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La biodiversité dulcicole sous influence du changement global : analyses des changements d'assemblages appliquées aux macroinvertébrés benthiques

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Théophile Lucas Mouton

*La biodiversité dulcicole sous influence du changement
global : analyses des changements d'assemblages
appliquées aux macroinvertébrés benthiques*

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« Rien n'est difficile aux gens qui ne cherchent rien. »

Anne Barratin ; Chemin Faisant (1894)

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Résumé

La vitesse et l'intensité du changement global nécessitent une analyse constante des changements qui opèrent dans la nature et sur la biodiversité. Afin de réellement comprendre les menaces que représentent les activités humaines sur les espèces de la Terre, il est nécessaire d'effectuer des études empiriques de séries temporelles de biodiversité. Malgré plus de 20 ans d'avancées scientifiques en écologie assortie d'une prise de conscience du public des effets du changement global sur la biodiversité, le déclin de celle-ci persiste, voire s'accroît. Cette thèse utilise une base de données de séries temporelles (1991-2016), sur la biodiversité de macroinvertébrés benthiques dans 64 sites de rivières de Nouvelle-Zélande. Elle représente un recensement unique de biodiversité dulcicole endémique au Sud-Ouest de l'Océan Pacifique et a pour but d'analyser les effets du changement global sur les patrons de biodiversité. Dans le premier article, nous montrons que la biodiversité des assemblages de macroinvertébrés s'homogénéise spatialement au cours du temps d'un point de vue taxonomique, mais se différencie d'un point de vue fonctionnel. Dans le deuxième article, nous montrons que la réorganisation temporelle des assemblages d'espèces observées se solde par, plus de gains que de pertes d'espèces et par un déplacement latitudinal des espèces d'en moyenne 50 kilomètres vers le sud par décennie. Dans le troisième article, nous montrons que la relation latitude/richeesse taxonomique des communautés s'est inversée au cours du temps et que cette inversion entraîne une augmentation de la redondance des traits, mais s'accompagne d'une diminution de leur richesse. En conclusion, cette thèse illustre les multiples facettes par lesquels le changement global altère la biodiversité et met en avant la nécessité d'analyser ces changements dans leur complexité.

Mots clés : Changement global, biodiversité, diversité fonctionnelle, diversité bêta, macroinvertébrés benthiques

Title - Freshwater biodiversity under global change: analyses of changes in assemblages applied to benthic macroinvertebrates

Abstract

The speed and intensity of global changes have pushed scientists to monitor and analyse changes that operate in nature and specifically on biodiversity. To truly understand the impact of human activities on the Earth's species, it is necessary to conduct empirical studies of biodiversity time-series. Despite more than 20 years of research in global change ecology and an increasing global public awareness, the decline of biodiversity is persisting and intensifying. Our knowledge in ecology is also incomplete, though of increasing interest to science. This PhD thesis uses a time-series database (1991-2016) of river macroinvertebrates located in 64 New Zealand River sites to analyse the effects of global changes on patterns of biodiversity. This database provides a unique picture of South-western pacific and endemic river benthic macroinvertebrates. In the first chapter, we show that macroinvertebrate biodiversity homogenises spatially with time from a taxonomic standpoint but differentiates through time from a functional standpoint. In the second chapter, we show that the observed temporal reorganisation of communities through time, involves greater gain than loss of species and latitudinal range shifts of species of 50 kilometres South on average per decade. In the third chapter, we show that the species richness/latitude relationship has reversed with time and that increases in species richness and trait redundancy come with the cost of reduced trait richness. To conclude, this PhD thesis demonstrates the multiple facets by which global change alters biodiversity and shows the need to analyse biodiversity changes considering all its complexity.

Keywords: Global change, biodiversity, functional diversity, beta diversity, benthic macroinvertebrates

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Publications scientifiques

Articles scientifiques présentés dans la thèse

Mouton, T. L., J. D. Tonkin, F. Stephenson, P. Verburg and M. Flourey (2020). "Increasing climate-driven taxonomic homogenization but functional differentiation among river macroinvertebrate assemblages." *Global Change Biology* 26(12): 6904-6915.

Mouton, T. L., F. Leprieur, M. Flourey, F. Stephenson, P. Verburg and J. D. Tonkin (2022). "Climate and land-use driven reorganisation of structure and function in river macroinvertebrate communities." *Ecography* 2022(3): e06148.

Mouton, T.L., A. Boyé, M. Mclean, J.D. Tonkin, S. Dolédec, N. Bonada, M. Flourey, P. Verburg, N. Mouquet, D. Mouillot, F. Leprieur (2022). "Climate change reverses the latitudinal species and trait richness gradients of river invertebrates." Submitted to: *Proceedings of the Royal Society B: Biological Sciences*.

Autres articles rédigés ou collaborés pendant la thèse

Stephenson, F., J. E. Hewitt, L. G. Torres, **T. L. Mouton**, T. Brough, K. T. Goetz, C. J. Lundquist, A. B. MacDiarmid, J. Ellis and R. Constantine (2021). "Cetacean conservation planning in a global diversity hotspot: dealing with uncertainty and data deficiencies." *Ecosphere* 12(7): e03633.

Stephenson, F., A. A. Rowden, T. Brough, G. Petersen, R. H. Bulmer, J. R. Leathwick, A. M. Lohrer, J. I. Ellis, D. A. Bowden, S. W. Geange, G. A. Funnell, D. J. Freeman, K. Tunley, P. Tellier, D. E. Clark, C. J. Lundquist, B. L. Greenfield, I. D. Tuck, **T. L. Mouton**, K. F. Neill, K. A. Mackay, M. H. Pinkerton, O. F. Anderson, R. M. Gorman, S. Mills, S. Watson, W. A. Nelson and J. E. Hewitt (2022). "Development of a Seafloor Community Classification for the New Zealand Region Using a Gradient Forest Approach." *Frontiers in Marine Science* 8 (792712).

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Pimiento C, Albouy C., Silvestro D., **Mouton T.L.**, Velez L., Mouillot D., Griffin J., Leprieur F. "Elasmobranch functional diversity is highly vulnerable and supported by unique species and locations worldwide". *Under review in: Nature Communications*.

Introduction générale

Une biodiversité en redistribution

La biosphère comprend environ 1.9 millions d'espèces décrites, avec un nombre total d'espèces estimé entre 3 et 100 millions (Mora et al. 2011, Grosberg et al. 2012, Costello et al. 2013, Roskov et al. 2013). Cette biodiversité est à la base du fonctionnement des écosystèmes et essentielle à l'existence humaine. Aujourd'hui, les activités d'origine humaine exercent une pression croissante sur les écosystèmes et la biodiversité (Dirzo et al. 2014, Díaz et al. 2019). Récemment, l'IPBES (Plateforme Intergouvernementale Scientifique et Politique sur la Biodiversité et les services écosystémiques) a réuni plus de 150 scientifiques pour rédiger le rapport de l'évaluation mondiale sur la biodiversité et les services écosystémiques (Díaz et al. 2019). Leurs conclusions révèlent la détérioration importante et globale des écosystèmes et de la biodiversité à travers le monde. Le rythme des changements de ces 50 dernières années est inédit dans l'histoire de l'humanité, avec 25% des espèces de plantes et d'animaux menacées d'extinction selon la Liste Rouge de l'Union Internationale pour la Conservation de la Nature (IUCN, 2020 ; Figure 1). Sur cette période, on estime que la biodiversité des communautés terrestres a diminué, en moyenne, de plus de 20% (Hill et al. 2018). La biomasse globale d'espèces végétales a diminué de moitié (Erb et al. 2018) et celle des mammifères sauvages a diminué de plus de 75%, représentant désormais 4% de la biomasse globale de mammifères, le restant étant les animaux élevés pour la production agricole et les êtres humains (Bar-On et al. 2018). En conséquence, la biodiversité s'homogénéise à travers les paysages, car seules certaines espèces persistent dans l'Anthropocène (McKinney & Lockwood 1999, Olden 2006, Gámez-Virués et al. 2015, Olden et al. 2018).

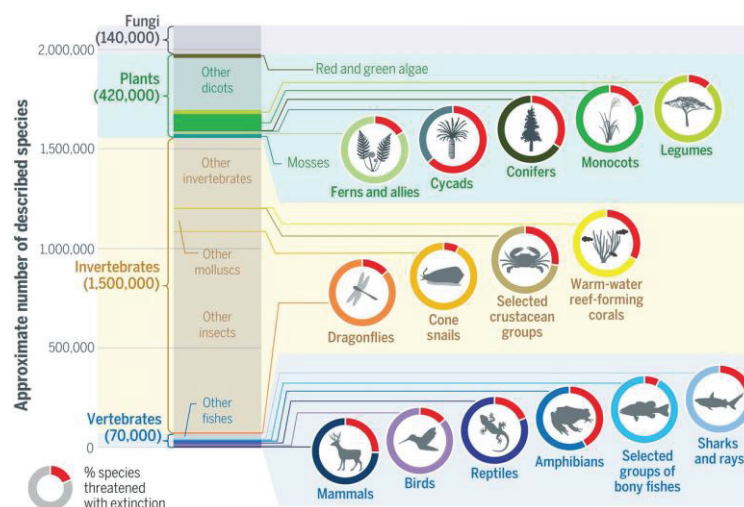


Figure 1 Pourcentage d'espèces menacées d'extinction par groupe taxonomique, adaptée de Díaz et al. 2019a

Alors qu'aucun écosystème n'est épargné par les impacts d'origines anthropiques, toutes les espèces ne sont pas sujettes aux mêmes déclin (Halpern et al. 2015, Dornelas et al. 2019). Chez les invertébrés, on ne connaît pas précisément combien d'espèces existent sur Terre, ni combien sont menacés d'extinction. Néanmoins d'après la Liste Rouge (IUCN 2020), ce groupe comprendrait plus de 1.3 millions d'espèces et le pourcentage d'espèces menacés d'extinction s'élèverait à environ 30%. D'après cette même liste rouge, à cela s'ajoutent 6.1% d'espèces quasi-menacées (« Near Threatened »), et 11.4% actuellement en déclin. Bien que constituant le groupe le plus divers et le plus abondant sur Terre, les invertébrés sont souvent sous-appréciés et sous-étudiés en termes de biodiversité par la communauté scientifique par rapport aux autres groupes zoologiques (Olden et al. 2016, Eisenhauer et al. 2019 ; Figure 2). Par exemple, la base de données BioTIME (Dornelas et al. 2018) – une compilation globale de séries temporelles de biodiversité – contient des données pour 22% des espèces d'oiseaux, mais seulement 3% des Arthropodes (le phylum dont font partie les insectes et les araignées).

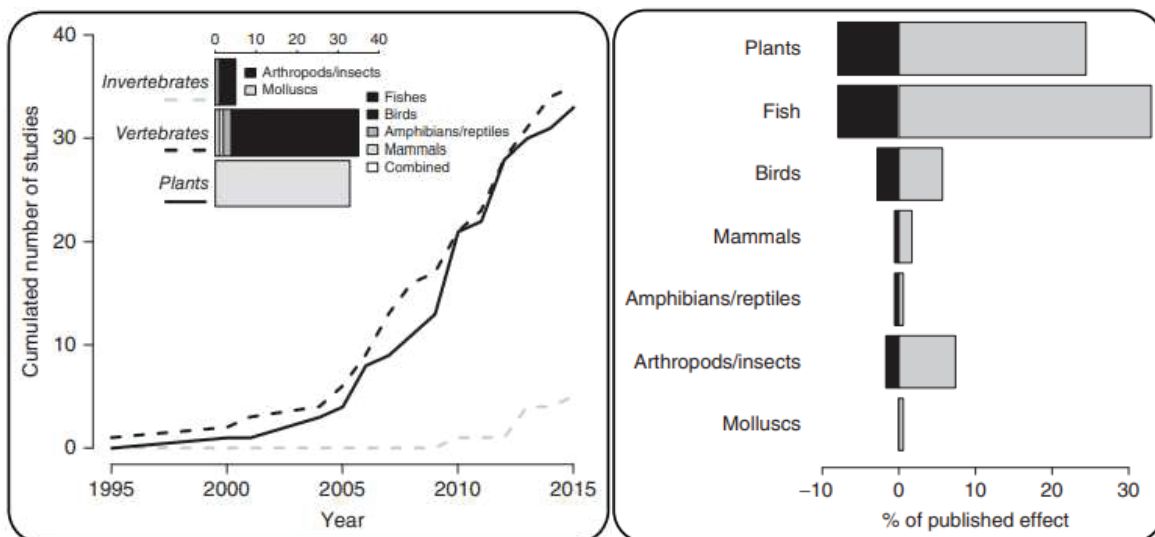


Figure 2 Panel de gauche : Nombre cumulé d'articles publiés sur l'homogénéisation de la biodiversité au cours du temps et classifié selon les groupes taxonomiques majeurs. Panel de droite : nombre d'études (en pourcentage) faisant état d'une augmentation (homogénéisation) ou d'une diminution (différentiation) de la similarité entre au moins deux communautés d'espèces au cours du temps (adapté de Olden et al. 2016).

La méta-analyse de séries temporelles de biodiversité d'invertébrés la plus complète à ce jour (Van Klink et al. 2020) a révélé des variations importantes, comprenant des hausses et des déclin en abondance et en biomasse. Cependant et de façon similaire aux découvertes faites chez d'autres taxa (Dornelas et al. 2014), cette méta-analyse n'a pas détecté de tendance générale à travers les 166 études utilisées totalisant 1676 sites d'études réparties dans 41 pays. Néanmoins, Van Klink et al. (2020) ont trouvé que l'abondance des invertébrés terrestres a diminué en abondance de 9% en

moyenne par décennie, tandis que celle des insectes d'eau douce a augmenté de 15%. Ces auteurs ont aussi noté des variations géographiques : l'Amérique du Nord et certains pays européens émergent comme points chauds (« hotspots ») de déclin d'abondance d'insectes.

Pour les invertébrés benthiques en rivières, Jähnig et al. (2021) ont noté premièrement que l'abondance totale ainsi que la biomasse des espèces, sont deux indicateurs faibles du statut des assemblages d'insectes d'eau douce et que cette augmentation d'abondance et de biomasse pourraient simplement être due à un remplacement des espèces dites « sensibles » aux pressions anthropiques par des espèces « tolérantes », plus abondantes dans ces milieux. Deuxièmement, que la majorité des jeux de données utilisés sont biaisés géographiquement, donc ne feraient pas une bonne représentation des tendances globales, mais plutôt celles de certaines conditions locales ou de sites sélectionnés a posteriori. En conclusion, et afin de mieux comprendre le statut de la biodiversité des invertébrés benthiques d'eau douce, il est nécessaire d'explorer davantage les changements temporels d'assemblages de ces espèces, dans des zones géographiques non-étudiées et en utilisant davantage de méthodes récemment développées en science de l'écologie (Olden 2006, Olden et al. 2018, Jähnig et al. 2021).

Encadré 1 - Qu'est que la biodiversité ?

Définition - La biodiversité ou diversité biologique désigne l'ensemble des **êtres vivants** ainsi que les **écosystèmes** dans lesquels ils vivent. Ce terme comprend également les interactions des espèces entre elles et avec leurs milieux. Bien que la biodiversité soit aussi ancienne que la vie sur Terre, ce concept n'est apparu que dans les années 1980. La **Convention sur la diversité biologique** signée lors du sommet de la Terre de Rio de Janeiro (1992) reconnaît pour la première fois l'**importance** de la conservation de la biodiversité pour l'ensemble de l'**humanité**.

Enjeux - La biodiversité répond aux **besoins primaires** de l'Homme en apportant oxygène, nourriture et eau potable. Elle contribue au développement des activités humaines en fournissant matières premières et énergies. C'est aussi une ressource extraordinaire pour le monde **médical** (e.g. la morphine (pavot)). En agriculture, la contribution des animaux pollinisateurs n'est plus à démontrer. La nature **protège** aussi des risques environnementaux (e.g. préservation et restauration de prairies inondables permettent de diminuer l'impact des inondations. Ce surplus d'eau alimente les nappes souterraines et sera utilisé lors de période de sécheresse).

Mesures - Toute mesure de biodiversité est à interpréter en termes d'échelles (Legendre and Fortin 1989). En écologie, la diversité est communément partitionnée en trois composantes : la diversité **alpha** (échelle locale), la diversité **gamma** (échelle régionale) et la diversité **beta**, représentant la variation de composition entre des communautés (Whittaker 1972) (Figure 3). Plusieurs indices de diversité existent à chacune de ces échelles, et peuvent prendre en compte (ou non) les abondances et propriétés des espèces au-delà de leur taxonomie.

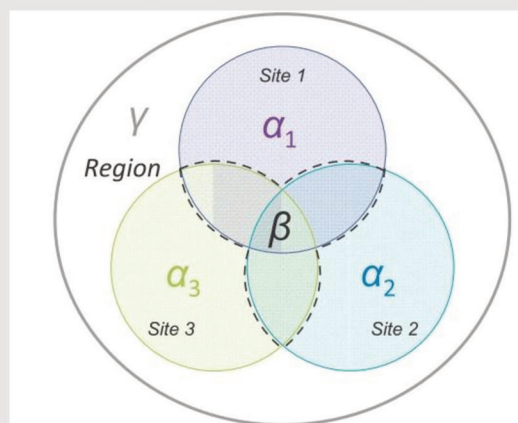


Figure 3 Schéma représentant la diversité alpha (en couleurs), beta (lignes noires en pointillés) et gamma (cercle gris) (adapté de Zinger et al. 2012)

Le changement climatique et la biodiversité

Tendances climatiques globales

L'augmentation de la concentration en gaz à effet de serre présente dans l'atmosphère (36.3 milliards de tonnes en 2021) a changé le climat global de la Terre, avec une estimation d'une augmentation globale des températures moyennes de surface de 1.5°C depuis 1880 et d'ici les prochaines années (IPCC, 2022). Malgré les politiques mises en place, ces changements continuent de s'accroître, suggérant que seuls d'énormes efforts pourraient permettre de ne pas dépasser les 2°C et de limiter les conséquences sur la biosphère (Leclère et al. 2020, Figure 4). Bien que la Terre ait connu de profondes modifications climatiques par le passé, la magnitude et la vitesse des changements climatiques actuels pourraient être dix fois supérieures au réchauffement constaté depuis le dernier maximum glaciaire (IPCC, 2022). Cette vision est cependant aujourd'hui remise en cause, par la mise en évidence de changements climatiques abrupts s'étant produits durant le Quaternaire (Steffensen et al. 2008, Pellissier et al. 2014).

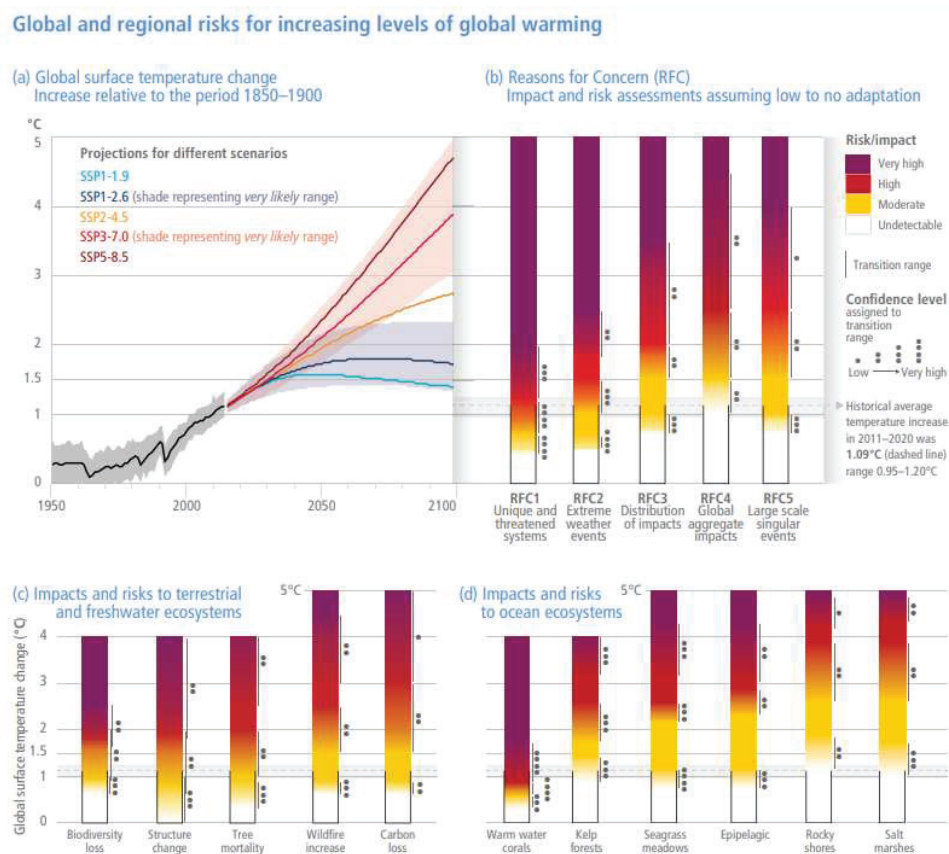


Figure 4 Risques globaux et régionaux liés à l'augmentation de la température de l'air. (a) Changements globaux de la température de l'air depuis 1850-1900 et projections selon les différents scénarios d'émissions de gaz à effets de serres. (b) Raisons de s'en préoccuper. (c) Impacts et risques sur les écosystèmes terrestres et d'eau douce. (d) Impacts et risques sur les écosystèmes océaniques (adapté de IPCC, 2022).

Enjeux pour la biodiversité

Ces changements climatiques ont des répercussions sur les facteurs contrôlant les patrons de biodiversité sur Terre et ont poussé la communauté scientifique à étudier la capacité des espèces à mettre en place des stratégies leur permettant de survivre aux changements climatiques (Parmesan 2006, Hof et al. 2011). Ainsi, un des enjeux majeurs pour la conservation de la biodiversité mondiale consiste à comprendre comment les espèces, et plus généralement les systèmes biologiques, sont d'ores et déjà en train de répondre aux changements climatiques actuels. Ces données constituent des éléments de réflexion primordiaux quant à notre capacité à initier des politiques de gestion adaptées, dont les missions futures ne peuvent désormais plus être conçues sans tenir compte de l'évolution du climat (Dawson et al. 2011, Hannah et al. 2020, Sala et al. 2021).

Les changements d'aires de répartition

Une des réponses majeures des espèces aux changements climatiques est de changer progressivement, quand cela leur est possible, leur aire de répartition en latitude (en direction des pôles) ou en altitude (vers des altitudes plus élevées) pour retrouver des conditions climatiques similaires (Walther et al. 2002, Parmesan 2006, Lenoir & Svenning 2015). Ces changements d'aires de répartition se produisent à l'échelle de populations, ils ne proviennent pas de mouvement individuel, mais de changements dans les ratios d'extinctions/colonisations aux limites des aires de répartition des espèces. La première étude scientifique menée à ce sujet (Parmesan et al. 1999) et couvrant la totalité de l'aire de répartition des espèces étudiées a concerné 35 espèces de papillons européens sédentaires, dont 63% avaient déplacé leur aire de répartition de 35 à 240 kilomètres en direction du Nord, durant le 20^{ème} siècle. Depuis cette première étude, des approches similaires et complémentaires ont été réalisées sur un grand nombre d'espèces et de localités dans le monde. Récemment, Lenoir et al. (2020) ont mis en forme et analysé une base de données recensant 30,534 déplacements d'aires de répartition sur l'ensemble du globe. Leurs conclusions ont premièrement mis en avant un déséquilibre spatial en direction des régions les plus développées de l'Hémisphère Nord et un biais taxonomique vers les espèces et plantes les plus charismatiques sur Terre. Néanmoins, et dans l'ensemble, les espèces marines suivent les changements d'isothermes plus rapidement que les espèces terrestres, et se déplacent en moyenne six fois plus rapidement que les espèces terrestres (Lenoir et al. 2020).

Plus précisément, les espèces marines suivent mieux les déplacements d'isothermes dans des eaux chaudes et relativement intactes (par exemple, dans le Bassin Centrale du Pacifique) ou dans des eaux froides sujettes à de fortes pressions humaines (par exemple, dans la Mer du Nord). Sur la terre, les activités humaines entravent la capacité des espèces à suivre les changements d'isothermes en

latitude. Le long de gradient d'altitude, les espèces suivent aussi les changements d'isothermes mais à un rythme inférieur que dans les océans (Lenoir et al. 2020). Les espèces terrestres sont donc plus en retard que les espèces marines lorsqu'il s'agit de suivre les changements d'isothermes, ce qui pourraient en partie être due à une marge de sécurité thermique plus large chez ces dernières, mais aussi à une plus faible capacité de dispersion due à un environnement physique plus contraint.

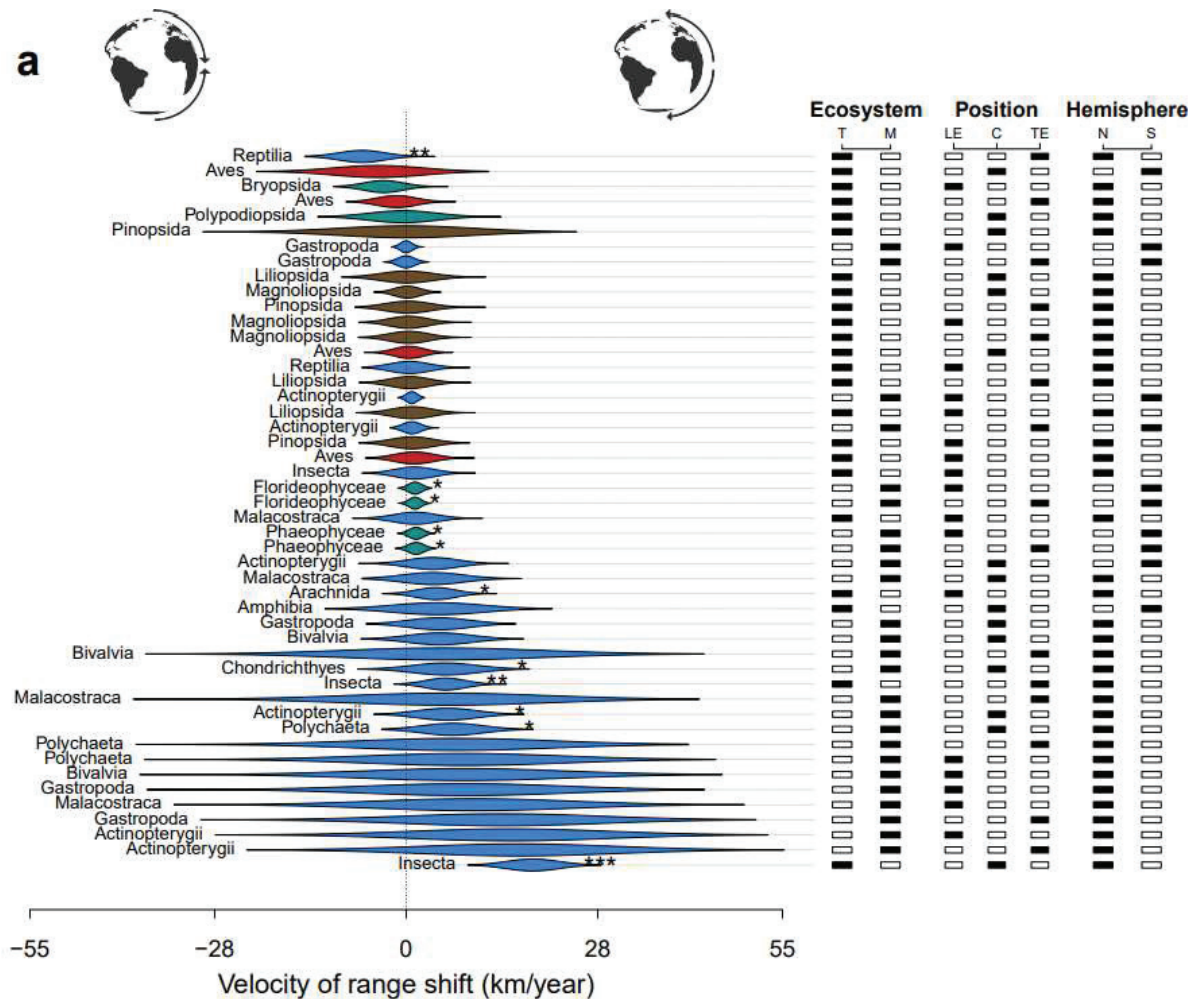


Figure 5 Vitesses moyennes des déplacements latitudinaux d'espèces par classe taxonomique et par combinaison d'écosystème (T : terrestre, M : marin), de position géographique au sein de l'aire de répartition de chaque espèce, i.e. à la limite de l'aire ou bien au centre de celle-ci (LE : « leading edge », C : « centroid », TE : « trailing edge ») et d'hémisphère (N : nord, S : sud) (adaptée de Lenoir et al. 2020).

Dans les cours d'eau, les changements climatiques se traduisent notamment, par une altération des régimes annuels de température (e.g. vagues de chaleurs en été), une fonte accélérée des glaciers, une perturbation des régimes d'écoulements, et par conséquent des cycles biogéochimiques fluviaux. Malgré leur valeur écologique et sociale, ces milieux subissent des déclin de leur biodiversité qui excèdent souvent ceux documentés dans les écosystèmes terrestres (Dudgeon et al. 2006). Par

ailleurs, la distribution de beaucoup d'espèces est hautement contrainte par la structure dendritique des réseaux hydrographiques, constituant un obstacle majeur à la dispersion (Peterson et al. 2013, Sarremejane et al. 2017, Thompson & Gonzalez 2017, Tonkin et al. 2018).

Notre connaissance de l'influence des changements climatiques sur la distribution spatiale des macroinvertébrés d'eau douce reste encore très faible. En effet, peu d'études ont mesurés les déplacements d'aires de répartition des macroinvertébrés d'eau douce. En Australie du Sud-Ouest cependant, Chessman (2012) a analysé 8928 échantillons de macroinvertébrés d'eau douce collectés durant une période de 16 ans et contenant des données pour 120 taxons. Ses résultats ont montré que les déplacements d'aire de répartition les plus fréquents (59%) concernaient une expansion de la limite froide de l'aire (« cool-edge expansion ») et une diminution de la limite chaude (« warm-edge contraction »), ainsi qu'une expansion de la limite humide (« wet-edge expansion ») et une diminution de la limite sèche (« dry-edge contraction »). Cependant, des diminutions des limites chaudes et froides (30%) et des limites humides et sèches (23%) étaient également fréquentes. Dans un contexte similaire, certaines projections et scénarios de changements climatiques pour les décennies à venir ont été appliqués aux aires de répartition de macroinvertébrés d'eau douce, notamment en Europe occidentale (Domisch et al. 2013). Ces scénarios ont été appliqués à 191 espèces de macroinvertébrés d'eau douce, pour lesquels les résultats ont suggérés une diminution de la quantité de zones climatique appropriées pour 57-59% des espèces. Les zones adaptées à ces espèces ont aussi été projeté de se déplacer, en moyenne, de 4.7°-6.6° Nord et 3.9-5.4° Est (Domisch et al. 2013). Pour les espèces adaptées aux climats froids, les modèles prédisaient une perte en quantité de zone(s) climatique(s) adaptée(s), tandis qu'une tendance inverse s'opérait pour les espèces adaptées aux climats chauds. Outre les effets généraux des changements climatiques, l'augmentation d'évènements climatiques extrêmes, comme une augmentation des vagues de chaleurs en été et une augmentation de l'amplitude et de l'intensité des crues (Tonkin et al. 2019), risquent aussi d'entraîner des conséquences importantes pour les populations aquatiques. Par conséquent, si l'empreinte des changements climatiques actuels est supportée par des résultats empiriques substantiels chez de nombreux groupes taxonomiques la capacité des macroinvertébrés d'eau douce, composés d'espèces holobiotiques et amphibiotiques, à se déplacer pour suivre les modifications du climat reste largement méconnue.

Les changements de diversité et de composition des communautés

A l'échelle de populations, ces effets peuvent affecter les règles d'assemblages des espèces au sein de communautés, et ainsi, favoriser le remplacement d'espèces, réduire ou augmenter leur richesse taxonomique, et éventuellement, leur diversité fonctionnelle. Dans ce contexte, Dornelas et al. (2014)

ont utilisé une suite de séries temporelles de biodiversité (c. 1850-2000), contenant plus de 50 000 séries temporelles de biodiversité provenant de 239 études et couvrant à la fois les milieux marins et terrestres. Ils ont trouvé un remplacement d'espèces supérieur à leurs attentes, mais aucune preuve d'une perte systématique de biodiversité. Ceci pouvant être due à l'homogénéisation des assemblages, aux changements d'aires de distribution et/ou à des changements asynchrones à travers la planète. De plus, Blowes et al. (2019), ont utilisé la même base de données pour identifier les patrons spatiaux mondiaux de changements de richesse et de composition d'espèces. Ils ont montré un remplacement d'espèces rapide et fréquent, plus important dans les milieux marins que terrestres. De plus, la richesse taxonomique ne changeait pas en moyenne à travers le globe, mais certains milieux marins présentaient des changements de richesse pouvant aller jusqu'à 20% par an. Aux échelles locales, le remplacement d'espèces est bien souvent découplé des changements de richesse taxonomique, et les changements de biodiversité sont plus importants et plus variables dans les océans.

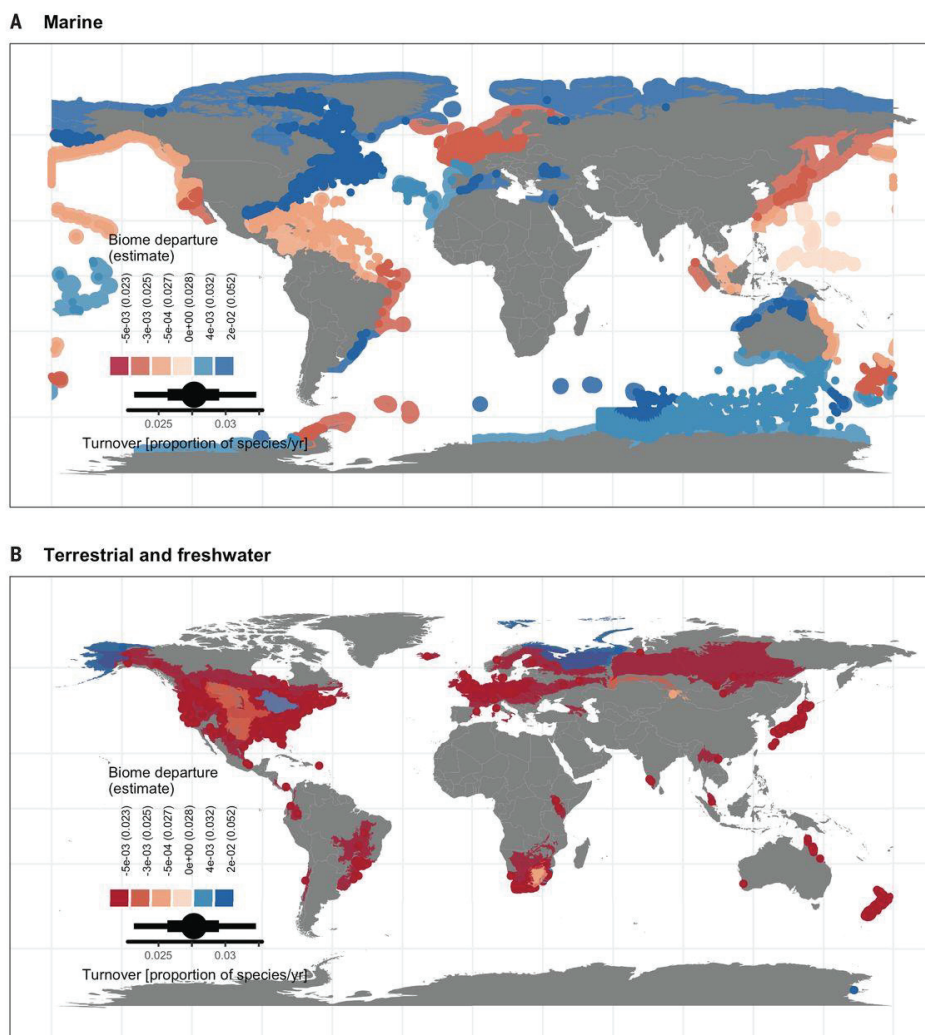


Figure 6 Cartes du monde illustrant le remplacement d'espèces global pour les biomes (A) marin et (B) terrestres et d'eau douce (adaptés de Blowes et al. 2019).

Enfin, et en guise de transition avec le paragraphe suivant, une étude menée à l'échelle des cours d'eau français a montré que la richesse taxonomique des macroinvertébrés benthiques d'eau douce avait augmenté de 42% en 25 ans (Van Looy et al. 2016). Dans ces mêmes cours d'eau français, la diversité fonctionnelle (FD) des macroinvertébrés benthiques a augmenté dans la majorité des sites étudiés (87%) en réponse aux changements climatiques. De plus, Floury et al. (2018) ont observé des variations latitudinales dans la contribution de la vulnérabilité climatique des macroinvertébrés d'eau douce aux changements temporels de FD (Figure 7).

Les relations avec la taxonomie et les traits des espèces

Outre les patrons géographiques généraux des changements d'aires de répartition, d'abondances ou d'occurrences d'espèces, une autre question concerne leurs relations avec la taxonomie et/ou les caractéristiques écologiques et biologiques (i.e. les traits) des espèces. Certaines études ont été réalisées, néanmoins avec des jeux de données parfois très diverses et des objectifs d'études différents. Par exemple, face aux changements globaux, les amphibiens sont les seuls taxons à connaître de nettes baisses d'abondances, tandis que les oiseaux, mammifères et reptiles connaissent des augmentations sur l'ensemble du globe (Daskalova et al. 2020). Dans un autre contexte, et pour des raisons paléontologiques, les espèces endémiques aux habitats de hautes altitudes sont particulièrement à risque vis-à-vis des changements climatiques, du fait d'une perte rapide des habitats forestiers de hautes altitudes plus vulnérable (Dirnböck et al. 2011).

De manière plus générale, les espèces dites « généralistes » remplacent les espèces « spécialistes » sous l'influence du changement global (Clavel et al. 2011). Une espèce est dite généraliste lorsque sa « niche environnementale » est relativement grande et variée, tandis qu'une espèce dite « spécialiste » a une niche environnementale relativement petite et est spécialisée pour vivre dans des habitats spécifiques. Ce phénomène de remplacement des espèces mène à l'homogénéisation

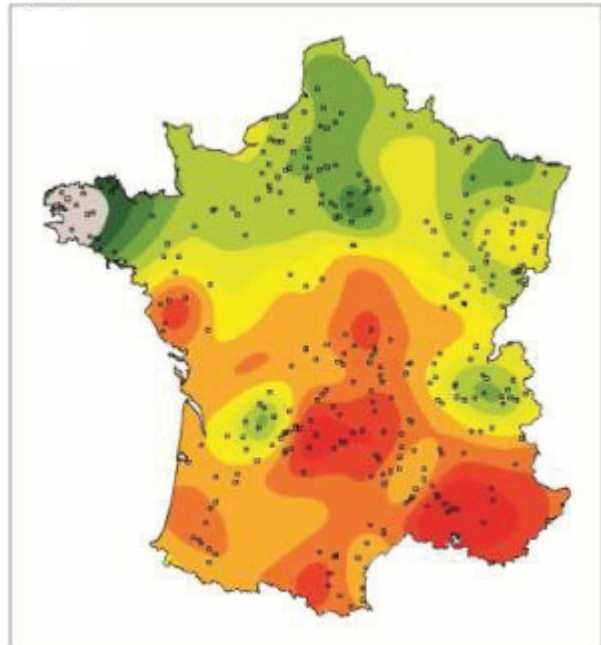
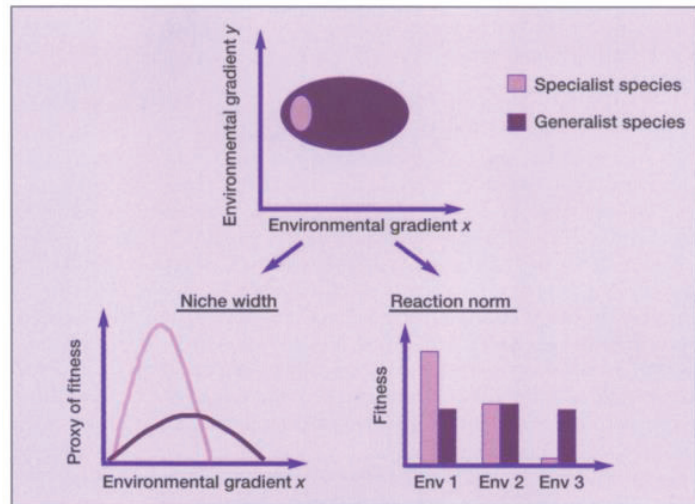


Figure 7 Carte de la France illustrant la contribution de la vulnérabilité climatique des macroinvertébrés benthiques aux changements temporels de diversité fonctionnelle (adapté de Floury et al. 2018).

fonctionnelle des communautés. Les données fossiles étudiées par les paléontologistes montrent que les épisodes passés d'extinctions massives d'espèces étaient largement associés à l'extinction d'espèces généralistes. La survie des espèces, tel qu'estimée par des données paléontologiques variait de manière non-aléatoire. Par exemple, au début du

Jurassique les espèces de foraminifères et d'invertébrés marin benthiques opportunistes et écologiquement généralistes ont vécu plus longtemps que les autres espèces, plus spécialistes (Erwin 1998).

Un des grands défis des écologistes est d'identifier et de comprendre quel(s) trait(s) des espèces permettent de prédire leurs réponses aux changements climatiques. De même que pour la taxonomie des espèces, plusieurs études se sont penchées sur le sujet, néanmoins, sans conclusion générale. Dans ce contexte, MacLean & Beissinger (2017) ont réalisé la première revue de littérature sur les liens entre traits des espèces et changements d'aires de répartition. Ils ont utilisé les résultats de 51 études comprenant la réponse de plus de 11 000 espèces. Leurs résultats ont montré que l'amplitude de la niche des espèces ainsi que la limite historique de leurs aires de répartition était des traits affectant significativement la vitesse de déplacements d'aires des espèces. Néanmoins, les autres traits étudiés (la taille du corps, la fécondité et l'amplitude de la niche alimentaire) n'avaient pas d'effet significatif sur les déplacements d'aires des espèces étudiées. Cela étant, parmi les facteurs de risque d'extinction, la taille et la masse des organismes semblent jouer un rôle, les espèces plus petites et plus grandes étant plus susceptibles d'être menacées ou éteintes que les espèces de taille intermédiaire (Ripple et al. 2017). D'autres traits d'histoire de vie sont également corrélés aux risques d'extinction, tels que l'âge à la maturité et la capacité de reproduction ou le régime alimentaire (Hutchings et al. 2012, Atwood et al. 2020). Les espèces ayant une durée de vie longue et se reproduisant tardivement sont naturellement plus impactées par des facteurs mortels, car les populations n'ont pas le temps de se régénérer (Reynolds et al. 2005). Au sein de populations de macroinvertébrés benthiques d'eau douce, la disparition progressive d'espèces adaptées aux eaux froides et courantes et leur remplacement par des espèces typiques d'eaux lentes et plus chaudes a été observé en Europe (Floury et al. 2013). De plus, les changements climatiques peuvent affecter la



capacité de dispersion, de locomotion ainsi que les modes d'alimentation des populations de macroinvertébrés d'eau douce, particulièrement chez les espèces les moins thermophiles (Floury et al. 2013, Aspin et al. 2019).

Encadré 2 - La biodiversité et l'Anthropocène

Qu'est-ce que l'anthropocène ? Le terme Anthropocène, qui signifie « L'Ère de l'humain », est une proposition d'époque géologique qui commencerait lorsque l'influence de l'être humain sur la géologie et les écosystèmes est devenue significative à l'échelle de l'histoire de la Terre. Sa date de début et sa reconnaissance en tant qu'ère géologique est toujours débattu par les experts. L'impact de l'activité humaine récente sera probablement enregistré dans les sédiments du futur pendant des millions d'années. Les marques de cette nouvelle époque géologique incluent : l'entrée en crise biologique globalisée, avec pour conséquence majeure une perte de biodiversité à un rythme jamais atteint au cours des âges géologiques et l'altération de la géologie et de la géochimie.

La biodiversité dans l'anthropocène : Le rythme des changements de ces 50 dernières années est inédit dans l'histoire de l'humanité, avec 25% des espèces de plantes et d'animaux qui sont menacées d'extinction par la Liste Rouge de l'Union Internationale pour la Conservation de la Nature. Il est estimé que la biodiversité des communautés terrestres a diminué, en moyenne, de plus de 20%. La biomasse globale d'espèces végétales a diminué de moitié et celle des mammifères sauvages a diminué de plus de 75%, représentant désormais 4% de la biomasse globale de mammifères, le restant étant les animaux élevés pour la production agricole et les êtres humains. En conséquence, la biodiversité s'homogénéise à travers les paysages, car seules certaines espèces persistent dans l'Anthropocène.

Enjeux et lacunes : Les activités humaines entraînent une répercussion sur les facteurs contrôlant les patrons de biodiversité sur Terre et ont poussé la communauté scientifique à étudier la capacité des espèces à mettre en place des stratégies leur permettant de survivre à ces changements environnementaux. Ainsi, un des enjeux majeurs pour la conservation de la biodiversité mondiale consiste à comprendre comment les espèces, et plus généralement les systèmes biologiques, répondent aux pressions humaines. Ces données constituent des éléments de réflexion primordiaux quant à notre capacité à initier des politiques de gestion adaptées, dont les missions futures ne peuvent désormais plus être conçues sans tenir compte de l'accroissement des activités humaines.

Les autres menaces sur la biodiversité

L'utilisation des terres

La cause majeure du déclin d'abondance des espèces sur Terre et de l'augmentation de leur risque d'extinction est l'utilisation des terres par l'Homme, qui induit une destruction des habitats naturels (IPBES, 2019). A l'échelle globale, des estimations suggèrent par exemple, que la surface continentale couverte par les espaces urbains et agricoles est passée de 5% en 1700 à 39% en 2000 (Ellis et al. (2010), Figure 9). Par conséquent, 75% de la surface continentale présentait en 2009 une empreinte écologique non nulle (i.e., avec des impacts d'activités humaines visibles depuis l'espace, d'après la mesure de la «Human Footprint»), avec des niveaux importants visibles sur tous les continents, particulièrement dans l'hémisphère Nord (Venter et al. 2016). Les zones importantes pour la biodiversité sont

particulièrement touchées puisque seuls 3% des points chauds de biodiversité (« Biodiversity Hotspots ») et 2% des zones à forte concentration d'espèces menacées de vertébrés sont dépourvues d'empreinte écologique mesurable (contre 25% globalement). Cette empreinte écologique a augmenté globalement de 9%

entre 1993 et 2009, avec cependant des nuances : une augmentation particulièrement forte sous les tropiques, mais une diminution dans plusieurs pays à haut PIB (Venter et al. 2016). La déforestation dure depuis des siècles avec une accélération mondiale au XXème siècle (Mouillot & Field 2005) et continue principalement dans les forêts tropicales, avec une perte de 129 millions d'hectares de forêt tropicale (3%) entre 1990 et 2015 (Hansen et al. 2013, Keenan et al. 2015). Cette déforestation affecte fortement la biodiversité, pouvant aller jusqu'à l'extinction locale de la quasi-totalité des espèces forestières (Gibson et al. 2013, Barlow et al. 2016).

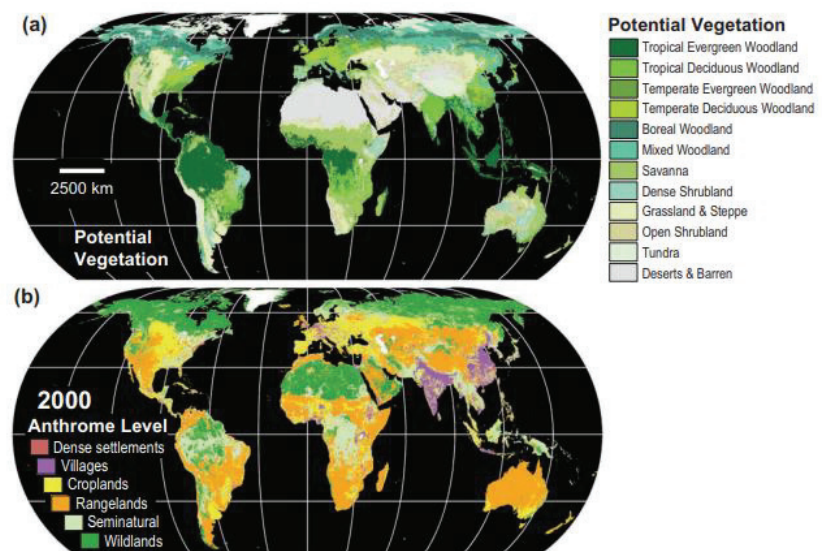


Figure 9 (a) Végétation potentielle naturelle sur Terre (b) Niveau de transformation de la biosphère terrestre en l'an 2000 (adapté de Ellis et al. 2010)

En Nouvelle-Zélande, la déforestation est emblématique de cette menace qui transforme les paysages et la biodiversité. Historiquement, la Nouvelle-Zélande était couverte de forêts primaires à l'aval de la limite forestière alpine (Ewers et al. (2006), Figure 10). Mais environ un siècle de colonisation polynésienne et européenne a abouti à la destruction de presque 75% de la couverture de forêt primaire (Ewers et al. 2006, Proce et al. 2006). A la destruction des habitats forestiers s'ajoute la dégradation des forêts restantes par des activités telles que l'introduction de mammifères herbivores, la coupe sélective des arbres, et l'augmentation de maladie due à des champignons ou des bactéries (Ogden et al. 1993, Proce et al. 2006). Cette dégradation impacte fortement la biodiversité, avec un effet d'une magnitude parfois proche de la déforestation (Jha & Bawa 2006), rendant le déclin des forêts primaires irréversible

(Harding 2003, Gibson et al. 2011).

Concernant les effets de la déforestation sur la biodiversité de macroinvertébrés benthiques en Nouvelle-Zélande, il a été estimé que 40-60% des forêts primaires en amont des bassins versants était nécessaire pour conserver environ 80% de la biodiversité de macroinvertébrés (Death & Collier 2010). De plus, tous les

indicateurs de biodiversité de macroinvertébrés utilisés par les collectivités territoriales Néo-Zélandaises répondent

négativement à la déforestation et un point d'inflexion dans la réponse de la biodiversité des macroinvertébrés benthiques est observable à partir de 10% de déforestation dans le bassin versant amont (Clapcott et al. 2010, Clapcott et al. 2012). Dernièrement, à travers la Nouvelle-Zélande, un nombre inconnu d'espèces s'est probablement éteint du fait de la déforestation, et les forêts primaires restantes sont certainement vitales à la conservation et préservation des espèces endémiques des rivières Néo-Zélandaises (Harding 2003).

La perte d'habitat

Bien que jouant un rôle majeur, la déforestation est loin d'être l'unique menace pesant sur la biodiversité. Les pratiques agricoles intensives et non-durables, sont également un facteur important

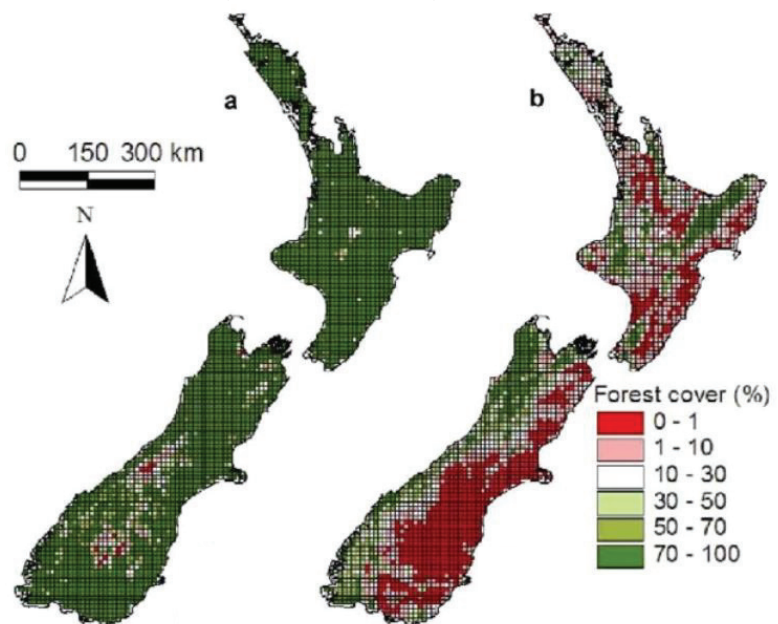


Figure 10 Patrons de changement de couverture forestière en Nouvelle-Zélande. a - Avant la colonisation humaine. b - Après la colonisation humaine. Image adaptée de Ewers et al. (2006)

du déclin global de la biodiversité sur Terre. Combiné avec l'exploitation directe de la nature via la chasse, la pêche, l'exploitation forestière et l'agriculture il est estimé que ces effets comptent pour plus de 50% des impacts humains qui affectent les écosystèmes terrestres et d'eau douce (IPBES, 2019). L'intensification de l'agriculture via les cultures, plantations et l'élevage est le facteur majeur de changement d'utilisation des terres dans le monde (IPBES, 2018). L'expansion et intensification de l'utilisation des terres a augmenté notre consommation des ressources de la Terre au détriment de la biodiversité et des services écosystémiques qu'elle fournit (Foley et al. 2005, Díaz et al. 2019). Généralement, l'utilisation des terres réduit la richesse taxonomique de manière conséquentes (Murphy & Romanuk 2014, Newbold et al. 2015, Gerstner et al. 2017, Beckmann et al. 2019), altère la composition des espèces (Dornelas et al. 2014, Newbold et al. 2016) et réduit leurs abondances (Collen et al. 2009, Gibson et al. 2011, Newbold et al. 2015). Les caractéristiques écologiques et fonctionnelles des espèces peuvent aussi répondre aux changements d'utilisation des terres, par exemple, les espèces aux habitudes alimentaires spécialisées, aux cycles d'activités courts et taille de corps relativement petites, sont sélectionnées en priorités dans les paysages fortement modifiés et aux pratiques agricoles intensives (Ribera et al. 2001, Gámez-Virués et al. 2015). En Nouvelle-Zélande, un changement des politiques économiques entraînant la suppression de nombreuses subventions agricoles a eu lieu au début des années 1970. Cela a eu pour conséquence une très forte augmentation de l'intensification de l'agriculture, et dans une moindre mesure, de sa diversification (MacLeod & Moller 2006). Ceci se traduisant par une augmentation de l'utilisation de fertilisants, de pesticides et d'intrants agricoles. Ainsi qu'une conversion des pratiques agricoles à des formes d'agricultures beaucoup plus intensives.

Les pollutions d'origines anthropiques

Une autre menace pesant sur la biodiversité est représentée par les pollutions provenant des activités humaines. Celles-ci peuvent être ponctuelles (dans le cas de rejets ponctuels de polluants dans un milieu) ou diffuses (la pollution des eaux par les nitrates et les pesticides de l'agriculture est un exemple de pollution diffuse). Ces pollutions peuvent avoir un impact direct (par exemple mortalité des individus (Wagenhoff et al. 2011)) ou indirect (par exemple en favorisant l'eutrophisation (Hilton et al. 2006 ; Figure 11)). De ce fait, dans de nombreux pays, les collectivités territoriales et les gouvernements ont inscrits dans la législation le devoir de contrôler la qualité de l'eau des milieux aquatiques en fixant des objectifs environnementaux portant notamment sur l'atteinte du bon état écologique de leurs masses d'eau. C'est par exemple le cas aux Etats-Unis avec le « Clean Water Act » (EPA 2008), de l'Union Européenne avec la « Directive-Cadre sur l'Eau » (Directive 2000) et de la Nouvelle-Zélande avec le « National Policy Statement for Freshwater Management » (MfE, 2020). A l'échelle de la France, une amplification trophique dans les communautés de macroinvertébrés (i.e.

une intensification des interactions trophiques et des voies à travers les réseaux alimentaires) a été suggéré comme étant la résultante principale du changement de composition des communautés de macroinvertébrés en réponse au réchauffement climatique et à une amélioration de la qualité des eaux en lien avec des mesures de gestion appropriées. En Nouvelle-Zélande, les apports excessifs d'azote, de phosphore et de sédiments (provenant de l'érosion des sols) dans les milieux aquatiques et provenant principalement de l'intensification de l'agriculture (Julian et al. 2017), sont considérés depuis plusieurs décennies comme étant une des principales menaces pour la qualité des états écologiques des milieux aquatiques et donc de leur biodiversité (Joy 2015). L'impact direct de ces pollutions a été relevé et étudié dans de nombreux cas, surtout sur les communautés de macroinvertébrés benthiques d'eau douce, par exemple, dans des cours d'eau néozélandais Wagenhoff et al. (2017) ont montré que l'abondance relative d'individus du genre *Pycnocentrode* et *Deleatidium* diminuait en réponse à une augmentation de concentration d'azote inorganique dissous.

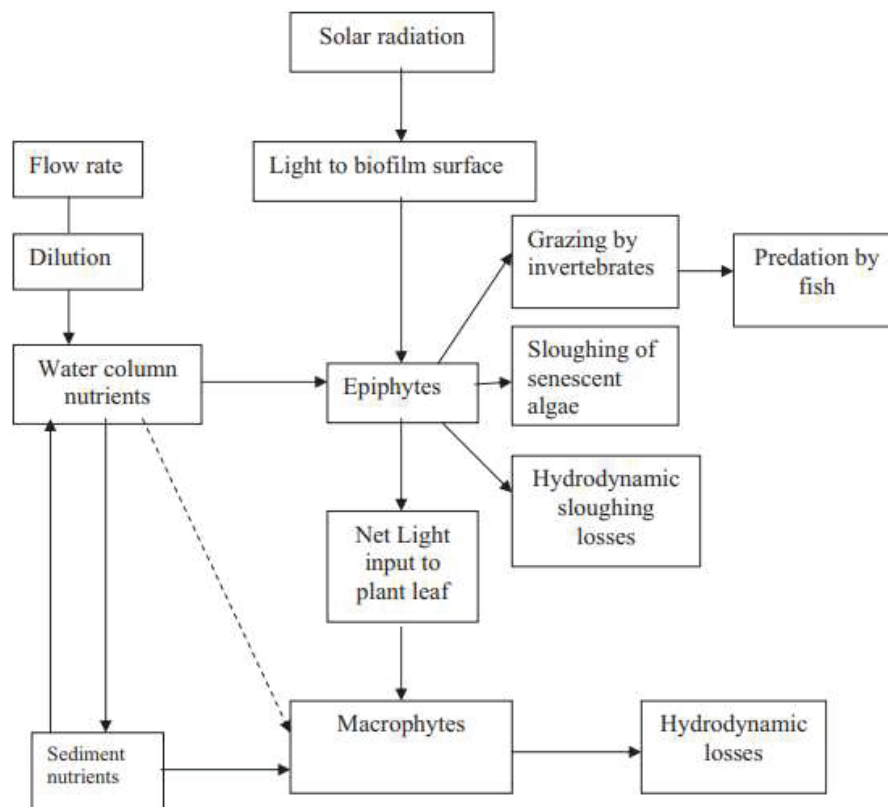


Figure 11 Diagramme schématisant les mécanismes de l'eutrophisation dans les rivières (adaptée de Hilton et al. 2006).

Enjeux et structure de la thèse

Les milieux aquatiques sont aujourd'hui sous l'influence de nombreuses pressions anthropiques (changement climatique, utilisation des terres, destruction d'habitat, pollutions) qui, en agissant simultanément, altèrent leur biodiversité et par conséquent leur fonctionnement ainsi que les services écosystémiques que ces milieux pourvoient aux sociétés humaines. Bien que la communauté scientifique ait réalisée de nombreuses avancées en écologie du changement global depuis plusieurs décennies, plusieurs lacunes persistent dans nos connaissances et notre compréhension des réponses de la biodiversité aux différentes facettes du changement global. Cela étant d'autant plus le cas dans les cours d'eau et chez les macroinvertébrés benthiques. Des analyses empiriques de séries temporelles de biodiversité, la prise en compte de zones géographiques sous-étudiées et l'utilisation de développement méthodologique récents sont nécessaires pour combler ces lacunes.

Les objectifs de cette thèse découlent de cet enjeu. Elle porte sur une analyse des changements de biodiversité de macroinvertébrés benthiques de rivières en Nouvelle-Zélande, sur une période s'étalant entre 1991 et 2016 inclus. Pour ce faire, nous avons utilisé une base de données de séries temporelles relativement unique au monde. Il s'agit d'un échantillonnage national des principales rivières de Nouvelle-Zélande, mené par l'Institut National pour la Recherche sur l'Eau et l'Atmosphère (NIWA). Dans cette thèse, je m'attache à (1) décrire les patrons de changements de biodiversité et (2) différencier les effets de l'ensemble des pressions décrites dans les parties précédentes (changements climatiques, utilisation des terres et pollutions des milieux aquatiques) sur les variations potentielles de biodiversité d'un point de vue taxonomique et fonctionnel.

Le corps de la thèse est composé de **trois articles scientifiques (p_i, p_{ii}, p_{iii})** dont les thématiques sont les suivantes : dans le **premier article (p_i)**, j'examine et j'analyse les variations temporelles de similarité spatiale (**diversité bêta spatiale**) des assemblages d'espèces à l'échelle de la Nouvelle-Zélande et je mesure les relations entre les changements taxonomiques et fonctionnels afin d'identifier les possibles causes environnementales de ces changements ; dans le **deuxième article (p_{ii})**, je m'intéresse aux patrons géographiques de réorganisation temporelle des communautés (**diversité bêta temporelle**) en examinant les possibles facteurs environnementaux, en déterminant les changements d'abondance et d'aire de répartition de chacun des taxons et analysant le(s) lien(s) potentiel(s) de ces changements avec la taxonomie des espèces ainsi que leurs traits fonctionnels ; Enfin, dans le **troisième article (p_{iii})**, je m'intéresse aux changements de **richesse taxonomique et fonctionnelle** et de **redondance fonctionnelle** à travers les paysages de Nouvelle-Zélande, je détermine la part d'effet(s)

direct(s) et indirect(s) des changements environnementaux et j'examine la contribution de chaque espèce aux changements observés.

English summary of the introduction section:

The general introduction section outlines the state of current biodiversity on Earth, including the fact that 25% of plant and animal species are threatened with extinction according to the Red List from the International Union for the Conservation of Nature. During the last 50 years, it is estimated that the global biomass of flora has reduced by halves and that the biomass of wild mammals has reduced by more than 75%. Consequently, biodiversity is homogenising across landscapes, as only certain species persist in the Anthropocene.

For invertebrates, it was found that the abundance of terrestrial species has reduced by 9% on average per decade, while that of freshwater species has increased by 15%. However, it is also recognised that to capture the full length of the effects of global change, analyses of temporal changes of biodiversity, including in poorly studied geographical areas are still necessary for freshwater benthic invertebrates.

Increases in global greenhouse gas emissions have changed the Earth's climate. Global surface air temperature has increased by approximately 1.5°C since 1880. Despite policy-development, these changes continue to increase, suggesting that only huge efforts would limit global warming by 2°C. Climate change impacts global biodiversity patterns, this has pushed scientists to study survival strategies of biodiversity. Therefore, a major challenge for the conservation of biodiversity, is to understand how species and ecosystems respond to climate change.

A major response of species to climate change is to shift their distribution ranges towards the poles or higher altitudes. These changes result from changes in the ratios of extinctions/colonisations at the margins of species ranges. Notably, it was found that marine species track the shifting isotherms faster in the oceans than on land. At the scale of communities, these changes can foster species temporal turn-over, increase or reduce species richness and eventually, alter functional diversity. For example, in French streams, macroinvertebrate species richness has increased by 42% in 25 years and functional diversity has increased at most sites (87%) in response to climate change.

Therefore, another challenge for ecologists, is to understand which species and traits mostly respond to climate change. Further, there is currently no consensus among ecologists regarding which species mostly respond to climate change, although it is thought that a phylogenetic signal exists. Similarly, studies identifying the traits that mostly define climatic sensitivity are sparse. However, traits such as body size, body mass, life duration, reproduction capacity and diet seem to influence extinction patterns.

The major cause of declines in the abundance and extinctions of species, is human land-use and the destruction of natural habitats by humans. At the global scale, urban and agricultural land-cover has increased from 5% to 39% globally from 1700 to 2000. As a result, more than 75% of the earth's surface has a positive human footprint, and only 3% of biodiversity hotspots are pristine. This is particularly the case in New-Zealand, which has lost more than 75% of its native forest cover since European settlement. In addition, agricultural intensification has increased since the 1970s with drastic changes in New Zealand's agricultural policy leading to greater uses of fertilisers and pesticides on land. Freshwater ecosystems are therefore under increasing threats and multiple anthropogenic pressures. This alters their biodiversity and ecosystem functioning. The objectives of this PhD thesis are to analyse temporal changes in the biodiversity of benthic river macroinvertebrate assemblages in New Zealand over a 26-year period. For so, we use high-resolution time series data of invertebrate biodiversity and environmental conditions to quantify and describe patterns of changes in the multiple facets of biodiversity and the effects of climate and land-use change.



Upper reaches of the Wairau River, Canterbury, New Zealand. Photo credit: Kéoni Saint-Pée

Chapitre 1

La biodiversité sous influence du changement global : mesures et bases de données

Préface :

Tel qu'énoncé dans l'Introduction générale, cette thèse a pour objectif de mesurer l'effet du changement global sur la biodiversité des macroinvertébrés benthiques dans les rivières de Nouvelle-Zélande, sur la période 1991 - 2016. Afin de répondre à cet objectif, j'ai utilisé des approches biostatistiques en écologie des communautés. Le premier chapitre est composé de deux parties distinctes : (1) une définition des mesures, et différentes facettes et composantes de la biodiversité et (2) une présentation détaillée des jeux de données utilisés pour répondre à chacun des objectifs de cette thèse. La mesure de la diversité biologique a en effet une histoire et son développement qui, bien que débutant approximativement à l'énoncé des concepts de Charles Darwin (1859) a subi une révolution de son développement méthodologique au début du XXI^{ème} siècle. Je m'efforcerais d'en définir les concepts et mesures principales. Ensuite, les analyses de cette thèse font appel à plusieurs bases de données dont un jeu de données de séries temporelles de biodiversité de macroinvertébrés benthiques de rivières et plusieurs bases de données décrivant l'environnement (climat, topographie, utilisation des terres, hydrographie et habitat) ainsi que les caractéristiques des espèces étudiées (traits fonctionnels et taxonomie). Ces bases de données seront présentées avec suffisamment de détails pour donner au lecteur les sources de leur origine et les raisons de leur utilisation.

Preface (english):

As outlined in the general introduction section, the objective of this PhD thesis is to measure the effects of global change on benthic macroinvertebrate biodiversity in New-Zealand Rivers, from 1991 to 2016. For so, I combine ecological theory with the use of statistical approaches in community ecology. The first chapter is divided in two distinct sections: (1) a definition of the measures, and different facets and components of biodiversity and (2) a detailed presentation of the databases used throughout the thesis. The measure of biodiversity has history and its development, although approximately starting with the publication of the first ecological concepts from Charles Darwin (1859), has seen a revolution in its methodological development during the early XXIst century. I define the major concepts and measures. Further, the analyses of this thesis use several databases, including a high-resolution benthic river macroinvertebrate time-series database, several databases describing the environment (climate, topography, land-use, hydrography, and habitat), and the characteristics of each studied species (taxonomy and functional traits). These databases will be presented with sufficient details to give the reader their origins and reasons for their use.

1. Mesurer la biodiversité

1.1 La diversité biologique

La description quantitative des communautés nécessite de mesurer la biodiversité qu'elles représentent. L'intérêt porté à la biodiversité et plus particulièrement sa quantification, s'est renforcée à l'émergence de problématiques en écologie et en biogéographie, car répondant à des besoins concrets de gestion de la conservation. Un problème majeur auquel sont confrontés les gestionnaires est le choix des systèmes à protéger, à restaurer et/ou à conserver en priorité (Brooks et al. 2006). Les écosystèmes plus riches et diversifiés doivent-ils être protégés en priorité ? Que signifie, écologiquement parlant, plus riches et/ou plus diversifiés ? Et surtout, comment, aux vues des effets croissants du changement global sur les communautés animales et végétales, ces écosystèmes les plus riches et diversifiés évoluent-ils ?

Une des définitions de la diversité, la plus acceptée de nos jours, est la suivante : "la variété des formes vivantes, à tous les niveaux des systèmes biologiques (i.e., de la molécule, de l'organisme, de la population, de l'espèce et de l'écosystème)" (Wilcox 1984). Aujourd'hui, la quantification de la diversité biologique est communément partitionnée en 3 composantes majeures : la diversité alpha (échelle locale), la diversité gamma (échelle régionale, c'est-à-dire de l'ensemble des communautés étudiées) et la diversité beta, représentant la variation de composition entre les communautés étudiées (Whittaker 1972). Plusieurs indices de diversité existent à chacune de ces échelles, et peuvent prendre en compte (ou non) les abondances et propriétés biologiques des espèces au-delà de leur taxonomie. Ainsi, les changements de biodiversité ne sont pas identiques à chaque échelle de perception et plusieurs indices complémentaires sont nécessaires pour évaluer la biodiversité d'un milieu donné.

1.2 La diversité fonctionnelle

La description de la diversité biologique, passe nécessairement par la prise en compte, des différences entre espèces (Webb et al. 2002). Un des premiers à considérer ces différences fut Darwin (1859), qui déclara que deux espèces d'un même genre sont davantage en compétition que deux espèces de genres distincts. Cette hypothèse induit que deux espèces proches phylogénétiquement, partagent des caractéristiques similaires, et ont des besoins et/ou exigences écologiques proches. Il souligne aussi que les espèces ne sont pas des entités indépendantes, mais qu'au contraire, elles partagent certaines caractéristiques du fait de leurs ancêtres communs, leur conférant des similitudes, plus ou moins fortes selon l'âge de l'ancêtre commun le plus récent.

Ainsi, la prise en compte de la diversité fonctionnelle et/ou phylogénétique permet de s'affranchir des hypothèses d'équivalence et d'indépendance des espèces. Ces deux facettes ont pris de l'importance dans les études en écologie à partir des années 1990 (e.g. Faith (1992); Keddy (1992); Weiher & Keddy (1995)). La diversité phylogénétique permet de quantifier l'histoire évolutive accumulée par les espèces coexistant (Harvey & Pagel 1991, Mace et al. 2003). La diversité fonctionnelle, quant à elle, mesure la diversité des traits, en intégrant les caractéristiques des espèces telles que, entre autres, la physiologie, l'écologie et/ou la morphologie dans les mesures de diversité biologique (Petchey & Gaston 2006, Violle et al. 2007). Les mesures de diversité fonctionnelle ont largement été développées et utilisées pour compléter la diversité taxonomique, notamment en écologie des communautés et biogéographie de la conservation (Champely & Chessel 2002, Mouillot et al. 2013, Stuart-Smith et al. 2013, Brum et al. 2017, Jarzyna & Jetz 2017). Dans mon travail de thèse, ne possédant pas de phylogénie datée pour l'ensemble des espèces étudiées (voir par exemple Múrria et al. (2018)), nous ne pouvions étudier la diversité phylogénétique propre et j'ai simplement considéré la taxonomie des espèces.

Dans une optique d'aide à la décision en conservation de l'environnement, la diversité fonctionnelle est particulièrement utile, car elle permet d'appréhender le fonctionnement des écosystèmes, ainsi que les services et biens prodigués par ces derniers à l'Homme (Tilman et al. 1997, Díaz & Cabido 2001, Isbell et al. 2017, Díaz et al. 2018). En effet, les écosystèmes fournissent aux êtres vivants, dont l'Homme, de nombreux services et biens parmi lesquels la production alimentaire, la purification de l'eau et de l'air, une protection contre certaines perturbations naturelles (e.g. inondations, tsunami), des services culturels et esthétiques, le recyclage de la biomasse morte, et d'autres. La perte de ces services est largement préjudiciable à l'humanité. Un exemple, concerne l'activité des pollinisateurs qui a été estimée, grossièrement, à environ 153 milliards d'euros en 2005 (Gallai et al. 2009). Or, en Chine, et plus particulièrement dans les pommeraies du Sichuan, l'abondance et biodiversité d'insectes pollinisateurs ont fortement chuté du fait de l'utilisation massive de produits phytosanitaires dans les cultures, obligeant les agriculteurs à polliniser manuellement leurs arbres fruitiers (Le Monde, 2014). Cet exemple de perte de services écosystémiques illustre l'intérêt économique que l'humanité a à préserver la diversité fonctionnelle (De Groot et al. 2012). Ainsi, la conservation de la diversité fonctionnelle peut aider à la conservation des écosystèmes, ainsi que de leur fonctionnement, dont dépendent les sociétés humaines.

1.3 Les différentes composantes de la biodiversité

La diversité peut être appréhendée et caractérisée à travers l'utilisation de différentes facettes, notamment : taxonomique, fonctionnelle et phylogénétique. Pour la diversité alpha, la richesse et l'équitabilité (« evenness ») sont les deux composantes taxonomiques les plus classiques et utilisées. Pour la diversité fonctionnelle, de nombreux indices ont été proposés, notamment : la richesse, l'équitabilité et la divergence (Mason et al. 2005, Villéger et al. 2008, Mouchet et al. 2010)

La richesse est une composante commune à toutes les facettes de la diversité, elle se mesure généralement en nombre d'espèces quand il s'agit de richesse taxonomique et en volume occupé dans un espace fonctionnel quand il s'agit de richesse fonctionnelle (e.g. Villéger et al. (2008)). Parce qu'elle permet d'intégrer la distribution des espèces et éventuellement de leurs abondances au sein d'un volume fonctionnel, l'équitabilité est également une composante largement utilisée. Dans sa version taxonomique, l'équitabilité correspond à la distribution des abondances entre les différentes espèces. Quand elle est fonctionnelle, elle décrit la distribution des individus et/ou des espèces dans l'espace fonctionnel. La divergence fonctionnelle mesure la variabilité des positions des espèces au sein de l'espace fonctionnel (Mason et al. 2005, Villéger et al. 2008). De plus, en utilisant les différences fonctionnelles entre espèces, il est possible d'estimer l'originalité (ou rareté et/ou redondance fonctionnelle (Flather & Sieg 2007, Violle et al. 2017, Kondratyeva et al. 2019)) d'une espèce. Ces différentes composantes de la diversité sont complémentaires, ainsi que mathématiquement et biologiquement indépendantes. Leur utilisation simultanée permet une meilleure compréhension de la structure des communautés.

Pour mesurer la diversité bêta, plusieurs méthodes existent et un intérêt grandissant pour son étude et son développement quantitatif a vu le jour au XXIème siècle (Legendre et al. 2005, Anderson et al. 2006). Il s'agit premièrement de choisir une méthode pour estimer les variations totales de composition entre les communautés étudiées. L'approche de Anderson et al. (2006) fut notamment très populaire en écologie. Elle proposait comme mesure, la dissimilarité moyenne des unités individuelles d'observation au centroïde de leur groupe, dans un espace multidimensionnel. Dans le même registre, la somme totale des carrés, proposée par Legendre et al. (2005) fut aussi très utilisée comme mesure de diversité bêta. Ensuite, il est possible de décomposer ces variations en remplacement d'espèces et/ou d'individus et en simples variations de richesses, et/ou d'abondance d'individus entre communautés (Baselga 2010, Baselga 2013, Legendre 2014, Baselga 2017). Ces dernières fut aussi décrites tel que l'emboîtement (« nestedness ») entre communautés (Baselga 2010, Mouillot et al. 2013).

2. Données biotiques et abiotiques

2.1 Données de biodiversité de macroinvertébrés

Les données utilisées pour examiner les patrons de changements de biodiversité au cours de cette thèse, sont des données d'abondance de macroinvertébrés benthiques de rivières en Nouvelle-Zélande. Elles proviennent d'un échantillonnage national (le « National River Water Quality Network (NRWQN) ») qui a été mis en place et est mené par NIWA (le « National Institute for Water and Atmospheric research »). Cet échantillonnage a pour but de contrôler la qualité physico-chimique et écologique des rivières de Nouvelle-Zélande. Dans la majorité des rivières, un point amont a été sélectionné et représente un site de référence (i.e. non-impacté par les activités humaines telles que la déforestation et l'agriculture), tandis que le point aval est un site impacté. Néanmoins, nombre de sites de référence ont vu leurs bassins versants en amont être modifiés au cours du temps et ne représentent aujourd'hui plus forcément de réelles conditions de références (comm. pers. J. Quinn).

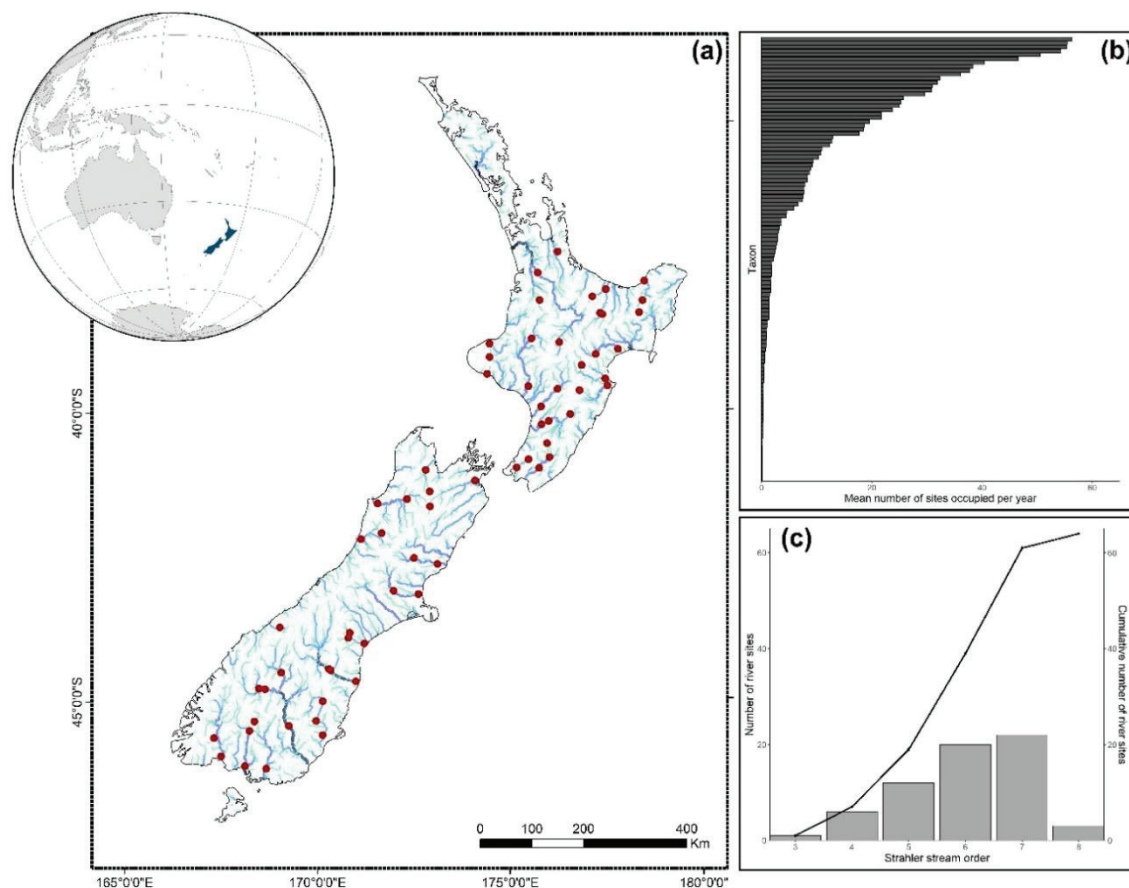


Figure 12 (a) Carte de la Nouvelle-Zélande montrant la position des sites d'échantillonnage (points rouges) de biodiversité de macroinvertébrés benthiques de rivières. (B) Nombre moyen de sites occupés par taxon et par an. (C) Nombre de sites (axe Y) et nombre cumulé de sites (axe Z) d'échantillonnage en fonction du rang de Strahler des sites.

Le NRWQN a échantillonné 82 sites au total qui recouvrent toutes la Nouvelle-Zélande du Nord au Sud et a débuté en 1989 (Quinn & Hickey 1990a, Quinn & Hickey 1990b). J'ai effectué ma demande d'extraction de données au début de 2018. Afin d'assurer une représentation temporelle uniforme à travers les sites étudiés, j'ai décidé de ne garder que 64 sites pour les analyses de ma thèse (Figure 12 (a)). Ces sites sont situés dans 35 rivières (rang de Strahler moyen = 6; max = 8, min = 3 ; Figure 12 (c)) et ont été échantillonnés de 1991 à 2016 inclus. Toutes les régions de Nouvelle-Zélande sont comprises dans l'échantillonnage sélectionné, sauf deux : Northland (aucun site) et la West Coast (un site uniquement). Le site le plus au Nord est situé sur la rivière Waihou et celui le plus au Sud sur la rivière Mataura (Figure 12 (a)).

