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Baptiste Bree

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THÈSE

UNIVERSITE DE PAU ET DES PAYS DE L'ADOUR
École doctorale des Sciences Exactes et leurs Applications
(ED 211 SEA)

Présentée et soutenue le 19 décembre 2023
par **Baptiste BRÉE**

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de l'Université de Pau et des Pays de l'Adour
Spécialité : Biologie évolutive

Radiations évolutives sur les archipels océaniques :
synthèse et analyses comparatives à large échelle
temporelle et spatiale

MEMBRES DU JURY

RAPPORTEURS

- Fabien LEPRIEUR
- Alain VANDERPOORTEN

Professeur / Université de Montpellier
Professeur / Université de Liège / Président du jury

EXAMINATEURS

- Laure GALLIEN
- Robin AGUILÉE
- Dominique STRASBERG

Chargé de recherche / Université Grenoble Alpes
Maître de conférences / Université de Toulouse
Professeur / Université de La Réunion

DIRECTEUR

- François RIGAL

Maître de conférences / Université de Pau et des Pays de l'Adour



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Le dimanche 8 juillet 2018 à 12h18, alors en pleine fête de famille, je reçois une notification de mail sur mon portable intitulé "IMPORTANT => place(s) à saisir [...]". En substance, le responsable du Master DARWIN m'expliquait qu'un grand nombre de désistements avait eu lieu, que les 7 personnes qui recevaient ce mail ayant des dossiers similaires, et que les deux premières qui répondraient gagnaient leur place au sein de la promotion 2018.

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Résumé

Depuis les premières observations de Darwin et Wallace, les radiations évolutives présentes sur les archipels océaniques (ROAs) n'ont cessé d'être étudiées par la communauté scientifique, et ont notamment joué un rôle majeur dans notre compréhension des mécanismes écologiques et évolutifs à l'origine de la biodiversité. La quantité d'information disponible concernant ces clades insulaires n'a cessé d'augmenter durant les dernières décennies, notamment suite à l'apparition des outils moléculaires, qui ont permis de mettre en évidence un certain nombre de patrons biogéographiques et (macro)évolutifs au sein des ROAs. Pourtant, les études comparatives trans-taxons et trans-archipels sont encore rares, alors même qu'elles pourraient contribuer à améliorer notre connaissance vis-à-vis des clades insulaires. C'est dans ce contexte que ce travail de thèse a donc été initié. Dans un premier temps, nous avons effectué un recensement de toutes les ROAs décrites à l'échelle mondiale, afin de faire le point sur les connaissances actuelles sur le sujet. Plus de 350 ROAs ont ainsi été identifiées à travers le monde sur plus d'une vingtaine d'archipels. Cette revue de la littérature, en plus de détecter un biais vers l'étude de certains archipels et ROAs emblématiques, a pu mettre en évidence un certain nombre de disparités méthodologiques, qui ne sont pas sans conséquences sur notre compréhension des mécanismes de diversification des ROAs. Par la suite, nous nous sommes intéressés plus particulièrement à l'effet des caractéristiques géo-environnementales des îles sur la diversité spécifique des ROAs, un aspect jusqu'alors peu étudié dans la littérature. L'aire, l'hétérogénéité environnementale et l'isolement géographique des îles ont ainsi été identifiés comme les principaux facteurs influençant les patrons de richesse spécifique émergeant au sein des ROAs. Plus important encore, nous avons également démontré que la force de l'effet de ces facteurs était fonction de l'archipel et, dans une moindre mesure, du taxon auquel appartenait la ROA. Enfin, dans une troisième et dernière partie, nous avons exploré le mode et le tempo de diversification des ROAs. Pour cette étude, 44 phylogénies de ROAs provenant de huit archipels différents ont été analysées. Les résultats montrent que la majorité des phylogénies présentaient une accumulation constante des espèces au cours du temps, contrastant avec l'idée d'équilibre. L'âge très jeune des ROAs ainsi que l'augmentation continue de l'aire des archipels océaniques par l'émergence de nouvelles îles permettrait d'expliquer ce résultat, même si d'autres hypothèses sont envisagées. Ce travail de thèse a permis de mettre en évidence un certain nombre de patrons biogéographiques et macroévolutifs communs aux ROAs, et de présenter de nouvelles perspectives concernant les mécanismes qui ont permis l'émergence de l'extraordinaire biodiversité endémique présente au sein des archipels océaniques.

Abstract

Since the first observations by Darwin and Wallace, evolutionary radiations occurring on oceanic archipelagos (ROAs) have not ceased to be studied by the scientific community and have played a major role in our understanding of the ecological and evolutionary mechanisms underlying biodiversity patterns. The amount of information available for these island clades has increased exponentially over the last few decades, particularly thanks to the development of molecular tools, which have enabled us to reveal biogeographical and (macro)evolutionary patterns within ROAs. However, cross-taxon and cross-archipelago comparative studies are still scarce in the literature, even though they could contribute to widen our general knowledge of ROAs. Therefore, as a first step, we carried out a literature review of all ROAs described worldwide, in order to evaluate current knowledge accumulated on the topic. More than 350 ROAs were identified worldwide in over twenty archipelagos. In addition to revealing a bias towards the study of certain emblematic archipelagos and ROAs, this literature review highlighted several methodological disparities, which are not without consequences for our understanding of ROA diversification mechanisms. In a second part, we focused on the effect of island geo-environmental characteristics on the species diversity of ROAs, an aspect that has received little attention in the literature. Island area, environmental heterogeneity and geographical isolation were thus identified as the main factors influencing specific richness patterns emerging from ROAs. More importantly, we also demonstrated that the strength of the effect of these factors was a function of the archipelago and, to a lesser extent, of the taxon to which the ROA belonged. Finally, in a third and final section, we explored the mode and tempo of diversification of the ROAs. For this study, 44 ROA phylogenies from eight different archipelagos were analyzed. The results show that a majority of phylogenies presented a constant rate of species accumulation over time, contrasting with the idea of equilibrium on islands. The very young age of the ROAs and the continuous growing of oceanic archipelagos through the emergence of new islands could explain this result, although other hypotheses are being considered. This thesis has highlighted a number of common biogeographical and macroevolutionary patterns among ROAs and has brought new perspectives on the mechanisms that have led to the emergence of the extraordinary endemic biodiversity of oceanic archipelagos.

Chapitre I : Introduction

Comprendre l'origine et le maintien de la biodiversité est une question centrale en écologie (Ricklefs 2004). Dans cette quête, les îles ainsi que les radiations évolutives qu'elles abritent ont toujours tenu une place fondamentale dans le développement des théories écologiques et évolutives, contribuant ainsi à approfondir notre compréhension du monde vivant (Whittaker et al. 2017). Outre la radiation emblématique des pinsons des Galápagos et son rôle pivot dans la formulation de la théorie de l'évolution (Darwin 1859), les études sur les radiations insulaires ont permis de mieux comprendre les processus éco-évolutifs qui sous-tendent la diversification des espèces et les patrons de biodiversité (Gillespie 2015, Whittaker et al. 2017, Whittaker et al. 2023). Cependant, et malgré l'essor sans précédent de l'étude des systèmes insulaires dans les sciences écologiques et évolutives (Patiño et al. 2017, Dos Santos et al. 2016), notre vision du phénomène radiatif insulaire reste très dispersée et fragmentée, centrée sur quelques clades et archipels emblématiques (Cerca et al. 2023). Bien que plusieurs auteurs aient proposé différentes synthèses, souvent centrées sur un archipel particulier (e.g., Hembry 2018, Hembry et al. 2021, Romeiras et al. 2019), ou un groupe taxonomique (e.g., Roderick & Gillespie 1998, 2002, Baldwin & Wagner 2010), nous manquons encore d'une véritable vision globale concernant les radiations insulaires. De plus, très peu d'analyses comparatives approfondies ont été réalisées jusqu'à présent (e.g., Lim & Marshall 2017, Roman-Palacios & Wiens 2018), et ce malgré le développement de modèles conceptuels sur le sujet ces dernières années (e.g., Whittaker et al. 2008, Valente et al. 2014, Borregaard et al. 2017).

Ce projet de thèse a donc pour objectif de mettre en œuvre une évaluation globale des radiations insulaires, afin d'examiner comment leurs patrons de diversité et de diversification émergents varient dans l'espace et entre groupes taxonomiques, et comment ces variations peuvent nous renseigner sur les mécanismes éco-évolutifs à l'origine de ces radiations. Devant l'extraordinaire diversité des systèmes insulaires présents sur Terre, je me suis concentré exclusivement sur les îles océaniques, pour deux raisons majeures : (i) elles représentent un groupe homogène partageant un certain nombre de caractéristiques communes, telles que leur origine volcanique, tout en présentant une forte variabilité sur des facteurs clés tels que l'aire, l'altitude et l'âge géologique (Nunn 2009, Whittaker et al. 2023) ; (ii) elles sont le groupe d'îles abritant le plus grand nombre de radiations évolutives documentées à ce jour (Emerson 2002).

L'introduction générale de ma thèse se structure de la manière suivante : dans une première partie, je présente un bref historique de la pensée évolutionniste et du concept de radiation évolutive, en m'attardant plus particulièrement sur les définitions passées et actuelles du concept de radiation et sur les différentes sous-catégories identifiées à ce jour. Dans la deuxième partie, je montre l'importance des environnements insulaires dans le développement des sciences écologiques et

évolutives ; je présente en détails les caractéristiques des archipels océaniques et montre leurs caractéristiques et la présence de radiations évolutives. La troisième partie est consacrée à la présentation des différentes méthodes et modèles principaux en macroécologie et macroévolution, et à la place que peuvent avoir les radiations évolutives en leur sein. La partie 4 présente les différents enjeux actuels dans l'étude des radiations évolutives et des environnements insulaires, en s'attardant notamment sur les dernières avancées en matière de compréhension de la dynamique évolutive des archipels océaniques, et la notion d'équilibre dynamique de diversité. Enfin, la partie 5 est une présentation de la méthode générale utilisée dans cette thèse et des différents chapitres qui la composent.

1. Radiations évolutives : histoire et définitions

Même s'il n'est pas nommé explicitement, le concept de radiation évolutive apparaît très tôt dans le développement de la théorie de l'évolution, ce phénomène évolutif étant l'expression même du processus d'émergence des espèces proposé par Charles Darwin et Alfred Russel Wallace il y a plus de 150 ans (Darwin 1859, Wallace 1870). Dans cette première partie, je reviendrai très brièvement sur les grandes étapes de la pensée évolutionniste, ainsi que sur l'évolution de l'idée de radiation dans la littérature. Je ferai également un point sur les différents types de radiations et leurs définitions.

1. a. (Très) brève histoire de la pensée évolutionniste

Au début du XIX^{ème} siècle, Jean-Baptiste Lamarck publie *Philosophie zoologique* (Lamarck 1809), ouvrage dans lequel il développe le concept de transformisme, considéré comme la première formalisation de l'idée d'évolution pour expliquer la diversité des êtres vivants. Selon Lamarck, les différentes espèces seraient d'abord apparues par génération spontanée, puis auraient évolué graduellement vers des formes de plus en plus complexes en fonction des circonstances auxquelles elles ont été confrontées (Lamarck 1809). C'est dans ce même ouvrage que Lamarck représente pour la première fois des relations de parenté entre groupes d'organismes sur un arbre phylogénétique buissonnant (**Figure I.1**). Dans cette première moitié du XIX^{ème} siècle, plusieurs scientifiques avancent le principe de sélection naturelle, comme William Charles Wells (Darwin 1861), Augustin Pyrame de Candolle (Darwin 1859, Bowler 2003), ou Patrick Matthew (Darwin 1861). En 1858, Charles Darwin et Alfred Russel Wallace proposent l'idée d'une théorie de l'évolution basée sur le principe de la sélection naturelle, qui propose d'appréhender l'évolution comme une série d'embranchements successifs à partir d'un ancêtre commun. Cette théorie,

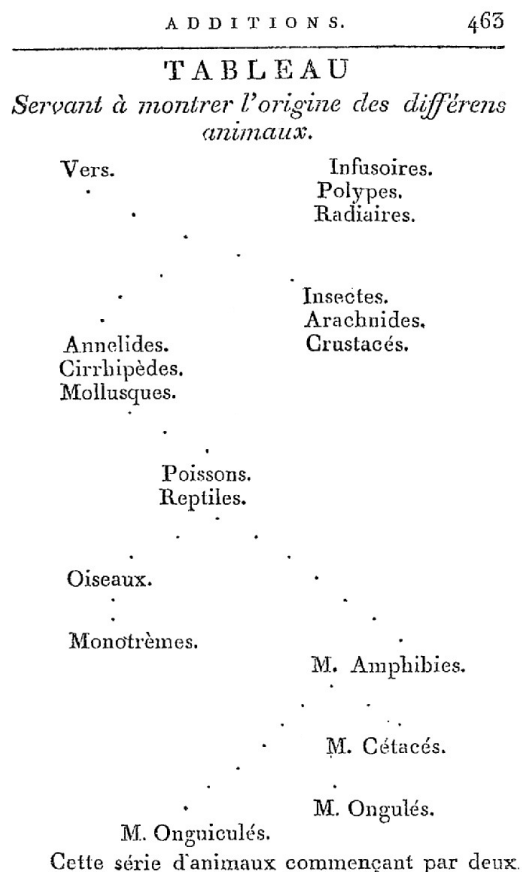


Figure I.1. La page 463 du livre *Philosophie zoologique* (Lamarck 1809), représentant l'un des plus anciens arbres phylogénétiques connus.

synthétisée dans “(On) The origin of species” (Darwin 1859), peut être résumée comme suit: (1) Au sein d’une même espèce, les individus peuvent présenter des variations morphologiques, physiologiques ou comportementales; (2) les individus ayant les caractéristiques les plus adaptées à leur environnement ont plus de chances de survivre et de produire des descendants; (3) ces descendants héritent des caractères spécifiques de leurs parents, faisant ainsi tendre la population générale vers les formes les plus adaptées. Ce sont ensuite les travaux successifs sur la notion d’hérédité, notamment grâce à la redécouverte des travaux de Gregor Mendel sur la génétique (Mendel 1866) au début du XXème siècle, qui permirent de convaincre une partie de la communauté scientifique quant à la validité de cette théorie. Durant cette période, plusieurs recherches vont contribuer à documenter et solidifier le principe de sélection naturelle (e.g., Fisher 1930, Haldane 1924), et vont finalement arriver à un consensus appelé *théorie synthétique de l’évolution*, ou *théorie néo-darwienne de l’évolution* vers les années 1930-1940 (Huxley 1942), qui s’inspire de plusieurs travaux sur l’évolution et la génétique (Dobzhansky 1937, Simpson 1944, Mayr 1942). Cette théorie

pose comme mécanismes fondamentaux de l'évolution (i) les mutations aléatoires du patrimoine génétique, (ii) les processus de migration, (iii) la sélection naturelle et (iv) la dérive génétique, souvent cités comme les *big four* de la génétique des populations (de la Harpe et al. 2017). Dans les années 1960, l'émergence de la théorie neutraliste de l'évolution, qui soutient que la plupart des mutations ont une influence négligeable sur la valeur sélective des individus (Kimura 1968, 1983), ouvre un vaste débat sur la prépondérance de la dérive génétique par rapport à la sélection naturelle.

1. b. Émergence du concept de radiation évolutive

Le 4 janvier 1837, Charles Darwin offre au Musée de la Société Zoologique une collection exceptionnelle de 450 oiseaux et 80 mammifères, la plupart ayant été collectés durant son voyage à bord du *Beagle* (1831-1836) (Steinheimer 2004). L'ornithologiste John Gould est chargé de classer les spécimens d'oiseaux. Un certain nombre de pinsons bruns d'apparence ordinaire provenant de l'archipel des Galápagos l'enthousiasment particulièrement, car ils se distinguent par leurs différentes tailles de bec. Gould identifie ainsi 13 nouvelles espèces de pinsons grâce à cette variation morphologique. Ce travail taxonomique va jouer un rôle fondamental pour Darwin dans la formulation de sa théorie de l'évolution. Dans son ouvrage *the voyage of HMS Beagle* de 1845, il écrit alors : “from an original paucity of birds in this archipelago, one species has been taken and modified for different ends.” (Darwin 1845, p.380). [“à partir d'un faible nombre d'oiseaux dans cet archipel, une espèce a été prise et modifiée à des fins différentes”]. Dans cette phrase se rencontrent déjà les deux idées fondamentales de la théorie de l'évolution : l'ancêtre commun et la différenciation. Darwin suppose alors qu'une espèce initiale peut donner naissance à de nombreuses populations dérivées (radiation), et que la morphologie de ses populations a été modifiée à des fins distinctes (adaptation). Sans encore utiliser le terme, il propose ainsi une première définition du processus de radiation évolutive, et plus précisément de radiation adaptative. Cinquante ans plus tard, Henry Fairfield Osborn formalise la terminologie “adaptative” pour décrire notamment l'évolution convergente des radiations de mammifères en de multiples formes/adaptations sur les différents continents (Osborn 1902). Le lien entre les caractéristiques des espèces et leur écologie n'est alors que supposé, mais les travaux de David Lack sur la corrélation entre la forme du bec et le régime alimentaire des pinsons de Darwin permet la reconnaissance du concept de radiation adaptative comme point fondamentale de la théorie synthétique (Lack 1947, Givnish 1997).

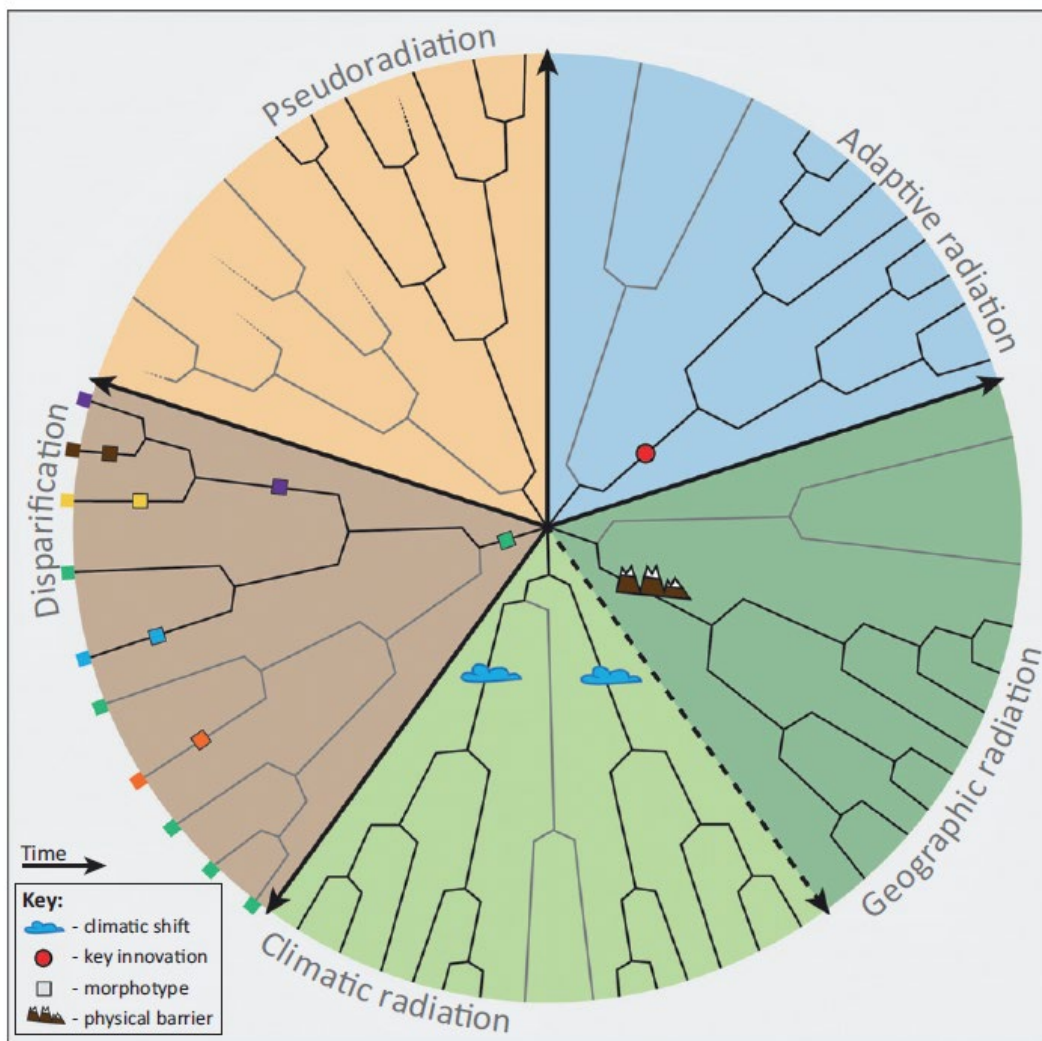
1. c. Les différents types de radiations : définitions et débats

Définir ce qu'est une radiation évolutive demeure encore aujourd'hui une tâche complexe, tant le débat s'est polarisé autour de la question de la nature adaptative ou non des radiations. Il apparaît donc essentiel de commencer par définir, ne serait-ce que brièvement, ces deux types de radiations. Les radiations dites "adaptatives" sont incontestablement les plus largement étudiées jusqu'à présent (Simões et al. 2016). Bien que le concept de radiation adaptative puisse sembler intuitif au premier abord, il n'existe pas de consensus clair concernant une définition précise de ce phénomène (Hernández-Hernández 2019, Gillespie et al. 2020). La définition la plus largement acceptée est certainement celle proposée par Schluter (2000) : "l'évolution de la diversité écologique au sein d'un clade qui se multiplie rapidement" ; cette évolution étant évaluée par un ensemble de quatre critères : (1) la présence d'un ancêtre commun, (2) la corrélation phénotype-environnement, (3) l'utilité du trait, et (4) un taux rapide de spéciation. Il s'est toutefois avéré difficile pour la plupart des études de satisfaire tous ces critères (Rundell & Price 2009). Par conséquent, le nombre de cas pouvant être considérés comme des "radiations adaptatives" selon Schluter (2000) reste aujourd'hui relativement faible (Gillespie et al. 2020). À l'opposé, plusieurs auteurs ont proposé des définitions beaucoup plus inclusives tels que Losos (2010) : "la divergence évolutive des membres d'un clade monophylétique en une variété de formes adaptatives" ou encore Givnish (2015) : "l'augmentation de la diversité des rôles écologiques et des adaptations associées au sein d'un clade, accompagnée d'un taux inhabituellement élevé d'accumulation de disparité morphologique/physiologique /comportementale et de divergence écologique". En 2020, Rosemary Gillespie, en collaboration avec plusieurs spécialistes des radiations adaptatives (Gillespie et al. 2020), proposent de classer une radiation comme adaptative s'il existe une indication quant à l'existence d'une divergence écologique entre des lignées phénotypiquement distinctes au sein du même clade. Cette définition, très large et très inclusive, sera reprise par Cerca et collaborateurs (Cerca et al. 2023 ; voir **Annexe 1**) pour identifier les radiations adaptatives dans les îles océaniques.

Seulement une dizaine d'années après la publication des travaux de Darwin, John Thomas Gulick, missionnaire à Hawaï et évolutionniste de la première heure, étudie la diversité des escargots terrestres de l'archipel, et ne parvient pas à identifier de différences écologiques majeures entre des espèces distribuées aussi bien dans des îles différentes que sur une même île. Il théorise alors le rôle de l'isolement géographique dans les processus de spéciation (Gulick 1872, voir aussi la synthèse de Rundell 2011), et met en lumière l'existence du caractère non-adaptatif de certaines radiations, même si le terme lui-même ne sera introduit que plus tard. Bien que ses idées aient été discutées par Darwin et Wallace, ainsi que par les chefs de file de la théorie synthétique (par exemple Wright et

Mayr), les travaux de Gulick restent encore très peu connus aujourd'hui (Rundell 2011, Simões et al. 2016). Au début des années 90, Edmund Gittenberger, malacologiste néerlandais, s'amuse à noter que si nous avons besoin d'ajouter l'épithète *adaptive* à radiation, c'est que le terme de radiation en tant que tel n'implique pas d'adaptation. Il propose donc pour la première fois l'utilisation de l'adjectif *non-adaptive* pour désigner une radiation évolutive dont les espèces présentent des niches écologiques similaires, et qui ont évolué principalement par spéciation parapatrique ou allopatrique (c.à.d. liée à des barrières géographiques) (Gittenberger 1991, Rundell & Price 2009). S'en suivent alors de nombreuses discussions quant à la caractérisation précise de ces deux types de radiations, poussant certains auteurs à suggérer l'abandon pur et simple du terme adaptatif, à moins que l'adaptation ne soit méthodologiquement démontrée (Hernández-Hernández 2019), ce qui est rarement le cas (Soulebeau et al. 2015).

Au-delà de ce débat, la communauté scientifique semble tout de même s'accorder sur le fait qu'une radiation évolutive est avant tout déclenchée par une opportunité écologique, c'est-à-dire un événement lié à la biologie et/ou l'environnement d'une espèce. La colonisation d'une nouvelle région géographique inoccupée, l'extinction d'espèces antagonistes, l'apparition de nouvelles ressources et l'évolution d'une innovation-clé sont considérées comme les déclencheurs fondamentaux des événements de radiations (Stanley 1979, Erwin 1992, Yoder et al. 2010, Stroud & Losos 2016). L'apparition d'une ou plusieurs de ces opportunités a pour conséquence la séparation et la différenciation souvent rapide d'une population initiale en plusieurs groupes écologiques et/ou morphologiques et/ou géographiques distincts, menant à une explosion du nombre d'espèces au sein du clade concerné (Rundell & Price 2009, Losos & Mahler 2010, Simões et al. 2016). De manière à englober toute la diversité du phénomène de radiation, certains auteurs ont donc proposé des définitions très générales de la radiation évolutive, comme l'"accumulation spectaculaire de lignées au sein d'un clade" (Simões et al. 2016) ou encore "un événement évolutif de diversification intense, où le taux de spéciation élevé au regard du taux d'extinction génère l'apparition rapide de nombreuses espèces" (Givnish 2015). L'utilisation de ce type de définition permet ainsi d'englober l'ensemble des phénomènes qui peuvent conduire à l'apparition d'une radiation, et d'inclure les radiations adaptatives et non-adaptatives, le mécanisme déclencheur pouvant tout aussi bien être de nature écologique qu'exclusivement géographique. Différentes tentatives de classification plus précises des radiations ont vu le jour récemment, en utilisant par exemple le type de déclencheur comme critère de classification (Simões et al. 2016, **Figure I.2**), ou bien les critères continus de divergence écologique, disparité phénotypique et richesse spécifique (Martin & Richards 2019, **Figure I.3**).



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Figure I.2. Présentation des différents types de radiations évolutives définies par leurs déclencheurs, et visualisation des phénomènes associés de disparification et de pseudoradiation. Pour chaque type, les branches de couleur grise permettent de comparer avec un clade n'ayant pas subi de radiation. La radiation adaptative (bleu) est déclenchée par une innovation clé indiquée par un point rouge, et mène vers une divergence écomorphologique des espèces en sympatrie (i.e., sur un même territoire). La radiation géographique (vert foncé) est déclenchée par une barrière physique permettant des événements de spéciation allopatrique (par isolement géographique). La radiation climatique (vert clair) est un type de radiation géographique (i.e., par spéciation allopatrique) mais qui est déclenchée par des changements climatiques. Le patron de disparification (marron) montre une plus grande variété de l'espace morphologique au sein de la radiation (5 morphotypes pour 5 espèces) par rapport au clade n'ayant pas subi de radiation (2 morphotypes pour 5 espèces). Le patron de pseudoradiation montre une baisse du taux d'extinction au sein de la radiation par rapport au clade n'ayant pas subi de radiation (1 lignée interrompue contre 4). Le fort taux d'accumulation d'espèces caractéristiques des radiations peut en effet être dû soit à une augmentation du taux de spéciation, soit à une baisse du taux d'extinction par rapport aux autres clades. Adaptée de Simões et al. (2016).

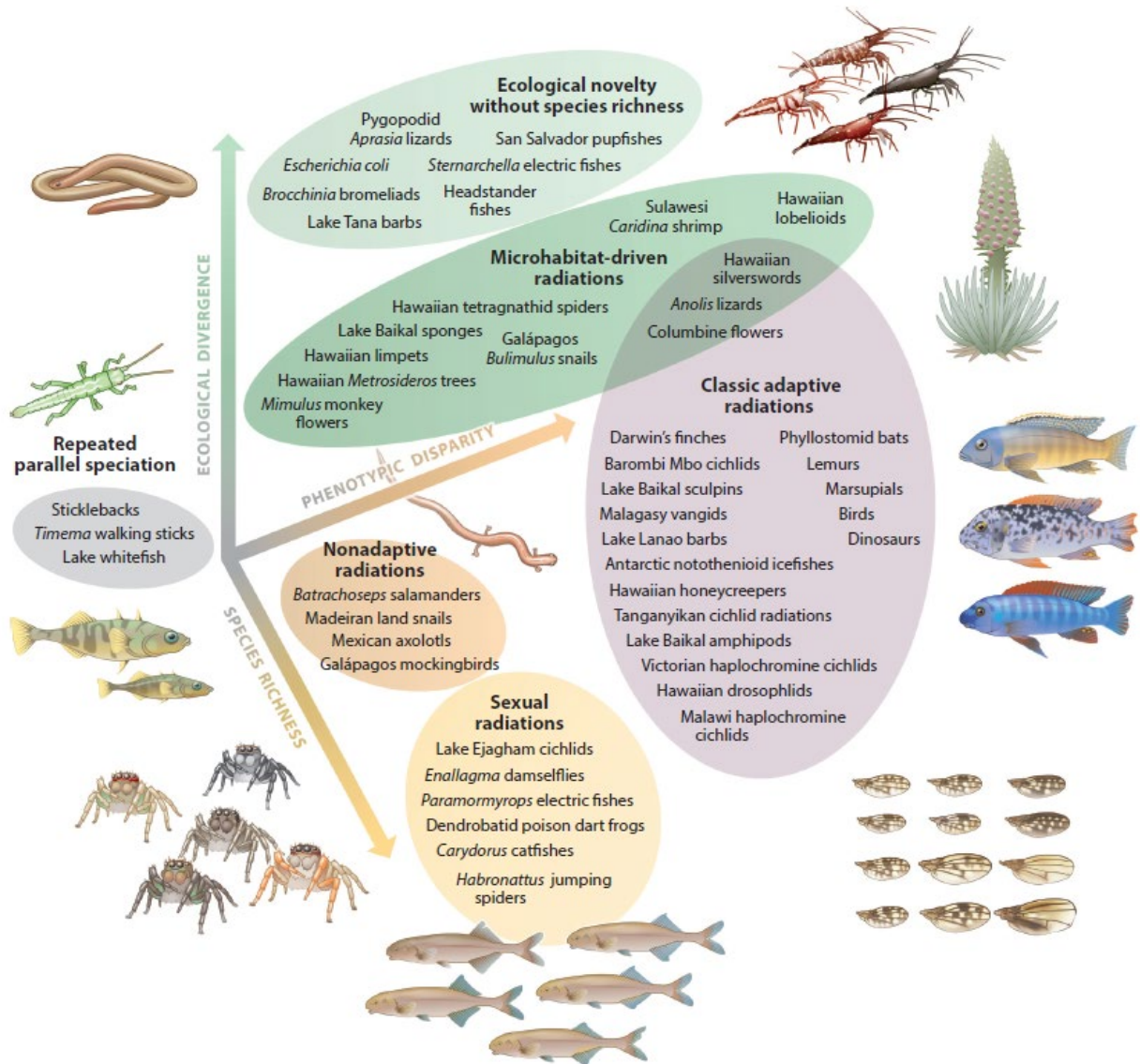


Figure I.3. Les différents types de radiations rapides et leur exemple associé, projetées dans l'espace selon trois grands axes majeurs : la divergence écologique, la disparité phénotypique et la richesse spécifique (nombre d'espèces). Sont présentés : la nouveauté écologique sans augmentation de la richesse spécifique (exemple illustré : les lézards pygopodes du genre *Aprasia*) ; les radiations induites par les microhabitats (microallopatrie) (exemple illustré : les crevettes des lacs Malili du genre *Caridina*). La spéciation parallèle répétée (exemples illustrés: les phasmes du genre *Timema* et les épinoches benthiques/limnétiques) ; les radiations non-adaptatives (exemple illustré: les salamandres du genre *Batrachoseps*) ; les radiations sexuelles (exemples illustrés: les araignées sauteuses du genre *Habronattus* et les poissons électriques du genre *Paramormyrops*) ; les radiations adaptatives classiques (exemples illustrés: les Cichlidae du Malawi, les drosophiles "picture-wing" d'Hawaï du genre *Drosophila* et l'alliance des « Silverswords » d'Hawaï). Adaptée de Martin & Richards (2019).

La richesse spécifique, c'est-à-dire le nombre d'espèces constituant la radiation, demeure un aspect encore relativement peu discuté dans la littérature. En effet, faut-il qu'un clade compte un nombre minimal d'espèces pour être qualifié de radiation ? À ce jour, il n'existe aucun consensus sur cette question, bien que de plus en plus de travaux tendent à considérer qu'un véritable événement radiatif commence à partir de trois espèces (Martin & Richards 2019, Matsubayashi & Yamaguchi 2021, Cerca et al. 2023), ce seuil devant être vu plus comme une convention que comme une réelle limite biologique.

Au cours de cette thèse, le terme de **radiation évolutive** fera donc référence à une **accumulation spectaculaire d'espèces au sein d'un même clade** ; un clade étant défini comme un groupe d'espèces proches partageant toutes un seul et même ancêtre commun, qui comprend la totalité des descendants de cet ancêtre et qui est composé d'au moins trois espèces (Funk 1995, Simoes et al. 2016, Martin & Richards 2019).

2. Radiations, îles et archipels océaniques

Dans cette section, je commence par présenter pourquoi les environnements insulaires sont reconnus comme de véritables laboratoires naturels pour l'étude de la biodiversité. Ensuite, j'adopte une perspective biogéographique pour introduire les différents types d'îles, avant de me concentrer sur les facteurs écologiques et évolutifs qui peuvent expliquer la prévalence des radiations évolutives au sein des archipels océaniques.

2. a. L'île comme laboratoire naturel

Comme abordé dans la section 1.1, l'étude de la biodiversité insulaire a joué un rôle clé dans le développement de la théorie de l'évolution (Wallace 1869, Darwin 1845). L'intérêt pour les îles au sein de la communauté scientifique n'a pas décliné au fil des décennies, conduisant certains chercheurs à évoquer "le paradigme du laboratoire naturel" à leur sujet (Whittaker et al. 2023). Plusieurs caractéristiques biologiques et environnementales expliquent pourquoi les îles sont des systèmes plus simples à appréhender que les systèmes continentaux (Losos & Ricklefs 2009). En effet, les îles sont, en règle générale, de taille modeste, et sont clairement délimitées par des barrières naturelles (le plus souvent, un océan), permettant ainsi un inventaire plus rapide et plus précis des espèces qui les peuplent par rapport aux régions continentales (Emerson 2002). Leur grand nombre et leur grande variété géologique et environnementale offrent de multiples réplicats écologiques et évolutifs naturels permettant ainsi de développer et de tester des théories d'importance plus générale (Whittaker et al. 2023). Dans le cas des îles d'origine volcanique, l'âge géologique des îles peut également fournir un cadre temporel propice à l'analyse des processus éco-évolutifs sur le long

terme (Borregaard et al. 2017). De plus, les communautés écologiques insulaires sont également généralement moins complexes, l'isolement des îles ayant rendu difficile voire impossible la colonisation active ou passive de certains organismes vivants. Par exemple, on retrouve une faible diversité d'amphibiens endémiques sur les îles très isolées, car leur faible capacité de dispersion couplée à leur intolérance à l'eau salée réduit fortement les chances de traversée réussie (Blaustein et al. 1994, Measey et al. 2007, mais voir aussi Fonte et al. 2019). Cette absence de certains taxons, appelé disharmonie (Carlquist 1974), n'empêche pas par ailleurs les environnements insulaires d'être de véritables points chauds de biodiversité : on estime en effet qu'ils représentent 20% de la biodiversité mondiale, pour seulement 6.67% de la surface terrestre (Kier et al. 2009, Sayre et al. 2018, Fernandez-Palacios et al. 2021). Il est également important de noter que les îles font partie des zones du globe les plus vulnérables et les plus menacées par les changements globaux actuels (Fernandez-Palacios et al. 2021). Elles sont le lieu d'environ 60% des extinctions récentes (c.-à-d. depuis 1500, début de la période historique d'exploration du globe par les Européens ; Whittaker et al. 2023). Cette proportion varie de 60% pour les mammifères (qui sont généralement absents dans les îles éloignées) à 79% pour les mollusques, 81% pour les oiseaux et jusqu'à 95% pour les reptiles. La perte d'espèces insulaires par l'action humaine s'explique par cinq facteurs principaux : la surexploitation, l'introduction d'espèces exotiques, la propagation des maladies, la dégradation ou perte d'habitat et le changement climatique (Leclerc et al. 2018, Fernandez-Palacios et al. 2021).

L'origine géologique des plus de 340000 îles recensées dans le monde (Sayre et al. 2018) est multiple et complexe (Ali 2017). Dans son livre *Island life* (Wallace 1880), Wallace propose de classer les îles en trois catégories distinctes, classification qui reste aujourd'hui abondamment utilisée dans la littérature, car toujours pertinente pour appréhender ces environnements d'un point de vue biogéographique (Whittaker et al. 2023). Notons cependant que certains travaux récents et orientés vers la communauté des biogéographes insulaires ont permis d'affiner, corriger et complexifier cette classification (Ali 2017, 2018, Ali & Meiri 2023). La classification de Wallace est la suivante :

- **Les îles continentales récentes.** Séparées du continent récemment au regard des temps géologiques, elles sont entourées d'eaux peu profondes, et peuvent avoir été régulièrement reconnectées avec le continent suite aux variations du niveau de la mer durant le Pléistocène. Ces îles restent donc très similaires aux continents d'un point de vue biologique et géologique. On peut citer comme exemple les îles de la Mer Egée.

- Les **îles continentales anciennes**. Ces masses terrestres se sont détachées du continent depuis une longue période (généralement plusieurs dizaines de millions d'années) : elles contiennent toujours un certain nombre d'espèces continentales ancestrales, mais peuvent également avoir eu un nouvel apport de diversité par le phénomène de spéciation *in-situ*, c'est à dire par l'évolution de nouvelles espèces strictement endémiques au sein même de l'île. On peut citer comme exemple l'île de Madagascar.
- Les **îles volcaniques**, aussi appelées **îles océaniques**. Ces formations géologiques sont le résultat d'une activité volcanique sous-marine intense ayant accumulé des roches magmatiques jusqu'à émergence au-dessus du niveau de la mer. Elles se forment typiquement dans les zones très actives de convergence ou de divergence de plaques tectoniques et produisent un ensemble de volcan appelé arc volcanique (**Figure I.4**) (e.g., les petites Antilles), mais peuvent également émerger directement sur la plaque, grâce au volcanisme dit de "point chaud" (e.g., Hawaï). Ce mécanisme géologique, mit en lumière pour la première fois par Wilson (Wilson 1963), est devenue l'hypothèse privilégiée pour expliquer l'émergence et la structure géographique de nombreux archipels océaniques à travers le monde (Morgan 1971, Wagner & Funk 1995, Ali 2017, **Figure I.5**). N'ayant jamais été en contact avec aucune autre terre émergée, la diversité observée sur les îles océaniques est donc uniquement le résultat de colonisations extérieures et/ou d'évènements de spéciation *in-situ*.

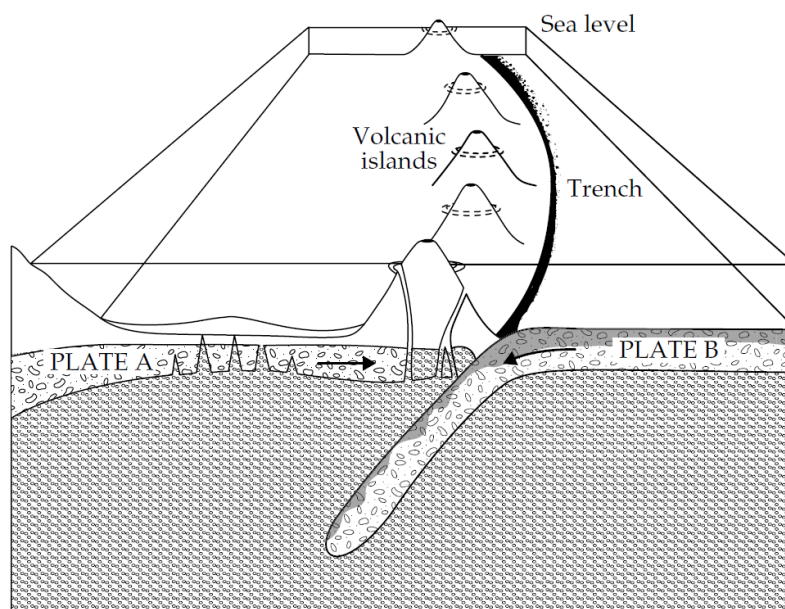


Figure I.4. Représentation simplifiée de la formation d'un archipel d'îles océaniques ou arc volcanique due à la subduction d'une plaque tectonique en dessous d'une autre. Adaptée de Whittaker & Fernández-Palacios (2007).

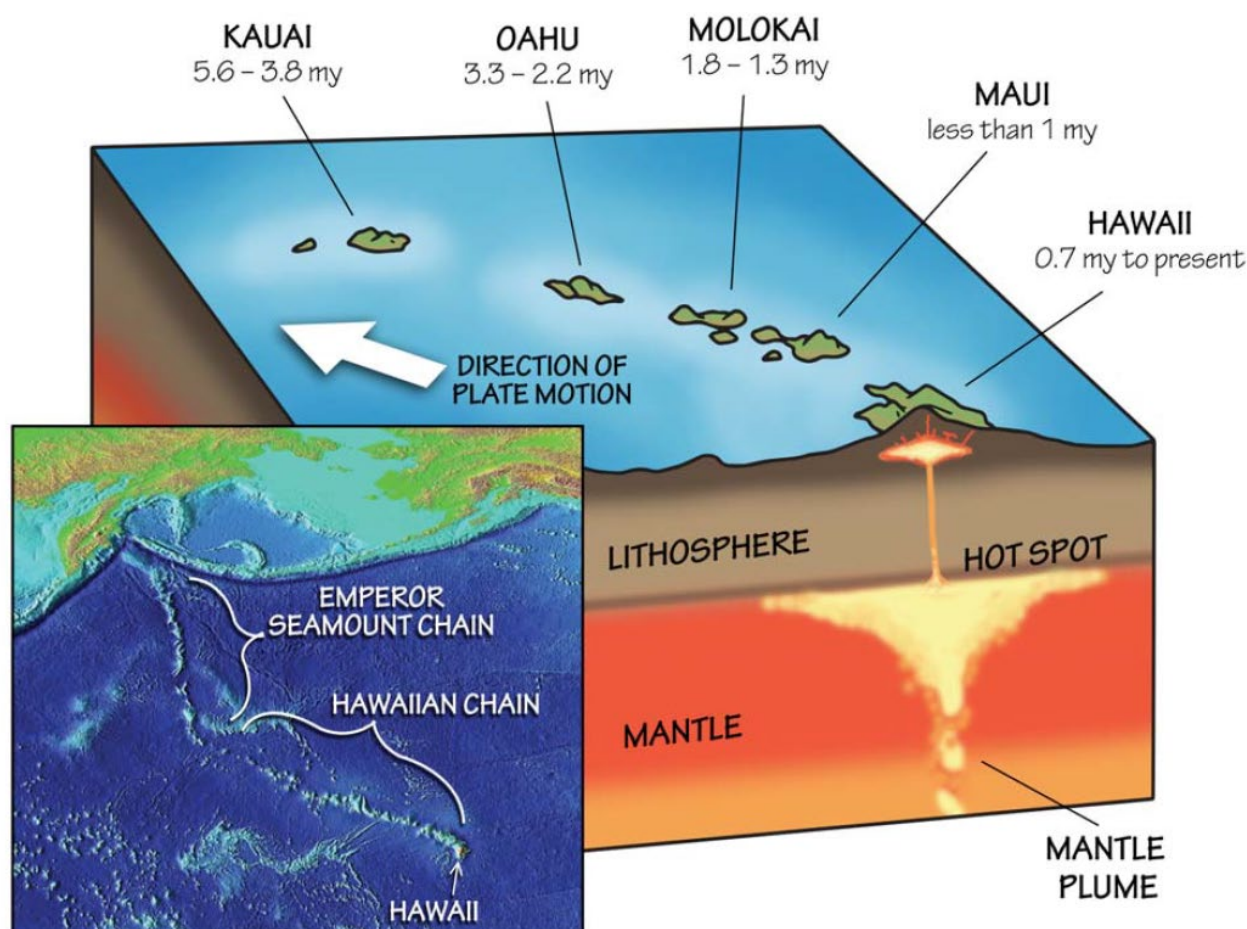


Figure I.5. Représentation schématique de la formation de l’archipel océanique d’Hawaï par l’interaction entre le point chaud d’Hawaï et la plaque tectonique Pacifique. Une remontée de roches chaudes dans le manteau, appelée panache (“Mantle plume”), crée une accumulation de magma basaltique (le point chaud), qui finit par traverser la lithosphère et mener à l’émergence de volcans sous-marins, puis d’îles volcaniques (voir **Figure I.6**). Le mouvement de la plaque tectonique Pacifique entraîne les îles ainsi formées vers le nord-est. Comme le point chaud reste relativement au même endroit dans le manteau, on observe la formation d’une chaîne d’îles volcaniques. La carte au premier plan montre la chaîne sous-marine Hawaï-Empereur, la Chaîne d’Hawaï et la position des îles actuelles émergées d’Hawaï (« Hawaii »). On suppose que ces monts sous-marins, s’étendant sur plus de 6000 kilomètres, sont des vestiges d’anciennes îles volcaniques dont les plus vieilles auraient émergé il y a 70 millions d’années (Keast and Miller 1996, Whittaker et al. 2023). Adaptée de Lucas et al. (2014).

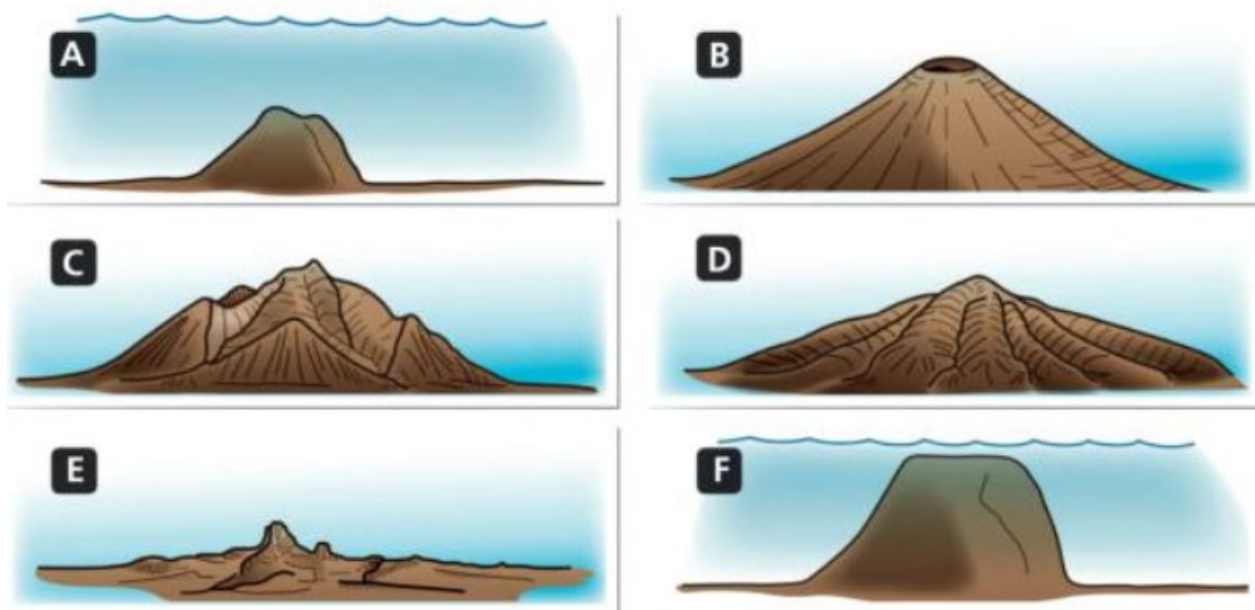


Figure I.6. Les différentes étapes théoriques de l'ontogénie d'une île volcanique. (A) La forte activité volcanique conduit à l'émergence d'un mont sous-marin par accumulation de roches basaltiques ; (B) L'île émerge et crée un volcan de forme conique aux rainures radiales caractéristiques (exemple réel : l'île de Tristan da Cunha). (C) Le volcan est au stade de planèze : il forme des plateaux triangulaires séparés par des rainures de drainage. L'érosion fluviale des plateaux est donc encore limitée (exemple réel : l'île de Sainte-Hélène). (D). Volcan résiduel, où les planèzes ont finalement disparu sous l'effet de l'érosion, mais où la forme conique est encore présente (exemples réels : l'île de Fuerteventura aux Îles Canaries, ou encore les îles de Sal, Boa Vista et Maio au Cap-Vert). (E) Squelette volcanique, où les necks et les dykes (reliefs volcaniques) restent les seuls marqueurs significatifs (exemples réels : l'île de Bora-Bora en Polynésie Française). (F) L'érosion et la subsidence ramène finalement l'île volcanique à l'état de mont sous-marin. Adaptée de Whittaker et al. (2023).

Parmi ces différents types d'îles, les îles océaniques sont incontestablement celles qui ont suscité le plus de fascination au sein de la communauté scientifique et qui, au fil des recherches qui leur ont été consacrées, ont émergé comme de formidables systèmes pour explorer les mécanismes écologiques et évolutifs sous-jacents à la diversification des espèces (Gillespie 2007). En effet, les événements volcaniques responsables de leur apparition génèrent le plus souvent un ensemble d'îles géographiquement proches et de même nature géologique qui peuvent cependant varier en taille, en âge ou en complexité topographique. Ces archipels volcaniques offrent ainsi une opportunité unique pour tester différentes hypothèses biologiques à l'échelle de plusieurs répliques tout en gardant une certaine intégrité géo-environnementale (Losos & Ricklefs 2009, Whittaker et al. 2023). De plus, la plupart de ces archipels sont jeunes d'un point de vue géologique (généralement entre Miocène et Pliocène ; i.e., de -23 à -2 million d'années), créant ainsi un cadre temporel restreint qui limite le nombre d'hypothèses évolutives. Il a récemment été suggéré que les archipels océaniques soient qualifiés de véritables provinces biotiques, c.-à-d. des environnements où la diversité reflète principalement un équilibre entre la spéciation et l'extinction, la colonisation jouant un rôle mineur (Triantis et al. 2016). Cette perspective réaffirme le statut de ces archipels en tant qu'unités d'analyse spatio-temporelle appropriées pour décrypter les schémas de biodiversité à des échelles plus vastes (Triantis et al. 2015, 2016).

Au cours de cette thèse, le terme d'**archipel océanique** fera donc référence ici à **une île ou un groupement d'îles géographiquement proches, ayant la même origine volcanique, et n'ayant jamais été en contact avec d'autres masses terrestres** (Nunn 2009, Whittaker et al. 2023). Une sélection de plusieurs archipels océaniques caractéristiques sont présentés en **Figure I.7**.

2. b. Archipels océaniques et radiations insulaires

Une des caractéristiques des archipels océaniques est le grand nombre de radiations évolutives décrites en leur sein (Emerson 2002, Gillespie 2007, Whittaker et al. 2023). Déterminer pourquoi les radiations sont fréquentes dans les archipels océaniques n'est pas un exercice trivial. Il est toutefois possible d'énumérer un certain nombre de facteurs déterministes et stochastiques qui pourrait favoriser la cladogenèse¹ et par conséquent l'apparition de radiations. Cependant, il est difficile de déterminer l'importance relative de ces facteurs, d'autant plus qu'ils peuvent varier d'une lignée, d'une île ou d'un archipel à l'autre.

¹ Cladogenèse : processus évolutif aboutissant à l'apparition de nouvelles espèces par la scission d'une lignée ancestrale en au moins deux lignées descendantes.

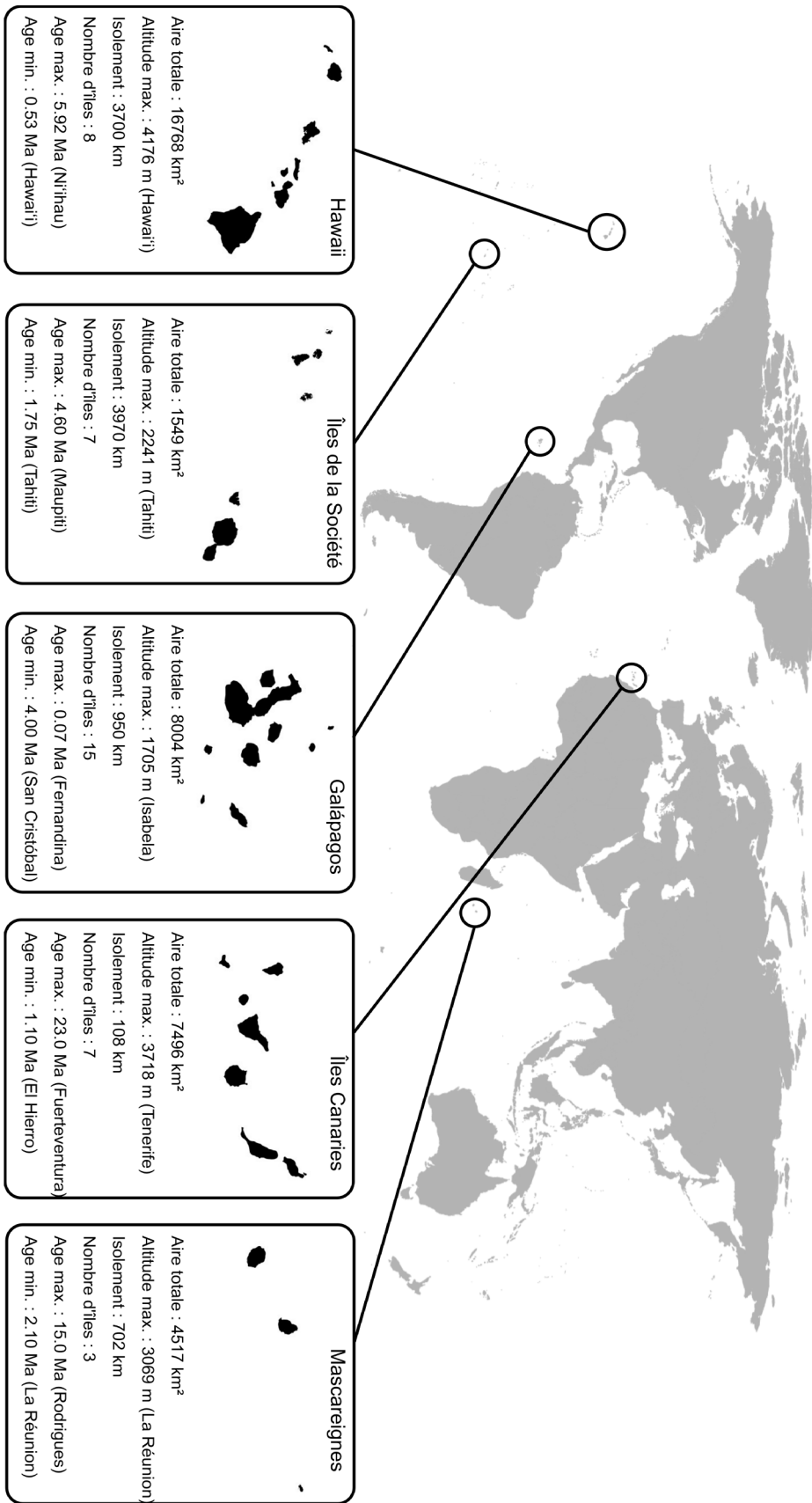


Figure I.7. Présentation de cinq archipels océaniques répartis dans trois océans à travers le monde. L'isolement correspond à la distance à la masse continentale la plus proche. Le nombre d'îles fait référence aux îles principales les plus grandes et les plus souvent utilisées dans la littérature. Les âges sont reportés par rapport à ces îles principales. Les informations sont tirées des références suivantes (et leur références internes) : Gillespie & Clague (2009), Weigel et al. (2015), Hembry & Balukjian (2016), Roell et al. (2021), Kraemer et al. (2022), van den Bogard (2013), Thébaud et al. (2009), Weigel et al. (2016).

La grande diversité des habitats sur de nombreuses îles océaniques, créée principalement par les conditions géologiques et climatiques, offre un large éventail d'opportunités écologiques. Par exemple, plusieurs îles dépassent les 3000 mètres (m) d'altitude, telles que Tenerife aux îles Canaries (3718 m), La Réunion aux Mascareignes (3070 m), ou Big Island à Hawaï (4207 m), ce qui engendre un gradient altitudinal marqué allant des habitats côtiers aux zones alpines. En outre, du fait de leur isolement géographique, peu d'organismes sont capables de coloniser ces îles, et les chances de colonisations répétées par une même espèce sont faibles, ce qui limite les flux de gènes. Ainsi, les individus immigrants qui réussissent à s'implanter peuvent se retrouver instantanément isolés de leur population d'origine (Paulay & Meyer 2002). Enfin, la compétition et la prédation exercées par les espèces déjà établies peuvent être considérées comme faibles (McArthur & Wilson 1967). Dans ces conditions, la spéciation *in-situ* va donc être favorisée (Carlquist 1974, Schluter 1988, Leigh et al. 2007, Losos and Ricklefs 2009, Losos & Mahler 2010), la diversification agissant comme l'unique moyen de “remplir” l'espace écologique disponible. Parfois, l'acquisition d'un ou plusieurs caractères particuliers peut prédisposer un taxon insulaire à une spéciation rapide, lui offrant ainsi l'accès à de nouvelles ressources jusqu'alors inexploitées (Jorgensen & Olesen 2001). Enfin, la configuration en archipel peut également être une source de spéciation potentielle: la colonisation de plusieurs îles par des individus d'une même population entraîne une séparation géographique, qui peut être suivie d'un isolement reproducteur si le taux de colonisation entre les îles reste limité, favorisant ainsi l'émergence d'espèces par spéciation allopatrique (dérive génétique), puis par spéciation sympatrique en cas de contact secondaire (Rosenzweig 1995, Losos & Ricklefs 2009, **Figure I.8**). Il est important de noter que toutes les lignées d'un archipel océanique donné ne connaissent pas le même succès, même si elles bénéficient des mêmes opportunités écologiques et sont exposées à la même dynamique géologique. L'apparition de nouvelles espèces peut simplement être dû à l'ordre de colonisation (effet fondateur, Waters et al. 2013) ou à des événements stochastiques (e.g., volcanisme) menant à l'extinction ou l'apparition d'une lignée et pas d'une autre. La variation du succès des lignées peut également être due à des différences dans leur potentiel évolutif (ou variabilité génétique) ou à des contraintes phylogénétiques (Hiller et al. 2019).

Les radiations évolutives occupent une part non négligeable de la biodiversité des archipels océaniques : sur l'archipel d'Hawaï par exemple, la seule radiation des *Lobelioideae* (Campanulaceae) représente un huitième de la totalité de la flore native (Givnish et al. 2009), et on estime que la radiation des papillons de nuit du genre *Hyposmocoma* (Lepidoptera) représente un tiers de la diversité totale des Lépidoptères de l'archipel (Haines et al. 2014). Un autre exemple

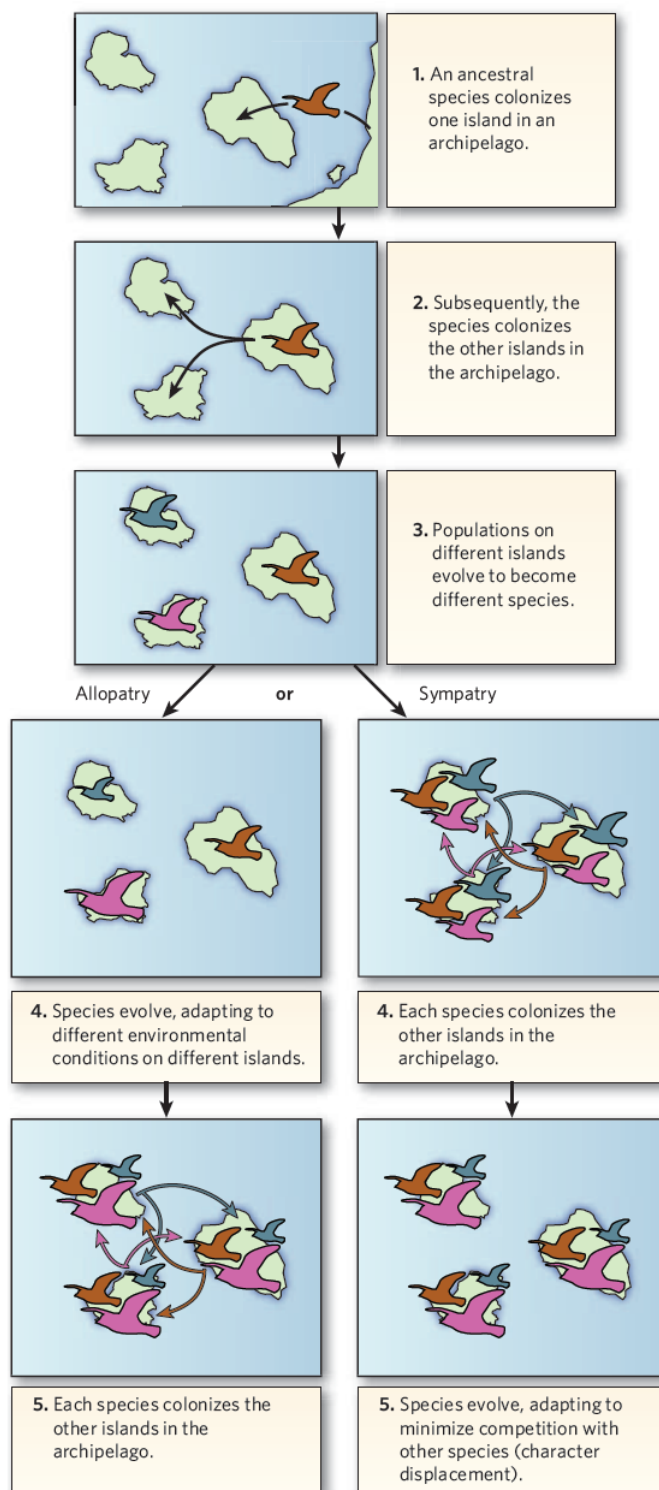


Figure I.8. Les deux modèles possibles de spéciation allopatrique avec sympatrie subséquente pouvant avoir lieu au sein d'un archipel. Les trois premiers panneaux s'appliquent aux deux modèles, tandis que les panneaux suivants montrent soit le rôle possible de la divergence écologique dans le processus d'allopatrie (gauche), soit celui du déplacement de caractère dans le processus de sympatrie (droite). Adaptée de Losos & Ricklefs (2009).



