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# Le rôle des traits des espèces dans la dispersion à différentes échelles - de la compréhension du passé profond aux processus actuels

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## THÈSE

Pour obtenir le grade de

### DOCTEUR DE L'UNIVERSITÉ GRENOBLE ALPES et de SWANSEA UNIVERSITY

École doctorale : Chimie et Sciences du Vivant  
Spécialité : Biodiversité – Écologie – Environnement  
Unité de recherche : Laboratoire d'Écologie Alpine et Biosciences

## Le rôle des traits des espèces dans la dispersion à différentes échelles - de la compréhension du passé profond aux processus actuels

## The role of species' traits in dispersal across scales - from deep past understanding to present-day processes

Présentée par : Sarah Sophie WEIL

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# Declaration

This work has not previously been accepted in substance for any degree and is not being concurrently submitted in candidature for any degree.

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Date 09/06/2023

This thesis is the result of my own investigations, except where otherwise stated. No correction services have been used. A bibliography is appended after each chapter.

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*A thesis between the sea and the mountains*



*This journey has no nameable ports of call, no identifiable destination, no placement in time and space. It is not a location, but a thought. It's a voyage of the mind to a world that is just a little to the left of reality.*

*Life isn't an orderly progression and it is frequently full of surprises.*

James C. Christensen, *A Journey of the Imagination*



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## **Le rôle des traits des espèces dans la dispersion à différentes échelles - de la compréhension du passé profond aux processus actuels**

**Mots clés :** biogéographie, dispersion, traits fonctionnels, tétrapodes, invasion biologique, modèles d'estimation des mouvements biogéographiques passés

L'un des défis les plus pressants de l'écologie consiste à comprendre les mécanismes qui régissent la répartition de la vie à l'échelle mondiale. Dans ce contexte, les événements rares de dispersion à travers des barrières biogéographiques et l'établissement d'espèces dans de nouvelles régions sont un facteur clé. En effet, ces événements peuvent influencer la répartition des espèces dispersantes et des espèces des communautés réceptrices, et à long terme initier des processus de spéciation. À plus petite échelle, la dispersion est essentielle pour la persistance des espèces et leur permet de réagir aux changements de leur environnement directement par le mouvement ou indirectement par l'adaptation. Toutes les espèces n'ont pas les mêmes capacités pour se disperser et s'établir. Mieux comprendre ces différences est devenu une nouvelle urgence aujourd'hui si nous voulons être pertinents et réalistes dans les actions de conservation à venir, dans le contexte des changements globaux (notamment des invasions biologiques, de l'utilisation des terres et du changement climatique). Les traits des espèces sont considérées comme un facteur important dans la réussite de la dispersion. Par exemple, les espèces de grande taille sont souvent de meilleurs disperseurs que les petites, et les plantes dont les graines peuvent flotter sont plus susceptibles de se disperser sur des archipels insulaires que celles dont les graines coulent. Cependant, peu de tests concernant le rôle des traits dans la dispersion à large échelle biogéographique ont été effectués.

Dans cette thèse, je combine des approches biogéographiques, macroécologiques et macroévolutives pour identifier le rôle des traits des espèces (taille et histoire de vie) dans la dispersion, et pour tester la transférabilité des relations trait-dispersion à travers de multiples échelles (taxonomiques, temporelles et géographiques). Premièrement, je quantifie et compare le rôle des traits dans l'histoire biogéographique de 56 clades de tétrapodes. Deuxièmement, je discute dans une synthèse conceptuelle si et comment les informations provenant d'études macroévolutives et biogéographiques peuvent être utilisées pour mieux prédire les futures espèces invasives, ainsi que la vulnérabilité des espèces natives face aux changements globaux actuels. Troisièmement, je teste les considérations conceptuelles de ce travail sur des données empiriques, en reliant les patrons observés dans la dispersion biogéographique passée aux invasions biologiques et aux changements d'aire de répartition actuels. Ensemble ces trois volets mettent en lumière l'importance des contextes taxonomiques, géographiques et temporels dans le rôle des traits des espèces pour la dispersion. Ceci constitue une étape importante vers de meilleures prédictions des capacités des espèces à répondre aux changements environnementaux.



## **The role of species' traits in dispersal across scales - from deep past understanding to present-day processes**

**Key words:** biogeography, dispersal, functional traits, tetrapods, biological invasion, trait-dependent biogeographic models

A pressing challenge in ecology is to unravel the mechanisms that underlie the distribution of life at a global scale. Rare dispersal events across biogeographic barriers and establishment in new regions are central to this: these events determine the distribution of both the dispersing species and of species in the receiving community, and they can open opportunities for speciation. On smaller scales, dispersal is integral to species' persistence, allowing them to respond to changes in their environment directly through movement or indirectly through adaptation. Not all species have the same ability to disperse and establish. Better understanding these differences has gained new urgency today if we are to accurately assess risks, challenges and conservation opportunities in the context of biological invasions, land-use and climate change. Species' traits are thought to be an important factor in successful dispersal. For example, large species are often better dispersers than small species, and plants with seeds that can float are more likely to disperse over island archipelagos than those with seeds that sink. However, there have been few tests of theory on how species traits might support dispersal at large biogeographic scales.

In this thesis, I combine biogeographic, macroecological and macroevolutionary approaches to identify the role of body size and life-history traits in dispersal, and to test the transferability of trait-dispersal relationships across scales. First, I quantify and compare the role of traits in biogeographic histories of 56 tetrapod clades. Second, I discuss in a conceptual synthesis if and how information from macroevolutionary and biogeographic studies can be used to better understand species present-day biological invasions, as well as present-day extinction risk due to changing environmental conditions. Third, I test conceptual considerations from this work on empirical data, linking the patterns observed in past biogeographic dispersal to present-day biological invasions and range shifts. Together these three strands highlight the importance of taxonomic, geographical and temporal contexts in the role of species traits in dispersal, which is an important step forward to better predictions of species' abilities to respond to changing environmental conditions.



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# Résumé détaillé de la thèse

Le rôle de la dispersion dans les patrons de distribution des espèces et dans la biogéographie globale est au cœur des débats depuis plusieurs siècles (Lomolino, Riddle, et al. 2017; Lomolino and Brown 2009; Morrone and Crisci 1995; Nelson 1978). D'un côté, des chercheurs défendaient l'hypothèse selon laquelle la dispersion est le processus le plus important qui détermine les distributions des espèces (dispersionnistes). D'autres scientifiques pensaient que les capacités individuelles de dispersion des espèces sont négligeables par rapport aux événements géologiques qui peuvent créer et éroder des barrières géographiques (hypothèse de la vicariance). Aujourd'hui, l'amélioration des méthodes de séquençage de l'ADN et l'estimation des dates de divergence des lignées sur la base des séquences moléculaires et de la datation des fossiles, ont fait avancer ce débat. Dans un grand nombre de cas, les dates de divergence des lignées montrent que les événements de spéciation sont trop récents pour être le produit de vicariance. La dispersion à travers des barrières importantes se produit chez un grand nombre de taxons, plus fréquemment et sur de plus grandes distances qu'on ne le pensait. Il a été démontré que la dispersion sur de longues distances est un facteur clé déterminant la distribution de certains mammifères (Ali and Vences 2019), reptiles (Vidal et al. 2008), amphibiens (Fonte et al. 2019; Vences et al. 2003), et qu'elle joue probablement un plus grand rôle encore chez les invertébrés (Hendriks et al. 2019) et les plantes (p. ex Nathan 2006). Certains auteurs ont même proposé que l'ensemble de la flore de Nouvelle-Zélande soit le produit d'évènements de dispersion (p. ex. Pole 1994; Winkworth et al. 2002).

Bien que le débat entre les dispersionnistes et ceux défendant l'hypothèse de la vicariance ne soit pas complètement clos (peut-être parce que l'importance relative de la dispersion et de la vicariance dépend des clades), il est clair que la dispersion joue un rôle décisif dans la biogéographie globale (Cowie and Holland 2006; Queiroz 2005). La dispersion peut étendre la distribution actuelle de l'espèce, elle peut affecter d'autres espèces dans la région nouvellement colonisée par le biais d'interactions biotiques et, à des échelles de temps évolutives, elle peut être à l'origine d'évènements de spéciation. Ainsi, un seul événement de dispersion peut déterminer le destin d'un clade ou d'une lignée entière. En outre, l'étude

des facteurs qui déterminent les issues d'événements de dispersion est devenue plus urgente aujourd'hui dans le contexte de la perte d'habitat, du changement climatique et des invasions biologiques (IPBES 2019). D'une part, le changement des conditions environnementales peut déplacer les niches abiotiques et biotiques des espèces hors de leur aire de répartition actuelle. Si les espèces ne peuvent pas s'adapter aux nouvelles conditions environnementales, le seul moyen d'éviter une extinction locale est de se disperser pour suivre le déplacement géographique de leur niche dans l'espace. Le taux de changement est rapide, ce qui signifie que la dispersion sur de longues distances ou à travers des barrières biogéographiques peut jouer un rôle crucial dans la survie future des populations et des espèces (Devictor et al. 2012; Trakhtenbrot et al. 2005). D'autre part, en raison d'une intervention humaine intentionnelle ou non, les espèces franchissent des barrières qu'elles n'auraient peut-être pas franchies naturellement, et ce en plus grand nombre. Des changements radicaux ont été observés dans des communautés envahies par des espèces provenant de régions lointaines (Simberloff et al. 2013).

Cependant, nous sommes encore loin de comprendre les déterminants des processus de dispersion, tant à l'échelle de l'évolution que dans les processus de dispersion actuels, tels que les changements d'aire de répartition et les invasions biologiques. Des questions restent en suspens, notamment en ce qui concerne les différences de capacités et de fréquences de dispersion entre les espèces, et le rôle que jouent les caractéristiques des espèces dans ces différences. En ce qui concerne la dispersion à l'échelle de l'évolution, le développement de nouvelles méthodes au cours des dernières années et la disponibilité des données ont rendu possible l'étude des questions que les scientifiques se posent depuis longtemps, telles que "La dispersion à travers des barrières majeures est-elle déterminée par le hasard et imprévisible ou existe-t-il des différences explicables dans les capacités de dispersion et d'établissement entre les espèces ?" (Lowe and McPeck 2014). Tenter de répondre à cette question contribuera à une meilleure compréhension des patrons de répartition des espèces et des processus qui les façonnent, et pourrait nous aider à mieux comprendre les processus de dispersion actuels.

La dispersion à travers des barrières majeures est un processus clé, qui détermine le destin des espèces et des lignées à des échelles temporelles et géographiques petites et grandes (Clobert et al. 2012; Queiroz 2005; Simpson 1940). Dans un monde changeant marqué par les crises conjointes du climat et de la biodiversité, il est plus urgent que jamais de comprendre les déterminants des capacités des espèces à se disperser à travers des barrières majeures et à établir des populations dans de nouvelles régions. Dans le cadre de ma thèse, j'apporte une contribution à cette compréhension. Ma thèse est composée de deux parties (Fig. 6 dans l'introduction). Dans la première partie, je me concentre sur les corrélats du succès de la dispersion biogéographique passée, d'abord chez les caméléons (**chapitre 1**) et ensuite dans 56 clades de tétrapodes (**chapitre 2**). Dans la deuxième partie

de ma thèse, je relie les informations du passé aux processus actuels. Je le fais d'abord dans une synthèse conceptuelle (**chapitre 3**) où je discute si et comment les informations provenant d'études macroévolutives et biogéographiques peuvent être utilisées pour mieux comprendre les processus actuels. Ensuite, je teste les considérations conceptuelles de ce travail relatives à la dispersion : tout d'abord, j'analyse si la dispersion passée est liée au succès actuel de la naturalisation de certains clades de tétrapodes (**chapitre 4**), puis j'étudie si la dispersion passée est liée à l'expansion actuelle de l'aire de répartition (**chapitre 5**). Je conclus cette thèse par une discussion générale sur mon travail, y compris les limites, et les perspectives de travail futur. Au cours de cette thèse, j'ai produit trois articles scientifiques : l'un (chapitre 1) est publié dans la revue *Ecography* (Weil, Gallien, et al. 2022), un deuxième (chapitre 2) est actuellement en révision dans la revue *Nature Ecology and Evolution*, et le troisième (chapitre 3) est en préparation. Deux autres articles non directement liés à cette thèse sont en préparation. L'un porte sur les stratégies d'histoire de vie des tétrapodes (Allen et al. in prep.), et l'autre sur les relations entre les menaces anthropogéniques et les stratégies fonctionnelles chez les reptiles (Weil, Rodriguez-Caro, et al. in prep.).

## **Partie I - Le passé**

Dans la première partie de ma thèse, j'étudie comment les caractéristiques des espèces sont liées à la dispersion biogéographique passée. Pour ce faire, j'utilise des modèles biogéographiques. Les modèles biogéographiques estiment les aires de répartition des ancêtres des espèces à travers la phylogénie, en se basant sur les occurrences des espèces existantes dans les régions biogéographiques définies a priori, et sur les informations phylogénétiques (Fig. P1.2a et b). Cela permet de déduire les événements de dispersion, de vicariance et de contraction de l'aire de répartition dans l'histoire d'un clade, c'est-à-dire de déduire l'histoire biogéographique d'un clade. Dans tous les modèles, deux paramètres clés sont estimés : le taux de dispersion  $d$  et le taux d'extinction  $e$ . Dans ce contexte, la "dispersion" fait référence à l'expansion réussie de l'aire de répartition et l'extinction fait référence à l'extinction locale dans une région, et non à l'extinction d'une lignée entière. Les taux de dispersion peuvent être modifiés pour refléter des caractéristiques importantes et des changements dans la géographie de la Terre au fil du temps (tels que les changements de la distance entre les régions, l'émergence ou la submersion d'îles). Cependant, dans les modèles de base indépendants des traits, les taux de dispersion sont toujours les mêmes pour toutes les lignées ("échangeabilité des lignées", Sukumaran and Knowles 2018), ce qui n'est pas réaliste car, dans la majorité des cas, on sait que les capacités de dispersion varient entre les espèces en raison des différences dans leurs traits. En réponse à ce problème, une extension

a été implémentée dans BioGeoBEARS (Klaus and Matzke 2020; Matzke 2013; Matzke 2014) permettant à un trait binaire, lui-même évolutif, d'influencer le taux de dispersion  $d$ . La comparaison des modèles indépendants et dépendants des traits avec des méthodes statistiques (critère d'information d' Akaike) permet de déduire si les traits des espèces sont susceptibles d'avoir joué un rôle dans l'histoire biogéographique d'un clade. Dans le cadre de ma thèse, j'ai développé une procédure plus sophistiquée, qui inclut le calcul de la moyenne des paramètres entre différents modèles basés sur différents scénarios de binarisation. Cette méthode permet de déduire des relations plus détaillées entre les traits et le succès de la dispersion biogéographique passée, y compris des relations en forme de U et en forme de cloche (chapitres 1 et 2).

Dans le **chapitre 1**, je cherche à déterminer la relation entre trois traits (distribution côtière, taille du corps, position sur le continuum rapide/lent du cycle de vie; "fast/slow life history continuum" en anglais) et la probabilité de dispersion passée sur une échelle de temps évolutive chez les caméléons (Chamaeleonidae). En utilisant les données de distribution des espèces, j'identifie les neuf régions biogéographiques les plus importantes pour tous les caméléons inclus (181/217 espèces). Avec l'aide de mes collaborateurs, je compile les données sur les traits d'histoire de vie et j'utilise l'analyse factorielle phylogénétique pour déduire des axes indépendants de taille corporelle et de traits d'histoire de vie rapides/lents. Enfin, j'étudie si les traits et les combinaisons de traits sont liés au succès de la dispersion biogéographique dans le passé, en utilisant des modèles biogéographiques indépendants et dépendants des traits, comme décrit ci-dessus. Je constate que les trois traits sont associés aux mouvements biogéographiques passés. Les lignées ayant des distributions côtières et celles ayant de grands corps ont des probabilités de dispersion plus élevées. Il est intéressant de noter que les caméléons avec des traits d'histoire de vie soit très rapide, soit très lent, réussissent mieux à se disperser que les espèces ayant une stratégie intermédiaire. Ensemble, les trois traits - côtier, gros corps et traits d'histoire de vie extrêmes - forment un syndrome de dispersion. Ce premier chapitre me permet de conclure que les caractéristiques des espèces ont joué un rôle important dans l'histoire biogéographique des caméléons. Alors que seuls les traits d'histoire de vie rapides ont été liés au succès actuel des invasions chez les reptiles, les deux extrêmes du spectre d'histoire de vie étaient probablement avantageux pour la dispersion et l'établissement au cours des mouvements biogéographiques passés. Une explication possible de ce résultat est que les espèces aux traits d'histoire de vie rapides peuvent être moins sensibles à l'extinction stochastique dans les premières phases d'une colonisation (en raison de la croissance rapide de la population), et que les espèces aux traits d'histoire de vie lents peuvent être moins vulnérables à la stochasticité environnementale (en raison d'une faible variabilité démographique).

Dans le **chapitre 2**, j'élargis l'analyse du chapitre 1 à 7009 espèces de té-

trapodes réparties en 56 clades. Je démontre que les événements de dispersion biogéographique passés dépendaient souvent des caractéristiques des espèces dans ces clades. L'incorporation de la taille du corps ou des traits d'histoire de vie dans les modèles biogéographiques améliore les performances des modèles dans 91% des clades et conduit à une augmentation des taux de dispersion de 28 à 32% pour les lignées ayant des traits de dispersion. Les différences entre les clades, en ce qui concerne l'ampleur de l'effet des traits d'histoire de vie sur les taux de dispersion, sont liées à la force et au type de barrières biogéographiques (continentales/océaniques), ainsi qu'à la variabilité des traits à l'intérieur des clades. Dans de nombreux cas, les grandes tailles et les histoires de vie rapides facilitent le succès de la dispersion, comme le prévoit la théorie (Andrews and Pough 1985; Blackburn et al. 2015; Caswell et al. 2003; Reynolds 2003). Cependant, les espèces de petite taille et/ou aux traits d'histoire de vie lents, ou celles ayant des traits moyens, ont un avantage dans une minorité de clades, avec des relations entre taille corporelle et dispersion dépendant de la taille corporelle moyenne et de la stratégie d'histoire de vie d'un clade. Ces résultats fournissent de nouvelles informations importantes sur la façon dont les traits d'espèces ont façonné la biogéographie historique des lignées de tétrapodes. En outre, la compréhension de la variation de l'ampleur des effets des traits et de la forme des relations de dispersion entre les clades peut faciliter l'extrapolation à d'autres clades et à d'autres circonstances.

## **Partie II - Relier le passé et le présent**

Dans la première partie, j'ai montré qu'il existe une multitude de formes de relations entre traits et capacités de dispersion biogéographique passée chez les tétrapodes. La dispersion biogéographique passée peut être comparée aux processus de dispersion contemporains, tels que les invasions biologiques et les déplacements d'aires de répartition, et des traits similaires peuvent être liés au succès des différents processus (voir l'introduction de cette thèse). Les résultats du chapitre 2 pourraient donc être utiles pour déterminer le potentiel actuel d'invasion et de déplacement de l'aire de répartition des espèces. Cependant, il y a aussi des raisons de penser que cela ne devrait pas être le cas, par exemple, des décalages dans les échelles temporelles ou l'influence humaine dans les processus actuels.

Dans la deuxième partie de ma thèse, j'étudie donc si et comment les informations provenant d'études du passé profond peuvent être utilisées pour éclairer les processus écologiques contemporains. Dans le chapitre 3, je le fais à travers une synthèse de la littérature où je relie différents types d'informations macroévolutives à deux processus actuels, à savoir l'extinction et les invasions biologiques. Cette idée repose sur le postulat que certaines espèces sont plus menacées d'extinction que d'autres, ou ont un potentiel d'invasion plus élevé, en raison de certaines

caractéristiques. Par exemple, les espèces dont la population est de petite taille ou dont l'aire de répartition est restreinte sont plus sujettes à l'extinction, tant à l'échelle locale que mondiale, car elles sont intrinsèquement plus sensibles aux changements environnementaux (Lavergne, Molina, et al. 2006; Lavergne, Thuiller, et al. 2005; Matthies et al. 2004). D'autre part, les espèces ayant de grandes capacités d'adaptation, de faibles degrés de spécialisation écologique et un fort potentiel de dispersion pourraient être des envahisseurs particulièrement efficaces (p. ex. Gallien, Saladin, et al. 2016; Gallien, Thornhill, et al. 2019; Lavergne, Evans, et al. 2013). Pourtant, les données sur la taille des populations et des aires de répartition, le degré de spécialisation, ainsi que les capacités de dispersion et d'adaptation ne sont pas facilement disponibles pour de nombreuses espèces, et les études macroévolutives pourraient fournir des proxys faciles à obtenir pour ces traits.

Dans le **chapitre 3**, je constate que les taux de diversification peuvent être utiles en tant qu'indicateurs de l'endémisme, de la spécialisation, de la taille de l'aire de répartition et des populations, mais que les hypothèses sous-jacentes doivent d'abord être testées au niveau des clades. Cependant, il est peu probable que les taux d'évolution soient pertinents pour estimer le potentiel d'adaptation à court terme des espèces aux changements mondiaux et le potentiel d'invasion, car les échelles de temps sont trop différentes. Le taux d'extinction passé peut être utile comme indicateur du risque d'extinction actuel, mais ce lien doit être étudié de manière plus approfondie. Enfin, je constate que les mouvements biogéographiques passés peuvent être un indicateur de la capacité d'établissement dans de nouveaux environnements pour les plantes, mais pas pour les tétrapodes. Mais ce dernier résultat est basé sur des études portant sur un très petit nombre de clades et nécessite également des recherches plus approfondies. Le plus grand défi que je souligne dans le chapitre 3 concernant le lien entre les processus passés et actuels concerne le défi de l'anthropocène : comment extrapoler les événements du passé profond aux événements actuels, alors que l'influence humaine est massive et conduit à des changements environnementaux sans précédent ? En outre, les menaces ne sont pas réparties de manière égale sur l'ensemble du globe et l'homme a également un impact direct sur les processus actuels, par exemple en modifiant les processus de dispersion (dispersion biogéographique naturelle passée comparée aux invasions biologiques actuelles). Si l'utilisation des informations du passé est une voie de recherche prometteuse pour éclairer les processus actuels et nous aider à identifier les espèces menacées d'extinction ou à fort potentiel invasif, il reste encore beaucoup à faire.

Dans le **chapitre 4**, je teste l'hypothèse selon laquelle la dispersion passée peut nous informer sur la performance des espèces dans les invasions biologiques actuelles dans un sous-ensemble d'espèces du chapitre 2. Il s'agit d'une hypothèse intéressante à tester car il a déjà été démontré que les capacités de dispersion passées sont liées au potentiel invasif dans trois clades de plantes (Gallien, Saladin,

et al. 2016; Gallien, Thornhill, et al. 2019). Ce chapitre s'appuie sur un travail réalisé avec Marceau Habrant, dont j'ai encadré le stage avec Laure Gallien entre mars et août 2022. Dans le chapitre 4, je montre que le succès de la dispersion biogéographique passée est lié au succès des invasions biologiques actuelles dans trois des 12 clades de tétrapodes. Chez les Phasianidae et les Diprotodontia, il est lié au succès de la phase d'introduction. Bien que le succès de la dispersion passée soit lié au succès de l'établissement chez les Colubrinae, ce résultat doit être considéré avec prudence car la taille de l'échantillon est assez faible. Lorsque l'on compare le succès de la dispersion passée à d'autres variables dans un modèle unique, il s'agit d'un meilleur prédicteur du succès de l'introduction uniquement chez les Diprotodontia. Dans l'ensemble, le succès de dispersion biogéographique passé n'est donc pas un prédicteur fort du succès d'invasion actuel dans la grande majorité de notre sélection de clades de tétrapodes. Toutefois, la dispersion passée pourrait être un proxy pertinent dans certaines circonstances. Il serait très utile d'approfondir cette question pour comprendre l'importance des facteurs intrinsèques et des contingences historiques dans la facilitation des invasions.

L'une des lignes possibles de recherche future que j'ai soulignée dans le chapitre 3 était de relier la dispersion passée à travers les barrières biogéographiques aux déplacements actuels de l'aire de répartition des espèces dans le contexte des changements environnementaux. C'est ce que j'ai entrepris de faire dans le **chapitre 5** : je détermine le potentiel de dispersion et de colonisation des espèces sur la base des relations entre les traits de taille corporelle et de stratégie d'histoire de vie et le succès de dispersion passé, tel que déterminé dans le chapitre 2. J'établis ensuite un lien entre ce potentiel de dispersion et de colonisation et les déplacements actuels de l'aire de répartition aux frontières principales, et je compare le pouvoir prédictif de cette variable à d'autres variables souvent utilisées. Je montre que la taille du corps et les traits d'histoire de vie ne sont pas de bons prédicteurs des déplacements de l'aire de répartition des espèces lorsqu'ils sont directement utilisés pour prédire les déplacements de l'aire de répartition des espèces. Cependant, les relations spécifiques aux clades entre les traits d'histoire de vie et les taux de dispersion biogéographiques passés, qui comprennent des relations en forme de U et de cloche, sont liées de manière significative aux déplacements de l'aire de répartition. Les informations relatives à la dispersion passée peuvent donc être utiles pour expliquer les déplacements actuels de l'aire de répartition. Il convient de noter que les relations entre les traits (ici la taille du corps et la stratégie de cycle de vie) ne sont pas simples et que différentes stratégies facilitent l'expansion des aires de répartition dans différents clades. En outre, des informations extrinsèques sur la vitesse locale des changements de température et les pressions humaines sont nécessaires pour compléter notre compréhension des patrons de déplacement de l'aire de répartition. Cependant, les différences de méthodologie expliquent encore une grande partie de la variation des déplacements latitudinaux de l'aire de

répartition des espèces. Ces premiers résultats prometteurs appellent à des analyses plus étendues sur le plan géographique et taxonomique, et éventuellement le long des gradients de pression humaine.

## **Conclusion**

Avec cette thèse, j'ai progressé sur le plan empirique et conceptuel en ce qui concerne le rôle des traits des espèces dans les processus de dispersion. Dans la première partie, je montre que la taille du corps et la stratégie d'histoire de vie jouent un rôle dans la dispersion passée à grande échelle. Alors que les travaux conceptuels sur ce sujet remontent à plus de 150 ans, il s'agit du premier test empirique à grande échelle portant sur plusieurs taxons tétrapodes, rendu possible par les progrès méthodologiques, l'augmentation de la disponibilité des données et la puissance de calcul. Je constate que les effets des traits et les formes des relations entre traits et capacité de dispersion varient entre les clades. Cette variation est en partie attribuable à la variation du type et de la force des barrières biogéographiques traversées, ainsi qu'à la variabilité des traits à l'intérieur des clades et à la taille moyenne du corps et à la stratégie d'histoire de vie des clades. Cette analyse confirme que les relations trait-dispersion sont souvent plus complexes que ce que l'on suppose généralement, comme l'ont déjà montré Stevens et al. (2014) pour la dispersion écologique.

Dans la deuxième partie, je contribue à la meilleure compréhension de la transférabilité des informations issues des analyses du passé profond à travers les échelles spatio-temporelles. Je constate que de multiples voies relient les indices macroévolutifs aux processus qui déterminent le potentiel d'invasion actuel des espèces et leurs besoins en matière de conservation. Les hypothèses sous-jacentes, par exemple les relations entre le taux d'évolution des traits et le potentiel adaptatif actuel des espèces, sont rarement testées, ce qui est pourtant nécessaire avant de faire des déductions. J'étudie ensuite plus en détail deux relations entre la dispersion passée et actuelle. Tout d'abord, la capacité de dispersion passée se révèle ne pas être un bon prédicteur du succès de l'invasion actuelle dans la majorité des 12 clades de tétrapodes testés, peut-être en raison de la labilité des traits évolutifs ou de l'influence de l'homme dans les filtres du processus d'invasion. Toutefois, certains éléments indiquent que la dispersion passée peut être un proxy pertinent dans certaines circonstances. Deuxièmement, les relations entre la stratégie d'histoire de vie et la dispersion, probablement liées à l'établissement de nouvelles populations, peuvent être comparables dans les dispersions biogéographiques passées et les déplacements actuels de l'aire de répartition.

Ce travail ouvre donc de nouvelles voies de recherche passionnantes qui pourraient faire progresser nos connaissances sur les processus de dispersion passés et

présents. Une meilleure connaissance des processus de dispersion à différentes échelles est essentielle pour mieux appréhender ce qui détermine les patrons biogéographiques, ainsi que les moteurs de la spéciation et de l'extinction. Dans le contexte des crises actuelles liées au climat et à la biodiversité, nous devons mieux comprendre les différences de capacité de dispersion entre les espèces et les différences de forme entre les relations trait-dispersion à différentes échelles. Seule une meilleure compréhension nous permettra de faire des prédictions utiles qui peuvent guider la politique concernant le potentiel d'invasion des espèces et les besoins en matière de conservation.

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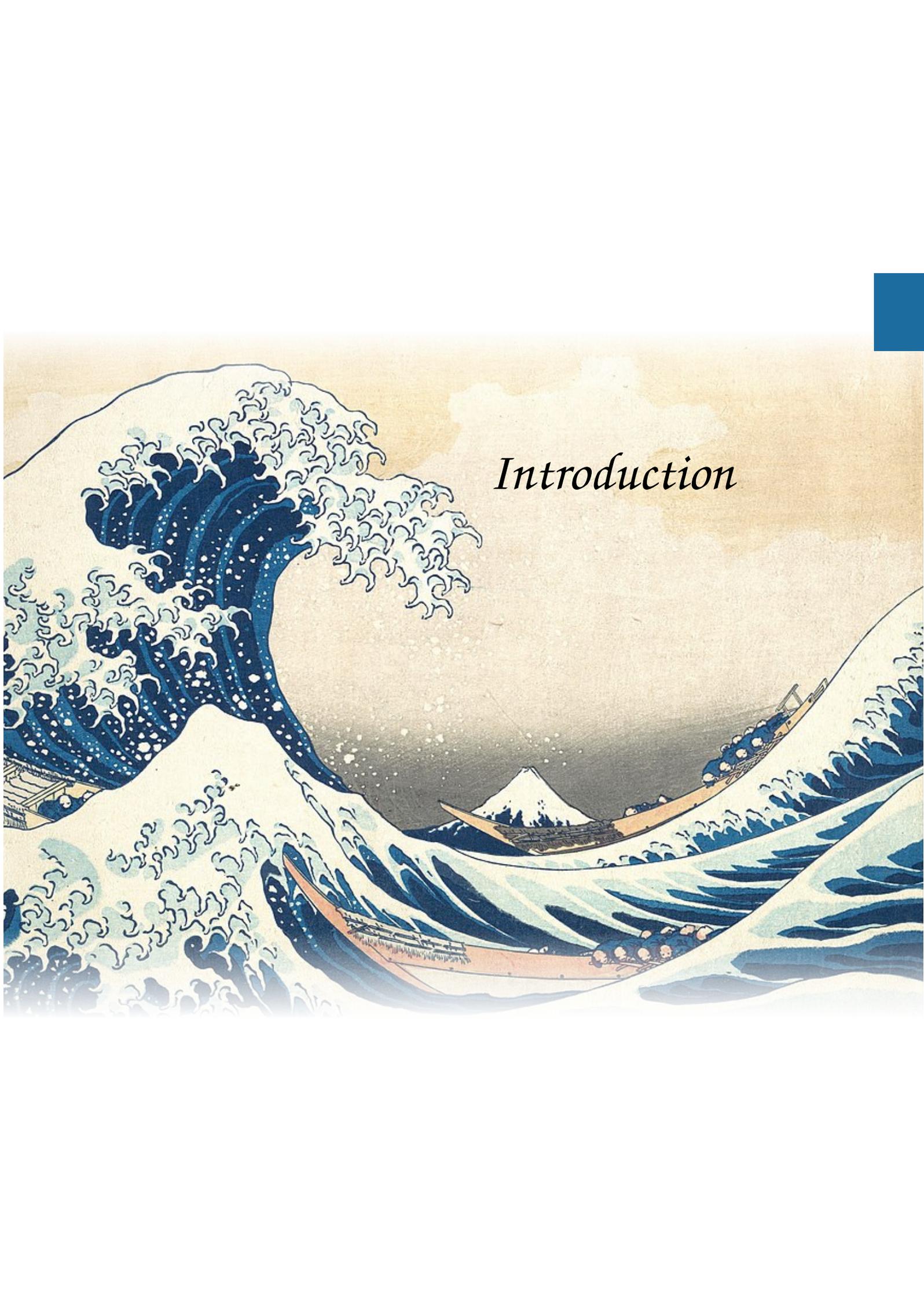
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*Introduction*



In March 2011, the strongest earthquake recorded in Japan's history generated a tsunami which wreaked havoc in the country and affected other countries throughout the Pacific basin; in Japan, it caused a major nuclear accident, more than 18 000 people died and more than 500 000 people lost their homes (National Oceanic and Atmospheric Administration, National Centers for Environmental Information 2018). One year later, and about 8 000 km away on the western coast of North America, debris began washing ashore. On this debris, more than 280 Japanese coastal species were reported that were still alive and had the potential to establish new populations (Carlton et al. 2017; Lindo 2020; Simkanin et al. 2019).

A few individuals surviving such an improbable journey are enough to establish a new population in a new region. The fate of that population has far-reaching consequences: it can expand the species' current distribution, it can affect other species' in the newly colonised region through biotic interactions, and on an evolutionary timescale it can provide opportunities for speciation. Thus, a single dispersal event has the potential to determine the fate of an entire clade or lineage.

Today, we know that these improbable and rare dispersal events are determinants of species' distributions and global biogeography, not only for coastal invertebrate species, but also for terrestrial vertebrates and marine species. We know this through contemporary observations (as described above; see also Batista et al. 2013; Censky et al. 1998; Gerlach et al. 2006; Ozgo et al. 2016), and through the statistical modelling of ancestral ranges of lineages (e.g. Ali and Vences 2019; Fonte et al. 2019; Kainulainen et al. 2017; Rieppel 2002; Sanmartín et al. 2007; Smith and Brown 2018; Veith et al. 2004). These latter techniques are only possible because of our knowledge of species' evolutionary relationships and because we have good estimations of how the geography of the Earth has changed over the last million years. However, this was not always the case (Fig. 1).

## **0.1 Dispersal and vicariance as drivers of global biogeography**

The role of dispersal in shaping species' distribution patterns and global biogeography has been the centre of debate for several centuries (Lomolino, Riddle, et al. 2017; Lomolino and Brown 2009; Morrone and Crisci 1995; Nelson 1978). On the one side were the proponents of the hypothesis that dispersal is the most important process determining species' distributions (dispersalists), and on the other hand were scientists who thought that species' individual dispersal capacities are negligible compared to the influence of a changing geographic template which can create and erode barriers (vicariance hypothesis). The relative importance of dispersal vs vicariance fluctuated over time and hinged on discoveries in other fields (Fig. 1).

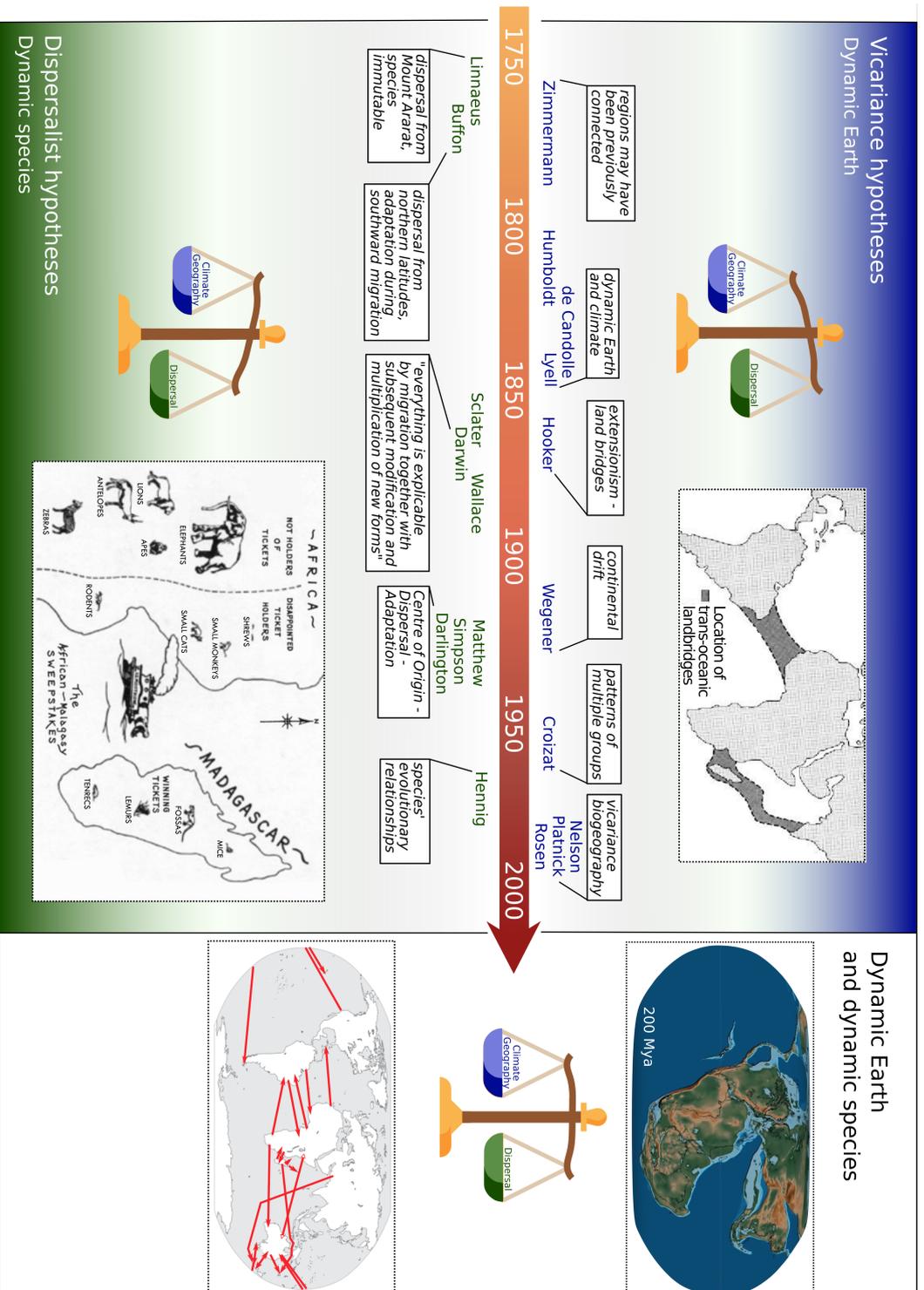


Figure 1: A timeline of dispersal versus vicariance ideas as drivers of species' distributions. Inset maps: topleft: proposed land bridges, adapted from Lomolino, Riddle, et al. (2017); bottomleft: sweepstakes routes between Africa and Madagascar; some species have the potential to disperse across the Mozambique Strait ("ticket holders"), but which ones manage to actually cross it depends on chance ("winning tickets"). Other species do not have the potential to disperse ("not holders of tickets"), adapted from Simpson (1940); topright: reconstruction of the position of the continents ca. 200 million years ago, adapted from Scotese (2019); bottomright: examples of historic transoceanic dispersal, adapted from Queiroz (2005). Icons: flaticon.com

About 250 years ago, Linnaeus and others considered Mount Ararat to be the centre of creation of all life forms, in accordance with myths of global flood (or deluge myths). Different species occupied different elevation bands of the mountain which explained why they had preferences for different environmental conditions. Once the flood receded, species then moved across the Earth to regions suitable for them according to their preferences. Dispersal was hence a key process explaining present-day distributions since that was the only mechanism by which species could have possibly moved from their centre of origin to where they occur today.

Similarly, Buffon believed dispersal to be key, however, he proposed a new theory to deal with contradictions of the flood myth theory with empirical evidence. By then it had been noted that different species occur in different regions of the world even if the abiotic conditions are the same (e.g. Buffon 1761). This conflicted with the flood myth theory whereby species spread out unhindered to habitats suitable for them; following this logic, regions with similar abiotic conditions should be inhabited by the same species. Buffon therefore developed the following theory (Buffon 1781 in Feuerstein-Herz 2004, p. 245): after the Earth's creation, our planet was hot. It started cooling down first at the poles which led to a first phase of life development once the climate was suitable. As temperatures continued to drop, those species migrated southward, following the conditions they were adapted to. In the course of their southward migration, he proposed that animals should have degenerated which would explain the occurrence of different species in similar abiotic conditions. With time, the cooling temperatures created successive "climatic zones" which led to successive phases of development of organisms adapted to these conditions, and successive southward migration events during which species "degenerated".

An alternative hypothesis was introduced to the scientific community by Zimmermann. He proposed that the geographic template may change through time ("fragmentation, flooding and sinking of various parts"<sup>1</sup>), and that these changes are drivers of species' distributions as we observe them today and not necessarily dispersal. He also proposed that islands may have been connected to continents if species known to be poor dispersers occurred in both regions (Zimmermann 1778, p. 29 in Feuerstein-Herz 2004, p. 249). Zimmermann's idea was supported by de Candolle who suggested that geographic distributions were "probably determined by geological causes that no longer exist today" but also cautioned that "this theory is touched by the uncertainty (...) of all of the ideas relating to the ancient state of our globe and to the primitive origin of living things" (Candolle 1820 and Candolle 1855 in Nelson 1978). Lyell and other geologists provided em-

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<sup>1</sup>"Zerstückung, Überschwemmen und Untersinken verschiedener Theile" (Zimmermann 1780, p. 232 in Feuerstein-Herz 2004, p. 255)

irical support for this theory: they inferred that the climate had changed over time through the discovery of fossils adapted to habitats different from those in which they were found, and they found similar evidence for changing sea levels, and mountain uplift and erosion (Lyell 1832). Hooker proposed that land bridges which may have formerly connected different landmasses could explain relationships of related species that were widespread (such as the southern beeches (*Nothofagus*) which he had noticed during his voyage on the HMS Erebus to occur in Australia, New Zealand and South America). In this theory, dispersal was a process acting only over short-distances and played a minor role in general species' distribution patterns compared to the dynamic geographic template.

Darwin and Wallace, on the other hand, supported the dispersalist theory with origins in the ideas of Linnaeus and Buffon. Darwin wrote: "I think all the grand leading facts are explicable on the theory of migration (...) together with subsequent modification and the multiplication of forms" (Darwin 1859 in Nelson 1978). In this theory, dispersal occurred over a stable geographic template, and "improbable dispersal", i.e. dispersal by "occasional means of transport" was central to their theory, contrasting with the extensionist point of view favoured by Hooker among others. Improbable dispersal as a general process was further emphasised by later dispersalists, such as Matthew, Simpson and Darlington, in the middle of the 20th century. Simpson for example provided mathematical support that, given enough time, the most improbable dispersal becomes not only probable but certain (Simpson (1952) in Nelson (1978)).

In the second half of the last century, three major advances brought new life into the debate. First, the development of Wegener's theory of continental drift provided a mechanism by which distributions could be determined through geological causes that was more satisfying than supposing numerous land bridges. Second, Croizat initiated a shift in biogeographic studies from studying individual taxa to studying several taxa simultaneously to discover underlying common patterns (Croizat 1958). Finally, with the development of cladistics (Hennig 1966), evolutionary relationships among organisms could be reconstructed based on shared, derived characteristics. These advances led to the development of cladistic vicariant biogeography (e.g. Brundin 1966; Nelson and Platnick 1981; Rosen 1978) which provided an analytical framework and made vicariance hypotheses testable by searching for congruence in phylogenetic and distribution patterns among several groups of organisms. This was a huge step forward from the previously narrative nature of studies (Donoghue and Moore 2003; Sanmartín 2012). Within this new framework, distributions of many disjunct taxa were found to be congruent with the breakup of Gondwanaland, and as a consequence, the perceived importance of dispersal in shaping species' distributions and global biogeographic patterns decreased tremendously.

However, a decisive element was still missing to reliably infer vicariance and

dispersal events: while the reconstruction of evolutionary relationships was great progress, estimation of the timing of lineage splits so crucial to verify or falsify a hypothesis of a clade's history remained largely unknown (Donoghue and Moore 2003). If the timing of diversification splits in the phylogeny coincides with the timing of fragmentation of regions, vicariance is likely the driving process. If lineages split considerably after the fragmentation of regions, on the other hand, vicariance cannot be the explanation and dispersal is more likely to be the driving process.

Today, improved methods of DNA sequencing and estimations of lineage divergence dates based on molecular sequences and fossil dating have evened out the balance of evidence between a dynamic geographic template and dynamic species dispersal in explaining species' distribution patterns and global biogeography (Fig. 1). In a great number of cases, lineage divergence dates show that speciation events are too young to be the product of vicariance. Dispersal and gene flow across major barriers occurs in a great number of taxa, and more frequently and across greater distances than previously expected. It has been shown to play a role in mammals (Ali and Vences 2019), reptiles (Vidal et al. 2008), amphibians (Fonte et al. 2019; Vences et al. 2003), and to perhaps have even more relative importance in invertebrates (Hendriks et al. 2019) and plants (e.g. Nathan (2006)). Some authors have even proposed that the entire flora of New Zealand is the product of long-distance dispersal (e.g. Pole 1994; Winkworth et al. 2002). While the debate between dispersalists and vicariance biogeographers is not completely laid to rest (perhaps because the relative importance of dispersal and vicariance is clade-dependent), it is clear that dispersal plays a decisive role in global biogeography (Cowie and Holland 2006; Queiroz 2005). However, we are still a long way from understanding the determinants of dispersal processes. There are still open questions, notably relating to differences in dispersal abilities and frequencies between species, and which role species' traits play in these differences.

## 0.2 The role of traits in biogeographic dispersal

Scientists supporting the dispersalist theory proposed early on that not all species are similarly able to disperse across major barriers. Darwin wrote: "The degree of dissimilarity (depends) on the migration of the more dominant forms of life from one region into another having been effected *with more or less ease*", and "widely-ranging species, abounding in individuals, which have already triumphed over many competitors in their own widely-extended homes *will have the best chance* of seizing on new places" (Darwin 1859, p. 350-351, in Nelson 1978). Although obviously influenced by a colonialist worldview, the implications and assumptions are clear: the actual 'migration', i.e. movement or transport, into a

new region and establishment once there is easier for some species than for others, and those differences may depend on intrinsic characteristics of species, here their competitive ability. Simpson (1940) expanded on this by conceptualising different types of barriers and the effect they may have had on the dispersal of species. He distinguished corridors (which all (mammal) species could indiscriminately traverse) from filter-bridges (which are selective and allow only some species to pass, depending on accessibility of the bridge and “character of the mammals themselves”) and sweepstakes routes. A sweepstakes route is “an adventitious route (where) it depends on chance whether (and when) a given type of animal that can cross it will really do so”. Thus, he emphasises the role of chance in these latter kind of dispersal events, but at the same time reaffirms that certain types of species can make use of these routes (he gives the example of “small arboreal types” when referring to a sweepstakes route between Asia and Australia) while others cannot. However, the rarity of these dispersal events and lacking empirical methodology precluded the testing of specific hypotheses regarding which role species’ characteristics play in these dispersal events across major barriers, and whether they differ depending on the barriers that are involved.

Today, the focus of the scientific community has shifted. The debate is no longer: “How important is dispersal relative to vicariance in shaping global biogeography?” but rather: “Is dispersal across major barriers determined by chance and unpredictable or are there explainable differences in dispersal and establishment abilities between species?” (Lowe and McPeck 2014). The development of new methods in recent years and the availability of data have now made the investigation of these questions possible. Attempting to answer them will contribute to better understanding patterns of species’ distributions and the processes that shape them, and therefore continue the path cleared by previous scientists.

In addition, studying what determines the outcomes of improbable dispersal events has gained new urgency today in the context of habitat loss, climate change and biological invasions, which are key drivers of ecosystem change and biodiversity loss (IPBES 2019). On one hand, changing environmental conditions can displace abiotic and biotic niches of species out of their current ranges. If they cannot adapt to the new environmental conditions of their current range, the only way to avoid local extinction is to disperse to track the geographic displacement of their most favourable niche in space. The rate of change is rapid which means that dispersal over long distances or major barriers may play a crucial role in populations and species’ future persistence (Devictor et al. 2012; Trakhtenbrot et al. 2005). On the other hand, due to intentional or unintentional human intervention, species overcome barriers that they might not have overcome naturally, and in greater numbers, too. Drastic changes have been observed in communities that were invaded by species from far-away regions (Simberloff et al. 2013).

Dispersal across major barriers is a key process, determining species and lin-

eages' fates at small and large temporal and geographical scales (Clobert et al. 2012; Queiroz 2005; Simpson 1940). In a changing world marked by the joint climate and biodiversity crises, it is more urgent than ever to understand the determinants of species' abilities to disperse across major barriers and establish populations in new regions. In the context of my thesis, I endeavour to contribute to this understanding. In the following sections I first provide necessary background information on dispersal, beginning with brief definitions and conceptual considerations. Then, I go into more detail about ecological and biogeographic dispersal, focusing especially on consequences at different scales and determinants of the outcomes of dispersal events. In the final section I consider how human influence has altered natural dispersal processes in present-day biological invasions and range expansions. In these sections I focus particularly, but not exclusively, on terrestrial dispersal of animals which is the main topic of this thesis. I conclude this introduction with an overview of the work I have conducted and detail the structure of the rest of the thesis.

### **0.3 The different scales of dispersal**

Dispersal is defined by Ronce (2007) as: "Any movement of individuals or propagules with potential consequences for gene flow across space". While every organism disperses at least once during its life, there is a wide variation in timing, frequency, distance and mechanisms of dispersal between and within taxonomic levels (Clobert et al. 2012). Some organisms mainly disperse as seeds or larvae before reproduction, i.e. pre-breeding or natal dispersal, others disperse after reproduction or between reproductive events, i.e. post-breeding dispersal. Some organisms disperse only once during their entire life before becoming sessile, such as plants or some aquatic organisms like giant clams, others disperse frequently. Mechanisms of dispersal can be active or passive: active dispersers move of their own will and energy, whereas passive dispersers are dependent on other vectors, such as gravity, wind, currents or other organisms. Both modes can happen in a single dispersal event, and both modes can coexist in populations and higher taxonomic levels. The distances that organisms disperse vary widely as well and depend on taxa and dispersal mechanisms. Passive dispersers can disperse further compared to active dispersers (Shigesada and Kawasaki 2002). Distributions of dispersal distances within populations and species are not symmetric; organisms frequently disperse over short distances, but long-distance dispersal is rare. This makes it difficult to observe and study contemporary long distance dispersal events, and studying their likelihood over large timescales (i.e. using phylogenetic data) may be more promising.

Consequences of dispersal are scale- and context-dependent (Fig. 2, Gillespie

et al. 2012). Short-distance dispersal or ecological dispersal (Nathan 2001) acts mainly on small temporal and spatial scales, within and between populations. Rare long-distance dispersal, in contrast, has a higher probability of involving the crossing of biogeographic barriers, with disproportionate consequences for a lineage's evolutionary and biogeographic future, including adaptive radiations (Alfaro 2017; Gillespie et al. 2012; Raxworthy et al. 2002). A link is therefore often implied between the distance over which an organism disperses and consequences of these events, e.g. gene flow between populations may drive less evolutionary change but allows persistence, whereas colonisation of a new region leads to expansion of a species' range and possibly speciation. However, this link is impractical because dispersal over short geographic distances can have far-reaching consequences as well, depending on the geographic context. At which point short-distance dispersal becomes long-distance dispersal is also a subjective decision and differs between taxa (Fig. 2). Nathan, Klein, et al. (2012) proposes two ways of classification: dispersal events could be classified as long-distance if they are in the top 1% (or top 1‰) in terms of distance of the dispersal kernel (the distribution of dispersal distances in a population), or generally if they are above a certain threshold distance depending on the biology of the organism and the environment.

I introduce here the notion of *biogeographic dispersal* (loosely based on Jordano's (2017) definition of strict-sense long-distance dispersal, see also Nathan (2001)) which is independent of the actual distance travelled by an organism, but instead indicates successful overcoming of significant biogeographic barriers. In the context of this thesis, I use biogeographic dispersal to denote dispersal that has the potential to influence a clade's biogeographic history, e.g. through opportunities for colonisation of new ecological space and/or speciation in a new region. Biogeographic dispersal is hence defined by its consequences rather than by properties of the actual dispersal event, such as distance or mechanism. It is part of the improbable dispersal that Simpson associated with his sweepstakes routes and applies also to most present-day biological invasions. Just as the classification of dispersal as short- or long-distance depends on a subjective threshold concerning the distance travelled, the classification of a dispersal event as biogeographic dispersal depends on the definition of the barrier that is crossed. As recognized by Simpson (1940) and Munroe among others, barriers can be physical (e.g. mountain chains or oceans), climatic (e.g. deserts), psychological or linked to biotic interactions. Barriers are taxon-specific, and they can change through time due to geological or climatic events. The delimitation of barriers, and the definition of distinct regions defined by them, is hence not a trivial task. I will come back to this in a later section (Intro Part I).