Les données comportent l'abondance de 113 taxons, dont 26% sont identifiés au niveau de l'espèce, 47% au genre et 21% au niveau de la famille d'après Quinn & Hickey (1990). Ils représentent 82 genres et 68 familles. La même résolution taxonomique a été utilisé tout au long de l'échantillonnage, afin d'assurer l'analyse de changements temporels au cours du temps (Scarsbrook et al. 2000). Ces échantillons sont prélevés une fois par an, durant la saison de débit minimale (entre le mois de février et d'avril). A chaque site, sept filets Surber (0.1 m² de surface et maille de 250 µm) ont été récoltés sur un maximum de substrats différents, les échantillons sont ensuite triés et les individus identifiés et comptés en laboratoire. Les trois taxons les plus présents dans la base de données sont : les Trichoptères *Aoteapsyche* spp., les Diptères Orthocladiinae et l'éphéméroptère *Deleatidium* spp. ; tandis que les trois moins présents sont : les Neuroptères de la famille des Osmylidae, les Diptères Podominae et *Zelandotipula* sp (Figure 12 (b)).

2.2 Données climatiques

Afin de relier les changements de biodiversité aux changements climatiques, j'ai utilisé la base de données climatiques du VCSN (« Virtual Climate Station Network »), mise en forme et commercialisée par le NIWA (<https://niwa.co.nz/climate/our-services/virtual-climate-stations>). Le VCSN contient des données climatiques horaires pour toute la Nouvelle-Zélande. Les données sont interpolées sur une grille de ~5 km à partir de données en temps réels, qui proviennent de plus de 600 stations d'enregistrement météorologique en Nouvelle-Zélande. Elles sont ensuite interpolées automatiquement à l'aide du logiciel ANUSPLIN (Hutchinson & Xu 2004). ANUSPLIN est un logiciel qui permet l'interpolation spatial de données à l'aide de « thin plate smoothing splines ». Pour mes analyses, j'ai utilisé les données de température de l'air et de précipitation horaire dans chaque cellule contenant un site d'étude.

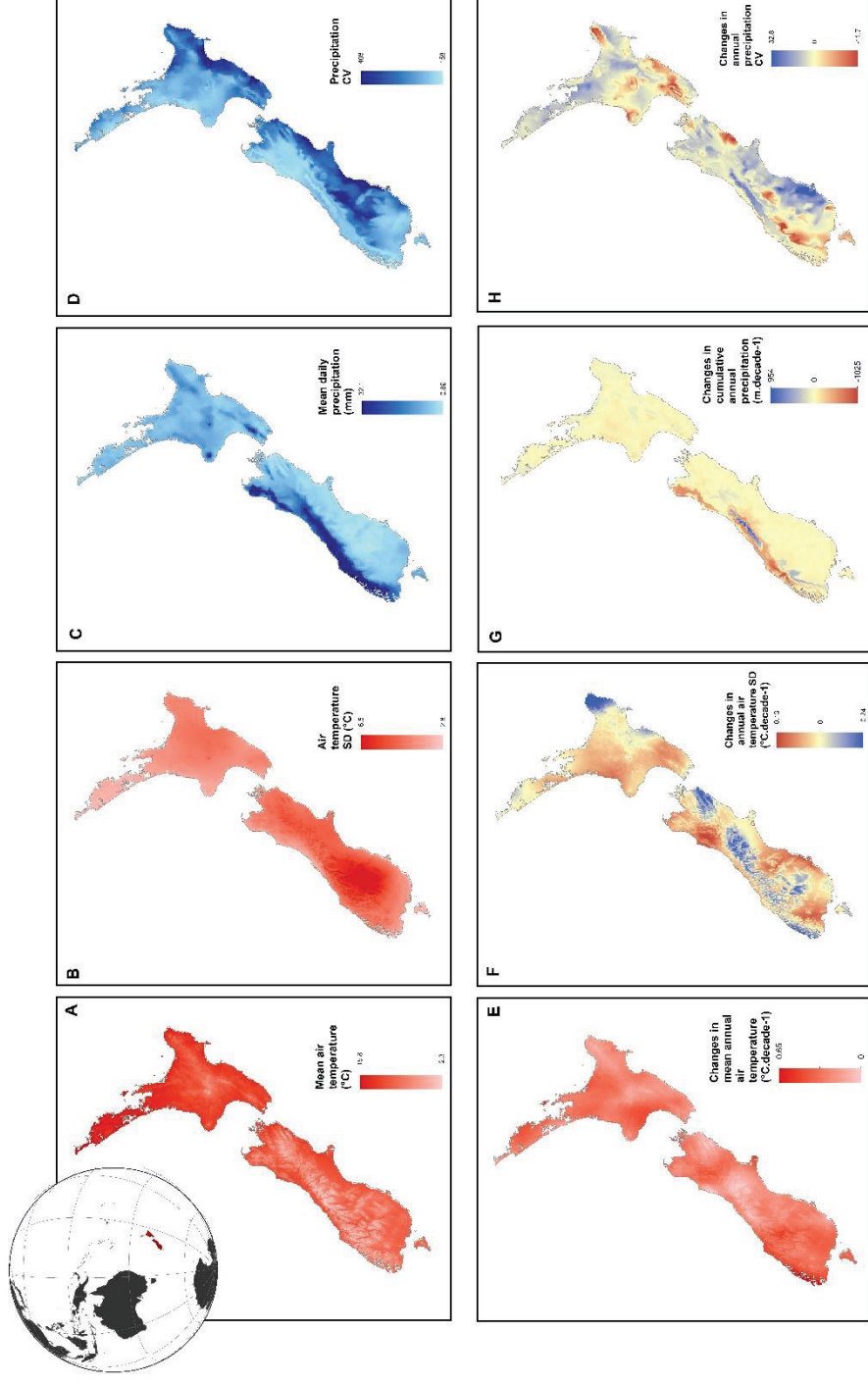


Figure 13 Cartes de la Nouvelle-Zélande montrant : A – D le climat pour la première année d'étude (1991). E – F les vitesses de changements climatiques par décennie pour les mêmes variables. De gauche à droite et pour chaque ligne : température moyenne annuelle (°C), écart type de la température de l'air annuel (°C), précipitation cumulative annuelle (mm) et coefficient de variation des précipitations annuelles.

Le changement climatique en Nouvelle-Zélande :

En Nouvelle-Zélande, de 1991 à 2016, d'après des modèles de régression linéaire : la température de l'air moyenne annuelle a augmenté de 0.25°C par décennie (maximum = 0.64°C). L'écart-type des températures annuelles a augmenté, en moyenne, de 0.02°C par décennie (minimum = - 0.24°C, maximum = 0.13). Les précipitations cumulatives annuelles ont diminué, en moyenne, de 44.1 millimètres par décennie (minimum = 1024, maximum = 954) et le coefficient de variation annuel de précipitations a augmenté, en moyenne, de 4.38 (minimum = -18.76, maximum = 32.83 ; Figure 13).

2.3 Données d'utilisation des terres

Pour quantifier l'utilisation des terres dans les bassins versant en amont de chacun des 64 sites d'étude, deux bases de données ont été utilisées. La première est la New Zealand Land Cover Data Base (LCDB, Landcare research). La LCDB est une classification thématique et multi-temporelle de la couverture des sols de Nouvelle-Zélande. Elle a été développée pour compléter une carte topographique de Nouvelle-Zélande, à une échelle de 1:50 000. Elle divise la couverture des sols en 75 classes différentes, que nous résumons en six classes pour les analyses de l'article I, décrivant : l'agriculture intensive, l'agriculture non-intensive, les forêts primaires, les espaces urbains, la couverture arbustive et les forêts exotiques.

La deuxième base de données est une base de densité de population de vaches laitières, de bœufs, de moutons et de cerfs d'élevages dans les bassins versant en amont des sites. Ces deux bases de données sont disponibles pour cinq pas de temps précédents nos échantillonnages : les étés 1990/91, 1996/97, 2001/02, 2008/09 et 2012/13. En nous appuyant sur les analyses de Julian et al. (2017) et pour les analyses des articles II et III de cette thèse, la différence (Δ) en couverture des sols et en densité de population de bétails entre 1990 et 2012, a été utilisé comme indicateur de changements temporels d'utilisation des terres.

2.4 Données de paysages, hydrographiques et d'habitat

Afin de décrire au mieux les bassins versants en amont des sites d'études, une classification des segments de cours d'eau de Nouvelle-Zélande décrivant leurs caractéristiques naturelles (i.e. de paysages) et de pressions humaines a été utilisée. Différentes échelles spatiales (tronçons, bassins versants amonts) ont été utilisé, afin d'extraire des variables pouvant influencer les dynamiques temporelles de macroinvertébrés benthiques de rivières. La base de donnée est : Freshwater

Ecosystems of New Zealand (FENZ; Leathwick et al. (2010)). FENZ est une base de données géo-spatialisée contenant des couches de données spatialisées décrivant des facteurs, tel que : les concentrations en phosphore et en calcium, ainsi que la dureté de la roche amont à chaque tronçon du réseau hydrographique Néo-Zélandais. Dans les articles I et II, les variables suivantes sont aussi utilisées : la surface des bassins versants en amont, la pente moyenne du bassin versant en amont et la largeur moyenne du lit mouillés à l'étiage de chaque tronçon.

Les 64 sites d'étude ont été tous équipés de jauges de débits qui enregistrent les débits horaires en continue. Les changements de débits moyen annuels et changements de coefficient de variation de débit annuels ont été utilisés comme indicateurs de changements de débits, dans les articles II et III. De plus, lors de chaque échantillonnage de macroinvertébrés, la taille des particules de substrat a été évaluée. Cent particules étaient aléatoirement collectées sur le site d'échantillonnage et leurs tailles mesurées et classées selon 8 classes de taille : roche mère, rochers (>300 mm), grande pierres (300–128 mm), petite pierre (128–64mm), gros gravier (32–64 mm), petit gravier (2–32 mm), sable (62.52 μm –2 mm) et limon (< 62.52 μm). Enfin, les sites d'études ont été échantillonnés pour la qualité physico-chimique de leurs eaux, mensuellement de 1991 à 2016 inclus. Dans les trois chapitres suivants, nous utilisons pour chaque site les valeurs médianes de concentration en nitrates ($\text{NO}_3\text{-N}$), d'azote ammoniacal ($\text{NH}_4\text{-N}$), de phosphore réactif dissous (DRP) et d'oxygène dissous (DO), ainsi que de la clarté de l'eau (CLAR).

2.5 Caractéristiques des espèces

2.5.1 Traits fonctionnels

Afin de décrire les caractéristiques de chaque taxon de la base de données, seize traits décrivant la morphologie, l'histoire de vie, les stratégies de dispersion et d'acquisition de ressources ont été utilisées. Ces traits proviennent d'une base de données de traits des macroinvertébrés d'eau douce de Nouvelle-Zélande, conçu par Dolédec et al. (2006). Les traits sont divisés en 59 modalités et un codage flou (de 0 à 3) est utilisé pour prendre en compte la variabilité intra-taxonomique ainsi que les lacunes dans les informations disponibles pour certains taxons plus rares (Chevenet et al. 1994).

2.5.2 Taxonomie des espèces

Afin d'identifier des changements potentiels propres aux taxons de la base de données, j'ai construit une classification taxonomique des taxons étudiés (contenant l'embranchement, le sous-embranchement, la classe, la sous-classe, la famille, la sous-famille, l'ordre, le genre et le nom de l'espèce) à l'aide du *National Center for Biotechnology Information* (et la fonction *taxonomy* du package *myTAI* (Drost et al. 2018) sous R (R Core Team, 2020)).

Chapitre 2

La biodiversité des macroinvertébrés
benthiques de rivières s'homogénéise-t-elle
d'un point de vue taxonomique et fonctionnel
au cours du temps ?

Préface :

Dans le chapitre précédent, nous avons présenté les différentes facettes et composantes qui constituent les mesures de biodiversité, ainsi que les jeux de données utilisés pour analyser les changements de biodiversité de macroinvertébrés au cours du temps et en identifier les causes potentielles. Le prochain chapitre s'attache à analyser les changements de diversité bêta spatiale d'un point de vue taxonomique et fonctionnelle et à en comprendre les causes potentielles de changements. Autrement dit, il pose la question suivante : les changements globaux mènent-ils à une homogénéisation taxonomique et fonctionnelle des assemblages de macroinvertébrés de rivières au cours du temps, à travers les bassins versants de Nouvelle-Zélande ?

Pour ce faire, nous analysons les variations spatiales de composition des communautés étudiées pour chaque année, à travers les 64 sites étudiés. Nous examinons si ces changements étaient principalement dus à un remplacement des espèces au cours du temps ou au contraire résultaient d'un changement unidirectionnel des abondances d'espèces. De plus, nous analysons les relations entre les changements de contribution des sites d'études à la diversité bêta spatiale taxonomique et fonctionnelle. Nous comparons aussi leurs vitesses de changements au cours du temps. Enfin, à l'aide de modèles additifs généralisés et hiérarchiques nous quantifions les effets corrélatifs de 16 variables environnementales, regroupés en 4 échelles environnementales.

En effet, l'homogénéisation taxonomique et fonctionnelle de la biodiversité étant une des conséquences importantes des changements globaux, il est nécessaire d'examiner si les patrons observés dans la littérature pour plusieurs groupes taxonomiques et localités à travers le monde s'expriment de façon similaire pour les macroinvertébrés benthiques de rivières. De plus, nous avons pu, grâce à une approche par modèles additifs hiérarchique généralisés, isoler les effets de plusieurs paramètres environnementaux (tel que les changements climatiques, l'utilisation des terres et les caractéristiques naturelles des rivières et de leurs bassins versant) afin de déterminer les causes de cette homogénéisation potentielle.

Preface (English):

In the previous chapter, we presented the different facets and components that constitute measures of biodiversity, and the databases used to analyse changes in biodiversity over time and their potential driving factors in the PhD thesis. The next chapter is focused on analysing changes in spatial taxonomic and functional beta diversity, and to understand its potential drivers of change. In other words, it asks the following question: does global change lead to taxonomic and functional homogenisation in river macroinvertebrate assemblages of New Zealand over time?

For so, we analyse spatial variation in the composition of communities for each year, across the 64 studied sites. Then, we analyse whether these changes were mostly due to the temporal replacement of species or, as opposed, results from unidirectional changes in the abundance of species. Further, we examine the relationship between changes in taxonomic and functional local contribution of sites to beta diversity. We also examine differences in their rates of change over time. Finally, we use hierarchical generalised additive models to quantify correlations between changes and 16 environmental variables, grouped within 4 spatial scales.

The taxonomic and functional homogenisation of biodiversity is one of the major consequences of global change, it is therefore necessary to examine whether the patterns observed for several taxonomic groups and localities worldwide, apply to New Zealand's River macroinvertebrates. In addition, with the use of hierarchical generalised additive models we were able to isolate the effects of several environmental factors (such as climate change, land-use change and the natural characteristics of catchments and river sections) to understand the drivers of spatial beta diversity changes.

Article I: Increasing climate driven taxonomic homogenisation but functional differentiation among river macroinvertebrate assemblages

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2.1 – Abstract

Global change is increasing biotic homogenisation globally, which modifies the functioning of ecosystems. While tendencies towards taxonomic homogenisation in biological communities have been extensively studied, functional homogenisation remains an understudied facet of biodiversity. Here, we tested four hypotheses related to long-term changes (1991 - 2016) in the taxonomic and functional arrangement of freshwater macroinvertebrate assemblages across space and possible drivers of these changes. Using data collected annually at 64 river sites in mainland New Zealand, we related temporal changes in taxonomic and functional spatial β -diversity, and the contribution of individual sites to β -diversity, to a set of global, regional, catchment and reach-scale environmental descriptors.

We observed long-term, mostly climate induced, temporal trends towards taxonomic homogenisation but functional differentiation among macroinvertebrate assemblages. These changes were mainly driven by replacements of species and functional traits among assemblages, rather than nested species loss. In addition, there was no difference between the mean rate of change in the taxonomic and functional facets of β -diversity.

Climatic processes governed overall population and community changes in these freshwater ecosystems, but were amplified by multiple anthropogenic, topographic, and biotic drivers of environmental change, acting widely across the landscape. The functional diversification of communities could potentially provide communities with greater stability, resistance, and resilience capacity to environmental change, despite ongoing taxonomic homogenisation. Therefore, our study highlights a need to further understand temporal trajectories in both taxonomic and functional components of species communities, which could enable a clearer picture of how biodiversity and ecosystems will respond to future global changes.

Keywords

β -diversity; Biotic homogenisation; Freshwater macroinvertebrates; Functional diversity; Climate change; Human disturbance

2.2 – Introduction

Global environmental changes are reducing biodiversity globally and altering the functioning of ecosystems through time, primarily through habitat change, pollution, and degradation (Cardinale et al. 2012, Hooper et al. 2012, Lefcheck et al. 2015). These processes are altering the distribution of species and the arrangement of communities across the landscape. At the global scale, native species extirpations exceed species colonisations (Urban 2015, Sobral et al. 2016, Jarzyna & Jetz 2018). Consequently, observations often indicate that human induced environmental changes homogenise biodiversity (i.e. reduces spatial β -diversity) through time (Clavel et al. 2011, Gámez-Virués et al. 2015, Magurran et al. 2015, Iacarella et al. 2018). The ecological and evolutionary consequences of this biotic homogenisation include reducing overall community and ecosystem functioning (Tilman et al. 1997), stability (Sankaran & McNaughton 1999), resilience (de Juan et al. 2013) and resistance to environmental change by narrowing the available range of species-specific responses to disturbances (*sensu* Mouillot et al. (2013)) (McKinney & Lockwood 1999, Olden et al. 2004, Olden 2006). Empirical biodiversity trends are however highly complex, and reports of a global biodiversity crisis are often seemingly contradictory to documented trends, including increases in β -diversity in response to anthropogenic disturbances (Gutiérrez-Cánovas et al. 2013, Hawkins et al. 2015). These latter observations imply that environmental changes may not always result in habitat simplification, and that a more general and comprehensive understanding of the factors that influence temporal changes in β -diversity is needed.

A trend towards taxonomic homogenisation (i.e. an increase in the similarity of species composition among species assemblages over time) has been demonstrated for many taxonomic groups across the globe (Haslem et al. 2015, Magurran et al. 2015, Kuczynski et al. 2018). Taxonomic diversity is,

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however, often recognised as providing only limited insight into the impacts of disturbance on ecosystem functioning, which may be better predicted using functional trait-based estimates of biodiversity (Tilman et al. 1997, Mouillot et al. 2013, Gagic et al. 2015). Increases in the similarity of functional trait composition among species assemblages over time, leading to functional homogenisation, are likely to decrease the resistance and resilience capacity of communities facing disturbances (Olden 2006, Clavel et al. 2011, de Juan et al. 2013). However, in some cases, there may be no direct relationship between changes in taxonomic and functional β -diversity among species assemblages (Sonnier et al. 2014, Villéger et al. 2014, White et al. 2018). For instance, assemblages that exhibit taxonomic homogenisation can be functionally differentiated if the newly introduced species in each assemblage are functionally dissimilar to each other (Villéger et al. 2014). Analyses of changes in functional β -diversity are therefore complementary to those of changes in taxonomic β -diversity (Sonnier et al. 2014, Villéger et al. 2014).

In ecosystems, biodiversity patterns are structured by factors operating at multiple, nested spatial scales (Townsend et al. 2003). At the global scale, climate is usually considered the predominant factor shaping biodiversity patterns, whilst at more local scales, factors including topography, land-use intensity and natural resource availability become increasingly important (Allan et al. 1997, Chase & Ryberg 2004, Mykrä et al. 2007, Chase & Knight 2013). For instance, an ecosystem might be buffered from the full magnitude of climate change by persisting in climate refugia (Hampe & Jump 2011, Keppel et al. 2012, Roberts & Hamann 2016). By contrast, local anthropogenic factors may interact with climate change processes to amplify their effects (Comte et al. 2016, Guo et al. 2018, Kuczynski et al. 2018). Hence, causal inferences on climate change effects in ecosystems may sometimes be difficult to distinguish from the potentially confounding effects of human driven local disturbances (Durance & Ormerod 2009, Floury et al. 2017, Radinger et al. 2017). However, attempts to disentangle the relative influence of global- to local-scale environmental drivers on the spatial arrangement of communities from both taxonomic and functional standpoints are lacking. This paucity of studies is

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particularly evident when considering how these patterns and relationships will change in response to global environmental change (Van Looy et al. 2017).

Here, we examined changes in the taxonomic and functional spatial β -diversity of freshwater macroinvertebrate assemblages in 64 New Zealand river sites over a 25-year period. Based on the knowledge gaps identified by Olden et al. (2018), we hypothesised an increasing taxonomic and functional homogenisation among freshwater macroinvertebrate assemblages (H_{1a} and H_{1b} , respectively). However, we hypothesised that the relationship between changes in each site's contribution to taxonomic and functional β -diversity over time, would differ due to contrasting taxonomic and functional responses to the environment (H_2 ; (Sonnier et al. 2014, Villéger et al. 2014)). Finally, we hypothesised that changes in climatic conditions over time would be the primary driver of observed changes in β -diversity (H_3 ; (Chase & Ryberg 2004, Chase & Knight 2013)).

2.3 – Methods

2.3.1 Macroinvertebrate community samples

Macroinvertebrate community samples were collected from 64 sites, located in 35 rivers (mean Strahler stream order = 6; max = 8, min = 3) of mainland New Zealand, between latitudes 46 and 35° S.

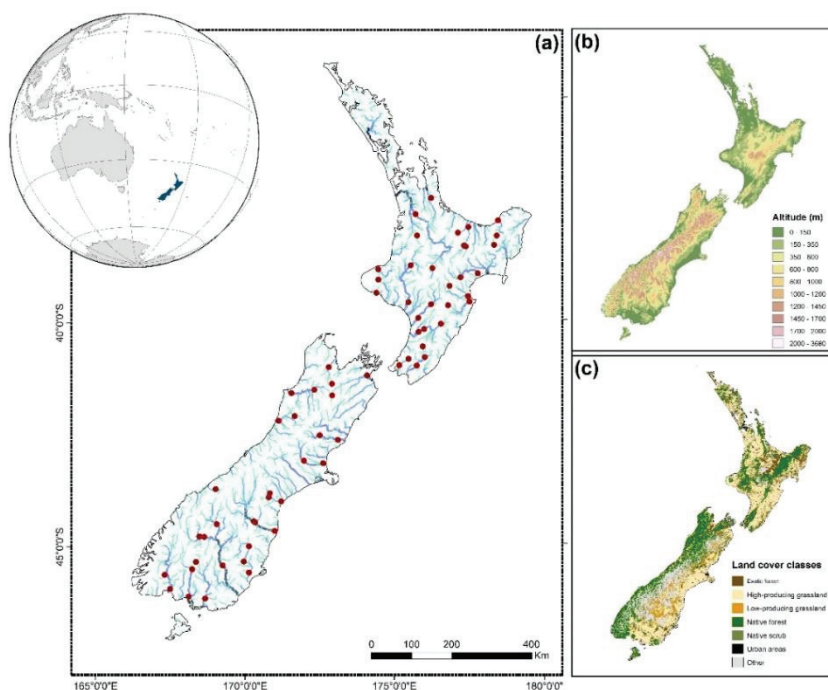


Figure 1 Maps of mainland New-Zealand showing (a) the location of the 64 sampling sites (red dots). Increases in river size (order > 3) are illustrated using increasing line width and darker blue color. The global inset map shows the location of New Zealand (blue country) in the world. (b) Altitude (m) and (c) Land-cover. For a definition of the land-cover classes, see Table S1.2

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Sampling surveys were conducted annually from 1991 to 2016, during late austral summers (February to April). These surveys were conducted for New Zealand's National Rivers Water Quality Network (NRWQN, Smith & McBride (1990)), which was operated and maintained by the National Institute of Water and Atmospheric Research (NIWA).

Sampling occurred under baseflow conditions ($Q < Q_{\text{median}}$) no less than 4 weeks after a flood exceeding three times the median flow. Seven Surber samples (0.1 m² and 250 µm mesh nets) were collected on all sampling occasions and macroinvertebrates were removed from the 0.1 m² area in the sampler down to a depth of c. 10 cm from as many substrate types as possible. Macroinvertebrates were identified to the lowest practicable taxonomic level (mostly species or genus) following Quinn & Hickey (1990). The same taxonomic resolution was maintained throughout the data set (Scarsbrook et al. 2000). Further information on site selection criteria, and sampling methodology are available in Smith & McBride (1990) and Davies-Colley et al. (2011).

Macroinvertebrate species were described by functional traits related to morphology, mobility, life-history, dispersal strategies and resource acquisition methods, extracted from the New Zealand freshwater macroinvertebrate trait database (NIWA; https://niwa.co.nz/sites/niwa.co.nz/files/nz_trait_database_v19_2_18.xlsx). Trait combinations govern species interactions through potential competition for habitat and food, or species contribution to ecosystem functioning through nutrient cycling, dispersal and trophic control (Sekercioglu 2010, Hevia et al. 2017). We used a total of 16 traits, divided into 59 modalities and fuzzy-coded from 0 to 3 following Chevenet et al. (1994) (Table S1.1; see also (Dolédec et al. 2006, Doledec et al. 2011)).

2.3.2 Environmental descriptors

Environmental characteristics to be used as predictors were grouped according to four different spatial scales: global, regional, catchment and reach scale (Table S1.2). Global-scale predictors used were temporal changes in air temperature and precipitation. At each site, we extracted daily values for the period 1991-2016, from 5 km² gridded layers of New Zealand, using NIWA's Virtual Climate

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Station Network (VCSN; <https://data.niwa.co.nz/>). We then regressed annual and seasonal (for the winter, spring and summer seasons) mean precipitation, precipitation variability (i.e. the coefficient of variation x 100), mean air temperature, and air temperature variability (i.e. the standard deviation of the mean) against time and used the slopes of each linear regression as estimates of temporal change. Principal Component Analyses (PCA; Pearson (1901)) were applied individually to air temperature and precipitation variables to reduce the multidimensionality and to eliminate multicollinearity within groups. We scaled all variables prior to PCAs and interpreted the respective first two axes of each PCA as synthetic descriptors of (1) changes in air temperature (TMean), (2) changes in air temperature seasonality (TSeas) (3) changes in precipitation seasonality (Prec CV) and (4) changes in precipitation (Prec; Table S1.3).

Regional scale predictors were described using four variables, reflecting landscape features that stretch beyond catchment boundaries. Altitude (m) at the sampling site, phosphorus and calcium concentrations and mean hardness (induration) in surface rocks of the upstream catchment (USPhosphorus, USCalcium and USHardness respectively). These variables were extracted for each site from the Freshwater Environments of New Zealand (FENZ) geodatabase, based on a thirty metre Digital Elevation Model (Leathwick et al. 2010), using ArcGIS version 10.7 (Esri, 2020).

For catchment-scale predictors, we used the proportion of upstream catchment covered by six land-cover types (intensive agriculture, light pastoral areas, native forest, urban areas, scrub and shrub cover and exotic forest; Table S1.2). We used static, spatial descriptors of land-cover *in lieu* of estimates of temporal changes in land-cover, as these were found to be major correlates of both spatial and temporal changes in the water-quality of New Zealand's freshwater systems (Julian et al. 2017, Snelder et al. 2018). We created the land cover types by aggregating fine-scale individual classes of the 75 land-cover classes from the New Zealand Land Cover database version 4.1 (Landcare Research 2015; Table S1.2). The six land-cover metrics were then ordinated using PCA, and the first two axes retained as synthetic land-use predictors (Land-use 1 and Land-use 2 respectively; Table

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S1.3). Area of the upstream catchment (km²; USCatchArea) and the average slope of the upstream catchment (degrees; USAvgSlope) from each river segment were also used as catchment-scale predictors.

Finally, reach-scale descriptors were defined by the slope (degrees) of the stream segment at each sampling site (SegSlope; Leathwick et al. (2010)), the predicted wetted river width (metres) at the 7-day mean annual low flow (WidthMALF; Booker (2015)), the estimated proportion of riparian shading at each river segment (SegRipShade; Leathwick et al. (2010) and temporal changes (1991-2016) in median annual values (mg.m⁻³) of nitrate (NO₃-N), ammoniacal-nitrogen (NH₄-N), dissolved reactive phosphorus (DRP) and dissolved oxygen (DO) concentrations and water clarity (metres; CLAR). Water quality variables were log₁₀-transformed prior to calculating temporal changes, which were then ordinated using PCA. The first axis was retained as a synthetic predictor of temporal changes in water quality (WQ; Table S1.3).

The final set of environmental variables consisted of 16 predictors which were not highly correlated (Pearson's $|r| < 0.65$; S1.1; Zuur et al. (2010)).

2.3.3 β - diversity measures

To evaluate temporal changes in taxonomic and functional spatial β -diversity we first log (x + 1) transformed macroinvertebrate abundances, and replaced the species by site matrix by a community-level (abundance) weighted means of functional trait values (CWM; Lavorel et al. (2008)) by site matrix for functional β - diversity analyses. We then measured β -diversity as the dissimilarity among all pairs of sampled sites ($N=64$) at each annual time step using the percentage difference index (%diff; Odum (1950); commonly referred to as Bray-Curtis dissimilarity). The percentage difference index between observation S_j and S_k is defined as:

$$\%diff = \frac{(B + C)}{(2A + B + C)}$$

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where A is the total abundance of all species found in both S_j and S_k , B is the total abundance of all species unique to S_j and C the abundance of each species unique to S_k . To assess the total variation in composition, we first computed the total sum of squares (SS_{total}) of the dissimilarity matrix by summing the dissimilarities in the lower triangular matrix and dividing it by the number of observations N . We then computed total β -diversity (BD_{Total}) for the North and South Island individually, by dividing SS_{total} by $N - 1$ (Legendre et al. 2005, Legendre & De Cáceres 2013).

We also measured temporal β - diversity for both islands individually using multiple-year and pairwise dissimilarity of all pairs of sampled years, by aggregating all samples across all sites ($N=64$) for each individual year ($n=25$). Pairwise β -diversity metrics and multi-site β -diversity metrics (i.e. spatial β -diversity aggregated across multiple sites) have been shown to reveal different patterns (Baselga 2010, Baselga 2013). To test whether temporal variations in β -diversity were mainly due to compensatory changes in abundances or fluctuations in total community abundance, we partitioned total β -diversity into two components, namely abundance replacement (β_{rep}) and abundance difference components (β_{diff}) following Baselga (2013), Legendre (2014) and Baselga (2017) as:

$$\beta_{\text{rep}} = \frac{2\min(B, C)}{(2A + B + C)}$$

and

$$\beta_{\text{diff}} = \frac{|B - C|}{(2A + B + C)}$$

Their contributions to total β - diversity were measured by computing the total sums of squares of each matrix and dividing them by $N - 1$.

Finally, to test the extent to which each sampled site contributed to long-term homogenisation or differentiation, we calculated temporal changes in the Local Contribution to Beta Diversity (LCBD;

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Legendre & De Cáceres (2013) of each community. LCBD indicates how unique an observation of macroinvertebrate composition is, by assessing its contribution to the total variation in community composition (Legendre & De Cáceres 2013). LCBD has been found to vary considerably through time in stream ecosystems (Li et al. 2020). We measured LCBD directly from the dissimilarity matrix of all observations as the diagonal elements of the matrix containing the centred dissimilarities, divided by SS_{total} . We then assessed temporal changes in LCBD at each site using the slope of a linear regression against years. Differences in the magnitude of temporal changes between taxonomic and functional LCBDs were tested for significance using paired samples t-tests.

2.3.4 Drivers of observed changes

Hierarchical Generalised Additive Mixed effects Models (GAMMs) were built to relate temporal changes in taxonomic and functional LCBD to global, regional, catchment and reach-scale processes respectively. Every variable (responses and predictors) was Box-Cox transformed and later standardised to their mean, one-unit variance. GAMMs were fitted with catchments nested within islands as random effects, using regression splines to account for potential non-linear relationships and restricted maximum likelihood (REML) to optimize the parameters estimates. For each change in LCBD, changes were primarily modelled against global climate change descriptors. We kept only the variables that maximised the coefficient of determination (adjusted- R^2) as the best model (Van Looy et al. 2017, Flourey et al. 2018). The relative importance of each variable in the model was assessed following methods described in Kuhn (2012). The same step was followed in a descendant way, using successively regional, catchment and reach scale descriptors as predictor variables and the residuals from the previous model as response variable. A smooth product between latitude and longitude was explored as a predictor variable using the residuals from the reach-scale models to account for spatial autocorrelation (Wood 2017). However, residual spatial autocorrelation was not observed ($p > 0.05$ for every model). Statistical analyses were all performed under the R environment (version 3.6.2; R Core Team, 2020). CWMs were calculated using the *FD* package (Laliberté et al. 2014), BD_{Total} and

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LCBD with the *adespatial* package (Dray et al. 2017), β -diversity partitioning with the *betapart* package (Baselga et al. 2018), GAMMs using the *mgcv* package (Wood & Wood 2015) and the relative influences of the environmental variables in the GAMMs with the *caret* package (Kuhn et al. 2020).

2.4 – Results

2.4.1 Changes in taxonomic and functional β -diversity

We observed overall tendencies towards taxonomic homogenisation but functional differentiation of macroinvertebrate communities on both islands of New Zealand (Figure 2A and B). Spatial taxonomic

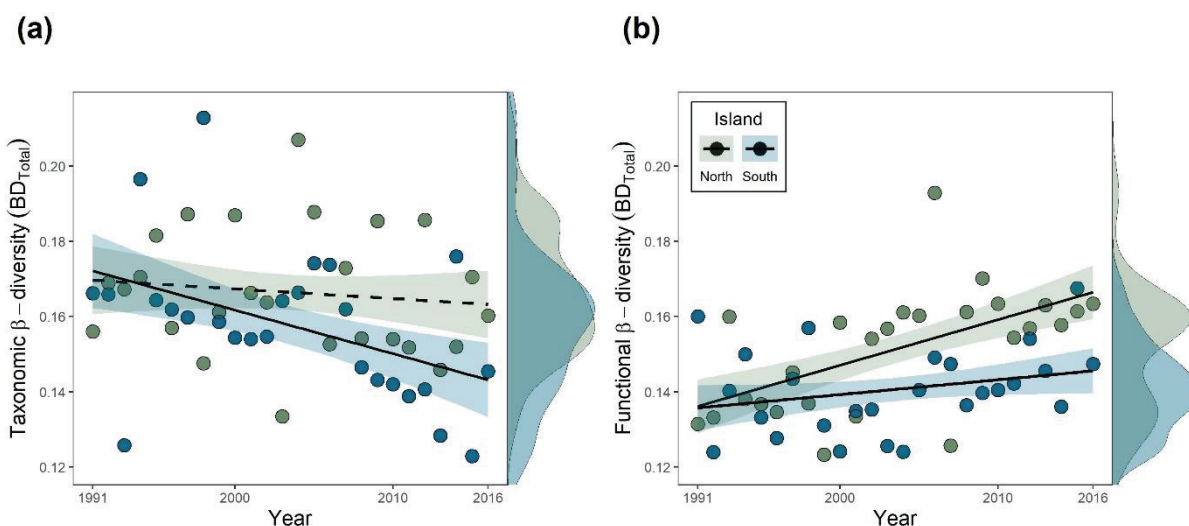


Figure 2 Scatter plots illustrating temporal changes in (a) taxonomic and (b) functional β -diversity (BD_{Total}) for the North and the South Island of mainland New Zealand (as indicated by the legend). Solid black lines represent significant ($p < .05$) linear regression models, whereas the black dashed line represents a nonsignificant model ($p > .05$). Density curves on the right of the figures illustrate the density distribution of the corresponding variable.

β -diversity declined over the 25-year period in the South Island ($R^2 = 0.19$, $F = 11.84$, $p < 0.01$), but not on the North Island ($p = 0.407$). In contrast, functional β -diversity increased on the North Island ($R^2 = 0.33$, $F = 24.62$, $p < 0.001$) but less so on the South Island ($R^2 = 0.069$, $F = 3.694$, $p = 0.06$).

Multiple-year and pairwise temporal β -diversity measures were highly similar on both islands and mainly driven by replacements of species abundances and functional traits among communities, rather than unidirectional abundance differences (Table 1

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). However, abundance replacements were much higher for taxonomic β -diversity (Multiple-year values: $\beta_{rep} = 61.1\%$ on both islands; $\beta_{diff} = 11.1\%$ and 11.2% for the North and the South Island respectively; Average pairwise dissimilarity: $\beta_{rep} = 37.2\%$ and 39.2% ; $\beta_{diff} = 20.8\%$ and 21.1% for the North and the South Island respectively. Table 1) than for functional β -diversity (Multiple-year dissimilarity: $\beta_{rep} = 20.4\%$ and 21.1% , $\beta_{diff} = 17\%$ and 16% ; Average pairwise dissimilarity: $\beta_{rep} = 12\%$ and 16.4% , $\beta_{diff} = 17.7\%$ and 20.3% , for the North and the South Island respectively; Table 1).

Finally, only 44% of the sites exhibited decreasing taxonomic LCBD, 56% showing flat trends or increasing taxonomic LCBD (Figure 3A), and 56% exhibiting decreasing functional LCBD – 44% showing flat trends or increasing functional LCBD (Figure 3B).

Table 1 Taxonomic and functional temporal β -diversity measured as the percentage difference index of dissimilarity (β_{diff}) and its decomposition into replacements of species abundances or functional traits (β_{rep}) and unidirectional abundance gradients (β_{diff}) of macroinvertebrate assemblages collected annually at 64 river sites in New Zealand from 1991 to 2016. To exclude potential spatial variations in species composition, samples were aggregated across all sampled sites (N=64) for each sampled year (N=25; 1991-2016) prior to analyses. Multiple-year dissimilarity corresponds to the dissimilarity after aggregating data across all years. Average pairwise dissimilarity is the average value of each pairwise comparison of sampled years. Values in the table are percentages.

| Island | Biodiversity facet | β_{diff} | β_{rep} | β_{diff} |
|---------------------------------------|--------------------|----------------|---------------|----------------|
| Multiple-year dissimilarity | | | | |
| North | Taxonomic | 72.2 | 61.1 | 11.1 |
| | Functional | 37.9 | 20.4 | 17.5 |
| South | Taxonomic | 72.3 | 61.1 | 11.2 |
| | Functional | 37.3 | 21.1 | 16.1 |
| Average pairwise dissimilarity | | | | |
| North | Taxonomic | 58.0 | 37.2 | 20.8 |
| | Functional | 29.7 | 12.0 | 17.7 |
| South | Taxonomic | 60.4 | 39.2 | 21.2 |
| | Functional | 36.7 | 16.4 | 20.3 |

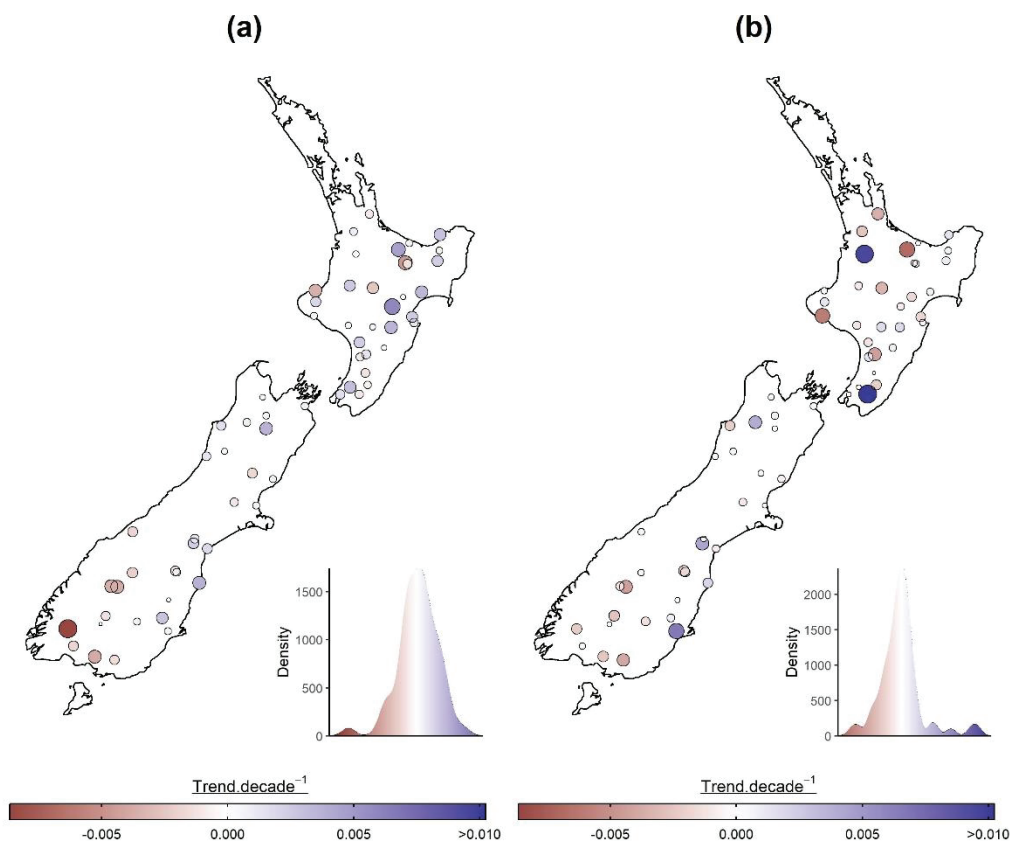


Figure 3 Maps of temporal changes (trend.decade⁻¹) in (a) taxonomic and (b) functional Local Contribution to Beta Diversity (LCBD) measured using log(x + 1) macroinvertebrate abundances and the percentage difference index of dissimilarity. Point size is proportional to the degree of change. Density curves at the bottom right corner of each map illustrate the density distribution of each variable.

2.4.2 Relationship between changes in taxonomic and functional local contribution to β -diversity

Changes in taxonomic and functional LCBD were weakly positively correlated on the South Island ($R^2 = 0.11$, $p = 0.07$; Figure 4A), but not on the North Island ($p = 0.69$; Figure 4A). Over both islands, 36% of the sites experienced increasing taxonomic LCBD but decreasing functional LCBD, whereas only 11% of the sites experienced increasing functional LCBD but decreasing taxonomic LCBD. Equal amounts (26%) of the remaining sites exhibited increasing or decreasing taxonomic and functional LCBD. In addition, there were no differences between changes in taxonomic and functional LCBD for all pairs of samples and on both islands individually ($0.20 < p < 0.76$; Figure 4B).

2.4.3 Drivers of observed changes

Hierarchical GAMMs explained 38% of the temporal changes for both taxonomic and functional LCBD (Table 2). Changes in taxonomic LCBD were mostly driven by global-scale variables ($R^2 = 0.25$) and further influenced by catchment- ($R^2 = 0.07$) and reach-scale descriptors ($R^2 = 0.07$; Table 2). Changes in functional LCBD mostly responded to global- ($R^2 = 0.23$) and catchment-scale descriptors ($R^2 = 0.21$; Table 2).

Eleven drivers of change in taxonomic LCBD were selected in

the GAMMs (Figure 5). These were: changes in precipitation seasonality (% of relative influence = 20.7), changes in air temperature (15.6%), altitude (12.1%), stream segment wetted river width at the 7-day mean annual low flow (11.2%), changes in precipitation (11.1%), stream segment slope (10.7%), upstream

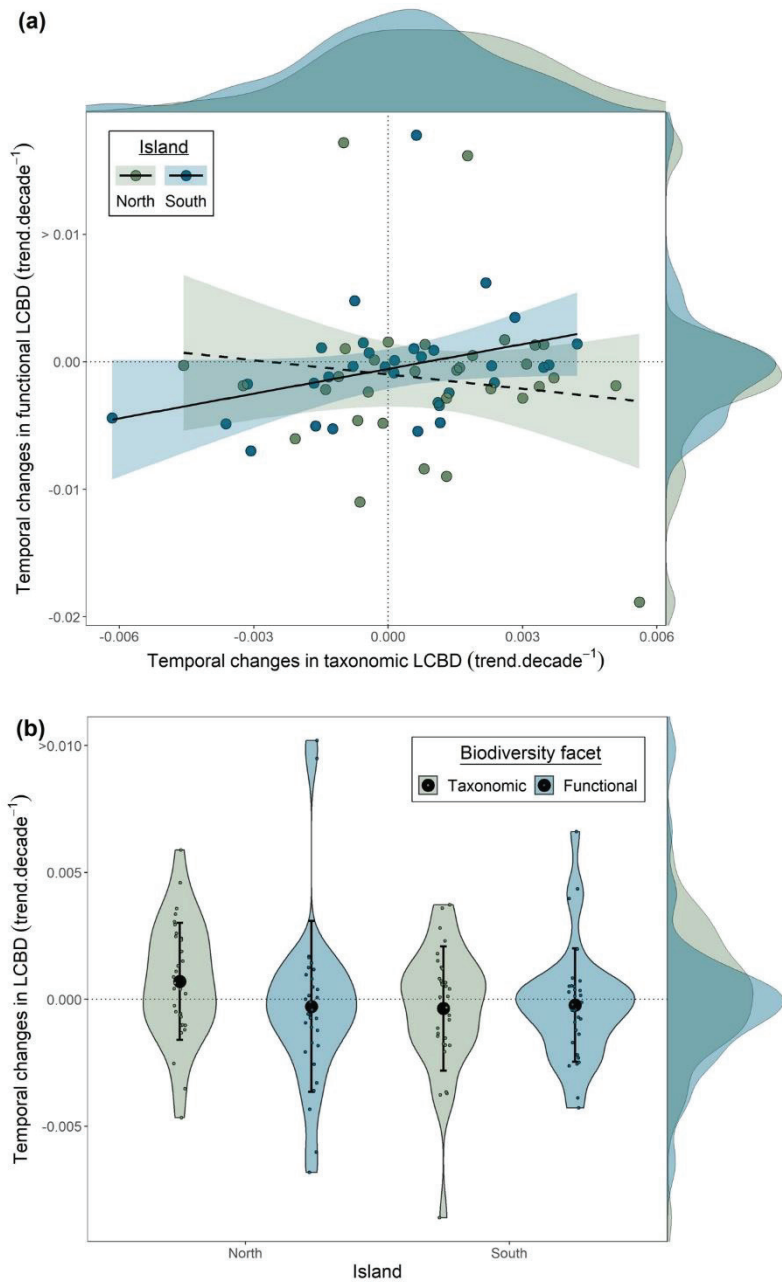


Figure 4 (a) Relationships between temporal changes in taxonomic and functional Local Contribution to Beta Diversity (LCBD) for both islands of mainland New Zealand. The solid black line represents a significant ($p < .05$) linear regression model. The black dashed line represents a nonsignificant model ($p > .05$). Shaded areas around the regression lines are 95% pointwise confidence intervals. (b) Violin plots illustrating differences between rates of changes in taxonomic and functional LCBD for the North and the South Island individually. The average rate of change is shown as black points and standard deviation as vertical black lines, in each violin plot. Raw values are shown as colored points. The horizontal dashed line on the plot shows the zero mark. The density curves on the margins of the figures illustrate density distribution of the corresponding variables

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calcium concentration in surface rocks (7.8%), land-use intensity (Land-use 1: 5.8%; Land-use 2: 5.7%;), upstream catch area (5.4%) and upstream average slope (4.9%).

Table 2 Coefficients of determination (adjusted-R²) of each generalised additive mixed effect model for each spatial scale and the full model (Total).

| Biodiversity facet | Spatial scale | | | | Total |
|--------------------|---------------|----------|-----------|---------|-------|
| | Global | Regional | Catchment | Reach | |
| Taxonomic | 0.25 | 0.05 | 0.07 | 0.07 | 0.38 |
| Functional | 0.23 | 0.01 | 0.21 | < 0.001 | 0.38 |

By contrast, changes in functional LCBD were driven by seven variables (Figure 5). Specifically, upstream catchment average slope (23.91%), changes in precipitation (22.4%), changes in air temperature (16.8%), land-use intensity (Land-use 1 and Land-use 2; 10.3% and 8.6% respectively), changes in temperature seasonality (9.2%), and upstream concentration of calcium in surface rocks (8.8%). Marginal effects plots of these relationships are presented in Figure S3.1.

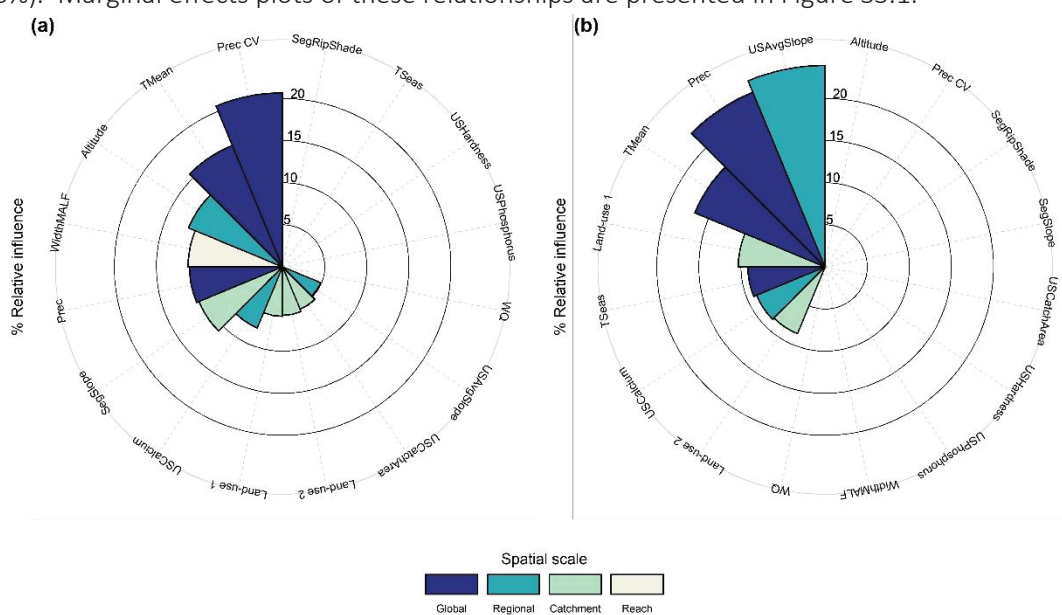


Figure 5 Polar diagrams illustrating the percentage of relative influence explained by each environmental predictor in the hierarchical Generalized Additive Mixed effects Models, for (a) taxonomic and (b) functional changes in Local Contribution to Beta Diversity

2.5 – Discussion

Our analyses revealed large-scale declines in taxonomic β -diversity but concurrent rises in functional β -diversity over the 25-year study period, which only partially supports our first hypothesis (fulfilling H_{1a} but rejecting H_{1b}). As expected, we found a weak relationship between changes in each site's contribution to taxonomic and functional β -diversity (accepting H_2). In addition, the mean rate of temporal change in these two metrics did not differ. Finally, our results support H_3 with global scale climatic factors being the primary determinants of the observed changes in taxonomic and functional β -diversity.

The functional differentiation among freshwater macroinvertebrate assemblages over the 25-year period was contrary to our expectation. However, similar climate-induced large-scale increases in functional diversity of freshwater macroinvertebrates were also recently observed in rivers of France (Floury et al. 2018, Bruno et al. 2019), and similar responses to climate change have been observed for other taxa and trophic levels globally (Walther et al. 2002, Araújo et al. 2006). In running waters, this climate-induced process could be due to the increasing prevalence of warm-water species in temperate systems, which are promoted by newly suitable (i.e. warmer) conditions (Buisson et al. 2008, Haase et al. 2019). Such a rise in functional β -diversity may also provide greater resilience and resistance capacity to macroinvertebrate communities facing disturbances (de Juan et al. 2013, Mori et al. 2013, Isbell et al. 2015, Van Looy et al. 2019).

Although a relationship between temporal changes in taxonomic and functional LCBD was observed on the South Island, the pattern did not hold on the North Island. This discrepancy highlights the need to consider explicitly both the taxonomic and functional facets of biodiversity, as changes in functional β -diversity cannot necessarily be predicted by changes in taxonomic β -diversity (Baiser & Lockwood 2011, Villéger et al. 2014, White et al. 2018). More importantly, 36% of the communities (measured as changes in their local contribution to β -diversity) in the present analyses, differentiated in taxonomic composition, but homogenised in functional composition with accrued time, as opposed to the rest of

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the communities. This may represent a key mechanism underlying the observed rise of generalist species and replacement of cold-tolerant species with warm-tolerant species that is being observed in temperate macroinvertebrate communities (Van Looy et al. 2016, Flourey et al. 2018, Haase et al. 2019). That is, communities comprising functionally similar but taxonomically diverse species are being replaced by functionally diverse but taxonomically similar species, as observed here.

Changes in precipitation seasonality was the most important correlate of taxonomic homogenisation. In contrast to temperature, which exhibited a consistent increase across all locations, changes in precipitation and precipitation seasonality were location-specific, with both increases and decreases present across the country (Fig. S2.2). These changes, whether an increase or a decrease, tended to reduce a site's contribution to β -diversity. Mainland New Zealand is composed of two mid-latitude islands, with a typically unpredictable climate (Tonkin et al. 2018) and flashy river flow regimes (Winterbourn et al. 1981) due to its oceanic position. The temporal turnover of stream communities in New Zealand streams tends to reflect this unpredictability, with limited intra-annual differentiation between seasons compared to trends in more predictable climates (Tonkin et al. 2017). However, our results indicate that patterns of precipitation seasonality in New Zealand has changed over this 25-year period, altering the spatial distribution of river macroinvertebrate communities through time. Similar climate driven environmental harshness has been observed not to only be important for dynamic systems like these, but also for other ecosystems worldwide. For instance natural flow intermittence is an important structuring agent for stream macroinvertebrate communities in Mediterranean streams (Belmar et al. 2019). Given the importance of natural cycles of flooding and drought in streams (Poff et al. 1997, Aspin et al. 2018, Tonkin et al. 2018, Aspin et al. 2019), it stands to reason that patterns in precipitation seasonality play a key role in structuring stream macroinvertebrate species communities.

Our results clearly highlighted a particularly dominant role of climate change, and less so land-use, in mediating changes in taxonomic and functional β -diversity of these river macroinvertebrate

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communities. These processes, together, contributed most of the relative influence explained by the variables in our models. Climate change, however, explained 3.6 times more of the variability in changes in taxonomic β -diversity, and 1.3 times more in functional β -diversity, than land-use related variables. This is despite New Zealand having experienced one of the highest rates of agricultural land intensification over recent decades (OECD/FAO 2015). However, we recognise that this result may be specific to our study area. For instance, the effects of climate change and land-use variables may have differed had we focused on streams of different realms (Heino 2011) or size (Floury et al. 2018, Radinger & García-Berthou 2020). Moreover, although we examined the effects of different environmental scales in our models, our findings could relate to the spatial extent of our analyses (Wiens 1989, Hewitt et al. 2010, Jarzyna & Jetz 2018). This can obscure the relative importance of anthropogenic factors that may only operate at local scales (Jouffray et al. 2019), such as human-induced flow alteration, eutrophication and sedimentation within single catchments. Whether a stronger anthropogenic signature would emerge at a finer extent of analyses, therefore, represents an important next step for future work that could better inform local community management.

The responses of communities to changes in climatic drivers were variable. Air temperature warming correlated with decreases in taxonomic and functional LCBD. However, decreasing precipitation correlated with decreasing taxonomic LCBD but increasing functional LCBD. Warming and decreasing precipitation theoretically reduces discharge, hence potentially reduces the connectivity among communities, but at the same time may homogenise mesohabitats in these systems (Rahel 2002, Rahel 2007, Aspin et al. 2018, Aspin et al. 2019). Such a mechanism would support the expansion of functionally diverse but homogeneous species assemblages. By contrast, Villéger et al. (2014) observed greater functional homogenisation than taxonomic homogenisation in European freshwater fish assemblages under climate change due to range expansions in non-native species distributions within European water basins, which supported similar functions to native species. Elucidating which species and functional traits contributed to the changes in β -diversity observed here, may allow

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further research to understand the evolutionary and ecological consequences of these changes in biodiversity.

Climate models suggest river flow regimes will increase in variability as the climate continues to change (Arnell & Gosling 2013, Schneider et al. 2013, Kakouei et al. 2018), opening the door to questions of how freshwater macroinvertebrate communities will respond to more intensified and variable flow disturbances. Although these New Zealand streams have seen an increase in functional diversity over the 25-year period, more intensified disturbances are likely to suppress or overturn this trend (Domisch et al. 2013, Kakouei et al. 2018). For example, an increasing number of colonising warm-water species could promote further species losses, by competitive exclusion (Buisson et al. 2008, Radinger et al. 2019). Moreover, the resilience of stream biodiversity in the face of continued global change could also be reduced if spatial insurance effects become less effective, as large-scale disturbances promote greater synchrony among ecosystems (Shanafelt et al. 2015). Our results therefore indicate that the responses of stream biodiversity to ongoing environmental change are overly complex with contrasting taxonomic and functional responses to change. The positive news of increasing functional β -diversity over time, which may provide a greater resilience capacity to communities despite taxonomic homogenisation, could only be a transient process that will be overturned in time. To better understand the biodiversity consequences of future global change, we need a greater uptake of studies exploring the combined and interacting responses of both taxonomic and functional components of biodiversity to ongoing environmental change. As river ecosystem reorganisation continues in the Anthropocene in response to climate change (Olden et al. 2018, Tonkin et al. 2019), the value of different ecosystem states and environmental management will likely hinge upon the capacity of those ecosystems to maintain key functional processes despite ongoing taxonomic homogenisation.

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Author contributions

TM, FS and PV compiled the data. TM and MF designed the study, computed analyses, and interpreted the results. TM and JDT wrote the manuscript with inputs from all co-authors.

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Data accessibility

The data that support the findings of this study are available from NIWA upon request. Restrictions apply to the availability of these data, which were used under license for this study. Data are available from the authors with the permission of NIWA.

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Supplementary materials

1: Species functional traits and observed environmental and biotic conditions in New Zealand large rivers from 1991 to 2016

Table S1.1 Category, Description and Modality of the macroinvertebrate functional traits used for analyses.

| Category | Description | Modality |
|---------------------|--|--------------------------------------|
| MORPHOLOGY | Maximum potential size | ≤5 mm |
| | | >5-10 mm |
| | | >10-20 mm |
| | | >20-40 mm |
| MORPHOLOGY | Body flexibility | >40 mm |
| | | none (<10°) |
| | | low (>10-45°) |
| MORPHOLOGY | Body form | high (>45°) |
| | | streamlined |
| | | flattened (dorso-ventral or lateral) |
| | | cylindrical |
| MORPHOLOGY | Respiration of aquatic stages (not including eggs) | spherical |
| | | tegument |
| | | gills |
| | | plastron |
| LIFE HISTORY | Maximum number of descendants per reproductive cycle | aerial |
| | | ≤100 |
| | | >100-1000 |
| | | >1000-3000 |
| | Maximum number of reproductive cycles per year | >3000 |
| semivoltine | | |
| | | uninvolving |

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| | | |
|-----------------|--|---|
| | | plurivoltine |
| | Number of reproductive cycles per individual | 1 ≥2 |
| | Life duration of adults | ≤1 day >1-10 days >10-30 days >30-365days >365 days |
| | Reproductive technique | single individual hermaphrodism male and female |
| | Oviposition Site | water surface submerged terrestrial endophytic |
| | Egg/egg mass | free cemented female bears eggs in/on body |
| | Aquatic stages | Adult, larva Adult or larva Larva, Pupa |
| MOBILITY | Dissemination potential (all stages) | low (<10 m) medium (10m - 1 km) high (>1km) |
| | Attachment to substrate of aquatic stages (excluding eggs) | swimmers (water column) crawlers (epibenthic) burrowers (infauna) |

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| | | |
|---------------------------------|---------------------|---------------------|
| | | attached |
| RESOURCE ACQUISITION | Feeding habits | shredders |
| | | scrapers |
| | | deposit-feeders |
| | | filter-feeders |
| | | predator |
| | | algal piercer |
| | Dietary preferences | strong (specialist) |
| | | moderate |
| | | weak (generalist) |

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Table S1.2 Spatial scale, abbreviation, description, and summary statistics of the environmental variables used for modelling, prior to calculating temporal changes and synthesising variable groups. Min = minimum; Max = Maximum.

| Spatial scale | Abbreviation | Description | Min | Max | Mean |
|---------------|--------------------|--|----------|----------|----------|
| Global | Temp | Mean annual air temperature (°C) | 6.14 | 16.73 | 11.93 |
| | Temp SD | Annual air temperature seasonality (°C; the standard deviation of the mean) | 2.87 | 5.86 | 4.15 |
| | Temp summer | Mean annual summer air temperature (°C) | 10.63 | 20.25 | 16.35 |
| | Temp SD summer | Annual summer air temperature variability (°C; the standard deviation of the mean) | 1.34 | 3.95 | 2.46 |
| | Temp winter | Mean annual winter air temperature (°C) | 0.74 | 13.51 | 7.45 |
| | Temp SD winter | Annual winter air temperature variability (°C; the standard deviation of the mean) | 1.33 | 3.92 | 2.26 |
| | Temp spring | Mean annual spring air temperature (°C) | 5.71 | 15.63 | 11.41 |
| | Temp SD spring | Annual spring air temperature variability (°C; the standard deviation of the mean) | 1.41 | 4.54 | 2.62 |
| | Prec | Mean daily precipitation (mm) | 0.80 | 20.51 | 3.51 |
| | Prec CV | Annual precipitation coefficient of variation (mm) | 149.60 | 440.38 | 249.23 |
| | Prec summer | Mean summer daily precipitation (mm) | 0.39 | 25.82 | 3.11 |
| | Prec CV summer | Summer precipitation coefficient of variation (mm) | 18.31 | 78.63 | 39.03 |
| | Prec winter | Mean winter daily precipitation (mm) | 0.22 | 18.26 | 4.01 |
| | Prec CV winter | Winter precipitation coefficient of variation (mm) | 17.59 | 86.12 | 47.9 |
| | Prec spring | Mean spring daily precipitation (mm) | 0.50 | 23.21 | 3.49 |
| | Prec CV spring | Spring precipitation coefficient of variation (mm) | 22.12 | 84.08 | 46.75 |
| Regional | Altitude | Altitude (m) | 0.30 | 672.26 | 164.44 |
| | USCalcium | Catchment-average Calcium concentration of underlying rocks (1 [very low]–4[very high]) | 1.01 | 2.01 | 1.46 |
| | USHardness | Catchment average hardness (induration) of surface rocks (1 [very low]–4[very high]) | 1.93 | 4.00 | 3.21 |
| | USPhosporus | Catchment-average Phosphorus concentration of underlying rocks (1 [very low]–4[very high]) | 1.03 | 4.00 | 2.38 |
| Catchment | USAvgSlope | Average slope in the upstream catchment (degrees), describes catchment-driven modification of flow variability | 3.48 | 30.5 | 19.0 |
| | USCatchArea | Area of the upstream catchment (m ²) | 1.37E+07 | 1.65E+10 | 2.48E+09 |
| | usintensiveAg | Proportion of catchment occupied by combination of high producing exotic grassland, short-rotation cropland, orchard, vineyard and other perennial crops (LCDB4.1 40,30,33) | 0 | 0.91 | 0.29 |
| | usPastorallight | Proportion of catchment occupied by low producing grassland (LCBD4.1 class 41) | 0 | 0.30 | 0.06 |
| | usNativeForest | Proportion of catchment in native forest (LCDB4.1 class 69) | 0 | 0.94 | 0.28 |
| | usUrban | Proportion of catchment occupied by combination of built-up areas, urban parkland, surface mines, dumps, transport, infrastructure (LCDB4.1 class 1,2,6,5) | 0 | 0.06 | 0 |
| | usScrub | Proportion of catchment in scrub and shrub cover (LCDB4.1 class, 50,51,52,54,55,56,58) | 0 | 0.38 | 0.11 |
| | usExoticForest | Proportion of catchment occupied by exotic forest (LCDB4.1 class 71) | 0 | 0.60 | 0.06 |
| Reach | WidthMALF | Wetted river width at the 7-day mean annual low flow (m) | 0.547 | 36.5 | 9.23 |
| | SegSlope | Segment slope (degrees), derived from GIS calculation using length and difference between upstream and downstream elevation for each segment | 0.00 | 1.72 | 0.260 |
| | SegRipShade | Riparian shading (proportion), the likely degree of riparian shading derived by using national, satellite image-based vegetation classification to identify riparian shading in each segment, with the degree of shading then estimated from river size and expected vegetation height | 0.00 | 0.49 | 0.07 |
| | DO | Dissolved oxygen concentration (mg.m ⁻³) | 3.35 | 12.80 | 10.53 |
| | CLAR | Black disk clarity (m) | 0.04 | 13.60 | 2.22 |
| | NH ₄ -N | Ammoniacal-Nitrogen concentration (mg.m ⁻³) | 0.00 | 85.42 | 11.46 |
| | NO ₃ -N | Nitrate-Nitrogen concentration (mg.m ⁻³) | 0.00 | 2419.50 | 233.45 |
| | DRP | Dissolved Reactive Phosphorus concentration (mg.m ⁻³) | 0.00 | 87.4 | 8.63 |

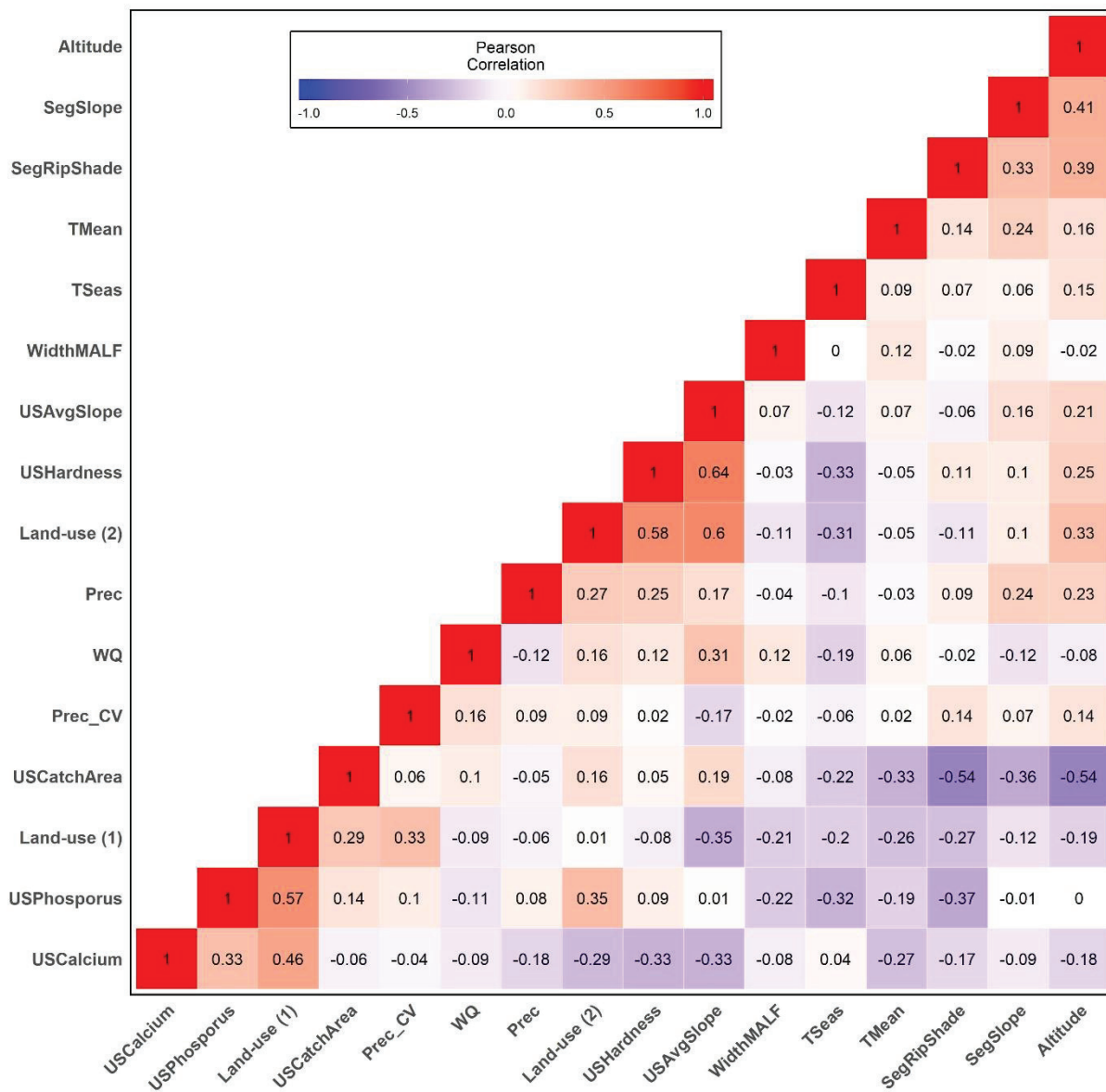
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Table S1.3 Correlation coefficient among input variables and principal components for each of the PCAs performed to synthesize groups of predictor variables. Temp = Temperature. Prec = Precipitation.

| Group | Variable | Principal component | |
|-----------------|--------------------|---------------------|--------|
| | | Axis 1 | Axis 2 |
| Air temperature | Temp annual | -0.97 | -0.01 |
| | Temp spring | -0.87 | -0.05 |
| | Temp summer | -0.79 | -0.45 |
| | Temp winter | -0.61 | 0.11 |
| | Temp SD | -0.04 | -0.92 |
| | Temp SD summer | 0.25 | -0.87 |
| | Temp SD spring | -0.03 | -0.77 |
| | Temp SD winter | 0.33 | -0.50 |
| Precipitation | Prec | 0.34 | -0.88 |
| | Prec spring | -0.35 | -0.53 |
| | Prec summer | 0.44 | -0.23 |
| | Prec winter | 0.18 | -0.77 |
| | Prec CV | 0.89 | 0.08 |
| | Prec CV summer | -0.71 | -0.28 |
| | Prec CV spring | -0.69 | -0.07 |
| | Prec CV winter | -0.20 | -0.19 |
| Land-cover | usintensiveAg | 0.62 | -0.63 |
| | usPastorallight | 0.62 | 0.60 |
| | usNativeForest | -0.87 | 0.16 |
| | usUrban | -0.10 | -0.68 |
| | usShrub | -0.53 | -0.10 |
| | usExoticForest | -0.12 | -0.33 |
| Water-quality | CLAR | 0.64 | 0.06 |
| | DO | -0.31 | 0.82 |
| | NH ₄ -N | -0.60 | -0.48 |
| | NO ₃ -N | -0.72 | 0.38 |
| | DRP | -0.52 | -0.38 |

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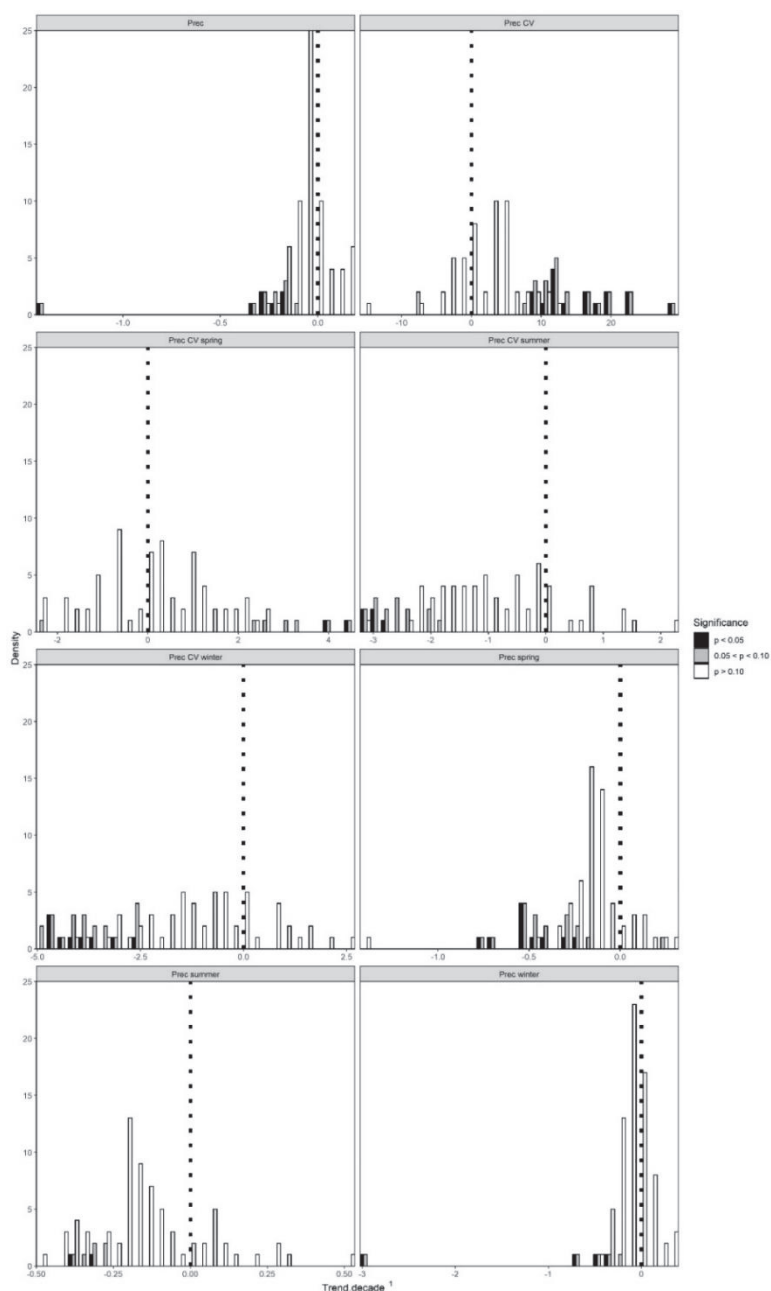
Figure S1.1 Pearson correlation matrix of predictor variables used as input variables in the Generalized Additive Mixed effects Models. For description of the variables see methods.



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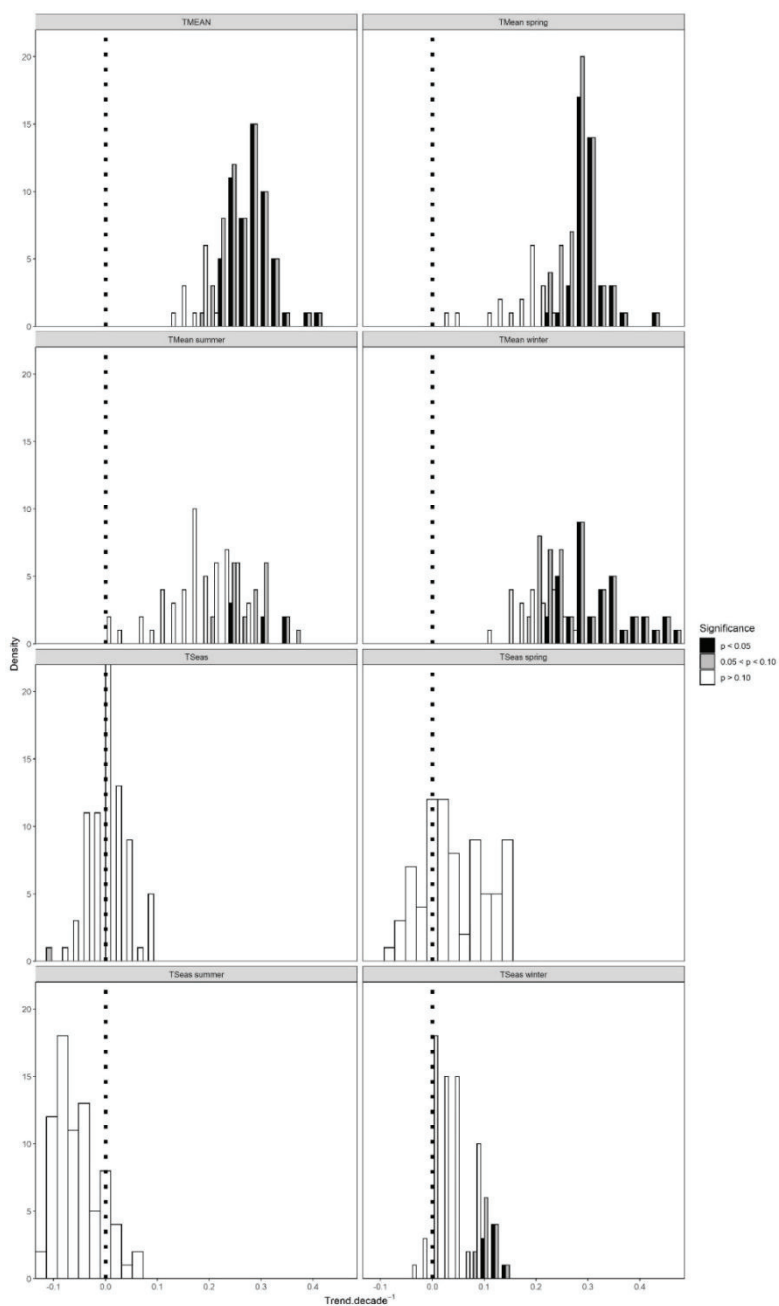
2: Observed environmental changes and biotic conditions in New Zealand large rivers between 1991 and 2016.

Figure S2.1 Histograms of measured temporal trends in mean annual and mean seasonal (winter, spring and summer) air temperature from 1991 to 2016 at the 64 sampled river sites. TMean = Mean air temperature. TSeas = Temperature seasonality (standard deviation of the mean). The dashed line shows the zero mark. The x axis (temporal trends) corresponds to the slope from linear regression models of each of the variables against years. Temporal trends were multiplied by ten to obtain a measure of change per decade (Trend.decade⁻¹). The significance indicated by the legend are those from the linear regression models. Y axis (density) corresponds to the number of sites.



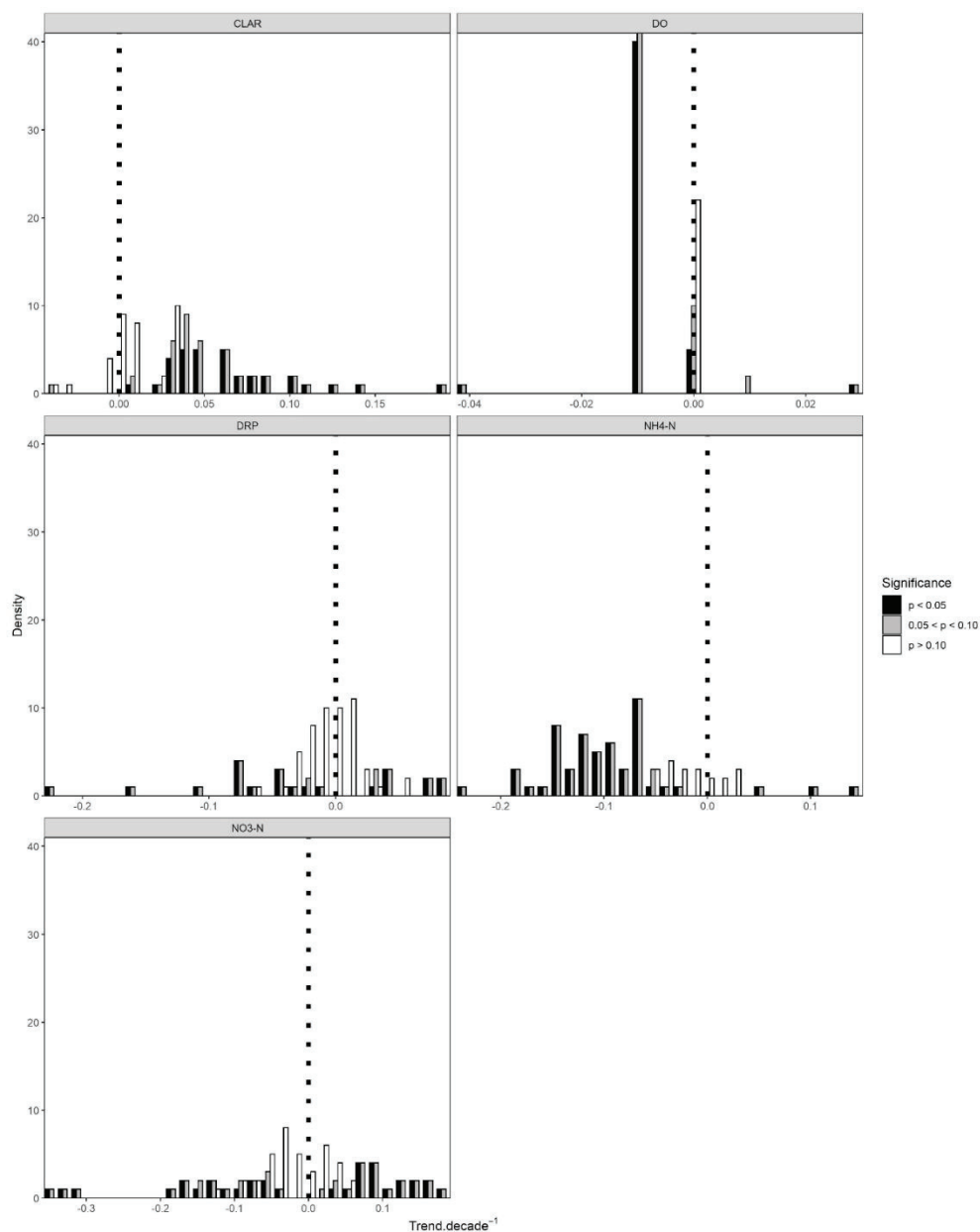
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Figure S2.2 Histograms of measured temporal trends in mean annual and mean seasonal (winter, spring and summer) precipitation and precipitation seasonality (coefficient of variation $\times 100$) from 1991 to 2016. Prec = Precipitation. Prec CV = Precipitation seasonality. The dashed line shows the zero mark. Temporal trends correspond to the slope from linear regression models of each of the variables against years. Temporal trends were multiplied by ten to obtain a measure of change per decade (Trend.decade⁻¹). The significance indicated by the legend are those from the linear regression models.