Figure I.9. Présentation de quatre radiations évolutives sur différents archipels océaniques. Figures adaptées de différentes références (voir en dessous de chaque figure). Les âges estimés correspondent à l'âge du nœud couronne (âge du premier événement de spéciation intra-radiation) le plus récent estimé dans la littérature (voir références).

concerne la flore endémique de l'ensemble des archipels de Macaronésie (Canaries, Açores, Madère, Selvagens et Cap-Vert), qui se compose à moitié d'espèces provenant uniquement de 12 radiations (Price et al. 2018). La littérature scientifique regorge par conséquent d'exemple de radiations évolutives dans les archipels océaniques, certaines comptant parmi les modèles biologiques les plus connus et étudiés aussi bien en biogéographie insulaire qu'en biologie évolutive, tel que les pinsons des Galápagos (Grant & Grant 2007), les Drosophiles d'Hawaii (Drosophilidae, O'Grady & DeSalle 2018) ou encore la radiation des "Silverswords" d'Hawaii (Asteraceae ; Baldwin & Sanderson 1998). En **Figure I.9** sont présentées une sélection quatre radiations iconiques provenant de différents archipels.

3. Comprendre les radiations évolutives dans les archipels océaniques : modèles macroécologiques et macroévolutifs.

Dans cette troisième section, je présente les principaux cadres théoriques qui ont guidé la recherche sur les radiations insulaires au cours des dernières décennies, en adoptant une perspective à la fois macroévolutive et biogéographique. Tout d'abord, j'aborde quelques aspects clés de l'approche macroévolutive ainsi que son application à l'étude des radiations insulaires, en expliquant comment ces travaux ont enrichi notre compréhension du phénomène radiatif dans les îles océaniques. Par la suite, je m'appuie sur la Théorie de la Biogéographie Insulaire (MacArthur & Wilson 1967) en tant que cadre général de l'étude de la biodiversité insulaire pour présenter les approches biogéographiques appliquées aux radiations. Je discuterai plus particulièrement du Modèle Dynamique Général de la biogéographie des îles océaniques (GDM, Whittaker et al. 2008, Borregaard et al. 2017), qui propose une meilleure intégration de la spéciation, et donc du processus radiatif, au sein de la Théorie de la Biogéographie Insulaire.

3. a. Approches macroévolutives

Le terme "macroévolution" désigne le domaine scientifique qui s'attache à observer et à comprendre la structuration de la diversité biologique à de larges échelles temporelles (i.e., temps géologiques, Simpson 1953, Stanley 1979). Basé initialement sur le registre fossile (Simpson 1944, Raup et al. 1973), l'analyse en macroévolution se repose aujourd'hui de plus en plus sur l'analyse d'arbres phylogénétiques. Ces derniers permettent notamment d'étudier l'histoire évolutive des espèces actuelles pour lesquelles les données fossiles sont inexistantes (Nee et al. 1992, Harvey et al. 1994, Ricklefs 2007) ; ce qui est le cas de la plupart des groupes présents dans les îles océaniques (Landis et al. 2018, García-Verdugo et al. 2019). L'analyse macroévolutive peut revêtir diverses formes : elle peut impliquer la description des schémas d'accumulation des lignées au fil du temps

(*lineage-through-time*), et également proposer une analyse plus approfondie de la configuration de l'arbre phylogénétique ainsi que l'étude des caractères phénotypiques sur le temps long. Étant donné que les approches macroévolutives abordées durant ma thèse se sont principalement axées sur l'analyse d'arbres phylogénétiques, je ne développerais pas ici les méthodes impliquant l'analyse de caractères phénotypiques (e.g., morphologiques) tels que, par exemple, les analyses de disparité dans le temps (*disparity-through-time*, Harmon et al. 2003).

Le développement de la théorie phylogénétique (Hennig 1966), la généralisation de la PCR et le séquençage de l'ADN à coût de plus en plus abordable (Douzery et al. 2016), l'augmentation de la puissance de calcul et la sophistication croissante des méthodes de reconstruction [i.e., l'approche du maximum de vraisemblance (Felsenstein 1973, 1981) et l'inférence bayésienne (Huelsenbeck et al. 2001)], ont conduit à une accumulation inédite de phylogénies de plus en plus robustes. Ces avancées ont ainsi permis d'identifier une diversité extraordinaire de groupes monophylétiques, qui sont aujourd'hui devenus des outils majeurs dans la recherche en macroévolution (McGill et al. 2019). On définit un groupe monophylétique comme un ensemble d'espèces que l'on considère comme provenant d'un seul ancêtre commun, dû à la présence d'au moins une synapomorphie commune à toutes les espèces (Ashlock 1971). Ces groupes permettent de placer les espèces au sein d'une histoire évolutive commune, et de poser ainsi un cadre clair pour l'étude des mécanismes qui sous-tendent les patrons de diversification (Funk & Wagner 1995). Le développement du concept d'horloge moléculaire (Zuckerkandl & Pauling 1965) puis d'horloge moléculaire relâchée (Sanderson 1997, Thorne et al. 1998) à la fin du XXème siècle a permis d'obtenir des estimations numériques quant aux dates de divergences entre espèces au sein des groupes monophylétiques, en se basant sur les distances génétiques estimées entre les nœuds d'une phylogénie (Bromham & Penny 2003, Donoghue & Benton 2007). Cette technique, couplée à un ou plusieurs points de calibrations tels que l'âge de fossiles et/ou d'événements géologiques connus, a ainsi permis de placer les arbres phylogénétiques au sein d'un cadre temporel plus ou moins précis.

Cette avancée a ainsi ouvert la voie à l'exploration de certaines problématiques clés de la macroévolution, tels que l'étude du tempo et du mode de diversification des clades (Morlon 2014) ou encore la question des variations de diversité entre clades (Rabosky 2009). De nombreux modèles statistiques, basé essentiellement le modèle "naissance-mort" (*birth-death models*) ont ainsi été développés afin d'évaluer un certain nombre d'hypothèses biologiques concernant les variations des taux de spéciation (λ) et d'extinction (μ) au cours du temps (Morlon 2014, **Encadré I.1**).

D'autres approches tels que les méthodes intégratives comme le Gamma (γ) (Pybus & Harvey 2000) ou le ρ (Pigot et al. 2010) ont proposé de résumer la forme d'un arbre en une seule valeur. L'indice γ est, de loin, le plus couramment utilisé, et se calcule comme suit :

$$\gamma = \frac{\left(\frac{1}{n-2} \sum_{i=2}^{n-1} \left(\sum_{k=2}^i k g_k \right) \right)^{-\frac{T}{2}}}{T \sqrt{\frac{1}{12(n-2)}}}, \quad T = \sum_{j=2}^n j g_j$$

Avec g_2, g_3, \dots, g_n représentant les distances entre les nœuds d'un arbre phylogénétique contenant n espèces.

Encadré I.1 : Fonctionnement des modèles de naissance-mort en macroévolution.

Au début des années 90, plusieurs chercheurs commencent à développer des modèles dit de "naissance-mort" (*birth-death models*) pour pouvoir étudier la diversification [i.e., la spéciation (λ) moins l'extinction (μ)] en ayant seulement recours à l'information contenu dans les phylogénies moléculaires (Hey 1992, Nee et al. 1992, 1994). Ces modèles sont basés sur un processus stochastique qui démarre d'une seule espèce à t_0 , et qui crée ou perd des espèces au cours du temps en fonction de λ et μ (Stadler 2013). Le modèle génère dans un premier temps un arbre phylogénétique complet comprenant toutes les lignées éteintes et actuelles, puis efface les branches menant aux lignées éteintes afin d'obtenir un arbre comparable à un phylogénétique empirique. Dans sa formulation la plus simple, λ et μ sont constants dans le temps et d'une espèce à l'autre, de sorte que $\lambda(t) = \lambda_0$ et $\mu(t) = \mu_0$, λ_0 et μ_0 étant les taux actuels. Ce modèle à taux constant a été largement utilisé comme modèle nul dans la littérature (Nee et al. 1994, Pybus & Harvey 2000). Par la suite, les modèles ont été complexifiés par l'ajout de différents paramètres dans l'expression des taux, afin de correspondre à différentes hypothèses biologiques (Morlon 2014). On trouve notamment des modèles avec λ et/ou μ variant de manière exponentiel et/ou linéaire au cours du temps (Morlon et al. 2010) ; des modèles propose également de corrélés λ et/ou μ avec les variations de certaines variables d'intérêt comme la température (Condamine et al. 2013), ou encore des modèles de diversité-dépendance, avec λ et μ qui convergent à l'approche de la capacité de charge K de l'environnement (Etienne et al. 2012). Traditionnellement, des critères tels que l'AIC (Akaike Information Criteria) basé sur la vraisemblance sont utilisés pour déterminer le ou les modèles s'ajustant le mieux à la phylogénie empirique (Morlon 2014). Cependant, une étude a récemment montré que les seules informations contenues dans les phylogénies ne permettaient pas de discriminer entre de multiples trajectoires évolutives possibles, remettant en cause l'utilisation de ce type d'approche (Louca & Pennel 2020). Malgré ces limites, la comparaison de modèles basée sur des hypothèses bien définies reste toujours utile pour pouvoir discriminer entre différentes histoires évolutives, sans s'intéresser nécessairement aux valeurs numériques exactes des taux de diversifications estimés (Morlon et al. 2020, Helmstetter et al. 2022).

La valeur de γ d'un arbre phylogénétique doit être comparée à zéro, qui est la valeur attendue sous l'hypothèse que l'arbre résulte d'un modèle de naissance pure (*Pure-birth model*, Yule 1925). Si γ est positif, cela signifie que les nœuds (événements de spéciation) sont concentrés vers le présent (i.e., l'hypothèse du *pull-of-the-present*), tandis qu'un γ négatif indique une concentration de nœuds vers la racine de l'arbre (i.e., l'hypothèse du *early burst*). Bien que plusieurs travaux aient pointé certaines faiblesses du γ [e.g., dépendance à la taille des clades ou au degré d'échantillonnage, e.g., McPeck 2008], cet estimateur continu d'être utilisé dans de nombreuses études empiriques afin de décrire les patrons de diversification (e.g., Borko et al. 2021, Stec et al. 2022).

L'application de diverses approches sur un grand nombre de phylogénies empiriques a permis de mettre en évidence des trajectoires évolutives communes au sein des radiations. Parmi elles a été observée une décélération du rythme de branchement au sein de nombreuses phylogénies indépendantes (i.e., *early burst*), pouvant être, dans certains cas, associée à un phénomène de diversité-dépendance sur les taux de diversification (e.g., Pybus & Harvey 2000, McPeck 2008, Phillimore & Price 2008, Morlon et al. 2010). Des recherches plus récentes ont également mis en évidence une corrélation entre les taux de spéciation et les fluctuations de l'environnement, en particulier les variations de température au cours du Cénozoïque (Condamine et al. 2019).

Enfin, l'utilisation de phylogénies moléculaires a également accéléré l'essor de la biogéographie historique, un sous-domaine de la macroévolution qui s'intéresse à la reconstruction de la distribution géographique passée des espèces à partir de leurs liens évolutifs (Hennig 1966, Nelson & Platnick 1981, Morrone & Crisci 1995, Ronquist & Sanmartín 2011). La biogéographie historique a initialement été façonnée par le principe de la vicariance, impliquant la fragmentation des masses terrestres due à des événements tectoniques (de Queiroz 2005). L'avènement de l'horloge moléculaire a cependant mis en évidence des histoires évolutives se déroulant sur des périodes trop courtes pour être en accord avec cette hypothèse, laquelle est principalement basée sur des processus géologiques lents (de Queiroz 2005, Sanmartín et al. 2008). En conséquence, une attention accrue est maintenant accordée à l'hypothèse de la dispersion à longue distance dans l'étude de l'histoire biogéographique des clades (de Queiroz, 2005, Sanmartín et al. 2008).

3. b. La macroévolution des radiations évolutives dans les îles océaniques

Vers la fin des années 1980, la publication d'un numéro spécial sur les îles d'Hawaii, édité par Chris Simon dans *Trends in Ecology and Evolution* (Simon 1987), joue un rôle essentiel dans le regain d'intérêt de la communauté scientifique envers les îles océaniques en tant que systèmes modèles en écologie et évolution (Gillespie 2015). Les années qui ont suivi ont ainsi vu une

explosion du nombre de publications de phylogénies moléculaires concernant des groupes insulaires, incluant, entre autres, l'alliance des Silverswords et les *Tetragnatha* d'Hawaii (Baldwin et al. 1990, 1991, Gillespie et al. 1994), les iguanes des Galápagos (Rassmann 1997) ou encore les coléoptères du genre *Pimelia* dans les Îles Canaries (Juan et al. 1995). Ces avancées ont été particulièrement cruciales pour la compréhension du phénomène radiatif dans les îles océaniques (Gillespie 2015). Ces phylogénies moléculaires ont avant tout permis de confirmer ou d'infirmer la monophylie des groupes d'espèces endémiques, permettant ainsi une meilleure délimitation des radiations. En effet, si les espèces insulaires s'avèrent former un groupe monophylétique, on peut alors supposer qu'elles ont toutes évolué à partir d'un ancêtre commun unique ayant colonisé l'archipel. L'inclusion dans l'analyse phylogénétique d'une large éventail taxonomique représentatif d'espèces provenant de plusieurs sources potentielles a également permis de déterminer l'origine géographique de la radiation, en examinant la provenance de l'espèce la plus proche phylogénétiquement (e.g., Price & Wagner 2018). Un arbre phylogénétique monophylétique facilite également l'évaluation des liens de parenté entre espèces, indépendamment de leurs similarités écologiques, offrant ainsi un cadre pertinent pour étudier l'évolution des adaptations morphologiques, écologiques, comportementales et physiologiques, ainsi que les circonstances qui ont favorisé la prolifération des espèces au sein de la radiation (Desalle et al. 1986, Baldwin et al. 1990, 1991, Gillespie et al. 1994). Avec l'accroissement de l'intérêt pour la biologie évolutive des îles océaniques, en grande partie facilité par la disponibilité croissante d'arbres phylogénétiques de plus en plus robustes, les chercheurs Warren Wagner et Vicki Funk du Smithsonian Institute (États-Unis) organisèrent en 1992 un symposium visant à explorer les développements de la biogéographie hawaïenne. Cette initiative déboucha sur la publication de l'ouvrage intitulé *Hawaiian Biogeography: Evolution on a Hot Spot Archipelago* (Funk et Wagner 1995), faisant aujourd'hui référence dans le domaine. Ce livre décrit de nombreuses radiations évolutives sur l'archipel d'Hawaï, mettant en lumière pour un grand nombre d'entre elles une tendance à suivre une progression biogéographique le long de la chaîne volcanique (*progression rule*, voir **Figure I.10**). Cette règle reflète des épisodes séquentiels de spéciation, se déroulant de l'île la plus ancienne à l'île la plus jeune. Cette dynamique de diversification a depuis été observée dans les radiations de nombreux groupes taxonomiques aux seins de multiples archipels océaniques (Wagner et Funk 1995, Roderick et Gillespie 1998, Shaw & Gillespie 2015).

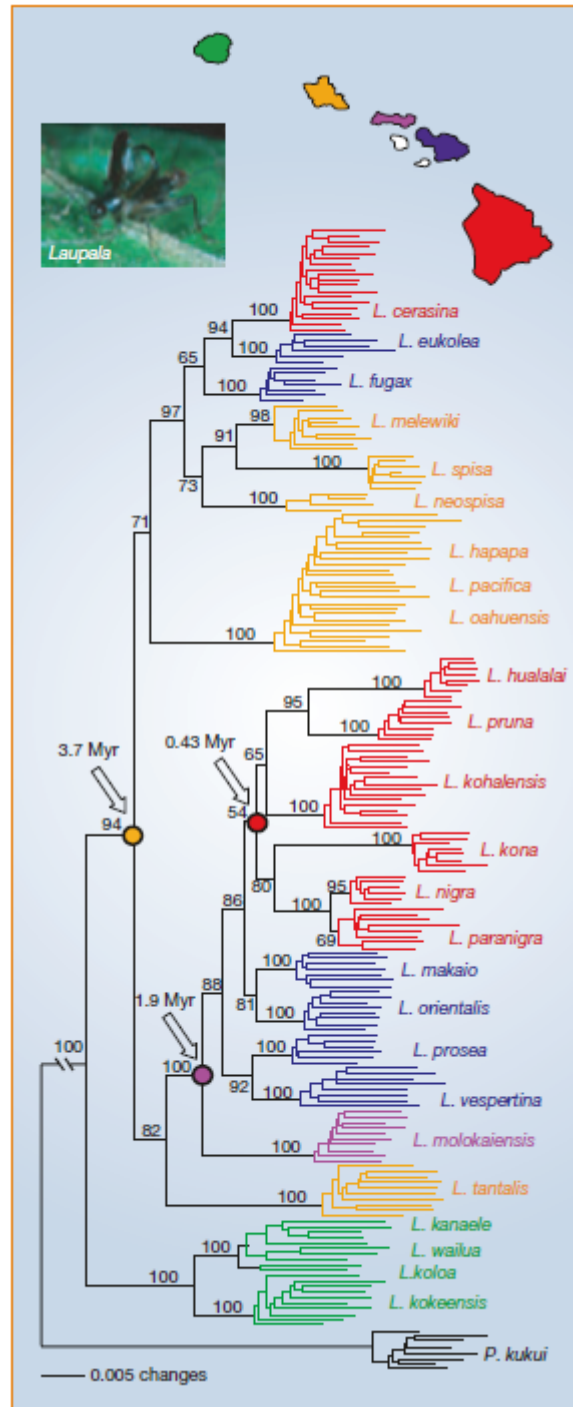


Figure I.10. Exemple de radiation suivant la *progression rule*. Reconstruction phylogénétique de 25 espèces sur 38 pour la radiation des criquets du genre *Laupala* sur l’archipel d’Hawaï. Les branches terminales représentent des individus, et sont codées par couleur pour indiquer l’île d’origine (vert = Kauai ; jaune = Oahu ; violet = Molokai ; bleu foncé = Maui ; rouge = Hawaï). A titre d’information : *Prolaupala kukui* est le groupe sœur supposé le plus proche des *Laupala*, et a été utilisé comme groupe externe. Les flèches indiquent la position et l’âge des trois ancêtres communs utilisés pour estimer les taux de spéciation. Un taux de 4.17 espèces par million d’années est notamment estimé pour l’île Hawaï. Adaptée de Mendelson & Shaw (2005).

La règle de progression a eu un impact significatif sur l'étude des radiations évolutives au sein des archipels océaniques et au-delà (Shaw & Gillespie 2015), car elle représente l'un des exemples les plus notables démontrant que, sous certaines conditions, la trajectoire évolutive de clades d'origines diverses peut être prédictible (Shaw & Gillespie, 2016). La recherche de ce patron va indirectement stimuler l'utilisation de la biogéographie historique dans l'étude des radiations, avec l'apparition de méthodes spécifiques aux environnements insulaires (Ronquist & Sanmartín 2011). En effet, les archipels sont propices à l'apparition d'événements de spéciation fondateurs (i.e., quand un petit nombre d'individus colonise un nouvel environnement et se retrouve instantanément isolé génétiquement de la population ancestrale, Paulay & Meyer 2002, Matzke 2014). Contrairement aux modèles biogéographiques classiques, l'aire de répartition de la lignée évolutive ne va donc ni s'agrandir ni se rétracter, mais passer directement d'une aire à une autre, ce qui nécessite certains ajustements au sein des modèles de reconstructions des aires géographiques (Matzke 2014).

La reconstruction phylogénétique des radiations évolutives au sein des archipels océaniques et leur étude macroévolutive reste toutefois un exercice complexe. Un des points les plus débattus encore à ce jour reste la question de la calibration des radiations (Bromham & Woolfit 2004, Heads 2005, 2011, Pillon & Buerki 2017, Landis et al. 2018). Le désaccord réside principalement dans l'utilisation des âges géologiques des îles (Heads 2011). Une méthode très populaire dans le domaine consiste en effet à identifier un ou plusieurs sous-clades à l'intérieur de la radiation comprenant uniquement des espèces strictement endémiques à une île spécifique, et à appliquer un âge maximal à ce sous-clade en utilisant l'âge géologique de l'île. L'argument sous-jacent à cette approche est que ces espèces endémiques n'ont pas pu évoluer avant l'émergence de leur substrat actuel (Fleischer et al. 1998, Baldwin et al. 1998, Richardson et al. 2001). Cependant, cette technique peut entraîner une sous-estimation de l'âge de la radiation, car elle ne tient pas compte d'éventuelles îles anciennes aujourd'hui submergées qui peuvent avoir existé au cours des millions d'années précédant l'émergence des îles contemporaines (Heads 2005, 2011, Fernández-Palacios et al. 2011). Plusieurs études ayant recours à d'autres stratégies de calibration (e.g., fossiles) ont d'ailleurs estimé un âge d'émergence de certaines radiations antérieur à l'existence de l'île actuelle la plus ancienne (e.g., Parent et al. 2008, Johns et al. 2018, **Figure I.11**).

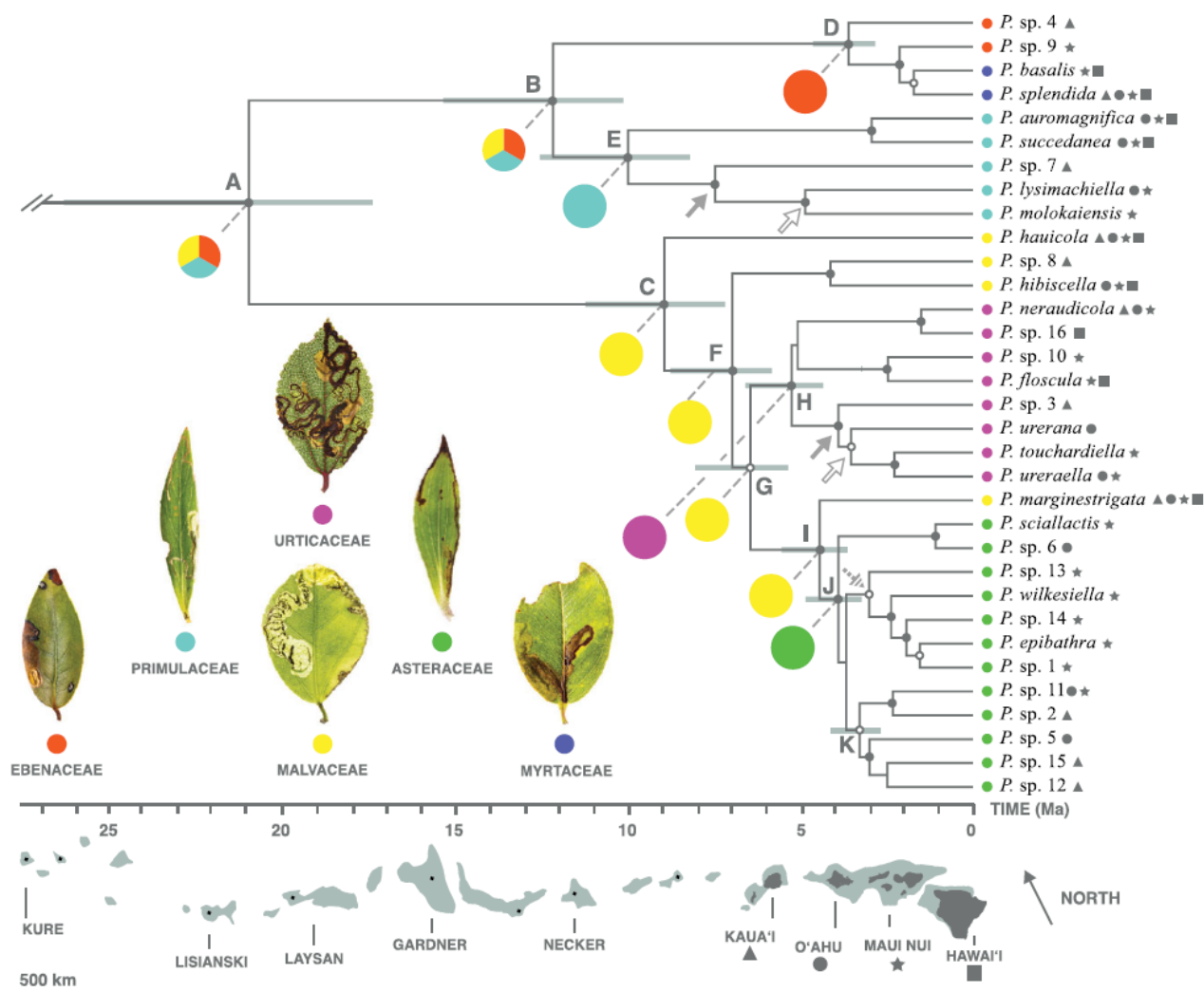


Figure I.11. Reconstruction phylogénétique pour la radiation des microlépidoptères du genre *Philodoria* (Lepidoptera, Gracillariidae) sur l’archipel d’Hawaï, montrant un âge de colonisation estimé à 20.95 millions d’années. L’estimation de l’âge de divergence a été déterminé comme étant le plus probable à travers un large panel de méthodes de datation (voir Johns et al. 2018). Les barres grises indiquent l’intervalle de densité postérieure à 95 %. A titre d’information : les formes à côté des noms d’espèces indiquent leur distribution par rapport aux îles indiquées sur la carte. Les petits cercles colorés indiquent la famille de plantes hôtes associée à chaque espèce. Les grands cercles indiqués aux nœuds internes indiquent le résultat de la reconstruction des caractères ancestraux concernant les plantes hôtes. Les flèches pleines pointent vers les nœuds utilisées dans la stratégie de calibration (voir Johns et al. 2018). Le soutien des nœuds est indiqué comme suit : cercles remplis = 100 % ; cercles vides = 99-70 % ; nœuds sans cercle = >70 %. Le dessin de l’archipel est repris de Price & Clague (2002). Les distances géographiques ne sont pas directement corrélées aux âges sur l’axe des x. Adaptée de Johns et al. (2018).

3. c. Approches biogéographiques

L'une des théories les plus influentes de la deuxième moitié du XXe siècle en écologie demeure sans conteste la Théorie de la Biogéographie Insulaire de MacArthur & Wilson (1963, 1967), tant elle a exercé une influence considérable sur notre manière d'envisager l'étude des patrons de biodiversité dans les îles (e.g., Warren et al. 2015, Patiño et al. 2017). En effet, la Théorie de la Biogéographie Insulaire, ou *Equilibrium Theory of Island Biogeography* (ETIB), a introduit pour la première fois une formalisation mathématique de la richesse spécifique observée au sein d'une île. Cette formalisation repose sur la combinaison de deux relations cruciales : (1) la relation entre la superficie de l'île et la richesse spécifique (i.e., la relation aire-espèces), concept fondamental formulé dès le XVIIIème siècle, et décrivant une corrélation positive entre la superficie d'une entité spatiale donnée et le nombre total d'espèces qu'elle abrite (Forster 1778, Triantis et al. 2012), et (2) la relation entre la distance de l'île et la richesse spécifique, qui illustre la corrélation négative entre le nombre d'espèces dans une île et la distance par rapport à sa principale source de colonisation (Mayr 1940, MacArthur & Wilson 1963). L'ETIB suggère que les îles les plus larges ont tendance à abriter une plus grande diversité d'espèces. Cela s'explique par le fait que ces îles ont une probabilité accrue d'intercepter des événements de dispersion, et que les populations d'espèces qui les habitent sont plus stables grâce à un apport fréquent d'individus. En conséquence, la probabilité d'extinction des espèces est réduite (MacArthur & Wilson, 1967, **Figure I.12**).

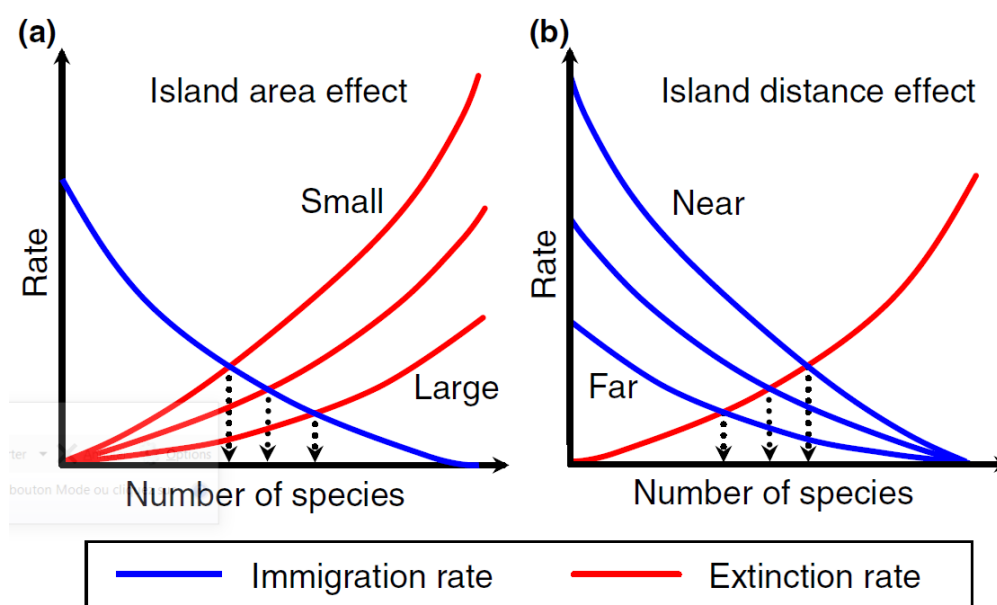


Figure I.12. Une représentation de la Théorie de la Biogéographie Insulaire illustrant les hypothèses de MacArthur et Wilson (1963, 1967) : (a) l'effet de la superficie de l'île sur le taux d'extinction, et (b) l'effet de la distance au continent sur le taux d'immigration. Le nombre d'espèces prédit apparaît sur l'axe des abscisses, et les flèches en pointillés marquent les points d'équilibre entre les taux d'immigration et d'extinction. Adaptée de Warren et al. (2015).

Cependant, cette relation est modulée par la distance entre l'île et sa source de colonisation. Un fort isolement réduit le taux d'immigration et augmente ainsi le taux d'extinction, car le faible nombre de colonisateurs diminue les chances de survie de l'espèce colonisatrice (**Figure I.12**). Bien que les faiblesses et les limites de ce modèle soient aujourd'hui bien identifiées dans la littérature (Brown & Lomolino 2000), le travail de MacArthur & Wilson a renouvelé l'intérêt des scientifiques pour les environnements insulaires, et a servi de base fondamentale à la majorité des développements actuels sur notre compréhension de la biodiversité des îles (Heaney 2007, Warren et al. 2015, Valente et al. 2020, Whittaker et al. 2023).

Bien que leur monographie de 1967 se concentre principalement sur l'influence des taux d'immigration et d'extinction sur la richesse spécifique, MacArthur et Wilson soulignaient déjà l'effet majeur que pourrait avoir la spéciation *in situ* sur la diversité totale des îles et archipels très éloignées du continent (MacArthur & Wilson 1963). En prenant pour exemple empirique les nombreuses radiations déjà décrites sur les archipels tels que Hawaï ou les Fidji, ils théorisèrent l'existence d'une "zone de radiation" (*radiation zone*), distance à partir de laquelle les espèces continentales peuvent se diversifier sur les îles en espèces endémiques par spéciation allopatrique (MacArthur & Wilson 1963). Cette dimension évolutive au sein de la dynamique biogéographique, d'abord mis à l'écart au sein de l'ETIB pour des raisons de simplicité mathématique (Whittaker et al. 2023), est peu à peu réapparue dans la littérature, notamment sous la forme de modèles conceptuels (Heaney 2000) et théoriques (e.g., Chen & He 2009, Rosindell & Phillimore 2011). D'un point de vue empirique, Losos et Schuller (2000) ont également avancé l'idée d'une relation aire-espèces évolutive (*Evolutionary species-area relationship*) à travers l'étude de la radiation des *Anolis* dans les Caraïbes. Ils ont pu montrer entre autres que le nombre d'événements de spéciation augmentait proportionnellement à la taille des îles, justifiant cette observation par l'accroissement des opportunités écologiques à mesure que la taille de l'île augmente (Losos et Schuller 2000). Les travaux d'Emerson et Kolm (Emerson & Kolm 2005) sur le lien entre richesse spécifique et diversification dans les îles océaniques vont populariser l'utilisation des espèces endémiques à une seule île (*single-island endemics*, SIE) comme une mesure de la diversification (spéciation - extinction) *in situ*, et donc représentatif de la part évolutive de la diversité insulaire (Emerson & Kolm 2005). Le nombre de SIE, d'abord perçu comme étant relié positivement à la diversité totale des îles (Emerson & Kolm 2005), fut ensuite réutilisé quelques années plus tard par Whittaker et collaborateurs (Whittaker et al. 2007, 2008) pour élaborer un nouveau modèle théorique permettant d'expliquer la diversité des îles par l'évolution de leurs caractéristiques géo-environnementales au cours du temps (Whittaker et al. 2007, 2008). Les études géologiques sur les archipels océaniques

(e.g., Moore & Clague 1992) ont en effet mis en évidence l'existence d'un véritable cycle de vie des îles (appelé ontogénie, voir **Figure I.6**), au cours duquel un certain nombre de facteurs géo-environnementaux tels que l'aire, l'altitude ou la complexité topographique varient de façon globalement prédictible (Whittaker et al. 2023) en fonction de l'âge de l'île (**Figure I.12**). Whittaker et collaborateurs formalisent alors en 2008 leur Modèle Général Dynamique de la biogéographie des îles océaniques (*General Dynamic Model*, GDM), qui exprime la variation des taux d'immigration, de spéciation *in-situ* (anagenèse² et cladogenèse) et d'extinction en fonction de l'ontogénie de l'île (Whittaker et al. 2008, **Figure I.13**). Ce modèle, aujourd'hui considéré comme l'un des travaux les plus influents en biogéographie insulaire depuis MacArthur & Wilson (Borregaard et al. 2017), se décline de la façon suivante (**Figure I.13**) :

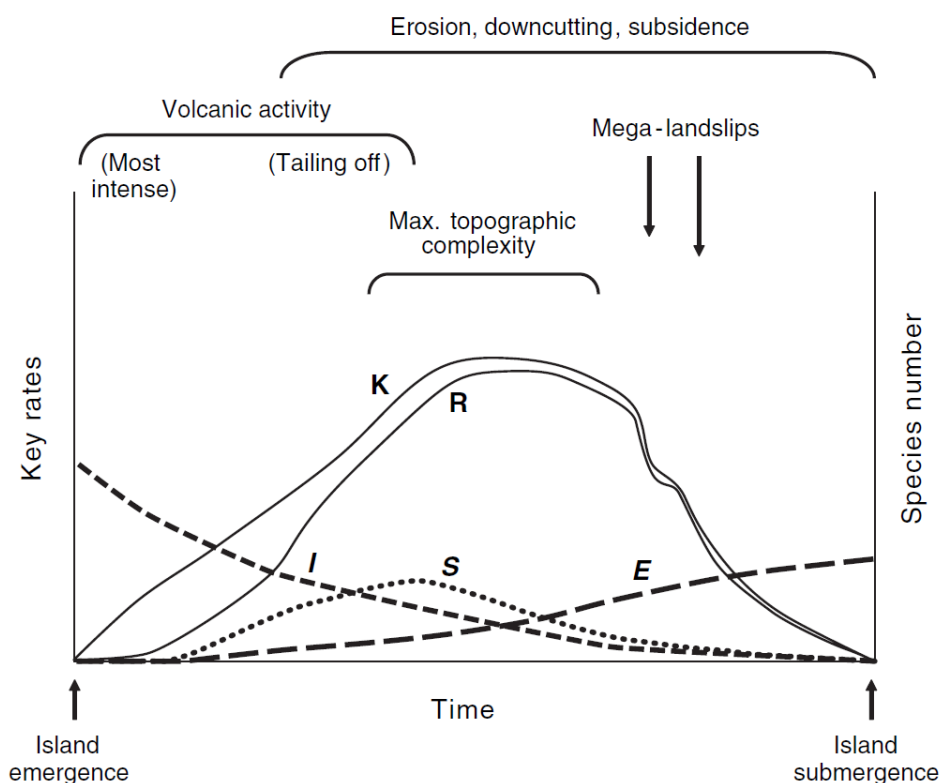


Figure I.13. Représentation graphique du modèle général dynamique (GDM) de la biogéographie des îles océaniques. Relation supposée entre les caractéristiques biologiques de l'ontogénie d'une île et les taux d'immigration (*I*), de spéciation (*S*) et d'extinction (*E*). *K* représente la capacité de charge (quantité maximum de biomasse et d'espèces atteignable sur l'île), et *R* le nombre d'espèces réalisées (nombre d'espèces effectivement atteint). Pour le cas des îles subissant des glissements de terrains (comme suggéré par les cassures dans les courbes *K* et *R*), la courbe du taux d'extinction devra être modifiée en conséquence. Adaptée de Whittaker et al. (2008).

² Anagenèse : processus de transformation lente et continue, généralement considérée comme graduelle, d'une espèce au fil du temps. L'évolution graduelle d'une espèce peut donner naissance à une nouvelle forme, sans qu'il y ait ramification.

(1) juste après l'émergence de l'île au-dessus du niveau de la mer, on observe l'arrivée d'espèces (par dispersion active ou passive) et leur établissement. A ce stade, la totalité des espèces au sein de l'île proviennent uniquement d'événements de colonisation. (2) L'augmentation progressive de l'aire et de l'altitude due à l'activité volcanique provoque l'apparition d'opportunités écologiques (e.g., augmentation du nombre d'habitats), permettant l'émergence de nouvelles espèces par spéciation *in-situ*, et donc l'augmentation du taux de spéciation. (3) Lorsque l'activité volcanique s'arrête, l'île arrive à maturité, et la complexité topographique augmente à cause de l'érosion, qui génère en retour des opportunités de spéciation allopatrique au sein de l'île (vicariance), permettant de maintenir un taux de spéciation élevé. (4) L'effet progressif de l'érosion et de la subsidence (l'île s'enfonce petit à petit dans l'océan sous l'effet de son propre poids et de la tectonique des plaques, qui l'éloigne progressivement des dorsales océaniques), fait progressivement baisser l'aire et l'altitude de l'île. Le taux de spéciation baisse suite à la diminution du nombre d'opportunités écologiques, et des événements catastrophiques tels que des glissements de terrains font également peu à peu augmenter l'extinction. (5) Enfin, l'île rétrécit jusqu'à passer sous le niveau de la mer, et toute la diversité terrestre est perdue.

D'après ce modèle, la diversité totale de l'île devrait donc suivre la forme d'une bosse (*hump-shaped relationship*) en fonction du temps : les îles jeunes en expansion ainsi que les îles vieilles en régression ont un nombre d'espèces plus faible que les îles d'âge moyen, qui sont à maturité en termes d'aire, d'élévation et de complexité topographique (Whittaker et al. 2008, **Figure I.13**). Dans le cadre de l'étude des radiations, il est important de noter que ce modèle inclut deux des principaux facteurs biogéographiques connus pour influencer positivement la spéciation : (1) l'aire, par la relation aire-espèces depuis repensé dans un cadre évolutif (Losos & Schuller 2000, Triantis et al. 2008), et (2) l'hétérogénéité environnementale (par l'altitude et la complexité topographique), également considéré comme un moteur essentiel de la diversification en général et sur les îles en particulier (Hortal et al. 2009, Steinbauer et al. 2012, Stein et al. 2014, Barajas-Barbosa et al. 2020). Par l'importance donnée à la spéciation, le GDM propose également un certain nombre de prédictions concernant les radiations évolutives. Selon le modèle, les radiations adaptatives émergent durant la phase de croissance de l'île grâce à l'augmentation des opportunités écologiques (augmentation de l'aire et de l'altitude). S'en suit ensuite l'émergence de radiations non-adaptatives due aux opportunités de spéciation allopatriques provoquées par l'augmentation de la complexité topographique (Whittaker et al. 2008). De même, les îles océaniques composites (e.g., Tenerife, formée à partir de trois systèmes volcaniques) devrait offrir plus d'opportunités pour la spéciation allopatrique que les îles aux histoires géologiques moins complexes. Enfin, l'intensité du

phénomène radiatif (nombre d'espèces résultant d'événements de cladogenèse) doit être proportionnelle à la distance au continent (Borregaard et al. 2016, Valente et al. 2020). En général, le GDM est évalué à l'aide d'une régression multiple qui inclut comme prédicteurs l'aire des îles et leur âge, auquel est ajouté un terme quadratique pour l'âge afin d'examiner la relation en forme de bosse due à l'ontogénie. Depuis sa première publication en 2008 (Whittaker et al., 2008), le modèle ATT² (Aire + Temp + Temps²) a été testé sur de nombreux archipels et groupes taxonomiques (e.g., Borges & Hortal 2009, Cameron et al. 2013, Patiño et al. 2013), démontrant en général un ajustement satisfaisant sur le nombre d'espèces par île, ainsi que sur nombre de SIEs. Plusieurs travaux récents ont également introduit diverses corrections et améliorations au modèle (Steinbauer et al. 2013, Otto et al. 2016, Barajas-Barbosa et al. 2020, Carey et al. 2023).

Il est pertinent de noter que, contrairement aux approches macroévolutives qui ont examiné les radiations en tant qu'objet d'étude à part entière, les approches macroécologiques ont principalement considéré le phénomène radiatif comme une composante de la diversité globale. En réalité, peu d'études ont cherché à déterminer si les principes de la biogéographie insulaire s'appliquent aux patrons de diversité émergents des radiations évolutives (mais voir par exemple Hamilton & Rubinoff 1964, Parent & Crespi 2006, Roell et al. 2021).

4. Enjeux actuels dans l'étude des radiations évolutives des archipels océaniques

L'étude des radiations évolutives au sein des archipels océaniques demeure un champ de recherche particulièrement dynamique. L'intérêt croissant pour la biogéographie insulaire, largement stimulé par la publication du GDM, ainsi que la disponibilité croissante de données géographiques et écologiques sur les systèmes insulaires à l'échelle globale, ont introduit de nouveaux enjeux et questionnements dans la recherche sur les îles (Santos et al. 2016, Patiño et al. 2017). Dans cette section, je propose un aperçu de quelques enjeux clés associés à l'analyse des radiations insulaires.

4. a. Effet des variations géo-environnementales sur la dynamique de diversification dans les îles océaniques

L'originalité du GDM réside indéniablement dans sa capacité à fournir un cadre intégratif, dynamique, et relativement simple pour appréhender la diversité insulaire, tout en proposant un modèle statistique facile à tester (modèle ATT²). Néanmoins, ce modèle est limité par son incapacité à prendre en compte la complexité inhérente aux dynamiques géo-environnementales des îles océaniques (Borregaard et al. 2017). Cette lacune pourrait expliquer certaines déviations aux prédictions du GDM rapportées dans la littérature (Borregaard et al. 2017, Steinbauer et al. 2013).

À titre d'exemple, le GDM se focalise sur l'ontogénie d'une seule île, négligeant ainsi le fait que la plupart des îles océaniques sont souvent regroupées en archipel (Borregaard et al. 2017). Cette configuration spatiale peut avoir un impact significatif sur la dynamique de la diversité. Par exemple, la probabilité d'extinction des espèces peut être réduite grâce à l'effet *rescue* (i.e., une espèce peut s'éteindre sur une île mais survivre sur d'autres îles) ou encore le maintien du flux de gènes entre les populations d'îles différentes pourrait limiter la spéciation allopatrique entre îles (Gascuel et al. 2016, Aguilée et al. 2021). L'utilisation de l'âge géologique des îles, correspondant souvent à l'âge de l'émergence au-dessus du niveau de la mer, offre une vision réductrice de la dynamique géo-environnementale des îles. En réalité, de nombreuses îles présentent des ontogénies plus complexes, caractérisées par exemple par des surfaces d'âges variables, reflétant différents stades géologiques et évolutifs de l'île (Otto et al. 2016). Dans un registre similaire, plusieurs études ont souligné les limites du modèle ATT² (e.g., Barajas-Barbosa et al. 2020, Carey et al. 2023). Certains auteurs ont suggéré d'incorporer des variables supplémentaires telles que l'altitude (Cameron et al. 2013), ou plus récemment l'hétérogénéité environnementale (Barajas-Barbosa et al., 2020), telle que la complexité topographique et la variabilité climatique, pour renforcer le pouvoir explicatif des modèles de régression. Plus récemment, Carey et ses collaborateurs (Carey et al. 2023) ont montré que l'utilisation de mesures directes de l'hétérogénéité environnementale s'avèrerait plus efficace que l'utilisation de l'âge de l'île comme proxy dans le cadre des tests du GDM sur des données empiriques. Par ailleurs, l'impact potentiel des variations du niveau de la mer au cours des cycles glaciaires et interglaciaires du Pléistocène a également influencé l'aire et la connectivité des îles, avec des conséquences sur la dynamique de la diversité et la diversification que nous commençons juste à comprendre (Ali & Aitchison 2014, Rijdsdijk et al. 2014, Weigelt et al. 2016, Norder et al. 2018, Jöks et al. 2020). Toutes ces questions représentent autant d'axes de recherche encore peu discutés dans le contexte des radiations insulaires. De manière plus générale, encore trop peu d'études ont cherché à comprendre comment la dynamique géo-environnementale des archipels océaniques peut moduler le processus d'accumulation des espèces durant un épisode radiatif (voir par exemple les travaux de Lim & Marshall 2017 sur l'impact de l'ontogénie des îles sur le taux d'accumulation des espèces dans les radiations évolutives d'Hawaï).

4. b. Diversification et équilibre

La question de savoir si les communautés insulaires ont atteint ou tendent vers un équilibre reste un problème central en biogéographie et macroévolution des systèmes insulaires. Deux visions s'opposent à ce sujet : la première soutient que la diversité insulaire évolue vers un équilibre dynamique. Autrement dit, les taux d'immigration, de spéciation et d'extinction maintiennent une richesse spécifique relativement stable au fil du temps, limitée par le nombre de niches écologiques disponibles et se traduisant par un phénomène de diversité-dépendance (MacArthur & Wilson 1967, Simberloff 1974, Valente et al. 2014). Il s'agit d'un équilibre qualifié de "dynamique" en raison de la variation potentielle de la composition en espèces au fil du temps. En effet, en cas d'extinction d'une espèce, une nouvelle espèce la remplace par le biais de l'immigration ou de la spéciation (Valente et al. 2014). La théorie alternative est celle du non-équilibre (Heaney 2000), qui avance que l'instabilité géologique et climatique des environnements insulaires, ainsi que la variabilité des taux de spéciation *in-situ*, rendent difficile, voire impossible, la présence d'un équilibre de diversité. Les deux scénarios susmentionnés ont été observés empiriquement pour un certain nombre de radiations insulaires : Rabosky & Glor (2010) et Valente et al. (2015) ont par exemple respectivement montré que la radiation des lézards du genre *Anolis* dans les Caraïbes et la radiation des pinsons de Galápagos avaient atteint l'équilibre. En revanche, Esselstyn et al (2009), tout comme Fritz et al. (2011), ont démontré une accumulation continue d'espèces au cours du temps au sein de clades endémiques des archipels Indo-Pacifique. Alors que la présence d'un équilibre est souvent justifiée par l'existence d'une limite écologique à la diversification (e.g., nombre de niche disponible, vicariance), l'absence d'équilibre peut s'expliquer, entre autres, par la dynamique géo-environnementale des archipels océaniques. En raison de leur constante expansion due à leur volcanisme, ces archipels continuent de fournir des opportunités de spéciation pour les clades qui s'y diversifient (Esselstyn et al. 2009). A ce jour, encore peu de radiations évolutives d'archipels océaniques ont fait l'objet d'une analyse de leur dynamique évolutive, et seules des études comparatives sur différents taxons et archipels pourraient contribuer à identifier de potentiels schémas évolutifs dominants.

5. Positionnement et objectifs de la thèse

Cette thèse a pour objectif d'entreprendre une évaluation globale des radiations évolutives dans les archipels océaniques, et de mettre en œuvre des analyses comparatives des patrons de diversité et de diversification émergents au sein de ces clades endémiques, afin d'en apprendre plus sur les mécanismes éco-évolutifs à l'origine de ces phénomènes. Comme il a été montré auparavant, nous manquons encore d'une véritable revue globale de la littérature sur le sujet, et malgré l'accumulation ces dernières décennies de données taxonomiques, phylogénétiques et biogéographiques (e.g., Weigelt et al. 2013, Shaw & Gillespie, Hembry 2018), très peu d'analyses comparatives approfondies ont été réalisées jusqu'à présent.

5. a. Description des chapitres

J'ai structuré cette thèse en trois chapitres distincts : dans un premier temps, j'ai conduit une revue de la littérature avec comme objectif d'établir un bilan global de la recherche sur les radiations évolutives dans les archipels océaniques (Chapitre II). Pour cela, j'ai construit une liste exhaustive de toutes radiations connues à travers le monde ayant diversifié dans ce type d'environnement, en visant spécifiquement celles ayant fait l'objet d'une analyse phylogénétique. J'ai également fait le point sur les principaux sujets de recherche abordés dans la littérature concernant ces radiations, en quantifiant leur popularité, en présentant les connaissances actuelles, et en proposant une discussion critique des principales méthodologies employées pour chacun d'entre eux. Ce premier chapitre de thèse a également permis d'identifier les lacunes existantes dans la littérature, et d'évaluer les opportunités d'études comparatives aux vues des données disponibles. Par la suite, j'ai concentré mes efforts sur l'étude des patrons biogéographiques au sein de ces radiations, en examinant les relations entre le nombre d'espèces par île pour chacune d'entre elle, et divers facteurs géo-environnementaux tels que l'aire, l'hétérogénéité environnementale et l'isolement des îles dans l'archipel (Chapitre III). Cette analyse a été menée sur près d'une centaine de radiations réparties dans quatre archipels, à savoir Hawaï, les Îles Canaries, les Galápagos et les Fidji. Un large éventail d'analyses statistiques a permis de mettre en lumière l'influence et l'importance de chacun des facteurs sur les patrons de distribution des espèces de chaque radiation. Pour finir, je me suis intéressé aux patrons de diversification de ces radiations (Chapitre IV) en testant plusieurs hypothèses sur les modes de diversifications attendues pour ce type de clades endémiques. J'ai pour cela réalisé des analyses de diversification sur plus d'une quarantaine de radiations, en utilisant les informations extraites de phylogénies moléculaires. Par ailleurs, l'ensemble de ces travaux s'est appuyé sur des approches comparatives utilisant uniquement des données extraites de la littérature et de base de données publiques (voir section suivante).

5. b. Approche générale

Cette thèse est avant tout un travail de revue scientifique et d'analyses comparatives. Autrement dit, la totalité des données empiriques utilisées dans chacun des chapitres est extraite de travaux de recherche déjà publiés, ou provient de bases de données publiques (e.g., données de distribution des espèces dans les Îles Canaries, <https://www.biodiversidadcanarias.es/>). Cette démarche est intrinsèquement liée à l'aire de l'information et du "big data" que la biologie traverse depuis le début du siècle (Spengler 2000, Hampton et al. 2013). En effet, la communauté scientifique ne cesse d'accumuler des données sur le vivant, et leur regroupement dans des bases de données bioinformatiques accessibles (exemples : GBIF, Edwards et al. 2000, GeneBank®, Sayers et al. 2023) a notamment permis la mise en place d'analyses taxonomiques, géographiques et/ou génétiques sans précédent. L'étude des radiations évolutives dans les archipels océaniques (et des environnements insulaires en général) n'échappent évidemment pas à ce phénomène, en témoigne la revue de littérature récente de Cerca et collaborateurs (voir Annexe 1) qui dénombre plus d'une centaine de radiations adaptatives insulaires étudiées à travers le monde (Cerca et al. 2023). Nous avons donc voulu étudier ces radiations en prenant le point de vue le plus large possible, c'est-à-dire en incluant un maximum de taxons et d'archipels différents, dans le but d'identifier les potentielles lacunes et disparités dans la littérature, et également de tenter de détecter des patrons globaux par le biais d'études comparatives.

**Chapitre II : Radiations évolutives sur les
archipels océaniques : synthèse
biogéographique et phylogénétique**

Résumé

Les radiations évolutives présentes au sein des archipels océaniques (ROAs) sont considérées par la communauté scientifique comme des modèles idéaux pour l'étude des mécanismes écologiques et évolutifs qui sous-tendent les patrons de biodiversité. Depuis plusieurs décennies, le développement des outils phylogénétiques, la génération de bases de données massives de séquences d'ADN ainsi que les progrès des méthodes analytiques en macroévolution et biogéographie ont abouti à une accumulation sans précédent de données pour ces radiations. Pourtant, la littérature manque encore d'une vision globale sur le sujet, aussi bien en termes des connaissances acquises que sur les méthodes employées pour leur étude. Ce chapitre met donc en œuvre une revue de littérature ayant pour but de faire un premier bilan global des connaissances concernant les ROAs. Plus de 350 ROA(s) réparties sur 22 archipels ont été identifiées sur la base d'une information phylogénétique. Par la suite, une évaluation quantitative a été mise en place afin de détecter les éventuelles disparités liées à ce domaine de recherche, puis cinq sujets clés concernant l'écologie, la biogéographie et l'évolution des ROAs sont identifiés et discutés : (1) l'âge de colonisation ; (2) les patrons de colonisations inter-îles ; (3) le type de radiation ; (4) les patrons biogéographiques ; et (5) les patrons de diversification. Un grand nombre de disparités géographiques, taxonomiques et méthodologiques sont mises en évidence, montrant notamment l'écrasante dominance d'Hawaï et des îles Canaries, ainsi que de certaines ROAs emblématiques dans la littérature associée. L'étude bibliographique de ces cinq sujets a montré de grandes variations en termes de popularité, et a également révélé un certain nombre de problèmes principalement liés au manque de standardisations des termes et méthodes employés. À la lumière de ces résultats, nous formulons plusieurs recommandations visant à améliorer les pratiques actuelles et à orienter les futures études comparatives, qui pourraient apporter un nouvel éclairage sur les mécanismes écologiques et évolutifs sous-tendant le phénomène des radiations évolutives dans les archipels océaniques.

Etat de publication

Ce manuscrit va bientôt être envoyé à plusieurs co-auteurs. Sont envisagés pour l'instant José María Fernández-Palacios (Université de La Laguna, Tenerife) avec qui nous avons déjà échangé sur les données de la revue, et José Cerca (Université d'Oslo), avec qui j'ai pu travailler sur la liste des radiations adaptatives connues dans le monde pour l'article présenté en Annexe 1.

Online Supplementary Data

Le tableau récapitulatif contenant toutes les données brutes utilisées dans ce chapitre est disponible à cette URL :

<https://drive.google.com/drive/folders/1RHrmW2BN1FrDU7U-B2DbnapCPysO1lsT?usp=sharing>

1. Introduction

1. a. General overview

Evolutionary radiations, defined as the proliferation of taxa from a single ancestral lineage (Simões et al. 2016, Naciri & Linder 2020), have intrigued biologists for centuries. In particular, evolutionary radiations on oceanic archipelagos (hereafter ROAs) hold an exceptional place in the literature as ideal models to uncover evolution in action (Losos & Rickelfs 2009, Gillespie 2015, Shaw & Gillespie 2015). Beyond the emblematic radiation of the Galápagos' finches (Darwin 1859, Grant & Grant 2008), many of the most known and studied evolutionary radiations to date have in fact been described on oceanic archipelagos, including the Hawaiian *Drosophila* (O'Grady & DeSalle 2018), the *Naesiotus* Galápagos land snails (Parent & Crespi 2006) or the *Echium* radiation in the Canary Islands (Böhle et al. 1996).

What truly makes ROAs so special is the unique feature of the archipelagos into which they have radiated. Indeed, oceanic archipelagos are of volcanic origin, and emerge above the ocean surface as blank slates for colonisation and subsequent diversification (Warren et al. 2015, Whittaker et al. 2023); their remoteness favors *in-situ* speciation over immigration in building diversity; they frequently feature significant ecological gradients, offering numerous opportunities for diversification (Emerson 2002); and the varying age of their volcanic islands provides a temporal framework that enables the role of long-term eco-evolutionary processes to be discerned (Whittaker et al. 2008). In addition, oceanic archipelagos are distributed across all oceans, vary in area, spatial configurations, geological age and climate (Triantis et al. 2016), and harbors co-distributed ROAs in many taxonomic groups (e.g., plants, birds, arthropods), therefore providing multiple experimental replicates across lineages and islands (Gillespie 2007, Losos & Ricklefs 2009).

In recent decades, the development of phylogenetic reconstruction techniques and the significant advances in statistical analyses have allowed the scientific community to address a wide array of questions related to ROAs, spanning from the timeframe of colonisation (García-Verdugo et al. 2019), their phylogeographic patterns (Shaw & Gillespie 2015), to the drivers of speciation (Salces-Castellano et al. 2020). This extensive research effort has yielded extraordinary progress, not only in improving our general understanding of ROAs, but also in shedding light on fundamental questions such as the equilibrium theory (e.g., Valente et al. 2015, Valente et al. 2017), density-dependence (e.g., Marshall & Quental 2016), trait-displacement (e.g., Schluter 2000, Goodman et al. 2014) or more generally, the mechanistic basis of adaptation (e.g., Givnish et al. 2009, Recuerda

et al. 2023, Cerca et al. 2023). It is evident, then, that ROAs research will continue to advance ecological and evolutionary science in the future.

As with any scientific field, ROAs research is likely to suffer from disparities, notably in terms of taxonomic and geographical focus (e.g., Emerson 2002, Cerca et al. 2023). The prevalence of certain methodological practices (e.g., Heads 2011) or the attractiveness of some specific topics over others (e.g., Cerca et al. 2023) have also influenced our general knowledge in the field. The extent to which such disparities may bias ROAs research remains however uncertain, and a comprehensive assessment of these literature discrepancies is lacking. Yet, undertaking such an endeavor will undoubtedly be valuable in order to sketch out current gaps, highlighting research opportunities and make practical suggestions for future investigations.

In the present study, we provided a thorough and critical review of the peer-reviewed literature focusing on ROAs. We organized it as follows: first, we set up a systematic review of the literature to identify all ROAs described so far and cross-tabulated their specific features, with a special emphasis on taxonomy and geographic distribution. In a second part, we identified five key research topics encountered in the ROAs literature and examined their popularity, major advances in the field and prevailing methodological practices. We used all this information to highlight knowledge disparities and make suggestions on how to overcome them. Finally, we capitalize on this review by encouraging the community to make use of the extensive data currently available on ROA to address important, yet unanswered questions on island ecology and evolution.

1. b. Definition used in this review

We defined an oceanic archipelago as an island or group of islands originating from submarine volcanic activity and that have never been connected to any other landmasses (Whittaker et al. 2023). This definition encompasses volcanic islands formed by different geological processes such as hotspot islands (e.g., Hawaii, Galápagos, Canary Islands, Society, Austral, Madeira, Mascarenes) resulting from the passage of tectonic plates over regions of melting in the mantle, or volcanic arc islands (e.g., Lesser Antilles, Sandwich Islands) formed by the subduction of plates into the mantle (a detailed review of the geology of oceanic islands can be found in Jones & Maclennan 2005, Nunn 2009, Ali 2017 and Ali & Meiri 2023, among others). Our selection excluded composite archipelagos that are formed of both continental and volcanic islands (e.g., the Philippines, Brown et al. 2013). We also discarded archipelagos that contain only atolls (e.g., Tuamotu in French Polynesia), as we consider them too depleted and unrepresentative in terms of ROAs diversity due to their advanced ontogeny cycle (Whittaker et al. 2008). To guide the literature

research procedure (See section 1.3), we generated a list of the major oceanic archipelagos worldwide based on our own expertise in the field and literature survey (**Table II.S1**).

We define a ROA as any monophyletic clade endemic to an oceanic archipelago that originates from a single colonisation event, and for which the monophyly have been validated by a phylogenetic reconstruction, at least for a fraction of the species that are thought to belong to the ROA. Following recent recommendations (Martin & Richards 2019, Matsubayashi & Yamaguchi 2021, Cerca et al. 2023), we considered an island clade as a ROA if it was composed of at least three species (i.e., two or more cladogenetic events). Our definition excludes all groups of species that have been described as island radiations only on a taxonomical basis [e.g., the Hawaiian *Mecyclothorax* (Hembry et al. 2021); the *Dinas* in Cabo Verde (Skuhrovec & Batelka 2014)]. We acknowledge that having a phylogeny for only a subset of the species obviously does not guarantee the monophyly of the entire group, but in most cases, it does ensure that the radiation has been subject to additional analyses such as dating, intra-archipelagic colonisation patterns or diversification analysis, among others.

2. Materials and Methods

2. a. ROA identification

We performed a standardized literature search in Web of Science (WOS) and Google Scholar indexing systems (last access March 2023) for each listed oceanic archipelago using the search string: TS = (“*name of each oceanic archipelago*” AND TS = (“*phylog**” OR “*radiation*” OR “*endemic*”). Results of the different searches were screened in order to identify every ROAs matching our definition (see section 1.2). To make sure that no relevant ROA had been overlooked, we also double-checked key reviews on the subject (e.g., Gillespie & Roderick 2002, Emerson 2002, Shaw & Gillespie 2015, de la Harpe et al. 2017, Price & Wagner 2018, Hembry & Balukjian 2016, Crawford & Archibald 2017, Hembry 2018, Hembry et al. 2021). However, we recognize that we may have missed ROAs for which the sampling fraction is extremely small, as well as those included in larger phylogenies and for which no publication directly referencing to the ROA itself has ever been published.

We conducted a second literature search to extract detailed metadata and information for each identified ROA. This step was carried out by combining the publications retrieved from the previous search with a second screening of the literature using the search string TS = (“*name of the ROA*” AND “*its archipelago provenance*”). The following information (when available) was recorded: taxonomic affiliation (Class, Order, Family, Genera), total number of species thought to belong the ROA, number of species including in the latest and most complete phylogeny, phylogenetic method

[DNA origin (mitochondrial, chloroplastic, nuclear), Sanger sequencing or phylogenomics, others including RFLP, RAPD, AFLP and SSR, tree reconstruction (Maximum Parsimony, Maximum Likelihood, Bayesian)], monophyly support (bootstrap and/or Posterior Probability values reported in the tree for the crown node of the radiation), crown and stem age of the latest dated phylogeny with associated variance [e.g., 95% HPD (height posterior density)] (if multiple dating were produced, all estimations were recorded), calibration strategy (Fossil, secondary, geology, rates). Finally, for each radiation, we performed a third search using the string: (AB = (“*name of the ROA*” AND “*its archipelago provenance*”) OR TI = (“*name of the ROA*” AND “*its archipelago provenance*”) OR (AB = “*name of the ROA*” AND TI = “*its archipelago provenance*”) OR (AB = “*its archipelago provenance*” AND TI = “*name of the ROA*”)) in order to obtain a list of studies specifically dedicated to the focal ROA (see **Table II.S2**). Specifically, we counted for each ROA the number of peer-reviewed publications and PhDs dealing specifically with taxonomy, phylogeny, biogeography, species traits or conservation of one or several species of the ROA (we removed duplicates and publications relating to human use, chemistry, pharmacology, parasites, pest control as well as publications in which the ROA was only cited in larger floristic or faunal records). It should be noted that, where applicable, searches have been run using the vernacular name of the radiation (see **online Supplementary Data**).