Dispersal is generally divided into three distinct phases or stages: emigration, movement/transport, and immigration/colonisation (Clobert et al. 2012; Ronce 2007). Different factors and processes govern each stage, and these factors and

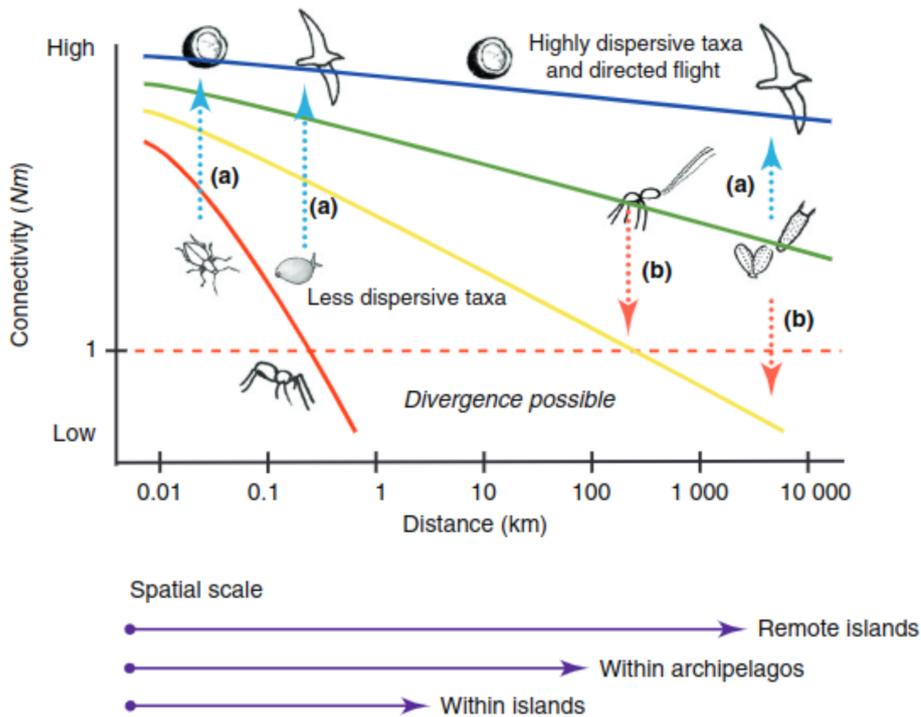


Figure 2: Consequences of dispersal are scale- and taxon-dependent. Connectivity ( $Nm$  = number of migrants/generation) between locations determines genetic isolation and thus opportunities for divergence and probability of population persistence. Connectivity generally decreases with distance, but the relationship varies between organisms. The tendency to disperse depends on the dispersal vector (e.g. species can become highly dispersive if dispersed by birds, (a) arrows) and can change through time (e.g. loss of ballooning ability in spiders, (b) arrows). Figure taken from Gillespie et al. (2012).

processes vary depending on the mechanism of dispersal and its scale, i.e. whether dispersal within and among populations (ecological dispersal henceforth), or biogeographic dispersal into a new region is considered. I detail these factors and processes separately for ecological and biogeographic dispersal in the next two sections.

### **0.3.1 Ecological dispersal**

Dispersal is costly for organisms. Their site of birth is generally suited to their abiotic needs otherwise their parents would not have been able to reproduce there. Moving away from the site of birth carries the risk of ending up in unsuitable habitat, and this risk increases with increasing distance from the site of birth due to spatial autocorrelation of the environment (Clobert et al. 2012). In addition, movement is energetically taxing, and developing locomotory structures may be associated with trade-offs, e.g. a lower investment in reproduction (e.g. Roff and Fairbairn 2001). What then can lead organisms to disperse despite these risks and costs?

In active dispersal, an individual's dispersal patterns depend on the perceived costs and benefits of dispersal. These costs and benefits depend on an individual's social and physical environment, as well as its own genotype, phenotype and condition (Kisdi et al. 2012; Matthysen 2012; Starrfelt and Kokko 2012). For instance, if local population density or the presence and number of relatives is high, dispersal reduces kin competition and inbreeding. If the quality of the natal habitat is low, dispersal can allow individuals to find more suitable habitat. Thus, dispersal can evolve as a strategy to exploit temporally variable or ephemeral habitats, because the general assumption that natal habitat is suitable is not met in these habitats. Costs and benefits are scale-dependent and landscape-dependent: benefits related to inbreeding avoidance, for example, diminish quickly at short distances, whereas effects of landscape structure operate at larger scales (Matthysen 2012). Landscape structure further affects the movement and immigration stage of dispersal; in highly fragmented landscapes, individuals need to disperse further to benefit from suitable habitat, whereas in homogeneous landscapes, longer dispersal distances might not result in substantial benefits compared to energetic costs.

Costs and benefits of dispersal are also specific to each individual, determined by its condition and phenotype (Kisdi et al. 2012). Thus, in the same environment, dispersal can be beneficial for one individual but not for another. The relationship between condition and dispersal propensity can further be influenced by the environment. For instance, individuals in good condition and with high competitive ability may be less likely to disperse if the current habitat patch is particularly favourable, while weaker and less competitive individuals may be driven to disperse. On the other hand, if the current habitat patch is of low quality,

individuals in better condition may disperse further. Dispersal can also be sex- and age-dependent and/or be related to traits determining movement ability (like body size) and orientation and information use (like cognitive ability or perception of the landscape structure including size and quality of habitat patches). Active dispersal therefore involves complex decision-making related to cues from the physical and social environment, and these cues may be interpreted differently by each individual depending on its phenotype and condition (Clobert et al. 2012).

On a population level, dispersal can have several functions and consequences, some of which I mentioned already (Matthysen 2012). On one hand, dispersal can have beneficial effects on population persistence by reducing inbreeding and kin competition, and it can allow an individual to escape locally unfavourable conditions (including diseases or pathogens Connell 1971; Janzen 1970; Matthysen 2012). In addition, it distributes offspring over different environmental conditions which increases the variance in expected fitness and can lead to the evolution of local adaptation. As dispersal can connect populations and increase gene flow between them it can be essential in assuring population persistence, especially in highly fragmented landscapes. Aside from having a lower risk of inbreeding, genetically diverse populations have been shown to be at lower risk of extinction due to additional effects, such as higher adaptability (Hoffmann et al. 2017; Kardos et al. 2021). On the other hand, dispersal can also increase extinction risk because it can increase synchronicity in population dynamics, which can result in synchronised periods of low population density leading to increased risk of stochastic local extinctions (Earn et al. 2000; Molofsky and Ferdy 2005).

Dispersal impacts on the two mechanisms that constitute species' responses to environmental change. On one hand, dispersal affects adaptation and microevolution by determining the magnitude of genetic differentiation between populations. Dispersal can impede local adaptation through gene flow swamping locally adapted gene pools, but it can also increase adaptation by importing adaptive genes from populations already experiencing new environmental conditions (Gandon et al. 1996; Lenormand 2002; reviewed in Lavergne et al. 2010). On the other hand, dispersal itself allows individuals and species to track their abiotic niche across space, increasing chances of global persistence despite local extinctions.

Propensity of ecological dispersal varies between individuals, populations, and species, and it is often correlated with morphological, behavioural, physiological and/or life history traits (Ronce and Clobert 2012). These associations between traits and dispersal are called dispersal syndromes, and they may be an effect of both mechanistic constraints and trade-offs, and the history of selection. Morphological traits are most consistently linked to dispersal, for example the presence of wings and dispersal structures in invertebrates and plants. Body size has been linked positively with dispersal distance in active natal dispersal of omnivores at the species-level, but via a bell-shaped relationship with dispersal distance in

herbivores and carnivores (Stevens et al. 2014). Physiological associations within species include differences in hormones (e.g. corticosterone, testosterone), and differences in metabolism. Correlations between dispersal and behaviour partly depend on hormones; residents are often less aggressive, more prone to collaboration, less exploratory and less bold than disperser phenotypes. Life-history has been frequently linked to disperser phenotypes, but the associations vary depending on other factors related to the physical and social environment (see e.g. Stevens et al. 2014). Different syndromes may be associated with different phases of the dispersal process (emigration, transport/movement, immigration) but these associations can vary with the environment (e.g. along disturbance or fragmentation gradients). Information about mortality during dispersal is scarce which makes it difficult to identify individual trait-dispersal correlations for different phases of the dispersal process (Clobert et al. 2012; Ronce 2007).

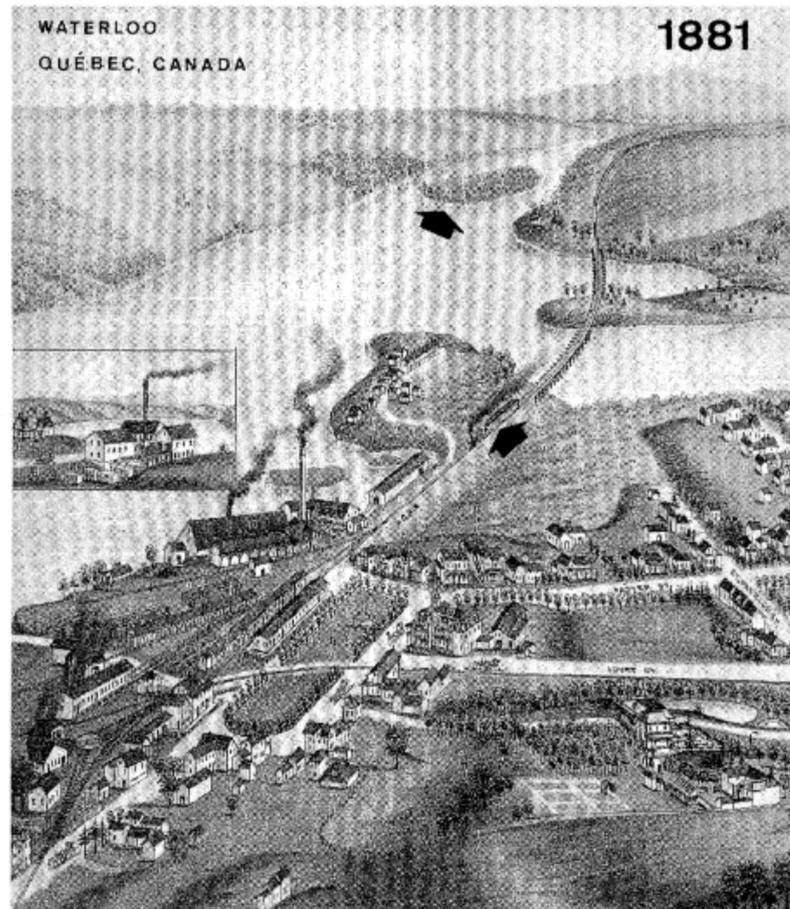
**In summary**, dispersal and variation in dispersal patterns within and between species are multicausal and context-dependent. Still relatively little is known about interactions of different factors that influence active dispersal, such as kin competition and an individual's condition, and an individual's decisions related to this process in different environments. This multicausality and context-dependency leads to varying associations between dispersal and other traits, depending on environmental context and cause of dispersal amongst others. Few generalities concerning dispersal syndromes have emerged to date which makes predictions difficult. While certain behavioural traits seem to be consistently linked to dispersal (such as boldness), life history strategy seems particularly inconsistent.

### **0.3.2 Biogeographic dispersal**

While we are far from completely understanding the evolution, costs, causes, and correlates of ecological dispersal, it has been relatively well studied compared to biogeographic dispersal or dispersal over longer distances. This is because biogeographic and long-distance dispersal events are rare, therefore difficult to study, and have generally been assumed to be largely determined by chance and hence unpredictable (Nathan 2001; Simpson 1940). Increasing recognition of the important role that dispersal across major barriers plays in global biogeography, biological invasions and species' responses to environmental changes has led to an increased interest in determinants of these events. An obvious hypothesis is that traits associated with short-distance dispersal may also be associated with long-distance dispersal. Selection for increased dispersal potential might then simultaneously select for biogeographic dispersal. General within-species associations of traits and dispersal across taxa could therefore also allow us to upscale to between species differences. However, there is increasing evidence that short- and long-distance dispersal events rely on different mechanisms and evolve independently (Higgins

et al. 2003) and that dispersal syndromes characterising within-population variation may poorly reflect syndromes at the scale of species (Ronce and Clobert 2012).

Organisms can overcome biogeographic barriers in a number of ways, and the dominant mechanism probably depends on the kind of barrier that is crossed (corridors, filter-bridges or sweepstakes; Simpson 1940). Lomolino, Riddle, et al. (2017)) distinguish between diffusion, secular migration and jump dispersal. Diffusion is defined as the expansion of a species' range along its edge over relatively short timescales (likely to play a role when traversing corridors). Secular migration is slow and progressive expansion of a species' range over geological timescales (likely to play a role when crossing filter-bridges). Jump dispersal is the extension of a species' range beyond its boundaries by a single event, leading to a disjunct distribution (likely the mechanism by which a sweepstakes route is taken). In contrast to diffusion and secular migration, where active dispersal is probably key, jump dispersal is likely to happen passively in most species. Dispersal vectors can be wind, ocean currents and other animals that are better active dispersers than the passively dispersing individual (e.g. migratory birds Gillespie et al. 2012; Nathan, Katul, et al. 2002). Today, humans act as dispersal vectors as well and have altered this process tremendously (see section 0.4.1). Passive dispersal is partly directed dispersal since large-scale patterns of oceanic and atmospheric currents, including regions of hurricanes, as well as main migratory routes are fairly constant (but not over geological timescales) and known (Box 1, Cowie and Holland 2006; Gillespie et al. 2012; Sanmartín et al. 2007). Ocean and wind currents have been shown to determine the direction of dispersal across taxa and regions (Ali and Huber 2010; Calsbeek and Smith 2003; Fajardo et al. 2019; Godinot 2020; Hawlitschek et al. 2017; Houle 1998; Nathan, Katul, et al. 2002). A potential mechanism for transoceanic dispersal was already proposed by Wallace (in Houle 1998) and Darlington Jr (1938): rafting on flotsam. Houle (1998) described it as the 'floating island model'. Such floating islands have been reported in the literature (see Houle 1998), including some with sizes up to 60 m by 23 m with trees up to 15m high. This means that rafting is not only relevant for organisms of small size but can be an important dispersal mechanism for organisms of intermediate size as well.



**Fig. 1.** A floating island near Waterloo in the Province of Québec, Canada, drawn in 1881 and recently reported by Hughes & Gaudet (1967). Compare the size of the train with the floating island (arrows).

Figure 3: Floating island, drawn in 1881 and reported by Hughes and Gaudet (1967) in Houle (1998). Arrows highlight the size of the island compared to the train.

### Box 1: Ocean and wind currents as dispersal vectors through time

Dispersal across major barriers, particularly transoceanic dispersal, is thought to occur via passive means of transport in most species. The best supported hypothesis is that organisms raft on mats of vegetation or 'floating islands' that have become adrift after tsunamis or hurricanes. While the organism itself has very little control in passive dispersal, passive dispersal is still often directed. This is because ocean and wind currents follow more or less predictable patterns that are physically determined. The sun heats up the Earth unevenly, with the equator receiving more energy than the poles, and this creates differences in atmospheric pressure and temperature. These differences in turn create atmospheric currents which, together with the position of the continents, determine in large parts oceanic surface currents. While smaller scale weather systems are more chaotic and annual and seasonal variation exists in wind and oceanic currents, the larger system remains mostly unchanged (Fig. 4).

This system consists of three main convective atmospheric cells in each hemisphere - the Hadley cells, the Ferrel cells, and the polar cells - which redistribute energy polewards from the equator. The flow of air in these cells (as well as oceanic currents) is affected by the Coriolis force as a result of the Earth's rotation. This deflects currents to the right in the Northern hemisphere and to the left in the Southern hemisphere, with respect to the travel direction. Hence, the differential heating of the Earth's surface by the sun causes not only latitudinal but also longitudinal movements. At the equator, air is heated up, decreases in density and rises. As the body of air moves polewards, it cools, becomes more dense and sinks at about 30°N and 30°S respectively. As air at the surface is heated up and rises in the equatorial region, a low pressure zone is created, and as air descends at 30° latitude, a high pressure zone is created. This leads to surface currents from 30° latitude towards the equator (northeasterly and southeasterly trade winds) to

replace the air that was "lost" at the equator, closing the loop of the Hadley cells. The polar cells are a similar system as the Hadley cells, with comparatively warm, humid air rising at 60° latitude, moving polewards where it cools and gets denser and descends as a result. It then moves back towards 60° latitude as a surface current. The Ferrel cells, located between the Hadley and polar cells, are known as a zone of mixing and are more unstable than the other cells, which are their main drivers. Additionally, air and ocean currents are determined by longitudinal movements which are a result of differential heat capacities of air and water. These movements act at smaller scales than the big convective cells.

Over geological timescales, wind systems and ocean currents are affected by tectonic events, such as mountain uplift or positional changes of continental plates. Historical biogeography, and particularly the inference of past dispersal events in clades' biogeographic histories, therefore strongly depends on geological, paleogeographical and paleoceanographical knowledge. The colonisation of Madagascar by African mammals, for instance, was a mystery for a long-time. Two hypotheses were proposed: either a land-bridge connection across the Mozambique Channel, or colonisation by rafting via a sweepstakes route. However, no evidence could be found for a landbridge, and prevailing winds and currents today flow westwards, in the opposite direction to those required by the sweepstakes hypothesis. Paleoceanographic modelling was necessary to bring new light into the matter: Ali and Huber (2010) showed that currents flowed, in fact, in the other direction before 20 million years ago, as a result of different positions of Africa, Madagascar and Australia. Thereby, they provided strong evidence for a colonisation of Madagascar by transoceanic dispersal, and an explanation why no further dispersal events were inferred in the last 20 million years.

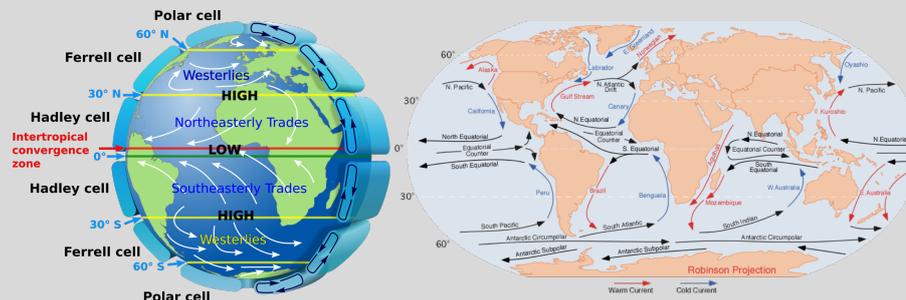


Figure 4: Atmospheric circulation and ocean surface currents. Atmospheric circulation: adapted from Wikimedia Commons contributors (2023) under a CC BY-SA 3.0 license; Ocean surface currents: Wikimedia Commons contributors (2023).

Successful biogeographic dispersal can have disproportionate consequences for a clade's biogeographic history and evolutionary future. Many adaptive radiations have been connected to jump dispersal events. This is most often the case on oceanic or continental islands (e.g. silverswords of Hawaii, chameleons of Madagascar), but also in continental settings (transatlantic rafting is, for instance, likely the origin of the New World monkey radiation (Platyrrhines), Bond et al. 2015, Alfaro 2017). Biogeographic dispersal does not only affect the dispersing lineage itself, it can also affect species in the receiving community through biotic interactions, such as predation or competition. A good example for this is the Great American Biotic Interchange (GABI). About 10 million years ago, the Isthmus of Panama began forming, connecting North and South America. This connection likely acted as a filter-bridge in the early stages but was more like a corridor once it had fully formed about 3 million years ago (Cody et al. 2010; Weir et al. 2009). Interestingly, we know today that successful dispersal across this corridor and consequences of the event were highly asymmetric (just like many other prehistorical interchanges of biotas, Vermeij 2005). Two North American mammal clades (Carnivora and Artiodactyla), for example, were significantly better dispersers than other North American clades (Carrillo et al. 2020), whereas birds predominantly dispersed from South America to North America (Weir et al. 2009). Extinction rates and successful immigrations also differed considerably between North and South America: in North America, the native mammal fauna decreased between the late Miocene and Pliocene by 25% and there was only a relatively low increase in the diversity of immigrant genera; in contrast, the native mammal fauna in South America decreased by 52% and immigrant diversity increased fourfold in the same period (Carrillo et al. 2020). This example illustrates how biogeographic and ecological processes (here biotic interactions) act in concert.

Biogeographic dispersal is a major determinant of species' distributions on Earth, and one single event can have far-reaching consequences. However, relatively little is known about why some species are better able to disperse across major barriers and establish populations elsewhere than others. One approach focuses on species' traits, which are thought to correlate with or facilitate biogeographic dispersal success, just as in ecological dispersal. A lot of theoretical and conceptual work has been done in this regard. Empirical work has been less extensive, due to methodological and computational limitations, focusing especially on island phenomena. Recently, scientists have called for the integration of species' biological differences (i.e. species' traits) in models of historical biogeography (Sukumaran and Knowles 2018). This has only just become possible because this integration is computationally very demanding. However, just like in ecological dispersal (0.3.1), there are a lot of different traits that are linked to biogeographic dispersal. Theory and emerging evidence suggest that several factors can influence relationships between dispersal and other traits, including the environment,

the mechanism of dispersal and the barriers that are crossed. In the following paragraphs I detail possible correlates with the overcoming of each phase of the dispersal process (emigration, transport/movement, immigration/colonisation).

Emigration is likely to depend more on chance in passive dispersal than in active dispersal (e.g. the probability of an individual sitting on a tree that will become adrift through a storm or hurricane). However, in some cases, emigration in passive dispersal can be based on cues from the environment. Spiders were found to prefer short-distance dispersal by rappelling in colder conditions, whereas warm temperatures were associated with higher probabilities of ‘ballooning’. These cases may be exceptions, however, and in many cases, passive dispersal may depend on opportunity and chance. In transoceanic dispersal, coastal species have a higher probability of emigrating than those living inland, and arboreality might also increase the probability of emigration if rafting on trees is hypothesised to be the main dispersal mechanism. Coastal habitat has been related to dispersal success in lizards (Blom et al. 2019). In active dispersers, e.g. birds, bats or butterflies, psychological barriers may be crucial in the emigration stage. Especially in tropical rainforests, several bird families are afflicted by a “fear of flying”, showing an aversion to crossing stretches of open water, even though they are physically clearly capable of doing so (Diamond 1981).

The transport/movement stage is characterised by movement or transport through unsuitable habitat, as well as food and water shortage. The reduction of metabolic rates and torpor has been suggested to have played a role in the colonisation of Madagascar by African lemurs, and possibly other mammals such as tenrecs (Kappeler 2000). Saltwater tolerance probably facilitates transoceanic dispersal in plants and other terrestrial organisms such as tortoises or crocodiles (e.g. Darwin 1855; Gerlach et al. 2006; Nicolai and Matzke 2019; Quilichini and Debussche 2000), and its lack may hinder dispersal in other groups (e.g. amphibians, who are completely absent from oceanic islands). Body size may play a role as well, because large-bodied species have a lower relative metabolic activity and may hence better withstand stress, like starvation. On the other hand, very small species are more likely to be transported by wind (as has been shown for snails and spiders, Ozgo et al. 2016, Bonte 2012). In addition, ecological tolerance is expected to influence the transport/movement stage (Nathan 2001). For instance, cold-adapted species might not easily be able to cross the equator. And in the tropics, mountains might constitute stronger barriers for resident species than mountains in temperate regions because of lower seasonality (Janzen 1967).

Some of the traits that might let species successfully pass the first two stages of the dispersal process might also be linked to the colonisation stage. Species with a wider niche are more likely to find suitable habitat wherever they arrive. Highly specialised species, in contrast, e.g. those with narrow climatic niches or those living in obligate symbiosis, are less likely to find suitable conditions far away from

their home range. Large species are typically better active dispersers than small species and can therefore explore a greater area more easily which increases their chance of finding suitable habitat (Vermeij 2005). Aside from these traits related to environmental conditions and active movement, population dynamics are thought to be crucial in the colonisation stage of dispersal. In jump dispersal, founder populations are typically small, and therefore especially vulnerable to environmental, demographic and genetic stochasticity. Rapid population growth may hence be advantageous because it allows the founder population to quickly overcome the period in which stochastic extinction is particularly high. In mammals, small size has been linked to a fast life history strategy which implies high reproductive rates and might increase survival probability of a founder population (e.g. Dobson and Oli 2007, see also Box 2). On the other hand, slow-lived species have longer lifespans and therefore more time to wait for favourable conditions (and mates) to reproduce. Propagule pressure has been shown to be a strong determinant of colonisation success; the bigger the founder population, the greater its probability of success (Blackburn, Lockwood, et al. 2015). This is partly because effects of environmental stochasticity decrease quickly with increasing population size. Small species may be more likely to arrive in higher numbers in a new region because smaller species often occur in greater numbers. Social system of the species likely plays a role as well. Mouse and dwarf lemurs, for instance, descendants of the ancestral lemurs that successfully crossed the Mozambique channel from Africa to Madagascar, typically spend daily and seasonal periods of inactivity in groups of up to 15 individuals in single tree holes (Kappeler 2000). This increases the chance of a bigger founder population in the case of a rafting dispersal event. In addition, bigger populations generally have higher genetic variability which decreases the risk of inbreeding depression and fixation of deleterious alleles (Frankham 2005; Kardos et al. 2021). It is also thought to favour adaptation in species (Hoffmann et al. 2017), which is advantageous during colonisation of a new habitat with many unknowns. Genetic variability in the founder population likely does not only depend on the size of the founder population, but also on the genetic variability in the source population.

In addition to a species' intrinsic traits, the properties of the receiving environment are likely to be crucial in determining the outcomes of dispersal events. The presence or absence of predators or food may impact an individual's survival, and so may the predictability of the environment. Safriel and Ritte (1980) proposed that a highly reproductive strategy may be more successful in unpredictable environment, whereas they predicted K-strategists, those investing more in survival and maintenance, to have an advantage in stable environments. This is because K strategists have reduced death rates and higher efficiency in resource utilisation which increases the carrying capacity of the environment. In unpredictable environments on the other hand, density-independent mortality is higher, and population

sizes may fluctuate more, therefore the ability to recover from lows may be more important, i.e. an r strategy.

**Box 2: Life history and the fast-slow continuum**

Species' traits often covary in distinct patterns related to survival, growth and reproduction, forming distinct life history strategies (Dobson and Oli 2007). To explain variation in these strategies, the concept of r- and K-strategists was developed in the 1970s (r = intrinsic growth rate, K = carrying capacity, MacArthur and Wilson 1967, Pianka 1970). This concept posited that different environmental conditions select for different modes of population regulation which leads to the evolution of covarying patterns in species' traits. r-strategists were species influenced by density-independent mortality that invested highly in reproduction, but less so in survival. In contrast to this, K strategists were seen as species influenced by competition, leading them to invest more in survival than in reproduction. Today we know that the trade-off between r- and K-strategies is often not valid, and that the mechanistic explanation of the r/K theory does not hold in many cases (Jeschke and Kokko 2009). Therefore, the r/K theory has been replaced in recent years by the concept of a fast-slow life history continuum, which is basically a descriptive analogue of the r/K selection theory without the mechanistic aspect (Dobson and Oli 2007; Jeschke and Kokko 2009). Life history traits of fast species can be equated to those of r-strategists (e.g. early reproduction, big litters/clutches), and life history traits of slow species to those of K-strategists (e.g. low fecundity, high investment in each offspring, long lifespan).

However, the theory of a fast-slow life history continuum is not without controversy. Early research was based purely on mammals, but

as more data became available, studies found that there is a multitude of trade-offs structuring species' life history strategies which can differ between taxonomic groups (Bauwens and Díaz-Uriarte 1997; Dobson and Oli 2007; Fisher et al. 2001; Jeschke and Kokko 2009; Stearns 1992). In addition, body size can affect other traits through allometric constraints (the scaling of traits with body size, see e.g. Meiri et al. 2021). Large species, for instance, have generally lower metabolisms and longer life spans. In reptiles, the number of eggs per clutch increases with body size, in contrast to mammals where large species typically have smaller litters. Some authors therefore consider body size-independent life history strategies while others include body size (e.g. Jeschke and Kokko 2009). In mammals, Bielby et al. (2007), for example, found two independent axes of life history covariation when body size effects were removed, one reflecting the trade-off between offspring size against offspring number, the other describing the timing of reproductive events. Healy et al. (2019), on the other hand, show across a large variety of animal species that 71% of the variation in life history strategies can be explained by traits associated with the fast-slow continuum, after accounting for body size effects. In plants, a fast-slow life history continuum has been identified as well, together with a second axis of variation reflecting the reproductive strategy (with highly reproductive iteroparous species on one side, and poorly reproductive semelparous species on the other side, Salguero-Gómez et al. 2016).



Figure 5: Examples of species with body size-independent fast and slow life history strategies. Left: *Chameleo senegalensis* Daudin, 1802 (Wikimedia Commons contributors 2021, under a CC BY-SA 4.0 license), a species with a fast life history strategy (hatchling size ca. 20% of adult size, average clutch size of 52, maximum lifespan in the wild 1.5 years); right: *Brookesia stumpffi* Boettger, 1894 (Wikimedia Commons contributors 2022, under a CC BY-SA 4.0 license), a species with a slow life history strategy (hatchling size ca. 45% of adult size, average clutch size of 3.5, maximum lifespan in the wild 4 years).

**In summary**, the dominant mechanism of biogeographic dispersal likely depends on characteristics of the barrier that is crossed. The mechanism and vector of dispersal in turn determine the traits that are linked to successful overcoming of each dispersal phase, in concert with conditions in the recipient community. Due to the rarity of natural long-distance dispersal, and lack of appropriate empirical methods, most hypotheses have not been tested yet.

## **0.4 Dispersal in a changing world**

In the previous sections I have laid out what we know about ‘natural’ dispersal, largely disregarding human influence. But human influence on other organisms is ubiquitous today, and the dispersal process is not excluded. Humans act, intentionally or unintentionally, as a dispersal vector. Through (pet) trade and increased human movement in the wake of globalisation, species are moved around the globe. Humans thus increase the frequency of dispersal and also change the dispersal process itself by possibly selecting for different traits than the natural process (Ricciardi 2007; Vermeij 2005, and following sections). In addition, humans impact on the causes of dispersal: through human influence, climate is changing faster than ever before (IPCC 2021). This can lead to mismatches between species’ abiotic niches and the current conditions in their range. Dispersal and adaptation are two ways through which species can react to these environmental changes. But land-use change and increased habitat fragmentation impact ecological dispersal and local and regional population dynamics. Dispersal is going to be key for population and species’ persistence in the future and may yet be the cause of other species’ demise in the context of biological invasions. But there are still many unknowns and it is difficult to predict which species are going to be successful in biological invasions (Gallien, Thornhill, et al. 2019), and our understanding of differences in species’ range shifts are limited (Angert et al. 2011; MacLean and Beissinger 2017). Little is known about how comparable the different kinds of biogeographic dispersal are (natural biogeographic dispersal, biological invasions and range expansions) and if the determinants of success are the same. But with new methods now available to investigate the role of traits in past biogeographic dispersal (Klaus and Matzke 2020), there is potential to gain new insight into present-day biological invasions and range expansions. In the following sections I introduce biological invasions and species’ range shifts, with a particular focus on what can explain differences in outcomes between species.

### **0.4.1 Biological invasions**

Biological invasions are the crossing of biogeographic barriers by species through dispersal associated with humans, followed by establishment and spread into a new region. Just like the ‘natural’ dispersal process, biological invasions are often described as a suite of consecutive stages (Blackburn, Pyšek, et al. 2011). *Transport* is the human-mediated transport of a species into a new region that is not part of its native range, *introduction* is the survival of the transport stage and successful arrival of a species in a new region, *naturalisation* is the effective colonisation of a new region and is characterised by a reproductively viable population of the introduced species. Some naturalised species expand their range in the new region beyond the location of the introduction, and this expansion characterises the *spread* stage of the invasion process. Each stage is characterised by different filters that species need to overcome to be successful (Blackburn, Pyšek, et al. 2011), e.g. the biogeographic barrier in transport, local climatic conditions in the introduction, biotic interactions in the establishment and landscape barriers in the spread stage. Species that are introduced are called alien, or exotic species (or the like), those that successfully naturalise are called established, and only species that spread beyond the region of their introduction are called invasive (Blackburn, Pyšek, et al. 2011). Humans have introduced species into new regions for thousands of years, but numbers have been increasing massively since the (re)discovery of the Americas by Christopher Columbus and the following ‘age of exploration’. At that time, many species were introduced intentionally, for example as food for the explorers (Simberloff et al. 2013). Another drastic increase in the number of invasive species came through globalisation. Transoceanic ships are estimated to transport ca. 7 000 species around the planet every day (Carlton 1999) and over 12 000 alien species have been identified just in Europe (Roy et al. 2020).

The consequences of successful introductions and naturalizations can be dramatic. Common examples include the introduction of cane toads, toxic to most animals if ingested, in Australia who have spread across the country in the last 80 years (Hudson et al. 2016), or the introduction of mammalian predators on islands which led to extinctions of the local avifauna, often groundbreeders unused to predators (Blackburn and Gaston 2005). While biological invasions can have positive effects for different societal segments (e.g. timber industry), impacts are generally negative from an ecosystem perspective and on ecological timescales, including homogenization of local biotas, community disassembly and species’ local extinctions (Simberloff et al. 2013; Vermeij 2005). The Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services considers biological introductions as one of the major causes for ecosystem declines and biodiversity loss (IPBES 2019). Due to these effects, the prediction and prevention of biological invasions is of major interest. However, it is also a major challenge.

Biological invasions and natural biogeographic dispersal are similar on a conceptual level, as both include the crossing of major biogeographic barriers. However, it is unclear to which degree the natural process is comparable to the human-mediated one, as human influence impacts all dispersal stages and the filters associated with them. Thus, traits linked to success across the individual stages of invasions may differ, or trait-dispersal relationships may be modified compared to natural biogeographic dispersal. The transport stage mainly depends on the pathways of introduction, going from intentional introductions for pest control (cane toads in Australia), over escaped exotic pets (chameleons in Florida), to unintentional transport of exotic seeds on hiker's boots. Due to this strong association with the dispersal vector in biological invasions (per definition), traits related to this stage are likely different from traits related to the emigration stage of "natural" biogeographic dispersal. Generally, species that have a strong association with humans and those that are 'charismatic' have a higher chance of being transported elsewhere, both unintentionally and intentionally (e.g. through pet trade, Lockwood et al. 2019, Theoharides and Dukes 2007).

Successful introduction has been linked to high reproduction and long reproductive lifespans in mammals, amphibians and reptiles (Allen, Street, et al. 2017; Capellini et al. 2015). Interestingly, body size was only related to introduction success in amphibians, whereas it is hypothesised to be a general determinant in transport and establishment of biogeographic dispersal.

The establishment stage in biological invasions is perhaps of all stages the most closely related to its biogeographic counterpart. In both cases, founder populations are small such that establishment success depends first and foremost on propagule pressure, i.e. the number of individuals that arrived at or were released in a given location (Blackburn, Lockwood, et al. 2015, see also discussion of successful colonisation in biogeographic dispersal above), as well as the environmental suitability in the exotic region. Potential range size has been linked to naturalisation success in two plant clades (Gallien, Thornhill, et al. 2019), which is related to ecological tolerance or niche breadth which is also hypothesised to play a role in natural biogeographic dispersal. In addition, invader competitive ability, and life history traits associated with a fast life history strategy have been linked to establishment success (Allen, Street, et al. 2017; Capellini et al. 2015; Hayes and Barry 2008; Sol et al. 2012; Theoharides and Dukes 2007). In birds, however, a fast life history has been proposed to be only advantageous in certain circumstances, whereas a bet-hedging strategy seems to be generally more effective (Sol et al. 2012). Historical factors have been proposed for consideration as well, for instance the history of invasive success (Hayes and Barry 2008), and the number of successful colonizations in a lineage's biogeographic history (Gallien, Saladin, et al. 2016; Gallien, Thornhill, et al. 2019), which might be indicative of traits related to invasion success that are difficult to measure.

Success in the spread stage of biological invasions has been linked to competitive ability, fast life history traits and introduction effort (Allen, Street, et al. 2017; Blackburn, Lockwood, et al. 2015; Capellini et al. 2015; Vermeij 2005). Palma et al. (2021) proposed that different traits might explain different metrics of spread, i.e. velocity of spread, geographic or environmental range sizes. It is also important to mention that the spread of invasive species can be strongly enhanced by their evolutionary potential. For instance, the length of cane toad's legs has been shown to be positively selected at their colonisation front in Australia (Phillips et al. 2006).

**In summary**, a lot of research has been done relating species' traits to success in the successive stages of invasion. However, there are differences in the trait-invasion relationships between different taxonomic groups, and depending on environmental conditions of the recipient community, including physical attributes such as climate, biotic factors and landscape structure (Allen, Street, et al. 2017; Theoharides and Dukes 2007; Wilgen and Richardson 2012). In addition, identified traits can be difficult to measure for a large number of species, such as phenotypic plasticity, which makes their practicality in applied circumstances questionable. Some of the traits linked to invasion success are similar to the ones that are hypothesised to be linked to success in biogeographic dispersal, especially in the establishment stage, but there are important differences, notably in the transport and introduction stages which are so closely associated with humans. Investigating the causes of differences in trait-dispersal relationships between natural biogeographic dispersal and biological invasions would be a step towards a mechanistic understanding of the role of traits in dispersal in different contexts.

## **0.4.2 Range expansions**

In response to temperature changes, many species' ranges are changing in size and shape. In most cases, poleward range edges are expanding towards high latitudes (leading edges), whereas equatorward edges are retracting (trailing edges), creating an overall range shift towards higher latitudes. In mountain contexts, species' ranges have been observed to be shifting towards higher elevations in a similar manner (Lenoir, Bertrand, et al. 2020; Parmesan and Yohe 2003). Altogether, marine species seem to be better at tracking their climatic niche, moving towards the poles six times faster than terrestrial species (ca. 6km/year vs 1km/year Lenoir, Bertrand, et al. 2020). However, there are a multitude of species' specific responses (Chen et al. 2011; Lenoir and Svenning 2015). In some cases, leading edges are not expanding, possibly due to dispersal barriers or biotic interactions inhibiting establishment, and in other cases, trailing edges are not retracting, possibly due to local adaptation or extinction debts. Some cases have been observed where trailing edges even expanded equatorward or towards lower elevations. In addition,

longitudinal changes may confound these range changes. Range changes are therefore highly specific, not only in the way the range changes shape, but also the degree of extension or retraction.

Differences in range changes between species can be due to several, possibly interacting, factors (see also Le Galliard et al. 2012). First, species' dispersal behaviour is more influenced by local changes in climate, but these do not always reflect changes at larger scales (Williams and Blois 2018). Second, species' niches are multidimensional, and their distributions are determined by other environmental factors than temperature. However, changes in different environmental factors are not necessarily correlated; changes in precipitation, for instance, are expected to be very variable across regions (VanDerWal et al. 2013). Third, as presented in previous sections, dispersal abilities differ between species, which may explain differences in the degree of poleward and high elevation expansions. Fourth, species' capacities of adaptation differ as well, which may be related to differing responses at the equatorward and valleyward edges. Fifth, species are not independent from each other but interact in complex ways. Range changes therefore can be contingent on other species. Lastly, current climate change is not the only process shaping species' distributions. Some species' ranges are still responding to past climate change and may not be at equilibrium with the environment. Range changes are therefore determined by a combination of extrinsic and intrinsic factors acting at different scales.

Species' abilities to adapt and shift their ranges to changing environmental conditions is essential for their persistence and survival. To focus conservation efforts, we hence need to understand what drives differences in their responses. Estrada et al. (2016) propose a framework similar to that of Ronce (2007) and Blackburn, Pyšek, et al. (2011), dividing the range shift process into emigration, movement, establishment and proliferation. Compared to biogeographic dispersal, which is probably jump dispersal in most cases, range expansions are more related to diffusive dispersal, happening over shorter geographic scales. The main mechanism of dispersal should therefore be active rather than passive dispersal, and emigration may be influenced by factors and traits that play a role in ecological dispersal (e.g. kin competition, local population density, curiosity, etc., see 0.3.1). However, the movement stages of biogeographic dispersal and range expansions may be comparable in heavily fragmented landscapes where suitable habitat patches may be separated by considerable barriers. These barriers may not necessarily be as strong filters as they would be in biogeographic dispersal. Hence, we might expect some similar traits to be important in both processes (e.g. body size which is hypothesised to be related to the movement ability) but with important differences: traits related to survival in areas characterised by strong human impact, e.g. small size or generalist diet, may be overrepresented in successful range extenders compared to successful dispersers across biogeographic

barriers. Establishment might be different in the two processes as range expansion happens over smaller geographic scales. Therefore, founder populations might be comparatively large and there might be a steady supply of newcomers, contrary to biogeographic dispersal. Nonetheless, we could expect reproductive strategy, competitive ability and ecological generalisation to be linked to both establishment and proliferation. Attempts have been made to link species' traits to range shifts empirically: a positive effect on range shifts was found for diet breadth and habitat breadth, but other traits, such as body size or fecundity, showed no significant effects (Angert et al. 2011; MacLean and Beissinger 2017). This may be due to any of the factors mentioned in the previous paragraph. Our understanding of the role of traits in range shifts therefore remains limited.

**In summary**, range shifts are the manifestation of complex interacting ecological and evolutionary processes, and presently difficult to predict. In particular, different processes are acting at different parts of the range (leading edge, trailing edge, core of the range), and local shifts in climate can lead to variable responses across a species' range. Range expansions are likely determined by diffusive dispersal, but in fragmented landscapes some comparisons can be made to biogeographic dispersal, and some traits may be similarly related to both processes.

## **0.5 This thesis**

In this introduction, I have outlined the consequences dispersal can have for evolutionary and biogeographical processes. All dispersal processes are context-dependent and influenced by a multitude of external and internal factors and processes. Generalities are hard to come by. A lot of work has been done regarding ecological dispersal, and conceptual work regarding biogeographic dispersal dates back about 250 years. However, empirical work and tests of specific hypotheses regarding correlates of biogeographic dispersal outcomes are lacking. This has many reasons, some of them historical (the dominance of vicariance biogeography in the latter half of the last century), others more practical (rarity of biogeographic dispersal events, limited data availability and computational constraints). As dispersal is species- and context-dependent and different processes are acting on the ecological and biogeographical scales, we cannot easily extrapolate from ecological to biogeographical dispersal. With this thesis, I aim to improve our understanding of biogeographic dispersal and its determinants. In the first part of this thesis, I therefore focus on correlates of past biogeographic dispersal success, first in chameleons (chapter 1) and then in 56 tetrapod clades (chapter 2, Fig. 6).

While humans have altered natural dispersal processes, conceptual similarities and similar correlates of dispersal success across different scales have been identified. Better understanding past dispersal across major barriers might improve our

knowledge of present-day processes and help us overcome the challenges associated with predicting biological invasions and range expansions. In a conceptual synthesis (chapter 3) I discuss if and how information from macroevolutionary and biogeographic studies can be used to better understand present-day biological invasions, as well as present-day extinction risk due to changing environmental conditions. I then test conceptual considerations from this work relating to dispersal: first, I analyse if past dispersal relates to present-day naturalisation success of selected tetrapod clades (chapter 4), then I investigate if past dispersal relates to present-day range expansions (chapter 5). Chapter 4 is based on work carried out together with Marceau Habrant, whom I co-supervised during his 5-month MSc internship at the Laboratoire d'Ecologie Alpine (March - August 2022).

I conclude this thesis with a general discussion of my work, including limitations and perspectives of future work.

In the course of this thesis I produced three scientific articles: one (chapter 1) is published in the journal *Ecography* (Weil, Gallien, et al. 2022), a second (chapter 2) is currently in revision in the journal *Nature Ecology and Evolution*, and the third (chapter 3) is in preparation. Two further articles not directly linked to this thesis are in preparation. One deals with life history strategies of tetrapods (Allen, Weil, et al. in prep.), and the other with the relationships between anthropogenic threats and functional strategies in reptiles (Weil, Rodriguez-Caro, et al. in prep.).

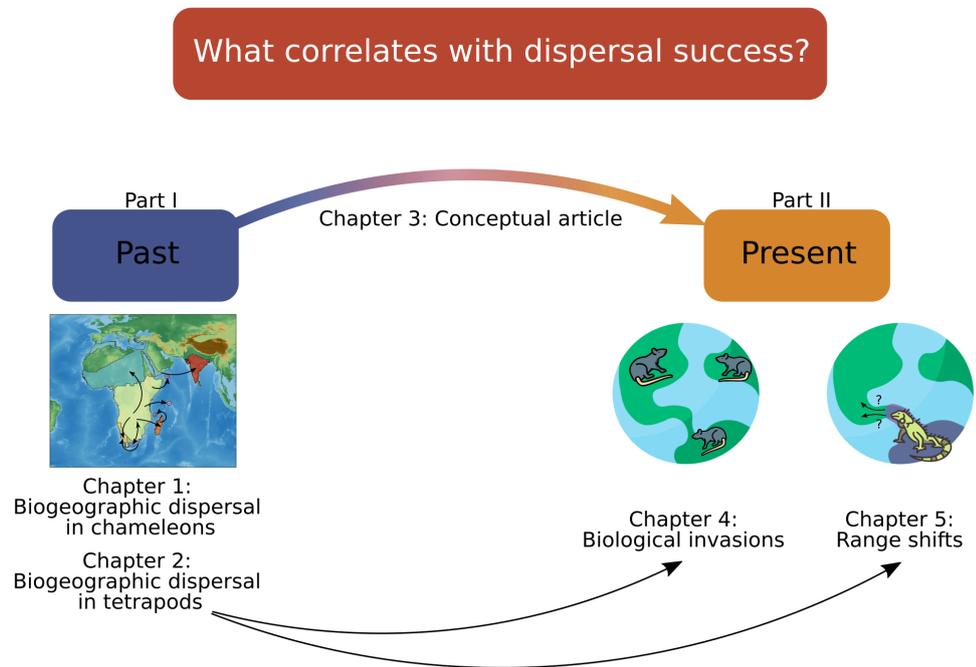


Figure 6: Outline of the thesis.

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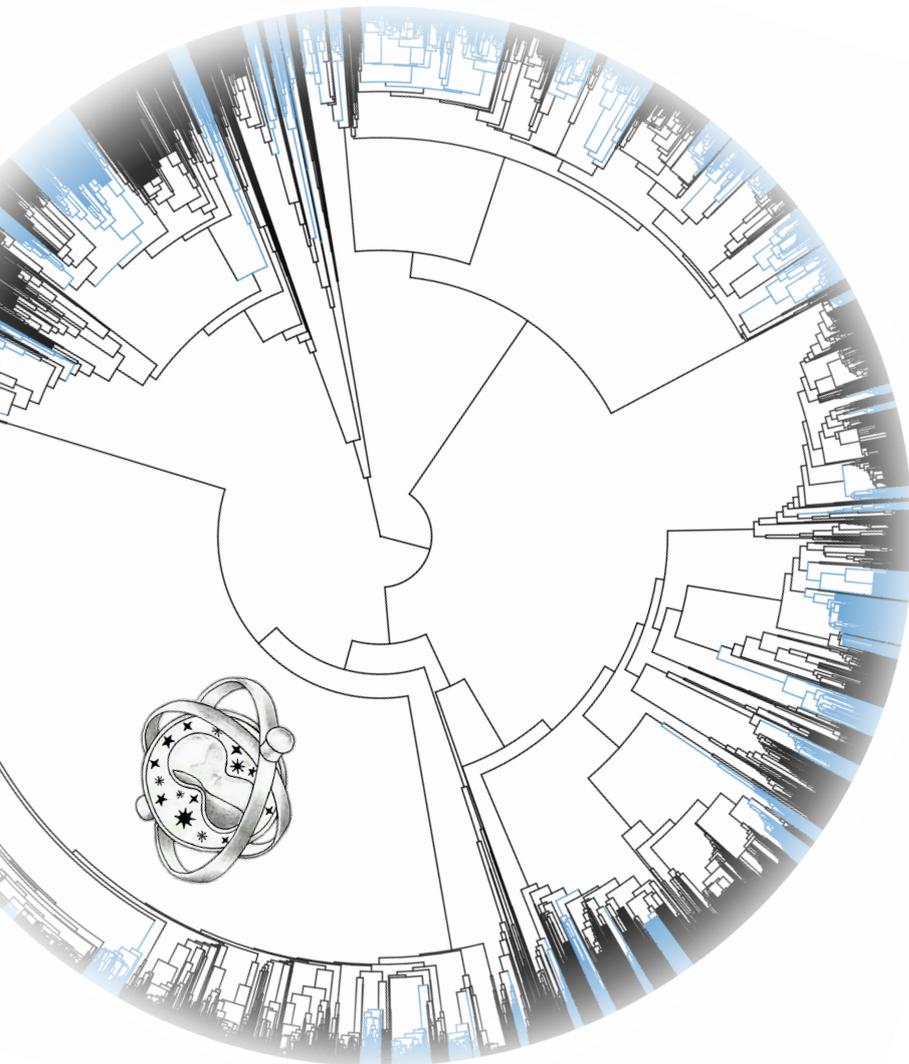
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# Part I

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## Past

*Mysterious thing, Time*



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"Mysterious thing, Time": J. K. Rowling, Harry Potter and the Prisoner of Azkaban.

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In this first part I investigate how species' traits are linked to past biogeographic dispersal. To do this, I use biogeographic models that jointly estimate past range evolution, i.e. range expansion through dispersal, range contraction and range splitting, and trait evolution across a phylogeny (Klaus and Matzke 2020). These new biogeographic models are an extension of trait-independent models which only estimate the range evolution across a phylogeny. All models have in common that they estimate range evolution in a clade's evolutionary history over discrete areas that need to be defined a priori. Here, I go into more detail regarding the definition of dispersal barriers and biogeographic regions between which dispersal is estimated in these biogeographic models. Then, I briefly describe the models and how the extension with traits is implemented.

## Bioregionalisation

*A spectre is haunting biogeography - the spectre of biogeographical regionalization.* Juan J. Morrone 2018

As highlighted in the introduction, the definition of biogeographic regions and the barriers that define them is no trivial task. Early regionalizations were based on expert knowledge and subjective differences between biotas. Species' assemblages within these regions should be taxonomically similar and assemblages of different regions maximally dissimilar. However, this depended much on the author's taxonomic knowledge, and the degree of dissimilarity necessary to justify the creation of a new region was also left to the author's discretion. Zimmermann (1778) is thought to have defined the first zoogeographical regions from occurrence patterns of mammal species' within continents (Glaubrecht 2022, Fig. P1.1a). During the 19<sup>th</sup> century, further regionalisations were proposed; based on distributions of bird species (Sclater 1858) and other vertebrate taxa (Wallace 1876, Fig. P1.1b), as well as various plant groups (Engler 1879). As these regionalisations were subjective, the exact delimitations of regions were a topic of debate (Ebach and Parenti 2015).