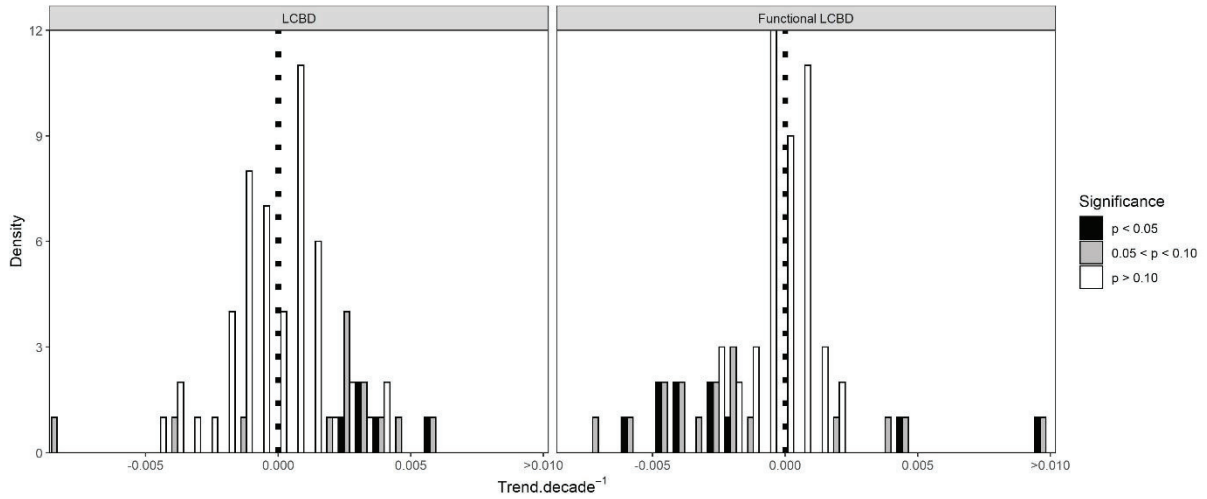
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Figure S2.3 Histograms of measured temporal trends in (log₁₀() transformed) median annual water quality at 64 New Zealand River sites from 1991 to 2016. CLAR: Black disc clarity (m). DO: Dissolved oxygen. DRP: Dissolved Reactive Phosphorus. NH₄-N: Ammoniacal Nitrogen. NO₃-N: Nitrate-nitrogen. The dashed line shows the zero mark. Temporal trends correspond to the slope from linear regression models of each of the variables against years. Temporal trends were multiplied by ten to obtain a measure of change per decade (Trend.decade⁻¹). The significance indicated by the legend are those from the linear regression models.



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Figure S2.4 Histograms of measured temporal trends in taxonomic and functional Local contribution to Taxonomic and Functional beta-diversity (LCBD and Functional LCBD, respectively) from 1991 to 2016. Temporal trends correspond to the slope from linear regression models of each of the variables against years. Temporal trends were multiplied by ten to obtain a measure of change per decade (Trend.decade⁻¹). The significance indicated by the legend are those from the linear regression models.



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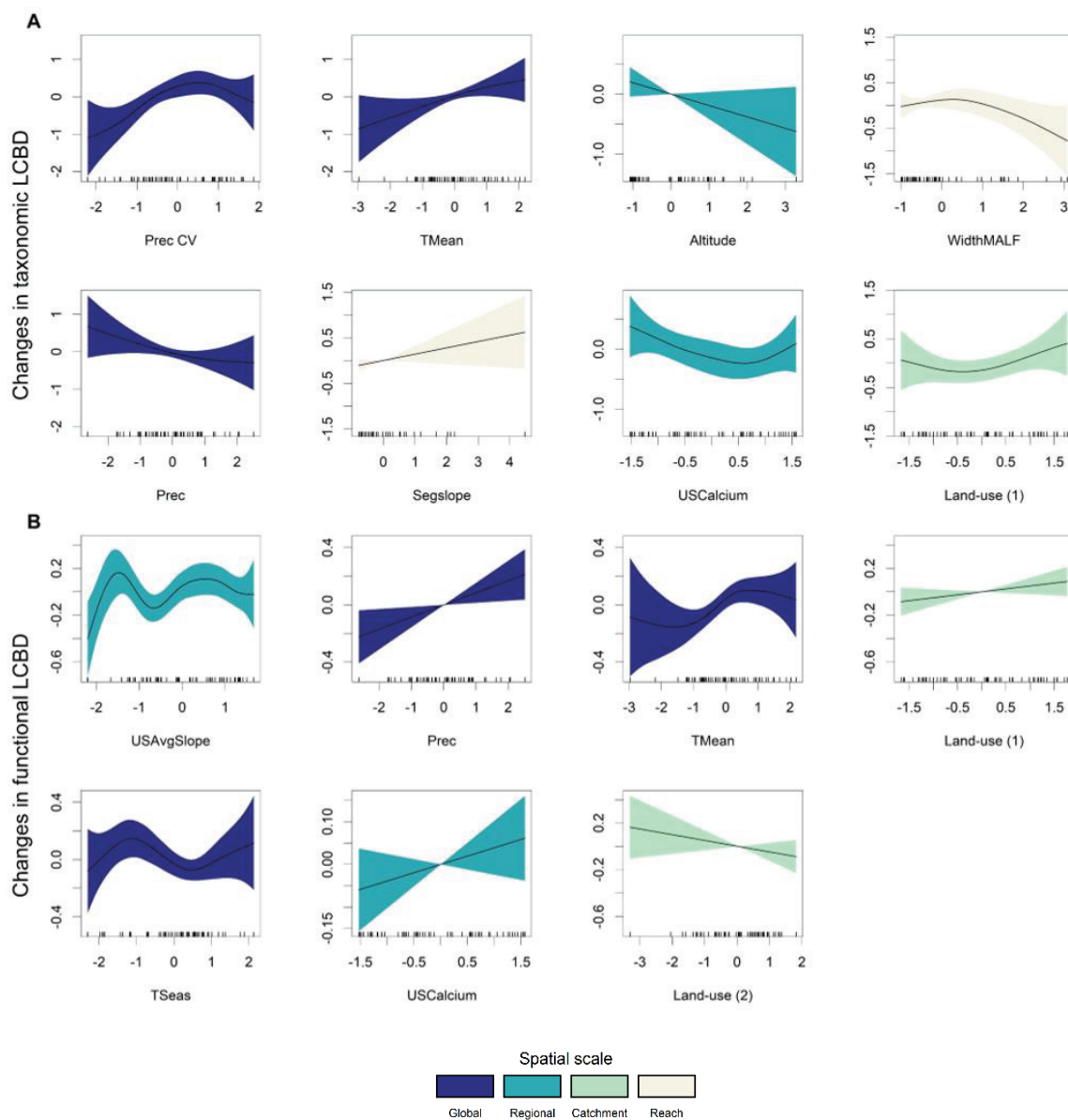
3: Results from Hierarchical Generalised Additive Mixed effect Models

Table S3.1 Results from the hierarchical Generalised Additive Mixed effects Models to predict temporal changes in taxonomic and functional Local Contribution to Beta Diversity. Edf: Estimated degrees of freedom; F: F value.

| Biodiversity facet | Spatial scale | Intercept (Std. Error) | Variable | edf | F | p | Cumulative R ² |
|--------------------|---------------|------------------------|--------------|-------|-------|-------|---------------------------|
| Taxonomic | Global | 0.02927 (0.12115) | Prec | 1.436 | 2.714 | 0.152 | 0.08 |
| | | | TMean | 1.329 | 4.340 | 0.050 | 0.13 |
| | | | Prec CV | 2.698 | 4.294 | 0.019 | 0.25 |
| | Regional | -0.01433 (0.13394) | USCalcium | 2.283 | 1.608 | 0.164 | 0.01 |
| | | | Altitude | 1.000 | 3.064 | 0.085 | 0.06 |
| | Catchment | -0.00669 (0.09821) | USCatchArea | 1.000 | 1.089 | 0.302 | 0.01 |
| | | | USAvgSlope | 1.961 | 0.656 | 0.499 | 0.03 |
| | | | Land-use (1) | 1.806 | 0.762 | 0.343 | 0.06 |
| | | | Land-use (2) | 1.972 | 1.172 | 0.276 | 0.07 |
| | Reach | -3.798e-10 (8.983e-02) | SegSlope | 1.000 | 1.770 | 0.189 | 0.01 |
| WidthMALF | | | 1.957 | 2.299 | 0.150 | 0.05 | |
| Functional | Global | -0.11727 (0.03303) | Prec | 1.000 | 5.821 | 0.019 | 0.05 |
| | | | TMean | 2.911 | 2.827 | 0.056 | 0.15 |
| | | | TSeas | 3.333 | 2.158 | 0.197 | 0.23 |
| | Regional | 0.001801 (0.031290) | USCalcium | 1.000 | 1.559 | 0.217 | 0.01 |
| | | | USAvgSlope | 5.678 | 2.808 | 0.015 | 0.19 |
| | Catchment | 0.002827 (0.027821) | Land-use (1) | 1.000 | 2.076 | 0.156 | 0.20 |
| | | | Land-use (2) | 1.000 | 1.554 | 0.218 | 0.22 |

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Figure S3.1 Marginal effects of the most influential variables in the Generalised Additive Mixed effects Models to predict changes in taxonomic and functional Local Contribution to Beta Diversity (LCBD). The eight most influential variables are shown for taxonomic LCBD and every variable is shown for functional LCBD. Solid lines represent the marginal effect of each variable. Shaded areas represent approximate 95% confidence intervals. Rug plots show the distribution of the values for each predictor. Predictor variables are scaled to their mean and one-unit variance. For description of the variables see Methods.



Chapitre 2 : Homogénéisation taxonomique et fonctionnelle

Chapitre 3

Réorganisation temporelle de la composition
des communautés : changements de tailles
de populations et d'aires de répartition

Préface :

Dans le chapitre précédent, nos mesures étaient basées sur les changements de variations spatiales de la composition des communautés. Nous n'avons pas pu mesurer le degré de réorganisation des communautés de macroinvertébrés au cours du temps. De plus, les espèces et traits potentiels qui profitent ou sont impactés par ces changements de composition n'ont pas été étudiés. Ce sont ces thématiques que nous allons aborder dans le chapitre qui suit. La diversité bêta temporelle est une méthode en plein essor, qui a récemment été utilisée à des fins macro-écologiques. Jusqu'à présent, elle avait majoritairement été utilisée comme outil de mesures de changements de composition entre quelques sites uniquement et sur un petit espace géographique. Dans ce chapitre, nous utilisons dans un premier temps la diversité beta temporelle afin de caractériser spatialement les patrons de changements de composition au cours du temps, ainsi que ceux de gains et de pertes d'espèces et de traits. D'une manière similaire au chapitre précédent, nous cherchons à en isoler les causes environnementales potentielles. Ensuite, l'accent est porté sur les changements de tailles de populations et d'aires de répartition ainsi que sur les vitesses de déplacement latitudinal des aires de répartition. Enfin, les liens entre les changements de populations et d'aires de répartition et la taxonomie et/ou les traits fonctionnels des espèces sont étudiés.

Preface (English):

In the previous chapter, our measures were based on changes in the spatial variation of composition in communities. We were not able to measure the degree of reorganisation of macroinvertebrate communities over time. In addition, the potential species and traits that gain or lose from these changes in composition were not studied. These topics will be tackled in the following chapter. The use of temporal beta diversity is rising in ecology and was recently applied in macro-ecological contexts. Until now, it had mainly been used as a tool to measure changes in the composition of a few communities in geographically restricted areas. In this chapter, we first use temporal beta diversity to spatially characterise patterns of changes in community composition over time, including gains and losses of species and traits. In a similar way to the previous chapter, we aim at identifying the environmental drivers of these changes. Then, we focus on changes in population and range sizes and latitudinal range shifts of our species pool. Finally, the links between changes in populations and species ranges with functional traits are studied.

Article II: Climate and land-use driven reorganisation of structure and function in river macroinvertebrate communities.

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3.1 – Abstract

Understanding temporal changes in the composition of species communities over spatial and temporal scales relevant to conservation management is crucial for preventing further biodiversity declines. Here, we assessed patterns and potential drivers of taxonomic and functional temporal β diversity over 26 years (1991 to 2016) of 64 river macroinvertebrate communities, and the length of New Zealand (-37°N, -46°S). We further examined changes in population size and range shifts of species pools and related these to taxonomy and functional traits. We found increasing climate and land-use driven differences in both the taxonomic and functional composition of communities over time, coupled with poleward species colonisations and increasing extirpations in northern locations. Increases in population and species range size were more prevalent than decreases in population and range size. Species shifted their ranges towards higher latitudes on average by 50 kilometres per decade. Despite little to no relationship with taxonomy, we uncovered distinct relationships between functional traits and population trends and latitudinal species range shifts. Species with a high number of reproductive cycles per year and long-life duration of adults tended to increase their population size, while larger size species with a high number of descendants per reproductive cycle tended to shift their range towards more southern latitudes. Our results suggest that the intensity of disturbances, the geographic location of individuals and communities, and species ecological and functional characteristics, are major determinants of riverine biodiversity reorganisation in the Anthropocene.

Keywords:

Temporal β diversity, Functional diversity, Climate change, Land use change, Population trends, Species range shifts, Biodiversity; Freshwater macroinvertebrates.

3.2 – Introduction

Current rates of biodiversity change correlate with recent human-induced climate change and land-use activities (IPCC 2014, Brondizio et al. 2019). These biodiversity changes are predicted to increase as human activities intensify (Urban 2015, Johnson et al. 2017), reflecting local extirpations and/or colonisations of species and populations across landscapes (Tilman et al. 1994, Maclean & Wilson 2011, Brondizio et al. 2019). Such demographic shifts could potentially lead to major alterations to the functioning of ecosystems. However, the responses of species likely vary in magnitude among regions of the world and across latitudes (Heino et al. 2009, Lenoir et al. 2019). Biodiversity trends are, however, overly complex, with observations of local biodiversity increases sometimes contradicting reports of a global climate-driven biodiversity crisis (Antão et al. 2020, Li et al. 2020, Outhwaite et al. 2020). There is therefore an imperative need for biodiversity time-series studies over wide and understudied geographical regions to inform conservation planning and policy (Olden et al. 2018, Magurran et al. 2019).

Uncovering the drivers of biodiversity change requires tools that can deconstruct the mechanisms underpinning such change. Research on changes in the composition of species communities (changing β diversity) has typically focused on temporal changes in spatial β diversity (Olden et al. 2018). However, ongoing temporal change in species composition is also a pressing (Kuczynski et al. 2018, Blowes et al. 2019, Antão et al. 2020), yet less investigated aspect of biodiversity change. Temporal β diversity can capture the biogeographical, ecological, functional and ecological processes involved in temporal changes in communities (Magurran et al. 2019), including local extirpations or colonisations (Legendre & Gauthier 2014, Shimadzu et al. 2015, Gotelli et al. 2017, Legendre 2019, Magurran et al. 2019).

The responses of species to environmental change, including local losses and gains associated with temporal β diversity, are underpinned by their ecological and life-history traits (Dawson et al. 2011, MacLean & Beissinger 2017, Pacifici et al. 2017, McLean et al. 2018). For example, populations of

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ecological specialists, with long generation times, and low reproductive output are predicted to be highly vulnerable to climate change (Vié et al. 2009, Chin et al. 2010, Conti et al. 2014). Similarly, the degree to which species reduce, expand and/or shift their ranges may depend on their ability to disperse and the geographic location of populations (Comte et al. 2014, Lenoir et al. 2019).

Theoretically, the lowest latitudinal margins of continents or islands are more likely to experience loss of taxa under climate change, because colonisations from lower latitudes are not possible (Heino et al. 2009, MacLean & Beissinger 2017).

In running waters, temporal β diversity is increasingly being used as a tool to understand the dynamics of change in macroinvertebrate communities, including identifying sites that are pivotal for maintaining biodiversity at the landscape scale (Ruhí et al. 2017). Changing climate or flow regimes has been identified as a common driver of change in community structure. For instance, Cañedo-Argüelles et al. (2020) found a strong relationship between structural changes in macroinvertebrate communities and changes in precipitation regimes. Similarly, Crabot et al. (2020) found that the temporal variability of community structure was related to the frequency and duration of drying events. However, few studies have examined temporal β diversity of stream invertebrate communities over large spatial and temporal scales.

Here, we complement recent findings from Mouton et al. (2020), who reported decreasing spatial taxonomic β diversity (taxonomic homogenisation) but increasing spatial functional β diversity (functional differentiation) among river macroinvertebrate assemblages. We capitalise on the same high-resolution time-series datasets, comprising macroinvertebrate communities collected annually from 1991 to 2016, at 64 mainstem river sites across New Zealand's two mainland islands. The two studies are complementary in the sense that Mouton, Tonkin et al. (2020) explored how climate change affects the spatial organization of assemblages while the present study aims at evaluating how both climate and land-use changes influence temporal differences in community composition within sites.

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We measured taxonomic and functional temporal β diversity over the period 1991-2016, which we decomposed into indices of colonisations and extirpations. We tested for the effects of climate and land-use change, nested within hierarchically organized environmental spatial scales, in mediating taxonomic and functional temporal β diversity of these communities. Finally, we examined changes in species' population and range size and latitudinal range shifts which we related to their taxonomic affiliation and a set of functional traits.

Given widespread evidence of freshwater macroinvertebrates response to ongoing climate change (Pyne & Poff 2017, Flourey et al. 2018, Mouton et al. 2020), we first expected a latitudinal pattern in temporal β diversity (E_1), owing to climate-driven species range shifts. Specifically, we expected (E_{1a}) increasing species colonisations at the leading edges (southern margins of New Zealand) but (E_{1b}) increasing extirpations at the rear edges (northern margin of New Zealand). Second, given globally observed species population declines and poleward range shifts (Urban 2015, Olden et al. 2018, Lenoir et al. 2019), we expected (E_2) greater decreases in species' population and range sizes than increases, and poleward range shifts. Finally, given the relationship between the taxonomic identity of species, their functional traits and demographic responses to environmental change (MacLean & Beissinger 2017, Pacifici et al. 2017, Daskalova et al. 2020), we expected a relationship between trends in population sizes and species range shifts with the taxonomic identity of species and with their functional traits (E_{3a} and E_{3b} , respectively).

3.3 – Methods

3.3.1 Data acquisition

3.3.1.1 Biodiversity data

Macroinvertebrate communities were sampled from mainstem rivers, at 64 wadeable sites (mean Strahler stream order = 6; min = 3, max = 8), located in 35 catchments of New Zealand, between latitudes 46 to 35° S (Figure S1). Surveys were conducted once a year, during late austral summers (February to April) from 1991 to 2016. These surveys were conducted for New Zealand's National

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Rivers Water Quality Network (NRWQN, Smith and McBride 1990), which is operated and maintained by the National Institute of Water and Atmospheric Research (NIWA). Samples were collected following a standardized protocol (Smith & McBride 1990) and under baseflow conditions ($Q < Q_{\text{median}}$). Seven Surber samples (0.1 m² and 250 µm mesh net) were collected on all sampling occasions during which macroinvertebrates were removed from a 0.1 m² area in the sampler down to a depth of c. 10 cm and from as many substrate types as possible. Individuals were later identified in the laboratory, to the lowest practicable taxonomic level (species = 26%; genus = 47%, family = 21%; Quinn and Hickey 1990). The same taxonomic resolution was maintained throughout the entire period to allow analyses of long-term changes (Scarsbrook et al. 2000).

We described each macroinvertebrate taxon ($n = 113$) using sixteen functional traits related to morphology, life-history, dispersal strategies and resource acquisition methods extracted from the New Zealand freshwater macroinvertebrate trait database (NIWA, https://niwa.co.nz/sites/niwa.co.nz/files/nz_trait_database_v19_2_18.xlsx). This trait database has been explicitly developed for New Zealand's standardised freshwater macroinvertebrate sampling protocols (Dolédec et al. 2006, Doledec et al. 2011). Functional traits were divided into 59 modalities and fuzzy-coded from 0 to 3 (Chevenet et al. 1994).

3.3.1.2 Environmental predictors

We defined a set of environmental predictors at four different spatial scales, commonly identified as prominent scales operating in river networks (Poff 1997, Allan 2004): the global, regional, catchment and reach scales.

Global-scale predictors were defined as temporal changes in air temperature and precipitation (Brown et al. 2013). At each site, we extracted daily values for the period 1991-2016, from 5 km² gridded layers of New Zealand, using NIWA's Virtual Climate Station Network (VCSN; <https://data.niwa.co.nz/>). We used the slopes of linear regressions between climate variables and years as estimates of rates of change (OLS; the *lm* function in R v.4.0.2; R Core Team, 2021). The following variables were used:

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annual and seasonal (for the winter, spring and summer seasons) mean precipitation, precipitation seasonality (i.e. the coefficient of variation x 100; Fick and Hijmans 2017), mean air temperature and air temperature seasonality (i.e. the standard deviation of the mean). We applied a Principal Component Analysis (PCA; the *dudi.pca* function in the *Ade4* package v. 1.7-15 Dray and Siberchicot 2020) individually to our sets of trends in air temperature and precipitation variables. Based on the correlations among each trend in climate variable and the axes of the PCAs, we created synthetic indices of climate change using the first two axes of each climate PCA. In the PCA of trends in air temperature variables, the first axis (35.9% of variation explained) described a gradient of increasing mean air temperature (TMean) and the second (33.0%) described changes in air temperature seasonality (TSeas). For precipitation variables, the first axis (28.2%) described changes in precipitation seasonality (Prec CV) and the second (22.7%) described changes in mean precipitation (Prec).

Regional-scale predictors were (1) altitude (metres above sea level) of the sampling site, (2) phosphorus and (3) calcium concentrations, and (4) mean hardness (induration) of surface rocks of the upstream catchment (respectively the variables USPhosphorus, USCalcium and USHardness extracted from Leathwick et al. 2010). The latter three variables are descriptors of catchment geology, hence likely reflect regional biogeochemical characteristics.

For catchment-scale predictors, we used descriptors of changes in catchment land-use and catchment hydro-morphology. For land-use, we used changes (1990-2012) in 4 land-cover types (defined as the proportion of catchment occupied by combinations of (1) high producing grassland, (2) shrub/grassland, (3) plantation forest and (4) non-plantation forest (Landcare Research, 2015, Julian et al. 2017). These data were available for the year 1990 and 2012, we used the difference in land-cover between these two dates as estimates of temporal change, following Julian et al. (2017). Similarly, we also used changes (1990-2012) in catchment stock unity density (SUD) of Dairy, Beef, Sheep and Deer ($SU \cdot ha^{-1}$; Statistics NZ (territorial authority), Julian et al. 2017). Changes in land-cover and changes in stock unity density were synthesised using the first two axes of two PCAs, which we interpreted as

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synthetic predictors of changes in land-cover (LC PC1, 61.4% and LC PC2, 23.9%; Table S1) and changes in stock unity density (SUD PC1, 44.3% and SUD PC2, 35.2%; Table S1), respectively.

Catchment hydro-morphology was given by the area of the upstream catchment (m²; USCatchArea) and the average slope of the upstream catchment (degrees; USAvgSlope) from each river segment (Leathwick et al. 2010).

For reach-scale descriptors, we used: (1) the slope (degrees) of the stream segment at each sampling site (SegSlope; Leathwick et al. 2010), (2) the predicted wetted river width (metres) at the 7-day mean annual low flow (WidthMALF; Booker 2005), (3) the estimated proportion of riparian shading at each river segment (SegRipShade; measured from satellite imagery by Leathwick et al. 2010), (4) temporal changes in water quality, (5) temporal changes in flow, and (6) temporal changes in substrate size.

Temporal changes in water-quality, flow and substrate size were all estimated as slopes of variables (described below) and years. For temporal changes in water-quality, we compiled data from 1991 to 2016 of median annual values (mg.m⁻³) of nitrate (NO₃-N), ammoniacal-nitrogen (NH₄-N), dissolved reactive phosphorus (DRP) and dissolved oxygen (DO) concentrations and water clarity (metres; CLAR).

These data originate from samples collected monthly, at the same sites as those sampled for macroinvertebrate communities (Davies-Colley et al. 2011). We log₁₀-transformed water-quality variables and calculated temporal changes for each variable at each site. We ordinated temporal changes in water-quality using PCA and retained the first axis (33.3%) as a synthetic indicator of temporal changes in water quality (WQ). For changes in flow, we compiled mean daily flow data from hydrological gauges located at each site, which we divided by upstream catchment area to obtain a measure of run-off per day (Vaughan & Gotelli 2019). We then calculated mean annual and seasonal (for winter, spring, and summer) flow and flow coefficient of variation, as was done for precipitation.

We ordinated temporal changes using PCA and kept the first two axes (Flow PC1, 54.1% and Flow PC2, 20.6%; Table S1) as indicators of temporal changes in flow. Finally, for changes in substrate size we used temporal changes in the substrate size index (SSI; Jowett et al. 1991). Substrate composition was

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measured by randomly selecting 100 particles at 1-m intervals along a path of 45 degrees to the riverbank in a zig-zag manner. Particles were assigned to each of 8 size classes: bedrock, boulders (>300mm), large cobbles (300–128mm), small cobbles (128-64mm), large gravel (32-64mm), small gravel (2-32mm), sand (62.52 μm – 2mm) and silt (< 62.52 μm). We measured the substrate size index (SSI) for each sampling occasion following Jowett et al. (1991) (1 = silt only, 8 = bedrock only). Temporal changes in SSI were then measured for each site. Detailed description of the variables and statistical outputs in regards to the environmental descriptors used for analyses are given in Mouton et al. (2020) and in Table S2.

3.3.2 Statistical analyses

3.3.2.1 Temporal β diversity indices

We used the Temporal β diversity Index from Legendre (2019) (TBI; the *TBI* function in the *adespatial* package v.0.3-8) to measure temporal changes in the taxonomic and functional composition of each of the 64 communities. This index has been specifically developed (i) to calculate differences in assemblage composition (dissimilarity) between two time periods from pairwise distances, and (ii) to decompose these temporal differences into indices of local colonisations and extirpations.

Macroinvertebrate abundances were $\log(x + 1)$ -transformed and pairwise distances in community composition were calculated using the percentage difference index of dissimilarity (*%diff*; Odum (1950), also known as the Bray-Curtis index). To estimate temporal changes in functional composition (i.e. the composition of species functional traits within each community), the species-by-site matrix was replaced by a trait-by-site matrix using the community-level abundance weighted means of functional trait values (CWM; Lavorel et al. 2008; using the *dbFD* function in the *FD* package v.1.0-12; Laliberté et al. 2014).

We used the first year of sampling (1991) as a baseline for each time-series, and then successively compared it to each of the following years (1992, onwards (Magurran & Henderson 2010, Dornelas et al. 2014, Antão et al. 2020)). This computation therefore yielded a value of dissimilarity, colonisations, and extirpations for each year (except the baseline year) and site. For each site, we regressed values of

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each index (taxonomic and functional dissimilarity, extirpations, and colonisations, respectively) against years and interpreted the slopes from the regression models (multiplied by ten) as a measure of trends per decade. This method allows to examine whether changes in composition of each assemblage (relative to the baseline year) consistently increase (positive slope) or decrease (negative slope) over time (Antão et al. 2020).

To test our first expectations (E_{1a} and E_{1b}), we tested for relationships between trends in temporal β diversity, including colonisations and extirpations with latitude using linear-mixed effects models (the *lme* function in the *nlme* package v.3.1-152 (Pinheiro et al. 2017)) setting island (North Island versus South Island) as random effect.

3.3.2.2 Drivers of temporal β diversity

We performed Hierarchical Generalised Additive Mixed effects Models (GAMMs; the *gamm* function in the *mgcv* package v.1.8-33 (Wood & Wood 2015)) to relate temporal changes in each of the six indices of trends in temporal β diversity to our set of environmental descriptors. Predictor variables were Box-Cox transformed prior to analyses (Box and Cox (1964); the *BoxCoxTrans* function in the *caret* package v. 6.0-84 (Kuhn et al. 2020)), and standardised to zero mean, one unit variance (using the *destand* function in the *vegan* package v. 2.5-6 (Oksanen et al. 2014)).

GAMMs were fitted with catchments nested within islands as random effects to account for spatial structure in data (Dormann et al. 2007). We used regression splines to account for potential non-linear relationships, restricted maximum likelihood (REML) to optimize the parameter estimates and assumed Gaussian-type distribution errors.

Each response variable was first modelled against global-scale descriptors. We kept only the global-scale descriptor(s) that maximised the coefficient of determination (adjusted- R^2) as the best model following Van Looy et al. (2017) and Floury et al. (2018). The same step was then repeated in a descending way, using successively regional, catchment and reach-scale descriptors as predictor variables and the residuals from the previous model as response variable. At each step, we quantified

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the percentage of relative importance of each variable in the model following methods described in Kuhn (2012) (the *varImp* function in *caret*). We tested for residual spatial autocorrelation in the residuals of the reach-scale model using Moran's index of spatial autocorrelation (the *Moran.I* function in the *ape* package v.5.5(Paradis et al. 2019)). Residual spatial autocorrelation was not observed ($p > 0.05$ for every model).

3.3.2.3 Population trends and species range shifts

To test our second expectation (H_2), we assessed temporal trends in the abundance, range size and the latitudinal distribution of 83 taxa that were recorded for at least 10 years (not necessarily consecutive; following Dornelas et al. 2019). For population trends (hereafter referred to as temporal trends in the abundance of each taxa), we did not include the time when a taxon was absent in the time series, because this would tend to flatten the slope towards zero. Macroinvertebrate abundances were $\log(x + 1)$ transformed and then standardised, so that each time-series had a mean of 0 and a standard deviation of 1. This transformation put all time-series into common units that are more appropriate for comparisons of taxa with disparate population sizes. We estimated population trends by fitting a linear regression model of abundances for each taxon individually, against years. Second, we measured the range size of each taxon as the convex hull area encompassing the sites where the taxon was present each year. We regressed range sizes against years using ordinary least squares models. Finally, we assessed latitudinal distribution shifts of each taxon, by regressing the centroid of its range against years. We used the slope of each linear regression model as an estimate of changes in population and range size and of latitudinal range shifts, for each taxon.

3.3.2.4 Relationships with taxonomy and functional traits

To test our third expectations (H_{3a} and H_{3b}), we started by relating changes in community composition to the taxonomic classification of our taxa (H_{3a}). For this purpose, we compiled a taxonomic classification of the studied taxa (using phylum, subphylum, class, subclass, family, subfamily, order, genus and species names), from the National Center for Biotechnology Information (using the

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taxonomy function in the *myTAI* package Drost et al. 2018). From this classification, we created a taxonomic tree by calculating taxonomic distances between taxa (using Gower's distance and the *taxa2dist* function in *vegan*). We used hierarchical clustering (the *hclust* function in R) to produce a tree from the taxonomic dissimilarity matrix. We checked for potential relationships between taxonomic distance and Euclidean dissimilarity in population size and/or species range shifts using a Mantel test (Mantel 1967) with 9999 permutations (the *mantel.rtest* function in *ade4*).

To relate changes in community composition to functional traits of macroinvertebrates (H_{3b}), we tested for relationships among population trends, changes in range size and latitudinal range shifts with the axes of a functional trait space (Loiseau et al. 2020). For this purpose, we built a functional trait space of the macroinvertebrate taxa by ordinating the species-by-trait matrix in a multidimensional space, using fuzzy correspondence analysis (the *dudi.fca* function in *Ade4*). We ensured that equal weights were given to each of the trait categories (e.g., for the trait "maximum potential size" which contained 5 categories, each category was given a weighting of 1/5). We retained the first three axes of the functional space as synthetic traits of macroinvertebrates (cumulative percentage of variation explained = 31.8%). We used non-parametric Spearman's rank correlation tests to relate changes in population and/or range size and latitudinal range shifts, respectively, to each axis of the trait space and mapped significant relationships on trait space to provide a better visual assessment of potential relationships. Statistical analyses were all performed under the R environment (R Core Team, 2021).

3.4 – Results

3.4.1 Spatial patterns of changes in temporal β diversity

Trends in taxonomic and functional temporal β diversity increased on average across New Zealand over the 26-year time-series (taxonomic dissimilarity: mean rate = 0.03, minimum = -0.08, maximum = 0.17; functional dissimilarity: mean = 0.02, min. = -0.07, max = 0.14; Figure 1). This increasing trend was driven by increasing taxonomic and functional colonisations and functional extirpations

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(taxonomic colonisations: mean = 0.04, min = -0.01, max = 0.2, functional colonisations: mean = 0.01, min = -0.03, max = 0.06, functional extirpations mean = 0.01, min = -0.04, max = 0.08) but decreasing taxonomic extirpations (mean = -0.01, min = -0.15, max = 0.14, Figure 1).

Trends in taxonomic temporal dissimilarity and colonisation decreased with latitude, while those of extirpations increased (Table 1; Figure 1). However, trends in functional temporal β diversity, colonisations and extirpations showed no or weak relationships with latitude (Table 1; Figure 1).

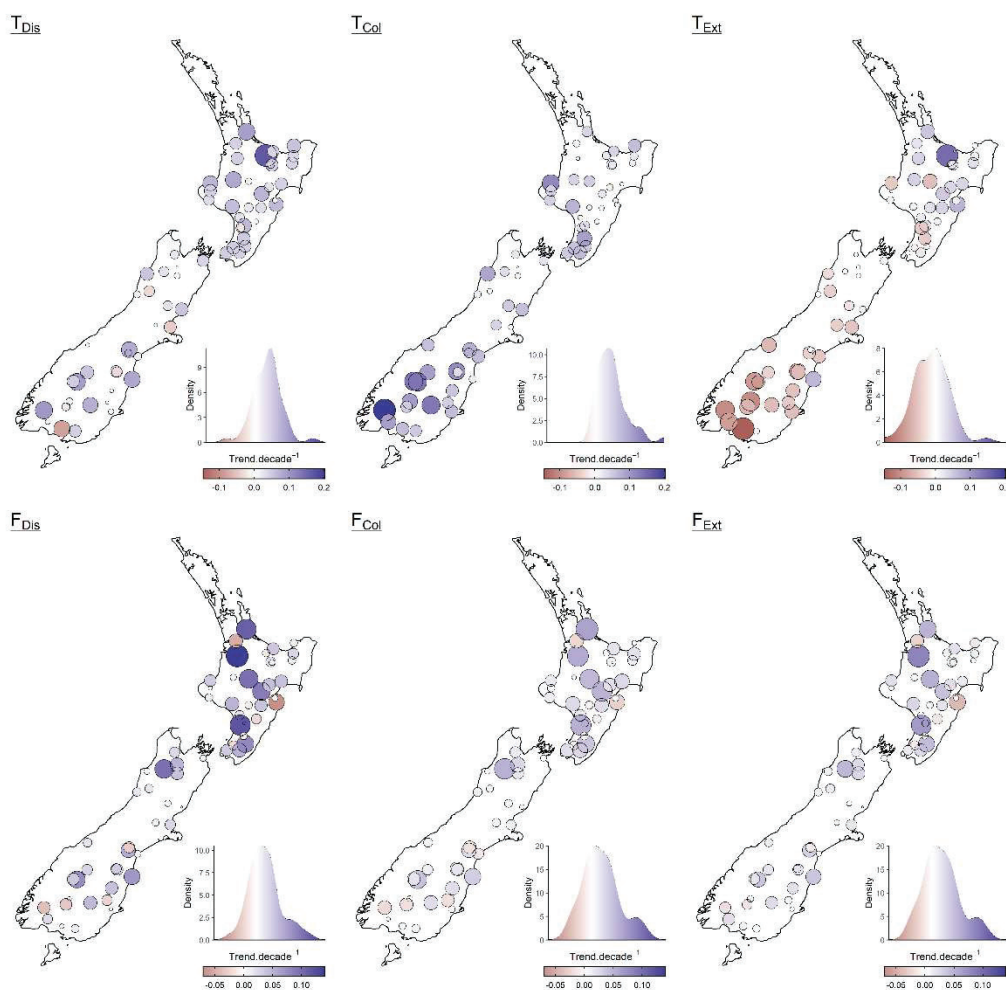


Figure 1 Maps of New Zealand illustrating rates of changes per decade (Trend decade⁻¹) in taxonomic and functional temporal β diversity indices of macroinvertebrate assemblages: dissimilarity (TDis and FDis respectively), colonisations (TCol and FCol) and extirpations (TExt and FExt). Temporal β diversity was measured by comparing the first year of sampling (1991) to each of the following years (1992–2016). Trends per decade are the slopes of linear regression models used to regress each temporal β diversity index against year. Point sizes are proportional to the absolute rate of change per decade. Red dots indicate decreasing trends, whereas blue dots indicate increasing trends. Density curves at the bottom right corner of each map illustrate the density distribution of each index. The x axis of each density curve corresponds to the limits of the legend.

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Table 1 Coefficients of determination (R^2), intercept (standard error), F-value (F) and p-value (p) of latitude in each generalised linear mixed effect model relating temporal β diversity indices to latitude with island as random effect. Values are the estimated mean values of the random intercept and slope.

| Temporal β diversity index | R^2 | Intercept (std. error) | Slope (std. error) | F | p | |
|----------------------------------|---------------|---------------------------|-----------------------|----------------|-------|--------|
| Taxonomic | Dissimilarity | 0.06 | 0.112 (0.044) | 0.111 (0.044) | 3.72 | 0.06 |
| | Colonisations | 0.41 | -0.238 (0.064) | -0.238 (0.064) | 13.8 | <0.001 |
| | Extirpations | 0.47 | 0.249 (0.034) | 0.249 (0.034) | 54.14 | <0.001 |
| Functional | Dissimilarity | 0.02 | 0.058 (0.046) | 0.058 (0.046) | 1.59 | 0.21 |
| | Colonisations | 0.06 | 0.088 (0.045) | 0.088 (0.045) | 3.7 | 0.06 |
| | Extirpations | < 0.01 | 0.028 (0.047) | 0.028 (0.047) | 0.36 | 0.55 |

3.4.2 Drivers of observed changes

Hierarchical GAMMs had good ($R^2 = 0.34 - 0.44$) and fair ($R^2 = 0.19 - 0.24$) fits for trends in taxonomic and functional indices, respectively (Table 2). Changes in taxonomic dissimilarity were mostly influenced by reach and catchment-scale descriptors (Table 2). However, trends in the five other indices were mostly influenced by global scale predictors (Table 2), followed by reach-scale predictors for taxonomic colonisations and catchment-scale predictors for all other indices (Table 2; Table S3).

Table 2 Coefficients of determination of each generalised additive mixed effect model for trends in each taxonomic and functional temporal β diversity index, spatial scale and the total of the four spatial scales.

| Temporal β diversity index | Global | Regional | Catchment | Reach | Total | |
|----------------------------------|---------------|----------|-----------|-------|-------|------|
| Taxonomic | Dissimilarity | 0.02 | 0.00 | 0.18 | 0.31 | 0.44 |
| | Colonisations | 0.22 | 0.05 | 0.00 | 0.12 | 0.34 |
| | Extirpations | 0.21 | 0.00 | 0.21 | 0.08 | 0.42 |
| Functional | Dissimilarity | 0.10 | 0.00 | 0.09 | 0.04 | 0.21 |
| | Colonisations | 0.14 | 0.00 | 0.10 | 0.02 | 0.24 |

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| | | | | | |
|--------------|------|------|------|------|------|
| Extirpations | 0.09 | 0.00 | 0.09 | 0.02 | 0.19 |
|--------------|------|------|------|------|------|

Changes in taxonomic dissimilarity were mostly influenced by changes in flow regimes (PC1: % of relative influence = 24.10), changes in stock unit density (PC2; 16.4%), upstream catchment area (9.2%) and changes in flow PC2 (10.8%; Figure 2 T_{Dis}). Changes in taxonomic colonisations were mostly influenced by changes in flow (PC2; 22.2%), changes in water quality (15.1%), upstream catchment hardness (13.7%) and changes in precipitation seasonality (12.8%; Figure 2 T_{Col}). Changes in taxonomic extirpations were mostly influenced by changes in land-cover (PC2; 18.5%), changes in stock unit density (PC2; 16.1%), segment slope (12.8%) and changes in precipitation seasonality (10.7%; Figure 2 T_{Ext}).

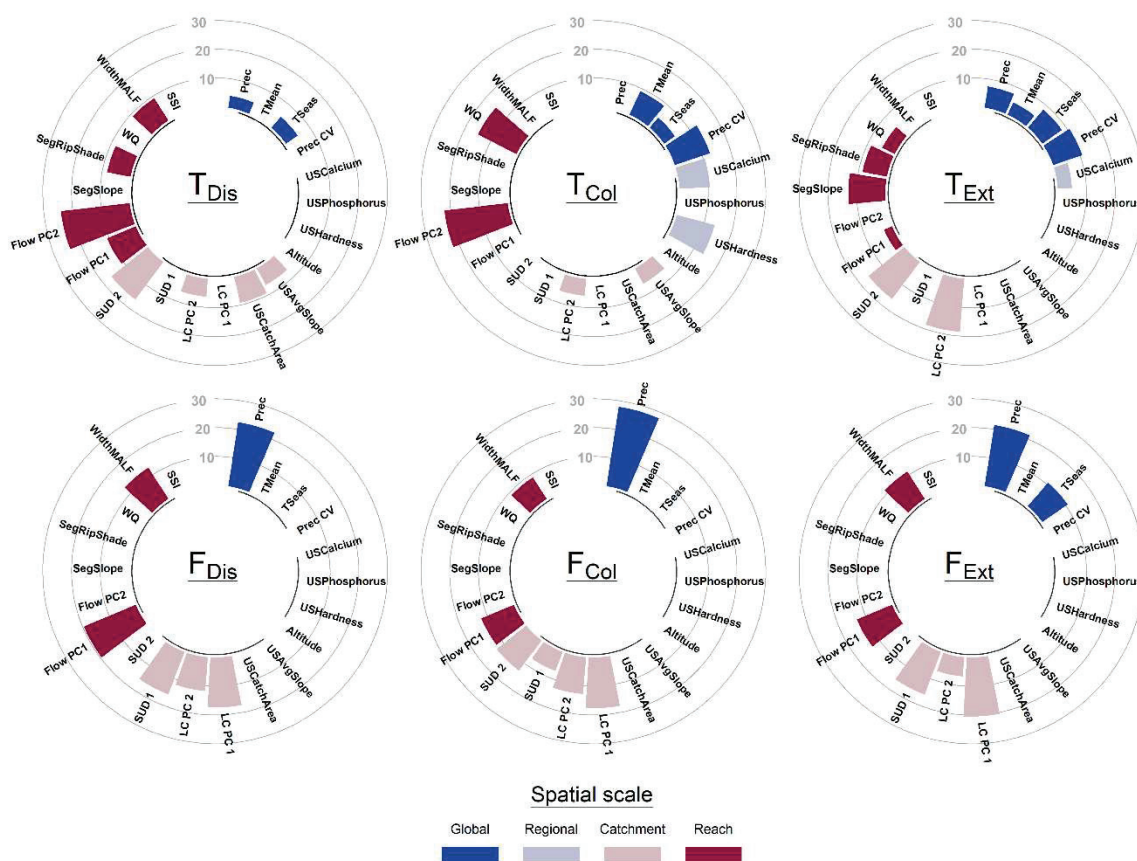


Figure 2 Relative influence of the environmental variables selected in each generalised additive mixed-effects model to explain rates of changes in taxonomic and functional temporal β diversity of macroinvertebrate assemblages. Bars are coloured by their respective spatial scale (as is indicated by the legend). T_{Dis} : taxonomic

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temporal β diversity; F_{Dis} : functional temporal β diversity; T_{Col} : taxonomic colonisations; F_{Col} : functional colonisations; T_{Ext} : Taxonomic extirpations; F_{Ext} : functional extirpations. Acronyms: Prec: Changes in precipitation; Prec CV: changes in precipitation coefficient of variation; TMean: changes in mean air temperature; TSeas: changes in temperature seasonality; USPhosphorus: phosphorus concentration of upstream surface rocks; USCalcium: calcium concentration of upstream surface rocks; USHardness: mean hardness of upstream surface rocks; Altitude: altitude of the sampled site; USAvgSlope: upstream average slope; USCatchArea: upstream catchment area; LC PC1: changes in land-cover (PC 1); LC PC2: changes in land-cover (PC2); SUD 1: changes in stock unit densities of sheep, deer, dairy and beef (PC1); SUD 2: changes in stock unit densities of sheep, deer, dairy and beef (PC2); Flow PC1: changes in flow regimes (PC1); Flow PC2: changes in flow regimes (PC2); SegSlope: average river segment slope; SegRipShade: estimated river segment riparian shading; WQ: changes in water-quality; WidthMALF: river width at mean annual low flow; SSI: changes in substrate size.

By contrast, changes in functional dissimilarity (Figure 2 F_{Dis}) were mostly influenced by changes in precipitation (22.4%, 27.9% and 21.5%, respectively), followed by changes in flow (PC1; 19.6%), changes in land-cover (PC1; 17.4%) and changes in stock unit density (15.8%). Changes in functional colonisations (Figure 2 F_{Col}) were mostly influenced by changes in changes in land-cover (PC1 & PC2; 17.7% & 12.9%) and changes in flow (PC1; 12.3%). Changes in functional extirpations (Figure 2 F_{Ext} ; Figure S2) were mostly influenced by changes in land-cover (PC1; 20.5%), changes in stock unit density (PC1; 15.9%) and changes in flow (PC1; 13.3%).

3.4.3 Population trends and species range shifts

Population sizes increased on average over the time series (mean slope = 0.002 ± 0.009), and this trend was driven by 16% of the taxa which exhibited significant population trends. Significantly increasing populations (12%; mean slope = 0.011, maximum = 0.022, minimum = 0.003) exceeded significantly decreasing populations (4%, mean slope = -0.015, min = -0.012, max = -0.018). Range sizes also increased on average over the 25-year time series (mean slope = $7,536 \pm 32,952 \text{ km}^2 \text{ decade}^{-1}$), but only 14% of taxa exhibited significant trends. Range expansions (11%; mean slope = $27,270$, min = 10,380, max = $63,330 \text{ km}^2 \text{ decade}^{-1}$) exceeded range contractions (3%; mean slope = $14,640$, min = 11,570, max = 17,700). Species shifted south on average by 56 kilometres per decade (mean = 56,31, min = 1,05, max = 242,98 km decade^{-1}), with 22% of taxa having significant poleward range shifts (mean slope = 108,14, min = 27,37, max = 242,98 km decade^{-1}).

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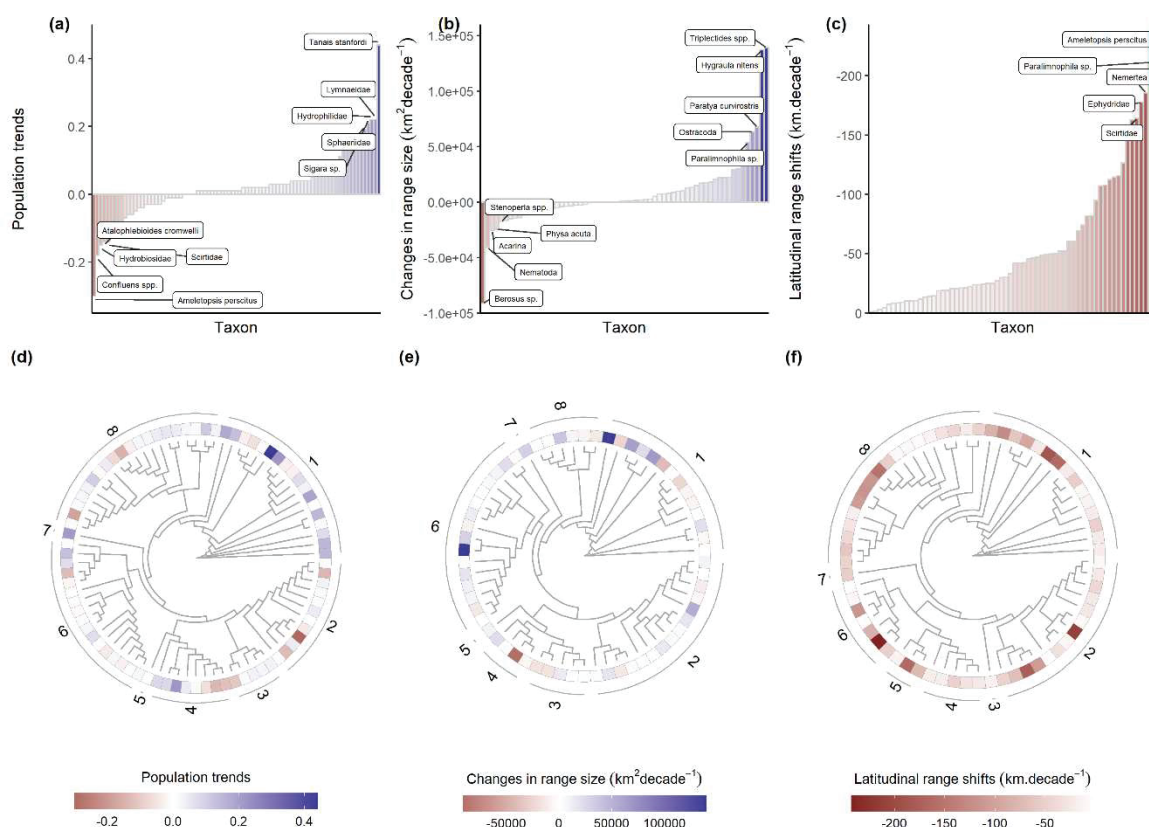


Figure 3 Population trends, species range shifts and relationships with taxonomy. Changes in population size (a), range size (b) and latitudinal range shifts (c) for each taxon. The name of the five most and/or least changing taxa are given on each plot. Relationships between taxonomy and changes in population size (d), range size (e) and latitudinal range shifts (f). The numbers around the taxonomic trees delineate major taxonomic orders: 1: Other, 2: Diptera, 3: Plecoptera, 4: Coleoptera, 5: Hemiptera, 6: Trichoptera, 7: Megaloptera, 8: Ephemeroptera

3.4.4 Relationship with taxonomy and functional traits

Dissimilarity in population trends was significantly, albeit weakly, related to taxonomic distance

(Mantel test: $r = 0.17$; $p = 0.03$, Table S4; Figure 3d). However, there was no relationship between

taxonomic distance and dissimilarity in changes in range size, nor with dissimilarity in latitudinal range shifts (Mantel's $r = 0.06$; $p = 0.27$ and Mantel's $r = 0.01$; $p = 0.40$, respectively; Figure 3 e & f).

Population trends were positively correlated with the first axis of the functional trait space ($r = 0.28$, $p < 0.01$; Figure S3 a). This axis was positively correlated with species with several reproductive cycles per year (two or more) and long-life duration of adults (> 30 days; Table S5). Changes in range size were not significantly related to functional trait space axes ($p > 0.05$). However, latitudinal range shifts were negatively correlated ($r = 0.30$, $p < 0.01$) with the third axis of the functional space, albeit with a

large amount of scatter (Figure S3 b; this included large size taxa (maximum potential size > 40mm), with a high number of descendants per reproductive cycle (> 1000), terrestrial oviposition sites and aerial respiration of aquatic stages; Table S4).

Changes in functional composition were evident on the ordinations (Figure 4 a & b): for changes in population size (Figure 4 a), most winners and losers occupied exclusive areas of trait space, signifying a temporal turnover of species populations and their traits over the 26-year time-series. However, taxa with the greatest latitudinal range shifts were mostly positioned in the centre of the functional space (Figure 4 b) indicating that these were rather generalists than specialist taxa (Mouillot et al. 2013).

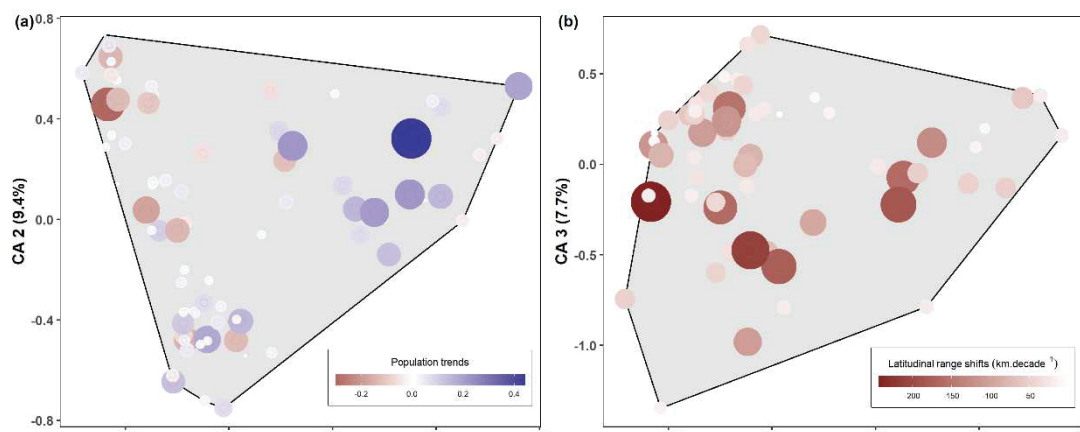


Figure 4 Differences in functional space occupancy between the species that experienced (a) population trends, and (b) latitudinal range shifts. Points size is proportional to the degree of change presented on each plot. Colour gradients also represent the degree of change presented on each plot. The black line delimits the convex hull (light grey polygon) occupied by the species pool within each bi-dimensional trait space.

3.5 – Discussion

We observed climate and land-use driven changes in temporal β diversity of taxa and functional traits across New Zealand rivers over a 25-year period relative to the first year of sampling. Trends in taxonomic colonisations increased with latitude while those of extirpations showed opposite patterns. Functional colonisations and extirpations showed weak or non-existent relationships with latitude (accepting our expectation E_{1a} but rejecting E_{1b}). Discrepancies among spatial patterns of taxonomic

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and functional diversity in river macroinvertebrate communities have also been reported elsewhere (Crabot et al. 2020, Sarremejane et al. 2020). This may suggest that communities are characterized by different degrees of functional redundancy across the landscape, allowing maintenance of functional diversity despite species losses, which may have important implications for ecosystem functions and services (McLean et al. 2019, Crabot et al. 2020).

Hierarchical models indicated a role of climate and land-use change in driving taxonomic and functional temporal β diversity. Increasing mean temperature, temperature variability and precipitation seasonality, tended to increase temporal turnover (*sensu* Anderson et al. 2011) in taxonomic composition. Many of the species that exhibited negative trends were those that specialise in cold-water pristine conditions, including the stonefly *Stenoperla prasina* and the mayfly *Amelotopsis perscitus*. One of the key mechanisms of climate change-related temporal turnover in stream communities globally has been a replacement of cold-dwellers with warm-dwellers, including in streams of North Western Europe (Haase, Pilotto et al. 2019) and New South Wales, Australia (Chessman 2009, Haase et al. 2019). By contrast, trends in functional temporal β diversity responded to changes in mean precipitation only (Figure S2). Changes in patterns of precipitation has been shown as a key structuring mechanism for freshwater temporal β diversity in many locations (Tonkin et al. 2017, Cañedo-Argüelles et al. 2020).

Moreover, land-use change (increasing intensively managed land and/or stock unit density of dairy and beef) was a predominant driver of temporal β diversity in our analyses. Increasing human land-use tended to increase taxa colonisations in these river systems (Figure S2). Human land-use intensification has been found to hasten biodiversity change in streams worldwide (Petsch et al. , Allan et al. 1997), and more particularly in New Zealand, which has experienced one of the highest rates of agricultural land intensification over recent decades (OECD/FAO 2015). Several studies have demonstrated that land use changes have profoundly impacted New Zealand's stream communities for several taxonomic groups (Clapcott et al. 2012, Foote et al. 2015, Joy et al. 2019). Such effects of

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human land-use could render freshwater ecosystems more susceptible to climate change (Verberk et al. 2016, Tickner et al. 2020), and our results indicate that their effects are currently operating in unison.

At the reach scale, changes in flow regimes were found to be the most important drivers of changes in taxonomic and functional β diversity. Riverine ecosystems are governed by patterns of temporal variation in flow regimes (Tonkin et al. 2018). As climate and land-use change modifies the natural flow regime in many river systems, components of flow regimes are expected to shift, even under the most conservative climate change scenarios (Rood et al. 2008, Ficklin et al. 2018). The results of our hierarchical models indicate how influential flow driven habitat changes are to the organization of river macroinvertebrate communities. Nevertheless, while flow change was important for almost all facets of beta diversity, it had only a small role as a driver of taxonomic extinctions, where land-use change was the predominant driver. This may reflect the relative flexibility of most New Zealand invertebrates to unpredictable flow regimes, given its oceanic climate (Tonkin et al. 2018, Winterbourn et al. 1981).

Contrary to our second expectation (E_2) our results identified greater amounts of increases in population and range size (i.e., winners) than decreases (i.e., losers) across the entire species pool. This suggests that the overall taxonomic homogenisation of these river macroinvertebrate communities recently observed (Mouton et al. 2020) is characterised by a greater amount of increase in population size and range size of winners than widespread declines of losers. Nonetheless, we found increasing rates of taxonomic extirpations at sites located at the north-eastern boundary of the North Island of New Zealand. Conversely, the greatest rates of taxonomic colonisations were located at the southern boundaries of each island. More importantly, almost a quarter of the taxa examined here also tracked the shifting isotherms by shifting their ranges towards the south pole. Given the geographic isolation of New Zealand and the observed latitudinal patterns of species distribution shifts here, the biodiversity of New Zealand's rivers could experience a 'cul-de-sac' effect, if it is to be exposed to more intense climate change (Sauer et al. 2011, Albouy et al. 2012). This trend may further

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be exacerbated for species dispersing exclusively along river networks (Hylander & Ehrlén 2013, Bush & Hoskins 2017, Tonkin et al. 2018).

We found that population trends were taxonomically structured, however no relationship was found with species range shifts (thus, partly accepting E_{3a}). We also found that changes in population size and latitudinal range shifts of taxa were associated with distinct functional traits, confirming our expectation of a relationship between the functional characteristics of species and their vulnerability to climate and land-use change (E_{3b}). Several mayflies (Ephemeroptera) and caddisflies (Trichoptera) exhibited decreasing abundances over the 26-year period, many species from these orders are widely considered as pollution-sensitive (Stark 1985, Usseglio-Polatera & Bournaud 1989). By contrast, we observed a rise in crustaceans (Crustacea), snails (Gastropoda) and scavenger beetles (Coleoptera), these groups being mainly composed of eurythermal taxa, typical from slow-flowing waters, and tolerant to a wide range of water quality conditions, including low oxygen but high nutrient concentrations (Stark, 1995). Increasing population sizes and latitudinal range shifts were strongly related to high numbers of reproductive cycles per year (two or more) and descendants per reproductive cycle, respectively. Such *r*-selected strategies have been found to correlate with other increasing population sizes and/or species range shifts in freshwater and marine organisms' facing climate change. For example, McLean et al. (2018) found that rapid warming drove marine pelagic fishes with *r*-selected life history traits to shift abruptly poleward. Similarly, Comte et al. (2014) found that species with high propagule pressure (i.e. *r*-strategists) and greater mobility, displayed the greatest range shifts in stream fishes facing climate change. Here, increasing population sizes and latitudinal range shifts were also related to traits like long-life duration of adults and large body sizes, which are more typical of *K*-strategists' species. This result is in agreement with previous studies highlighting that such strategies can be promoted under climate change (e.g. del Cacho et al. 2012), especially in running waters experiencing climate-driven flow reduction (Floury et al. 2017).

3.6 – Conclusion

We found that rates of changes in macroinvertebrate taxonomic composition in New Zealand's River systems over a 25-year period are latitudinally structured but not changes in their trait composition. We observed increasing rates of taxonomic extirpations at the rear edge of mainland New Zealand but increasing taxonomic colonisations at the leading edges. Further, we found that most taxa tended to increase in population and range size rather than decrease. Changes in community composition correlated with recent climate and land-use change. Macroinvertebrate functional traits related to life-history and morphology explained changes in population size and species latitudinal range shifts. Our findings highlight the critical need to move beyond observation of emergent state-level variables to understanding the mechanisms underpinning taxonomic and functional reorganisation of biodiversity under ongoing environmental changes (Tonkin et al. 2019).

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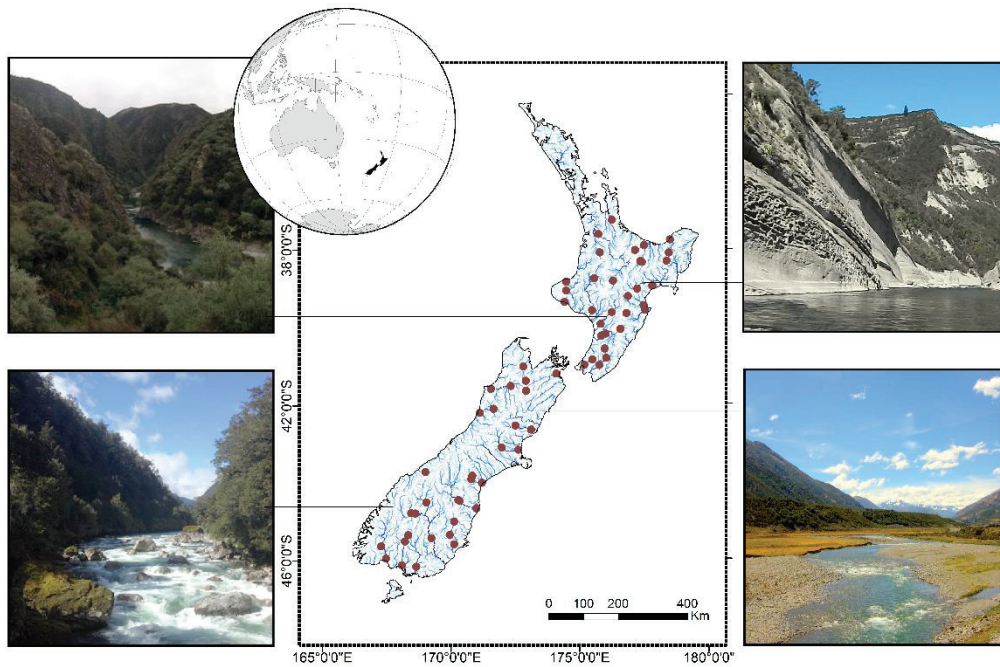
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Supplementary materials

1 – Study area

Figure S1 Map of Mainland New Zealand showing the location of the 64 sampling sites (red dots). Rivers (streams of order > 3) are illustrated using blue segments. The global inset map shows the location of New Zealand (black country) in the world. Photo credits: Théophile L. Mouton, Kéoni Saint-Pée and Tom Drinan.



2 – PCAs of environmental predictors

Table S1 Correlations among input variables and the axis of the PCAs used to define synthetic predictors of changes in land-cover, changes in stock unit density and changes in flow, respectively (three PCAs in total). Percentages are the percentage of variation explained by each axis in its respective PCA.

| | PC1 | PC2 |
|----------------------------------|---------|---------|
| <u>Land-cover</u> | (61.1%) | (23.9%) |
| NF | 0.42 | 0.87 |
| PF | -0.99 | 0.03 |
| SG | 0.90 | -0.02 |
| HG | 0.70 | -0.45 |
| <u>Stock unit density</u> | (44.3%) | (35.2%) |
| Dairy SUD 2012-1990 | -0.67 | 0.62 |
| Beef SUD 2012 - 1990 | 0.64 | 0.59 |
| Sheep SUD 2012 - 1990 | 0.83 | -0.38 |
| Deer SUD 2012 - 1990 | 0.48 | 0.73 |
| <u>Flow</u> | (54.1%) | (20.6%) |
| Flow mean annual | 0.93 | 0.07 |
| Flow CV annual | -0.90 | -0.19 |
| Flow mean Summer | 0.85 | -0.26 |
| Flow mean Spring | 0.55 | -0.51 |
| Flow mean Winter | 0.55 | 0.69 |
| Flow CV Summer | -0.77 | 0.28 |
| Flow CV Spring | -0.81 | 0.21 |
| Flow CV Winter | -0.34 | -0.83 |

3 - Hierarchical Generalised Additive Mixed-effect Models

Table S2 Results from the hierarchical Generalised Additive Mixed-effect Models relating temporal β -diversity indices (taxonomic and functional dissimilarity, colonisations, and extirpations) to environmental descriptors nested within environmental spatial scales. Std. Error: Standard error; Edf: Estimated degrees of freedom; F: F value. Acronyms: Prec: Changes in precipitation; Prec CV: changes in precipitation coefficient of variation; TMean: changes in mean air temperature; TSeas: changes in temperature seasonality; USPhosphorus: phosphorus concentration of upstream surface rocks; USCalcium: calcium concentration of upstream surface rocks; USHardness: mean hardness of upstream surface rocks; Altitude: altitude of the sampled site; USAvgSlope: upstream average slope; USCatchArea: upstream catchment area; LC PC1: changes in land-cover (PC 1); LC PC2: changes in land-cover (PC2); SUD 1: changes in stock unit densities of sheep, deer, dairy and beef (PC1); SUD 2: changes in stock unit densities of sheep, deer, dairy and beef (PC2); Flow PC1: changes in flow regimes (PC1); Flow PC2: changes in flow regimes (PC2); SegSlope: average river segment slope; SegRipShade: estimated river segment riparian shading; WQ: changes in water-quality; WidthMALF: river width at mean annual low flow; SSI: changes in substrate size.

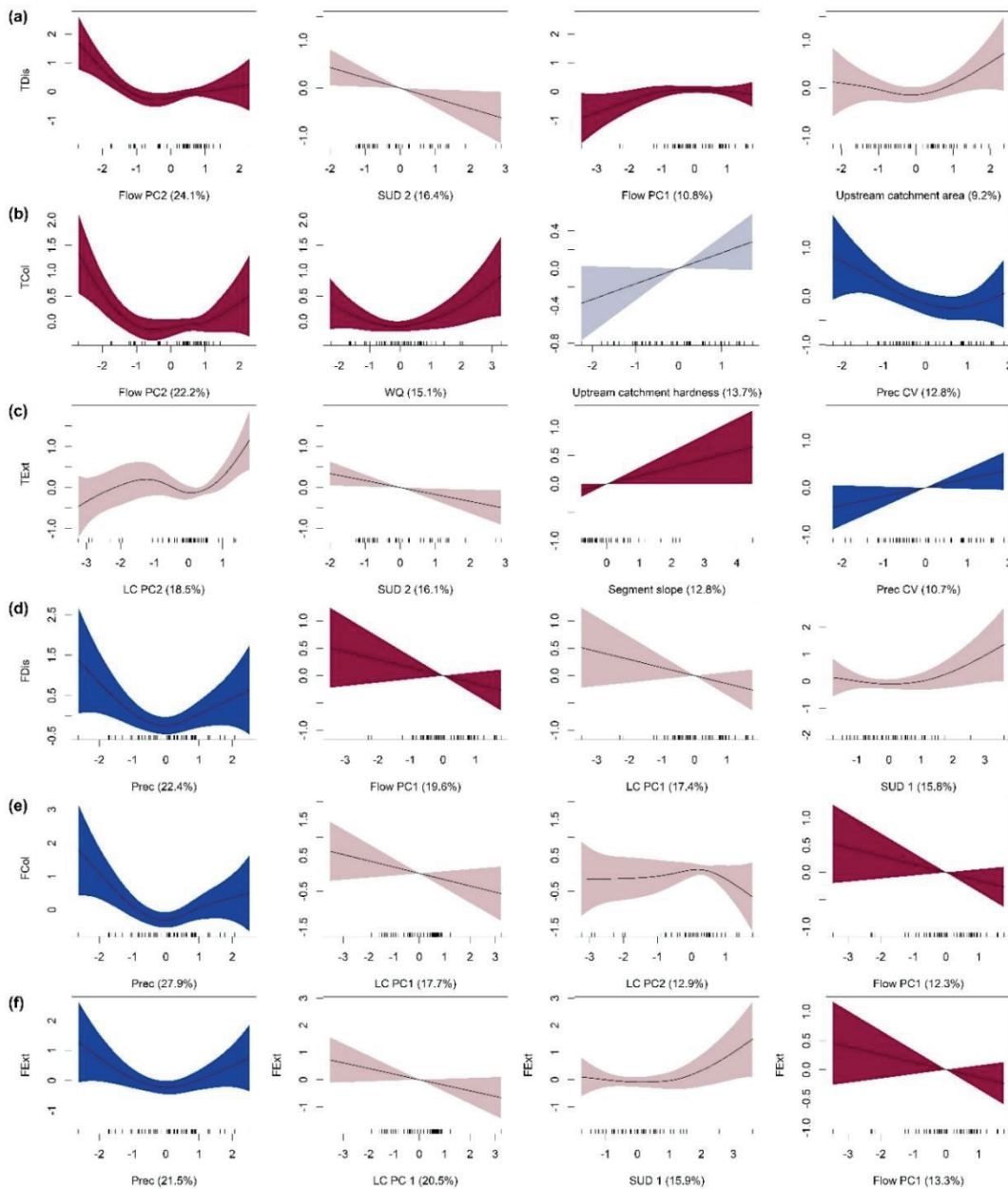
| Temporal β -diversity index | Spatial scale | Intercept (std. error) | Variable | Edf | F | p-Value |
|-----------------------------------|---------------|---------------------------|------------------|-------|-------|---------|
| Dissimilarity | Global | 0.040 (0.223) | TSeas | 1 | 0.999 | 0.321 |
| | | | Prec | 1 | 0.759 | 0.387 |
| | Catchment | 1.613e-11 (8.633e-02) | USCatchArea | 2.269 | 2.186 | 0.139 |
| | | | USAvgSlope | 1.00 | 1.645 | 0.205 |
| | | | LC PC2 | 2.509 | 1.895 | 0.287 |
| | | | SUD PC2 | 1.000 | 5.254 | 0.026 |
| | | | SegRipShade | 2.588 | 1.265 | 0.195 |
| | Reach | 0.022 (0.068) | WidthMALF | 2.015 | 2.282 | 0.112 |
| | | | Flow PC1 | 2.212 | 2.358 | 0.096 |
| | | | Flow PC2 | 3.509 | 4.739 | 0.003 |
| Taxonomic | Global | 0.023 (0.279) | TMean | 1.475 | 2.595 | 0.167 |
| | | | TSeas | 1.000 | 0.715 | 0.401 |
| | | | Prec CV | 2.192 | 2.424 | 0.077 |
| | Regional | -0.0005 (0.095) | USHardness | 1.000 | 3.528 | 0.065 |
| | | | USCalcium | 1.314 | 2.896 | 0.121 |
| | Catchment | -2.963e-11 (7.222e-02) | USAvgSlope | 1 | 1.101 | 0.298 |
| | | | LC PC2 | 1 | 1.067 | 0.306 |
| | Reach | 0.0018 (0.0898) | WQ | 2.577 | 2.977 | 0.049 |
| | | | Flow PC2 | 3.142 | 3.542 | 0.012 |
| | Extirpations | Global | 0.013 (0.422) | Prec | 1.926 | 2.211 |
| TMean | | | | 1.000 | 0.942 | 0.3358 |
| TSeas | | | | 1.000 | 2.214 | 0.1422 |

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| | | | | | | |
|--|----------------------|--------------------------|-------------|-------|-------|--------|
| | | | Prec CV | 1.000 | 3.164 | 0.0805 |
| | Regional | 3.735e-11 (7.942e-02) | USCalcium | 1.000 | 1.058 | 0.308 |
| | | | SegSlope | 1.000 | 4.277 | 0.043 |
| | Reach | 0.001 (0.068) | SegRipShade | 1.000 | 3.329 | 0.073 |
| | | | Flow PC1 | 1.000 | 0.755 | 0.389 |
| | | | WQ | 2.565 | 2.901 | 0.062 |
| | Dissimilarity | | | | | |
| | Global | -0.0003 (0.121) | Prec | 2.612 | 2.332 | 0.063 |
| | | | LC PC1 | 1.000 | 2.776 | 0.101 |
| | Catchment | 8.032e-10 (1.132e-01) | LC PC2 | 2.560 | 1.662 | 0.339 |
| | | | SUD PC1 | 2.112 | 1.852 | 0.147 |
| | Reach | -0.035 (0.105) | WidthMALF | 1.000 | 1.550 | 0.218 |
| | | | Flow PC1 | 1.000 | 1.964 | 0.166 |
| | Colonisations | | | | | |
| | Global | -0.0006 (0.118) | Prec | 2.964 | 3.312 | 0.019 |
| | | | LC PC1 | 1.000 | 2.240 | 0.140 |
| | Catchment | 6.892e-11 (1.110e-01) | LC PC2 | 2.418 | 1.120 | 0.544 |
| | | | SUD PC1 | 1.631 | 1.109 | 0.455 |
| | | | SUD PC2 | 1.000 | 2.399 | 0.127 |
| | Reach | -0.034 (0.103) | WidthMALF | 1.000 | 1.774 | 0.188 |
| | | | Flow PC1 | 1.000 | 2.113 | 0.151 |
| | Extirpations | | | | | |
| | Global | 5.816e-05 (1.209e-0) | Prec | 2.538 | 2.745 | 0.078 |
| | | | TSeas | 1.780 | 0.916 | 0.278 |
| | Catchment | 2.124e-10 (1.113e-01) | LC PC1 | 1.000 | 3.022 | 0.087 |
| | | | LC PC2 | 2.493 | 1.321 | 0.451 |
| | | | SUD PC1 | 2.240 | 1.634 | 0.151 |
| | Reach | -0.038 (0.102) | WidthMALF | 1.000 | 1.281 | 0.262 |
| | | | Flow PC1 | 1.000 | 1.630 | 0.207 |

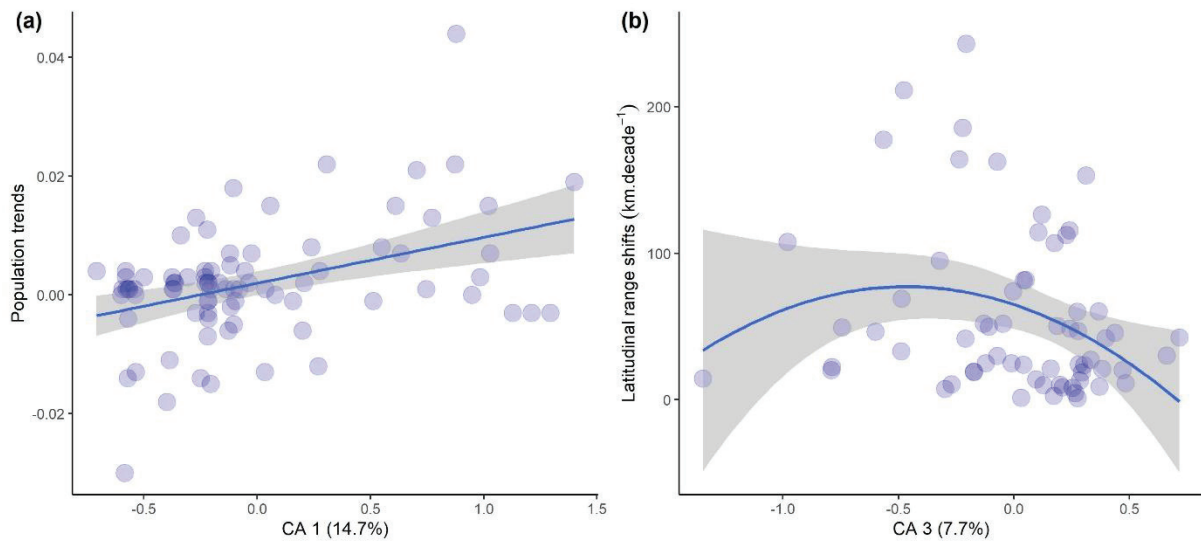
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Figure S2 Marginal effects plots of the four most influential predictor variables in the Generalised Additive Mixed effect Models. (a) Taxonomic dissimilarity, (b) Taxonomic colonisations, (c) Taxonomic extirpations, (d) Functional dissimilarity, (e) Functional colonisations and (f) functional extirpations. The colours for each plot are those used in Figure 2 of the main text. Rug plots on the bottom margins of each plot show the distribution of sites across that variable. Acronyms: Prec: Changes in precipitation; Prec CV: changes in precipitation coefficient of variation; TMean: changes in mean air temperature; TSeas: changes in temperature seasonality; USPhosphorus: phosphorus concentration of upstream surface rocks; USCalcium: calcium concentration of upstream surface rocks; USHardness: mean hardness of upstream surface rocks; Altitude: altitude of the sampled site; USAvgSlope: upstream average slope; USCatchArea: upstream catchment area; LC PC1: changes in land-cover (PC 1); LC PC2: changes in land-cover (PC2); SUD 1: changes in stock unit densities of sheep, deer, dairy and beef (PC1); SUD 2: changes in stock unit densities of sheep, deer, dairy and beef (PC2); Flow PC1: changes in flow regimes (PC1); Flow PC2: changes in flow regimes (PC2); SegSlope: average river segment slope; SegRipShade: estimated river segment riparian shading; WQ: changes in water-quality; WidthMALF: river width at mean annual low flow; SSI: changes in substrate size.



5 – Functional trait space

Figure S3 Relationships between (a) the first axis of functional trait space (CA 1) and population trends, (b) the third axis of the functional trait space and latitudinal range shifts. Latitudinal range shifts are shown as positive values for illustration purpose but are all negative values (southward shifts). The blue lines are second order polynomial regressions. Percentages indicate the percentage of the functional trait space explained by the trait space axes.



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Table S3 Position of the species trait modalities on the first 3 axes of the functional space (CA). Functional space was generated using a fuzzy correspondence analysis (CA) of 16 functional traits, based on dissimilarities among the 59 fuzzy coded trait modalities of macroinvertebrates (n=83).

| Category | Functional traits | Modalities | CA 1 | CA 2 | CA 3 | |
|--|--|----------------------------------|---------|-------|-------|-------|
| Morphology | Maximum potential size | <=5 mm | 0.71 | -0.15 | 0.90 | |
| | | >5-10 mm | -0.11 | 0.13 | 0.12 | |
| | | >10-20 mm | -0.05 | -0.21 | -0.02 | |
| | | >20-40 mm | -0.34 | 0.49 | -0.57 | |
| | | >40 mm | 0.17 | -0.21 | -2.58 | |
| Life history | Maximum number of descendants per reproductive cycle | <=100 | 1.00 | 0.08 | -0.10 | |
| | | >100-1000 | -0.27 | -0.16 | 0.15 | |
| | | >1000-3000 | -0.98 | 0.98 | -1.26 | |
| | Maximum number of reproductive cycles per year | >3000 | -0.52 | 0.88 | -0.36 | |
| | | semivoltine | -1.10 | 0.91 | -1.74 | |
| | | univoltine | -0.28 | -0.01 | 0.00 | |
| | Number of reproductive cycles per individual | plurivoltine | 1.02 | -0.13 | 0.29 | |
| | | 1 | -0.38 | -0.09 | 0.02 | |
| | Life history | Life duration of adults includes | > or =2 | 1.77 | 0.41 | -0.07 |
| | | | <=1 day | -0.80 | 0.54 | -0.53 |
| >1-10 days | | | -0.56 | -0.01 | 0.14 | |
| >10-30 days | | | -0.39 | -0.42 | 0.41 | |
| >30-365days | | | 0.92 | 0.30 | -0.33 | |
| Reproductive technique | | >365 days | 0.95 | 0.10 | -0.73 | |
| | | single individual | 1.54 | 0.12 | 0.08 | |
| | | hermaphrodism | 1.93 | 0.43 | -0.19 | |
| | | male and female | -0.29 | -0.06 | 0.02 | |
| Oviposition Site | | water surface | -0.79 | 0.74 | 0.19 | |
| | | submerged | 0.48 | -0.31 | 0.19 | |
| | | terrestrial | -0.17 | -0.70 | -1.55 | |
| | | eggs endophytic | 1.21 | 0.02 | -0.12 | |
| Egg/egg mass | | free | -0.36 | 0.35 | -0.26 | |
| | | cemented | 0.14 | -0.69 | 0.37 | |
| | | female bears eggs in/on body | 1.30 | 0.85 | -0.07 | |
| Mobility | Dissemination potential (all stages) | low (10 m) | 0.16 | 0.18 | 0.34 | |
| | | medium (1 km) | -0.15 | 0.10 | 0.09 | |
| | | high (>1km) | 0.02 | -0.40 | -0.59 | |
| | | swimmers (water column) | 0.56 | 0.39 | -0.13 | |
| | | crawlers (epibenthic) | -0.11 | 0.08 | 0.10 | |
| Attachment to substrate of aquatic stages (excluding eggs) | | burrowers (infauna) | 0.12 | -0.23 | -0.78 | |
| | | attached | 0.09 | -0.52 | 0.74 | |
| | | none (<10°) | 0.68 | 0.28 | 0.38 | |
| Morphology | Body flexibility | low (>10-45°) | -0.50 | 0.50 | 0.15 | |

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| | | | | | |
|----------------------|--|--------------------------------------|-------|-------|-------|
| | | high (>45°) | 0.08 | -0.83 | -0.49 |
| | | streamlined | -0.45 | 0.80 | 0.04 |
| | Body form | flattened (dorso-ventral or lateral) | 0.11 | 0.78 | 0.10 |
| | | cylindrical | -0.08 | -0.40 | -0.07 |
| | | spherical | 2.15 | 0.64 | 0.60 |
| | | shredders | -0.37 | -0.27 | 0.24 |
| | | scrapers | -0.02 | 0.48 | 0.23 |
| | Feeding habits | deposit-feeders | 0.14 | 0.19 | -0.53 |
| Resource acquisition | | filter-feeders | 0.16 | -0.38 | 0.88 |
| | | predator | 0.04 | -0.51 | -0.55 |
| | | algal piercer | -0.16 | -0.91 | 1.84 |
| | | strong (specialist) | -0.12 | -0.76 | -0.44 |
| | Dietary preferences | moderate | -0.14 | -0.08 | -0.03 |
| | | weak (generalist) | 0.08 | 0.22 | 0.12 |
| | | tegument | 0.06 | -0.22 | 0.28 |
| Morphology | Respiration of aquatic stages (not including eggs) | gills | -0.29 | 0.60 | 0.12 |
| | | plastron | 0.83 | 0.38 | -0.17 |
| | | aerial | 0.23 | -0.85 | -1.28 |
| | | Adult, larva | 1.31 | 0.38 | -0.27 |
| Life history | Aquatic stages | Adult or larva | -0.84 | 0.81 | -0.42 |
| | | Larva, Pupa | -0.33 | -0.80 | 0.47 |

Chapitre 4

Quelles conséquences des changements globaux sur la diversité alpha et la redondance fonctionnelle des communautés ?