2. b. Key topics in ROA research

The majority of ROAs literature seek in one way or another to understand the ecological and evolutionary processes driving ROAs. While this overarching goal united ROAs research, the field has also been structured around several distinct concepts, questions and approaches, varying in popularity within the literature. For this review, we decided to focus on five key topics which we believe encompass the breadth of ROAs research. We acknowledge that delineating these topics is somewhat arbitrary as they are all interconnected, but we believe that alternative classifications will undoubtedly lead to the same conclusions. Our five topics are: (1) *timing of colonisation*, referring to all research including an estimation of the time of island colonisation by the ancestor of the ROA via molecular dating, (2) *inter-islands biogeographical patterns*, referring to all research investigating intra-archipelagic colonisation routes (e.g., the progression rule, Funk & Wagner 1995), (3) *type of radiation*, referring to all studies addressing the adaptive and/or non-adaptive nature of the ROA, and more generally studies attempting to identifying the drivers of diversification (Givnish et al. 2009, Takayama et al. 2018, Cerca et al. 2023) (4) *mode of diversification*, which refers to studies aimed at estimating the pace of species accumulation over time (Diversity equilibrium, Valente et al. 2015; Slowdown of diversification, Bennett & O'Grady

2013) and (5) *species diversity and distribution*, referring to all research focusing on diversity patterns and its determinants with or without reference to the evolutionary relationship between species (Species-isolation relationship: Hamilton & Rubinoff 1963; Species-area relationship; Parent & Crespi 2006). For each topic, we used all relevant references retrieved from prior searches to ascertain for each ROA whether the topic was covered (YES) or not (i.e., data deficient). We also provided for each topic a brief overview and outlined the main advances in the field, with a specific focus on the prevailing methodological practices and pitfalls.

All detailed metadata and information extracted from the literature, together with associated references, are listed in a table available in the **online Supplementary Data** of this thesis.

3. Results and discussion

3. a. Geographic and taxonomic distribution of the ROA worldwide

Our literature review enabled us to retrieve a total of 354 ROAs in 22 of the 60 oceanic archipelagos on our initial list. (**Figure II.1, online Supplementary Data**). As expected, the distribution of ROA was highly unequal across archipelagos and taxonomic groups (Chi Square-test $P < 0.001$). Hawaii and the Canary Islands were the archipelagos for which we retrieve the most ROAs, accounting respectively for 31% (109 ROAs) and 21% (75) of all identified ROAs. Only four other archipelagos harbored more than ten ROAs, namely Mascarenes (36), Galápagos (22), Fiji (19) and Madeira (18). Altogether, these six oceanic archipelagos nearly hosted 80% of all ROAs retrieved (**Figure II.1**). A similar pattern was also detected for the radiation size (**Figure II.2A**), with 10 of the 11 ROAs exceeding 100 species being in Hawaii, the remaining one being in the Canary Islands (**Figure II.2B**). In the same way, for the 30 ROAs with more than 50 species, 22 were reported in Hawaii and 4 in the Canary Islands (**Figure II.2B**). These marked disparities can be attributed to various non-exclusive factors. Initially, variations in archipelagic biogeographical features such as area, spatial configuration, elevation, topographical complexity, and isolation are known to modulate the magnitude of in-situ diversification (Keast 1996, Emerson 2002, Hembry et al. 2013, Hembry & Balukjan 2016). These factors certainly had a positive effect on the presence of ROA and their respective size in Hawaii and the Canary Islands (Emerson 2002, Gillespie 2007, Gillespie et al. 2008) and could also explain why there are only a few radiations of smaller size in less complex archipelagos such as Lord Howe (14 km², 875 m.a.s.l.) or St. Helena (122 km², 820 m.a.s.l.).

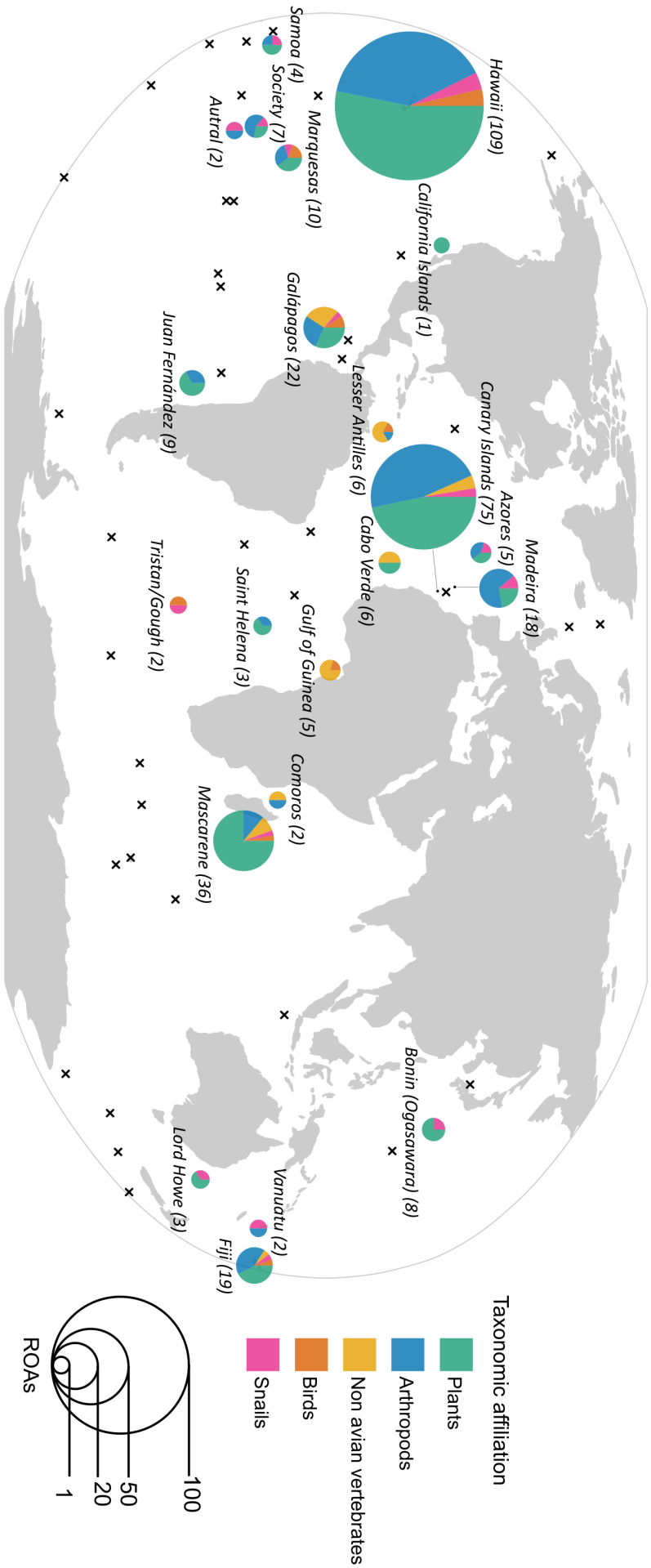


Figure.II.1. Worldwide repartition of all the 354 evolutionary radiations on oceanic archipelagos (ROAs) found in literature review.

CHAPITRE II : RADIATIONS EVOLUTIVES SUR LES ARCHIPELS OCEANIQUES : SYNTHESE BIOGEOGRAPHIQUE ET PHYLOGENETIQUE

In this context, we detected a statistically significant positive relationship between elevation and the \log_{10} -transformed number of ROA ($R^2 = 41\%$; $P < 0.001$), although the \log_{10} -transformed area, the number of islands, latitude, and isolation did not feature. Along with the Galápagos, both Hawaii and the Canary Islands are probably the best studied oceanic archipelagos in the world, both in terms of their natural history and the phylogenetic origin of their biota (Juan et al. 2000, Emerson 2002). The connections of Hawaii with North America and the Canary Islands with continental Europe have definitely play a role here (Funk & Wagner 1995, Hembry et al. 2013), as human presence, area accessibility and high socioeconomic indicators have been shown to be positively correlated to sampling and research effort (Ficetola et al. 2014, Rudbeck et al. 2022, Hickisch et al. 2018). In this context, the number of ROA obtained for Fiji appears to be greatly underestimated. Fiji is indeed as big as Hawaii but with five times less ROAs retrieved. Phylogenetic knowledge on Fiji archipelago is, in fact, estimated at just 40% for seed plants, and no part of the country's Gross domestic product (GDP) has been allocated to academic research (Rudbeck et al. 2022). This is also interesting to note that none of the publications related to the Fijian ROA involved a local institution. The limited number of ROA reported for the southeastern Polynesian archipelagos (7 for Society Islands, 10 for Marquesas and 2 for Austral Islands) aligns with recent reviews on the topic (Hembry & Balukjan 2016, Hembry 2018). This discrepancy can be attributed, in part, to the relatively small size and low elevations of these archipelagos. For instance, the Society Islands or the Marquesas are an order of magnitude smaller than Hawaii (Gillespie & Clague 2009). Additionally, the apparent lower degree of isolation in southeastern Polynesia when compared with Hawaii has probably contributed to this disparity. Unlike Hawaii, the southeastern Polynesia comprises hundreds of interconnected islands, spanning over 2,000 kilometers (Hembry et al. 2013). This configuration has enabled frequent inter-islands/archipelagos colonisation events and has been proposed as an explanation for why the Society Islands exhibit more non-monophyletic groups than radiations (Hembry & Balukjan 2016). Another contributing factor is the lack of phylogenetic and taxonomic research in this region, as underlined in Hembry & Balukjan (2016) and Hembry (2018). The case of the Azores is also of interest. In contrast to the other archipelagos discussed above, the Azores (5 ROAs, **Figure II.1**) is a well-studied archipelago (e.g., Borges et al. 2010) and the apparent lack of endemic clades and endemism in general has been intensely debated in the literature as the "Azorean diversity enigma" (Carine & Schaefer 2010). Various hypotheses have been proposed, ranging from the absence of environmental triggers for speciation during the Quaternary (Carine & Schaefer 2010) to the archipelago relatively young age and low environmental heterogeneity (Triantis et al. 2012).

CHAPITRE II : RADIATIONS EVOLUTIVES SUR LES ARCHIPELS OCEANIQUES :
SYNTHESE BIOGEOGRAPHIQUE ET PHYLOGENETIQUE

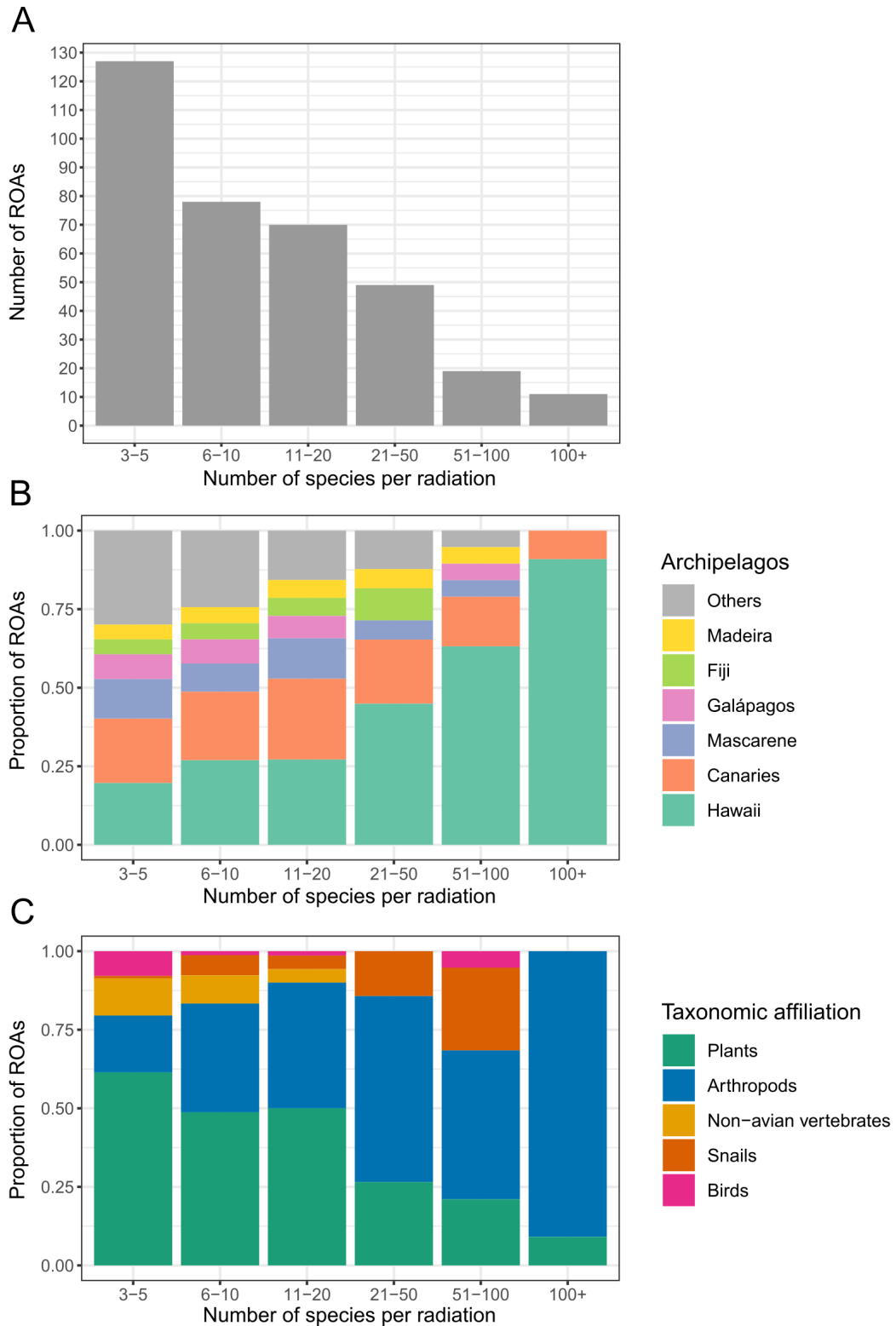


Figure.II.2. The 354 evolutionary radiations on oceanic archipelagos (ROAs) found in literature sorted in seven different categories according to their total number of species thought to belong to the ROA. A) Number of ROAs by category; B) Proportion of the six archipelagos containing most of the ROAs in each category; C) Proportion of the five main ROAs taxonomic groups in each category.

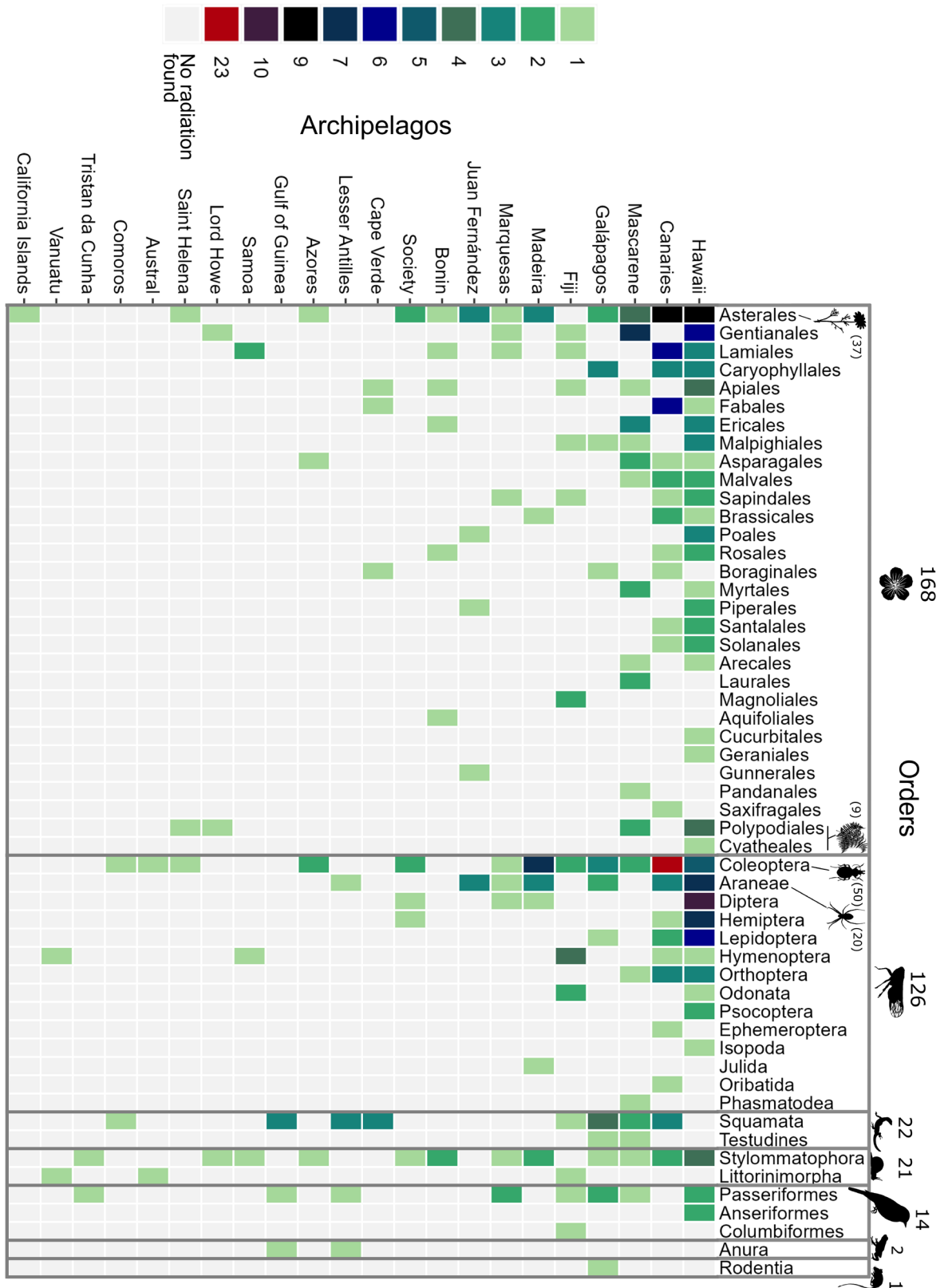
CHAPITRE II : RADIATIONS EVOLUTIVES SUR LES ARCHIPELS OCEANIQUES : SYNTHESE BIOGEOGRAPHIQUE ET PHYLOGENETIQUE

Furthermore, the absence of ROAs in the 18 (30%) archipelagos located below -40° or above 40° latitude can be simply attributed to climatic constraints. Despite having complete knowledge of phylogenetic relationships for some Sub-Antarctic archipelagos (Rudbeck et al. 2022), these regions exhibit very low numbers of endemic species and virtually no endemic clades.

Concerning the taxonomic coverage of our 354 retrieved ROAs, we found a dominance of vascular plants (169 ROAs) followed by arthropods (101 among which 25 beetles and 20 spiders), reptiles (22), snails (21), birds (14), ferns (9), amphibians (2) and mammals (1) (**Figure II.2C**, **Figure II.3**). Among the vascular plant ROAs, the highest numbers were found in Hawaii (58 ROAs), the Canary Islands (35 ROAs), and the Mascarene Islands (27 ROAs). The plant ROAs were not evenly distributed across orders and families (Chi-square test, $P < 0.001$). Notably, the Asteraceae was the most dominant family, accounting for 32 ROAs; a trend previously documented by Cerca et al. (2023) in the context of adaptive ROAs. Interestingly, Asteraceae is the second-largest flowering plant family globally after Orchidaceae (Christenhusz & Byng 2016), the latter being represented by only two ROAs. The limited diversity of Orchidaceae on islands, particularly in remote archipelagos, is not new and has been attributed to their particular life forms and functional traits (Taylor et al. 2019, 2021). Conversely, the success of Asteraceae in colonising and diversifying on islands remains a complex issue, probably involving multiple factors (Katinas et al. 2013). In contrast to vascular plants, ferns, which are disproportionately represented on islands (Kreft et al. 2008), contributed to a relatively small number of ROAs. This can be attributed to their extreme dispersal abilities, which may have limited diversification by maintaining gene flow with source populations (Hennequin et al. 2014, Weigelt et al. 2015).

Concerning arthropod ROAs, most of them were retrieved in Hawaii (58), the Canary Islands (35) and Madeira (12). Intriguingly, the Mascarene Islands, which were the third-best represented archipelago in our study, featured only 4 ROAs. This finding underscores therefore the well-documented deficiency in knowledge for arthropods in the Mascarene Islands (Legros et al. 2020). Within arthropods, approximately two-thirds of the ROAs were insects, with Coleoptera (beetles) representing half of them (50 ROAs). Coleoptera included some of the largest radiations retrieved in our dataset, such as the genus *Blackburnia* in Hawaii and the *Laparocerus* in the Canary Islands, with 140 and 182 species, respectively. A noteworthy observation is that nearly half of the Coleoptera ROAs were found in the Canary Islands (23), where a long-standing tradition of coleopterists exist since the 19th century, resulting in an extensive knowledge of this group for these islands (Machado & Oromi 2000) (see **Figure II.3**).

Figure II.3. Taxonomic diversity of all the 354 evolutionary radiations on oceanic archipelagos (ROAs) found in our literature review.



CHAPITRE II : RADIATIONS EVOLUTIVES SUR LES ARCHIPELS OCEANIQUES : SYNTHESE BIOGEOGRAPHIQUE ET PHYLOGENETIQUE

The remaining insect radiations encompassed 13 Diptera, 9 Lepidoptera, 9 Hemiptera, 8 Hymenoptera, and 7 Orthoptera. Several of these radiations were among the largest ever described on islands, all exclusive to Hawaii. These included the *Drosophila* with 416 species, the moth genus *Hypomocoma* with 400 species, the leafhopper *Nesophrosyne* with 215 species, and the fly genus *Campsicnemus* with 188 species. In addition to insects, there were twenty ROAs of spiders (Araneae) spanning ten families, along with a single radiation of mites (Oribatida), Diplopoda, and Malacostraca.

Additionally, we also identified a few ROAs of snails (21), a number that is likely to be underestimated. Land snails, with their low mobility and high passive dispersal ability are seen as especially prone to radiate on islands (Chiba & Cowie 2016). Moreover, a recently published global list of island land snail species (Proios et al. 2021) indicates that 75% of the 11,139 island species are endemic to a single island, another indication that land snails might have undergone significant diversification on islands (Holland & Cowie 2009). Despite this potential for diversification, their diversity on islands is still poorly known even in the most studied archipelagos like Hawaii (Chiba & Cowie 2016, Yeung & Hayes 2018). Moreover, these organisms have been significantly impacted by anthropogenic extinction, with a large part of their fauna being known solely from dead shells, hampering therefore phylogenetic works.

Vertebrates were noticeably underrepresented in our dataset with only 38 ROAs (10%). Many vertebrate groups exhibit a minimum area required for speciation, limiting their potential for diversification on relatively small systems like oceanic islands and archipelagos (Kisel & Barraclough 2010). Of the non-volant vertebrates, reptiles were the most represented group, with 22 ROAs identified, in contrast to amphibians (2) and mammals (1). Reptiles are known to be highly effective island colonisers due to their capacity to endure extended overwater journeys (Vidal et al. 2008). On the other hand, terrestrial mammals and amphibians are less suited to long-distance dispersal due to their high metabolic rates and limited desiccation resistance, respectively. Consequently, terrestrial mammals and amphibians are generally rare on oceanic archipelagos (e.g., Galápagos archipelago: Swash & Still 2005) or even absent (e.g., Cabo Verde: Duarte & Romeiras 2009). Within our dataset, birds accounted for only 14 ROAs, with 11 belonging to the Passeriformes order, two to the Anseriformes, and one to the Columbiformes. This number may appear to be underestimated, considering the extensive knowledge accumulated about island birds in recent decades (Johnson & Stattersfield 1990, Hume 2017, Matthews et al. 2022). Two main reasons may contribute to this situation: first, although islands host disproportionately high levels of endemic avian biodiversity, the frequency of cladogenesis remains low (Valente et al. 2017,

2020). Second, many island birds have already gone extinct, particularly on oceanic islands (e.g., >70% of Hawaii's known native birds are thought to have been driven extinct by humans; Matthews et al. 2023), making the recovery of certain radiations impossible (e.g., Rando et al. 2020).

Overall, the huge geographic and taxonomic disparities we have documented for ROAs results certainly from the interaction between the dispersal abilities of the clade ancestor, its speciation capacities and abiotic and biotic conditions of the colonised islands. However, sampling bias, long standing interest of some specific groups, availability of research funding, accessibility to specific regions as well as historical extinctions, have undoubtedly contributed to current ROA geographical and taxonomic distribution reported here.

3. b. Knowledge disparity among ROA.

Beside the aforementioned important disparities across archipelagos and taxa, we performed a bibliographic analysis to assess the number of peer-reviewed publications with as a focus each of the ROA. This approach aimed to provide insights into the popularity of each radiation and serve as a basic indicator of the extent of knowledge available for each of them. Our findings revealed some striking patterns. For 27 ROAs (7%), no publication was found meaning that these radiations were primarily mentioned within the study of a larger clade and were not individually explored. For 71 ROAs (20%), only a single publication was available. Overall, 244 ROAs (68%) had fewer than five publications while 293 ROAs (83%) had fewer than ten. On the contrary, we only found 7 ROAs with more than 50 publications namely: *Drosophila* in Hawaii: 323 publications; The Galápagos Finches: 249; the Hawaiian Honeycreepers: 177; the plant genus *Metrosideros* in Hawaii: 61, the genus of crickets *Laupala* in Hawaii, the Hawaiian Silversword Alliance: 66 and the genus of wall lizards *Gallotia* in the Canary Islands (**Figure II.4**). Some iconic ROAs were also among the most extensively studied such as the Hawaiian Lobeliads (45 publications) or the radiation of plant genus *Echium* (22) and the Aeonium Alliance (24) both in the Canary Islands. Additionally, only 15 ROAs were investigated for our five topics, with most of them originating from Hawaii. These included most of the emblematic ROAs: the plants Lobeliads, *Cyrtandra*, *Schiedea*, the Silversword Alliance and *Psychotria*; the *Laupala*, the genus of damselflies *Megalagrion*, *Drosophila*, the spiders *Tetragnatha*, *Ariamnes* and *Orsonwelles* and the Honeycreepers, some of them being among the largest retrieved ROAs (see **online Supplementary Data**). The only non-Hawaiian ROA that has been investigated in all five topics was the Galápagos Finches. In contrast, 108 ROAs were exclusively investigated in just one of the five topics, most of them being for their timing of colonisation (69).

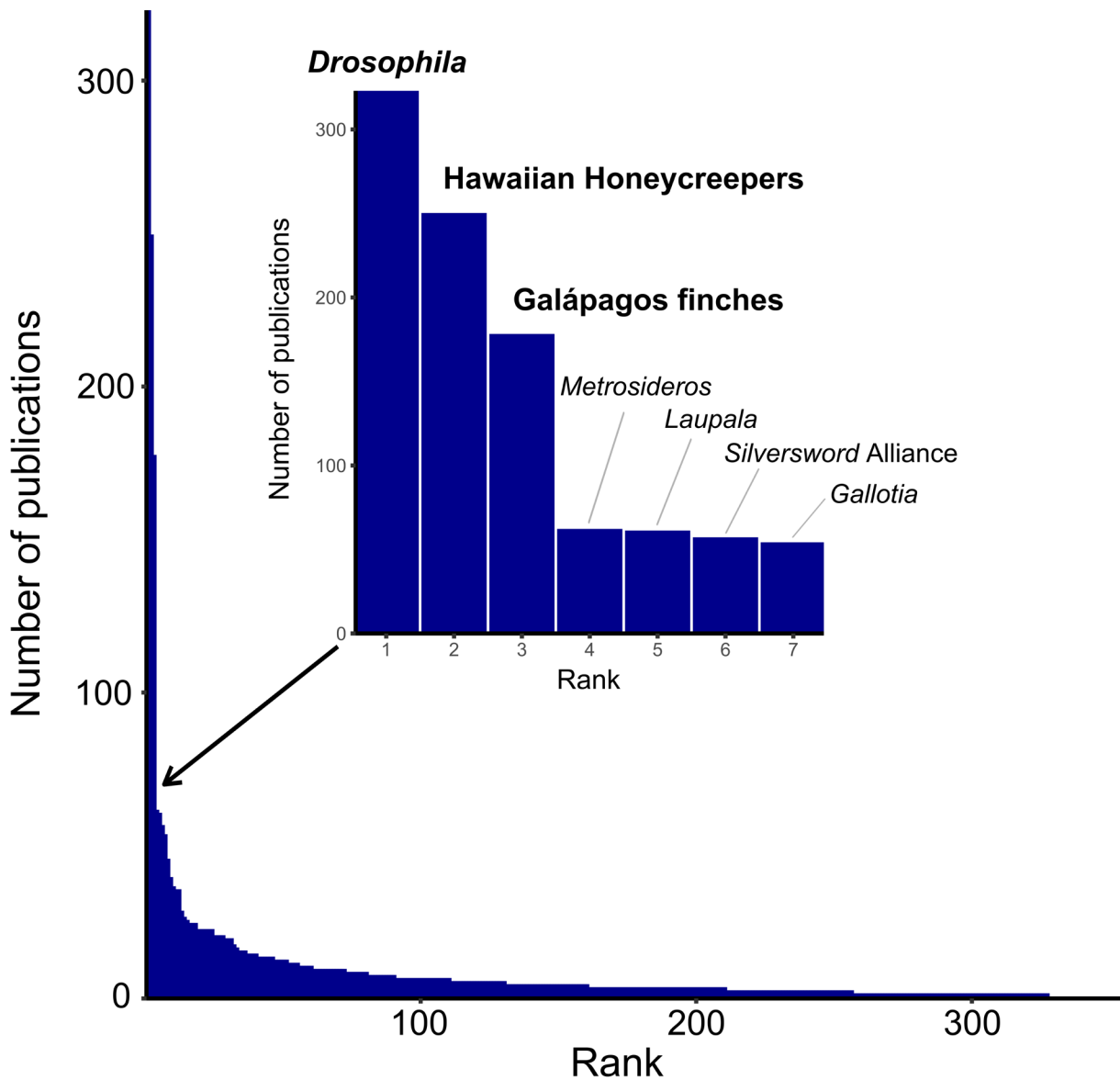


Figure.II.4. Ranking of all 354 evolutionary radiations on oceanic archipelagos (ROAs) based on the number of peer-reviewed publications found for each of them in our bibliometric analysis. The insert zooms on the seven ROAs with the most publications referenced, and highlighted the top 3 in bold.

Such knowledge disparities were also revealed in some ROA features such as the sampling fraction, which represents the ratio between the number of species included in the phylogeny and the total number of species believed to belong to the radiation (Poe 1998). This ratio serves multiple purposes: first, it gives an indication of the degree of monophyly validation, and second, it indicates the extent to which subsequent analyses on the phylogeny are representative of the entire clade. Indeed, most empirical phylogenies do not contain representatives of all species such that dating, diversification rates or even biogeographical patterns are typically estimated from incompletely sampled data (Chang et al. 2020). Overall, we found a median sampling fraction of 94% (Q25 at

70%; Q75 at 100%), suggesting a generally robust sampling effort across all ROAs. However, larger radiations tend to have lower sampling fractions, as evidenced by the significant and negative Spearman correlation between the sampling fraction and the estimated number of species within the radiation ($r_s = -0.51$; $P < 0.001$). Furthermore, we identified substantial variations in the sampling fraction among the archipelagos, with significant differences observed (Kruskal-Wallis test $P < 0.001$). Fiji, for instance, shows a median sampling fraction of 100%, while Hawaii had a median of 80%, partly due to the presence of very large ROAs. In contrast, Samoa and the Marquesas had the lowest median sampling fractions, at 52% and 57%, respectively. Additionally, land snails were the taxonomic group with the lowest median sampling fraction (61%), mostly because of their high number of extinct species, as previously mentioned. Notably, we observed no significant correlation between the sampling fraction and either the number of peer-reviewed publications (Spearman's correlation $r_s = -0.03$; $P = 0.52$) or the number of topics addressed ($r_s = -0.08$; $P = 0.12$) indicated that best-known ROA did not necessarily have the most complete phylogeny. An interesting example is the Hawaiian *Laupala* which, despite being one of the most iconic and best-studied ROAs, displayed a sampling fraction of 63%. This is important since missing taxa are likely to not be randomly distributed in the tree. Indeed, missing basal or recent species can substantially affect the outcomes of any kind of analyses involving the phylogeny (Brock et al. 2011).

In summary, these findings highlight that most of the ROAs we identified have received limited research attention. Much of our understanding of these phenomena stems from a relatively small number of well-studied radiations. Such bias is not without consequences as it may lead exceptions to become the rules if a larger range of ROA is not thoroughly explored.

3. c. Key research topics

In the following section, we presented the outcomes of the literature survey quantifying the popularity of each of the five research topics delineated above across our identified 354 ROAs (**Figure II.5**). For each topic, we provided a brief overview, highlighted the main advances and discussed the results of our survey with a specific focus on the prevailing methodological practices and pitfalls.

CHAPITRE II : RADIATIONS EVOLUTIVES SUR LES ARCHIPELS OCEANIQUE :
SYNTHESE BIOGEOGRAPHIQUE ET PHYLOGENETIQUE

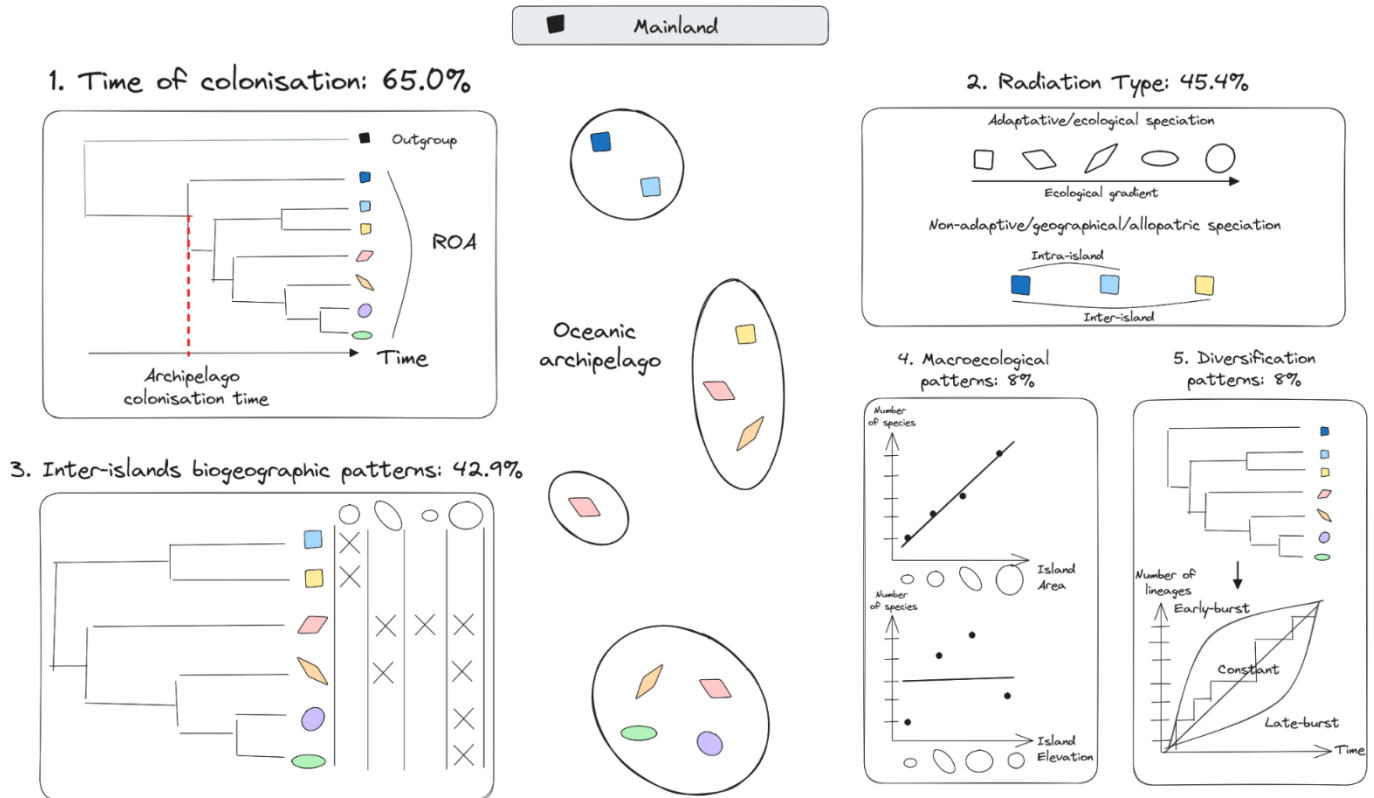


Figure.II.5. Graphical representation of the five key research topics related to evolutionary radiations on oceanic archipelagos (ROAs) detailed in our review. The percentage after each topic name represent the fraction of the 354 ROAs for which this topic has been investigated. In the center is represented an oceanic archipelago composed of four islands of different shapes. On it is displayed a ROA composed of seven species characterize by seven different colors (blue, cyan, yellow, red, orange, green and purple), and which have either one (e.g., the blue species) or several (e.g., the red species) populations on different islands. Panel 1 represent a calibrated phylogenetic tree including the ROA species and a mainland outgroup, that are used to estimate a time of colonisation of the common ancestor of the ROA. Panel 2 represent the same phylogenetic tree without the outgroup, but linked to the actual distribution of the species. Panel 3 present the two ways of speciation that can occur in ROAs: on top is display the evolution of a trait (represented by shapes) into several species according to an ecological gradient, representing speciation by ecological adaptation. The second one illustrates the evolution of new species without ecological speciation, but due to intra or inter-island isolation. Panel 4 presents an example of a biogeographical analysis involving ROAs. Two hypothetical linear regressions between the number of species of the ROA on each island and two geo-environmental factors, namely area and elevation, are shown. Finally, Panel 5 illustrates an example of a diversification analysis. Here, the calibrated phylogenetic tree is transformed into a Lineages-Through-Time (LTT) plot (stepped line), in which is added the species accumulation curve of three hypothetical simulated phylogenies, showing either an *early burst* (i.e., a decrease of species accumulation through time), a *constant* (the one fitting the phylogeny) and a *late burst* (i.e., an increasing of species accumulation through time) pattern of diversification.

3. c. 1. Time of colonisation

3.c.1.a. Brief overview

Since to the discovery of the molecular clock (Zuckerandl & Pauling 1962, 1965) and its further refinements (Thorne et al. 1998, Donoghue & Benton 2007, Donoghue and Yang 2016, Bromham et al. 2018), researchers are routinely applying sophisticated models on molecular phylogenies in order to place their clade of interest within the course of evolution (e.g., r8s, Sanderson 2003; BEAST2, Bouckaert et al. 2014). Establishing such a temporal framework is particularly relevant in ROAs research, as it permits to estimate the time of arrival of the ancestor in the archipelago. Because of the inherent characteristics of phylogenetic trees – which only depict nodes representing full lineage divergence – this time of colonisation inevitably falls between the time of divergence from the outgroup mainland species (Stem age) and the first splitting event in the ROA (Crown node). Although these two estimations are not always clearly distinguished in ROAs studies, crown nodes are usually preferred, as they are considered less biased proxies for the actual colonisation time (García-Verdugo et al. 2019). Indeed, outgroup identification can be especially difficult for ROAs, mainly because dispersal routes to oceanic archipelagos can be multiple, which makes the sampling of putative closest relatives complex (Price & Wagner 2018). In addition, taxonomic knowledge may be limited for some ROAs, hindering accurate outgroup selection (Haines et al. 2014, Jones et al. 2014, Machado et al. 2017). These crown node estimates, together with our growing knowledge of archipelago geology, have given rise to new hypotheses concerning the evolution of ROAs, such as the importance of old and now submerged islands in the establishment and diversification of lineages on some oceanic archipelagos (e.g., Bradler et al. 2015, Zaher et al. 2018, see **Figure II.S1**).

3.c.1.b Popularity of the topic and prevailing methodological approaches

Our survey reveals that almost two third (230/354) of the ROAs we recovered have been subject to at least one molecular dating, making *Time of colonisation* the dominant and most investigated topic in ROA literature (**Figure II.5**). In **Figure II.S1** are represented all ROAs crown nodes ages we recovered from the literature. Despite the attractiveness of this topic, our survey also revealed wide methodological disparities in phylogenetic calibration methods (**Figure II.6**), reflecting a long standing but still ongoing discussion in the literature about specific calibration of island clades (Bromham and Woolfit 2004, Heads 2005, 2011, Pillon & Buerki 2017, Landis et al. 2018). Approximately $\frac{1}{4}$ of all dated ROAs were calibrated using at least one fossil-informed calibration point (**Figure II.6**). This method consists in identifying one or several fossils that share sufficient synapomorphies with species closely related to or directly from the clade of interest, and

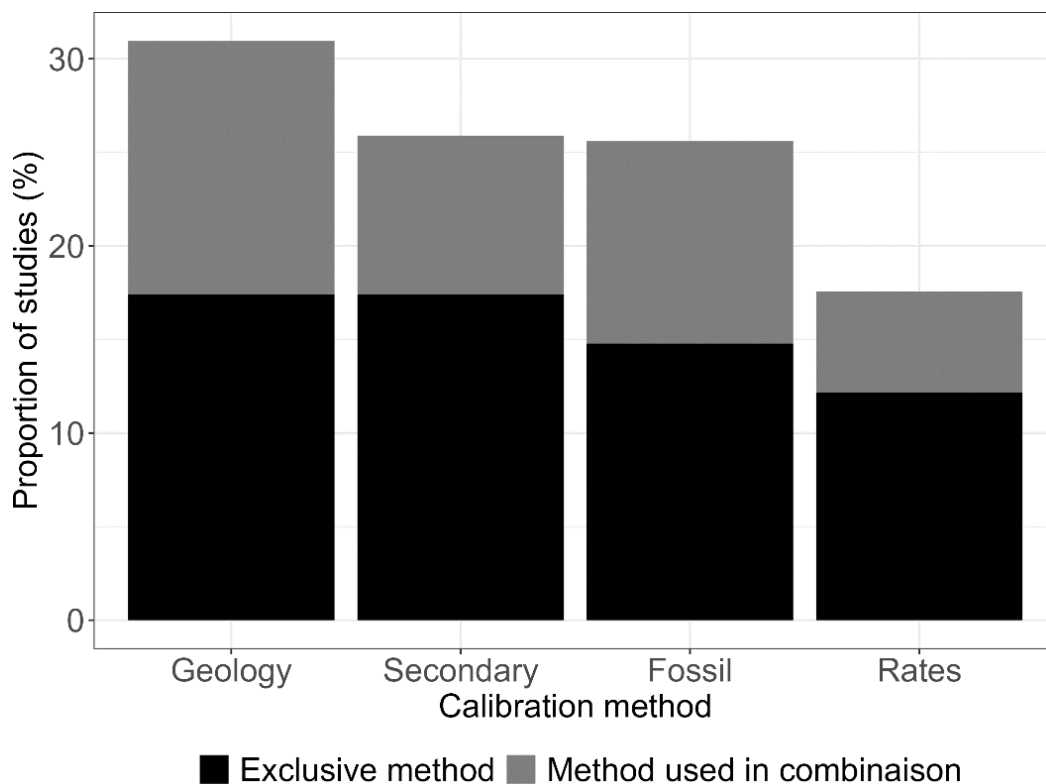


Figure II.6. Popularity of each of the four methods that have been used to calibrate phylogenetic trees of evolutionary radiations on oceanic archipelagos (ROAs). “Exclusive method” mean that the calibration was performed only with one type of calibration point(s) (either geological, secondary, or fossil) or a rate, where “Method used in combinaison” refer to studies that used at least one calibration point or a rate in addition to one or several over calibration types. Proportions are calculated on a total of 230 ROAs for which an age was available in the literature. If several independent publications have produced estimations, we selected the method that have been used in the most recent one.

then use the age of the fossil to constrain one or several nodes in the phylogeny (Ho & Phillips 2009). However, information on fossils is often scarce or even absent for ROA species (Landis et al. 2018, García-Verdugo et al. 2019, and references herein), which make this method only the third most used for ROA calibration (**Figure II.6**). Due to these limitations, researchers turned early on to the use of an alternative procedure using island geological ages. This method, which has been the most popular in the field (**Figure II.6**), consists of constraining a node of the phylogeny with the age of an island, used either a fixed or a maximum age. This has been used for example to create a maximum bound at the root of the ROA phylogeny with the age of the oldest known island (e.g., Kim et al. 2008, Nietlisbach et al. 2013). A perhaps more common approach consists in identifying sub-clades within the ROA that are strictly endemic to a specific island, and to apply the age of the island to the oldest splitting event of the subclade (e.g., Willyard et al. 2011, Bennett & O'Grady 2013). The rationale behind this method is that the ROA or the sub-clade could not have evolved

before the emergence of the island (Fleischer et al. 1998, Baldwin et al. 1998, Richardson et al. 2001). Another frequently employed calibration method is the use of secondary calibration points (~26% of the cases, **Figure II.6**), which consists in identifying calibrated nodes in published phylogenies, and use their age estimates to further calibrate the same node in the phylogeny of interest. Sometimes, additional outgroups therefore need to be included in the phylogeny of interest in order to recreate the specific node required for the calibration. Lastly, approximately 18% of ROAs (**Figure II.6**) have been calibrated using substitution rates, which consists in using a previously estimated mean evolutionary rate of a specific group of taxa. For instance, the constant molecular clock estimate of 2.3% pairwise sequence divergence per million years of Brower (1994) has been commonly used to calibrate phylogenies of arthropods (e.g., Arnedo et al. 2008, Gillespie et al. 2018).

3.c.1.c Limitations of current approaches and recommendations

Each of the calibration methods has its own biases and pitfalls (Hipsley and Müller 2014), that we will briefly present hereafter. First, despite the large body of literature dedicated to this subject (e.g., Benton & Donoghue 2007, Parham et al. 2012, Ksepka et al. 2015), estimating an accurate age and phylogenetic placement for fossils remains challenging, and often lead to somewhat arbitrary temporal uncertainties (Hipsley and Müller 2014). Second, using geological events as calibration points has faced criticism, as it may underestimate the time of colonisation. By relying solely on the age of existing islands, this method inevitably excludes the role of older islands, now submerged, that could have played in the evolutionary history of the clade (Heads 2005, 2011, Fernández-Palacios et al. 2011). In fact, several studies using alternative calibration strategies have dated the emergence of ROAs before the age of the oldest present-day island (e.g., Parent et al. 2008, Johns et al. 2018, see **Figure I.11**). This approach also introduces circular reasoning when attempting the investigation of biogeographical patterns (Waters & Craw 2006, Kodandaramaiah 2011, Ho et al. 2015), as the timing of cladogenetic events cannot be linked with biogeographical events like island emergence if island age was used for the initial calibration. Third, while substitution rates are now typically incorporated into methods assuming uncorrelated rates between branches under log-normal or exponential distributions (e.g., Drummond et al. 2006), they are not without their issues. Substitution rates appear to be influenced by the time scale at which they are measured, the lineages, or the genes in the estimation (Ho et al. 2011, Hipsley & Müller 2014). Finally, the use of secondary calibration points seems a promising alternative, as it relies on larger fossil-calibrated phylogeny. However, the retrieved calibrations are not always accurately capturing the uncertainties of the node age estimation in the source phylogeny and has been shown to yield

biased and falsely precise age estimates, at least when used without other relevant (i.e., fossil) calibration points (Graur and Martin 2004, Forest 2009, Schenk 2016). We recommend the reading of Hipsley and Müller (2014) for a more thorough review on pros, cons, and current advances in calibrations methods.

Considering these problems, some recent ROA studies have opted for alternative strategies. For example, several works have proposed to test, compare, and discuss multiple calibration methods (e.g., Arnedo & Hormiga 2020), sometimes using log-likelihood based indices to rank methods (Johns et al. 2018). Other authors have suggested preferring rates from geological island age to primarily avoid circularity in the interpretation of the evolutionary history of the clade (e.g., Gillespie et al. 2018). Others even assume to not attempt any calibration at all (e.g., Hochkirch et al. 2009). With the exponential increase in DNA sequences available for most groups, an interesting alternative is the use of mega-trees in which multiple ROAs can be included and calibrated simultaneously, the mega-tree being more easily dated accurately with multiple fossils. A good example is the work of Huysduynen et al. (2021), who estimated the time of colonisation of 39 plant species and clades in the Canary Islands using a megaphylogeny of 23,776 species and 42 fossil calibration points. In general, we recommend that potential future comparative studies on this subject should as much as possible reassess old geological, substitution rates, and secondary calibrations in light of these propositions, and by taking into account potentially newly discovered fossils for the clade or from close continental sister groups. Additionally, we encourage the development of alternative fossil-free calibration methods – like the recently developed time-stratified biogeographic stochastic process of Michael Landis (Landis 2017, Landis et al. 2018) – that could be used for ROAs for which no close fossil has never (and might never) been found.

3. c. 2. Radiation type

3.c.2.a. Brief overview

Historically, the study of evolutionary radiations has been in practice the study of adaptive radiations (Simpson 1953, Simões et al. 2016). Many of the most iconic adaptive radiations have been described on island and island-like systems [e.g., Darwin's finches, *Anolis* lizards, African Great Lake cichlids; Gillespie et al. 2020], and are partially coherent with Schuller's definition of 2000 which involve common ancestry, phenotype-environment correlation, trait utility and rapid speciation (Schuller 2000). Yet, the progressive accumulation of knowledge and empirical examples in the last decades have led to the emergence of several new alternative radiation categories (Simões et al. 2016, Martin & Richards 2019, Moen et al. 2019). Gittenberger (1991) notably proposed the

term “non-adaptive” radiations in reference to clades that diversified without relevant niche differentiation. This adaptive/non-adaptive dichotomy rely on the presence or absence of ecomorphological divergence between species, and also on the type of speciation process involve in the radiation emergence: adaptive radiation typically refer to a clade of ecologically differentiated sympatric species, where non-adaptive radiation are the result of allopatric divergence through geographical isolation, that does not necessarily necessitate niche differentiation (Gittenberger 2004, Rundell and Price 2009). In the specific case of ROAs, both processes have been invoked to explain the emergence of new species. In fact, on one hand, allopatric speciation can arise between islands of the archipelago, and also inside islands through geographical fragmentation caused by volcanism, landslides, climate changes or sea level fluctuations (Cook et al. 2008, Goodman et al. 2012, Whittaker et al. 2023). On the other hand, sympatric speciation is believed to occur via adaptive divergence to different ecological niches in the same environment/island (Schulter 2000), but can also emerge through secondary contact: an species can colonize multiple islands of an archipelago, create several reproductively isolated populations with or without ecological differentiation on each islands, and then enter in secondary contact, provoking sympatry with character displacement (Losos & Ricklefs 2009, Losos & Mahler 2010).

3.c.1.b Popularity of the topic and prevailing methodological approaches

One the basis of author discussions and keywords found in the literature (see **Online Supplementary Data**), we found that nearly 45% of all ROA have been assessed as either adaptive, non-adaptive or both, making it the second most investigated topic in ROAs research (**Figure II.5**). The vast majority of investigated ROAs have been described as “adaptive” (~73%), followed by “both” (~16%) and “non-adaptive” (~11%). The dominance of adaptive ROAs is not a surprising result, as this type of denomination has always been predominant in the literature (Simões et al. 2016) and especially in oceanic archipelagos (Soulebeau et al. 2015). However, this highlights a more general issue: researchers are often identifying radiations as adaptive without performing any statistical tests, or by using information that has been shown to not always be restricted to adaptive clades (Lieberman 2012, Soulebeau et al. 2015). For example, the observation of a high speciation rate is often invoked to prove the adaptive nature of a clade (e.g., Schulter 2000, Magnacca & Danforth 2006). One of the ideas behind this reasoning is that non-ecological speciation is a slower process than ecological differentiation (Coyn & Orr 2004), but it has been shown that this assumption is not always true (Czekanski-Moir & Rundell 2019). We found out that most researchers generally use the adaptive terminology for ROAs when they are witnessing huge morphological disparities or habitat diversity between closely related species (e.g., Barber et al.

2000, Strijk et al. 2012); and such observation may sound reasonable in order to characterize a clade as adaptive. But the absence of standardized methods and a definitive and objective set of criteria makes the “adaptive” epithet mostly unusable for relevant comparison between clades. The same problem arises for putative non-adaptive ROAs, which are identified when there is an apparent but non-tested lack of ecological diversity between species (e.g., Pillon et al. 2013, Beatty et al. 2017), or just because of their geographical isolation between islands (e.g., Benavides et al. 2008).

3.c.1.c Limitations of current approaches and recommendations

As mentioned above, the main issue about identifying the type of radiation is the lack of methodological consensus and a clear definition of adaptive and non-adaptive radiations, despite the numerous attempts and discussion on the subject (Simpson 1953, Schluter 2000, Rundell & Price 2009, Olson & Arroyo-Santos 2009, Hernández-Hernández 2019 and reference herein). Regarding the specific case of ROAs, we are convinced that the dichotomy adaptive/non adaptive makes little sense, as it is difficult to conceive that these clades are composed exclusively of species that are either completely ecologically differentiated between each other, or all ecologically identical but geographically separated. As already supposed for few ROAs (our category “both”, e.g., Goodson et al. 2006, Harter et al. 2015), both processes can play a significant role in the diversification of ROAs, as the geological and environmental dynamic of an oceanic archipelago can generate many opportunities for ecological adaptation and vicariance (Whittaker et al. 2008). We think therefore that the literature would really gain clarity by being careful about the use of adaptive and non-adaptive terms for ROAs, and recommend as much as possible the use of a statistical procedure (e.g., the evolution of disparification through time, demonstrating the use, by species of the same clade, of different habitats or resources, Soulebeau et al. 2015) before making any conclusion about the process behind species diversification in a ROA.

3. c. 3. Inter-islands biogeographic patterns

3.c.2.a. Brief overview

The historical biogeography of a clade can be explored by examining the actual distribution of its species and related it to their positions in the phylogenetic tree. The concept that phylogenetic relationships can inform us about the spatial distribution of lineages across geological times is not new (Hennig 1966) and has undergone extensive debate and paradigm shifts concerning the role of vicariance and dispersal (Morrone & Crisci 1995, de Queiroz 2005, Cowie & Holland 2006). Contemporary biogeographic models now encompass a wide array of biogeographical hypotheses

and are routinely applied to time-calibrated molecular phylogenies by means of maximum likelihood or Bayesian methods (e.g., Ree & Smith 2008, Sanmartín et al. 2008, Matzke 2014).

Oceanic islands have been the subject of specific discussions and model developments in order to account for their biogeographic specificities such as overwater dispersal and founder-event speciation (Cowie & Holland 2006, Sanmartín et al. 2008, Matzke 2014). Recent years have seen a substantial focus on the historical biogeography of oceanic archipelagos, driven in part by the observation that several endemic clades exhibit a correlation between species age and the geological age of the island they inhabit, with old and young species found on older and younger islands, respectively (Funk & Wagner 1995). This pattern, known as the "progression rule", was mainly described for Hawaiian ROAs, but has now also been reported in other archipelagos (Shaw & Gillespie 2016), and undoubtedly remains one of the most discussed and debated island phenomena (Borregaard et al. 2017, Hembry et al. 2021).

3.c.1.b Popularity of the topic and prevailing methodological approaches

We discovered that approximately 43% (151 out of 354) of all ROAs included in our study have been examined for their intra-archipelago biogeographic patterns (see Figure X). Notably, this analysis encompassed half of the Hawaiian ROAs (52% or 58 out of 109), 45% of those in the Canary Islands (35 out of 75), and a substantial 59% within the Galápagos archipelago (13 out of 22), as depicted in **Figure II.5**. Conversely, the remaining best-studied archipelagos were less explored, with Fiji at 32%, the Mascarene at 31%, and Madeira at 17% (see **Figure II.5**). The lack of research interest for the Mascarene may be partly attributed to its relatively low number of primary islands, having only three main islands and most ROA being found only on La Réunion et Mauritius. Most studies that have discussed an intra-archipelago biogeographic pattern for a ROA have done so within the framework of the progression rule (Funk & Wagner 1995). The underlying idea behind this pattern is that species present on older islands progressively colonize emerging islands over time, thus linking the diversification dynamics of the ROA with the geological history of the archipelago. Our literature review revealed that information was available on this particular biogeographical pattern for 15 archipelagos (**Figure II.5**). Interestingly, our results show that the progression rule is far from a clear and ubiquitous pattern, despite its historical significance in oceanic archipelago biogeography (Borregaard et al. 2017).

We also wanted to point out that oceanic archipelagos are not necessarily sinks of biodiversity, and that they can be part of a larger colonisation route. Indeed, we found that 64 ROAs (18%) have further colonised other oceanic archipelagos or have undergone a “boomerang effect” (Caujapé-

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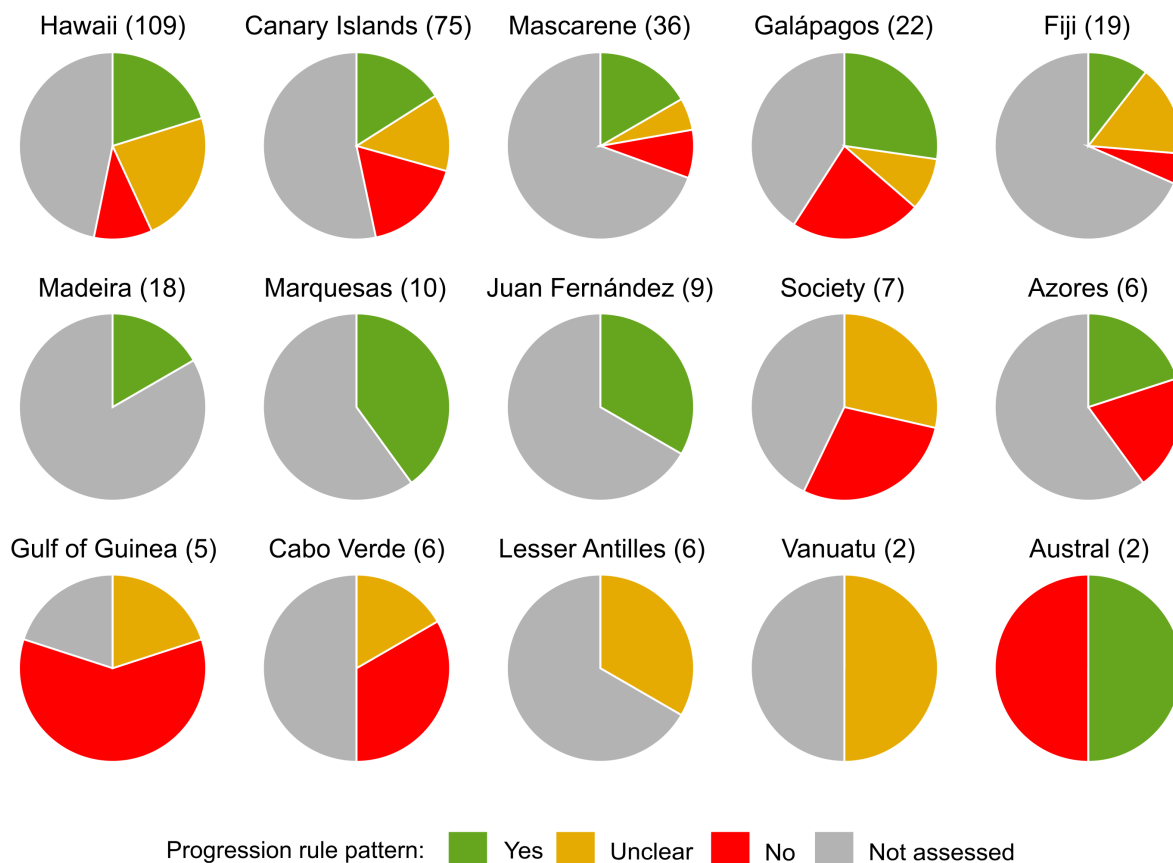


Figure.II.7. Assessment of the progression rule pattern for 15 oceanic archipelagos around the world based on the evaluation described and/or tested in the literature. Green slices represent the proportion of ROAs for which most dispersal events have been inferred or are believed to be from older to younger islands, and when the oldest current island has been inferred or is believed to be the ancestral range. Orange slices represent the proportion of ROAs for which dispersal from older to younger island have been detected but is not clearly dominant in the phylogeny, and the oldest island has not necessarily been inferred/believed to be the ancestral range. Red slices represent the proportion of ROAs for which the majority of dispersal events have been reported to barely/not follow the progression rule, and when the oldest island has not been inferred/believed to be the ancestral range. Grey slices represent the proportion of ROA that have not been investigated at all for their inter-islands biogeographic patterns.

Castells 2004, 2011) by back-colonizing mainland areas. Unsurprisingly, nearly half of these events concerned Canary islands ROAs (35/64), probably because their central position in the Macaronesian meta-archipelago and their past and current proximity to north Africa, that make them more prone to such types of colonisation pathways (Fernández-Palacios et al. 2011). Only seven ROAs have extended their range beyond Hawaii, primarily dispersing to the French Polynesian archipelagos (Austral, Marquesas, Society), but also to Bonin (Harbaugh et al. 2010) and Samoa (Holland & Cowie 2009). Eleven other archipelagos display between one to four occurrences of such secondary dispersal events (see **online Supplementary Data**).

3.c.1.c Limitations of current approaches and recommendations

Several reasons can explain why inter-islands biogeographic patterns have only concern less than 50% of the ROA studied in the literatures (**Figure II.5**): (i) a low phylogenetic resolution at certain nodes and/or a low sampling fraction obviously limit the description and interpretations of clades historical biogeography; (ii) even if larger ROAs (>10 species) usually hold a majority of single island endemics (see Chapter III), the presence of multiple island endemics complexify the detection of inter islands colonisation route (e.g., Jordal et al. 2004, Liu et al. 2020), as it requires a thorough sampling of multiple populations for each species (e.g., Garb & Gillespie 2009); (iii) ROAs restricted to a single island (e.g., Saint-Helena, Lord Howe) are obviously not concerned by such an investigation (15 ROAs fall into this category). (iv) some ROAs have only been studied within the context of large-scale studies, that have been primarily focused on the global biogeographic history of specific taxonomic groups, with little to no interest for the ROA itself, apart from identifying the original source pool of the ancestral colonisation (e.g., Razafimandimbison et al. 2017, Xu et al. 2019); (v) the limited knowledge of the archipelago's geology might also explain why no assessment has been conducted as it is probably the case for the Bonin archipelago (Davison and Chiba 2006).