Towards the end of the 20th century, several quantitative methods were developed to define biogeographic regions more objectively, based on the concept of endemism, i.e. congruence in distributions of several taxa (e.g. Cladistic Analysis of Distributions and Endemism (Porzecanski and Cracraft 2005), Parsimony Analysis of Endemicity (Morrone 1994), Analysis of Endemicity (Szumik, Cuezco, et al. 2002; Szumik and Goloboff 2004)). In recent years, methods using similarity indices and cluster analysis, as well as network-based approaches have become especially popular, which allow to quantify relationships between regions (Bradshaw et al. 2015; Kreft and Jetz 2010; Newman 2006; Rosvall et al. 2009). In addition, new criteria have been proposed to identify regionalisations, one of them the "naturalness" of the region (Ebach and Parenti 2015). This is to say that biota

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within a region should share a historical relationship, and that if subareas of a region are more closely related to subareas of another region, then none of the two regions is natural (Ebach and Parenti 2015; Parenti and Ebach 2009). Picking up on the criterion of historical relationship, Holt et al. (2013) proposed to also include phylogenetic information in bioregionalisation methods, in addition to species' distribution data. The idea behind this proposition is that assemblages that are phylogenetically similar are/were determined by barriers that are/were relatively stable through time. This is important information in the context of historical biogeography which not only deals with species' present-day movements but range evolution over millions of years. Including phylogenetic information resulted in different regions than regions defined purely based on distributional data (Holt et al. 2013, Fig. P1.1). In particular, there were notable differences between regionalisations of different classes (amphibians, reptiles and birds) which they suggest may be due to differences in dispersal abilities and sensitivity to environmental conditions between taxa. This is an important result as it implies that bioregions are class- or taxon-specific, which thus needs to be taken into account in all studies where biogeographic regions are the basic unit of analysis (which is frequently the case in the fields of macroevolution, biogeography and macroecology, amongst others, Kreft and Jetz 2010)

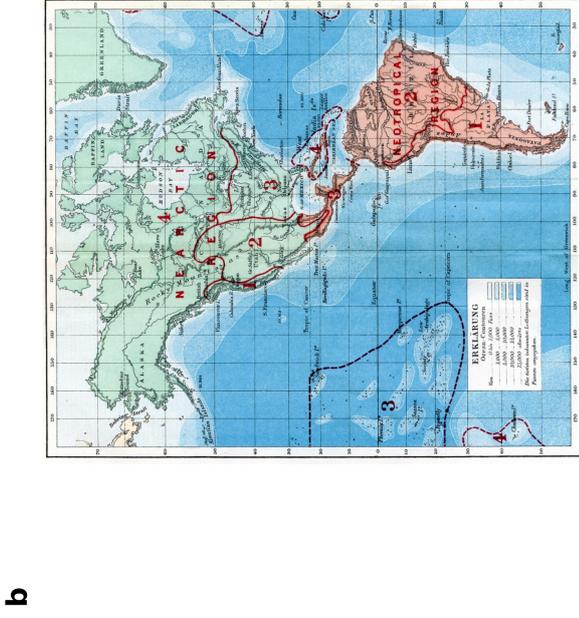
Several studies have compared some of the existing methods of bioregionalisation, but there is no consensus over which method is most appropriate (Bloomfield et al. 2018; Escalante 2015; Ferrari 2018; Morrone 2018; Vilhena and Antonelli 2015). And while these methods are more objective than the first expert-based bioregions, there are still a number of subjective decisions to make (e.g. grain of analysis, betadiversity metric in clustering approaches). Ferrari (2018) suggested testing several bioregionalisation scenarios to evaluate the robustness of the results to the adopted schemes.

## **Biogeographic models and traits**

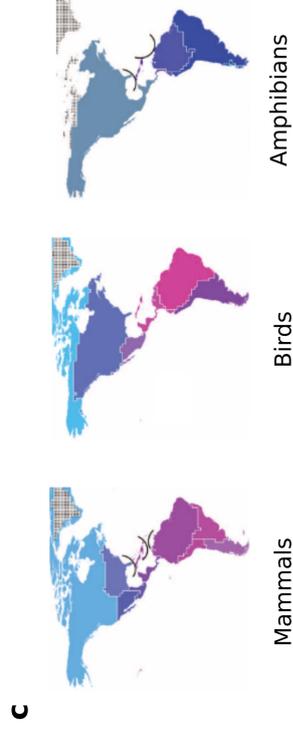
Biogeographic models estimate the ranges of species' ancestors across the phylogeny, based on extant species' occurrences in the a priori defined biogeographic regions and phylogenetic information (Fig. P1.2a and b). This allows the inference of dispersal, vicariance and range contractions in the history of a clade, i.e. the inference of a clade's biogeographic history. Three models for ancestral range estimation are implemented in the R package BioGeoBEARS (Matzke 2013; Matzke 2014): DEC (Ree, Moore, et al. 2005; Ree and Smith 2008), and a likelihood version of DIVA (Ronquist 1997) (DIVALIKE) and BAYAREA (Landis et al. 2013) (BAYAREALIKE). They all implement slightly different range inheritance scenarios (Fig. P1.3). For instance, DEC models always assume one daughter lineage to have a single area range whereas DIVA also allows for widespread vicariance.



Zoogeographic regions based on tetrapod distributions according to Zimmermann (1783)



Zoogeographic regions based on bird, mammal, reptile and insect distributions according to Wallace (1876)



Zoogeographic regions according to Holt et al. (2013)

Figure P1.1: Extracts of different proposed bioregionalisations. a) Zimmermann's *Tabula mundi geographico zoologica sistens quadrupedas* (Zimmermann et al. (1783), available at <https://cata.log.princeton.edu/cataLog/9955253523506421>), b) Wallace's zoogeographical regions (Wikimedia Commons contributors 2021), and c) Holt et al.'s updated zoogeographical regions (Holt et al. 2013).

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In BioGeoBEARS, the three models are implemented in a common likelihood framework which makes it possible to compare the different models and determine which range inheritance scenario best fits the data.

In all models, two key parameters are estimated: the dispersal rate  $d$  and the extinction rate  $e$ . In this context, “dispersal” refers to successful range expansion and extinction refers to local extinction in a region, not extinction of an entire lineage. In the basic models, the dispersal rate is the same for all lineages and between all regions. This is unrealistic because several factors can influence dispersal rates, e.g. kind of barrier that is crossed (oceanic, continental, with oceanic currents, against oceanic currents), distance between regions, or species’ traits. However, a number of adjustments can be made to include these factors and increase the realism in these models.

First, a manual dispersal multiplier matrix (MDMM) can be implemented (Fig. P1.2c). This is a matrix that defines multipliers applying to dispersal between pairs of regions. This way, it is possible to make dispersal between certain regions impossible (e.g. jumps between non-adjacent regions, Fig. P1.2). In addition, weights can be applied to dispersal between regions depending on the barrier, e.g. to make dispersal across oceans “harder” than dispersal across land for terrestrial species.

A second way to increase realism is to implement a time-stratified analysis. This way, changes in the geographic template through time can be taken into account, e.g. the emergence or submergence of islands. Through areas allowed matrices, colonization of certain regions becomes possible/impossible for certain periods of time (Fig. P1.2c).

Lastly, it is possible to let the distance between regions influence dispersal by adding a distance matrix and introducing a new parameter in the models (parameter  $x$ , Van Dam and Matzke 2016). Dispersal between any two regions A and B,  $d_{AB}$ , is thus defined in the following manner:  $d_{AB} = d_0 * D_{AB}^x$ , where  $d_0$  the general dispersal rate estimated by the model,  $D_{AB}$  the distance between A and B given by the distance matrix, and  $x$  the additional parameter estimated by the model. Its estimated value can inform about the importance of distance in the biogeographic history of the clade. If  $x$  is 0, distance effectively does not play a role (since any  $D^0 = 1$ , and  $d = d_0 * 1 = d_0$  in the above equation). If  $x$  is negative, dispersal becomes less likely with increasing distance.

In these biogeographic models, dispersal rates can thus be modified to reflect important characteristics of and changes in the geographic template through time. However, dispersal rates are still the same for all lineages (“lineage exchangeability”, Sukumaran and Knowles 2018) which is unrealistic because in the majority of cases it is known that dispersal capacities vary between species due to differences in their traits (see Introduction). In response to this problem an extension was implemented in BioGeoBEARS (Klaus and Matzke 2020) allowing a binary trait,

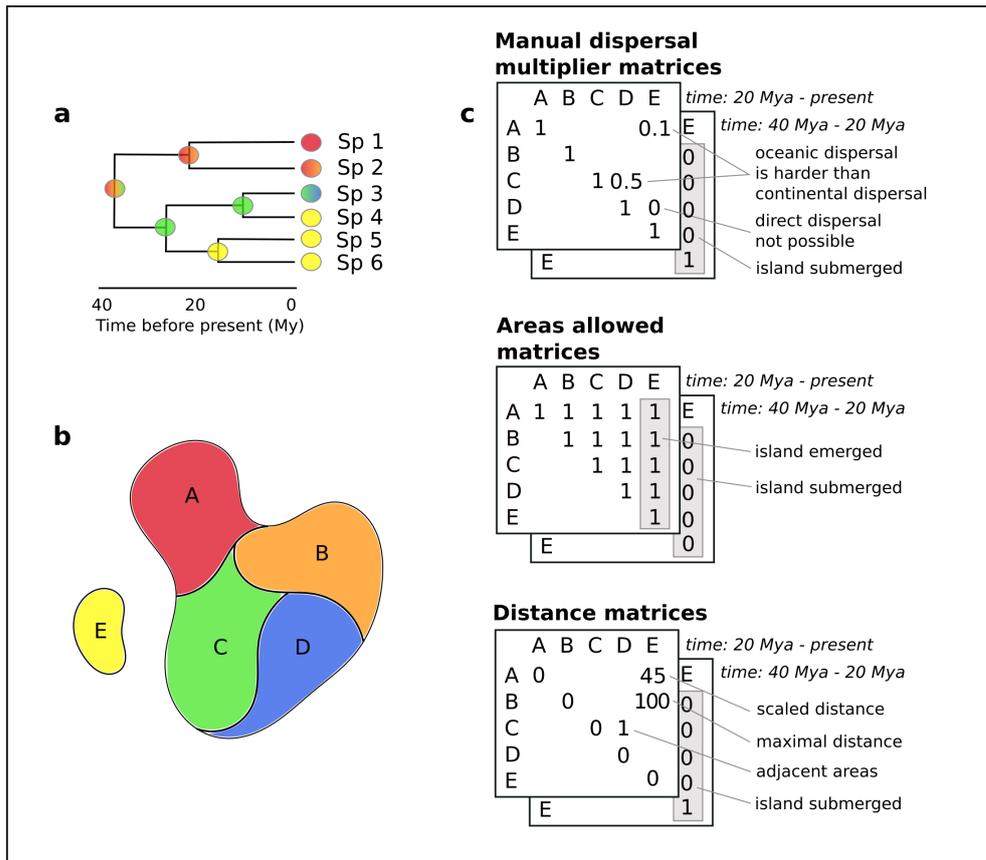


Figure P1.2: Biogeographic models allow us to estimate ranges of species' ancestors, based on extant species' phylogenetic relationships (a) and occurrences in a priori defined biogeographic regions (b). A number of adjustments can be made to increase realism in these models through manual dispersal multiplier matrices, areas allowed matrices and distance matrices (c). These modify dispersal rates of the model by taking into account the strength of barriers (e.g. oceanic vs continental dispersal), changes in the geographic template, such as island submergence or emergence, and distances between regions.

	Process	Ranges		Character mapping	DIVA	DEC (GeoSSE, LAGRANGE)	BayArea, BBM (RASP)	Parameter of BioGeoBEARS Supermodel
		Before	After					
Anagenetic	Dispersal				✓	✓	✓	$d$ (& $x, b$ )
	Extinction				✓	✓	✓	$e$ (& $u, b$ )
	Range-switching			✓				$a$ (& $x, b$ )
Cladogenetic	Sympatry (narrow)			✓	✓	✓	✓	$y$ (& $mx0ly$ )
	Sympatry (widespread)						✓	$y$ (& $mx0ly$ )
	Sympatry (subset)					✓		$s$ (& $mx0ly$ )
	Vicariance (narrow)				✓	✓		$v$ (& $mx0ly$ )
	Vicariance (widespread)				✓			$v$ (& $mx0ly$ )
	Founder							$j$ (& $x, mx0ly$ )

Figure P1.3: Processes assumed by different biogeographic models (from Matzke 2013).

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which is itself evolving, to influence the dispersal rate  $d$ . In this extension, several additional parameters are necessary:  $t_{12}$  and  $t_{21}$  are the rates of trait evolution from trait state 1 to 2 and from 2 to 1, and  $m_1$  and  $m_2$  are multipliers with which the dispersal rate  $d$  is multiplied depending on the trait state of a lineage. In practice,  $m_1$  is fixed to 1 so that the dispersal rate for lineages in trait state 1 corresponds to  $d$  (which can still be modified according to possible additions reflecting the geographic template).  $m_2$  is estimated by the model; if it is greater than 1 this implies that lineages in trait state 2 were better dispersers than those in trait state 1, if it is smaller than 1, they were worse dispersers than those in trait state 1.

This trait-dependent extension is computationally expensive partly due to the number of parameters that are estimated (three more than in trait-independent models) but more so due to the size of the range transition matrix (the size of which is quadrupled due to the inclusion of a binary trait, see Sukumaran and Knowles 2018 for a detailed explanation). This transition matrix depends on the number of region combinations that are allowed which in turn depends on the number of regions that are defined a priori. Inference with more than nine regions quickly becomes impossible to solve with current typical supercomputing capacity if species are allowed to occur in more than two regions simultaneously.

In the following chapters I develop and apply a methodology based on a phylogenetically-informed bioregionalisation approach and trait-dependent biogeographic models to understand how traits were related to past biogeographic dispersal success. I do this in the family of chameleons (Chamaeleonidae) as a case study (chapter 1). Then, I apply a slightly modified analysis pipeline to 56 clades of tetrapods, which I follow up by post-hoc analyses to understand differences between clades in trait-dispersal relationships (chapter 2).

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# **Chapter 1**

**Case study: Chameleon  
biogeographic dispersal is associated  
with extreme life history strategies**



# ECOGRAPHY

## Research

### Chameleon biogeographic dispersal is associated with extreme life history strategies

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Understanding the role of traits in dispersal is necessary to improve our knowledge of historical biogeography, community assembly processes and predictions of species' future movements. Here we aimed to determine the relationship between three traits (coastal distribution, body size, position on the fast/slow life history continuum) and past dispersal probability on an evolutionary timescale in chameleons (Chamaeleonidae). Using species' distribution data we identified the nine most important biogeographic regions for all included chameleons (181/217 species). We compiled life history trait data and used phylogenetic factor analysis to infer independent body size and fast/slow life history trait axes. Finally, we tested whether traits and trait combinations related to biogeographic dispersal success in the past, using trait-dependent biogeographic models. All three traits were associated with past biogeographical movements. Lineages having coastal distributions and those with large bodies had higher dispersal probabilities. Interestingly, chameleons with either a very fast or very slow life history were more successful dispersers than species with an intermediate strategy. Together, the three traits – coastal, large-bodied and extreme life history – form a dispersal syndrome. Traits have played an important role in the biogeographic history of chameleons. While only fast traits have been linked to present-day invasion success in reptiles, both extremes of the life history spectrum were likely advantageous for dispersal and establishment during past biogeographic movements. Fast-living species may be less susceptible to stochastic extinction in the first phases of a colonization (due to rapid population growth), and slow-living species may be less vulnerable to environmental stochasticity (due to low demographic variability). Our results call for broader analyses testing the general influence of life history strategy in biogeographic dispersal success, which would help explain species distribution patterns on Earth.

Keywords: biogeography, Chamaeleonidae, dispersal, life history continuum, species' traits, trait-dependent biogeography

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## Introduction

Species' traits can impact biogeographic processes such as dispersal, extinction and cladogenesis and likely play a part in shaping the distribution of life on Earth (Ronce and Clobert 2012, Zamudio et al. 2016, Chichorro et al. 2019). While associations between traits and short-distance dispersal at the level of individuals and populations have been studied extensively (Whitmee and Orme 2013), the role of traits in broad-scale historical biogeographic dispersal outcomes at the species level is only just beginning to be formally investigated (Sukumaran and Knowles 2018, Klaus and Matzke 2020). Integrating dispersal events and species' trait evolution on evolutionary timescales offers potential insight into the role of traits in species' biogeographic movements. This will advance our understanding of processes in historical biogeography and community assembly, which may enable better predictions of species' movements in the future (Lowe and McPeck 2014, Estrada et al. 2016).

To colonize a distant location, species must succeed at three sequential stages of dispersal: emigration, movement (or 'passage' if referring to passive dispersal) and establishment (Nathan 2001). Different types of traits might be linked to successfully overcoming each stage (Estrada et al. 2016). The emigration stage in biogeographic dispersal is strongly influenced by species' geographic distributions; coastal species, for example, are more likely to be moved from their native range by storms and cyclones than species living far away from the coast (Blom et al. 2019). In the movement and establishment stages, larger animals might have a survival advantage since their relative metabolic rate (relative to body size) is lower than that of smaller species (Andrews and Pough 1985, White et al. 2019), which improves their resistance to stress (including long periods of food and water shortage; Van Bocxlaer et al. 2010). On the other hand, transoceanic, cyclone-driven rafting dispersal of small organisms has long been reported (Ozgo et al. 2016, Lindo 2020). Establishment at a new location depends first and foremost upon the arrival of a reproductively viable founding population, which is determined by population size and species' life history traits (Safriel and Ritte 1980). While some traits are likely linked to specific stages of the dispersal process (e.g. coastal distribution to emigration), other traits may be related to several dispersal stages at the same time (such as body size). In addition, traits may have multiplicative effects, i.e. a species holding several dispersal traits may have a much higher probability of dispersal success than could be expected based on estimations from the individual traits. It is therefore important to consider combinations of traits that might form a successful disperser phenotype (Van Bocxlaer et al. 2010).

Further clues to understanding how traits influenced biogeographic movements in the past can be found in today's biological invasions. In some groups, invasive species belong to lineages with particularly frequent historical biogeographical movements (e.g. in pines: Gallien et al. 2016; and in Australian acacias and eucalypts: Gallien et al. 2019). Furthermore, in both processes taxon-specific barriers need

to be overcome for a successful range expansion (e.g. large water bodies). While some barriers may be very different in the two processes (e.g. those related to emigration), others may be comparable (e.g. those related to establishment) and the traits associated with overcoming them may be similar.

In today's biological invasions, a species' position on the fast/slow life history continuum has been linked to its invasion success (Sol et al. 2012, Capellini et al. 2015, Allen et al. 2017). The fast/slow life history continuum (Dobson and Oli 2007, Jeschke and Kokko 2009) is a descriptive analogue of the mechanistic r/K selection theory of life history evolution (MacArthur and Wilson 1967, Pianka 1970). Life history traits of fast species can be equated to those of r-strategists (e.g. early reproduction, big litters/clutches), and life history traits of slow species to those of K-strategists (e.g. low fecundity, long lifespan). Birds with traits associated with slow life history and bet-hedging strategies, such as large brains and iteroparous reproduction, are more successful invaders (Sol et al. 2012). Slow and bet-hedging species may have the resources (and lifespans) to wait for favourable environmental conditions to produce offspring (Cáceres 1997), and they exhibit less demographic variability over the years, which buffers the effects of environmental stochasticity (Sæther and Bakke 2000, Jeppsson and Forslund 2012). On the other hand, in mammals, amphibians and (non-avian) reptiles, the opposite pattern has been found: species with fast life histories are more successful throughout the invasion pathway than slow species (Capellini et al. 2015, Allen et al. 2017). Fast species are able to quickly establish sizable populations, hence they may be able to quickly overcome the period in which founder populations are particularly vulnerable to stochastic extinction (Caswell et al. 2003, Blackburn et al. 2015). The relationship between life history strategy and present-day biological invasions and species' movements has inspired us to investigate the role these strategies have played as drivers of global biogeography in the past.

Here, we use recently developed trait-dependent biogeographic models (Klaus and Matzke 2020) to test the effect of three binary traits (coastal distribution, body size and life history strategy) and their combination in dispersal outcomes on an evolutionary timescale. We investigate these traits in the family of chameleons (Chamaeleonidae) which comprises 217 species in 12 genera (according to <[www.reptile-database.org](http://www.reptile-database.org)>, accessed 20 May 2021). Most species occur in Madagascar and Africa, but some species can be found in southern Europe, the Middle East, India and Indian Ocean islands (IUCN 2019). Chameleons are situated within the squamate clade of Acrodonta, and are hypothesized to have diverged from their sister clade Agamidae ca 90 million years ago (Mya) (Townsend et al. 2011, Tolley et al. 2013). Chameleon phylogeography suggests an African origin with multiple oceanic dispersal events to Madagascar, the Comoros Islands, Arabia, the Seychelles, India and Europe (Raxworthy et al. 2002, Townsend et al. 2011, Tolley et al. 2013), which makes the group well-suited for investigating how traits relate to dispersal patterns.

First, we analysed whether chameleon distributions (coastal versus non-coastal) and body size (and associated life history trait covariation) are related to past dispersal outcomes, two traits identified as affecting historical dispersal in other reptile clades (Blom et al. 2019, Nicolai and Matzke 2019). Body size is known to evolve under different selective pressures from life history (e.g. temperature; Tinkle et al. 1970), but through allometric constraints selection pressures on body size can indirectly influence traits that are related to the fast/slow life history spectrum (Bauwens and Díaz-Uriarte 1997, Bakewell et al. 2020, Meiri et al. 2021). We therefore placed species on a body size-independent fast/slow life history continuum using phylogenetic factor analysis. We then evaluated the relationship between this body size-independent life history strategy and past dispersal outcomes, which has not been done in the context of historical biogeographic dispersal before. Finally, we combined all three traits (coastal distribution, body size and life history strategy) and investigated the possibility of a successful dispersal syndrome. We used trait-dependent biogeographic models to test the following hypotheses:

- 1) Coastal lineages and large-bodied lineages were better dispersers than non-coastal and small-bodied lineages, respectively, in the past, as demonstrated in other reptile clades.
- 2) Chameleon lineages with fast life histories were better biogeographic dispersers than lineages with slow traits in the past, following patterns in invasive reptiles.
- 3) Chameleon lineages holding all traits hypothesized to favour dispersal (coastal distribution, large body and fast life history strategy) were better dispersers than lineages holding only one of these traits.

### Material and methods

To assess whether, and how, three traits (coastal distribution, body size and body size-independent life history strategy) have influenced past dispersal success of chameleons we built and compared trait-independent and trait-dependent biogeographical models (Fig. 1). Biogeographical models estimate ancestral ranges of species based on species' extant distributions and allow us to estimate past movements between discrete

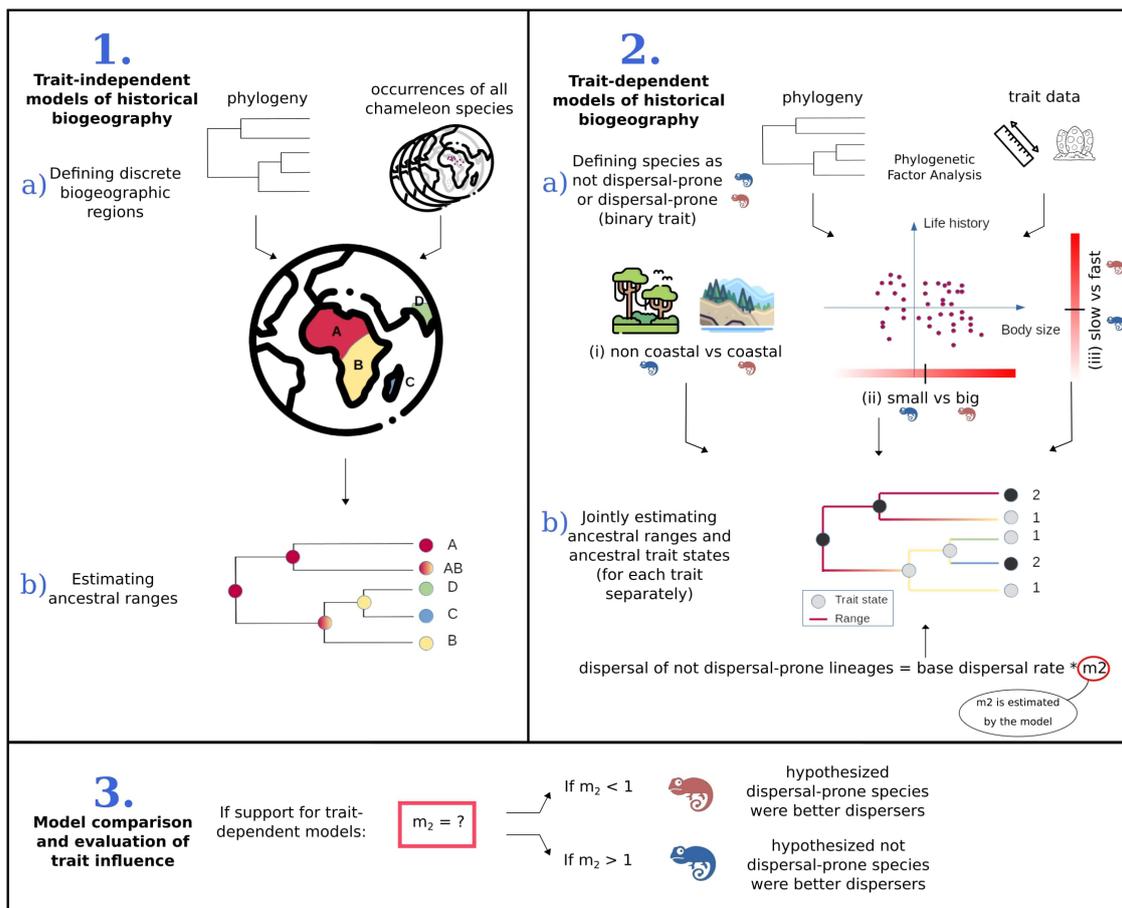


Figure 1. Schematic presentation of analysis workflow. Icons: <www.flaticon.com>.

biogeographic regions (see ‘Chamaeleonidae biogeographic regions’ section for details on the definition of these regions). In trait-dependent biogeographical models, a binary trait can influence dispersal rates of lineages. To define this binary trait and classify species according to body size and body size-independent life history strategy we used phylogenetic factor analysis (see ‘Trait data and phylogenetic factor analysis’ section for details). Comparison between trait-dependent and trait-independent models reveals whether a given trait had an influence on dispersal success in the past. If this is the case, the direction of the relationship between a given trait and dispersal success will be investigated (with the estimated parameter  $m_2$ ; see ‘Trait-dependent dispersal: ‘BioGeoBEARS’ section for details). All analyses were performed using R ver. 3.6.3 (<www.r-project.org>) unless otherwise specified.

### Chamaeleonidae phylogeny and distribution

We focused only on chameleon species for which genetic data were available (181/217 species, ca 83%), using a subset of the Tonini et al. (2017) squamate consensus tree. To quantify the effect of phylogenetic uncertainty in results we repeated the analyses on a set of 100 uniformly sampled trees from a sample of the posterior distribution of Tonini et al. (2017) (Supporting information). Species’ distribution data were obtained from IUCN (2019). We kept records where presence was defined as extant and origin as native. We transformed the data into rasters in cylindrical equal area projection (Behrmann with standard parallels at 30° to avoid distortion of area at higher latitudes, which allows for a better comparison between different raster cells at different latitudes) with a resolution of ca 93 × 93 km.

### Chamaeleonidae biogeographic regions

To estimate species’ movements in the past, the first step is to identify the most important biogeographic regions specific to chameleon species. We did so with a data-driven approach using extant species’ distribution data. After evaluating alternative bioregionalization methods (Supporting information) we chose to use a clustering algorithm (unweighted pair group with arithmetic mean, Kreft and Jetz 2010) on between-site phylogenetic distances (modified Simpson’s phylogenetic beta-diversity index (Lennon et al. 2001 after Simpson 1943); Eq. 1). This method calculates the phylogenetic distance between raster cells based on extant species’ distribution data and their phylogenetic relationships, and then groups raster cells together according to the amount of evolutionary history they share. Hence, this method identifies barriers that have acted as actual barriers to gene flow over evolutionary time, and dispersal that is estimated between regions can be considered biogeographic dispersal (Kreft and Jetz 2010) (Eq. 1):

$$\text{Simpson} = \frac{\min(b,c)}{\min(b,c) + a} \quad (1)$$

where  $a$  = length of shared branches on the phylogenetic tree between two different raster cells, and  $b$  and  $c$  = length of unique branches in two different raster cells.

The phylogenetic beta-diversity matrix was weighted by a geographical distance matrix (great-circle distances on latitude/longitude coordinates). Non-contiguous regions were separated manually. In this way, we identified nine biogeographic regions: North Africa and Arabia, Central Africa, Southeast Africa, Southwest Africa, India, Socotra, Madagascar, the Comoros Islands and the Seychelles (Fig. 2). Extant species occupy three biogeographical regions at maximum. We therefore allowed ancestral distributions to extend to a maximum of three regions (Supporting information).

### Trait data and phylogenetic factor analysis

Trait-dependent biogeographic models can presently only take binary traits into account (see ‘Trait-dependent dispersal: ‘BioGeoBEARS’ section). We hence defined four binary trait datasets, based on three focal traits and their combination: 1) coastal distribution: coastal species (species living within 10 km of the coast) versus non-coastal species; 2) body size and associated life history trait covariation: large-bodied species versus small-bodied species; 3) body size-independent life history: fast versus slow life history; and 4) dispersal syndrome: species holding all three hypothesized dispersal traits (coastal distribution + large bodied + fast life history) versus species that do not have all three traits.

We identified species as coastal if they lived less than 10 km away from the sea (74 coastal species, ca 41%) using QGIS (QGIS Development Team 2020) and a global terrain model for ocean and land (GEBCO Bathymetric Compilation Group 2021). To assess sensitivity to the 10 km threshold, we analysed three additional classifications where we defined species as coastal if they lived less than 2, 15 or 25 km away from the sea. To rank species according to body sizes and life history strategies, we compiled a dataset of life history traits and identified the main axes of variation with a phylogenetic factor analysis (PFA, Tolkoﬀ et al. 2018). The trait data included: snout–vent length (SVL, 100% coverage) as a proxy for body size, clutch size (67% coverage), number of clutches per year (24% coverage), age at sexual maturity (29% coverage), gestation time (28% coverage) and reproductive lifespan (18% coverage; Nečas 1999, Glaw and Vences 2007, Tilbury 2010, Allen et al. 2017, Meiri 2018, Hughes and Blackburn 2020).

We performed PFA using the Julia package PhylogeneticFactorAnalysis.jl ver. 0.1.4 (Hassler et al. 2022) which relies on a development version of BEAST (Suchard et al. 2018) to be released with BEAST ver. 1.10.5. Missing data were handled in PFA through integrating out missing values in likelihood calculations, allowing inclusion of species with incomplete trait data, while avoiding biases associated with data imputation (Supporting information). To identify a size-specific fast/slow continuum (cf. Jeschke and Kokko 2009) independent from allometric constraints,

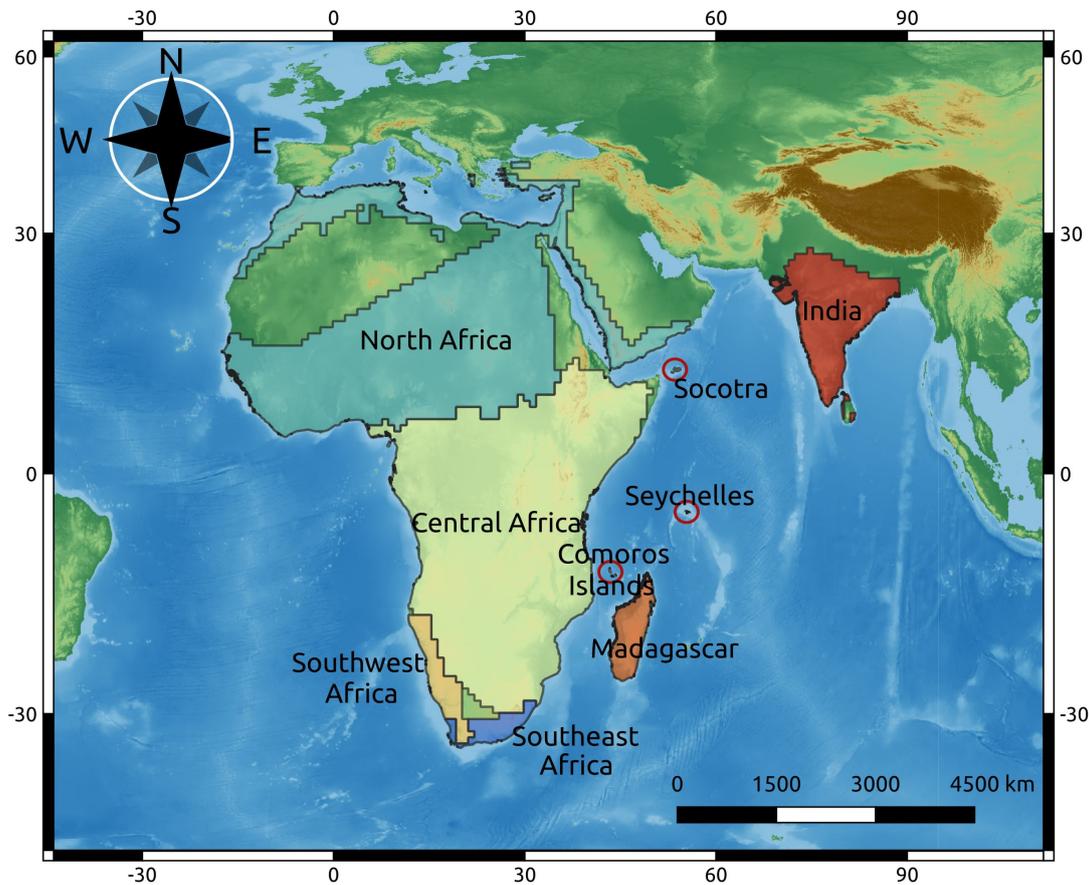


Figure 2. The nine biogeographic regions for Chamaeleonidae, identified through unweighted pair group with arithmetic mean (UPGMA) clustering on a modified Simpson's phylogenetic beta-diversity distance matrix. (Global terrain model of oceans and land taken from GEBCO Compilation Group (2021).)

we structured the PFA so that body size (as captured by SVL) loaded only onto the first factor while all other traits loaded onto all factors. This forced life history trait variation associated with body size onto the first factor with any additional factors capturing size-independent patterns of life history covariation (Supporting information). The first factor capturing size-dependent relationships was defined by positive loadings on SVL and clutch size (Fig. 3). The second factor was associated with size-independent fast/slow strategies and defined by gestation time and sexual maturity, with fast species of early sexual maturity and short gestation time on one side, and species with opposing traits on the other. Altogether, 32% of trait variance was attributable to the first factor and 16% to the second.

We used the first factor of the PFA to assess the role of body size and associated allometric relationships by median-splitting the species along this factor (i.e. using the median to assign species as small or large). We used the second factor as a representation of the fast/slow spectrum and median-split species along this factor to differentiate fast from slow species and obtain the life history trait dataset. We further

tested alternative splitting thresholds (Supporting information): 1) the fastest 25% of species versus the rest; 2) the fastest 75% versus the rest; and 3) the fastest 25% and slowest 25% ('extreme' life history) versus the rest. According to the results of these splits our definition of the dispersal syndrome changed. Finally, we assessed the sensitivity of our main results to the binarization of the continuous traits by moving the cutoff 10% in either direction.

#### Trait-dependent dispersal: 'BioGeoBEARS'

To assess the effect of traits on dispersal outcomes in the biogeographic history of chameleons, we used three biogeographic models that estimate ancestral ranges implemented in the R package 'BioGeoBEARS' ver. 1.1.2 (Matzke 2013, 2014): 1) dispersal-extinction-cladogenesis (DEC; Ree et al. 2005, Ree and Smith 2008); 2) DIVA-like (a likelihood implementation of DIVA; Ronquist 1997); and 3) BAYAREA-like (a likelihood implementation of BayArea; Landis et al. 2013). In the 'BioGeoBEARS' implementation of these models, biogeographical movements (i.e. anagenetic and cladogenetic

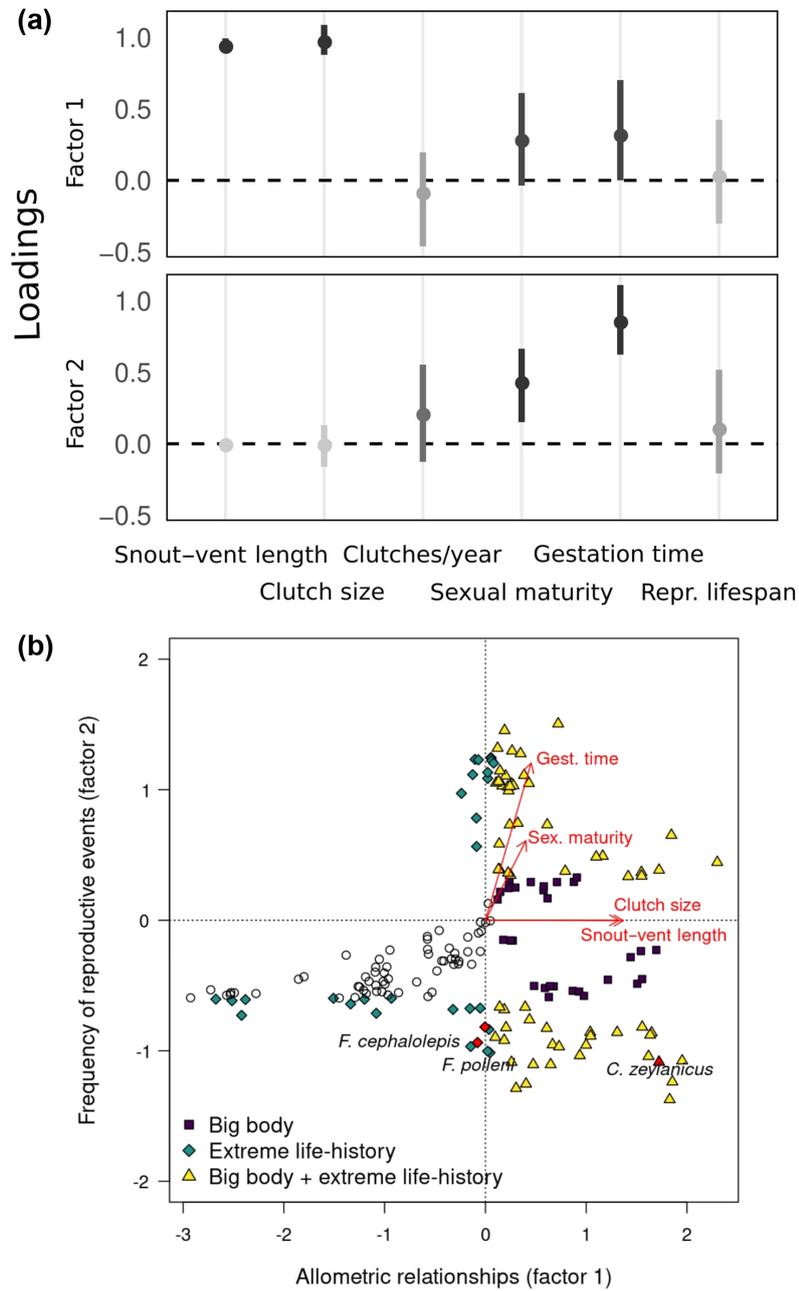


Figure 3. Results of the phylogenetic factor analysis. The estimates for the loadings of the body size and life history variables onto the two identified factors are given in (a). Points represent the posterior mean while error bars represent the 95% highest posterior density interval. Shading indicates the posterior probability  $p$  that loadings are of the same sign as their posterior means. The light end of the spectrum corresponds to  $p = 0.5$  (i.e. the loadings value has equal probability of being positive or negative), while the dark end corresponds to  $p = 1$  (i.e. the parameter's sign is certain). In (b), chameleon species are plotted in the factor space with different symbols depending on whether the species were classified as large-bodied (square), having an extreme life history strategy (diamond) or as being both large-bodied and having an extreme life history strategy (triangle). Small-bodied species with an intermediate life history strategy are indicated by simple dots. The original variables that loaded most strongly on the two identified factors are represented by red arrows. The three species that are associated with recent oceanic dispersal are labelled and indicated by red symbols.

dispersal rates) can be influenced by lineages' trait values. These models go beyond investigating correlations between traits and species' distributions to allow quantitative estimations of the importance of traits in dispersal processes at large temporal and spatial scales (Sukumaran and Knowles 2018, Klaus and Matzke 2020). At present the trait can take only two states (i.e. it is a binary trait) and it is itself evolving on the phylogeny, i.e. ancestral trait states and ranges are jointly estimated on the phylogeny. All models are implemented in a common likelihood framework which allows for model comparison.

The influence of trait states on dispersal rates is implemented via dispersal multipliers  $m_1$  and  $m_2$ . If a lineage is in trait state 1 (e.g. large body size), the base dispersal rate  $d$  is multiplied by  $m_1$ , and if a lineage is in trait state 2 (e.g. small body size),  $d$  is multiplied by  $m_2$  (Klaus and Matzke 2020 and <http://phylo.wikidot.com/biogeobears>). In practice,  $m_1$  is fixed to 1, and only  $m_2$  is inferred:  $m_2 > 1$  indicates that lineages in trait state 2 (e.g. small-bodied) were more successful dispersers than lineages in trait state 1, and  $m_2 < 1$  indicates the inverse. The transition rates from one trait state to the other,  $t_{12}$  and  $t_{21}$ , are inferred as well. To compare trait-independent models to trait-dependent '+ $m_2$ ' models, the log-likelihood from the independent trait evolution on the tree is combined with the log-likelihood from the independent geographic data. Therefore, we ran just the trait data under binary discrete character models as implemented in the 'BioGeoBEARS' package to independently estimate the parameters  $t_{12}$  and  $t_{21}$  (Klaus and Matzke 2020). The log-likelihood of the trait-independent models was then the sum of the log-likelihood of these independent trait data and the log-likelihood of the geographic data (i.e. log-likelihood from 'BioGeoBEARS' runs without parameters  $m_2$ ,  $t_{12}$  and  $t_{21}$ ). The log-likelihood reflects whether incorporating the trait (e.g. body size) improves model fit and  $m_2$  indicates which trait state the dispersal is associated with (e.g. large body size).

Plate tectonics and island uplift influenced species' past movements between biogeographic regions. We therefore implemented a time-stratified analysis and defined manual dispersal multiplier matrices (MDMMs) to account for islands uplifts and differences in the ease of continental versus oceanic-with-currents versus oceanic-against-currents dispersal (Supporting information). We also took changing geography into account by modifying dispersal probabilities between any two areas depending on the distance between them (+ $x$  model variant). Based on GPlates (Müller et al. 2018) and the global plate and rotation model of Matthews et al. (2016), we accounted for changing distances between regions by recalculating the distances for every time slice (Supporting information). We further introduced a root constraint in Central Africa to reflect findings from the literature (Tolley et al. 2013, Supporting information).

In summary, we first evaluated 30 trait-independent models: three types of biogeographical models (DEC, DIVA and BAYAREA)  $\times$  two types of influence of geographic distances (base model and + $x$ -variant)  $\times$  five different MDMMs. We compared these 30 models with the corrected Akaike information criterion (AICc), and identified the best base model:

DEC with MDMM distinguishing continental versus oceanic barriers and paleo-current directions (Supporting information). Second, for each of the traits (coastal distribution, body size, four life history strategies, dispersal syndrome) we ran the two trait-dependent biogeographic models (+ $m_2$  and + $m_2x$ ) using the previously selected best base model. Third, for each trait, we used AICc to compare the four final models (two trait-independent models: base, base+ $x$  and two trait-dependent models: base+ $m_2$ , base+ $m_2x$ ). In addition, we ran founder event models (+ $j$ ) for two traits (body size and extreme life history strategy) but, since they did not affect the  $m_2$  parameter estimates significantly (Supporting information) and a critique of Ree and Sanmartín (2018) highlighted conceptual problems, we did not pursue this avenue further to reduce computation time.

To assess phylogenetic uncertainty, we reran the trait-dependent model for every trait (coastal distribution, body size, life history strategy and dispersal syndrome) for every tree across the set of 100 trees from the posterior. Each new run included a new phylogenetic factor analysis to reclassify species as large versus small, to reclassify the life history strategies and to recalculate the dispersal phenotype (Supporting information).

All 'BioGeoBEARS' analyses were performed on R ver. 3.6.2 ([www.r-project.org](http://www.r-project.org)) using the GRICAD infrastructure (<https://gricad.univ-grenoble-alpes.fr>). The biogeographical analyses amounted to more than 44 600 h  $\times$  cores of computation time.

## Results

### Trait-dependent biogeographic models

#### Coastal distribution and body size

Non-coastal lineages did not disperse at all and large chameleons had a higher dispersal probability than lineages with small body sizes in the past. The trait-dependent models were selected as best models by the AICc-based model comparison for coastal distribution and body size (Table 1; Supporting information), split between just trait-dependent (coastal distribution: 63%, body size: 74%) and distance-and-trait-dependent models (coastal distribution: 37%, body size: 26%; Supporting information). The multiplier of the non-dispersal-prone forms ( $m_2$ ) was 0 for both traits. Phylogenetic uncertainty had little effect on dispersal multiplier estimates in the coastal distribution and body size analyses (Fig. 4). Using different distances to the sea (2, 15, 25 km) to classify species as coastal did not change interpretation of our results (Supporting information). Neither did moving the cutoff during binarization of body size 10% in either direction, i.e. considering the first 40% and 60% of species as large, respectively (Supporting information).

#### Life history strategy

Initial results suggested that fast lineages had generally higher dispersal probabilities than slow lineages:  $m_2$  of the

Table 1. Best models per trait as selected by model comparison with AICc. Only models with an AICc weight greater than 1% are included. m2: dispersal multiplier of species in the non-dispersal-prone form: non-coastal distribution, small bodied, intermediate life history (m2 > 1 indicates that species with non-dispersal-prone traits were more successful dispersers than species in trait state 1, and m2 < 1 indicates the inverse); x: dispersal multiplier of geographic distance.

Trait set	Best models	LnL	AICc weight (%)	m2	x
Coastal distribution	DECm2	-272	63	0	0
	DECm2x	-271	37	0	-0.11
Body size	DECm2	-253	74	0.0028	0
	DECm2x	-253	26	0.0028	-10 <sup>-6</sup>
Extreme life history	DECm2	-248	74	0.15	0
	DECm2x	-248	26	0.15	-10 <sup>-6</sup>
Dispersal syndrome	DECm2	-234	74	0.02	0
	DECm2x	-234	26	0.02	-10 <sup>-6</sup>

median-split classification of life history strategies was 0.84, trait-dependent models accruing an AICc weight of 27% (Supporting information), and m2 was 0.22 when comparing the fastest 25% of all species against the rest, trait-dependent models accruing an AICc weight of 93% (Supporting information). However, when comparing the fastest 75% against the rest, m2 of the best model was 2.19 (AICc weight of trait-dependent models = 68%; Supporting information), indicating that the slowest 25% of all species had a higher dispersal probability than the fastest 75%, contrary to the initial results. We therefore developed an ad hoc hypothesis and tested whether the extremes of the life history spectrum may be advantageous to dispersal. When comparing the fastest 25% and slowest 25% of species jointly against the rest, m2 was 0.15 and trait-dependent models accrued an AICc weight of 100% (Table 1, Supporting information), indicating that

species with an extreme life history strategy had an 85% higher dispersal probability than species with an intermediate one. Phylogenetic uncertainty influenced the extreme life history result more than coastal distribution and body size, with the median m2 being at  $0.33 \pm 0.07$ . Moving the cutoff during binarization 10% in either direction, i.e. hypothesizing the extreme 40% and 60% of species to be dispersal-prone, respectively, did not change our results (Supporting information).

**Dispersal syndrome**

According to the life history results, our prediction for the dispersal syndrome changed to expecting that chameleons dispersed more when they were at the same time coastal, large-bodied and with extreme life history strategy (instead of only a fast one). We identified 34 species (ca 19%) as having such a dispersal syndrome, significantly more than could have been expected by chance (Supporting information). Species that did not hold this combination of traits had a 98% lower probability of dispersal (m1 was fixed to 1, m2 estimated as 0.02; Fig. 4), and trait-dependent models accrued an AICc weight of 100% (Table 1, Supporting information). When running the trait-dependent model on a set of trees, m2 values varied around  $0.03 \pm 0.14$  but a small number of trees (3%) generated low log-likelihood models with m2 parameters close to 1 (Supporting information).

**Biogeographic history of chameleons and trait evolution**

Trait-dependent models were consistently better supported by AICc comparison than trait-independent models. Notably, two nodes were estimated identically in all trait-dependent models but differently in the trait-independent

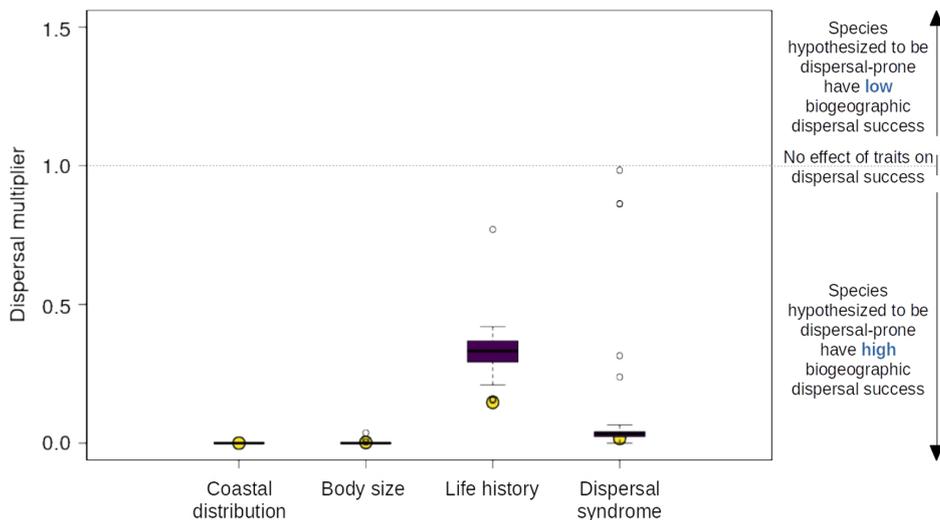


Figure 4. Values of the dispersal multiplier parameters as estimated by trait-dependent DEC models (DEC + m2). m1 (multiplier of the dispersal-prone forms) was fixed to 1. All multipliers presented here are estimations of m2, the multiplier for the non-dispersal-prone forms. The yellow points indicate the m2 parameter estimation from the consensus tree; the boxplots reflect the uncertainty in m2 parameter estimates due to phylogenetic uncertainty: the models were run on a set of 100 trees from the posterior.

model (Supporting information). All trait-dependent models agreed on the most recent common ancestor (MRCA) of *Bradypodion pumilum* and *B. damaranum* occupying Southeast and Southwest Africa (Supporting information). The trait-independent model, however, inferred this node to be restricted to Southeast Africa which then led to the inference of two independent range expansions by *B. pumilum* and *B. damaranum* to Southwest Africa (Supporting information). Similarly, the trait-dependent models estimated a more widespread ancestor for part of *Trioceros* than the trait-independent model (Supporting information).

Despite all trait-dependent models being better supported than trait-independent models, there were also differences in estimations of ancestral ranges within trait-dependent models. Shortly after the split of Brookesiinae and Chamaeleoninae, the ancestor of the Chamaeleoninae developed a dispersal-prone form and expanded its range to the Seychelles and Madagascar, but the order of events is unclear (coastal distribution and life history models inferred that Madagascar was colonized first; body size and dispersal syndrome models inferred that the Seychelles were colonized first; Supporting information).

The biogeographic history of the genus *Chamaeleo* was well supported by all models, except for the timing of the colonization of Socotra and North Africa and Arabia. The coastal distribution and dispersal syndrome models agreed on an ancestor occupying Central Africa, North Africa and Arabia, and Socotra ca 20 Mya. In other models this same ancestor was restricted to Central Africa and colonized Socotra about 18 Mya (Supporting information).

Several range expansions and retractions took place in *Bradypodion* but the order and timing of events is uncertain (Supporting information). The MRCA of *Bradypodion* either occupied Central Africa and Southeast Africa (body size, life history and trait-independent models) or Central Africa, Southeast and Southwest Africa (coastal distribution and dispersal syndrome models). All trait-dependent models then agreed on the MRCA of *B. pumilum* and *B. damaranum* occupying Southeast and Southwest Africa. The MRCA of *Bradypodion* excluding *B. pumilum* and *B. damaranum* (Supporting information) was estimated to have occupied the same model-specific range as the MRCA of the whole genus; only the coastal distribution model inferred a range retraction. Furthermore, in the body size and life history models the ancestor of *B. thamnobates* occupied Southeast Africa and dispersal into Central Africa only took place with *B. thamnobates*, which occurs today on the edge of both regions. In the other models, the ancestor of *B. thamnobates* was already present in both regions. Similarly, it is unclear whether *B. gutturale* expanded its range from Southeast to Southwest Africa or if the expansion happened before.

In *Trioceros*, range expansions to North Africa took place repeatedly, but the number of range expansion events differed between trait-dependent models (coastal distribution, body size: 6; life history: 4; dispersal syndrome: 5; Fig. 5, Supporting information).

## Discussion

We tested on an evolutionary timescale whether three traits (coastal distribution, body size and life history) and their combination in chameleons were related to biogeographic dispersal success. Lineages of coastal chameleons and large chameleons were more likely to disperse than non-coastal and small lineages in the past. Instead of a fast life history strategy, an extreme life history strategy, i.e. either particularly early sexual maturity and short gestation time (fast) or late maturity and a long gestation time (slow) relative to body size, was linked to dispersal success. Our analyses revealed uncertainties in ancestral range estimations: there were differences in timing of dispersal events between trait-independent and trait-dependent models, as well as within trait-dependent models depending on which trait was included. However, trait-dependent models were better supported by AICc comparison than trait-independent models in all cases, demonstrating that including traits in analyses of historical biogeography is essential for more accurate estimations of species' pasts.