Préface :

Dans le chapitre 3, nous nous sommes intéressés aux patrons géographiques des pertes et des gains d'espèces et de traits au cours du temps, ainsi qu'aux changements latitudinaux d'aires de répartition des espèces. Nous avons notamment identifié de forts gains d'espèces aux limites sud des deux îles principales que forment la Nouvelle-Zélande. Mais comment ces changements de composition des communautés affectent-ils les gradients latitudinaux de richesse taxonomique et fonctionnelle ? Et comment, la redondance fonctionnelle des communautés évolue-t-elle au cours du temps en réponse à ces multiples changements ?

Ce sont ces deux questions que nous abordons dans le chapitre 4. Le gradient latitude/richeesse est un des patrons géographiques les plus étudiés en biogéographie. Cependant, sont changement potentiel au cours du temps est peu étudié. De plus, l'effet des changements potentiels de richesse et de redondance fonctionnelle sur la biodiversité est inconnu. La diversité fonctionnelle reflète le fonctionnement des communautés, tandis que la redondance fonctionnelle en reflète les capacités de résistance et de résilience de ceux-ci. Par les analyses effectuées dans le chapitre qui suit, je pourrais donc émettre des hypothèses sur l'effet des changements globaux sur le rôle que joue la biodiversité des macroinvertébrés benthiques dans les hydrosystèmes.

Preface (English):

In chapter 3, we were interested in geographical patterns of gains and losses of species and traits, and in latitudinal shifts of species ranges. We identified high gains of species at the southern limits of both mainland islands of New Zealand. But how do these changes in community composition affect latitudinal gradients in species and trait richness of macroinvertebrates? And how, does trait redundancy change with time given these multiple changes?

We tackle these two questions in chapter 4. The latitude/species richness gradient is one of the most studied geographical patterns in biogeography. However, its potential to change with time is understudied. In addition, the effects of potential changes in trait richness and redundancy on biodiversity is unknown. Functional diversity reflects the functioning of ecological communities, whereas redundancy reflects resistance and resilience capacities. By the analyses undertaken in the chapter to come, I will therefore be able to discuss the effects of global changes on the role that macroinvertebrate biodiversity has in these freshwater ecosystems.

Article III: Climate change reverses the latitudinal species and trait richness gradients of river invertebrates

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4.1 – Abstract

Latitudinal trends in species richness, traits, and diversity are well-studied biogeographical patterns, but there is limited understanding of how they might be altered by climate, land use and local habitat changes. We examined changes in species richness, trait richness, and trait redundancy in relation to climate change, land-use and local habitat in a 26-year time-series of 1,561 macroinvertebrate samples distributed across 64 river sites in New Zealand. We observed an inversion in the latitudinal species and trait richness gradients over time, whereby species richness decreased in the northernmost regions but increased in the southernmost. Increases in species richness correlated with a reduction in trait richness but with an increase in trait redundancy. Changes in climate were the greatest direct correlates of changes in species richness but changes in trait richness and in trait redundancy were mainly associated with changes in flow regimes, indirectly driven by climate and land-use changes. Increasing trait redundancy was also partly explained by reductions in niche position (generalisation) of species for flow regimes and water quality. Our results highlight that climate change and land-use intensification may increase species richness and trait redundancy at several locations but come with the cost of reduced trait richness.

KEYWORDS

Climate change; Species richness; Trait diversity; Latitude; Trait redundancy; Kernel density; Niche breadth

4.2 – Introduction

Although the latitudinal diversity gradient is one of the most well-studied of all biogeographical patterns, there is now significant interest in how it will be affected by global change (Chaudhary et al. 2021). Climate and land-use changes are altering global biodiversity patterns (Guo et al. 2018), in many cases homogenising biological assemblages over large spatial scales (McGill et al. 2015). These changes have direct and indirect consequences on ecosystems through interactions and feedback loops (Barnes et al. 2017). At more local scales, long-term trends in biodiversity are complex, reflecting a balance between local species colonisations and extirpations (Dornelas et al. 2019, Williams et al. 2022). While recent meta-analyses and empirical studies report a latitudinal shift in species richness (Chaudhary et al. 2021), the trends observed reflect both positive and negative changes in local species diversity (Blowes et al. 2019). Thus, we need to better understand under which contexts positive and negative changes occur to better predict the effect of global changes on biodiversity (Chaudhary et al. 2021, Comte et al. 2021).

Changes in community structure and composition may or may not propagate to ecosystem functioning. The strength of this propagation depends on the extent and direction of trait changes within communities (de Bello et al. 2021). Trait diversity reflects the breadth of ecological roles played by species in each community (Mihalitsis et al. 2021, Sosiak & Barden 2021), and therefore relates to ecosystem functioning (Díaz & Cabido 1997, Tilman et al. 1997). By contrast, trait redundancy within a community theoretically relates to resilience and resistance capacities (Walker 1995, Moretti et al. 2006). Two species may be deemed redundant if they share similar trait values and likely perform similar functions in ecosystems. Trait redundancy can thus buffer functional diversity erosion when some species are locally extirpated from a community (Laliberté et al. 2010, Mouillot et al. 2014, McLean et al. 2019). Therefore, understanding how the reorganisation of biodiversity under global change relates to changes in trait diversity and redundancy is a fundamental aspect of community ecology (Teixidó et al. 2018, Luza et al. 2021).

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Trends in trait diversity and redundancy under global change are less well investigated than trends in taxonomic diversity, however some studies have found that environmental disturbances can impact trait diversity and redundancy (Etard et al. 2021, Luza et al. 2021). For example, Luza et al. (2021) found that human impacts may increase trait redundancy in communities of non-volant small terrestrial mammals, whereas Etard et al. (2021) found that functional diversity of terrestrial mammals decreased in response to human land-use intensification. In addition, many studies observed expansions in generalist species distributions and abundances, leading to ecological generalisation of communities (Stuart-Smith et al. 2021). Species with unique and specialised traits may be more frequently extirpated (Pimiento et al. 2020), as their environmental niche breadth and position are reduced over time with increasing anthropogenic disturbances (Stuart-Smith et al. 2021). Given that some traits may be favoured by anthropogenic stressors (Gámez-Virués et al. 2015), one may expect gains in redundancy for some traits at the expense of others (Luza et al. 2021). Nonetheless, patterns of temporal changes in the organisation of communities across large spatial scales remain poorly studied, limiting our capacity to assess the effects of spatially extended anthropogenic alterations such as climate and land-use changes on biodiversity.

Streams and rivers are among the most vulnerable ecosystems on the planet, however their biodiversity is understudied compared to marine and terrestrial systems (Lenoir et al. 2020). Global patterns of air temperature and precipitation regimes are changing rapidly in the Anthropocene (IPCC, 2019), altering river flow regimes and impacting riverine organisms (Tonkin 2021). The impacts of land-use change, such as deforestation or agriculture intensification may interact with climate change to intensify impacts (Comte et al. 2021). Climate change may directly affect the distribution ranges of species such as insects (Outhwaite et al. 2022) and amphibians (Tiberti et al. 2021) that use both freshwater and terrestrial systems during their life-stages. However, climate change may also have indirect effects, for example, by altering the frequency and duration of drying and/or flooding events, and more generally the natural flow regimes of rivers throughout the year (Tonkin et al. 2018).

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In this study, we expand on recent findings from Mouton et al. (2020, 2022), which examined spatial and temporal changes in both taxonomic and functional beta diversity of 64 river macroinvertebrate communities comprising 113 taxa, sampled sequentially for 26 years across New Zealand rivers. They reported increasing spatial taxonomic homogenisation but functional differentiation, and temporal reorganisation of communities including greater increases than decreases in population and range sizes. While it is largely reported that taxonomic homogenization is generally accompanied by increases in alpha diversity, and more particularly species richness (Daru et al. 2021), how functional differentiation translates to changes in functional richness and trait redundancy remains unknown. Here, we disentangle spatial and temporal changes in species richness, trait richness and trait redundancy and examine the potential direct and indirect effects of environmental changes underlying observed patterns. We also examine how changes in environmental niche breadth and position of all taxa relate to their changes in trait redundancy within communities. For this, we use a unique, quality-controlled database comprising high resolution data on macroinvertebrate communities (Smith & McBride 1990), climate and land-use change, flow regimes, water quality and river substrate size. This database is ideal to study the combined effects of climate and land-use changes on freshwater macroinvertebrate biodiversity, since it broadly spans the entire distributional range of all taxa present in the database (Winterbourn et al. 1981). New Zealand's climate is undergoing rapid change (Hopkins et al. 2015) and its landscape has suffered from one of the highest rates of agricultural intensification on the planet over recent decades (OECD/FAO 2015), rapidly impacting its freshwater ecosystems (Foote et al. 2015).

First, we expect that increases in species richness would result in decreased trait richness but increased trait redundancy, because species that benefit from global change are mostly functionally similar to each other (E2; Luza et al. (2021); Carmona et al. (2021)). Second, we expect the species richness latitudinal gradient to change across years as a result of species range shifts (E1; Lenoir et al. (2020), Mouton et al. (2022)). Third, we expect direct and indirect effects of climate change and land-

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use in driving changes in species richness, trait richness and trait redundancy through changes in flow regimes, water quality and river substrate size (E3; Vollstädt et al. (2017), Chu et al. (2019)). Finally, we predict that increasing trait redundancy in communities is influenced by the increasing niche breadth and changes in niche position of generalist species that track novel environmental conditions (E4; Stuart-Smith et al. (2021)).

4.3 – Methods

4.3.1 Macroinvertebrate community sampling

We used a time-series database of macroinvertebrate community samples collected from 64 sites, located in 35 mainstem rivers of New Zealand (between latitudes 46 and 35°S). Sampling surveys were conducted, operated, and maintained by the National Institute of Water and Atmospheric Research (NIWA) for New Zealand's National Rivers Water Quality Network (NRWQN, Smith & McBride, 1990). Sampling operations were conducted yearly from 1991 to 2016, during late austral summers (from February to April). At each sampling occasion, seven Surber samples (0.1 m² and 250 µm mesh nets) were collected down to a depth of approximately 10 centimetres and from as many substrate types as possible. Macroinvertebrates were removed from the sampler and individuals were later identified to the lowest taxonomic levels possible (mostly species or genus) in the laboratory, and the same taxonomic level was used for every survey across sites and years (Scarsbrook et al. 2000).

4.3.2 Environmental variables

We used a set of environmental predictors known to influence the distribution of macroinvertebrates in running waters (Poff et al. 1997, Allan 2004): changes in air temperature and precipitations (climate change), changes in land cover and stock unit densities of dairy, beef, sheep and deer cattle (land use change), changes in flow regimes, substrate size of the riverbed and in water quality (local habitat change). Metrics of temporal changes in these variables are detailed in the following section.

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For changes in air temperature and precipitation, we used daily mean air temperature and precipitation for the period 1991-2016. We extracted these values from 5 km² gridded layers of New Zealand, as provided by NIWA's Virtual Climate Station Network (VCSN; <https://data.niwa.co.nz/>). We calculated annual and seasonal (for the three seasons preceding sampling: winter, spring and summer seasons) means and variability (i.e. the standard deviation of the mean for temperature and the coefficient of variation for precipitation; Fick and Hijmans (2017)).

For land use changes, we used measures of temporal changes (1990-2012) in four land cover types (defined as the proportion of catchment occupied by combinations of (1) high producing grassland, (2) shrub/grassland, (3) plantation forest and (4) non-plantation forest), as provided by the New Zealand Land Cover database (LCDB, Landcare Research, 2015; Julian et al. (2017)) and in catchment stock unity density (SUD) of dairy, beef, sheep and deer cattle (SU ha⁻¹; Statistics NZ (territorial authority), Julian et al. (2017)). These two databases are updated every four to five years and, therefore, only four layers of land cover and SUD were available for our studied period (1990, 1994, 1998 and 2012).

To assess changes in local habitat, we first compiled mean daily flow data from hydrological gauges implemented at each site and during the entire study period. We divided mean daily flow by upstream catchment area to obtain a measure of run-off per day (Vaughan and Gotelli 2019). Then, we calculated the mean annual and seasonal (for winter, spring, and summer, as was done for precipitation) run-off per day (hereafter, referred to as flow and flow coefficient of variation). Changes in substrate size were quantified measurements conducted at each macroinvertebrate sampling survey. 100 particles were selected randomly at 1 m. intervals along a path of 45 degrees to the riverbank in a zig-zag manner. Particles were then assigned to each of eight size classes: bedrock, boulders (>300mm), large cobbles (300–128mm), small cobbles (128-64mm), large gravel (32- 183 64mm), small gravel (2-32mm), sand (62.52 µm – 2mm) and silt (< 62.52 µm). We used the substrate size index (SSI) for each sampling occasion following Jowett, Richardson et al. (1991) (1 = silt only, 8 = bedrock only). Finally, changes in water quality were assessed through median annual values (mg.m⁻³)

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of nitrate ($\text{NO}_3\text{-N}$), ammonium nitrogen ($\text{NH}_4\text{-N}$), dissolved reactive phosphorus (DRP) and dissolved oxygen (DO) concentrations and water clarity (metres; CLAR). These data originated from samples collected monthly, at the same sites as those sampled for macroinvertebrate communities and from 1991 to 2016 (Davies-Colley et al. 2011).

4.3.3 Quantifying temporal changes

To estimate temporal changes throughout the entire time-series (26 years) and in each of the environmental variables described above (except land use variables, see below), we regressed each variable, at each site, against the time series year ($n = 26$). We used the slope of each regression model as our estimates of temporal change, for each environmental variable. Then, we synthesised temporal changes (i.e. the slopes from the regression models) in our sets of variable groups using Principal Component Analyses (PCAs; using the *dudi.pca* function in the *ade4* package v. 1.7-15 (Thioulouse et al. 2018)).

A PCA was performed for air temperature variables and another for precipitation variables and the first two axes of each PCA were kept as synthetic indicators of climate change (Table S1). For air temperature, the first axis (PC1; 35.9% of explained variation) described a gradient of increasing mean air temperature (Tmean), while the second (PC2; 33.0%) described a gradient of increasing air temperature seasonality (Tseas). For precipitation, the first axis (PC1; 28.2%) described a gradient of increasing precipitation seasonality (Prec CV) and the second (PC2; 22.7%) a gradient of decreasing mean precipitation (Prec).

Similarly, for changes in flow we ordinated temporal changes using PCA and kept the first two axes (Flow PC1, 54.1% and Flow PC2, 20.6%; Table S1) as indicators of temporal changes in flow regimes. To improve the normality of water quality variables, we used a \log_{10} -transformation prior to measuring temporal changes. We then ordinated temporal changes using PCA and retained the first axis (WQ,

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33.3%; Table S1) as a synthetic indicator of temporal changes in water quality. For land-use, given that the variables were only available at four-time steps over our study period, we estimated temporal changes as the difference in land cover between the last and first year of the time-series (2012 and 1990, respectively), following Julian et al (2017). Further, we synthesised temporal changes in land cover and in stock unity density, individually, using the first two axes of two PCAs (Table S1). We interpreted the first two axes of each PCA as synthetic predictors of changes in land cover (Land cover 1, 61.4% and Land cover 2, 23.9%), and changes in stock unity density (SUD 1, 44.3% and SUD 2, 35.2%; Table S1), respectively. We tested for correlations among every pair of predictor variables used for analyses, including latitude, using Pearson's correlation test. Variables were not highly correlated (Pearson's $r < 0.75$ for all variables; Fig. S1).

4.3.4 Species traits and trait space

We used the New Zealand freshwater macroinvertebrate trait database (https://niwa.co.nz/sites/niwa.co.nz/files/nz_trait_database_v19_2_18.xlsx) to create a multidimensional trait space of macroinvertebrate taxa ($n=111$). This database contains a total of 16 traits describing the morphology, life history, mobility and resource acquisition methods of macroinvertebrates (Table S2), divided into 59 modalities and fuzzy coded from 0 to 3 following Chevenet et al. (1994); see also Dolédec et al., (2006, 2011). The combinations of these traits relate to key ecological and functional processes, such as resistance and resilience to disturbances, recovery dynamics, secondary production, and trophic specialisation (Table S2). We built our trait space of macroinvertebrate taxa by ordinating the species-by-trait matrix in a multidimensional space (Mouillot et al. 2013, Mouillot et al. 2021), using fuzzy correspondence analysis (FCA; the *dudi.fca* function from ade4 package in R; Chevenet et al. (1994)).

4.3.5 Species richness, trait diversity and redundancy

Taxonomic diversity was measured using taxon richness (SR; hereafter referred to as species richness), measured as the sum of taxa occurrences present in a community. Trait diversity was measured using two kernel based multidimensional probabilistic hypervolume indices: trait richness (FRic) and 1 - trait originality as a measure of trait redundancy (FRed; Mammola & Cardoso (2020)). Trait originality has been shown to be an indicator of trait redundancy within trait space (Mouillot et al. 2013). We created a functional probabilistic hyperspace using the first five axes of our trait space (using Gaussian kernel density estimation; the *kernel_build* function with default settings in the BAT package v. 2.7.0 (Cardoso et al. 2015)). The first five axes were chosen because five is the maximum number of dimensions recommended to be used by Mammola and Cardoso (2020). Because we wanted to link changes in functional diversity to changes in SR, kernels were not weighted by species abundances. We measured trait richness of the trait space as the total volume of the functional hyperspace (using the *kernel_alpha* function with default settings in BAT) and trait originality of each observation as the average distance between each observation to a sample of stochastic points within the boundaries of the hypervolume (using the *kernel_originality* function with default settings; Mammola and Cardoso (2020)).

4.3.6 Species niche breadth and position

We measured changes in the realised niche breadth and niche position of each taxon in the database and for each year using Within Outlying Mean Indexes (WOMI) calculations (Karasiewicz et al. 2017). This method uses the relationships between species abundances (a site-by-species matrix) and environmental variables to produce indices describing species niches, including: "OMI" or the niche position of a species and "tolerance" or the niche breadth of a species (Dolédec et al. 2000). The OMI metric measures the distance of each species to the average environmental conditions in the study area (i.e., niche position), whereas the tolerance metric measures the amplitude in the species

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distributions across the studied environmental gradients (i.e., niche breadth) (Dolédec et al. 2000, Karasiewicz et al. 2017). In this sense, generalist species with broad niches are expected to have a lower OMI score than species with small-sized niches. Similarly, niche breadth is expected to decrease for species occurring in marginal habitats with environmentally more restricted conditions, than non-marginal species (Dolédec et al. 2000, Heino & Grönroos 2014). We performed WOMI calculations three times individually, for three sets of environmental variables (as are described above, using the *niche* and *subniche* functions in Ade4 and the subniche package v.1.4, respectively; Karasiewicz & Karasiewicz (2021)): (1) air temperature conditions, (2) flow regimes and (3) water-quality. We tested for statistical significance of the species niches (using the *rtest* function), by comparing between the observed species position and simulated values, using 999 random permutations, under the null hypothesis that the species is indifferent to its environment. We then assessed temporal trends in niche breadth and position of each species contained in the database.

4.3.7 Statistical analyses

To test our first expectation (**E₁**), we measured temporal changes in species richness, trait richness and trait redundancy at each site using OLS, as was done for most environmental variables. Second, we tested for relationships between trends in species richness, trait richness and trait redundancy with latitude using linear-mixed effects models (the *lme* function in the *nlme* package ver. 3.1-152 (Pinheiro et al. 2017)) setting island (North Island versus South Island) as random effect. Third, we regressed temporal changes in species richness, trait richness and trait redundancy against one another to assess relationships among changes in each index with the two other indices.

To test our second expectation (**E₂**), we used ordinary least squares models to regress values of species richness, trait richness and trait redundancy at each site ($n = 64$) against latitude for each year of the time-series ($n = 26$). We used the slope of each regression model as our estimates of latitudinal

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diversity gradient and regressed these against year to assess changes in the latitudinal diversity gradient over time.

To test our third expectation (**E₃**), we assessed the total, direct and indirect effects of environmental factors in mediating biodiversity changes. We used a multilevel path analysis ('piecewise' structural equation modelling) derived from a subset of Gaussian linear mixed effects models using the *piecewiseSEM* v.2.1.2 and *nlme* v.3.1 packages in R (Lefcheck 2016, Pinheiro et al. 2017). We built a total of seven linear models, in which we included a maximum of predictor variables and included sites nested within catchments as random effect (Mouton et al. 2020). We employed the *dredge* function from the *MuMIn* v.1.46 package in R and the corrected version of Akaike Information Criterion for small samples (AIC_c ; Hurvich & Tsai (1989)) to rank each possible combination of variables with the lowest AIC_c . We kept all variables contained in models with $\Delta AIC_c < 4$. We used these final models in the piecewise structural equation model.

We tested the potential for multicollinearity in all models using the variance inflation factor (VIF; the *vif* function in the *car* package v. 3.0-12, Fox et al. (2012)), all variables had $VIF < 1.5$. We used Fisher's C test of directed separation to evaluate whether any non-hypothesized independent relationships were significant and whether including a missing path could improve the goodness-of-fit of the model (Shipley 2000). We reported marginal coefficients of determination for each linear mixed effect model included in our final piecewise SEM (Nakagawa & Schielzeth 2013). We used 100 bootstraps model effects to examine standardized path coefficients of each variable (the *bootEff* function in the *semEff* package v.0.6.1). To quantify the strength of indirect effects in our model, we estimated these by multiplying standardised path coefficients in the SEM (Bowd et al. 2021).

Finally, to test our fourth expectation (**E₄**), we primarily related changes in species trait redundancy to their taxonomy and functional traits. To do this, we related (euclidean) dissimilarity in changes in trait redundancy to taxonomic dissimilarity (using a taxonomic classification of the studied species

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compiled by Mouton et al. (2022) and Gower's distance of dissimilarity) and dissimilarity in trait space (using euclidean distances of the axis from the FCA, as was used to calculate functional diversity indices) using multiple regression on distance matrices with 999 permutations (the *MRM* function in the *ecodist* v.2.0.9 package (Goslee et al. 2020)). Second, we related changes in species trait redundancy to changes in niche breadth and niche position (for climatic conditions, flow regimes and water quality as is described above), using multiple regression models. We standardised all predictor variables (changes in niche breadth and position) to mean zero and standard deviation one and tested all combinations of the six variables as potential predictors of changes in trait redundancy. We ranked each possible model by AIC_c using MuMIn and averaged all models with $\Delta AIC_c < 2$. Finally, we used MRM again, to relate (euclidean) dissimilarity in all six indicators of changes in niche breadth and position to taxonomic dissimilarity and dissimilarity in trait space.

4.4 – Results

Environmental conditions have changed widely at our studied sites during our study period (supplementary text & Fig. S2-S5). The broadest picture of change is that air temperature has increased on average by 0.26°C per decade and precipitation decreased by 33 mm per decade on average (Fig. S2). Within-year variations in air temperature and precipitation are also now higher on average (Fig. S2), which may reflect increases in extreme weather events (e.g. heatwaves, frosts, floods and droughts) in most areas. Deforestation is also increasing over time at the expense of increasing wood production and agriculture has switched from mostly sheep farming to intensive dairy farming (Fig. S3). Consequently, river run-off per day and dissolved oxygen concentrations have mostly decreased at the studied sites, despite notable decreases in nutrient concentrations at most river sites (Fig. S4 & Fig. S5).

4.4.1 Changes in diversity and redundancy

At the sampled sites, species richness ranged from 1 to 39 within communities (mean = 18). Patterns of changes in species richness were strong across the country over the 26 year time-series (mean = + 9.6 % decade⁻¹, max = + 52.4, min = -35.3, SD = 14.8, Fig. 1 A) and negatively correlated with latitude ($R^2 = 0.42$, $F = 52.2$, $p < 0.001$): species richness decreased at northernmost sites but increased at the southernmost (i.e. poleward; Fig. 1 A). Changes in trait richness broadly showed opposite trends to changes in species richness (Fig. 1 B) but were less correlated with latitude ($R^2 = 0.15$, $F = 5.23$, $p < 0.05$). By contrast, there was no latitudinal pattern of changes in trait redundancy (Fig. 1 C; $R^2 = 0.03$, $F = 1.49$, $p = 0.22$).

Changes in species richness were negatively related with changes in trait richness ($R^2 = 0.20$, $F = 17.3$, $p < 0.001$; Fig. 1 D), and positively correlated with changes in trait redundancy ($R^2 = 0.06$, $F = 5.32$, $p = 0.02$; Fig. 1 E). Changes in trait richness were highly and negatively related with changes in trait redundancy ($R^2 = 0.75$, $F = 187.7$, $p < 0.001$; Fig. 1 F).

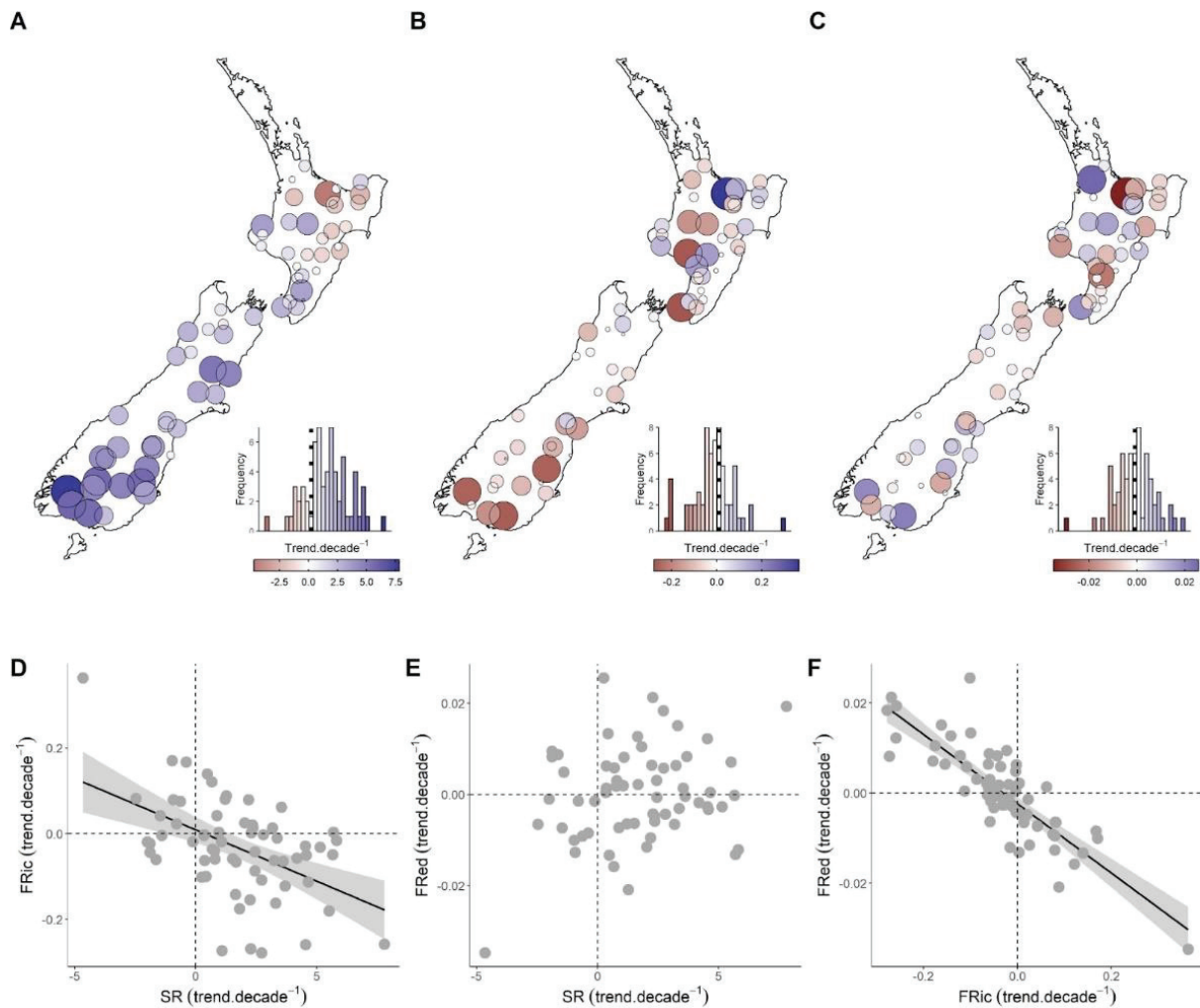


Fig. 1 Maps of temporal changes (1991-2016) in (A) species richness (SR), (B) trait richness (FRic) and (C) trait redundancy (FRed). Temporal changes (trend.decade⁻¹) are given by the slopes of the linear regression models against year, at each site. Point size is proportional to the degree of community change at each site over time and points are coloured according to the same degree of change (as is indicated by the legends). **D – F**: Relationships between (D) changes in SR and changes in FRic, (E) changes in SR and changes in FRed, (F) changes in FRic and changes in FRed. The points are shown as grey dots (n=64) and the blue polygons show the density distributions of these points. The black lines represent significant linear relationships with 50% confidence intervals.

4.4.2 Changes in the latitudinal diversity gradient

There was a strong decrease in the latitudinal species richness relationship over the 26-year period ($R^2 = 0.54$, $F = 32.97$, $df = 26$, $p < 0.001$; Fig. 2 A). The latitudinal species richness gradient was positive on average, prior to the year 2002, but became negative in 2003 onwards (Fig. 2 A). By contrast, the

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latitudinal trait richness relationship increased over the 26-year period, however, at a lower magnitude than species richness ($R^2 = 0.16$, $F = 5.69$, $df = 26$, $p = 0.02$; Fig. 2 B). Changes in the latitudinal trait redundancy relationship showed no steady trend over the 26 years ($p = 0.37$; Fig. 2 C).

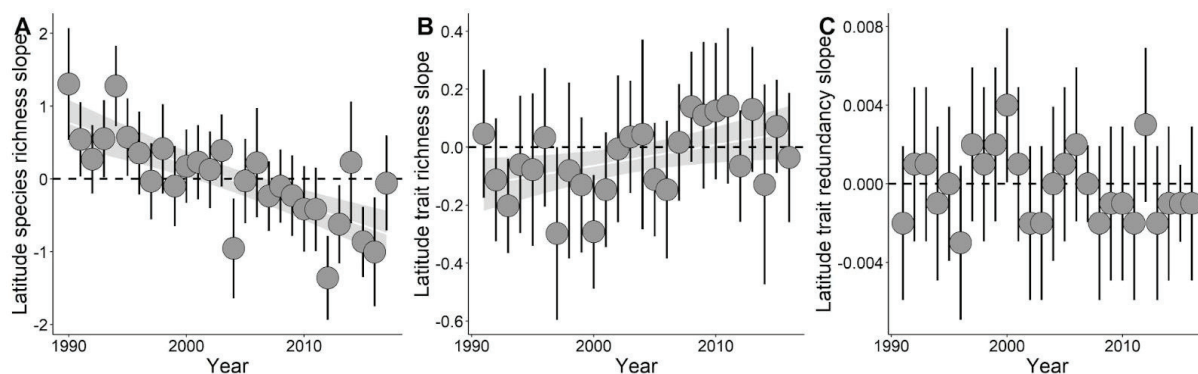


Fig. 2 A – C: Changes in the latitudinal diversity gradient for **A** - Species richness; **B** - Trait richness; **C** - Trait redundancy from 1991 to 2016. Blue dots are the slopes from linear regression models against latitude, for each year of the time series. Black vertical bars on the dots are 95% confidence intervals. The grey ribbons and white solid lines in panels A & B are significant linear regression models (see text for results). The horizontal dashed lines delimit the zero mark. A value above this line indicates the index is increasing northward, and vice versa.

4.4.3 Drivers of observed changes

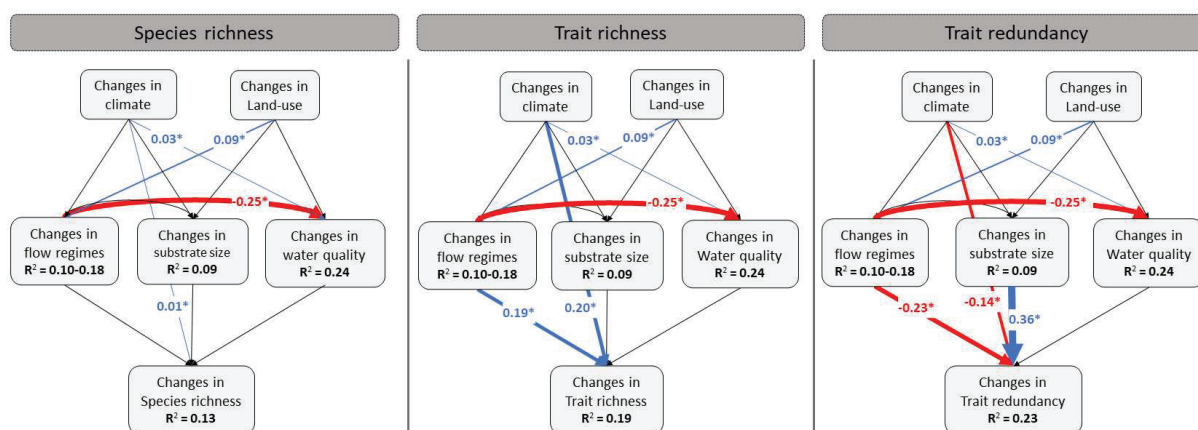


Fig. 3 Path diagrams showing results from Piecewise Structural Equation Models used to quantify direct and indirect relationships between climate and land-use change with changes in flow regimes, substrate size and water quality to determine changes in macroinvertebrate species richness, trait richness and trait redundancy in New Zealand's mainstem rivers. R^2 are marginal coefficients of determination. Blue and red arrows show significant bootstrapped (mean) standardised effect size(s). Black arrows are non-significant relationships. Changes in flow regimes have two R^2 because this includes two models (changes in flow regimes PC1 and PC2). Asterisks indicate significant relationships with $p < 0.05$.

All three final piecewise Structural Equation Models (pSEMs) had adequate model fits (Fisher's C test of direct separations: $p > 0.01$). Changes in flow regimes, substrate size and water quality were all

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significantly related to climate and land-use changes ($R^2 = 0.09 - 0.24$; Fig. 3). Specifically, there were significant direct and positive effects of changes in land-cover (PC2) and changes in stock unit densities (PC2) on changes in flow regimes (PC2). Similarly, changes in land-cover (PC1) had significant indirect and negative effects on changes in substrate size mediated through changes in flow regimes (PC1). Changes in water-quality were directly and positively driven by changes in precipitation CV, directly and negatively driven by changes in flow (PC2) and therefore indirectly and negatively driven by changes in land-cover (PC2) and by changes in stock-unit-densities (PC2).

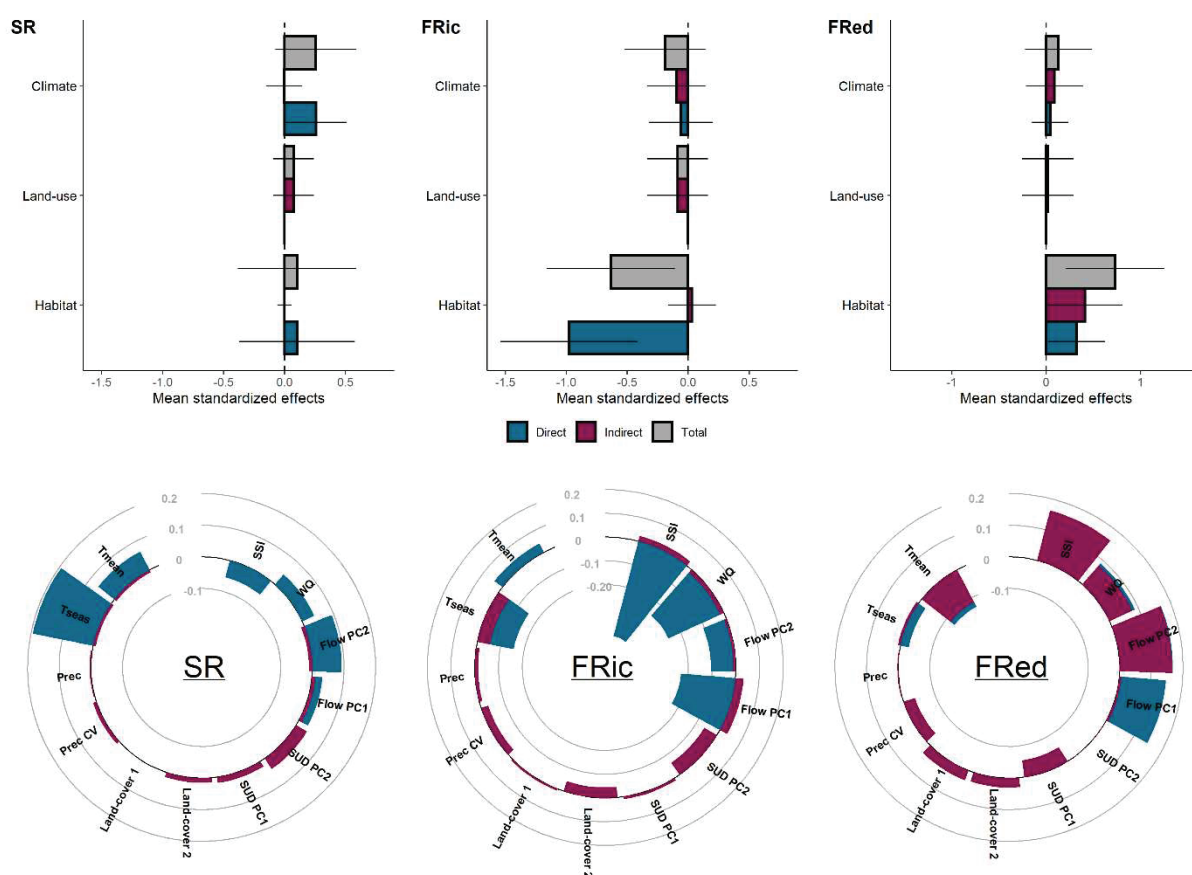


Fig. 4 Top row: Magnitude and direction of mean standardised effects (standard error) of changes in climate, land use and habitat as provided by piecewise SEM. SR - species richness, FRic - trait richness, FRed - trait redundancy. Total (dark grey), direct (blue) and indirect effects (dark pink). Bottom row: Direction and magnitude of standardized effects of all variables used in piecewise structural equation modelling, for changes in species richness (SR), trait richness (FRic) and trait redundancy (FRed). Direct effects are shown in blue and indirect effects in dark pink. Tmean: Changes in mean air temperature, Tseas: changes in air temperature seasonality; Prec: changes in precipitation; Prec CV: changes in precipitation coefficient of variation; SUD: Stock Unit density; WQ: Changes in water quality; SSI: changes in substrate size.

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pSEMs also had fair to good prediction of changes in species richness ($R^2 = 0.13$; Fig. 3; Fig. S1), trait richness ($R^2 = 0.19$; Fig. 3) and trait redundancy ($R^2 = 0.23$, Fig. 3).

Mean standardised effects of changes in precipitation CV were significant direct and negative predictors of changes in species richness (Fig. 3, Fig. 4). By contrast, mean standardised effects of changes in air temperature and in flow regimes (PC2) were significant direct and positive drivers of changes in trait richness (Fig. 3, Fig. 4). Changes in air temperature and in stock unit densities (PC2) were significant indirect and negative drivers of changes in trait richness through changes in flow regimes (PC2; Fig. 3, Fig. 4). Finally, changes in air temperature and changes in flow regimes (PC1 and PC2) were significant direct and positive drivers of changes in trait redundancy, whereas changes in substrate size were significant direct but negative drivers (Fig. 3, Fig. 4). Changes in flow regimes (PC2) was also a significant indirect and positive driver of changes in trait redundancy through changes in substrate size.

4.4.4 Changes in trait redundancy, niche breadth and position

Species realised niches were significant for 58, 33 and 56% of the species, for air temperature, flow regimes and water quality, respectively. Dissimilarity in changes in species realised niches and dissimilarity of changes in species trait redundancy were not significantly related to dissimilarity in taxonomic or trait space (MRM: $p > 0.05$ for every model). As illustrated on the ordination (Fig. 5 A & B), patterns of changes in trait redundancy were over-dispersed in trait space and unrelated to baseline trait redundancy (Fig 5. A & B).

However, changes in trait redundancy were well related to changes in species niche breadth and position ($R^2 = 0.25$, $F = 8.539$, $p < 0.001$; Fig. 5 C). A single multiple regression model was selected, which contained changes in niche position (OMI) for air temperature, flow regimes and water-quality, and changes in niche breadth (Tol) relative to water-quality (Fig. 5 C). Trait redundancy was positively associated with an increase in niche breadth relative to water quality and increases in niche position

relative to air temperature. But negatively correlated with increasing niche position in flow and in water quality (Fig. 5 C).

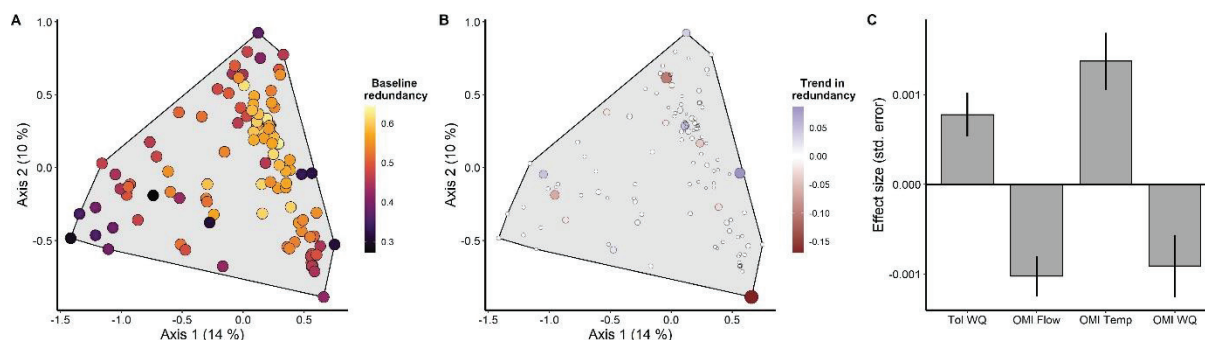


Fig. 5 A – B: First two axes of the trait space of macroinvertebrates illustrating (A) baseline trait redundancy and (B) trends in trait redundancy over time (B). C: Standardised effects (standard error) of changes in niche position and niche breadth on changes in species' trait redundancy derived from a multiple regression model.

4.5 – Discussion

4.5.1 Spatial patterns and mismatches among changes in biodiversity

Our analyses revealed a negative relationship between (1) changes in species richness and changes in functional richness and (2) between changes in functional richness and changes in functional redundancy, but (3) a positive relationship between changes in species richness and changes in trait redundancy, confirming our first expectation (E_1). These patterns possibly reveal that climate and land-use changes, by homogenising species assemblages (Mouton et al. 2020) and favouring the expansion of a majority of generalist species, as well as the decline of specialist species in these river systems (Mouton et al. 2022), may lead to increases in species richness in most locations. However, these changes reduce the hypervolume occupied by species pools in trait space, as these species are located close to each other in trait space (Sobral et al. 2016). Trait richness is therefore reduced in most locations, which can weaken the capacity of whole ecosystems to withstand growing anthropogenic disturbances and ensure ecosystem functioning (Yan et al. 2022). In addition, this process results in a greater density of functionally redundant species in similar areas of trait space

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(Pigot et al. 2016, Carmona et al. 2021). These species that colonise disturbed habitats, could further promote functional specialisation for resource exploitation under global change (Pigot et al. 2016). We also note that trait richness increased in northern locations of both islands, while species richness decreased, which may drive the spatial functional differentiation observed by Mouton et al. (2020). These increases may also be the result of the expansion of previously poorly sampled species, with ecological and biological features that allow them to thrive in highly disturbed river systems, such as a high number of reproductive cycles per year and/or long-life duration of adults (Mouton et al. 2022).

Our results also revealed that climate change induces latitudinal changes in species richness of river macroinvertebrates, likely shifting the climatic niches of species poleward, confirming our second expectation (**E₂**). The latitudinal gradient in species richness is perhaps the most well-known biogeographic pattern and has been presumed to be stable over centuries (Chaudhary et al. 2021). Here, we observe an inversion in the latitudinal species richness gradient across New Zealand mainland islands. This phenomenon resulted in declining species richness at higher latitudes, suggesting that it is already too warm for some species to persist and that further high-latitude declines in species richness are likely to happen with continued climate change. This decline is a consequence of the isolation of New Zealand from potential colonists from warmer (i.e. northern) habitats; a finding that could indicate what could happen globally at the edge of climatic gradients.

Overall, our results suggest a reduction of ecological functions but the potential for a higher insurance of specific functions in these homogenised ecological communities. More specifically, an increase in trait redundancy may result in a potential increase in trait insurance of specific portions of trait space (Yachi & Loreau 1999). It is difficult to forecast how this negative effect of homogenisation on trait richness, but positive effect on trait redundancy, will balance and affect ecosystem functioning in the long term. However, it may depend on how the traits concerned are linked to functioning and opens interesting research directions for modelling the consequences of climate change on ecosystem functioning.

4.5.2 Direct and indirect effects of climate and land-use changes

Our models showed that the switch from native forest to high producing grassland overtime with increased stock units of dairy, beef and/or deer instead of sheep in upstream river catchments correlated with decreases in winter river run-off, increased variability in winter run-off and increased nutrient concentrations in river waters. We also find that warming and increases in high producing grassland correlated reductions in mean annual river run-off and increases in its variability, which correlated to reduced river substrate size. These changes were correlated with changes in freshwater macroinvertebrate taxonomic and functional diversity in agreement with our third expectation (E₃).

Changes in species richness were mainly correlated to climate change related variables. Our findings therefore primarily indicate that climate change is a likely major driver of shifts in species richness. Similar multi-decadal, climate change impacts on freshwater macroinvertebrate taxonomic diversity have been observed in running waters of Western Europe (Floury et al. 2018). However, across the functional diversity components, changes in flow regimes had predominant direct effects, followed by changes in substrate size and changes in climate variables. This highlights the influence of flow driven habitat changes to the assembly of river communities. Flow regimes govern community assembly in running waters for several reasons, including by filtering out species with life histories that are unsuitable for the conditions, controlling species dispersal through hydrological connectivity and determining habitat heterogeneity (Tonkin et al. 2018). Accounting for the effects of land-use change on river flow regimes and riverbed conditions, therefore, appears to be essential when aiming to predict the functional diversity of river communities. Spatial and temporal mismatches between patterns of taxonomic and functional diversity have been observed for several organisms and locations globally including terrestrial birds (Devictor et al. 2010) and marine fish (Parravicini et al. 2014).

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In addition, we show that changes in species niche position and niche breadth predict their changes in trait redundancy (confirming **E4**). Specifically, trait redundancy increases as species track changing water quality regimes, with increased niche breadth and decreased niche position for water quality. Trait redundancy also increases as generalist's species sustain novel flow regimes (decreased niche position for flow) but are specialists (increased niche position) for novel air temperature conditions. This results in the ecological generalisation of communities which are composed of functionally redundant species (Stuart-Smith et al. 2021). Functional redundancy has been shown to correlate low niche position and large niche breadth in forests of southern China (Wang et al. 2023). Overall, our findings therefore start to disentangle the multifaceted effects of climate and land-use change in running water ecosystems and demonstrate differences between the responses of taxonomic and functional diversity dimensions.

4.5.3 Final remarks

Taxonomic and functional diversity in biological communities is believed to influence ecological systems through links between organismal functions and ecosystem processes (Loreau et al. 2001). Our findings provide novel insights into previously poorly understood patterns of biodiversity change. Importantly, our results suggest that by neglecting trait richness and redundancy, and their respective relationship with changes in species richness, traditional diversity approaches based on taxonomic diversity to biodiversity research may be vastly underestimating global change impacts in ecological systems (Mouillot et al. 2013).

To our knowledge, this study represents the most comprehensive empirical evidence of changes in species richness, trait richness, and redundancy in any natural ecosystem, and corroborates recent results from spatial diversity examinations (Luza et al. 2021). For example, Luza et al. (2021) found that greater species richness in human-modified habitats does not result in greater functional diversity. Yet, they also found an increase in functional redundancy because species which profit from

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human modification do not bring new functions into human-modified habitats. Therefore, they concluded that greater species richness in human-modified habitats may not yield greater function. Similarly, Crabot et al. (2021) found that functional redundancy does not compensate for biodiversity loss associated with increasing stream flow intermittence. Instead, a specific set of functional trait modalities are selected with increasing flow intermittence. While research on biodiversity time series is increasing, including with the creation of global scale databases (e.g. Dornelas et al. (2018)), our study contributes to a growing body of empirical studies on how global change can impact biodiversity and its multiple facets (Antão et al. 2020, Dornelas & Daskalova 2020, Williams et al. 2022). Increases in species richness and trait redundancy are usually seen as positive for biodiversity, however, here the resulting communities mostly had lower trait richness which instead, could weaken the ecosystem services provided by biodiversity (de Bello et al. 2010, Díaz et al. 2018).

The insurance hypothesis of biodiversity states that the maintenance of high diversity and redundancy in functional traits contributes to increased stability of biological assemblages and their associated ecological processes (Yachi & Loreau 1999, Loreau et al. 2003). However, for trait redundancy to enhance the resilience of high-richness regions, redundant species must exhibit a diversity of responses, that is, have different tolerances to environmental change (Elmqvist et al. 2003). Indeed, the loss of trait diversity despite gains in redundancy may reduce the potential for response diversity, given that only a reduced set of functions is dominant in the community. Thus, a further key challenge for biodiversity research is to understand the role of response diversity, within functionally redundant communities, especially in the context of global change, and to identify the traits that enhance the resistance or recovery of assemblages.

River ecosystems face an uncertain future, and, already, the goal of returning degraded rivers to their original state is no longer an option in many cases (Tonkin et al. 2019). Instead, the global challenge in the face of climate change is to maintain river ecosystems in a way that preserves their ecological functions, recognizing that their species composition is already changing rapidly. Across the world's

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ivers, there is an increasing prevalence of heavily impacted macroinvertebrate assemblages, where more tolerant or regenerative species are favoured (Floury et al. 2013). In many regions, the extent of shifts in ecosystem function or the prospects of returning to a normal functioning state are unknown. Ultimately, the degree of ecological change by river, depends on shifts in the presence or abundance of species and on the level of trait similarity between persistent and declining species. The critical task of understanding and preserving river ecosystem functioning likely rests on our comprehension of these phenomena, including the degree of change in functional diversity of ecological communities under global environmental change.

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Supplementary materials

Table S1 Correlations among input variables and each PCA axis (six PCAs in total) used to define synthetic predictors of changes in air temperature (Temp), air temperature standard deviation (Temp SD), precipitation (Prec), precipitation coefficient of variation (Prec CV), land-cover (NF: Natural Forest, PF: Production Forest, SG: Low producing grassland and HG: High Producing Grassland), stock unit density, flow (CV: Coefficient of variation) and water quality (CLAR: Water clarity, DO: Dissolved oxygen, NH₄-N: Ammoniacal-Nitrogen, NO₃-N: Nitrate-Nitrogen and DRP: Dissolved Reactive Phosphorus).

| Group | Variable | Principal component | |
|--------------------|--------------------|---------------------|--------|
| | | Axis 1 | Axis 2 |
| Air temperature | Temp annual | 0.97 | 0.01 |
| | Temp spring | 0.87 | 0.05 |
| | Temp summer | 0.79 | 0.45 |
| | Temp winter | 0.61 | -0.11 |
| | Temp SD | 0.04 | 0.92 |
| | Temp SD summer | -0.25 | 0.87 |
| | Temp SD spring | 0.03 | 0.77 |
| | Temp SD winter | -0.33 | 0.50 |
| Precipitation | Prec | 0.34 | -0.88 |
| | Prec spring | -0.35 | -0.53 |
| | Prec summer | 0.44 | -0.23 |
| | Prec winter | 0.18 | -0.77 |
| | Prec CV | 0.89 | 0.08 |
| | Prec CV summer | -0.71 | -0.28 |
| | Prec CV spring | -0.69 | -0.07 |
| | Prec CV winter | -0.20 | -0.19 |
| Land cover | NF | 0.42 | -0.87 |
| | PF | -0.99 | -0.03 |
| | SG | 0.90 | 0.02 |
| | HG | 0.70 | 0.45 |
| Stock unit density | Dairy | -0.67 | 0.62 |
| | Beef | 0.64 | 0.59 |
| | Sheep | 0.83 | -0.38 |
| | Deer | 0.48 | 0.73 |
| Flow | Flow mean annual | -0.93 | -0.07 |
| | Flow CV annual | 0.90 | 0.19 |
| | Flow mean Summer | -0.85 | 0.26 |
| | Flow mean Spring | -0.55 | 0.51 |
| | Flow mean Winter | -0.55 | -0.69 |
| | Flow CV Summer | 0.77 | -0.28 |
| | Flow CV Spring | 0.81 | -0.21 |
| | Flow CV Winter | 0.34 | 0.83 |
| Water-quality | CLAR | 0.64 | 0.06 |
| | DO | -0.31 | 0.82 |
| | NH ₄ -N | -0.60 | -0.48 |
| | NO ₃ -N | -0.72 | 0.38 |
| | DRP | -0.52 | -0.38 |

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Table S2 Type and name of each biological trait used to characterise functional diversity in this study. Potential ecological and functional processes associated to each trait are given aside.

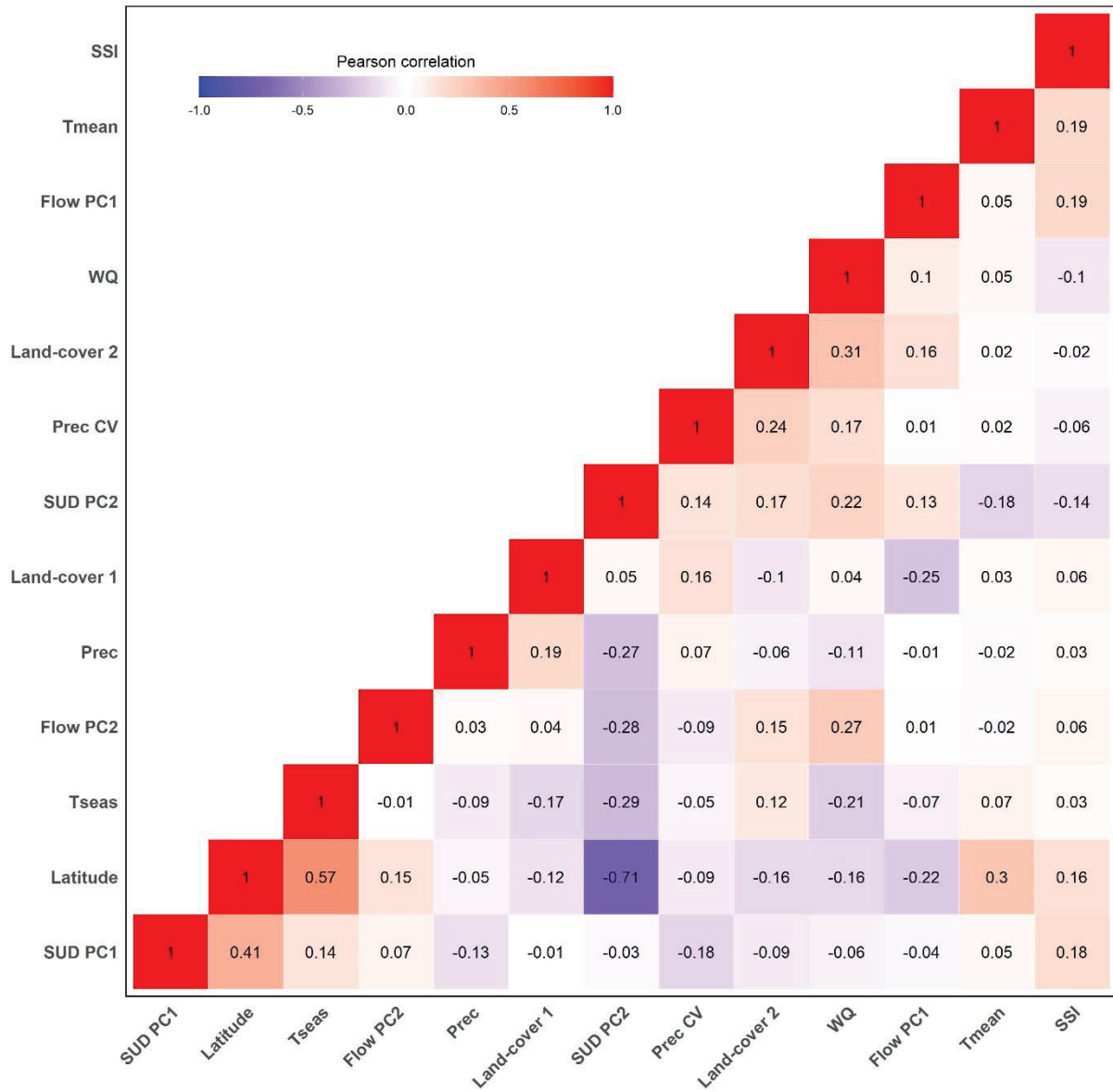
| <u>Trait type</u> | <u>Biological trait</u> | <u>Ecological processes</u> | <u>Functional processes</u> |
|----------------------|---|---|--|
| Life history | <p>Maximum potential size</p> <p>Maximum number of descendants per reproductive cycle</p> <p>Maximum number of reproductive cycles per year</p> <p>Number of reproductive cycles per individual,</p> <p>Life duration of adults</p> <p>Oviposition site</p> <p>Egg/egg mass</p> <p>Aquatic stages</p> | <p>Resistance/Resilience to disturbances (Townsend & Hildrew, 1994)</p> | <p>Secondary production (Statzner & Bêche, 2010)</p> |
| Morphology | <p>Body flexibility</p> <p>Body form</p> <p>Respiration of aquatic stages (not including eggs)</p> | <p>Resistance to disturbances (Townsend & Hildrew, 1994)</p> <p>Resistance to oxygen depletion (Statzner & Bêche, 2010)</p> | - |
| Dispersal | <p>Dissemination potential (all stages)</p> <p>Attachment to substrate of aquatic stages (excluding eggs)</p> | <p>Resistance/Resilience to disturbances (Townsend & Hildrew, 1994)</p> | <p>Bioturbation</p> <p>Nutrient cycling</p> <p>Energy transfer</p> |
| Resource acquisition | <p>Feeding habits</p> <p>Dietary preferences</p> | <p>Trophic specialization</p> <p>Complexity of trophic network</p> | <p>Resource utilisation,</p> <p>Energy transfer</p> <p>Nutrient cycling</p> <p>Leaf litter decomposition</p> <p>Primary production</p> |

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Biomass production

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Fig. S1 Pearson correlation matrix of all predictor variables used for analyses, including latitude. All predictor variables are described in the methods section of the manuscript.



Supplementary text:

Changes in climate, land-use, flow, and water-quality

At the studied sites and from 1991 to 2016, mean air temperature has increased on average by 0.26°C per decade (min = 0.13, max = 0.41; Fig. S2). Annual air temperature seasonality also increased on average across sites (mean = 0.002, min = -0.10, max = 0.09; Fig. S2). Mean daily precipitation has decreased on average by 33 mm per decade (max = 69.35, min = - 507.35; Fig. S2) and the annual precipitation coefficient of variation has increased on average across sites (mean = 5.31, min = -14.9, max = 29.2; Fig. S2).

From the year 1990 to 2012 the percentage of upstream catchment covered by native forest has decreased over the studied sites (mean = -0.15, max = 0.1, min = -1.0; Fig. S3 A). Similarly, the percentage of shrub and grassland has declined on average and at most sites (mean = -1.15, max = 0.9, min = -13.0; Fig. S3 A)). As opposed, there was an increase in the percentage of plantation forest (mean = 1.38, max = 13.4, min = -3.30; Fig. S3 A) and a balanced change in the percentage of high-producing grassland (mean = -0.16, max = 3.4, min = -4.8, Fig. S3 A).

However, stock unit densities of dairy have increased on average and at most sites (mean = 0.59, max = 2.1, min = -1.5; Fig S3 B) while those of sheep have decreased at all sites (mean = -0.89, max = -0.1, min = -2.2; Fig. S3 B). Changes in stock unit densities of beef have decreased on average and those of deer were rather balanced across sites (beef: mean = -0.22, max = 0.4, min = -1.8; Deer: mean = 0.01, max = 0.2, min = -0.2; Fig. S3 B).

Regarding changes at the scale of sites from 1991 to 2016, mean annual run-off per day has decreased on average and at 53.5 % of sites (Fig. S4). The opposite pattern was found for run-off coefficient of variation with an average increase over time and at 55% of sites.

For water quality, water clarity has increased on average and at 80% sites. Water conductivity has also increased on average and at 75% of sites (23% no change, 2% decreased; Fig. S5). Dissolved oxygen concentrations have decreased on average and at 55% of sites (2% increased and 43% no change; Fig. S5). Concentrations of ammoniacal-nitrogen have decreased on average and at 85% of sites (12% increased and 3% no change; Fig. S5). Concentrations of nitrate-nitrogen have decreased on average and at 54% of sites (45% increased, 1% no change; Fig. S5) and concentrations of dissolved reactive phosphorus have decreased on average and at 48% of sites (38% increased and 14% no change; Fig. S5).

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Fig. S2 Temporal changes (change per decade) in mean annual air temperature (Tmean), annual air temperature standard deviation (Tseas), cumulative annual precipitation (Prec) and annual precipitation coefficient of variation (Prec CV). Changes per decade were obtained from the slopes of linear regression models of each variable against year multiplied by 10.

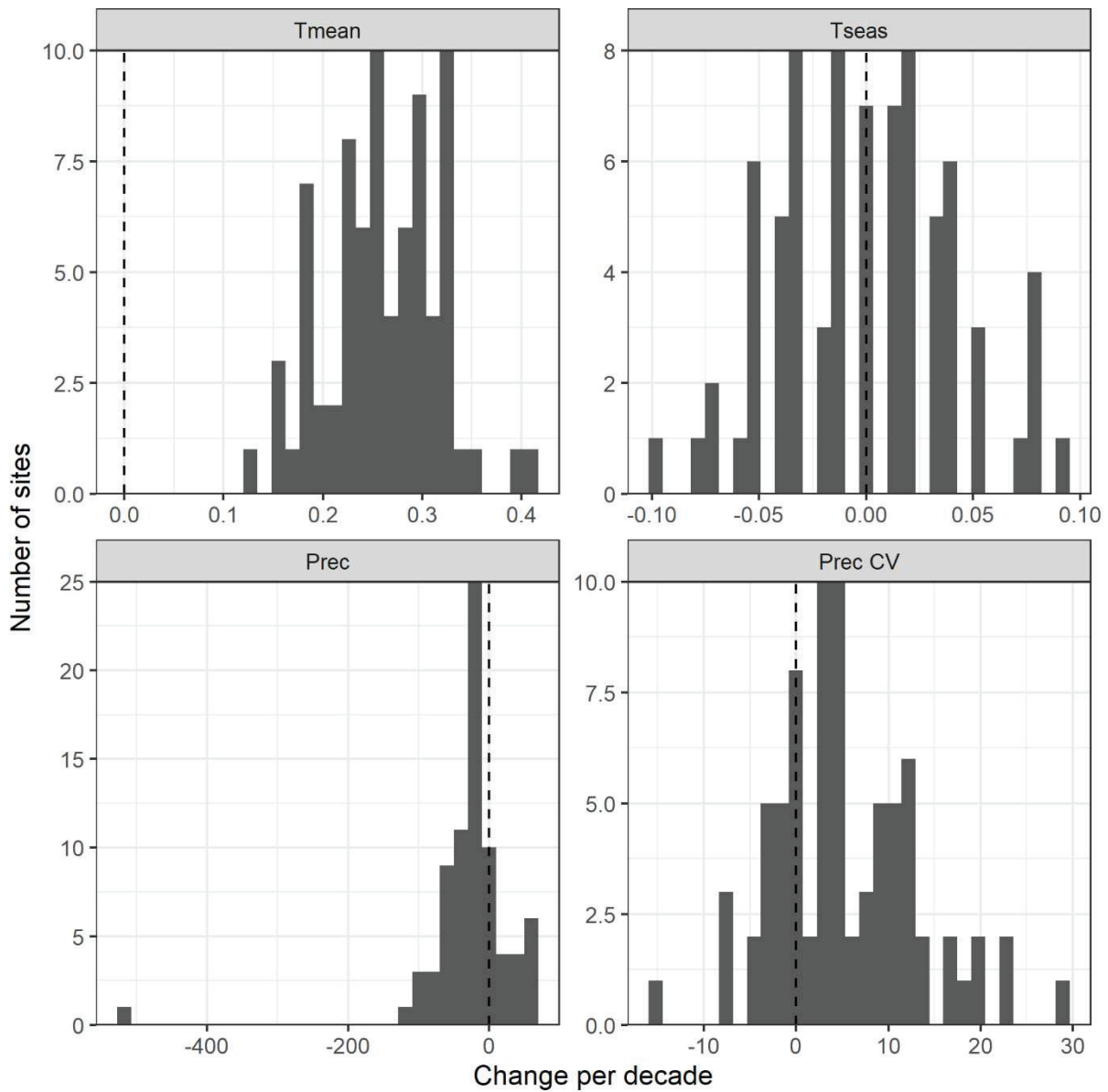
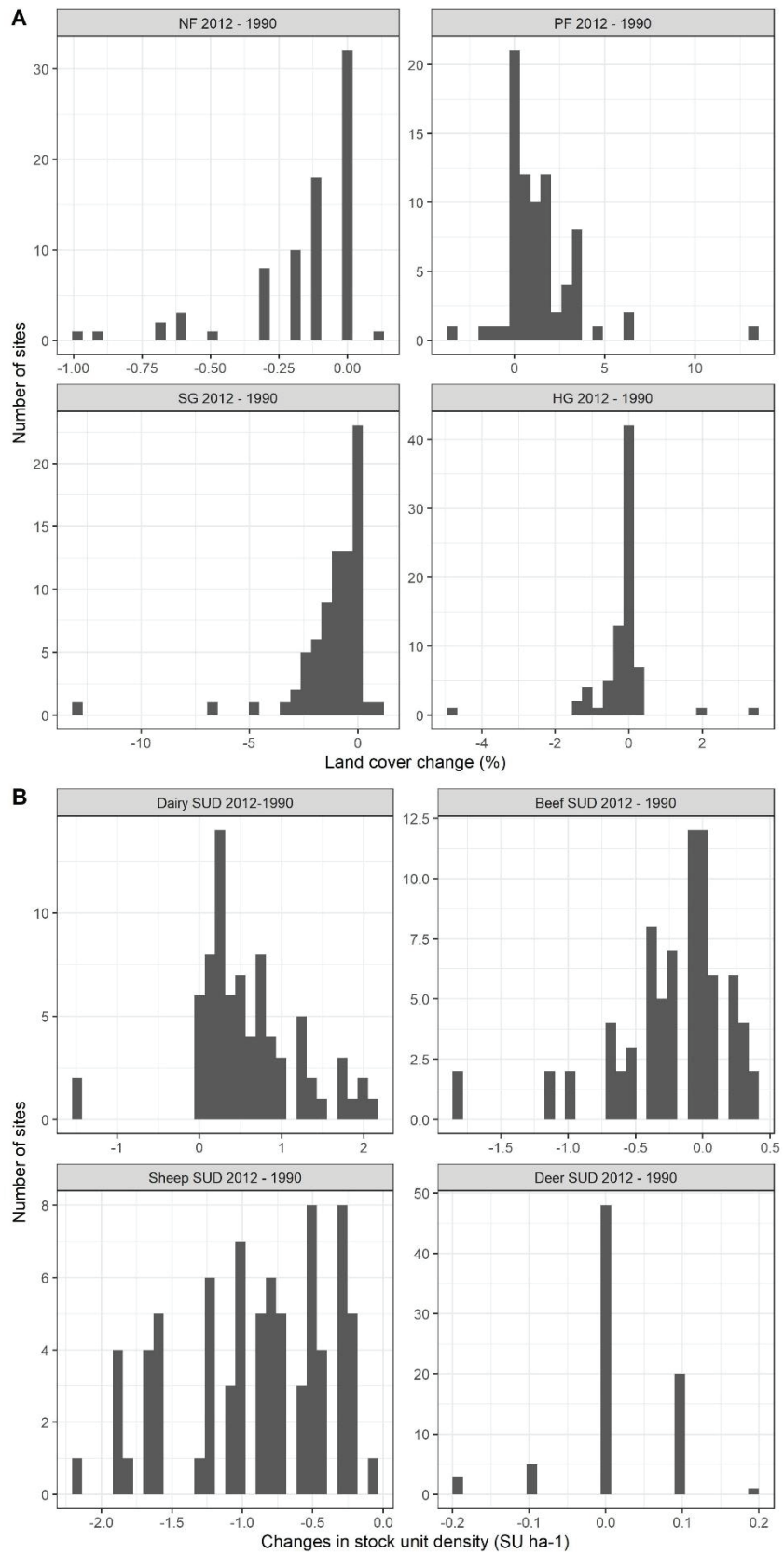


Fig S3 Changes in (A) the average percentage of land-cover and (B) in the average stock unit density (SUD) per hectare of Dairy, Beef, Sheep and Deer in the upstream catchment of each site and for the period 1990 to 2012. These data were extracted from Julian et al. (2017). NF = Non-plantation Forest; PF = Plantation Forest; SG = Scrub and Grassland; HG = High producing grassland.

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Fig. S4 Temporal changes (standardised slopes) in mean annual run-off (left panel) and mean annual run-off CV (right panel). Standardised slopes were obtained from linear regressions of log transformed run-off per second metrics (multiplied by 10^7) against year.

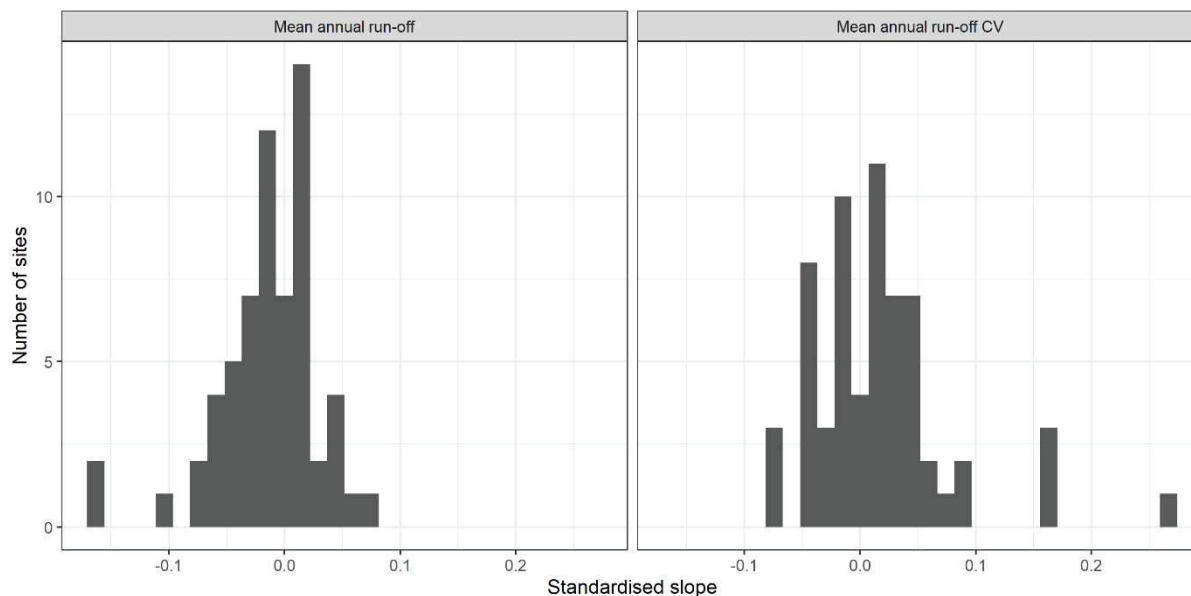
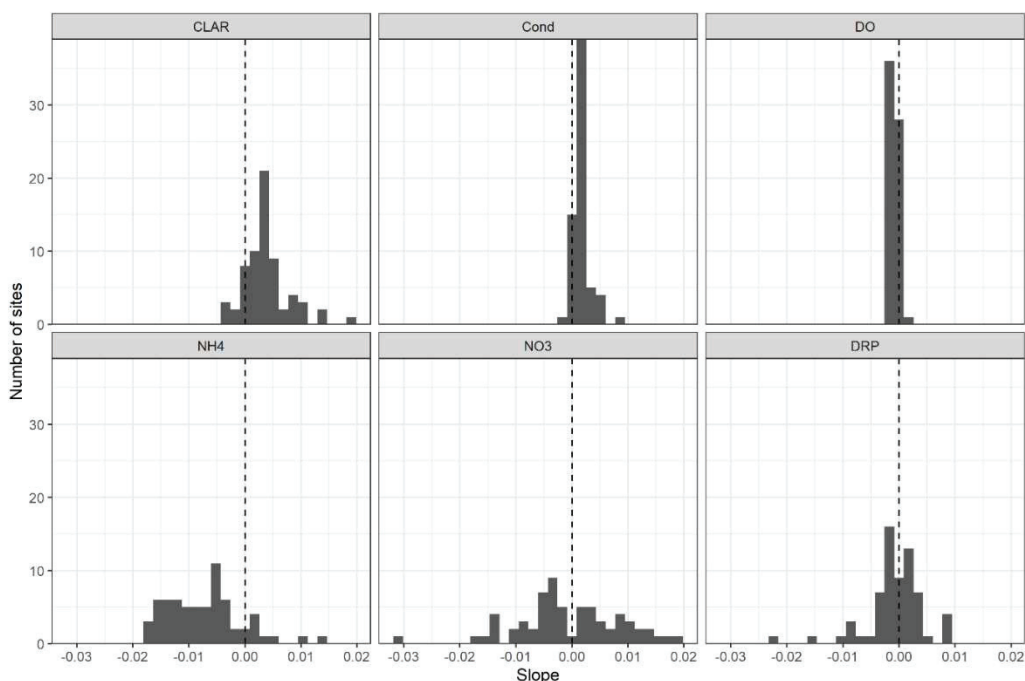


Fig. S5 Temporal changes in median annual water quality variables. Temporal changes (slopes) were obtained from linear regressions of log₁₀ transformed median annual water quality variables against year. CLAR: Water back disk clarity. Cond: Conductivity. DO: Dissolved oxygen concentration. NH₄: Ammoniacal-nitrogen concentration. NO₃: Nitrate-nitrogen concentration. DRP: Dissolved reactive phosphorus concentration.