It is important to highlight that most discussions on ROA intra-archipelago biogeographic patterns have primarily relied on visual examination of the tree topology and the species distribution on islands. Merely 45 out of approximately 350 studies (around 13%) have delved into the historical biogeography of ROAs using probabilistic models, with about 19 of them testing and comparing at least two distinct biogeographic models. This lack of statistical evidence can pose significant problems for comparative analyses of progression rules (Hembry et al. 2021). Classifying intra-archipelago biogeographic patterns is a complex task. Although Funk & Wagner (1995) proposed multiple scenarios of intra-archipelago colonization routes within the Hawaiian archipelago, the literature is still lacking a set of reliable tests that can specifically assess all the intricacies of dispersal patterns between islands at the scale of ROAs. We believe that reevaluating older phylogenies using modern biogeographic models such as *BioGeoBEARS* (Matzke 2014) could greatly benefit the field and pave the way for meaningful comparative analyses in the future. We also call for the establishment of a standard procedure for statistically evaluating the progression rule, or at least for the development of an index to objectively quantify the presence of the progression rule in an ROA phylogeny. A simple correlation between the age of islands and the age of the species inhabiting them could be a first test. For their studies on the *Bidens* in Hawaii, Knope

et al. (2020) also proposed counting the number of speciation events that shifted from an older to a younger island, as a way of quantifying the rule of progression.

3. c. 4. Macroecological patterns

3.c.2.a. Brief overview

Thanks to the pioneering work of MacArthur & Wilson (1963, 1967), the investigation of biogeographical patterns on islands has remained a prominent focus in the field of island biology over the past sixty years (Warren et al. 2015, Patiño et al. 2017). Comprehending the mechanisms behind the variations in species richness among islands has been proven to be fundamental for our understanding of broader ecological and evolutionary patterns. Predictive statistical models were initially developed to explain island diversity using two simple parameters: the distance of the island from the source pool and the island area (MacArthur & Wilson 1963, 1967). Current models include island area, isolation island geological age, environmental heterogeneity and past configurations at the last glacial maximum (LGM) (e.g., Whittaker et al. 2008, Weigelt & Kreft 2013, Weigelt et al. 2016, Barajas-Barbosa et al. 2020). Yet, an evaluation of the geo-environmental factors influencing island species richness patterns emerging from ROAs could prove crucial for our understanding of the diversification dynamics taking place in oceanic archipelagos (Economo et al. 2015). It is worth noting that such approaches were initiated very early in the study of ROAs, as evidenced by Terrell Hamilton and Ira Rubinoff's work on Darwin's finches (Hamilton & Rubinoff 1963, 1964) in the Galápagos.

3.c.1.b Popularity of the topic and prevailing methodological approaches

We found 29 ROAs (~8%) for which ROA island species richness was studied as a response variable in biogeographical models (**Figure II.5**). Probably because of its apparent ubiquity in nature (Lomolino 2000), all but one of the studies retrieved have searched for evidence of a positive relationship between ROA island species richness and island area. Relation with island geological age has also been widely tested (26/29), and more precisely, the combined effect of area and age via the general dynamic model (GDM, Whittaker et al. 2008) have been widely discussed (see below). Only four studies have tried to correlate ROA diversity patterns with more specific ecological proxies, such as elevation (Givnish et al. 2009) or plant diversity per island (Hamilton & Rubinoff 1963). Finally, the effect of island insularity (via its distance from the continent and/or from other islands) have been studied for four ROAs. Regarding the paucity of data available, it is difficult to extract any relevant trends on the influence of geo-environmental factors on the diversity patterns of ROAs. Most of the studies came from two meta-analyses focused on Hawaiian ROAs (Gillespie

& Baldwin 2010, Lim & Marshall 2017), that have both found a positive effect of area and island geological age on ROAs island species richness, in accordance with the GDM.

3.c.1.c Limitations of current approaches and recommendations

Even though it seems obvious to ask why, in a given archipelago, some islands have accumulated more species than others during the radiation process, very few works on ROAs have addressed this topic (Roell et al. 2021, Wagner et al. 2014, Economo et al. 2015, Lim & Marshall 2017, Tao et al. 2021), as demonstrated by our literature review. However, we see great potential for exploring such an approach given that species distribution on islands for several archipelagos and taxa already exists and is freely available with minimal effort (e.g., Nishida 2002, Imada 2012). Islands characteristic can be easily retrieved from global databases (Weigelt et al. 2013, Norder et al. 2018, Barajas-Barbosa et al. 2020) or reconstructed through open-access geographical databases (Global Administrative Areas: <http://www.gadm.org/version1>). Several questions related to such "classic" biogeographical approach remain unanswered, such as the prevalence of a species-area relationship for island radiated clades (Losos & Schluter 2000), or whether island species richness for adaptive ROAs better scale to island elevation and climatic variability (Givnish et al. 2009).

3. c. 5. Diversification patterns

3.c.2.a. Brief overview

Understanding how and why biodiversity varies through time is one of the fundamental questions of macroevolution (Morlon 2014). The study of diversification rates, i.e., the balance between the rate of species emergence (speciation) and species extinction through time, have first been investigated with fossil data (Raup et al. 1973), but the development of molecular tools in the last decades have made possible the inference of diversification rates directly from time-calibrated molecular phylogenies of extant taxa, via the use of birth-death models (Nee et al. 1994, Ricklefs 2007, Stadler 2013). Today, a wide variety of phylogenetic-related tools are available for investigate clade's diversification, from the detection of rate-shifts (e.g., Rabosky et al. 2014, May & Moore 2016) to model-fitting techniques that can correlate diversification rates with biotic (e.g., Etienne et al. 2012) or abiotic (e.g., Condamine et al. 2013) variations through geological times. These implementations have notably triggered many discussions regarding the causes of emergence and evolution of the diversity inside radiating clades (Moen & Morlon 2014, Rabosky & Lovette 2008, Martin & Richards 2019).

Since the earliest days of island biogeography (MacArthur and Wilson 1963, 1967), the macroevolution of island biodiversity as mainly focuses on the emergence of species assembly:

diversification rates have been explored in concert with immigration rate and within the framework of the equilibrium theory (Whittaker et al. 2008, Rabosky & Glor 2010, Valente et al. 2015). Yet, despite their valuable temporal framework, time-calibrated molecular phylogenies have rarely been used to investigate the mode and tempo of diversification on island systems (Valente et al. 2018, Lim & Marshall 2017), with a general lack of interest in the diversification dynamic of ROAs.

3.c.2.b Popularity of the topic and prevailing methodological approaches

We only identified 30 ROAs (~8%) for which at least one study has explicitly investigated the diversification dynamic through time (**Table II.1**). As for macroecological patterns, nearly half of them have been examined by Lim & Marshall (2017), who predicted a decline in the rate of species accumulation over time for 14 Hawaiian radiations. The paradox is that Lim & Marshall (2017) did not use time-calibrated phylogenies, but rather the actual species richness of clades in a geologically informed model. For the remaining 16 ROAs, diversification patterns were explored using time-calibrated phylogenies. For five of them, a slowdown in the diversification rate through time, also known as an *early burst* pattern, was documented (**Table II.1**). In contrast, eight showed an opposite *late burst* pattern, i.e., showing an increase in the diversification rate toward the present, while the other three displayed a constant rate of species accumulation through time (**Table II.1**). Regarding the analytical approaches used in these studies, most discussions were based on a Lineage-Through-Time (LTT) plots (i.e., a plot with time along the x-axis and the reconstructed number of lineages on the y-axis) and/or simple summary statistics such as the γ -statistic (Pybus & Harvey 2000). Finally, very few studies carried out more in-depth research such as comparing the fit of several birth-death models on the ROA phylogenies (**Table II.1**).

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Table II.1. Information on the 28 evolutionary radiations on oceanic archipelagos (ROAs) that have been investigated for their diversification patterns, with details on the method(s) used and the main resulting diversification pattern retrieved.

Radiation	Archipelago	Type of taxa	Method(s) used	Result	Reference
14 Hawaiian radiations	Hawaii	6 Plants 7 Invertebrates 1 Birds	Custom geologically informed model (Lim & Marshall 2017)	Early burst	Lim & Marshall 2017
<i>Badula</i>	Mascarene	Plants	LTT plot observation Gamma statistic (Pybus & Harvey 2000)	Early burst	Strijk et al. 2014
<i>Ruiza</i>	Mascarene	Plants	LTT plot observation Gamma statistic (Pybus & Harvey 2000) Models fits (TreePar, Stadler 2011)	Early burst	Le Péchon et al. 2015
<i>Nesophrosyne</i>	Hawaii	Invertebrates	LTT plot observation Models fits (LASER, Rabosky 2006) Gamma statistic (Pybus & Harvey 2000)	Early burst	Bennett & O'Grady 2013
Galápagos Finches	Galápagos	Birds	DAISIE (Valente et al. 2015)	Early burst	Valente et al. 2015
<i>Mandarina</i>	Bonin	Land snails	LTT plot observation Gamma statistic (Pybus & Harvey 2000) Colless Index (Colless, 1982) B1 statistic (Kirkpatrick and Slatkin 1993)	Early burst	Davison & Chiba 2006
<i>Aphanarthurum</i>	Canaries	Invertebrates	LTT plot observation	Constant	Jordal & Hewitt 2014
<i>Phesulma</i> (2 radiations)	Mascarene Comoros	Reptiles	LTT plot observation Gamma statistic (Pybus & Harvey 2000)	Constant	Harmon et al. 2008
<i>Pholcus</i>	Canaries	Invertebrates	LTT plot observation Models fits (LASER, Rabosky 2006) B1 statistic (Kirkpatrick and Slatkin 1993)	Late burst	Dimitrov et al. 2008
<i>Melanobasis & Nesobasis</i> (2 radiations)	Fiji	Invertebrates	Generalized Mixed Yule Coalescent (GMYC) (Fujisawa & Barraclough, 2013) LTT plot observation	Late burst	Beatty et al. 2017
<i>Homalictus</i> (3 radiations)	Fiji Vanuatu Samoa	Invertebrates	LTT plot observation	Late burst	Groom et al. 2013
<i>Melicope</i>	Hawaii	Plants	LTT plot observation BAMM (Rabosky, 2014)	Late burst	Paetzold 2019
<i>Aeonium Alliance</i>	Canaries	Plants	LTT plot observation	Late burst	Thiv et al. 2010

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The three main diversification patterns (*early burst*, constant and *late burst*) have been associated with several hypotheses regarding the emergence of ROAs. Clades showing a progressive decline of diversification through time (*early burst*) appear to be a common outcome in the literature (McPeck 2008, Rabosky & Lovette 2008), and have been associated with several biological hypotheses but also to some methodological biases (Moen & Morlon 2014). Adaptive radiations are thought to be especially prone to produce a slowdown of diversification, as they are believed to progressively fill available niche space until competition limits clade richness through diversity-dependent feedbacks (Phillimore & Price 2008, Etienne & Haegeman 2012, Scantlebury 2013). Recent developments in island biogeography, such as the proposal of the General Dynamic Model of Oceanic Island Biogeography (GDM; Whittaker et al. 2008, Borregaard et al. 2017) also suggest the diversification slowdown as the main outcome for ROAs. In their model, such a pattern should result from a three-stage process: (i) a rapid accumulation of lineages due to an increase in ecological space as the island emerges and grows; (ii) a slowdown in the rate of species accumulation, reflecting the non-adaptive phase (intra-island allopatry) when the island reaches its maximum topographical complexity; (iii) an equilibrium phase, reflecting the island's finite resources, which in turn impose a limit on diversity.

Late burst signals in ROAs have been proposed to be the consequence of recent geo-environmental fluctuations affecting diversification rates such as Pleistocene sea-level variations (Groom et al. 2013), or to be linked with specific ecological features like trait shifts (Papadopoulou & Knowles 2017, Salces-Castellano et al. 2020, Paetzold 2019) or sexual selection (Dimitrov et al. 2008), which can give a selective advantage and rapidly increase speciation rates. It is also plausible that the high extinction rates recorded over the last million years, because of volcanic eruptions, mega landslides, or tropical storms (Whittaker et al. 2023), have wiped out most of the ancient lineages within the ROA, leaving only the most recent burst of speciation recorded in molecular phylogeny.

Finally, constant rates of diversification have also been documented for several island clades. Although poorly discussed in the context of ROAs, some studies on composite archipelagos in the Indo-Pacific have highlighted the fact that endemic clades have not yet reached their ecological limit (archipelagos are young systems) and continued to expand into new niches due to the recent emergence of islands that increases the likelihood of speciation (Esselstyn 2009, Fritz et al. 2011).

3.c.2.c Limitations of current approaches and recommendations

As with biogeographical patterns, the study of ROA diversification patterns has been neglected in the field. This may seem paradoxical, especially when we consider on the one hand the large number of phylogenies available for ROAs, and on the other hand that remarkable theoretical and methodological advances have been made in the field of models of evolution applied to molecular phylogenies in recent years (e.g., Stadler 2013, Morlon 2014, Rabosky et al. 2016). In addition, examining the tempo and mode of diversification in phylogenetic trees enables us to address key topics in island biogeography, such as the concepts of equilibrium, diversity-dependence, or adaptive radiations (e.g., Rabosky & Glor 2010, Valente et al. 2015, 2017). We therefore encourage island biogeographers to add macroevolutionary perspectives to their studies in order to gain a complementary and broader view of the process driving diversification patterns through time, and to add further lines of evidence to their discussion of ROA ecology and evolution. Several analyses are now available in R packages and are not required to have an expert level to be implemented (*RPANDA*, Morlon et al. 2016; *BAMM*, Rabosky et al. 2014). We recommend, however, to pay a particular attention to the current debate concerning the validity of parameters (i.e., speciation and extinction rates) estimated by likelihood-based models such as those implemented in the *RPANDA* package (Louca & Pennel 2020). Despite these limitations, model comparison based on well-defined assumptions is still a useful approach for discriminating between different evolutionary histories, without necessarily focusing on the exact numerical values of the estimated diversification rates (Morlon et al. 2020, Helmstetter et al. 2022).

4. Conclusion

Here, we have presented for the first time a literature review of all recognized evolutionary radiations occurring on oceanic archipelagos (ROAs) worldwide based on phylogenetic evidence. This endeavor has shed light on geographical, taxonomical, and methodological disparities within the field, notably the pronounced dominance of a handful of well-studied ROAs, archipelagos, and research topics. While a substantial amount of ecological, evolutionary, and biogeographical data has been accumulated over the past decade, the field appears to lack a consensus on several definitions and methodological aspects that should be addressed before attempting any meaningful comparative analyses.

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5. Supplementary information

Table.II.S1. List of the 60 oceanic archipelagos investigated to identify evolutionary radiations on oceanic archipelagos (ROAs).

Oceans/Region	Oceanic archipelagos
North Atlantic Ocean	Azores
	Bermuda
	Canary Islands
	Cape Verde
	Faroe
	Gulf of Guinea
	Lesser Antilles
	Madeira
	Savage
South Atlantic Ocean	Ascension
	Fernando de Noronha
	Saint Helena
	Trindade (and Martim Vaz)
	Tristan/Gough
Indian Ocean	Christmas
	Comoros
	Mascarene
Antarctic Ocean	South Sandwich
	Amsterdam
	Antipodes
	Balleny
	Bouvet
	Crozet
	Heard and McDonald
	Kerguelen
	Macquarie
	Peter I
	Prince Edward
	Scott
Arctic Ocean	Jan Mayen

Oceans/Region	Oceanic archipelagos
Bering Sea	Saint-Paul
North Pacific Ocean	Bonin (Ogasawara)
	Guadalupe
	Hawaii
	Line islands
	Marianas
	Oki
	Revillagigedo
South Pacific Ocean	Austral
	Campbell
	Chatham
	Cocos (Costa-Rica)
	Cook
	Desventuradas
	Easter (Rapa Nui)
	Fiji
	Galápagos
	Gambier
	Juan Fernández
	Kermadec
	Lord Howe
	Malpelo
	Marquesas
	Pitcairn
	Salas y Gómez
	Samoa
	Society
Tonga	
Vanuatu	
Wallis and Futuna	

Table II.S2. Web of Science strings used for each archipelago in our bibliometric research, in order to obtain an estimation of the number of studies specifically dedicated to each evolutionary radiations on oceanic archipelagos (ROAs). We use the same string construction for every ROA in each archipelago (the ROAs names used here serve as examples).

Archipelago	Example of Web of Science implementation
Austral	(AB = (Rhyncogonus AND Austral) OR TI = (Rhyncogonus AND Austral) OR (AB = Austral AND TI = Rhyncogonus))
Azores	(AB = (Leptaxis AND Azor*) OR TI = (Leptaxis AND Azor*) OR (AB = Leptaxis AND TI = Azor*) OR (AB = Azor* AND TI = Leptaxis))
Bonin	(AB = (Crepidiastrium AND Bonin) OR TI = (Crepidiastrium AND Bonin) OR (AB = Crepidiastrium AND TI = Bonin) OR (AB = Bonin AND TI = Crepidiastrium) OR AB = (Crepidiastrium AND Ogasawara) OR TI = (Crepidiastrium AND Ogasawara) OR (AB = Crepidiastrium AND TI = Ogasawara) OR (AB = Ogasawara AND TI = Crepidiastrium))
California Islands	(AB = (Deinandra AND California Islands) OR TI = (Deinandra AND California Islands) OR (AB = Deinandra AND TI = California Islands) OR (AB = California Islands AND TI = Deinandra))
Canary Islands	(AB = (Adenocarpus AND Canar*) OR TI = (Adenocarpus AND Canar*) OR (AB = Adenocarpus AND TI = Canar*) OR (AB = Canar* AND TI = Adenocarpus))
Cape Verde	(AB = (Daucus AND Verde) OR TI = (Daucus AND Verde) OR (AB = Daucus AND TI = Verde) OR (AB = Verde AND TI = Daucus))
Comoros	(AB = (Phelusuma AND Comor*) OR TI = (Phelusuma AND Comor*) OR (AB = Phelusuma AND TI = Comor*) OR (AB = Comor* AND TI = Phelusuma))
Fiji	(AB = (Strumigenys AND Fiji*) OR TI = (Strumigenys AND Fiji*) OR (AB = Strumigenys AND TI = Fiji*) OR (AB = Fiji* AND TI = Strumigenys))
Galápagos	(AB = (Lecocarpus AND Galapag*) OR TI = (Lecocarpus AND Galapag*) OR (AB = Lecocarpus AND TI = Galapag*) OR (AB = Galapag* AND TI = Lecocarpus))
Gulf of Guinea	(AB = (Zosterops AND Gulf of Guinea) OR TI = (Zosterops AND Gulf of Guinea) OR (AB = Zosterops AND TI = Gulf of Guinea) OR (AB = Gulf of Guinea AND TI = Zosterops))
Hawaii	(AB = (Ochrosia AND Hawai*) OR TI = (Ochrosia AND Hawai*) OR (AB = Ochrosia AND TI = Hawai*) OR (AB = Hawai* AND TI = Ochrosia))
Juan Fernández	(AB = (Neomaso AND Fernandez) OR TI = (Neomaso AND Fernandez) OR (AB = Neomaso AND TI = Fernandez) OR (AB = Fernandez AND TI = Neomaso))
Lesser Antilles	(AB = (Cyrtognatha AND Lesser Antilles) OR TI = (Cyrtognatha AND Lesser Antilles) OR (AB = Cyrtognatha AND TI = Lesser Antilles) OR (AB = Lesser Antilles AND TI = Cyrtognatha))
Lord Howe	(AB = (Coprosma AND Howe) OR TI = (Coprosma AND Howe) OR (AB = Coprosma AND TI = Howe) OR (AB = Howe AND TI = Coprosma))
Madeira	(AB = (Boettgeria AND Madeira*) OR TI = (Boettgeria AND Madeira*) OR (AB = Boettgeria AND TI = Madeira*) OR (AB = Madeira* AND TI = Boettgeria))
Marquesas	(AB = (Pomarea AND Marquesa*) OR TI = (Pomarea AND Marquesa*) OR (AB = Pomarea AND TI = Marquesa*) OR (AB = Marquesa* AND TI = Pomarea))
Mascarene	(AB = (Bertiera AND Mascare*) OR TI = (Bertiera AND Mascare*) OR (AB = Bertiera AND TI = Mascare*) OR (AB = Mascare* AND TI = Bertiera))
Saint Helena	(AB = (Commidendrum AND Helena) OR TI = (Commidendrum AND Helena) OR (AB = Commidendrum AND TI = Helena) OR (AB = Helena AND TI = Commidendrum))
Samoa	(AB = (Cyrtandra AND Samoa*) OR TI = (Cyrtandra AND Samoa*) OR (AB = Cyrtandra AND TI = Samoa*) OR (AB = Samoa* AND TI = Cyrtandra))
Society	(AB = (Sclerotheca AND Society) OR TI = (Sclerotheca AND Society) OR (AB = Sclerotheca AND TI = Society) OR (AB = Society AND TI = Sclerotheca))
Tristan/Gough	(AB = (Nesospiza AND Tristan) OR TI = (Nesospiza AND Tristan) OR (AB = Nesospiza AND TI = Tristan) OR (AB = Tristan AND TI = Nesospiza) OR AB = (Nesospiza AND Gough) OR TI = (Nesospiza AND Gough) OR (AB = Nesospiza AND TI = Gough) OR (AB = Gough AND TI = Nesospiza))
Vanuatu	(AB = (Fluviopupa AND Vanuatu) OR TI = (Fluviopupa AND Vanuatu) OR (AB = Fluviopupa AND TI = Vanuatu) OR (AB = Vanuatu AND TI = Fluviopupa))

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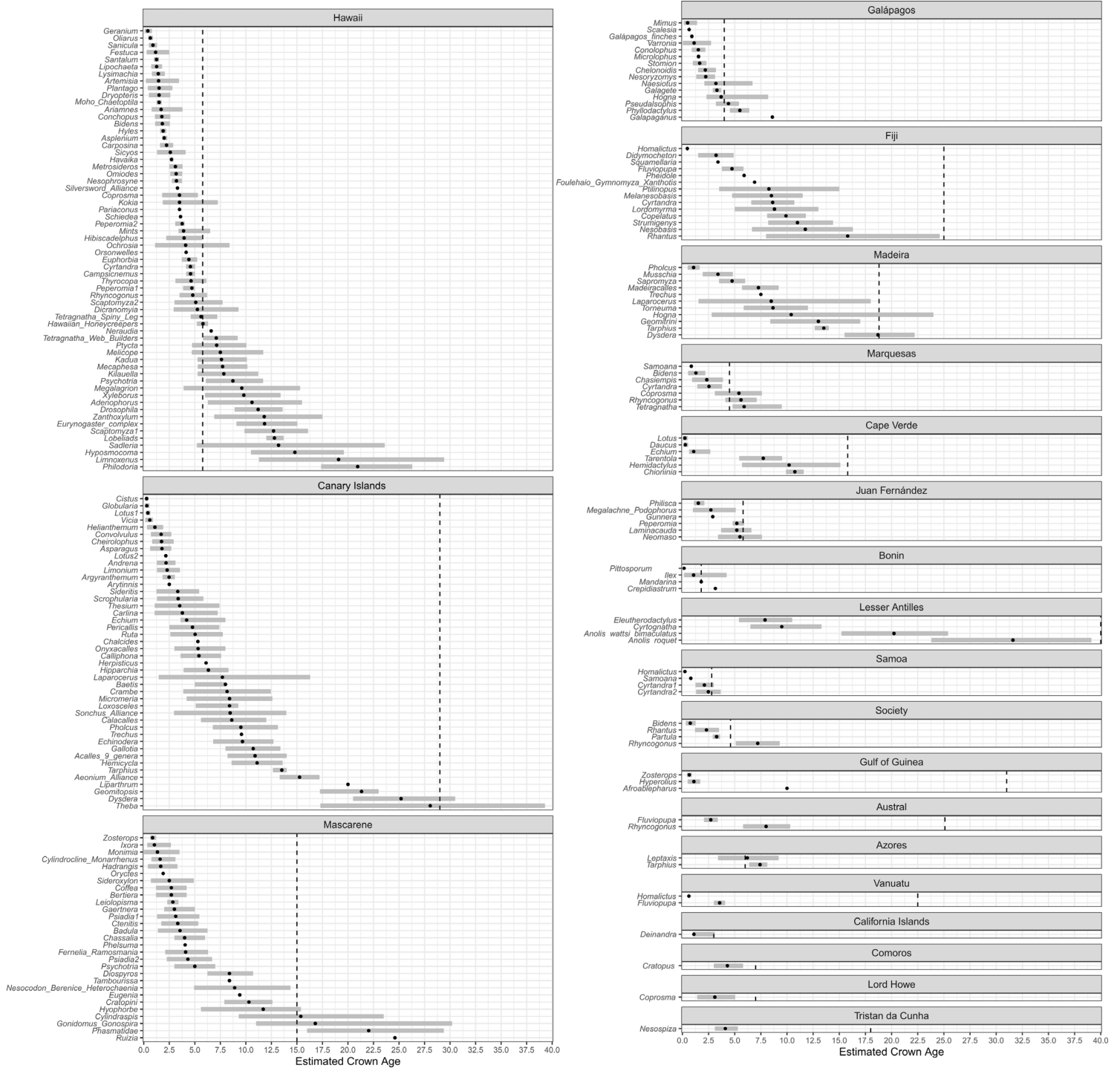


Figure.II.S1. Estimation of the time of colonization for all ROAs we recovered in our literature review and for which the information was available. For each archipelago, the dashed-line correspond to the age of the oldest current emerged major island. We can see that sometimes, and especially on Hawaii, the time of colonization is recovered as being oldest that the age of this oldest island.

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**Chapitre III : Patrons biogéographiques des
radiations évolutives sur les archipels
océaniques**

Résumé

Certainement en raison de la nature dynamique des îles volcaniques, les radiations évolutives sur les archipels océaniques (ROAs) ont toujours servi de modèles de choix pour comprendre les processus évolutifs et écologiques qui sous-tendent la diversification des espèces. Pourtant, les patrons de diversité émergeant des ROAs ont peu attiré l'attention des biogéographes, alors même qu'une évaluation des effets des facteurs géo-environnementaux sur la distribution des espèces de ces clades insulaires pourrait s'avérer cruciale pour notre compréhension des dynamiques de diversification au sein les archipels océaniques. Dans ce chapitre, nous avons effectué une analyse comparative combinant les valeurs de richesse spécifique par île de près d'une centaine de ROAs réparties dans plusieurs archipels océaniques et taxons. L'objectif de notre étude était double : (1) tester si les patrons de richesses spécifiques étaient influencés par les caractéristiques géo-environnementales des îles, et (2) tester si l'importance relative de ces facteurs sur les patrons de richesse différait entre les archipels et les taxons. Nous avons ainsi quantifié l'influence de l'aire, de l'âge géologique, de l'hétérogénéité environnementale et de l'isolement géographique des îles, et avons révélé leur effet significatif sur les patrons de richesse spécifique des ROAs, pour tous les taxons et archipels analysés. Plus important encore, nous avons démontré que la force de l'effet de ces facteurs était fonction de l'archipel et, dans une moindre mesure, du taxon auquel appartenait la ROA. Ce résultat indique donc que les ROA au sein d'un archipel donné sont principalement régies par la même dynamique géo-environnementale, en interaction avec les caractéristiques écologiques des espèces.

État de publication

Ce manuscrit est prêt à être soumis à *Peer Community In* après avoir apporté quelques dernières modifications, et après une relecture finale de tous les co-auteurs. La soumission devrait être effectuée d'ici la soutenance de thèse. Cinq co-auteurs ont participé à cette étude (les détails des noms et affiliations sont présentés en page suivante).

Online Supplementary Data

Les matrices de distributions des espèces utilisées dans ce chapitre sont disponible à cette URL : <https://drive.google.com/drive/folders/1RHrmW2BN1FrDU7U-B2DbnapCPysO1lsT?usp=sharing>

The biogeography of evolutionary radiations on oceanic archipelagos

Baptiste Brée¹, Thomas J. Matthews^{2,3}, José María Fernández-Palacios⁴, Christian Paroissin⁵, Robert J. Whittaker^{6,7}, Kostas A. Triantis⁸, François Rigal¹

¹ Université de Pau et des Pays de l'Adour (UPPA), Energy Environment Solutions (E2S), Centre National de la Recherche Scientifique (CNRS), Institut des Sciences Analytiques et de Physico-Chimie pour l'Environnement et les Matériaux (IPREM), Pau, France

² GEES (School of Geography, Earth and Environmental Sciences) and Birmingham Institute of Forest Research, University of Birmingham, Birmingham, UK

³ cE3c—Centre for Ecology, Evolution and Environmental Changes/Azorean Biodiversity Group/CHANGE—Global Change and Sustainability Institute and Universidade dos Açores—Faculty of Agricultural Sciences and Environment, Angra do Heroísmo, Azores, Portugal

⁴ Island Ecology and Biogeography Group, Instituto Universitario de Enfermedades Tropicales y Salud Pública de Canarias (IUETSPC), Universidad de La Laguna (ULL), La Laguna, Spain

⁵ Université de Pau et des Pays de l'Adour (UPPA), Energy Environment Solutions (E2S), Centre National de la Recherche Scientifique (CNRS), Laboratoire de Mathématiques et de leurs Applications de Pau (LMAP), Pau, France

⁶ School of Geography and the Environment, University of Oxford, Oxford, UK

⁷ Center for Macroecology, Evolution and Climate, GLOBE Institute, University of Copenhagen, Copenhagen, Denmark

⁸ Faculty of Biology, Department of Ecology and Taxonomy, National and Kapodistrian University of Athens, Athens, Greece

1. Introduction

Evolutionary radiations on oceanic archipelagos (hereafter ROAs) have served as invaluable models for understanding evolutionary and ecological processes underlying species diversification, due to the dynamic nature of volcanic islands (Losos & Ricklefs 2009, Gillespie 2015, Shaw & Gillespie 2015, Whittaker et al. 2023). Here we define a ROA as a monophyletic clade endemic to an oceanic archipelago that originates from a single colonisation event. Since the description of the Darwin's finches radiation more than 150 years ago (Darwin 1845), many ROAs have been described for multiple taxa, including the iconic Hawaiian Lobeliads (Givnish et al. 2009), the *Naesiotus* Galápagos land snails (Parent & Crespi 2006) and the *Echium* radiation in the Canary Islands (Böhle et al. 1996). In recent decades, our understanding of ROAs has significantly expanded thanks to the development of advanced molecular and analytical tools offering opportunities to track back ancestor origin (e.g., Keeley & Funk 2011), timing of colonisation and diversification (e.g., Church & Extavour 2022), intra-archipelagic colonisation patterns (e.g., Shaw & Gillespie 2015), as well as the mechanistic basis of speciation through adaptive and non-adaptive processes (e.g., Salces-Castellano et al. 2020).

Surprisingly, diversity patterns emerging from ROAs, although being the most impressive macroecological outcome of the diversification processes, have attracted little attention from macroecologists. Yet, an evaluation of the geo-environmental factors influencing the island species richness pattern emerging from radiating processes could prove crucial for our understanding of the diversification dynamics taking place in oceanic archipelagos (Economato et al. 2015). In other words, it might be informative to address why, within a given archipelago, some islands have accumulated more species than others during the radiation process. However, despite recent works on oceanic and other island-like systems (e.g., Roell et al. 2021, Wagner et al. 2014, Economato et al. 2015, Lim & Marshall 2017, Tao et al. 2021), evolutionary radiations have been rarely studied from this perspective.

Since the publication of the Equilibrium Theory of Island Biogeography (ETIB) by MacArthur & Wilson (1963, 1967), many strong and predictable relationships between island characteristics and species richness have been identified (Warren et al. 2015). Current models include island area and isolation (both past and current) as well as geological age and environmental heterogeneity as primary predictors (e.g., Whittaker et al. 2008, Weigelt & Kreft 2013, Barajas-Barbosa et al. 2020). Hence, we hypothesize that the same factors will also affect the species richness of a ROA in a given island (hereafter Island S_{ROA}). The positive relationship of species richness with island area (i.e., the

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island species-area relationship, ISAR) is probably one of the best-documented patterns in island biogeography (Triantis et al. 2012, Matthews et al. 2021). We may expect a positive ISAR for ROAs given that larger islands offer more ecological opportunities for speciation (Losos & Schluter 2000). However, few empirical ISARs have been previously reported for ROAs (e.g., Parent & Crespi 2006, Beatty et al. 2017). Isolation is expected to decrease the probability of dispersal to an island, leading to a negative correlation between island isolation and species richness (MacArthur & Wilson 1967). In the context of ROAs, it is primarily the way in which islands within an archipelago are isolated from one another that is expected to determine Island S_{ROA} patterns. Hence, as the ROA spreads throughout an archipelago, species will be more likely to colonise the less-isolated islands within the archipelago (Parent 2012). Note that while nearby islands might increase their Island S_{ROA} by colonisation, the comparative lack of isolation could also hamper between-island allopatric speciation by maintaining gene flow between populations (e.g., Aguilée et al. 2021). Island geological age might also play a fundamental role in controlling diversification on oceanic islands. Indeed, many factors affecting speciation, such as area, environmental heterogeneity and volcanic/geomorphological dynamism vary over time following the island geological ontogeny. This covariation of factors with age and its consequence for island diversity has been incorporated into the General Dynamic Model of oceanic island biogeography (hereafter GDM), with species richness predicted to rise and fall throughout the island ontogeny (Whittaker et al. 2008). The model also predicted that the ROA diversity at the scale of one island will vary with island geological age (Whittaker et al. 2008, Borregaard et al. 2017, Lim & Marshall 2017). Building on these predictions, we make the following hypotheses: (i) Island S_{ROA} is low on young and small islands due to insufficient time for *in situ* speciation and lack of ecological opportunities; (ii) when the island rises to its maximum elevation, increasing ecological opportunities foster speciation (adaptive phase); (iii) as the island erodes and subsides, increasing topographic complexity triggers within-island allopatry (non-adaptive phase) and (iv), as the island declines, Island S_{ROA} decreases until the island founders (Lim & Marshall 2017, Roell et al. 2021). Consequently, Island S_{ROA} should also scale positively with elevation and topographic complexity, with the relative importance of each depending on the adaptive nature of the ROA. It should be noted that a hump-shaped relationship with age is expected for archipelagos with the full range of island development stages. As this is not always the case, the relationship can be either positive or negative according to the range of ages involved.

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Given the numerous ROAs that have been described worldwide, it is likely that the contribution of the aforementioned factors in explaining Island S_{ROA} will vary considerably between them. A growing body of evidence has substantiated the prevalence of geo-environmental context in shaping diversification patterns of groups that radiated on oceanic archipelagos (Funk & Wagner 1995, Roman-Palacios & Wiens 2018). It is therefore reasonable to hypothesize that Island S_{ROA} patterns of ROAs belonging to the same archipelago should be governed by the same factors. On the other hand, the intrinsic biological characteristics of the ROA itself could also explain why some factors hold greater significance than others. For instance, elevation gradients have been suggested to drive diversification for several plants ROAs (Itow 1995, Baldwin & Sanderson 1998), for which a positive correlation between Island S_{ROA} and elevation is expected (See the Hawaiian Lobeliads, Givnish et al. 2009). However, such correlation is unlikely to hold for arthropods ROAs in Hawaii that appear to have diversified within narrow elevation belts (Hiller et al. 2019). In a general manner, the differences of dispersal abilities between taxa, for instance between birds and land snails, will also potentially greatly influence the resulting biogeographical patterns.

In this study, we carried out an extensive analysis using a unique dataset that combines Island S_{ROA} values for nearly one hundred ROAs distributed across several oceanic archipelagos and taxa. The aims of our study were twofold: (1) to test whether Island S_{ROA} scales as a function of island geo-environmental factors and (2) to test whether the strength of the effect of factors on Island S_{ROA} differed between archipelagos and higher taxon (specifically plants, invertebrates and vertebrates); higher taxon being used here as a coarse proxy for biological characteristics, as previously done in similar contexts (Triantis et al. 2012, Matthews et al. 2016, 2019). Specifically, we hypothesized that the island geo-environmental factors should scale with the Island S_{ROA} for most of the ROAs in a way similar to our predictions (i.e., positive relationship with area, elevation and topographic complexity, negative with isolation and hump-shaped with geological age). We also hypothesized that, overall, environmental heterogeneity and island geological age should be the predominant drivers of Island S_{ROA} , as they are both known to trigger diversification by offering ecological opportunities and time for speciation (Givnish 1997, Losos and Ricklefs 2009). Lastly, we anticipated that the variation in the contribution of factors would be explained equally by both archipelagos and taxon, as the effect of a factor on Island S_{ROA} stems from complex interactions between the dynamics of the archipelago and the biological characteristics of the ROA itself.

2. Materials & Methods

2. a. Data collection

We have restricted our study to oceanic archipelagos of exclusively volcanic origin that have never been connected to any other landmasses (Triantis et al. 2016). We excluded island systems composed of both volcanic islands and continental fragments such as the Philippines (Brown et al. 2013). We then established a list of criteria to determine whether a radiation should be included in our study. First, we selected ROAs with a minimum of 10 species, as ROAs with fewer species have less chance to statistically scale with potential predictors. Therefore, for ROAs that diversified across more than one oceanic archipelago, we treated each archipelago independently, only keeping the ones that harbour a monophyletic clade of at least 10 species (e.g., the *Tarphius* beetle radiation, Amorim et al. 2012). To facilitate comparison between archipelagos, we excluded clades that reach 10 species only at the scale of the meta-archipelago (e.g., South Pacific, Macaronesia). Second, the ROA needed to be distributed on at least six islands within a given archipelago. This threshold was set to allow for the inclusion of Hawaiian ROAs, as most of them are distributed on only the six main islands of the archipelago (i.e., on Kaua‘i, O‘ahu, Moloka‘i, Lāna‘i, Maui and Hawai‘i; see further details on the island selection procedure for Hawaii in **Appendix III.1**). As such, oceanic archipelagos such as Juan Fernández and the Mascarene, comprising two and three islands respectively, were discarded. Third, the monophyly of the ROA should have been validated by a phylogenetic reconstruction for at least three of the species known to belong to the ROA.

To guide our literature search, we first made a list of the major oceanic archipelagos that contain at least six main islands (**Table III.S1**) and then performed a targeted search of ROAs studies with ISI Web of Knowledge and Google Scholar indexing systems (last access December 2022), using archipelago names in combination with “island”, “phylog*”, “radiation” and “endemic” strings. Additionally, we also checked the references list of both the studies we retrieved and some key reviews on the topic (e.g., Shaw & Gillespie 2015, Gillespie et al. 2020, de La Harpe et al. 2017, Hembry et al. 2021, Florencio et al. 2022) to make sure that no relevant ROAs had been overlooked. An archipelago was then selected for our study when it harboured a minimum of five ROAs meeting our criteria; a threshold of five was required in order to make meaningful comparisons between archipelagos. Overall, a total of 95 ROAs distributed across four oceanic archipelagos were recovered from the literature, Hawaii being by far the most represented of the four with 53 ROAs, followed by the Canary Islands (29), Galápagos (7) and Fiji (6) (**Figure III.1A**). Further details on the discarded archipelagos and ROAs are provided in **Table III.S1** and **Table III.S2**.

For each selected ROA, we created an occurrence matrix with islands as rows and species as columns for all the species known to belong to the ROA in the focal archipelago (available in the **Online Supplementary Data** of this thesis), using the most recent taxonomy and sampling published works we found in the literature (**Table III.S3**). When the information was available, we included globally and locally (i.e., species extirpated from individual islands) extinct species. We also created two alternative versions of the matrix (1) by replacing species by their sub-species where appropriate, since some authors consider subspecies to represent more significant evolutionary units than species, particularity in the island context (Lasky et al. 2017), and (2) by sub-setting only the Single Island Endemic (SIE) species to account specifically for within-island speciation. The number of species per island was then calculated for each ROA separately to form the Island S_{ROA} vector. We made an exception for the *Naesiotus* radiation in the Galápagos, for which the Island S_{ROA} vector was retrieved directly from Roell et al. (2021). Note that all *Naesiotus* species are SIE. For each ROA, we recorded four distinct features: (1) the archipelago it belongs to, (2) the taxon it belongs to, (3) ROA size (i.e., number of constituent species) and (4) proportion of SIE. For the taxon classification, ROA were classified into three higher taxonomic ranks (i.e plants, invertebrates, and vertebrates). We did not use lower ranks in order to maintain sufficient sample sizes, but we recognized that variability within each taxon could add noise to the analyses. We also attempted to source from the literature whether the ROA is considered adaptive, non-adaptive, or both. Here, we followed authors point of views in the literature as well as the recent classification of Cerca et al. (2023), who used the relaxed definition of adaptive radiation proposed by Gillespie et al. (2020): a radiation is adaptive if there is an indication of ecological distinction among phenotypically distinct lineages. The full list of selected ROAs, along with their characteristics and original literature resources is available in **Table III.S3**.

2. b. Island characteristics

To assess the role of island characteristics on Island S_{ROA} , we gathered information for island area, environmental heterogeneity, geological age and isolation. We used the database of Global Administrative Areas (GADM: <http://www.gadm.org/version1>) to obtain high-resolution present coastlines for all islands included in our dataset. Island area (Area, km²) was then calculated for each GADM polygon in cylindrical equal area projection. Environmental heterogeneity was assessed using two distinct variables: (1) the maximum elevation, and (2) the variation of the rate of elevational change over the horizontal surface quantified as the standard deviation of slope (hereafter SDS). Maximum island elevation is used as a proxy of the climatic gradient while SDS quantifies the topographic complexity of an island by measuring the roughness of the terrain. The

island of Hawai‘i exemplifies the contrast between elevation and SDS, as it has the largest maximum elevation of the Hawaiian archipelago, but a comparatively low topographic complexity due to its young age (its surface is relatively smooth compared to older, more eroded islands; Barajas-Barbosa et al. 2020). The maximum elevation and SDS were calculated based on the 30-m digital elevation model (DEM) Advanced Land Observing Satellite (ALOS) from the OpenTopography Portal: <https://opentopography.org>). Intra archipelagic island isolation (hereafter isolation) was calculated using the neighbor index (*NI*) of Kalmar & Currie (2006), which postulates that the importance of an island as a potential source of colonisation to the focal island is proportional to its area and to the coast-to-coast distance that separates it from the focal island. Since the way *NI* is calculated can give more or less weight to area and distance, we identified three distinct configurations for *NI*: (1) no effect of area; proportional to distance, (2) proportional to area and distance (3) proportional to area and to the squared distance. We then calculated these three configurations for each ROA (taking into account only islands where the ROA species occurs) and selected the one that maximized the correlation with Island S_{ROA} (details of the calculations are given in **Appendix III.1**). Finally, we obtained the geological age of the islands from a literature search. All island characteristics and the associated literature sources are available in **Table III.S4**.

2. c. Statistical analyses

All the following statistical analyses were carried out within the R programming environment (R Development Core Team 2023).

2. c. 1. Univariate relationships

We first aimed to investigate univariate relationships between geo-environmental factors and Island S_{ROA} for each ROA separately. Prior to the analyses, area and elevation were \log_{10} transformed to approximate normality. Univariate relationships were assessed using generalized linear models (GLM) using a Poisson distribution (O'Hara & Kotze 2010). To account for overdispersion, GLMs were also run using a Negative Binomial distribution (Zuur et al. 2009). We evaluated each univariate relationship between geo-environmental factors and Island S_{ROA} in two ways. (1) We first classified each relationship as significant or not. Because a total of 95 GLMs were performed for each factor, we also corrected the P-values using the False Discovery Rate method (FDR, Benjamini & Hochberg 1995) to guard against inflation of Type-I errors. Applying such a correction could, however, hamper the detection of important but less strong relationships due to the small number of data points (Borges & Hortal 2009). Therefore, both results before and after the FDR correction were presented. (2) We calculated the standardized β coefficient for each relationship as a normalized measure of the strength of the effect of each individual factor on Island

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S_{ROA} . The higher or lower the value of the coefficient, the greater the positive or negative effect respectively. To evaluate the presence of a hump-shaped relationship between age and Island S_{ROA} , we performed the GLM with age and its quadratic term (age^2) and considered the relationship as hump-shaped when it met the three following criteria: (1) the sign of the slope is positive for the linear term and negative for the quadratic term, (2) the two slopes are significant, and (3) the inflection point predicted by the fitted model is present within the range of age values contained in the data (Hortal et al. 2009). Finally, for area exclusively, we also fitted the log–log model (log-transformed Island S_{ROA} against log-transformed Area, Triantis et al. 2012) to extract the slope of the relationship (i.e., commonly referred to as the z values) for comparison with published ISAR z values.

To provide an overview of our univariate GLMs, we summed the number of significant positive or negative univariate relationships across archipelagos and taxon for each individual geo-environmental factor. For age + age^2 , we simply counted how many ROAs presented a hump-shaped pattern meeting our three criteria. Next, for each factor, we ran a multiple regression to test whether (i) archipelago, (ii) taxon, (iii) the proportion of SIEs and (iv) the size of the ROA can explain the variation in the standardized β coefficient. Note that we did not include in the model whether the ROA was adaptive or not since we were unable to retrieve this information for roughly a third of the ROAs (See discussion). Initially, we did not include any interaction terms, as the variable taxon and archipelago were both highly unbalanced. Therefore, to test for interactions, we reduced our dataset to only Hawaii and the Canary Islands and to plants and invertebrates in order to obtain a more balanced design. We then reran the multiple regressions as detailed above. We only tested for an interaction between archipelago and taxon because preliminary tests for all the other interactions did not indicate significance. Multiple regressions were fitted using ordinary least squared models (OLS). For the specific case of age + age^2 , we used a binomial GLM to test whether the presence or absence of a hump-shaped pattern could be explained by archipelago, taxon, the proportion of SIEs and the ROA size. All models were subsequently reduced using backward selection to obtain a final model comprising only significant terms.

2. c. 2. Global models

Given that none of the factors is expected to fully account for Island S_{ROA} variation on its own, and that a combination of several (if not all) factors is probably necessary (Roell et al. 2021), we ultimately carried out a global analysis to identify the best set of predictors for Island S_{ROA} across ROAs. Analyses were performed using generalized linear mixed models (GLMMs) with a Poisson distribution, or a negative binomial distribution when overdispersion was detected. The GLMMs were implemented with all geo-environmental factors [$\log_{10}(\text{area})$, age, $\log_{10}(\text{elevation})$, SDS and isolation] including the quadratic term for age to account for potential hump-shaped relationships (i.e., six predictors). We implemented a GLMM for each individual archipelago. For Hawaii and the Canary Islands only (as these were the only archipelagos with sufficient sample size for this analysis), we also reran the GLMMs for plants and invertebrates subsets. Note that we did not run a global model encompassing all ROAs since our goal was not to find common predictors across all archipelagos and taxa but rather to determine if there was a distinct archipelagic or taxonomic signature in how geo-environmental factors contribute to explain Island S_{ROA} .

We constructed each GLMM by combining all the Island S_{ROA} values belonging to an archipelago (or a taxon within an archipelago) in such a way that if, for a given archipelago of 10 islands, we have recovered 5 ROAs and each has an Island S_{ROA} value on each island, the length of the response variable in our GLMM will be 50. Each geo-environmental factor was then repeated as many times as there were ROAs. ROA identity was added as the random intercept as well as a random slope for the six predictors to let the intercept and the slope of the relationships to vary between ROAs. Because the same island appears multiple times in the model, island identity was also included as a separate random effect (intercept only). Note that our factors were somewhat correlated between each other (**Figure III.S1**), but collinearity shortcomings were overcome by evaluating and comparing models containing all possible combinations of variables (Patiño et al. 2013). The GLMMs were fitted using the R package *glmmTMB* (Brooks et al. 2017). All factors were scaled to zero mean and unit variance to improve model convergence (Harrison et al. 2018). We used a top-down strategy for model selection (Zuur et al. 2009). First, the best random effect structures, with all fixed effects considered, were selected using the function *buildglmmTMB* in the R package *buildmer* (Voeten 2023) (See **Appendix III.1** for further details on the procedure). Second, we employed an information theoretic approach to determine the best set of fixed effects explaining Island S_{ROA} by fitting all possible models and calculating Akaike's information criterion (AIC) corrected for small sample size for each model; the best model being the one with the smallest AICc (Anderson & Burnham 2002). All models with a $\Delta AICc$ value < 2 (the difference between each

model's AICc and the lowest AICc) were considered as receiving equal statistical support (Anderson & Burnham 2002). The selection procedure was performed with the function dredge in the *MuMIn* package (Bartoń 2023) specifically customized to include age² in a model only if age was also included. For each LMM, both the conditional R²c (all factors, including the random effects) and marginal R²m (fixed factors only) were computed with the *r.squaredGLMM* function. Finally, we derived a measure of variable importance for each predictor using AIC-weighted standardized regression coefficients (Weigelt et al. 2016; **Appendix III.1**). Residuals of the best models were surveyed in order to detect deviations from normality and homoscedasticity and to identify outliers using the R package *DHARMA* (Hartig 2018).

2. c. 3. Additional analyses

We undertook all the aforementioned analyses using the alternative presence-absence matrices that included subspecies included in order to assess the robustness of our results with regard to the choice of taxonomic unit. Moreover, recent studies have demonstrated that past archipelago configurations during the Pleistocene sea levels fluctuations have influenced the distribution and evolution of insular biota (Weigelt et al. 2016, Norder et al. 2018). It is therefore reasonable to assume that the present-day island S_{ROA} values might have been shaped by past archipelago configurations. To test this, we used an intermediate sea level of -85 m – which is the most frequent long-term sea level stand of the Pleistocene – and the R code provided by Norder et al. (2018) to calculate the paleo-area and paleo-Neighbor Index for all. Analyses were then rerun using the new paleo-variables (area and isolation). Geological age was also added to the analysis. When a group of islands fused into a larger island at -85 m, we kept the oldest age of all present islands included in the past island. Elevation and SDS were not included due to the absence of reliable paleo environmental heterogeneity data.

3. Results

All the following results were also obtained with the subspecies included. Since no specific differences were noticed, we only present below the results obtained without considering subspecies. Detailed results including subspecies are provided in **Table III.S5 to III.S8** and **Figure III.S2**.

3. a. Radiation characteristics

The 95 selected ROAs covered a great taxonomic range including 30 orders and 64 families (**Figure III.1B** and **Table III.S3**). They were largely dominated by invertebrates (60%: 58 ROAs) and plants (37%: 35 ROAs), with only two bird- (Hawaiian Honeycreepers and Galápagos finches) and one reptile- radiation (Galápagos *Chelonoidis* tortoises) (**Figure III.1B**). Overall, 77% of ROAs had fewer than 50 described species (median = 22). Conversely, only six had a hundred or more species, five being in Hawaii and one in the Canary Islands (the *Laparocerus* beetles, 182 species). Overall, the difference in ROA size between archipelagos was marginally significant (Kruskal-Wallis, $H = 8.226$, $P = 0.04$) with Hawaiian ROAs being significantly larger than the ones in the Galápagos (Post-hoc Dunn test $P = 0.02$). Most ROAs constituent species were SIE (median = 70%) (**Figure III.1C**, **III.1D**) and this proportion did not vary significantly between archipelagos (Kruskal-Wallis, $H = 3.962$, $P = 0.265$).

Large ROAs had a higher proportion of SIEs than smaller ones (Spearman Rank correlation $\rho = 0.44$, $P < 0.001$; **Figure III.S3**), but when analyzed for each archipelago separately, the relationship remained significant only for Hawaii ($\rho = 0.62$, $P < 0.001$). For both Hawaii and the Canary Islands, where comparisons between plants and invertebrates were possible (**Figure III.1C**, **III.1D**), we found that invertebrates ROAs in Hawaii were on average larger and with a higher proportion of SIEs than plants ROAs (Wilcoxon test, $P = 0.002$ and $P = 0.025$ respectively), while no specific differences were found for the Canary Islands (Wilcoxon test, $P = 0.702$ and $P = 0.392$ respectively).

3. b. Univariate relationships between geo-environmental factors and island S_{ROA}

The results of the univariate GLMs revealed significant relationships between Island S_{ROA} and elevation for about 45% of the ROAs, followed by isolation (40%), area (39%), SDS (14%) and age (12%) (**Figure III.2A**). Notably, most of the observed significant relationships for area, elevation, SDS and isolation had a sign aligned with our predictions (see examples in **Figure III.2B**). Specifically, 100% of the significant relationships with area, 98% with elevation, and 70% with SDS were positive, while 92% of the significant relationships with isolation were negative.

Regarding the effect of age, for which both positive and negative relationships can be expected, eight of the 11 significant relationships (72%) were positive. Additionally, 13 ROAs (14%) exhibited a hump-shaped relationship between age and Island S_{ROA} meeting our three criteria. Similar trends were obtained after FDR correction of the P -values, but with a substantial decrease in the proportion of significant relationships from one-third to twice as low (**Figure III.2A**). This indicates that many initially significant relationships were only marginally significant.

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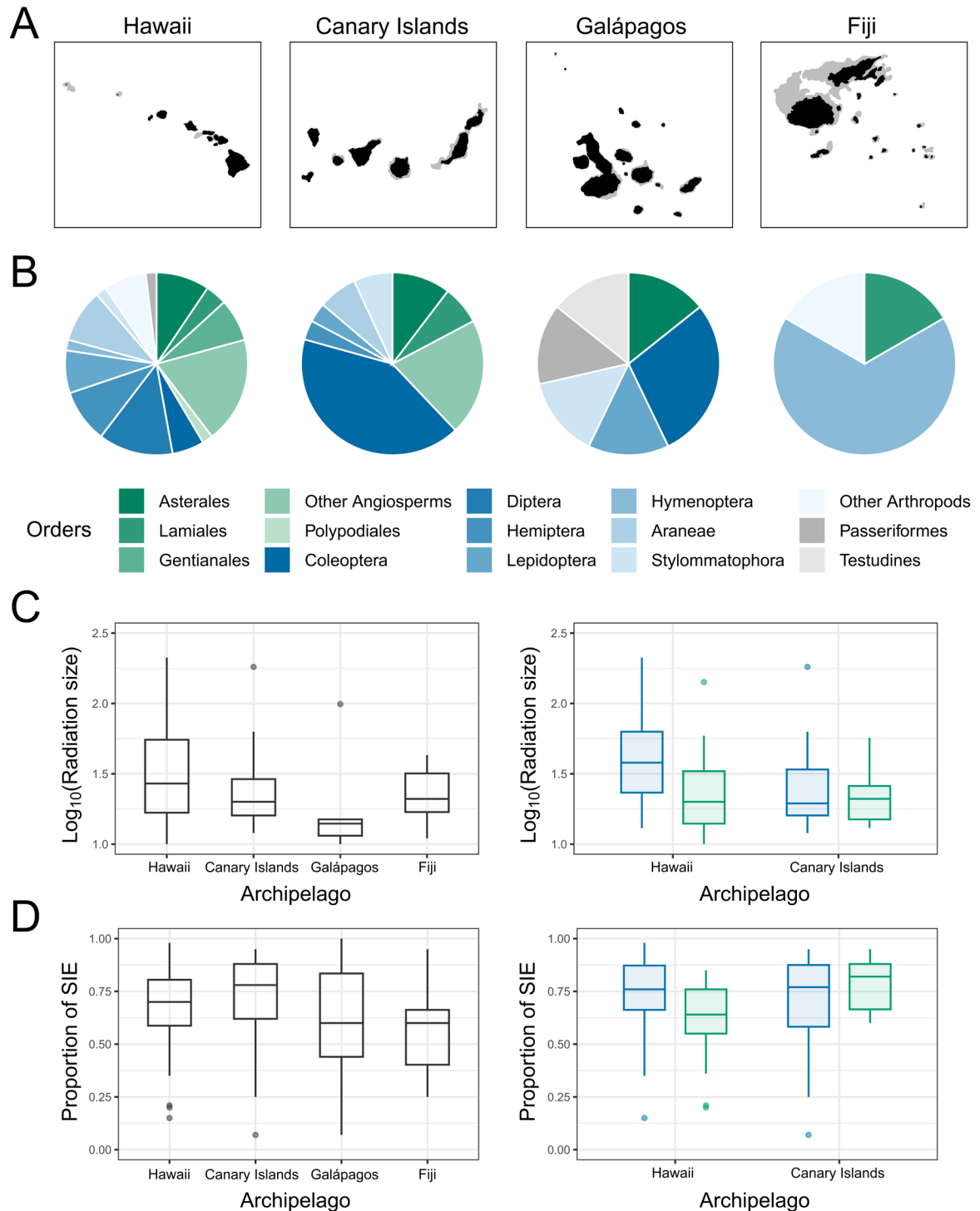


Figure III.1. A) Maps of the four selected archipelagos. The current islands are shown in black while the paleo-islands at -85m are depicted in grey. B) Pie charts showing the proportion of the main orders to which the radiations belong for each archipelago. C) Distribution of the size of the radiation (\log_{10} -transformed number of species, without subspecies) for each archipelago (left panel) and between invertebrates (blue) and plants (green) for both Hawaii and Canary Islands (right panel). D) Distribution of the proportion of SIEs for each archipelago (left panel) and between invertebrates (blue) and plants (green) for both Hawaii and the Canary Islands (right panel).

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Table III.1 presents the results of the multiple regression examining the effect of archipelago, taxon, ROA size and proportion of SIEs on the strength of the effect of the geo-environmental factor on Island S_{ROA} , here quantified by the standardized β coefficient. Notably, archipelago emerged as the primary factor explaining the strength of the effect of all factors. Post-hoc tests revealed that area and age had a greater effect on Fiji's Island S_{ROA} , while the effect of elevation exhibited greater strength on Island S_{ROA} for both the Canary Islands and Fiji. Additionally, most of the hump-shaped relationships meeting our criteria were found for Canary Islands ROA, and the effect of isolation on Island S_{ROA} was more pronounced for this archipelago, with all relationships being negative. In contrast to the archipelago, we only found one marginal but significant effect of taxon on the standardized β coefficient of SDS.

Table III.1 Results of the multiple regressions testing whether the effect of the geo-environmental factors on the radiation S_{ROA} can be explained by archipelagos, taxon, radiation size and proportion of SIE. The effect of a given geo-environmental factor on a given S_{ROA} is quantified by its standardized β coefficient for the factors area, age, elevation, SDS and isolation while the effect of age + age² is coded as binary variable with 1 if S_{ROA} follows a hump-shaped relationship with Age according to our three criteria (See main text) and 0 if not. All models were fitted with OLS except for the age + age² model, for which a GLM with binomial distribution was used. The R^2 is given for each model and the P-value is provided for each significant predictor remaining in the model after backward elimination procedure. Analyses were initially performed for all radiations without testing the interaction between archipelago and taxon because of a too unbalanced design. The models with the interaction term were performed for a subset of the data including only the radiations of Hawaii and the Canary Islands and for plants and invertebrates.

	Factors	Archipelago	Taxon	Size	Proportion SIE	A x T	R2
<hr/>							
All radiations							
<hr/>							
<i>z values</i>							
	Area		0.019		0.030 (+)	-	
	Area	0.005			0.004 (+)	-	0.222
	Age	<0.001				-	0.257
Standardized β coefficient	Age + Age ²	0.009				-	0.137
	Elevation	<0.001		0.008 (+)		-	0.204
	SDS	<0.001	0.008	0.025 (+)		-	0.372
	Isolation	<0.001		0.007 (-)		-	0.239
<hr/>							
Subset							
<hr/>							
<i>z values</i>							
	Area		0.003				
	Area		0.009				0.118
	Age					0.001	0.184
Standardized β coefficient	Age + Age ²	0.007					0.112
	Elevation	0.005		0.025 (+)		0.002	0.242
	SDS	0.009	0.011	0.001 (+)			0.247
	Isolation	<0.001		0.010 (-)			0.242

Interestingly, the Island S_{ROA} of larger ROAs exhibited stronger fits with elevation, SDS and isolation (**Table III.1**), while the effect of area on Island S_{ROA} was stronger for ROAs with higher proportions of SIE. Similar outcomes were obtained when we conducted the multiple regressions with a more balanced subset including only Hawaii, the Canary Islands, plants and invertebrates. Furthermore, this last analysis allowed us to detect a significant interaction between archipelagos and taxon for age and elevation, supporting the fact that the difference between archipelagos in the effect of these two factors was taxon dependent. Lastly, the z value of the ISAR was found to range from - 0.19 to 0.93 (median = 0.25) and was only marginally explained by taxon and the proportion of SIEs (**Table III.1**); the latter effect becoming non-significant when the analysis was repeated for the subset analysis.

3. c. Testing the relative contribution of the geo-environmental factors in explaining Island S_{ROA} across archipelago and taxon

Results of the GLMMs are presented in **Table III.2** and **Figure III.3**. Further details including the best random structures and family distribution are given in **Table III.S5**. For Hawaii, the model selection procedure yielded four best models, all recovering a positive effect of area and SDS (**Table III.2**). The averaged R^2_m of the best models (fixed effects only) accounted for approximately 40% of the variation in Island S_{ROA} (**Figure III.3**). For the Canary Islands, three best models were recovered, each including a hump-shaped relationship with age and a strong negative effect of isolation (**Table III.2**). A positive effect of elevation was also included in the best model but disappeared in the next two in favour of area. Collectively, these best models had an average R^2_m of 32% (**Figure III.3**). Galápagos exhibited high model uncertainty, yet most of the best models featured a positive effect of elevation. However, these models explained only a small fraction of the variation in Island S_{ROA} ($R^2_m = 18\%$). For Fiji, two best models were retrieved, both including a positive effect of age and elevation and displaying an average R^2_m of 63%. Importantly, for most archipelagos and subsets, the variance captured by the random structure was high (**Figure III.3**), ranging from 18% for Fiji to 54% for Galápagos. When we performed the analysis solely on plants ROAs, the best models identified for Hawaii highlighted hump-shaped patterns with age associated with a positive effect of elevation. Similarly, for the Canary Islands, a positive effect of elevation emerged, along with a negative effect of isolation and a less pronounced hump-shaped age pattern. Both Hawaii and Canary Islands' best models for plants ROAs exhibited R^2_m values of 58% on average.