### Trait-dependent biogeographic models

#### Coastal distribution and body size

Coastal distributions are positively related to biogeographic movement in chameleons, as has been shown for *Cryptoblepharus* lizards and crocodiles (Blom et al. 2019, Nicolai and Matzke 2019). While it seems logical that coastal distributions should promote trans-oceanic dispersal, most dispersal events that we identified were continental. Possibly chameleons dispersed along the coast, either by their own movement on land, or on vegetation adrift on the sea. Alternatively, coastal lineages may have dispersed through the interior of the continent. Coastal lineages tend to have larger ranges and there may be other factors that facilitate their overland and overwater dispersal, e.g. an underlying trait correlated with coastal distribution, possibly related to micro-habitat (e.g. arboreal species having a higher chance of being transported on vegetation compared to terrestrial species) or other morphological traits (da Silva and Tolley 2013, 2017).

Furthermore, body size (and associated life history trait covariation) also strongly influenced natural biogeographic dispersal processes, as in crocodylians (Nicolai and Matzke 2019). Large size possibly favours dispersal success because the lower metabolic rate relative to body size of large species is related to lower relative energy requirements (Andrews and Pough 1985) which may improve resistance to stress, such as long periods of food and water shortage, and increase survival probability during the dispersal process. Moreover, body size in reptiles is highly correlated to clutch size (Meiri et al. 2020) and species with big clutches may have an advantage at the establishment stage. To distinguish between the correlated effects of body size and clutch size, further research should explore the role of body size in biogeographic dispersal in taxonomic groups where body size does not correlate positively with clutch size (e.g. reptile clades with relatively invariant clutch sizes, such as geckos, or in mammals).

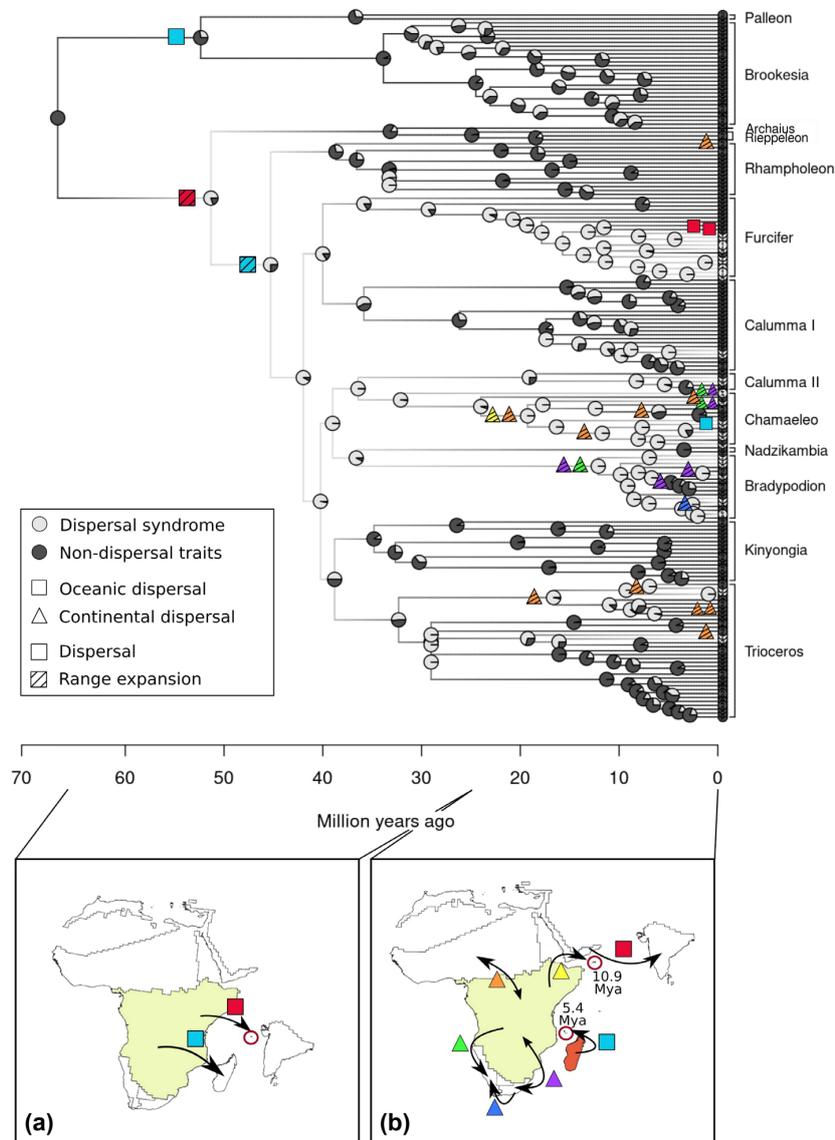


Figure 5. Biogeographical movements and evolution of the dispersal syndrome of chameleons mapped onto their phylogeny (using trait-dependent biogeographical model). The pie charts represent the probabilities of nodes being in a certain trait state: white indicates species holding all three hypothesized biogeographic dispersal traits (coastal distribution, large body and extreme life history strategy), and black indicates a form with two, one or no dispersal traits. Estimated dispersal (i.e. lineage completely left the previously occupied region; plain symbols) and range expansion events (i.e. the new regions were added to the lineage's range; striped symbols) are indicated on the tree by coloured symbols next to the pie charts. Different symbols correspond to oceanic (square) and continental (triangle) dispersal events and the colours indicate the direction of the dispersal events. The maps below the tree show where these dispersal and range expansion events took place, and where chameleons presumably occurred at the beginning of the period (coloured regions). Note: although we included five time slices in our analysis, only two maps are presented here for simplification. (a) shows the geography between 65 and 23 Mya and (b) between 23 Mya and the present. The times of emergence of the Comoros Islands and of Socotra's split-off from Africa are indicated in (b).

### Life history strategy

Model selection did not confirm that chameleons with a fast life history were better dispersers than slow chameleons in the past. Instead, lineages with an extreme life history strategy had a higher dispersal probability than lineages with an intermediate life history strategy.

Our results for historical dispersal may indeed reconcile two seemingly conflicting theories on how life history strategy influences range expansion and dispersal. On one hand, species with a fast life history strategy may be successful establishers because they have the capacity for fast population growth and can quickly overcome the period in which stochastic extinction is particularly probable (Caswell et al. 2003, Reynolds 2003, Blackburn et al. 2015). Also, fast population growth facilitates local adaptation in niche requirements if newly colonized areas are ecologically different from areas of origin (Lavergne et al. 2010). In present-day invasions, for instance, a fast life history strategy was found to be more successful than a slow one in non-avian reptiles (Fujisaki et al. 2010, van Wilgen and Richardson 2012, Allen et al. 2017). On the other hand, species with a slow life history strategy can wait for favourable conditions to reproduce (Cáceres 1997) and they are less vulnerable to environmental stochasticity since they exhibit less demographic variability (Sæther and Bakke 2000, Jeppsson and Forslund 2012). This is apparent in bird invasions today where characteristics of a slow life history strategy, such as long lifespan and big brain size, are linked to success (Sol et al. 2012). Our results confirm that one strategy is not necessarily better than the other and that there might be more than one road to dispersal success.

Another reason for an extreme life history strategy being related to dispersal success in our study, rather than a fast one, may be that we did not exclusively study oceanic dispersal. Sol et al. (2012) proposed that a founder population needs to be very small for a strategy of fast population growth to be advantageous for colonization success. A small founder population is most likely the origin of island populations, but it may not always be the case for continental dispersal (e.g. climatic barriers can be temporarily alleviated over evolutionary time scales). Indeed, all recent purely oceanic dispersals in chameleons (*Furcifer polleni* and *F. cephalolepis* to the Comoros Islands and *Chamaeleo zeylanicus* to India) were associated with an extremely fast life history strategy (Fig. 3b). However, since there were few clear oceanic dispersal events in the history of chameleons, it is impossible to draw strong conclusions from this fact. More research is necessary to distinguish between the effect of life history strategy in continental versus oceanic dispersal; maybe a different strategy is advantageous for different modes of dispersal.

### Dispersal syndrome

While we suggest the three traits tested are linked to specific stages of the dispersal process, it is possible that they are also linked to other stages of the dispersal process, either directly or indirectly through correlations with other traits (Uyeda et al. 2018). In addition, traits may have multiplicative effects on

dispersal probability. This underlines the importance of also testing dispersal syndromes in relation to biogeographic dispersal success (Van Bocxlaer et al. 2010, Nicolai and Matzke 2019). We found the combination of coastal distribution, large body size and an extreme history strategy had ca 98% higher dispersal rate than lineages with a non-dispersal syndrome. Moreover, more than one-third of all identified dispersal and range expansion events took place in the genus *Chamaeleo*, a relatively small genus (14/181 species) in which most extant species and their ancestors were identified to hold or to have held all three hypothesized dispersal traits. Since coastal distributions were strongly related to dispersal success (the dispersal multiplier for non-coastal species was 0 which is the maximum detectable effect), we were not able to formally detect an additive or multiplicative effect of all hypothesized dispersal traits.

The number of species that held the dispersal syndrome was significantly higher than expected by chance, which may indicate that lineages with a dispersal syndrome have higher speciation rates. In other clades (birds: *Zosterops*, Moyle et al. 2009; amphibians: Bufonidae, Van Bocxlaer et al. 2010), patterns of high dispersal ability combined with high speciation rates were found as well. Rare dispersal to distant locations may open opportunities for divergence by creating isolated populations (Gillespie et al. 2012). However, the fact that more species than expected held the dispersal syndrome may be a result of coevolving traits that produce convergent trait syndromes. Several traits can, for example, be jointly selected for by a given environment (Ronce and Clobert 2012, Stevens et al. 2014). More detailed studies are necessary to elucidate the link between dispersal and speciation in chameleons, and to determine whether the dispersal syndrome may be a product of coevolution.

### New insights into the biogeographic history of chameleons

Trait-dependent models accrued 100% of the AICc weight for all four traits that we tested. This underlines the importance of including species' ecology in models of historical biogeography and emphasizes that different biogeographic processes may be relevant to different lineages, which means that they should not be treated interchangeably (Sukumaran and Knowles 2018).

The inclusion of traits allows us to pinpoint which parts of a clade's biogeographic history are subject to uncertainty. While in some nodes there were uncertainties throughout all models, two nodes were estimated identically in all trait-dependent models but differently in the trait-independent model (MRCA of *Bradypodion pumilum* and *B. damaranum*, and the ancestor of part of *Trioceros*; Supporting information). In both cases, the trait-independent model inferred a more restricted ancestral range, which led to more estimated range expansion events later on. In *Bradypodion*, there is an indication that the MRCA of *B. pumilum* and *B. damaranum* may have occupied a more widespread range including Southwest and Southeast Africa (Tolley et al. 2006), supporting results

from trait-dependent models in our study. In *Trioceros*, all trait-dependent models inferred an ancestor already occupying parts of Central Africa and the region comprising North Africa and Arabia ca 15 Mya, whereas the trait-independent model inferred two separate dispersal events later on. For clades with an uncertain biogeographic history, an analysis at a smaller spatial scale is preferable to allow a tailored definition of biogeographic regions and more detailed estimations (see Tolley et al. 2006 for *Bradypodion* and Ceccarelli et al. 2014 for *Trioceros*).

## Conclusions

Our study emphasizes the importance of including species' ecological and biological characteristics in historical biogeography. Coastal distribution, body size and life history strategy are likely to have indeed played a decisive role in shaping the biogeographic history of chameleons. We found evidence that lineages with extreme life histories were more successful dispersers than lineages with an intermediate life history. Our results complement findings from invasion ecology but indicate that dispersal on an evolutionary timescale and in the Anthropocene may not be directly comparable. We show how life history strategy has influenced the biogeographic history of chameleons, which invites new key questions: Which effect has life history strategy had in the biogeographic history of other clades? How has it influenced and will it influence range shifts, invasions and global biodiversity patterns?

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## Author contributions

**Sarah-Sophie Weil:** Conceptualization (equal); Data curation (equal); Formal analysis (lead); Writing – original draft (lead); Writing – review and editing (equal). **Laure Gallien:** Conceptualization (equal); Funding acquisition (equal); Supervision (equal); Writing – review and editing (equal). **Sébastien Lavergne:** Supervision (equal); Writing – review and editing (equal). **Luca Börger:** Supervision (equal); Writing – review and editing (equal). **Gabriel W. Hassler:** Formal analysis (supporting); Methodology (equal); Writing – original draft (supporting); Writing – review and editing (equal). **Michaël P. J. Nicolai:** Data curation (equal);

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Data and R code are available from the Dryad Digital Repository: <<https://doi.org/10.5061/dryad.hqbzkh1jx>> (Weil et al. 2022).

## Supporting information

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

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## **Chapter 2**

# **Uncovering how traits have shaped the historical biogeography of tetrapods**

# Uncovering how traits have shaped the historical biogeography of tetrapods

Sarah-Sophie Weil<sup>1,2</sup>, Laure Gallien<sup>1\*</sup>, Michaël P. J. Nicolai<sup>3</sup>, Sébastien Lavergne<sup>1</sup>, Luca Börger<sup>2</sup>, William L. Allen<sup>2\*</sup>

**Dispersal across biogeographic barriers is a key process determining global patterns of biodiversity as it allows lineages to colonise and diversify in new realms<sup>1,2</sup>. However, biogeographic dispersal is rare and difficult to observe, so we know little about its determinants<sup>3</sup>. Here, we demonstrate that past biogeographic dispersal events often depended on species' traits by analysing 7009 tetrapod species in 56 clades. Incorporating body size or life history into biogeographic models improves model performance in 91% of clades and leads to an increase in dispersal rates of 28-32% for lineages with disperser traits. Differences between clades in the effect magnitude of life history on dispersal rates are linked to the strength and type of biogeographic barriers (continental/oceanic), and intra-clade trait variability. In many cases, large body sizes and fast life histories facilitate dispersal success, as expected by theory<sup>4,5,6,7</sup>. However, small and/or species with slow life histories, or those with average traits, have an advantage in a significant minority of clades, with body size-dispersal relationships depending on a clade's average body size and life history strategy. These results provide important new insight into how traits have shaped the historical biogeography of tetrapod lineages and may impact present-day and future biogeographic dispersal.**

The rare occasions in species' evolutionary histories when populations successfully disperse across major geographic barriers such as oceans, mountain ranges or deserts, can have major consequences for the distribution of life on Earth. For example, long-distance dispersal from Africa to South America led to the evolution of over 90 species of New World monkeys<sup>8,9</sup>, and a few chameleons rafting on vegetation from Africa to Madagascar is why today half of all living chameleon species are found in Madagascar<sup>10,11</sup>. However, we still know little about the determinants of these biogeographic dispersal events.

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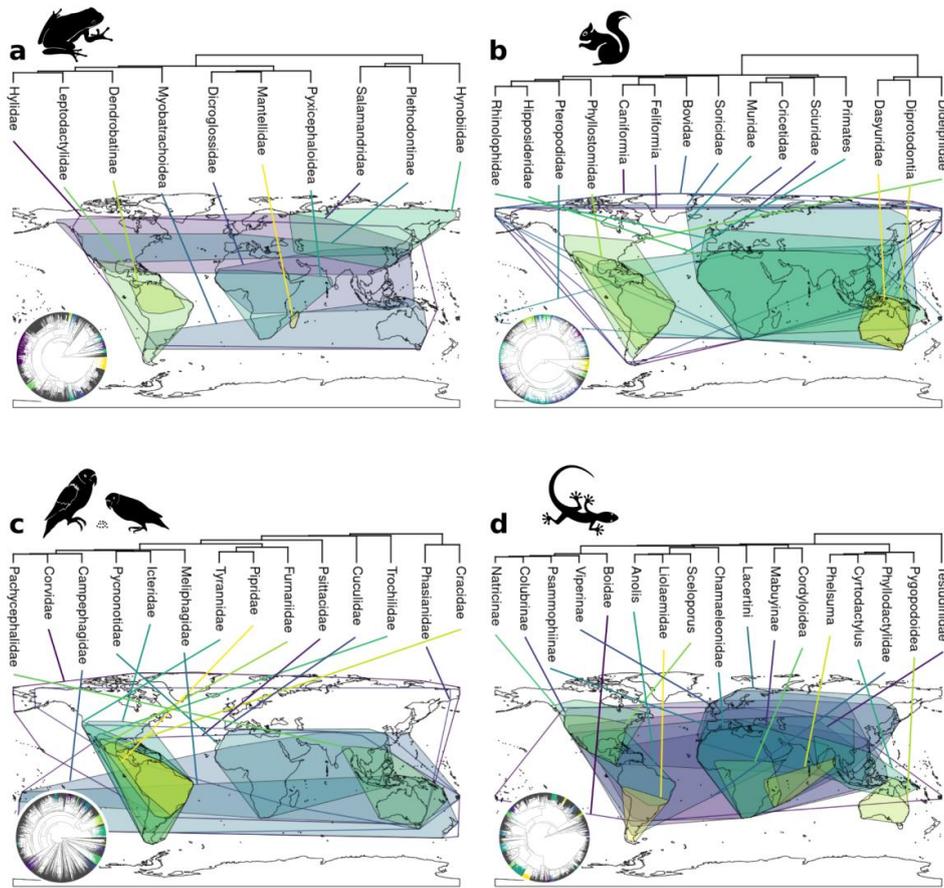
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While chance has a large role to play, species' traits could also influence outcomes of biogeographic dispersal events<sup>12</sup>. Species' traits are known to mediate active, short-distance dispersal<sup>13,14</sup>, however, traits are not necessarily related to biogeographic dispersal in the same manner because the mode of dispersal differs. Short-distance dispersal is primarily determined by species' active movements, whereas in biogeographic dispersal (e.g. in transoceanic dispersal) passive transportation plays a bigger role<sup>12</sup>. Several traits may be related to biogeographic dispersal success, and body size and life history are likely to be crucial: Body size determines relative energy requirements<sup>4</sup> and hence resistance to stress, such as water and food shortage. Indeed, recent findings show that large-bodied species have crossed biogeographic barriers more often than small ones in three reptile clades<sup>15,16,17</sup>. Life history strategy, defined by the trade-offs between traits related to growth, reproduction and survival<sup>18</sup>, can influence the likelihood of populations establishing in new locations. Species with a fast life history strategy reproduce quickly which makes founder populations more resistant to stochastic extinction<sup>5,6,7</sup>. Species with a slow life history strategy, on the other hand, exhibit less demographic variability which makes their populations more resistant to environmental stochasticity<sup>19,20,21</sup>. Both effects are documented in chameleons, for which successful biogeographic dispersal is associated with both extremely fast and extremely slow life history strategies<sup>17</sup>. However, we do not know whether these initial findings in three small reptile groups represent a general trait-dispersal bias in tetrapods, or whether multiple relationships exist across highly different clades.

Here, we use trait-dependent models of historical biogeography at a global scale to fill this gap. We aim to understand whether species' traits (body size and life history strategy) facilitate or hinder dispersal across major biogeographic barriers, and how trait-dispersal relationships vary across tetrapods. We then test how observed patterns relate to potential ecological drivers to examine mechanisms underlying any differences between clades. Understanding whether and how traits determine biogeographic dispersal outcomes, and what explains variation in trait-dispersal relationships between clades, gives insight into the history of life on Earth<sup>22</sup> and how species might respond to future global changes<sup>14</sup>.



**Figure 1: Geographic and phylogenetic extent of the analysis for a) amphibians (10 clades), b) mammals (15 clades), c) birds (14 clades) and d) reptiles (17 clades).** Clades included in the analysis are coloured on the class-level phylogenies in the bottom left of each panel according to the convex hulls of their ranges on the map. Icons: [Frog](#) by GREY Perspective, [Squirrel](#) by R Diepenheim, [Bird](#) by yudi yanto, [Gecko](#) by Kevin from Noun Project, [CC BY 3.0](#).

### Traits in biogeographic models

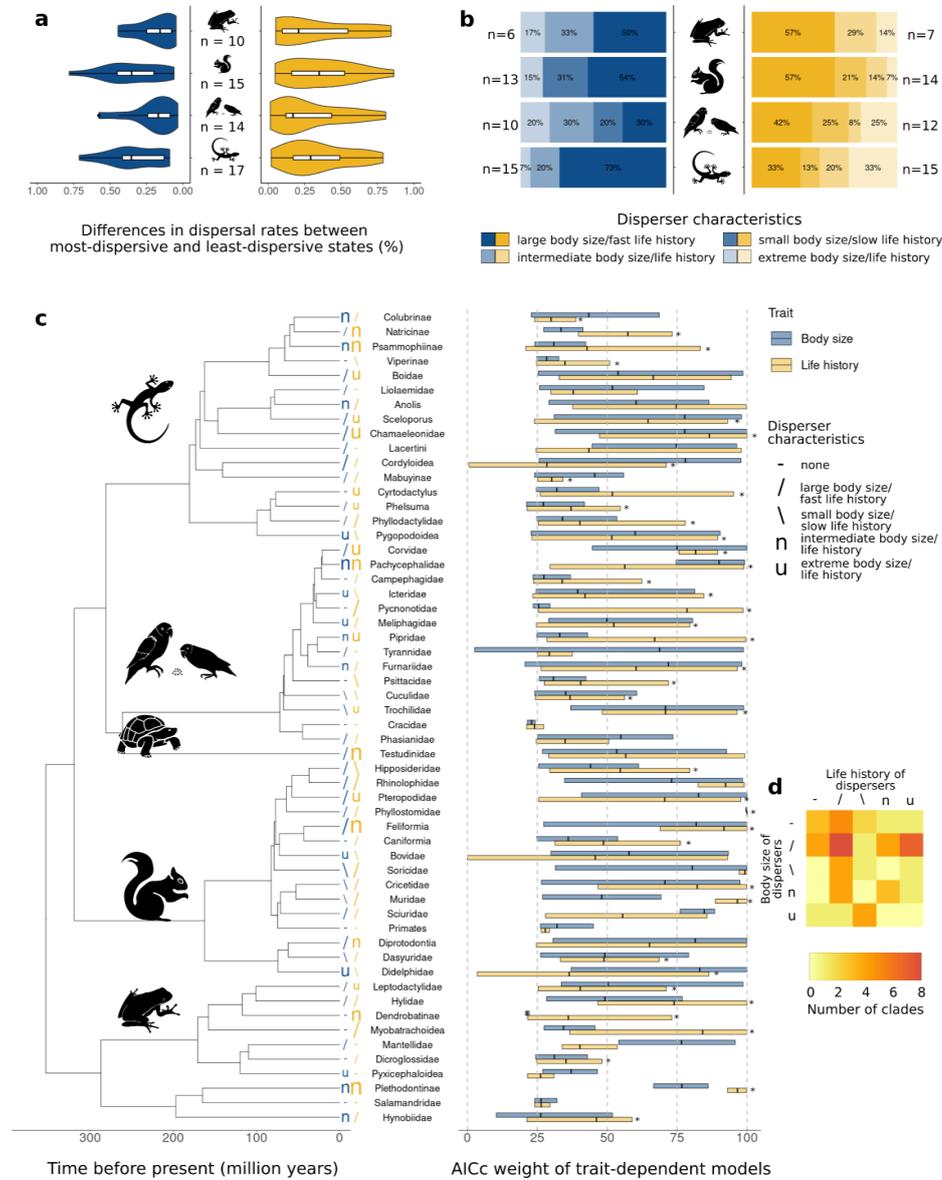
First, we investigate the importance of traits in the biogeographic histories of 56 tetrapod clades for which sufficient data are available to address our research questions. We compiled phylogenetic data, extant species' distributions, and trait data for 7009 species (on average 125 species per clade, minimum: 32 species, maximum: 491 species) spread across 10 amphibian clades, 15 mammal clades, 17 reptile clades, and 14 bird clades (Fig. 1, Extended Data Tab. 1, methods). To determine the two traits of interest (body size and life history strategy), we used phylogenetic factor analysis<sup>23,24</sup> to position species along two main axes of trait variation per clade. The first axis represented body size and related life history trait covariation, and the second axis body size independent life history covariation. We then determined the relationship between species' positions on these two trait axes and their past dispersal rates, developing further the methodology of Weil et al.<sup>17</sup>. Briefly, we defined informative biogeographic regions for each clade using a data-driven approach (after Holt et al.<sup>25</sup> and Kreft & Jetz<sup>26</sup>) and used these biogeographic regions to estimate ancestral range changes along the phylogeny. We employed both biogeographic models where dispersal rates were independent of species' traits (trait-independent models), and models where dispersal rates depended on traits (trait-dependent models)<sup>27</sup>. We included distance-independent and distance-dependent extensions of each model, in the latter of which dispersal probabilities decrease with increasing distance between biogeographic regions (see Weil et al.<sup>17</sup> for details). To assess whether the chosen traits have played a role in clades' biogeographic histories we compared the performance of trait-dependent and trait-independent models using their relative AIC weights. We studied trait-dispersal relationships across the trait spectrum in binary trait-dependent models by analysing four binary splits of the continuous traits (see Methods for details).

Our results show that the inclusion of traits generally improves models of historical biogeography, providing the strongest evidence at this scale that biological differences between lineages impact biogeographic movements<sup>22</sup>. In 91% of clades the best trait-dependent model accrued more than 50% of the AICc weight (body size: 40 clades = 71%, life history: 48 clades = 86%). Even when accounting for multiple binarization thresholds by averaging trait-dependent AIC weights per clade, trait-dependent models were better supported than trait-independent models in 66% of clades (Fig. 2c).

To understand the consequences of including traits in estimations of biogeographic histories of clades, we evaluated three metrics: (i) ancestral range resolution (measured as the proportion of the most likely ancestral range at each node), (ii) the average number of dispersal events per clade, and (iii) the proportion of node ranges that were estimated differently between trait-dependent and trait-independent models. To benchmark this comparison, we included distance-dependent and distance-independent model extensions in this assessment (see Methods for details). There were no significant differences in the resolution of ancestral range estimations between trait-dependent, trait-independent, distance-dependent and distance-independent models (using mixed effect models,  $\chi^2(3) = 7.27$ , p-value = 0.064). The number of estimated dispersal events per clade did not differ significantly between trait-dependent and trait-independent models (contrasts among estimated marginal means,  $t(389) = 1.53$ , p-value = 0.42), but including distance between regions increased the number of dispersal events by ca.

2% ( $t(389) = 7.38$ ,  $p\text{-value} < 0.001$ ). The most likely ancestral ranges differed in 6% of phylogeny nodes on average, both between trait-dependent and trait-independent estimations, and between distance-dependent and distance-independent models.

In summary, including traits in biogeographic models changes neither the resolution of ancestral range estimations, nor does it change the number of dispersal events estimated on the phylogeny. However, in a small but significant number of nodes, the identity of ancestral ranges differs between trait-dependent and trait-independent estimations. These differences might be due to a change in the dispersal path and/or the timing of dispersal events. If the timing of dispersal events changes due to the inclusion of traits, then this may impact estimations of speciation modes (e.g. dispersal of the ancestor followed by sympatric speciation, or two separate dispersal events followed by founder-event speciation), with implications for our understanding of different speciation processes.



**Figure 2: The role of traits in biogeographic dispersal.** a) Distributions of maximal differences of dispersal rates between most-dispersive and least-dispersive states per tetrapod class, in blue for body size-dispersal relationships, in yellow for life history-dispersal relationships. b) Proportions of different trait-dispersal relationships per class, including only clades where maximal differences in dispersal rates between trait states were greater than 10%. c) Relative AICc weight of trait-dependent models compared to the entire set of candidate models, and across the entire range of binary trait thresholds (center line, median; box limits, minimum and maximum). The identified biological characteristics of better disperser lineages are indicated by symbols at the tip of the phylogeny, the size of which indicates the maximal

difference in dispersal rates between trait states. Clades with life history trade-offs consistent with a fast-slow life history continuum are indicated by “\*” at the end of the life history bars. d) Relationship between disperser characteristics in body size and life history analyses. The colours indicate the number of clades in which a given combination of body size-dispersal and life history-dispersal relationships were found. Icons: credit as in Fig. 1, [Galapagos turtle](#) by parkjisun from Noun Project, [CC BY 3.0](#).

### The effect of traits on dispersal rates

Incorporating body size and life history traits resulted in better biogeographic models in 91% of tetrapod clades studied. To understand the role of these traits in dispersal, we next investigated the magnitude of their effects within each clade, i.e. the difference in dispersal rates between most-dispersive and least-dispersive lineages. To do so, we combined the dispersal parameters of all models for each clade via AIC-weighted averages.

On average across all 56 clades, including body size led to differences in dispersal rates of 28% (standard deviation: 19%) between most-dispersive and least-dispersive lineages, and including life history led to differences of 32% (standard deviation: 24%) in the 47/56 clades where life history was consistent with a fast-slow continuum (Extended Data Fig. 1). The magnitude of body size effects within clades differed significantly between classes ( $F(3,52) = 3.03$ ,  $p$ -value = 0.04, Fig. 2a). The largest effects were detected in mammals and reptiles, and the smallest ones in amphibians and birds (contrast among estimated marginal means:  $t(52) = 3.00$ ,  $p$ -value = 0.004). Stevens et al.<sup>14</sup> found high phylogenetic signal in dispersal distances of aerial dispersers which might explain the small body size effects in bird clades: high phylogenetic signal indicates little intra-clade variability which might lead to small trait effects in our intra-clade analyses. On the other hand, there were no significant differences between classes in the magnitude of life history effects on dispersal ( $F(3,52) = 0.31$ ,  $p$ -value = 0.82), although the largest effects were again found in mammals, and the smallest effects in birds (Fig. 2a).

To better understand the variation in magnitude of trait effects between clades we investigated the influence of the following five variables and their associated hypotheses (Tab. 1): (i) the number of dispersal events per lineage as a proxy of barrier strength, (ii) the proportion of estimated dispersal events that are oceanic, (iii) the variability of traits within clades, (iv) the number of species within a clade, and (v) trait data coverage. We used a stepwise selection process on multivariate regressions to identify the variables that could best explain the maximal difference in dispersal rates between trait states across clades.

For body size-dispersal relationships, none of the tested variables could explain significant variation in dispersal rate differences between trait states across clades (Tab. 1, Extended Data Tab. 2). However, for life history-dispersal relationships, we found that the difference in dispersal rates between trait states increases in clades with (i) less frequent dispersal events, (ii) smaller and greater proportions of oceanic dispersal events (i.e. clades with mostly oceanic dispersal or mostly continental dispersal; Extended Data Fig. 2), and (iii) lower life history variability (Fig. 3a). These results suggest that life history traits played a larger role in the past

dispersal of clades that had to cross more stringent barriers, i.e. clades where fewer dispersal events were estimated on the phylogeny, and that weak barriers may dilute the signal in trait-dispersal relationships. Further, our results suggest that oceanic and continental barriers filter species differently, as differences in dispersal rates between trait states were more marked in clades with mostly oceanic dispersal or mostly continental dispersal, than for clades with mixed oceanic and continental dispersal events. Different life history traits may therefore be related to successful dispersal in both processes and mixing both continental and oceanic barriers can obscure life history-dispersal relationships. Biogeographic dispersal may hence be context-dependent (depending on the type of barrier, and possibly their characteristics, i.e. environmental harshness, degree of landscape fragmentation as has been shown for active, short-distance dispersal previously<sup>28,29</sup>). In future analyses, different types of barriers should therefore be considered separately (which is not possible in the present study due to computational constraints, Supplementary Information). That both the number of dispersal events in a clade's biogeographic history and the proportion of oceanic dispersal events were selected in the best model also underlines the importance of choosing meaningful barriers for biogeographic models, which are specific to each clade, using for example data-driven bioregionalisation approaches<sup>26,30</sup>. Furthermore, we found a negative effect of trait variability on the differences in maximal dispersal rates between clades, which is surprising and may indicate that other traits additionally influence dispersal success in clades with high life history variability (e.g. habitat, diet, or climatic tolerance<sup>14,31</sup>). Both variables accounting for potential methodological biases were not significant, suggesting that they had a negligible impact on the outcome of our analyses. Our results remained qualitatively similar when we restricted the analysis to those clades that showed the strongest fast-slow life history continuum (Extended Data Tab. 2).

In summary, we found strong variation in the magnitude of trait effects on dispersal rates between clades. The variation in the magnitude of body size effects could not be explained by any of the variables we tested. The variation in the magnitude of life history effects, on the other hand, was related to intra-clade trait variability, as well as the strength and type of biogeographic barriers, indicating that different barriers may filter species differently according to their life history in the dispersal process.

### **The traits of successful dispersers**

To identify the traits of successful dispersers, we further determined the shapes of the relationships between traits (body size and life history) and dispersal rates in all clades where the difference in estimated dispersal rates between trait states was greater than 10% (79% of all body size-dispersal relationships, and 83% of the 47 life history-dispersal relationships in which fast-slow consistent trade-offs structured life history). We distinguished between the following relationships: (i) positive (large/fast-lived species were better dispersers than small/slow-lived species), (ii) negative (small/slow-lived species were the better dispersers), (iii) u-shaped (species with extreme traits were better dispersers than intermediate ones), and (iv) bell-shaped (species with intermediate traits were the better dispersers).

Within clades, large-bodied species were generally better dispersers than small species (55% of all significant body size-dispersal relationships were positive), especially in reptile (73%) and mammal (54%) clades (Fig. 2b). This result is in accordance with previous findings of a large body size dispersal advantage in dispersal in general<sup>32</sup> and in historic biogeographic dispersal in particular<sup>15,16,17</sup>. Nevertheless, intermediate-sized species were better dispersers in 18% of clades, and small body size or extreme body sizes provided a dispersal advantage in 14% of clades. There were significant differences in the distributions of body size-dispersal relationships between ectotherms and mammals and birds (Fisher's exact test,  $p$ -value = 0.02), notably there were no amphibian or reptile clades in which only small species had a dispersal advantage. Our results contrast with findings of Stevens et al.<sup>14</sup>, who found a positive body size-dispersal relationship in rodents (in our study: 1/3 rodent clades), and a u-shaped one in passerines (in our study: 3/9 passerine clades). This indicates that body size-dispersal relationships depend on the type and stage of dispersal considered (Stevens et al.<sup>14</sup> studied active, natal dispersal at the movement stage, we studied successful biogeographic dispersal).

Life history-dispersal relationships were more varied in their shape than body size-dispersal relationships (Fig. 3b). Within clades, fast species were generally better dispersers than slow species (44% of the 39 clades with fast-slow consistent life history and significant dispersal relationships). However, species with an extreme life history strategy (i.e. either fast or slow) were better dispersers than those with an intermediate strategy in 23% of clades, slow species were better dispersers than fast species in 18% of clades, and intermediate species were better dispersers in 15% of clades. There were no differences in life history-dispersal shapes among classes (Fisher's exact test,  $p$ -value = 0.84). These results remained qualitatively similar when we included only clades with differences in dispersal rates between trait states greater than 20%, or when we restricted the analysis to those clades that showed the clearest fast-slow life history continuum (Extended Data Fig. 1, Extended Data Tab. 3). When considering phylogenetic uncertainty, the identification of successful disperser's characteristics was robust for some clades, but not for all (e.g. Natricinae, Extended Data Fig. 4, Extended Data Tab. 4, Methods, Supplementary Information). Future studies should take phylogenetic uncertainty explicitly into account, but such an endeavour is clearly out of the scope of present study which is already computationally demanding.

Overall, when analysing the trait-dispersal relationships of the two traits together, large bodied-species were generally more likely to disperse, as well as species with a fast life-history strategy, but a dispersal advantage of the two strategies did not necessarily occur simultaneously in the same clades (Fig. 2d). For instance, in some clades, large species with an extreme life history strategy were better dispersers (e.g. Chamaeleonidae and Corvidae); and in other clades species with fast life history strategies but small body sizes were better dispersers (e.g. Cricetidae and Dasyuridae). Multiple traits may therefore interact in their influence on biogeographic dispersal<sup>33</sup>, and that influence may be mediated by the environment and/or biotic interactions<sup>28,29</sup>.

Finally, we investigated the potential mechanisms that can explain why the characteristics of the best dispersers vary between clades. We specifically explored the influence of the following five ecological and methodological variables and their associated hypotheses: (i) a clade's

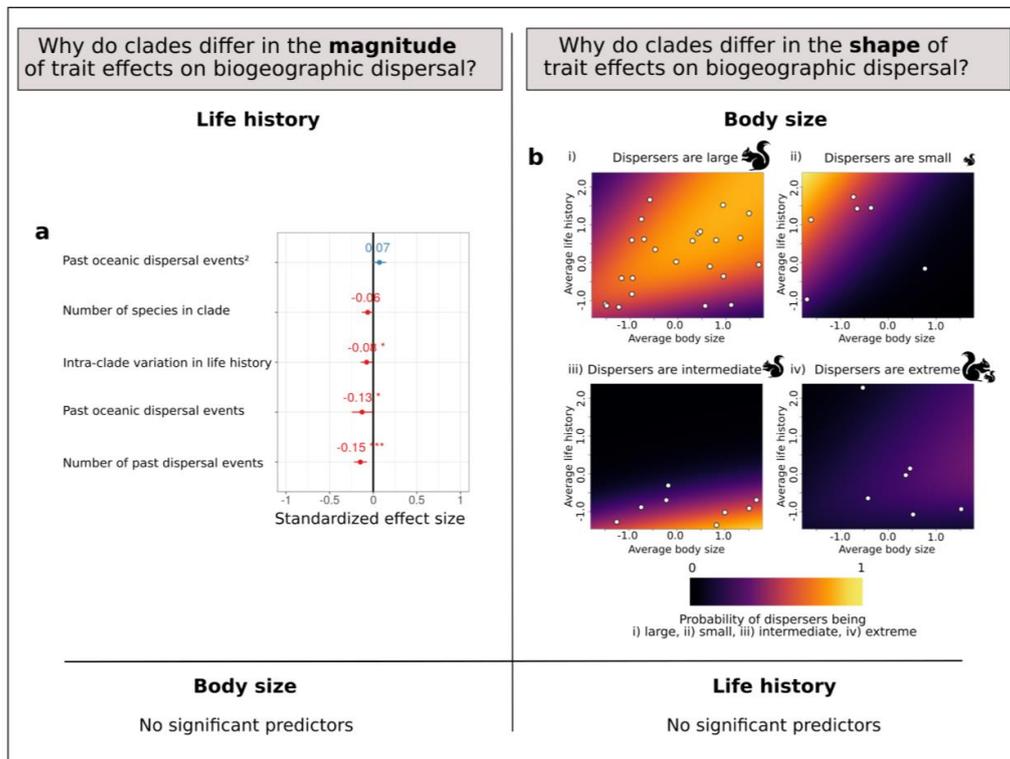
average trait value (absolute trait values are more important than relative trait values within clades, e.g. advantage of large size may only be apparent in large-bodied clades), (ii) the variability of traits within clades (more complex relationships, e.g. u- and bell-shaped ones, may only appear in clades with sufficient trait variability), (iii) the proportion of observed dispersal events that are oceanic (different traits are linked to different biogeographic barriers), (iv) the number of species within a clade (more complex relationships, e.g. u- and bell-shaped ones, may only appear in species-rich clades), and (v) trait data coverage (little available trait data makes it difficult to correctly identify species' life histories, and may obscure trait-dispersal relationships). We used a stepwise selection process on multivariate multinomial regressions to identify the variables that could best explain the different categories of trait-dispersal relationships (positive, negative, bell- or u-shaped).

Differences in the shape of the body size-dispersal relationships between clades were partly explained by both the average body size and life history of the clades (predictive accuracy = ca. 64%, McFadden  $R^2 = 0.19$ , Fig. 3b, Extended Data Tab. 5). This means that a clade's life history strategy may explain which body sizes are advantageous in dispersal, and that both traits interact to influence dispersal outcomes. A first noteworthy result is that, while large body size was a dispersal advantage in most clades, small size generally was a dispersal advantage in clades with small average body sizes and fast life histories. There are indeed instances where very small animals have been reported to disperse over long distances (e.g. land snails<sup>34</sup>, invertebrates<sup>35</sup>), but this has not been shown for tetrapods before. Small body size could be advantageous in oceanic dispersal because it might increase the probability of several individuals dispersing at once, increasing propagule pressure which is a strong predictor of colonization success in present-day biological invasions<sup>36</sup>. In clades with relatively fast life histories, small body size might not only be an advantage but rather a constraint: fast-lived species have short lifespans, and if not enough individuals arrive at a far-away location at the same time to reproduce, these individuals might die before a new chance event leads to more individuals arriving. Interestingly, small body size was mainly related to successful dispersal in bird and mammal clades. Only two clades of herpetofauna (=10% of significant relationships) showed a u-shaped relationship between body size and dispersal success, and none showed a negative relationship. One possible explanation for these differences between tetrapod classes is that small body sizes lead to higher cooling rates in ectotherms and less thermal stability<sup>37</sup>. This is disadvantageous both for active movement and when passing through cold environments, which one might expect during long distance dispersal events. Small ectotherms may hence only have a dispersal advantage in specific circumstances, for example when passing through hot environments where a high cooling rate is desirable.

A second important result is that intermediate sizes were of advantage in clades with overall large body sizes and slow life histories. This indicates that large absolute body sizes do not confer an advantage in biogeographic dispersal if a clade's average life history is very slow. This might be related to lower propagule pressure since chances might be low of several large individuals dispersing passively at once. In addition, species with slow life histories have generally slow population growth rates which may lead potential founder populations to fail due to stochastic extinction<sup>5</sup>. When exploring variability in life history-dispersal relationships,

none of the tested variables could significantly explain differences between clades (Extended Data Tab. 5).

In summary, there is significant variation in trait-dispersal relationships between clades, and in body size-dispersal relationships also between tetrapod classes. Small species only had a dispersal advantage in two clades of ectotherms, but in a much larger proportion of mammal and bird clades. Intermediate body size only conferred a dispersal advantage in some mammal clades. We tested several variables that might explain the variation in trait-dispersal relationships, but none of them could explain the variation in life history-dispersal relationships. The shapes of body size-dispersal relationships, on the other hand, were related to the average body size and life history of the entire clade, indicating that both traits may interact in their influence on biogeographic dispersal.



**Figure 3: Factors explaining the differences between clades in magnitude and shapes of trait effects.** a) Coefficients of a model regressing the differences in estimated dispersal rates between life history traits across clades against a number of explanatory variables (explained in the text and Tab. 1). b) Probabilities of different dispersal shapes depending on a clade's body size and life history relative to other clades of the same class. Each point corresponds to one clade where disperser characteristics were as indicated in the title of each panel. The background represents predicted probabilities of specific characteristics being linked to successful dispersal within a clade, where lighter colours correspond to higher probabilities. No variables were significantly related to differences between clades in the magnitude of body size effects on biogeographic dispersal, and no variables were related significantly to differences between clades in shapes of life history-dispersal relationships (indicated by a “?”). Icon: credit as in Fig. 1.

### **The future of traits in biogeography**

To conclude, we show here for the first time that morphological and life-history traits are related to, and interact in their influence on, biogeographic dispersal in a large number of tetrapod clades. We find that species' traits have played a key role in shaping global biogeography and the diversity of life on Earth. Traits are part of what determines which lineages have opportunities to colonise and radiate in new biogeographic realms, and which become geographically constrained, making them paramount to understanding historical biogeography and in projecting to the future. The ability of species to overcome large barriers is critical for both climate niche tracking and species' invasions of new biogeographical regions. Both climate change and biological invasions are key challenges of our time because they are key drivers of ecosystem declines and biodiversity shifts<sup>38,39</sup>. Therefore we urgently need to better understand how species differ in their potential to disperse across biogeographic barriers. We find that traits of successful dispersers vary across clades and we took first steps to find sources of this variation. The magnitude of life history effects on dispersal rates depends on intra-clade trait variability, as well as strength and type (oceanic/continental) of biogeographic barriers. The shape of body size-dispersal relationships, on the other hand, depends on a clade's average body size and life history. Our analysis offers exciting perspectives and ideas for future work relating to species' dispersal and colonization. For instance, species' past biogeographic dispersal capacities have been linked to present-day invasion success in plants<sup>40,41</sup>, and species' past dispersal capacities might be indicative of species' capacities to track suitable habitat as climate changes. The new knowledge presented here on how traits influence dispersal outcomes could be used to predict and manage biological invasions, improve species distribution modelling predictions, and in conservation planning for a rapidly changing world where species' survival will primarily depend on biogeographic dispersal<sup>42</sup>.

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**Table 1: Ecological and methodological variables tested to understand the magnitude of trait effects on historical dispersal rates across clades.**

	Explanatory variables	Hypotheses relating variables to the magnitude of trait effects in historical dispersal rates	Influence on the magnitude of body size effects	Influence on the magnitude of life history effects
Ecological variables	Variability of body size within clade	Traits with low variability rarely generate large differences in dispersal potential between species <sup>43,44</sup>		
	Variability of life history within clade			coef = <b>-0.08</b> (pval = <b>0.03</b> )
	Number of dispersal events per lineage	Proxy for strength of biogeographic barrier. Too few dispersal events decrease statistical power (a problem of small sample size <sup>45</sup> ), too many dispersal events indicate weak barriers <sup>46</sup> and thus reduced potential for traits to influence dispersal. This could either lead to a quadratic effect (if both hypotheses are supported), or a linear effect (if only one of them is confirmed)	coef = -0.03 (pval = 0.17)	coef = <b>-0.15</b> (pval < <b>0.001</b> )
	(Number of dispersal events per lineage) <sup>2</sup>		coef = -0.04 (pval = 0.08)	
	Proportion of past oceanic dispersal	Continental dispersal might be less selective than oceanic dispersal.		coef = <b>-0.13</b> (pval = <b>0.03</b> )
	(Proportion of past oceanic dispersal) <sup>2</sup>	Oceanic and continental barriers might filter species differently <sup>13,47</sup> , which could confound the results when both types of dispersal are combined.		coef = 0.07 (pval = 0.06)
Methodological variables	Number of species within clade	Too few species may limit statistical power (a problem of small sample size <sup>45</sup> ).		coef = -0.06 (pval = 0.06)
	Trait data coverage	Little available trait data makes it difficult to correctly identify species' life histories, and may obscure trait-dispersal relationships.		
	Full model Adjusted R <sup>2</sup>		5%	27%

The hypothesis underlying each variable is described. Effect size (standardized coefficient) and p-values are reported if selected in the final models (stepwise variable selection procedure). Trait data coverage was not tested for body size-dispersal relationships since body size was available for all species. Variability of body size within clade was not tested for the effect magnitude of life history, and inversely, variability of life history within clade was not tested for the effect magnitude of body size since we do not assume a causal link between these variables and effects. Variables with a “<sup>2</sup>” were included to test for quadratic effects.

## Methods

### Taxon selection

We only included clades for which sufficient data was available: for clades that are estimated to contain between 50-99 species (according to Bánki et al.<sup>48</sup>) we required more than 60% of data coverage (i.e. at least 60% of all species had to have phylogenetic and species distribution data, and trait data for at least one trait; for details see section Trait data); for clades estimated to contain more than 99 species we required a coverage of at least 50%.

### Phylogenies

To analyse the role of traits in biogeographic dispersal we used dated species-level phylogenies of 56 monophyletic clades of amphibians (10 clades), reptiles (17 clades), birds (14 clades) and mammals (15 clades, Extended Data Tab. 1). We extracted clades where long-distance dispersal is assumed to have occurred and clades where sufficient data was available from bigger trees (amphibians<sup>49</sup>; squamates<sup>50</sup>; mammals<sup>51</sup>). For birds we grafted subclades of the Hackett MCC tree from Jetz et al.<sup>52</sup> onto nodes of the backbone of Prum et al.<sup>53</sup>, following Cooney et al.<sup>54</sup>. We excluded non-sedentary birds using data from Dufour et al.<sup>55</sup>. Where available, we used clade-specific trees (Extended Data Tab. 1). In all cases, we excluded taxonomically imputed species from the phylogenies.

For phylogenetic factor analyses at the class level (to determine clade positions in the higher-level trait space and intra-clade trait variability, see also section “Explaining the magnitude of trait effects and the shape of trait-dispersal relationships”), we used class-level phylogenies: for amphibians the consensus tree from Pyron & Jetz<sup>49</sup>. For mammals we used a node-dated maximum clade credibility tree<sup>51</sup>. To analyse all non-avian reptiles together, we combined the squamate tree<sup>50</sup> with a crocodile phylogeny<sup>56</sup> and a turtle phylogeny<sup>57</sup>. For birds we used the combined tree as explained above.

### Species distributions

We extracted species distribution data from IUCN<sup>58</sup> for amphibians, mammals and reptiles, and from Birdlife<sup>59</sup> for birds. We only kept records of species where presence was defined as extant, possibly extinct or extinct; where origin was defined as native or reintroduced and where seasonality was defined as resident or breeding season. For species for which we did not find a direct match between phylogeny and occurrence data we used the R package *taxize* to look up synonyms in the Integrated Taxonomic Information System (ITIS; functions *get\_tsn* and *itis\_getrecord*, package *taxize* v0.9.99<sup>60,61</sup>). In addition, we used the function *synonymMatch* (package *rangeBuilder* v1.5<sup>62</sup>) which looks up synonyms in AmphibiaWeb<sup>63</sup>, the reptile database<sup>64</sup>, the BirdLife Taxonomic Checklist (v8.0<sup>65</sup>) and Wilson & Reeder<sup>66</sup>. Where we could not find distribution data for a given species in the IUCN database, we downloaded point occurrence data from the Global Biodiversity Information Facility (<https://www.gbif.org/>), using the R package *rgbif* (v.2.2.0<sup>67</sup>). We cleaned this data using the package *CoordinateCleaner*<sup>68</sup>. We then merged the IUCN shapefiles with gbif rasters per clade and reprojected the resulting shapefile into Behrmann cylindrical equal area projection (so that cells close to the poles can be compared to cells close to the equator in terms of area). Finally,

for each species we plotted the range map to visually assess it and look for outliers which we removed if there were any.

### **Trait data**

For detailed descriptions of data collation see Supplementary Information. For amphibians we combined different trait databases<sup>69-72</sup> and extracted snout-vent-length (SVL), egg size (ES), clutch size (CS), clutches per year (CY), age at sexual maturity (SM) and longevity (LG). For non-avian reptiles we combined data<sup>69,70,73-77</sup> and extracted SVL, hatchling body mass (HBM), CS, CY, SM and LG. For mammals we combined trait databases<sup>76,78-87</sup> and extracted body mass (BM), neonate body mass (NBM), litter size (LS), litters per year (LY), LG, SM, gestation time (GT) and weaning age (WA). Finally, for birds we combined data<sup>55,76,80,83,84,88-96</sup> and extracted BM, egg mass (EM), LS, LY, LG, SM, GT and WA.

### **Matching phylogenetic and trait data**

The phylogenies and combined trait databases did not follow the same taxonomies. We therefore looked up synonyms for all species for which we could not find a match in the trait databases. To do so, we again used the Integrated Taxonomic Information System (ITIS; functions `get_tsn` and `itis_getrecord`, package `taxize` v0.9.99<sup>60,61</sup>) and the package `rangeBuilder` (v1.5<sup>62</sup>; function `synonymMatch`) which looks up synonyms in `AmphibiaWeb`<sup>63</sup>, the reptile database<sup>64</sup>, the `BirdLife Taxonomic Checklist` (v8.0<sup>65</sup>) and `Wilson & Reeder`<sup>66</sup>. In addition, we looked up species by hand that still did not have a match after this process. Where several matches in the trait databases for a species with phylogenetic data was found, we averaged the trait values.

### **Bioregionalisation and paleoreconstruction**

For every clade we identified relevant biogeographic barriers by calculating phylogenetic beta-diversity<sup>97,98</sup> between raster cells (using an equal area projection, Behrmann projection with standard parallels at 30° to make raster cells between higher and lower latitudes comparable). To do this, we used the R package `betapart` v1.5.6<sup>99</sup>. We weighted the phylogenetic beta-diversity matrix with a geographical distance matrix (great-circle distances on latitude/longitude coordinates) and applied an unweighted pair group method with arithmetic mean (UPGMA) following methodology in Weil et al.<sup>17</sup>. We reconstructed movement of biogeographic regions using `Gplates`<sup>100</sup> and a global plate and rotation model<sup>101</sup>. Based on those reconstructions we implemented a time-stratified analysis if necessary to reflect plate tectonic movements and island uplifts. In addition, we implemented root constraints where strong indications for the root distribution were available (Extended Data Tab. 1). Dispersal across oceanic barriers may be less likely than dispersal across continental barriers. To take these differences in dispersal abilities into account we implemented three different manual dispersal multiplier matrices (MDMMs), adapted from Weil et al.<sup>17</sup>. We defined these MDMMs based on the assumption that continental dispersal is more likely than trans-oceanic dispersal. Using biogeographic models implemented in `BioGeoBEARS` (`DEC`, `DIVALIKE`, `BAYAREALIKE`<sup>102</sup>), we used model comparison based on AIC weight to identify the best MDMM for each clade (choosing between (i) an equal weight MDMM with no difference between continental and oceanic dispersal probabilities, (ii) a 0.5 version where continental

dispersal was set to 0.5 and oceanic dispersal to 0.125, and (iii) a 0.1 version where the probability of oceanic dispersal was set to 0.05, i.e. 10 times less likely than continental dispersal) (see Extended Data Tab. 1 for which model and MDMM was chosen for each clade).