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Table S3 Results from model selection to predict Flow PC1. Combinations of variables are ranked according to their AICc, from the lowest to the highest. (Int) = intercept. Df = degrees of freedom. logLik = log link. Delta = difference in AICc with the lowest scoring model.

| (Int) | Land-cover 1 | Land-cover 2 | Prec | Prec CV | Tmean | Tseas | SUD_PC1 | SUD_PC2 | df | logLik | AICc | delta | weight |
|-------|--------------|--------------|------|---------|-------|-------|---------|---------|------|--------|--------|-------|--------|
| 0.00 | -0.22 | | | | | | | | 5.00 | -83.09 | 177.30 | 0.00 | 0.13 |
| 0.00 | | | | | | | | | 4.00 | -84.62 | 177.90 | 0.67 | 0.09 |
| 0.00 | -0.20 | 0.12 | | | | | | | 6.00 | -82.67 | 178.90 | 1.61 | 0.06 |
| 0.00 | | 0.15 | | | | | | | 5.00 | -83.96 | 179.00 | 1.73 | 0.06 |
| 0.00 | -0.23 | | | | | -0.11 | | | 6.00 | -82.76 | 179.10 | 1.80 | 0.05 |
| 0.00 | -0.23 | | | | | | 0.11 | | 6.00 | -82.80 | 179.10 | 1.88 | 0.05 |
| 0.00 | -0.22 | | | 0.09 | | | | | 6.00 | -82.82 | 179.20 | 1.92 | 0.05 |
| 0.00 | -0.23 | | 0.06 | | | | | | 6.00 | -82.96 | 179.50 | 2.20 | 0.04 |
| 0.00 | -0.23 | | | 0.06 | | | | | 6.00 | -82.98 | 179.50 | 2.24 | 0.04 |
| 0.00 | -0.22 | | | | | | -0.01 | | 6.00 | -83.09 | 179.70 | 2.45 | 0.04 |
| 0.00 | | | | 0.08 | | | | | 5.00 | -84.41 | 179.90 | 2.63 | 0.04 |
| 0.00 | | | | | | | | 0.09 | 5.00 | -84.42 | 179.90 | 2.66 | 0.03 |
| 0.00 | | | | | | -0.08 | | | 5.00 | -84.46 | 180.00 | 2.75 | 0.03 |
| 0.00 | | | 0.03 | | | | | | 5.00 | -84.59 | 180.30 | 2.99 | 0.03 |
| 0.00 | | | | 0.03 | | | | | 5.00 | -84.59 | 180.30 | 2.99 | 0.03 |
| 0.00 | | | | | | | 0.00 | | 5.00 | -84.62 | 180.30 | 3.05 | 0.03 |
| 0.00 | -0.22 | 0.13 | | | | -0.13 | | | 7.00 | -82.24 | 180.60 | 3.33 | 0.03 |
| 0.00 | -0.21 | 0.11 | | 0.09 | | | | | 7.00 | -82.41 | 180.90 | 3.65 | 0.02 |
| 0.00 | -0.23 | | | 0.11 | | | | 0.12 | 7.00 | -82.43 | 181.00 | 3.70 | 0.02 |
| 0.00 | | 0.16 | | | | -0.10 | | | 6.00 | -83.72 | 181.00 | 3.72 | 0.02 |
| 0.00 | -0.21 | 0.11 | | | | | 0.09 | | 7.00 | -82.44 | 181.00 | 3.72 | 0.02 |
| 0.00 | -0.24 | | | 0.10 | | -0.12 | | | 7.00 | -82.44 | 181.00 | 3.72 | 0.02 |
| 0.00 | | 0.15 | | 0.08 | | | | | 6.00 | -83.74 | 181.00 | 3.77 | 0.02 |
| 0.00 | | 0.14 | | | | | 0.07 | | 6.00 | -83.82 | 181.20 | 3.92 | 0.02 |
| 0.00 | -0.21 | 0.11 | 0.06 | | | | | | 7.00 | -82.54 | 181.20 | 3.92 | 0.02 |
| 0.00 | -0.24 | | 0.09 | | | | 0.13 | | 7.00 | -82.54 | 181.20 | 3.93 | 0.02 |

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Table S4 Results from model selection to predict Flow PC2. Combinations of variables are ranked according to their AICc, from the lowest to the highest. (Int) = intercept. Df = degrees of freedom. logLik = log link. Delta = difference in AICc with the lowest scoring model.

| (Int) | Land-cover 1 | Land-cover 2 | Prec | Prec CV | Tmean | Tseas | SUD.PC1 | SUD.PC2 | df | logLik | AICc | delta | weight |
|-------|--------------|--------------|----------|----------|----------|---------|---------|---------|----|---------|-------|-------|--------|
| 0 | | 0.2053 | | | | | | -0.315 | 6 | -82.16 | 177.9 | 0 | 0.137 |
| 0 | | | | | | | | -0.2807 | 5 | -83.548 | 178.2 | 0.31 | 0.117 |
| 0 | | 0.2298 | | | | -0.143 | | -0.3607 | 7 | -81.525 | 179.2 | 1.29 | 0.072 |
| 0 | | 0.2279 | | -0.1028 | | | | -0.3045 | 7 | -81.817 | 179.7 | 1.87 | 0.054 |
| 0 | | 0.2098 | | -0.08733 | | | | -0.3316 | 7 | -81.904 | 179.9 | 2.05 | 0.049 |
| 0 | | 0.2123 | | | | | 0.07994 | -0.3141 | 7 | -81.94 | 180 | 2.12 | 0.048 |
| 0 | 0.07904 | 0.2142 | | | | | | -0.3207 | 7 | -81.946 | 180 | 2.13 | 0.047 |
| 0 | | | | | | -0.1013 | | -0.3102 | 6 | -83.236 | 180 | 2.15 | 0.047 |
| 0 | | | | | -0.07653 | | | -0.2945 | 6 | -83.336 | 180.3 | 2.4 | 0.041 |
| 0 | | 0.2048 | -0.04251 | | | | | -0.3265 | 7 | -82.102 | 180.3 | 2.44 | 0.04 |
| 0 | | | | | | | 0.06199 | -0.2791 | 6 | -83.421 | 180.4 | 2.52 | 0.039 |
| 0 | 0.05556 | | | | | | | -0.2836 | 6 | -83.446 | 180.4 | 2.57 | 0.038 |
| 0 | | | | -0.05313 | | | | -0.2733 | 6 | -83.457 | 180.5 | 2.59 | 0.038 |
| 0 | | | -0.04533 | | | | | -0.2931 | 6 | -83.485 | 180.5 | 2.65 | 0.036 |
| 0 | | | | | | | | | 4 | -86.051 | 180.8 | 2.94 | 0.032 |
| 0 | | 0.2552 | | -0.1107 | | -0.1492 | | -0.3514 | 8 | -81.119 | 181 | 3.13 | 0.029 |
| 0 | | 0.2418 | | | | -0.1604 | 0.1039 | -0.3651 | 8 | -81.154 | 181.1 | 3.2 | 0.028 |
| 0 | | 0.234 | | | -0.08558 | -0.1419 | | -0.3766 | 8 | -81.275 | 181.3 | 3.44 | 0.025 |
| 0 | | 0.2312 | -0.0714 | | | -0.1567 | | -0.3845 | 8 | -81.364 | 181.5 | 3.62 | 0.022 |
| 0 | 0.06006 | 0.2349 | | | | -0.1335 | | -0.362 | 8 | -81.402 | 181.6 | 3.7 | 0.022 |
| 0 | 0.1008 | 0.2434 | | -0.1218 | | | | -0.3098 | 8 | -81.476 | 181.7 | 3.85 | 0.02 |
| 0 | | 0.1527 | | | | | | | 5 | -85.331 | 181.8 | 3.88 | 0.02 |

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Table S5 Results from model selection to predict changes in water quality. Combinations of variables are ranked according to their AICc, from the lowest to the highest. (Int) = intercept. Df = degrees of freedom. logLik = log link. Delta = difference in AICc with the lowest scoring model.

| (Int) | Land-cover 1 | Land-cover 2 | Prec | Prec CV | Tmean | Tseas | SUD PCI | SUD PC2 | df | logLik | AICc | delta | weight |
|-------|--------------|--------------|----------|---------|---------|---------|----------|---------|----|---------|-------|-------|--------|
| 0 | | 0.3161 | | | | | | | 5 | -80.119 | 171.3 | 0 | 0.19 |
| 0 | | 0.3337 | | | | -0.2041 | | | 6 | -79.092 | 171.7 | 0.41 | 0.154 |
| 0 | | 0.3156 | | | 0.07743 | | | | 6 | -79.903 | 173.4 | 2.03 | 0.069 |
| 0 | | 0.321 | | | | | -0.0858 | | 6 | -79.91 | 173.4 | 2.05 | 0.068 |
| 0 | | 0.3104 | | | | | | 0.08429 | 6 | -79.943 | 173.4 | 2.11 | 0.066 |
| 0 | | 0.3113 | | 0.04078 | | | | | 6 | -80.068 | 173.7 | 2.36 | 0.058 |
| 0 | 0.02731 | 0.3211 | | | | | | | 6 | -80.091 | 173.7 | 2.41 | 0.057 |
| 0 | | 0.3334 | | | 0.08534 | -0.2095 | | | 7 | -78.823 | 173.8 | 2.43 | 0.056 |
| 0 | | 0.316 | 0.005556 | | | | | | 6 | -80.118 | 173.8 | 2.46 | 0.055 |
| 0 | | 0.3349 | | | | -0.1959 | -0.06089 | | 7 | -78.984 | 174.1 | 2.75 | 0.048 |
| 0 | | 0.3276 | | 0.04663 | | -0.2045 | | | 7 | -79.023 | 174.2 | 2.83 | 0.046 |
| 0 | | 0.3293 | | | | -0.1934 | | 0.04913 | 7 | -79.029 | 174.2 | 2.84 | 0.046 |
| 0 | | 0.3342 | -0.01926 | | | -0.2068 | | | 7 | -79.079 | 174.3 | 2.94 | 0.044 |
| 0 | 0.01023 | 0.3353 | | | | -0.2028 | | | 7 | -79.088 | 174.3 | 2.96 | 0.043 |

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Table S6 Results from model selection to predict changes in substrate size. Combinations of variables are ranked according to their AICc, from the lowest to the highest. (Int) = intercept. Df = degrees of freedom. logLik = log link. Delta = difference in AICc with the lowest scoring model.

| (Int) | Flow PCI | Flow PC2 | Land-cover 1 | Land-cover 2 | Prec | Prec CV | Tmean | Tseas | SUD PCI | SUD PC2 | df | logLik | AICc | delta | weight |
|-------|----------|----------|--------------|--------------|---------|----------|--------|----------|---------|----------|----|---------|-------|-------|--------|
| 0 | | | | | | | | | | | 4 | -84.559 | 177.8 | 0 | 0.054 |
| 0 | 0.1799 | | | | | | | | | | 5 | -83.575 | 178.2 | 0.41 | 0.044 |
| 0 | | | | | | | 0.1785 | | | | 5 | -83.592 | 178.3 | 0.44 | 0.043 |
| 0 | | | | | | | | | 0.1695 | | 5 | -83.734 | 178.6 | 0.73 | 0.038 |
| 0 | 0.1863 | | | | | | | | 0.1756 | | 6 | -82.652 | 178.9 | 1.03 | 0.032 |
| 0 | 0.1711 | | | | | | 0.1696 | | | | 6 | -82.677 | 178.9 | 1.08 | 0.032 |
| 0 | | | | | | | 0.1715 | | 0.1609 | | 6 | -82.819 | 179.2 | 1.36 | 0.027 |
| 0 | | | | | | | | | | -0.1259 | 5 | -84.119 | 179.3 | 1.5 | 0.026 |
| 0 | 0.1978 | | | | | | | | | -0.1503 | 6 | -82.928 | 179.4 | 1.58 | 0.025 |
| 0 | 0.1786 | | | | | | 0.1629 | | 0.1681 | | 7 | -81.799 | 179.7 | 1.88 | 0.021 |
| 0 | | | 0.05684 | | | | | | | | 5 | -84.46 | 180 | 2.18 | 0.018 |
| 0 | 0.2054 | | | | | | | | 0.1761 | -0.1512 | 7 | -81.963 | 180 | 2.21 | 0.018 |
| 0 | 0.2053 | | 0.1054 | | | | | | | | 6 | -83.243 | 180 | 2.21 | 0.018 |
| 0 | | | | | | | | | 0.1693 | -0.1259 | 6 | -83.276 | 180.1 | 2.28 | 0.017 |
| 0 | | 0.03967 | | | | | | | | | 5 | -84.51 | 180.1 | 2.28 | 0.017 |
| 0 | | | | | | -0.0383 | | | | | 5 | -84.518 | 180.1 | 2.29 | 0.017 |
| 0 | | | | | 0.02884 | | | | | | 5 | -84.532 | 180.2 | 2.32 | 0.017 |
| 0 | | | | -0.009237 | | | | | | | 5 | -84.556 | 180.2 | 2.37 | 0.017 |
| 0 | | | | | | | | 0.006629 | | | 5 | -84.558 | 180.2 | 2.37 | 0.017 |
| 0 | | | | | | | 0.1627 | | | -0.09713 | 6 | -83.327 | 180.2 | 2.38 | 0.016 |
| 0 | | | 0.04959 | | | | 0.1765 | | | | 6 | -83.515 | 180.6 | 2.75 | 0.014 |
| 0 | 0.1813 | | | | | -0.04508 | | | | | 6 | -83.515 | 180.6 | 2.75 | 0.014 |
| 0 | 0.1874 | | | | | | 0.1492 | | | -0.1232 | 7 | -82.239 | 180.6 | 2.76 | 0.014 |
| 0 | | 0.04755 | | | | | 0.1805 | | | | 6 | -83.521 | 180.6 | 2.77 | 0.014 |

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Table S7 Results from model selection to predict changes in species richness. Combinations of variables are ranked according to their AICc, from the lowest to the highest. (Int) = intercept. Df = degrees of freedom. logLik = log link. Delta = difference in AICc with the lowest scoring model.

| (Int) | Flow PC1 | Flow PC2 | Tmean | Tseas | SSI | WQ | df | logLik | AICc | delta | weight |
|-------|----------|----------|----------|---------|----------|---------|----|--------|-------|-------|--------|
| 0 | | | | | | | 4 | 17.641 | -26.6 | 0 | 0.166 |
| 0 | | | | -0.1935 | | | 5 | 18.602 | -26.1 | 0.45 | 0.133 |
| 0 | | -0.07174 | | | | | 5 | 18.016 | -24.9 | 1.63 | 0.074 |
| 0 | | -0.08446 | | -0.2064 | | | 6 | 19.116 | -24.7 | 1.89 | 0.065 |
| 0 | | | -0.06004 | | | | 5 | 17.835 | -24.6 | 1.99 | 0.062 |
| 0 | | | | | -0.04924 | | 5 | 17.789 | -24.5 | 2.08 | 0.059 |
| 0 | -0.04574 | | | | | | 5 | 17.762 | -24.4 | 2.13 | 0.057 |
| 0 | | | | | | 0.02843 | 5 | 17.684 | -24.3 | 2.29 | 0.053 |
| 0 | | | | -0.2039 | -0.06656 | | 6 | 18.871 | -24.2 | 2.38 | 0.051 |
| 0 | | | -0.0682 | -0.1975 | | | 6 | 18.85 | -24.1 | 2.42 | 0.05 |
| 0 | -0.04658 | | | -0.1936 | | | 6 | 18.728 | -23.9 | 2.67 | 0.044 |
| 0 | | | | -0.1914 | | 0.01319 | 6 | 18.611 | -23.7 | 2.9 | 0.039 |
| 0 | | -0.07432 | -0.06321 | | | | 6 | 18.233 | -22.9 | 3.66 | 0.027 |
| 0 | | -0.08871 | | | | 0.0623 | 6 | 18.203 | -22.9 | 3.72 | 0.026 |
| 0 | | -0.07398 | | | -0.05171 | | 6 | 18.182 | -22.8 | 3.76 | 0.025 |
| 0 | | -0.08772 | | -0.2171 | -0.06966 | | 7 | 19.419 | -22.7 | 3.84 | 0.024 |
| 0 | | -0.08827 | -0.07302 | -0.2111 | | | 7 | 19.401 | -22.7 | 3.88 | 0.024 |
| 0 | -0.03662 | -0.06775 | | | | | 6 | 18.093 | -22.6 | 3.94 | 0.023 |

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Table S8 Results from model selection to predict changes in trait richness. Combinations of variables are ranked according to their AICc, from the lowest to the highest. (Int) = intercept. Df = degrees of freedom. logLik = log link. Delta = difference in AICc with the lowest scoring model.

| (Int) | Flow PC1 | Flow PC2 | SR | Tmean | Tseas | SSI | WQ | df | logLik | AICc | delta | weight |
|-------|----------|----------|---------|---------|----------|---------|----------|----|---------|--------|-------|--------|
| 0 | | 0.2204 | -0.5074 | | | -0.1869 | | 7 | 200.587 | -385.1 | 0 | 0.153 |
| 0 | | 0.2137 | -0.4752 | | | | | 6 | 199.071 | -384.6 | 0.47 | 0.12 |
| 0 | | 0.2298 | -0.4763 | 0.1384 | | -0.2083 | | 8 | 201.404 | -384 | 1.02 | 0.092 |
| 0 | | | -0.5399 | | | -0.1851 | | 6 | 198.493 | -383.4 | 1.63 | 0.068 |
| 0 | | | -0.5087 | | | | | 5 | 197.18 | -383.3 | 1.79 | 0.062 |
| 0 | 0.09274 | 0.2155 | -0.5188 | | | -0.2115 | | 8 | 200.921 | -383.1 | 1.99 | 0.057 |
| 0 | | 0.2203 | -0.4487 | 0.1052 | | | | 7 | 199.529 | -382.9 | 2.12 | 0.053 |
| 0 | | 0.2407 | -0.5005 | | | -0.1938 | -0.06838 | 8 | 200.781 | -382.8 | 2.27 | 0.049 |
| 0 | | 0.2169 | -0.5279 | | -0.0387 | -0.189 | | 8 | 200.637 | -382.5 | 2.55 | 0.043 |
| 0 | | 0.2277 | -0.4695 | | | | -0.0477 | 7 | 199.162 | -382.2 | 2.85 | 0.037 |
| 0 | 0.04362 | 0.2127 | -0.4794 | | | | | 7 | 199.153 | -382.2 | 2.87 | 0.036 |
| 0 | | 0.2114 | -0.4884 | | -0.02538 | | | 7 | 199.091 | -382.1 | 2.99 | 0.034 |
| 0 | | | -0.5143 | 0.1215 | | -0.2 | | 7 | 199.077 | -382 | 3.02 | 0.034 |
| 0 | | 0.2556 | -0.4655 | 0.1478 | | -0.2183 | -0.08494 | 9 | 201.709 | -381.9 | 3.17 | 0.031 |
| 0 | 0.1267 | | -0.5479 | | | -0.2321 | | 7 | 198.993 | -381.9 | 3.19 | 0.031 |
| 0 | 0.07997 | 0.2284 | -0.4878 | 0.1344 | | -0.2247 | | 9 | 201.69 | -381.9 | 3.21 | 0.031 |
| 0 | | | -0.4867 | 0.09094 | | | | 6 | 197.502 | -381.4 | 3.61 | 0.025 |
| 0 | | 0.227 | -0.4925 | 0.1369 | -0.02994 | -0.2096 | | 9 | 201.435 | -381.3 | 3.72 | 0.024 |
| 0 | | | -0.5729 | | -0.06429 | -0.187 | | 7 | 198.621 | -381.1 | 3.93 | 0.021 |

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Table S9 Results from model selection to predict changes in trait redundancy. Combinations of variables are ranked according to their AICc, from the lowest to the highest. (Int) = intercept. Df = degrees of freedom. logLik = log link. Delta = difference in AICc with the lowest scoring model.

| (Int) | Flow PC1 | Flow PC2 | SR | Tmean | Tseas | SSI | WQ | df | logLik | AICc | delta | weight |
|-------|----------|----------|--------|---------|----------|--------|-----------|----|---------|--------|-------|--------|
| 0 | -0.2257 | -0.1983 | 0.2755 | | | 0.3783 | | 8 | 341.56 | -664.4 | 0 | 0.138 |
| 0 | -0.2288 | | 0.3057 | | | 0.3718 | | 7 | 340.067 | -664 | 0.33 | 0.117 |
| 0 | | -0.2017 | 0.2454 | | | 0.3301 | | 7 | 339.692 | -663.3 | 1.08 | 0.08 |
| 0 | -0.2191 | -0.2079 | 0.2434 | -0.1386 | | 0.3982 | | 9 | 342.269 | -663 | 1.34 | 0.07 |
| 0 | | | 0.2757 | | | 0.3228 | | 6 | 338.238 | -662.9 | 1.43 | 0.067 |
| 0 | -0.2223 | | 0.2784 | -0.1234 | | 0.3893 | | 8 | 340.603 | -662.4 | 1.91 | 0.053 |
| 0 | | -0.2119 | 0.2117 | -0.1495 | | 0.3531 | | 8 | 340.47 | -662.2 | 2.18 | 0.046 |
| 0 | -0.2235 | -0.2234 | 0.2681 | | | 0.3888 | 0.08491 | 9 | 341.817 | -662.1 | 2.25 | 0.045 |
| 0 | | -0.2445 | | -0.1964 | | 0.3264 | | 7 | 338.954 | -661.8 | 2.56 | 0.038 |
| 0 | | -0.2375 | | | | 0.2887 | | 6 | 337.621 | -661.7 | 2.66 | 0.036 |
| 0 | -0.1862 | -0.2452 | | -0.1931 | | 0.3614 | | 8 | 340.204 | -661.6 | 2.71 | 0.035 |
| 0 | -0.1896 | -0.2384 | | | | 0.3249 | | 7 | 338.862 | -661.6 | 2.74 | 0.035 |
| 0 | -0.2257 | -0.1981 | 0.2766 | | 0.002142 | 0.3784 | | 9 | 341.56 | -661.6 | 2.76 | 0.035 |
| 0 | | | 0.2468 | -0.1342 | | 0.3432 | | 7 | 338.837 | -661.6 | 2.79 | 0.034 |
| 0 | -0.2285 | | 0.3189 | | 0.02569 | 0.3732 | | 8 | 340.085 | -661.4 | 2.95 | 0.032 |
| 0 | -0.2309 | | 0.3049 | | | 0.3739 | 0.01912 | 8 | 340.08 | -661.4 | 2.96 | 0.031 |
| 0 | -0.2296 | -0.2384 | 0.2321 | -0.1493 | | 0.4123 | 0.101 | 10 | 342.638 | -660.9 | 3.47 | 0.024 |
| 0 | | -0.2188 | 0.2395 | | | 0.3359 | 0.05785 | 8 | 339.805 | -660.8 | 3.51 | 0.024 |
| 0 | | -0.2013 | 0.2479 | | 0.004777 | 0.3303 | | 8 | 339.692 | -660.6 | 3.74 | 0.021 |
| 0 | | | 0.2905 | | 0.02873 | 0.3244 | | 7 | 338.26 | -660.4 | 3.94 | 0.019 |
| 0 | | | 0.276 | | | 0.3222 | -0.006165 | 7 | 338.239 | -660.4 | 3.99 | 0.019 |

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Supplementary references

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Upper reaches of the Mokihinui River, West Coast, New Zealand. Photo credit: Kéoni Saint-Pée

Discussion générale

5.1 - Rappel des principaux résultats

Les deux premiers articles de cette thèse avaient pour but de quantifier les subtiles changements spatiaux et temporels de composition taxonomique et fonctionnelle, de 64 communautés de macroinvertébrés benthiques de rivières en Nouvelle-Zélande, sur la période 1991 à 2016.

L'article 1, basé sur les changements de similarité spatiale, montre que les assemblages s'homogénéisent au cours du temps, d'un point de vue taxonomique, mais se différencient d'un point de vue fonctionnel. Ces changements résultent principalement d'un remplacement d'espèces et de traits au sein des communautés, plutôt que d'un changement unidirectionnel en abondance.

L'article 2, montre un gradient latitudinal dans les gains et les pertes d'espèces au sein des communautés, le long de la Nouvelle-Zélande. Une perte d'espèce marquée au Nord des deux îles principales, et des gains plus élevés en direction du Sud. De plus, j'ai pu tester qu'un nombre plus important d'espèces accroît la taille de leurs populations et celle de leurs aires de répartition, plutôt que la diminue. J'ai également trouvé que les espèces se déplacent en moyenne de 50 kilomètres par décennie vers le Sud. Les espèces avec plusieurs cycles de reproduction par an et une longue durée de vie adulte augmentent leur taille de populations, tandis que les espèces de plus grandes tailles avec un nombre élevé de descendants par cycle de reproduction tendent à déplacer leur aire de répartition vers le Sud (les pôles). Enfin, j'ai pu montrer que le changement climatique est le premier acteur des changements de composition taxonomique tandis que la composition fonctionnelle répond d'avantage aux changements d'utilisation des terres.

L'article 3, utilise également cette base de données de biodiversité de macroinvertébrés de rivières, pour se focaliser sur la redondance fonctionnelle dans les communautés. Les résultats montrent que les gradients « latitude/richeesse taxonomique » et « latitude/richeesse fonctionnelle » s'inversent linéairement au cours du temps. La richesse taxonomique devient plus importante vers le Sud, tandis

que la richesse fonctionnelle augmente en direction du Nord. Je ne trouve, cependant, aucune relation entre la latitude et les changements temporels de redondance fonctionnelle au sein des communautés. De plus, de nombreuses espèces ont gagné en redondance de traits, ce qui s'explique par des diminutions de position de niche de chaque espèce vis-à-vis de la température de l'air, des débits et de qualité de l'eau. Tandis que les changements climatiques dominent clairement les changements de richesse taxonomique des communautés, les changements de richesse fonctionnelle, ainsi que ceux de redondance fonctionnelle, sont principalement influencés par la modification des débits et de la qualité de l'eau.

Dans leur ensemble, ces travaux contribuent à une meilleure compréhension de l'impact des changements globaux sur la biodiversité. Ils montrent une réponse rapide de la biodiversité aux changements environnementaux, dans des milieux où le climat et l'utilisation des terres n'avaient jamais changé aussi rapidement précédemment. Les résultats sont alarmants et inquiétants quant au devenir de la biodiversité dans un monde où les pressions humaines sur les écosystèmes sont de plus en plus importantes. Je détaille ci-dessous les différents apports de cette thèse à la biogéographie du changement global, la biologie de la conservation et l'écologie des communautés. J'identifie ensuite des perspectives de poursuite des recherches en ce sens, avant de rappeler la nécessité de mesures de gestion adaptées.

5.2 - Apports de cette thèse en biogéographie du changement global

La contribution de cette thèse à la littérature en biogéographie du changement global porte premièrement sur la description des patrons de changements de biodiversité le long d'un gradient latitudinal. Ces travaux sont uniques, car la totalité de l'aire de répartition de chaque espèce étudiée est comprise dans la base de données que nous avons analysée. Les patrons identifiés dans les

analyses que j'ai menées avec mes collègues peuvent donc théoriquement s'apparenter aux changements qui opèrent sur chaque continent, en fonction de l'intensité des changements environnementaux qui opèrent sur ces derniers. Par les deux premiers articles, nous renforçons la littérature empirique sur les changements de composition d'espèces et de traits dans le temps et l'espace, à partir de séries temporelles de biodiversité relativement longues et précises.

En particulier, ce travail de thèse apporte de nouveaux résultats concernant la différenciation fonctionnelle spatiale des assemblages au cours du temps. La majorité des études précédentes ont suggéré une homogénéisation taxonomique et fonctionnelle des communautés au cours du temps et dans l'Anthropocène (Clavel et al. 2011, Villéger et al. 2014, Gámez-Virués et al. 2015, Saladin et al. 2020). Or les résultats présentés ici indiquent un patron inverse. De plus, les changements climatiques apparaissent bien comme un acteur majeur de l'homogénéisation biotique dans ces milieux, car ils favorisent l'expansion et le déplacement vers les pôles des aires de répartition des espèces généralistes et tendent à réduire l'abondance ou faire disparaître les espèces spécialistes, souvent contraintes à la dispersion au sein des réseaux fluviaux uniquement. De ce fait, un gradient important de perte d'espèces vers le Nord et de gain vers le Sud est patent dans nos résultats. De tels résultats ont été observés dans la littérature, notamment celle sur la diversité beta temporelle (Magurran et al. 2019) ainsi que celle sur les changements d'aires de répartition des espèces (Parmesan et al. 1999, Steinbauer et al. 2018, Lenoir et al. 2020). Cependant, ils restent peu nombreux, relativement à l'importance de connaître la vitesse et l'intensité des changements de la biodiversité planétaire face au réchauffement climatique. Bien que non évalué directement dans les chapitres de cette thèse, les résultats obtenus ne rejoignent pas ceux de Blowes et al. (2019), qui suggèrent que les patrons de changements de richesse taxonomique et de diversité beta temporelle sont découplés dans l'espace. Dans les résultats des chapitres 2 et 3, les deux indices suivent un gradient latitudinal et présentent des patrons de changements temporels relativement similaires.

Parmi les résultats les plus frappants, l'inversion latitudinale des relations « latitude/richeesse » est un résultat unique. Ces changements sont parfaitement linéaires, et aucune étude n'avait jusqu'à présent montré de changements si nets et précis, en biogéographie du changement global. Ces patrons de tendances inversées pour la richesse taxonomique et fonctionnelle sont nouveaux et d'autant plus intéressants. De nombreux travaux restent néanmoins nécessaires dans le futur, afin d'identifier et de comprendre d'avantage les changements qui opèrent sur la biodiversité. Notons d'ailleurs qu'ils seront de fait toujours nécessaires. En effet, la biodiversité et les écosystèmes étant dynamique dans le temps et l'espace, la mesure de tels changements devra régulièrement être mise à jour.

Un premier axe à creuser, dans l'optique de confirmer les tendances temporelles de similarité spatiale identifiées dans le premier chapitre de cette thèse, serait de répéter les analyses effectuées à différentes échelles spatiales (Barton et al. 2013, Jarzyna & Jetz 2018, Sreekar et al. 2018). En effet, l'échelle spatiale à laquelle un indice de biodiversité, et notamment la diversité beta, est calculé, peut grandement affecter les résultats d'une étude et donc ses conclusions (Hewitt et al. 2010, Jarzyna & Jetz 2018). L'utilisation de différentes échelles spatiales (tel que le site, le bassin versant, l'écorégion et l'île) permettrait d'identifier si les patrons identifiés à l'échelle de la Nouvelle-Zélande sont les mêmes pour toutes les échelles spatiales inférieures. En effet, il se peut que l'échelle spatiale à laquelle nos analyses ont été effectuées influence les résultats. Une homogénéisation taxonomique et fonctionnelle des communautés pourrait avoir lieu à une échelle spatiale plus fine, par exemple, entre certains sites, ou certaines écorégions. De plus, la méthode utilisée pour mesurer l'homogénéisation biotique peut aussi grandement affecter les résultats. Par exemple, Villéger et al. (2014) conclurent que chez les poissons d'eau douce européens, la similarité fonctionnelle était 6 fois plus importante que la similarité taxonomique. La méthode utilisée dans cette étude consistait néanmoins à compter le nombre de paires de sites devenant plus ou moins similaires en composition taxonomique et fonctionnelle entre une période historique et une période contemporaine. Contrairement à mon

travail de thèse, qui dans l'article 1 utilise la variance totale des assemblages entre sites comme indicateur de diversité bêta (Legendre & De Cáceres 2013).

De plus, dans cet article, la forme des changements de composition (replacements d'espèces ou gradients unidirectionnels d'abondances) a été mesuré à l'échelle temporelle annuelle, mais son évolution spatiale n'a elle pas été évaluée. Il se peut, par exemple, que les assemblages deviennent davantage des sous-ensembles de chacun d'eux (« nestedness ») avec le temps, et que le remplacement spatiale d'espèces diminue avec le temps (Villéger et al. 2014, Jarzyna & Jetz 2018) en conséquence de l'homogénéisation taxonomique.

Par ailleurs, la diversité bêta fonctionnelle a été évaluée pour tous les traits disponibles pour ces espèces. Cependant, il se peut que les patrons de changements de composition fonctionnelle diffèrent en fonction des traits utilisés (Lefcheck et al. 2015). Chez les oiseaux et à l'échelle globale, les patrons de changement temporelle de diversité fonctionnelle varient fortement d'un groupe de traits à un autre (Jarzyna & Jetz 2018). Le choix des traits dans le calcul de la composition ou de la diversité fonctionnelle d'une communauté est en effet un facteur fondamental de son calcul (Lefcheck et al. 2015, Maire et al. 2015, Mouillot et al. 2021) et les biais dans les résultats associés à ce dernier ne sont que très rarement présentés dans les études. La méthode la plus utilisée à ce jour, consiste généralement à définir un espace fonctionnel, comme un ensemble équilibré de traits décrivant la majorité des fonctions exercés par une espèce dans son écosystème (Mouillot et al. 2013b) . De ce fait, l'espace fonctionnel décrit la niche biologique et écologique d'une espèce. A partir de cet ensemble de traits, une réduction adéquate et représentative de la dimensionnalité de l'espace est définie et un nombre approprié d'axes représentant l'espace fonctionnel est choisi. Ce choix des axes a constitué un élément clé du calcul adéquate de l'espace fonctionnel (Maire et al. 2015, Mouillot et al. 2021). Il se peut néanmoins, qu'un choix préalable de traits inclus dans le calcul de l'espace fonctionnel soit un élément fondamental à sa réponse aux gradients environnementaux et/ou variation taxonomique étudiée(s). Certaines études récentes se sont penchées notamment, sur

l'influence du nombre de traits utilisé dans le calcul de la diversité fonctionnelle (Lefcheck et al. 2015, Legras et al. 2020). De mon point de vue, un travail de développement méthodologique pourrait être fait sur le choix des traits, préalable au calcul de diversité et de composition fonctionnelle dans l'optique de déterminer des indices de vulnérabilité ou de sensibilité des organismes aux facteurs étudiés. Un tel développement méthodologique permettrait l'amélioration et la standardisation d'approches déjà expérimentés dans certain cas (e.g. Flourey et al. 2018, Kling et al. 2018).

5.3 - Apports de cette thèse en écologie des eaux douces

De manière générale, ces travaux de thèse centrés sur les macroinvertébrés benthiques de rivières néo-zélandaises sont assez novateurs puisque la majorité des connaissances dans ce domaine se concentrent sur des rivières d'Europe de l'Ouest (Flourey et al. 2013, Flourey et al. 2018, Jourdan et al. 2018) ou d'Amérique du Nord (Lawrence et al. 2010) et d'Australie (Chessman 2009, Chessman 2012) ou sur d'autres organismes, notamment sur les poissons d'eau douce (Kuczynski et al. 2018) ou sur des espèces terrestres (Brice et al. 2019). Mes résultats sont d'autant plus importants que la Nouvelle-Zélande est un point chaud de biodiversité, combinant un fort taux d'endémisme et de perte d'habitat et doit donc faire l'objet d'un contrôle permanent.

De plus, la base de données que j'ai mise en forme pour réaliser mon travail de thèse est d'excellente qualité aussi bien en termes de biodiversité que de données environnementales. Il n'existe peu de bases de séries temporelles de biodiversité qui couvrent un pas de temps aussi long avec une couverture spatiale aussi large pour un groupe taxonomique tel que les macroinvertébrés de rivières. De plus, la majorité des facteurs environnementaux pouvant être mesurés et agissant potentiellement sur la biodiversité des macroinvertébrés sont présent dans la base de données. Une variable majeure est néanmoins manquante : la température de l'eau. En effet, la température de l'eau est un facteur

crucial dans la distribution des macroinvertébrés benthiques, particulièrement dans un contexte de changements climatiques. Malheureusement, cette variable n'était mesurée qu'une fois par mois, à une heure aléatoire du jour (non mentionnée dans la base de données), et lors des échantillonnages de qualité de l'eau. La température de l'eau pouvant fortement changer au cours d'une journée dans un cours d'eau, en fonction de la météo, et d'autres facteurs environnants tel que la profondeur de l'eau, j'ai jugé la qualité de cette variable insuffisante et j'ai donc décidé de ne pas l'intégrer à mes analyses. Un dernier point, concernant les variables environnementales utilisées dans les analyses, concerne les changements de précipitations. Dans mes analyses, j'ai mesuré ces derniers à l'échelle de chaque site d'échantillonnage, ce qui ne reflète pas les changements potentiels s'étant produit dans le bassin versant amont ou la région du site en question. Cette limitation est à prendre en compte dans des travaux futurs, il serait intéressant d'améliorer la qualité de cette variable environnementale et donc de la mesurer à l'échelle du bassin versant amont ou de la région du site d'échantillonnage.

Enfin, dans mes analyses des chapitres 1 et 2, j'ai défini les variables de changements climatiques comme appartenant à l'échelle globale. Dans les cours d'eau, les variations de température de l'air et de précipitation sont communément considérées à l'échelle régionale (Allan 2004). J'ai trouvé plus intéressant de dissocier ces variables de celles décrivant la géologie des bassins versants en amont des sites d'échantillonnages et de les positionner à une échelle hiérarchique supérieure.

5.4 - Perspectives

Malgré les résultats mis en avant dans ces travaux de thèse, il est de plus en plus reconnu que les communautés écologiques ne répondent pas nécessairement de façon immédiate aux changements environnementaux qu'elles subissent. En effet, elles peuvent présenter un décalage temporel (i.e. un retard) entre les extinctions attendues étant donné le changement enduré et les extinctions effectivement observées : c'est le principe de la dette d'extinction (Tilman et al. 1994). La dette d'extinction est généralement quantifiée en nombre d'espèce qui devrait être perdue étant donné le

changement supporté (Cowlshaw 1999, Helm et al. 2006). Des études ont ensuite proposé de prendre en compte les préférences thermiques des espèces (Devictor et al. 2008, Devictor et al. 2012) ou la dynamique des déplacements d'aires de répartition des espèces dans un cadre métapopulation (Talluto et al. 2017). L'étude de la dette d'extinction semble particulièrement intéressante dans notre contexte, il serait intéressant de l'appliquer à notre cas d'étude. De plus, une approche complémentaire consisterait à relier la dette d'extinction des espèces à leurs caractéristiques fonctionnelle(s) et donc, à partir de calculs de la dette potentiel de chaque espèce, en déduire une dette fonctionnelle.

S'ajoutant à l'inertie observée dans la dynamique des communautés, les synergies entre les composantes des changements globaux et entre les changements climatiques et leurs valeurs au début de la période étudiée (la « baseline value ») sont de plus en plus documentées. En effet, les différentes composantes du changement global telles que la perte d'habitat et les changements climatiques peuvent affecter la diversité de façon individuelle mais également en agissant en synergie. Dans ce cas, l'effet d'un facteur est exacerbé par un second et les conséquences observées sont plus fortes que la somme des conséquences individuelles de chaque facteur. Dans le cas de la biodiversité, des synergies entre différents changements environnementaux ont été mis en cause à plusieurs reprises, y compris chez les macroinvertébrés d'eau douce ainsi que chez d'autres espèces (Piggott et al. 2012, Peters et al. 2019, Williams et al. 2022). Plus récemment, c'est la synergie entre le climat au début de la période étudiée et la vitesse des changements climatiques qui est mis en avant comme une approche optimale pour mesurer l'effet des changements climatiques sur la biodiversité (Antão et al. 2020). En effet, il a été démontré que plus les communautés étaient proches des pôles, plus leur biodiversité répondait rapidement aux changements climatiques (Antão et al. 2022). En prenant en compte les dettes d'extinctions et synergies potentielles entre les changements environnementaux, il est vraisemblable que les changements de biodiversité soient d'avantage documentés et explicités.

Enfin, l'idée que la diversité influence la stabilité des communautés est un concept ancien en écologie et connaît depuis un intérêt grandissant (MacArthur 1955, Margalef 1969, May 1975, Tilman 1996, Lehman & Tilman 2000). La stabilité peut être définie de différentes façons. Par exemple, la constance au cours du temps de la structure et de la composition d'une ou de plusieurs communauté(s), a été utilisée pour définir la stabilité de celles-ci. D'autres définitions ont été proposées, telles que la persistance des populations au cours du temps, l'inertie d'une communauté (i.e. sa capacité à revenir à un état initial à la suite d'une perturbation) ou encore la vitesse d'inertie d'une communauté. Un des mécanismes par lequel la diversité peut affecter la stabilité est l'hypothèse d'assurance (« the insurance hypothesis »; (Yachi & Loreau 1999, Loreau et al. 2003)). L'hypothèse d'assurance propose qu'une communauté subissant des variations de conditions environnementales de son milieu sera d'autant moins touchée qu'elle est taxonomiquement riche du fait des réponses différentielles des espèces aux fluctuations environnementales (Tilman et al. 1998, Yachi & Loreau 1999, Elmqvist et al. 2003). En effet, lorsque le nombre d'espèces est important au sein d'une communauté, les dynamiques de populations se compensent de façon globale en raison de la covariance négative entre elles. Néanmoins, dans le contexte du changement global et étant donnée les résultats de cette thèse, qui démontrent une généralisation des communautés vers des caractéristiques fonctionnelles similaires (i.e. les espèces gagnantes dans l'anthropocène), il semblerait particulièrement intéressant d'examiner la stabilité des communautés dans le temps et comment cette dernière est affectée par les variations de populations et déplacement d'aires géographiques des espèces aujourd'hui et dans le cadre de scénarios futures de changement global.

5.5 - Conserver la biodiversité dulcicole dans

l'Anthropocène

Lors de mon parcours universitaire, j'ai toujours été fortement attiré par la voie de la recherche, principalement par curiosité personnelle, mais régulièrement incertain sur l'utilité concrètes des travaux réalisés en biologie de la conservation. N'en sait-on pas déjà assez ? Ne vaudrait-il mieux pas travailler sur la sensibilisation, l'influence de politiques publiques ou simplement adopter un mode de vie correspondant à mes idéaux ? Après de nombreuses réflexions et un parcours professionnel initié dans le milieu de la recherche. J'ai moi-même décidé de croire au travail académique et de proposer ce sujet de thèse, qui découle de mon propre intérêt scientifique et de mes expériences passées. Il me semble aujourd'hui essentiel de penser l'utilité réelle de ces travaux et d'exposer en toute transparence si je pense avoir participé à quelque chose d'utile ou bien si ma thèse n'était en réalité qu'un exercice académique. Les résultats apportés par cette thèse passent nécessairement par un point de synthèse sur leur utilité dans la conservation de la biodiversité dans le contexte actuel, qu'est l'Anthropocène.

La Nouvelle-Zélande est un pays où l'écologie des eaux douces est une thématique qui comporte un nombre de scientifiques significatif en rapport avec la taille du pays et de sa population. Il y a souvent eu des écologistes d'eau douce connus en Nouvelle-Zélande, notamment Colin R Townsend, éditeur de la revue *Freshwater Biology*, qui a apporté une contribution significative à la recherche et reçu la visite de nombreux chercheurs internationaux dont plusieurs français. Malgré cela, et à ma grande stupeur, bien que la communauté scientifique soit assez active en Nouvelle-Zélande, il n'y avait jusqu'à ce jour, aucune étude empirique sur les effets des changements climatiques et des utilisations des terres sur la biodiversité dans les cours d'eau. Les travaux dans ce domaine en Nouvelle-Zélande ont été fortement axés sur les effets de l'utilisation des terres uniquement sur la biodiversité des cours d'eaux ou sur l'écologie des espèces en générale. C'est pour cela, que le plan de gestion

gouvernementale actuel (NPSFM), comporte un nombre important de mesures visant à protéger les cours d'eau des pollutions anthropiques, néanmoins aucun intérêt n'est porté sur les effets du changement climatique ou des mesures visant à les mitiger. J'espère que mon travail de thèse sera lu et utilisé par les politiques publiques pour appuyer à la gestion des cours d'eau en Nouvelle-Zélande.

Dans un premier temps, il est compréhensible qu'engager ou proposer des mesures de gestion visant directement à atténuer les effets du changement climatique sur la biodiversité des cours d'eau puisse paraître penne perdue, tant l'ampleur du phénomène paraît incontrôlable à l'échelle d'une discipline qu'est la biologie de la conservation. Néanmoins et après réflexion, il semblerait que nous faisons actuellement face à un des plus grands défis qu'a pu connaître notre humanité. Nos capacités scientifiques nous permettent de comprendre et de suivre exactement les phénomènes se produisant et leur mitigation ainsi que leur contrôle, devraient être la priorité de nos politiques environnementales et de gestion au regard de la dangerosité qu'ils représentent pour notre santé et nos sociétés humaines. D'autant plus que la majorité des mesures actuellement proposées, tel que la conservation et restauration des forêts amonts et rivulaires aux cours d'eau, ainsi que des zones humides, la préservation des sites naturelles et l'interdiction de la destruction d'habitat naturel par l'homme, sont d'autant de mesures qui bénéficieraient la gestion de l'impact des activités anthropiques dans leur ensemble (Canadell & Raupach 2008, Shin et al. 2022). Il paraîtrait donc essentiel aujourd'hui d'intégrer dans nos plans de gestions mais aussi d'aménagement urbain, de transports, d'alimentation et d'énergie, des mesures et adaptation visant à mitiger les effets des changements climatiques et la préservation de la biodiversité.

Dans un deuxième temps, l'intensité, la vitesse ainsi que la complexité à laquelle les espèces répondent actuellement aux changements environnementaux mettent en avant la nécessité de continuer à contrôler et recenser cette biodiversité qui est de plus en plus sujette aux pressions humaines. Le développement de méthodes de recensement efficace et rapide tel que les travaux portés sur l'ADN environnementale dans les milieux aquatiques et terrestres sont autant d'atouts à

notre portée aujourd'hui pour connaître d'avantage la biodiversité et perfectionner nos moyens de gestion (Bohmann et al. 2014, Balint et al. 2018). Notamment à des échelles plus fines et une résolution plus forte nous permettant d'obtenir une vision plus complète de l'état de la biodiversité.

English summary of the discussion section:

This PhD thesis had the objective of quantifying subtle changes in the taxonomic and functional spatial and temporal alpha and beta diversity of 64 river macroinvertebrate communities in New Zealand from 1991 to 2016. Several major findings were obtained from our analyses, including an increasing taxonomic homogenisation but functional differentiation of assemblages across New Zealand over time. Latitudinal patterns in gains and losses of species and greater increases in population and range size of species than decreases. We also found that species were shifting their ranges south by approximately 50 km per decade on average. Species with several reproduction cycles per year and long-life duration of adults tend to increase in population size, while species of greater size and with a higher number of descendants by reproductive cycle tend to shift their ranges towards the south (the poles). We also showed that climate change was the major driver of changes in taxonomic diversity and composition while trait diversity was more driven by changes in land-use and habitat (flow and water-quality). Finally, we show that the « latitude/species richness » gradient and “latitude/trait richness” gradient have reversed steadily over time and our study area. Overall, these findings contribute to a better understanding of the impacts of global change on biodiversity. They show a rapid response of biodiversity to environmental changes, where climate and land-use had never changed so rapidly before. Results are rather worrying regarding the future of biodiversity in a world where human pressures continue to increase over time.

The contribution of this thesis to the literature in global change biogeography is primarily focused on the description of patterns of changes in biodiversity along a latitudinal gradient. Our results are unique, given that the entire range distribution of each species is approximately present in the database. The patterns found here may therefore reflect what could happen at the edge of climatic gradients globally. We bring interesting findings, including with the increasing functional differentiation of assemblages over time. Many previous studies had suggested a taxonomic and functional homogenisation of communities over time (Clavel et al. 2011, Villéger et al. 2014, Gámez-

Virués et al. 2015, Saladin et al. 2020). In addition, we show that climate change is a major driver of biotic homogenisation in these communities, because it drives the expansion and latitudinal shifts of generalists' species ranges but tends to reduce the abundance and distributions of specialists' species. Consequently, an important gradient of losses of species towards the North and gains towards the South is appeared in our results. Such results were also observed elsewhere, including in temporal beta diversity analyses (Magurran et al. 2019) and in studies of species range shifts (Parmesan et al. 1999, Steinbauer et al. 2018, Lenoir et al. 2020), but remain scarce given the importance of knowing the speed and intensity of biodiversity changes under climate change.

Among the most striking results, the latitudinal inversion in the species richness gradient is a unique result, which had never been found elsewhere. Though many further works are needed to continue monitoring and understanding global change impacts on biodiversity. Notably, analysing and identifying whether the patterns of changes in diversity and composition observed here, are similar across spatial scales (such, as the catchment, ecoregion, and scale of islands) (Barton et al. 2013, Jarzyna & Jetz 2018, Sreekar et al. 2018). Taxonomic and functional homogenisation may appear at finer scale of analyses such as within or between a few catchments or ecoregions. The methods used to quantify changes in diversity may also affect results, for example Villéger et al. (2014) counted the pair of sites becoming similar overtime, as opposed to here, where the total variance in community structure was used. In addition, in our analyses, we measured weather temporal changes in composition where mostly due to nestedness or turn-over components of beta diversity, however, we did not measure spatial changes in these components over time. Spatial nestedness could increase over time because of homogenisation, while spatial turn-over may be decreasing (Villéger et al. 2014, Jarzyna & Jetz 2018).

Further, functional diversity was measured using the full set of traits available for these species in each of our analyses. However, patterns of functional diversity may differ when considering only a limited set of traits (Lefcheck et al. 2015). For example, for the global bird fauna, patterns of temporal

changes in functional diversity greatly vary from a group of traits to another (Jarzyna & Jetz 2018). Indeed, the choice of traits in functional diversity research is another, yet often overlooked aspect of its calculation (Lefcheck et al. 2015, Maire et al. 2015, Mouillot et al. 2021) and biases associated to its choice are rarely assessed in ecological studies. The mostly used method, consist of defining a functional space, as a full set of traits best describing ecological and functional strategies in the species pool (Mouillot et al. 2013b). From this functional space, dimensionality reduction is performed, and a few trait axes are kept as best representing the functional space. However, it is possible that the initial choice of traits is a fundamental aspect of the response of functional diversity indices to environmental gradients and/or variation in species identity. Few studies have looked at the influence of the number of functional traits (Lefcheck et al. 2015, Legras et al. 2020). From my perspective, methodological development could be undertaken on the choice of traits, prior to measuring functional diversity, for example to define indices of vulnerability or sensitivity of organisms to environmental factors as was already attempted in some cases (e.g. Flourey et al. 2018, Kling et al. 2018).

Broadly speaking, this PhD focus on New-Zealand's benthic river macroinvertebrates is rather novel as most previous studies of these organisms were undertaken in rivers of Western Europe (Flourey et al. 2013, Flourey et al. 2018, Jourdan et al. 2018), the USA (Lawrence et al. 2010) or Australia (Chessman 2009, Chessman 2012) or on other organisms such as freshwater fish (Kuczynski et al. 2018) and terrestrial species (Brice et al. 2019). New Zealand is also a biodiversity hotspot combining high rate of endemism and habitat loss and therefore must be monitored with priority. In addition, the database used throughout my PhD is of excellent quality. There exist only a few databases of such quality, that cover such a large spatial scale and time step. Nevertheless, a variable was missing, water temperature. This variable was only measured with point samples once a month, we therefore judged its quality to be insufficient for it to be included in our analyses. Another point regarding the variables used is precipitation. In my analyses, I used precipitation data from the sampled sites, which does not

reflect patterns of precipitation at the scale of the upstream catchments or regions. Considering changing patterns of precipitation in upstream catchments or regions may be a valuable addition to future work.

Despite the results from this thesis, it is increasingly recognised that biological communities do not necessarily respond immediately to environmental changes. A lag between the extinction of a species and an environmental change may occur: called the extinction debt (Tilman et al. 1994). The extinction debt is generally quantified using the number of species that should have been lost given the environmental change (Cowlshaw 1999, Helm et al. 2006). Studies have further proposed to use the thermal preferences of species (Devictor et al. 2008, Devictor et al. 2012) or the dynamics of species range shifts in a metapopulation context (Talluto et al. 2017). The study of extinction debt seems particularly interesting in our case and would be interesting to measure in future work. Further research could then extend this concept to the concept of functional debt.

Adding to the inertia observed in the dynamics of biological communities, synergies between environmental drivers (such as climate and land-use change) and with the “baseline value” of an environmental parameter, are increasingly studied. These environmental parameters may affect biological diversity individually but also acting synergistically. In this case, the effect of an environmental parameter is exacerbated by a second and the observed consequences are greater than the sum of individual effects. By considering both the extinction debts and potential synergies among environmental drivers, further research may better document changes in biodiversity.

Finally, the fact that the stability of a community influences diversity is an old concept in ecology and has been increasingly studied (MacArthur 1955, Margalef 1969, May 1975, Tilman 1996, Lehman & Tilman 2000). Stability may be defined using several measures, for example using the consistency over time of the structure and composition of communities. Other measures also exist, such as the persistence of populations through time and the inertia of a community (its capacity to return to an original state following disturbance). One of the mechanism by which diversity may affect stability is

« the insurance hypothesis » (Yachi & Loreau 1999, Loreau et al. 2003). The insurance hypothesis states that the richer a community is in species, the lower its response to environmental changes given differences in the responses of species. However, in the context of global change and given the results from this thesis, which demonstrates a generalisation of communities towards functionally similar characteristics, it would be interesting to examine changes in community stability over time and how is stability affected by variations in population sizes and species range shifts now and under future climate change scenarios.

To conclude, I understand that suggesting management measure that aim at mitigating the effects of climate change on river biodiversity may sound overwhelming for conservation biologists, given the magnitude and intensity of climate change which may seem out of control. Nonetheless, it seems that humanity is now facing its greatest challenge and that our scientific knowledge and capacity, allows us to perfectly understand and follow exactly the phenomena that are occurring. Therefore, its mitigation and control by humans should be the priority of our environmental policies. This is especially the case as most measures proposed, such as riparian and catchment forest and wetland conservation and restoration, the protection of pristine areas and ban of the destruction of natural areas, are measures that would also benefit the management of human impacts. It therefore seems essential to integrate in our management frameworks but also urban planning, transports, food industry and energy, measures and adaptations that aim to mitigate the effects of climate change and preserve biodiversity.

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Increasing climate-driven taxonomic homogenization but functional differentiation among river macroinvertebrate assemblages

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Abstract

Global change is increasing biotic homogenization globally, which modifies the functioning of ecosystems. While tendencies towards taxonomic homogenization in biological communities have been extensively studied, functional homogenization remains an understudied facet of biodiversity. Here, we tested four hypotheses related to long-term changes (1991–2016) in the taxonomic and functional arrangement of freshwater macroinvertebrate assemblages across space and possible drivers of these changes. Using data collected annually at 64 river sites in mainland New Zealand, we related temporal changes in taxonomic and functional spatial β -diversity, and the contribution of individual sites to β -diversity, to a set of global, regional, catchment and reach-scale environmental descriptors. We observed long-term, mostly climate-induced, temporal trends towards taxonomic homogenization but functional differentiation among macroinvertebrate assemblages. These changes were mainly driven by replacements of species and functional traits among assemblages, rather than nested species loss. In addition, there was no difference between the mean rate of change in the taxonomic and functional facets of β -diversity. Climatic processes governed overall population and community changes in these freshwater ecosystems, but were amplified by multiple anthropogenic, topographic and biotic drivers of environmental change, acting widely across the landscape. The functional diversification of communities could potentially provide communities with greater stability, resistance and resilience capacity to environmental change, despite ongoing taxonomic homogenization. Therefore, our study highlights a need to further understand temporal trajectories in both taxonomic and functional components of species communities, which could enable a clearer picture of how biodiversity and ecosystems will respond to future global changes.

KEYWORDS

β -diversity, biotic homogenization, climate change, freshwater macroinvertebrates, functional diversity, human disturbance

1 | INTRODUCTION

Global environmental changes are reducing biodiversity globally and altering the functioning of ecosystems through time, primarily through habitat change, pollution and degradation (Cardinale et al., 2012; Hooper et al., 2012; Lefcheck et al., 2015). These processes are altering the distribution of species and the arrangement of communities across the landscape. At the global scale, native species extirpations exceed species colonizations (Jarzyna & Jetz, 2018; Sobral et al., 2016; Urban, 2015). Consequently, observations often indicate that human-induced environmental changes homogenize biodiversity (i.e. reduces spatial β -diversity) through time (Clavel et al., 2011; Gámez-Virués et al., 2015; Iacarella et al., 2018; Magurran et al., 2015). The ecological and evolutionary consequences of this biotic homogenization include reducing overall community and ecosystem functioning (Tilman et al., 1997), stability (Sankaran & McNaughton, 1999), resilience (de Juan et al., 2013) and resistance to environmental change by narrowing the available range of species-specific responses to disturbances (sensu McKinney & Lockwood, 1999; Moullot et al., 2013; Olden, 2006; Olden et al., 2004;). Empirical biodiversity trends are however highly complex, and reports of a global biodiversity crisis are often seemingly contradictory to documented trends, including increases in β -diversity in response to anthropogenic disturbances (Gutiérrez-Cánovas et al., 2013; Hawkins et al., 2015). These latter observations imply that environmental changes may not always result in habitat simplification, and that a more general and comprehensive understanding of the factors that influence temporal changes in β -diversity is needed.

A trend towards taxonomic homogenization (i.e. an increase in the similarity of species composition among species assemblages over time) has been demonstrated for many taxonomic groups across the globe (Haslem et al., 2015; Kuczynski et al., 2018; Magurran et al., 2015). Taxonomic diversity is, however, often recognized as providing only limited insight into the impacts of disturbance on ecosystem functioning, which may be better predicted using functional trait-based estimates of biodiversity (Gagic et al., 2015; Moullot et al., 2013; Tilman et al., 1997). Increases in the similarity of functional trait composition among species assemblages over time, leading to functional homogenization, are likely to decrease the resistance and resilience capacity of communities facing disturbances (Clavel et al., 2011; de Juan et al., 2013; Olden, 2006). However, in some cases, there may be no direct relationship between changes in taxonomic and functional β -diversity among species assemblages (Sonnier et al., 2014; Villéger et al., 2014; White et al., 2018). For instance, assemblages that exhibit taxonomic homogenization can be functionally differentiated if the newly introduced species in each assemblage are functionally dissimilar to each other (Villéger et al., 2014). Analyses of changes in functional β -diversity are therefore complementary to those of changes in taxonomic β -diversity (Sonnier et al., 2014; Villéger et al., 2014).

In ecosystems, biodiversity patterns are structured by factors operating at multiple, nested spatial scales (Townsend et al., 2003). At the global scale, climate is usually considered the predominant

factor shaping biodiversity patterns, while at more local scales, factors including topography, land-use intensity and natural resource availability become increasingly important (Allan et al., 1997; Chase & Knight, 2013; Chase & Ryberg, 2004; Mykrä et al., 2007). For instance, an ecosystem might be buffered from the full magnitude of climate change by persisting in climate refugia (Hampe & Jump, 2011; Keppel et al., 2012; Roberts & Hamann, 2016). By contrast, local anthropogenic factors may interact with climate change processes to amplify their effects (Comte et al., 2016; Guo et al., 2018; Kuczynski et al., 2018). Hence, causal inferences on climate change effects in ecosystems may sometimes be difficult to distinguish from the potentially confounding effects of human-driven local disturbances (Durance & Ormerod, 2009; Flourey et al., 2017; Radinger et al., 2017). However, attempts to disentangle the relative influence of global-to local-scale environmental drivers on the spatial arrangement of communities from both taxonomic and functional standpoints are lacking. This paucity of studies is particularly evident when considering how these patterns and relationships will change in response to global environmental change (Van Looy et al., 2017).

Here, we examined changes in the taxonomic and functional spatial β -diversity of freshwater macroinvertebrate assemblages in 64 New Zealand river sites over a 25-year period. Based on the knowledge gaps identified by Olden et al. (2018), we hypothesized an increasing taxonomic and functional homogenization among freshwater macroinvertebrate assemblages (H_{1a} and H_{1b} respectively). However, we hypothesized that the relationship between changes in each site's contribution to taxonomic and functional β -diversity over time, would differ due to contrasting taxonomic and functional responses to the environment (H_2 ; Sonnier et al., 2014; Villéger et al., 2014). Finally, we hypothesized that changes in climatic conditions over time would be the primary driver of observed changes in β -diversity (H_3 ; Chase & Knight, 2013; Chase & Ryberg, 2004).

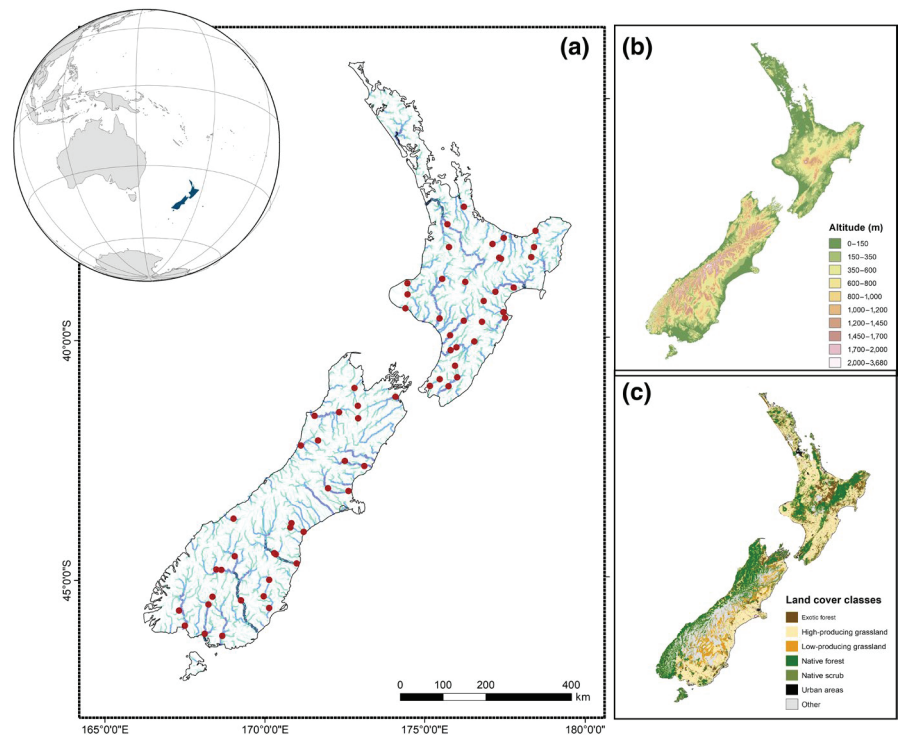
2 | METHODS

2.1 | Macroinvertebrate community samples

Macroinvertebrate community samples were collected from 64 sites, located in 35 rivers (mean Strahler stream order = 6; max = 8, min = 3) of mainland New Zealand, between latitudes 46 and 35°S (Figure 1). Sampling surveys were conducted annually from 1991 to 2016, during late austral summers (February to April). These surveys were conducted for New Zealand's National Rivers Water Quality Network (NRWQN, Smith & McBride, 1990), which was operated and maintained by the National Institute of Water and Atmospheric Research (NIWA).

Sampling occurred under baseflow conditions ($Q < Q_{\text{median}}$) no less than 4 weeks after a flood exceeding three times the median flow. Seven Surber samples (0.1 m² and 250 μ m mesh nets) were collected on all sampling occasions and macroinvertebrates were removed from the 0.1 m² area in the sampler down to a depth of c. 10 cm from as many substrate types as possible. Macroinvertebrates

FIGURE 1 Maps of mainland New Zealand showing (a) the location of the 64 sampling sites (red dots). Increases in river size (order > 3) are illustrated using increasing line width and darker blue color. The global inset map shows the location of New Zealand (blue country) in the world. (b) Altitude (m) and (c) Landcover. For a definition of the land-cover classes, see Table S1.2



were identified to the lowest practicable taxonomic level (mostly species or genus) following Quinn and Hickey (1990). The same taxonomic resolution was maintained throughout the dataset (Scarsbrook et al., 2000). Further information on site selection criteria, and sampling methodology are available in Smith and McBride (1990) and Davies-Colley et al. (2011).

Macroinvertebrate species were described by functional traits related to morphology, mobility, life-history, dispersal strategies and resource acquisition methods, extracted from the New Zealand freshwater macroinvertebrate trait database (NIWA; https://niwa.co.nz/sites/niwa.co.nz/files/nz_trait_database_v19_2_18.xlsx). Trait combinations govern species interactions through potential competition for habitat and food, or species contribution to ecosystem functioning through nutrient cycling, dispersal and trophic control (Hevia et al., 2017; Sekercioglu, 2010). We used a total of 16 traits, divided into 59 modalities and fuzzy-coded from 0 to 3 following Chevenet et al. (1994; Table S1.1; see also Dolédec et al., 2006, 2011).

2.2 | Environmental descriptors

Environmental characteristics to be used as predictors were grouped according to four different spatial scales: global, regional, catchment and reach scale (Table S1.2). Global-scale predictors used were temporal changes in air temperature and precipitation. At each site, we extracted daily values for the period 1991–2016, from 5 km² gridded layers of New Zealand, using NIWA's Virtual Climate Station Network (VCSN; <https://data.niwa.co.nz/>). We then regressed annual and seasonal (for the winter, spring and summer seasons) mean precipitation, precipitation variability (i.e. the coefficient of

variation $\times 100$), mean air temperature and air temperature variability (i.e. the standard deviation of the mean) against time and used the slopes of each linear regression as estimates of temporal change. Principal component analyses (PCA; Pearson, 1901) were applied individually to air temperature and precipitation variables to reduce the multidimensionality and to eliminate multicollinearity within groups. We scaled all variables prior to PCAs and interpreted the respective first two axes of each PCA as synthetic descriptors of (a) changes in air temperature (TMean), (b) changes in air temperature seasonality (TSeas), (c) changes in precipitation seasonality (Prec CV) and (d) changes in precipitation (Prec; Table S1.3).

Regional-scale predictors were described using four variables, reflecting landscape features that stretch beyond catchment boundaries. Altitude (m) at the sampling site, phosphorus and calcium concentrations and mean hardness (induration) in surface rocks of the upstream catchment (USPhosphorus, USCalcium and USHardness respectively). These variables were extracted for each site from the Freshwater Environments of New Zealand geodatabase, based on a 30 m Digital Elevation Model (Leathwick et al., 2010), using ArcGIS version 10.7 (Esri Inc., 2020).

For catchment-scale predictors, we used the proportion of upstream catchment covered by six land-cover types (intensive agriculture, light pastoral areas, native forest, urban areas, scrub and shrub cover and exotic forest; Table S1.2). We used static, spatial descriptors of land-cover in lieu of estimates of temporal changes in land-cover, as these were found to be major correlates of both spatial and temporal changes in the water-quality of New Zealand's freshwater systems (Julian et al., 2017; Snelder et al., 2018). We created the land cover types by aggregating fine-scale individual classes of the 75 land-cover classes from the New Zealand Land Cover database

version 4.1 (Landcare Research 2015; Table S1.2). The six land-cover metrics were then ordinated using PCA, and the first two axes retained as synthetic land-use predictors (Land-use 1 and Land-use 2 respectively; Table S1.3). Area of the upstream catchment (km^2 ; USCatchArea) and the average slope of the upstream catchment (degrees; USAvgSlope) from each river segment were also used as catchment-scale predictors.

Finally, reach-scale descriptors were defined by the slope (degrees) of the stream segment at each sampling site (SegSlope; Leathwick et al., 2010), the predicted wetted river width (metres) at the 7-day mean annual low flow (WidthMALF; Booker, 2015), the estimated proportion of riparian shading at each river segment (SegRipShade; Leathwick et al., 2010) and temporal changes (1991–2016) in median annual values (mg/m^3) of nitrate ($\text{NO}_3\text{-N}$), ammoniacal-nitrogen ($\text{NH}_4\text{-N}$), dissolved reactive phosphorus and dissolved oxygen concentrations and water clarity (metres; CLAR). Water quality variables were log₁₀-transformed prior to calculating temporal changes, which were then ordinated using PCA. The first axis was retained as a synthetic predictor of temporal changes in water quality (Table S1.3).

The final set of environmental variables consisted of 16 predictors which were not highly correlated (Pearson's $|r| < .65$; Figure S1.1; Zuur et al., 2010).

2.3 | β -diversity measures

To evaluate temporal changes in taxonomic and functional spatial β -diversity, we first $\log(x + 1)$ transformed macroinvertebrate abundances, and replaced the species by site matrix by a community-level (abundance) weighted means of functional trait values (CWM; Lavorel et al., 2008) by site matrix for functional β -diversity analyses. We then measured β -diversity as the dissimilarity among all pairs of sampled sites ($n = 64$) at each annual time step using the percentage difference index (%diff; Odum, 1950; commonly referred to as Bray–Curtis dissimilarity). The percentage difference index between observation S_j and S_k is defined as:

$$\%diff = \frac{(B+C)}{(2A+B+C)},$$

where A is the total abundance of all species found in both S_j and S_k , B is the total abundance of all species unique to S_j , and C the abundance of each species unique to S_k . To assess the total variation in composition, we first computed the total sum of squares (SS_{total}) of the dissimilarity matrix by summing the dissimilarities in the lower triangular matrix and dividing it by the number of observations N . We then computed total β -diversity (BD_{Total}) for the North and South Island individually, by dividing SS_{total} by $N - 1$ (Legendre et al., 2005; Legendre & De Cáceres, 2013).

We also measured temporal β -diversity for both islands individually using multiple-year and pairwise dissimilarity of all pairs of sampled years, by aggregating all samples across all sites ($N = 64$) for each individual year ($N = 25$). Pairwise β -diversity

metrics and multi-site β -diversity metrics (i.e. spatial β -diversity aggregated across multiple sites) have been shown to reveal different patterns (Baselga, 2010, 2013a). To test whether temporal variations in β -diversity were mainly due to compensatory changes in abundances or fluctuations in total community abundance, we partitioned total β -diversity into two components, namely abundance replacement (β_{rep}) and abundance difference components (β_{diff}) following Baselga (2013b), Legendre (2014) and Baselga (2017) as:

$$\beta_{\text{rep}} = \frac{2 \min(B, C)}{(2A+B+C)},$$

and

$$\beta_{\text{diff}} = \frac{|B-C|}{(2A+B+C)}.$$

Their contributions to total β -diversity were measured by computing the total sums of squares of each matrix and dividing them by $N - 1$.

Finally, to test the extent to which each sampled site contributed to long-term homogenization or differentiation, we calculated temporal changes in the Local Contribution to Beta Diversity (LCBD; Legendre & De Cáceres, 2013) of each community. LCBD indicates how unique an observation of macroinvertebrate composition is, by assessing its contribution to the total variation in community composition (Legendre & De Cáceres, 2013). LCBD has been found to vary considerably through time in stream ecosystems (Li et al., 2020). We measured LCBD directly from the dissimilarity matrix of all observations as the diagonal elements of the matrix containing the centred dissimilarities, divided by SS_{total} . We then assessed temporal changes in LCBD at each site using the slope of a linear regression against years. Differences in the magnitude of temporal changes between taxonomic and functional LCBDs were tested for significance using paired samples t tests.

2.4 | Drivers of observed changes

Hierarchical Generalized Additive Mixed effects Models (GAMMs) were built to relate temporal changes in taxonomic and functional LCBD to global, regional, catchment and reach-scale processes respectively. Every variable (responses and predictors) was Box-Cox transformed and later standardized to their mean, 1 unit variance. GAMMs were fitted with catchments nested within islands as random effects, using regression splines to account for potential non-linear relationships and restricted maximum likelihood to optimize the parameter estimates. For each change in LCBD, changes were primarily modelled against global climate change descriptors. We kept only the variables that maximized the coefficient of determination (adjusted- R^2) as the best model (Floury et al., 2018; Van Looy et al., 2017). The relative importance of each variable in the model was assessed following methods described in Kuhn (2012). The same step was followed in a descendant way, using successively regional,

catchment and reach-scale descriptors as predictor variables and the residuals from the previous model as a response variable. A smooth product between latitude and longitude was explored as a predictor variable using the residuals from the reach-scale models to account for spatial autocorrelation (Wood, 2017). However, residual spatial autocorrelation was not observed ($p > .05$ for every model). Statistical analyses were all performed under the R environment (version 3.6.2; R Core Team, 2020). CWMs were calculated using the *FD* package (Laliberté et al., 2014), BD_{Total} and LCBD with the *adespatial* package (Dray et al., 2017), β -diversity partitioning with the *betapart* package (Baselga et al., 2012), GAMMs using the *mgcv* package (Wood & Wood, 2015) and the relative influences of the environmental variables in the GAMMs with the *caret* package (Kuhn et al., 2020).

3 | RESULTS

3.1 | Changes in taxonomic and functional β -diversity

We observed overall tendencies towards taxonomic homogenization but functional differentiation of macroinvertebrate communities on both islands of New Zealand (Figure 2a,b). Spatial taxonomic β -diversity declined over the 25 year period in the South Island ($R^2 = .19$, $F = 11.84$, $p < .01$), but not on the North Island ($p = .407$). In contrast, functional β -diversity increased on the North Island ($R^2 = .33$, $F = 24.62$, $p < .001$) but less so on the South Island ($R^2 = .069$, $F = 3.694$, $p = .06$).

Multiple-year and pairwise temporal β -diversity measures were highly similar on both islands and mainly driven by replacements of species abundances and functional traits among communities, rather than unidirectional abundance differences (Table 1). However, abundance replacements were much higher for taxonomic β -diversity (Multiple-year values: $\beta_{rep} = 61.1\%$ on both islands; $\beta_{diff} = 11.1\%$ and 11.2% for the North and the South Island respectively; Average

pairwise dissimilarity: $\beta_{rep} = 37.2\%$ and 39.2% ; $\beta_{diff} = 20.8\%$ and 21.1% for the North and the South Island respectively; Table 1) than for functional β -diversity (Multiple-year dissimilarity: $\beta_{rep} = 20.4\%$ and 21.1% , $\beta_{diff} = 17\%$ and 16% ; Average pairwise dissimilarity: $\beta_{rep} = 12\%$ and 16.4% , $\beta_{diff} = 17.7\%$ and 20.3% , for the North and the South Island respectively; Table 1).

Finally, only 44% of the sites exhibited decreasing taxonomic LCBD, 56% showing flat trends or increasing taxonomic LCBD (Figure 3a), and 56% exhibiting decreasing functional LCBD – 44% showing flat trends or increasing functional LCBD (Figure 3b).

TABLE 1 Taxonomic and functional temporal β -diversity measured as the percentage difference index of dissimilarity ($\beta_{\%diff}$) and its decomposition into replacements of species abundances or functional traits (β_{rep}) and unidirectional abundance gradients (β_{diff}) of macroinvertebrate assemblages collected annually at 64 river sites in New Zealand from 1991 to 2016. To exclude potential spatial variations in species composition, samples were aggregated across all sampled sites ($N = 64$) for each sampled year ($N = 25$; 1991–2016) prior to analyses. Multiple-year dissimilarity corresponds to the dissimilarity after aggregating data across all years. Average pairwise dissimilarity is the average value of each pairwise comparison of sampled years. Values in the table are percentages

| Island | Biodiversity facet | $\beta_{\%diff}$ | β_{rep} | β_{diff} |
|--------------------------------|--------------------|------------------|---------------|----------------|
| Multiple-year dissimilarity | | | | |
| North | Taxonomic | 72.2 | 61.1 | 11.1 |
| | Functional | 37.9 | 20.4 | 17.5 |
| South | Taxonomic | 72.3 | 61.1 | 11.2 |
| | Functional | 37.3 | 21.1 | 16.1 |
| Average pairwise dissimilarity | | | | |
| North | Taxonomic | 58.0 | 37.2 | 20.8 |
| | Functional | 29.7 | 12.0 | 17.7 |
| South | Taxonomic | 60.4 | 39.2 | 21.2 |
| | Functional | 36.7 | 16.4 | 20.3 |

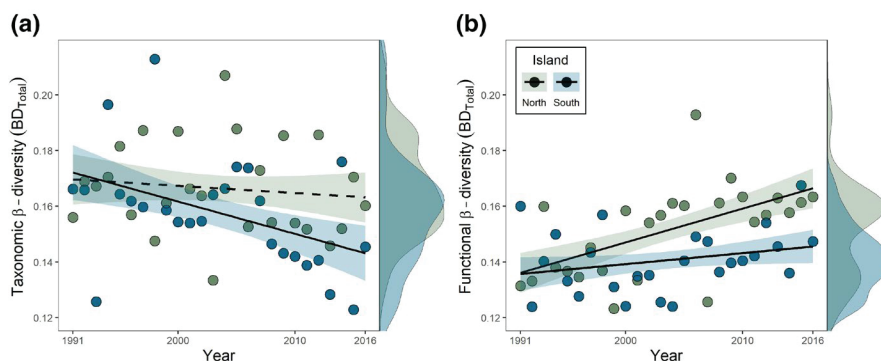


FIGURE 2 Scatter plots illustrating temporal changes in (a) taxonomic and (b) functional β -diversity (BD_{Total}) for the North and the South Island of mainland New Zealand (as indicated by the legend). Solid black lines represent significant ($p < .05$) linear regression models, whereas the black dashed line represents a nonsignificant model ($p > .05$). Density curves on the right of the figures illustrate the density distribution of the corresponding variable

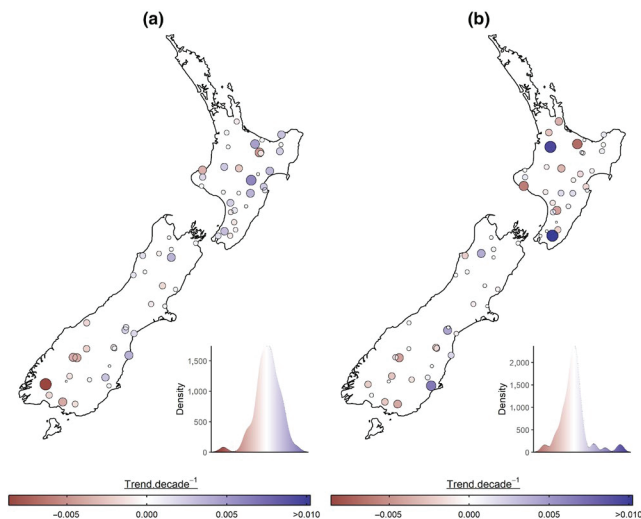


FIGURE 3 Maps of temporal changes ($\text{trend} \cdot \text{decade}^{-1}$) in (a) taxonomic and (b) functional Local Contribution to Beta Diversity (LCBD) measured using $\log(x + 1)$ macroinvertebrate abundances and the percentage difference index of dissimilarity. Point size is proportional to the degree of change. Density curves at the bottom right corner of each map illustrate the density distribution of each variable

3.2 | Relationship between changes in taxonomic and functional local contribution to β -diversity

Changes in taxonomic and functional LCBD were weakly positively correlated on the South Island ($R^2 = .11$, $p = .07$; Figure 4a), but not on the North Island ($p = .69$; Figure 4a). Over both islands, 36% of the sites experienced increasing taxonomic LCBD but decreasing functional LCBD, whereas only 11% of the sites experienced increasing functional LCBD but decreasing taxonomic LCBD. Equal amounts (26%) of the remaining sites exhibited increasing or decreasing taxonomic and functional LCBD. In addition, there were no differences between changes in taxonomic and functional LCBD for all pairs of samples and on both islands individually ($.20 < p < .76$; Figure 4b).

3.3 | Drivers of observed changes

Hierarchical GAMMs explained 38% of the temporal changes for both taxonomic and functional LCBD (Table 2). Changes in taxonomic LCBD were mostly driven by global-scale variables ($R^2 = .25$) and further influenced by catchment- ($R^2 = .07$) and reach-scale descriptors ($R^2 = .07$; Table 2). Changes in functional LCBD mostly responded to global- ($R^2 = .23$) and catchment-scale descriptors ($R^2 = .21$; Table 2).

Eleven drivers of change in taxonomic LCBD were selected in the GAMMs (Figure 5). These were: changes in precipitation seasonality (% of relative influence = 20.7), changes in air temperature (15.6%), altitude (12.1%), stream segment wetted river width at

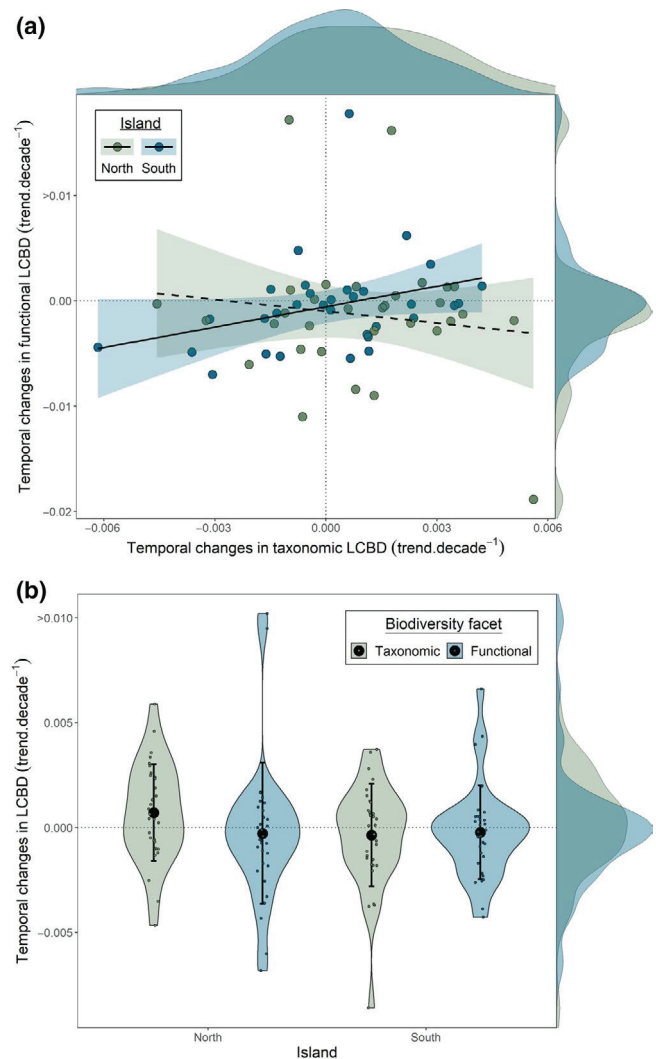


FIGURE 4 (a) Relationships between temporal changes in taxonomic and functional Local Contribution to Beta Diversity (LCBD) for both islands of mainland New Zealand. The solid black line represents a significant ($p < .05$) linear regression model. The black dashed line represents a nonsignificant model ($p > .05$). Shaded areas around the regression lines are 95% pointwise confidence intervals. (b) Violin plots illustrating differences between rates of changes in taxonomic and functional LCBD for the North and the South Island individually. The average rate of change is shown as black points and standard deviation as vertical black lines, in each violin plot. Raw values are shown as colored points. The horizontal dashed line on the plot shows the zero mark. The density curves on the margins of the figures illustrate density distribution of the corresponding variables

the 7 day mean annual low flow (11.2%), changes in precipitation (11.1%), stream segment slope (10.7%), upstream calcium concentration in surface rocks (7.8%), land-use intensity (Land-use 1:5.8%; Land-use 2:5.7%;), upstream catch area (5.4%) and upstream average slope (4.9%).

By contrast, changes in functional LCBD were driven by seven variables (Figure 5). Specifically, upstream catchment average slope (23.91%), changes in precipitation (22.4%), changes in air temperature (16.8%), land-use intensity (Land-use 1 and Land-use 2;

differentiated in taxonomic composition, but homogenized in functional composition with accrued time, as opposed to the rest of the communities. This may represent a key mechanism underlying the observed rise of generalist species and replacement of cold-tolerant species with warm-tolerant species that is being observed in temperate macroinvertebrate communities (Floury et al., 2018; Haase et al., 2019; Van Looy et al., 2016). That is, communities comprising functionally similar but taxonomically diverse species are being replaced by functionally diverse but taxonomically similar species, as observed here.

Changes in precipitation seasonality was the most important correlate of taxonomic homogenization. In contrast to temperature, which exhibited a consistent increase across all locations, changes in precipitation and precipitation seasonality were location-specific, with both increases and decreases present across the country (Figure S2.2). These changes, whether an increase or a decrease, tended to reduce a site's contribution to β -diversity. Mainland New Zealand is composed of two mid-latitude islands, with a typically unpredictable climate (Tonkin, Death, et al., 2018) and flashy river flow regimes (Winterbourn et al., 1981) due to its oceanic position. The temporal turnover of stream communities in New Zealand streams tends to reflect this unpredictability, with limited intra-annual differentiation between seasons compared to trends in more predictable climates (Tonkin, Death, et al., 2018). However, our results indicate that patterns of precipitation seasonality in New Zealand has changed over this 25 year period, altering the spatial distribution of river macroinvertebrate communities through time. Similar climate-driven environmental harshness has been observed not only to be important for dynamic systems like these, but also for other ecosystems worldwide. For instance, natural flow intermittence is an important structuring agent for stream macroinvertebrate communities in Mediterranean streams (Belmar et al., 2019). Given the importance of natural cycles of flooding and drought in streams (Aspin et al., 2018, 2019; Poff et al., 1997; Tonkin, Merritt, et al., 2018), it stands to reason that patterns in precipitation seasonality play a key role in structuring stream macroinvertebrate species communities.