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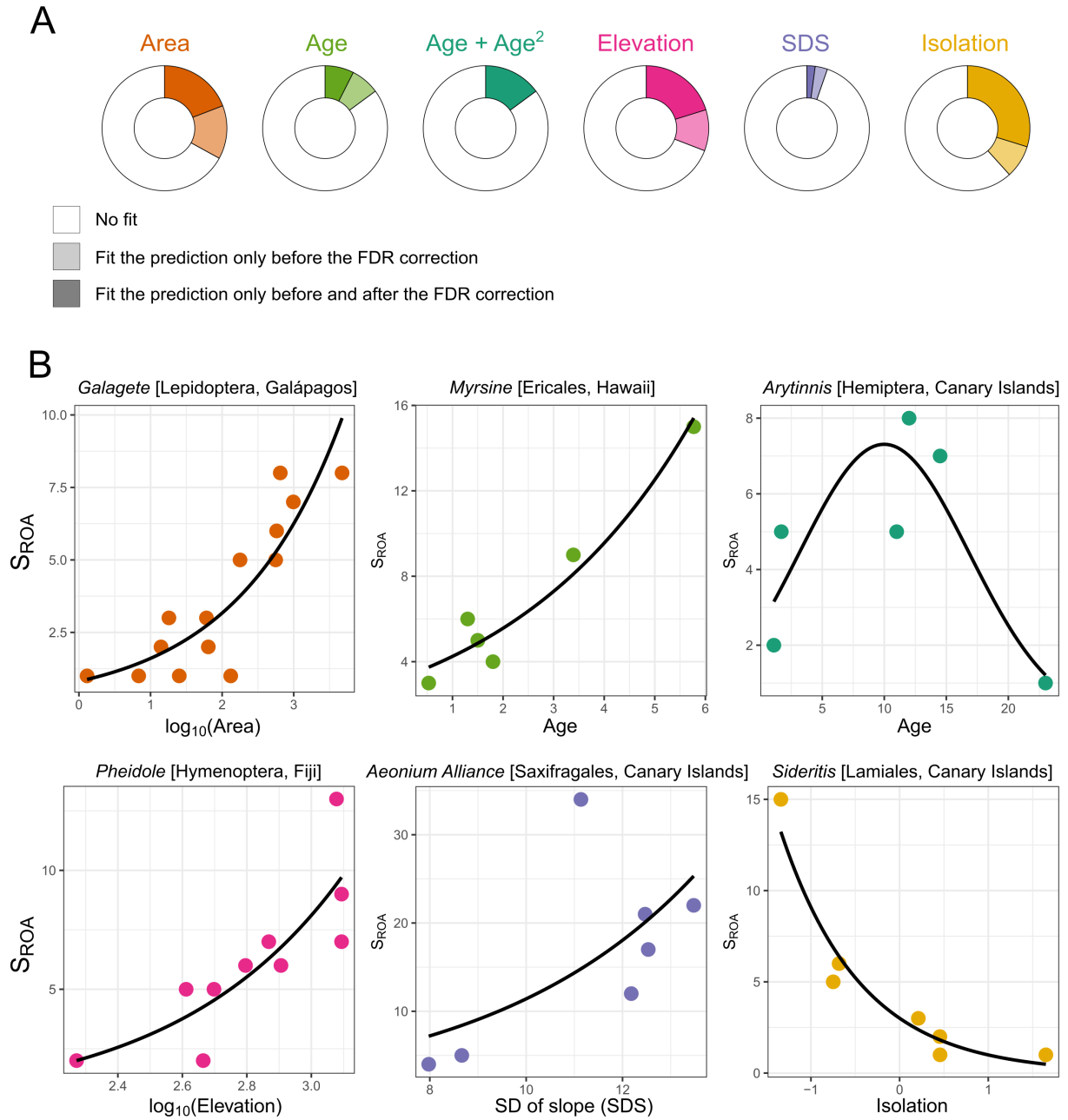


Figure III.2 A) Summary of the results of the univariate GLMs between S_{ROA} and each geo-environmental factor separately. Each pie chart illustrates the proportion of radiations having a significant relationship between island S_{ROA} and the factor. The colored part of the pie chart represents the proportion of significant relationship before the FDR correction, while the transparent part shows the proportion after FDR correction. Specifically for age + age², only the proportion of radiations having a hump-shaped relationship with age that met our three criteria is shown. B) Selection of significant relationships between S_{ROA} and the geo-environmental factors. One radiation was selected for each factor namely log₁₀(area), age, age+age², log₁₀(elevation), SDS and isolation. Dots indicate islands and the black curves show the fitted values extracted from the Poisson / Negative binomial generalized linear model. All relationships were significant at 5% after the FDR correction. Plots for all ROAs and all factors are available in **Figures III.S4 to III.S15**.

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Regarding the invertebrates data subset, the best models identified for Hawaii underlined the importance of area, elevation and SDS, while for the Canary Islands, results were more uncertain, although a dominant hump-shaped pattern with age and a negative effect of isolation were evident. The best models for Hawaii still explained a high proportion of the variation in Island S_{ROA} ($R^2_m=58\%$) contrasting with the 39% captured by the best models of the Canary Islands.

Lastly, the analyses carried out with archipelago paleo-configurations revealed substantial differences with the main analyses (**Table III.S5, III.S9, Figure III.S16**), although comparisons and SDS were not included in the paleo models. Overall, we noted that area and the hump-shaped relationship with age became dominant in all the best models identified for the four archipelagos. We also observed an abrupt decrease in the effect of isolation for the Canary Islands, which contrasts with our main results. We also observed a sharp reduction in the variance explained by the fixed effects, with most R^2_m values being half those from the main analyses (**Figure III.S16**).

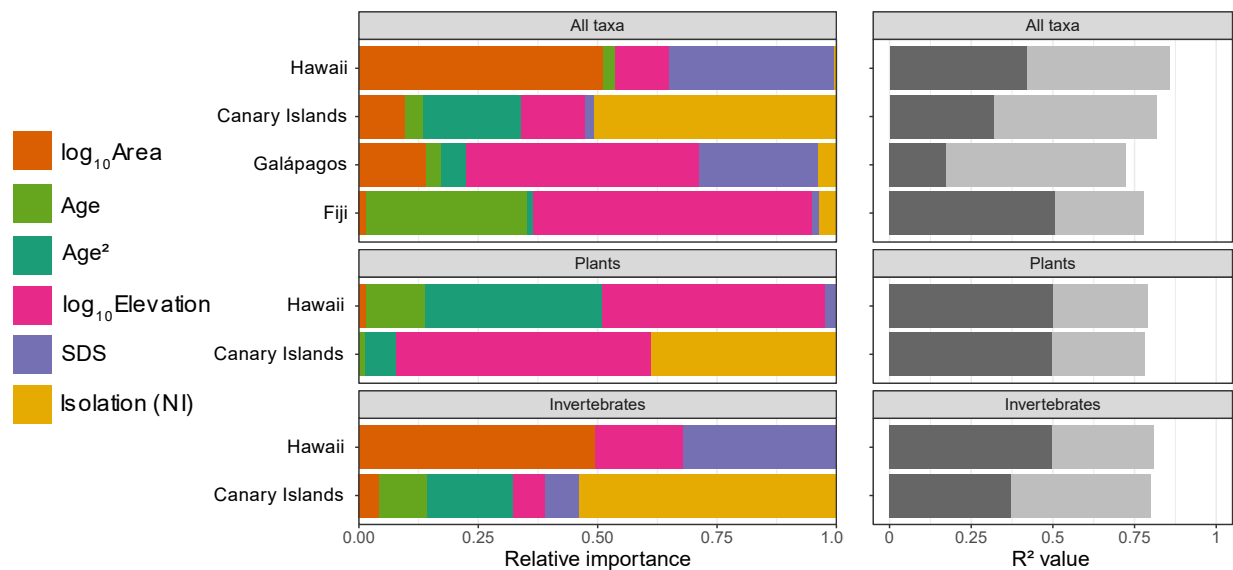


Figure III.3 Left panels: relative importance of each fixed effect as predictor of the S_{ROA} for each archipelago, and for the plants and invertebrates subsets separately. Results for the plants and invertebrate subsets are given only for Hawaii and the Canary Islands, for which enough radiations were available for each taxon in each archipelago (See **Table 2** for detailed results). Right panel: decomposition of the variance explained by the best model(s) (conditional R^2_c) into its components assigned to the fixed (marginal R^2_m , dark grey) and random effects ($R^2_c - R^2_m$, light grey) for each archipelago, and the plants and invertebrates subsets for Hawaii and the Canary Islands (mean R^2 of all best models).

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Table III.2 Results of the Generalized Linear Mixed Models (GLMM) analyses testing the effect of the geo-environmental factors on S_{ROA} variation simultaneously for all the radiation in each archipelago. Results for the plant and invertebrates subsets are given only for Hawaii and the Canary Islands for which enough radiations were available in each taxon. Model selection was performed using AICc. The best-fit models ($\Delta AICc < 2$) are presented. For each best model, we provide the coefficient of the factors included in the model, the degree of freedom (df), the AICc, $\Delta AICc$ and $wAICc$. For each model, the significance of each factor was estimated using an analysis of variance. Significant factors are marked in bold. It should be noted that the calculation of P -values for fixed effects in GLMMs remains controversial. Further details including the best random structure, and family distribution are given in **Table III.S5**.

	Area	Age	Age2	Elevation	SDS	Isolation	df	AICc	$\Delta AICc$	$wAICc$	
Hawaii	0.480			0.201	0.346		15	1935.429	0	0.253	
	0.601	-0.120			0.394		15	1936.681	1.252	0.135	
	0.663				0.381		14	1937.039	1.61	0.113	
	0.474			0.197	0.343	-0.025	16	1937.045	1.616	0.113	
Canary Islands		0.116	-0.131	0.207		-0.305	12	943.841	0	0.245	
	0.134	-0.043	-0.159			-0.406	12	944.115	0.274	0.214	
	0.123	-0.070	-0.157		-0.072	-0.433	13	945.565	1.724	0.104	
Galápagos				0.354	-0.313		6	335.752	0	0.103	
				0.336	-0.298	-0.085	7	336.261	0.509	0.08	
				0.366			5	336.92	1.168	0.057	
		0.053	-0.093	0.383	-0.277		8	336.961	1.208	0.056	
				0.347		-0.089	6	337.212	1.46	0.05	
	0.470	0.047	-0.116				7	337.27	1.518	0.048	
		0.077	-0.095	0.409			7	337.454	1.702	0.044	
Fiji		0.380		0.651			7	249.079	0	0.388	
		0.345		0.648		-0.103	8	250.303	1.224	0.21	
Plants		0.155	-0.462	0.544			10	708.403	0	0.246	
	Hawaii	0.129	-0.393	0.529	0.074		11	708.655	0.252	0.217	
		-0.086	0.164	-0.482	0.625		11	709.86	1.457	0.119	
	Canary Islands			0.384		-0.304	5	311.312	0	0.231	
		-0.032	-0.146	0.377		-0.223	7	312.823	1.511	0.109	
Invertebrates	Hawaii	0.522		0.308	0.374		15	1178.358	0	0.263	
		0.793			0.428		14	1180.238	1.88	0.103	
			0.149	-0.130	0.142		-0.334	11	629.542	0	0.172
		0.090	0.033	-0.147			-0.409	11	629.645	0.103	0.163
	Canary Islands	0.077	0.015	-0.144		-0.117	-0.443	12	630.414	0.872	0.111
			0.114	-0.129	0.120	-0.115	-0.379	12	630.416	0.874	0.111
			0.053	-0.130		-0.150	-0.498	11	630.632	1.09	0.1
			0.083	-0.129			-0.467	10	631.055	1.513	0.081

4. Discussion

Despite the large amount of work performed on ROAs in recent decades, little research has focused on the emergent diversity patterns, with the few studies that have done so focusing on the effect of island area and geological age (e.g., Lim & Marshall 2017, Gillespie & Baldwin 2010). To our knowledge, the land snail radiation of *Naesiotus* in the Galápagos is the only ROA for which the effect of multiple drivers of Island S_{ROA} have been tested (e.g., Parent & Crespi 2006, Roell et al. 2021). In this study, we examined how the Island S_{ROA} of almost a hundred ROAs scales with five major biogeographic factors (area, age, elevation, topographic complexity and isolation), and whether the magnitude of their effects was archipelago or taxon specific. Our results revealed that, overall, island geo-environmental features are strong drivers of Island S_{ROA} and that the unique geo-environmental settings of each archipelago dictate the species accumulation processes of clades that radiated into it, with a low to moderate effect of the taxon. As such, the results presented here have important implications for our understanding of the diversification processes in oceanic archipelagos.

4. a. An overview of the selected ROA

Our dataset reveals a clear dominance of ROAs from Hawaii and the Canary Islands in the literature. This was somewhat expected since these two archipelagos are known to host a tremendous number of successful ROAs (e.g., Machado et al. 2017, Hembry et al. 2021, Cerca et al. 2023). Both Hawaii and the Canary Islands are also two of the best studied volcanic island systems in the world, both in terms of their natural history and the phylogenetic origin of their biota (Juan et al. 2000, Emerson 2002). On the other hand, the Galápagos, which are more ecologically uniform (Naciri & Linder 2020), are home to smaller ROAs, many of which number fewer than 10 species (Parent et al. 2008). The few ROAs retrieved for Fiji can be explained by the overall less advanced phylogenetic understanding of Fijian endemic groups compared to the other three archipelagos (Rudbeck et al. 2022). Interestingly, we documented a very high proportion of SIEs overall (median 70%), confirming the role of within-island speciation and, in turn, the role of island environmental heterogeneity (both available ecological space and topographic complexity) in driving the radiation process (Cowie & Holland 2008). The study of evolutionary radiations invariably raises the question of whether they are adaptive or not. As an attempt to classify our 95 ROAs as adaptive or not, we followed the recent classification proposed by Gillespie et al. (2020) and found that half of our ROAs can be classified as adaptive (52%). For one third, no indication of the speciation mode was recovered and only five ROAs were classified as non-adaptive by the authors (i.e., the two *Cyrtandra* radiations in Hawaii and in Fiji, the *Pholcus* spider radiation in

Canary Islands and the *Homalictus* and *Nesobasis* radiations in Fiji). We should, however, be very cautious with this result, as the lack of consensus on what an adaptive radiation actually prevents us from drawing robust conclusions on this issue (Hernández-Hernández 2019, Gillespie et al. 2020, Cerca et al. 2023). In particular, we found that discussions of potential non-adaptive processes are rare, even though they could potentially explain the bulk of ROAs speciation events (see Dimitrov et al. 2008, Benavides et al. 2008, Groom et al. 2013, Vitales et al. 2015, Chiba & Cowie 2016, Whittaker et al. 2023). A recent study on the plant trait diversity on the island Tenerife in the Canary Islands even suggested that the vast majority of plants radiations on this archipelago might be non-adaptive (Barajas-Barbosa et al. 2023).

4. b. Island geo-environmental factors are strong drivers of island S_{ROA}

Our study confirms our predictions that the selected geo-environmental factors were overall good predictors of Island S_{ROA} , but they were not all equally important. Indeed, about 75% of all the significant relationships recovered were attributed, in decreasing order, to elevation, isolation and area. As importantly, the signs of these relationships were in line with our predictions, i.e., positive for area and elevation and negative for isolation. In this respect, these results corroborate what is usually reported in studies on island species richness of larger groups (vascular plants, Kreft et al. 2008; spiders, Cardoso et al. 2010; birds, Kalmar & Currie 2006). The predominance of elevation partially confirmed our prediction that both environmental heterogeneity and age should explain Island S_{ROA} . To our knowledge, the effect of elevation on species richness remains poorly tested in the context of ROAs (but see Parent & Crespi 2006). The importance of elevation in our results implies an important role for adaptive processes (e.g., Ricklefs and Lovette 1999). Several radiated species (mostly plants) have developed into locally adapted ecotypes in response to elevational gradients, such as Lobeliads in Hawaii or the *Aeonium* Alliance and *Micromeria* in Canary Islands, all three showing a significant positive relationship between Island S_{ROA} and elevation. However, we did not find any general association between adaptive radiation and elevation, since of the 14 ROAs classified as adaptive in the Canary Islands, 9 showed a significant relationship with elevation, whereas in Hawaii the relationship was significant for only 10 out of 29. Moreover, elevation might not be exclusively associated with adaptive processes. For example, high elevation zones can provide refugia during periods of climate change, allowing relict populations of ancient species to persist (Irl et al. 2015). Furthermore, elevation can also act as a surrogate of topographic complexity, as high elevation is a prerequisite for the presence of a complex landscape structure promoting within island allopatry (Brown et al. 2006). For SDS, the absence of a significant effect on Island S_{ROA} was somewhat anticipated, since its effect seems to

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become apparent only after controlling for other factors such as area or age, as reported by Roell et al. (2021) and Barajas-Barbosa et al. (2020).

Contrary to our prediction, age was found to not scale with Island S_{ROA} for most of the ROAs, neither through a linear nor a hump-shaped relationship. We cannot exclude the possibility that the lack of hump-shaped relationship (only 14% of all ROAs) is due to our small samples ($n_{islands}=6$ or 7). Such small samples hinder our ability to identify significant effects, particularly when more than one predictor is tested (age + its quadratic terms), due to the low degree of freedom. The weak effect of age echoes a recent study by Carey et al. (2023) in which the authors suggest that, for islands in volcanic hotspot archipelagos, accounting for the effect of environmental heterogeneity on species richness is best achieved using direct measurements rather than using island age as a proxy. In addition, our results may also show the limitation of assigning a single age to an island, given that many of the oceanic islands we considered are formed by different basaltic shields of varying ages (Irl et al. 2015, Otto et al. 2016). This calls into question the idea that the number of species on an island is a simple function of its effective biological age, as implicitly postulated by the GDM.

Although not dominant in our univariate analyses (one third of significant relationship with Island S_{ROA}), our results show that island area remains an important biogeographic factor for diversification on islands (Losos & Schluter 2000, Triantis et al. 2008). As not only Island S_{ROA} , but also speciation rate is expected to increase with island area, Losos & Schluter (2000) postulated that the z value of systems where speciation prevails should be steeper than for classic archipelagic ISARs (Rosenzweig 1995). Regarding this last point, we found two different but not necessarily contrasting patterns. On the one hand, we reported a huge variance of z ranging from 0.01 to 0.93 for the positive values and thus encompassing, although much expanding, the typical range of 0.2-0.4 for archipelagic ISARs (MacArthur & Wilson 1967, Rosenzweig 1995, Triantis et al. 2012). On the other hand, we have also shown that ROAs with a high proportion of SIEs tend to have a steeper z value (**Table III.1**). This positive SIE effect on z values as been previously detected at the scale of higher taxonomic groups (Triantis et al. 2008) and would mean that higher within-island speciation rate could therefore lead to steeper ISARs in the case of ROA as well. However, the relationship between the proportion of SIEs and z was only marginally significant. Therefore, much of the variation in z might instead be attributed to ecological disparities between ROAs, as suggested by the weak but significant effect of taxon on z values (**Table III.1**). Further work is needed to properly assess the characteristics of ROA ISARs.

4. c. Drivers of the effect of the geo-environmental factors on island S_{ROA} : Archipelago takes (almost) all

One of the most notable findings of our study is that the strength of the effect of geo-environmental factors on Island S_{ROA} depends on the archipelago to which the ROA belongs to and, to a lesser extent, to its taxonomic group (**Table III.1, III.2** and **Figure III.2, III.3**). This result implies that the unique geo-environmental dynamics of each archipelago play a crucial role in shaping species accumulation for clades that have radiated into it. The idea that the geographic and chronological settings of an archipelago can channel the diversification process into predictable patterns is not new. Perhaps the best example of such an archipelagic effect is the progression rule (Funk & Wagner 1995, Shaw & Gillespie 2015) where, in archipelagos with a linear age progression, radiating clades tend to colonise the archipelago from the oldest to the youngest islands, leading to a particular topology for the phylogenies of these radiations. To take another example, by observing congruence in macroevolutionary patterns between the radiation of Darwin's finches and the tortoises on Galápagos, Román-Palacios & Wiens (2018) suggested the idea of a “place-dependent” effect on diversification. However, to our knowledge, our study is the first to highlight such an archipelagic effect in the factors driving diversity patterns of ROAs across multiple archipelagos. It should be noted, however, that previous studies have already attempted to find common predictors for Island S_{ROA} , but that these analyses were limited either by the number of predictors or the number of clades considered (e.g., Parent 2012, Lim & Marshall 2017).

A strong effect of area and topographic complexity (SDS) on Island S_{ROA} thus appears to be a signature of Hawaii. Interestingly, SDS, which had no significant effect on Hawaii's Island S_{ROA} within the univariate GLM, became the second most important factor in the GLMM. The explanation for this likely lies in the role of the island of Hawai'i in explaining the variation in Island S_{ROA} . Indeed, in most ROAs, Hawai'i has an Island S_{ROA} value lower than predicted by the ISAR of the other Hawaiian Islands. This deviation is then captured by its comparatively lower topographic complexity, indicative of its smooth and young terrain, compared to the older and more rugged terrain of the older islands (Price & Wagner 2011, Barajas-Barbosa et al. 2020). In contrast to Hawaii, isolation and age (hump-shaped) appears to shape the Island S_{ROA} patterns for the Canary Islands (**Table 2** and **Figure 3**). This predominance of a negative effect of isolation reveals therefore that species accumulation during the radiation process was higher in the central, least isolated islands, namely Tenerife and Gran Canaria. This result aligns with previous studies that have positioned these two islands as primary centers of diversification (e.g., Francisco-Ortega et al. 2002, Allan 2004, Fernández-Mazuecos & Vargas 2011). In that respect, our data indicate that two-thirds

of the ROAs reached their peak species richness and SIE richness in Tenerife (**Figure III.S17**). Because of this, these two islands are the main sources of dispersal for the peripheral islands. For example, using a Bayesian framework to infer dispersion processes within the Canary Islands, Sanmartín et al. (2008) identified a stepwise dispersal pattern from the central islands to the smaller islands of La Palma and El Hierro in the west. In addition, a recent literature review also suggests a colonisation route to the eastern islands (Lanzarote and Fuerteventura) following the establishment of a xerophytic climate, which may have provided new ecological opportunities for recent (re)colonisation (García-Verdugo et al. 2019). This distinctive feature of Tenerife and Gran Canaria relies also on their intrinsic characteristics, such as elevation (3,715 and 1,956 meters above sea level respectively) and topographic complexity, both resulting from their intermediate age (12 and 14.5 Ma respectively) within the range of the Canary Islands (1.1 to 23 Ma). According to the GDM, intermediate-age islands reach 'maturity' through the slowing down of island-building processes in favour of erosive processes, generating a more complex topography (Borregaard et al. 2017). This relationship with age is reflected in the importance of the hump-shaped relationship detected for the Canary Islands (**Table III.2**), with young and old islands being species-poor compared to the central islands. However, it should be noted that Lanzarote and Fuerteventura (the two oldest islands) have sustained high levels of extinction during the Pleistocene due to climatic fluctuations (García-Verdugo et al. 2019), which can therefore artificially drive the effect of age in our analyses.

Results obtained for the Galápagos emphasized the role of elevation and topographic complexity in driving Island S_{ROA} patterns. These findings are in accordance with a recent study highlighting the role of environmental heterogeneity in driving SIE richness for diverse taxonomic groups in this archipelago (Roell et al. 2021). However, our model for the Galápagos only accounted for a very small portion of Island S_{ROA} variation (18% captured by the fixed effect). This limited explanatory power can possibly be attributed to the wide taxonomic range covered by the seven ROAs analyzed (two beetles, one moth, one bird, one reptile, one land snail and one flowering plants lineages), which might have hindered the identification of common drivers. In contrast to the results for the Galápagos, the prevalence of elevation and age for Fiji (**Table III.2** and **Figure III.3**) was straightforward to interpret since all six Fijian ROAs had their highest Island S_{ROA} values on Viti Levu, which is both the oldest, highest, and largest island of the archipelago.

Results obtained with the paleo configurations of the archipelagos highlighted that a simple combination of age and paleo-area was able to significantly explain a substantial amount of S_{ROA} variation (even if R^2_m were lower than our initial models) (**Figure III.S16** and **Table III.S9**). While these models cannot be directly compared with our initial analyses due to the absence of reliable

paleo environmental heterogeneity data, this suggests that the past archipelago configuration may have played a key role in driving the radiation process, in line with Fernández-Palacios et al. (2016) predictions and Norder et al. (2018) conclusions.

4. d. The effect of the geo-environmental factors on island S_{ROA} is also taxon dependent

Despite its lesser importance, the effect of taxon, mainly in interaction with archipelago, also appears to wield a significant role in driving the effect of the geo-environmental factors on Island S_{ROA} . Probably the most striking finding was the strong effect of elevation detected for the plants subset of both Hawaii and the Canary Islands. The explanation of such a pattern certainly lies in the fact that many plants ROAs span the entire elevation gradient of these archipelagos, with different species each found exclusively in narrow habitats ranging from dry coastal areas to mesic environments and wet forests [e.g., in Hawaii: Lobeliads (Givnish et al. 2009), Silversword Alliance (Baldwin & Sanderson 1998), *Schiedea* (Sakai et al. 2006), *Euphorbia* (Yang et al. 2018); in the Canary Islands: *Aeonium* Alliance (Kim et al. 2008), *Argyranthemum* (White et al. 2020), *Echium* (García-Maroto et al. 2009), *Sonchus* (Kim et al. 2008)]. In contrast, the relative contribution of elevation for invertebrates (**Figure III.3**) was very limited in both archipelagos. This finding aligns with previous work indicating that strong environmental conservatism dominates for arthropod ROAs as they largely occur within a restricted environmental envelope (Hiller et al. 2019, Dorey et al. 2020). In this sense, the important contribution of area for Hawaiian invertebrates may be due to the fact that area serves as a better proxy of habitat diversity for invertebrates rather than elevation and SDS.

Interestingly, we found that the effect of elevation, SDS and isolation was more pronounced for larger ROAs, irrespective of their archipelago or taxon. We see two non-exclusive explanations for these results: (i) it could simply be a statistical artefact since more species in the clade could increase the likelihood to detect a scaling with the geo-environmental variables; (ii) large ROAs are large because they have accumulated many species through within-island speciation triggered by elevation and topographic complexity (SDS; see the positive correlation between radiation size and the proportion of SIEs, **Figure III.S3**). Finally, the decomposition of the R^2 in the GLMMs revealed that a nearly equal proportion of variance was captured by both the fixed factors (the geo-environmental factors) and the random structure (slopes and intercepts). In some cases, the random structure demonstrated even stronger explanatory power than the fixed factors, as observed in the Galápagos. This is an interesting outcome because it shows that the inclusion of radiation identity as random effects (slope and intercept) in our analyses likely captures finer differences between ROAs regarding their ecological and evolutionary features (e.g., dispersal capabilities, speciation

rate). For instance, ROAs with rapid rates of speciation such as the Hawaiian *Plagithmysus* beetles may rapidly saturate even the young islands, resulting in a positive correlation between Island S_{ROA} and island area. In contrast, for ROAs with a lower speciation rate, such as the flightless Hawaiian *Rhyncogonus* weevils or the *Megalagrion* damselflies, Island S_{ROA} is expected to correlate with island age (Paulay 1994, Jordan et al. 2003).

4. e. Limitations

Our approach undoubtedly comes with some limitations. First, our values of Island S_{ROA} can be potentially biased due to unrecorded human mediated species extinctions or local (islands) extirpations (Paulay 1994, Whittaker et al. 2023, Lim & Marshall 2017). Moreover, we cannot exclude the possibility that inconsistencies among taxonomists and the varying degrees of completeness of these endemic clades may have generated noise in our analyses. However, the analyses that included subspecies did not show any specific differences with the analyses run without subspecies, suggesting that our results may be robust to marginal variation in species number (**Appendix III.1**). Second, we acknowledge that the limited number of islands within each archipelago poses a challenge in terms of statistical power and restricts the use of complex models. This situation, which affects many island biogeography studies (Whittaker et al. 2023), becomes even more complicated when using paleo-islands, which reduces the main Hawaiian archipelago to just four islands. Third, the ten species threshold we chose to ensure sufficient variance in Island S_{ROA} between islands introduces a bias toward “successful” ROAs, and our conclusions therefore might not apply for more modest ROAs. Fourth, some of our geo-environmental factors may not be entirely suitable for some specific ROAs. For example, the environmental heterogeneity variables (elevation and SDS) were chosen according to common practice in the literature, but there is no doubt that other variables such as climatic variations or direct measurement of habitat diversity might provide better fits for certain ROAs (Yu et al. 2015).

5. Conclusion

The approach proposed in this study revealed that the diversity patterns of ROAs are predictable from a set of classical geo-environmental factors, for all the taxa and archipelagos analyzed. More precisely, it highlights that, along with area, environmental heterogeneity and geographical isolation have played a significant role in shaping diversity patterns of oceanic archipelagos. We also demonstrated that the strength of the effect of geo-environmental variables is a function of the archipelago and, to a lesser extent, of the taxon to which the ROA belonged. This result indicates that the ROAs within a given archipelago are mainly governed by the same

geological and geographical dynamics, in interaction with the ecological features of the radiated species. We conclude that the adoption of simple macroecological approaches can contribute significantly to our understanding of the diversification processes occurring on islands.

6. Supplementary information

Appendix III.1

Island selection for Hawaii

The number of Hawaiian Islands historically included in island biogeography analyses have varied greatly between studies (from 5 to 18 islands; Price 2004, Price & Wagner 2011). After a careful review of the literature, we made our own selection by considering biological and statistical matters, as detailed hereafter. First, we remove Kure, Midway, and Pearl & Hermes, because of their islet nature (see Whittaker et al. 2008) and because we consider them too degraded/advanced in their island ontogeny. Then, we excluded Kaula Rock and Kaho‘olawe, due to their highly degraded biota resulting from military explosives testing and alien ungulates presence (King 1973, Whittaker et al. 2008 and reference herein). Finally, we choose to remove Lisianski and Laysan as these small, far, and old Northwestern Hawaiian Islands greatly cluster the data and, in turn, increased collinearity between our geo-environmental factors. Our final set for the main analyses therefore comprises nine islands: Necker, Nihoa, Ni‘ihau, Kaua‘i, O‘ahu, Moloka‘i, Lāna‘i, Maui and Hawai‘i. Among the 53 ROAs (Evolutionary radiations on oceanic archipelagos) retrieved for Hawaii, 33 ROAs were on 6 islands, 12 on 7 islands, 7 on 8 islands, and 1 on 9 islands.

Neighbor Index (NI) calculation

The Neighbor Index (NI) (Kalmar & Currie 2006) postulated that the importance of an island as a potential source of colonisation to the focal island is proportional to its area (A) and inversely proportional to the distance (D) that separates it from the focal island. The general formula of NI for a given island is written as follow:

$$NI = \sum_{i=1}^{n-1} \frac{A_i^a}{D_i^b}$$

where n is the number of islands in the archipelago, and a and b are empirical constants. Kalmar & Currie (2006) suggested estimating a and b iteratively for each dataset until they maximize the correlation with RSI. Because we have few data points per ROA, we did not follow this approach to avoid spurious values for a and b . Instead, we identified three significant pairs of a and b , and calculated NI for each ROA using the pair that maximizes the correlation with RSI. The three pairs

were: (1) $a = 0$ and $b = -1$, where NI is simply the sum of the distance (no effect of area); (2) $a = 1$ and $b = 1$, where NI is proportional to the area, and inversely proportional the distance and (3) $a = 1$ and $b = 2$, where NI is proportional to their area, and inversely proportional to the square of their distance. Each of the three NI calculations was done specifically for each ROA, only accounting for islands where the ROA occurs.

Finding the best random structure for GLMM

The best random effect structures, with all fixed effects considered, were selected using the function `buildmer` in the R package *buildmer* (Voeten 2023). The function performs a backward stepwise elimination of the random terms while guaranteeing model convergence at the same time, which is a critical issue for models with complex random structures such as ours. The backward stepwise procedure was performed using the Likelihood Ratio Test (LRT) as implemented by default. The selection of the best random structures for the SIE analysis was performed using the *buildglmmTMB* function in the *buildmer* package.

Measuring of variable importance

For a given predictor, we first averaged the standardized regression coefficients across best models (all models with $\Delta AICc < 2$) including the predictor, weighted by the models' AICc weights. The average coefficients of all predictors were then transformed into absolute values and scaled to sum up to one to obtain an importance value per predictor, expressed as its relative contribution to all best models.

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Table III.S1. List of the 20 oceanic archipelagos fitting all our criteria (i.e., fully oceanic with at least six main islands) and results of our literature research for ROA description. FP=French Polynesia; MAC=Macaronesia.

Archipelago name	ROA presence (10 species or more)
Austral (FP)	Yes
Azores (MAC)	Yes
Canary Islands (MAC)	Yes
Cabo Verde (MAC)	Yes
Cook	No
Faroe	No
Fiji	Yes
Galápagos	Yes
Gambier (FP)	No
Hawaii	Yes
Kermadec	No
Lesser Antilles	Yes
Line islands	No
Mariana	No
Marquesas (FP)	Yes
Ogasawara (Bonin)	Yes
Samoa	No
Society (FP)	Yes
Tonga	No
Vanuatu	Yes

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Table III.S2. List of the ROAs with at least 10 species and occurring on our four selected oceanic archipelagos but removed from our final dataset for specific reasons detailed below.

Archipelago	ROA name	Reason for removal
Hawaii	<i>Tetragnatha (Web Builders)</i>	Distributed on five Hawaiian islands only
	<i>Orsonwelles</i>	Distributed on five Hawaiian islands only
	<i>Lysimachia</i>	Distributed on five Hawaiian islands only
	<i>Auriculellinae</i>	Distributed on five Hawaiian islands only
	<i>Hyposmocoma</i>	Too many undescribed species: at least 600 species are known, but hundreds of them are yet to be formerly described (Hembry et al. 2021)
	<i>Kilauella</i>	Too many undescribed species: over 200 species are estimated based on museum collections, but only seven of them have been published (Gero 2015, Kevin Johnson personal communication)
	Sap beetles	Too many undescribed species (see Ewing 2007)
	Succineidae	Succineidae land snails have colonized the Hawaiian Islands twice according to molecular data (Holland & Cowie 2009), but the species repartition between those two independent colonizations can't be assessed properly.
	<i>Campsicnemus</i>	Too many undescribed species: Goodman et al. (2014) estimated that 60 species await description, and most of them have yet to be published to date.
	<i>Drosophila</i>	Too many undescribed species: hundreds of species are still awaiting description (O'Grady & DeSalle 2018)
Canary Islands	<i>Calathus</i>	Distributed on five Canary islands only
	<i>Cheirolophus</i>	Distributed on five Canary islands only
	<i>Pericallis</i>	Distributed on five Canary islands only
Fiji	<i>Copelatus</i>	Distributed on five Fijian islands only
	<i>Fluviopupa</i>	Distributed on two Fijian islands only
	<i>Phyllanthus</i>	The only published reference of <i>Phyllanthus</i> data distribution is Smith (1991) book "Flora Vitiensis Nova" (David H. Hembry personal communication), which lacks information/precision on the matter.

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(Table III.S3 continued)

Radiation name	Publication showing monophyletic proof	Archipelago	Number of species	Number of species + subspecies	%SIE	Taxonomic rank	Order	Family	Radiation Type	Radiation Type reference	Island with maximum SKOA	Island with maximum SIE	Best Invasibility factor	Number of Islands occurrence	Distribution references(s)
<i>Myrsine</i>	Appelblans et al. 2020	Hawaii	21	21	0.67	Plants	Ericales	Primulaceae	ND	-	Kauai'i	Kauai'i	AD_NI	6	Appelblans et al. 2020
<i>Nothofagus</i>	Phillips et al. 2020	Galapagos	99	99	1	Invertebrates	Stylommatophora	Brulialidae	Adaptive	Parent & Crespi 2006	Santa Cruz	Santa Cruz	D_NI	11	Phillips et al. 2020
<i>Neohabris</i>	Beatty et al. 2017	Fiji	36	36	0.56	Invertebrates	Odonata	Cleptidae	Non-adaptive	Beatty et al. 2017	Viti Levu	Viti Levu	D_NI	6	Beatty et al. 2017
<i>Neophrosyne</i>	Bennett & O'Grady 2013	Hawaii	212	214	0.88	Invertebrates	Hemiptera	Ceangroniidae	Both	Bennett & O'Grady 2013	Hawaii'i	Hawaii'i	AD_NI	6	Nishida 2002; Bennett & O'Grady 2012
<i>Nesozela</i>	Goodman et al. 2010	Hawaii	112	114	0.79	Invertebrates	Hemiptera	Dipluchidae	Both	Goodman et al. 2010	O'ahu	O'ahu	D_NI	6	Nishida 2002
<i>Nesozela</i>	Rees et al. 2001	Canaries	19	21	0.42	Invertebrates	Coleoptera	Tenebrionidae	Adaptive	Rees et al. 2001	Tenerife	Tenerife	D_NI	8	www.biodiversidadcanarias.es
<i>Ollaris</i>	Wessel et al. 2013	Hawaii	63	86	0.75	Invertebrates	Hemiptera	Cixiidae	Both	Wessel et al. 2013	O'ahu	O'ahu	AD_NI	7	Nishida 2002
<i>Ombodes</i>	Haines 2011	Hawaii	23	23	0.35	Invertebrates	Lepidoptera	Crabulidae	ND	-	Hawaii'i	Hawaii'i	D_NI	6	Nishida 2002
<i>Panicum</i>	Edwards & Shi 2008	Hawaii	11	11	0.09	Plants	Poales	Poaceae	ND	-	Hawaii'i	Hawaii'i	D_NI	6	Imada 2012
<i>Paracianina</i>	Perey 2017	Hawaii	36	36	0.92	Invertebrates	Hemiptera	Triozidae	Adaptive	Amada et al. 2020	Hawaii'i	Hawaii'i	D_NI	6	Perey 2017
<i>Peperomia</i>	Lim et al. 2019	Hawaii	16	16	0.44	Plants	Piperiales	Piperaceae	ND	-	Maui	Maui	AD_NI	6	Imada 2012
<i>Phidole</i>	Darwell et al. 2019	Fiji	16	16	0.25	Invertebrates	Hymenoptera	Formicidae	Adaptive	Darwell et al. 2019	Viti Levu	Viti Levu	D_NI	10	Samat 2008; Samat & Moreau 2011; Fischer et al. 2016; Darwell et al. 2019
<i>Phidolaria</i>	Johns et al. 2018	Hawaii	51	51	0.71	Invertebrates	Lepidoptera	Gracillariidae	Both	Johns et al. 2018	Maui	Maui	D_NI	6	Kobayashi et al. 2021
<i>Phidola</i>	Dimitrov et al. 2008	Canaries	20	20	0.9	Invertebrates	Araneae	Phididae	Non-adaptive	Dimitrov et al. 2008	Tenerife	Tenerife	D_NI	7	www.biodiversidadcanarias.es
<i>Pinosporum</i>	Gemmill et al. 2002	Hawaii	11	11	0.64	Plants	Apiales	Piptoporenaceae	Adaptive	Gemmill et al. 2002	Kauai'i	Kauai'i	D_NI	6	Imada 2012
<i>Polystichus</i>	Costello & Moleley 2007	Hawaii	11	11	0.64	Plants	Apiales	Araliaceae	Adaptive	Costello & Moleley 2007	Kauai'i	Kauai'i	D_NI	6	Imada 2012
<i>Pritchardia</i>	Bacon et al. 2012	Hawaii	24	24	0.79	Plants	Arecales	Arecaceae	Adaptive	Bacon et al. 2012	Kauai'i	Kauai'i	D_NI	8	Bacon et al. 2012
<i>Psychotria</i>	Zhang 2016	Hawaii	11	12	0.55	Plants	Gentianales	Rubiaceae	ND	-	Kauai'i	Kauai'i	AD_NI	6	Imada 2012; Zhang 2016
<i>Pycna</i>	Bess et al. 2014	Hawaii	63	72	0.78	Invertebrates	Psoocoptera	Psoocidae	ND	-	O'ahu	Hawaii'i	AD_NI	8	Nishida 2002; Bess et al. 2014
<i>Rhynchospora</i> (Hawaii)	Claridge et al. 2017	Hawaii	47	47	0.94	Invertebrates	Coleoptera	Curtulionidae	ND	-	O'ahu	O'ahu	D_NI	6	Samuelson 2003
<i>Sarona</i>	Asquith 1995	Hawaii	40	40	0.98	Invertebrates	Hemiptera	Miridae	Both	Asquith 1995	O'ahu	O'ahu	AD_NI	8	Nishida 2002
<i>Scalotia</i>	Fernández-Mazuecos et al. 2020	Galapagos	15	15	0.67	Plants	Asterales	Asteraceae	Adaptive	Fernández-Mazuecos et al. 2020	Santa Cruz	Santa Cruz	D_NI	10	Fernández-Mazuecos et al. 2020
<i>Scaptomyza</i> 1	Katoh et al. 2017	Hawaii	134	135	0.69	Invertebrates	Diptera	Drosophilidae	Adaptive	Lapoint et al. 2013	Hawaii'i	Hawaii'i	AD_NI	6	Nishida 2002; O'Grady et al. 2003; Magnacca & O'Grady 2008
<i>Scaptomyza</i> 2	Katoh et al. 2017	Hawaii	14	14	0.50	Invertebrates	Diptera	Drosophilidae	Adaptive	Katoh et al. 2017	Hawaii'i	Hawaii'i	D_NI	6	Nishida 2002
<i>Schizela</i>	Williard et al. 2011	Hawaii	34	35	0.82	Plants	Diptera	Caryophyllaceae	Adaptive	Kapralov & Filatov 2006	Kauai'i	Kauai'i	D_NI	6	Imada 2012
<i>Sicyos</i>	Sebastian et al. 2012	Hawaii	14	14	0.21	Plants	Cucurbitales	Cucurbitaceae	ND	-	Hawaii'i	Hawaii'i	D_NI	7	Imada 2012
<i>Sideritis</i>	Barber et al. 2007	Canaries	28	31	0.86	Plants	Lamiales	Lamiaceae	Adaptive	Barber et al. 2007	Tenerife	Tenerife	D_NI	6	www.biodiversidadcanarias.es
<i>Silversward</i> Alliance	Baldwin et al. 2021	Hawaii	33	45	0.85	Plants	Asterales	Asteraceae	Adaptive	Schlüter 2000	Kauai'i	Kauai'i	D_NI	7	Imada 2012
<i>Sonchus</i> Alliance	Lee et al. 2005	Canaries	29	30	0.66	Plants	Asterales	Asteraceae	Adaptive	Santiago & Kim 2009	Tenerife	Tenerife	D_NI	7	www.biodiversidadcanarias.es
<i>Stomion</i>	Wuhenpfeimig 2012	Galapagos	11	12	0.55	Invertebrates	Coleoptera	Tenebrionidae	ND	-	Santa Cruz	Espanola	D_NI	15	Peel 2006; https://www.darwinfoundation.org/en/datazone/checklist
<i>Strangomyza</i>	Liu et al. 2020	Fiji	20	20	0.35	Invertebrates	Hymenoptera	Formicidae	Adaptive	Liu et al. 2020	Viti Levu	Viti Levu	AD_NI	9	Samat et al. 2019; Liu et al. 2020
<i>Tarphax</i> (Canaries)	Anonim et al. 2012	Canaries	31	32	0.77	Invertebrates	Coleoptera	Zopheridae	Adaptive	-	Tenerife	Tenerife	D_NI	6	www.biodiversidadcanarias.es
<i>Tephrinidae</i>	Viale et al. 2015	Hawaii	28	28	0.79	Invertebrates	Diptera	Tephrinidae	Adaptive	Viale et al. 2015	Hawaii'i	Hawaii'i	AD_NI	8	Nishida 2002; Viale et al. 2015
<i>Tetragonata</i> Spiny Leg	Kennedy et al. 2022	Hawaii	17	17	0.71	Invertebrates	Araneae	Tetragonathidae	Both	Kennedy et al. 2022	Maui	Maui	AD_NI	7	Kennedy 2018; Kennedy et al. 2022
<i>Tetrazomolophilum</i>	Suncho & Karaman-Castro 2008	Hawaii	11	15	0.36	Plants	Asterales	Asteraceae	Adaptive	Lowry et al. 2001	Maui	O'ahu	D_NI	6	Imada 2012
<i>Thaba</i>	Böckers et al. 2016	Canaries	12	12	0.5	Invertebrates	Stylommatophora	Helicidae	Both	Greve et al. 2012	Fuerteventura	Fuerteventura	AD_NI	7	Hase et al. 2014
<i>Theridion</i>	Bellvert et al. 2021	Hawaii	16	16	0.69	Invertebrates	Araneae	Therididae	Adaptive	Bellvert et al. 2021	Maui	Maui	AD_NI	6	Bellvert et al. 2021
<i>Thyrocopa</i>	Medeiros & Gillespie 2011	Hawaii	36	36	0.67	Invertebrates	Lepidoptera	Xylopetalidae	Both	Medeiros et al. 2015	Kauai'i	Kauai'i	D_NI	6	Medeiros 2009
<i>Tolpis</i>	Mort et al. 2022	Canaries	13	13	0.62	Plants	Asterales	Asteraceae	Adaptive	Gruenstaedt et al. 2013	Tenerife	Tenerife	AD_NI	7	https://www.biodiversidadcanarias.es; Mort et al. 2022
<i>Trechus</i>	Comeras-Diaz et al. 2007	Canaries	16	17	0.88	Invertebrates	Coleoptera	Carabidae	Adaptive	Comeras-Diaz et al. 2007	Tenerife	Tenerife	D_NI	7	www.biodiversidadcanarias.es
<i>Tree crickets</i>	Shaw 1995	Hawaii	68	68	0.91	Invertebrates	Orthoptera	Gryllidae	ND	-	O'ahu	O'ahu	D_NI	6	Nishida 2002
<i>Xylocopa</i>	Cognato et al. 2018	Hawaii	21	21	0.48	Invertebrates	Coleoptera	Curculionidae	ND	-	Hawaii'i	Hawaii'i	D_NI	7	Samuelson 1981

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Table III.S4. Islands characteristics for the four oceanic archipelagos selected in our study. SDS correspond to the standard deviation of the slope (see main text). The three $_NI$ columns correspond to the three Neighbor Index calculations (D_NI = only distances, AD_NI = area & distances, AD^2_NI = area & distances², see main text and **Appendix III.1**). Note: These values of NI are indicative since, for a given ROA, they have been calculated only with the islands on which the species constituent of the ROA occurs.

Archipelago	Islands	Area (km ²)	Age (Ma)	Elevation (m)	SDS	D_NI	AD_NI	AD^2_NI	Age References
Hawaii	Hawai'i	10457.22	0.53	4176.00	5.57	2914.00	65.61	0.07	Gillespie & Clague 2009; Weigelt et al. 2015 and references herein
	Mauı	1894.11	1.30	2993.00	11.56	2208.88	348.83	1.09	
	Lāna'i	366.60	1.50	999.00	8.95	2111.30	319.93	1.20	
	Moloka'i	680.42	1.80	1377.00	13.86	1970.43	311.68	1.20	
	O'ahu	1545.40	3.39	1220.00	12.23	1773.52	106.44	0.03	
	Kaua'i	1442.95	5.77	1530.00	13.76	2022.75	60.20	-0.28	
	Ni'ihau	197.31	5.92	340.00	8.48	2292.37	96.00	0.34	
	Nihoa	0.80	7.30	275.00	14.31	3373.19	32.84	-1.11	
Necker	183.00	11.00	84.00	6.76	5312.93	20.22	-1.59		
Canaries	El Hierro	278.00	1.10	1503.00	12.18	1188.09	51.53	-0.28	Staudigel et al. 1986; van den Bogard 2013
	La Palma	729.00	1.70	2425.00	13.48	1118.29	49.96	-0.28	
	La Gomera	378.00	11.00	1484.00	12.47	861.09	114.54	0.51	
	Tenerife	2058.00	12.00	3718.00	11.14	672.24	66.40	0.08	
	Gran Canaria	1532.00	14.50	1950.00	12.53	842.06	69.98	-0.01	
	Lanzarote	796.00	15.00	670.00	7.98	1532.07	198.96	1.26	
	Fuerteventura	1725.00	23.00	807.00	8.66	1188.64	116.29	0.94	
Galápagos	Fernandina	648.63	0.07	1494.00	7.01	1634.86	1344.94	2.56	Roell et al. 2021; Kraemer et al. 2022 and references herein
	Genovesa	14.00	0.30	64.00	4.62	1782.25	72.56	-0.15	
	Darwin	1.44	0.40	165.00	7.02	3356.63	42.05	-0.63	
	Marchena	131.83	0.60	343.50	4.86	1479.83	102.94	0.16	
	Pinta	60.39	0.70	550.00	7.32	1667.40	103.74	0.18	
	Isabela	4731.51	0.80	1705.00	5.53	992.35	272.18	1.74	
	Wolf	1.30	1.00	253.00	14.63	2911.36	52.00	-0.44	
	Rábida	6.84	1.30	367.00	8.93	1258.16	423.81	1.69	
	Santiago	576.77	1.40	906.00	4.84	1102.93	402.31	1.41	
	Pinzón	18.07	1.70	458.00	9.20	1281.64	456.45	1.51	
	Floreana	177.83	2.30	640.00	5.25	1747.84	141.05	0.43	
	Santa Cruz	986.28	2.30	864.00	2.69	1125.30	249.64	1.00	
	Santa Fe	25.18	2.90	259.00	9.27	1529.30	168.46	0.78	
	Española	64.12	3.50	198.00	4.69	2212.39	78.35	-0.03	
San Cristóbal	559.76	4.00	715.00	3.78	1956.07	71.99	-0.11		
Fiji	Lakeba	62.11	8.50	187.00	7.29	3072.64	81.07	-0.42	Barajas-Barbosa et al. 2020 and references herein
	Koro	106.89	5.00	499.00	10.30	2867.65	282.06	0.70	Gillespie et al. 2017 and references herein
	Rambi	67.30	3.00	463.00	8.64	3669.97	1245.39	2.37	Groom et. 2013
	Taveuni	434.00	3.00	1241.00	8.51	3061.57	872.17	2.04	
	Kadavu	411.00	3.43	805.00	8.77	3703.81	190.69	0.39	
	Vanua Levu	5753.54	8.60	881.00	8.45	2970.85	269.25	1.15	Nunn 1990
	Beqa	36.00	3.07	462.00	8.50	3827.48	1185.98	2.08	
	Moala	67.07	8.40	409.00	7.94	2467.39	127.12	-0.02	Nunn 1995
	Matuku	57.00	3.50	385.00	9.03	2878.00	106.87	-0.16	Sarnat & Economo 2012
	Ngau	136.10	5.00	738.00	8.70	2552.85	248.85	0.57	
	Ovalau	106.00	5.70	625.00	8.59	3066.29	821.30	1.69	
	Totoya	28.00	4.90	366.00	8.43	2648.80	101.29	-0.19	
	Kabara	31.00	15.00	29.00	6.79	3024.59	74.66	-0.47	
	Namuka-i-Lau	5.00	15.00	79.00	6.41	3264.97	70.71	-0.44	
	Ogea	13.30	15.00	82.00	5.85	3711.71	62.52	-0.44	
	Ono-i-Lau	7.90	15.00	113.00	5.60	5231.09	48.36	-0.88	
	Vulaga	18.50	15.00	79.00	6.17	3464.09	65.85	-0.44	
	Yathata	6.00	15.00	94.00	6.21	3053.90	151.64	0.21	
Viti Levu	10693.22	25.00	1197.00	8.98	3027.25	125.91	0.45		

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Table III.S5. The best random structure and family distribution selected for the GLMMs performed for data including all current geo-environmental factors (The initial model) and for the paleo-analyses including only paleo-area, paleo isolation and geological age. The best random structures were selected using the function *buildmer* in the R package *buildmer* (Voeten 2023). The function performs a backward stepwise elimination of the random terms while guaranteeing model convergence at the same time. A negative binomial was selected when the GLMM with Poisson showed significant overdispersion.

	Best random structure		Family distribution
	Random slope	Random intercept	
Initial model			
Hawaii	SDS, elevation, isolation	Radiations, Islands	Poisson
Canary Islands	SDS, age	Radiations, Islands	Poisson
Galapagos	SDS	Radiations	Poisson
Fiji	Age2	Radiations	Poisson
Plants Hawaii	Elevation, Age2	Radiations	Poisson
Plants Canary Islands		Radiations	Poisson
Invertebrates Hawaii	SDS, elevation, isolation	Radiations, Islands	Negative binomial
Invertebrates Canary Islands	SDS, age	Radiations	Poisson
Subspecies models			
Hawaii	SDS, elevation, isolation	Radiations, Islands	Poisson
Canary	SDS, elevation	Radiations	Poisson
Galapagos	SDS	Radiations	Poisson
Fiji	Age2	Radiations	Negative binomial
Plants Hawaii	Elevation, Age2	Radiations	Poisson
Plants Canary Islands		Radiations	Poisson
Invertebrates Hawaii	SDS, elevation, isolation	Radiations, Islands	Negative binomial
Invertebrates Canary Islands	SDS	Radiations	Poisson
Paleo models			
Hawaii	Isolation, Area, Age2	Radiations, Islands	Poisson
Canary	Age	Radiations, Islands	Poisson
Galapagos	Area	Radiations	Poisson
Fiji		Radiations, Islands	Poisson
Plants Hawaii	Area	Radiations, Islands	Poisson
Plants Canary Islands		Radiations	Poisson
Invertebrates Hawaii	Isolation, Area, Age2	Radiations, Islands	Negative binomial
Invertebrates Canary Islands	Age, Isolation	Radiations, Islands	Poisson

Table III.S6. Number and proportion of significant relationship between Island S_{ROA} and the geo-environmental factors, before and after the FDR corrections of the P-values for the dataset with the subspecies included. For age + age², an exception is made as we only counted the number of ROAs for which a hump-shaped relationship with age that met our three criteria was recovered.

	Before FDR correction		After FDR correction	
	# of significant relationships	% of significant relationships	# of significant relationships	% of significant relationships
Area	37	0.39	18	0.19
Age	12	0.13	6	0.06
Age + Age ²	15	0.16	-	-
Elevation	43	0.45	35	0.37
SDS	12	0.13	3	0.03
Isolation	38	0.4	26	0.27

Table III.S7. Results of the multiple regressions testing whether the effect of the geo-environmental factors on the Island S_{ROA} can be explained by archipelagos, taxon, radiation size and proportion of SIE. The analyses were performed including subspecies. The effect of a given geo-environmental factor on a given Island S_{ROA} is quantified by its standardized β coefficient for the factors area, age, elevation, SDS and isolation while the effect of age +age² is code as binary variable with 1 is S_{ROA} follows a hump-shaped relationship with Age according to our three criteria (See main text) and 0 if not. All models were fitted with OLS except for age + age² for which a GLM with binomial distribution was used. The R^2 is given for each model and the P-value is provided for each significant predictor remaining in the model after backward elimination procedure. Analyses were initially performed for all ROAs without testing the interaction between archipelago and taxon because of a too unbalanced design. The models with the interaction term were performed for a subset of the data including only the ROAs of Hawaii and the Canary Islands and for plants and invertebrates.

	Factors	Archipelago	Taxon	Size	Proportion SIE	A x T	R ²
All radiations							
<i>z values</i>							
	Area		0.019		0.030 (+)	-	
	Area	0.005			0.009 (+)	-	0.162
	Age	<0.001				-	0.229
	Age + Age ²	0.001				-	0.155
Standardized β coefficient	Elevation	<0.001		0.005 (+)		-	0.212
	SDS	<0.001	0.02	0.025 (+)		-	0.385
	Isolation	<0.001		0.005 (-)		-	0.214
Subset							
<i>z values</i>							
	Area		0.003				
	Area		0.008				0.096
	Age				0.015	0.004	0.187
	Age + Age ²	<0.001					0.126
Standardized β coefficient	Elevation	0.005		0.025 (+)		0.005	0.204
	SDS	<0.001		0.006 (+)			0.268
	Isolation	<0.001	<0.001	0.001 (-)			0.215

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Table III.S8. Results of the Generalized Linear Mixed Models (GLMM) analyses testing the effect of the geo-environmental factors on S_{ROA} variation simultaneously for all the ROAs including the subspecies in each archipelago. Results for the plants and invertebrates subsets are given only for Hawaii and the Canary Islands for which enough ROAs were available in each taxon. Model selection was performed using AICc. The best-fit models ($\Delta AICc < 2$) are presented. For each best model, we provide the coefficient of the factors included in the model, the degree of freedom (df), the AICc, $\Delta AICc$ and $wAICc$. For each model, the significance of each factor was estimated using an analysis of variance. Significant factors are marked in bold. It should be noted that the calculation of P-values for fixed effects in GLMMs remains controversial. Further details including the best random structure, and family distribution are given in **Table III.S5**.

	Area	Age	Age2	Elevation	SDS	Isolation	df	AICc	$\Delta AICc$	$wAICc$	
Hawaii	0.482			0.207	0.353		15	1949.236	0	0.257	
	0.606	-0.123			0.403		15	1950.564	1.328	0.132	
	0.476			0.203	0.35	-0.024	16	1950.856	1.62	0.114	
	0.67				0.39		14	1950.947	1.711	0.109	
Canary Islands		0.107	-0.125	0.255		-0.293	11	959.39	0	0.495	
Galápagos				0.354	-0.313		6	335.752	0	0.103	
				0.336	-0.298	-0.085	7	336.261	0.509	0.08	
				0.366			5	336.92	1.168	0.057	
		0.053	-0.093	0.383	-0.277		8	336.961	1.208	0.056	
				0.347		-0.089	6	337.212	1.46	0.05	
		0.47	0.047	-0.116			7	337.27	1.518	0.048	
Fiji		0.077	-0.095	0.409			7	337.454	1.702	0.044	
	0.44						5	337.612	1.859	0.041	
		0.38		0.651			7	249.079	0	0.388	
Plants Hawaii		0.345		0.648		-0.103	8	250.303	1.224	0.21	
		0.17	-0.484	0.573			10	716.008	0	0.279	
Plants Canary Islands		0.145	-0.42	0.559	0.07		11	716.384	0.376	0.231	
		-0.088	0.18	-0.504	0.656		11	717.392	1.384	0.14	
			-0.029	-0.208	0.403		-0.192	7	320.3	0	0.213
			0.122	-0.214	0.527	0.157		7	321.44	1.14	0.121
Invertebrates Hawaii		0.024	-0.234	0.544			6	321.889	1.59	0.096	
			0.043	-0.199	0.425	0.098	-0.152	8	321.909	1.609	0.095
Invertebrates Canary Islands		0.517		0.317	0.376		15	1185.368	0	0.256	
		0.794			0.435		14	1187.334	1.966	0.096	
		0.511		0.313	0.375	-0.03	16	1187.367	1.999	0.094	
Invertebrates Canary Islands		0.139	-0.093	0.165		-0.358	8	635.987	0	0.17	
		0.097	-0.095	0.148	-0.137	-0.391	9	636.514	0.526	0.13	
		0.106	0.003	-0.119		-0.436	8	636.724	0.737	0.117	
		0.095	-0.026	-0.118		-0.463	9	637.107	1.12	0.097	
			0.158		0.176		-0.406	7	637.9	1.912	0.065

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Table III.S9. Results of the Generalized Linear Mixed Models (GLMM) analyses testing the effect of the paleo area, isolation, and geological factors on S_{ROA} variation simultaneously for all the ROAs in each archipelago. Results for the plants and invertebrates subsets are given only for Hawaii and the Canary Islands for which enough ROAs were available in each taxon. Model selection was performed using AICc. The best-fit models ($\Delta AICc < 2$) are presented. For each best model, we provide the coefficient of the factors included in the model, the degree of freedom (df), the AICc, $\Delta AICc$ and $wAICc$. For each model, the significance of each factor was estimated using an analysis of variance. Significant factors are marked in bold. It should be noted that the calculation of P-values for fixed effects in GLMMs remains controversial. Further details including the best random structure, and family distribution are given in **Table S5**.

	Area	Age	Age2	Isolation	df	AICc	$\Delta AICc$	$wAICc$
Hawaii	1.085	0.475	-0.686		15	1435.825	0	0.754
Canary Islands	0.309	-0.127	-0.398	-0.071	9	882.712	0	0.576
	0.334	-0.154	-0.415		8	884.374	1.662	0.251
Galápagos	0.456	0.087	-0.14		7	332.123	0	0.501
Fiji	0.684			0.234	5	200.281	0	0.594
Plants	0.916	0.515	-0.656		8	548.296	0	0.683
Hawaii	0.925	0.538	-0.657	0.034	9	550.042	1.745	0.285
Plants	0.399	-0.302		-0.494	6	288.578	0	0.529
Canary Islands	0.426	-0.387	-0.177	-0.341	7	289.153	0.575	0.397
Invertebrates	1.472	0.771	-0.655		11	858.02	0	0.687
Hawaii	0.289	-0.015	-0.292		11	584.955	0	0.528
Canary Islands	0.275	-0.051	-0.299	-0.069	12	586.575	1.62	0.235

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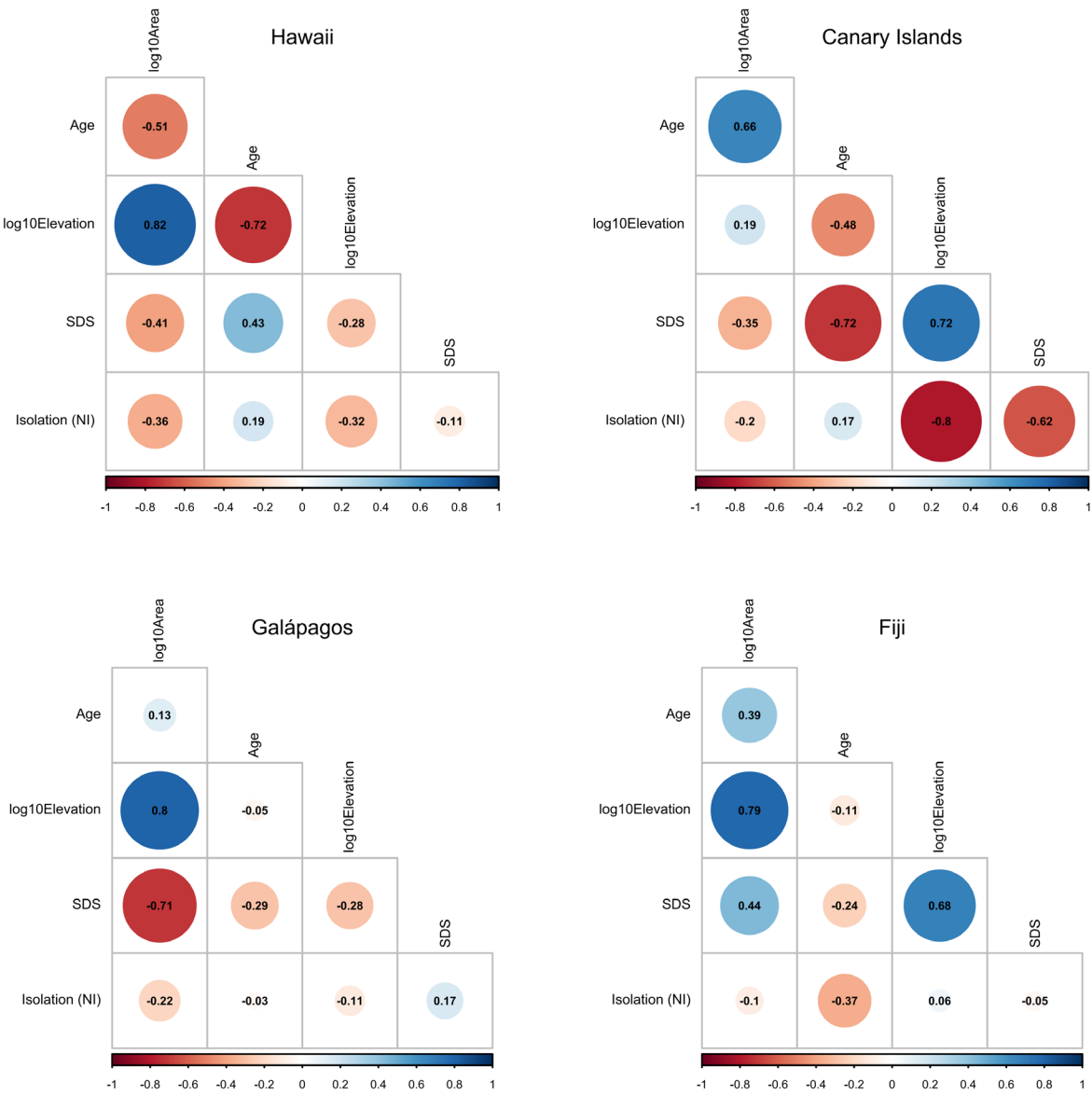


Figure III.S1. Pairwise correlations between the biogeographical factors for each archipelago. SDS: Standard deviation of slopes and NI: Neighbor index.