### Phylogenetic factor analysis

To detect latent variables that structure life histories across taxonomic groups, we used a phylogenetic factor analysis (PFA<sup>23</sup>) that allows for missing data (for more details see Hassler et al.<sup>103</sup>; Weil et al.<sup>17</sup>). This PFA is implemented in the Julia package `PhylogeneticFactorAnalysis.jl` v0.1.4<sup>24</sup> which relies on a development version of BEAST<sup>104</sup> to be released with BEAST v1.10.5. Body size can influence life history traits through allometric constraints while evolving under different selection pressures. We therefore structured the PFA so that body size (as captured by SVL for amphibians and non-avian reptiles, and BM for birds and mammals) loaded only onto the first factor while all other traits loaded onto all factors, following Weil et al.<sup>17</sup>. Hence, life history trait variation associated with body size was forced onto the first factor and the second factor we extracted captured size-independent patterns of life history covariation. We analysed all clades separately, and then repeated the analyses separately for amphibians, mammals, birds and reptiles to determine position and variation of individual clades in the higher-level trait space (data coverage per clade: Extended Data Tab. 6).

### Trait-dispersal relationships

As in Weil et al.<sup>17</sup> we first determined the best base model (DEC, DIVALIKE or BAYAREALIKE) and manual dispersal multiplier matrix (MDMM null, MDMM 0.5 or MDMM 0.1) for each clade. We then ran trait-dependent and trait-and-distance-dependent models only on the best base model applying the most supported MDMM (see Extended Data Tab. 1 for which combination was chosen for which clade). In trait-dependent models, the dispersal probability of a lineage is multiplied by a parameter  $m$ , depending on which trait state the lineage is in. Due to computational constraints, most studies of trait-dependent biogeography currently only include binary traits. In practice, the multiplier of trait state 1, parameter  $m_1$ , is fixed to 1 and the multiplier of trait state 2, parameter  $m_2$ , is estimated by the model. If  $m_2$  is greater than 1, this indicates that trait state 2 is positively related to dispersal, and inversely, if  $m_2$  is smaller than 1, it indicates that trait state 1 is positively related to dispersal. Since the inclusion of binary traits can only offer limited information, we tested four different binarizations: for each trait we tested the first 50% of species against the rest (i.e. using a median split on the factors of the PFA), the first 25% against the rest, the last 25% against the rest, and the extreme 50% (first and last 25% taken together against the rest). We then calculated weighted averages of the dispersal multipliers for the different intervals on the two factors of the PFA to obtain an estimate of the relationship between trait (i.e. factor) and dispersal probability for each clade.

To quantify the magnitude of the effect of traits on dispersal rates, we calculated the maximal difference in dispersal rates between trait states per clade. We then determined the exact shape of the relationship for those clades in which the maximal difference in dispersal rates between trait states exceeded 10%, separately for body size and life history strategy. We distinguished between positive (large/fast-lived species were better dispersers than small/slow-lived species),

negative (small/slow-lived species were better dispersers than large/fast-lived species), bell-shaped (species with intermediate traits were better dispersers than species with extreme traits) and u-shaped relationships (species with extreme traits were better dispersers than species with intermediate traits).

To assess the effect of phylogenetic uncertainty on the classification of trait-dispersal relationships, we selected 10 trees for one reptile, one amphibian and one mammal clade and repeated phylogenetic factor analyses, as well as trait-independent and trait-dependent biogeographic models (Extended Data Fig. 4, Tab. 4) for all individual trees, using the best base model and MDMM as identified in the main analysis. For one bird clade, we repeated all analyses on a tree where we used the backbone of Prum et al.<sup>53</sup> that included the fossil *vegavis*.

The computation time of all biogeographic analyses combined amounted to ca. 262 800 h\*cores of calculations on a high-performance computing cluster (GRICAD infrastructure, <https://gricad.univ-grenoble-alpes.fr>), corresponding to emissions of ca. 1,2t of CO<sub>2</sub>eq.

### The effect traits in biogeographic estimations

To assess how the inclusion of traits impacted biogeographic estimations, we analysed the following three metrics: (i) average resolution of ancestral range estimates, (ii) average number of dispersal events in a clade's biogeographic history, and (iii) proportion of nodes that were estimated differently between trait-dependent and trait-independent models (and between distance-dependent and distance-independent models, as a comparison).

(i) The average resolution of ancestral range estimates for each clade was calculated in two steps. First, we calculated AIC-weighted averages for ancestral range estimations at each node of the phylogeny, separately for trait-dependent and trait-independent models (+m2 and +m2x models vs base model and +x model). We repeated this for each trait (both body size and life history) and binarization split (4 splits: median split, first 25%, last 25%, extreme 25%). To have a point of comparison, we also calculated AIC-weighted averages for distance-dependent and distance-independent models (+x and +m2x vs base model and +m2 models). Second, we calculated mean resolutions of ancestral range estimations, i.e. the proportion of most likely range per node divided by number of nodes in the phylogeny, excluding tips. The results were averaged across binarization splits per trait, which led to 8 values per clade in total: 2 traits (body size and life history) x 4 model groups (trait-dependent, trait-independent, distance-dependent, distance-independent).

(ii) To calculate the total number of dispersal events in the biogeographic history of a clade, we created 100 biogeographic stochastic maps<sup>105</sup> for all models (base model, base\_model+x, base\_model+m2, base\_model+m2x) and all binarization splits (median split, first 25%, last 25%, extreme 25%, for both body size and life history). We counted the total number of dispersal events for each of the 100 maps we created per model, trait and binarization split (1800 maps in total), and divided it by the number of species in the clade to be able to compare values between clades. We then calculated AIC-weighted averages for trait-dependent and -independent, and distance-dependent and -independent models, and averaged across binarization splits per trait (which again led to 8 values per clade, as above).

(iii) Finally, we calculated the proportion of nodes that were estimated differently between the different groups of models (trait-dependent vs. trait-independent, distance-dependent vs. distance-independent models). To do so, we first determined the most likely ancestral range for each node in each model group for each binarization split. We then calculated differences between trait-dependent and -independent models, as well as distance-dependent and -independent models, and averaged across binarization splits per trait. This led to 4 values per clade (2 traits (body size and life history) x 2 comparisons (trait-dependent vs -independent, distance-dependent vs -independent)).

We used mixed effects models (R packages lme4 v1.1.30<sup>106</sup>, and car v3.1.0<sup>107</sup>) to assess how resolution and number of dispersal events in a clade's biogeographic history varied between the different model groups (trait-dependent, trait-independent, distance-dependent and distance-independent estimations), using clade identity as a random effect. Where these models were significant, we followed with contrasts among estimated marginal means (contrasting trait-dependent and trait-independent models, distance-dependent and distance-independent models, distance-dependent and trait-dependent models, and distance-independent and trait-independent models, using a Šidák correction for multiple comparisons, R package emmeans v1.8.2<sup>108</sup>). We checked normality of residuals visually with histograms, and homoscedasticity by plotting residuals against fitted values.

### **Explaining differences between clades**

We first used linear regressions to test whether the differences between clades in the maximal difference in dispersal rates between trait states could be explained by (i) total average number of dispersal events within a clade' biogeographic history, (ii) percentage of oceanic dispersal events in a clade's biogeographic history, (iii) intra-clade variability in body size or LH, (iv) a clade's species richness, (v) data coverage. To understand why trait-dispersal relationships vary across clades, we performed multinomial logistic regressions to test if the different categories of relationships (positive, negative, bell-shaped and u-shaped) could be explained by (i) a clade's average body size or life history strategy, (ii) intra-clade variability in body size or LH, (iii) percentage of oceanic dispersal events in a clade's biogeographic history, (iv) a clade's species richness, (v) data coverage. (Hypotheses relating the individual variables to the magnitude of trait effects or trait-dispersal relationships can be found in the main text and in Tab. 1). For multinomial regressions we used the R packages nnet v7.3.17<sup>109</sup> and mlogit v1.1.1<sup>110</sup>. In both cases, we used a stepwise selection process (in both directions, R package MASS v7.3.55<sup>109</sup>) to identify those variables that were significantly related to the variables of interest. To determine the average position of all clades in the higher-level trait space and intra-clade trait variability, we conducted class-level phylogenetic factor analyses for amphibians, mammals, reptiles and birds. We scaled clades' median positions in those higher class trait spaces between -1 and 1, with 0 coinciding with the median position of the entire class. We expressed intra-clade trait variability as a percentage of variability in the entire class. To calculate the total number of dispersal events in the biogeographic history of a clade, as well as the percentage of oceanic dispersal, we created 100 biogeographic stochastic maps<sup>106</sup> for all models (base model, base model+x, base\_model+m2, base\_model+m2x) and all binarization splits (median split, first 25%, last 25%, extreme 25%). We counted the number of oceanic

dispersal events and the total number of dispersal events for each of the 100 maps we created per model and binarization split, averaged them across the 100 maps, and then calculated an AIC-weighted average per binarization split. Finally, we averaged the number of oceanic dispersal events and the total number of dispersal events across binarization splits, and expressed the number of oceanic dispersal events as a percentage of the total number of dispersal events.

Since the distributions of the variables total average number of dispersal events, percentage of oceanic dispersal events and clades' species richness were skewed, we log-transformed these variables before conducting the regressions. All variables were scaled before the regressions to compare their influence in a single model.

### **Data availability**

Data for analyses of historical biogeography (trait-dependent and otherwise), as well as data related to the analysis of differences in the magnitude of trait effects and differences in trait-dispersal patterns are archived on Figshare at <https://doi.org/10.6084/m9.figshare.21897003> (the link will become active upon publication, in the meantime material is available from the first author upon request). Further data and for preliminary and intermediate analyses will be made available by the authors upon reasonable request.

### **Code availability**

R scripts for analyses of historical biogeography (trait-dependent and otherwise), as well as code related to the analysis of differences in the magnitude of trait effects and differences in trait-dispersal patterns are archived on Figshare at <https://doi.org/10.6084/m9.figshare.21897003>. Further code for preliminary and intermediate analyses will be made available by the authors upon reasonable request.

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### **Author contributions**

L.G. and W.L.A. conceived the project. L.G., W.L.A. and S.S.W. conceptualised the study; S.S.W., with help of W.L.A. and M.P.J.N., collected the data; S.S.W., with help of M.P.J.N., performed bioregionalisations; S.S.W. performed all further analyses and wrote the original draft of the manuscript; all co-authors reviewed and edited the manuscript; L.G. and W.L.A. acquired financial support for the project.

### **Competing interests**

The authors declare no competing interests.

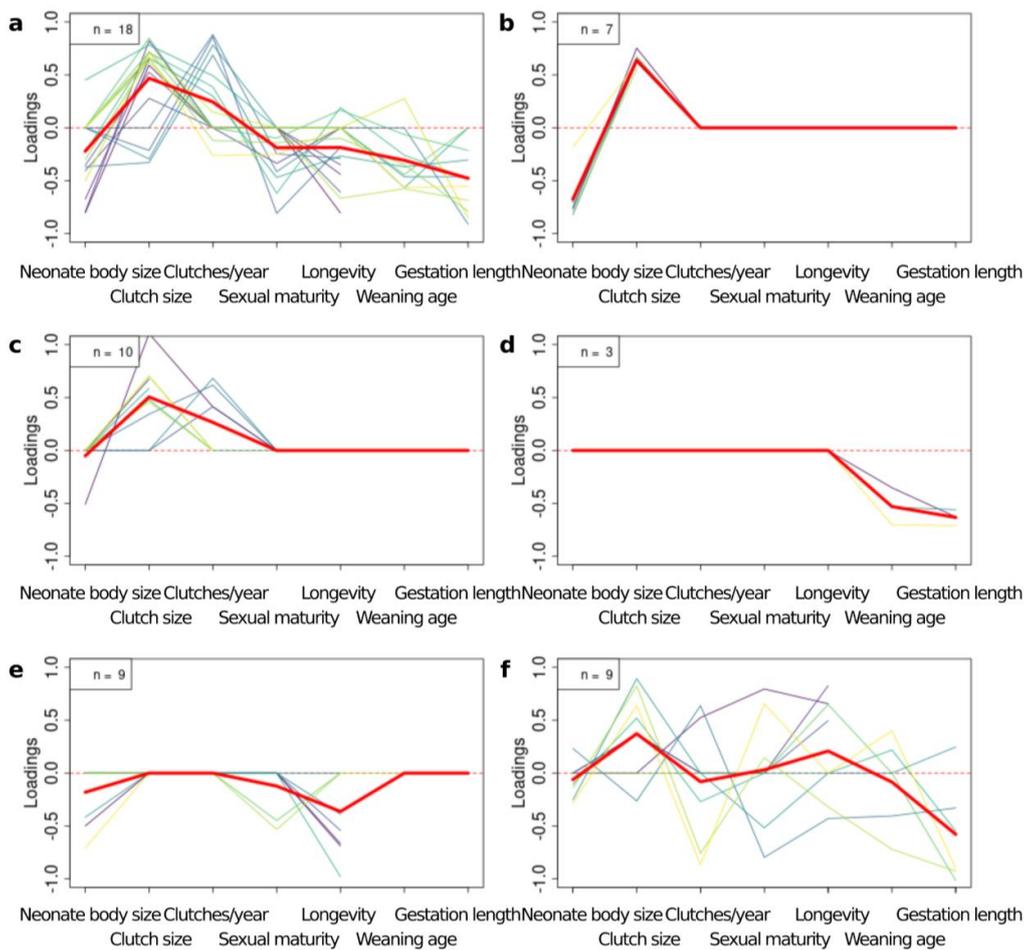
Supplementary Information is available for this paper (see Annex).

## **Extended Data Figures and Tables**

### **Extended Data Table 1 | Overview of clades included in the study.**

Details of included genera and families if a monophyletic subclade of a taxon was used, number of species per clade (as per Bánki et al.<sup>48</sup>), percent of species included in the clade-level analysis, reference of the phylogeny used. Details of the biogeographic models that were run for each clade, including the base model, which manual dispersal multiplier matrix (MDMM) was used, if a time-stratified analysis or a root constraint were implemented. If a root constraint was implemented, a reference to literature is given.

This table is provided as a separate .csv file upon publication. It is available upon request from the first author.



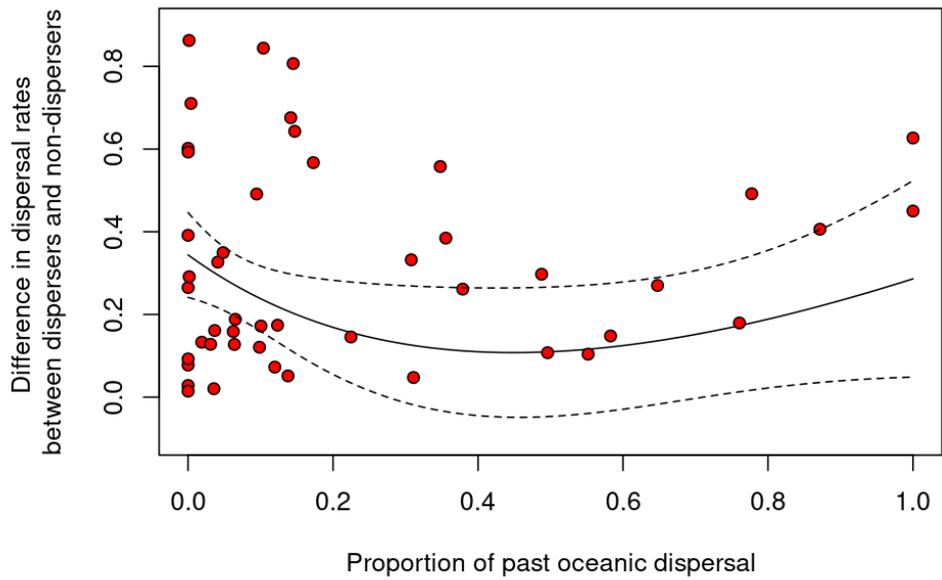
**Extended Data Figure 1 | Summary of variable loadings on the second factor of phylogenetic factor analyses, grouped by interpretation of main life history trade-offs.** One thin line corresponds to one clade; the thick red line is the average of all clades in a panel. a) Clades in which we found a clear fast-slow life history spectrum (where fast species reproduced quickly and were short-lived and slow species had opposing traits;

18/56 clades=32%). b), c), d) Clades in which other fast-slow consistent trade-offs structured life history (20 clades=36%). e) Clades in which only one trait loaded onto the second factor (9 clades=16%). f) Clades in which trait covariation did not suggest any trade-off between survival and reproduction consistent with the fast-slow life history spectrum (9 clades=16%).

Extended Data Table 2 | Model selection results for the magnitude of trait effects.

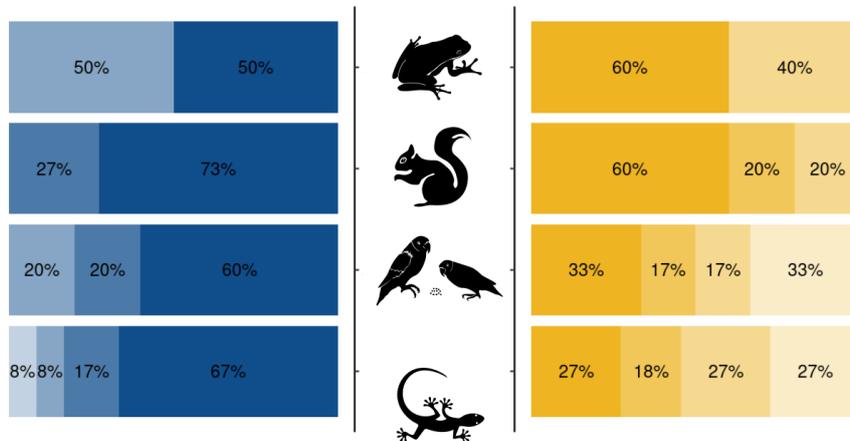
Variables	Body size (56 clades)	Life history 1 (47 clades)	Life history 2 (38 clades)
Variability of body size within clade		n.t.	n.t.
Variability of life history within clade	n.t.	coef = -0.08 (pval = 0.03)	coef = -0.11 (pval = 0.005)
Number of dispersal events per lineage	coef = -0.03 (pval = 0.17)	coef = -0.15 (pval < 0.001)	coef = -0.17 (pval < 0.001)
Number of dispersal events per lineage <sup>2</sup>	coef = -0.04 (pval = 0.08)		
Proportion of past oceanic dispersal		coef = -0.13 (pval = 0.03)	coef = -0.13 (pval = 0.05)
Proportion of past oceanic dispersal <sup>2</sup>		coef = 0.07 (pval = 0.06)	coef = 0.06 (pval = 0.15)
Number of species		coef = -0.06 (pval = 0.06)	coef = -0.10 (pval = 0.01)
Trait data coverage	n.t.		
Adjusted R <sup>2</sup>	5% (pval 0.11)	27% (pval 0.003)	35% (pval 0.002)

We conducted linear regressions to explain the effect of several variables (in rows) on the differences between clades in the maximal differences in dispersal rates between trait states (in columns). For variables that were selected in the stepwise model selection process we give coefficients and p-values of variables. Variables that were not tested for a given dataset because we did not hypothesize them to causally influence the magnitude of trait effects are indicated by n.t.. Life history 1 is the dataset presented in the main manuscript, including 47 clades in which we identified a fast-slow life history continuum (Extended Data Fig. 2); in Life history 2 we excluded clades where only one variable loaded onto the second factor of the phylogenetic factor analysis.



**Extended Data Figure 2 | Relationship between proportion of past oceanic dispersal and magnitude of life history effects on dispersal rates.** Each point corresponds to a clade; the line was fitted based on the selected model explaining

differences between clades in dispersal rate differences between most-dispersive and least-dispersive lineages. Dotted lines correspond to confidence intervals.



### Disperser characteristics

- large/fast life history
- small/slow life history
- intermediate traits
- extreme traits

**Extended Data Figure 3 | Distribution of trait-dispersal relationships by class.** Only clades where the maximal difference in dispersal rates between most-dispersive and least-dispersive trait states was greater than 20% are included (4 amphibian clades, 5 bird clades, 11 mammal clades, 12 reptile clades for body size-dispersal

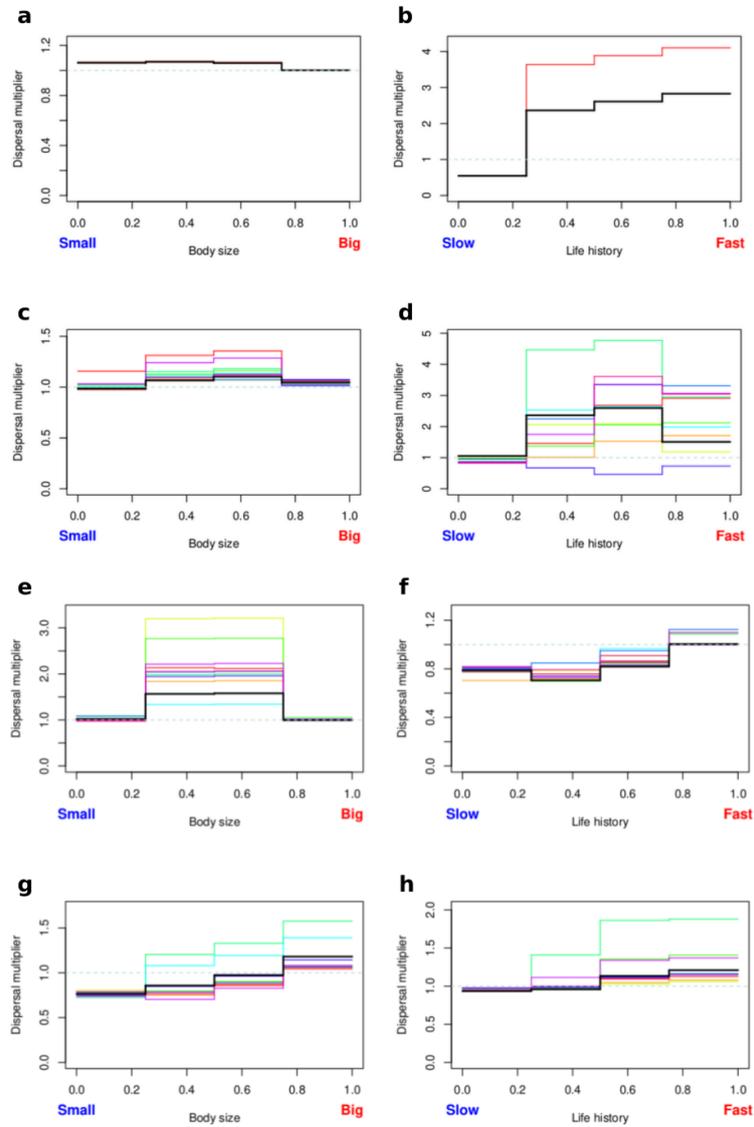
relationships; 5 amphibian clades, 6 bird clades, 10 mammal clades, 11 reptile clades for life history-dispersal relationships (only including clades where a fast-slow life history spectrum was identified)). Icons: [Frog](#) by GREY Perspective, [Squirrel](#) by R Diepenheim, [Bird](#) by yudi yanto, [Gecko](#) by Kevin from Noun Project, [CC BY 3.0](#).

## Chapter 2. Tetrapods

**Extended Data Table 3 | Sensitivity of trait-dispersal relationships to different inclusion thresholds and life history datasets.**

Dataset	Identified relationships					Number of clades
	NONE	POS	NEG	BELL	U	
Body size 10%	12 (21%)	24 (43%)	6 (11%)	8 (14%)	6 (11%)	56
Life history 1 10%	8 (17%)	17 (36%)	7 (15%)	6 (13%)	9 (19%)	47
Life history 2 10%	7 (18%)	16 (42%)	5 (13%)	4 (11%)	6 (16%)	38
Body size 20%	24 (43%)	21 (38%)	6 (11%)	4 (7%)	1 (2%)	56
Life history 1 20%	22 (47%)	10 (21%)	5 (11%)	6 (13%)	4 (9%)	47
Life history 2 20%	18 (47%)	10 (26%)	4 (11%)	4 (11%)	2 (5%)	38

10% (20%) indicates the threshold of maximum difference in dispersal rates between trait states below which we decided not to identify the shape of a relationship. Life history 1 is the dataset presented in the main manuscript, including 47 clades in which we identified a fast-slow life history continuum (Extended Data Fig. 2); in Life history 2 we excluded clades where only one variable loaded onto the second factor of the phylogenetic factor analysis.



**Extended Data Figure 4 | Effect of phylogenetic uncertainty on trait-dispersal relationships.** In black: the trait-dispersal relationship we identified with the maximum consensus tree; in different colours: the trait-dispersal relationships when

different phylogenetic trees from the posterior were used (methodology to choose those trees as in Weil et al.<sup>17</sup>). a) and b) Pycnonotidae, c) and d) Natricinae, e) and f) Hynobiidae, g) and h) Sciuridae.

## Chapter 2. Tetrapods

**Extended Data Table 4 | Assessing phylogenetic uncertainty in trait-dispersal relationships.**

Clade	Trait	Identified relationships					Correctly identified
		NONE	POS	NEG	BELL	U	
Hynobiidae	Body	0	0	0	10	0	100%
Hynobiidae	LH	0	10	0	0	0	100%
Sciuridae	Body	0	10	0	0	0	100%
Sciuridae	LH	2	8	0	0	0	80%
Pycnonotidae	Body	1	0	0	0	0	100%
Pycnonotidae	LH	0	1	0	0	0	100%
Natricinae	Body	2	5	0	3	0	50%
Natricinae	LH	0	5	0	4	1	40%

None indicates that the differences in dispersal rates between most-dispersive and least-dispersive lineages was less than 10%. POS: large/fast-lived species were better dispersers than small/slow-lived species; NEG: small/slow-lived species were better dispersers than large/fast-lived species; BELL: species with intermediate traits were better dispersers than species with extreme traits; U: species with extreme traits were better dispersers than species with intermediate traits.

**Extended Data Table 5 | Model selection results for the shape of trait-dispersal relationships.**

Variables	Body size		Life history 1		Life history 2	
	10% (44 clades)	20% (32 clades)	10% (39 clades)	20% (25 clades)	10% (31 clades)	20% (20 clades)
Average body size of clade						
Average life history of clade						
Variability of body size within clade			n.t.	n.t.	n.t.	n.t.
Variability of life history within clade	n.t.	n.t.				
Proportion of past oceanic dispersal						
Number of species						
Trait data coverage	n.t.	n.t.				
<b>Predictive accuracy</b>	64%	91%	51%	52%	55%	75%
<b>McFadden R<sup>2</sup></b>	0.19	0.62	0.08	0.12	0.09	0.43

We used multinomial regressions to assess the effect of several variables (in rows) on the trait-dispersal relationships in different datasets (in columns). Variables that were selected are highlighted in blue; variables that were not tested for a given dataset because we did not hypothesize them to causally influence the magnitude of trait effects are indicated by n.t.. Life history 1 is the dataset presented in the main manuscript, including 47 clades in which we identified a fast-slow life history continuum (Extended Data Fig. 2); in Life history 2 we excluded clades where only one variable loaded onto the second factor of the phylogenetic factor analysis. 10% (20%) indicates the threshold of maximum difference in dispersal rates between trait states below which we decided not to identify the shape of a relationship.

## Chapter 2. Tetrapods

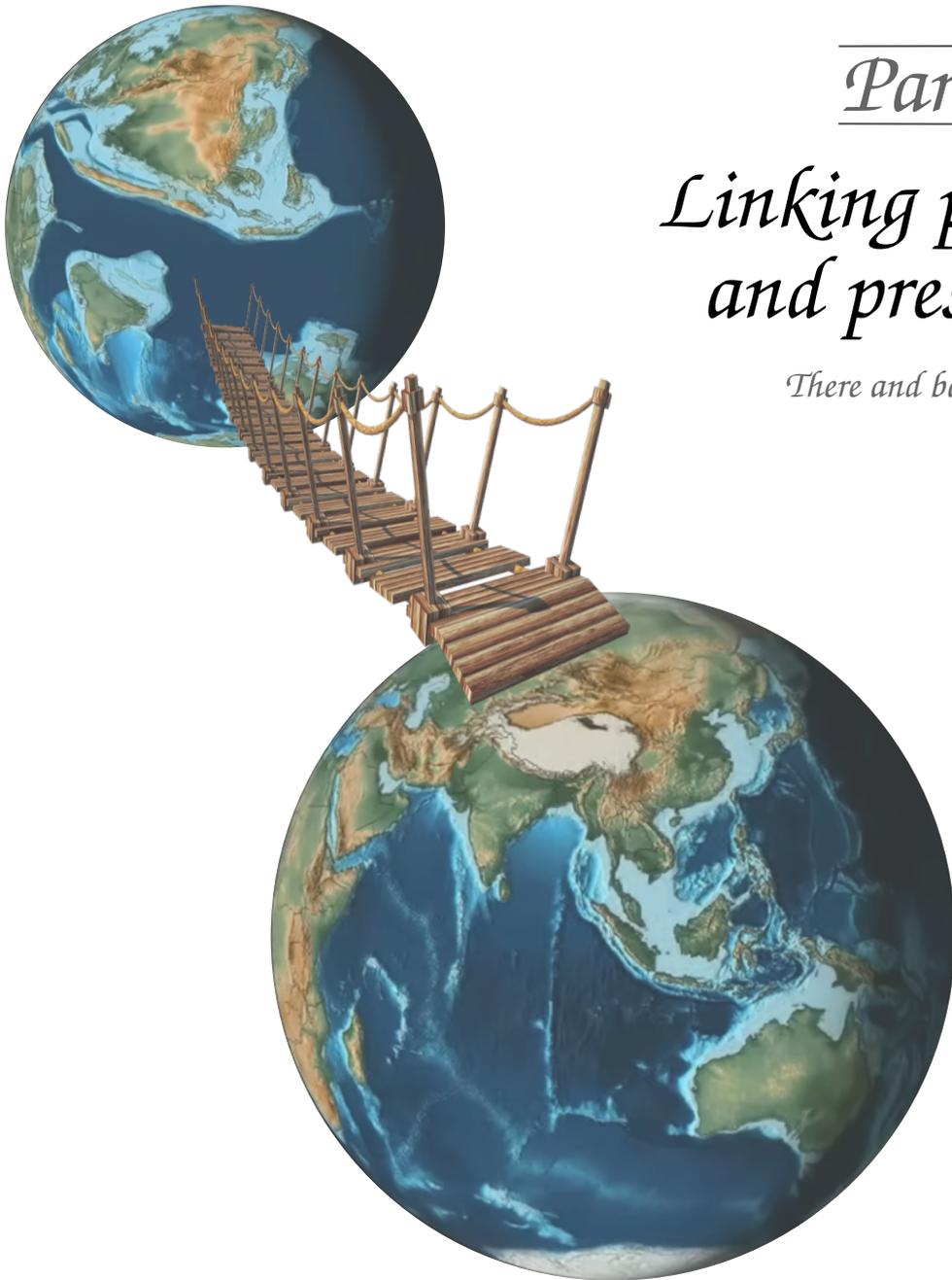
**Extended Data Table 6 | Data coverage overview for class-level phylogenetic factor analyses.**

Clade	Number of species included	SVL/BM	HBM/EM/ES	CS/LS	CY/LY	SM	LG	GT	WA
Amphibians	3447	3421 (99%)	401 (12%)	1621 (47%)	1267 (37%)	347 (10%)			
Reptiles	5657	5619 (99%)	2143 (38%)	3806 (67%)	1412 (25%)	963 (17%)	1563 (28%)		
Mammalia	3874	3874 (100%)	1538 (40%)	2794 (72%)	1844 (48%)	1675 (43%)	2121 (55%)	1847 (48%)	1692 (44%)
Aves	6589	6589 (100%)	3449 (52%)	6427 (98%)	1519 (23%)	1157 (18%)	1441 (22%)	1814 (28%)	1542 (23%)

For reptiles and amphibians: snout-vent-length, for mammals and birds: body mass. For amphibians: egg size, for birds: egg mass, for reptiles: hatchling body mass, for mammals: neonate body mass. Abbreviations: SVL/BM: snout-vent-length/body mass, HBM/ES: hatchling body mass/egg size, CS/LS: clutch/litter size, CY/LY: clutches/litters per year, SM: average age of females at sexual maturity, LG: maximum longevity, GT: gestation time, WA: weaning age/fledgling age.







Part II

*Linking past  
and present*

*There and back again*



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Credits previous page:

Paleo reconstruction of the Earth: Scotese, C. R., 2013. Collision of India and Tectonic Evolution of Southeast Asia, PALEOMAP Project Animation. Available at [www.youtube.com](http://www.youtube.com).

Wooden bridge illustration: [www.pngwing.com](http://www.pngwing.com).

"There and back again": J. R. R. Tolkien, *The Hobbit*.

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In the last chapter I showed that a multitude of trait-dispersal relationships exists in past biogeographic dispersal in tetrapods. Past biogeographic dispersal can be compared to contemporary dispersal processes, such as biological invasions and range shifts, and similar traits might be linked to success in the different processes (see Introduction of this thesis). Results from chapter 2 might therefore be useful to determine species' present-day invasion and range shift potential. However, there are also reasons to think that this should not be the case, for example, mismatches in timescales or human influence in present-day processes.

In this second part of my thesis I explore if and how information from deep past studies can be used to inform contemporary processes. In chapter 3 I do this through a literature synthesis where I include other processes than dispersal, such as adaptation (this article is still in progress). In chapter 4 I test the hypothesis that past dispersal can inform us about species' performance in present-day biological invasions in a subset of species from chapter 2. I finish this part with chapter 5 where I test the hypothesis that past dispersal can inform us about species' present-day range shifts, again in a subset of species from chapter 2.



## **Chapter 3**

# **Can macroevolution inform contemporary extinction risk and invasion potential?**

# Can macroevolution inform contemporary extinction risk and invasion potential?

Sarah-Sophie Weil<sup>1,2</sup>, Sébastien Lavergne<sup>1</sup>, Marceau Habrant<sup>1</sup>, Florian Boucher<sup>1</sup>, William Allen<sup>2\*</sup>, Laure Gallien<sup>1\*</sup>

## Introduction

Biodiversity loss and ecosystem declines are key challenges of our time, driven in large parts by climate change and species' invasions (IPBES 2019). It is therefore essential to identify species which are likely to become especially threatened or have a high potential for becoming invasive. Over the last decades, conservation science has significantly progressed towards this goal by taking advantage of approaches from a diversity of fields, including population ecology and genetics (e.g. Sakai, Allendorf, et al. 2001), metapopulation studies (e.g. Huang, Pimm, et al. 2020), macroecology (e.g. Santini et al. 2021), as well as the study of adaptive processes (e.g. Marin et al. 2020). Now, a new approach is emerging with recent studies investigating macroevolutionary events and processes to better understand the current processes that influence species range changes and species' responses to global changes (e.g. Davies, Smith, et al. 2011; Gallien, Thornhill, et al. 2019; Greenberg, Pyron, et al. 2021; Lavergne, Evans, et al. 2013; Tanentzap et al. 2020).

Conceptually, macroevolutionary and biogeographic events and processes can be linked to contemporary issues in several ways. First, events and processes that happened in the past (such as extinction, trait or niche evolution, species diversification, as classically inferred from paleontological and neontological data) are still happening today, influencing species' contemporary population and range dynamics. These processes thus partly determine species' responses to changing environmental conditions: species can disperse to track suitable conditions, species' niches can evolve through adaptation to match the new conditions, or species can

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ultimately go extinct (e.g. Edwards and Donoghue 2013; Román-Palacios and Wiens 2020). Similarly, present-day biological invasions can be viewed as a human-mediated analogy of a natural phenomenon: biogeographic dispersal followed by colonisation of distant locations in the deep past, which usually had profound impact on the native biotas that were confronted with the colonist species (e.g. the colonisation of South America from Africa by Platyrrhini (Alfaro 2017; Bond et al. 2015); or the radiation of silverswords on Hawaii (Judd et al. 1999; Landis et al. 2018)). Thus, parallels can be drawn between past events and processes and contemporary processes influencing species' population and range dynamics.

Second, evolutionary rates have been suggested to be useful proxies for species' probabilities of extinction and abilities of adaptation through indirect connections with extinction-/invasion-promoting characteristics. For example, high species diversification rates may be correlated with endemism and smaller range and population sizes which would indicate higher extinction risk of species belonging to lineages with high diversification rates (e.g. Schmidt et al. 2021). Species belonging to lineages with high rates of trait evolution may have higher capacities to adapt to new environmental conditions, which may make them less vulnerable to climate change and more prone to becoming invasive (e.g. Gallien, Saladin, et al. 2016; Gallien, Thornhill, et al. 2019; Lavergne, Evans, et al. 2013).

The proposal that macroevolution can inform contemporary ecological dynamics is appealing, but also raises a number of concerns. Undoubtedly, there is a mismatch of temporal and taxonomic scales. Current environmental changes are occurring at high rates whereas past change has almost always been much slower (e.g. IPCC 2021; Ricciardi 2007). Another obvious temporal mismatch is speciation which happens over tens of thousands to million years. In addition, while many contemporary issues (species vulnerability to extinction or probability of invasion) are at the population or species level, macroevolutionary rates are often measured at higher taxonomic levels (e.g. Schmidt et al. 2021).

Here, we propose to explore in detail if macroevolution can inform contemporary extinction risk and invasion potential to answer the question: Can we use information from macroevolutionary and historical biogeographic studies to help understand contemporary ecological dynamics, and if so, under what conditions? We synthesise studies that use macroevolutionary and past biogeographical analyses to understand two types of present-day dynamics: (1) population and species' declines and extinction threat in the face of global changes, and (2) biological invasions and risk of naturalisation and invasion. Specifically, we identify the implicit assumptions made in these studies to link past and current processes and evaluate whether these assumptions are supported by scientific evidence. We further highlight potential ways forward.

## **Can past macroevolutionary rates help us identify species at high risk of extinction?**

Some species are more vulnerable to global changes and at higher risk of extinction than others due to certain characteristics. Species with small population sizes or small ranges, for instance, are more prone to extinction both at local and global scales because they are inherently more sensitive to environmental changes (Lavergne, Molina, et al. 2006; Lavergne, Thuiller, et al. 2005; Matthies et al. 2004). Species with low capacities of adaptation, high degrees of ecological specialisation and poor dispersal potential are also at a disadvantage (e.g. McKinney and Lockwood 1999; Román-Palacios and Wiens 2020). Yet, data on population and range sizes, degree of specialisation, as well as dispersal and adaptation capacities is not readily available for many species, which is why identification of threatened species can be difficult. In the following sections we explore how the study of past diversification rates, past trait evolution rates and past extinctions may help us to identify species that are especially at risk of extinction due to global changes even when they lack key data.

### **Past diversification rate as proxy for current extinction risk**

Clades with high diversification rates are suggested to be more vulnerable to global changes than clades with low diversification rates. At the core of this link are two underlying assumptions: (1) High diversification rates are the signal of localised radiations, which tend to create species with small range and/or population sizes and a high degree of specialisation. (2) In turn, these characteristics are assumed to be key drivers of species' extinction risk.

#### **The evidence for underlying assumptions**

Evidence for the second assumption has clearly been demonstrated. Extinction risk is associated with narrow dietary and habitat/environment breadth (Boyles and Storm 2007; Colles et al. 2009; Devictor et al. 2008; Ducatez et al. 2014; Harnik et al. 2012; Heim and Peters 2011; McKinney and Lockwood 1999; Olden et al. 2008; Smits 2015), limited geographic distribution (Koh et al. 2004; Lavergne, Molina, et al. 2006; Lavergne, Thuiller, et al. 2005; Sakai, Wagner, et al. 2002), and small population size (Caughley 1994; Purvis et al. 2000). These characteristics are not independent from each other, and synergistic effects may further increase species' vulnerability: highly specialised species, especially those with a narrow habitat or environmental niche, are often geographically restricted (Brown 1995, Slatyer et al. 2013, Huang, Chen, et al. 2021, but see Fargallo et al. 2022). Since

range size and abundances are generally positively correlated (Gaston and Gaston 1994), specialist, narrow-ranging species often have small population sizes (but some tropical taxa have been shown to be simultaneously small-ranged and highly abundant, Freeman et al. 2022 and references therein). Narrow-ranging endemics should hence be the most prone to extinction. Nevertheless exceptions exist, some local endemic species have for example become invasive elsewhere (e.g. *Pinus radiata*, consisting of a handful of native populations from California to Mexico, but which showed worldwide naturalisation).

However, evidence for the first assumption that high diversification rates generate species with these extinction-promoting characteristics is mixed. This concerns both the link with specialisation and with range size. First, the relationship between specialisation and diversification may be positive or negative (Rolland and Salamin 2016 and references therein, Sexton et al. 2017). On one hand, specialisation can promote diversification if specialists have isolated and disconnected populations, increasing rates of allopatric speciation (Futuyma and Moreno 1988; Vrba 1987). On the other hand, generalists can also have high diversification rates if they have large ranges, which are more likely to be fragmented by geographical barriers over evolutionary time-scales, also leading to allopatric speciation. In addition, large ranges increase the variability of environmental conditions a species encounters, which may increase opportunities for local adaptations and hence probabilities of diversification (Rolland and Salamin 2016). Empirical evidence leans toward supporting the hypothesis of specialists having higher diversification rates than generalists. This was found for (1) biome specialisation in ruminants, squirrels and butterflies (Cantalapiedra et al. 2011; Gamboa et al. 2022; Menéndez et al. 2021), (2) host-plant specialisation in butterflies (Hardy and Otto 2014), and (3) climatic niche specialisation in amphibian, mammal and bird species (Rolland and Salamin 2016). Aside from the uncertain link between diversification rates and specialisation, specialisation can be a labile trait through time. Although specialised ancestors tend to have specialist descendents (Allen, Moreno, et al. 2020; Brändle et al. 2002), there are numerous counterexamples showing that specialists can evolve into generalists (reviewed in Colles et al. 2009), and even that specialist-to-generalist biases exist (i.e. higher probabilities of specialists evolving into generalists than the other way around, Sexton et al. 2017). Another tricky point is that different dimensions of a species' niche (e.g. diet, habitat, environmental tolerances, Sexton et al. 2017) are not necessarily correlated (Carscadden et al. 2020; Emery et al. 2012) and specialisation in one dimension may be compensated for by generalisation in another (Litsios, Kostikova, et al. 2014). As concluded by Schluter (2000), the direction of evolution of niche breadth may just be unpredictable, so that past diversification rates may hence not be a good proxy for the present-day degree of specialisation of species.

Second, the relationship between diversification rate and species range size was

also found to be positive or negative depending on the taxonomic group. Negative relationships were found in many taxa of plants and tetrapods (Davies, Smith, et al. 2011; Fu et al. 2022; Greenberg and Mooers 2017; Greenberg, Pyron, et al. 2021), while positive relationships were found in turtles, crocodiles, primates and Australian mammals (Cardillo et al. 2003; Colston et al. 2020; Redding et al. 2010). The relationship between diversification rates and range size appears to be variable, which can be due to several factors. On one hand, geographic context is likely to play an important role: diversification in a geographically restricted context favours both specialisation and narrow ranges via niche packing. On the other hand, speciation mode influences the relationships between diversification and range size. In allopatric and peripatric speciation, recently diverged species may indeed occupy narrower geographic and adaptive spaces than parent species (Castiglione et al. 2017). However, post-speciation changes in range size can blur such potential relationships, but the relationship between species age and range size seems like an unsettled matter (Miller 1997; Taylor and Gotelli 1994; Webb and Gaston 2000; Willis et al. 1922). The impact of speciation rate on range size requires further investigation.

### **The evidence for linking past to present**

Confronting the expectation of a link between diversification rates and species' present-day extinction risk to empirical observations, it seems that the relationship between diversification rates and extinction risk strongly depends on geographic and taxonomic context. Indeed, positive relationships between diversification rates and proportion of threatened species were found in some families and genera in plants (Davies, Smith, et al. 2011; Fu et al. 2022; Schmidt et al. 2021; Tanentzap et al. 2020) and tetrapods (Greenberg and Mooers 2017; Greenberg, Pyron, et al. 2021). However, no significant link between diversification rates and extinction risk was found in angiosperm genera endemic to China (Yu et al. 2022), and a negative relationship was found in angiosperm families in temperate biodiversity hotspots (Fu et al. 2022). Studies at high taxonomic scales in mammals (Verde Arregoitia, Blomberg, et al. 2013), birds (Jetz, Thomas, Joy, Redding, et al. 2014) or squamate reptiles (Tonini et al. 2016) generally do not find any significant relationships between evolutionary distinctiveness (a species-level proxy of diversification rate; Jetz, Thomas, Joy, Hartmann, et al. 2012) and extinction risk, whereas in analyses conducted at smaller taxonomic scales phylogenetically isolated species were disproportionately at risk (in turtles and crocodiles (Colston et al. 2020) and primates (Verde Arregoitia, Blomberg, et al. 2013)).

Similarly, results contrary to the initial hypothesis have been found when diversification rates are replaced by other proxies, such as potential loss of phylogenetic diversity through species at risk of extinction compared to expected loss of

phylogenetic diversity by chance. Extinction risk that is concentrated in groups with long terminal branches (implying low speciation or high extinction rates in the past) would lead to higher loss of phylogenetic diversity than expected under random extinction scenarios. Extinction in clades with fast diversification rates, i.e. extinction of short terminal branches, would lead to lower loss of phylogenetic diversity than expected by chance (Heard and Mooers 2000; Purvis 2008). Loss of phylogenetic diversity has been shown to be higher than expected by chance, indicating that slowly-diversifying clades, and especially monotypic ones, have a particularly high risk of extinction, in primates (Purvis et al. 2000), marsupials (Johnson et al. 2002), mammals and birds on a global scale (Purvis et al. 2000; Von Euler 2001) as well as angiosperms (Vamosi and Wilson 2008).

### **Conclusion**

Overall, literature shows that the relationships between diversification rates and species' degree of specialisation and range sizes are inconsistent and likely dependent on geographic context and speciation mode. Hence, it is clearly preferable to directly use species' characteristics known to promote extinction risk (e.g. niche or diet breadth, range size, population size) to assess vulnerability (as does the IUCN). However, in the absence of trait or distribution data, and in clades where the relationship between diversification rates and extinction-promoting characteristics has been confirmed, diversification rates may be used to identify species likely to be especially threatened.

### **Niche evolution rates as proxies for current extinction risk**

Species' adaptive potential is an emerging focus of conservation ecology and predictions of species' persistence in changing environmental conditions (Catullo et al. 2015; Gonzalez et al. 2013; Hanson et al. 2020; Hoffmann, Griffin, et al. 2015; Olivieri et al. 2016), but data are scarce. Slow evolution of niches in the past has been proposed as a potential indicator of the risk of species' extinction. This suggestion comes from the theoretical expectation that rates of niche or trait evolution are faster in species with higher genetic diversity, which in turn should give them an adaptive advantage in the context of current environmental changes (Lavergne, Evans, et al. 2013; Salamin et al. 2010). In particular, the link between niche evolution rates and current extinction risk is based on three underlying assumptions: (1) species belonging to lineages with low rates of niche evolution in the past have lower genetic diversity, (2) low genetic diversity leads to low evolutionary potential to face the current rates of environmental changes, (3) species with low adaptive potential are at higher risk of extinction.

### **The evidence for underlying assumptions**

Literature supports the second and third underlying assumptions. Species with low genetic diversity are indeed less likely to adapt to novel conditions (shown theoretically (Falconer and Mackay 1996), experimentally in *Drosophila melanogaster* (Frankham et al. 1999), see also Hoffmann, Sgrò, et al. 2017, Kardos et al. 2021, de Villemereuil et al. 2019). On the contrary, high capacities of adaptation can prevent extinctions by favouring evolutionary rescue against adverse environmental change (Gonzalez et al. 2013; Vander Wal et al. 2013). In addition, low genetic diversity may directly increase extinction rates via inbreeding depression (e.g. Frankham 2005; Hufbauer et al. 2015; Kardos et al. 2021). However, there are no studies, to our knowledge, assessing the first part of the hypothesis, i.e. the link between past niche evolution rates and present-day genetic diversity.

An alternative hypothesis linking past rates of niche evolution to present-day extinction risk is that, within a geographically restricted area, high rates of niche evolution may imply adaptive evolution and hence increased specialisation (Gudde and Venditti 2016). Specialisation in turn is generally linked to narrow ranges and small population sizes, possibly leading to a positive relationship between high niche evolution rates and present-day extinction risk (see discussion in previous section). This effect could be compounded by the associations between degree of specialisation, population size and genetic diversity, implying that specialist species with isolated populations have low genetic diversity (Habel and Schmitt 2012) and lower capacities of adaptation, increasing present-day extinction risk even further. However, no consistent relationships between rates of climatic niche evolution and niche breadth were found in salamanders, and relationships with some climatic variables were positive, indicating higher rates of niche evolution in clades with more generalist niches (Fisher-Reid et al. 2012). Similar results were found in mammals and damselfish (Cooper et al. 2011, Litsios, Pellissier, et al. 2012, but see Satterwhite and Cooper 2015). A recent analysis found significant relationships between rates of climatic niche evolution and niche breadth in less than 20% of ca. 1900 plant and animal species, without a consistent direction of positive or negative relationships (Liu et al. 2020).

### **The evidence for linking past to present**

The association between past rates of niche evolution and species' extinction risk has received mixed empirical support. It has been confirmed for European birds, where slow evolution of the climatic and habitat niche was related to demographic declines (Lavergne, Evans, et al. 2013). However, a large-scale study covering more than 11 000 terrestrial vertebrates did not find any consistent relationship between niche evolutionary rates and current IUCN threat status (Rolland, Davies,

et al. 2020).

### **Conclusion**

In conclusion, there are two contradictory links between high past rates of niche evolution and present-day extinction risk; one possibly decreasing extinction risk via adaptation, the other possibly increasing extinction risk via specialisation and associated narrow ranges and small population sizes. Therefore, before using rates of trait evolution as an indicator of species extinction risk, it is necessary to first determine whether high evolutionary rates do indeed lead to increased intraspecific genetic variability or if they lead to increased specialisation, especially in geographically constrained areas.

Linking macroevolutionary rates and microevolution, i.e. adaptation, is further complicated by two major challenges: temporal shifts in evolutionary rates, and varying rate estimates depending on the taxonomic level considered. The histories of lineages have been shown to be characterised by long periods of little evolution followed by periods of rapid change (punctuated equilibrium, Gould and Eldredge 1977). For example, it took only about 30 generations for the Italian wall lizard to adapt to the new ecological conditions after introduction on a remote island (i.e. shifting from an insectivorous to an herbivore diet, Herrel et al. 2008), but the inferred rate of niche evolution will necessarily decrease when measured on a larger time interval. This has an important consequence: the largest evolutionary rates are always measured on shorter timescales, but low evolutionary rates can be inferred at all timescales (Harmon et al. 2021). So a key challenge becomes to predict high potential evolutionary rates which are occurring in a matter of generations. This might be done by quantifying punctual niche or trait change from phylogenetic comparative methods (e.g. Pearman et al. 2014), which would therefore identify which niche axes or which clades are more likely to evolve punctually rather than gradually. Several studies indeed found that projected climate change is much faster than historical rates of niche evolution (on species-level in plants and vertebrates: Quintero and Wiens 2013, Cang et al. 2016, and population-level across taxonomic groups: Jezkova and Wiens 2016). However, averaged rates were used in these analyses, potentially underestimating instantaneous rates in times of rapid change. In addition, it has been questioned at which taxonomic level niches and rates of niche evolution should be estimated to inform conservation actions (Smith, Godsoe, et al. 2019). Rates of niche evolution vary depending on the taxonomic level, and adaptations of e.g. populations to local environmental conditions have been recorded frequently (e.g. Valladares et al. 2014). However, while modelling at sub-species level is promising, it requires good data coverage and may be impractical or impossible in many cases (Smith, Godsoe, et al. 2019).

### **Past extinction rate as proxy for current extinction risk**

Extinction rates have varied throughout Earth's history, going from relatively low background rates to mass extinction events where more than 75% of biodiversity was lost (Barnosky et al. 2011). While extinction rates today are up to 1000 times higher than historical background rates (Pimm et al. 2014), studying past extinctions may help us better understand causes of extinction and what biodiversity is especially under threat (Condamine et al. 2013). Greenberg, Pyron, et al. (2021) outline two contrasting pathways of how past extinction rates may be linked to present-day extinction risk: (1) Rates of extinction vary among clades due to lineage-specific traits and characteristics, such as range size or degree of specialisation. Species descending from lineages with high extinction rates may hence be especially at risk of extinction. (2) Alternatively, species descended from lineages with high extinction rates may be less at risk of extinction because they possess the features that made them particularly resistant to past extinctions (since they are the survivors). Hypothesis 1 assumes that traits were linked to past extinctions, that the same traits are related to present-day extinction risk, and that these traits are conserved on the phylogeny. Hypothesis 2 agrees with the first part of hypothesis 1 but assumes in contrast that extinction-promoting traits are not conserved, i.e. that surviving species of lineages with high extinction rates do not share the traits of their extinct sister species.