Our results clearly highlighted a particularly dominant role of climate change, and less so land-use, in mediating changes in taxonomic and functional β -diversity of these river macroinvertebrate communities. These processes, together, contributed most of the relative influence explained by the variables in our models. Climate change, however, explained 3.6 times more of the variability in changes in taxonomic β -diversity, and 1.3 times more in functional β -diversity, than land-use related variables. This is despite New Zealand having experienced one of the highest rates of agricultural land intensification over recent decades (OECD/FAO, 2015). However, we recognize that this result may be specific to our study area. For instance, the effects of climate change and land-use variables may have differed had we focused on streams of different realms (Heino, 2011) or size (Floury et al., 2018; Radinger & García-Berthou, 2020). Moreover, although we examined the effects of different environmental scales in our models, our

findings could relate to the spatial extent of our analyses (Hewitt et al., 2010; Jarzyna & Jetz, 2018; Wiens, 1989). This can obscure the relative importance of anthropogenic factors that may only operate at local scales (Jouffray et al., 2019), such as human-induced flow alteration, eutrophication and sedimentation within single catchments. Whether a stronger anthropogenic signature would emerge at a finer extent of analyses, therefore, represents an important next step for future work that could better inform local community management.

The responses of communities to changes in climatic drivers were variable. Air temperature warming correlated with decreases in taxonomic and functional LCBD. However, decreasing precipitation correlated with decreasing taxonomic LCBD but increasing functional LCBD. Warming and decreasing precipitation theoretically reduces discharge, hence potentially reduces the connectivity among communities, but at the same time may homogenize mesohabitats in these systems (Aspin et al., 2018, 2019; Rahel, 2002, 2007). Such a mechanism would support the expansion of functionally diverse but homogeneous species assemblages. By contrast, Villéger et al. (2014) observed greater functional homogenization than taxonomic homogenization in European freshwater fish assemblages under climate change due to range expansions in non-native species distributions within European water basins, which supported similar functions to native species. Elucidating which species and functional traits contributed to the changes in β -diversity observed here, may allow further research to understand the evolutionary and ecological consequences of these changes in biodiversity.

Climate models suggest river flow regimes will increase in variability as the climate continues to change (Arnell & Gosling, 2013; Kakouei et al., 2018; Schneider et al., 2013), opening the door to questions of how freshwater macroinvertebrate communities will respond to more intensified and variable flow disturbances. Although these New Zealand streams have seen an increase in functional diversity over the 25 year period, more intensified disturbances are likely to suppress or overturn this trend (Domisch et al., 2013; Kakouei et al., 2018). For example, an increasing number of colonizing warm water species could promote further species losses, by competitive exclusion (Buisson et al., 2008; Radinger et al., 2019). Moreover, the resilience of stream biodiversity in the face of continued global change could also be reduced if spatial insurance effects become less effective, as large-scale disturbances promote greater synchrony among ecosystems (Shanafelt et al., 2015). Our results therefore indicate that the responses of stream biodiversity to ongoing environmental change are overly complex with contrasting taxonomic and functional responses to change. The positive news of increasing functional β -diversity over time, which may provide a greater resilience capacity to communities despite taxonomic homogenization, could only be a transient process that will be overturned in time. To better understand the biodiversity consequences of future global change, we need a greater uptake of studies exploring the combined and interacting responses of both taxonomic and

functional components of biodiversity to ongoing environmental change. As river ecosystem reorganization continues in the Anthropocene in response to climate change (Olden et al., 2018; Tonkin et al., 2019), the value of different ecosystem states and environmental management will likely hinge upon the capacity of those ecosystems to maintain key functional processes despite ongoing taxonomic homogenization.

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AUTHOR CONTRIBUTION

T.L.M., F.S. and P.V. compiled the data. T.L.M. and M.F. designed the study, computed analyses and interpreted the results. T.L.M. and J.D.T. wrote the manuscript with inputs from all co-authors.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available from NIWA upon request. Restrictions apply to the availability of these data, which were used under license for this study. Data are available from the authors with the permission of NIWA.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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ECOGRAPHY

Research

Climate and land-use driven reorganisation of structure and function in river macroinvertebrate communities

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Understanding temporal changes in the composition of species communities over spatial and temporal scales relevant to conservation management is crucial for preventing further biodiversity declines. Here, we assessed patterns and potential drivers of taxonomic and functional temporal β diversity over 26 years (1991–2016) of 64 river macroinvertebrate communities, and the length of New Zealand (37°00'N, 46°00'S). We further examined changes in population size and range shifts of species pools, and related these to taxonomy and functional traits. We found increasing climate and land-use driven differences in both the taxonomic and functional composition of communities over time, coupled with poleward species colonisations and increasing extirpations in northern locations. Increases in population and species range size were more prevalent than decreases in population and range size. Species shifted their ranges towards higher latitudes on average by 50 km per decade. Despite little to no relationship with taxonomy, we uncovered distinct relationships between functional traits and population trends and latitudinal species range shifts. Species with a high number of reproductive cycles per year and long-life duration of adults tended to increase their population size, while larger size species with a high number of descendants per reproductive cycle tended to shift their range towards more southern latitudes. Our results suggest that the intensity of disturbances, the geographic location of individuals and communities, and species ecological and functional characteristics, are major determinants of riverine biodiversity reorganisation in the Anthropocene.

Keywords: biodiversity, climate change, freshwater macroinvertebrates, functional diversity, land use change, population trends, species range shifts, temporal β diversity



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Introduction

Current rates of biodiversity change correlate with recent human-induced climate change and land-use activities (IPCC 2014, Brondizio et al. 2019). These biodiversity changes are predicted to increase as human activities intensify (Urban 2015, Johnson et al. 2017), reflecting local extirpations and/or colonisations of species and populations across landscapes (Tilman et al. 1994, Maclean and Wilson 2011, Brondizio et al. 2019). Such demographic shifts could potentially lead to major alterations to the functioning of ecosystems. However, the responses of species likely vary in magnitude among regions of the world and across latitudes (Heino et al. 2009, Lenoir et al. 2019). Biodiversity trends are, however, overly complex, with observations of local biodiversity increases sometimes contradicting reports of a global climate-driven biodiversity crisis (Antão et al. 2020, Li et al. 2020, Outhwaite et al. 2020). There is therefore an imperative need for biodiversity time-series studies over wide and understudied geographical regions to inform conservation planning and policy (Olden et al. 2018, Magurran et al. 2019).

Uncovering the drivers of biodiversity change requires tools that can deconstruct the mechanisms underpinning such change. Research on changes in the composition of species communities (changing β diversity) has typically focused on temporal changes in spatial β diversity (Olden et al. 2018). However, ongoing temporal change in species composition is also a pressing (Kuczynski et al. 2018, Blowes et al. 2019, Antão et al. 2020), yet less investigated aspect of biodiversity change. Temporal β diversity can capture the biogeographical, ecological, functional and ecological processes involved in temporal changes in communities (Magurran et al. 2019), including local extirpations or colonisations (Legendre and Gauthier 2014, Shimadzu et al. 2015, Gotelli et al. 2017, Legendre 2019, Magurran et al. 2019).

The responses of species to environmental change, including local losses and gains associated with temporal β diversity, are underpinned by their ecological and life-history traits (Dawson et al. 2011, MacLean and Beissinger 2017, Pacifici et al. 2017, McLean et al. 2018a). For example, populations of ecological specialists, with long generation times, and low reproductive output are predicted to be highly vulnerable to climate change (Vié et al. 2009, Chin et al. 2010, Conti et al. 2014). Similarly, the degree to which species reduce, expand and/or shift their ranges may depend on their ability to disperse and the geographic location of populations (Comte et al. 2014, Lenoir et al. 2019). Theoretically, the lowest latitudinal margins of continents or islands are more likely to experience loss of taxa under climate change, because colonisations from lower latitudes are not possible (Heino et al. 2009, MacLean and Beissinger 2017).

In running waters, temporal β diversity is increasingly being used as a tool to understand the dynamics of change in macroinvertebrate communities, including identifying sites that are pivotal for maintaining biodiversity at the landscape scale (Ruhí et al. 2017). Changing climate or flow regimes has been identified as a common driver of change in community

structure. For instance, Cañedo-Argüelles et al. (2020) found a strong relationship between structural changes in macroinvertebrate communities and changes in precipitation regimes. Similarly, Crabot et al. (2020) found that the temporal variability of community structure was related to the frequency and duration of drying events. However, few studies have examined temporal β diversity of stream invertebrate communities over large spatial and temporal scales.

Here, we complement recent findings from Mouton et al. (2020), who reported decreasing spatial taxonomic β diversity (taxonomic homogenisation) but increasing spatial functional β diversity (functional differentiation) among river macroinvertebrate assemblages. We capitalise on the same high-resolution time-series datasets, comprising macroinvertebrate communities collected annually from 1991 to 2016, at 64 mainstem river sites across New Zealand's two mainland islands. The two studies are complementary in the sense that Mouton et al. (2020) explored how climate change affects the spatial organization of assemblages while the present study aims at evaluating how both climate and land-use changes influence temporal differences in community composition within sites.

We measured taxonomic and functional temporal β diversity over the period 1991–2016, which we decomposed into indices of colonisations and extirpations. We tested for the effects of climate and land-use change, nested within hierarchically organized environmental spatial scales, in mediating taxonomic and functional temporal β diversity of these communities. Finally, we examined changes in species' population and range size and latitudinal range shifts which we related to their taxonomic affiliation and a set of functional traits.

Given widespread evidence of freshwater macroinvertebrates response to ongoing climate change (Pyne and Poff 2017, Floury et al. 2018, Mouton et al. 2020), we first expected a latitudinal pattern in temporal β diversity (E_1), owing to climate-driven species range shifts. Specifically, we expected (E_{1a}) increasing species colonisations at the leading edges (southern margins of New Zealand) but (E_{1b}) increasing extirpations at the rear edges (northern margin of New Zealand). Second, given globally observed species population declines and poleward range shifts (Urban 2015, Olden et al. 2018, Lenoir et al. 2019), we expected (E_2) greater decreases in species' population and range sizes than increases, and poleward range shifts. Finally, given the relationship between the taxonomic identity of species, their functional traits and demographic responses to environmental change (MacLean and Beissinger 2017, Pacifici et al. 2017, Daskalova et al. 2020), we expected a relationship between trends in population sizes and species range shifts with the taxonomic identity of species and with their functional traits (E_{3a} and E_{3b} , respectively).

Methods

Data acquisition

Biodiversity data

Macroinvertebrate communities were sampled from mainstem rivers, at 64 wadeable sites (mean Strahler stream

order=6; min=3, max=8), located in 35 catchments of New Zealand, between latitudes 46 and 35°S (Supporting information). Surveys were conducted once a year, during late austral summers (February–April) from 1991 to 2016. These surveys were conducted for New Zealand's National Rivers Water Quality Network (NRWQN, Smith and McBride 1990), which is operated and maintained by the National Institute of Water and Atmospheric Research (NIWA). Samples were collected following a standardized protocol (Smith and McBride 1990) and under baseflow conditions ($Q < Q_{\text{median}}$). Seven Surber samples (0.1 m² and 250 μm mesh net) were collected on all sampling occasions during which macroinvertebrates were removed from a 0.1 m² area in the sampler down to a depth of ca 10 cm and from as many substrate types as possible. Individuals were later identified in the laboratory, to the lowest practicable taxonomic level (species=26%; genus=47%, family=21%; Quinn and Hickey 1990). The same taxonomic resolution was maintained throughout the entire period to allow analyses of long-term changes (Scarsbrook et al. 2000).

We described each macroinvertebrate taxon (n=113) using sixteen functional traits related to morphology, life-history, dispersal strategies and resource acquisition methods extracted from the New Zealand freshwater macroinvertebrate trait database (NIWA, <https://niwa.co.nz/sites/niwa.co.nz/files/nz_trait_database_v19_2_18.xlsx>). This trait database has been explicitly developed for New Zealand's standardised freshwater macroinvertebrate sampling protocols (Dolédec et al. 2006, Doledec et al. 2011). Functional traits were divided into 59 modalities and fuzzy-coded from 0 to 3 (Chevenet et al. 1994).

Environmental predictors

We defined a set of environmental predictors at four different spatial scales, commonly identified as prominent scales operating in river networks (Poff 1997, Allan 2004): the global, regional, catchment and reach scales.

Global-scale predictors were defined as temporal changes in air temperature and precipitation (Brown et al. 2013). At each site, we extracted daily values for the period 1991–2016, from 5 km² gridded layers of New Zealand, using NIWA's Virtual Climate Station Network (VCSN; <<https://data.niwa.co.nz/>>). We used the slopes of linear regressions between climate variables and years as estimates of rates of change (OLS; the *lm* function in R ver. 4.0.2; <www.r-project.org>). The following variables were used: annual and seasonal (for the winter, spring and summer seasons) mean precipitation, precipitation seasonality (i.e. the coefficient of variation $\times 100$; Fick and Hijmans 2017), mean air temperature and air temperature seasonality (i.e. the standard deviation of the mean). We applied a principal component analysis (PCA; the *dudi.pca* function in the Ade4 package ver. 1.7-15 Dray and Siberchicot 2020) individually to our sets of trends in air temperature and precipitation variables. Based on the correlations among each trend in climate variable and the axes of the PCAs, we created synthetic indices of climate change using the first two axes of each climate PCA. In the PCA of

trends in air temperature variables, the first axis (35.9% of variation explained) described a gradient of increasing mean air temperature (TMean) and the second (33.0%) described changes in air temperature seasonality (TSeas). For precipitation variables, the first axis (28.2%) described changes in precipitation seasonality (Prec CV) and the second (22.7%) described changes in mean precipitation (Prec).

Regional-scale predictors were 1) altitude (metres above sea level) of the sampling site, 2) phosphorus, 3) calcium concentrations and 4) mean hardness (induration) of surface rocks of the upstream catchment (respectively the variables USPhosphorus, USCalcium and USHardness extracted from Leathwick et al. 2010). The latter three variables are descriptors of catchment geology, hence likely reflect regional biogeochemical characteristics.

For catchment-scale predictors, we used descriptors of changes in catchment land-use and catchment hydro-morphology. For land-use, we used changes (1990–2012) in 4 land-cover types (defined as the proportion of catchment occupied by combinations of 1) high producing grassland, 2) shrub/grassland, 3) plantation forest and 4) non-plantation forest (Landcare Research 2015, Julian et al. 2017). These data were available for the year 1990 and 2012, we used the difference in land-cover between these two dates as estimates of temporal change, following Julian et al. (2017). Similarly, we also used changes (1990–2012) in catchment stock unity density (SUD) of dairy, beef, sheep and deer (SU ha⁻¹; Statistics NZ (territorial authority), Julian et al. 2017). Changes in land-cover and changes in stock unity density were synthesised using the first two axes of two PCAs, which we interpreted as synthetic predictors of changes in land-cover (LC PC1, 61.4% and LC PC2, 23.9%; Supporting information) and changes in stock unity density (SUD PC1, 44.3% and SUD PC2, 35.2%; Supporting information), respectively. Catchment hydro-morphology was given by the area of the upstream catchment (m²; USCatchArea) and the average slope of the upstream catchment (degrees; USAvgSlope) from each river segment (Leathwick et al. 2010).

For reach-scale descriptors, we used: 1) the slope (degrees) of the stream segment at each sampling site (SegSlope; Leathwick et al. 2010), 2) the predicted wetted river width (m) at the 7-day mean annual low flow (WidthMALF; Booker 2015), 3) the estimated proportion of riparian shading at each river segment (SegRipShade; measured from satellite imagery by Leathwick et al. 2010), 4) temporal changes in water quality, 5) temporal changes in flow and 6) temporal changes in substrate size. Temporal changes in water-quality, flow and substrate size were all estimated as slopes of variables (described below) and years. For temporal changes in water-quality, we compiled data from 1991 to 2016 of median annual values (mg m⁻³) of nitrate (NO₃-N), ammoniacal-nitrogen (NH₄-N), dissolved reactive phosphorus (DRP) and dissolved oxygen (DO) concentrations and water clarity (metres; CLAR). These data originate from samples collected monthly, at the same sites as those sampled for macroinvertebrate communities (Davies-Colley et al. 2011). We log₁₀-transformed water-quality variables and calculated temporal

changes for each variable at each site. We ordinated temporal changes in water-quality using PCA and retained the first axis (33.3%) as a synthetic indicator of temporal changes in water quality (WQ). For changes in flow, we compiled mean daily flow data from hydrological gauges located at each site, which we divided by upstream catchment area to obtain a measure of run-off per day (Vaughan and Gotelli 2019). We then calculated mean annual and seasonal (for winter, spring and summer) flow and flow coefficient of variation, as was done for precipitation. We ordinated temporal changes using PCA and kept the first two axes (Flow PC1, 54.1% and Flow PC2, 20.6%; Supporting information) as indicators of temporal changes in flow. Finally, for changes in substrate size we used temporal changes in the substrate size index (SSI; Jowett et al. 1991). Substrate composition was measured by randomly selecting 100 particles at 1-m intervals along a path of 45 degrees to the riverbank in a zig-zag manner. Particles were assigned to each of 8 size classes: bedrock, boulders (> 300 mm), large cobbles (300–128 mm), small cobbles (128–64 mm), large gravel (32–64 mm), small gravel (2–32 mm), sand (62.52 μm –2 mm) and silt (< 62.52 μm). We measured the substrate size index (SSI) for each sampling occasion following Jowett et al. (1991) (1 = silt only, 8 = bedrock only). Temporal changes in SSI were then measured for each site. Detailed description of the variables and statistical outputs in regards to the environmental descriptors used for analyses are given in Mouton et al. (2020) and in the Supporting information.

Statistical analyses

Temporal β diversity indices

We used the temporal β diversity index from Legendre (2019) (TBI; the *TBI* function in the *adespatial* package ver. 0.3-8) to measure temporal changes in the taxonomic and functional composition of each of the 64 communities. This index has been specifically developed 1) to calculate differences in assemblage composition (dissimilarity) between two time periods from pairwise distances, and 2) to decompose these temporal differences into indices of local colonisations and extirpations. Macroinvertebrate abundances were $\log(x+1)$ -transformed and pairwise distances in community composition were calculated using the percentage difference index of dissimilarity (*%diff*; Odum 1950, also known as the Bray–Curtis index). To estimate temporal changes in functional composition (i.e. the composition of species functional traits within each community), the species-by-site matrix was replaced by a trait-by-site matrix using the community-level abundance weighted means of functional trait values (CWM; Lavorel et al. 2008; using the *dbFD* function in the *FD* package ver. 1.0-12; Laliberté et al. 2014).

We used the first year of sampling (1991) as a baseline for each time-series, and then successively compared it to each of the following years (1992, onwards (Magurran and Henderson 2010, Dornelas et al. 2014, Antão et al. 2020)). This computation therefore yielded a value of dissimilarity, colonisations and extirpations for each year (except the baseline year) and

site. For each site, we regressed values of each index (taxonomic and functional dissimilarity, extirpations and colonisations, respectively) against years and interpreted the slopes from the regression models (multiplied by ten) as a measure of trends per decade. This method allows to examine whether changes in composition of each assemblage (relative to the baseline year) consistently increase (positive slope) or decrease (negative slope) over time (Antão et al. 2020).

To test our first expectations (E_{1a} and E_{1b}), we tested for relationships between trends in temporal β diversity, including colonisations and extirpations with latitude using linear-mixed effects models (the *lme* function in the *nlme* package ver. 3.1-152 (Pinheiro et al. 2017)) setting island (North Island versus South Island) as random effect.

Drivers of temporal β diversity

We performed hierarchical generalised additive mixed effects models (GAMMs; the *gamm* function in the *mgcv* package ver. 1.8-33 (Wood and Wood 2015)) to relate temporal changes in each of the six indices of trends in temporal β diversity to our set of environmental descriptors. Predictor variables were Box–Cox transformed prior to analyses (Box and Cox 1964; the *BoxCoxTrans* function in the *caret* package ver. 6.0-84 (Kuhn et al. 2020)), and standardised to zero mean, one unit variance (using the *decostand* function in the *vegan* package ver. 2.5-6 (Oksanen et al. 2014)).

GAMMs were fitted with catchments nested within islands as random effects to account for spatial structure in data (Dormann et al. 2007). We used regression splines to account for potential non-linear relationships, restricted maximum likelihood (REML) to optimize the parameter estimates and assumed Gaussian-type distribution errors.

Each response variable was first modelled against global-scale descriptors. We kept only the global-scale descriptor(s) that maximised the coefficient of determination (adjusted- R^2) as the best model following Van Looy et al. (2017) and Floury et al. (2018). The same step was then repeated in a descending way, using successively regional, catchment and reach-scale descriptors as predictor variables and the residuals from the previous model as response variable. At each step, we quantified the percentage of relative importance of each variable in the model following methods described in Kuhn (2008) (the *varImp* function in *caret*). We tested for residual spatial autocorrelation in the residuals of the reach-scale model using Moran's index of spatial autocorrelation (the *Moran.I* function in the *ape* package ver. 5.5 (Paradis et al. 2019)). Residual spatial autocorrelation was not observed ($p > 0.05$ for every model).

Population trends and species range shifts

To test our second expectation (H_2), we assessed temporal trends in the abundance, range size and the latitudinal distribution of 83 taxa that were recorded for at least 10 years (not necessarily consecutive; following Dornelas et al. 2019). For population trends (hereafter referred to as temporal trends in the abundance of each taxa), we did not include the time when a taxon was absent in the time series,

because this would tend to flatten the slope towards zero. Macroinvertebrate abundances were $\log(x + 1)$ transformed and then standardised, so that each time-series had a mean of 0 and a standard deviation of 1. This transformation put all time-series into common units that are more appropriate for comparisons of taxa with disparate population sizes. We estimated population trends by fitting a linear regression model of abundances for each taxon individually, against years.

Second, we measured the range size of each taxon as the convex hull area encompassing the sites where the taxon was present each year. We regressed range sizes against years using ordinary least squares models. Finally, we assessed latitudinal distribution shifts of each taxon, by regressing the centroid of its range against years. We used the slope of each linear regression model as an estimate of changes in population and range size and of latitudinal range shifts, for each taxon.

Relationships with taxonomy and functional traits

To test our third expectations (H_{3a} and H_{3b}), we started by relating changes in community composition to the taxonomic classification of our taxa (H_{3a}). For this purpose, we compiled a taxonomic classification of the studied taxa (using phylum, subphylum, class, subclass, family, subfamily, order, genus and species names), from the National Center for Biotechnology Information (using the *taxonomy* function in the myTAI package Drost et al. 2018). From this classification, we created a taxonomic tree by calculating taxonomic distances between taxa (using Gower's distance and the *taxa-2dist* function in *vegan*). We used hierarchical clustering (the *hclust* function in R) to produce a tree from the taxonomic dissimilarity matrix. We checked for potential relationships between taxonomic distance and Euclidean dissimilarity in population size and/or species range shifts using a Mantel test (Mantel 1967) with 9999 permutations (the *mantel.rtest* function in *Ade4*).

To relate changes in community composition to functional traits of macroinvertebrates (H_{3b}), we tested for relationships among population trends, changes in range size and latitudinal range shifts with the axes of a functional trait space (Loiseau et al. 2020). For this purpose, we built a functional trait space of the macroinvertebrate taxa by ordinating the species-by-trait matrix in a multidimensional space, using fuzzy correspondence analysis (the *dudi.fca* function in *Ade4*). We ensured that equal weights were given to each of the trait categories (e.g. for the trait 'maximum potential size' which contained 5 categories, each category was given a weighting of 1/5). We retained the first three axes of the functional space as synthetic traits of macroinvertebrates (cumulative percentage of variation explained = 31.8%). We used non-parametric Spearman's rank correlation tests to relate changes in population and/or range size and latitudinal range shifts, respectively, to each axis of the trait space and mapped significant relationships on trait space to provide a better visual assessment of potential relationships. Statistical analyses were all performed under the R environment (<www.r-project.org>).

Results

Spatial patterns of changes in temporal β diversity

Trends in taxonomic and functional temporal β diversity increased on average across New Zealand over the 26-year time-series (taxonomic dissimilarity: mean rate = 0.03, minimum = -0.08, maximum = 0.17; functional dissimilarity: mean = 0.02, min = -0.07, max = 0.14; Fig. 1). This increasing trend was driven by increasing taxonomic and functional colonisations and functional extirpations (taxonomic colonisations: mean = 0.04, min = -0.01, max = 0.2, functional colonisations: mean = 0.01, min = -0.03, max = 0.06, functional extirpations mean = 0.01, min = -0.04, max = 0.08) but decreasing taxonomic extirpations (mean = -0.01, min = -0.15, max = 0.14, Fig. 1).

Trends in taxonomic temporal dissimilarity and colonisation decreased with latitude, while those of extirpations increased (Table 1, Fig. 1). However, trends in functional temporal β diversity, colonisations and extirpations showed no or weak relationships with latitude (Table 1, Fig. 1).

Drivers of observed changes

Hierarchical GAMMs had good ($R^2 = 0.34-0.44$) and fair ($R^2 = 0.19-0.24$) fits for trends in taxonomic and functional indices, respectively (Table 2). Changes in taxonomic dissimilarity were mostly influenced by reach and catchment-scale descriptors (Table 2). However, trends in the five other indices were mostly influenced by global scale predictors (Table 2), followed by reach-scale predictors for taxonomic colonisations and catchment-scale predictors for all other indices (Table 2; Supporting information).

Changes in taxonomic dissimilarity were mostly influenced by changes in flow regimes (PC1: % of relative influence = 24.10), changes in stock unit density (PC2; 16.4%), upstream catchment area (9.2%) and changes in flow PC2 (10.8%; Fig. 2 T_{Dis}). Changes in taxonomic colonisations were mostly influenced by changes in flow (PC2; 22.2%), changes in water quality (15.1%), upstream catchment hardness (13.7%) and changes in precipitation seasonality (12.8%; Fig. 2 T_{Col}). Changes in taxonomic extirpations were mostly influenced by changes in land-cover (PC2; 18.5%), changes in stock unit density (PC2; 16.1%), segment slope (12.8%) and changes in precipitation seasonality (10.7%; Fig. 2 T_{Ext}).

By contrast, changes in functional dissimilarity (Fig. 2 F_{Dis}) were mostly influenced by changes in precipitation (22.4, 27.9 and 21.5%, respectively), followed by changes in flow (PC1; 19.6%), changes in land-cover (PC1; 17.4%) and changes in stock unit density (15.8%). Changes in functional colonisations (Fig. 2 F_{Col}) were mostly influenced by changes in changes in land-cover (PC1 and PC2; 17.7% and 12.9%) and changes in flow (PC1; 12.3%). Changes in functional extirpations (Fig. 2 F_{Ext} ; Supporting information) were mostly influenced by changes in land-cover (PC1; 20.5%), changes in stock unit density (PC1; 15.9%) and changes in flow (PC1; 13.3%).

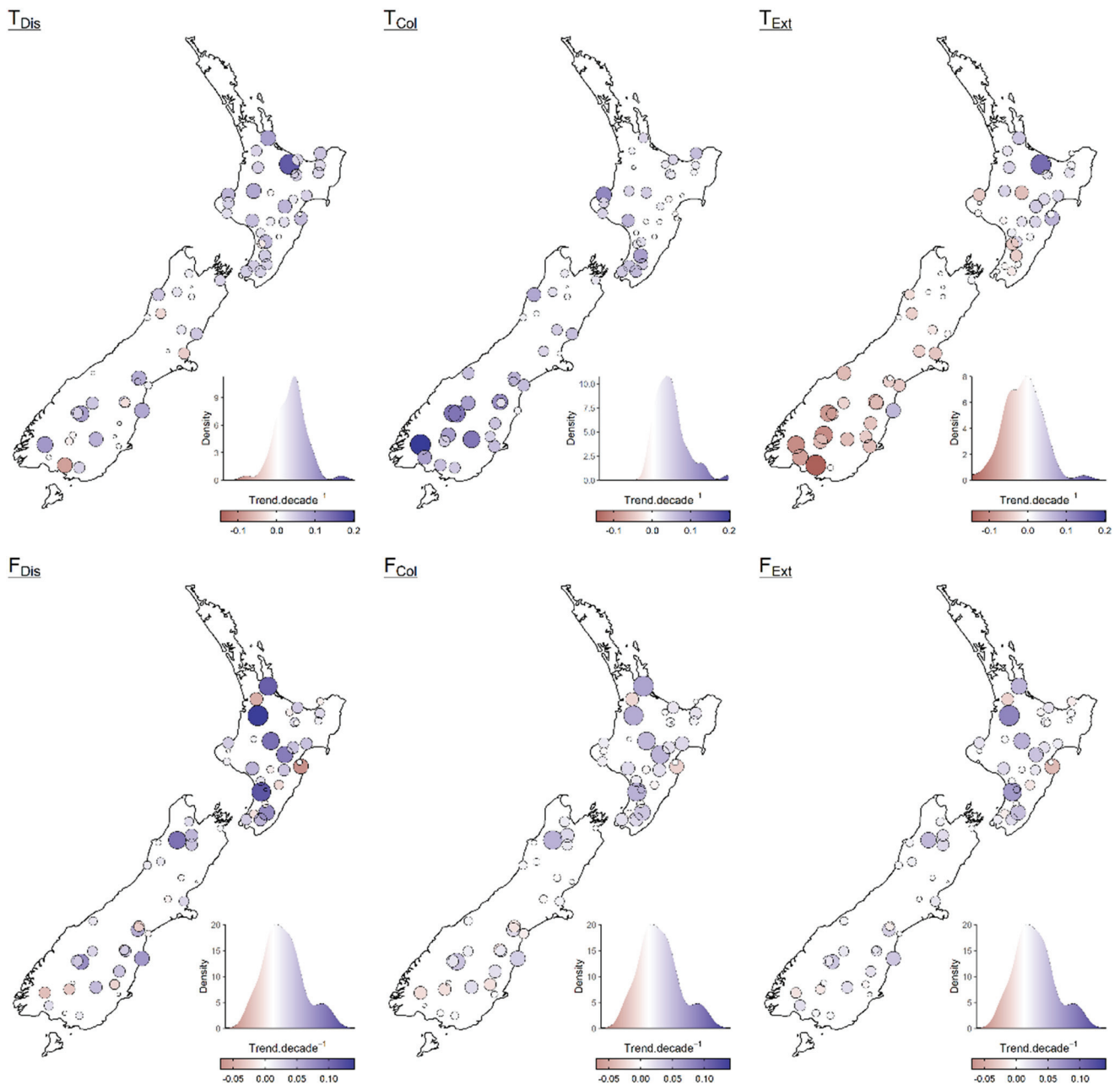


Figure 1. Maps of New Zealand illustrating rates of changes per decade (Trend decade^{-1}) in taxonomic and functional temporal β diversity indices of macroinvertebrate assemblages: dissimilarity (T_{Dis} and F_{Dis} respectively), colonisations (T_{Col} and F_{Col}) and extirpations (T_{Ext} and F_{Ext}). Temporal β diversity was measured by comparing the first year of sampling (1991) to each of the following years (1992–2016). Trends per decade are the slopes of linear regression models used to regress each temporal β diversity index against year. Point sizes are proportional to the absolute rate of change per decade. Red dots indicate decreasing trends, whereas blue dots indicate increasing trends. Density curves at the bottom right corner of each map illustrate the density distribution of each index. The x axis of each density curve corresponds to the limits of the legend.

Population trends and species range shifts

Population sizes increased on average over the time series (mean slope = 0.002 ± 0.009), and this trend was driven by 16% of the taxa which exhibited significant population trends. Significantly increasing populations (12%; mean slope = 0.011, maximum = 0.022, minimum = 0.003)

exceeded significantly decreasing populations (4%, mean slope = -0.015 , min = -0.012 , max = -0.018). Range sizes also increased on average over the 25-year time series (mean slope = $7536 \pm 32\,952 \text{ km}^2 \text{ decade}^{-1}$), but only 14% of taxa exhibited significant trends. Range expansions (11%; mean slope = 27 270, min = 10 380, max = $63\,330 \text{ km}^2 \text{ decade}^{-1}$) exceeded range contractions (3%; mean slope = 14 640,

Table 1. Coefficients of determination (R^2), intercept (standard error), F-value (F) and p-value (p) of latitude in each generalised linear mixed effect model relating temporal β diversity indices to latitude with island as random effect. Values are the estimated mean values of the random intercept and slope.

| Temporal β diversity index | R^2 | Intercept (SE) | Slope (SE) | F | p |
|----------------------------------|--------|----------------|----------------|-------|---------|
| Taxonomic | | | | | |
| Dissimilarity | 0.06 | 0.112 (0.044) | 0.111 (0.044) | 3.72 | 0.06 |
| Colonisations | 0.41 | -0.238 (0.064) | -0.238 (0.064) | 13.8 | < 0.001 |
| Extirpations | 0.47 | 0.249 (0.034) | 0.249 (0.034) | 54.14 | < 0.001 |
| Functional | | | | | |
| Dissimilarity | 0.02 | 0.058 (0.046) | 0.058 (0.046) | 1.59 | 0.21 |
| Colonisations | 0.06 | 0.088 (0.045) | 0.088 (0.045) | 3.7 | 0.06 |
| Extirpations | < 0.01 | 0.028 (0.047) | 0.028 (0.047) | 0.36 | 0.55 |

min = 11 570, max = 17 700). Species shifted south on average by 56 km per decade (mean = 56.31, min = 1.05, max = 242.98 km decade⁻¹), with 22% of taxa having significant poleward range shifts (mean slope = 108.14, min = 27.37, max = 242.98 km decade⁻¹).

Relationship with taxonomy and functional traits

Dissimilarity in population trends was significantly, albeit weakly, related to taxonomic distance (Mantel test: $r = 0.17$; $p = 0.03$, Supporting information; Fig. 3d). However, there was no relationship between taxonomic distance and dissimilarity in changes in range size, nor with dissimilarity in latitudinal range shifts (Mantel's $r = 0.06$; $p = 0.27$ and Mantel's $r = 0.01$; $p = 0.40$, respectively; Fig. 3e–f).

Population trends were positively correlated with the first axis of the functional trait space ($r = 0.28$, $p < 0.01$; Supporting information). This axis was positively correlated with species with several reproductive cycles per year (two or more) and long-life duration of adults (> 30 days; Supporting information). Changes in range size were not significantly related to functional trait space axes ($p > 0.05$). However, latitudinal range shifts were negatively correlated ($r = 0.30$, $p < 0.01$) with the third axis of the functional space, albeit with a large amount of scatter (Supporting information; this included large size taxa (maximum potential size > 40 mm), with a high number of descendants per reproductive cycle (> 1000), terrestrial oviposition sites and aerial respiration of aquatic stages; Supporting information).

Changes in functional composition were evident on the ordinations (Fig. 4a and b): for changes in population size (Fig. 4a), most winners and losers occupied exclusive areas of

trait space, signifying a temporal turnover of species populations and their traits over the 26-year time-series. However, taxa with the greatest latitudinal range shifts were mostly positioned in the centre of the functional space (Fig. 4b) indicating that these were rather generalists than specialist taxa (Mouillot et al. 2013).

Discussion

We observed climate and land-use driven changes in temporal β diversity of taxa and functional traits across New Zealand rivers over a 25-year period relative to the first year of sampling. Trends in taxonomic colonisations increased with latitude while those of extirpations showed opposite patterns. Functional colonisations and extirpations showed weak or non-existent relationships with latitude (accepting our expectation E_{1a} but rejecting E_{1b}). Discrepancies among spatial patterns of taxonomic and functional diversity in river macroinvertebrate communities have also been reported elsewhere (Crabot et al. 2020, Sarremejane et al. 2020). This may suggest that communities are characterized by different degrees of functional redundancy across the landscape, allowing maintenance of functional diversity despite species losses, which may have important implications for ecosystem functions and services (McLean et al. 2019, Crabot et al. 2020).

Hierarchical models indicated a role of climate and land-use change in driving taxonomic and functional temporal β diversity. Increasing mean temperature, temperature variability and precipitation seasonality, tended to increase temporal turnover (sensu Anderson et al. 2011) in taxonomic composition. Many of the species that exhibited negative

Table 2. Coefficients of determination of each generalised additive mixed effect model for trends in each taxonomic and functional temporal β diversity index, spatial scale and the total of the four spatial scales.

| Temporal β diversity index | Global | Regional | Catchment | Reach | Total |
|----------------------------------|--------|----------|-----------|-------|-------|
| Taxonomic | | | | | |
| Dissimilarity | 0.02 | 0.00 | 0.18 | 0.31 | 0.44 |
| Colonisations | 0.22 | 0.05 | 0.00 | 0.12 | 0.34 |
| Extirpations | 0.21 | 0.00 | 0.21 | 0.08 | 0.42 |
| Functional | | | | | |
| Dissimilarity | 0.10 | 0.00 | 0.09 | 0.04 | 0.21 |
| Colonisations | 0.14 | 0.00 | 0.10 | 0.02 | 0.24 |
| Extirpations | 0.09 | 0.00 | 0.09 | 0.02 | 0.19 |

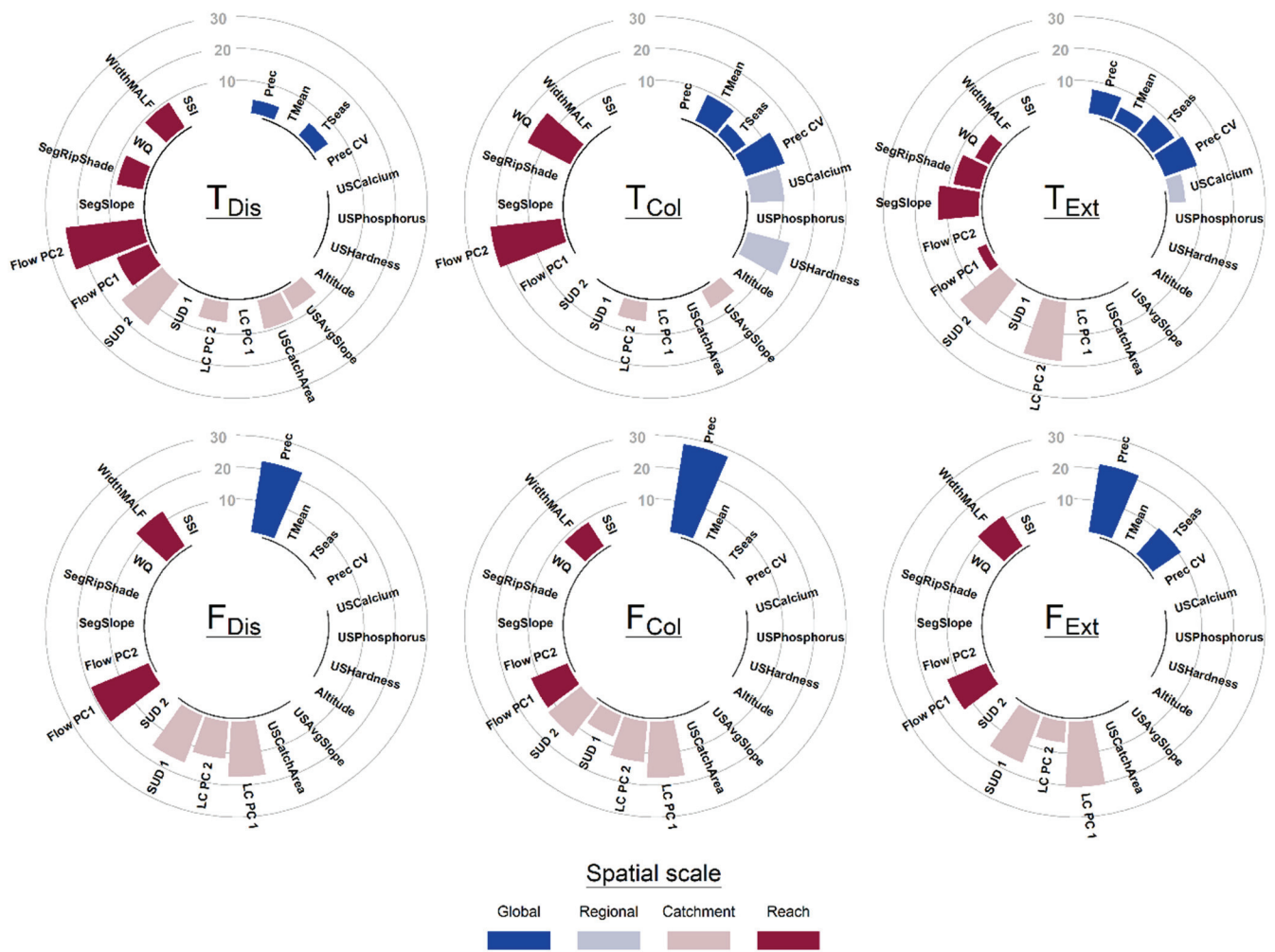


Figure 2. Relative influence of the environmental variables selected in each generalised additive mixed-effects model to explain rates of changes in taxonomic and functional temporal β diversity of macroinvertebrate assemblages. Bars are coloured by their respective spatial scale (as is indicated by the legend). T_{Dis} : taxonomic temporal β diversity; F_{Dis} : functional temporal β diversity; T_{Col} : taxonomic colonisations; F_{Col} : functional colonisations; T_{Ext} : taxonomic extirpations; F_{Ext} : functional extirpations. Acronyms: Prec: changes in precipitation; Prec CV: changes in precipitation coefficient of variation; TMean: changes in mean air temperature; TSeas: changes in temperature seasonality; USPhosphorus: phosphorus concentration of upstream surface rocks; USCalcium: calcium concentration of upstream surface rocks; USHardness: mean hardness of upstream surface rocks; Altitude: altitude of the sampled site; USAvgSlope: upstream average slope; USCatchArea: upstream catchment area; LC PC1: changes in land-cover (PC 1); LC PC2: changes in land-cover (PC2); SUD 1: changes in stock unit densities of sheep, deer, dairy and beef (PC1); SUD 2: changes in stock unit densities of sheep, deer, dairy and beef (PC2); Flow PC1: changes in flow regimes (PC1); Flow PC2: changes in flow regimes (PC2); SegSlope: average river segment slope; SegRipShade: estimated river segment riparian shading; WQ: changes in water-quality; WidthMALF: river width at mean annual low flow; SSI: changes in substrate size.

trends were those that specialise in cold-water pristine conditions, including the stonefly *Stenoperla prasina* and the mayfly *Amelotopsis perscutus*. One of the key mechanisms of climate change-related temporal turnover in stream communities globally has been a replacement of cold-dwellers with warm-dwellers, including in streams of northwestern Europe (Haase et al. 2019) and New South Wales, Australia (Chessman 2009, Haase et al. 2019). By contrast, trends in functional temporal β diversity responded to changes in mean precipitation only (Supporting information). Changes in patterns of precipitation has been shown as a key structuring mechanism for freshwater temporal β diversity in many locations (Tonkin et al. 2017, Cañedo-Argüelles et al. 2020).

Moreover, land-use change (increasing intensively managed land and/or stock unit density of dairy and beef) was a predominant driver of temporal β diversity in our analyses. Increasing human land-use tended to increase taxa colonisations in these river systems (Supporting information). Human land-use intensification has been found to hasten biodiversity change in streams worldwide (Allan et al. 1997, Petsch et al. 2021), and more particularly in New Zealand, which has experienced one of the highest rates of agricultural land intensification over recent decades (OECD/FAO 2015). Several studies have demonstrated that land use changes have profoundly impacted New Zealand's stream communities for several taxonomic groups (Clapcott et al. 2012, Foote et al. 2015,

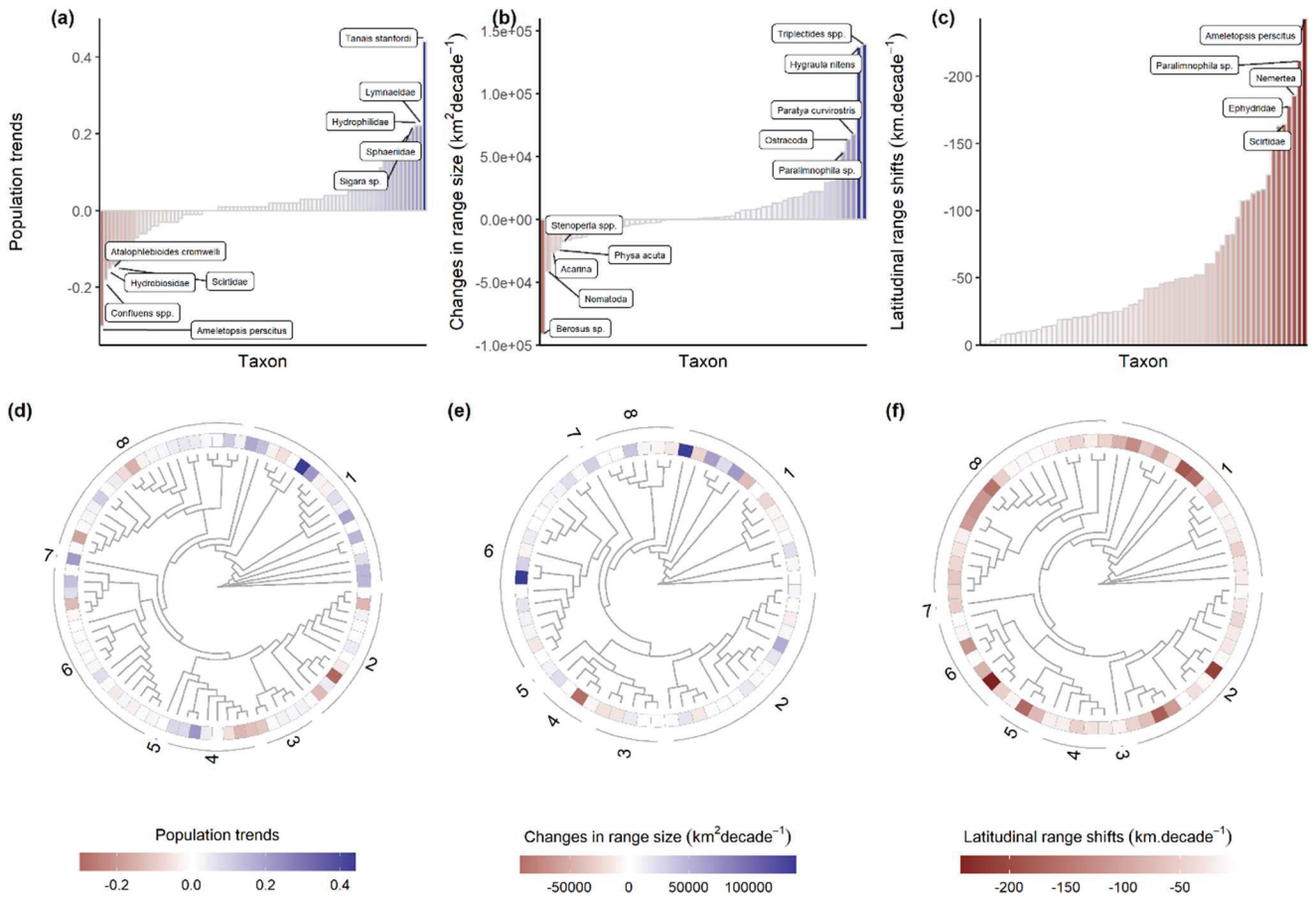


Figure 3. Population trends, species range shifts and relationships with taxonomy. Changes in population size (a), range size (b) and latitudinal range shifts (c) for each taxon. The name of the five most and/or least changing taxa are given on each plot. Relationships between taxonomy and changes in population size (d), range size (e) and latitudinal range shifts (f). The numbers around the taxonomic trees delineate major taxonomic orders: 1: Other, 2: Diptera, 3: Plecoptera, 4: Coleoptera, 5: Hemiptera, 6: Trichoptera, 7: Megaloptera, 8: Ephemeroptera.

Joy et al. 2019). Such effects of human land-use could render freshwater ecosystems more susceptible to climate change (Verberk et al. 2016, Tickner et al. 2020), and our results indicate that their effects are currently operating in unison.

At the reach scale, changes in flow regimes were found to be the most important drivers of changes in taxonomic and functional β diversity. Riverine ecosystems are governed by patterns of temporal variation in flow regimes (Tonkin et al. 2018a). As climate and land-use change modifies the natural flow regime in many river systems, components of flow regimes are expected to shift, even under the most conservative climate change scenarios (Rood et al. 2008, Ficklin et al. 2018). The results of our hierarchical models indicate how influential flow driven habitat changes are to the organization of river macroinvertebrate communities. Nevertheless, while flow change was important for almost all facets of beta diversity, it had only a small role as a driver of taxonomic extinctions, where land-use change was the predominant driver. This may reflect the relative flexibility of most New Zealand invertebrates to unpredictable flow regimes, given its oceanic climate (Winterbourn et al. 1981, Tonkin et al. 2018a).

Contrary to our second expectation (E_2) our results identified greater amounts of increases in population and range size (i.e. winners) than decreases (i.e. losers) across the entire species pool. This suggests that the overall taxonomic homogenisation of these river macroinvertebrate communities recently observed (Mouton et al. 2020) is characterised by a greater amount of increase in population size and range size of winners than widespread declines of losers. Nonetheless, we found increasing rates of taxonomic extirpations at sites located at the north-eastern boundary of the North Island of New Zealand. Conversely, the greatest rates of taxonomic colonisations were located at the southern boundaries of each island. More importantly, almost a quarter of the taxa examined here also tracked the shifting isotherms by shifting their ranges towards the south pole. Given the geographic isolation of New Zealand and the observed latitudinal patterns of species distribution shifts here, the biodiversity of New Zealand's rivers could experience a 'cul-de-sac' effect, if it is to be exposed to more intense climate change (Sauer et al. 2011, Albouy et al. 2012). This trend may further be exacerbated for species dispersing exclusively along river networks

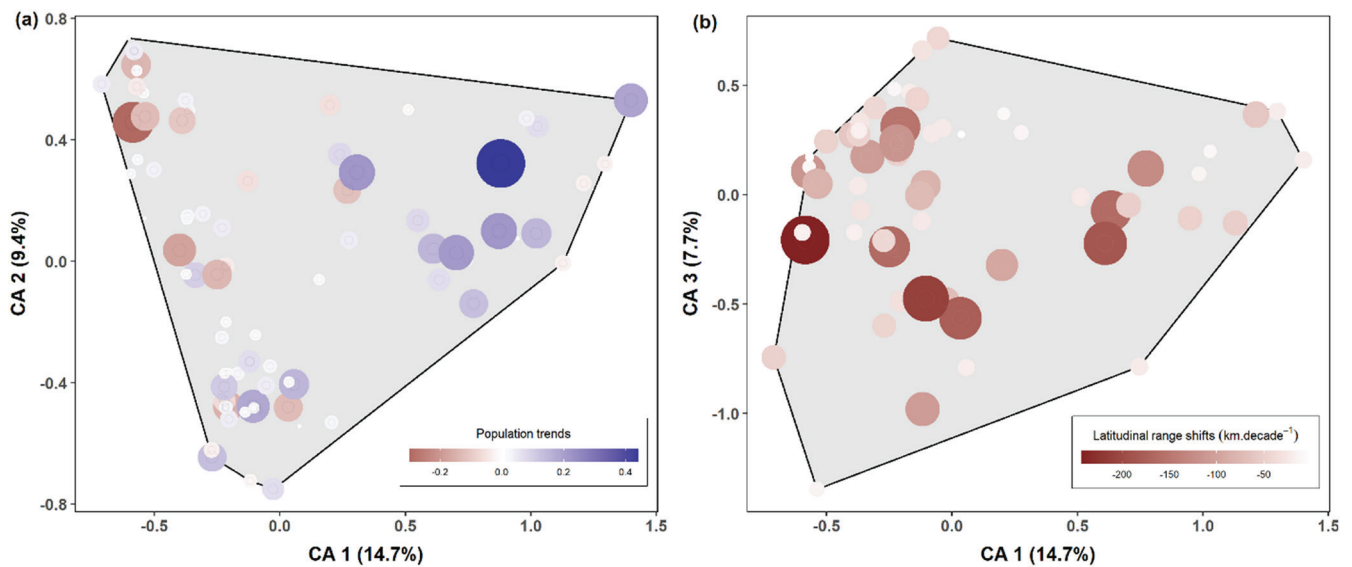


Figure 4. Differences in functional space occupancy between the species that experienced (a) population trends, and (b) latitudinal range shifts. Points size is proportional to the degree of change presented on each plot. Colour gradients also represent the degree of change presented on each plot. The black line delimits the convex hull (light grey polygon) occupied by the species pool within each bi-dimensional trait space.

(Hylander and Ehrlén 2013, Bush and Hoskins 2017, Tonkin et al. 2018b).

We found that population trends were taxonomically structured, however no relationship was found with species range shifts (thus, partly accepting E_{3a}). We also found that changes in population size and latitudinal range shifts of taxa were associated with distinct functional traits, confirming our expectation of a relationship between the functional characteristics of species and their vulnerability to climate and land-use change (E_{3b}). Several mayflies (Ephemeroptera) and caddisflies (Trichoptera) exhibited decreasing abundances over the 26-year period, many species from these orders are widely considered as pollution-sensitive (Stark 1985, Usseglio-Polatera and Bournaud 1989). By contrast, we observed a rise in crustaceans (Crustacea), snails (Gastropoda) and scavenger beetles (Coleoptera), these groups being mainly composed of eurythermal taxa, typical from slow-flowing waters, and tolerant to a wide range of water quality conditions, including low oxygen but high nutrient concentrations (Stark 1995). Increasing population sizes and latitudinal range shifts were strongly related to high numbers of reproductive cycles per year (two or more) and descendants per reproductive cycle, respectively. Such r-selected strategies have been found to correlate with other increasing population sizes and/or species range shifts in freshwater and marine organisms' facing climate change. For example, McLean et al. (2018b) found that rapid warming drove marine pelagic fishes with r-selected life history traits to shift abruptly poleward. Similarly, Comte et al. (2014) found that species with high propagule pressure (i.e. r-strategists) and greater mobility, displayed the greatest range shifts in stream fishes facing climate change. Here, increasing population sizes and latitudinal range shifts were

also related to traits like long-life duration of adults and large body sizes, which are more typical of K-strategists' species. This result is in agreement with previous studies highlighting that such strategies can be promoted under climate change (del Cacho et al. 2012), especially in running waters experiencing climate-driven flow reduction (Floury et al. 2017).

Conclusion

We found that rates of changes in macroinvertebrate taxonomic composition in New Zealand's River systems over a 25-year period are latitudinally structured but not changes in their trait composition. We observed increasing rates of taxonomic extirpations at the rear edge of mainland New Zealand but increasing taxonomic colonisations at the leading edges. Further, we found that most taxa tended to increase in population and range size rather than decrease. Changes in community composition correlated with recent climate and land-use change. Macroinvertebrate functional traits related to life-history and morphology explained changes in population size and species latitudinal range shifts. Our findings highlight the critical need to move beyond observation of emergent state-level variables to understanding the mechanisms underpinning taxonomic and functional reorganisation of biodiversity under ongoing environmental changes (Tonkin et al. 2019).

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Data availability statement

The data that support the findings of this study are available from the National Inst. of Water and Atmospheric research (NIWA) upon request. Restrictions apply to the availability of these data, which were used under license for this study.

Supporting information

The supporting information associated with this article is available from the online version.

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Cetacean conservation planning in a global diversity hotspot: dealing with uncertainty and data deficiencies

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Abstract. Many cetacean species are at risk from anthropogenic disturbances including climate change, pollution, and habitat degradation. Identifying cetacean hotspots for conservation management is therefore required. Aotearoa–New Zealand waters are used by 53% of the world’s cetacean species and are a global cetacean diversity hotspot. Using geographic predictions of cetacean taxa, we aimed to identify important areas within New Zealand waters using two methods: estimates of cetacean richness and a spatial prioritization analysis. For both methods, we investigated how varying levels of uncertainty in predictions of the taxa’ occurrence layers would affect our interpretation of cetacean hotspots. Despite some marked spatial differences in distribution of important areas for cetacean diversity, both methods, across all uncertainty scenarios, highlighted six distinct deep offshore regions as important habitat. Generally, inshore areas had lower richness estimates than offshore areas, but these remain important for conservation for species with limited ranges (e.g., the endemic Māui and Hector’s dolphins), and in some places had similar richness values to offshore hotspots. Furthermore, inshore hotspots had lower uncertainty in predicted taxa distribution and richness estimates. The use of two different uncertainty estimates allows the integration of distributional information from differing sources (different modeling methods with varying numbers of cetacean records) to be integrated in a robust and conservative way. Identification of cetacean hotspots with varying levels of uncertainty provides a robust and efficient step toward prioritizing areas for conservation management in a participatory process.

Key words: New Zealand; richness; spatial prioritization; species distribution models; uncertainty.

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INTRODUCTION

Marine mammals play key roles in the world's ecosystems and are important to people through economic and social benefits from related tourism, culture, and recreation (Schipper et al. 2008, Hammerschlag et al. 2019). Despite their importance, there remains a paucity of information for a number of marine mammal taxa due to their elusive behavior and offshore habitat use. However, it is well established that many populations are at risk from anthropogenic disturbances through habitat degradation, including climate change, pollution, underwater noise, and fisheries competition, and direct hunting (Schipper et al. 2008, Albouy et al. 2017, Ramírez et al. 2017, Clapham and Baker 2018, Reeves 2018, Hammerschlag et al. 2019, Albouy et al. 2020). Broad global-scale estimates of cetacean distribution and richness have been developed (Kaschner et al. 2006, 2011) providing crucial information for assessing potential large-scale effects of anthropogenic impacts on different populations and taxa (e.g., Pershing and Stamieszkin 2020). For example, Albouy et al. (2017) identified global multifaceted biodiversity hotspots (based on functional diversity, phylogenetic diversity, and species richness) for marine mammals and their potential spatial overlap with human threats. More recently, Albouy et al. (2020) used a trait-based approach to assess the vulnerability of all marine mammals to global warming. The latter work demonstrated that potential extinctions of marine mammals that were most at risk from global warming could induce a disproportionate loss of functional diversity in marine ecosystems. There are well-documented shifts in the spatiotemporal distribution of cetaceans (e.g., Friday et al. 2013, Ramp et al. 2015, Meyer-Gutbrod and Greene 2018), pinnipeds (Szpak et al. 2018, e.g., Hückstädt et al. 2020), and polar bears (*Ursus maritimus*; e.g., Laidre et al. 2020) due to climate change-induced ecosystem shifts. In addition, several other studies have documented the impact of localized anthropogenic activities on marine mammals, such as underwater noise, pollution, ship strikes, and over-harvesting of prey species (Davidson et al. 2012, Jepson et al. 2016, Azzellino et al. 2017, Scales et al. 2017, Abrahms et al. 2019).

Global-scale conservation practices are widely acknowledged as having positive effects on biodiversity (Hoffmann et al. 2010, Costello 2019, Purvis et al. 2019); however, regional (national) conservation efforts may be equally important, given current challenges for transboundary conservation efforts (Mason et al. 2020) and for highly mobile species (Woinarski et al. 1992). Conservation efforts in New Zealand may be particularly important because it is recognized as a globally important cetacean diversity hotspot (Myers et al. 2000, Davidson et al. 2012, Albouy et al. 2017). In total, 53% ($n = 47$) of the world's known cetacean species, subspecies, and/or ecotypes including resident, migrant, or vagrant taxa have been identified in the New Zealand Exclusive Economic Zone (EEZ; Baker et al. 2019). Seven of these, including the endemic Hector's (*Cephalorhynchus hectori hectori*) and Māui dolphins (*C. h. maui*), are listed as Endangered or Critically Endangered under the IUCN threat classification system (IUCN 2001), and 28 are considered Data Deficient, hence are unable to be classified (IUCN 2015). All cetacean species in New Zealand's marine environment are protected under national law by the New Zealand Marine Mammals Protection Act (1978). Recent species distribution models (SDMs) developed by Stephenson et al. (2020b) produced a comprehensive understanding of cetacean distribution in New Zealand for 30 species, subspecies, and species complexes. Such work can inform the management of potential threats to cetaceans such as fishing, shipping, mineral extraction, and other threats that are heterogenous in space (Baker et al. 2019). However, questions remain as how to best use this information for management given differing levels of uncertainty and the implications of ignoring species that are either rare or for which little information exists. To date, we are not aware of any studies that have attempted to identify hotspots of cetacean diversity within the New Zealand EEZ. This lack of information is a major limitation with respect to the effective conservation of New Zealand's biodiversity, including highly migratory species crossing jurisdictional waters, facing intensifying anthropogenic threats.

The most commonly used approach to identify areas of conservation priority is the biodiversity hotspot approach. This approach was originally

used by Myers (1988) to identify areas facing exceptional degrees of threat and supporting exceptional concentrations of species with high levels of endemism (Myers et al. 2000). A commonly used approach to identify biodiversity hotspots is to estimate species richness. However, distribution of species richness may be biased toward areas where species with large overlapping ranges occur; that is, those species with restricted non-overlapping ranges will not contribute greatly toward the summed species richness (Veach et al. 2017). Furthermore, areas with high richness may represent marginal habitats for several species but may not represent ideal habitats (i.e., those habitats likely to support healthy populations) for any of these taxa.

Spatial prioritization analyses that account for range size bias can also be used for identifying biodiversity hotspots (e.g., Hillman et al. 2020). Both richness estimates and spatial prioritization analyses require knowledge of the geographical distributions of target species. SDMs offer a recognized correlative method of predicting species' probability of occurrence (Guisan and Thuiller 2005, Elith et al. 2006). Information on the presence of species, such as from incidental sightings, is used as an input response variable to model a species' ecological niche based on the assumption that the distribution of known encounters reflects the species' environmental preferences. The performance of SDMs is, however, highly dependent on sample size and sampling extent (Stockwell and Peterson 2002, Wisz et al. 2008, Bean et al. 2012). Hence, rare species may be highly challenging to incorporate into SDM analyses (Granger et al. 2015, Ferrer-Sánchez and Rodríguez-Estrella 2016), possibly introducing bias in the designation of areas of high importance for the conservation of biodiversity and ecosystem functions (Mouillot et al. 2013, Ferrer-Sánchez and Rodríguez-Estrella 2016). In addition to a lack of distributional data for rare taxa, the uncertainty in distribution data and/or accounting for data availability is rarely considered for conservation planning (Moilanen et al. 2006b, Rowden et al. 2019). Given that many of the cetacean species occurring in New Zealand are data deficient or inhabit poorly surveyed offshore waters with very few observation records, it is important to not only consider these species but also consider the uncertainty surrounding their distributions.

Furthermore, understanding the effects of using several, differing, measures of uncertainty for spatial management is crucial for impact assessment of marine activities and conservation efforts (Beale and Lennon 2012), as well as for highlighting potential data gaps.

Here, we seek to identify cetacean diversity hotspots in a globally important location for cetaceans, the New Zealand EEZ. Despite some criticisms (Marchese 2015, Veach et al. 2017), models of species richness and the concept of diversity hotspots are widely used to develop cost-effective strategies for biodiversity conservation (Myers et al. 2000, Norman 2003, Orme et al. 2005). Using mean long-term geographic predictions of species' occurrences (at a 1-km grid resolution, annual scale) from Stephenson et al. (2020a), we aim to identify important areas within the New Zealand EEZ for cetacean taxa using two methods: estimates of cetacean richness and a spatial prioritization analysis. For both methods, we investigate how varying levels of uncertainty in spatial predictions of occurrence influence the interpretation of cetacean hotspots and their efficacy for informing national and global conservation efforts.

METHODS

Study area

The study area extends over 4.2 million km² of the South Pacific Ocean within the New Zealand EEZ (~25–57° S; 162° E to 172° W; Fig. 1). New Zealand's two long and narrow main islands span a wide latitudinal range, resulting in a diverse array of environmental conditions within the waters of the EEZ (Bradford-Grieve et al. 2006, Stephenson et al. 2018).

Distribution models of cetacean taxa

At-sea cetacean sighting records of 30 cetacean species, subspecies, and species complexes (herein referred to as cetacean taxa), collected over the period 1980–2017, were collated from multiple databases (Stephenson et al. 2020a). Depending on the number of records available for each taxa, different analyses were undertaken to estimate distributions (Table 1). For those taxa with fewer than 50 recorded sightings, relative environmental suitability (RES) models (Kaschner et al. 2006) were used to predict probability

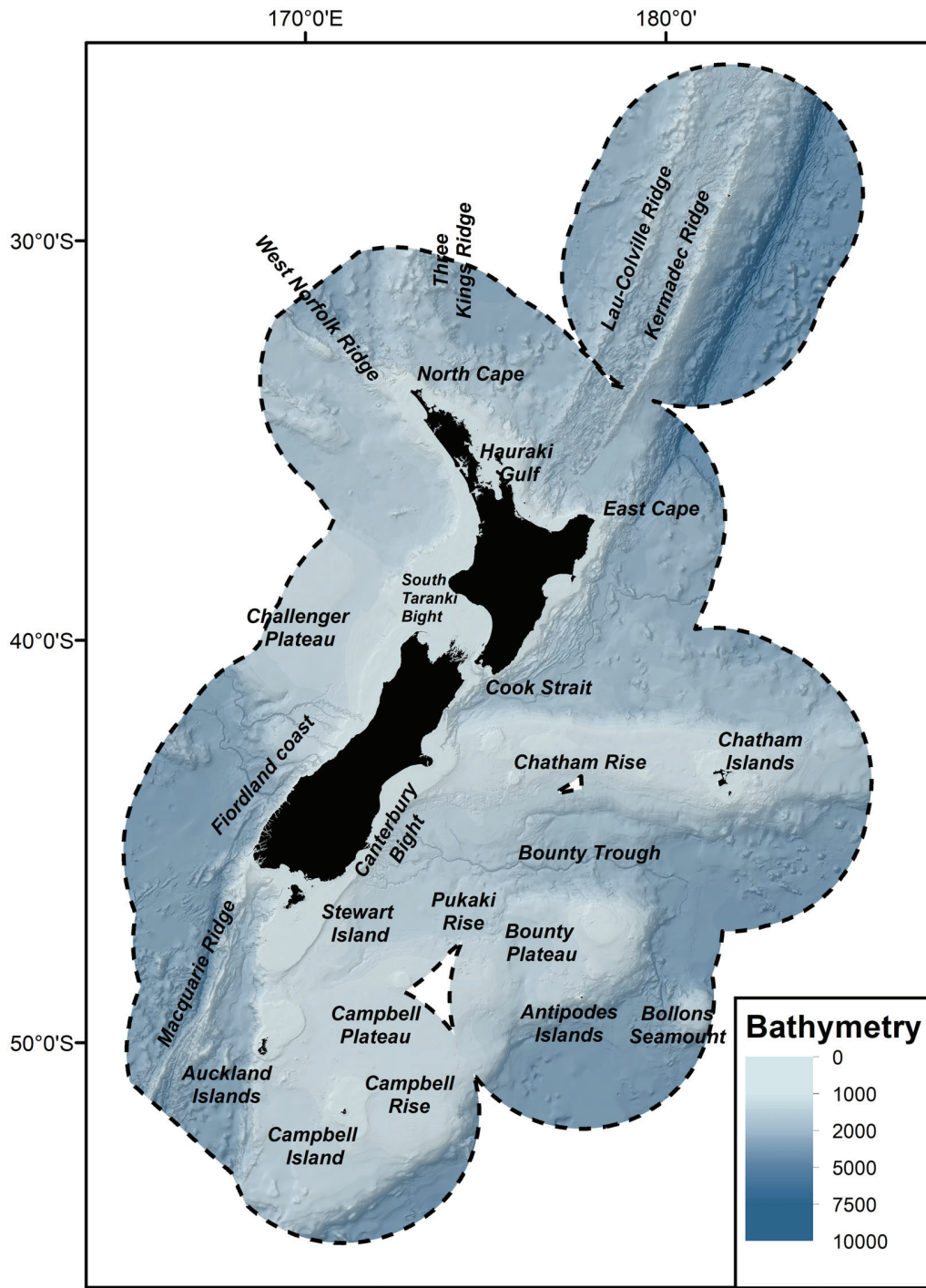


Fig. 1. Map of the study region (New Zealand Exclusive Economic Zone [EEZ], black dashed line), bathymetry, and feature names used throughout the text; figure modified from Stephenson et al. (2020a).

Table 1. Number of cetacean sighting records per species, subspecies, or species complexes included in Stephenson et al. (2020a).

| Taxa common names | Species/subspecies | No. of sighting records | AUC calculated from evaluation data |
|---|---------------------------------------|-------------------------|-------------------------------------|
| Common dolphin | <i>Delphinus delphis</i> | 4411 | 0.90 ± 0.01 |
| Māui dolphin | <i>Cephalorhynchus hectori maui</i> | 1051 | 0.99 ± 0.00 |
| Hector's dolphin | <i>C. h. hectori</i> | 3688 | 0.99 ± 0.00 |
| Dusky dolphin | <i>Lagenorhynchus obscurus</i> | 823 | 0.95 ± 0.01 |
| Pilot whale (2 spp.) | <i>Globicephala melas</i> | 680 | 0.91 ± 0.02 |
| | <i>G. macrorhynchus</i> | | |
| Humpback whale | <i>Megaptera novaeangliae</i> | 629 | 0.85 ± 0.02 |
| Bryde's whale | <i>Balaenoptera edeni brydei</i> | 593 | 0.93 ± 0.01 |
| Killer whale | <i>Orcinus orca</i> | 569 | 0.79 ± 0.02 |
| Bottlenose dolphin | <i>Tursiops truncatus</i> | 498 | 0.81 ± 0.02 |
| Sperm whale | <i>Physeter macrocephalus</i> | 497 | 0.92 ± 0.01 |
| Southern right whale | <i>Eubalaena australis</i> | 477 | 0.94 ± 0.01 |
| Blue whale (2 recognized sub spp.) | <i>Balaenoptera musculus musculus</i> | 355 | 0.95 ± 0.02 |
| | <i>B. m. breviceauda</i> | | |
| Sei whale | <i>Balaenoptera borealis</i> | 70 | 0.81 |
| Fin whale | <i>Balaenoptera physalus</i> | 61 | 0.79 |
| Minke whale | <i>Balaenoptera acutorostrata</i> | 57 | 0.81 |
| Arnoux's beaked whale | <i>Berardius arnuxii</i> | 31 | na |
| False killer whale | <i>Pseudorca crassidens</i> | 28 | na |
| Southern right whale dolphin | <i>Lissodelphis peronii</i> | 27 | na |
| Gray's beaked whale | <i>Mesoplodon grayi</i> | 9 | na |
| Cuvier's beaked whale | <i>Ziphius cavirostris</i> | 7 | na |
| Risso's dolphin | <i>Grampus griseus</i> | 5 | na |
| Shepherd's beaked whale | <i>Tasmacetus shepherdi</i> | 5 | na |
| Southern bottlenose whale | <i>Hyperoodon planifrons</i> | 4 | na |
| Andrew's beaked whale | <i>Mesoplodon bowdoini</i> | 2 | na |
| Hourglass dolphin | <i>Lagenorhynchus cruciger</i> | 2 | na |
| Pygmy sperm whale | <i>Kogia breviceps</i> | 2 | na |
| Blainville's beaked whale | <i>Mesoplodon densirostris</i> | 1 | na |
| Dwarf minke whale | <i>Balaenoptera acutorostrata</i> | 1 | na |

Notes: Taxon names in boldface indicate taxa for which boosted regression tree probability of occurrence models was fitted; roman text indicates taxa for which relative environmental suitability models were run. AUC values were calculated using evaluation data and for those models that were bootstrapped are shown as the mean ± SD.

of occurrence (Table 1). Briefly, RES models predict the geographical ranges of taxa using basic descriptive, widely available data (i.e., the relationships between taxa and three environmental variables: sea surface temperature, water depth, and distance to shore) that are available for most taxa, including those for which few (or no) recorded locations are available (Kaschner et al. 2006). Although RES is a conceptually simple modeling approach, it is a well-established method that has been successfully applied to predict global distributions of cetaceans and other marine taxa (Kesner-Reyes et al. 2016). Stephenson et al. (2020a) concluded that estimated probability distributions using RES were consistent

with the limited sighting records available for 15 rarely sighted taxa, providing some evidence that the environmental niche of an individual taxa was at least encompassed within the RES prediction. RES predictions are currently the best available information for rare taxa; however, given the low levels of information, these predictions should be used cautiously (Stephenson et al. 2020a).

For taxa with more than 50 recorded sightings (bold typeface in Table 1), boosted regression tree (BRT) models (Elith et al. 2006) were fitted using 14 gridded environmental variables (1-km grid resolution, annual scale), bootstrapped 100 times, to predict probability of occurrence and a

spatially explicit measure of uncertainty (measured as the standard deviation of the mean [SD]; Stephenson et al. 2020b). BRT models used to predict cetacean taxon occurrence performed well (model goodness of fit: AUC > 0.75; Table 1). Distributions of individual taxon occurrence aligned with information on known distributions of some taxa and were visually congruent with recorded sighting data (used to train the models) and evaluation data. A separate independent statistical validation of models for a subset of taxa (bottlenose [*Tursiops truncatus*], common [*Delphinus delphis*], Hector's and dusky dolphins [*Lagenorhynchus obscurus*], and Bryde's [*Balaenoptera edeni brydei*] and killer whales [*Orcinus orca*]) provided further evidence that these model predictions were robust. See Stephenson et al. (2020a) for further details on methodology, description of environmental predictors, model parametrization, and results.

Spatially explicit measures of uncertainty

Two measures of spatially explicit uncertainty were produced by Stephenson et al. (2020a): an estimate of the coverage of the environmental space by all cetacean sighting records (herein referred to as environmental coverage; Appendix S1: Fig. S1A), and estimates of the uncertainty of the distributions for those taxa with sufficient data (herein referred to as taxa uncertainty, example shown in Appendix S1: Fig. S1B). All maps of taxa distributions and associated estimates of spatially explicit uncertainty are available in Stephenson et al. (2020a).

When model predictions are projected into areas for which no occurrence data exist, it is important to understand the similarity between the new environments and those used in training the model (Elith et al. 2010). The environmental coverage (Smith et al. 2013, Stephenson et al. 2020a) provides an indication of which parts of this environmental space contain many sighting records (across all taxa) and are presumed to have more certain predictions of taxa distributions. Similarly, parts of the environmental space containing few sighting records are identified with the assumption that the relationship between the environment and the sighting records is poorly understood and predictions are less certain (Smith et al. 2013). Methods and the

mapped coverage of the environmental space are provided in Appendix S1.

Associated uncertainty estimates of taxon distributions were provided as standard deviation (SD) of the mean predicted probability of occurrence (estimated through bootstrapping of the BRT models, described in section *Cetacean systematic conservation planning*). An important consideration for these uncertainty layers is that the BRT model predictions are not well extrapolated into unsampled environmental space (i.e., the predicted values shown will simply be those of the closest environmental space). In addition, the confidence estimates may remain low in poorly sampled areas because the bootstrapping requires variability between samples to produce estimates of error.

Cetacean richness hotspots

Two methods were used to identify important areas for multiple cetacean taxa: (1) distribution of cetacean richness; and (2) spatial prioritization analyses. For both methods, we investigated how varying levels of uncertainty in the spatial layers affect interpretation of cetacean hotspots (Fig. 2). Here, we present results of three uncertainty scenarios for both the cetacean richness and spatial prioritization analyses: (1) no inclusion of uncertainty estimates (herein referred to as the "baseline" scenario); inclusion of moderately weighted uncertainty estimates (herein referred to as "moderate-uncertainty" scenarios); and the inclusion of highly weighted uncertainty estimates (herein referred to as "high-uncertainty" scenarios; Fig. 2).

Cetacean richness

Cetacean richness for the baseline scenario (without inclusion of uncertainty) was estimated by summing the occurrence probability predictions from individual modeled taxon distributions (Fig. 2; Ferrier and Guisan 2006, Calabrese et al. 2014, Stephenson et al. 2020b).

Cetacean richness for moderate- and high-uncertainty scenarios was produced by down-weighting the individual taxon occurrence layers prior to summing (Fig. 2). Down-weighting for taxon occurrence layers predicted using BRTs was done by multiplying individual taxon distribution layers by their associated cross-validation AUC scores (Table 1). Uncertainty discounting

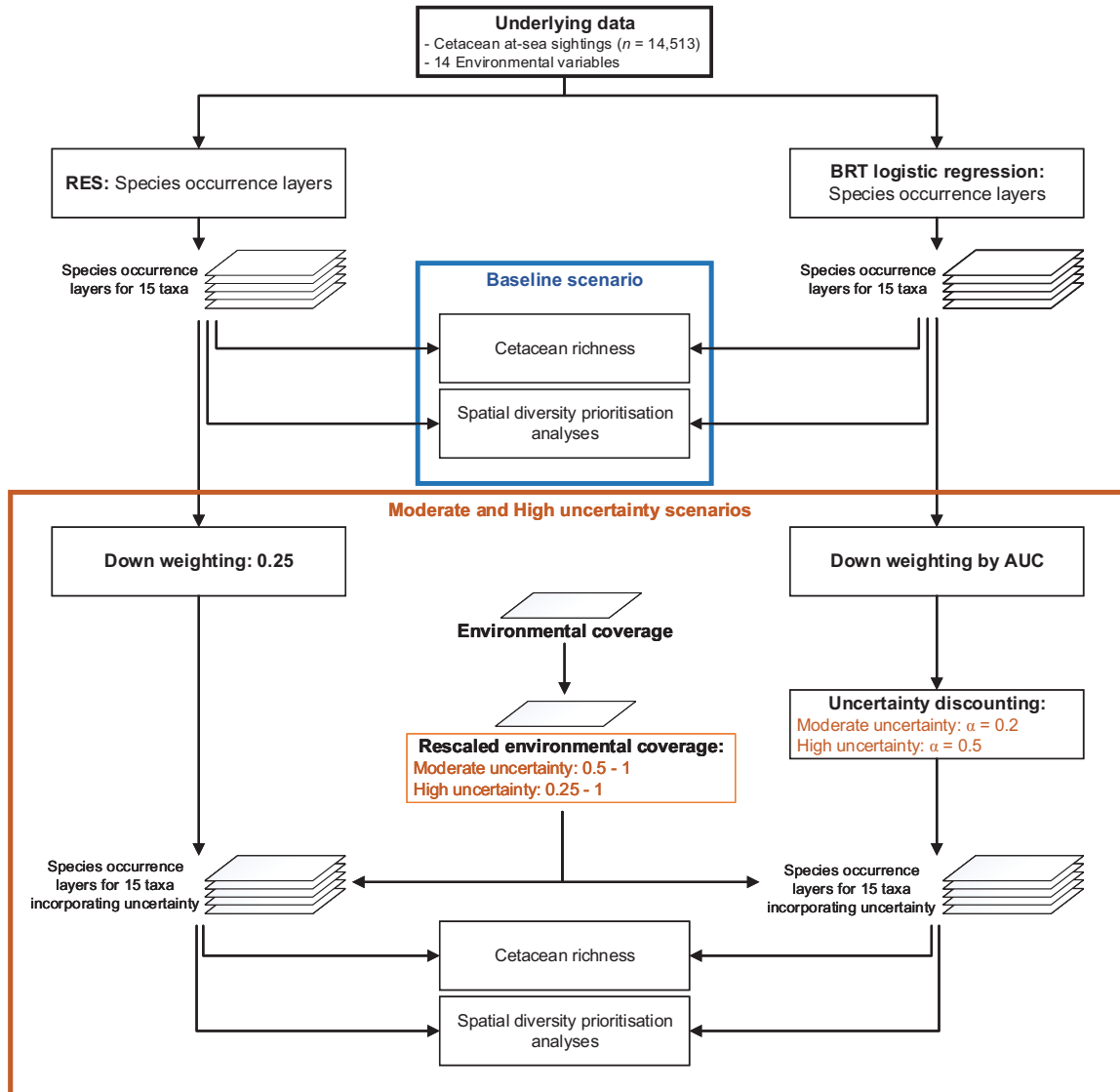


Fig. 2. Infographic depicting key steps in the preparation of spatial data layers and their use for estimating cetacean richness and spatial prioritization analyses with varying levels of incorporation of uncertainty (baseline, moderate-uncertainty, and high-uncertainty scenarios).

was then applied to these layers using methods described in Moilanen et al. (2006a), where info-gap theory is applied to achieve conservation targets given the most adverse choice of probabilities (in other words, when all probabilities are at their lower bounds). For all taxon layers, this was implemented following Eq. 1 (described in Moilanen et al. 2006a):

$$P_{ij} = P^*_{ij} - \alpha W_{ij} \quad (1)$$

where α is the degree of uncertainty, and W_{ij} is any error measure (here, the SD of each cell from the spatially explicit uncertainty maps) related to the accuracy of P^*_{ij} (the mean probability of occurrence for cetacean taxa j in cell i ; Moilanen and Wintle 2006). A range of α values were

trialed: 0.1, 0.2, 0.3, 0.4, and 0.5. Results using a moderate ($\alpha = 0.2$)- and a high-uncertainty weighting ($\alpha = 0.5$) were subsequently used in the moderate-uncertainty and high-uncertainty scenarios, respectively.

Since model evaluation metrics and spatially explicit estimates of uncertainty are not available when using RES models, RES layers were subjectively down-weighted using a 0.25 multiplier. This value was arbitrary but reflects expert evaluation of the relative value of RES values compared with BRT models.