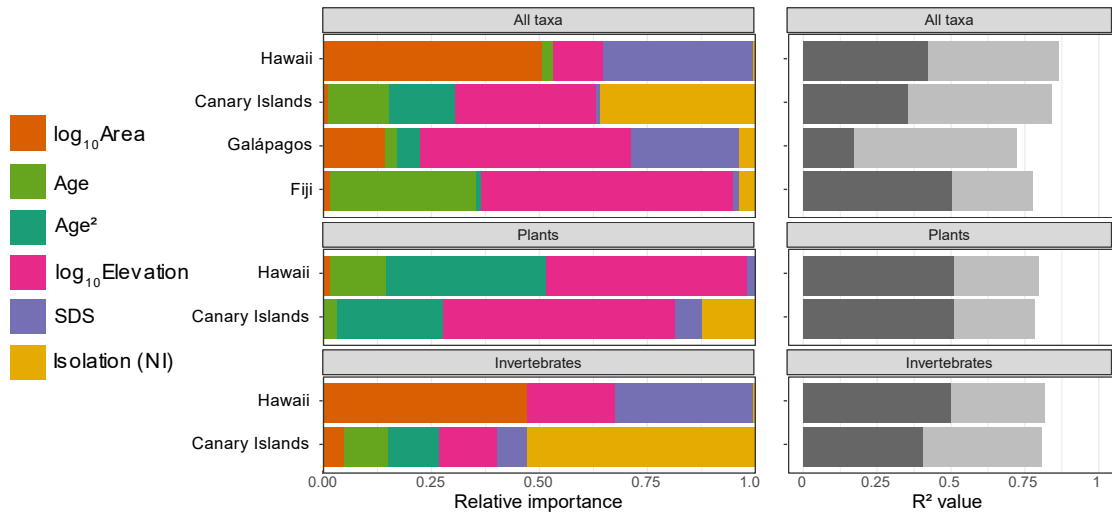


Figure III.S2. Results of the GLMMs with the subspecies included. Left panels: relative importance of each fixed effect as predictor of the S_{ROA} for each archipelago and the plants and invertebrates. Results for the plants and invertebrates subsets are given only for Hawaii and the Canary Islands for which enough ROAs were available in each taxon. in each archipelago (See Table 2 for detailed results). Right panel: Decomposition of the variance explained by the best model(s) (conditional R^2_c) into its components assigned to the fixed (marginal R^2_m , dark grey) and random effects ($R^2_c - R^2_m$, light grey) for each archipelago and the plants and invertebrates subsets for Hawaii and the Canary Islands (mean R^2 of all best models).

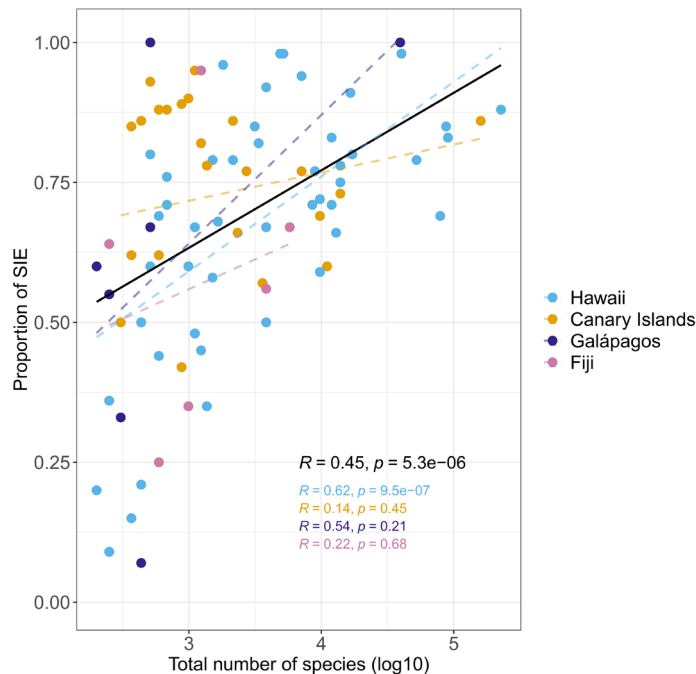


Figure III.S3. Linear relation between ROAs species richness and their percentage of Single Island Endemics (SIE). Black line represents the global linear regression (n=95). Dashed lines represent linear regressions for each archipelago independently.

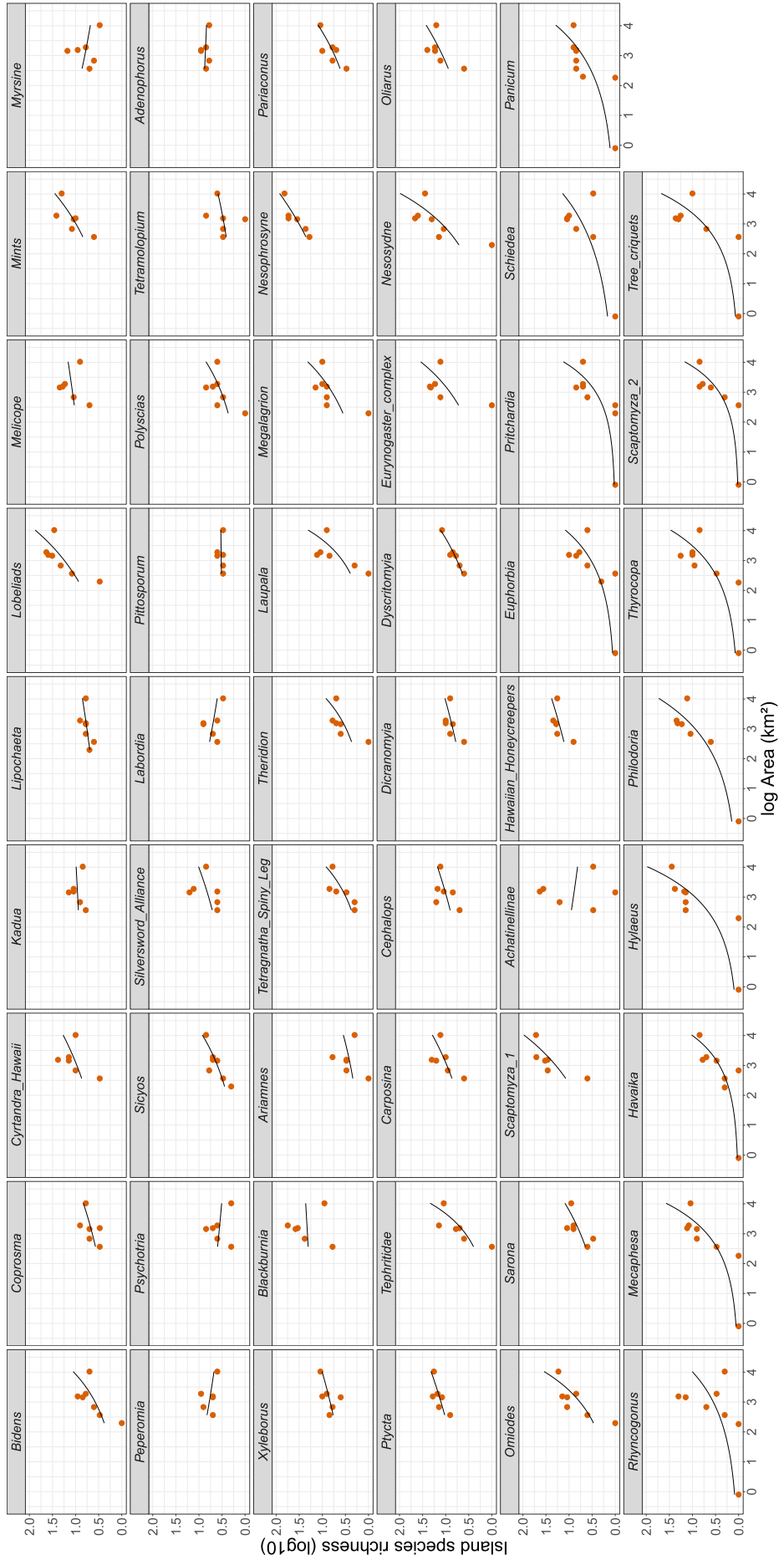


Figure III.S4. Relationships between S_{ROA} and $\log_{10} \text{area}$ for the Hawaiian archipelago. Dots indicate islands, and the black curves show the fitted values extracted from the Poisson/Negative binomial generalized linear models.

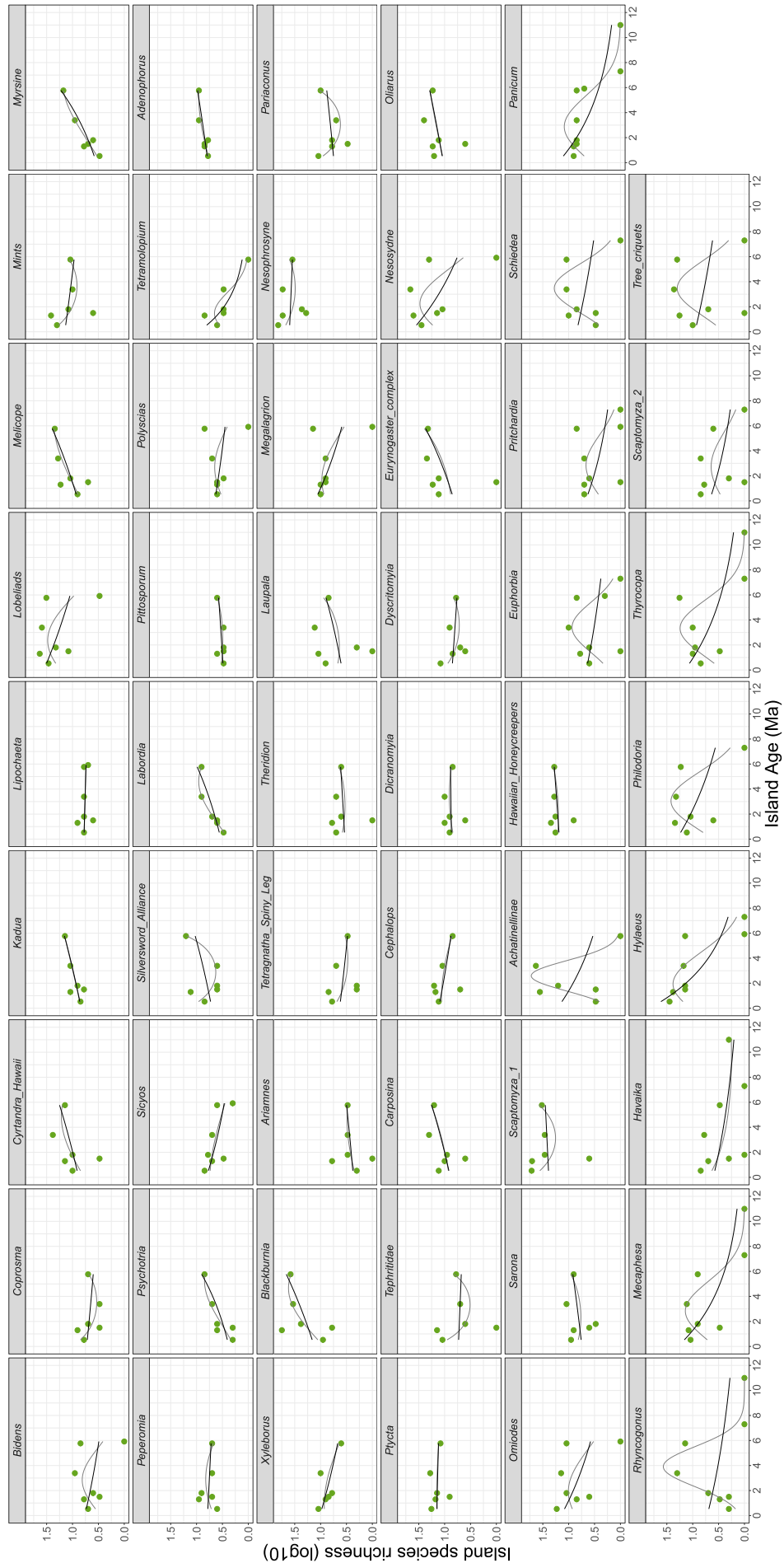


Figure III.S5. Relationships between S_{ROA} and age (black lines) and S_{ROA} and $age+age^2$ (grey lines) for the Hawaiian archipelago. Dots indicate islands, and the black curves show the fitted values extracted from the Poisson/Negative binomial generalized linear models.

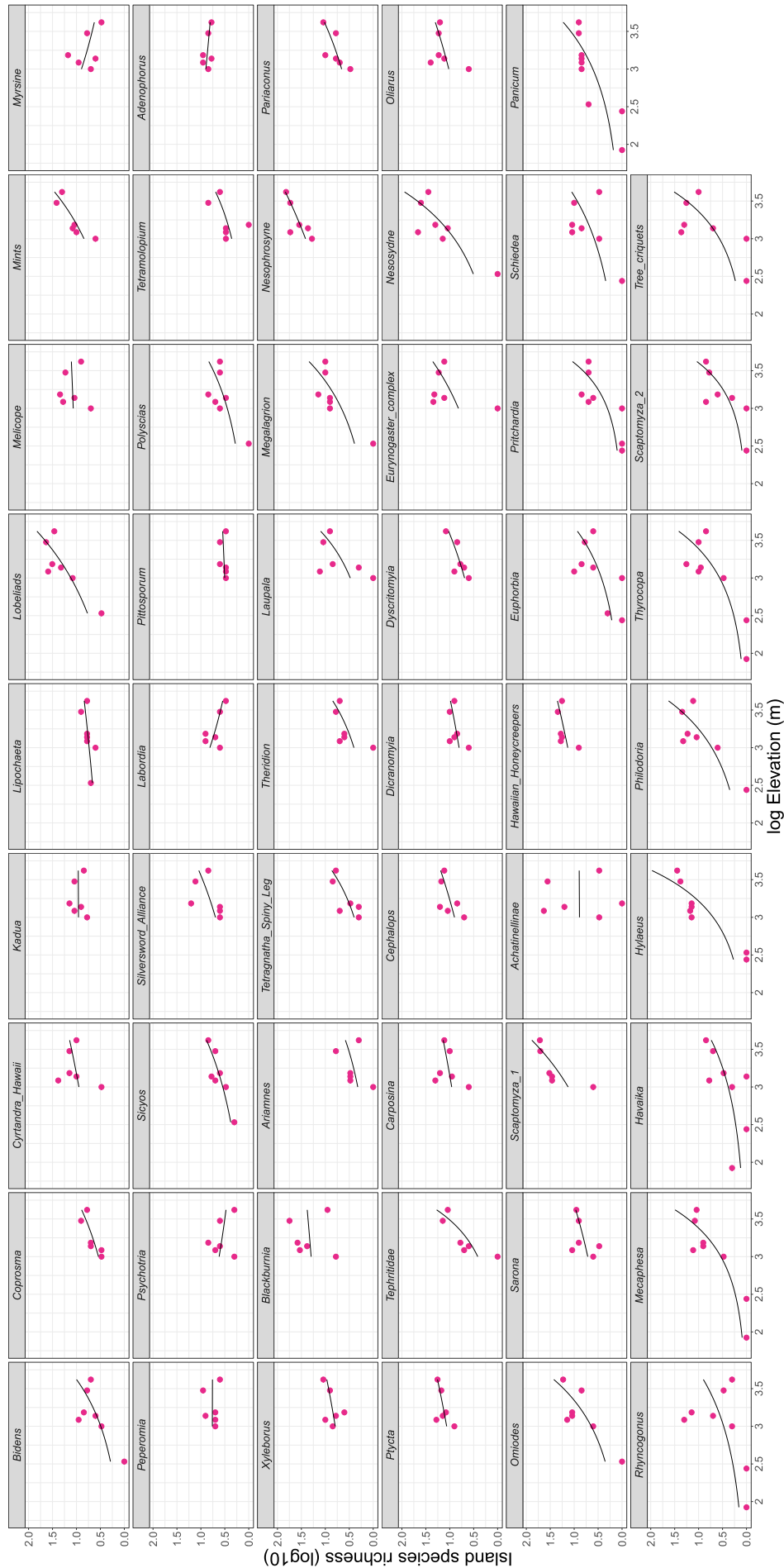


Figure III.S6. Relationships between S_{ROA} and \log_{10} elevation for the Hawaiian archipelago. Dots indicate islands, and the black curves show the fitted values extracted from the Poisson/Negative binomial generalized linear models

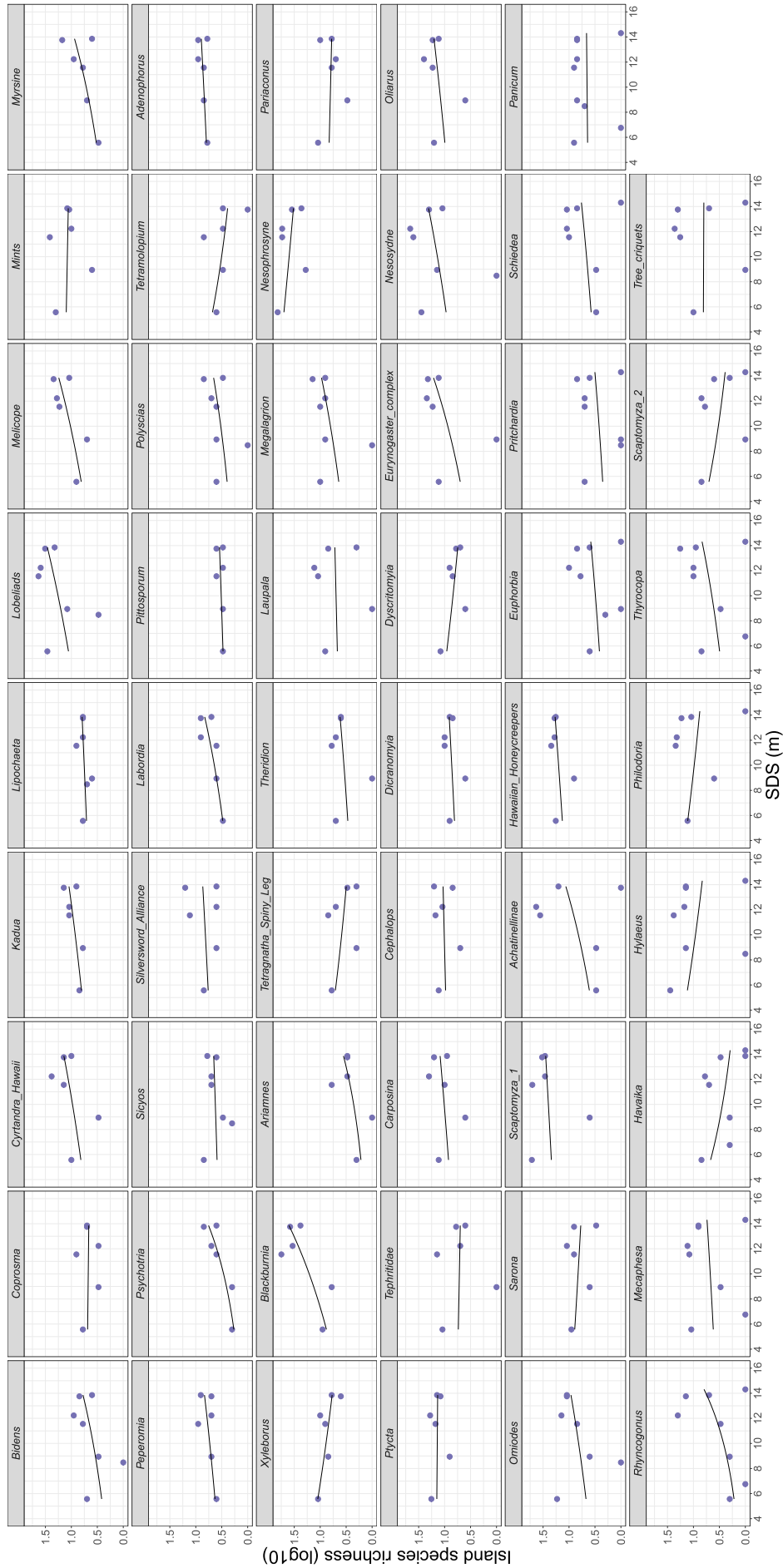


Figure III.S7. Relationships between S_{ROA} and SDS for the Hawaiian archipelago. Dots indicate islands, and the black curves show the fitted values extracted from the Poisson/Negative binomial generalized linear models

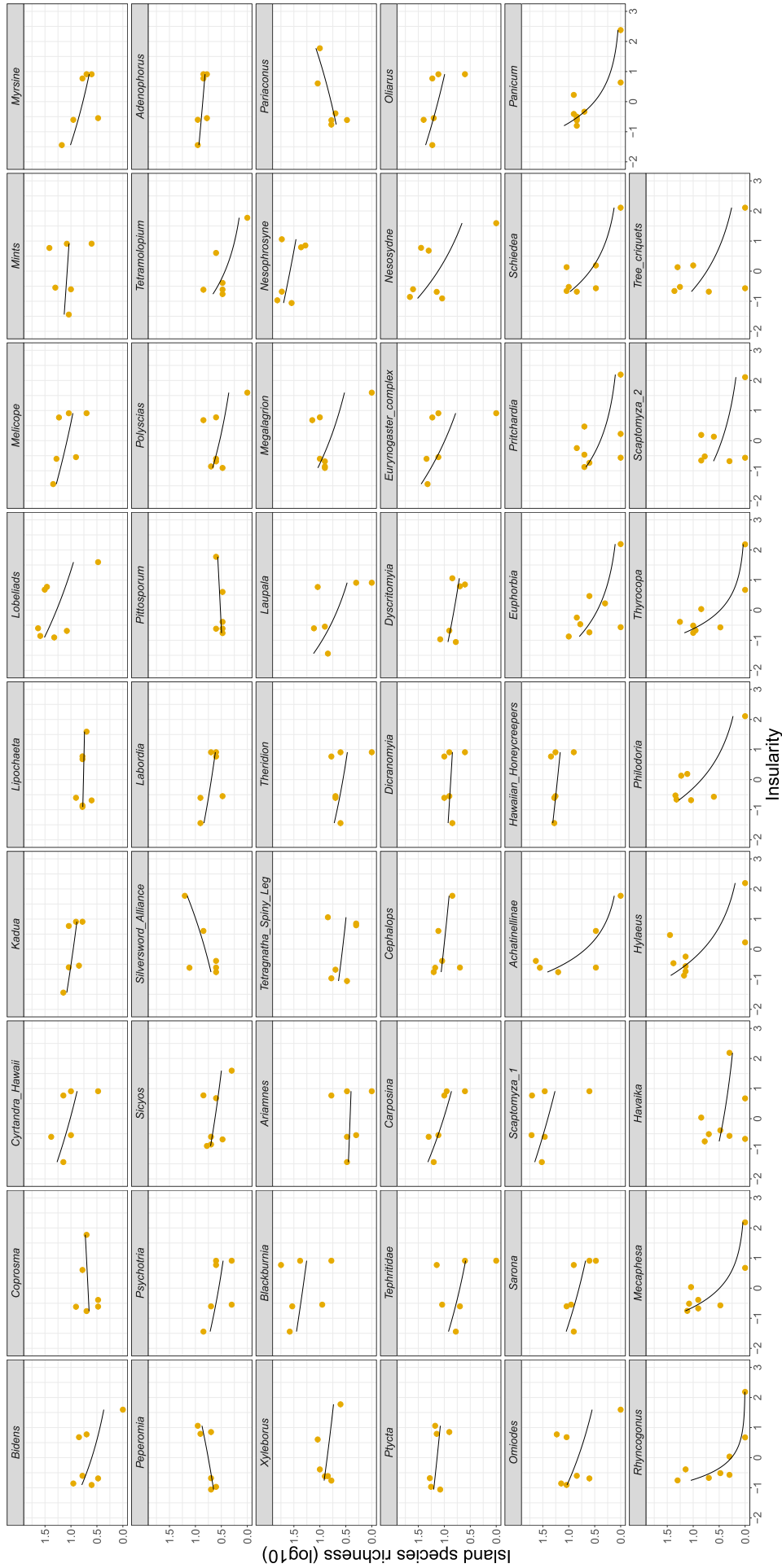


Figure III.S8. Relationships between S_{ROA} and isolation (NI) for the Hawaiian archipelago. Dots indicate islands, and the black curves show the fitted values extracted from the Poisson/Negative binomial generalized linear models

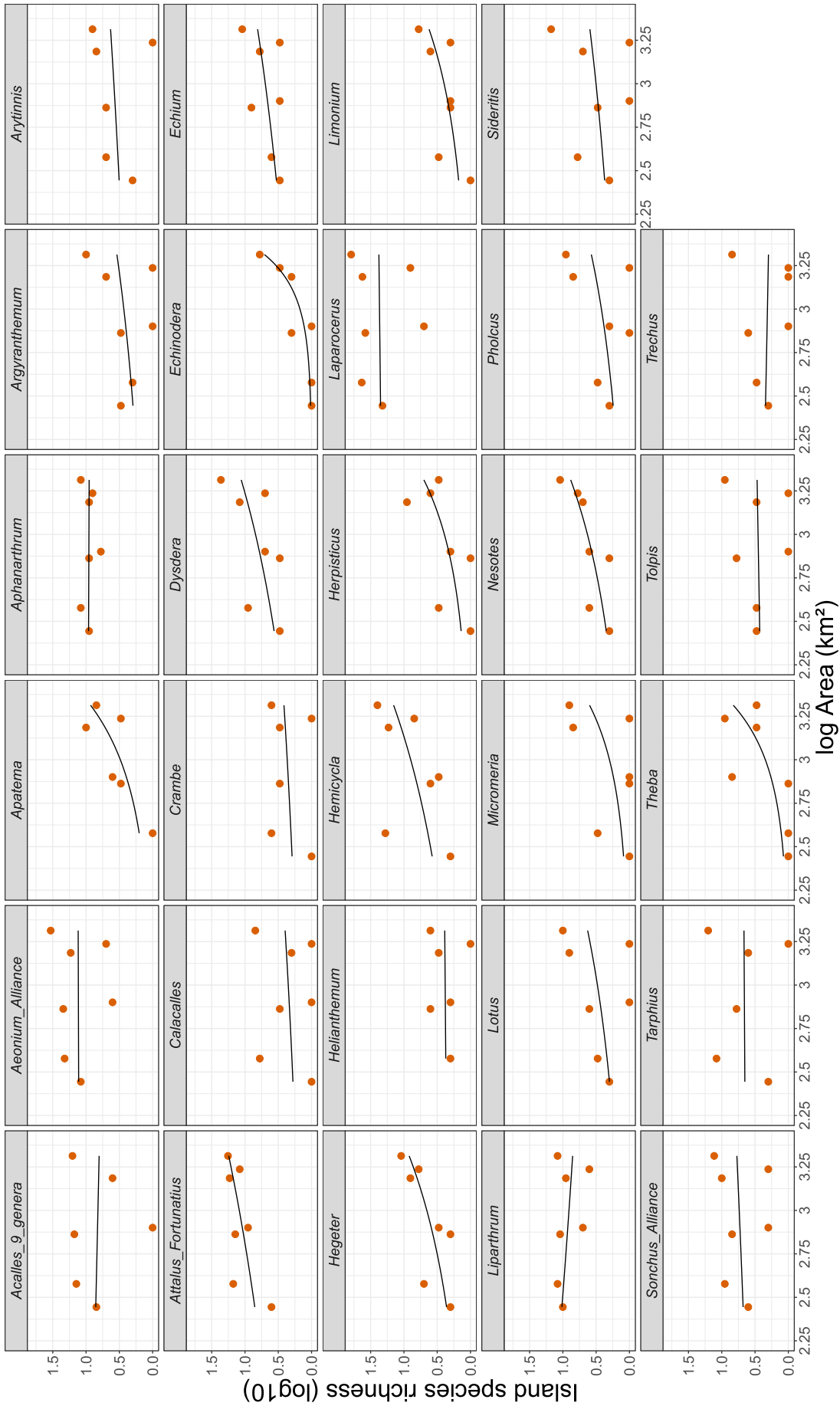


Figure III.S9. Relationships between S_{rOA} and $\log_{10}area$ for the Canary Islands. Dots indicate islands, and the black curves show the fitted values extracted from the Poisson/Negative binomial generalized linear models.

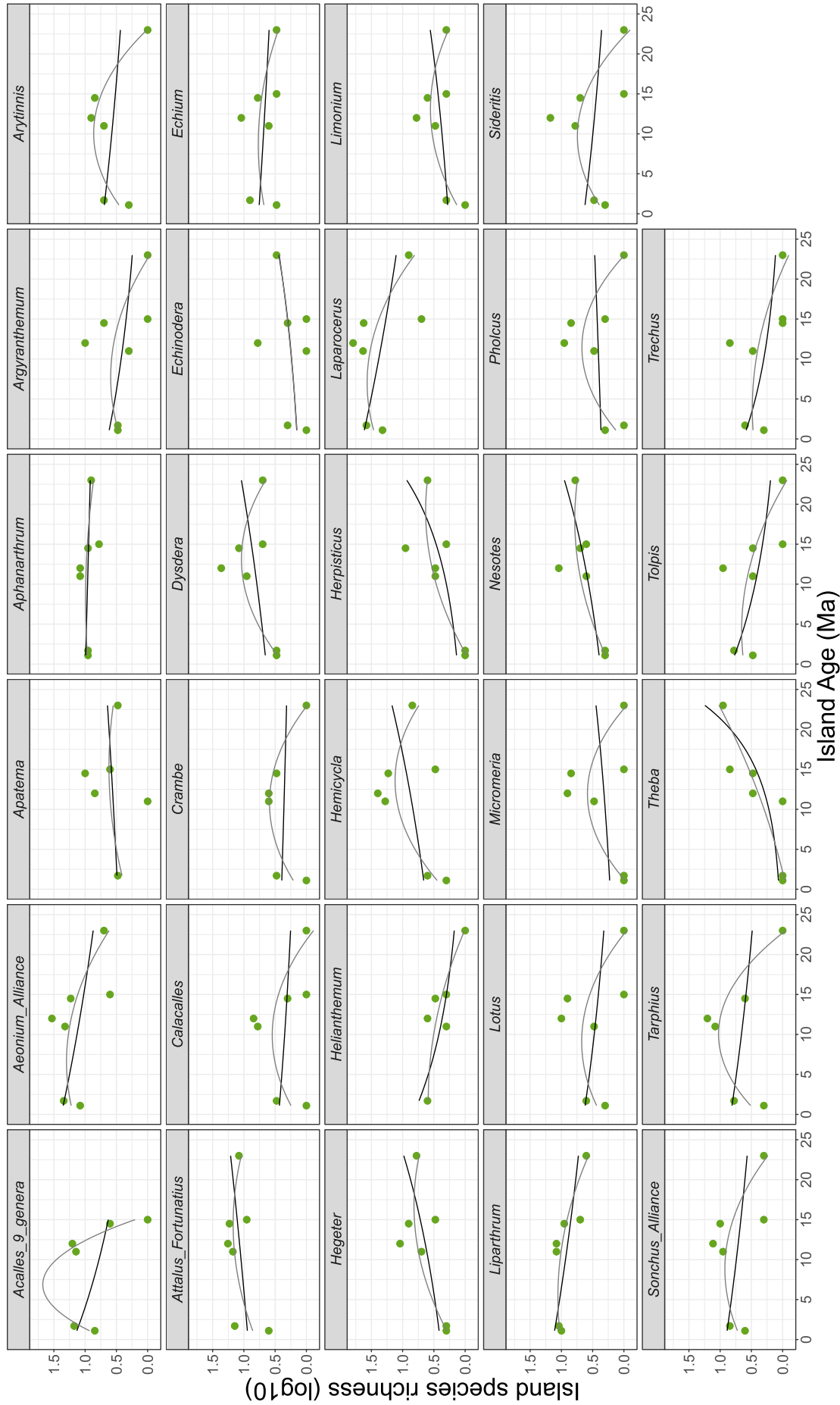


Figure III.S10. Relationships between S_{ROA} and age and S_{ROA} and age+age² for the Canary Islands. Dots indicate islands. The black (age) and grey (age+age²) curves show the fitted values extracted from the Poisson/Negative binomial generalized linear models.

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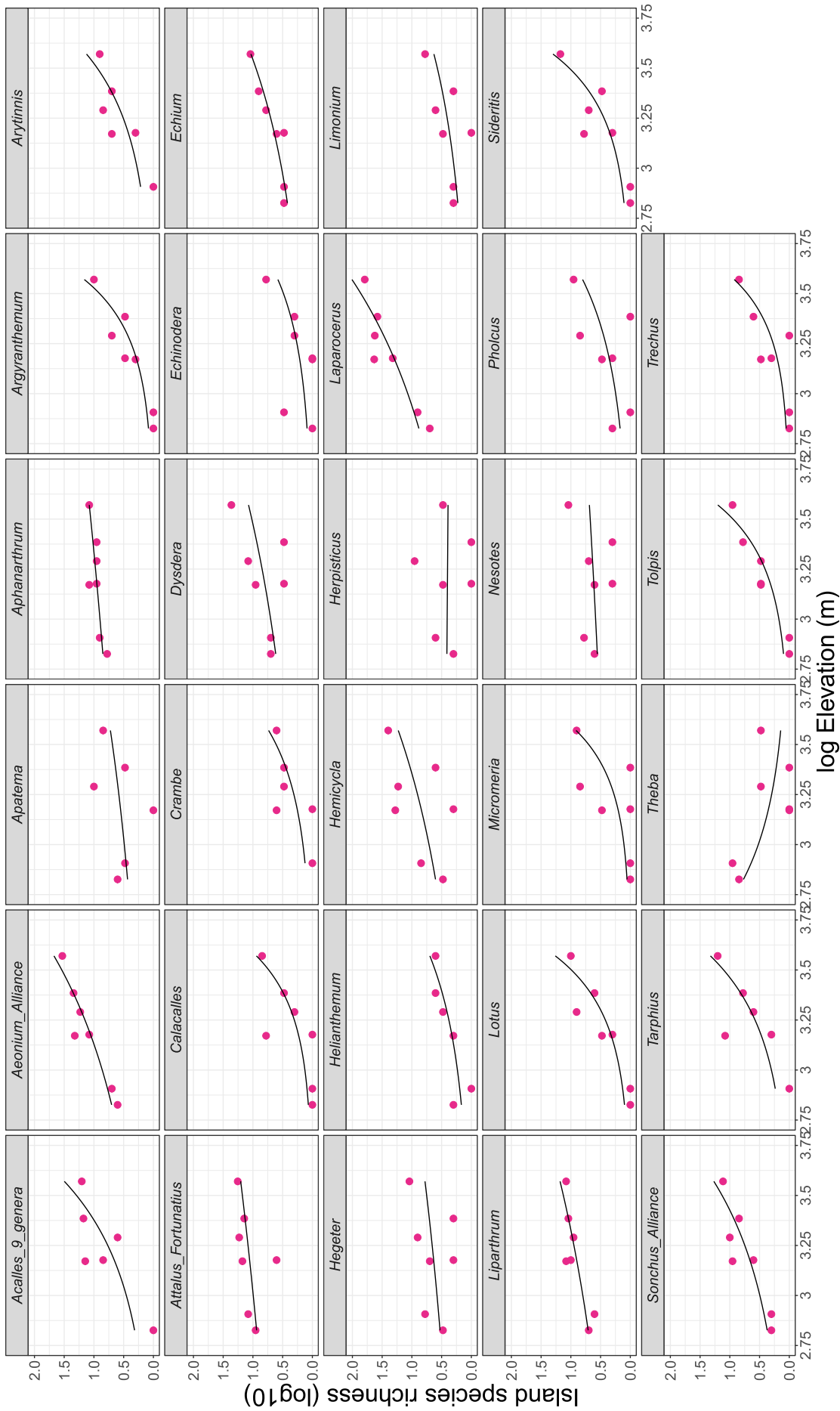


Figure III.S11. Relationships between S_{ROA} and \log_{10} elevation for the Canary Islands. Dots indicate islands, and the black curves show the fitted values extracted from the Poisson/Negative binomial generalized linear models

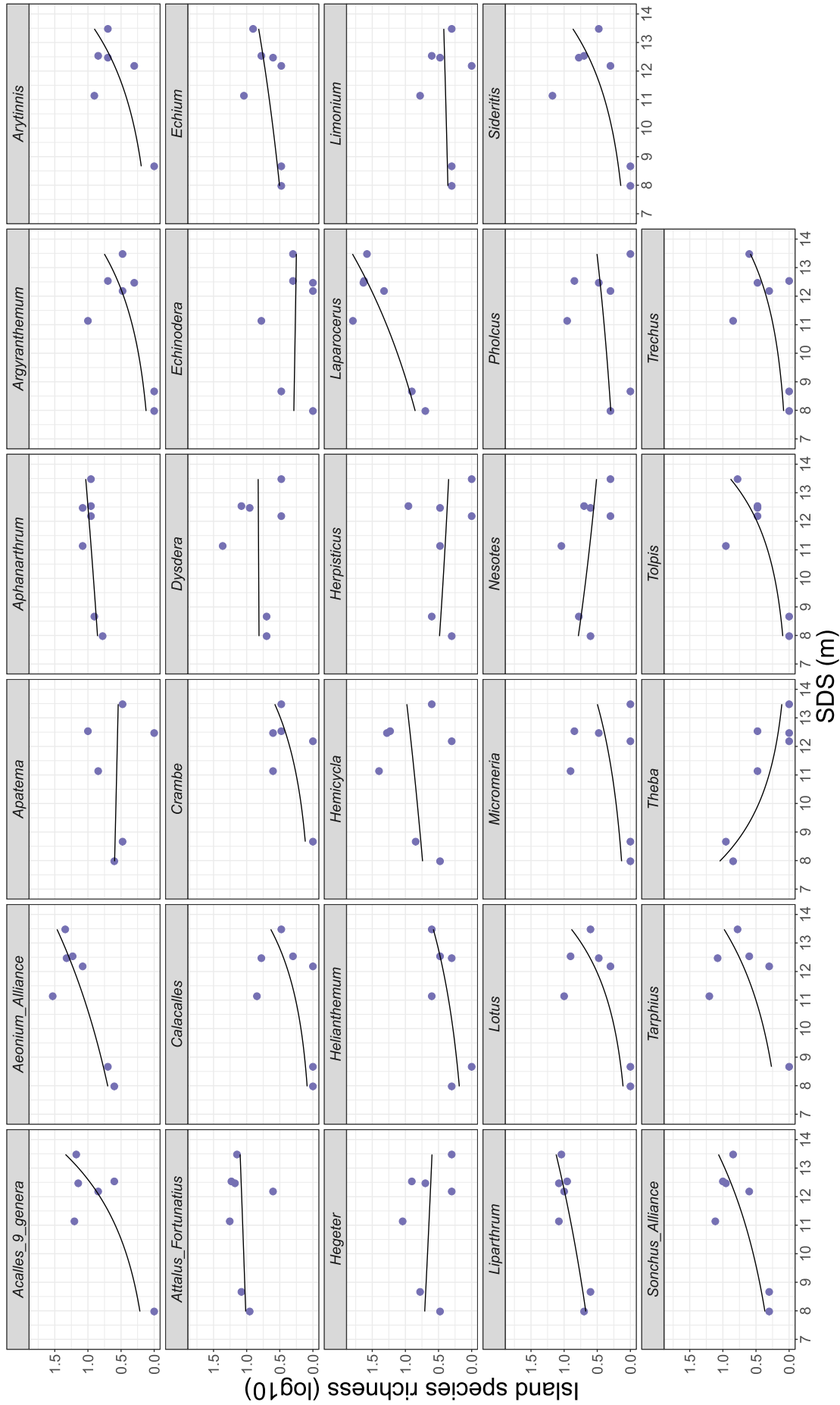


Figure III.S12. Relationships between S_{ROA} and SDS for the Canary Islands. Dots indicate islands, and the black curves show the fitted values extracted from the Poisson/Negative binomial generalized linear models

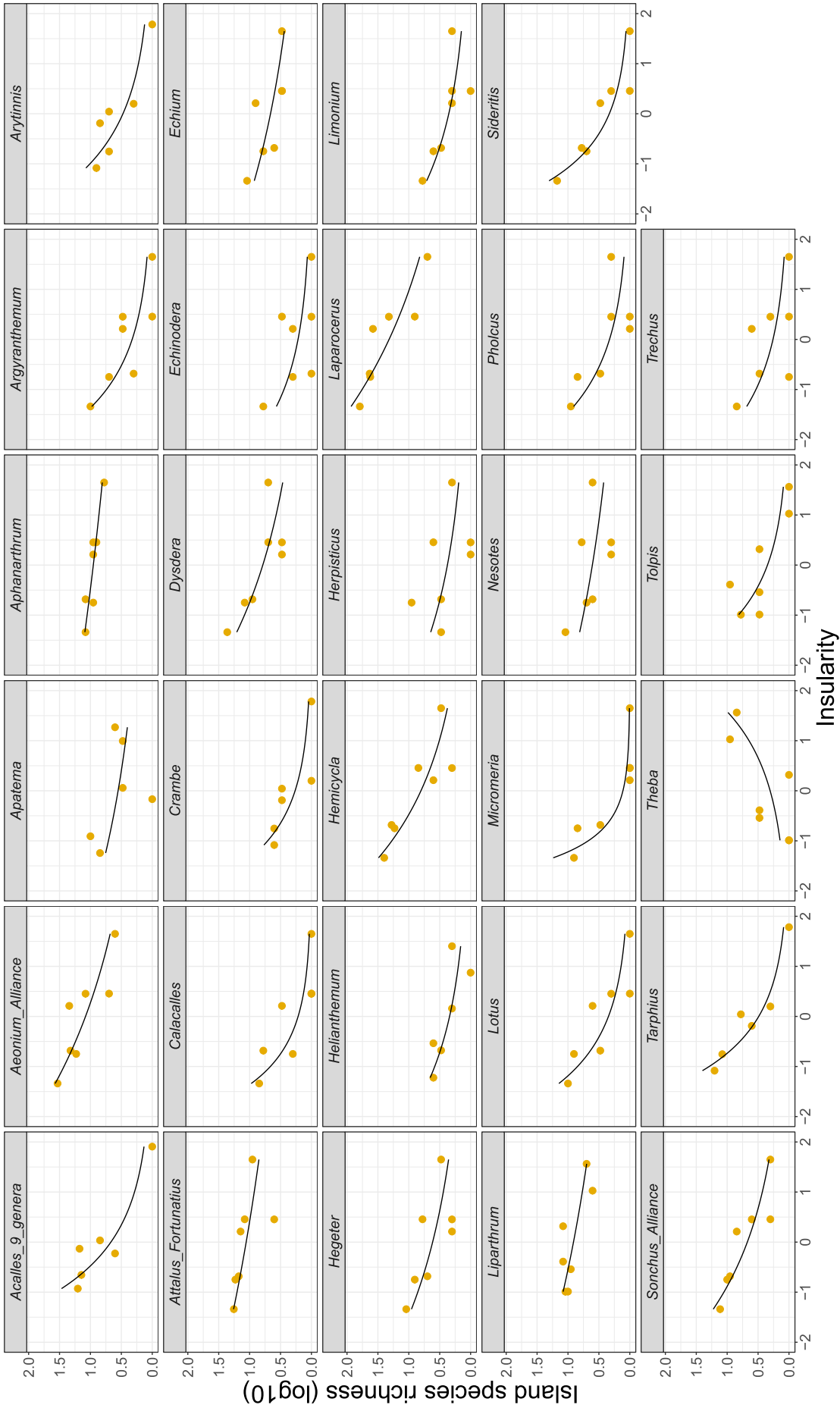


Figure III.S31. Relationships between S_{ROA} and isolation (NI) for the Canary Islands. Dots indicate islands, and the black curves show the fitted values extracted from the Poisson/Negative binomial generalized linear models

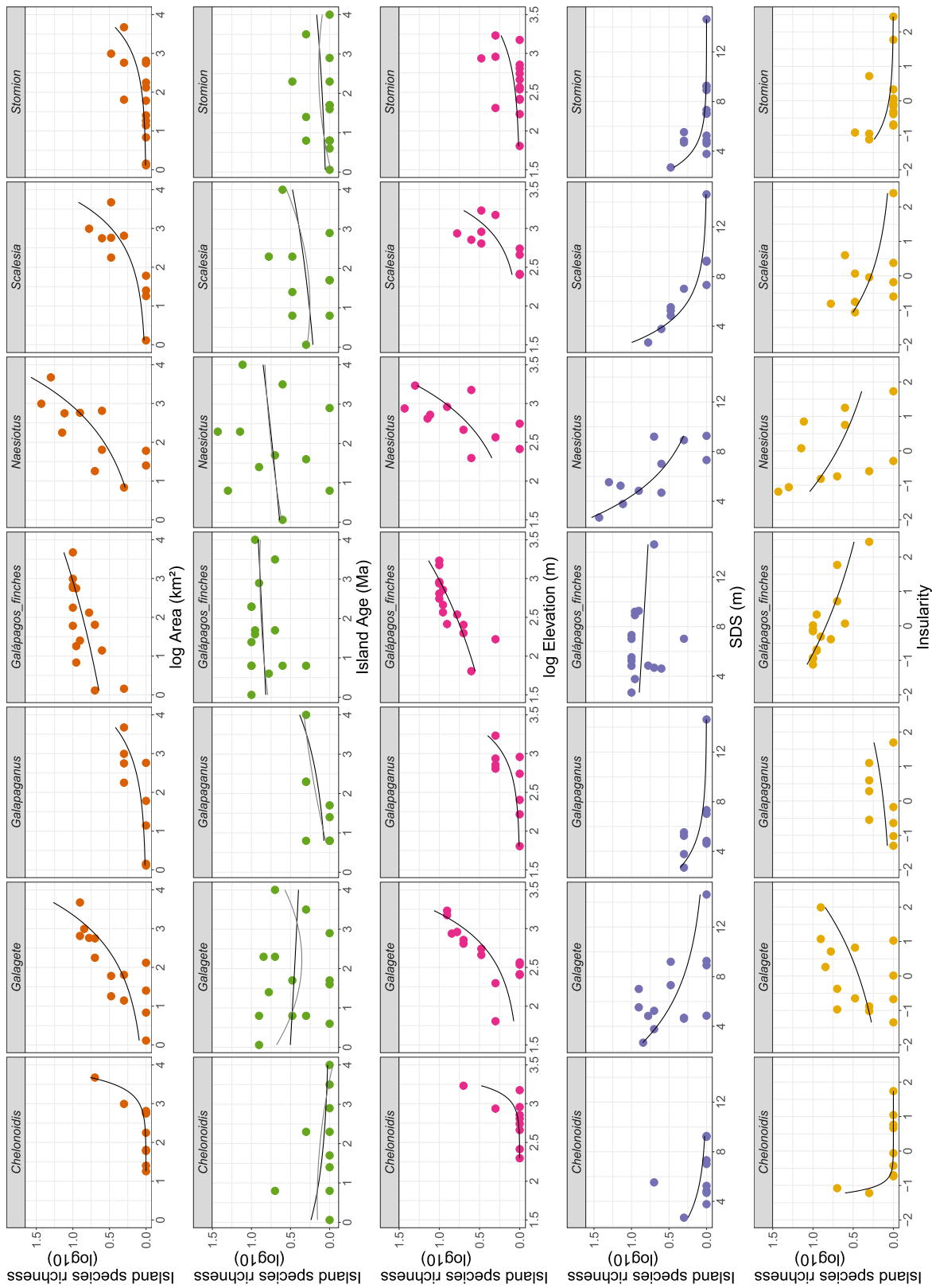


Figure III.S14. Linear and humped shaped relationships between S_{ROA} and the six geo-environmental factors tested in our study, for the seven ROAs from Galápagos. The colors correspond to the six factors as in **Figure 2**. Black lines represent linear regressions, and grey lines in the Age plots represent the humped shape relationship with $age+age^2$.



Figure III.S15. Linear and humped shaped relationships between S_{ROA} and the six geo-environmental factors tested in our study, for the six ROAs from Fiji. The colors correspond to the six factors as in **Figure 2**. Dots indicate islands, and the black curves show the fitted values extracted from the Poisson/Negative binomial generalized linear models

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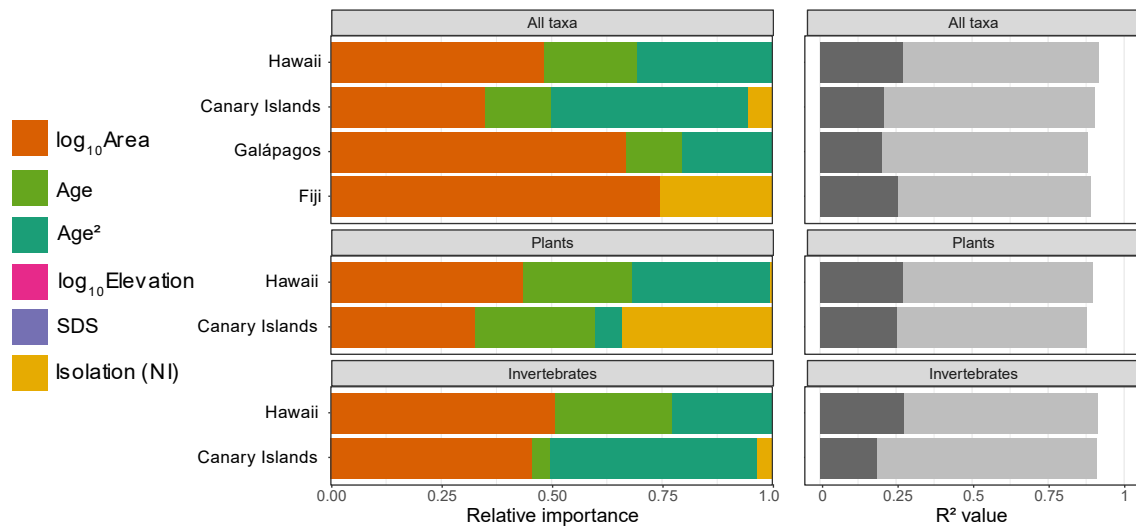


Figure III.S16. Results of the GLMMs performed with the paleo variables. Left panels: relative importance of each fixed effect as predictor of the S_{ROA} for each archipelago and the plants and invertebrates. Results for the plants and invertebrates subsets are given only for Hawaii and the Canary Islands for which enough ROAs were available in each archipelago (See Table 2 for detailed results). Right panel: Decomposition of the variance explained by the best model(s) (conditional R^2_c) into its components assigned to the fixed (marginal R^2_m , dark grey) and random effects ($R^2_c - R^2_m$, light grey) for each archipelago and the plants and invertebrates subsets for Hawaii and the Canary Islands (mean R^2 of all best models).

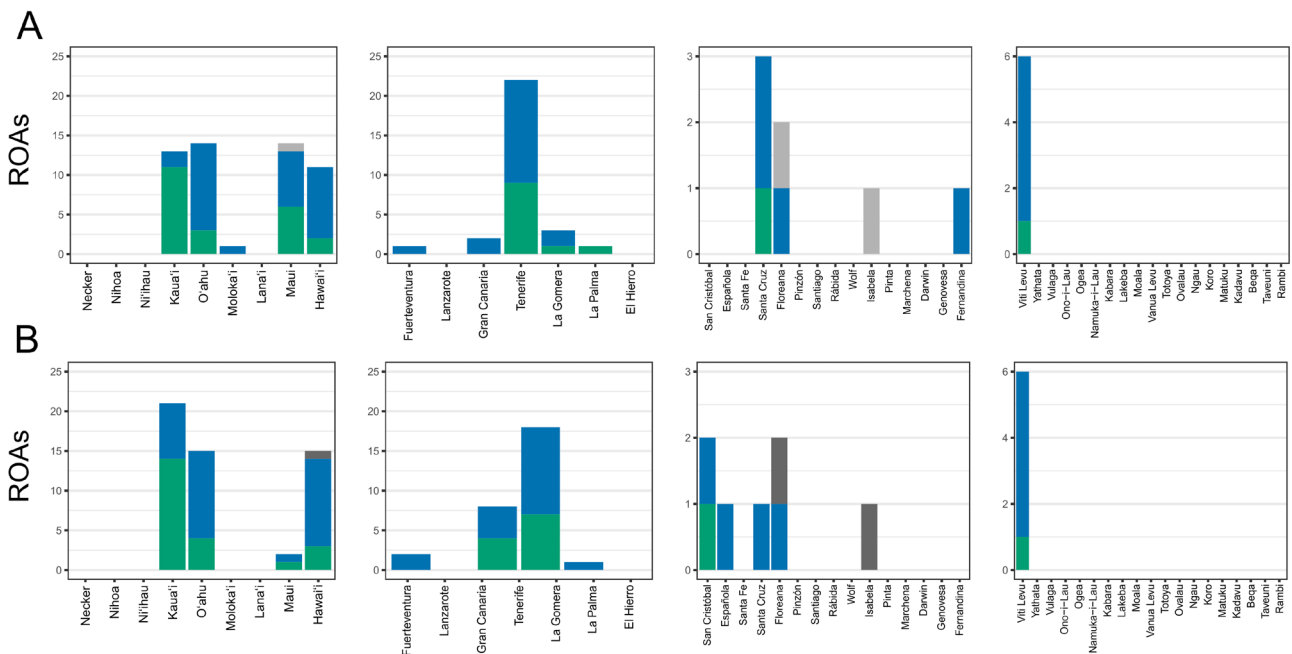


Figure III.S17. Number of ROAs per island that have their highest Island S_{ROA} (A) and highest number of Single Island Endemics (B) on the island. For instance, 22 ROAs reach their maximum Island S_{ROA} on Tenerife, and 18 ROAs reach their maximum number of SIE on this same island. Colors show the type of taxon (invertebrates=blue, plants=green, vertebrates=grey).

**Chapitre IV : Tempo et mode de
diversification des radiations évolutives sur
les archipels océaniques**

Résumé

Depuis la publication de la théorie de l'équilibre de la biogéographie insulaire par MacArthur et Wilson, de nombreuses études ont tenté de mettre en évidence la présence ou non d'un équilibre dynamique au sein des communautés insulaires. Cette notion d'équilibre, qui implique un ralentissement dans l'accumulation des espèces au cours du temps, souvent lié à un phénomène de diversité-dépendance, n'a été que très rarement testé à l'échelle des radiations évolutives des archipels océaniques (ROAs). Pourtant, étudier la dynamique d'accumulation des espèces pour les ROA permettrait de mieux comprendre les mécanismes sous-jacents à la diversification biologique dans îles océaniques. Dans cette étude, le mode de diversification de 44 phylogénies de ROAs dans huit archipels différents a été analysé. Les résultats montrent que la majorité des ROAs présentait une accumulation constante des espèces au cours du temps, contrastant avec l'idée d'équilibre. Un ralentissement a cependant été détecté pour un quart des ROAs étudiées. Trois hypothèses non exclusives ont été mises en avant pour expliquer nos résultats (i) l'âge généralement très jeune des ROAs, expliquant pourquoi elles n'ont pas encore atteint leur équilibre ; (ii) la dynamique d'expansion des archipels océaniques permettant aux radiations de continuer à s'étendre vers de nouveaux espaces écologiques ; (iii) le taux élevé d'extinction dans ce type d'archipels, qui aurait pu atténuer le signal d'un ralentissement du taux d'accumulation des espèces. Nos résultats soulignent la pertinence d'une théorie du non-équilibre pour ce type de système insulaire.

Etat de publication

Ce manuscrit n'est encore qu'à l'état de chapitre de thèse. En effet, comme expliqué dans la partie matériels et méthodes du chapitre, un certain nombre de phylogénies n'ont pas encore été inclus dans les analyses, faute de temps et/ou de problèmes liés à leur reconstruction et/ou leur datation. Nous espérons dans le futur pouvoir en ajouter d'autres et ainsi obtenir une meilleure vision d'ensemble des patrons macroévolutifs des ROAs.

1. Introduction

Oceanic islands have long fascinated scientists thanks in part to their unique biotas, which encompass many endemic species (Whittaker et al. 2023). These particularly isolated landmasses have also been proven powerful models for understanding diversification mechanisms, and a large body of theory have provided testable predictions on how island geographic and ecological properties influence endemic diversity (Schluter 2000, Givnish et al. 2008, Warren et al. 2015, Whittaker et al. 2023). Among these, MacArthur & Wilson's landmark island biogeography has been one of the most influential theories in the field of biogeography and ecology (MacArthur & Wilson 1963, 1967). Inspired by the concept of density-dependent regulation of populations (Lack 1954), they introduced the idea that the species diversity on islands should be viewed as a dynamic equilibrium balanced by immigration and extinction. Their theory is that the rate of species accumulation will progressively slow-down as it reaches the maximum carrying capacity of the islands (i.e., diversity-dependent mechanism) (Rabosky 2013). This space filling can be seen as a neutral process in which immigration rate decreases and extinction rate increases as the system reaches its carrying capacity, in line with the classical logistic growth (Marshall & Quental 2016). In contrast, the deterministic view of equilibrium interprets carrying capacity as the maximum number of niches available in the system, with competition for niche space limiting species richness through diversity-dependent feedbacks (Rabosky & Glor 2010, Valente et al. 2014). The nature and prevalence of this equilibrium have been subject of extensive discussions (Simberloff 1974, Heaney 2000, Rabosky & Glor 2010, Valente et al. 2015) and have especially been challenged in the case of oceanic islands (Heaney 2000, Whittaker et al. 2008). Indeed, the sometimes-extreme isolation of oceanic islands limits colonisation, resulting in a biota formed primarily by *in situ* speciation (Whittaker et al. 2008). In addition, oceanic islands are characterized by frequent and severe climatic and geological events throughout their relatively short life cycle, contributing to high extinction rates. Given that speciation takes time, it has therefore been suggested that the net diversification rate (speciation minus extinction) may be too slow to reach equilibrium (Heaney 2000, Whittaker et al. 2008). However, to date, few empirical studies have been conducted to test the extent to which dynamic equilibrium theory could effectively be applied to oceanic islands (but see Valente et al. 2015, 2017).

In this context, molecular phylogenies are a primary source of information, as the rate of species accumulation can be inferred from the timing of divergence between lineages (Ricklefs 2007, Morlon 2014). However, very few studies have taken advantage of the temporal information encoded in molecular phylogenies to assess the tempo and mode of diversification on oceanic

CHAPITRE IV : TEMPO ET MODE DE DIVERSIFICATION DES RADIATIONS EVOLUTIVES SUR LES ARCHIPELS OCEANIQUES

islands (Valente et al. 2015, 2018). Evolutionary radiations on oceanic archipelagos (hereafter ROAs) such as the Darwin's Finches (Grant & Grant 2008) or the Hawaiian Lobeliads (Givnish et al. 2009) can serve here as ideal models. Indeed, ROAs are monophyletic groups endemic to a given oceanic archipelago, therefore resulting solely from *in situ* speciation. Their taxonomic diversity is also well-known, and the diversification process of many of them is thought to have been driven by divergent natural selection generated through competition (Schluter 2000). Moreover, ROAs have been extensively studied from a phylogenetic perspective, resulting in several well-resolved, time-calibrated phylogenies covering a wide range of taxonomic groups and oceanic island systems. (e.g., Cowie & Holland 2008, Parent et al. 2008, Gillespie et al. 2008).

One of few conceptual models existing for the diversification pattern of ROAs is the proposition of the General Dynamic Model of oceanic island biogeography (GDM; Whittaker et al. 2008). Basically, the premise of the GDM implies that ROAs should be one of the most recurrent patterns in oceanic islands, at least during the period where islands grow up in size and complexity (Whittaker et al. 2008). In the model, diversification patterns could be decomposed in three successive and distinct phases: (i) a fast accumulation of lineages due to an increase of ecological opportunities as the island emerges and grows (the adaptive phase) ; (ii) a slowdown of species accumulation rate, reflecting the transition to the non-adaptive phase (intra-island allopatry) as the island reaches its maximum elevation and topographic complexity ; (iii) an equilibrium phase, reflecting the finite resources of the island which imposes, in turn, a limit to diversity. According to this proposal, the relationship between the number of lineages and their respective ages should be asymptotic, resulting from a slowdown in diversification. Using simulations, Valente et al. (2014) have shown the presence of diversification slowdown for ROAs restricted to old oceanic islands (Valente et al. 2014). Yet, such predictions remain difficult to test, as ROAs in these contexts have been primarily seen as evolving at the scale of a single island. However, most ROAs described today have diversified throughout several islands, making them more likely to be influenced by geo-environmental dynamics at the scale of an entire archipelago, which might be more than just the sum of island individual contributions. Indeed, the spatio-temporal configuration of the islands within the archipelago has for example been shown to play a significant role in shaping island diversity (Gascuel et al. 2016, Aguilée et al. 2021).

In this study, we aimed to investigate the tempo and the mode of diversification of several ROAs from multiple taxa and archipelagos. We identified and tested three general diversification patterns that are likely to emerge for ROAs at the archipelago scale. Hypothesis 1: ROAs tend toward equilibrium at the archipelago scale. Several studies have already identified a trend towards

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equilibrium in some ROAs (Strijk et al. 2014, Le Péchon et al. 2015, Bennett & O'Grady 2013, Valente et al. 2015). The rationale is that what occurs on a single island should also prevail for the archipelago level, with the number of speciation opportunities across the archipelago increasing at a slower pace than the rate of species accumulation of the ROA. Moreover, this *early burst* pattern of diversification has been shown to be prevalent in macroevolutionary literature (Morlon et al. 2010) and is often associated with adaptive radiations (Moen & Morlon 2014), which are believed to be common among ROAs (Cerca et al. 2023). Hypothesis 2: ROAs show a constant rate of species accumulation through time. The main cause behind this diversification pattern could be that most ROAs did not reach their ecological limit yet, and will potentially continue their expansion into new niche spaces in the future, due for example to the emergence of new islands (Esselstyn et al. 2009, Fritz et al. 2011, Justiniano et al. 2015). This reasoning implies that archipelagos are continually expanding their ecological space. While comprehensive geological data for entire archipelagos are scarce, recent simplified reconstructions of the geological histories of several oceanic archipelagos (e.g., Hawaii, The Canary Islands, Galápagos) seem to support the idea of an increase of area over time (Lim & Marshall 2017, Jöks et al. 2020). Hypothesis 3: ROAs show a *late burst* pattern of diversification, where the rate of diversification accelerates through time (i.e., the pull-of-the-present hypothesis, Nee et al. 1992). The rationale here is that oceanic archipelagos are prone to catastrophic events that can drive lot of endemic species to extinction, such as the sterilization of large surfaces due to volcanic eruptions, mega-landslides cutting large areas down into the ocean and generating tsunamis on neighbors islands, and also tropical storms and earthquakes (Fernández-Palacios et al. 2021, Whittaker et al. 2023). The late rise of diversification detected might therefore be the result of a recent pulse of speciation due to the vacant ecological space left by older species that have been wiped out (Pybus & Harvey 2000).