#### **The evidence for underlying assumptions**

Traits that were related to past extinctions (short duration in the stratigraphic record), such as small geographic range size and narrow niche breadth, have been shown to be good predictors for present-day extinction risk (IUCN threat status) in amphibians (Tietje and Rödel 2018). In addition, small geographic range size has been associated independently with past and present-day extinction risk (Kiessling and Kocsis 2016; Payne and Finnegan 2007; Purvis et al. 2000). Generally, range size has been shown to be phylogenetically conserved across taxa (e.g. mammals: Cardillo 2015, Pie and Meyer 2017; squamates: Pie and Meyer 2017; birds: Waldron 2007; tropical plants: Loza et al. 2017; ammonites: Zacaï et al. 2017). However, the strength of phylogenetic signal is highly variable across clades, and completely absent in some of them. It is therefore likely that the relationship between past and present-day extinction risk is clade-dependent.

#### **The evidence for linking past to present**

We did not find any study testing the hypothesis that past extinction rates are linked to present-day extinction. This may be because extinction rates are difficult to estimate from molecular phylogenies (Rabosky 2010), and other metrics such

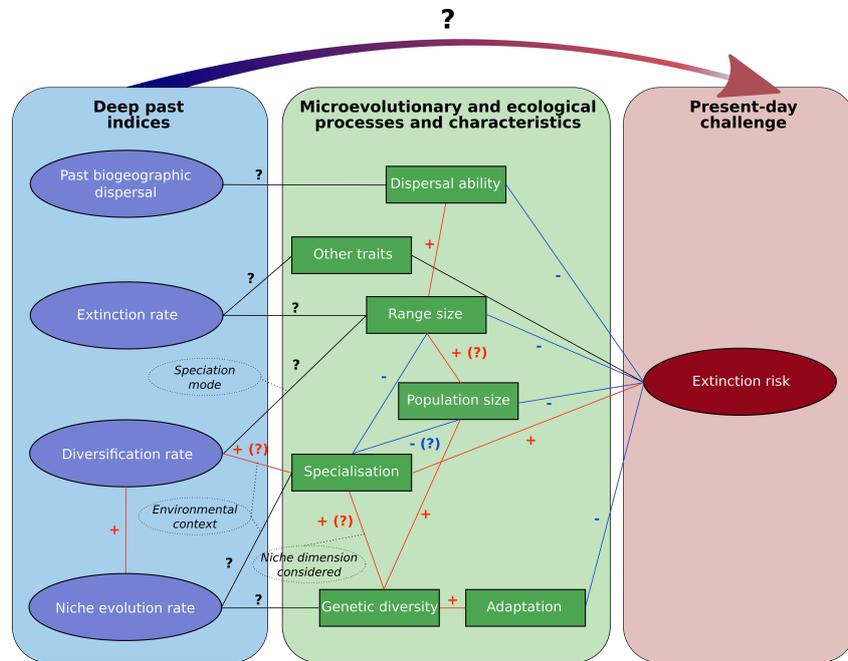


Figure 1: Summarising links between deep past indices and present day processes linked to species' extinction risk and conservation needs. Direction of links is indicated by + (positive), - (negative), or ? (unknown or context-dependent).

as diversification rates are more robust (e.g. Pyron and Pennell 2022). However, we can assess evidence for the underlying hypotheses of the proposed pathways. There is literature about trait selectivity of past mass extinctions (e.g. Guinot and Condamine 2023), which serve identifying how extinction process may be related to particular life history traits, niches etc. However, this literature has yet to be linked to current extinction threat to identify whether extant species sharing the same traits may be prone to extinction nowadays. This was done on Amphibians (reference below). Also, there is still very little paleontological analyses of extinction events with traits ... to be developed further.

## **Can past macroevolutionary rates and biogeographical movements help us identify species with high naturalisation potential?**

Just as some species are thought to be at higher risk of extinction due to certain characteristics, species' naturalisation potential in the context of biological invasions is thought to be linked to traits as well. These traits include, amongst others, the degree of specialisation, population growth rates, adaptive potential, as well as dispersal and establishment capacities. In the following sections we explore how macroevolutionary rates and past biogeographic dispersal might be used as proxies for these traits and hence inform us about species' present-day naturalisation potential.

### **Evolutionary rates as proxies for current potential of naturalisation**

Evolutionary rates have also been linked to naturalisation potential of introduced species. There are several potential mechanistic pathways linking evolutionary rates and naturalisation potential that partly conflict with each other: (1) fast diversifying clades are hypothesised to give rise to specialised endemics which are expected to perform poorly in biological invasions, (2) fast diversifying clades are often observed in clades of organisms with short generation times and high population growth, characteristics which are expected to be advantageous in biological invasions, and (3) fast diversifying clades may also have high rates of niche evolution which possibly indicate high adaptive potential, an advantage in biological invasions. In addition, it has been proposed that the link between high diversification rates and naturalisation success is purely correlative; the evolution of lineage-specific traits, such as fruit size or phenotypic plasticity, may have increased past diversification rates and may be simultaneously advantageous during the invasion process (Lenzner et al. 2020, and references therein).

### **The evidence for underlying assumptions**

We have shown above that the links between diversification rates and degree of specialisation and range size are not straightforward. It is hence difficult to infer species' present-day naturalisation potential from diversification rates if the underlying hypotheses relating to specialisation and range size have not been explicitly tested. Geographic context may play an important role in the link between diversification rates and degree of specialisation, too. Lenzner et al. (2020) found a significant interaction between range size and diversification rates in tropical

regions and that naturalisation success was higher for families with large ranges and high diversification rates. They propose that high diversification rates, especially in the tropics, are associated with high degrees of specialisation and possibly the evolution of mutualistic interactions, limiting naturalisation potential.

There is more empirical support for the second proposed pathway involving population characteristics. High diversification rates have been linked to traits often correlated with short generation times and higher population growth rates: small size and early age at sexual maturity in plants (Boucher et al. 2017; Verdú 2002), fast demographic turnover times in Amazonian trees (Baker et al. 2014), large litters in Australian mammals (Cardillo et al. 2003), and small size in actinopterygian fish (Tedesco et al. 2017). High rates of molecular evolution have also been linked to short generation times in invertebrates and plants (Smith and Donoghue 2008; Thomas et al. 2010). These characteristics are beneficial in the colonisation of new habitats (Allen, Street, et al. 2017, Capellini et al. 2015, but see Sol et al. 2012) because populations with high population growth rates can quickly overcome the period in which probability of stochastic extinction is high, and may have greater adaptive potential (see also following paragraph). This might create a positive association between diversification rates and naturalisation potential.

Empirical support for the third pathway, involving the link between diversification rates, niche evolution rates and adaptive potential is mixed. Lineages with high diversification rates have indeed been shown to have high rates of niche evolution (Kozak and Wiens 2010; Title and Burns 2015). However, niche border shifts in invaded ranges have been shown to be uncorrelated to past rates of niche evolution in pines (Gallien, Saladin, et al. 2016) and little is known about the link between rates of niche evolution and adaptive potential (see discussion above). Generally, higher levels of genotypic and phenotypic diversity have been found to increase establishment success of invaders (Forsman 2014). However, the high adaptability of invasive species is a paradox since they often have small founder population sizes to begin with and hence limited genetic variability, which should limit their adaptive potential (Carneiro and Lyko 2020; Chown et al. 2015). Many species have indeed spread successfully with low genetic diversity (Darling et al. 2008; Myburgh et al. 2007; Richards et al. 2012), which has been linked to the nature of the invaded environment (agricultural vs natural landscapes, Moran and Alexander 2014, Chown et al. 2015). But on the other hand, there are numerous examples of invasive species evolving rapidly after introduction (Fetters and Mcglathlin 2017; Gallien, Thuiller, et al. 2016; Hudson et al. 2016; Pili et al. 2020; Whitney and Gabler 2008; Wiens et al. 2019).

In addition, an important question is which adaptability in which niche dimension or which trait of invasive species is considered. Different dimensions of the niche may be important in different contexts. While persistence in an already occupied region (relating to extinction risk) depends principally on a species' ability to

adapt its climatic niche to changing conditions, naturalisation can be for example be promoted by evolution of a disperser type by changing morphology (cane toads in Australia Phillips et al. 2006), or adaptation to new host plants (soapberry bugs Carroll et al. 2001).

### **The evidence for linking past to present**

Schmidt et al. 2021 found a negative relationship between diversification rates and proportion of naturalisation success in angiosperm families. In contrast to this, Lenzner et al. 2020 found a positive relationship between diversification rates and naturalisation success in angiosperm families.

### **Conclusion**

To conclude, conflicting pathways link past evolutionary rates to contemporary naturalisation potential. Some of them (e.g. ‘fast’ population characteristics) are empirically more supported than others, and other underlying hypotheses remain to be tested.

### **Past biogeographical movements as proxy for current potential of naturalisation**

Past biogeographic movements may be related to species’ present-day capacity of establishment in new environments, and therefore a proxy for species’ naturalisation potential in biological invasions. This has been suggested because successful biogeographic movement may depend on traits which may show phylogenetic signal (Gallien, Saladin, et al. 2016). Species descended from lineages that were successful colonisers in the past may hence be better invaders today because they may have retained good dispersal and establishment capacities.

### **The evidence for underlying assumptions**

The link between past biogeographic movements and species’ naturalisation potential has been proposed based on the assumptions that species’ biogeographic movements are related to traits, which are heritable and phylogenetically conserved. Species’ past biogeographic dispersal success has indeed been shown to depend on traits, such as body size and life-history related traits (Klaus and Matzke 2020; Weil, Gallien, Lavergne, et al. 2022; Weil, Gallien, Nicolai, et al. submitted). These traits were also found to be heritable (Kingsolver et al. 2001; Mousseau and Roff 1987; Réale et al. 2003). However, we do not always know which traits drive

dispersal and establishment success, and these traits may change depending on geographical and environmental context (Clobert et al. 2012).

### **The evidence for linking past to present**

The association of successful past dispersal and present-day naturalisation success has been confirmed for pines (Gallien, Saladin, et al. 2016), as well as Australian eucalyptus and acacias (Gallien, Thornhill, et al. 2019). However, we do not know whether these trends reflect a general rule across the tree of life, or whether they are specific to a few clades. Here, we test this association in 12 clades of tetrapods (Box 1). We find that in those clades, past dispersal success does not seem to be a good predictor of present-day naturalisation success.

### **Conclusion**

In summary, while a positive association between past dispersal and naturalisation success was found previously, corroborating underlying hypotheses, we could not confirm this for 12 tetrapod clades. It is hence possible that in the naturalisation process, other factors or traits may dominate (e.g. propagule pressure; Blackburn et al. 2015; Cassey et al. 2018) compared to natural biogeographic dispersal. This conclusion, however, is based on a small number of clades and more investigation is necessary.

**Box 1: Is the number of past colonisations a good proxy for invasiveness?**

We tested if species' past biogeographic dispersal success can be used as a proxy for their present-day naturalisation capacity in biological invasions. To do so, we used phylogenetic and species distribution of 12 clades of tetrapods from Weil, Gallien, Nicolaï, et al. (submitted) and additionally compiled naturalisation data. We estimated species' past movements between biogeographic regions defined at clade-level using 100 biogeographic stochastic maps (BSMs, Dupin et al. 2017). Movements of species between bioregions were counted as the number of dispersal events for each species' lineage averaged across all 100 BSMs. To be able to compare clades with each other, we standardised the number of past colonisations at clade level. Finally, we compared introduced and naturalised species with introduced but not naturalised species and tested if the number of past colonisations was related to present-day naturalisation success using phylogenetic logistic regressions (R package 'phy-

loim', Ho and Ane 2014). While previous work showed in three plant clades (pines, eucalypts and acacias) that there is a significant relationship between past colonisations and present-day naturalisation success (Gallien, Saladin, et al. 2016; Gallien, Thornhill, et al. 2019), we did not find any significant relationships in tetrapod clades. One possible explanation for this is that the pool of introduced species was already heavily biased (Allen, Street, et al. 2017; Capellini et al. 2015). Among the 12 tetrapod clades, 91% of introduced species crossed major barriers due to intentional human transport (see also Hulme 2009), and human activities have been shown to favour species' with certain traits (Street et al. 2023). It is also possible that other factors are more important than species past colonisation capacities; introduction effort (or propagule pressure) has been shown to be a consistent predictor of species naturalisation success (Cassey et al. 2018).

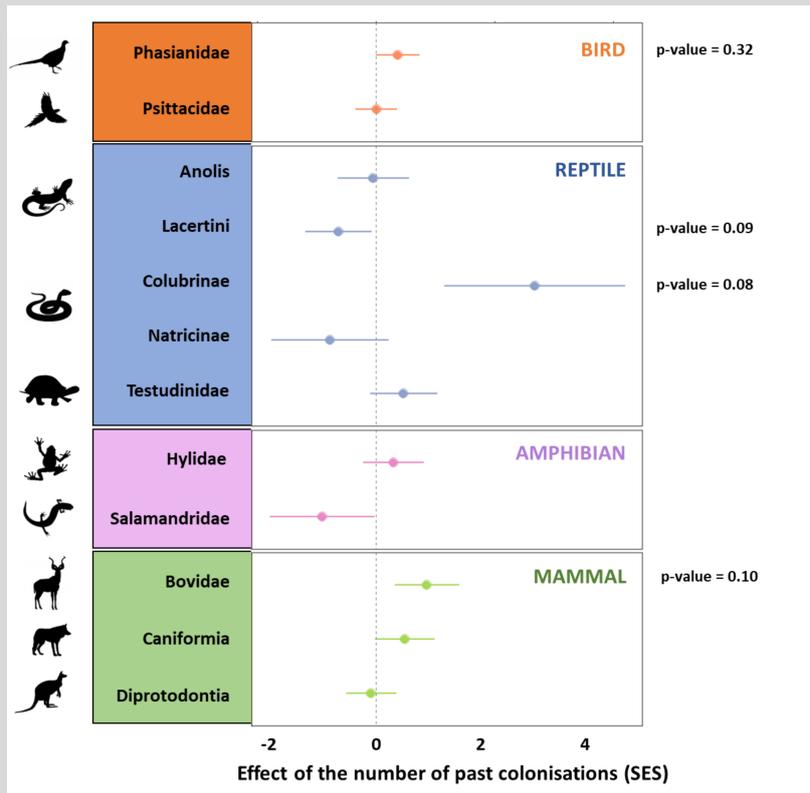


Figure 2: Effect of the number of past colonisation events in present-day naturalisation success (comparing introduced to established species in binomial logistic regressions).

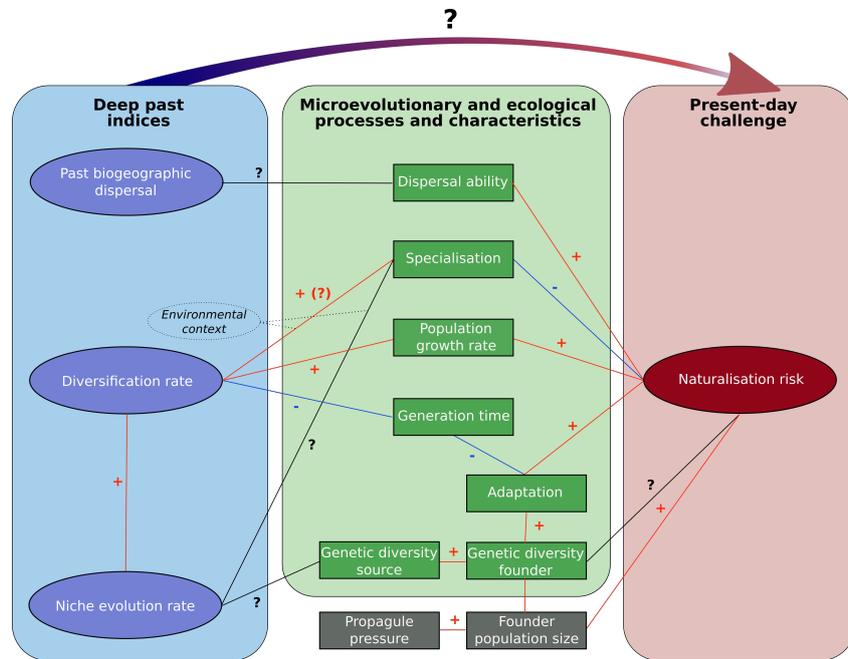


Figure 3: Summarising links between deep past indices and present day processes linked to species' naturalisation risk. Direction of links is indicated by + (positive), - (negative), or ? (unknown or context-dependent).

## Perspectives

In this review, we have shown a multitude of pathways linking macroevolutionary events and processes to present-day dynamics with implications for invasion and conservation ecology. Integrating past information to inform present-day processes holds a lot of promise, but we also show that underlying hypotheses need to be explicitly formulated and tested. Particularly obvious is the lack of studies investigating the effect of macroevolutionary rates on range size, population size and genetic diversity and how these relationships vary depending on different processes, e.g. speciation mode, and environmental context (temperate/tropical). Furthermore, different extinction/invasion-promoting characteristics and processes interact in complex ways and jointly determine species' extinction risk and invasion potential (Fig. 1, 3). However, in most studies, these processes were considered separately. The integration of several involved processes might be an important step forward. Concerning studies linking macroevolutionary rates to present-day extinction risk, the majority of studies used IUCN threat categories as a proxy for extinction risk. However, actual extinction data for the last century is

(unfortunately) available. This data could be very useful to validate relationships that were found using IUCN data; did the species that went extinct belong to lineages with high or low diversification or niche evolution rates?

Given that underlying assumptions are sufficiently tested, we see two lines of future research using macroevolutionary and biogeographic information to inform contemporary processes. First, past dispersal capacities have been linked to invasion success (Gallien, Saladin, et al. 2016; Gallien, Thornhill, et al. 2019, this article), but we did not find any study investigating the relationship between past biogeographic movements and species' range expansions related to climate change. Especially in high-latitude environments, long-distance dispersal has been shown to be an important driver of plant species' range expansions (Alsos, Ehrich, Eidesen, et al. 2015; Alsos, Ehrich, Seidenkrantz, et al. 2016; Alsos, Pernille, et al. 2007), and this could prove to be an exciting opportunity for future research.

Second, another new avenue of research may lie in the study of patterns in multiple groups to identify ecological interactions that proved to be consistent at macroevolutionary scale (see also Condamine et al. 2013). This may help us identify potential dependencies in existing assemblages and anticipate species' interactions in novel assemblages. Biotic interactions may prove to be more important than abiotic limits in species' persistence (Cahill et al. 2013; Ockendon et al. 2014), and they can hinder or facilitate species' establishment (Kleunen et al. 2018). Indeed, coextinctions have been proposed to dominate future vertebrate losses.

However, several methodological challenges are evident. The first one concerns the joint reconstruction of past biogeographic movements and trait evolution. Currently, methods only allow the use of binary traits and few regions, limiting their useability in complex situations. Second, small phylogenies can tell us little about the past given the high number of parameters to estimate and small statistical power. However, well-resolved species-level phylogenies are becoming increasingly available which is a great opportunity (e.g. Tonini et al. 2016; Upham et al. 2019). Phylogenetic uncertainty remains and should be taken explicitly into account. Third, extinction rates are also difficult to estimate (Rabosky 2010) because fossils are scarce, and our knowledge of past extinctions is biased towards taxa that leave them (e.g. animals and marine life, Davies 2019).

One of the greatest challenges is related to the magnitude of current human impact: How do we extrapolate from deep past events to current ones, when human influence is massive and leads to unprecedented environmental change (rate of warming and increase of CO<sub>2</sub> in atmosphere both higher than what has been observed in the past, extinction rates are about 1000 times higher than background rates (Pimm et al. 2014))? In addition, human impact is widespread but not evenly distributed across the globe. The geography of threat may override ecological differences between species and evolutionary history (Lenzner et al. 2020; Verde

Arregoitia, Leach, et al. 2015). Prevalence of risk has been shown to be higher in the Old World than in the New World and higher on islands than on continents (Davies, Fritz, et al. 2008). The uneven distribution of threat may also make it difficult to distinguish between geographic and phylogenetic structure: closely related species have a tendency to live close to each other and may hence be affected by the same threats (Purvis et al. 2000), independently from their intrinsic characteristics. These patterns may be lost in global analyses, and geographically explicit studies are necessary to disentangle the effects.

Lastly, a large body of literature exists on general barriers to the implementation of ecological research into conservation practice. Dealing with uncertainties and scalability of results has been identified as a key challenge (see e.g. Rapacciuolo 2019; Santini et al. 2021; Zizka et al. 2022) and this holds true for the integration of macroevolutionary studies into conservation science.

## **Conclusion**

Altogether, we found evidence that diversification rates might be useful as proxies for endemism, specialisation, small range and population sizes. However, underlying assumptions need to be tested first at clade-level. Evolutionary rates, on the other hand, are unlikely to be relevant for approximating species' short-term adaptative potential to global changes and invasion potential as the time scales are too different. Past extinction rate are potentially useful as a proxy for present-day extinction risk, but this link requires further investigation. Lastly, past biogeographical movements may be a proxy for capacity of establishment into novel environments for plants, but not for tetrapods. This last result is based on studies of very few clades and also requires further research.

The greatest challenges regarding the link between past and present-day processes concern the anthropocene challenge: How do we extrapolate deep past events to current ones, when human influence is massive and leads to unprecedented environmental change? In addition to this, threats are not equally distributed across the globe and humans further impact the actual processes as well, e.g. by modifying dispersal processes (natural past biogeographic dispersal compared to present-day biological invasions). While using past information to inform present-day processes and help us identify species at risk of extinction or with high invasive potential is a promising research avenue, much work still needs to be done.

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# Chapter 4

## Past dispersal and present-day invasions

In Box 1 of chapter 2 we already saw a brief glimpse of the results of this chapter. Here, I present this analysis about the role of past biogeographic dispersal success in present-day biological invasions in more detail. This chapter is based on work that was carried out together with Marceau Habrant, whose internship I supervised together with Laure Gallien between March and August 2022. I provided data (from chapter 2) and some of the code for the analysis, he carried out the analysis, and we jointly interpreted the results. The following chapter is based in parts on his report of the internship.

### Introduction

Biological invasions are key drivers of ecosystem declines and incur considerable economic costs to society, but despite continued efforts to prevent them, the rate of biological invasions is increasing, and is projected to continue to do so (Diagne et al. 2021; IPBES 2019; Seebens et al. 2021). We therefore need to better understand the determinants of success at each phase of the invasion process: transport, introduction, naturalisation and spread (Blackburn, Pyšek, et al. 2011).

A number of variables have been used to predict success in the consecutive stages of the invasion process in tetrapods. Generally, species that have a high association with humans and those that are ‘charismatic’ have a higher chance of being transported elsewhere, both unintentionally and intentionally (e.g. through pet trade; Lockwood et al. 2019, Theoharides and Dukes 2007). Transport pathways may affect introduction and establishment success as in some cases success may be actively encouraged by humans (e.g. in introductions for conservation purposes or hunting). Survival at the introduction site tends to increase for these

transported species with high reproduction and long reproductive lifespans (as found in mammals, amphibians and reptiles; Allen et al. 2017, Capellini et al. 2015). Population persistence, ie. establishment success, appears to depend first and foremost on propagule pressure (Blackburn, Lockwood, et al. 2015), as well as suitability of the environment at the introduction site and a fast life history strategy (Allen et al. 2017; Capellini et al. 2015; Hayes and Barry 2008; Sol et al. 2012; Theoharides and Dukes 2007). In birds, however, a fast life history has been proposed to be only advantageous in certain circumstances, whereas a bet-hedging strategy seems to be generally more effective (Sol et al. 2012). Lastly, high levels of genotypic and phenotypic diversity have been found to increase establishment success of invaders (Forsman 2014). Success in the spread stage has been linked to competitive ability, fast life history traits and introduction effort (Allen et al. 2017; Blackburn, Lockwood, et al. 2015; Capellini et al. 2015; Vermeij 2005). Body size has been linked to various stages of the invasion process in reptiles, mammals and birds, and sometimes in antagonistic manner, i.e. relationships between body size and success changed from one stage to the next (Jeschke and Strayer 2006; Kolar and Lodge 2001; Reed et al. 2012).

Traits have been used to predict species' potential to cross the barriers associated with each phase of the invasion process, however, they vary among taxonomic groups and can be difficult to measure (e.g. genotypic diversity). Gallien, Thornhill, et al. (2016; 2019) therefore proposed to use successful past biogeographic colonisations as a proxy for species' dispersal and establishment capacity in the invasion process. This is because past dispersal across major biogeographic barriers can be considered conceptually similar to the invasion process: both involve the crossing of biogeographic barriers, and the establishment in new conditions starting from a small founder population. Success in past and present colonisations may hence be due to the same underlying traits. Gallien, Thornhill, et al. (2016; 2019) found a positive relationship between the past number of colonised biogeographic regions and species' naturalisation success in three plant clades (pines, Australian eucalypts and acacias). However, whether this relationship is consistent across clades is not known.

Tetrapods are among the most human-transported clades (Lockwood et al. 2019) and they belong to the group that causes the greatest environmental damage in biological invasions (Pimental 2007). Here, we test if past colonizations can be a useful predictor of success in the introduction and establishment stages of the invasion process in 12 tetrapod clades. We then compare this predictor to previously identified determinants of invasion success, including specific traits (body size and life history strategy), association with humans and area on Earth with suitable climatic conditions (potential range size).

## Material and methods

We selected those clades of Weil et al. (submitted) in which at least two naturalised and two introduced but not naturalised species occurred. Data on invasion status was extracted from Capellini et al. (2015), Allen et al. (2017), and Sol et al. (2012). 12 clades fulfilled this criterion: two amphibian clades (Hylidae, Salamandridae), two bird clades (Phasianidae, Psittacidae), three mammal clades (Bovidae, Caniformia, Diprotodontia) and five reptile clades (Anolis, Colubrinae, Lacertini, Natricinae, Testudinidae)(for sample sizes per clade and invasion stage see Fig. 4.2a,b). For each species of these clades we calculated the number of successful dispersal events in their biogeographic history. We then used binomial logistic regressions to assess the relationship between those variables and success in the introduction and establishment stages of biological invasions.

### Calculating the number of past dispersal events

To determine the number of past dispersal events in each lineage, we first extracted each clade's biogeographic history using biogeographic models from Weil et al. (submitted). Briefly, for each clade, Weil et al. (submitted) used a data-driven approach to define biogeographic regions (by calculating phylogenetic beta-diversity followed by a UPGMA clustering algorithm). Then, they defined three manual dispersal multiplier matrices (MDMM) for each clade which allows to define differences in dispersal probabilities depending on the barriers that are crossed. In one MDMM, oceanic and continental dispersal had the same probability, in another MDMM, continental dispersal was set to 0.5 and oceanic dispersal was half as likely, and in the last MDMM, continental dispersal was set to 0.5 and oceanic dispersal was 1/10 as likely. They ran all combinations of biogeographic models (3 base models x 3 MDMMs) with and without the +x extension of BioGeoBEARS which takes geographic distance between regions into account. This resulted in 18 models per clade which they compared with the corrected Akaike Information Criterion (AICc). To take uncertainties in these biogeographic estimations into account, we calculated AICc-weighted averages of all estimated parameters (including only models where AICc was greater than 5%). Based on the model-weighted parameters, we performed Biogeographic Stochastic Mapping (BSM, Dupin et al. 2017) to generate 100 possible biogeographic histories per clade. We then extracted the number of past dispersal events in each lineage for each of these maps and averaged them to obtain the mean number of past dispersal events per species.

### **Additional variables known to influence invasion success**

In order to assess the performance of the number of past colonisations as a predictor of introduction and establishment success, respectively, we compared it with a number of variables known to influence invasion success: species' intrinsic traits, potential range size, and association with humans. We extracted species' body size and body size-independent life history strategy from Weil et al. (submitted) which corresponds to species' positions on the two factors per clade they identified through phylogenetic factor analysis (Hassler et al. 2022; Tolkoﬀ et al. 2018).

We calculated each species' potential range size following Higgins and Richardson (2014). Briefly, we conducted a principal component analysis (PCA) on the following climatic variables from the WorldClim database (Fick and Hijmans 2017): mean diurnal range, maximum temperature of the warmest month, minimum temperature of the coldest month, annual precipitation and precipitation seasonality (variables BIO2, BIO5, BIO6, BIO12, BIO15, extracted at a 10m resolution). We then defined each species' native realised niche by calculating its convex hull in the PCA space of the first two principal components (`tri.mesh` function in R package `tripack` (Gebhardt et al. 2020)). This was based on species' distribution data, see Weil et al. (submitted) for details. Finally, we determined the number of pixels on Earth in which the climatic conditions were suitable for the species, i.e. contained in the convex hull, which corresponds to a species' potential range size.

As a proxy for the association with humans, we calculated for each species the overlap between its realised niche and the human niche (human footprint overlap, HFO, henceforth). Species with high values have thus a climatic niche similar to that of highly urbanised areas, and are more likely to be introduced and used by humans. To calculate HFO, we used the human footprint map (Venter et al. 2016) and extracted human occurrences (arbitrarily using 50% as a threshold to transform this map into a binary one). We then extracted the PCA coordinates where humans were considered as present and estimated the overlap between those coordinates and species' climatic conditions with the R package 'ecospat' (v.3.3 (Di Cola et al. 2017), using "T", a modified Hellinger metric (Warren et al. 2008)). Measures of HFO ranged between 0 and 1, with greater values indicating greater overlap, i.e. higher association with humans.

Finally, we also compiled information about transport pathways, which can affect success across the invasion process (Jeschke and Strayer 2006), from the literature (Allen et al. 2017; Ballari et al. 2016; Biancolini et al. 2021; Blythman and Porter 2020; CABI International 2022; Camposano et al. 2008; Carpio, Álvarez, et al. 2020; Carpio, Guerrero-Casado, et al. 2017; Carrete and Tella 2008; Centre 2022; Desenvolvimento e Conservação Ambiental (The Horus Institute for Environmental Conservation and Development) 2022; Dyer et al. 2016; Frith and

Calaby 1974; Garrido and Jaume 1984; Gortázar et al. 2000; Groupe de travail national Invasions biologiques en milieux aquatiques 2022; Heinsohn 2001; ISSG 2015; King and Krakauer 1966; Lever 2003; Medway 2010; Mittermeier and Plotkin 1980; NOBANIS 2022; Ruiz, Carlton, et al. 2003; Rutkowski et al. 2015; Saul et al. 2017; Toda et al. 2010; U.S. Geological Survey 2022; Yokoyama 2012).

## **Association between past number of dispersal events and success in present-day invasions**

To assess the relationship between the past number of dispersal events and success in present-day invasions, we used a methodology similar to that of Gallien, Saladin, et al. (2016). Data on invasion status allowed us to create two binary variables: (1) introduced vs not introduced species, and (2) established vs introduced but not established species. Not enough data was available to extend this to the spread stage of invasions. For each of these response variables, we built binomial logistic regressions using generalised linear models. We first built bivariate regressions for each clade, assessing only the effect of past dispersal success. If phylogenetic signal was present in the residuals we repeated this step with phylogenetic regressions (R package ‘phylolm’, Ho and Ane 2014). In a second step, we repeated these regressions for the establishment stage, but excluded species that were introduced intentionally for conservation or hunting purposes. This is because in introductions for conservation or hunting purposes, humans may actively encourage invasion success which might confound the results.

To compare the performance of the predictor “past dispersal success” to other variables known to influence invasion success, we built multivariate binomial regressions. We did this only for the introduction stage due to low establishment data availability, and only for those clades where past dispersal success was a significant predictor of introduction success (i.e.  $p$ -value < 0.05). The goodness-of-fit was evaluated through a likelihood-ratio-test, using the adjusted  $D^2$  (Zuur et al. 2009), calculated as  $D^2 = 1 - (L_{model}/L_{null})$  where  $L$  is the likelihood of the model with predictors and the null model.  $D^2$  can vary between 0 and 1 and is maximal when the model fits perfectly to the data. All variables were centred and scaled for all regressions.

## **Results**

### **Linking past dispersal to success biological invasions**

The number of successful past dispersal events in a species’ biogeographic history was a significant predictor of species’ introduction success in biological invasions

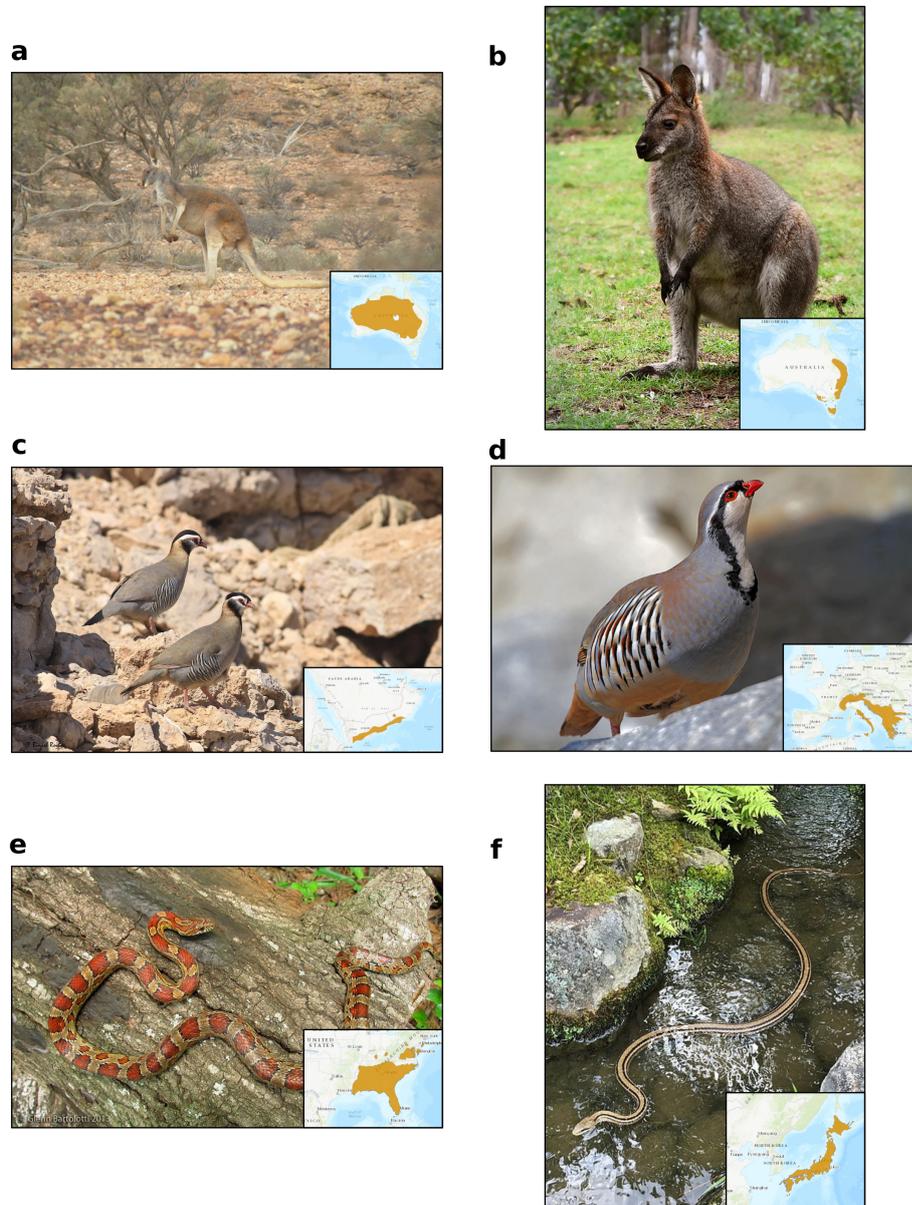


Figure 4.1: Examples of species that reached different stages of the invasion process. a) *Osphranter rufus* Desmarest, 1822 (Diprotodontia), not introduced (Wikimedia Commons contributors 2023a, under a CC BY 2.0 license); b) *Notamacropus rufogriseus* Desmarest, 1817 (Diprotodontia), established (Wikimedia Commons contributors 2023b, under a CC BY-SA 3.0 license); c) *Alectoris melanocephala* Rüppell, 1835 (Phasianidae), not introduced (Wikimedia Commons contributors 2022a, under a CC BY-SA 4.0 license); d) *Alectoris graeca* Meisner, 1804 (Phasianidae), introduced (Wikimedia Commons contributors 2020b, under a CC BY-SA 3.0 license); e) *Pantherophis guttatus* Linnaeus, 1766 (Colubrinae), introduced but not established (Wikimedia Commons contributors 2020a, under a CC BY-SA 4.0 license); f) *Elaphe quadrivirgata* H. Boie, 1826 (Colubrinae), established (Wikimedia Commons contributors 2022b, under a CC BY-SA 4.0 license). Distribution maps are from IUCN (2022).

in two of 12 tetrapod clades, Phasianidae and Diprotodontia (Fig. 4.2a). It was a successful predictor of establishment success only in Colubrinae (Fig. 4.2b). Excluding species that were intentionally introduced for conservation or hunting for the analysis of established *vs* not established species did not change the results in a significant way (the p-values of Lacertini and Bovidae increased above the 0.10 threshold, however).

### **Comparing past dispersal to other predictors**

The variable “past dispersal success” performed better than other predictors in Diprotodontia (Fig. 4.2d,  $D^2 = 0.33$ ). For each additional past colonisation, the odds of success in introductions increased by 2. In Phasianidae, however, past dispersal success was not significantly related to introduction success when comparing it to other variables in a single model. Instead, species’ life history and potential range size were better predictors of introduction success (Fig. 4.2c,  $D^2 = 0.38$ ). This may be because the variable past colonisation was positively correlated with life history (Pearson correlation 0.59,  $pval < 0.001$ ).

## **Discussion**

We showed that past biogeographic dispersal success was related to success in present-day biological invasions in three of 12 tetrapod clades. In Phasianidae and Diprotodontia it was related to success in the introduction stage. Although past dispersal success was related to establishment success in Colubrinae, this result should be regarded with caution as sample size was quite low (ten species not established, three species established). When comparing past dispersal success to other variables in a single model, it was a better predictor of introduction success only in Diprotodontia, but not significant in Phasianidae. Overall, past biogeographic dispersal success is not a strong predictor of present-day invasion success in the large majority of our selection of tetrapod clades. However, there is indication that it may be relevant in some circumstances. Investigating this further would be highly relevant to understanding the importance of intrinsic factors and historical contingency in facilitation invasions.

### **Why is past biogeographic dispersal not a good predictor in most clades?**

The fact that the number of past successful biogeographic dispersal events is not a good predictor of tetrapod invasion success suggests either evolutionary lability in traits facilitating past dispersal and colonisation of species, and/or differences

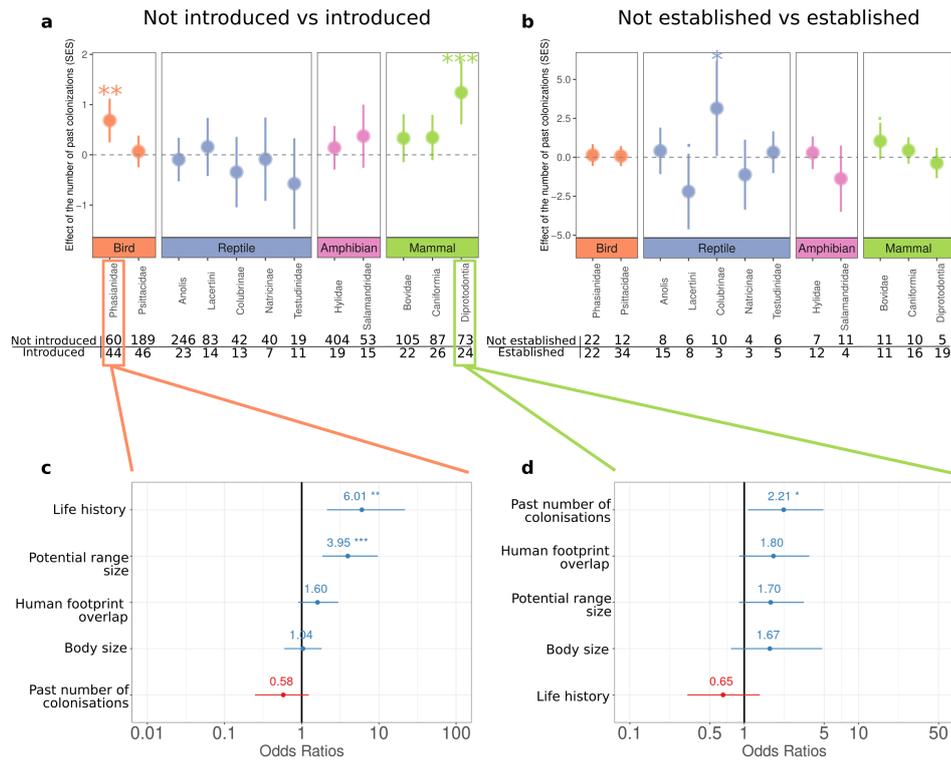


Figure 4.2: Results of binomial logistic regressions. a) Evaluating the effect of the number of past dispersal events on success in the introduction stage of biological invasions. b) Evaluating the effect of the number of past dispersal events on success in the establishment stage of biological invasions. Sample sizes are given in the tables below a) and b). c) and d) Odds ratios for different predictors that were assessed in multivariate logistic regressions, separately for Phasianidae (c) and Diprotodontia (d).

between the traits favouring historical colonisations and present-day invasions. While body size may be phylogenetically conserved, life history traits have been found to be more labile (Blomberg et al. 2003; Kamlar and Cooper 2013). An argument in favour of trait lability in Phasianidae is that life history was positively related to introduction success, just like it was to past biogeographic dispersal success in Weil et al. (submitted). The relationship between life history and success is thus conserved in both processes. The fact that the variable past number of dispersal success did not show a higher correlation with the trait life history may thus indicate that the trait is evolutionary labile. In future studies, it may hence be useful to use methods that take trait evolution on the phylogeny into account, for instance trait-dependent biogeographic models (Klaus and Matzke 2020). These models can integrate binary traits and determine relative dispersal rates for the two trait states. It would be interesting to test whether introduced (or established species) would be estimated to have had higher dispersal rates in the past than not-introduced (not-established) species. At this point in time, however, these models perform poorly with very unbalanced traits (which is the case for introduced/not-introduced comparisons) and many missing species (which is the case for established/not-established comparisons).

We know that human-mediated transport in biological invasion constitutes a modification of the geographic filter compared to natural biogeographic dispersal. Indeed, past introductions of species in new regions were led by rare stochastic meteorological (e.g. storms, Ozgo et al. 2016; Raxworthy et al. 2002) or demographic events (e.g. curious individuals, Canestrelli et al. 2016), whereas nowadays most introductions are led by more frequent human-mediated voluntary or accidental transports (Hulme 2009; Lockwood et al. 2019). In more than 80% of cases vertebrates have been introduced intentionally (Saul et al. 2017). Being aesthetically pleasing to humans or useful for humans may thus be a better predictor of introduction success than past correlates of dispersal success (Essl et al. 2011; Hulme et al. 2008). Indeed, we found different relationships between traits and invasion success than Weil et al. (submitted) for the two clades in which we explicitly included traits, except for the life history-dispersal relationship in Phasianidae. In Phasianidae, body size was not related to introduction success, but it was positively related to past biogeographic dispersal success. In Diprotodontia, neither body size nor life history were significantly related to introduction success, whereas Weil et al. (submitted) found a positive relationship between body size and biogeographic dispersal success and a bell-shaped one between life history and past biogeographic dispersal success. Different traits thus seem to have facilitated past biogeographic dispersal and present-day invasion success at both the introduction and naturalisation stages in these two clades.

The fact that most species today are introduced intentionally is likely to also affect the establishment stage. First, the introduction filter biases the pool of species

that arrives at the second stage of the invasion process. For instance, species with high reproductive rates are intentionally selected for in the context of pet trade such that there may be little variability in life history traits of introduced species (Street et al. 2023). This may explain why there may be no further significant relationship in the establishment stage. Second, voluntary transport of animal species is usually followed by care for the reproduction in captive conditions (e.g. pet trade, Lockwood et al. 2019) leading to a bigger population size and more frequent immigration when accidental release occurs. In such cases, introduced species avoid demographic stochastic events such as Allee effects (Taylor and Hastings 2005).

Past dispersal was a better predictor of introduction success than other variables in Diprotodontia. Interestingly, at least five of the 24 successfully introduced species were already introduced in prehistoric times, including for example *Phalanger orientalis* which was transported to New Ireland around 20 000 BP (Haberle et al. 2010). Dispersal processes were certainly less modified than they are today which may explain why past biogeographic dispersal success may be a significant predictor in this clade. It is also possible that a trait related to biological invasions, e.g. attractiveness for humans (Essl et al. 2011; Hulme et al. 2008), incidentally correlates with past biogeographic dispersal success in Diprotodontia and that this may be the reason for the significant correlation. This could also be the case in Phasianidae and Colubrinae, which contain many species that are highly associated with humans (gamebirds in the case of Phasianidae, or aesthetically pleasing species often sold in the pet trade in the case of Colubrinae). In fact, traded species were found to have relatively high reproductive rates which are likely more lucrative in industries involving large-scale captive breeding (Street et al. 2023). These same traits are hypothesised to favour success in natural dispersal. Investigating in which clades attractiveness and traits favouring past dispersal success coincide could be helpful to better understand in which cases past dispersal capacities may be a good indicator of invasion success.

### **Why is past dispersal success related to invasion success in plants but not in animals?**

It is surprising that past dispersal success was not generally related to invasion success in the tetrapod clades we tested when it explained almost 10% of species' naturalisation success in three plant clades (Gallien et al., 2019, 2016). There may be several reasons for these contrasting results. As mentioned above, animals show high rates of evolution for behavioural and life history traits (Blomberg et al. 2003; Kamilar and Cooper 2013). Thus, if behavioural traits or life history traits were key in tetrapods' past biogeographical success, their lack of phylogenetic signal might

explain the poor predictive quality of past biogeographic dispersal success. However, measures of phylogenetic signal are susceptible to trait measurement error, and behavioural traits are difficult to measure accurately and consistently across species. In addition, alien plant species follow more unintentional introduction pathways than vertebrates (Saul et al. 2017) which may explain why relationships in biological plant invasions may resemble more past relationships than in tetrapods. In future studies it might therefore be interesting to take information on transport pathways into account. Finally, sample sizes for our study were generally quite small compared to the studies of Gallien, Saladin, et al. (2016) and Gallien, Thornhill, et al. (2019) (e.g. acacia: 315 of 1020 species successfully introduced, 71 successfully naturalised) which might explain why we did not observe many significant associations between past dispersal and invasion success, particularly in the establishment stage. It might therefore be of interest to repeat this study at a larger scale, e.g. order-level instead of clade-level. However this is currently challenging due to a lack of data on success across the invasion process and phylogenetic relationships. In addition, estimating biogeographic histories at such high taxonomic levels is not straightforward (e.g. only a limited number of bioregions can be considered due to computational constraints, and a single bioregionalisation scenario would be required but barriers are species-specific, see also part I).

In this study we investigated whether it is possible to use past biogeographic dispersal success as a predictor of success in present-day biological invasions. We show that past dispersal success can be linked to success in biological invasions in three out of 12 tetrapod clades. These results therefore suggest that past dispersal success is generally not a good predictor of invasion success in tetrapods (with the exception of Diprotodontia). Several methodological and ecological factors can explain this lack of signal, including our limited sample sizes, evolutionary labile traits and/or changes in trait-dispersal relationships related to human influence. Processes of historical biogeography are major factors explaining current spatial patterns of biodiversity but the domination of ecosystems by humans has changed processes of spatial and taxonomic evolution. In this context, results of this study highlight the shift in the selection of species crossing geographic and environmental barriers. However, our study was limited by small sample sizes of introduced and established species in individual clades, and higher-level studies are necessary to confirm these results. Studies at the interface of historical biogeography, evolution and ecology have great potential for improving our understanding of current processes, and especially for better understanding how human influence has changed natural processes.

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## Chapter 5

# Past dispersal and present-day range shifts

One of the possible lines of future research we highlighted in chapter 3 was to relate past dispersal across biogeographic barriers to species' present-day range shifts in the context of environmental changes. Dispersal at leading edges of ranges most likely occurs through diffusive dispersal, but considerable barriers exist in today's human-modified landscapes. Therefore, trait-dispersal relationships derived from past dispersal across major biogeographic barriers may be informative and useful to explain differences in present-day range shifts at leading edges between species. In this chapter I present the beginnings of an investigation testing this hypothesis. This work is preliminary but already shows interesting results.

In chapter 4 we used the number of dispersal events in a species' past biogeographic history as a proxy for species' present-day invasion success. However, the past number of dispersal events was a weak and inconsistent predictor for present-day invasion success, possibly because traits can be evolutionarily labile. Therefore, I use here a slightly different approach: I determine species' dispersal and colonisation potential based on relationships between the traits body size and life history strategy and past dispersal success, as determined in chapter 2. I then relate this dispersal and colonisation potential to present-day range shifts at leading edges. This approach further allows me to directly test if trait-dispersal relationships are conserved in different dispersal contexts, i.e. in past biogeographic dispersal and in present-day ecological dispersal in the context of range shifts.

## Introduction

Latitudinal and elevational shifts of species' ranges in response to changing environmental conditions have been observed in many taxa in the last decades (Kerr 2020;

Lenoir, Bertrand, et al. 2020; Parmesan and Yohe 2003). Generally, species' ranges are shifting towards higher latitudes and higher elevations in response to rising temperatures. However, there are a multitude of species' specific responses (Chen et al. 2011; Lenoir and Svenning 2015). In some cases, poleward or high-elevation edges are not expanding, possibly due to dispersal barriers or biotic interactions inhibiting establishment, and in other cases, equatorward or low-elevation edges are not retracting, possibly due to species' local adaptations or plastic responses (Boutin and Lane 2014). Some cases have been observed where trailing edges even expanded towards the equator or towards lower elevations. Range changes are therefore highly species specific, not only in the way the range changes shape, but also in the magnitude of extension or retraction. Species-specific range changes could lead to a large-scale reshuffling of the Earth's biota, and difficulties in predicting which species will be able to track their niches across space in response to climate change. Determinants of differences in range shifts between species are still not well known. To better predict species' responses to changing environmental conditions, we need to have a greater understanding of which species will be able to track their niche across space, and which ones will instead depend on sufficient plasticity or adaptation to avoid extinction.

Several factors have been linked to the velocity of species' range shifts, among them the velocity of isotherm shifts and human pressures in a given region (Lenoir, Bertrand, et al. 2020), as well as species' intrinsic traits (Angert et al. 2011; MacLean and Beissinger 2017). Lenoir, Bertrand, et al. (2020) found for example that human impact (measured through the human footprint index) is negatively related to range shifts in terrestrial species. Among traits, diet breadth and habitat breadth were positively correlated with range shift velocities, but other traits, such as body size or fecundity, showed no significant effects (Angert et al. 2011; MacLean and Beissinger 2017). However, even models including significant variables had low explanatory power (Angert et al. 2011). Lenoir, Bertrand, et al. (2020) further found that differences in methodologies between studies explained the largest part of the variance.

It is perhaps surprising that previous work did not show significant associations between body size, life history traits and velocities of range shifts, especially at leading edges where dispersal is the major determinant of range shifts. These traits have been associated with dispersal capacity and range expansions at individual and population level, and dispersal capacities in different contexts. For instance, at leading edges of populations, species with large bodies, high growth rates, and fast life history strategies (early age of sexual maturity, greater reproductive output, shorter lifespans) were found to be overrepresented (Chuang and Peterson 2016). Stevens et al. (2014) found that body size and life history traits were related to dispersal capacities at species level, via complex (U-shaped or bell-shaped) relationships. Similarly complex relationships between these traits and dispersal

and establishment success were also found on a historic biogeographic scale (Weil et al. submitted). Both Stevens et al. (2014) and Weil et al. (submitted) found that trait-dispersal relationships were clade-specific and could include positive linear and negative as well as U-shaped and bell-shaped relationships. Limited explanatory power in previous studies associating traits and range shifts could therefore stem in part from the disregard of more complex clade-specific trait-dispersal relationships.