Finally, the environmental coverage was used to down-weight both RES- and BRT-derived taxon distribution layers. The environmental coverage layer was rescaled so that values ranged from 0.5 to 1 and 0.25 to 1 for the moderate-uncertainty and high-uncertainty, scenarios, respectively. The rescaled environmental coverage layer was multiplied with the taxon distribution layers, resulting in areas with high environmental coverage retaining their predicted occurrence values, whereas less certain areas with lower environmental coverage were down-weighted. The rescaling of environmental coverage ensured that many offshore areas were retained yet reflect that these areas are poorly understood (but still provide some useful information). The adjusted RES- and BRT-derived taxon distribution layers were summed to produce a single conservative estimate of richness for the study area (Fig. 2).

Spatial diversity prioritization

A spatial diversity prioritization analysis, using the software Zonation (Moilanen et al. 2009), was undertaken to identify a representative set of areas with the highest conservation value for cetacean taxa in New Zealand (incorporating the importance of range-restricted species that do not contribute greatly to summed estimates of richness). Zonation initially assumes that the entire area of interest (study area) is protected, sequentially removing in a stepwise fashion those cells making the lowest contribution to the representation of a full range of biodiversity features, in this case, cetacean distribution layers (Moilanen et al. 2014). For all analyses presented here, the additive benefit function (ABF) algorithm was used for prioritization (Moilanen 2007). This method generally gives greater value

to areas with overlapping distributions of species (Moilanen 2007, Virtanen et al. 2018).

Spatial prioritization analysis for the baseline scenario (without inclusion of uncertainty) was undertaken with all layers equally weighted and no estimates of uncertainty (Fig. 2). Default settings were used for other parametrization options (e.g., edge removal, no aggregation algorithm, no cost layers, and no administrative unit analysis).

Spatial prioritization analysis for moderate- and high-uncertainty scenarios was produced by down-weighting the individual taxon occurrence layers based on confidence in model predictions, the individual taxon uncertainty layer (if available), and the environmental coverage prior to analysis (Fig. 2). As for richness estimates for moderate- and high-uncertainty scenarios, BRT taxon distribution layers were down-weighted according to their cross-validation AUC scores and their respective spatially explicit uncertainty layer with a weighting of $\alpha = 0.2$ and $\alpha = 0.5$. RES taxon occurrence layers were down-weighted (layer weighting: 0.25). Finally, the rescaled environmental coverage (ranging from 0.5 to 1.0 and 0.25 to 1.0 for the moderate-uncertainty and high-uncertainty scenarios, respectively) was again used to down-weight all taxon distribution layers using the condition function in Zonation (which implements the same down-weighting as that described for the richness estimates). Default settings were used for other parametrization options.

Zonation outputs included a single map of biodiversity prioritization, with areas identified from the highest to lowest priority in terms of conservation value (Moilanen et al. 2011). In this study, outputs were presented as maps that identified the top 5%, 10%, 20%, and 30% priority areas for cetacean diversity. Other Zonation outputs included the proportion of each taxon's (assumed) range protected across the range of prioritization (i.e., 0–100% of total area selected collated into tables). At each priority conservation level (top 5%, 10%, etc.), the ranges of individual taxa contained within these areas can be examined providing information on whether taxa are adequately represented. Prioritizations can then be judged according to whether a greater proportion of the taxon's range is protected than the proportion of the priority area

(e.g., if taxon X has $\geq 5\%$ of its range protected within the top 5% priority areas, this would be considered an adequate solution for taxon X). It should be noted that the proportion of each taxon's range will tend to decrease (reduced in spatial extent) with increasing uncertainty because the taxon's occurrence values have been down-weighted to the point of removal for some cells resulting in a smaller total (assumed) range. Comparison between uncertainty scenarios was nevertheless considered because erroneous areas (most likely those areas with higher uncertainty) would not be included.

RESULTS

Cetacean richness

Cetacean richness estimates for the baseline scenario ranged from 1 to 8 inshore (<50 km from the coast) and 9 to 18 for offshore areas (Fig. 3A). Unsurprisingly, the highest richness estimates were lower (maximum: 18, Fig. 3A) than the 30 taxa modeled since not all taxon distributions overlapped. The highest estimates were observed in deep offshore waters (>50 km from the coast) along the southern part of the Lau-Colville and Kermadec Ridges (see Fig. 1 for place names, Fig. 3A, iii), Macquarie Ridge and along the western edge of the Campbell Plateau (Fig. 3, ii), and the northern and western edges of the Bounty Trough and the north and south of the Chatham Rise (Fig. 3A, iv). Much of the high richness offshore areas had lower confidence (as measured by the coverage of the environmental space—crisscross black lines in Fig. 3A). Closer to shore (<50 km), cetacean richness was generally predicted to be lower (predominately between 3 and 4), although the Fiordland coast, North Cape, South Taranaki Bight, Kaikōura Coast, Cook Strait, and eastern Bay of Plenty all had regions of moderate cetacean richness (richness 5–8; Fig. 3A).

There were clear differences in predicted cetacean richness with the inclusion of uncertainty compared with the baseline scenario, although broad patterns in richness hotspots were similar (moderate- and high-uncertainty scenarios; Fig. 3B, C, respectively). Maximum predicted richness was 9 in the high-uncertainty scenario (Fig. 3C) compared with 11 in the moderate-uncertainty scenario (Fig. 3B) and 18 in the baseline scenario

(Fig. 3A). With increasing weighting of uncertainty, vast areas offshore displayed lower richness (Fig. 3B, C). However, there was greater contrast between areas with low and high estimated richness in these maps that incorporated uncertainty; that is, many hotspots of cetacean richness remained the same but were more easily observed (e.g., compare Fig. 3A, B, C, iii, ii, iv). The higher weighting of uncertainty further highlighted areas closer to shore as important regions, which had only moderate-richness values in the baseline scenario, including North Cape (Fig. 3B, C, i), Kermadec Islands (Fig. 3B, C, ii), East Cape, South Taranaki Bight (Fig. 3B, C), and the west coasts of South Island and North Island (Fig. 3B, C, i). Some offshore areas with low environmental coverage (crisscross black lines in Fig. 3) still displayed relatively high richness estimates for both moderate- and high-uncertainty scenarios (~8–10 and 6–8, respectively), including the Aotea Basin, along the Norfolk Ridge, Challenger Plateau, and Campbell Plateau (Fig. 3B, C).

Cetacean systematic conservation planning

Spatial prioritization.—The top 30% of priority areas for cetacean diversity for the baseline scenario were broadly distributed across the study area (Fig. 4A). The highest priority areas identified for cetacean diversity (i.e., top 5% of areas, dark red; and top 10%, light red in Fig. 4A) were located in both inshore and offshore areas. Inshore areas included most parts of the South Island (see Fig. 1 for place names, Fig. 4A, iv) and the North Island (North Taranaki Bight and Hauraki Gulf; Fig. 4A, i). Similar to richness hotspots identified in the baseline scenario, offshore priority areas included the Lau-Colville and Kermadec Ridges (Fig. 4A, iii), the areas on the Puysegur Trench (Fig. 4A, ii), and Bounty Trough extending onto the Campbell Plateau and the south Chatham Rise (Fig. 4A, iv). Areas with the next highest priority (top 20% of areas—orange in Fig. 4A) were predominately located along the Aotea Basin (Fig. 4A, i), along the western edge of the Campbell Plateau in the waters west of North East Island (Fig. 4A, ii), and the northern parts of the Lau-Colville Ridge, Kermadec Ridge, and Kermadec Trench (Fig. 4A, iii), and the Bounty Trough (Fig. 4A, iv).

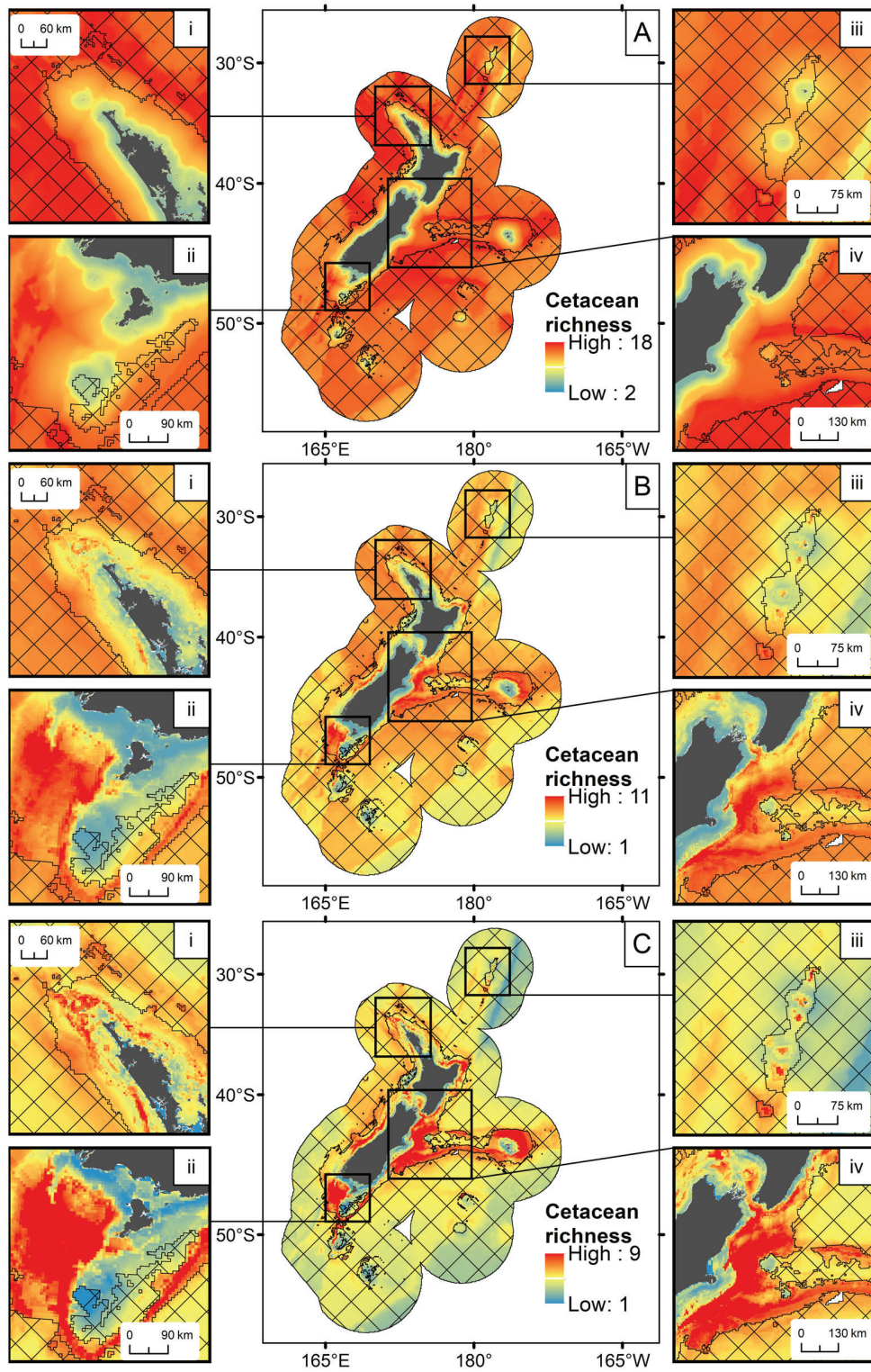


Fig. 3. Cetacean richness estimates in New Zealand derived from the addition of probability occurrences of

(Fig. 3. *Continued*)

individual taxon distributions for (A) baseline scenario (modified from Stephenson et al. 2020a); (B) moderate-uncertainty scenario; and (C) high-uncertainty scenario. Crisscross black lines indicate areas of low predicted environmental coverage depicting the lower confidence that can be placed in the predicted probability occurrence. Inset maps: (i) northern North Island including the North Cape and Hauraki Gulf; (ii) south of the South Island including Snares Island, Stewart Island, and parts of Fiordland Coast; (iii) Kermadec Islands, Lau-Colville Ridge, and Kermadec Ridge; (iv) south of the North Island including the South Taranaki Bight and Cook Strait and north of the South Island including the western Chatham Rise. Note the different scales for each inset map.

There were clear differences in the location of high-priority areas with the inclusion of uncertainty (Fig. 4B, C) compared with the baseline scenario (Fig. 4A). The high-priority areas very close to shore (<10 km) in most parts of the North and South Islands (i.e., top 5% of areas, dark red in Fig. 4) were present across all scenarios. With increasing weighting of uncertainty, these areas extended further from shore (Fig. 4B, C). Some high-priority sites further offshore (>50 km) were identified in all scenarios, for example, parts of the Kermadec Ridge (Fig. 4A, B, C, iii), parts of the Puysegur Trench (Fig. 4A, B, C, ii), and the Bounty Trough and south Chatham Rise (Fig. 4A, B, C, iv). However, there was a large shift from high priority further offshore in areas with low environmental coverage in the baseline scenario (Fig. 4) to high-priority offshore sites. These shifts were within areas classified as having adequate environmental coverage (Fig. 4B), and these shifts increased for the high-uncertainty scenario (Fig. 4C). Areas identified as high-priority areas in the moderate- and high-uncertainty scenarios included large parts of the North Cape (Fig. 4B, C, i), East Cape, South Taranaki Bight, Cook Strait (Fig. 4B, C), Kaikōura coast, and the western and eastern slopes of the Chatham Rise (Fig. 4B, C, iv). In both moderate- and high-uncertainty scenarios, some top priority areas were still selected in areas with low environmental coverage despite the increasing incorporation of uncertainty (e.g., parts of the Three Kings Ridge, Fig. 4B, C, i; Lau-Colville Ridge, Fig. 4B, C, iii) although these had reduced priority values compared to other areas with greater certainty in model predictions.

Taxon range.—For each priority level of the baseline scenario, at least some of each taxon distribution was represented; that is, the taxa with the lowest percentage distribution included in

the top 5% of the baseline prioritization were Blainville's beaked whale and pygmy sperm whale with 3.6% of their distribution included in these areas (Table 2). Seventeen cetacean taxa were adequately represented in the top 5% of the area in the baseline scenario, that is, those taxa with >5% of their distribution included in the top 5% of prioritized area (boldface italic numbers in Table 2). However, 13 of these taxa were those with low number of observations modeled using RES (considered less robust than the BRT models used for taxa with >50 sightings at sea). The number of adequately represented taxa increased with decreasing priority; that is, in the top 20% of baseline priority areas for cetacean diversity, 22 taxa out of 30 included in the analysis were adequately represented (boldface italic numbers in Table 2). However, 7 of the 15 taxa modeled with BRTs were not adequately represented at any priority level within the top 30% of areas selected in the baseline scenario prioritization analysis (bottlenose dolphin, Bryde's whale, common dolphin, dusky dolphin, humpback whale, killer whale, and southern right whale; Table 2).

For each priority level of the moderate- and high-uncertainty scenarios, at least some of each taxon distribution was represented; for example, the taxon with the lowest percentage distribution included in the top 5% of the prioritization in both scenarios was the southern bottlenose whale with 2.7% of its distribution included in the top 5% of priority areas (Table 2). With increasing weighting of uncertainty, there was a shift from taxa with efficient solutions being predicted using RES models (i.e., offshore taxa, with fewer recorded sightings) to those taxa whose distributions were predicted using BRT models (Table 2). For example, in the high-uncertainty scenario, in the top 5% of priority areas, out of the 16 taxa that were adequately represented, 15

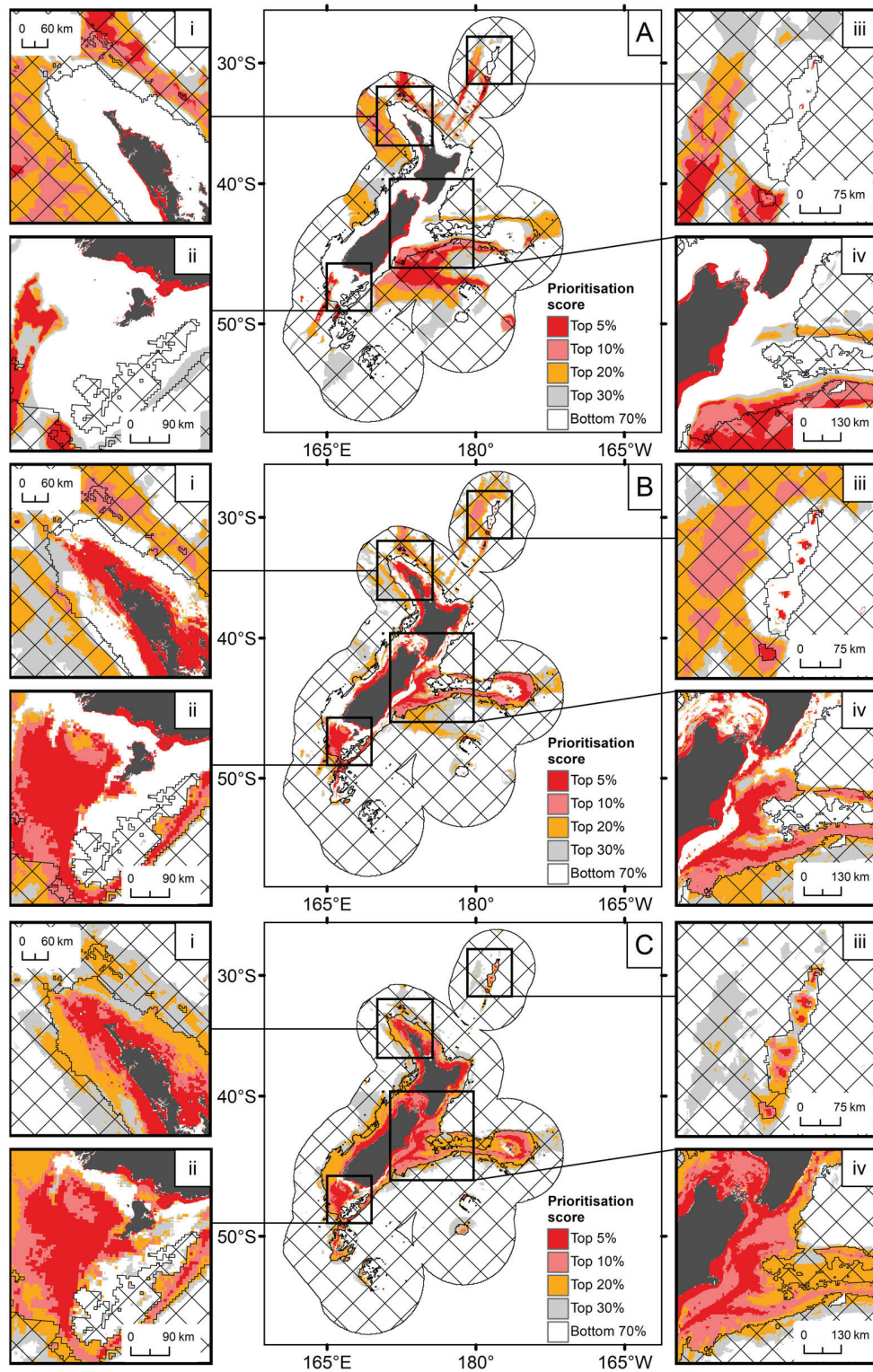


Fig. 4. Spatial diversity prioritization in New Zealand's EEZ (using the additive benefit function in Zonation

(Fig. 4. *Continued*)

software) for the (A) baseline scenario; (B) moderate-uncertainty scenario; and (C) high-uncertainty scenario. Areas were identified from the highest to lowest priority in terms of conservation prioritization (top 5%, 10%, 20%, and 30% priority areas). Crisscross black lines indicate areas of low predicted environmental coverage depicting the lower confidence that can be placed in the predicted probability occurrence. Inset maps: (i) northern North Island including the Aotea Basin, North Cape, and Hauraki Gulf; (ii) south of the South Island including Snares Island, Stewart Island, and parts of Fiordland Coast; (iii) Kermadec Islands, Lau-Colville Ridge, and Kermadec Ridge; and (iv) east of the South Island including the Cook Strait, the western Chatham Rise, the Bounty Trough, and Bounty Plateau. Note the different scales for each inset map.

of these were taxa modeled using the more robust BRT models (taxa with >50 sightings at sea). The number of taxa whose proportion (%) exceeded the prioritization percentage increased markedly with decreasing priority and with increasing weighting of uncertainty. For the high-uncertainty scenario, the top 30% of priority areas were deemed an efficient solution for all

Table 2. Proportion (%) of cetacean taxon distribution within priority areas (top 5%, 10%, 20%, and 30% priority areas) for each scenario: baseline (B); moderate uncertainty (MU); and high uncertainty (HU).

| Taxa | Top 5% of area | | | Top 10% of area | | | Top 20% of area | | | Top 30% of area | | |
|------------------------------|----------------|--------------|-------------|-----------------|--------------|--------------|-----------------|--------------|--------------|-----------------|--------------|--------------|
| | B | MU | HU | B | MU | HU | B | MU | HU | B | MU | HU |
| Mean across all taxa | 8.8 | 8.7 | 11.2 | 14.6 | 14.3 | 18.1 | 26.0 | 25.2 | 29.3 | 37.0 | 35.9 | 39.8 |
| Bottlenose dolphin | 4.1 | 5.7 | 10.7 | 8.4 | 10.7 | 17.1 | 17.5 | 21.1 | 26.6 | 27.3 | 31.3 | 35.9 |
| Blue whale | 4.1 | 3.7 | 7.9 | 10.0 | 10.0 | 14.5 | 22.6 | 23.0 | 25.5 | 33.2 | 35.7 | 37.4 |
| Bryde's whale | 4.8 | 12.0 | 20.5 | 9.3 | 17.4 | 28.1 | 18.5 | 27.5 | 37.9 | 27.9 | 36.8 | 46.4 |
| Common dolphin | 4.8 | 14.6 | 27.4 | 9.4 | 21.5 | 39.0 | 18.3 | 32.1 | 49.7 | 26.9 | 41.9 | 57.7 |
| Dusky dolphin | 4.5 | 8.3 | 13.7 | 8.8 | 14.0 | 24.0 | 16.7 | 21.8 | 37.8 | 25.5 | 29.2 | 46.1 |
| Humpback whale | 5.0 | 6.3 | 11.5 | 9.5 | 11.5 | 18.7 | 19.0 | 21.9 | 29.1 | 28.9 | 31.8 | 38.2 |
| Hector's dolphin | 100.0 | 100.0 | 99.9 | 100.0 | 100.0 | 100.0 | 100.0 | 100.0 | 100.0 | 100.0 | 100.0 | 100.0 |
| Killer whale | 4.6 | 6.3 | 11.3 | 8.9 | 11.2 | 18.4 | 17.8 | 20.5 | 29.2 | 27.3 | 29.9 | 38.4 |
| Māui dolphin | 14.8 | 20.7 | 31.1 | 18.8 | 24.9 | 35.4 | 26.8 | 33.5 | 41.9 | 35.4 | 41.7 | 48.9 |
| Pilot whales | 4.5 | 4.6 | 7.4 | 10.0 | 9.6 | 14.5 | 20.2 | 19.2 | 26.4 | 30.5 | 29.0 | 36.6 |
| Southern right whale | 5.9 | 7.3 | 11.9 | 9.9 | 11.8 | 19.9 | 18.1 | 19.2 | 31.2 | 27.5 | 26.5 | 40.0 |
| Sperm whale | 4.9 | 4.4 | 6.9 | 10.6 | 9.9 | 13.3 | 21.8 | 20.8 | 24.5 | 32.9 | 31.6 | 35.2 |
| Sei whale | 4.5 | 3.4 | 8.6 | 10.1 | 8.2 | 15.1 | 20.2 | 18.9 | 25.3 | 30.4 | 29.7 | 35.3 |
| Fin whale | 4.5 | 4.9 | 10.5 | 10.2 | 10.3 | 18.0 | 20.4 | 21.1 | 28.7 | 30.7 | 31.9 | 38.9 |
| Minke whale | 4.7 | 5.1 | 10.5 | 10.0 | 10.3 | 18.0 | 20.1 | 20.7 | 29.4 | 30.2 | 31.0 | 39.4 |
| Andrew's beaked whale | 6.2 | 4.1 | 4.8 | 13.6 | 10.6 | 11.3 | 28.1 | 23.5 | 24.9 | 41.0 | 36.4 | 37.8 |
| Arnoux's beaked whale | 5.7 | 3.8 | 4.5 | 12.5 | 9.7 | 10.5 | 26.2 | 21.6 | 23.2 | 39.1 | 33.5 | 35.3 |
| Blainville's beaked whale | 3.6 | 3.3 | 4.4 | 10.3 | 11.0 | 10.2 | 27.6 | 27.2 | 24.7 | 40.4 | 43.0 | 40.1 |
| Cuvier's beaked whale | 6.0 | 4.0 | 4.7 | 13.2 | 10.6 | 11.1 | 27.4 | 24.1 | 24.3 | 40.3 | 37.2 | 37.0 |
| Dwarf minke whale | 5.5 | 3.8 | 4.7 | 12.2 | 9.8 | 10.9 | 25.4 | 22.1 | 23.3 | 38.2 | 34.2 | 35.2 |
| False killer whale | 6.6 | 3.2 | 3.3 | 14.4 | 9.8 | 8.5 | 29.9 | 24.0 | 20.0 | 43.1 | 38.0 | 33.2 |
| Gray's beaked whale | 5.7 | 3.8 | 4.5 | 12.5 | 9.7 | 10.5 | 26.2 | 21.6 | 23.2 | 39.1 | 33.5 | 35.3 |
| Hourglass dolphin | 8.0 | 3.3 | 3.0 | 14.8 | 6.8 | 7.8 | 23.1 | 14.1 | 15.7 | 35.8 | 21.5 | 23.0 |
| Pygmy sperm whale | 3.6 | 3.3 | 4.4 | 10.3 | 11.0 | 10.2 | 27.6 | 27.2 | 24.7 | 40.4 | 43.0 | 40.1 |
| Risso's dolphin | 6.7 | 4.8 | 5.7 | 14.8 | 12.4 | 13.2 | 30.4 | 26.8 | 28.2 | 44.5 | 40.5 | 41.9 |
| Southern bottlenose whale | 5.4 | 2.7 | 2.7 | 12.0 | 7.9 | 7.1 | 25.1 | 19.2 | 17.3 | 37.2 | 30.9 | 30.0 |
| Shepherd's beaked whale | 6.2 | 3.0 | 3.1 | 13.8 | 9.0 | 8.1 | 28.7 | 21.6 | 20.1 | 42.1 | 34.3 | 31.8 |
| Striped dolphin | 6.0 | 4.0 | 4.7 | 13.2 | 10.6 | 11.1 | 27.4 | 24.1 | 24.3 | 40.3 | 37.2 | 37.0 |
| Spectacled porpoise | 7.9 | 4.2 | 4.4 | 14.7 | 8.2 | 10.6 | 22.9 | 15.5 | 20.2 | 35.8 | 22.8 | 27.7 |
| Southern right whale dolphin | 5.7 | 3.8 | 4.5 | 12.5 | 9.7 | 10.5 | 26.2 | 21.6 | 23.2 | 39.1 | 33.5 | 35.3 |

Notes: Adequate solutions for cetacean species are shown by boldface italic numbers (e.g., if more than 5% of a cetacean taxa's range is included in the top 5% of prioritized area, this would be considered an adequate solution). Cetacean taxon names are boldface for those cetacean taxa whose distributions were predicted using BRTs.

but two taxa (hourglass dolphin, 23.0%; spectacled porpoise, 27.7%; Table 2).

DISCUSSION

Uncertainty is part of any decision-making process, and therefore, a transparent and robust method for dealing with gaps in information and data is required (Stelzenmüller et al. 2020). Knowledge gaps of marine species distributional data are common, yet spatial conservation management efforts must proceed while accounting for inherent uncertainty (Ansong et al. 2017). Here, we present an approach to estimate cetacean richness and spatial prioritization that explicitly accounts for varying levels of spatial uncertainty to provide a comprehensive overview of cetacean distribution in New Zealand waters. The use of uncertainty estimates allows the integration of distributional information from differing sources (different modeling methods with varying number of cetacean records) to be integrated in a robust and conservative way. This method is particularly important because it allows the integration of the limited spatial information available for rare taxa (RES models), which are seldom considered in a quantitative way for conservation planning.

Cetacean hotspots

Richness estimates and spatial prioritization methods provided complementary measures to identify diversity hotspots. Richness estimates highlight areas with high overlap of taxa distributions, whereas spatial prioritizations account for representativeness of cetacean taxa, thus highlighting the most efficient spatial arrangement to include the maximum ranges of all taxa. Despite some differences, both methods, across all uncertainty scenarios, highlighted several deep offshore waters as important for cetaceans. The congruence between methods and uncertainty scenarios provides evidence that these offshore areas are important for cetaceans. The complex topography in the New Zealand's EEZ spans subtropical to subantarctic waters and enables migratory or wide-ranging species to move across ocean basins (e.g., Thompson et al. 2016, Riekkola et al. 2018). Some species take advantage of prey (Torres et al. 2013) or may use ridges and seamounts or other cues to navigate

(Bouchet et al. 2015). This enables wider genetic connectivity of species seen in New Zealand waters, for example, Gray's beaked whales (Thompson et al. 2016), sperm whales (Alexander et al. 2016), and humpback whales (Riekkola et al. 2018) beyond the EEZ, highlighting the importance of global management approaches to such wide-ranging animals with few boundaries to dispersal. There is limited ability to corroborate the offshore hotspots identified in this study with independent data sets or anecdotal information although historical whaling data could be used (e.g., as in Torres et al. 2013, Carroll et al. 2014). However, the offshore locations identified here provide strong guidance for areas of importance requiring protection from anthropogenic impacts, or priority areas to undertake dedicated surveys to confirm species richness and ecosystem interactions.

Inshore areas generally had lower richness estimates; however, these areas were highlighted as important in all three uncertainty scenarios using the spatial prioritization method, and remain important for conservation for species with limited ranges, for example, Māui and Hector's dolphins and coastal bottlenose dolphins. With increased weighting of uncertainty, areas of moderate and high richness inshore (5–9) became more apparent because these areas were more certain and therefore retained their richness values. These areas included the following: Cook Strait, North Cape, Kermadec Islands, East Cape, South Taranaki Bight, and the west coast of South Island and northern parts of the North Island (Fig. 1). These inshore areas were also highlighted as important in the spatial prioritization analysis for scenarios with moderate- and high-uncertainty discounting. The high productivity and cetacean diversity within the waters of the South Taranaki Bight region (~70–300 m) are assumed to be due to localized wind-driven upwelling system that leads to an abundance of krill (Bradford-Grieve et al. 1993). High densities of this prey resource make the region an important foraging ground for pygmy blue whales (Torres 2013, Barlow et al. 2020) and possibly other species of baleen whale such as sei whales and Bryde's whales observed in this broader region. There is some evidence that corroborates the other inshore locations highlighted as important in this study for several species

(Childerhouse et al. 1995, Lusseau and Slooten 2002, Benoit-Bird et al. 2004, Barlow et al. 2018), but in most cases, there are no published summaries of species richness. This lack of information reflects the species-specific, localized studies that dominate cetacean research in New Zealand, which is largely focused on immediate conservation issues (Baker et al. 2019). Given the lack of information on cetacean hotspots in New Zealand, understanding the implications of incorporating uncertainty is particularly relevant.

Incorporating uncertainty

Environmental and ecosystem models provide a way for conservation practitioners to make management decisions for threatened species under significant uncertainty. While frameworks for formal decision-making have been applied in conservation contexts (Possingham 1997), uncertainty is rarely considered (Regan et al. 2002). Failure to acknowledge sources of uncertainty can lead to poor management decisions (Regan et al. 2005, Link et al. 2012). While uncertainty can readily be incorporated into single-species or single-sector models, for example, by quantifying the error around estimates, incorporation of uncertainty into multi-taxa models or for ecosystem-based management is more difficult. Here, we develop a methodological approach that explicitly incorporates two sources of uncertainty for 30 cetacean taxa. The two spatially explicit measures of uncertainty estimated here should not be considered in isolation and provide two complementary measures to be considered by managers. The environmental coverage provides an indication of which areas of the taxon's probability of occurrence are likely to have been extrapolated into unsampled space, that is, where there is limited information to validate the predicted relationships (Stephenson et al. 2020*b*). Associated uncertainty estimates of species' distribution provide an important indication of the variability in the modeling estimates (Leathwick et al. 2006). The cetacean distributions and the associated spatial uncertainty used here were estimated using occurrence records collected over the period of 40 yr (Stephenson et al. 2020*b*). This broad temporal window means that the spatial predictions presented here should be interpreted as a temporally smoothed representation of cetacean hotspots. The uncertainty

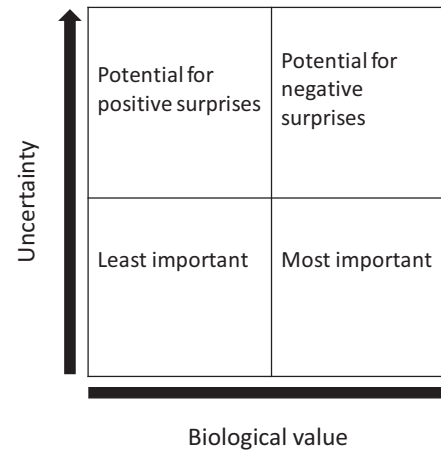


Fig. 5. Four broad outcomes for conservation based on biological quality and the certainty of that information (figure adapted from Moilanen et al. 2006*a*).

associated with any potential temporal changes in taxon distributions is not quantified here but may be important to consider in a management context (Azzellino et al. 2012, 2017).

The goal of uncertainty analysis in the context of conservation planning is to implement and evaluate trade-offs between biological quality and the certainty of that information (Moilanen et al. 2014). If uncertainty information is available, there are four broad considerations and outcomes for conservation (Moilanen and Wintle 2006, Moilanen et al. 2006*b*, Fig. 5). Areas with high biological value (e.g., high richness or core habitat of endangered species) with low uncertainty should be highlighted as most important (Fig. 5). Conversely, areas with low biological value and with low uncertainty should be highlighted as least important (Fig. 5). Areas with high biological value and with high uncertainty should be avoided for conservation—these are areas that may result in much lower conservation benefits than expected (Fig. 5). Finally, areas with low biological value and with high uncertainty have the potential for being higher value than initially estimated, although this potential benefit requires careful consideration (Fig. 5).

The adequate weighting of uncertainty remains a subjective decision. Here, we provide two examples to highlight differences and consistencies. For conservation planning, several analysis decisions would need to be made, including

the appropriate levels of uncertainty to incorporate, whether all taxa are equally important in the analysis, and whether levels of uncertainty for all taxa are equal. Ideally, these somewhat subjective decisions would be made through a participatory process to ensure buy-in and acceptance of any subsequent policy decisions (Love 2017).

The aim of our moderate- and high-uncertainty scenarios was to highlight areas with high biological value and low uncertainty. Despite only having two uncertainty scenarios, we can draw conclusions on the importance of our areas for cetacean diversity. If an area is always highlighted as important irrespective of the weighting value of uncertainty, then we can be confident that the area is important for conservation (Moilanen et al. 2006b). For example, the offshore areas of the Lau-Colville and Kermadec Ridges, Macquarie Ridge, and along the western edge of the Campbell Plateau, the northern and western edges of the Bounty Trough, and the north and south of the Chatham Rise, and the areas surrounding the Chatham Islands were consistently highlighted in all our scenarios of richness and spatial prioritization analyses. If an area is highlighted as important with low weighting of uncertainty but not with high weighting of uncertainty, then we can conclude that the area contains high biological values, but these are uncertain, for example, many of the offshore areas within the environmental coverage. These areas can still be considered as important, but further investigation is required into the specific levels of uncertainty, the taxa driving these differences, and whether these taxa are considered more important than those in other areas. If the area is not highlighted as important with low weighting of uncertainty but is with high weighting of uncertainty, then we can conclude that the area may have moderate levels of importance with high certainty. For example, inshore areas in the Cook Strait, North Cape, Kermadec Islands, East Cape, South Taranaki Bight, and the west coast of South Island and northern parts of the North Island had moderate levels of richness (5–8) but low uncertainty. These areas became more clearly highlighted as important with increasing weighting of uncertainty.

Spatial management of cetaceans

New information on spatial hotspots in cetacean diversity can provide environmental managers with opportunities to mitigate a range of threats to these taxa. While new information on the distribution of cetacean diversity across the whole EEZ may be considered the best available information, it is still important to acknowledge that much of this habitat, both inshore and offshore, remains unsampled. Thus, decision-makers should carefully consider this uncertainty when considering management actions, such as the approach presented here. Helpfully, the uncertainty measures generated in this study, particularly coverage of the environmental space, allow for stakeholder-friendly representation of this uncertainty as part of a participatory decision-making process (Stelzenmüller et al. 2020).

Spatial models that depict probability of species presence are useful to establish important locations for cetacean diversity (Kaschner et al. 2011, Tobeña et al. 2016). However, the species often have marked variation in abundance as a function of variable residency patterns, migratory patterns, and local/regional endemism. Modeling the relative abundance or density of species would allow the incorporation of such effects into spatial prioritization—and would likely improve the effectiveness of any spatial management (Williams et al. 2014, Johnston 2015). Williams et al. (2014) found high-density areas of most species was inversely related to richness—thus, spatial management based on richness alone would not select areas important for certain species (Albouy et al. 2017). The decision whether to favor diversity or density for individual taxa is a consideration best deliberated during stakeholder participatory processes in conservation planning. However, data to calculate abundance/density are not currently available for many cetacean species, including in New Zealand due to a lack of targeted surveys (but see some taxa modeled in Stephenson et al. 2020a). Targeted surveys that fill data gaps should be prioritized with future research.

The hotspots in cetacean diversity identified in this study can enable spatially explicit management of threats to these taxa, some of which would otherwise be afforded no management efforts due to knowledge gaps. Rather than discounting taxa with few data points from our effort

to describe cetacean diversity, we incorporated all relevant data and accounted for the associated uncertainty. Hence, our results allow managers to scale management decisions along spectrums of diversity and uncertainty simultaneously based on species' importance and/or levels of acceptable risk (e.g., as discussed in Incorporating uncertainty). Such spatially explicit results can be considered alongside threats such as fishing effort and shipping traffic to quantify risk, direct research and monitoring efforts, and ultimately apply effective management schemes. Cetaceans may be impacted by different anthropogenic drivers; for example, climate change is likely to impact many of New Zealand's cetacean species (Learmonth et al. 2006, Simmonds and Isaac 2007). The large EEZ may provide space for the deep-water cetaceans that make up a substantial part of New Zealand's cetacean taxa to adapt to changing ocean conditions (e.g., through foraging plasticity as observed in the Gulf of St. Lawrence, Canada, by Ramp et al. 2015). Greater knowledge on hotspots for deep-diving species may allow the identification of climate change refugia so that management can reduce potential threats in these areas. Shifts in prey availability associated with oceanographic phenomena (Scales et al. 2017) or fishing pressures (Bearzi et al. 2006) may drive variation in distribution and habitat use over different spatial and temporal scales. In addition, pressure from tourism, recreational vessels, shipping, and industrial development can drive cetaceans away from critical habitat (Allen and Read 2000, Azzellino et al. 2017, Derville et al. 2019). Thus, understanding the functional relationships between oceanography, prey, and cetacean behavior that drive predator distribution patterns (e.g., Guerra et al. 2017, Izadi et al. 2018, Barlow et al. 2020) will likely improve the potential for management policies to effectively adapt under a changing climate. For the non-migratory, nearshore species, understanding behavioral plasticity and prey preferences is important when considering the effects of climate change in addition to other anthropogenic threats.

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Development of a Seafloor Community Classification for the New Zealand Region Using a Gradient Forest Approach

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To support ongoing marine spatial planning in New Zealand, a numerical environmental classification using Gradient Forest models was developed using a broad suite of biotic and high-resolution environmental predictor variables. Gradient Forest modeling uses species distribution data to control the selection, weighting and transformation of environmental predictors to maximise their correlation with species compositional turnover. A total of 630,997 records (39,766 unique locations) of 1,716 taxa living on or near the seafloor were used to inform the transformation of 20 gridded environmental variables to represent spatial patterns of compositional turnover in four biotic groups and the overall seafloor community. Compositional turnover of the overall community was classified using a hierarchical procedure to define groups at different levels of classification detail. The 75-group level classification was assessed as representing the highest number of groups that captured the majority of the variation across the New Zealand marine environment. We refer to this classification as the New Zealand “Seafloor Community Classification” (SCC). Associated uncertainty estimates of compositional turnover for each of the biotic groups and overall community were also produced, and an added measure of uncertainty – coverage of the environmental space – was developed to further highlight geographic areas where predictions may be less certain owing to low sampling effort. Environmental differences among the deep-water New Zealand SCC groups were relatively muted, but greater environmental differences were evident among groups at intermediate depths in line with

well-defined oceanographic patterns observed in New Zealand's oceans. Environmental differences became even more pronounced at shallow depths, where variation in more localised environmental conditions such as productivity, seafloor topography, seabed disturbance and tidal currents were important differentiating factors. Environmental similarities in New Zealand SCC groups were mirrored by their biological compositions. The New Zealand SCC is a significant advance on previous numerical classifications and includes a substantially wider range of biological and environmental data than has been attempted previously. The classification is critically appraised and considerations for use in spatial management are discussed.

Keywords: species distributions, spatial management, biodiversity, coastal, deep-sea, macroalgae, demersal fish, benthic invertebrates

INTRODUCTION

Robust identification of priority areas for marine spatial planning is often hampered by a lack of comprehensive knowledge of biodiversity patterns (Ferrier et al., 2007; Arponen et al., 2008; Hortal et al., 2015). Species distribution models (SDMs) are correlative models that predict the occurrence of species in relation to environmental variables and can provide estimates of biodiversity patterns across broad spatial scales where data are often sparse. SDMs have become an important tool for resource management and conservation biology (Moilanen et al., 2011). However, species' distribution estimates using SDMs are often only available for more common species, i.e., there are often large numbers of species that are either poorly described or for which there are not enough records to generate robust distribution estimates (Ellingsen et al., 2007; Anderson et al., 2016). As a consequence, the full complement of biodiversity is typically not represented in marine spatial planning, despite the important roles that biodiversity and rare species can play in the stability and functioning of marine ecosystems (Ellingsen et al., 2007).

In marine spatial planning, there is interest in understanding how communities as a whole respond to environmental gradients, and in identifying the environmental variables that best predict patterns of biodiversity (rather than individual species' distributions). Multivariate or community-based modelling methods, which account for multiple species, can be used to summarize biodiversity patterns by classifying readily available environmental data into groups that are likely to have similar biological characteristics (e.g., Gregr and Bodtker, 2007; Dunstan et al., 2012; Leathwick et al., 2012). One such method, Gradient Forests (GF; Ellis et al., 2012; Pitcher et al., 2012), uses species distribution data to control the selection, weighting and transformation of environmental predictors to maximise their correlation with species compositional turnover and establish where along the range of environmental gradients important compositional changes occur (Ellis et al., 2012). These transformed environmental layers (representing species compositional turnover) can then be classified to define spatial groups that capture variation in species composition and turnover. A GF-based classification was recently used to describe spatial patterns of demersal fish species turnover in New Zealand using an extensive demersal fish dataset (>27,000 research

trawls) and high-resolution environmental data layers (1 km² grid resolution) (Stephenson et al., 2018b, 2020a). Using a large set of independent data for evaluation, this 30-group classification was found to be highly effective at summarising spatial variation in both the composition of demersal fish assemblages and species turnover (Stephenson et al., 2018b).

Such classifications have several key features that make them particularly useful for resource management and marine spatial planning. Firstly, they can be created at various hierarchical levels of group-detail [e.g., 30 groups as presented in Stephenson et al. (2018b), to 500+], a feature that makes them particularly useful when they need to be applied at differing spatial scales (national to regional to local scales) (Stephenson et al., 2020a). Secondly, because the classification is based on GF (tree-based) models of species turnover across environmental gradients, it can readily describe non-linear changes in species composition in relation to the environment, such as decreases in species turnover at depths >1,500 m (Stephenson et al., 2018b). Together, these two attributes mean that a single classification can reflect dynamic inshore environments with a greater number of groups compared to fewer groups in the relatively less dynamic environments in deeper offshore areas. Thirdly, because classifications contain spatial information on inter-group similarities (i.e., estimate of species compositional turnover), it is possible to locate and therefore implement appropriate management of areas that contain relatively unusual environments that are likely to support unique species assemblages (i.e., groups with low inter-group similarity). Finally, a GF-based classification condenses large numbers of individual species distribution layers down to a relatively small number of groups (e.g., <100 groups compared to several hundreds of species), which is generally more comprehensible and useful for managers, stakeholders and the general public.

One challenge with these classifications is the communication of a statistically complex product in a way that facilitates their use by management agencies and others involved in marine planning (Rowden et al., 2018; Stephenson et al., 2020a). This challenge can be overcome, at least in part, through the provision of maps and descriptions of the habitats and biotic assemblages associated with each classification group. A detailed description for a 30-group demersal fish classification was produced by Stephenson et al. (2020a), which aimed to bridge the gap

between the typical output from numerical classifications and the readily understandable habitat and fish assemblage descriptions that result from thematic (non-numerical) classifications. The descriptions of Stephenson et al. (2020a) included geographic locations, environmental characteristics, and demersal fish assemblages in a hierarchy based on the dominant environmental variables identified in the analysis (e.g., depth, tidal current, and productivity).

Here, a numerical environmental classification and associated spatially explicit estimates of uncertainty was developed for the New Zealand marine environment with the future goal of supporting ongoing marine spatial planning at regional and national scales. This classification used a broad suite of biotic groups [benthic invertebrates, macroalgae, reef fish, as well as demersal fish data as used in Stephenson et al. (2020a)] and high-resolution environmental predictor variables. The classification – termed the New Zealand Seafloor Community Classification (New Zealand SCC) – extends from the coastal marine area to the full extent of New Zealand's Exclusive Economic Zone (EEZ). Here we describe the development of the New Zealand SCC, and present key results including classification group descriptions.

MATERIALS AND METHODS

Study Area and Environmental Data

The study area extended over 4.2 million km² of the South Pacific Ocean within the New Zealand Territorial Sea (TS) and Exclusive Economic Zone (EEZ), herein referred to as the New Zealand marine environment (≈25–57°S; 162°E–172°W; **Figure 1**).

New Zealand's marine environment was described using 36 gridded environmental variables (**Supplementary Table 1**), collated at two resolutions: a 250 m resolution grid from the coastline to the edge of the TS (12 NM from shore), and a 1 km resolution grid from the edge of the TS to the edge of the EEZ (**Figure 1**). Spatial layers were projected using an Albers Equal Area projection centred at 175°E and 40°S (EPSG:9191). The 36 environmental variables were thought to influence the distribution of benthic and demersal taxa, and therefore distribution of species composition, richness, and turnover (e.g., see Leathwick et al., 2006; Compton et al., 2013; Smith et al., 2013; Anderson et al., 2016; Rowden et al., 2017; Stephenson et al., 2018b; Georgian et al., 2019). Several environmental variables showed some co-linearity within records for biotic groups but all levels of co-linearity were considered acceptable (Pearson correlation < 0.9) for tree-based machine learning methods (Elith et al., 2010; Dormann et al., 2013) and more specifically GF modelling (Ellis et al., 2012).

A subset of twenty environmental variables were selected for GF modelling for all biotic groups (grey rows, **Supplementary Table 1**) through a model-tuning process which aimed to maximise model fit (see section “Estimating Compositional Turnover”). These were: bathymetry, benthic sediment disturbance, bottom nitrate, dissolved oxygen at depth, bottom phosphate, salinity at depth, bottom silicate, temperature at depth, broadscale Bathymetric Position Index, fine-scale Bathymetric Position Index, chlorophyll-a concentration

spatial gradient, detrital absorption, seabed incident irradiance, downward vertical flux of particulate organic matter at the seabed, turbidity, annual amplitude of sea floor temperature, sediment classification, slope, sea surface temperature gradient, and tidal current speed.

In most cases, conventional modelling approaches seek to fit the most parsimonious model and the inclusion of many variables generally only provide minimal improvement in predictive accuracy and complicate interpretation of model outcomes (Leathwick et al., 2006). However, here, the interpretation of model outcomes (i.e., the drivers of distribution) was of secondary interest, the primary focus being on maximising the predictive accuracy of the model.

Biological Data

Occurrence records of four biotic groups (demersal fish, benthic invertebrates, macroalgae, and reef fish) were collated from various sources (**Supplementary Table 2**). All records were groomed: records located on land, outside the New Zealand marine environment and/or duplicated within and between databases were removed. Taxonomy was standardised across datasets and years to the most recent nomenclature. Demersal fish, reef fish and macroalgae were identified to species level, whereas benthic invertebrates were identified to genera. Further information on the data treatment and assumptions and distributions of taxa records are provided for each biotic group in **Supplementary Materials 1**.

Records for each of the biotic groups were separately aggregated to unique locations of different spatial resolutions: demersal fish and benthic invertebrates were aggregated to 1 km grid resolution, whereas macroalgae and reef fish taxa (coastal taxa) were aggregated to a 250 m grid resolution. Taxa with ≥10 unique sample locations were retained for the analysis (e.g., Stephenson et al., 2018b) because this ensured that there were sufficient samples to run GF models. Following quality control and spatial aggregation, a total of 630,997 records across the four biotic groups occurring at 39,766 unique locations were retained for final analysis. Values for environmental variables were derived for each taxa record location by overlaying them onto the environmental predictor layers using the “raster” package in R (Hijmans and van Etten, 2012). For demersal fish and benthic invertebrate records this procedure was undertaken using 1 km grid resolution environmental variables (including in areas where information was available at a 250 m grid resolution in order to match the spatial scale at which these were sampled), whereas environmental values for reef fish and macroalgae records were extracted from the 250 m grid resolution environmental variables.

Demersal fish, macroalgae, and reef fish were collected using consistent methods for each of the biotic groups (e.g., demersal fish were collected by research trawls). In contrast, benthic invertebrate records were collected using a variety of sampling methods (208 different gear types). Many of the gear types used were name variants of commonly used sampling gear types, but for most records, the specific sampling parameters (e.g., mesh size, tow length, etc.) were not recorded. In

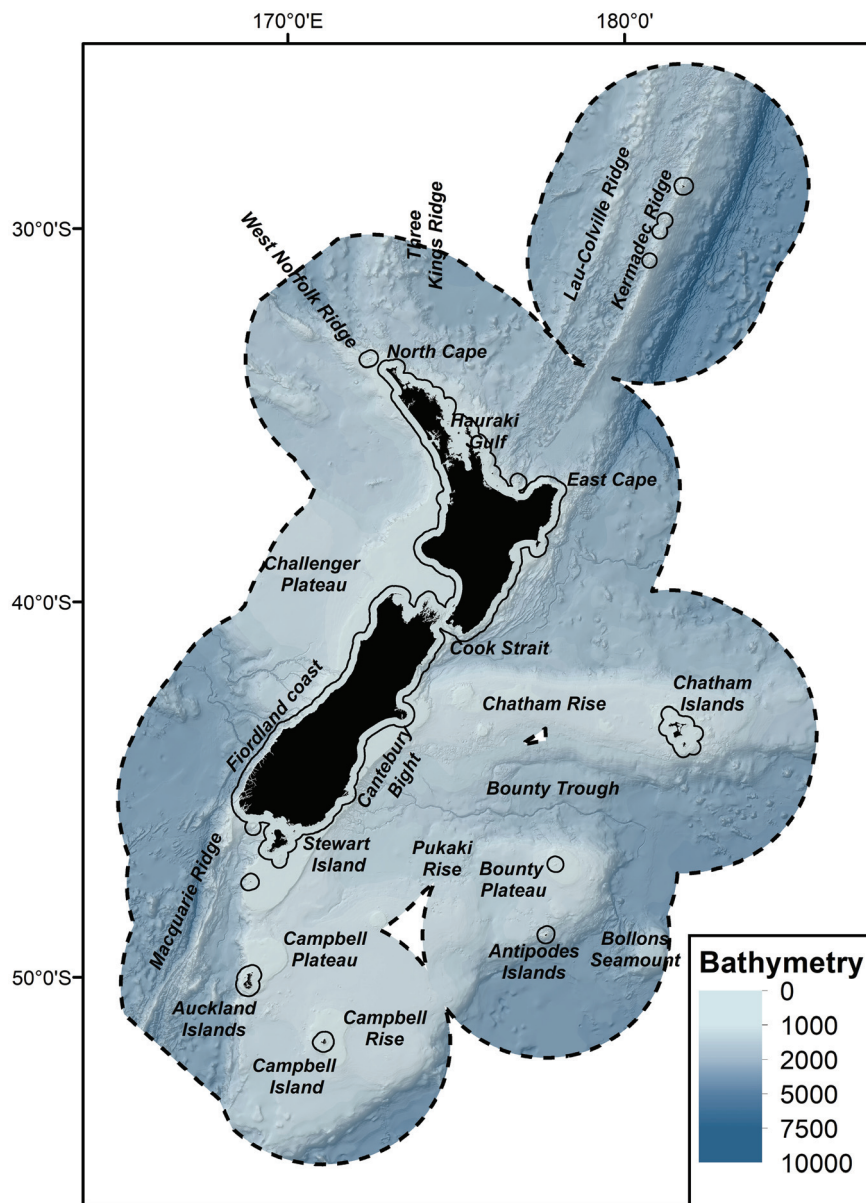


FIGURE 1 | Map of the study region. New Zealand Exclusive Economic Zone (EEZ, black dashed line), Territorial Sea (TS, solid black line), water depth and feature names used throughout the text are displayed.

order to account for both the large number of gear types recorded and the differences in sampling parameters, gear types were grouped into “catchability categories.” Catchability was assumed to be influenced by gear size, deployment area and selectivity (**Supplementary Table 3**; Stephenson et al., 2018a). Sampling gear types were assigned codes for each of the catchability categories (**Supplementary Table 4**). Out of 18 possible catchability categories, the available invertebrate samples occurred in six categories: LLG – Large gear types, deployed over large areas, which were not selective (e.g., otter trawls); LMG – Large gear types, deployed over medium-sized areas, which were not selective (e.g., beam trawls);

MMG – Medium sized gear types, sampling medium sized areas, which were not selective (e.g., benthic sled); SMG – Small gear types, sampling medium sized areas, which were not selective (e.g., Devonport dredge); SMHS – Small gear types, sampling medium sized areas, which were highly selective (e.g., collected by hand, bottom longline); SSG – Small gear types, sampling small areas, which were not selective (e.g., box corer). Records of LLG and LMG were combined as these catchability categories represent commercial fishing practices with similar catches of invertebrates likely to be more demersal in nature (i.e., some squid species). All records collected from highly selective gear catchability category (e.g., SMHS) were

excluded from the analysis, because methods classified within this category were considered too variable to provide reliable records of absence (20,010 records were excluded across 412 genera and 2,097 unique locations, including 190 genera unique to selective methods).

Estimating Compositional Turnover

For the demersal fish, macroalgae, and reef fish biotic groups, and for the four benthic invertebrate catchability categories (LLG.LMG, MMG, SMG, and SSG), GF models were fitted using the “extendedForest” (Liaw and Wiener, 2002) and “gradientForest” (Ellis et al., 2012) R packages. GF model aggregates results from a collection of Random Forest (RF) models (Breiman, 2001), each of which describes the environmental relationships of an individual species. Information from the individual Random Forest models about the relative importance of each environmental predictor, and information on where changes in the presence (or abundance) of the modelled species occur along their environmental ranges is aggregated to generate a transformed set of environmental predictors that represent species turnover (Pitcher et al., 2012).

GF models were fitted with 500 trees and default settings for the correlation threshold used in the conditional importance calculation of environmental variables. For each of the 7 GF models, we extracted information on the predictive power of the individual RF models (R^2_f for each taxon measured as the proportion of out-of-bag variance explained) (Ellis et al., 2012) and the importance of each environmental variable (R^2 assessed by quantifying the degradation in performance when each environmental variable was randomly permuted¹ (Pitcher et al., 2012). The environmental variables used in each GF model were selected to maximise the number of taxa effectively modelled (i.e., taxa with $R^2_f > 0$) and increase model fits for the most poorly modelled taxa (i.e., taxa with low R^2_f).

Gradient forest aggregates the values of the tree-splits from the RF models for all taxon models with positive fits ($R^2_f > 0$) to develop empirical distributions that represent taxa compositional turnover along each environmental gradient (Ellis et al., 2012; Pitcher et al., 2012). The turnover function is measured in dimensionless R^2 units, where taxa with highly predictive random forest models (high R^2_f values) have greater influence on the turnover functions than those with low predictive power (lower R^2_f). The shapes of these monotonic turnover

curves describe the rate of compositional change along each environmental predictor; steep parts of the curve indicate fast assemblage turnover, and flatter parts of the curve indicate more homogenous regions (Ellis et al., 2012; Pitcher et al., 2012; Compton et al., 2013).

The use of the dimensionless R^2 to quantify compositional turnover enables information from multiple taxa to be combined, even if that information comes from different sampling devices, surveys or regions (Ellis et al., 2012). In the first instance, the compositional turnover functions from each of the benthic invertebrate catchability category GF models were combined using the “combinedGradientForest()” function to provide a combined benthic invertebrate GF model (hereafter referred to simply as “benthic invertebrate” GF model). In the second instance, a final combined GF model was created using the “combinedGradientForest()” function across all biotic groups (demersal fish, reef fish, benthic invertebrates, and macroalgae), which we hereafter refer to as the “community” model. Broadly, this method of combining GF models accounts for the number of taxa, the number of samples, and the taxa R^2_f along the gradient of each environmental variable from individual GF models to provide a cumulative estimate of compositional turnover [for further details see, Ellis et al. (2012) and Pitcher et al. (2012)].

The compositional turnover functions from each biotic group and the community GF models (shapes of the turnover curves) were used to transform the gridded environmental layers (both 250 m and 1 km grid resolutions), creating a “transformed environmental space” representing compositional turnover. Variation within this transformed environmental space was summarised using principal components analysis (PCA) (Pitcher et al., 2011). The colours used in the PCA of each biotic group/community model were based on the first three axes of their respective PCA analysis so that similarities/differences in colour corresponded broadly to pairwise similarities/differences in the transformed environmental space and thus, by inference, describe differences in taxa composition (Stephenson et al., 2018b). Predicted taxa compositional turnover for each biotic group and community model was plotted geographically using the colour scheme derived from their respective PCA analyses.

GF models for each biotic group, as well as the community GF model, were bootstrapped 100 times. That is, 100 community GF models were fitted (as for the main model described above) to separate randomly selected subsets of the full input dataset. For biotic groups with $\geq 5,000$ samples (Supplementary Table 2), a random selection of 5,000 samples was selected from the full dataset. This number of samples was selected both to ensure reasonable computational time for the analysis, and

¹Note that R^2 described by Ellis et al. (2012) and Pitcher et al. (2012) refers to a unitless measure of cumulative importance and should not be confused with the more commonly used R -squared (R^2) denoting coefficient of determination.

TABLE 1 | Mean (\pm SD) model fit metrics of individual taxa (R^2_f) from bootstrapped gradient forest (GF) models.

| Model fit metric | Demersal fish (317 taxa) | Benthic invertebrates (958 taxa) | Macroalgae (349 taxa) | Reef fish (92 taxa) |
|--|--------------------------|----------------------------------|-----------------------|---------------------|
| Mean taxa effectively modelled (\pm SD) | 313.76 (\pm 1.57) | 955.20 (\pm 3.36) | 335.99 (\pm 0.11) | 91.99 (\pm 0.11) |
| Min Taxa R^2_f (\pm SD) | 0.36 (\pm 0.04) | 0.26 (\pm 0.05) | 0.19 (\pm 0.08) | 0.25 (\pm 0.04) |
| Mean Taxa R^2_f (\pm SD) | 0.52 ($<$ 0.01) | 0.48 ($<$ 0.01) | 0.47 ($<$ 0.01) | 0.53 (\pm 0.01) |
| Max Taxa R^2_f (\pm SD) | 0.91 (\pm 0.01) | 0.84 (\pm 0.05) | 0.61 (\pm 0.04) | 0.94 (\pm 0.04) |

The number of taxa retained in biotic group datasets is provided in brackets in the group headings.

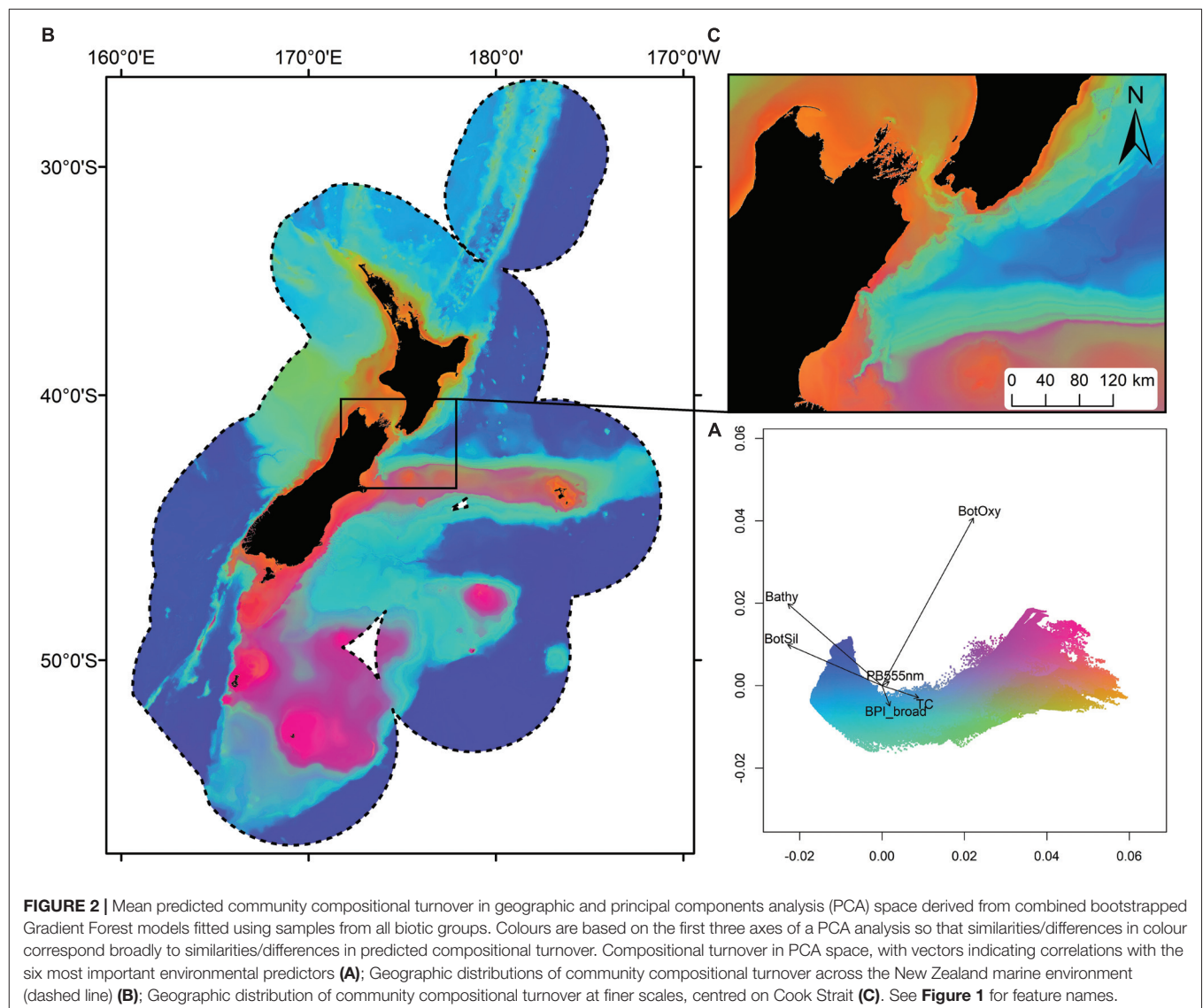
because previous analysis using demersal fish data indicated that this number of samples provided stable (consistent) model outputs (Stephenson et al., 2018b). For biotic groups with <5,000 samples (**Supplementary Table 2**), 75% of the dataset was randomly selected for each bootstrap iteration. The bootstrapping process was repeated 100 times, and at each iteration, species compositional turnover functions were used to transform the gridded environmental layers (both 250 m and 1 km grid resolutions). Mean (± 1 standard deviation of the mean) estimates of taxa R^2_f and environmental variable importance (R^2) were calculated for each GF model from the 100 bootstrapped iterations.

Spatial Predictions and Uncertainty

Spatial estimates of compositional turnover from each GF model (i.e., for each biotic group and community model), were averaged (mean). A spatially explicit measure of uncertainty [measured as the standard deviation of the mean (SD) compositional turnover

averaged across each environmental variable] was calculated for each grid cell using the 100 bootstrapped transformed environmental layers.

As an added measure of model uncertainty, for each GF model, we estimated “coverage of the environmental space” (Smith et al., 2013; Stephenson et al., 2020c). The “environmental space” is the multidimensional space produced by considering each of the environmental variables as a dimension. Some parts of this environmental space will contain many samples – meaning we can be more confident of the relationships and the predictions (Smith et al., 2013) – while other parts will contain few samples. Predictions for the less sampled parts of the environmental space are considered less reliable, and should be interpreted with greater caution (Smith et al., 2013). We modelled variation in sampling density within the environmental space by combining our samples (assigned as “present”) with an equal number of randomly sampled values from the environmental space (i.e., where we did not have any taxonomic samples – assigned as



“absences”). A Boosted Regression Tree (BRT; Elith et al., 2006) model was then used to model the relationship between these “present” (true) samples and “absent” (random) samples for the 20 environmental variables used in the GF analyses. The “Dismo” package (Hijmans et al., 2017) was used with BRT models fitted using a Bernoulli error distribution, a learning rate that yielded 2,000 trees and an interaction depth of 2 (so that only pair-wise combinations of the environmental variables were considered). Predictions using this model yielded estimates of the probability of a sample occurring in each part of the environmental space, these estimates ranging between 0 and 1, where 0 indicated very low sampling of the environmental space and 1 a very high level of sampling (Stephenson et al., 2020c).

Defining the Classification

The mean spatial estimate of compositional turnover from the community GF model (i.e., the bootstrapped GF model which included samples from all biotic groups) was classified using a two-stage approach (Leathwick et al., 2011; Stephenson et al., 2018b) using the R package “cluster” (Maechler et al., 2017). For the first stage, mean spatial estimates of compositional turnover were clustered to form 500 initial groups using

non-hierarchical, k-medoids clustering. Average values for the transformed environmental predictors were then computed for each of these initial groups. For the second stage, a hierarchical clustering approach – flexible unweighted pair group method with arithmetic mean (UPGMA) – using the Manhattan metric, and a value for beta of -0.1 (Belbin et al., 1992) was used to define each group from the initial 500. This second classification step was undertaken at various levels of classification detail ranging from 5 to 150-group levels in increments of 5 representing seafloor communities at various spatial scales.

Given the hierarchical nature of the GF-based classification, the most appropriate level of classification detail for planning purposes will vary depending on the spatial scale of the application and the level of information required for management. Using the biological data included in the GF models, the discrimination across classification levels was assessed [5–150 groups in increments of 5, e.g., as in Snelder et al. (2007)] using an analysis of similarities test (ANOSIM) analysis (Clarke and Warwick, 2001). The global R statistic was calculated as the difference in ranked biological similarities arising from all pairs of replicate sites between different groups, and the average of all rank similarities within groups, adjusted by

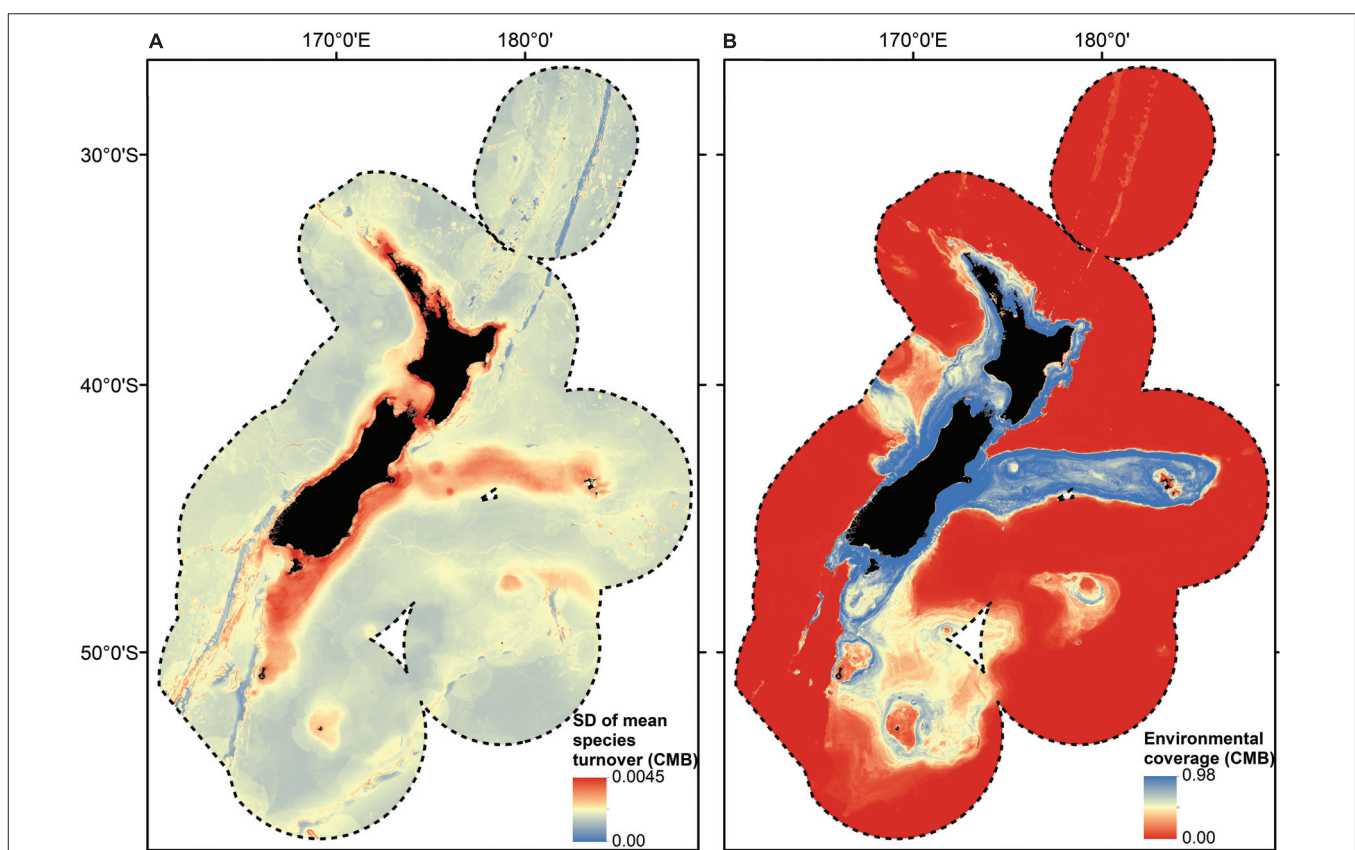


FIGURE 3 | Spatially explicit estimate of uncertainty and environmental coverage from the combined bootstrapped Gradient Forest model fitted using samples from all biotic groups. Uncertainty estimate (SD) of compositional turnover modelled using bootstrapped Gradient Forest model fitted with demersal fish, benthic invertebrate, macroalgae and reef fish samples (A). Predicted environmental coverage depicting the confidence that can be placed in the predictions, ranging from low (i.e., no samples in the dataset with those environmental conditions) to high (i.e., many samples with those environmental conditions) within the New Zealand marine environment (B). See Figure 1 for feature names.

the total number of sites. Global R is equal to 1 if all replicates within groups are more like each other than any replicates from different groups and is approximately 0 if there is no group structure. Significance levels of the ANOSIM statistics were tested with a randomisation procedure based on the null hypothesis of no group structure. All ANOSIM analyses were undertaken in R using the “Vegan” package (Oksanen et al., 2013). We only analysed groups with adequate biological data (≥ 5 unique occurrences). Group means for each of the transformed environmental variables were calculated and plotted in a PCA and geographical distributions were plotted for each classification from 5 to 150 groups (**Supplementary Materials 2**).

Finally, we describe the 75-group level classification in greater detail. We refer to this classification as the New Zealand “Seafloor Community Classification” (NZ SCC). This classification level represented the highest number of groups that captured the majority of the variation across the New Zealand marine environment, based on examining the ANOSIM global R statistic for each classification group, and which contained an adequate number of biological records (see “Results” below). Following methods developed by Stephenson et al. (2020a), individual classification group descriptions for the New Zealand SCC (75-group classification) are provided in **Supplementary Materials 3**. This included: (1) The location of the New Zealand SCC group

within the New Zealand marine environment. (2) Descriptions of a subset of each groups’ environmental characteristics, termed “characterising environmental conditions.” (3) Descriptions of each groups’ biological characteristics, calculated as mean frequency occurrence of each taxon within classification groups and investigating the contribution of individual taxa to intra-group similarity (SIMPER analysis using Bray-Curtis similarity, in PRIMER v7.0.13) (Stephenson et al., 2020a). Characterising species were defined as those species contributing more than 4% to the SIMPER intra-group similarity. (4) A measure of model confidence, for each classification group, represented by the mean, 25 and 75% quantile for the uncertainty estimate of compositional turnover (SD of the combined bootstrapped GF) and the overall predicted environmental coverage.

RESULTS

Compositional Turnover and Uncertainty

Models were able to be fitted for most taxa across all biotic groups (i.e., $R^2_f > 0$, **Table 1**). However, individual taxon R^2_f values varied widely, ranging from 0.19 (macroalgae, **Table 1**) to 0.94 (reef fish, **Table 1**). On average, the GF models explained 47–53%

TABLE 2 | Results of the pair-wise analysis of similarities test (ANOSIM) analysis for the biotic groups at varying levels of classification detail.

| | Classification detail (number of groups) | Proportion of groups ≥ 5 unique occurrences | Proportion of significant inter-class differences | Mean significant ANOSIM R-statistic |
|-----------------------|--|--|---|-------------------------------------|
| Demersal fish | 5 | 1.00 | 1.00 | 0.57 |
| | 25 | 0.84 | 1.00 | 0.65 |
| | 50 | 0.82 | 1.00 | 0.70 |
| | 75 | 0.76 | 0.99 | 0.72 |
| | 100 | 0.73 | 1.00 | 0.73 |
| | 125 | 0.74 | 0.99 | 0.73 |
| | 150 | 0.73 | 0.99 | 0.74 |
| Benthic invertebrates | 5 | 1.00 | 1.00 | 0.22 |
| | 25 | 0.92 | 0.94 | 0.21 |
| | 50 | 0.96 | 0.93 | 0.23 |
| | 75 | 0.91 | 0.93 | 0.25 |
| | 100 | 0.91 | 0.93 | 0.27 |
| | 125 | 0.90 | 0.92 | 0.26 |
| | 150 | 0.87 | 0.92 | 0.26 |
| Reef fish | 5 | 0.60 | 1.00 | 0.20 |
| | 25 | 0.40 | 0.98 | 0.32 |
| | 50 | 0.32 | 0.92 | 0.41 |
| | 75 | 0.24 | 0.92 | 0.41 |
| | 100 | 0.23 | 0.91 | 0.49 |
| | 125 | 0.18 | 0.94 | 0.49 |
| | 150 | 0.15 | 0.92 | 0.49 |
| Macroalgae | 5 | 0.80 | 1.00 | 0.01 |
| | 25 | 0.72 | 0.91 | 0.03 |
| | 50 | 0.66 | 0.81 | 0.04 |
| | 75 | 0.55 | 0.84 | 0.05 |
| | 100 | 0.50 | 0.84 | 0.04 |
| | 125 | 0.44 | 0.80 | 0.04 |
| | 150 | 0.45 | 0.71 | 0.04 |

of variation in occurrence across biotic groups (mean taxa R^2_f : 0.47–0.53, **Table 1**).

Although all environmental variables contributed to predicting compositional turnover for all models (positive R^2 , **Supplementary Table 5**), their relative importance (in terms of mean cumulative importance) varied across biotic groups. The most consistently important variables in the biotic group GF models were dissolved oxygen at depth and bottom salinity (**Supplementary Table 5**). Tidal current speed was important in GF models of demersal fish, benthic invertebrates and the community GF model. Many of the environmental variables had moderate cumulative importance across all biotic groups and in the community GF model, e.g., dissolved oxygen at depth, seabed incident irradiance, downward vertical flux of POC at the seabed (R^2 : 0.0015–0.004, **Supplementary Table 5**). The predicted cumulative changes in compositional turnover along each environmental variable for each biotic group and the overall community are presented in **Supplementary Materials 1**.

Spatial patterns in overall community compositional turnover reflected broadscale patterns in environmental variables linked to well-defined oceanographic patterns observed in New Zealand's waters. Briefly, compositional turnover was minimal in the deepest water (>2,000 m), although with progression into shallower waters (1,000–2,000 m) there appeared to be differences in taxa occurring in the northwest of the study area compared

to all other deep-water areas (**Figure 2**). With progression into intermediate depths (70–1,000 m), there was a clear latitudinal separation in taxa composition along the boundaries of the Subtropical Front (STF), a highly productive zone of mixing between high salinity, nutrient poor, warm, northern waters, and low salinity, nutrient rich, cold, and southern waters (Bradford-Grieve et al., 2006; Leathwick et al., 2006, 2012; Stephenson et al., 2018b; **Figure 2**). In shallow water (0–70 m), patterns in community compositional turnover were more closely associated both with latitude and with more localised environmental conditions. Namely, turbidity, tidal currents, and broadscale and fine-scale Bathymetric Position Index (**Figure 2**).

The SD for all GF models was low compared to the mean compositional turnover, i.e., the uncertainty in the compositional turnover was low even for the most variable areas. The SD of mean compositional turnover for the community GF model was highest close to shore in areas of high compositional turnover, for example, in Cook Strait and the Marlborough Sounds (**Figure 3A**). Much of the continental shelf (areas shallower than 200 m) and the Chatham Rise displayed moderate to high variability in mean compositional turnover (**Figure 3A**). Deep water areas (>2,000 m) displayed the lowest variability in mean compositional turnover, in part reflecting the relative environmental homogeneity associated with these abyssal waters, but also likely reflecting, at least in part, the relative lack of sampling in these areas as environmental coverage was low for most areas deeper than 2,000 m (**Figures 3A,B**). Environmental coverage was high in areas close to shore and along the Chatham Rise (**Figure 3B**) and moderate for parts of the Challenger and Campbell plateaus (**Figure 3B**).

Seafloor Community Classification Assessment of Classification Strength

There was adequate unique occurrences of benthic invertebrate and demersal fish (i.e., ≥ 5 unique occurrences in a given group) for more than 70% of all groups (up to 150 groups, **Table 2**), however, for the more coastally restricted taxa from the macroalgae and reef fish biotic groups, there were fewer groups with adequate occurrences (**Table 2**). All the global ANOSIM R values were significant at the 1% level. The global R values generally increased for all data sets as the classification detail was increased, indicating that finer levels of classification detail defined more biologically distinctive environments (**Table 2**). The ANOSIM R values were higher for demersal and reef fish classifications than those for the benthic invertebrates and the macroalgae. However, the classification strength became more gradual for all biotic groups, once the number of classification groups exceeded 55–75 groups (**Table 2**). Furthermore, pairwise differences between groups (with adequate sample number) declined with increasing classification detail (**Table 2**).

The New Zealand Seafloor Community Classification

The 75-group classification – termed the New Zealand SCC – was used because it was the highest number of groups that captured the majority of the variation across the New Zealand marine environment (as assessed by global ANOSIM R values) and contained an adequate number of biological records.