The tempo and mode of diversification of a given ROA can also be influenced not only by the dynamic of the archipelago into which it has radiated, but also by its intrinsic characteristics such as its reproduction cycle, dispersal capacities or adaptability (Paulay 1994, Borges & Hortal 2009, Lim & Marshall 2017). For instance, some ROAs might produce species at a high rate and therefore quickly saturate the ecological space available, while others will speciate much more slowly and show no specific correlation with the geo-environmental changes induced by the oceanic archipelago dynamic. These modulations have also to be paired up with the age of emergence of the ROA: indeed, a ROA that have colonised the archipelago only recently might not show yet a slowdown of diversification, even if it might tend toward equilibrium in the future (Esselstyn et al. 2009).

In this study, we conducted a comparative analysis of diversification patterns across different island taxa from various oceanic archipelagos. Our approach involved tree reconstructions and diversification analyses, in order to discern whether there is an emerging global diversification pattern for ROAs, or if the pattern is idiosyncratic. We will discuss the results obtained in the light of some key ROA features (e.g., taxa, age, size, diversification rate) and acknowledge the potential of such macroevolutionary analysis for our understanding of ROAs evolutionary history.

2. Materials & Methods

2. a. ROAs selection and characteristics

We performed a standardized literature search in Web of Science (WOS) and Google Scholar indexing systems (last access March 2023) to identify all ROAs that have been the subject of at least one molecular phylogenetic analysis. We then first generated a list of the major oceanic archipelagos worldwide based on our own expertise in the field and literature survey (**Table II.S1**) and use the search string TS = (“*name of each oceanic archipelago*” AND TS = (“*phylog**” OR “*radiation*” OR “*endemic*”) for each of them. Results of the searches were then screened in order to identify every ROAs with a phylogenetic tree. We also double-checked key reviews on the topic (e.g., Gillespie & Roderick 2002, Emerson 2002, Shaw & Gillespie 2015, Price & Wagner 2018, Hembry & Balukjian 2016, Crawford & Archibald 201, Hembry 2018, Hembry et al. 2021) to ensure that no relevant ROA had been missed. Because macroevolutionary analyses require to have a minimum amount of phylogenetic information in order to recover unbiased estimators (Cusimano & Renner 2010, Brock et al. 2011, Beaulieu & O’Meara 2015), we choose to keep only ROAs which presented a phylogenetic completeness higher than 50% (i.e., the ratio between the number of species in the phylogeny and the number of species thought to belong to the ROA) (McPeck 2008) and that include at least 10 species. We then identified 98 ROAs fitting our criterion, that are reported and detailed in **Table IV.S1**. From this initial pool, 44 ROAs were further selected for the present study on the basis of data availability, lineage consistency and possible calibration strategy (see **Table IV.S1**). Of these 44 ROAs, 28 were time-calibrated phylogenies that we either reconstructed or retrieved from the literature (mainly plants), and 16 were phylogenies that we reconstructed using relative time (mainly invertebrates), although for most of these, a calibration has been proposed in the literature, but has not yet been implemented. A total of 39 ROA phylogenies (mainly invertebrates) will be added in the near future, but not all of them have been time-calibrated. Finally, 15 ROAs were removed from our final list of 98 ROAs due to high taxonomic uncertainties, unresolved topology and/or data inaccessibility (see **Table IV.S1**). For each of the 44 selected ROAs, we gathered the following information: (i) archipelago of origin (ii), broad taxon classification (either

plants, invertebrates, birds, or reptiles), (iii) number of species including in the phylogeny, (iv) phylogenetic sampling fraction, (v) crown age – either taken from the reconstructed time-calibrated phylogenies or from the literature, (vi) net diversification rate (see below) and (vii) type of radiation (i.e., either adaptive, non-adaptive or both).

2. b. Reconstructing ROAs phylogenies

The 44 ROAs phylogenetic trees were acquired through different strategies, mainly depending on the type of data that have been used to reconstruct the most recent and complete phylogenetic tree published. We identified three categories of phylogenies: (1) *Phylogenies reconstructed from Sanger genetic data and time-calibrated (20)*: 17 phylogenies were reconstructed from DNA sequences and dated with BEAST (Suchard et al. 2018), and three were retrieved from publication. (2) *Phylogenies reconstructed from genomic data and time-calibrated (8)*: six Maximum Likelihood (ML) trees were recovered from the literature or after request to corresponding authors and were time-calibrated using TreePL (Smith & O'Meara 2012), and two genomic time-calibrated trees were directly retrieved from publication. *Phylogenies reconstructed from Sanger genetic data but calibrated with relative time (16)*: all phylogenies in this group were reconstructed from DNA sequence and time-calibrated with BEAST2 (Bouckaert et al. 2014).

2.b.1. Phylogenetic tree reconstruction

Sanger tree phylogenetic reconstruction was performed using the following pipeline: all sanger data that has been used in the most recent and complete phylogenetic study were retrieved using the NCBI research engine in Geneious 10.0.9 (Kearse et al. 2012). If necessary, these data were completed with other literature sources in order to add further genetic markers and/or outgroups for calibration purposes (see **Table IV.S2-S3** for the list of markers and references). Each genetic marker was then aligned independently using MAFFT 7.490 (Katoh & Standley 2013) with default settings (automatic model selection option), and all markers were further concatenated to form one global genetic matrix. The optimal partition scheme and model of evolution for each partition was then inferred with PartitionFinder 2.1.1 (Lanfear et al. 2017), using the greedy algorithm and an AICc model selection (branchlengths = linked, models = all, Lanfear et al. 2012). Phylogenetic reconstruction and divergence time estimations were performed using BEAST 1.10.4 (Suchard et al. 2018), or BEAST 2.6.7 (Bouckaert et al. 2014) for relative-time inferences. The matrix, partition scheme and models of evolution were then implemented in BEAUti, as well as an uncorrelated lognormal relaxed-clock model for each partition (Drummond et al. 2006) and a birth-death process tree prior (Gernhard 2008). One or several priors were specified to calibrate the tree in real or relative time (see **Table S2** and below). The BEAST analysis was run for 100 million

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generations, sampling every 10000th generations. MCMC convergence was checked using Tracer 1.7.1 (Rambaut et al. 2018), and a Maximum Clade Credibility (MCC) tree was obtained using Treeannotator v 2.6.6, after applying a 10% burnin.

2.b.2. Time-calibrations

Calibrating ROA phylogenies in time is challenging, as fossil information is often very scarce or even non-existent for oceanic island clades (Landis et al. 2018, García-Verdugo et al. 2019 and references herein). Consequently, alternatives or mixed methods involving fossil, geological information and/or substitution rates have often been used to calibrate ROAs phylogenies (Baldwin et al. 1998, Richardson et al. 2001, Landis et al. 2018, Arnedo & Hormiga 2020). In order to standardize our calibrations as much as possible, we have implemented a calibration strategy that involves only fossil-related information (as direct or secondary calibrations) for all recovered plant ROAs (See **Table IV.S2**). Unfortunately, we were not able to find enough information in the literature to apply a similar approach to the remaining phylogenies (mainly invertebrates). As we did not yet have time to establish an alternative approach for these ROAs, we opted for a relative-time calibration so that we could still retrieve ultrametric trees to study the diversification pattern of these phylogenies. Specifically, we took inspiration from the method used in Scantlebury (2013) and established in BEAUti an arbitrary uniform prior between 9.99 and 10.01 at the root of the ROA clade. Finally, for the six ML phylogenies that were reconstructed with genomic data, calibration in time was performed using the penalized likelihood method implemented in TreePL (Smith & O'Meara 2012). Because performing a state-of-the-art calibration strategy would imply adding outgroups from which genomic information was not available, we simply constraint the ROA root age following the latest literature estimations (See **Table IV.S2**).

The 44 trees were then pruned to remove outgroups, as well as species representing further colonisation routes outside the archipelago. In several cases, multiple individuals from the same species were sampled in the phylogeny. When the species was monophyletic, we kept only one individual; otherwise, paraphyletic species were kept as lineages if they were acknowledged as potentially distinct lineages in the literature (see **Table IV.S1**).

2. c. Diversification analyses

All the following statistical analyses were carried out within the R programming environment (R Development Core Team 2023).

We carried out a series of diversification analyses to quantify the variation in the rate of species accumulation over time for the 44 ROA phylogenies. Diversification analysis focused on two main variables: the branching times, which are the branch lengths (expressed in Ma or in relative time) in a phylogeny between two nodes (i.e., cladogenetic events), and the cumulative number of nodes (i.e., lineages). Both variables are traditionally plotted together in a Lineages-Through-Time (LTT) plot to evaluate the dynamic of diversification of a given clade graphically. Examples of retrieved LTT plots are given in **Figure IV.1**. The analysis of diversification has undergone significant statistical development over the last decade, with several methods and statistical frameworks now available (Condamine et al. 2013, Morlon 2014, Rabosky et al. 2014).

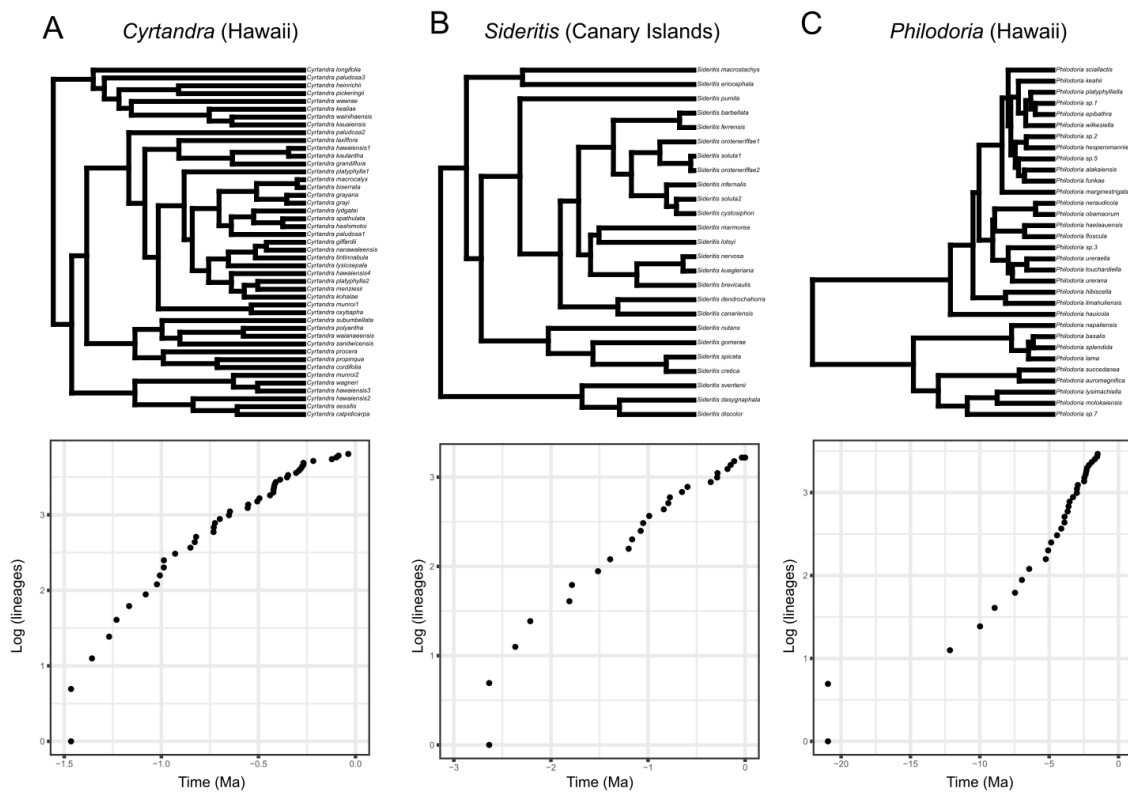


Figure IV.1 Examples of three time-calibrated phylogenetic trees of evolutionary radiations on oceanic archipelagos (ROAs), with their associated Lineages-Through-Time (LTT) plots. A) Phylogenetic tree of the Hawaiian *Cyrtandra* (Lamiales, Gesneriaceae), showing an apparent decrease in species accumulation rate through time (i.e., *early burst* pattern). B) Phylogenetic tree of the Canary Islands *Sideritis* (Lamiales, Lamiaceae), showing a somewhat constant rate of species accumulation through time. C) Phylogenetic tree of the Hawaiian *Philodoria* (Lepidoptera, Gracillariidae), showing a progressive increase in species accumulation rate through time (i.e., *late burst* pattern).

2.c.1. Gamma statistic

As a first approach, we used the γ statistic, which summarizes the distribution of the internode distances of a phylogeny (Pybus & Harvey 2000). Under a pure birth model, the value γ follows a normal distribution with a mean of 0 and a standard deviation of 1. If $\gamma > 0$, the phylogeny's internal nodes are closer to its tips than expected under the pure birth process (i.e., *late burst* pattern). Conversely, if $\gamma < 0$, the internal nodes are closer to the root than expected under the pure birth model (i.e., *early burst* pattern) (Pybus & Harvey 2000). We calculate a γ value for each of our 44 trees using the function *MCCR* in the R package *phytools* (Revell 2012). For each phylogeny, we assessed the statistical significance of γ by simulating a null distribution of 10,000 trees under a pure-birth model (with the function *sim.bd.taxa* in the R package *TreeSim*; Stadler 2019), using the speciation rate estimated from the empirical tree (function *fit.yule* in *phytools*), and accommodating for incomplete phylogenetic sampling. We then calculated γ values for all simulated trees and compared the null distribution to the γ value of the empirical tree. We considered γ as significant if it falls outside the bounds of the 95% confidence interval of the null distribution.

2.c.2. Diversification models in a maximum-likelihood framework

We fitted eight distinct diversification models on our 44 phylogenies using the *RPANDA* package (Morlon et al. 2016) to determine whether models with varying speciation and/or extinction rates through time were more likely to fit our empirical phylogenies than simple constant rates models. These models are birth-death models of cladogenesis, involving speciation (λ) and extinction (μ), which can be fitted to reconstructed phylogenies using maximum likelihood (Morlon 2014). Specifically, we use two constant rates models: a pure birth (λ *cst*; $\mu=0$) and a constant birth-death model (λ & μ *cst*); and six time-dependent models: two with the speciation rate varying either exponentially or linearly over time, with no extinction (λ *expo*; $\mu=0$ and λ *linear*; $\mu=0$), two with the speciation rate varying either exponentially or linearly over time and with constant extinction (λ *linear*; μ *cst* and λ *expo*; μ *cst*) and two with the extinction rate varying either exponentially or linearly over time with constant speciation (λ *cst*; μ *linear* and λ *cst*; μ *expo*). We did not fit models with both time-varying speciation and extinction, as preliminary analyses showed either very poor fits or overfits with unrealistic parameter estimates for most phylogenies. Several recent studies comparing diversification models tend to include models that explicitly account for diversity-dependence (e.g., Condamine et al. 2019, Kong et al. 2022). However, recent work has shown that these diversity-dependent models (DDD models, Etienne et al. 2012) tend to overfit the data and produce unreliable parameter estimates (Etienne et al. 2016, Pannetier et al. 2021). Furthermore, it seems that the models currently available fail to distinguish between a diversity-dependent

branching model and a time-dependent branching model (Pannetier et al. 2021). In view of these recent results, we refrain from fitting any of the available DDD models. Nevertheless, we interpret time-varying patterns with decreasing speciation rate over time as potential signatures of diversity-dependence.

We employed an information theoretic approach to compare the performance of our eight models in fitting our empirical phylogenies. For each model, we calculated the Akaike's information criterion corrected for small sample size (AICc), the ΔAICc (i.e., the difference between each model's AICc and the lowest AICc), and AICc weights representing the relative likelihood of each model. We identified the best model as the one with the smallest AICc (Anderson & Burnham 2002). However, all models with a ΔAICc value < 2 were considered as receiving equal statistical support (Anderson & Burnham 2002). We further implemented the one-tailed statistical test proposed by Rabosky (2006) to detect if the best time-dependent model was statistically better than the best constant rate model. To do this, we initially calculated for each ROA the $\Delta\text{AICc}_{\text{CRC}}$ between the AICc of the best constant and the AICc of the best time-dependent model ($\Delta\text{AICc}_{\text{CRC}} = \text{AICc}_{\text{CST}} - \text{AICc}_{\text{TD}}$). If $\Delta\text{AICc}_{\text{CRC}} < 0$, then the best model is constant, and conversely, if $\Delta\text{AICc}_{\text{CRC}} > 0$, the best model is time-dependent. To test the significance of the $\Delta\text{AICc}_{\text{CRC}}$, we simulated 1000 yule trees using a speciation rate of one and the same number of tips as in the empirical phylogeny. We then fit on these trees the best constant and the best time-dependent models and recalculated the $\Delta\text{AICc}_{\text{RC}}$. We then used the 1000 simulated $\Delta\text{AICc}_{\text{CRC}}$ to test if the empirical $\Delta\text{AICc}_{\text{CRC}}$ was greater than the null distribution (one-tailed statistical test) i.e., if the best time-dependent model was significantly better than the best constant model.

2.c.3. Net diversification rate

The net diversification rate of the 44 ROAs trees was calculated using the method-of-moments estimator (ME) (Magallón & Sanderson 2001), implemented in the *bd.ms* function in the *geiger* R package (Pennel et al. 2014). Despite criticism regarding the accuracy of this method (e.g., Rabosky 2010), it has been shown to perform at least as well as other more complex approaches for the estimation of diversification rate in a single clade (Meyer & Wiens 2018, Roman-Palacios & Wiens 2018). Given that relative extinction rates (ϵ) were unknown, three different values were considered: low ($\epsilon = 0$), medium ($\epsilon = 0.5$), and high ($\epsilon = 0.9$), following standard practices (e.g., Magallón & Sanderson 2001). However, these different values generally gave concordant results, and only those for $\epsilon = 0.5$ are further presented.

2.c.4. Testing the effect ROA features on diversification patterns

In a last set of analyses, we investigated the relationship between diversification patterns and ROA characteristics. First, we performed a series of Spearman's rank correlations, examining the γ -statistic of all 44 ROAs in relation to their age, radiation size, and net diversification rate. These correlations were performed separately for Hawaii and the Canary Islands, the two archipelagos with the largest number of ROAs (See Results). Second, we conducted an ordinary least square (OLS) multiple regression on a restricted dataset including only taxa and archipelago with a minimum of 3 ROAs, namely Hawaii, Canary Islands, Mascarene et Fiji, and for plants and invertebrates (36 ROAs). We included age, radiation size and net diversification rate (all \log_{10} -transformed), as well as taxon and archipelago as predictors in the model. Model selection was performed using AICc (Burnham & Anderson 2002) to identify the best set of predictors explaining γ -statistic. The same procedure was applied to Hawaii and the Canary Islands separately and without the predictor archipelago. To explore the relationship between the diversification patterns identified in the diversification models, we performed a constrained analysis of principal coordinates (CAP, function *capscale* in the R package *vegan*) (Anderson & Willis 2003, Oksanen et al 2007) where we use the matrix of AIC weight (with ROAs as rows and models as columns) as a response variable and the same set of predictors as above. We used the Manly distance (Manly 1994) to characterize pairwise dissimilarities between the AICc weights profiles of the ROAs. Model selection was performed using the function *ordiR2step* in the package *vegan*, which performs a forward selection solely on the adjusted R^2 and the P-value. This analysis was performed on the restricted dataset including only taxon and archipelago with a minimum of 3 ROAs performed. We conducted a separate CAP analysis for Hawaii and The Canary Islands.

3. Results

The 44 selected ROAs include 24 plants, 18 invertebrates and two vertebrates (Table S1) unequally distributed among eight archipelagos, namely Hawaii (16 ROAs), The Canary Islands (15), Fiji (3), Galápagos (3), Mascarene (2), Madeira (1), Austral (1) and Azores (1). Radiation size varied from 11 for the ROA of *Tarphius* in Azores to 186 species for the ROA of *Laparocerus* in the Canary islands. Our data also revealed a sampling fraction of 100% for 15 ROAs, with further 30 ROAs exhibiting a sampling fraction exceeding 90%. The lowest sampling fraction was recorded at 62.7% for the ROA of Hawaiian moths *Philodoria*. Crown ages also exhibited significant variation among ROAs, spanning from 0.31 million years for *Pericallis* in the Canary Islands to 20.95 million years for the Hawaiian *Philodoria*.

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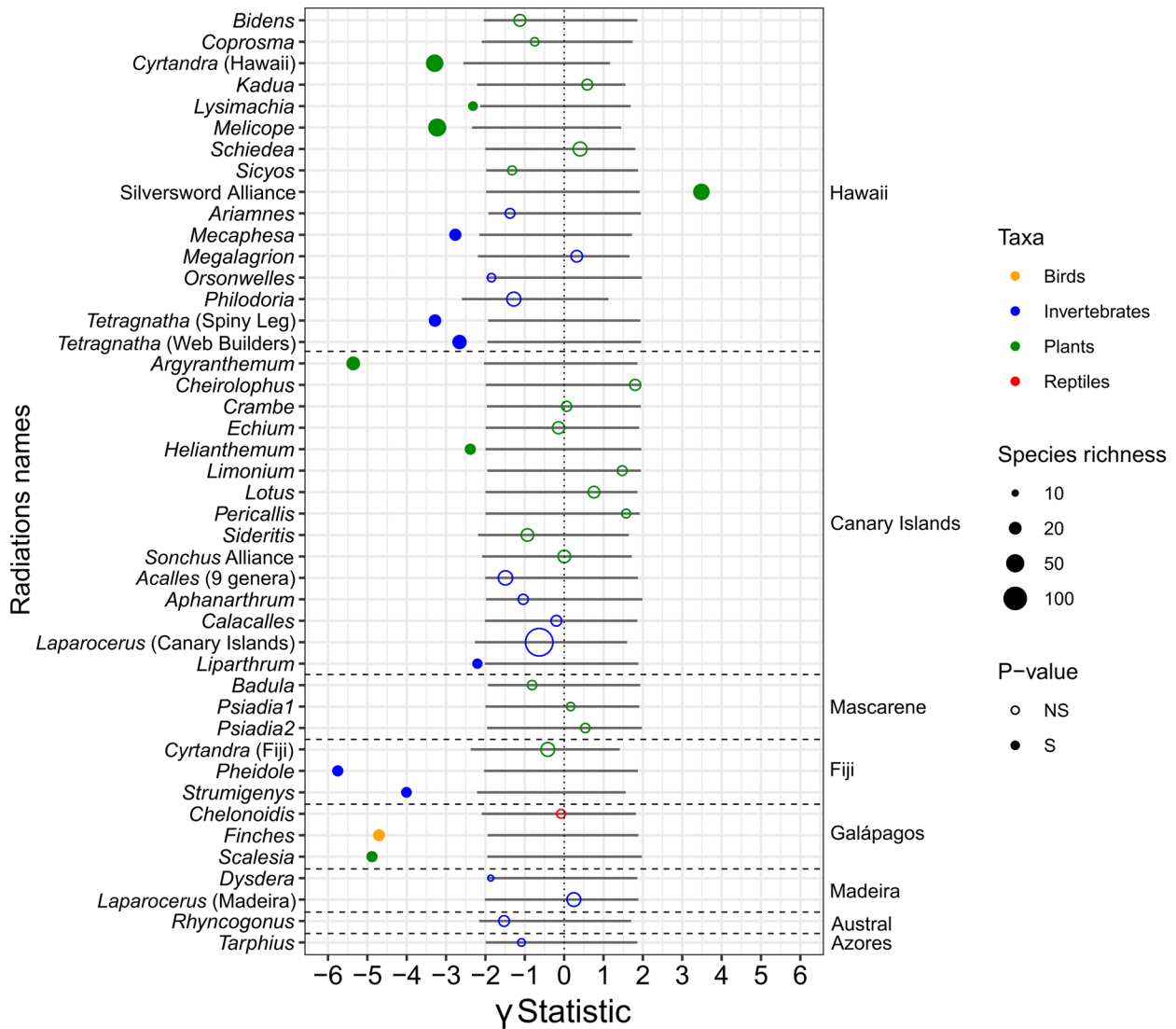


Figure IV.2. Results of the *MCCR* test performed on the 44 phylogenies of evolutionary radiations on oceanic archipelagos (ROAs) selected in our study. Color represents the four types of taxon. Circle sizes is proportional to the number of lineages included in the phylogeny. “NS” imply that the statistical test was non-significant, meaning that the γ value was not significantly lower or higher than the null distribution of γ values from constant rate simulated phylogenetic trees. “S” means that the test was significant.

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We found that γ varied from -5.75 for *Pheidole* in Fiji to 3.48 for the Silversword Alliance in Hawaii, with an average γ across phylogenies of -1.21 (standard deviation: 1.96). Based on the *MCCR* test, we were not able to reject a constant diversification rate for 30 phylogenies (68%), while 13 showed significant *early burst*. Only one phylogeny exhibited a *late burst* (**Figure IV.2**).

The AICc weights for each of the eight *RPANDA* diversification models and for each ROA are shown in **Figure IV.3**. For all but two phylogenies (Silversword Alliance and *Philodoria*), most AICc weights were assigned to models that did not include an extinction parameter. The λ *cst*; $\mu=0$ model was the one with the highest AICc weights (i.e., the best-fitting model) for 24 trees, followed by the λ *linear* model (13 trees) and the λ *expo*; $\mu=0$ model (5 trees). The λ & μ *cst* model and the λ *cst*; μ *expo* model were found to be the best model for only one phylogeny each (see **Table IV.S4**). Among the two constant-rate models, the best model was the λ *cst*; $\mu=0$ model for all phylogenies, with the exception of the three ROAs for which a birth-death model λ & μ *cst* came out on top. Among the six best time-dependent models, the λ *linear*; $\mu=0$ model was the best for 35 phylogenies, followed by the λ *expo*; $\mu=0$ model (7 phylogenies), the λ *cst*; μ *expo* model (1 phylogeny) and the λ *linear*; μ *cst* model (1 phylogeny).

Our $\Delta\text{AICc}_{\text{CRC}}$ statistical test reveals that 32 (72%) phylogenies did not deviate from a constant-rate model of diversification (one-tailed test $P > 0.05$). In contrast, the best time-dependent model significantly outperforms the best constant rate model for only 12 phylogenies (**Figure IV.S1**). In all but one case, these time-dependent models featured a speciation rate decreasing over time (positive α value) either linearly (λ *linear*, 6 phylogenies) or exponentially (λ *expo*, 5 phylogenies), and with no extinction. For a single phylogeny, the time-dependent model that performed statistically better than the best constant rate was the λ *cst*; μ *expo* model, with an extinction rate decreasing over time (positive β value). Regarding our three hypotheses (*early burst*, constant and *late burst*), ROAs with a positive α (λ decreases) or negative β (μ increases), as detected above, are interpreted as decreasing net-diversification, and are considered as showing an *early burst*. The results between the *MCCR* test and the *RPANDA* analysis were globally consistent. Ten of the 14 trees with a significantly negative γ value were also better fitted by a model including a speciation rate decreasing over time (either λ *linear* or λ *expo*). The main incongruency concerned the Hawaiian Silversword Alliance, for which a significant positive γ value was found, but the constant-rate model was proved to be the best model with $\Delta\text{AICc}_{\text{CRC}}$ statistical test. The phylogeny best fitted by the λ *cst*; μ *expo* (*Philodoria*) model showed no deviation from a constant rate of species accumulation in the *MCCR* test.

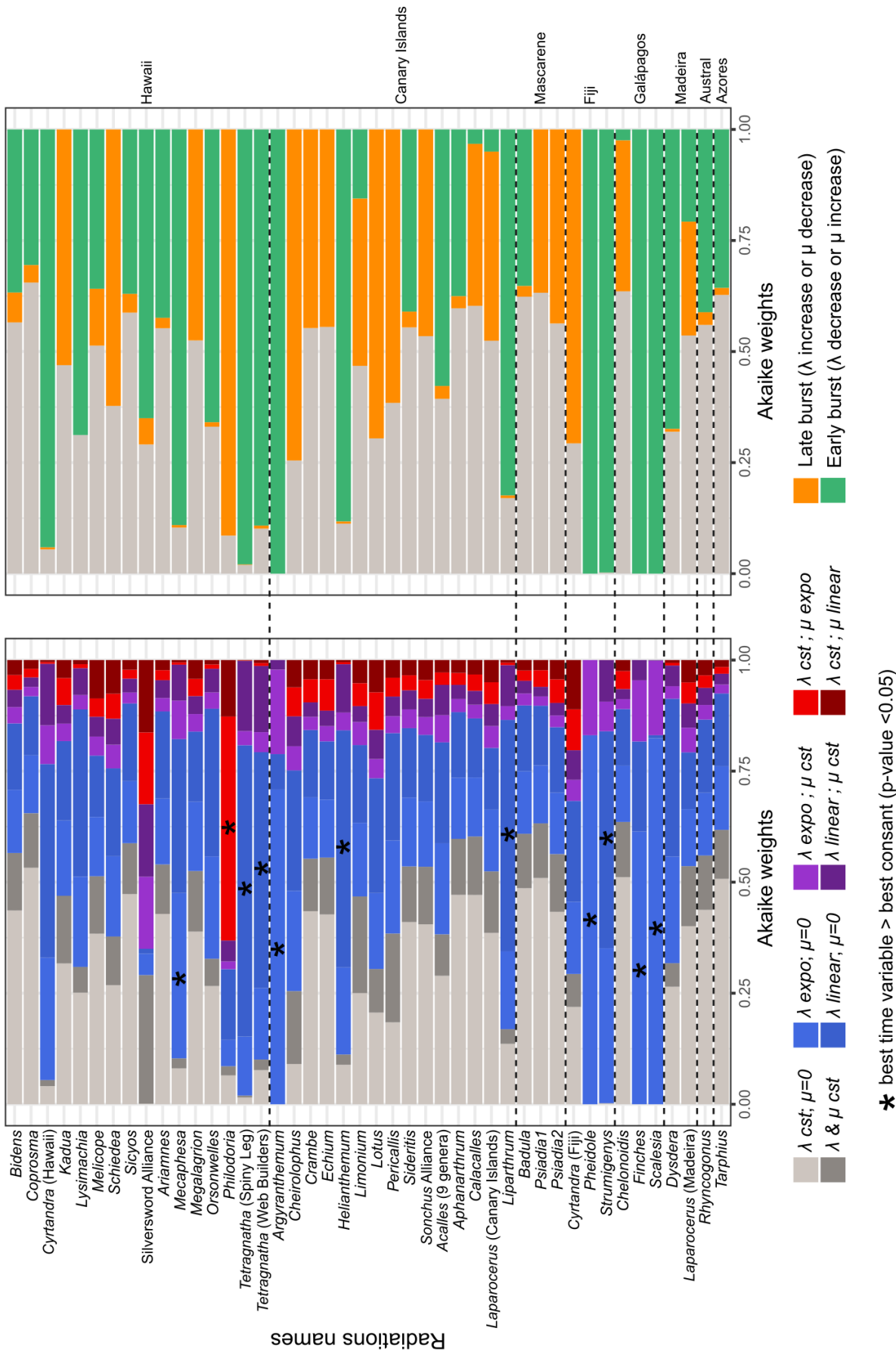


Figure IV.3 Results of our *RPANDA* analysis, showing the AICc weights of each of our eight diversification models (i.e., the relative likelihood of each model) for all of the 44 phylogenies of evolutionary radiations on oceanic archipelagos (ROAs) investigated. For each ROA, a star is displayed on the best time-variable model when the ΔAIC_{CR} between this model and the best constant model was recovered as significant (see main text and **Figure IV.S1**).

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Our analyses of the relationship between diversification patterns and ROA characteristics did not reveal any specific trends (**Figure IV.4**). Spearman's correlation between γ values and age, radiation size and net diversification rate were all insignificant ($\rho = -0.177$, $P=0.253$; $\rho = 0.025$, $P = 0.872$ and $\rho = 0.225$; $P = 0.142$ respectively), even when correlations were performed for Hawaii and the Canary Islands separately. AICc-based model selection on OLS multiple regression identified four competing models ($\Delta AICc < 2$), a first with taxon as the sole predictor ($R^2 = 15\%$, $P=0.020$), a second with net diversification rate ($\epsilon=0.5$) ($R^2 = 14\%$, $P=0.023$), a third with age ($R^2 = 13\%$, $P=0.034$) and a fourth with both age and taxa ($R^2 = 17\%$, $P=0.045$). When applied separately to Hawaii and the Canary Islands, the best model was the one with no predictor in either case. The model selection procedure applied to the CAP analysis reveals a marginal effect of archipelago ($R^2 = 16\%$, $P=0.046$) on ROA AICc weights profiles, while for Hawaii and the Canary Islands, no effect was detected.

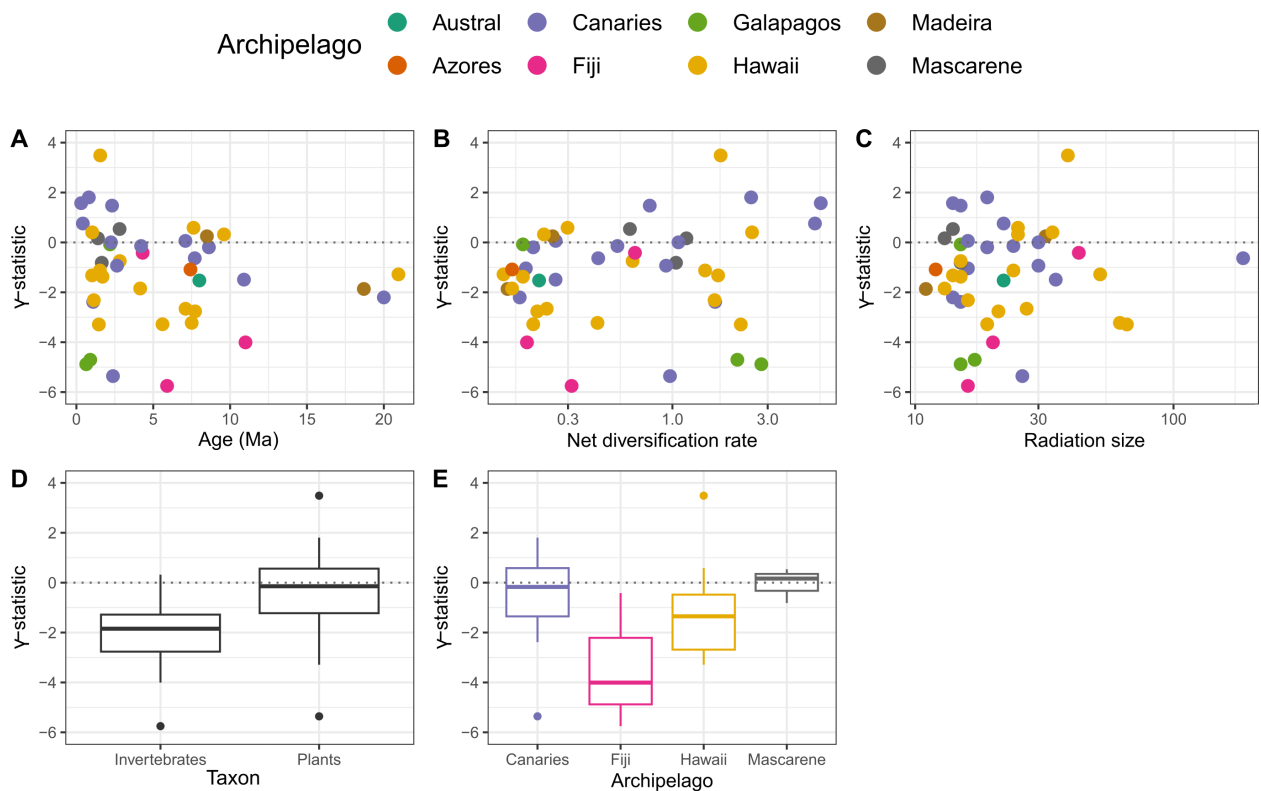


Figure IV.4 Relationship between the γ -statistic and some key ROA features. (A) Age (Ma), (B) Net diversification rate calculated with the method-of-moments estimator (Magallón & Sanderson 2001), (C) Radiation size (i.e., the total number of species in the ROA), (D) Taxon, and (E) the archipelago where the ROA diversified. Note that for net diversification rate, results are shown for an extinction parameter ϵ fixed at 0.5. Similar results were obtained with $\epsilon = 0$ and $\epsilon = 0.9$ (data not shown). Statistical analyses were performed on a restricted dataset including only taxon and archipelago with a minimum of three ROAs namely Hawaii, Canary Islands, Mascarene et Fiji and for Plants and Invertebrates (36 ROAs).

4. Discussion

4. a. Most ROAs accumulate species over time at a constant rate

Our findings revealed that a significant proportion of the investigated ROAs exhibit a constant rate of species accumulation over time, comprising approximately 68% to 72% of the phylogenies (**Figure IV.2, IV.3**). This outcome deviates from classic expectations of the literature, where slowdown of diversification is the prevalent pattern recovered from molecular phylogenies (McPeck 2008, Morlon et al. 2010, Moen & Morlon 2014, Condamine et al. 2019). Why, then, most of the clades studied here do not conform to this apparently general pattern? A first explanation could be the age of ROAs. In one of the latest studies confirming the dominance a slowdown in molecular phylogenies (Condamine et al. 2019), the authors analysed a total of 218 phylogenies of tetrapod families, most of which originated in the late Cretaceous and early Paleocene (-100 to -60 Ma). In comparison, most ROAs are by far more recent, having evolved between the Miocene and Pliocene (-23 to -2 Ma). As an indication, the mean age of our ROAs was 5.3 Ma (median 2.82), of which only 5 were older than 10 Ma. Therefore, a logical consequence of this young age could be that most ROAs are still in their "immature" phase, where the rate of species accumulation over time is not yet constrained by limited environmental resources (Rabosky 2009, Esselstyn et al. 2009). This explanation does not rule out the existence of a possible equilibrium at the archipelago scale, as ROAs could experience a gradual decline in diversification in the future, and eventually reach diversity-dependence.

Diversification patterns within ROAs are undeniably influenced by the characteristics of the archipelago in which the clade diversified. From a broad perspective, oceanic archipelagos represent dynamic ecosystems (Whittaker et al. 2023), and the continuous variations of abiotic factors over time, such as area, elevation and topographic complexity can significantly impact the diversification rate on their soil (Heaney 2000, Borregaard et al. 2017). The ongoing emergence of new islands within an archipelago can also potentially trigger both parapatric and sympatric speciation processes, by rapidly increasing area and habitat diversity, which will produce new ecological opportunities that will trigger speciation (Whittaker et al. 2008, Losos and Ricklefs 2009, Bennett & O'Grady 2013). The continuous arrival of ecological space may help limit interspecific competition and diversity-dependent feedbacks over extended time periods, like what was observed in large and complex mixed-origin archipelagos such as those in the Indo-Pacific (Esselstyn et al. 2009, Fritz et al. 2011). Indeed, if the rate of ecological space emergence matches or exceeds the rate at which species accumulate over time, a relatively constant species accumulation rate can be sustained over long periods of time. However, such hypotheses remain difficult to verify, as data on

the geological dynamics of entire archipelagos is scarce. Nevertheless, a few clues do exist: since the emergence of Kauaʻi (5.9 million years ago), the Hawaiian archipelago has accumulated islands without losing any (Hembry et al. 2021); although Kauaʻi and Oʻahu are now in decline, recent simplified reconstructions of Hawaii's geological history have shown that the total area has been steadily increasing (Lim & Marshall 2017, Jöks et al. 2020). Similar reconstructions have also been proposed for the Canary Islands and Galápagos, reaching the same conclusion (Jöks et al. 2020).

This presumed increase in ecological opportunities through the growth of the archipelago is not without consequences, as this expansion is due to volcanic activity, which can be destructive to the endemic flora and fauna (Ramalho et al. 2013, Fernández-Palacios et al. 2023). Consequently, we cannot rule out that the apparent constant rate could be the result of a high past extinction rate, that have eroded the *early burst* phylogenetic signal (Rabosky & Lovette 2008, Quental & Marshall 2009). Our inability to detect non-null extinction rate in most of our best diversification models is probably due to technical issues, as estimating extinction rates from molecular phylogenies is notoriously difficult and often leads to zero-extinction (Quental & Marshall 2009, Rabosky 2010). However, for the three ROAs for which the best constant model estimated an extinction rate (λ & μ *cst* model), all rate values were particularly high (see *Cheirolophus*, *Silversword Alliance* and *Pericallis* in **Table IV.S4**). We cannot also exclude that recent human-driven extinction within ROAs might have dragged the diversification patterns away from equilibrium (Valente et al. 2017).

4. b. Few evidence for a diversification slow-down in ROAs

While the dominant diversification pattern observed was a constant rate, we also detected a significant slowdown of diversification over time in 10 ROAs (22%) (**Figure IV.3**). This pattern is one of the most common in molecular phylogenies, and it has prompted various explanations (for a comprehensive review, see Moen & Morlon 2014). One of the primary biological explanations, often invoked for adaptive radiations, is diversity-dependence. In this scenario, a clade initially experiences rapid diversification due to adaptations to various niches. However, as new species emerge and niches become filled, competition increases and gradually slows down the rate of new species formation (McPeck 2008, Rabosky & Lovette 2008, Etienne & Haegeman 2012). Notably, for many ROAs, the designation as adaptive is common in the literature, even though quantitative statistical evidence of niche partitioning or ecological diversification is often lacking (Soulebeau et al. 2015). Furthermore, while all but one of the 10 ROAs exhibiting an *early burst* pattern have been considered adaptive in the literature (except for the beetle ROA of *Liparthrum* in the Canary Islands), most ROAs displaying a constant rate were also categorized as adaptive (see **Table IV.S1**). Interestingly however, some ROAs showing the *early burst* pattern have been extensively

investigated for their adaptive components. For instance, the Galápagos finches are among the best-known examples of adaptive radiation with multiple lines of evidence (e.g., Burns et al. 2002, Navalón et al. 2020). Various works on *Tetragnatha* spider radiations have uncovered numerous morphological and ecological features linked to adaptations (Gillespie 2004, Kennedy et al. 2022). Finally, intense ecomorphological diversification has been observed in the two Fijian ant lineages (*Strumigenys* and *Pheidole*), which are both filling a substantial portion of the global morphospace known in each genus (Darwell et al. 2019, Liu et al. 2020). Several alternative hypotheses concerning the *early burst* pattern have been proposed in the literature (Moen & Morlon 2014), such as the effect of extinction and/or protracted speciation at the tips of phylogenetic trees. Larger phylogenies may also be more prone at displaying a slowdown just by chance (e.g., Pennel et al. 2012), but we found no significant relationship between radiation size, nor with γ or the AICc weights distribution. Only a weak significant signal was detected when we performed the analyses with the restricted data.

4. c. No evidence for a *late burst* of diversification in ROAs

Our analyses yielded limited evidence for the presence of a *late burst* pattern in ROAs (**Figure IV.2, IV.3**). Only the Hawaiian *Philodoria* exhibited a best-fitting diversification model including a slowdown in the extinction rate with constant speciation. This pattern might be linked to the colonisation of new plant families in the archipelago, enabling multiple host shifts throughout the clade evolutionary history (Johns et al. 2018). The development of such adaptations or other key innovations, if they emerged later in the clade's history, could contribute to the observed "pull-of-the-present." However, this information is missing for this particular clade. Another hypothesis regarding *late burst* involves the role of the geo-environmental dynamics of the archipelago. Recent climatic fluctuations and Pleistocene sea-level variations have been shown to positively impact diversification on archipelagos by creating a "species pump", where populations experience repeated isolation and reconnection (Papadopoulou & Knowles 2017, Salces-Castellano et al. 2020). An empirical example supporting this assumption can be found for the several ROAs of *Homalictus* bees (not included in our study), which exhibited a recent burst of diversification on South Pacific archipelagos, synchronized with Pleistocene climate changes (Groom et al. 2014). Like the constant-rate pattern discussed earlier, it is plausible that high extinction rates in the past million years (a reasonable hypothesis for oceanic archipelagos, as mentioned above) may have erased most of the ancient lineages within ROAs, leaving only the most recent burst of speciation recorded in the molecular phylogeny.

4. d. Limitations

First, as nicely pointed out by Fritz et al. (2011): “*The interpretation that our analyses show patterns of constant net diversification rates should be taken cautiously because our failure to reject the null hypothesis does not prove its validity.*” Second, most of the ROAs investigated in this study rarely exceed 20 species (**Table IV.S1**). However, small ROAs offer less statistical power compared to larger ones due to their fewer nodes and branches for analysis (Harmon et al. 2008). Third, the majority of current ROA research has been focused on Hawaii and the Canary Islands (see Chapter II), and data availability for phylogenetic reconstruction is therefore concentrated in these two archipelagos (31 out of 44 ROAs). This limitation undoubtedly restricts our capacity to draw general conclusions. Furthermore, the number and type of molecular markers used for phylogenetic reconstruction vary considerably between ROAs, ranging from a single ITS marker to large genomic datasets (see **Table IV.S1**). Some researchers have emphasized the importance of utilizing phylogenies from as many different, independent sources as feasible rather than, for instance, simply slicing up previously constructed “megaphylogenies” (Diaz et al. 2019). By doing so, we expect to minimize the correlation of error across datasets, and by utilizing the most recent published phylogenies, we ensured to use the best available tree for each ROA. However, it remains uncertain whether the diversification dynamics displayed by the molecular phylogeny of a given ROA would remain consistent if fewer, more, or alternative markers were used. Notably, our data revealed that six out of eight trees reconstructed with phylogenomic information displayed a significant *early burst* pattern. Nevertheless, since this pattern does not affect all our phylogenetic trees – the *Melicope* tree was determined to be constant, and the *Philodoria* tree is the sole significant *late burst* tree – and given that we didn’t find any evidence regarding any potential bias in the literature due to the use of genomic data, this trend might have just appeared by chance. On a final note regarding sampling bias, it is important to acknowledge that while the methods used in our study considered incomplete sampling, the way it is handled may not be optimal, as exemplified by the *MCCR* test, which assumes that missing species are randomly distributed throughout the phylogeny (Cusimano & Renner 2010).

Finally, we would like to emphasize that fitting macroevolutionary models to molecular phylogenies provides only one piece of evidence concerning the evolutionary history of a clade. Further study of other key aspects of ROAs, such as the evolution of phenotypic traits over time or other ecological aspects, will be essential to distinguish between several hypotheses and uncover new pieces of information that will explain or contrast our initial assessment of ROA diversification history (García-Verdugo et al. 2014, Blonder et al. 2016, Takayama et al. 2018, Miles et al. 2023). For

example, the recent development of several state-dependent speciation and extinction (SSE) models would be of great use in assessing the influence of trait evolution on lineage diversification patterns (Maddison et al. 2007, FitzJohn 2012, Beaulieu and O'Meara 2016). In addition, these models seem relatively robust to the identifiability problems of diversification patterns that have recently been (re)discovered (Louca & Pennel 2020, O'Meara & Beaulieu 2021).

5. Conclusion

To our knowledge, this work is the first comparative study that examined diversification patterns of ROA across various taxa and oceanic archipelagos. Our analyses brought some important insights, revealing that most ROAs exhibit a constant rate of species accumulation over time. We suggest that the dynamics of oceanic island systems allow for sustained high diversification rates through several possible mechanisms, including high extinction rate and continuous increase of ecological space. As demonstrated in our study, a comprehensive understanding of diversification dynamics requires data from an extensive range of cases, encompassing both species-poor and species-rich taxa, and spanning various systems across the globe. In this sense, we expect to increase the number of phylogenies analyzed in the near future. Overall, our study will benefit from linking our patterns to additional biogeographic and ecological data.

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Table IV.S2. Calibration method, list of genetic markers and associated references for the 28 dated phylogenetic trees of evolutionary radiation on oceanic archipelagos (ROAs) reconstructed in this study.

Radiation name	Archipelago	Phylogenetic tree of reference	Calibration type	Source/details of the calibration	Node where the calibration was applied	Parameterization (prior and likelihood boundary)	Comments/Justifications	List of genetic markers used	Data retrieving details
<i>Agave/Anemone</i>	Canaries	White et al. (2020)	Secondary	White et al. (2020) Crown node of <i>Agave/Anemone</i> : 2.48 Ma (1.84 - 3.04 Ma)	Crown node of <i>Agave/Anemone</i> genera	Point calibration: 2.48 Ma	-	Genomic	Mt. (RAML) phylogenetic tree directly retrieved from authors.
<i>Bulbia</i>	Masarene	Stijfk et al. (2014)	Fossil	Bremer et al. (2004), Smith & Donoghue (2008) Split between traditionally defined Primulaceae and Myrsinaceae 45 Ma (30-60 Ma) Chandler (1957), Donohue (1983), Frits (1985), Mai (2001), Mai & Walther (1988) + fossils from middle Miocene and middle Pliocene Pole (1998, 2008) Ardebe about 20 Ma	Root (divergence between Primulaceae and Myrsinaceae) Stem node of <i>Lymnophila</i> Stem node of <i>Ardisia</i>	Uniform Lower=30, Upper=60 Lower=23.03, Upper=50 Lower=5.3, Upper=50 Lower=1.3, Upper=3.1	Calibration strategy from Stijfk et al. (2014). They described a stepwise calibration strategy in which supplementary materials for the stem node of <i>Lymnophila</i> and <i>Ardisia</i> . As calibration from the supplementary materials are more conservative and follow recommendations of Ho & Phillips (2009) (Posterior = minimum bound, not maximum), we use those.	Nuclear: ITS Chloroplast: psbA-trnH, rbcL, psbI-trnA, psbK-trnH, accD, psbE	Accession numbers retrieved from Stijfk et al. (2014).
<i>Blechnum</i>	Hawaii	Kroppe et al. (2020)	Secondary	Kroppe et al. (2020) Crown node Hawaiian <i>Blechnum</i> : 2.1 Ma (1.3-3.1 Ma)	Hawaiian <i>Blechnum</i> crown node	Uniform Lower=10.6, Upper=12.7	Calibration strategy from Herando-Molina et al. (2019).	Nuclear: ITS, ETS Chloroplast: psb2-trnL, psb-trnH, and P16000	Accession numbers retrieved from Kroppe et al. (2020).
<i>Chenopodium</i>	Canaries	Viala et al. (2014)	Secondary	Herando-Molina et al. (2019) node 60: 11.63 Ma (10.60 - 12.71 Ma)	Root	Uniform Lower=10.6, Upper=12.7	Calibration strategy from Herando-Molina et al. (2019).	Nuclear: ITS, ETS Chloroplast: psb2-trnL, psb-trnH, and P16000	Accession numbers retrieved from Viala et al. (2014).
<i>Coprosma</i>	Hawaii	Canfield et al. (2016)	Fossil	MacDougal (1989), Guibaud (2009) <i>Phalaenoptilus nuttallii</i> zelandicus, Oligocene to Pleistocene	Crown of <i>Coprosma</i> and <i>Melicope</i>	Uniform Lower=23.03, Upper=47	Calibration strategy from Canfield et al. (2016). We use the fossil age as a minimum bound for the crown node of <i>Coprosma</i> . Secondary calibration as it has no impact on the result (see Canfield et al. (2016) for details). We used the same strategy to avoid calibrate phylogenies with rates when other calibrations strategy are available.	Nuclear: ITS, ETS Chloroplast: psb16, rbcL, psbI-trnA	Accession numbers retrieved from Canfield et al. (2016).
<i>Cymbala</i>	Canaries	Francisco-Ortega et al. (2012)	Fossil	Ving (1987), Baileton et al. (2010) <i>Thapsia primivum</i> , Oligocene	Split between <i>Alliaria parvifolia</i> and <i>Thapsia avarosa</i>	Uniform Lower=23.2, Upper=125 Lower=36.3, Upper=60.7	Calibration strategy from Añe et al. (2014), except for the upper bound of the fossil calibration, set to 125 Ma as in Baileton et al. (2010).	Nuclear: ITS Chloroplast: ap1-slight, psbD-trnT, psb2-trnL, ycf6-psbM.	Accession numbers retrieved from Francisco-Ortega et al. (2012), Añe et al. (2014) and Añe et al. (2014).
<i>Cyatodia</i> (two radiations)	Hawaii Fiji	Johnson et al. (2017)	Secondary	Johnson et al. (2017) Crown node of <i>Cyatodia</i> stem node: 30.45 Ma (14.79 - 37.54 Ma) Crown node of <i>Cyatodia</i> crown node: 1.1 Ma (0.32 - 2.17 Ma) Pacific <i>Cyatodia</i> crown node: 6.29 Ma (0.5 - 3.85 Ma)	<i>Cyatodia</i> stem node <i>Cyatodia</i> crown node Pacific <i>Cyatodia</i> crown node	Uniform Lower=14.79, Upper=37.54 Lower=3.25, Upper=21.78 Lower=3.85, Upper=9.5	Calibration strategy inspired from Johnson et al. (2017). We used uniform instead of point calibration for secondary calibrations. We didn't label the used calibrations.	Nuclear: ITS, ETS Chloroplast: psb16, trnL-trnF, psb2-trnL	Accession numbers retrieved from Johnson et al. (2017).
<i>Echium</i>	Canaries	Niik et al. (2019)	Fossil	Chandler (1950), Mai & Walther (1981), Ozaki (1991) Earliest fossil record of <i>Echium</i> in the Early Eocene Dawson & Thompson (2007) <i>Cryptantha auriculata</i> , Late Miocene, Clarendonian	Root (Crown of <i>Echium</i>)	Uniform Lower=10.3, Upper=88	Calibration strategy from Niik et al. (2019), except for the upper bound of the fossil calibration, set to 125 Ma as in Baileton et al. (2010).	Nuclear: ITS, ETS Chloroplast: psb16, trnL-trnF, psb2-trnL	Accession numbers retrieved from Niik et al. (2019).
<i>Galapagos finches</i>	Galapagos	Lamichhane et al. (2015)	Secondary	Lamichhane et al. (2015) Crown node of Galapagos finches: 0.901 Ma (0.123-1.69 Ma)	Crown node of Galapagos finches	Point calibration: 0.901 Ma	-	Genomic	Mt. (E-pAML) phylogenetic tree directly retrieved from the corresponding author of Lamichhane et al. (2015).
<i>Helianthemum</i>	Canaries	Albaladejo et al. (2021)	Secondary	Albaladejo et al. (2021) Crown node of Canarian <i>Helianthemum</i> : 1.09 Ma (0.32-1.90 Ma)	Crown node of Canarian <i>Helianthemum</i>	Point calibration: 1.09 Ma	-	Genomic	Mt. (RAML) phylogenetic tree directly retrieved from authors.
<i>Kalua</i>	Hawaii	Neupane et al. (2017)	Fossil	Morales-Chavez et al. (2016), Late Eocene, 38 Ma. <i>Syphyphora</i> sp.: Early Miocene, 16 Ma. Mai & Walther (1985, 2000) <i>Cephalanthus parviflorus</i> , Late Eocene, 34 Ma. Collinson et al. (2012) Alstonia Middle Eocene, 47 Ma. Gentiana-like crown node: 7.5 Ma (SD=2.7 Ma)	Rubiaceae crown node Ichoridaceae crown node Chlorobaceae crown node Cinchonaceae crown node	Uniform Lower=38, Upper=128 Lower=16, Upper=128 Lower=34, Upper=128 Lower=34, Upper=128 Mean=7.5, SD=2.7	Calibration strategy from Neupane et al. (2017). We used uniform instead of point calibration for secondary calibrations. We didn't label the used calibrations.	Nuclear: ITS, DDEES Chloroplast: rbcL, trnL-trnF	BEAST MCC dated tree retrieved directly from Niik et al. (2019) publication.
<i>Limonium</i>	Canaries	Koutroumpa et al. (2021)	Fossil	Van Campo (1976), Muller (1981) <i>Artemisa</i> sp.: Upper Miocene Baucher (1975), Muller (1981) Cecobran (1976), Muller (1981) Cecobran (1976), Muller (1981) <i>Rhaphites maulenbeckii</i> sp. nov.: Upper Eocene	Limoniaceae crown node Ceratophyllaceae stem node Coccoloba stem node Maulenbeckiaceae stem node	Uniform Lower=5.333, Upper=78.21 Lower=2.56, Upper=78.21 Lower=5.333, Upper=78.21 Lower=33.9, Upper=78.21	Calibration strategy from Koutroumpa et al. (2021). We used uniform instead of point calibration for secondary calibrations. We didn't label the used calibrations.	Nuclear: ITS Chloroplast: trnL-F, rbcL, matK	BEAST MCC dated tree retrieved directly from the corresponding author of Koutroumpa et al. (2021).
<i>Lotus</i>	Canaries	Jain-Molina et al. (2021)	Secondary	Jain et al. (2005) Split between <i>Coronilla verna</i> and <i>Lotus apollonicus</i> : 14.4 Ma (11.7-18.6 Ma)	Root (<i>Coronilla</i> as outgroup)	Uniform Lower=11.7, Upper=18.6	Jain-Molina et al. (2021) compared the effect of 1 or 2 calibrations, their results shown highly overlapping 95% HPDs, so we only took the secondary calibration to avoid using island calibration.	Nuclear: ITS	ITS Aligned matrix retrieved directly from the corresponding authors of Jain-Molina et al. (2021) about using only the ITS dataset for the molecular dating analysis.
<i>Lymnophila</i>	Hawaii	Yin et al. (2018)	Fossil	Oh et al. (2020), Yin (2018) Fossil seeds similar to <i>Lymnophila vulgaris</i> , Middle Miocene (12-16 Ma), Stijfk et al. (2014) core <i>Lymnophila</i> and <i>Anagallis</i> crown age: 28.47 Ma (23.03-37.67 Ma) Stijfk et al. (2014) Lymnophila stem node: 27.88 Ma (26.94-50.46 Ma). Lymnophila stem node: 4.1 Ma (23-52 Ma).	crown node of <i>Chabe IV</i> crown node of <i>Chabe I-VIII</i> Root (3 calibrations tested for the stem node of the <i>Lymnophila</i>)	Uniform Offset=12, Mean=1, SD=2 Lower=23.03, Upper=37.67 Lower=23.04, Upper=52	Calibration strategy from Yin et al. (2018). We used uniform instead of point calibration for secondary calibrations. The secondary calibration was used to avoid using island calibration. We have taken the lowest and highest 95% HPD bounds of the two estimations.	Nuclear: ITS Chloroplast: rbcL, trnL-trnF, psbI-trnA, psbK-trnH, psb2-trnL, psb16, trnS-trnG, psb2-trnL	Aligned matrix and PartitionFinder information retrieved from Yin et al. (2018) publication.