Here, I propose to use information on past trait-dispersal relationships inferred from species' biogeographic histories to explain differences in species' present-day shifts at leading range edges. On a conceptual level, range expansions at leading edges can be considered as diffusive dispersal, whereas biogeographic dispersal might be considered as jump dispersal. However, results from Lenoir, Bertrand, et al. (2020) suggest that movement of terrestrial species today is strongly impacted by human activities, indicating that considerable barriers impede species' movement in our heavily fragmented landscapes. Hence, we might expect some similar traits to be important in both processes (e.g. body size, which is hypothesised to be related to movement, and life history traits, which are linked to the establishment process in new locations), but also with differences: for example traits related to survival in urban areas such as small size or generalist diet (Pacifci et al. 2020), may be overrepresented in successful range expanders when compared to successful dispersers across biogeographic barriers. To test how past trait-dispersal relationships can explain differences in present-day range shifts, I first used clade-level relationships between traits and past biogeographic dispersal success to determine species' potential dispersal capacity. Then, I used linear mixed effects models to relate these dispersal capacities to present-day range shifts and estimated their effect compared to other variables, including traits, local velocities of temperature change, human pressures, and methodological variables. Past biogeographic trait-dispersal relationships may help us better understand differences in species' shifts at leading range edges today, and lead to progress on a conceptual level regarding the comparability of dispersal processes across different spatiotemporal scales.

## **Materials and methods**

### **Relationships between traits and past biogeographic dispersal success**

Weil et al. (submitted) determined the relationships between two traits, body size and body size-independent life history strategy, and dispersal probabilities in biogeographic histories of 56 tetrapod clades containing 7009 species. I extracted

species' positions on the body size and life history factors that Weil et al. (submitted) used as traits (from hereon  $f_{body}$  and  $f_{LH}$ ) and determined each species' dispersal rate based on their trait-dispersal relationships. I did this separately for body size and life history strategy, which resulted in two variables of past dispersal rates ( $past\_disp\_body$  and  $past\_disp\_LH$ ). I scaled these variables at clade level for later inter-clade comparisons.

## Velocities of latitudinal range shifts and further extrinsic variables

I extracted velocities of latitudinal leading edge shifts from Lenoir, Bertrand, et al. (2020) for tetrapods. This variable describes the rate or velocity of species' range shifts along the elevational or the latitudinal gradient (in m/year and km/year, respectively) and is based on a collection of studies that cover different time periods. I excluded data where quality was low and families with less than three observations (leaving 312 species) to standardise the extracted velocities at family level (by subtracting the mean and dividing by the standard deviation). Finally, I selected those species for which data on past biogeographic dispersal was available (in total 31 observations).

Along with velocities of range shifts, I extracted local velocities of temperature shifts ( $LatVeloT$ ) and human pressures (the human footprint index,  $HFI$ ) provided by Lenoir, Bertrand, et al. (2020). I scaled  $HFI$  and  $LatVeloT$  at family-level, but due to low resolution in these variables this resulted in a loss of three species, leaving a total dataset of 28 observations in 22 species in 6 clades (Tab. 5.1). I further extracted the following methodological information relating to the individual studies that are included in Lenoir, Bertrand, et al. (2020) BioShifts database: hemisphere, type of observation (occurrences or abundances), grain (coarse or medium), significance (if significance was reported, binary variable), area (total surface area of polygons for a given case study, three levels), start date of the baseline survey (grouped in three time periods), and total number of species considered in the study (grouped in two levels). For more information regarding these variables see supplementary tables of Lenoir, Bertrand, et al. (2020).

## Statistical analysis

To relate variables to differences in leading edge range shifts between species, I adapted the methodology from Lenoir, Bertrand, et al. (2020). First, to estimate effects of methodological biases in range shifts, I built linear mixed effects models (lmer from the lme4 R package (Bates et al. 2015), setting REML to FALSE for maximum likelihood estimations) for each methodological variable separately and

Table 5.1: Species included in the analysis and number of latitudinal range shift observations at leading edges per species. The columns body size/dispersal relationship and life history/dispersal relationship show which relationship between a trait and past biogeographic dispersal success was identified in Weil et al. (submitted).

Class	Clade	Species	Number of observations	Body size-past dispersal	Life history-past dispersal
Aves	Corvidae	<i>Aphelocoma californica</i>	1	positive	U-shaped
		<i>Corvus ossifragus</i>	2	positive	U-shaped
		<i>Garrulus glandarius</i>	3	positive	U-shaped
		<i>Pica nuttalli</i>	1	positive	U-shaped
		<i>Pica pica</i>	2	positive	U-shaped
		<i>Pyrrhocorax pyrrhocorax</i>	2	positive	U-shaped
	Icteridae	<i>Quiscalus major</i>	1	U-shaped	negative
		<i>Quiscalus mexicanus</i>	1	U-shaped	negative
	Tyrannidae	<i>Sayornis nigricans</i>	1	positive	none
	Reptilia	Colubrinae	<i>Coronella austriaca</i>	1	bell-shaped
<i>Coronella girondica</i>			1	bell-shaped	positive
<i>Zamenis longissimus</i>			1	bell-shaped	positive
Lacertini		<i>Lacerta bilineata</i>	1	positive	none
		<i>Lacerta schreiberi</i>	1	positive	none
		<i>Podarcis hispanicus</i>	1	positive	none
		<i>Podarcis muralis</i>	1	positive	none
		<i>Timon lepidus</i>	1	positive	none
		<i>Zootoca vivipara</i>	2	positive	none
Viperinae		<i>Vipera aspis</i>	1	none	negative
	<i>Vipera berus</i>	1	none	negative	
	<i>Vipera latastei</i>	1	none	negative	
	<i>Vipera seoanei</i>	1	none	negative	

compared them with a null model based on corrected AICs (using the function AICc from the MuMIn package (Barton 2022)). In the following models, I included those methodological variables that had a lower AICc than the null model as random effects. To relate past dispersal rates to present-day range shifts and estimate their effect compared to other variables, I built linear mixed effects models separately for each non-methodological variable, including previously chosen methodological variables as random effects. The fixed variables included in this step were: *past\_disp\_body*, *past\_disp\_LH*, *f\_body*, *f\_LH*, *LatVeloT* and *HFI*. Then, I compared these models again by AICc, selecting those variables that explained scaled range shifts better than the null model. I finally combined the random and fixed variables chosen in previous steps in a single model and computed the marginal (i.e. variance explained by the fixed effects) and conditional (i.e. variance explained by both the fixed and random effects)  $R^2$  values using the *r.squaredGLM* function from the MuMIn package (Barton 2022).

## Results

Body size and life history traits were not good predictors of species' range shifts when they were directly used in the models (models including these variables performed worse than the null model). However, using clade-specific relationships between life history and past biogeographic dispersal rates, which included U- and bell-shaped relationships, significantly improved the model ( $\Delta AICc > 2$  compared to the null model;  $AICc_{past\_disp\_LH} = 70.48$  compared to  $AICc_{null} = 73.3$ ). Based on Tab. 5.1, a fast life history strategy was thus linked to range shift success in Colubrinae, whereas a slow life history strategy was linked to range shift success in Viperinae and Icteridae. Both a fast and a slow life history strategy was linked to range shift success in Corvidae. In two out of the six clades (Lacertini and Tyrannidae, eight observations), there was no detectable relationship between species' life history and range shift success.

In addition to *past\_disp\_LH*, the inclusion of *HFI* and *LatVeloT* also increased model performance (both with  $\Delta AICc > 2$  compared to the null model;  $AICc_{HFI} = 66.9$ ,  $AICc_{LatVeloT} = 70.41$ ). Both variables were positively related to the velocity of range shifts (Fig. 5.1). Furthermore, the spatial resolution of the raw data on which the velocities of range shifts were based (methodological variable "grain") was related to range shift estimates ( $AICc_{grain} = 72.4$ ). Studies at coarse spatial resolutions (estimating range shifts based on range maps or atlas grids with a spatial resolution greater than 100km) detected much smaller range shifts than studies at higher spatial resolutions. In the full model combining all variables that improved the null model, 25.8% of the variance was attributable to fixed effects and 36.8% to random effects, resulting in a total of 62.6% explained variance.

## Discussion

Altogether, this analysis shows that relationships between traits (here body size and life history strategy) and range shifts at leading edges are not straightforward, but that information from past dispersal can be useful to explain present-day range shifts. Importantly, relationships between life history and past dispersal success, including more complex U- and bell-shaped relationships, varied between clades (Tab. 5.1, Weil et al. (submitted)). Thus different strategies are predicted to facilitate range expansions at leading edges in different clades.

While life history strategy was linked to range shift abilities, body size was not: neither as untransformed nor as transformed variable. Life history strategy is hypothesised to be linked to the establishment stage of the dispersal process whereas body size is thought to be more related to the movement stage (Safriel and Ritte 1980; Stevens et al. 2014; Vermeij 2005). Therefore, this is initial evidence

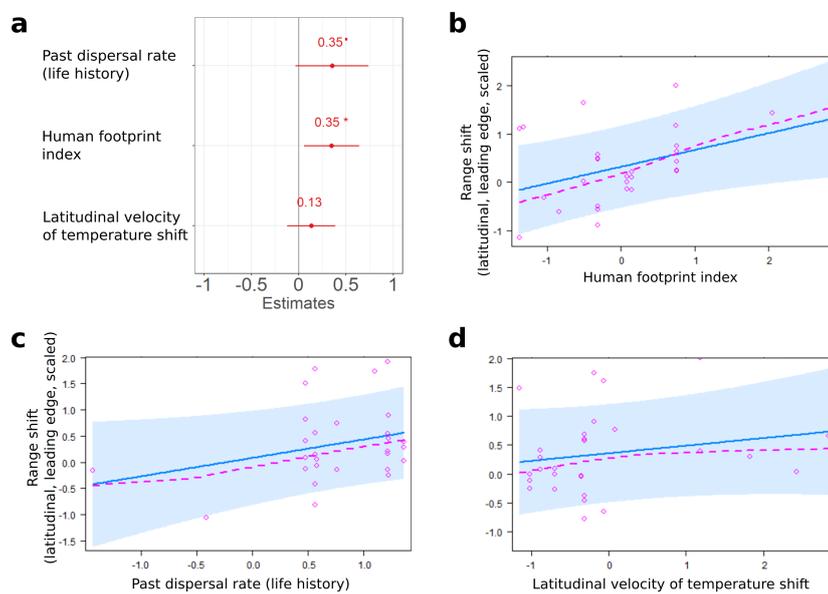


Figure 5.1: Variables related to present-day range shifts. a) Effect sizes of past dispersal rate (based on relationships between life history and past biogeographic dispersal success), human footprint index and latitudinal velocities of temperature shifts, based on a linear mixed effects model which also included grain of the analysis as a random factor. b), c) and d) Predictor effect plots of the individual variables.

that establishment might be comparable between past biogeographic dispersal and present-day range expansions, but that movement is different in both processes. This may be because biogeographic dispersal is generally thought to happen passively, whereas range expansions are more likely to occur via active dispersal (Gillespie et al. 2012; Lomolino et al. 2017). Alternatively, different body sizes may facilitate dispersal in biogeographic dispersal compared to human-modified landscapes (large size may be advantageous for active dispersal in more natural landscapes, whereas small size may be advantageous for survival in more urban areas, see also Pacifici et al. 2020). Stevens et al. (2014) found that relationships between body size and natal dispersal distance in terrestrial animals were order-specific, and these relationships were partly different to those found by Weil et al. (submitted). For instance, they found a U-shaped relationship for Passeriformes whereas Weil et al. (submitted) found a positive relationship for Corvidae and Tyrannidae. It would be interesting to test whether the relationships found by Stevens et al. (2014) are more informative for range shifts, or possibly jointly with the life history-dispersal relationships determined by Weil et al. (submitted).

The results of this study confirm the importance of extrinsic factors, particularly local velocities of temperature shifts and human pressures, in determining species' range shifts (Lenoir, Bertrand, et al. 2020). However, in contrast to previous studies (Lenoir, Bertrand, et al. 2020) I did not find human pressures to impede species' range shifts. On the contrary, the relationship was significantly positive. One reason for this disparity might be that we could not test for interactions between several variables due to low sample size. In addition, human influence was small to moderate (median HFI 0.25, maximum HFI 0.42), and this relationship might be different in more modified landscapes. To fully understand and predict range shifts, using a combination of extrinsic and intrinsic factors is undoubtedly necessary.

Despite being better than the null model, the explanatory power of fixed effects was still weaker than that of random effects. The spatial resolution of the raw data on which the velocities of range shifts were based (methodological variable "grain") explained more variance than the fixed effects of past dispersal success (based on life history strategy), latitudinal velocity of temperature shifts and human footprint index together (37% compared to 26%). This reflects findings of Lenoir, Bertrand, et al. (2020), where methodological variables explained close to 40% and fixed effects only about 8%.

Further, a number of limitations of this study need to be mentioned. First, most of the included observations showed positive range shifts, i.e. range expansions, and only 21% (six observations) showed negative ones. The sample of observations included in the present analysis is therefore not representative of the 350 observations in Lenoir, Bertrand, et al.'s (2020) database of good quality terrestrial latitudinal range shifts at leading edges, where range shifts were negative in 36% of all cases (126 observations). Second, the species selected for this analysis also hap-

pened to be good dispersers to begin with (based on the relationship between life history and past biogeographic dispersal success). I used data scaled at clade-level, but only two data points were negative (first quartile of dispersal rate based on life history was at 0.56, median at 0.76). More data on poor dispersers is necessary to elucidate if the relationship holds across the full distribution of dispersal capacities. Third, this analysis is spatially biased, as only data from the northern hemisphere were available. In addition, data were mostly available from regions characterised by low to moderate human pressures (median HFI 0.25, maximum HFI 0.42, HFI is scaled between 0 and 1). We might expect differences in traits being linked to successful range expansions in different geographic contexts (e.g. biogeographic realms, Pacifici et al. (2020)) and along gradients of human pressure.

Lastly, the sample size of this study is generally very low, and included few taxonomic groups (only birds and reptiles). It would be interesting to extend this analysis to other groups of organisms to test if the relationship between traits and past biogeographic dispersal success is ubiquitously conserved in trait-range shift relationships. In particular plants might be an interesting study subject, as information on past biogeographic dispersal capacities has already been shown to be a good predictor of present-day invasion success (Gallien, Saladin, et al. 2016; Gallien, Thornhill, et al. 2019). In addition, more good quality data of latitudinal range shifts at leading edges is available for plants than for animals (at least in the BioShifts database). More extensive spatial and taxonomic sampling is necessary to test hypotheses linking past biogeographic dispersal and present-day dispersal in the context of range expansions across spatial and taxonomic scales.

In summary, I show that species' life history strategy can be useful to understand present-day range shifts when relationships between life history and past biogeographic dispersal success are taken into account. This supports the hypothesis that past biogeographic dispersal and present-day range shifts may be comparable to a certain degree. In addition, extrinsic information on local velocities of temperature shifts and human pressures is necessary to complete our understanding of this pattern. However, differences in methodology still explain a lot of the variation in species' latitudinal range shifts at leading edges. These initially promising results call for analyses with wider geographic and taxonomic scope, and possibly along gradients of human pressure.

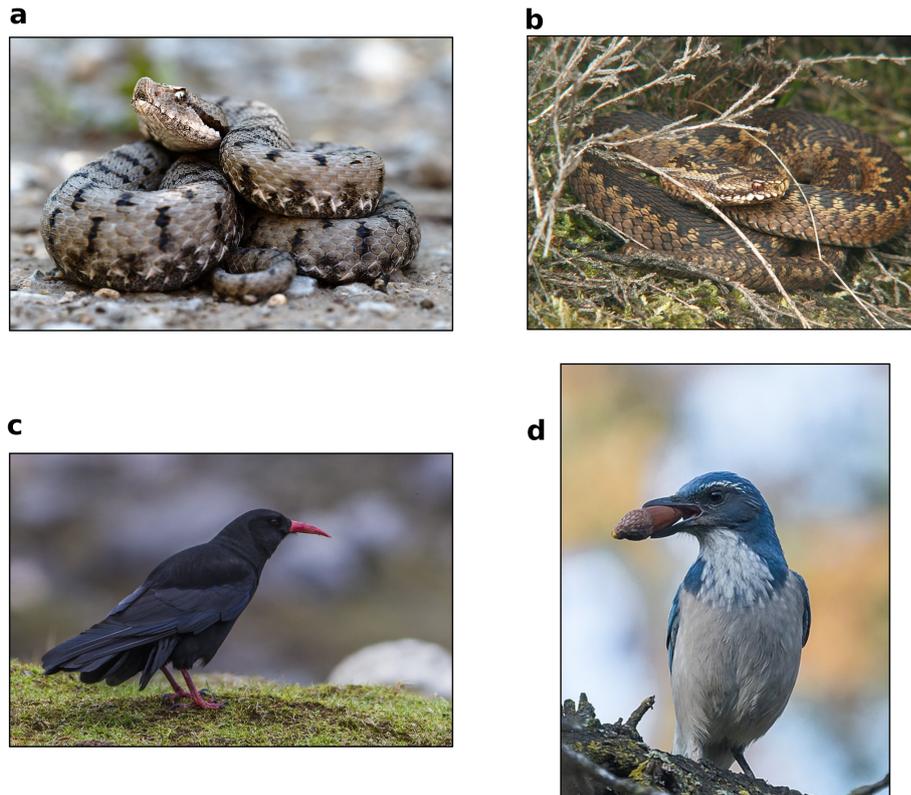


Figure 5.2: Examples of species with different range shift velocities. a) *Vipera aspis* Linnaeus, 1758 (Wikimedia Commons contributors 2022b, under a CC BY-SA 3.0 license) whose latitudinal leading edge is estimated to expand by ca. 0.60 km/year (family-scaled range shift of -0.67); b) *Vipera berus* Linnaeus, 1758 (Wikimedia Commons contributors 2022c, under a CC BY-SA 2.5 license) whose latitudinal leading edge is estimated to expand by ca. 2.43 km/year (family-scaled range shift of 0.73); c) *Pyrrhocorax pyrrhocorax* Linnaeus, 1758 (Wikimedia Commons contributors 2022a, under a CC BY-SA 3.0 license), whose latitudinal leading edge is estimated to retract by ca. 0.27 km/year (family-scaled range shift of -0.36); d) *Aphelocoma californica* Vigors, 1839 (Wikimedia Commons contributors 2020, under a CC BY 2.0 license) whose latitudinal leading edge is estimated to expand by ca. 7.4 km/year (family-scaled range shift of 1.24).

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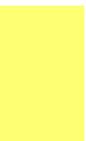
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## *Discussion*



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*"It looks like the journey ahead is going to be tough," said Tiny Dragon.*

*Big Panda grinned, "It looks like an adventure to me."*

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Available at [www.jamesnorbury.com](http://www.jamesnorbury.com). See also [www.instagram.com](http://www.instagram.com).

I started this thesis with a rare description of an observed biogeographic dispersal event, the rafting of species on debris from Japan to North America after a major earthquake. These seemingly chance dispersal events can be natural or human-mediated and are known to shape clades' biogeographic histories; they determine the distribution of both the dispersing species and of species in the receiving community, and they can open opportunities for speciation (Lomolino et al. 2017; Queiroz 2005). On smaller scales, dispersal is integral to species' persistence and it allows species to react to changes in their environment directly through movement or indirectly through adaptation (Clobert et al. 2012; Garant et al. 2007). Dispersal is thus an essential process in the present-day context of climate and land-use changes. Multiple factors influence dispersal ability and propensity of organisms which leads to variability at different scales; there are differences between individuals, populations, species and higher taxonomic levels (Clobert et al. 2012). Differences in dispersal abilities and propensities on ecological scales have been linked to organisms' traits, and the relationship between traits and dispersal outcomes is relatively well understood at these scales. However, it is unclear whether these relationships are conserved across taxonomic scales and across different geographic contexts. The role of traits in large-scale biogeographic dispersal is thus not well understood.

With this thesis I have made progress on an empirical and conceptual level regarding the role of species' traits in dispersal processes. In part I we showed that body size and life history strategy matter in past dispersal on a grand scale. While conceptual work on this topic dates back more than 150 years, this was the first large-scale empirical test spanning multiple tetrapod taxa, made possible by methodological advances, increased data availability and computational power. I found that trait effects and shapes of trait-dispersal relationships vary between clades and that this variation is in part attributable to variation in type and strength of crossed biogeographic barriers, as well as intra-clade trait variability and clades' average body size and life history strategy. This analysis further confirmed that trait-dispersal relationships are often more complex than what is generally assumed, as was already shown by Stevens, Whitmee, et al. (2014) for ecological dispersal.

In part II I endeavoured to better understand the transferability of information from deep past analyses across spatiotemporal scales. We found that multiple pathways link macroevolutionary indices to processes which determine species' present-day invasion potential and conservation needs. Underlying assumptions, e.g. regarding the relationships between the rate of past trait evolution in a lineage and species' current adaptive potential, are rarely tested, but this is necessary before any inferences are made. I then explored two relationships between past and present dispersal in more detail. First, past dispersal ability revealed itself to not be a good predictor of present-day invasion success in the majority of the 12 tested tetrapod clades, possibly due to evolutionary trait lability or human influence in the

filters of the invasion process. However, there is indication that it may be relevant in some circumstances. Second, life history-dispersal relationships, likely related to the establishment of new populations, may be comparable in past biogeographic dispersal and present-day range shifts.

This work thus opens exciting new avenues of research that have the potential to advance our knowledge of past and present dispersal processes. Better understanding dispersal processes at different scales is essential to increase our understanding of what determines global biogeographic patterns and to identify species' invasion potential and conservation needs. In the following sections I detail several of these research avenues.

## **5.1 The role of traits in dispersal**

In previous studies, traits have been linked to dispersal outcomes on various scales and in various contexts: at within-species level in ecological dispersal, in biological invasions and in range shifts. Trait-dispersal relationships were found to vary between taxa and between environmental contexts (Allen, Street, et al. 2017; Angert et al. 2011; Capellini et al. 2015; MacLean and Beissinger 2017; Ronce and Clobert 2012; Stevens, Whitmee, et al. 2014; Theoharides and Dukes 2007). Similarly, we found in chapter 2 that neither body size nor life history strategy were consistently linked to past biogeographic dispersal success, and that the magnitude of trait effects and trait-dispersal relationships varied between clades. We further found in chapters 4 and 5 that trait-dispersal relationships are not or only partly conserved between past and present-day processes. We do not yet have a good understanding of why trait-dispersal relationships are inconsistent. However, given the results from previous chapters, it is possible that the strength of barriers, as well as differences in relative strengths of filters across the dispersal process may play a role (see also following sections). The inconsistency of trait-dispersal relationships is an intrinsically interesting problem which requires investigation to further our understanding of the natural world. In addition, it is desirable to better understand these inconsistencies if we want to make reliable predictions of trait-dispersal relationships in different contexts. The reliability of predictions, particularly under changing environmental conditions, depends on our ability to transfer knowledge into different situations, and this is only possible if we have a deeper understanding of underlying mechanisms and processes (Evans 2012; Sequeira et al. 2018). To make efficient decisions regarding policy and conservation measures, reliable predictions are crucial, especially given the role that dispersal plays in today's context of climate and land-use changes.

### 5.1.1 Strength of barriers

In chapter 2 we proposed one factor that may influence the role traits play in dispersal: strength of barriers that are crossed. To test the influence of barrier strength, we used the average number of dispersal events on the phylogeny for a given bioregionalisation scenario as a proxy for the strength of barriers (the more dispersal detected, the weaker the barrier), and we found this proxy to be an important explanatory variable of differences in trait effects between clades. This reflects findings from ecological dispersal, where matrix harshness (characterised through nutrient availability or predation pressure) has already been found to modify the degree of association between traits and dispersal (Bestion et al. 2014; Cote, Dahirel, et al. 2022; Jacob et al. 2020). This may be because increased matrix harshness raises the cost of dispersal and consequently acts as a stronger filter on phenotypes (Cote, Bestion, et al. 2017; Cote, Dahirel, et al. 2022; Jacob et al. 2020).

Barrier strength may consequently affect trait-dispersal relationships in different dispersal processes. In chapter 2 we compared different clades with each other and thus used a proxy for barrier strength as no absolute measure of barrier strength exists. However, it is possible to test the isolated effect of barrier strength more explicitly. This can be done by creating several bioregionalisation scenarios of different strengths within one clade: the bioregionalisation procedure we used creates a dendrogram that describes the degree of phylogenetic similarity between individual raster cells (Fig. D1a). Biogeographic regions are then constructed by choosing a cut-off threshold (arbitrarily or via some optimization rules; e.g., R package ‘*phyloregion*’, Salvador and Chan 2004) which groups all raster cells below that threshold into one region. By choosing a series of cut-off thresholds, it is thus possible to create a series of hierarchical bioregions (Fig. D1b). The different levels of bioregionalisation should then correspond to bioregionalisations of different strengths and the effect of traits can thus be evaluated as a function of barrier strength within individual clades (Fig. D1c).

However, this approach would be influenced by three major limitations which may also have affected our analysis in chapter 2: the constraints in biogeographic models regarding the number of bioregions and trait states, the stability of barriers through time, and measuring absolute barrier strength. First, it would still rely on trait-dependent biogeographic models to assess the effect of traits in the different bioregionalisation scenarios. Yet, current trait-dependent models are severely limited by the number of regions that can be considered, as well as the fact that only a binary trait can be considered. This is due to computational constraints that are unlikely to change soon. In chapter 2 we proposed an approach that circumvents the problem of the binary trait which consists of testing different binarization thresholds. Unfortunately, very detailed bioregionalisation scenarios cannot be

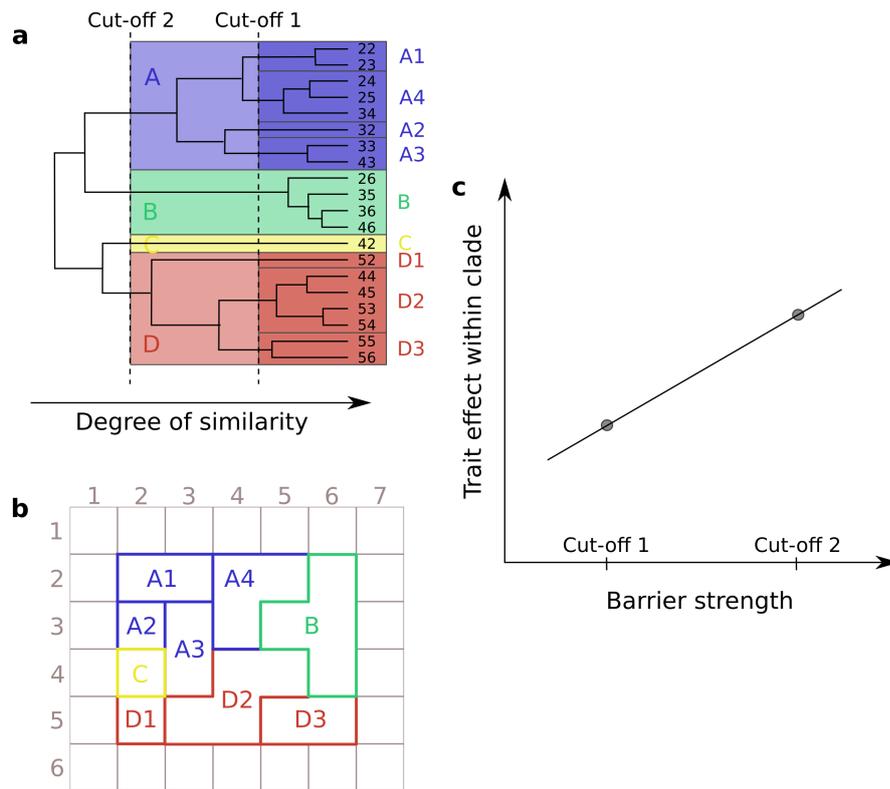


Figure D1: Proposed methodology for testing the influence of barrier strength in trait effects. a) Dendrogram describing phylogenetic similarity between raster cells which are depicted in b) (individual raster cells are indicated at tips of the dendrogram, first digit corresponds to lines of raster, second digit corresponds to column of raster). Two cut-off thresholds are indicated which lead to two different bioregionalisation scenarios: cut-off 1 results in nine bioregions, cut-off 2 in four. These bioregions are visualised in b). c) Hypothesised relationship between barrier strength and trait effects.

tested with current methods. However, there are different methods that could be and have been used to test the effect of barriers on trait-dispersal relationships on ecological scales. These include experimental approaches where habitat matrices of different harshness degrees are created and the traits of successful individual dispersers are measured (Cote, Dahirel, et al. 2022; Jacob et al. 2020). In the field, cost-distance modelling could be useful to identify strengths/costs of different landscape elements and associate them with trait-dispersal patterns (Etherington 2016; Stevens, Verkenne, et al. 2006). Comparisons of barrier effects on trait-dispersal relationships at different scales would be helpful to understand to which degree these effects are transferable between scales.

The second major limitation when testing the effect of barrier strength on a biogeographic level concerns the stability of barriers through time, which is essential but difficult to determine. Including phylogenetic information in the bioregionalisation process is an important step but at the moment the resulting bioregionalisations are likely impacted by uncertainty in phylogenetic relationships, as well as geographic and taxonomic biases in sampling effort (which also counts for species' distribution data). In future studies, robustness of bioregionalisations in respect to phylogenetic uncertainty as well as biases in species' distribution data needs to be explicitly assessed.

Finally, there is no absolute measure of barrier strength. Comparisons within clades may be feasible as bioregionalisations with different cut-off thresholds let us identify the relative strengths of bioregionalisation scenarios. However, comparisons between clades are more difficult and may continue to rely on proxies such as the average number of dispersal events on the phylogeny we used in chapter 2.

### **5.1.2 Relative filter effects across dispersal stages**

Another factor that may influence trait-dispersal relationships is the relative strength of different filters across the dispersal process. The consecutive stages of dispersal processes are associated with different filters, which in turn are linked to specific traits (Blackburn et al. 2011; Clobert et al. 2012; Estrada et al. 2016; Ronce 2007). Body size, for instance, is thought to be linked to the movement or transport stage whereas life history is more likely to be key in the establishment stage. The relationship between one given trait and success in different dispersal stages may vary as well. For instance, large size might be advantageous in the movement or transport stage, but it may hinder establishment because it might reduce the chance that several individuals arrive simultaneously at the same location, decreasing propagule pressure. In biogeographic dispersal, especially past biogeographic dispersal, we have no information about failures at different stages, as we often do for biological invasions. Therefore, it is impossible with current data and

methodologies to test associations of traits with specific dispersal stages in this context. We can only look at the final relationship between traits and combined dispersal and establishment outcomes. However, it is likely that the relative strength or selectivity of the filters related to the different dispersal stages varies depending on the context (e.g. Bonte et al. 2012; Theoharides and Dukes 2007). This may then affect the traits that are linked to the overall dispersal success. The emigration filter, for instance, is likely to be strong in transoceanic dispersal, i.e. opportunities of dispersal are mostly determined by a coastal distribution. In continental dispersal, on the other hand, the establishment filter may be of greater importance, and hence those traits associated with it (e.g. life history). Differing relative filter strengths may also affect the relationship between a given trait and dispersal success; for instance, the correlation between body size and dispersal success might be positive or negative depending on whether the movement/transport or establishment stage is more determinant.

One way to test the influence of changing selectivity of filters on traits associated with dispersal could be to compare clades across a gradient of filter strength. Mountain passes have been suggested to be “higher in the tropics” (Janzen 1967), i.e. a stronger movement/transport filter, because tropical species may have narrower physiological niches compared to temperate species which have to deal with strong seasonal climatic differences. But there is also considerable evidence that biotic interactions determine distributions of tropical species more strongly than distributions of temperate species (LaManna et al. 2017; Paquette and Hargreaves 2021; Schemske et al. 2009; Zvereva and Kozlov 2021). The strength of the filter associated with the establishment stage should consequently decrease with latitude, and traits related to establishment (e.g. life history strategy) might be less decisive than movement traits (Fig. D2). As a next step, it might thus be interesting to test for a latitudinal gradient in associations between traits and dispersal outcomes (by comparing for example the effect of movement/transport and establishment traits in relatively restricted temperate and tropical clades).

### **5.1.3 Proportions of dispersal modes**

A third factor that may explain differences in trait-dispersal relationships between clades is the mode of dispersal. Different kinds of physical barriers may be associated with different proportions of active vs passive dispersal, and with different modes of active dispersal or passive dispersal vectors (Fig. D3). Different dispersal modes and different dispersal vectors, in turn, may select for different traits (Bonte et al. 2012; Gillespie et al. 2012). Low propagule mass, for instance, is an advantage for wind dispersal in plants whereas relatively heavy, fleshy fruits may be predominantly dispersed through endozoochory. Similarly, the traits related to the emigration and transport stages of dispersal in animals certainly depend on

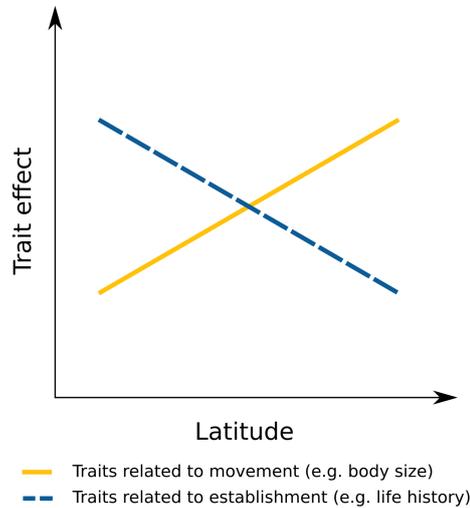


Figure D2: Testing the effect of relative strength of filters in the dispersal process. The relative strength of the filter associated with the establishment stage is hypothesised to decrease with latitude.

the mode of transport (active *vs* passive), and general trait-dispersal relationships should therefore be influenced by the proportion of active compared to passive dispersal that occurs. Different modes of transport and different dispersal vectors also impact the establishment stage and the filters and barriers associated with it because they may determine distance and direction of the movement (e.g. birds migrating preferentially north-south whereas atmospheric and oceanic currents move preferentially east-west; Gillespie et al. 2012). This in turn influences the characteristics of the receiving environment, e.g. presence/absence or abundance of kin, biotic and abiotic similarity of natal and receiving environment. These characteristics may determine which life history strategies are particularly successful for establishment.

To test hypotheses related to this idea on a biogeographic scale it would be possible to compare trait-dispersal relationships of sister clades in different settings, for instance island settings where only passive dispersal occurs with continental settings. The genus *Anolis* (iguanian lizards native to the Americas, including the Caribbean) could be a good case study for such an analysis. Differences in strength of biogeographic barriers should not affect this analysis since differences in strength were shown to impact effect size of traits and not the shape of trait-dispersal relationships (Weil, Gallien, et al. submitted).

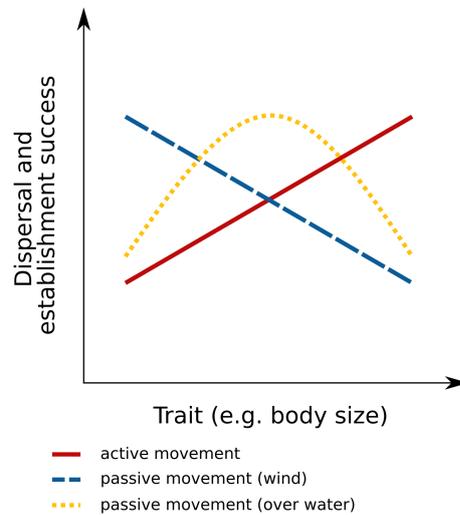


Figure D3: Trait-dispersal relationships depending on dispersal mode.

### 5.1.4 Towards spatio-temporal transferability of trait effects and shapes of trait-dispersal relationships

Altogether, these factors (strength of barriers, relative selectivity of filters across the dispersal process depending on environmental context, and proportion of dispersal modes) may explain a part of the variation we saw in trait effects and shapes of trait-dispersal relationships in chapter 2. They may also explain why trait-dispersal relationships are not easily transferable across taxonomic and spatial scales (see also chapters 2, 4 and 5). Different species may rely on different dispersal modes, and geographic specificities may determine the strength of barriers, as well as the relative importance of the individual dispersal filters. Integrating these factors into a general framework is necessary for the spatiotemporal transferability of trait effects and trait-dispersal relationships.

Concerning taxonomic transferability of trait-dispersal relationships, another important point to consider is intraspecific trait variability. In large-scale analyses of biogeographic dispersal, species' mean trait values are generally used. However, as seen in section 0.3.1, dispersal is not a species-level event, but rather an individual- or population-level event. And there is considerable intra-specific variation in traits related to dispersal (Evangelista et al. 2019; Milles et al. 2020). At this point, data availability is unlikely to be sufficient for analyses at large scales that include intra-specific trait variability, but conceptually it is certainly something that should be taken into account.

Finally, how do we choose which traits to test? With today's computing power there is a risk of massive undirected, not well thought out tests of traits but this

increases the risk of false positives (e.g. Burnham and Anderson 2002; Klaus and Matzke 2020). As I outlined in the introduction, a lot of conceptual work has already been done when it comes to traits that could be linked to biogeographic dispersal outcomes. These and further conceptual considerations should be the basis for future studies linking traits to biogeographic dispersal outcomes. In addition, physiological constraints and trade-offs between different traits can conceal similar trait-dispersal relationships between taxa, which is why the effect of traits on dispersal should not be considered in isolation but rather in concert. An attempt to do so was to combine species' life history traits into a single life history strategy in chapter 2. However, this is also a limitation because the identifiability of a species' life history strategy likely depends on trait data availability. In addition, it makes it more difficult to compare life history-dispersal relationships between clades. A multitude of trade-offs structure life history traits (chapter 2; Stearns 1992) and differences between taxa are still not very well understood (Allen, Weil, et al. in prep.).

## **5.2 From traits to dispersal to species' vulnerability in changing environments**

Above, I outlined several ideas about what factors might influence the role of traits in dispersal and lead to variation at taxonomic and spatial scales. But why do we need to know which traits facilitate dispersal in which situation or context? Dispersal is a major process determining species' responses to changing environmental conditions. It does so directly by allowing organisms to escape unfavourable conditions, and indirectly through its effects on population connectivity and gene flow which influence local adaptation and extinction (Clobert et al. 2012; Garant et al. 2007). The relationship between traits and dispersal might thus ultimately inform us about the ways that different species are most likely to cope or not cope with changing environmental conditions. However, the interaction of these different processes is complex (see also chapter 3) and it is therefore challenging to predict which species are especially vulnerable to climate change or increasing landscape fragmentation.

In chapter 5 I investigated how traits are linked to dispersal in the context of species' range shifts at leading edges. Despite it being a preliminary analysis, initial results indicate that the relationships between traits and past biogeographic dispersal success may be conserved to a certain degree and might thus inform us of species' abilities to track their niche through space. Firming up this finding and investigating in which contexts it holds is important to get a better understanding of how human impact modifies natural dispersal processes. But dispersal is only one

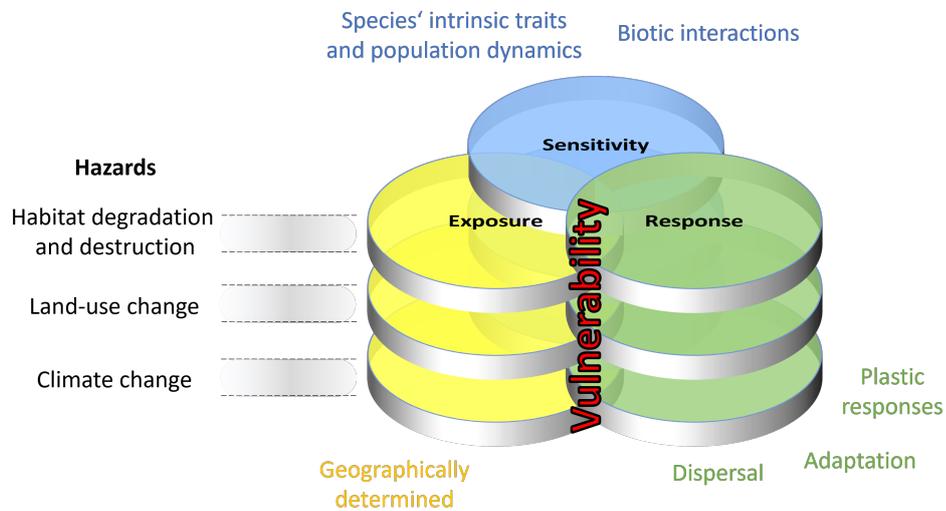


Figure D4: Determining species' vulnerability to global changes. Their risk depends on the interaction of different factors: exposure to individual hazards, such as climate or land-use change, individual sensitivity to given hazards, and possible responses.

side of the coin. To truly be able to determine species' vulnerability to changing environmental conditions, several additional factors need to be taken into account, in particular species' sensitivity, exposure and other possible responses to changing conditions (Dawson et al. 2011; Williams et al. 2008, Fig. D4).

First, the environment is changing today in multiple ways, related to climate change (e.g. increased temperature and changed precipitation patterns) and human influences (e.g. habitat fragmentation and destruction, pollution). These changes are not ubiquitous, but some regions of the Earth are more affected than others (e.g. Cox et al. 2022). Exposure to these pressures thus varies between species. In addition, sensitivity of species varies as well: species characterised by combinations of certain traits have been shown to be more vulnerable than others, and different pressures affect functional strategies to different degrees (Carmona et al. 2021; Rodriguez-Caro et al. 2022; Weil, Rodriguez-Caro, et al. in prep.). Biotic interactions are a crucial factor to take into account in this context (Berg et al. 2010). They can lead to extinction cascades, especially in communities with low functional redundancy, and can impede species' responses to changing conditions, namely establishment in new locations (Fowler 2010; Sanders et al. 2018).

Finally, apart from dispersal, species can also respond through adaptation or plastic changes in phenotypes to changes in their environment (e.g. Donelson et al. 2019; Lavergne et al. 2010). Adaptation allows species to persist in their current habitat in the face of changing environmental conditions. Adaptation is not independent from species' dispersal capacities: generally it is assumed that

an intermediate level of dispersal allows the greatest adaptive divergence (Garant et al. 2007). A second response to changing environmental conditions are plastic changes in phenotypes, i.e. phenotypic changes that are not genetically based. These processes are not mutually exclusive, but it is difficult to clearly attribute observed changes to evolutionary adaptation (Merilä and Hendry 2014). In fact, most changes attributed to ongoing climate change seem to be plastic (Boutin and Lane 2014).

To accurately assess species' vulnerability to global changes, integration of all the above-mentioned factors is necessary, i.e. exposure, sensitivity, and possible responses. For some of these processes we can use traits as proxies (general adaptation ability, dispersal capacities). But there are taxonomic and geographic idiosyncrasies (biotic interactions, barriers, human pressures) that call for spatially explicit analyses. In the majority of current projections of species' future distributions, the above-detailed factors are not taken into account, however, it is an essential aspect to incorporate in future studies as we know that including them can change predictions (Kubisch et al. 2013; Pollock et al. 2014; Valladares et al. 2014).

### **5.3 Concluding remarks**

Large-scale analyses, such as the present one, can help to uncover which factors and processes are influential, and can indicate which responses are possible. This thesis thus highlights the important role that traits play in dispersal across scales, and which traits in particular are associated with dispersal in different tetrapod clades. However, we still need a better mechanistic understanding of variation in trait-dispersal relationships across scales, especially if we want to make useful predictions that can guide policy and conservation measures. To do this, I indicated several possible ways to investigate factors that could mediate trait-dispersal relationships in different contexts (e.g. barrier strength, relative strength of filter effects across dispersal stages, proportions of dispersal modes). In the long term, however, it is necessary to move towards more integrative analyses that take species' exposure and sensitivity to threats into account, as well as other possible responses (e.g. plasticity, adaptation). Only then will we be able to accurately determine the vulnerability of species to global change and act accordingly.

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# Appendices

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# Supplementary material to „Chameleon biogeographic dispersal associated with extreme life history strategies”

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## **1. Methodology to assess phylogenetic uncertainty**

When assessing the effect of phylogenetic uncertainty on parameter estimates, we wanted to represent the whole tree space while maintaining a reasonable computation time. We thus calculated pairwise distances (using the Kendall Colijn metric with emphasis on branch lengths) between 1000 trees of the posterior distribution (using the 7th 1000 posterior sample from Tonini et al. 2017) and performed a principal coordinates analysis using the R package ‘treespace’ (Jombart et al. 2017). We selected a set of 100 trees in a way that maximized the distance between the trees within this set, and simultaneously minimized the distance between trees outside the set to the nearest within-set tree.

Then we repeated the phylogenetic factor analysis for each of the 100 trees to reclassify species as big bodied vs. small bodied and as having a fast vs. slow (or extreme vs. intermediate) life history strategy. We also reclassified the dispersal syndrome where species were hypothesized to be dispersal prone if they held all three dispersal traits: coastal distribution, big body and fast (or extreme) life history strategy. Finally, we ran the best trait-dependent BioGeoBEARS model (DEC+m2) on the selected 100 trees.

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## 2. Details about the bioregionalization methodology

Biogeographic regions can be estimated in many ways. Recent approaches for bioregionalization propose to either (i) apply clustering algorithms on matrices of phylogenetic beta-diversity (Holt et al. 2013, Kreft and Jetz 2010), or (ii) use network methods (McDonald-Spicer et al. 2019, Newman 2006, Vilhena and Antonelli 2015). The performance of several methods has been compared in the literature but results are inconclusive because of changes in the methods compared and performance criteria used to assess them (Bloomfield et al. 2018, Casagrande et al. 2012, Vilhena and Antonelli 2015). We thus tested several approaches: (i) a network method (modularity simulated annealing, R package ‘netcarto’, Doucier and Stouffer 2015, Guimerà et al. 2007), and (ii) two different phylogenetic beta-diversity indices (modified Simpson’s phylogenetic beta-diversity index - “Simpson” (Lennon et al. 2001 after Simpson 1943) - and Kulczynsky - “K2” (Kulczyński 1927 as cited in Shi 1993), equations Eq. S1 and Eq. S2) at two different raster resolutions (93x93km and 186x186km) followed by a UPGMA clustering algorithm (Fig. S1). We chose the UPGMA clustering method as it was identified as the best clustering algorithm for our dataset (function `select_linkages` in the R package ‘phyloregion’, Daru et al. 2020). The optimal number of clusters was based on the ‘elbow’ of the graph where explained variance was plotted against the number of clusters (Salvador and Chan 2004; function `optimal_phyloregion`, package ‘phyloregion’). The phylogenetic beta-diversity matrix was weighted by a geographical distance matrix (Great Circle Distances on Lat/Long coordinates) to introduce a contiguity constraint (based on packages ‘HiClimR’, Badr et al. 2015, and ‘ClustGeo’, Chavent et al. 2017). The different bioregionalization methods were evaluated based on their capacity to determine continuous bioregions and to explain a maximum of variance with a minimum of regions. If non-contiguous regions were identified, we separated them manually and assigned two different areas. In the end, the Simpson phylogenetic beta-diversity and UPGMA approach was selected at a resolution of 93x93km, and identified nine biogeographical regions: north Africa and Arabia, central Africa, southeast Africa, southwest Africa, India, Socotra, Madagascar, the Comoros Islands and the Seychelles (Fig. 2 in the main text).

$$\text{Eq. S1} \quad \text{Simpson} = \frac{\min(b,c)}{\min(b,c)+a}$$

$$\text{Eq. S2} \quad \text{Kulczynsky} = \frac{1}{2}a \frac{2a+b+c}{(a+b)(a+c)}$$

where  $a$  = length of shared branches on the phylogenetic tree between two different raster cells,  $b$  &  $c$  = length of unique branches in two different raster cells.

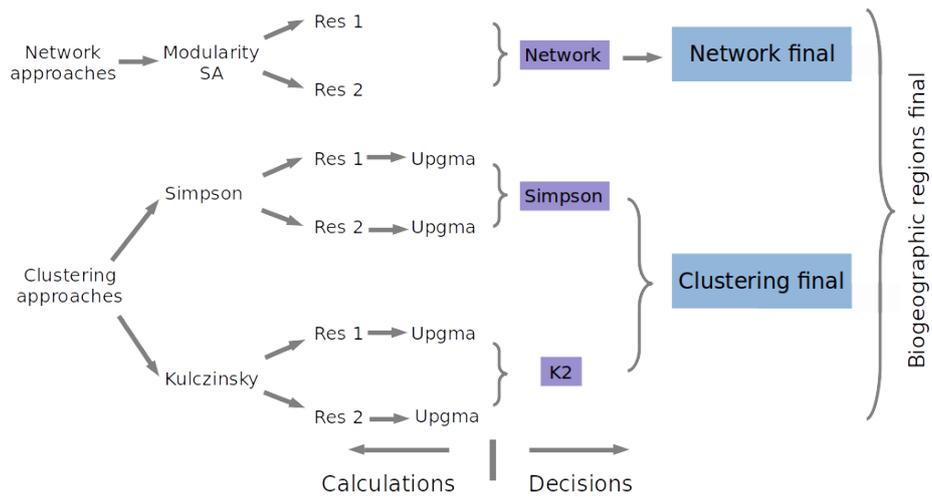


Figure S1: Determining the method for calculating biogeographic regions. Upgma: Unweighted pair group method with arithmetic mean; Res: Resolution of the rasters, K2: Kulczinsky diversity index.

### 3. Species range combinations in BioGeoBEARS

To reduce computation time, we manually specified the ranges that were possible for species to inhabit in the BioGeoBEARS models. Since all extant species occupy three or less biogeographic regions, we allowed all single and two-region ranges. We added all three-region ranges that are currently occupied by an extant species and all three-region ranges that were plausibly occupied in the past (Tab. S1).

Table S1: Three-region combinations that were allowed in the BioGeoBEARS analysis.

North Africa & Arabia	Central Africa	Seychelles	Comoros Islands	southwest Africa	Madagascar	southeast Africa	Socotra	India
1	1		1					
1	1			1				
1	1					1		
1	1						1	
1							1	1
	1	1	1					
	1	1			1			
	1		1		1			
	1		1			1		
	1			1		1		
	1				1	1		
	1						1	1
		1	1				1	
		1	1					1
		1			1			1

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#### 4. Classification of coastal species

We classified species that lived less than 10km away from the sea as coastal (74 species). In addition, we also tested other classifications: 2km (63 coastal species), 15km (82 coastal species), 25km (88 coastal species). These different classifications did not alter our results (Tab. S2).

Table S2: Results of the BioGeoBEARS analyses where species were classified as coastal according to different distances from the sea. Only models with an AICc weight greater than 1% are included. m2: dispersal multiplier of species in trait state 2 (the non dispersal prone form); x: dispersal multiplier of geographic distance.

Trait set	Best models	LnL	AICc weight (%)	m2	x
Coastal distribution: 2km	DECm2	-259	68	0	0
	DECm2x	-259	32	0	-0.08
Coastal distribution: 15km	DECm2	-270	59	0	0
	DECm2x	-269	41	0	-0.12
Coastal distribution: 25km	DECm2	-267	57	0	0
	DECm2x	-266	43	0	-0.13

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## 5. Phylogenetic factor analysis

We employed phylogenetic factor analysis (PFA, Tolkoﬀ et al. 2018) to identify the axes along which the life history phenotypes have evolved. We applied a cross-validation model selection strategy to infer the number of factors. Our cross-validation procedure generated 20 partitions of the data into a training set containing 90% of the data and a test set containing the remaining 10%. We then performed PFA assuming the number of factors  $k = 1, \dots, 5$  and used the posterior of the inferred parameters and the training data to predict the values of the removed observations. The model with the lowest average mean squared-error (MSE) between the inferred observations and their true values (in this case a 2-factor model) was selected as the “best” and used in the final analysis.

Note that PFA readily accommodates missing data and computes the posterior distribution conditional on the observed data only. Specifically, PFA assumes an ignorable missing data mechanism (Little and Rubin 1987) and analytically integrates out all missing observations from the complete likelihood (i.e. the likelihood conditional on both missing and observed data) as in Hassler et al. (2020). Essentially, rather than computing  $p(\theta|Y^{obs}, Y^{mis})$ , where  $\theta$  represents the parameters of interest,  $Y^{obs}$  represents the observed data, and  $Y^{mis}$  represents the missing data, we analytically compute  $p(\theta|Y^{obs}) = \int p(\theta|Y^{obs}, Y^{mis})p(Y^{mis}|Y^{obs})dY^{mis}$ , which simultaneously accounts for all possible values of the missing data (i.e. integrates them out). This integration ensures posterior inference uses all available information while avoiding bias introduced by other missing data control mechanisms such as imputation. This ready accommodation of missing data is particularly useful in light of the fact that some traits have low coverage (e.g. only 18% of species have observations of reproductive lifespan). As a general rule, however, posterior certainty decreases with increasing missing data. While we are confident in the signal that we do observe, we emphasize that the lack of clear association between either of the factors with clutches per year or reproductive lifespan is not evidence that those traits are not related to the other traits of interest. Rather, the posterior distribution of the relevant entries of the loadings matrix have large variances, suggesting that with more data we may better discern their roles. Regardless, we observe clear signals related to age at sexual maturity and gestation time which have only 28% and 29% coverage, respectively.