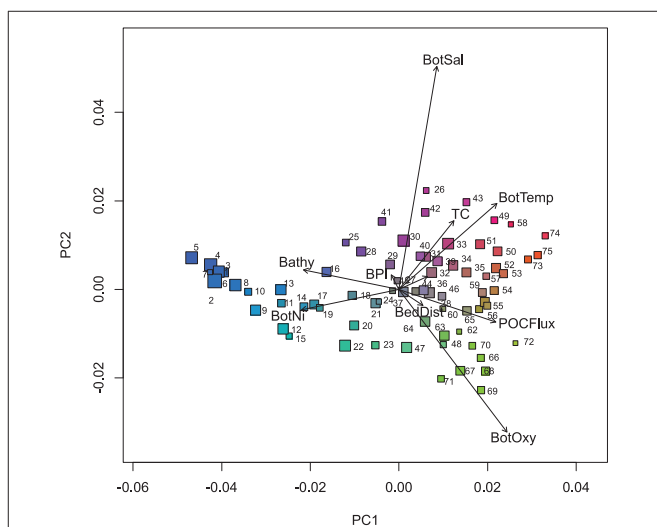
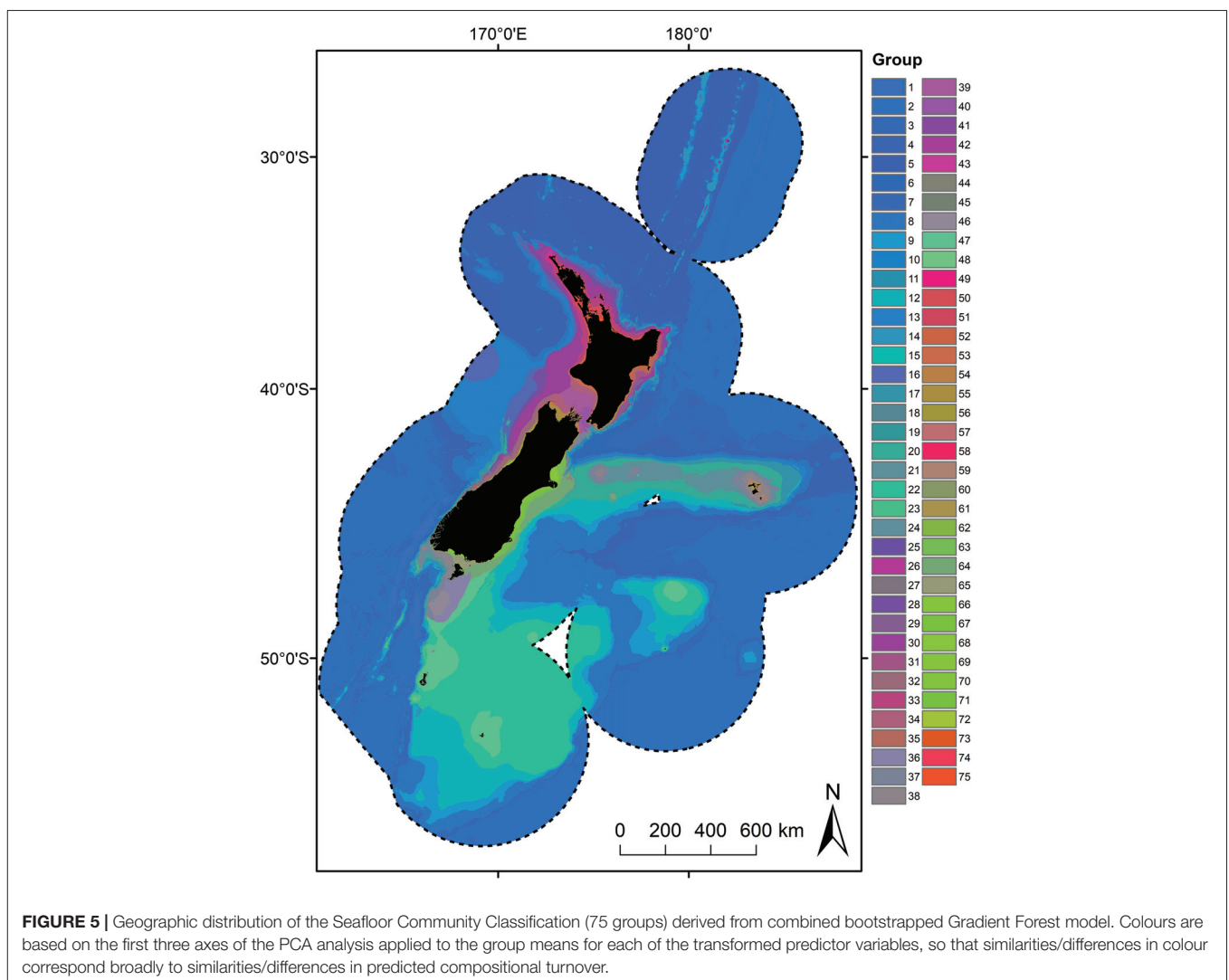


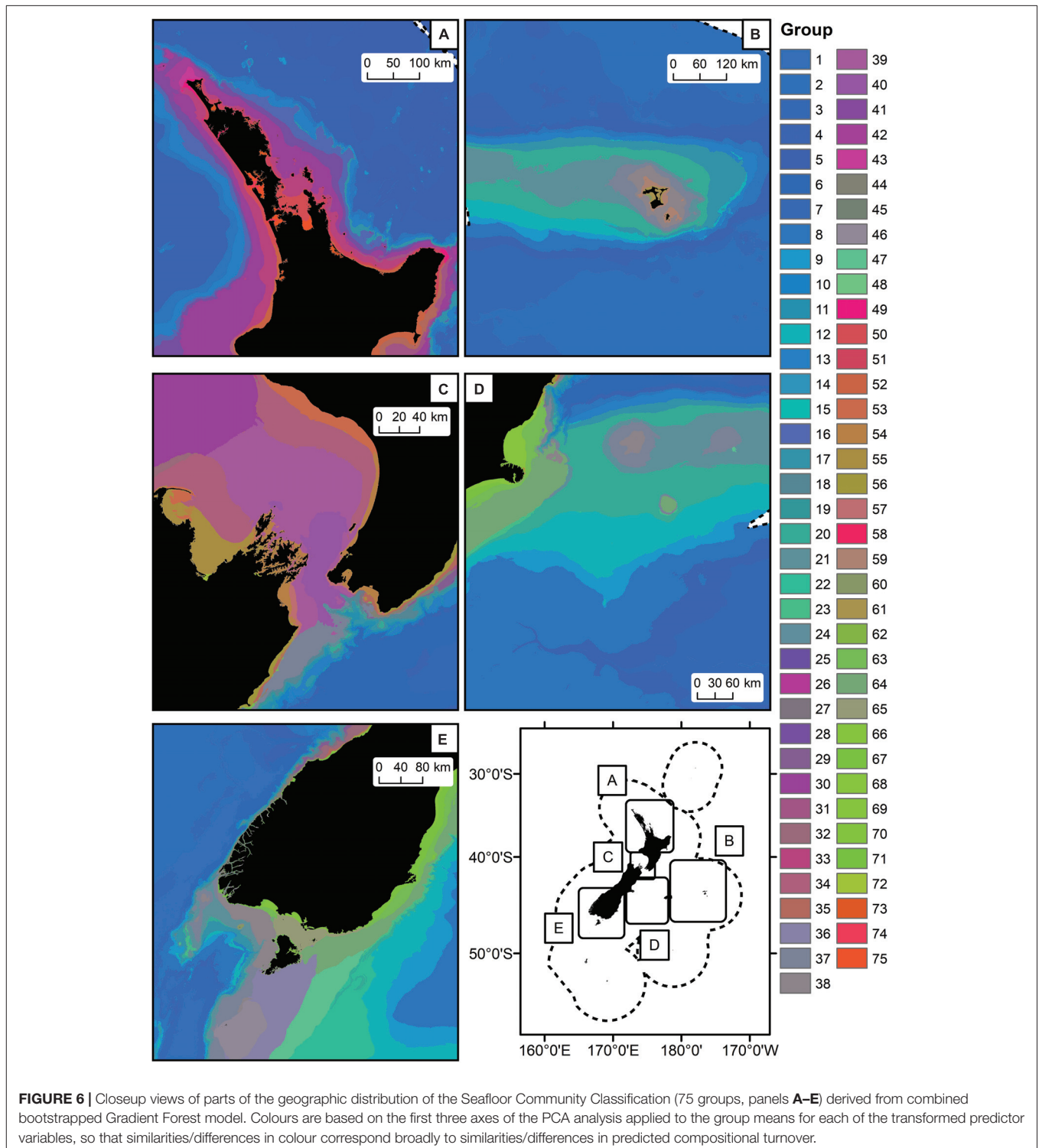
FIGURE 4 | Principal component analysis of the seafloor community classification groups (75 groups) for the New Zealand marine environment. Vectors indicate correlations with the nine most important environmental predictors and symbol size indicates the relative spatial area represented by the group. Colours are based on the first three axes of the PCA analysis applied to the group means for each of the transformed predictor variables, so that similarities/differences in colour correspond broadly to similarities/differences in predicted compositional turnover. Environmental predictors include: bathymetry (*Bathy*), benthic sediment disturbance (*BedDist*), bottom nitrate (*BotNi*), dissolved oxygen at depth (*BotOxy*), salinity at depth (*BotSal*), temperature at depth (*BotTemp*), broadscale Bathymetric Position Index (*BPI*), downward vertical flux of particulate organic matter at the seabed (*POCFlux*) and tidal current speed (*TC*).

The New Zealand SCC exhibited clear differences in terms of environmental conditions (summarised in **Figure 4**) and geographic distributions (**Figures 5, 6**). Not surprisingly, geographic and environmental patterns of the New Zealand SCC closely reflect the patterns of the community compositional turnover on which the New Zealand SCC was based. At broad scales, New Zealand SCC groups were differentiated primarily according to oceanographic conditions such as depth (along PC1 in **Figure 4**) and bottom temperature (co-linear with bottom salinity and bottom oxygen, along PC2 in **Figure 4**). Environmental differences among New Zealand SCC groups in deep water (groups 1–19, mean depths between 4,156 and 537 m) were relatively muted, but greater environmental differences were evident among New Zealand SCC groups at intermediate depths (group 20–48, primarily mean depths between 537 and 52 m), particularly with respect to bottom temperature, bottom oxygen concentration and bottom salinity. These more pronounced environmental differences among groups at intermediate depths were aligned with well-defined oceanographic patterns observed in New Zealand's oceans, with a clear latitudinal separation along

the boundaries of the Subtropical Front (STF). Intermediate depth groups to the north of the STF included groups 27–35; 41–43 and south of the STF included 20–23; 36–40; 46–48 (**Figure 5**). Environmental differences became even more pronounced at shallow depths (groups 49–75, primarily mean depths between 54 and 1 m), where variation in more localised environmental conditions such as productivity (downward vertical flux of particulate organic matter at the seabed), seafloor topography (broad-scale Bathymetric Position Index and slope), seabed disturbance (benthic sediment disturbance) and tidal currents (**Figure 4**) were important differentiating factors (**Figure 5**).

Environmental differences between New Zealand SCC groups were mirrored by differences in biological composition. For example, the New Zealand SCC groups varied in their characterising taxa with many taxa occurring in several groups sharing similar environmental characteristics [e.g., orange roughly (*Hoplostethus atlanticus*), and smooth oreo (*Pseudocyttus maculatus*) were most frequently observed in deep cold-water groups], whereas a large number of species occurred infrequently or in a small number of groups. A detailed description





of the characterising demersal fish, benthic invertebrate, macroalgae, and reef fish characterising taxa is provided in **Supplementary Materials 3**.

In addition, mean values for the two spatially explicit estimates of uncertainty differed between New Zealand SCC groups (summarised in **Supplementary Materials 3**). Broadly,

with decreasing depth, the mean environmental coverage increased, although some small localised New Zealand SCC groups with few biological samples had low environmental coverage (e.g., group 26). Several New Zealand SCC groups had low or variable number of samples across biotic groups, but moderate to high combined environmental coverage (e.g.,

shallow coastal groups 58–60, 66, 72), suggesting sampling in similar environmental conditions had occurred for these taxa in other New Zealand SCC groups.

DISCUSSION

The New Zealand SCC developed here is a significant advance on previous numerical classifications, in New Zealand and globally. Firstly, it combined a larger number of taxonomic records (630,997 records of 1,716 taxa occurring at 39,766 unique locations) from multiple biotic groups, across a large area (>4.2 million km²), with a comprehensive and high-resolution set of environmental predictor variables compared to previous studies (e.g., Snelder et al., 2007; Stephenson et al., 2020a). Secondly, because flexible machine learning modelling methods were used, non-linear relationships between taxa and environment were incorporated (Pitcher et al., 2012). For the first time globally, spatial estimates of confidence were provided for the predicted compositional turnover through the use of bootstrapping techniques, which can in turn be used to partially assess the confidence that can be placed in the individual New Zealand SCC groups.

Critical Appraisal of the New Zealand Seafloor Community Classification

The methods and data used to develop the New Zealand SCC build on those used in previous classifications of New Zealand's marine environment: the New Zealand Marine Environment Classification (MEC, Snelder et al., 2007) and the Benthic Optimised Marine Environment Classification (BOMECE, Leathwick et al., 2012). Although the classification is environment-based, in broad terms the classification can be understood as a spatial summary of variation in seafloor community composition and turnover in the New Zealand marine environment (Stephenson et al., 2020a). Overall, the spatial distribution of the New Zealand SCC is consistent with the MEC and BOMECE which identified depth, and to a lesser extent, water temperature and water mass, and major oceanographic features as important drivers of taxa composition. However, the New Zealand SCC also identified finer-scale environmental differences for community groups at shallow depths, where variation in more localised environmental conditions such as productivity, seafloor topography, seabed disturbance, and tidal currents were important differentiating factors.

The New Zealand SCC groups represent taxa that share the same suite of environmental preferences, and therefore inhabit the same locations. These groups can be considered communities as they describe groups of spatially and temporally co-occurring taxa, which may interact to some extent with one another (Morin, 2009). Some species in a community will interact either directly (e.g., through predator-prey interactions) or indirectly (e.g., by feeding on the same organisms), while other taxa may not necessarily interact with each other and may only be “associated” because they inhabit the same physical space (Francis et al., 2002). There is still a paucity of information with regards to species interactions at the spatial scales of the communities identified by

the New Zealand SCC. Nevertheless, the inferred communities from the New Zealand SCC provide useful descriptions of habitat and biotic assemblages for spatial resource management and conservation planning, particularly when considered alongside the estimates of confidence for each of the groups.

Management Application

Describing spatial variation in species compositional turnover and richness is central both to our understanding of the scaling of diversity, and for identification of priority sites for marine spatial planning and conservation (McKnight et al., 2007). New Zealand SCC groups are based on estimated taxa compositional turnover, which allows spatially explicit measures of within-group and between-group similarity in taxonomic composition to be produced (Stephenson et al., 2021a). In turn, these similarity metrics can allow identification of environments that are likely to host rare or unusual communities as well as identifying geographic areas (which may consist of multiple New Zealand SCC groups) that are most representative of New Zealand seafloor communities as a whole, for example, in a spatial conservation prioritisation analysis (Leathwick et al., 2011).

Given the hierarchical nature of the New Zealand SCC classification, consideration will be required as to what constitutes the most appropriate level of classification detail for planning purposes. At the scale of the New Zealand marine environment, the 75-group New Zealand SCC may be appropriate. Using a higher number of classification groups (100–200 groups) is likely to be more appropriate for regional scale management planning, particularly for inshore areas where there is greater heterogeneity in environmental conditions and biological communities (Stephenson et al., 2018b). As part of any spatial planning process, information from the New Zealand SCC could be supplemented with the inclusion of other spatial layers to facilitate selection of areas of particular importance [e.g., see Stephenson et al., 2018a; Lundquist et al., 2020] for a comprehensive list and description of spatial layers available in New Zealand to inform the identification of Key Ecological Areas]. The New Zealand SCC aims to represent seafloor communities; however, to achieve comprehensive representation for marine spatial planning, information on other species, including pelagic species, will likely need to be included. By itself, the New Zealand SCC is unlikely to be an appropriate proxy for pelagic species distributions (Hewitt et al., 2015). Spatial layers relating to other values and uses, such as social, cultural and economic value, would also need to be factored in as part of a marine planning process.

A spatial planning analysis using the 75-group New Zealand SCC would need to include the classification uncertainty measures developed here because failure to acknowledge sources of uncertainty can lead to poor management decisions (Regan et al., 2005; Link et al., 2012). Here we provide two spatially explicit measures of uncertainty: model variability and environmental coverage, which provide two complementary measures to be considered by managers (Stephenson et al., 2021b). The environmental coverage provides an indication of the parts of the environmental space that, for example, contain many samples – meaning we can be more confident of the

relationships and the predictions for compositional turnover and SSC groupings in such areas (Smith et al., 2013). The uncertainty estimates of community compositional turnover (i.e., standard deviation of the mean (SD) compositional turnover averaged across each environmental variable) provide an important indication of the variability in the modelling estimates. Given that uncertainty estimates of compositional turnover will only vary in areas where samples are present, we suggest that the uncertainty associated with individual SCC groups first be assessed by examining the number of samples and environmental coverage values. Where these values are adequate [e.g., environmental coverage > 0.05 as in Stephenson et al. (2020c) or another suitable cut-off], the uncertainty estimates of compositional turnover will provide further insight into the variability (and therefore the confidence) of the underlying models used for the classification. However, it should be noted that both of these uncertainty estimates are not propagated through the model to include any uncertainty in the classification. That is, we only quantify parts of the model uncertainty (albeit arguably the most important parts) and there are no estimates of classification uncertainty *per se* (Hill et al., 2020). This means that for parts of the environmental space our estimate of model uncertainty will be an under-estimate (i.e., particularly for those parts of the environmental space that could be classified as either in one group or another similar group). However, spatial predictions of inter- and intra-group (biological) similarity can be generated from the classification and be used to highlight those areas in the classification groups that may be classified in one group or another and therefore may represent less certain classifications [e.g., see methods and use of these layers in Stephenson et al. (2021a)].

One challenge with numerical classifications, such as the New Zealand SCC, is the communication of results from a statistically complex product in a way that facilitates their use by management agencies and others involved in spatial planning processes (Rowden et al., 2018). Individual group descriptions for the New Zealand SCC are provided in **Supplementary Materials 3**. These descriptions are provided to facilitate use of the classification by both managers and stakeholders and, at least in part, help bridge the gap between the typical output from numerical classifications and the readily understandable habitat and assemblage descriptions that result from thematic classifications. As new data become available, the underlying numerical methodology underpinning the classification can be updated allowing the New Zealand SCC to be continually improved over time.

Improving the Classification

Despite the large datasets collated for the development of the New Zealand SCC, there remain limitations associated with the classification, which at least in part, can be attributed to the available biological and environmental data. The long temporal span over which taxa samples were collected means that there is a mismatch between the temporal window of biological data and that of the environmental variables which were mostly compiled from data collected in the last few decades. This mismatch means that the compositional turnover presented here should be interpreted as a spatially and temporally smoothed representation

(Stephenson et al., 2018b). Furthermore, it is worth noting that data were collected over a time span that includes the establishment of widespread commercial fishing in the region (Baird and Wood, 2018), and the impact of this disturbance on seafloor communities has not been incorporated into the modelling methodology.

Although the species occurrence data we used mostly provided adequate spatial coverage of our study area close to shore and further offshore on the Chatham Rise and the Challenger and Campbell Plateaus (as assessed by the coverage of the environmental space), several large, outlying sections had few or no biological samples, notably the vast majority of waters deeper than 2,500 m. For deeper waters where few samples are available, lower confidence can be placed in the predictions of compositional turnover that underpin the New Zealand SCC.

The “quality” of the available biological data varied by biotic group based on differences in sampling gear and method. Records for demersal fish and reef fish were collected using (relatively) consistent sampling gears and methods (Smith et al., 2013; NIWA, 2014, 2018). Abundance estimates were available for both these biotic groups, and few assumptions were required to use these data as presence/absence in GF models to make them consistent with benthic invertebrate and macroalgae group data. In contrast, multiple sampling gears and methods were used to sample benthic invertebrates, which required division of these data into gear catchability categories. However, it should be noted, that there was a high proportion of unique taxa associated with each gear type and therefore it was deemed important to include each of these because they sampled different parts of the community. Information on sampling methods for macroalgae was not easily available but given their localised nature (collected on or close to shore), this was not deemed to be critical. Neither the benthic invertebrate nor the macroalgal data here can be considered true presence/absence (because of variations in the survey designs used to collect these data), and therefore the classification results from these biotic groups should be used with greater caution [although care was taken to account for differences in the biases associated with sampling method as per Phillips et al. (2009)]. Future iterations of the New Zealand SCC may benefit from being tuned using abundance estimates and, for benthic invertebrates, records at the species level [e.g., using data from comprehensive surveys as in Bowden et al. (2019)]. Despite these limitations, the taxa data used here form a valuable dataset that will have uses outside the development of the New Zealand SCC (e.g., see Lundquist et al., 2020) and represents the best available compiled biotic information at present for the New Zealand marine environment. The ability of the classification to represent variation in taxa composition at different scales using independent or newly collected data [e.g., as in Bowden et al. (2011) or as in Stephenson et al. (2018b)] would be of interest in order to independently validate the accuracy of the New Zealand SCC.

The lack of consistent spatially explicit abundance information, means that despite the comprehensive SCC group descriptions of the environmental and biotic characteristics, SCC groups may still lack some of the key features that stakeholders

may more readily associate with, or understand as habitats and communities. For example, the lack of abundance information means there is no spatial information about the locations of biogenic habitats, despite biogenic habitat forming taxa being present (and identified as characterising taxa) in several groups (e.g., bivalves, stony corals – see **Supplementary Materials 3**).

CONCLUSION

The New Zealand SCC and associated spatially explicit uncertainty layers are particularly well suited as inputs for marine spatial planning, and more specifically, marine protection planning and reporting at regional and national scales. Firstly, spatially explicit estimates of within and between group similarity of the New Zealand SCC make it particularly well suited to support developing an effective network of marine protected areas and other tools [goal 10.6.3 of Te Mana o te Taiao – The Aotearoa New Zealand Biodiversity strategy, Department of Conservation (2020)] and complement work currently underway to map Key Ecological Areas within New Zealand's marine environment. Secondly, the development of two spatially explicit measures of uncertainty allow for the nuanced use of the New Zealand SCC in a marine spatial planning context. Thirdly, the New Zealand SCC summarises a large and complex dataset spanning four seafloor biotic groups in a single community classification layer that could greatly facilitate communication of complex spatial biodiversity patterns during participatory stakeholder processes. Despite the advances and utility of the New Zealand SCC for conservation planning, there remain several limitations, including a lack of abundance data, and the identification of the key features that some stakeholders may more readily associate with, or understand as, habitats and communities. These limitations can, at least in part, be overcome through the use of other spatial layers to complement the New Zealand SCC (e.g., as collated for the identification of Key Ecological Areas, Stephenson et al., 2018a; Lundquist et al., 2020) such as spatial estimates of fish spawning grounds and biogenic habitats.

DATA AVAILABILITY STATEMENT

The datasets presented in this study can be found in online repositories. The names of the repository/repositories and accession number(s) can be found below: <https://doc-deptconservation.opendata.arcgis.com/documents/4050708cbf274e26a978448c4caf2b3d>.

AUTHOR CONTRIBUTIONS

FS, AR, TB, RB, DB, DC, BG, KN, KM, MP, OA, RG, SM, and WN collated and groomed the biological and environmental data. FS, TB, GP, and JL led the data analysis with input from CL, AR, SG, GF, DF, KT, PT, IT, and JH. FS, TB, SW, GP, and JL produced the figures. FS, AR, TB, GP, and JH led the writing, but all authors

contributed to the development of ideas, writing and editing of this article, and approved the submitted version.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: <https://www.frontiersin.org/articles/10.3389/fmars.2021.792712/full#supplementary-material>

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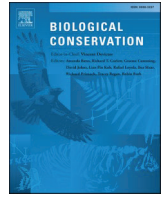
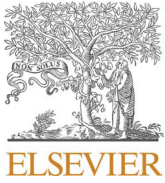
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Spatial mismatch in diversity facets reveals contrasting protection for New Zealand's cetacean biodiversity

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ABSTRACT

Cetaceans play key roles in the world's ecosystems and provide important economic and social benefits. New Zealand's Exclusive Economic Zone is a global biodiversity hotspot for cetaceans and benefits from a system of marine protected areas (MPAs). However, spatial patterns of cetacean biodiversity and their overlap with MPAs have never been assessed.

We quantify this overlap by using a comprehensive cetacean at-sea sightings database, high-resolution environmental data layers, and information on ecological and evolutionary characteristics of each species to model spatial patterns of taxonomic, functional, and phylogenetic diversity of cetaceans. We examine areas of congruence among hotspots of richness and uniqueness components of biodiversity and measure the contribution of species to biodiversity.

We find that cetacean taxonomic and phylogenetic diversity are spatially mismatched with MPAs, but this is less true for functional diversity. Hotspots of congruence among richness indices are located on the continental shelf break, whereas hotspots of uniqueness indices are located closer to shore on the continental shelf. Seven species have high contributions to biodiversity, with blue whale being the only species being evolutionarily distinct, functionally unique, specialised and globally endangered.

Our results underline the potential of multicomponent biodiversity indices, their spatial congruence, and the contribution of species to biodiversity to be used as guides for a strategic placement and expansion of MPAs to protect biodiversity.

1. Introduction

Biodiversity is facing globally intensifying threats, with multiple potential consequences for ecosystems and human well-being (Cardinale et al., 2012; Hooper et al., 2012; Isbell et al., 2017). Despite increasing effort and investment in the protection of biodiversity globally, there remains a requirement for increased protection (Sala et al., 2021) and accurate identification of biodiversity hotspots (Daru et al., 2015; Brum et al., 2017). In this context, taxonomic diversity remains the most

widely used measure of biodiversity, despite growing recognition that it does not account for the ecological functions that species perform within ecosystems, nor represent species evolutionary histories (Devictor et al., 2010; Thuiller et al., 2015; Li et al., 2020). Adopting an integrated view from taxonomic, functional, and phylogenetic standpoints may, however, improve our understanding of biodiversity distribution across large spatial scales (Devictor et al., 2010; Stuart-Smith et al., 2013; Runge et al., 2015; Thuiller et al., 2015; S.L. Maxwell et al., 2020; S.M. Maxwell et al., 2020).

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Protected areas are viewed as essential tools to protect biodiversity and ecosystems (Davidson and Dulvy, 2017; Cazalis et al., 2020; Mouillot et al., 2020). Conservation planning, however, has mainly focused on identifying priority areas that protect a proportion of the geographic range of specific biological features, such as species ranges. The assumption underpinning this approach is that maximising the representation of species within protected areas will ensure their persistence. However, planning protected areas in such a way as to capture maximum biodiversity, may not necessarily safeguard important ecological processes mediated by a wide range of functionally important species (Pimiento et al., 2020a, 2020b). Few studies have demonstrated a discrepancy between the design of protected areas and spatial patterns of biodiversity (Daru et al., 2015; Venter et al., 2018; Franke et al., 2020), especially with regards to protecting key functional roles and the diversity of species evolutionary history (Mouillot et al., 2016; Pollock et al., 2017; Daru et al., 2019). In this context, identifying which species contribute the most to measures of taxonomic, functional, and phylogenetic diversity and are threatened at the global scale, is of particular importance for targeting species-based conservation priorities (Isaac et al., 2007, Pool et al., 2014, Pimiento et al., 2020a, 2020b).

The New Zealand Exclusive Economic Zone (EEZ) is a global cetacean biodiversity hotspot (Kaschner et al., 2006; Albouy et al., 2017; Stephenson et al., 2021): in total, 47 cetacean species, subspecies and/or ecotypes including resident, migrant or vagrant taxa are known to occur in New Zealand waters (Baker et al., 2019). All cetaceans in New Zealand's EEZ are protected under national law by the New Zealand Marine Mammals Protection Act (1978). New Zealand has pioneered marine protection with the establishment of the Marine Reserves Act in 1971 and the creation of one of the world's first no-take marine reserves in 1975 (Ballantine and Gordon, 1979). Marine protection has increased in New Zealand's waters since then (Ballantine, 2014; Scott, 2016), with the creation of 44 no-take marine reserves and a network of partly no-take protected areas. These areas were mostly designed to promote recovery of exploited species (e.g., reef fish and benthic invertebrates), and more recently, also include areas of set netting restrictions for the protection of endemic coastal dolphins. Identifying hotspots of congruence among multiple components of cetacean biodiversity and the species that mostly contribute to this biodiversity is necessary to assess the effectiveness of current MPAs at protecting cetacean biodiversity and guide the expansion and placement of future MPAs.

Here, we model spatial patterns of taxonomic, functional, and phylogenetic diversity of cetaceans in New Zealand's EEZ to assess patterns of biodiversity and protection by MPAs to guide conservation planning. We measure overlap among biodiversity indices and their hotspots with MPAs. We assess spatial congruence among multiple components of biodiversity and calculate species contributions to biodiversity coupled with their global IUCN red list threat status. To do so, we used a database of high resolution at-sea sightings of cetaceans collected within the New Zealand EEZ and spanning more than 14,000 sightings occasions. We develop spatial predictions of cetacean species potential geographic distributions across the New Zealand EEZ and calculated measures of taxonomic, functional, and phylogenetic diversity. We then assess the extent to which MPAs overlap cetacean biodiversity. We finally examine the contribution of each species to patterns of functional and phylogenetic cetacean biodiversity coupled with their global IUCN red list status to inform conservation priorities for endangered species contributing much to cetacean biodiversity in New Zealand waters.

2. Methods

2.1. Cetacean at-sea sightings records

We used a comprehensive database of cetacean at-sea sightings records collected within the New Zealand Exclusive Economic Zone (EEZ). New Zealand's EEZ area extends over 4.2 million km² of the South

Pacific Ocean, between latitude 25 to 57°S and longitude 162 to 172°W (Fig. 1). Sightings data originated from a variety of sources (citizen scientists, seismic vessels, tourist charters, scientific surveys, fishing vessels, aircrafts, and New Zealand ferries) and are described by Stephenson et al. (2020). Following quality control, that is, removing ~6000 records that lacked species identification or location, were located on land or outside the New Zealand EEZ, we used a total of 14,513 at-sea cetacean sightings records for 28 cetacean species (Table S1).

2.2. Environmental data

We used high resolution (1km²) gridded data for thirteen environmental variables (Table S2) to describe cetacean environmental niches and habitat (i.e., physical processes and oceanographic features that may either influence cetaceans directly, or indirectly such as by influencing prey distribution; Bluhm et al., 2007, Lambert et al., 2014, Mannocci et al., 2020). These included: bathymetry, chlorophyll-a concentration in surface waters, distance to the 500-metre isobath, distance to shore, coloured dissolved organic matter concentration in surface waters, diffuse downwelling attenuation, mixed layer depth, seabed slope, sea surface temperature, tidal current speed, the residuals of a GLM relating temperature to depth using natural splines (positive residual values represent waters "abnormally" warm considering how deep they are, and vice-versa), and estimates of surface water primary productivity (Table S2). Predictor variables were not highly correlated (Pearson's $|r| < 0.7$; Stephenson et al. (2020)).

2.3. Species distribution models

2.3.1. Ensemble models for highly sighted species

We modelled geographic distributions of species with high sighting frequency (≥ 50 sightings, Stephenson et al. (2020); $n = 13$ species) using an ensemble modelling approach (Araújo and New, 2007). To maximise the benefits of competing statistical frameworks with different strengths and weaknesses and reduce the reliance on a single model algorithm, we used seven statistical algorithms of species distribution models (SDMs; generalised linear models (GLM), generalised additive models (GAM), generalised boosted regression tree models (GBM), random forests (RF), multivariate adaptive regression splines (MARS), artificial neural networks (ANN) and support vector machine (SVM)) (using the *ensemble_modelling()* function in the *SSDM* package (Schmitt et al., 2017)).

We generated pseudo-absences for each species following recommendations from Barbet-Massin et al. (2012). This includes the generation of 10,000 equally weighted and randomly distributed pseudo-absences for regression models (GLM, GAM and MARS), and an equal number of absences to the number of presences for each species for machine learning models (GBM, RF, ANN and SVM). This procedure was repeated 10 times for each species to generate 10 pseudo-absence data sets. We also used spatial thinning of species occurrences to deal with potential spatial autocorrelation in sightings records following Aiello-Lammens et al. (2015). The aim of thinning is to remove the fewest possible records needed to reduce the effect of sampling bias, while retaining the greatest possible amount of environmental variability for each species. The relative importance of environmental variables was estimated for each species using a jack-knife approach; i.e. the difference in Area Under the Curve (AUC) between an SDM containing all environmental variables and one with each environmental variable omitted in turn (Phillips et al., 2006).

The performance of each model was evaluated using holdout cross-validation; models were calibrated using 70% of the data and evaluated using the remaining 30%. Model performance was evaluated using AUC. We used Pearson's correlation coefficient to compare performance for each pair of statistical algorithms. Then, we performed an ensemble forecasting approach: if an SDM had an AUC superior or equal to 0.75, it

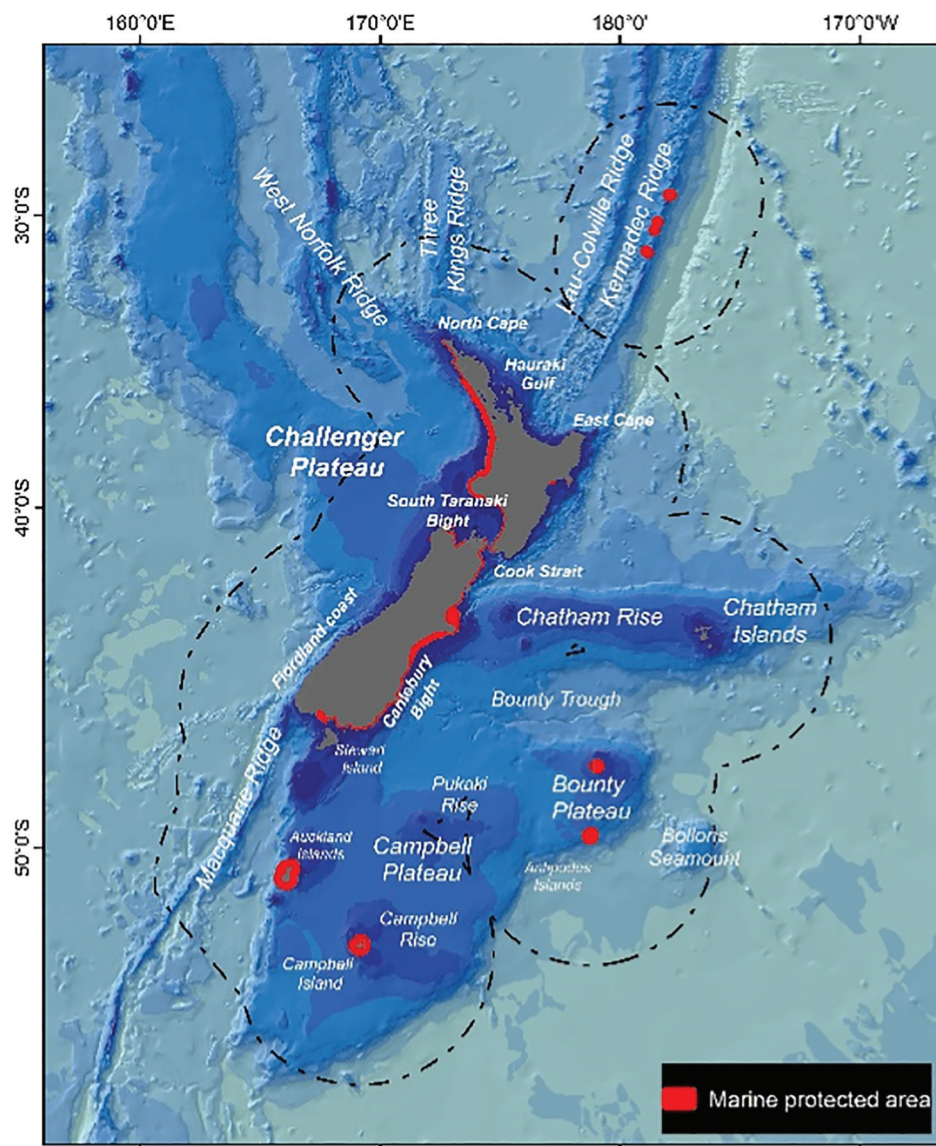


Fig. 1. Map of the New Zealand Exclusive Economic Zone (black dashed line) and surrounding areas. Bathymetry is shown as blue background. Marine protected areas are shown in red. The land is shown in grey colour. Feature names used throughout the text are written in white. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

was used to weight the means of predicted habitat suitability, and to combine ensembles of predicted species distributions (Marmion et al., 2009; Gritti et al., 2013). Finally, we generated binary (presence or absence) outputs of ensemble models using a threshold that maximised the True Skill Statistic (TSS) score (Thuiller et al., 2009).

2.3.2. Relative environmental suitability models for rarely sighted taxa

For species with few sightings ($n < 50$), we used Relative Environmental Suitability (RES) models from Stephenson et al. (2020). For RES modelling, cetacean sightings data are not used as inputs in the model but as a visual validation only (Stephenson et al., 2020). RES models were built using three environmental variables (sea surface temperature, water depth and distance to shore) to describe species' geographic ranges following methods described in Kaschner et al. (2006). Broadly, the relationships between species and the three environmental variables are described using a trapezoidal response curve based on four parameters: MinA, MinP, MaxP and MaxA. Where MinA and MaxA refer to absolute minimum and maximum variable ranges. While MinP and MaxP describe the "preferred" range of each environmental variable for

each species (Kaschner et al., 2006). While these simplistic models are likely less reliable than those using empirical relationships between species occurrence and habitat, they may be useful for discerning broad geographic distributions of rarely sighted species (Fig. 2).

Geographic ranges for each taxon were obtained by converting predicted relative environmental suitability into strict presence or absence. We use a probabilistic approach (the *convertToPA* function in the *virtuallspecies* package v.1.5.1; Leroy et al., 2016), in which the probability of getting a presence of the species in each grid cell is dependent on its suitability in this grid cell. We defined the probability of presence as a logistic transformation of environmental suitability (Meynard and Kaplan, 2012; Meynard and Kaplan, 2013). Using this approach, the only parameter that can be customised is the parameter that determines the threshold of suitability above which the species is present and below which the species is absent (β). We randomly simulated β for each species 999 times and used the mean value of simulations as a cut-off to define presence or absence (Meynard and Kaplan, 2013).

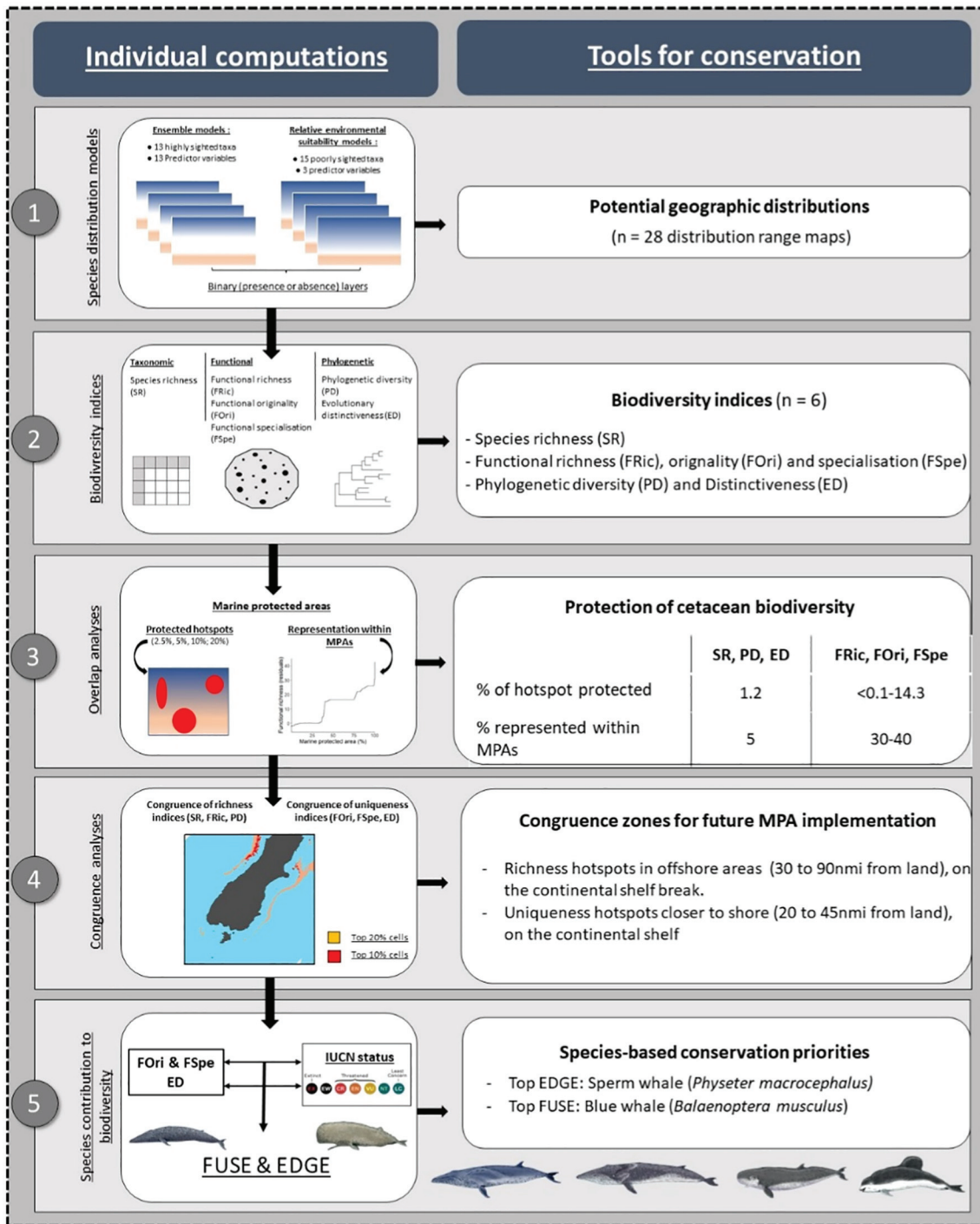


Fig. 2. Workflow diagram depicting each step of the individual computations performed in this study and their expected output for cetacean conservation in New Zealand. (1) Species distribution models were developed using two different methods: ensemble species distribution models were performed using thirteen environmental predictor variables for highly sighted species (≥ 50 at-sea sightings). Relative environmental suitability models were developed using three environmental predictor variables for poorly sighted species (< 50 at-sea sightings). Both models were then transformed into binary layers of presence or absence for each species and used for further analyses. (2) A complementary set of biodiversity indices were measured at the scale of the Exclusive Economic Zone for the taxonomic (species richness, SR), functional (functional richness, FRic; functional originality, FOr; and functional specialisation, FSpe) and phylogenetic (phylogenetic diversity, PD; and evolutionary distinctiveness, ED) diversity components of biodiversity. (3) Overlap with marine protected areas (MPA) was measured using two complementary methods: the percentage of hotspots (i.e. the top 2.5, 5, 10 and 20% cells of each biodiversity index) overlapping MPAs; and the values of each biodiversity index represented within MPAs. (4) Congruence analyses were developed to identify areas of importance for biodiversity for future MPA implementation. For this purpose, indices were grouped into two sets, those that represent richness (species richness, functional richness, and taxonomic diversity) and those that represent uniqueness (functional originality, functional specialisation, and evolutionary distinctiveness) facets of biodiversity. Congruence was measured for pairwise combinations of two indices within each group and for three indices simultaneously. (5) Species contribution to biodiversity was measured to classify species for conservation priorities. We measured the contribution of species to (a) FOr and FSpe, (b) ED. We then coupled these contributions with their global degree of endangerment (IUCN red list status) to identify Functional Unique, Specialised and Endangered species (FUSE) and Evolutionary Distinct and Globally Endangered species (EDGE).

2.4. Functional traits

We built a database of thirteen functional traits following [Albouy et al. \(2017\)](#) for all at-sea sighted cetacean species contained in our database. These fourteen traits spanned five categories: resource acquisition, life-history, reproduction, social behaviour, and morphology; and included: diet composition, foraging depth range, foraging location, fasting, female sexual maturity, weaning, gestation length, inter-litter interval, breeding site, social group size, social behaviour, adult maximum body mass and sexual dimorphism (Table S3). We coded all traits following a quantitative, semi-quantitative or binomial coding framework (Table S3). Most values (>85%) were retrieved from the literature (encyclopaedias, books, scientific literature, and the grey literature), but expert knowledge (LT, WR, TB) was also used to parameterise a subset (c. 5%) of values.

There was a total of 28 trait values (7.1%) for which information was unavailable. We imputed these values to the trait database using a regularised iterative Principal Component Analysis algorithm (the *imputePCA* function in the *missMDA* package v.1.17; [Josse and Husson, 2016](#)). However, we used the original functional trait matrix for further analyses as it was highly correlated with the imputed matrix (Mantel test; $r = 0.97$, $p < 0.001$).

2.5. Biodiversity indices

We measured cetacean biodiversity for each grid cell of the EEZ using species richness as an indicator of taxonomic diversity, three indices of functional diversity and two indices of phylogenetic diversity. Species richness (SR) was measured by summing the individual probability of presence or absence of each species in each grid cell. Functional diversity was measured using the mean value of the following multidimensional indices in each grid cell ([Villéger et al. \(2008\)](#)); using the R function *multidimFD* downloaded in December 2020 from: <http://villeger.sebastien.free.fr/>): functional richness (FRic), functional originality (FOri) and functional specialisation (FSpe). For these, we first produced a multidimensional functional space, using Principal Coordinates Analysis (PCoA) based on a Gower's distance dissimilarity matrix of each pairwise combination of all 28 species according to their 14 functional traits. Gower's distance was used as it allows the use of both binary and semi-quantitative values and can also deal with missing trait values. We ensured that equal weights were given to each of the trait categories (e.g. for the resource acquisition category which contained 3 traits, each trait was given a weighting of 1/3; Table S3). We

then synthesised functional traits using the first four axes of the functional space (as determined, using the R function *quality_funct_space*; [Maire et al. \(2015\)](#); Fig. 3). We built our functional space using four dimensions because the difference between mean squared deviations of a five-dimensional space and a four-dimensional space was negligible (0.0000001). Then, we calculated FRic as the total convex hull volume occupied by the species pool in the functional space ([Villéger et al., 2008](#)). FOri was calculated as the mean distance between each species and its closest neighbour in the functional space ([Villéger et al., 2008](#)). FOri increases as species contained in a community share fewer traits with other species. It may therefore be seen as equivalent to the inverse functional redundancy of a community ([Mouillot et al., 2013a, 2013b](#)). Finally, we calculated FSpe as the mean distance of each species to the centroid of the functional space ([Villéger et al., 2008](#)). Increases in functional specialisation show how specialist species (i.e., having extreme trait combinations) tend to increase in occurrence ([Mouillot et al., 2013a, 2013b](#)).

For phylogenetic diversity, we retrieved cetacean phylogeny from a molecular phylogenetic tree of cetaceans ([Steeman et al., 2009](#)). First, we used Faith's index (PD; using the *pd* function in the *picante* package v.1.8.2; [Kembel et al., 2010](#)), which represents the minimum total length of all the phylogenetic branches required to span a given set of species on the phylogenetic tree ([Faith, 1992](#)). Second, we measured evolutionary distinctiveness (ED; [Isaac et al. \(2007\)](#)); using the *evol.distinct* function in *picante*), which is a measure of phylogenetic isolation of a species in the species pool. It is calculated as the ratio between total branch length and the number of species within a clade. ED increases as species have a long unshared branch length with all other species.

PD is mathematically correlated to SR ([Tucker and Cadotte, 2013](#)). Thus, we calculated the standardized effect size of phylogenetic diversity (*ses.pd*, using the *ses.pd* function in *picante*), which is the difference between the observed phylogenetic diversity in an assemblage and the mean phylogenetic diversity obtained with null assemblages generated by randomizing species from the regional pool 999 times, divided by the standard deviation of phylogenetic diversity in the null model ([Gotelli and Graves, 1996](#)). Positive *ses.pd* values indicate higher phylogenetic diversity than expected given SR, and vice-versa.

FRic is also mathematically correlated to species richness ([Laliberté and Legendre, 2010](#)). Thus, we calculated the residuals from a local regression model (frequently referred to as a loess curve) with SR as predictor variable and PD as response variable (*res.pd*). We then tested for a relationship between *ses.pd* and *res.pd* using Pearson's correlation coefficient (r). We found a high correlation ($r = 0.77$) among *ses.pd* and

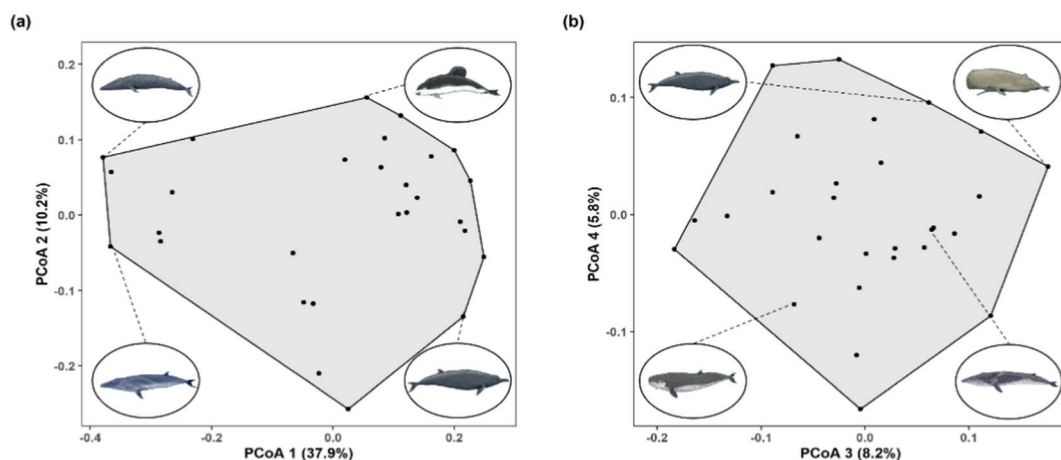


Fig. 3. Functional space of cetacean species considered in this study. Functional space was generated using the first four axes of a Principal Coordinates Analysis (PCoA) of 13 functional traits, based on dissimilarities among trait modalities. (a) Axis 1 versus axis 2; (b) axis 3 versus axis 4. Silhouettes illustrate the position of key species in the functional space, from top, right, bottom to left: (a) Blue whale (*Balaenoptera musculus*), speckled porpoise (*Phocoena dioptrica*), Arnoux's beaked whale (*Berardius arnuxii*) and sei whale (*Balaenoptera borealis*); (b) Arnoux's beaked whale (*Berardius arnuxii*), sperm whale (*Physeter catodon*), fin whale (*Balaenoptera physalus*) and pygmy sperm whale (*Kogia breviceps*).

res.pd. For all analyses, we therefore replaced PD and FRic by the residuals from a loess model involving SR as predictor variable and PD or FRic as response variable, respectively. A negative PD or FRic index indicates lower diversity than expected given SR, and vice-versa.

2.6. Congruence analyses

To map the spatial congruence between all cetacean biodiversity indices themselves we used spatial congruence analyses. Spatial congruence analyses were undertaken between hotspots of complementary biodiversity indices. That is, indices that describe richness (SR, PD and FRic) and those that describe distinctiveness (ED, FOr and FSpe). Congruence analysis allows the identification of whether two biodiversity indices present similar spatial patterns of high values, which may not be visible if only correlations among indices are displayed (Albouy et al., 2017). For example, for a pairwise comparison between SR and FRic, we calculated the observed number of overlaps, which corresponds to the number of cells recorded as a hotspot for SR and FRic. We then performed a randomization procedure, to assess whether the observed number of overlaps (Oo) was significantly different from that obtained by chance (Oe; Mouillot et al., 2011). The values contained in the cells for one of the two variables considered were randomly permuted 9999 times, and the number of overlaps was estimated for each. We tested for congruence among all pairwise combinations of indices within these two sets. We then tested for overall congruence among the three indices for each set of index individually (Albouy et al., 2017).

2.7. Marine protected areas

We aggregated gridded layers (1km²) containing detailed polygons of a set of MPAs (n = 135) for New Zealand's EEZ, covering a total of 74,373 km² (1.8%) of the EEZ. We considered all MPAs that restrict set-net and/or trawl fishing year-round. That is, we considered (1) New Zealand's 44 no-take marine reserves (<https://koordinates.com/layer/6026-doc-marine-reserves/>), (2) 26 partly no-take MPAs and (3) 59 areas of set netting restrictions designed to protect endemic coastal dolphins (Set netting prohibitions | Ministry for Primary Industries Open Data Site (arcgis.com)).

2.8. Overlap analyses

We measured overlap between cetacean biodiversity hotspots and MPAs. We defined hotspots as all grid cells with values in the upper 2.5, 5, 10 and 20% of cells of each biodiversity index for comparison. Overlap analyses were performed: (1) between hotspots of the different biodiversity indices and MPAs, (2) for the biodiversity represented in each protected grid cell of the EEZ. First, we overlaid gridded MPA locations with the hotspots of each biodiversity index. We then measured the percentage of hotspots overlapped by MPAs, considering that even if a subset of a cell overlapped a protected area, the value of the index belonging to this cell potentially benefits from a protection effect. Second, we measured the diversity represented within each protected grid cell, following Mouillot et al. (2011). This approach provides a synthesised and continuous assessment of whether MPAs overlap areas of high biodiversity. For each biodiversity index, we extracted all grid cells overlapping MPAs, which we ranked from the least to the most diverse. We then plotted these ranked values of protected biodiversity against the cumulative percentage of protected area.

2.9. Species contribution to biodiversity

We measured the contribution of each species to biodiversity using a range of evolutionary and functional metrics. Globally, many species that are evolutionarily and/or functionally distinct, and globally endangered do not benefit from existing conservation projects or protected

areas (Isaac et al., 2007; Pimiento et al., 2020a, 2020b). However, species contribution to biodiversity has been suggested as an effective tool to guide species-based conservation priority (Redding and Mooers, 2006; Isaac et al., 2007; Pimiento et al., 2020a, 2020b). We retrieved up-to-date IUCN red list status for all species of the database from the IUCN website (IUCN, 2021).

For phylogenetic diversity, we used the evolutionary distinctiveness of each species as described above (Isaac et al., 2007). We then combined evolutionary distinctiveness with the IUCN red list status of each species, to define evolutionarily distinct and globally endangered species (EDGE species; Isaac et al. (2007)). The EDGE index is defined as:

$$\text{EDGE} = \ln(1 + \text{ED}) + \text{GE} * \ln(2)$$

where ED is the evolutionary distinctiveness of each species, and GE is the IUCN red list category weight (Least Concern = 0, Near Threatened and Conservation Dependent = 1, Vulnerable = 2, Endangered = 3, Critically Endangered = 4; Butchart et al. (2004)).

For functional diversity, we measured the functional originality and specialisation of each species from our functional space, as described above (Villéger et al., 2008). These contributions were then integrated and combined with extinction risk to identify species that are both important contributors to functional diversity and endangered (FUSE species; (Pimiento et al., 2020a, 2020b)). To measure the FUSE index, we used the following formula:

$$\text{FUSE} = \text{FUGE} + \text{FSGE}$$

where

$$\text{FUGE} = \ln(1 + (\text{FOr} \times \text{GE}))$$

and

$$\text{FSGE} = \ln(1 + (\text{FSpe} \times \text{GE}))$$

where FOr is the standardized functional originality (also referred to as functional uniqueness by Pimiento et al. (2020a, 2020b)) of each species and FSpe the standardized functional specialisation. GE is the IUCN red list scores, from LC = 0 to CR = 4 (see above).

3. Results

3.1. Species distribution models

Ensemble modelling of species distribution for highly sighted taxa (n = 13) performed well across species and algorithms (mean AUC = 0.89 ± 0.06; sensitivity = 0.89 ± 0.07; specificity = 0.90 ± 0.05; Table S4). Across all species, environmental variables having the highest relative influence were distance to shore (% relative influence = 19.2 ± 10.5), temperature residuals (10.3 ± 8.5); mixed layer depth = 9.00 ± 9.90; bathymetry (9.35 ± 4.3), VGPM (7.6 ± 3.1) and sea surface temperature (7.2 ± 3.11; Table S5).

3.2. Functional trait space of cetaceans

The first axis of the trait space (37.9%, Fig. 3(a)) was strongly related to diet composition, foraging depth range and foraging location but strongly negatively related to fasting (Table S6). Southern right whale dolphin (*Lissodelphis peronii*) scored the highest value along the first axis, whereas blue whale (*Balaenoptera musculus*) scored the lowest value. The second axis (10.2%; Fig. 3(a)) was negatively related to foraging location, social behaviour and sexual dimorphism (Table S6). Sperm whale (*Physeter catodon*) scored the lowest value on the second axis, whereas dusky dolphin (*Lagenorhynchus obscurus*) scored the highest. The third axis (8.2%; Fig. 3(b)) of the trait space was negatively correlated to gestation length, weaning and female sexual maturity but positively related to breeding site and foraging location (Table S6).

Killer whale (*Orcinus orca*) scored the lowest value on the third axis, and hourglass dolphin (*Lagenorhynchus cruciger*) scored the highest value. Lastly, the fourth axis of the functional space (5.8%; Fig. 3(b)) was positively correlated to female sexual maturity and adult maximum body mass, but negatively correlated to diet composition (Table S6). Spectacle porpoise (*Phocoena dioptrica*) scored the lowest value on the fourth axis and blue whale (*Balaenoptera musculus*) scored the highest.

3.3. Spatial patterns of cetacean diversity

Species richness, phylogenetic diversity and evolutionary distinctiveness reached their highest values offshore (i.e. at a distance of 40 to 100 nautical miles from the land, Fig. 4(a)–(c)). In contrast, functional richness, originality and specialisation were highest in areas closer to shore (i.e. 0 to 40 nmi from the land, Fig. 4(d)–(e)).

Species richness ranged from 0 to 21 species (Fig. 4(a)). The highest values (>16 species) were in offshore areas along the west and east coasts of both mainland islands, the Chatham Islands, the eastern margins of the Challenger Plateau and the western margins of Chatham Rise. Predicted phylogenetic diversity was also highest in offshore areas (Fig. 4(b)). The highest values of phylogenetic diversity were located off the west and east coasts of both mainland islands, Chatham Rise and Islands, Stewart Island, the Kermadec Ridge and the Auckland Islands.

Northern waters of the EEZ had greater phylogenetic diversity than southern waters (Fig. 4(b)). Evolutionary distinctiveness showed similar broad-scale spatial patterns to species richness (Fig. 4(c)).

Functional richness peaked along the edge of the continental shelf (i.e. 25–35 nmi from the land; Fig. 4(d)), on the Canterbury Bight, East Cape and the Hauraki Gulf (Fig. 4(d)). Finally, functional originality and functional specialisation were high along most of the continental shelf close to shore (0 to 25 nmi from the land) of both mainland islands and Chatham Island (Fig. 4(d) & (f)).

3.4. Spatial congruence among diversity indices

Congruence analyses using two indices, showed that the most congruent indices were SR and FRic (Fig. S1a, b, c & d; SR/FRic). In contrast, SR and PD, and PD and FRic were poorly congruent for the 2.5, 5% and 10% top cells (Fig. S1a, b & c; SR/PD & PD/FRic). ED & FOri and ED & FSpe, were not congruent for the 2.5% top cells (Fig. S1a), nor were ED and FSpe for the 5% top cells (Fig. S1b).

Congruence using three indices (SR, FRic and PD, ED, FOri and FSpe) was extremely low for the top 2.5 and 5% top cells (data not shown). Congruence of SR, FRic and PD was however apparent for the 10% and 20% top cells (Fig. S2(a)). Areas of congruence were in offshore areas (30 to 90 nmi from land), on the continental shelf break, especially in the

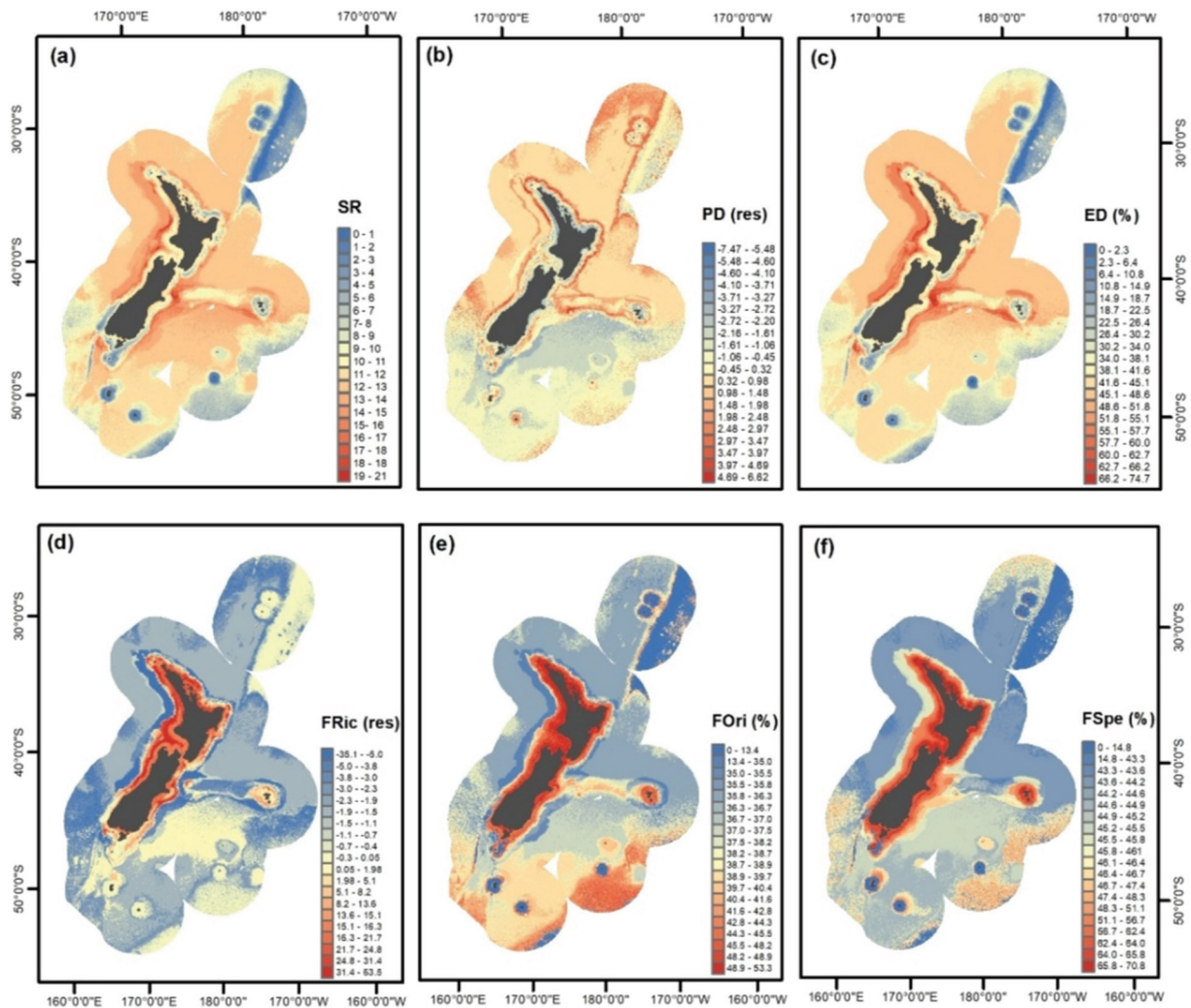


Fig. 4. Modelled spatial patterns of cetacean biodiversity in New Zealand's Exclusive Economic Zone as measured and predicted using six indices. (a) SR: species richness; (b) PD: phylogenetic diversity; (c) ED: evolutionary distinctiveness; (d) FRic: functional richness; (e) FOri: functional originality; (f) FSpe: functional specialisation. Res: residuals from relationships with species richness using local regression models. ED, FOri, and FSpe are represented as the percentage of their maximum possible value.

outer Hauraki Gulf, East Cape, Chatham Islands, the north-west of the North Island, the South Taranaki Bight and the Canterbury Bight (Fig. S2 (a)).

There was a higher congruence among ED, FOrI and FSpe indices (Fig. S2(b)). Most congruence zones were located closer to shore (20 to 45 nmi from land), especially on the continental shelf around the South Taranaki Bight and Challenger Plateau, but also the West Coast of the South Island, Canterbury Bight and the northernmost part of the North Island (Fig. S2(b)).

3.5. Biodiversity overlaps with marine protected areas

There was little overlap (<1.2%) between species richness, phylogenetic diversity, and evolutionary distinctiveness hotspots with MPAs (Fig. 5(a) & (b)). In contrast, hotspots of functional richness, originality and specialisation had a greater amount of overlap with MPAs, yet this overlap was still relatively low (% of overlap \leq 0.1–14.3%; Fig. 5(a) & (b)).

Regarding the representation of diversity indices within MPAs (Fig. 5 (c) & (d)): values within the top 10% hotspots of species richness, phylogenetic diversity and evolutionary distinctiveness were represented in only c. 5% of MPAs. In contrast, values within the top 10% hotspots of functional richness, originality and specialisation were represented in c. 60–70% of MPAs (Fig. 5(c) & (d)).

3.6. Species' contribution to biodiversity

The three most evolutionarily distinct species were southern right whale (*Eubalaena australis*; 7.2%), sperm whale (*Physeter macrocephalus*; 6.9%) and pygmy sperm whale (*Kogia breviceps*; 6.9%; Fig. 6, Table S5), while the three most evolutionarily distinct and endangered species were sperm whale (EDGE = 3.44), southern right whale (EDGE = 3.41) and blue whale (*Balaenoptera musculus*; 3.36; Fig. 6, Table S5). In contrast, species contributing the most to functional originality were pygmy sperm whale (5.47%), spectacled porpoise (*Phocoena dioptrica*; 5.6%) and Arnoux's beaked whale (*Berardius arnuxii*; 5.1%; Fig. 6, Table S5), while the three most functionally specialised species were blue whale (6.7%), sei whale (*Balaenoptera borealis*; 5.8%) and fin whale (*Balaenoptera physalus*; 5.7%; Fig. 6, Table S5). Finally, the most functionally unique, specialised, and endangered species were blue whale (FUSE = 2.31), sei whale (2.19) and fin whale (1.67; Fig. 6, Table S5).

4. Discussion

Our analyses identified a spatial mismatch between hotspots of taxonomic, functional, and phylogenetic cetacean diversity and MPAs in New Zealand's Exclusive Economic Zone. Our results suggest that current MPAs poorly overlap hotspots of richness and uniqueness of cetacean diversity. We further show that New Zealand's MPAs are not representative of cetacean biodiversity for at least 30% of MPAs. Finally, we identify hotspots of congruence among multiple components of biodiversity and rank species contributions to biodiversity, revealing

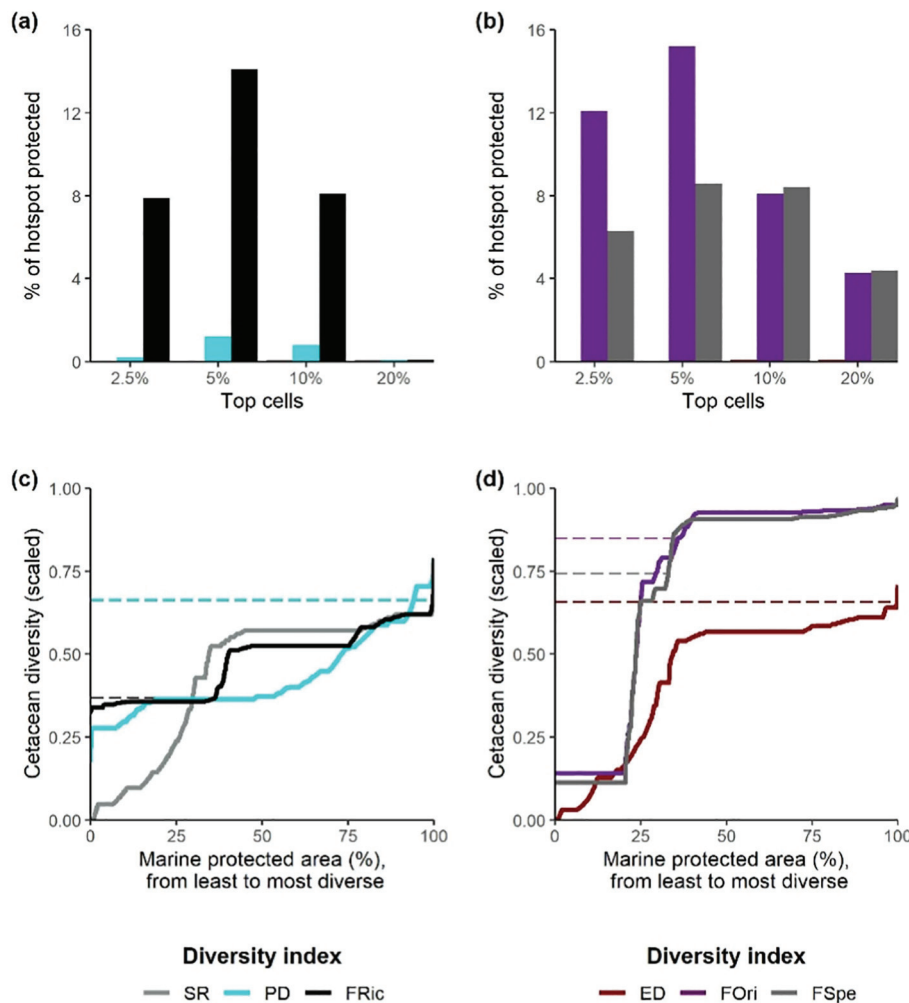


Fig. 5. (a) & (b): Percentage of cetacean biodiversity hotspots (top cells) overlapped by MPAs in the New Zealand Exclusive Economic Zone. (c) & (d) Cetacean biodiversity represented in New Zealand's MPAs. Each plot gives the values of the corresponding diversity index represented within protected grid cells of the New Zealand Exclusive Economic Zone. To produce these plots, we first scaled each of the six indices to their range values (0 to 1). Then, we extracted the values of each index within each protected grid cell and ranked values from the lowest to the highest. Finally, we plotted the cumulative percentage of protected cells in New Zealand's Exclusive Economic Zone (horizontal axis) against the ranked diversity values (vertical axes). The coloured bands indicate values within the top 10% cells of each index. (a) & (c) SR: species richness; PD: phylogenetic diversity; FRic: functional richness; (b) & (d) ED: evolutionary distinctiveness; FOrI: functional originality; FSpe: functional specialisation.

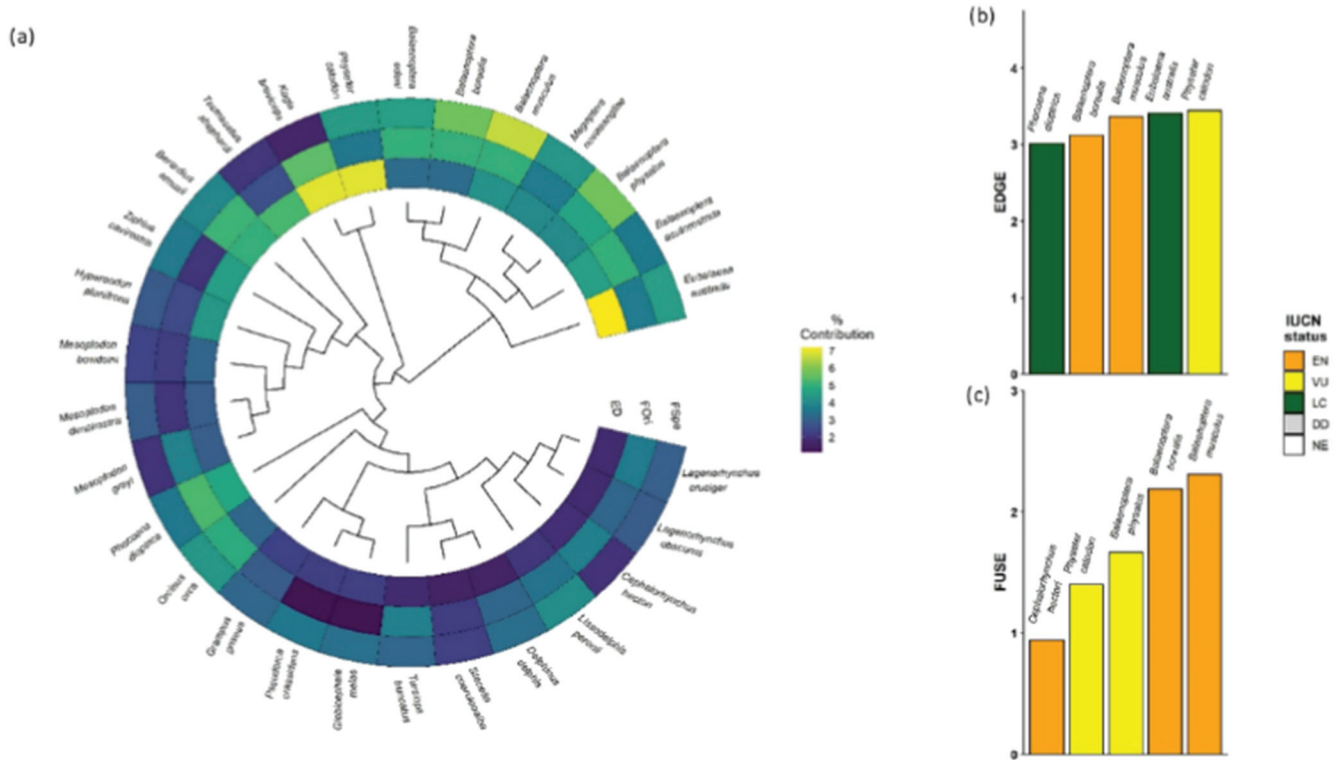


Fig. 6. Species contribution to biodiversity. (a) Phylogenetic tree of cetacean species used in this study showing values of Evolutionary distinctiveness (ED), functional originality (FOri) and specialisation (FSpe) (b). Top five scoring Evolutionary Distinct and Globally Endangered (EDGE) species. (c) Top five scoring = Functionally Unique Specialised and Endangered (FUSE) species. IUCN (red list) status: EN = endangered; VU = vulnerable; LC = least concern; NE: not evaluated; DD = data deficient. All values of species contribution to biodiversity are given in Table S6.

priorities and guidance for future cetacean distribution hotspots and species-based conservation efforts.

Our results revealed that species richness, phylogenetic diversity and evolutionary distinctiveness reached their highest values in areas 40 to 100 nautical miles from the coast. The location of these hotspots represent overlap areas between the ranges of species inhabiting inshore waters and those favouring offshore waters (Stephenson et al., 2020). Species distribution models of cetacean distributions at the scale of New Zealand’s EEZ, have suggested that many of the cetacean species accounted for here (e.g., common dolphin, Māui dolphin, blue whale, fin whale, bottlenose dolphin and Bryde’s whales) display preferences for northern, warmer, and high salinity, nutrient poor subtropical waters located to the west and north of New Zealand (Stephenson et al., 2020; but see Derville et al. (2016) and Barlow et al. (2020)). This result reflects the greater phylogenetic diversity found in northern areas of the EEZ. However, it is unclear whether preferences for northern waters are an indication of the environmental niches of these species or those of their prey. Nevertheless, we show that these areas have high conservation value for New Zealand’s cetacean species evolutionary history.

Functional diversity measures increased toward near-shore zones of New Zealand. The New Zealand cetacean fauna comprises a diverse array of species, including endemic species that inhabit nearshore habitats only and other resident, migratory or vagrant taxa (Baker et al., 2019). An increase in functional originality toward near shore zones suggests a decrease in functional redundancy, which may reflect increased vulnerability and sensitivity of functions to environmental change in near-shore areas of the EEZ, as has been reported for other coastal areas worldwide (Mouillot et al., 2014; McLean et al., 2019). Increasing functional specialisation suggests that species inhabiting near-shore areas are also specialist species, performing unique functional roles (Mouillot et al., 2013a, 2013b). Here, the use of these two indices simultaneously was necessary to fully describe ecological

patterns, which was also the case for other studies (e.g., Colin et al., 2018 and Pimiento et al., 2020b). Together these two patterns of functional originality and specialisation suggest that the loss of a single species in near shore areas may destabilize ecological processes (Pimiento et al., 2020a, 2020b). Given that taxonomic and phylogenetic diversity measures were lowest in nearshore areas, the spatial patterns of functional diversity that were observed here, have important implications for conservation planning.

New Zealand is considered a global biodiversity hotspot for cetaceans, encompassing exceptional taxonomic, functional, and phylogenetic diversity (Kaschner et al., 2006; Albouy et al., 2017; Stephenson et al., 2021). Given this status, making well-informed decisions is crucial at both national and international scales to promote the long-term conservation of this biodiversity. Our study provides fruitful results in this sense, including that around 30% of MPAs in New Zealand are currently located in areas of low cetacean biodiversity. This indicates that despite the recent increase in MPA coverage over the last decade in New Zealand’s EEZ, one third are generally not located in the most suitable or important sites to protect cetacean biodiversity. This lack of congruence between cetacean biodiversity and existing MPAs likely reflects a lack of consideration for this aspect of marine biodiversity within the current network. For example, most no-take marine reserves are established in relatively small areas in coastal habitat to promote recovery of exploited species (e.g., reef fish, invertebrates). Additionally, historical MPA planning processes were unlikely to have detailed information available on cetacean biodiversity to draw upon, and instead, designation for protection of cetaceans has been targeted at single species such as Hector’s and Maui dolphins (Derville et al., 2016). Expanding MPAs with large and/or offshore MPAs and Important Marine Mammal Areas appears to be necessary for cetacean conservation in New Zealand, as was also suggested for other ecosystems worldwide (Singleton and Roberts, 2014, Davies et al., 2017, Agardy et al., 2019, S.

L. Maxwell et al., 2020; S.M. Maxwell et al., 2020).

We identified congruent areas among indices of both richness and distinctiveness. Areas of congruence among richness indices were mostly located along the edge of the continental shelf. In contrast, areas of congruence among indices of distinctiveness were located closer to shore, on the continental shelf. Shelf-break areas may function as transition zones where both coastal and offshore species overlap within a narrow band of highly variable habitat characteristics. The New Zealand continental slope environment is punctuated by diverse topographical features (e.g., submarine canyons, seamounts, plateaus) and this diversity in habitat types may be reflected by the high diversity of species that use this area. The western boundary currents that define New Zealand's broad oceanographic setting are steered by seafloor topography at approximately the depth of the continental shelf break (Smith et al., 2013), which likely promotes mesoscale features (e.g., eddies, fronts) that may provide foraging opportunities for diverse cetacean species. Mobile species such as cetaceans may provide different functions in different areas, particularly those that use certain habitats for different life-history stages (e.g., breeding/calving areas for baleen whales; Rayment et al., 2015). Protecting these areas may represent strategic investment to increase conservation gains by MPAs in New Zealand's waters.

The fact that functional diversity indices spatially differed from our estimates of phylogenetic diversity suggests that our set of traits are not phylogenetically conserved; i.e. that closely related species do not necessarily share similar traits (Thuiller et al., 2015). This discrepancy supports the notion that prioritizing phylogenetic diversity for conservation does not capture functional diversity reliably (Mazel et al., 2018). Thus, this study highlights the need to integrate multiple components of biodiversity in conservation frameworks (Devictor et al., 2010; Mazel et al., 2018). The relationship between evolutionary and functional distinctiveness depends on the mode of trait evolution, the rates of speciation and extinction in a clade, and the interaction between these processes (Grenié et al., 2018). The influence of factors such as convergent evolution and niche conservatism on the relationship between evolution and functional strategies at the assemblage level is still poorly explored (Mazel et al., 2017; McLean et al., 2021). A comprehensive perspective on how functional and evolutionary distinctiveness relate across different taxa, is necessary to further guide conservation prioritization.

We found that the most evolutionarily distinct, functionally original and/or specialised species differed from those being threatened at the global scale. As functionally original and specialised species differ in trait composition from the rest of the species pool, these may support unique ecosystem functions (Mouillot et al., 2013a, 2013b), yet do not seem to be considered by conservation strategies as species needing prioritized protection. Sperm whales and pygmy sperm whales are deep diving specialists, that contribute to the recycling of nutrients stored in the deep ocean and enhance carbon sequestration (Lavery et al., 2010). Southern right whales are also ecological specialists that forage on dense aggregations of zooplankton consisting largely of euphausiids and copepods (Tormosov et al., 1998). The significant spatial separation between foraging and breeding grounds promotes large scale transport of micronutrients that enhance productivity in the micronutrient poor southern ocean (Wing et al., 2014). The mismatch between red list status and functional traits validates the use of functional diversity metrics as an important component to identify species that are not threatened at the global scale, but likely support unique functions in ecosystems, such as the New Zealand Exclusive Economic Zone.

Our study provides novel results and highlights conservation gaps for cetaceans in New Zealand's waters, that can be used to improve MPA planning. However, we recognise that it may represent a starting point. Further research effort should be focused in improving fine-scale knowledge on cetacean ecology and distribution, such as, increasing sampling effort and diversifying sampling methods, for example, using targeted eDNA (Juhel et al., 2021) or tracking data (Hays et al., 2019).

Comparing mapping approaches among different distribution maps and modelling approaches (Albouy et al., 2017; Herkt et al., 2017; Derville et al., 2018), will further strengthen our capacity to protect this biodiversity.

New Zealand waters are among the most diverse areas for cetaceans on Earth and face increasing environmental changes. Given the increasingly recognised link between biodiversity, its protection and human well-being (Ban et al., 2019), protecting such biodiversity should therefore be a priority (Sala et al., 2021). Thus, it is important to establish systematic conservation planning for the multiple components and facets of biodiversity (Brum et al., 2017), as a key process within government agencies responsible for conservation and development planning. Our results can be used by managers to identify areas that should be considered for cetacean conservation planning in New Zealand waters. Priorities for conservation should be continuously updated as solutions are implemented when knowledge of changes in species contribution to biodiversity and degree of endangerment changes. Our study identifies novel, yet important, challenges for increasing the protection of cetacean biodiversity in New Zealand's marine environment.

CRediT authorship contribution statement

Théophile L. Mouton, Fabien Leprieur, Fabrice Stephenson and Camille Albouy: Conceptualization. Fabrice Stephenson, Théophile L. Mouton, Leigh Torres, Will Rayment and Tom Brough: Data curation. Théophile L. Mouton: Formal analysis, Writing - original draft. All authors: Writing - review & editing.

Declaration of competing interest

Authors declare no conflict of interest.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.biocon.2022.109484>.

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