We sought to identify size-independent life history structure because body size may evolve under different selection pressures but influences life history traits through allometric

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constraints. When performing the model selection we hence assumed that snout-vent length (SVL) loaded only onto the first factor. Doing so allowed us to separate variation in life history traits related to body size (Hypothesis 1 of our work) and size-independent life history variation (Hypothesis 2 of our work) since factors  $2, \dots, k$  were independent of allometric influences. The loadings associated with factors  $2, \dots, k$  were then assumed to be orthogonal to each other, which is required to induce posterior identifiability in the loadings without requiring ordering of the life history phenotypes (Holbrook et al. 2016).

This model selection procedure identified a 2-factor model (one factor associated with body size and one size-independent factor) as the optimal representation of trait variation across species. Code associated with this analysis is publically available at <https://gabehassler.github.io/PhylogeneticFactorAnalysis.jl/stable/>.

## **6. Paleoreconstruction and manual dispersal multiplier matrices**

Plate tectonics and island uplift influenced species' past movements between biogeographic regions. To account for changing distances between regions and island uplifts in the biogeographic reconstruction we used GPlates (<https://www.gplates.org>, Müller et al. 2018) and the global plate and rotation model of Matthews et al. (2016). Furthermore, paleocurrents are assumed to be an important factor in oceanic dispersal, especially for the Madagascan fauna (Ali and Huber 2010). Today, currents flow westward from Madagascar to Africa but they may have changed directions at the Oligocene/Miocene boundary (23 Mya) as a result of Madagascar changing its latitudinal position (Ali and Huber 2010). Also, a large freshwater outflow to the east through what is Kenya today could have contributed to eastward currents from Africa to Madagascar in the past (Markwick and Valdes 2004, Townsend et al. 2011). Based on these paleocurrents and the paleoreconstruction of the biogeographic regions we implemented a time-stratified analysis with the following five time periods (Fig. S2) :

80 - 65.1 mya: Socotra is connected to the Arabian Peninsula, Seychelles are connected to India, Comoros Islands do not exist yet, and oceanic currents flow eastward between Africa and Madagascar

65 - 23.1 mya: Seychelles are separated from India

23 - 11 mya: currents flow westward between Madagascar and Africa

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10.9 - 5.5 mya: Socotra is separated from the Arabian Peninsula

5.4 mya - present: Comoros Islands emerge

Dispersal probabilities generally decrease with distance between biogeographic regions (spatial effect), and may differ depending on the type of barrier to overcome: continental dispersal may be more probable than oceanic dispersal for terrestrial species, and oceanic dispersal with oceanic currents may be more probable than against them. To account for the spatial effect, we calculated minimal geographic distances (great-circle distances) between geographic regions at different points in time. The distances were logged and scaled to range between 1 (adjacent regions) and 100 (maximally distant). To account for differences in the ease of continental vs. oceanic-with-currents vs. oceanic-against-currents dispersal, we defined manual dispersal multiplier matrices (MDMMs). Since it is difficult to estimate the resistance associated with each type of barrier, we generated five sets of MDMMs using different weights of resistance.

To adapt dispersal probabilities between biogeographic regions, manual dispersal multiplier matrices (MDMMs) were defined based on the assumptions that dispersal across continents is more likely than trans-oceanic dispersal, and that oceanic dispersal in the same direction as the paleocurrent flows was easier than against the currents. The direction of the currents was based on present currents (<https://earth.nullschool.net>) and reconstructions of paleocurrents (Ali and Huber 2010). The MDMMs were adapted for all time slices that were identified based on the paleoreconstruction. We tested five different MDMMs:

- equal weight MDMM: no difference between oceanic and continental dispersal probabilities.
- simple version: continental dispersal was set to 0.5, and oceanic dispersal to 0.125 (i.e. the direction of the paleocurrents has a negligible effect).
- medium complex version: continental dispersal was set to 0.5, and oceanic dispersal to 0.125, except for oceanic dispersal between central Africa and Madagascar, the Comoros Islands and the Seychelles where paleocurrents may have played an important role and dispersing in the same direction as the current flows was assumed easier and set to 0.25.
- full complexity: continental dispersal was set to 0.5, oceanic dispersal with currents

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(based on paleocurrents and present-day currents) to 0.25, and oceanic dispersal against currents to 0.125.

- version full complexity 0.1: same as in full complexity, but the probability of oceanic dispersal was assumed 10 times harder than continental dispersal (oceanic dispersal with currents was set to 0.05, and against currents to 0.025).

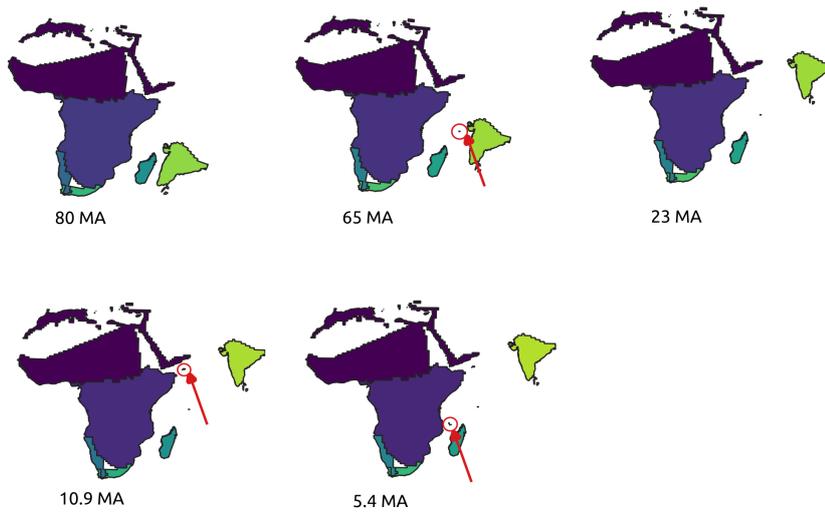


Figure S2: Paleoreconstruction of biogeographic regions and identified time slices for the time-stratified analysis. Emergence of islands and disconnection of land masses are highlighted with red circles and arrows.

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## 7. Inverted root constraint

Our preliminary analyses estimated that the common ancestor of all chameleons occupied central Africa, Madagascar and the Seychelles, however Tolley et al. (2013) suggests a narrower ancestral distribution in Africa only, which is likely the better estimation due to the inclusion of outgroups. Therefore, we constrained the root node to central Africa. Ancestral ranges and trait states are jointly estimated in trait-dependent models, hence we had to constrain the trait state of the root node. To do so, we used stochastic character mapping (R package ‘phytools’ version 0.7.70; Revell 2012) with a trait evolution model that allowed for all trait transition rates to be different to estimate the most likely trait state of the root node. We generated 100 stochastic character maps per trait (coastal distribution, body size and life history strategy). Stochastic character mapping yielded the following root trait states: coastal, big bodied and having a slow or intermediate life history strategy, depending on how the life history trait was transformed. The models were constrained at the root accordingly. When testing the dispersal syndrome (Hypothesis 3) we set the root as “non-disperser”, since the root node was estimated to have had a slow or intermediate life history strategy.

To investigate how the root constraints affected the estimation of the m2 parameter, we compared the Akaike Information Criterion (AIC) of the models with these constraints against models using the opposite trait values for the root (i.e. the trait state that was *not* estimated by stochastic character mapping). The inverted root constraint did not change our main results, although m2 estimations changed slightly for the body size and life-history models (Tab. S3).

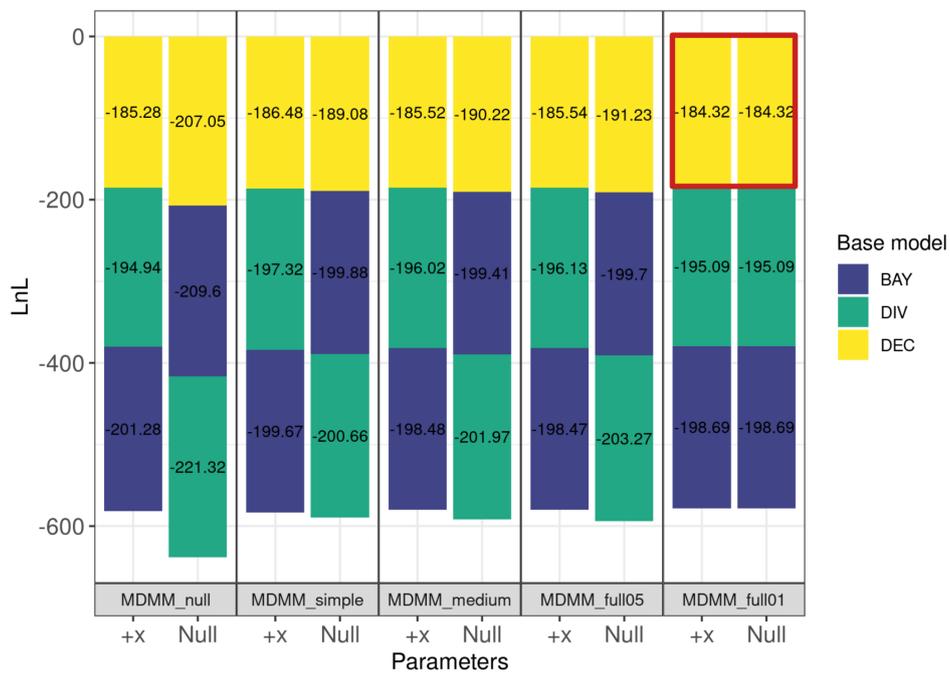
Table S3: Results of the BioGeoBEARS analyses where the root trait state was constrained to be *not* the trait state estimated by stochastic character mapping. Only models with an AICc weight greater than 1% are included. m2: dispersal multiplier of species in trait state 2 (the non dispersal prone form); x: dispersal multiplier of geographic distance.

Set	Best model	LnL	AICc weight (%)	m2	x
Coastal	DECm2	-274.19	63	0	0

distribution	DECm2x	-273.64	37	0	-0.11
Body size	DECm2	-257.43	74	0.13	0
	DECm2x	-257.43	25	0.13	-1E-06
Extreme life history	DECm2	-246.44	74	0.02	0
	DECm2x	-246.44	26	0.02	-1E-06

## 8. Choice of best base model and manual dispersal multiplier matrix

When selecting the base model and MDMM on which to run the trait-dependent models, the DEC base model and DEC+x with MDMM full 0.1 were selected with AICc weights of 57% and 20%, respectively (Fig. S3). We therefore ran the trait-dependent models only with DEC models and including MDMM full 0.1.



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Figure S3: Comparison of base models DEC, DIVA- and BAYAREA-like (indicated by “Null” parameters) and base models that take geographic distance into account (indicated by the “+x” parameters). We tested four different sets of MDMMs of different complexity, as well as an equal weight model where dispersal probability was not modified based on different kinds of barriers (continental vs. oceanic; MDMM\_null). DEC and DEC+x of the MDMM\_full01 set were selected as the best models (combined AICc weight of 77%).

## 9. BioGeoBEARS optimization

We built up model complexity sequentially, starting with the simplest model and using the estimated parameter values as input values for the next level of complexity. For example, we started with the DEC base model, then ran DEC+x and DEC+m2 with previously estimated parameter values for dispersal and extinction rates as starting values, and finally ran DEC+x+m2. Furthermore, we defined what we assumed to be the dispersal-prone form as trait 1 because this way the m2 parameter is predicted to fall between 0 and 1 which should facilitate its identification (Klaus and Matzke 2020). For each trait, we then compared all four possible models (base model, +x, +m2, +m2x) with the corrected Akaike Information Criterion (AICc). Finally, we reran the best trait-dependent models through the function “rerun\_optimization\_w\_HiLow,” which reruns the optimization three times, starting at the estimated parameters, the parameters perturbed downwards, and the parameters perturbed upwards (we used a perturbation of 25%).

## 10. Founder-event speciation models (+j)

We ran founder-event speciation models (+j) on two trait sets: body size and extreme life history strategy. The estimates of m2 parameters did not change significantly (Tab. S4).

Table S4: Best models per trait as selected by model comparison with AICc. Only models with an AICc weight greater than 1% are included. m2: dispersal multiplier of species in the non dispersal prone form: small bodied, intermediate life history (m2 > 1 indicates that species with non dispersal prone traits were more successful dispersers than species in trait

state 1, and  $m2 < 1$  indicates the inverse);  $x$ : dispersal multiplier of geographic distance;  $j$ : relative weight of founder-event jump dispersal during cladogenesis.

Trait set	Best models	LnL	AICc weight (%)	m2	x	j
Body size	DECm2j	-252	37	0.0028	0	0.0096
	DECm2	-253	35	0.0028	0	0
	DECm2jx	-252	15	0.0027	$-10^{-6}$	0.0138
	DECm2x	-253	12	0.0028	$-10^{-6}$	0
Extreme life history	DECm2	-248	40	0.15	0	0
	DECm2j	-247	34	0.15	0	0.0166
	DECm2x	-248	14	0.15	$-10^{-6}$	0
	DECm2jx	-247	12	0.16	$-10^{-6}$	0.0165

## 11. Sensitivity analysis of phylogenetic factor analysis

To assess the effect of phylogenetic uncertainty, we ran the phylogenetic factor analysis on each of the 100 trees chosen from the posterior. Only three of these 100 analyses yielded a factor model with more than two factors. The corresponding three trees were excluded from all further analyses of life history strategy and the dispersal syndrome since the second factor of the PFA was not comparable with the second factors of all other PFAs. The remaining 97 trees yielded a factor model nearly identical to that of the consensus tree (Fig. 2a in the main text). There was little variation in the mean estimations of loadings of the variables onto the two identified factors (Fig. S4). The classification of chameleon species as having an extreme

vs. intermediate life history strategy changed relatively little: 76% of all species were always classified the same (in all analyses 76 species always had an extreme life history strategy and 61 species always an intermediate one), and 24% switched classification at least once.

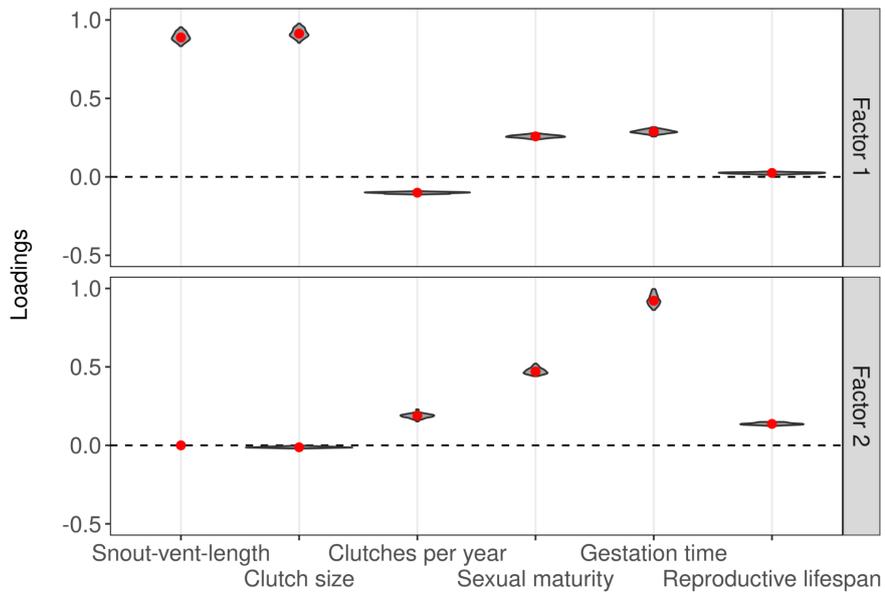


Figure S4: Results of phylogenetic factor analysis on 97 trees of the posterior. The violin plots show the distribution of posterior mean estimates of the loadings onto the factors.

## 12. Model results for different trait datasets

Table S5: Results of model comparison for the different trait sets: (a) coastal distribution, (b) body size, (c-f) life history, and (g) dispersal syndrome. For trait-independent models the biogeographic data (geog LnL) and the trait evolution (trait LnL) were estimated separately. Then both were combined (joint LnL) to offer a reference likelihood for comparison with the trait-dependent models. The main parameters estimated are: d: dispersal, e: extinction, x: geographic distance, t12: trait transition from trait state 1 to trait state 2 (i.e. from dispersal prone form to less dispersive form), t21: trait transition from trait state 2 to trait state 1, m1: dispersal multiplier of species in trait state 1 (not estimated but fixed to 1), m2: dispersal multiplier of species in trait state 2. The models with highest support are highlighted in bold.

Table S5a. Model comparison for coastal distribution (coastal vs. non-coastal).

	geog LnL	trait LnL	joint LnL	number of parameters	d	e	x	t12	t21	m1 (always fixed)	m2	AICc	AICc weight
DEC	-184.32	-108.36	-292.68	4	0.01	0	0 (fixed)	0.03	0.02	1	1 (fixed)	593.58	0
<b>DECm2</b>	-	-	<b>-271.62</b>	<b>5</b>	<b>0.04</b>	<b>0</b>	<b>0 (fixed)</b>	<b>0.04</b>	<b>0.02</b>	<b>1</b>	<b>0</b>	<b>553.59</b>	<b>0.63</b>
DECx	-184.32	-108.36	-292.68	5	0.01	0	0	0.03	0.02	1	1 (fixed)	595.7	0
DECm2x	-	-	-271.11	6	0.05	0	-0.11	0.04	0.02	1	0	554.7	0.37

Table S5b: Model comparison for the body size trait (big-bodied vs. small-bodied).

	geog LnL	trait LnL	joint LnL	number of parameters	d	e	x	t12	t21	m1	m2	AICc	AICc weight
DEC	-184.32	-79.23	-263.55	4	0.01	0	0 (fixed)	0.02	0	1	1 (fixed)	535.33	0
<b>DECm2</b>	<b>0</b>	<b>0</b>	<b>-253.36</b>	<b>5</b>	<b>0.02</b>	<b>0</b>	<b>0 (fixed)</b>	<b>0.02</b>	<b>0</b>	<b>1</b>	<b>0</b>	<b>517.06</b>	<b>0.74</b>
DECx	-184.32	-79.23	-263.55	5	0.01	0	0	0.02	0	1	1 (fixed)	537.44	0
DECm2x	0	0	-253.36	6	0.02	0	0	0.02	0	1	0	519.2	0.26

Table S5c: Results of model comparison with AICc for life history strategy (fast vs. slow, median split).

	geog LnL	trait LnL	joint LnL	number of parameters	d	e	x	t12	t21	m1	m2	AICc	AICc weight
<b>DEC</b>	<b>-184.32</b>	<b>-42.94</b>	<b>-227.26</b>	<b>4</b>	<b>0.01</b>	<b>0</b>	<b>0 (fixed)</b>	<b>0</b>	<b>0.01</b>	<b>1</b>	<b>1 (fixed)</b>	<b>462.75</b>	<b>0.55</b>
DECm2	0	0	-227.23	5	0.01	0	0 (fixed)	0	0.01	1	0.84	464.81	0.20
DECx	-184.32	-42.94	-227.26	5	0.01	0	0	0	0.01	1	1 (fixed)	464.87	0.19
DECm2x	0	0	-227.23	6	0.01	0	0	0	0.01	1	0.84	466.95	0.07

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Table S5d: Results of model comparison with AICc for life history strategy (fastest 25% vs. the rest).

	geog LnL	trait LnL	joint LnL	number of parameters	d	e	x	t12	t21	m1	m2	AICc	AICc weight
DEC	-184.32	-51.27	-235.59	4	0.01	0	0 (fixed)	0	0.01	1	1 (fixed)	479.4	0.05
<b>DECm2</b>	<b>0</b>	<b>0</b>	<b>-232.02</b>	<b>5</b>	<b>0.04</b>	<b>0</b>	<b>0 (fixed)</b>	<b>0</b>	<b>0.01</b>	<b>1</b>	<b>0.22</b>	<b>474.38</b>	<b>0.67</b>
DECx	-184.32	-51.27	-235.59	5	0.01	0	0	0	0.01	1	1 (fixed)	481.52	0.02
DECm2x	0	0	-231.9	6	0.04	0	-0.06	0	0.01	1	0.2	476.27	0.26

Table S5e: Results of model comparison with AICc for life history strategy (fastest 75% vs. the rest).

	geog LnL	trait LnL	joint LnL	number of parameters	d	e	x	t12	t21	m1	m2	AICc	AICc weight
DEC	-184.32	-31.7	-216.02	4	0.01	0	0 (fixed)	0	0.01	1	1 (fixed)	440.27	0.24
<b>DECm2</b>	<b>0</b>	<b>0</b>	<b>-214.21</b>	<b>5</b>	<b>0.01</b>	<b>0</b>	<b>0 (fixed)</b>	<b>0</b>	<b>0.01</b>	<b>1</b>	<b>2.19</b>	<b>438.76</b>	<b>0.51</b>
DECx	-184.32	-31.7	-216.02	5	0.01	0	0	0	0.01	1	1 (fixed)	442.38	0.08
DECm2x	0	0	-214.21	6	0.01	0	0	0	0.01	1	2.19	440.9	0.17

Table S5f: Results of model comparison with AICc for life history strategy (extremes (50% together) vs. the rest).

	geog LnL	trait LnL	joint LnL	number of parameters	d	e	x	t12	t21	m1	m2	AICc	AICc weight
DEC	-184.32	-70.94	-255.26	4	0.01	0	0 (fixed)	0.01	0.01	1	1 (fixed)	518.76	0
<b>DECm2</b>	<b>0</b>	<b>0</b>	<b>-247.83</b>	<b>5</b>	<b>0.02</b>	<b>0</b>	<b>0 (fixed)</b>	<b>0.01</b>	<b>0.01</b>	<b>1</b>	<b>0.15</b>	<b>506.01</b>	<b>0.74</b>
DECx	-184.32	-70.94	-255.26	5	0.01	0	0	0.01	0.01	1	1 (fixed)	520.87	0
DECm2x	0	0	-247.83	6	0.02	0	0	0.01	0.01	1	0.15	508.15	0.25

Table S5g: Results of model comparison with AICc for the dispersal syndrome (coastal-big-extreme LH vs. the rest).

	geog LnL	trait LnL	joint LnL	number of parameters	d	e	x	t12	t21	m1	m2	AICc	AICc weight
DEC	-184.32	-68.93	-253.25	4	0.01	0	0 (fixed)	0.05	0	1	1 (fixed)	514.73	0
<b>DECm2</b>	<b>0</b>	<b>0</b>	<b>-234.3</b>	<b>5</b>	<b>0.06</b>	<b>0</b>	<b>0 (fixed)</b>	<b>0.06</b>	<b>0.01</b>	<b>1</b>	<b>0.02</b>	<b>478.94</b>	<b>0.74</b>
DECx	-184.32	-68.93	-253.25	5	0.01	0	0	0.05	0	1	1 (fixed)	516.85	0
DECm2x	0	0	-234.4	6	0.06	0	0	0.06	0.01	1	0.02	481.08	0.26

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### 13. Effect of binarization: Moving the cutoff by 10%

Since trait-dependent biogeographic models currently only accept binary traits, we transformed the continuous body size and life history traits that we obtained by using PFA on our trait data into binary traits. To assess how the subjective cutoff points (50% for body size, first and last 25% for extreme life history) affected our results, we ran additional analyses on trait sets where we moved the cutoff points by 10%. For body size we tested the largest 40% against the rest and the largest 60% against the rest, and for life history we classified the first and last 20% and first and last 30% as dispersal-prone (Tab. S6). While the m2 parameter estimates changed, these additional analyses confirmed our initial results that large species and species with an extreme life history strategy were better dispersers than small and intermediate species, respectively, in the past.

Table S6: Results of the BioGeoBEARS analyses where different cutoff points were used to binarize the continuous body size and life history traits. Only models with an AICc weight greater than 2% are included. m2: dispersal multiplier of species in trait state 2 (the non dispersal prone form, i.e. small and intermediate species, respectively); x: dispersal multiplier of geographic distance.

Trait set	Best models	LnL	AICc weight (%)	m2	x
Body size: first 40%	DECm2	-259	74	0.12	0
	DECm2x	-259	25	0.12	-10 <sup>-6</sup>
Body size: first 60%	DECm2	-246	74	0.0183	0
	DECm2x	-246	26	0.0183	-10 <sup>-6</sup>
Life history: extreme 40% (first and last 20%)	DECm2	-240	74	0.14	0
	DECm2x	-240	26	0.14	-10 <sup>-6</sup>

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Life history: extreme 60% (first and last 30%)	DECm2	-244	73	0.26	0
	DECm2x	-244	25	0.26	-10 <sup>-6</sup>

#### 14. Dispersal syndrome: additional effects of life history strategy

To assess the added value of an extreme life history strategy to coastal distribution and big body size, we ran additional simulations. We simulated 100 times a random trait evolution on the chameleon phylogeny (using a Brownian Motion model; R package ‘geiger’, Pennell et al. 2014) and created 100 “pseudo” life history trait datasets where species in the upper and lower quartiles were coded as dispersal prone and the others as not dispersal prone. We then combined these simulated life history trait datasets with the coastal distribution and body size data: species were coded as dispersal prone when they held dispersal prone traits in all three trait datasets. We ran the best trait-dependent model (DEC+m2) on these 100 “pseudo” dispersal syndrome datasets. In the real dispersal syndrome dataset, 34 species were coded as dispersal prone because they held all three traits hypothesized to promote dispersal. In the simulated dispersal syndrome datasets, a maximum of 31 species held all three traits; the median was 20 (Fig. S5a). Only 19% of simulated trait datasets had an m2 value lower than 0.02, the value of the real dispersal syndrome dataset. That these values were lower than 0.02 might be a floor effect related to the very low m2 values of the coastal distribution and body size traits (Fig. S5b).

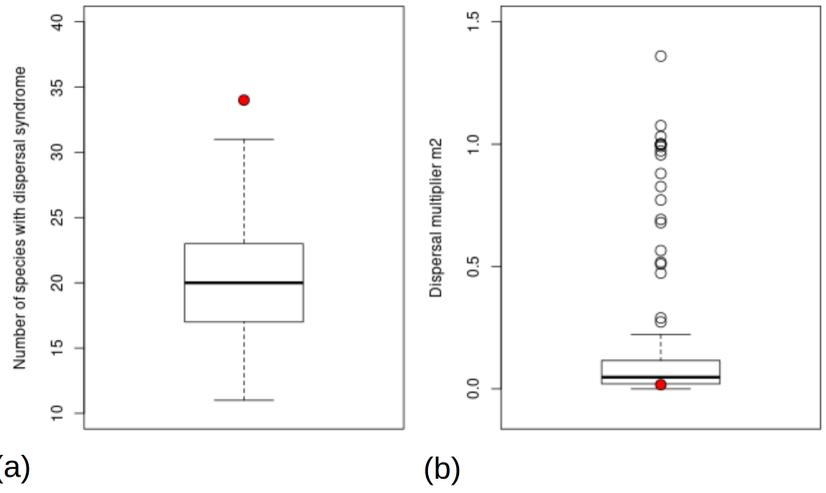


Figure S5: Distribution of number of species that were classified as having a dispersal syndrome in the simulation (a) and distribution of dispersal multipliers  $m_2$  (b). The values of the “real” dispersal syndrome analysis are indicated by red dots.

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## 15. Analysis of phylogenetic uncertainty

When running the trait-dependent model on a set of trees for the dispersal syndrome,  $m_2$  values varied around 0.03. But for some trees  $m_2$  values close to 1 were estimated. The log-likelihoods of these models were comparatively low (Fig. S6). A possible reason for the three most extreme outliers is the age of the trees: two of the trees have a root that is older than 80 million years (compared to ca. 67 million years for the consensus tree), and the third has a root of 58 million years. Due to our definition of the time stratification, only four time slices were defined for this last tree which may have affected the estimations.

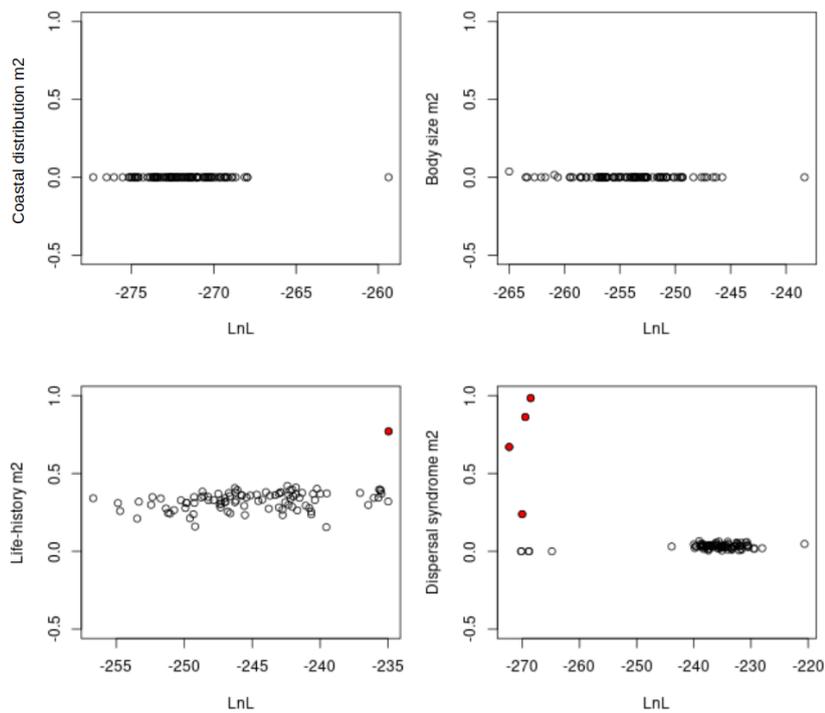


Figure S6: The relationship between log-likelihood and  $m_2$  parameter values in the sensitivity analysis of phylogenetic uncertainty. The  $m_2$  values that are outliers in the life history and dispersal syndrome analyses (Fig. 3 in the main text) are highlighted in red.

## 16. Differences between trait-dependent and trait-independent model estimations

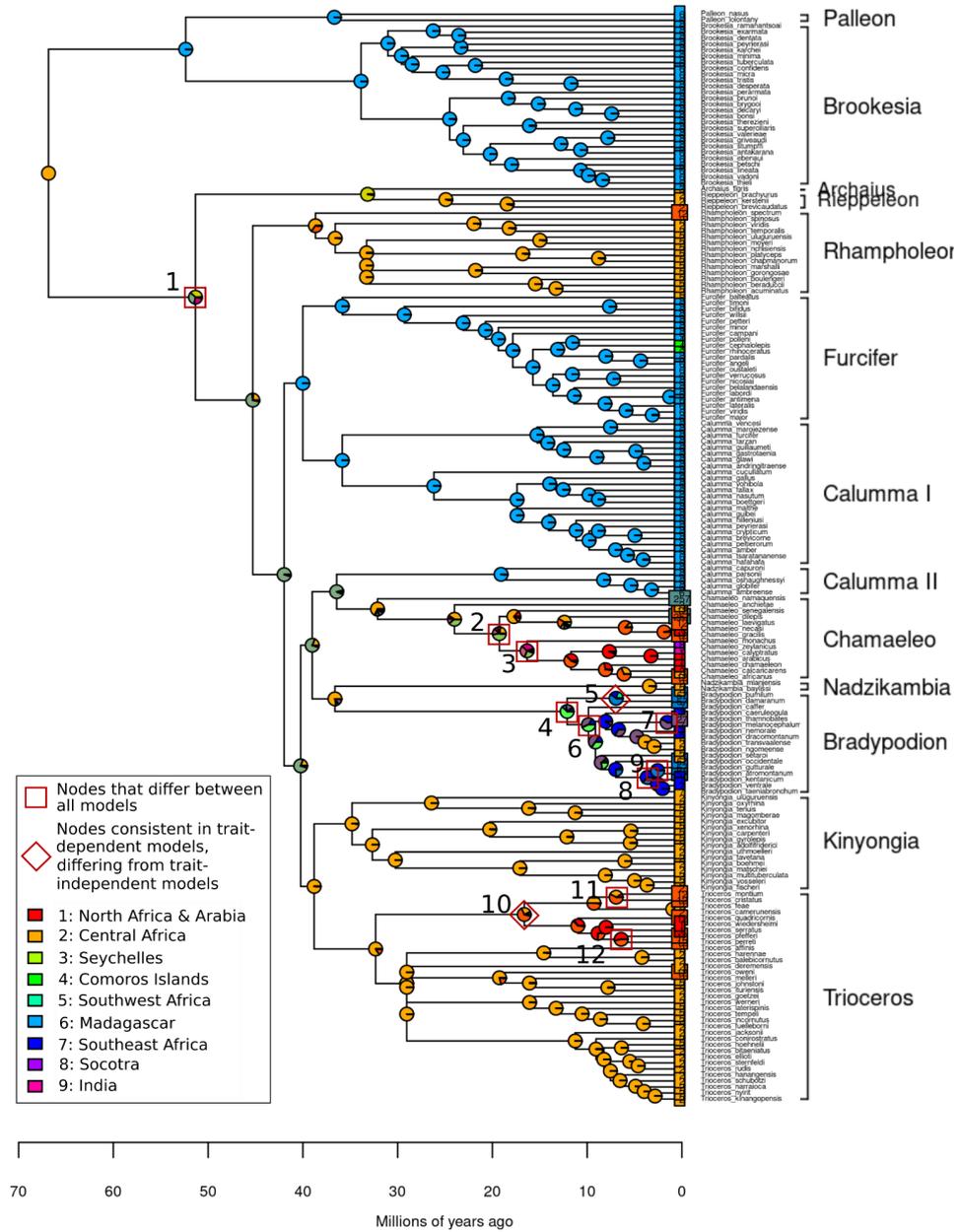


Figure S7: Estimation of ancestral areas of chameleons of the **dispersal syndrome analysis as estimated by DEC+m2**. Nodes that were estimated to have different most likely ancestral areas are indicated by a red square (where there are differences between the different trait-dependent models) or diamond (where the nodes are consistent in trait-dependent models, but trait-independent models estimated different ancestral ranges). Which ancestral ranges were estimated by which model is shown in Tab. S7. Colours of nodes are only indicated for single-area ranges in the legend; colours of multiple-area ranges are a mix of colours of the individual areas that make up the range. The grey/green colour in the basal nodes, for example, corresponds to the range Central Africa+Madagascar.

Table S7: Ancestral ranges at nodes that differ between the different models. Relevant node numbers are indicated in Fig. S7 and S8. Numbers denote biogeographic regions: 1: north Africa and Arabia, 2: central Africa, 3: Seychelles, 4: Comoros Islands, 5: southwest Africa, 6: Madagascar, 7: southeast Africa, 8: Socotra, 9: India.

Node number	Trait-independent DEC	Coastal distribution	Body size	Life history (extreme)	Dispersal syndrome
1	26	26	23	26	23
2	2	128	2	2	128
3	28	28	28	28	18
4	27	257	27	27	257
5	7	57	57	57	57
6	27	27	27	27	257
7	7	27	7	7	27
8	7	7	57	7	7
9	7	57	57	7	57
10	2	12	12	12	12
11	2	2	2	12	12
12	1	1	1	12	1

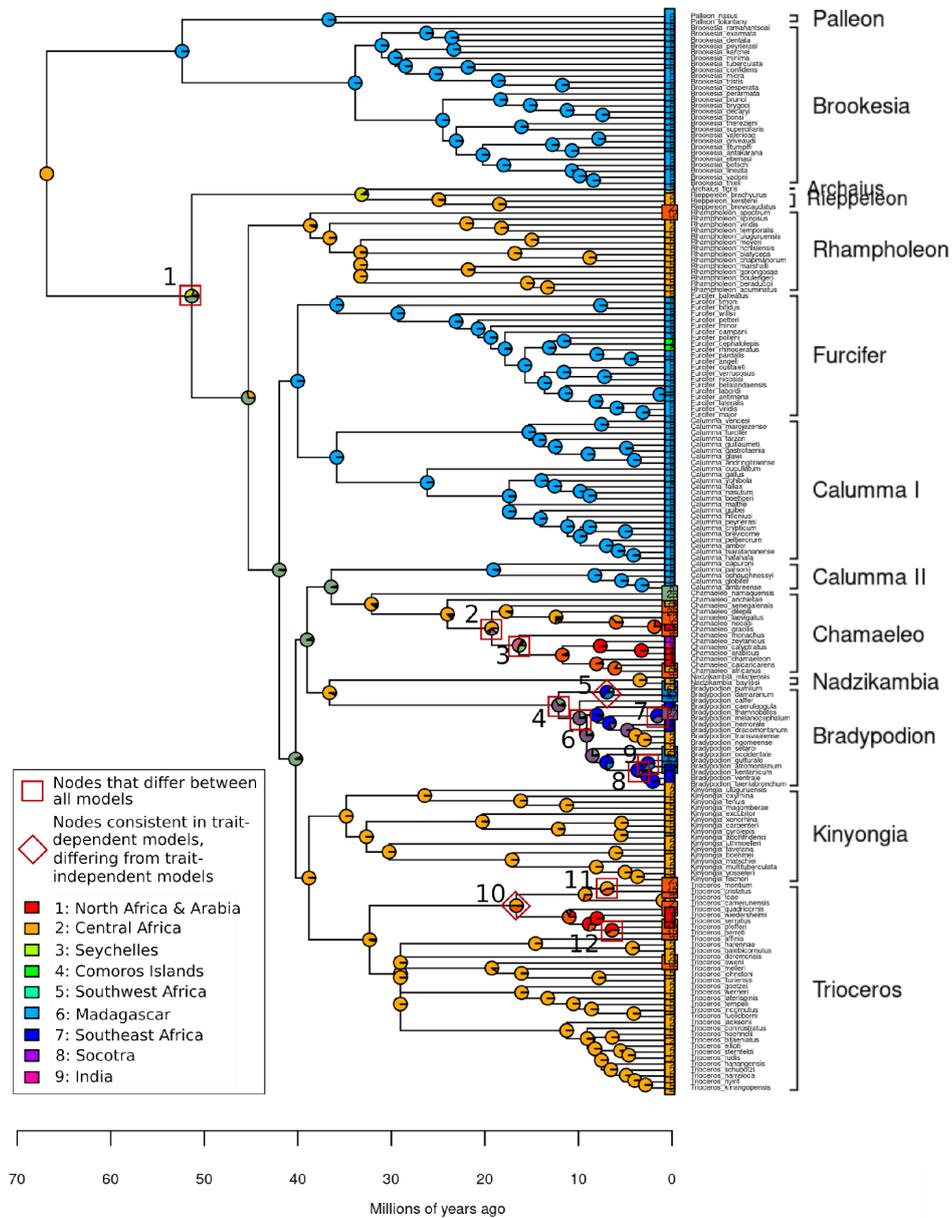
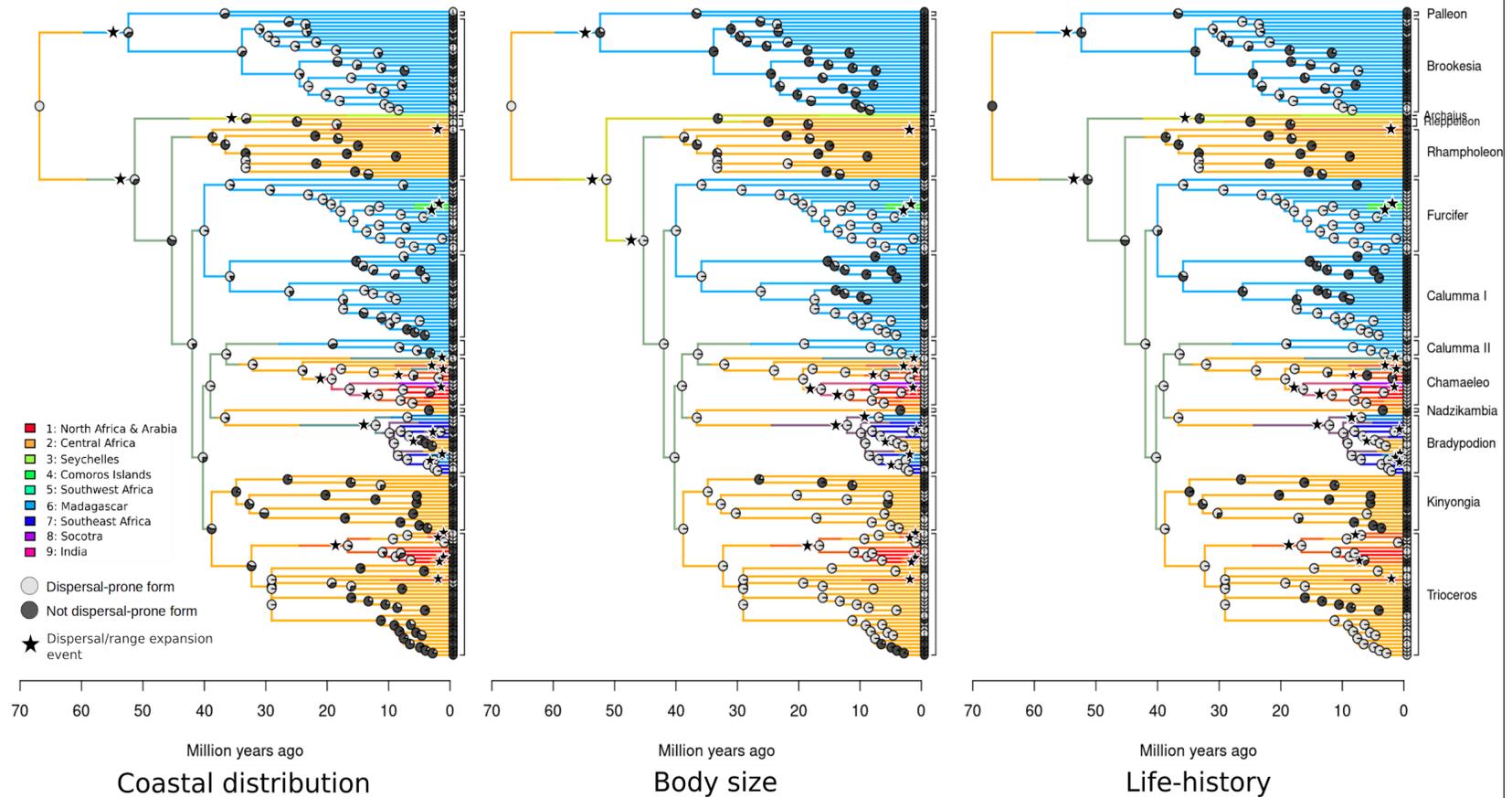


Figure S8: Estimation of ancestral areas of chameleons as estimated by **trait-independent DEC**. Nodes that were estimated to have different most likely ancestral areas are indicated by

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a red square (where there are differences between the different trait-dependent models) or diamond (where the nodes are consistent in trait-dependent models, but trait-independent models estimated different ancestral areas). Colours of nodes are only indicated for single-area ranges in the legend; colours of multiple-area ranges are a mix of colours of the individual areas that make up the range.

## 17. Representation of three different trait-dependent models



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Figure S9: Biogeographic estimations of three different trait-dependent models (coastal distribution, body size and life history) represented on the chameleon phylogeny. Most likely ancestral ranges are indicated by coloured edges (only indicated for single-area ranges in the legend; colours of multiple-area ranges are a mix of colours of the individual areas that make up the range). The pie charts represent the probabilities of

the nodes of being in a certain trait state: light colour indicates species holding hypothesized dispersal traits (coastal distribution, big body, extreme life history strategy), and dark colours indicate a non dispersal-prone form. Dispersal or range expansion events are indicated by black stars.

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## Supplementary Information to Uncovering how traits have shaped the historical biogeography of tetrapods

### Phylogenetic uncertainty

We assessed the effect of phylogenetic uncertainty on the classification of trait-dispersal relationships by rerunning analyses on a selection of clades (one clade per class). For reptiles, amphibians and mammals we selected a clade at random (Natricinae, Hynobiidae, Sciuridae), and extracted ten phylogenies from their respective posteriors<sup>17</sup>. For the bird clade (Pycnonotidae) we repeated analyses on a phylogeny where we used the backbone of Prum et al.<sup>53</sup> that included the fossil *vegavis*. For each clade and phylogeny, we (1) repositioned species on the body size and life history axes using phylogenetic factor analyses (PFAs). We then (2) repeated all biogeographic models, using the same base models and manual dispersal multiplier matrices as for the main analyses (Extended Data Tab. 1), and (3) reclassified trait-dispersal relationships. For Hynobiidae, Sciuridae and Pycnonotidae, trait-dispersal relationships varied little (Extended Data Fig. 4, Extended Data Tab. 4). However, there was considerable variation for Natricinae. The main analysis identified a positive relationship between body size and dispersal rates in Natricinae, i.e. large species were better dispersers than small ones. However, we identified the same body size-dispersal relationship in only five of the selected trees from the posterior, in three trees we identified intermediately-sized species to be better dispersers, and in two trees the difference in dispersal rates between most-dispersive and least-dispersive species was less than 10%. The results were similar for life history-dispersal relationships in Natricinae.

The trees selected from the posterior for Natricinae were more different than those of any of the other clades (minimum correlation Natricinae: 0.945; for other clades: 0.9804, function `cor.dendlist` from R package `dendextend` v1.16.0<sup>151</sup>), which suggests more uncertainty in the phylogenetic estimations in this clade than in others. Consequently, species scores from the different PFAs were less strongly correlated for Natricinae than those of other clades (minimum correlation Natricinae: 0.42; for other clades: 0.99). This indicated that we had difficulties identifying species' positions

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on the body size and life history axes which led to differences in categorizations of species as dispersal-prone and not dispersal-prone. This uncertainty in turn cascaded down to the biogeographic estimations and classifications of trait-dispersal relationships. In the present study, we analyse the global signal emerging from the responses of a large number of clades, and thus assume that using a single phylogeny per clade (with a potential clade-specific phylogenetic bias) generates noise to the overall signal. Adding noise should decrease the probability of detecting a signal, making our tests more conservative. In practice, the global character of this study was already computationally demanding (ca. 262800h\*cores of calculations), and any replication for uncertainty analyses multiplies the computation time (and associated carbon emission), which we believe is not necessary.

### **Barriers in biogeographic dispersal**

Barriers are species-specific: what constitutes a dispersal barrier for one species is not necessarily a barrier for another species<sup>1</sup>. To define barriers as objectively as possible, we used a data-driven bioregionalisation approach, based on species' phylogenetic relationships and extant distribution data (see Weil et al.<sup>17</sup> for details concerning the methodology). Our bioregionalisation approach showed that for most clades continental barriers were stronger than oceanic ones. Since traits might be related in a similar manner to dispersal success across both types of barriers, we combined both barriers in our analyses. Large body size may be advantageous in oceanic dispersal because of increased stress tolerance<sup>4</sup>, and it may be advantageous in continental dispersal because large-bodied species are generally better active dispersers than small species<sup>13,32</sup>. In both kinds of dispersal we expect founder populations to be small and life history effects should therefore be comparable, with either fast-lived species having advantage due to being more resistant to stochastic extinction<sup>5,6,7</sup>, or slow-lived species having an advantage due to less demographic variability<sup>19,20,21</sup>. In addition, biogeographic dispersal is rare and difficult to observe. Combining both types of dispersal hence increased statistical power (if we had only included oceanic dispersal, the sample size would have been too small to statistically detect the influence of traits on these scales since very few dispersal events would have been estimated on the phylogeny).

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## Combining trait databases

Amphibians: We used trait data from Allen et al.<sup>69</sup>, which includes snout-vent-length (SVL, mm), clutch size (CS, number of eggs), clutches per year (CY), egg size (ES, mm), sexual maturity (SM, years) and reproductive lifespan (RL, years). We calculated longevity (LG, years) from SM and RL ( $LG = RL + SM$ ). To this database we added body size (BS) data from Cooney & Thomas<sup>70</sup>, maximal SVL, maximum CS and maximum LG from Trakimas et al.<sup>71</sup>, and SVL and CS from Pincheira-Donoso et al.<sup>72</sup>. We inferred SVL values for species without SVL data based on BS data using phylogenetic linear models (R package *phylolm* v2.6<sup>152</sup>), separately for Caudata and all other amphibians. When adding data to Allen et al.<sup>69</sup>, we first looked up synonyms in the Integrated Taxonomic Information System (ITIS; functions `get_tsn` and `itis_getrecord`, package *taxize* v0.9.99<sup>60,61</sup>) and AmphibiaWeb (2016; function `synonymMatch`, package *rangeBuilder* v1.5<sup>62</sup>) for all species in the new database. We also checked for outliers per order, using Tukey's fences where a value is considered an outlier if it is outside the bounds of  $[Q1 - 3 \cdot IQR, Q3 + 3 \cdot IQR]$ , where Q1 and Q3 are the lower and upper quartiles, respectively, and IQR the inter-quartile range  $Q3 - Q1$ . These calculations were done on logged trait values. Overall, we compiled SVL, ES, CS, SM and LG for amphibians.

Reptiles: We again used trait data from Allen et al.<sup>69</sup> as a starting point, which included SVL, hatchling SVL, CS, CY, SM (in months), LG, RL and hatchling body mass (HBM, g). If hatchling SVL was available but not HBM for a given species, we inferred HBM from hatchling SVL using phylogenetic regressions. We did this separately for Anguimorpha, Gekkota, Iguania, Lacertoidea and Scincoidea. We then added CS from Meiri et al.<sup>73</sup>, BS from Cooney & Thomas<sup>70</sup>, CS and CY from Schwarz & Meiri<sup>74</sup>, SVL and BS from Feldman et al.<sup>75</sup>, CS, CY, SM, LG and body mass (BM) from Myhrvold et al.<sup>76</sup>, and CS, LG and BM from Stark et al.<sup>77</sup>. As for amphibians we first checked if synonyms of species in the new databases already existed in Allen et al.<sup>69</sup> (using ITIS and the reptile database<sup>64</sup>) and excluded outliers before adding values. We estimated SVL from BS and BM measures where possible using phylogenetic regressions. Overall, we compiled SVL, HBM, CS, CY, SM and LG for non-avian reptiles.

Mammals: We combined data from PanTHERIA<sup>78</sup> (BM (g), gestation time (GT, days), litter size (LS), litters per year (LY), LG (months), SM (days) and weaning age (WA,

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days), neonate body mass (NBM, g)), Phylacine<sup>79</sup> (BW), AnAge<sup>80</sup> ( BM, GT, LS, LY, LG, SM female, SM male, WA, NBM), Ernest<sup>81</sup> (BM, GT, LS, LY, LG, WA, NBM), Fisher et al.<sup>82</sup> (GT, LS, LG, SM female, WA, NBM), Myhrvold et al.<sup>76</sup> (BM, GT, LS, LY, LG, SM female, SM male, WA, NBM), Tsuboi et al.<sup>83</sup> (BM), Williams et al.<sup>84</sup> (BM, LS, LY, LG), Smith et al.<sup>85</sup> (BM), COMBINE<sup>86</sup> (BM, GT, LS, LY, LG, SM, SM female, SM male, WA) and Capellini et al.<sup>87</sup> (BM, GT, LS, LY, LG, SM, WA). Before combining the databases, we used the function `getAcceptedNames` (R package `rangeBuilder`) to update the taxonomies of the individual databases according to Wilson & Reeder<sup>66</sup>. From the AnAge database<sup>80</sup> we only used data from wild species that were flagged as “high” or “acceptable” data quality. We again checked for outliers per trait as described above. We also checked for outliers across databases if more than one database contained a value for a given trait and species. Where female sexual maturity was not available, we completed with male or unknown sexual maturity. When combining values across databases, we did a median of unique values, except for longevity, where we kept the maximum value. Overall, we compiled BM, NBM, LS, LY, LG, SM, GT and WA for mammals.

Birds: We combined data from Sheard et al.<sup>88</sup> (BM), Myhrvold et al.<sup>76</sup> (BM, CS, CY, LG, SM female, SM male, egg mass (EM), fledging age (FA)), Botero et al.<sup>89</sup> (BM), O’Gorman & Hone<sup>90</sup> (BM), Tsuboi et al.<sup>83</sup> (BM), AnAge<sup>80</sup> (BM, GT, CS, CY, LG, SM female, SM male), Garnett et al.<sup>91</sup> (BM, CS), Burgio et al.<sup>92</sup> (BM), Williams et al.<sup>84</sup> (BM, CS, CY, LG, SM), Dufour et al.<sup>55</sup> (BM), Storchová & Hořák<sup>93</sup> (BM, CS, CY, LG, SM), Tobias & Pigot<sup>94</sup> (CS), Rotenberry & Balasubramaniam<sup>95</sup> (EM) and DATLife<sup>96</sup> (SM, LG). Before combining the databases, we used the function `getAcceptedNames` (R package `rangeBuilder`) to update the individual databases according to the BirdLife Taxonomic Checklist (v8.0<sup>65</sup>). From the AnAge database<sup>80</sup> we only used data from wild species that were flagged as “high” or “acceptable” data quality. We excluded values of captive individuals from the DATLife database and only used SM of females. We excluded inferred values from Burgio et al.<sup>92</sup>. We again checked for outliers as described above per trait. We also checked for outliers across databases if more than one database contained a value for a given trait and species. Where female sexual maturity was not available, we completed with male or unknown sexual maturity. When combining values across databases, we did a median of unique values, except for

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longevity, where we kept the maximum value. Overall, we compiled BM, EM, LS, LY, LG, SM, GT and WA for birds.

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