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(Table IV.S2 continued)

Radiation name	Archipelago	Phylogenetic tree of reference	Calibration type	Sources/details of the calibration	Node where the calibration was applied	Parametrisation (prior density function, bounds)	Comments/Justifications	List of genetic markers used	Data retrieving details
Melicope	Hawaii	Petold et al. (2019)	Secondary	Apehrens et al. (2019) Crown node of Hawaiian Melicope (4.7-11.7 Ma)	Crown node of Hawaiian Melicope	Point calibration: 7.5 Ma	-	Genomic	Mt. (EwAML) phylogenetic tree directly retrieved from authors.
Feralls	Carnaries	Jones et al. (2014)	secondary	Huchvalson et al. (2021): Stem node of Feralls: 1.37 Ma (0.34 - 2.83 Ma)	Emilia/Feralls divergence node	Uniform Lower=0.34, Upper=2.83	Secondary calibration from the latest fossil calibrated phylogeny (Huchvalson et al. 2021)	Nuclear: ITS Chloroplast: matK, trnL-pstA, trnD-trnE	Accession numbers retrieved from Jones et al. (2014) and Huchvalson et al. (2021).
Phedusa	Fiji	Dawel et al. (2019)	Secondary	Economou et al. (2015) Crown node of Fijian Phedusa: 5.9 Ma	Crown node of Fijian Phedusa	Point calibration: 5.9 Ma	-	Genomic	Mt. (RAxML) phylogenetic tree directly retrieved from Dawel et al. (2019) publication.
Phideria	Fiji	Jones et al. (2018)	Secondary	Wang et al. (2013) Most recent common ancestor of Phideria and Gacallariidae. Price & Chase (2022) Oldest geological age of the Maui Nui complex: 2.2 Ma	Root Crown node Maui Nui Phidodaria	Uniform Lower=88.5, Upper=141.2642 Normal Mean=2.2, SD=0.73	This calibration strategy used island age in addition to secondary, but the authors did not mention the calibration strategy (see Jones et al. 2018 for details)	Genomic	BEAST MCC dated tree retrieved directly from Jones et al. (2018) publication.
Paladia (two radiations)	Miscarane	Stijk et al. (2012)	Fossil	Hobbs & Baldwin (2013) and references therein; Mandel et al. (2019) Altemian, Late Eocene and Early and Middle Miocene	<i>Araucarioxylum</i> / <i>Chrysanthemum</i> /Cordia divergence node	lognormal offset=0, mean=1, SD=1.5	Calibration strategy from Stijk et al. (2012). We modified the fossil calibration in order to follow Ho & Phillips (2009) recommendations for fossil calibrations. We used the fossil calibration from Stijk et al. (2012). We did not use the secondary from Kim et al. (2005), as the root of the tree do not correspond to the crown node of <i>Araucarioxylum</i> . As if the fossil calibration from Stijk et al. (2012) was used, the secondary from Kim et al. (2005) secondary calibration as it is in fact a tertiary calibration. Furthermore, the calibration don't have any impact on the date of the divergence between <i>Araucarioxylum</i> and <i>Chrysanthemum</i> . Bogh & Under (2009) pollen calibration, it doesn't appear in more recent literature calibrated phylogeny as a valid fossil (Mandel et al. 2019). Accession numbers retrieved from Stijk et al. (2012). We contrast the monophyly of the <i>Graptaleae</i> .	Nuclear: ITS Chloroplast: atpB, ypsb, psbA-trnH	Accession numbers retrieved from Stijk et al. (2012). We contrast the monophyly of the <i>Graptaleae</i> .
Scalasa	Galapagos	Fernandez-Mazaucos et al. (2020)	Secondary	Fernandez-Mazaucos et al. (2020) Crown node of Scalasa: 0.64 Ma (0.63 - 0.74 Ma)	Crown node of Scalasa	Point calibration: 0.64 Ma	-	Genomic	Mt. (RAxML) phylogenetic tree directly retrieved from the corresponding author of Fernandez-Mazaucos et al. (2020).
Schedea	Hawaii	Wilyard et al. (2011)	Fossil	Jordan & Macphail (2003) Caryophyllida paleogenetics, Middle-Late Eocene	Root (Almioidae/Caryophyllidae crown node)	lognormal Offset: 33.9, Mean=0.0, SD=1.37	Calibration strategy from Gzaw et al. (2016).	Chloroplast: psbA-psbM, psbE-psbL, psbM-trnD, trnD-trnE, trnD-psbE, trnK, trnL, trnM, trnS-trnM, matK, rbcL, trnL-trnF, trnS-trnM	Accession numbers retrieved from Wilyard et al. (2011) and Greenberg & Donoghue (2011). We followed authors' recommendations about using only the chloroplast dataset for the molecular dating analysis.
Seyos	Hawaii	Sebastian et al. (2012)	Fossil Secondary	Saint-Chedelaeff (1978) <i>Hexaploites schottii</i> : Oligocene (63.9 to 23 Ma) Schaerer et al. (2009): 3 Ma Root of the Sicyoaeae	split between <i>Limnacozygos</i> and the remaining New World Sicyoaeae Root of the Sicyoaeae	Uniform Lower=23, Upper=40 Uniform Lower=34, Upper=40	Calibration strategy from Sebastian et al. (2012). We connected the Oligocene minimum bound (Cohen et al. 2013) and the Upper bound from Schaerer et al. (2009) (2008). We used uniform instead of normal distributions.	Nuclear: ITS Chloroplast: trnL-trnF, trnS-G, psbA-trnH, rbcL	Accession numbers retrieved from Sebastian et al. (2012).
Sermitis	Carnaries	Barber et al. (2007)	Fossil	Mai (2001) <i>Stachyris talpacoti</i> , Middle Miocene (Seravallian)	Root (Stachyris crown node)	Lognormal Offset=14.63, Mean=0.5, SD=0.8	Calibration strategy from Roy et al. 2013, with a correction on the minimum bound (following Ho & Phillips (2009) recommendations).	Nuclear: ITS, ETS, 5SNTS	Accession numbers retrieved from Barber et al. (2007) and Sasaki et al. (2019). We followed authors' recommendations in Barber et al. (2007) for the molecular dating analysis.
Skinnerd/Alliance	Hawaii	Baldwin et al. (2021)	Secondary Secondary	Barnede et al. 2016 and Lande et al. (2018) Madriane crown node: 5.77 Ma (4.14 - 3.79 Ma) Barnede et al. 2016 and Lande et al. (2018): <i>Halea</i> → <i>Amica</i> + <i>Madriane</i> : 15.99 Ma (22.65 - 9.13 Ma)	Madriane crown node Root (<i>Halea</i> → <i>Amica</i> as outgroups)	Uniform Lower=3.79, Upper=14.14 Uniform Lower=9.13, Upper=22.85	Calibration strategy from Baldwin et al. (2021).	Nuclear: ITS	ITS Aligned matrix and partitions retrieved from the corresponding author of Baldwin et al. (2021).
Stachyris Alliance	Carnaries	Lee et al. (2005)	Fossil	Bloxmore et al. (1996) <i>Sinchus grazius</i> pollen: Late Miocene <i>Stachyris</i> <i>Alapaka</i> type pollen: Middle Pliocene Hochuli (1978)	Hyosinidiace stem node Scorzonera stem node Stem node of the core group (Cichorieae without Scorzonerae)	Uniform Lower=3.33, Upper=100 Lower=3.4, Upper=100 Lognormal Offset=22, Mean=1.16, SD=0.42	Calibrations strategy from Tremblay et al. (2013).	Nuclear: ITS Chloroplast: trnT-trnF, matK	Accession numbers retrieved from Lee et al. (2005) and Tremblay et al. (2013).
Strumignys	Fiji	Liu et al. (2020)	Secondary	Ward et al. (2015) Crown node of <i>Strumignys</i> : 33.1 Ma (27.2 - 39.2 Ma)	Crown node of <i>Strumignys</i>	Uniform Lower=27.2, Upper=39.2	-	Genomic	BEAST MCC dated tree retrieved directly from Liu et al. (2020) publication.

Table IV.S3. List of genetic markers and associated references for the 16 phylogenetic trees of evolutionary radiation on oceanic archipelagos (ROAs) reconstructed in relative time for this study.

Radiation name	Archipelago	Phylogenetic tree of reference	List of genetic markers used	Data retrieving details
<i>Acalles</i> (9 genera)	Canaries	Stüben et al. (2021)	Nuclear: 28S Mitochondrial: COI, 16S	Accession numbers retrieved from Stüben et al. (2021).
<i>Aphanarthrum</i>	Canaries	Jordal & Hewitt (2004)	Nuclear: EF1a, Enolase Mitochondrial: COI, 16S	Accession numbers retrieved from Jordal & Hewitt (2004).
<i>Ariamnes</i>	Hawaii	Gillespie et al. (2018)	Nuclear: EF1a Mitochondrial: COI	Alignment directly retrieved from Gillespie et al. (2018) publication.
<i>Calacalles</i>	Canaries	Stüben et al. (2021)	Nuclear: 28S Mitochondrial: COI, 16S	Accession numbers retrieved from Stüben et al. (2021).
<i>Chelonoidis</i>	Galápagos	Poulakakis et al. (2020)	Mitochondrial genome	Alignment directly retrieved from Poulakakis et al. (2020) publication.
<i>Dysdera</i>	Madeira	Crespo et al. (2021)	Nuclear: NADH1, 28S, H3 Mitochondrial: COI, 16S, L1	Accession numbers retrieved from Crespo et al. (2021).
<i>Laparocerus</i> (2 radiations)	Canaries Madeira	Machado et al. (2017)	Nuclear: EF1a, 28S Mitochondrial: COI, 12S, 16S	Accession numbers retrieved from Machado et al. (2017).
<i>Liparthrum</i>	Canaries	Jordal et al. (2004)	Nuclear: EF1a Mitochondrial: COI	Accession numbers retrieved from Jordal et al. (2004).
<i>Mecaphesa</i>	Hawaii	Garb & Gillespie 2009	Nuclear: EF1a, 28S, H3 Mitochondrial: COI, 12S, NADH1, 16S	Accession numbers retrieved from Garb & Gillespie (2009) & Piacentini & Ramirez (2019).
<i>Megalagrion</i>	Hawaii	Jordan et al. (2003)	Nuclear: EF1a, A6, A8 Mitochondrial: COI	Alignment directly retrieved from Jordan et al. (2003) publication.
<i>Orsonwelles</i>	Hawaii	Hormiga et al. (2003)	Nuclear: ITS2 Mitochondrial: COI, 16S, NADH1	Accession numbers retrieved from Hormiga et al. (2003).
<i>Rhyncogonus</i>	Austral	Claridge et al. (2017)	Nuclear: EF1a Mitochondrial: COI, 12S, 16S	Accession numbers retrieved from Claridge et al. (2017).
<i>Tarphius</i>	Azores	Borges et al. (2017)	Nuclear: EF1a Mitochondrial: COI, COII	Accession numbers retrieved from Borges et al. (2017).
<i>Tetragnatha</i> (Spiny Leg)	Hawaii	Kennedy et al. (2022)	Nuclear: ITS2, H3, 18S, 28S, Actin Mitochondrial: COI, 12S, 16S, CyIB	Alignment + PartitionFinder directly retrieved from the corresponding author of Kennedy et al. (2022) authors.
<i>Tetragnatha</i> (Web Builders)	Hawaii			

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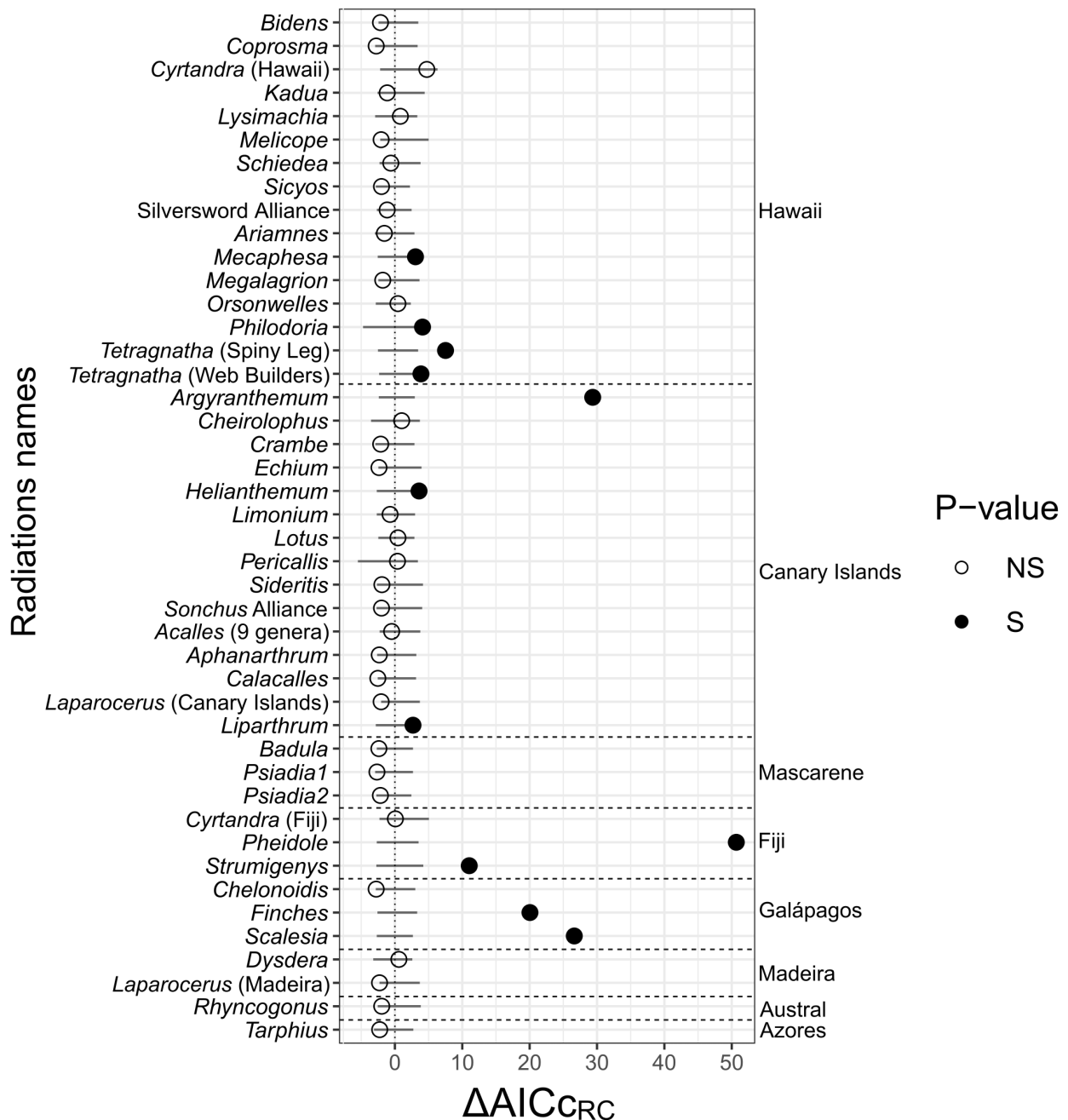


Figure IV.S1. Results of our ΔAIC_{CRC} statistical test. “NS” imply that the statistical test was non-significant, meaning that the ΔAIC_{CRC} for the empirical tree was not significantly higher than the null distribution of ΔAIC_{CRC} values from constant rate simulated phylogenetic trees. “S” means that the test was significant.

Chapitre V : Discussion générale

Les trois chapitres de cette thèse, grâce à leur approche globale et comparative, apportent un éclairage nouveau sur les phénomènes écologiques et évolutifs en jeu au sein des environnements insulaires, en prenant pour principal objet d'étude les radiations évolutives dans les archipels océaniques (ROAs). Dans ce chapitre, je vais d'abord synthétiser les principaux résultats obtenus dans le cadre de ce travail de thèse, puis je présenterai certaines recommandations et pistes de réflexion pour des recherches futures sur les ROAs. Je discuterai enfin de certaines limites inhérentes aux analyses comparatives, et finirai en présentant trois perspectives.

1. Synthèse des résultats

Bien que les radiations évolutives au sein des archipels océaniques (ROAs) aient fait l'objet de nombreuses études au cours des dernières décennies, il n'existait encore aucune revue de littérature à l'échelle mondiale sur le sujet, ni même de quantification précise du nombre de ROAs répertoriées jusqu'à présent. Jusqu'ici, les revues sur les ROAs étaient globalement restreintes à certaines groupes taxonomiques (e.g., insectes d'Hawaï : Hembry et al. 2021 ; arthropodes : Gillespie & Roderick 2002) ou certains archipels (e.g., Marquises : Hembry 2018 ; Hawaï : Cowie & Holland 2008). De plus, bien que plusieurs auteurs aient précédemment signalé des disparités significatives dans la littérature concernant l'étude des archipels océaniques et leurs ROAs (e.g., Meiri 2017, Cerca et al. 2023), ces problèmes n'avaient pas encore été systématiquement évalués. Par conséquent, l'objectif du premier chapitre de ma thèse était de combler ces lacunes, en fournissant une revue aussi complète que possible des ROAs dans le monde, tout en cherchant à quantifier précisément les disparités existantes dans ce domaine.

Sur la base de la disponibilité d'une information phylogénétique, le premier chapitre a donc permis d'identifier plus de 350 ROAs sur 22 archipels océaniques différents. La majeure partie d'entre elles sont composées de plantes (~45%) ou d'arthropodes (~36%), eux-mêmes dominés par les ordres et familles parmi les plus diverses de la planète (e.g., Asteraceae, Coleoptera). Les archipels d'Hawaï et des Îles Canaries abritent à eux seuls plus de la moitié des ROAs décrites à ce jour (51% à eux deux), le reste étant principalement distribué sur les archipels des Mascareignes (~10%), les Galápagos (~6%), Madère (~5%) et les Fidji (~5%). Cette simple observation est intéressante en elle-même, car elle souligne la prépondérance (parfois problématique, voir Farris 2020) de certains systèmes et/ou organismes modèles dans les connaissances accumulées sur un domaine spécifique. Dans un article d'opinion au ton provocateur, Shai Meiri parlait de la biogéographie des îles océaniques comme d'une science nomothétique de l'anecdote [*Oceanic island biogeography: Nomothetic science of the anecdotal*, Meiri 2017] et ajoutait :

“Thus studies of oceanic islands [...] usually focus on very few systems, namely the European and USA (controlled) oceanic island archipelagos of the Canaries, the Azores, Cape Verde and Hawaii, with the emblematic Galápagos thrown in for good measure. Our general dynamic theories are thus general to the level of these five archipelagos, and not so many other, much less well studied ones.”

Ces propos traduisent parfaitement l'état de la littérature concernant les ROAs. Bien sûr, ces disparités sont attribuables en partie à des facteurs naturels, tels que l'isolement exceptionnel et la grande complexité topographique d'Hawaï, qui ont sans aucun doute favorisé la prolifération d'un grand nombre de ROAs (Emerson 2002, Gillespie 2007, Gillespie et al. 2008). Cependant, les facteurs socio-économiques sont tout aussi importants : l'accessibilité, le financement de la recherche, ou même la présence de longues traditions naturalistes pour certains groupes spécifiques tels que les araignées à Hawaï (Gillespie 2016) ou les coléoptères des îles Canaries (Machado & Oromi 2000), explique sûrement pourquoi tant de ROAs ont été décrites sur ces archipels. Notre revue de littérature démontre également que ces fortes disparités se manifestent dans la popularité des ROAs dans la littérature, avec seulement quelques-unes ayant fait l'objet de nombreuses études couvrant un large éventail de sujets (tels que les pinsons de Darwin ou encore les Drépanidinés d'Hawaï), tandis que la grande majorité des ROAs répertoriées ont été largement négligées sur le plan de la recherche.

Cette revue de la littérature offre aussi une présentation à la fois qualitative et quantitative de la notoriété des sujets abordés dans la littérature portant sur les ROAs. De nouveau, nos résultats mettent en lumière le monopole de certains thèmes/sujets, tandis que d'autres ont manifestement été négligées. L'estimation de l'âge de la colonisation apparaît ici comme le sujet le plus populaire, avec deux-tiers des 354 ROAs pour lesquelles une estimation existe. Même si cela reste anecdotique, il est intéressant de noter que cet intérêt pour l'âge de la colonisation apparaît dès les premières publications de phylogénies de ROAs. Par exemple, en 1985, Beverley & Wilson (1985) proposaient déjà un âge de 42 Ma pour la colonisation de l'ancêtre des Drosophiles d'Hawaï, en utilisant des comparaisons immunologiques de protéine de l'hémolymphe larvaire. Malgré leur popularité, la calibration des phylogénies insulaires, en particulier sur les archipels océaniques, demeurent un sujet de débat au sein de la communauté scientifique. Il existe en effet une grande variabilité d'approches, chacune présentant des biais méthodologiques plus ou moins marqués. Parmi elles, on trouve notamment l'utilisation controversée de l'âge géologique des îles comme points de calibration (Heads 2005, 2011, Fernández-Palacios et al. 2011), qui reste toujours utilisé dans certaines publications récentes (e.g., Ahlstrand et al. 2019, Martins et al. 2020).

Le deuxième thème de recherche le plus couramment abordé dans la littérature concerne le type de radiation (45% des ROAs), qui a pour but de déterminer si la ROA est adaptative ou non. Ce thème se distingue des autres par un manque évident de cadre méthodologique. En effet, il n'existe à ce jour aucun consensus concernant les approches ou méthodes qui permettraient de confirmer ou d'infirmer le caractère adaptatif d'une radiation, bien que plusieurs propositions aient été récemment avancées (Soulebeau et al. 2015, Moen et al. 2021). La validité/l'utilité même du terme "radiation adaptative", abondamment utilisé dans la littérature sur les ROAs (et souvent sans aucune justification), fait d'ailleurs débats au sein de la communauté scientifique (voir Hernández-Hernández 2019). Il semble par ailleurs que la fréquence des événements de spéciation non-adaptatifs (par allopatrie intra et/ou inter-îles) aient été aussi largement sous-estimés (Barajas Barbosa et al. 2023).

Le troisième sujet d'intérêt (43% des ROAs) concerne la biogéographie historique, qui fait état des différents événements de colonisations ayant lieu entre les îles de l'archipel au cours du temps pour une ROA donnée. L'accès à cette information, grâce à la reconstruction phylogénétique, a permis de mettre en évidence le phénomène de la "règle de progression" (*progression rule*, PR, Funk & Wagner 1995), révélant une corrélation positive entre l'âge des espèces et l'âge de l'île sur laquelle elles sont distribuées. Toutefois, malgré l'émergence de méthodes de plus en plus sophistiquées pour reconstruire l'histoire biogéographique des clades (e.g., Matzke 2014), l'étude de la biogéographie historique des ROAs est rarement soumise à une évaluation statistique. De plus, bien que la PR soit un sujet de discussion fréquent dans la littérature, les données empiriques montrent que ce patron est loin d'être dominant. Enfin, l'étude de la biogéographie historique, en particulier la détection de la PR, souffre d'un manque flagrant de cadre statistique bien défini, comme l'ont déjà relevé Hembry et al. (2021) :

“We further lack any kind of agreement about what a statistical “threshold” would be above which a Hawaiian phylogeny would be significantly consistent with a progression rule and distinguishable from a stochastic pattern”.

Nous reviendrons sur ce point précis dans la section 2 de cette discussion, où une proposition d'un indice permettant de quantifier la PR dans une phylogénie de ROA est présentée.

Enfin, notre étude révèle que deux thèmes de recherche semblent avoir été négligés dans la littérature, ces derniers ayant été traités pour moins de 10% des ROAs. Le premier thème concerne l'étude des patrons de diversité émergent au sein des ROAs, visant à établir des liens entre la répartition des espèces (ici, celles qui composent les ROAs) et les caractéristiques des îles. Le

deuxième thème porte sur la caractérisation du mode de diversification, c'est-à-dire l'analyse de la distribution temporelle des événements de spéciation depuis la colonisation de l'archipel. Ces deux thèmes feront l'objet des deux chapitres suivants de cette thèse.

En conclusion, ce premier chapitre a mis en évidence les nombreuses disparités qui existent dans la recherche sur les ROAs, et a permis de dresser un bilan de l'état actuel des approches mises en œuvre (ou non) dans l'étude de ces clades insulaires. Plusieurs recommandations y sont formulées sur la manière d'améliorer nos pratiques actuelles ainsi que sur la mise en place de futures études comparatives, qui pourraient apporter un nouvel éclairage sur les mécanismes éco-évolutifs sous-tendant les phénomènes radiatifs dans les archipels océaniques.

En guise de point final sur ce premier chapitre, nous pouvons dresser le portrait-robot d'une ROA typiquement retrouvée au sein de la littérature. Ainsi, si l'on devait choisir une ROA au hasard parmi les 354 référencées, il est probable que :

- Elle ait fait l'objet de moins de cinq études dans la littérature.
- Elle soit endémique de l'archipel d'Hawaï.
- Elle soit constituée de plantes.
- Elle ne compte pas plus d'une dizaine d'espèces.
- Elle appartienne à l'ordre des Asterales, voire à la famille des Asteraceae.
- Son âge ait été estimé en utilisant l'âge géologique des îles.
- Elle soit considérée comme adaptative.
- Les schémas de colonisation entre les îles de l'archipel aient été discutés, sans que la PR n'ait été clairement détectée.
- Il n'y ait pas d'informations concernant sa biogéographie, son tempo et son mode de diversification.

Le second chapitre de cette thèse (Chapitre III) avait pour objectif d'explorer les patrons biogéographiques émergents au sein des ROAs, en établissant les relations entre le nombre d'espèces par île au sein de chaque radiation et les caractéristiques géo-environnementales des îles. Cette analyse a été réalisée pour près d'une centaine de ROAs réparties sur quatre archipels, à savoir Hawaï, les Îles Canaries, les Galápagos et les Fidji. Comme précédemment mentionné, peu d'études se sont intéressées à ces patrons à l'échelle des ROAs, même si il est intéressant de noter certaines tentatives initiées très tôt, comme les travaux de Terrell Hamilton et Ira Rubinoff sur les pinsons de Darwin (Hamilton & Rubinoff 1963, 1964). Ces chercheurs se sont penchés sur le rôle des facteurs

biogéographiques, tels que la superficie des îles et la distance entre les îles, pour expliquer le nombre d'espèces et de sous-espèces de pinsons présents sur les îles des Galápagos.

Le travail présenté dans ce chapitre représente donc à ce jour la première tentative d'une analyse comparative de la biogéographie des ROAs. Différents résultats découlent de cette étude : premièrement, de manière générale, les hypothèses classiques de la biogéographie insulaire habituellement étudiées à l'échelle de grands groupes taxonomiques (e.g., oiseaux, Matthews et al. 2023 ; plantes, Price & Wagner 2011 ; fourmis, Ohyama et al. 2021 ; araignées, Cardoso et al. 2010) semble également s'appliquer aux ROAs. On y retrouve une relation positive entre la richesse spécifique et l'aire et l'hétérogénéité environnementale. Plus précisément, trois facteurs affectent plus particulièrement les patrons de diversité des ROAs dans les îles : l'aire, l'isolement géographique, et l'altitude. De manière surprenante, l'âge des îles n'a pas semblé être déterminant dans nos analyses. Etant donnée que l'âge est un proxy de l'aire et de l'hétérogénéité environnementale (ces deux derniers facteurs covariants avec l'âge durant l'ontogénie des îles, voir le modèle GDM ; Whittaker et al. 2008), nous faisons l'hypothèse que les mesures directes de l'hétérogénéité environnementale sont plus performantes sur le plan explicatif que l'âge (voir les récents travaux de Carey et al. 2021 sur cette question). Deuxièmement, nous avons mis en évidence que l'archipel d'origine, et dans une moindre mesure le groupe taxonomique (plantes ou invertébrés), explique une part considérable de la variabilité des patrons biogéographiques observés entre les ROAs. En dépit des différences écologiques entre ROAs qui pourraient influencer leurs patrons de distribution, l'identité de l'archipel semble ici jouer un rôle prédominant dans l'explication de la variation de l'importance relative des facteurs géo-environnementaux sur la diversité spécifique des ROAs au sein des îles. Parmi les résultats marquants, on constate que les ROAs de plantes semblent être principalement influencées par l'altitude, et ceci tant sur Hawaï que sur les Îles Canaries. Cela fait écho à l'extraordinaire diversité de phénotypes que l'on observe le long du gradient altitudinal au sein des ROAs de plantes de ces deux archipels (e.g., les Lobelioideae d'Hawaï, ou les *Echium* et les *Aeonium* des îles Canaries). Dans leur ensemble, ces résultats renvoient à un concept clé dans l'étude des îles océaniques : la prédictibilité (e.g., Shaw & Gillespie 2016, Whittaker et al. 2017, Roman-Palacios & Wiens 2018). En effet, l'histoire géologique et environnementale des archipels océaniques est fréquemment perçue comme très structurante, et donc façonnant de manière plus ou moins similaire les patrons écologiques et évolutifs des organismes qui s'y établissent. Cette notion est en partie corroborée par la règle de progression, qui montre que des clades très différents ont suivi des trajectoires de colonisation similaires au sein de l'archipel (Shaw & Gillespie 2016). Cette perspective renvoie aussi à l'idée d'envisager l'archipel océanique comme une véritable province

biotique, où chaque groupe qui s'y développe est soumis aux mêmes contraintes géo-environnementales (Triantis et al. 2015, 2016).

Enfin, dans le dernier chapitre (Chapitre IV), nous nous sommes penchés sur l'étude des patrons macroévolutifs se manifestant au sein des ROAs. De manière étonnante, notre revue de la littérature avait révélé une quasi-absence de traitement de la question du tempo et du mode de diversification dans l'étude des clades insulaires. Cela peut sembler paradoxal, surtout lorsque l'on considère d'une part le grand nombre de phylogénies disponibles pour les ROAs, et d'autre part les avancées théoriques et méthodologiques remarquables des dernières années dans le domaine des modèles d'évolution appliqués aux phylogénies moléculaires (e.g., Stadler 2013, Morlon 2014, Rabosky et al. 2014). En outre, l'examen du tempo et du mode de diversification dans les arbres phylogénétiques permet d'aborder des points clés de la biogéographie insulaire, tels que les concepts d'équilibre, de diversité-dépendance, ou de radiations adaptatives (e.g., Rabosky & Glor 2010, Valente et al. 2015, 2017). Ainsi, nous avons entrepris dans ce chapitre une étude comparative des patrons de diversification des ROAs, en analysant une quarantaine de phylogénies moléculaires. Notre étude s'est articulée autour de trois hypothèses simples, chacune correspondant à un attendu clair sur la dynamique de l'accumulation des espèces au cours du temps : (1) le taux d'accumulation des espèces à ralentie au cours du temps. Ce patron peut être interprété comme un signe de diversité-dépendance au sein des ROAs (Strijk et al. 2014, Le Péchon et al. 2015, Bennett & O'Grady 2013, Valente et al. 2015). En outre, ce patron est dominant dans la littérature (Morlon et al. 2010) et est souvent associé aux radiations adaptatives (Moen & Morlon 2014) ; (2) le taux d'accumulation des espèces est resté constant au cours du temps. Ce patron peut être dû au fait que la plupart des ROAs n'ont pas encore atteint leur limite écologique, et continuent ainsi de se diversifier grâce à l'émergence de nouvelles îles ; (3) le taux d'accumulation des espèces a augmenté au cours du temps. Ce patron pourrait s'expliquer, entre autres, par le fait que les archipels océaniques sont sujets à des événements catastrophiques entraînant l'extinction de nombreuses espèces endémiques (e.g., éruptions volcaniques ou glissements de terrain). La phylogénie ne conserverait ainsi que la trace du dernier *boost* de spéciation, expliquant une augmentation tardive du taux d'accumulation.

Contrairement à certains attendus de la littérature, nos résultats ont donc montré que seul un faible nombre de ROAs présentaient un ralentissement significatif de leur taux d'accumulation des espèces au cours du temps. En réalité, un taux constant d'accumulation est observé pour environ trois quarts des ROAs, tandis que notre troisième hypothèse (augmentation progressive du taux au fil du temps) n'est rencontrée que dans un seul cas. La corrélation de ces résultats avec diverses caractéristiques clés des ROAs, telles que leur groupe taxonomique, leur âge ou leur taux de diversification net, ne

semble pas permettre d'expliquer cette répartition. Même si ce résultat nécessite d'être interprété avec prudence, la mise en évidence d'un tel patron à l'échelle de multiples ROAs est une première dans la littérature. Plusieurs hypothèses peuvent être formulées pour expliquer la prédominance du taux constant. J'aimerais souligner ici trois d'entre elles, qui me semblent être particulièrement pertinentes dans le contexte spécifique des archipels océaniques : (i) L'âge généralement très jeune des ROAs, qui permettrait d'expliquer pourquoi elles n'ont pas encore atteint leur équilibre. (ii) La dynamique géologique des archipels, qui permettrait aux radiations de continuer à s'étendre vers de nouveaux espaces écologiques (la plupart des archipels étant considérés comme en expansion, Ali & Meiri 2023). (iii) Le taux élevé d'extinction dans les archipels océaniques, qui aurait pu atténuer le signal d'un ralentissement du taux d'accumulation en éliminant les espèces les plus anciennes des phylogénies. Aussi, nos résultats soulignent la nécessité d'une remise en question de la notion d'équilibre de diversité au sein des les archipels océaniques (Whittaker et al. 2008), justifiant la pertinence d'une théorie du non-équilibre ou du déséquilibre pour ce type de systèmes (Heaney 2000).

2. Recommandations et pistes de réflexions

À la lumière des résultats présentés dans cette thèse, et en particulier dans la revue de littérature (Chapitre II), il m'a semblé opportun de regrouper quelques recommandations et pistes de réflexion dans une section distincte. Ces recommandations revêtent une importance particulière selon moi, compte tenu des disparités, des problèmes et des débats que j'ai pu rencontrer dans la littérature et au cours des discussions que j'ai pu avoir durant ces trois années de thèse.

2. a. Tendre vers un rééquilibrage de nos connaissances sur les ROAs

Même si cela peut paraître dérisoire de mentionner ce type de recommandations dans une discussion générale de thèse, j'aimerais tout de même souligner que la recherche sur les ROAs et les archipels océaniques pourrait grandement bénéficier de l'augmentation de l'effort d'échantillonnage dans certains archipels jusqu'ici quelque peu mis à l'écart, tels que ceux du Pacifique Sud. Par exemple, les îles Fidji, malgré leur grande similitude géo-environnementale avec Hawaï, semblent largement sous-étudiées en termes de ROAs. De plus, il existe un manque général d'investissements et de connaissances concernant la biodiversité de cet archipel (Rudbeck et al. 2022). Il convient également de mentionner les îles Samoa et les îles Vanuatu comme d'autres archipels qui mériteraient une exploration approfondie.

2. b. Multiplier les techniques de calibrations pour les phylogénies de ROA

Il me semble essentiel d'essayer d'appliquer un éventail plus large de méthodes lors de l'estimation de l'âge d'une ROA. Étant donné la complexité des problèmes liés à la calibration moléculaire, je pense que l'approche la plus judicieuse consisterait à tester un ensemble de points de calibration en parallèle. Deux articles récemment publiés illustrent très bien cette démarche : dans Johns et al. (2018), les auteurs testent 29 combinaisons différentes entre différents points de calibration et priors sur l'arbre phylogénétique des *Philodoria* (Lepidoptera, Gracillariidae) d'Hawaii. Ils utilisent ainsi plusieurs calibrations secondaires et âges géologiques des îles, et discutent de celles qui présentent les plus fortes valeurs de vraisemblance. Dans Arnedo & Hormiga (2020), les auteurs ont comparé et discuté trois techniques de calibration différentes pour trois ROAs de Linyphiidae sur l'archipel de Juan Fernández (les radiations de *Juanfernandezia*, *Laminacauda* et *Neomaso*). La première technique utilise une calibration basée sur un fossile, la deuxième est une calibration basée sur l'âge d'une île, et la troisième utilise des taux de substitution des gènes mitochondriaux. Bien que ce type d'approche puisse nécessiter un peu plus de temps et d'efforts, elle me semble plus appropriée que de faire un choix arbitraire d'une méthode plutôt qu'une autre. Ce genre d'exercice permettrait également de faciliter les analyses comparatives.

2. c. Encadrer l'utilisation de l'épithète « adaptative » pour les ROAs

La question de la classification des ROAs en différents types mérite d'être abordée avec précaution. Il semble pertinent de limiter autant que possible l'emploi du terme "radiation adaptative" pour décrire une ROA, sans avoir préalablement effectué une ou plusieurs analyses statistiques sur la majorité des espèces qui composent cette radiation (Soulebeau et al. 2015). Il est important de noter que la perception du caractère adaptatif d'une ROA peut sembler évidente pour les experts du groupe en question, et l'objectif de cette recommandation n'est bien sûr pas de remettre en question leur expertise. Cependant, dans un souci de clarté et de rigueur scientifique, il me semble essentiel d'identifier clairement un ensemble de preuves avant d'utiliser l'épithète « adaptative » pour qualifier une ROA. Les récentes discussions sur le sujet (e.g., Hernández-Hernández 2019, Martin & Richards 2019, Moen et al. 2021, Cerca et al. 2023), les propositions de classifications (e.g., Simões et al. 2016, Martin & Richards 2019) et les recommandations méthodologiques (e.g., Soulebeau et al. 2015) de ces dernières années vont dans ce sens, offrant des bases solides pour espérer une clarification progressive des types de ROAs. On peut notamment citer les cinq méthodes proposées par Soulebeau et al. (2015) afin de mettre en évidence le caractère adaptatif d'une radiation donnée : (1) le test expérimental, (2) la déduction de l'adaptation locale à partir de comparaisons QST-FST, (3) l'étude de l'évolution de la disparification dans le

temps, (4) l'élucidation de l'utilisation, par les membres d'un clade, du même habitat ou des mêmes ressources par différents moyens, (5) la démonstration de l'utilisation, par des spécimens du même clade, d'habitats ou de ressources différents.

2. d. Mieux quantifier la règle de progression (PR)

Comme mentionné précédemment, la PR est l'un des modèles éco-évolutifs les plus étudiés dans la littérature sur les ROAs. Cependant, nous avons pu constater que ce modèle de colonisation inter-îles était trop rarement soumis à une évaluation statistique, un problème déjà soulevé par Hembry et al. (2021). À ce jour, il n'existe pas de protocole clairement établi pour détecter l'existence de la PR au sein des phylogénies de ROAs. Ce manque entrave la mise en œuvre d'une véritable étude comparative, qui pourrait notamment déterminer quand, où et chez qui la PR prévaut exactement. Durant mon travail de revue de la littérature pour le Chapitre II, et en l'absence de cadre statistique clair, j'ai souvent dû relire attentivement les discussions des articles afin de comprendre comment les auteurs interprétaient la topologie de l'arbre en fonction de la distribution des espèces dans les îles. Je souhaiterais donc proposer ici une méthode directement inspirée d'une idée de Knope et al. (2020), et qui permettrait de quantifier de manière plus précise la présence de la PR dans une phylogénie de ROA. Les détails de cette méthode sont exposés dans la section suivante.

2. e. Calcul d'un indice de PR

La méthode présentée ici nécessite d'avoir à disposition la phylogénie moléculaire datée (en temps réel ou relatif) d'une ROA, ainsi qu'une matrice de distribution des espèces au sein des différentes îles de l'archipel (ou des différents volcans sur la même île si cette information est connue, Funk & Wagner 1995). La première étape consiste à reconstruire les aires ancestrales à chaque nœud de l'arbre à l'aide du package R *BioGeoBEARS* (Matzke 2013, 2014). Cette méthode permet de tester plusieurs modèles alternatifs de reconstruction des aires ancestrales qui admettent différents types d'événements biogéographiques (voir **Figure V.1**). Une fois les différents modèles testés, la méthode utilise le critère d'information d'Akaike corrigé (AICc) pour identifier le meilleur modèle. La reconstruction effectuée avec le meilleur modèle est donc sélectionnée, ce qui permet d'obtenir pour chaque nœud interne de la phylogénie une estimation de l'aire la plus vraisemblable (voir **Figure V.2**).

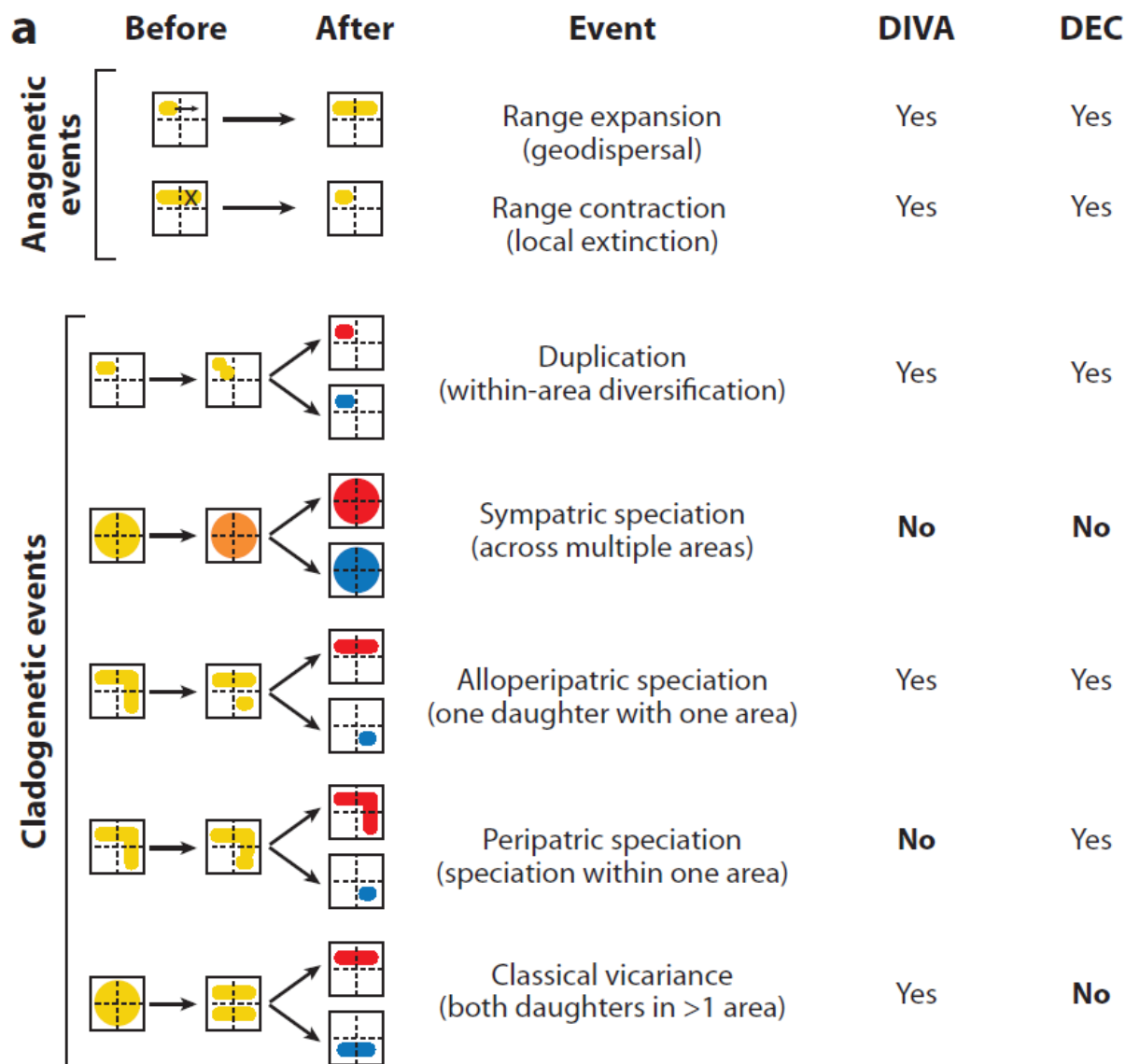


Figure.V.1. Présentation des différents processus pris en compte dans les modèles de biogéographie phylogénétique DIVA (Dispersal-vicariance analysis, Ronquist 1997) et DEC (Dispersal-extinction-cladogenesis, Ree et al. 2005), qui figure parmi les modèles testés dans *BioGeoBEARS* (Matzke 2013). Les événements anagénétiques impliquent une évolution de l'aire de répartition au sein d'une même lignée (pas d'événement de spéciation), tandis que les événements cladogénétiques impliquent une évolution de l'aire de répartition couplée à une séparation en deux lignées distinctes (spéciation). Adaptée de Ronquist & Sanmartín (2011).

A partir de cette information, je propose ensuite de compter le nombre d'événements en accord ou non avec la PR, selon les critères suivants : soit, A, B et C trois îles ayant chacune un âge géologique différent tel que âge $A >$ âge $B >$ âge C.

Cas 1 : On compte un événement en accord avec la PR lorsque qu'il y a, pour un nœud donné, un changement d'une aire ancestrale vers une aire comportant une ou plusieurs îles plus jeunes (e.g., $A \rightarrow AB$, $AB \rightarrow BC$), ou si un événement fondateur est détecté, c'est-à-dire une bascule d'une aire ancestrale vers une autre aire indépendante plus jeune (e.g., $B \rightarrow C$, $A \rightarrow BC$).

Cas 2 : On compte un événement comme étant inverse à la prédiction de la PR lorsque qu'il y a, pour un nœud donné, un changement d'une aire ancestrale vers une aire comportant une ou plusieurs îles plus vieilles (e.g., $B \rightarrow AB$, $C \rightarrow BC$), ou si un événement fondateur est détecté, c'est-à-dire une bascule d'une aire ancestrale vers une autre aire indépendante plus vieille (e.g., $C \rightarrow B$, $C \rightarrow AB$).

Cas 3 : Lorsque l'on observe un changement d'une aire ancestrale vers une aire comportant à la fois une ou plusieurs îles plus vieilles et plus jeunes (e.g., $B \rightarrow ABC$, $B \rightarrow AC$), on comptabilise pour moitié en accord et pour moitié en contradiction avec la PR.

Cas 4 : Dans les cas où l'aire ne change pas (e.g., $A \rightarrow A$) ou se rétrécit sans nouvelle colonisation (e.g., $AB \rightarrow B$), le nœud en question n'est pas comptabilisé.

Une fois tous les nœuds classés, on additionne les nœuds en accord avec la PR (1 point par Cas 1 et un demi-point par Cas 3 recensé), et on divise par le nombre total de nœuds comptabilisés (c-à-d l'addition des Cas 1, Cas 2 et Cas 3, mais sans les Cas 4).

Dans notre exemple (**Figure.V.2**), on comptabilise huit changements d'aire en accord et cinq en désaccord avec la PR : on quantifie donc ici la PR à 61,5% (8/13). On peut ensuite imaginer des étapes subséquentes, tels qu'un test statistique permettant de savoir si le pourcentage de PR observé est supérieur à un attendu aléatoire à la vue de la topologie et de la distribution des espèces de la ROA. Une autre proposition pourrait être de calculer le pourcentage sur 1000 arbres *pure-birth*, et d'évaluer si le pourcentage observé est supérieur à la borne à 95% de la distribution nulle.

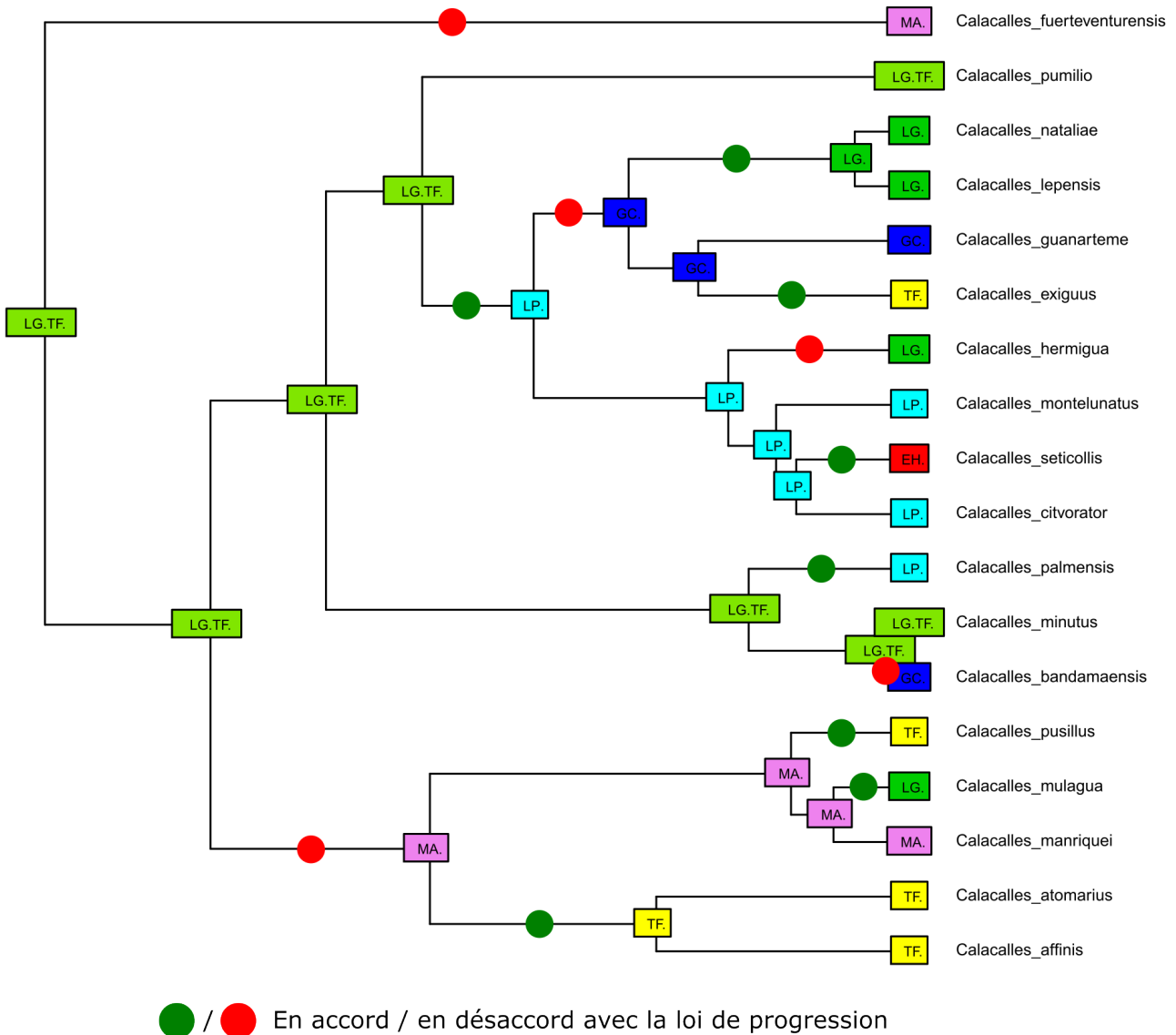


Figure.V.2. Présentation de notre méthode de quantification de la PR pour la ROA des *Calacalles* sur îles Canaries. Les aires de reconstruction ancestrales ont été estimées avec le modèle BAYAREALIKE+J, sélectionné comme modèle le plus vraisemblable dans BioGeoBEARS. Les lettres correspondent aux noms des différentes îles (leur âge géologique est spécifié entre parenthèses) : MA=Mahan (23 Ma), qui représente la combinaison des îles actuelles de Lanzarote et Fuerteventura, ces dernières ayant été reliées durant la majeure partie de leur cycle géologique. GC= Gran Canaria (14.5 Ma), TF = Tenerife (12 Ma), LG = La Gomera (11 Ma), LP = La Palma (1.7 Ma), EH = El Hierro (1.10 Ma).

3. Critique des approches comparatives

Les résultats de cette thèse démontrent clairement l'importance des analyses comparatives à grande échelle pour la recherche en écologie de l'évolution. Cependant, il est essentiel de noter que la comparaison de nombreuses données provenant de sources diverses peut présenter des limites significatives, qui sont souvent attribuables au manque de standardisation des pratiques et des méthodes couramment utilisées au sein de la communauté scientifique.

Au commencement de cette thèse, nos premières investigations de la littérature nous avaient laissé entrevoir la possibilité de mener des analyses comparatives à très large échelle, portant sur plus d'une centaine de ROAs réparties dans divers archipels du globe. Cependant, il est rapidement apparu que de nombreuses données taxonomiques, phylogénétiques et géo-environnementales étaient soit lacunaires, soit tout simplement inexistantes au sein de la littérature (e.g., données phylogénétiques sur le Sud-Pacifique, géologie des Bonins (Ogasawara), de Vanuatu). De plus, certaines caractéristiques essentielles concernant les ROAs, bien que disponibles, étaient loin de la standardisation nécessaire leur permettant d'être incluses dans nos études comparatives. En fin de compte, et au risque d'être caricaturale, les informations exploitables étaient principalement disponibles pour Hawaï, les îles Canaries et les Galápagos, ce qui, malgré leurs importances dans le domaine, ne représente qu'une portion très limitée de la grande variété des archipels océaniques dans le monde.

D'un point de vue plus technique, il convient de mentionner certaines limites générales liées à nos études comparatives, qui méritent d'être gardées à l'esprit à la suite de la lecture des résultats. Tout d'abord, il est important de reconnaître que l'incertitude associée à l'échantillonnage et à la taxonomie engendre un biais dans les données, difficilement quantifiable tant dans les matrices de distribution que dans les arbres phylogénétiques. Par exemple, l'inadéquation entre la taxonomie et la phylogénie pose des problèmes pour la délimitation des unités taxonomiques opérationnelles nécessaires aux analyses biogéographiques et macroévolutives. Dans plusieurs radiations, de nombreuses espèces restent à décrire, comme c'est le cas pour certaines radiations d'insectes à Hawaï (Hembry et al. 2021). De plus, lors de notre recherche bibliographique, nous avons identifié un nombre indéterminé de radiations potentielles, c'est-à-dire des groupes d'espèces endémiques, parfois très diversifiés (e.g., les *Mecyclothorax* avec 239 espèces, les *Proterhinus* avec 177 espèces, voir Hembry et al. 2021), qui n'ont toutefois jamais fait l'objet d'études phylogénétiques. Faute de preuves de leur monophylie, nous n'avons pas pu les inclure dans nos analyses, créant ainsi un déséquilibre de représentation au sein de nos données. La quantification de ces radiations

potentielles pourrait cependant être très pertinente pour de futures recherches. Je voudrais ici mentionner le travail de l'étudiante en thèse, Lizzie Roeble du National Research Institute for Biodiversity aux Pays-Bas, qui travaille actuellement sur les radiations des Asteraceae. Elle a en effet produit une estimation de l'ensemble des ROAs potentielles (*putative radiations*) au sein de ce groupe dans le monde, et a cartographié leur distribution, créant ainsi un moyen d'orienter les futures études vers les zones prioritaires.

Pour conclure cette section sur les défis liés à la mise en place d'analyses comparatives avec des phylogénies, plusieurs aspects méritent d'être pris en considération. Il est légitime de se questionner sur la comparabilité des phylogénies obtenues à partir de sources différentes, car il est possible que des phylogénies estimées indépendamment ne représentent pas des histoires évolutives totalement comparables. Compte tenu du fait que toutes les espèces sont apparentées, l'idéal serait de construire des méga-phylogénies par grand taxons (e.g., angiospermes, oiseaux, coléoptères) qui regrouperaient des ensembles de ROAs. Ces dernières pourraient ensuite être réextraites pour des analyses individuelles. Cette approche pourrait être également pertinente pour résoudre les problèmes de calibration des ROAs, un méga-arbre étant plus facile à dater avec précision grâce à la possibilité d'y placer plusieurs fossiles (e.g., Huysduynen et al. 2021). Cependant, cela a comme conséquence potentielle l'augmentation de la corrélation des erreurs. Dans ce cas, l'utilisation de phylogénies provenant de sources différentes, comme nous l'avons fait durant cette thèse, peut permettre d'éviter ce type de problème. De manière plus générale, nous manquons de recul sur l'impact du nombre et du type de marqueurs sur les patrons de diversification des ROAs, les variations de vitesse d'évolution entre marqueurs pouvant peut-être poser des problèmes. Enfin, l'hétérogénéité concernant la robustesse des nœuds dans les phylogénies (mesurée par les valeurs de bootstraps ou des probabilités postérieures) constitue un défi majeur pour toutes les analyses comparatives qui dépendent d'une topologie robuste, comme l'évaluation de la PR.

4. Perspectives

Ce travail de thèse a tenté d'apporter un nouvel éclairage sur la recherche en biogéographie et en macroévolution concernant les ROAs. Cependant, comme tout travail scientifique, il ne constitue qu'une petite contribution à l'édifice des connaissances bâti par la communauté scientifique depuis des décennies sur ce sujet. En réalité, il soulève au moins autant de nouvelles questions qu'il ne fournit de réponses. Dans cette section, je présente donc plusieurs pistes de développement potentielles pour compléter et prolonger ce travail de thèse.

4. a. Prendre en compte les caractéristiques écologiques des espèces dans les analyses comparatives sur les ROAs

Une perspective évidente qui émerge à la suite de ce travail de thèse est la nécessité d'intégrer des informations écologiques (traits fonctionnels, données morphologiques, préférences d'habitats) au niveau spécifique dans les analyses comparatives entre ROAs. Cette perspective revête une importance capitale, tant pour mieux appréhender le caractère adaptatif de la ROA dans son ensemble (e.g., l'étude de l'évolution de la disparification au fil du temps), que pour discriminer différentes hypothèses biogéographiques et/ou évolutives [e.g., adaptation versus allopatrie (Barajas-Barbosa et al. 2023) convergence évolutive (Gillespie 2004 ; Mahler et al. 2013), innovations clés (Burress & Muñoz 2022)]. En effet, la richesse spécifique et la phylogénie, toutes deux abondamment utilisées au cours de cette thèse, sont aveugles aux différences écologiques entre espèces. L'essor de l'étude des traits fonctionnels produit un nombre de données de plus en plus conséquent pour plus en plus de groupes taxonomiques (plantes : Kattge et al. 2011 ; oiseaux : Tobias et al. 2022 ; araignées : Pekár et al. 2021 ; papillons : Shirey et al. 2022), qui seront clé pour le futur du domaine. On rencontre également de plus en plus d'études prenant en compte des caractères fonctionnels dans l'étude des ROAs (*Argyranthemum*, White et al. 2020 ; *Scalesia*, Fernandez-Mazuecos et al. 2020 ; *Pheidole*, Darwell et al. 2019). L'accessibilité des données écologiques pour un grand nombre de ROAs ouvre la voie à la formulation de nouvelles hypothèses/questions, comme la possibilité de quantifier la part des processus non-adaptatifs dans les patrons de diversification des ROAs. Par exemple, dans une récente étude sur la diversité des traits végétaux sur l'île de Tenerife dans les îles Canaries, Barajas-Barbosa et al. (2023) ont montré que la grande majorité des radiations de plantes sur cet archipel résultait en majorité de processus non-adaptatifs, car seules les radiations des *Aeonium* et des *Polycarphaea* auraient contribué de manière significative (adaptative) à l'expansion de l'espace des traits. De plus, la comparaison des espaces écologiques occupés par différentes radiations dans différents archipels pourrait permettre de déterminer si les changements dans les caractéristiques des espèces sont directionnels et donc prédictibles entre archipels (Schrader et al. 2021).

4. b. Explorer les patrons biogéographiques et macroévolutifs des radiations évolutions dans d'autres systèmes insulaires

Dans cette thèse, notre travail s'est porté exclusivement sur les archipels océaniques définis comme une île ou un groupement d'îles géographiquement proches, ayant la même origine volcanique, et n'ayant jamais été en contact avec d'autres masses terrestres (Nunn 2009, Whittaker et al. 2023). Ce choix a été fait dans le but de créer un cadre de recherche clair et cohérent qui

délimite sans ambiguïté notre travail sur les ROAs. De plus, l'étude de ces systèmes nous a permis de nous appuyer sur un cadre théorique solide, principalement basée sur la formalisation du Modèle Général Dynamique de la biogéographie des îles océaniques (General Dynamic Model, GDM, Whittaker et al. 2008, Borregaard et al. 2017).

Il serait pertinent et relativement aisé d'appliquer les hypothèses et les méthodes utilisées dans cette thèse à d'autres types d'environnements insulaires. Par exemple, les îles d'Asie du Sud-Est (Indonésie, Philippines), constituées en partie d'îles volcaniques, abritent plusieurs grandes radiations insulaires de vertébrés (e.g., Esselstyn et al. 2009, Blackburn et al. 2013, Rowe et al. 2019). Certaines hypothèses sur la prévalence des taux constants dans les patrons de diversification, exposées dans le chapitre IV, reposent en grande partie sur des travaux réalisés dans cette région géologiquement très dynamique (Esselstyn et al. 2009, Fritz et al. 2011). Il serait aussi pertinent d'étudier les patrons de diversification des radiations évolutives dans des îles continentales, telles que Madagascar ou la Nouvelle-Zélande, en ayant à l'esprit l'hypothèse que les radiations dans ces îles (plus anciennes et géologiquement plus stables) pourraient présenter des profils de ralentissement des taux, comme cela a été suggéré pour certains groupes (e.g., les vangas de Madagascar, Reddy et al. 2012 ; les hébés de Nouvelle-Zélande, Thomas et al. 2023), même si des contre-exemples existent (e.g., les lémuriens de Madagascar, Herrera 2017). Le cas de la Nouvelle-Calédonie serait également intéressant à explorer, car bien que cette île ait longtemps été considérée comme une île continentale en termes de biotope, il semble que son histoire géo-environnementale soit plus proche de celle d'une île océanique (Grandcolas et al. 2008).

Une autre piste de recherche intéressante serait d'examiner comment les profils biogéographiques et macroévolutifs évoluent lorsque l'on considère les ROAs à l'échelle des méta-archipels (Whittaker et al. 2019). En effet, de nombreuses ROAs préservent également leur monophylie à cette échelle, notamment dans l'Atlantique Nord à l'échelle de la Macaronésie (qui englobe les Açores, Madère, le Cap-Vert, et les Selvagens). On peut citer par exemple les coléoptères du genre *Tarphius* (Amorim et al. 2012), les plantes du groupe *Aeonium* (Mort et al. 2002) ou encore le genre *Argyranthemum* (White et al. 2020). Un phénomène similaire se produit dans le Pacifique, avec des radiations monophylétiques à l'échelle de l'ensemble de la région (comme le cas des coléoptères du genre *Rhyncogonus*, Claridge et al. 2017).

4. c. L'étude des ROAs dans un contexte de conservation biologique

Bien que les îles présentent un ratio disproportionné entre leur surface totale sur le globe et leur richesse spécifique (6.67% de la surface terrestre pour 20% de la biodiversité, Kier et al. 2009,

Sayre et al. 2018, Fernandez-Palacios et al. 2021), elles abritent également 50 % des espèces menacées et 75 % des extinctions connues depuis l'expansion européenne autour du globe (Fernández-Palacios et al. 2021). Dans ce contexte, l'étude des ROAs revête une importance capitale en raison de la vulnérabilité des espèces qui les composent. En effet, beaucoup d'espèces sont souvent présentes sur une seule île de l'archipel (SIE, *single islands endemic*) (voir Chapitre III ; environ 75% des espèces des ROAs sont des SIEs) ; et se caractérisent également par des tailles de populations réduites, des niches climatiques souvent restreintes, et des abondances locales plutôt faibles en comparaison avec les lignées qui n'ont pas ou très peu diversifiées (Fernández-Palacios et al. 2021). Les ROAs sont donc directement et fortement affectées par l'impact de l'activité humaine sur la biodiversité insulaire, que ce soit en termes de dégradation de l'habitat, de surexploitation des ressources naturelles, d'introduction d'espèces exotiques ou des perturbations liées au changement climatique (Harter et al. 2015, Whittaker et al. 2017, Fernández-Palacios et al. 2021, Matthews et al. 2022).

Ainsi, une approche approfondie et interdisciplinaire de l'étude des ROAs s'avère plus nécessaire que jamais. Cette démarche constitue un prérequis essentiel pour élaborer des stratégies de conservation efficaces (Caujapé-Castells et al. 2010) en vue de préserver ces espèces endémiques d'une importance cruciale d'un point de vue scientifique (Warren et al. 2015, Patiño et al. 2017), écologique (e.g., Albert-Daviaud et al. 2020) et sociétal (e.g., Duarte et al. 2022). L'étude des patrons biogéographiques et macroévolutifs des ROAs contribue ainsi de manière significative à cette entreprise globale, offrant des pistes pour orienter la recherche future en matière de conservation. Par exemple, une perspective intéressante consisterait à évaluer, à travers la littérature scientifique et la Liste rouge de l'IUCN, le degré de connaissance de la communauté scientifique concernant le statut de conservation des 354 ROAs et des espèces qui les composent (e.g., espèce vulnérable, en danger, etc). Il serait également pertinent d'analyser combien d'entre elles font l'objet de politiques de conservation à l'échelle locale et régionale. Un tel travail de synthèse permettrait de dresser un état des lieux des enjeux de conservation spécifiques aux ROAs. De plus, la disponibilité d'arbres phylogénétiques pour les ROAs pourrait constituer un atout précieux pour orienter des futures initiatives de conservation. En effet, dans le cas où la conservation intégrale de la ROA s'avère impossible, la diversité phylogénétique pourrait guider les efforts vers les zones, habitats ou îles abritant l'héritage phylogénétique le plus diversifié, maximisant ainsi l'impact des mesures de conservation (Faith 2018).

5. Conclusion

L'objectif général de ce travail de thèse était d'entreprendre une évaluation globale des radiations évolutives dans les archipels océaniques du monde entier, et de mettre en œuvre des analyses comparatives des patrons de diversité et de diversification de ces clades insulaires, afin d'éclairer sur les mécanismes éco-évolutifs à l'origine de leur émergence. Comme montré en introduction de cette thèse, nous manquions d'une véritable revue globale de la littérature concernant ces radiations, et malgré l'accumulation ces dernières décennies de données taxonomiques, phylogénétiques et biogéographiques sur le sujet (e.g., Weigelt et al. 2013, Shaw & Gillespie, Hembry 2018), très peu d'analyses comparatives approfondies avaient été réalisées jusqu'à présent. Ce travail de thèse a permis de combler un certain nombre de ces lacunes, même s'il a soulevé un certain nombre de problèmes inhérents à l'état actuel des connaissances et méthodes sur le sujet. Il est fascinant de constater à quel point un domaine aussi étudié et populaire que les radiations insulaires est encore soumis à de fort biais de représentativité et de méthodologie, certains semblant particulièrement difficiles à surmonter (par exemple, la méconnaissance de certains archipels ou le manque de données fossiles). Ce travail a donc tenté d'apporter un nouvel éclairage sur les mécanismes ayant permis l'émergence de cette extraordinaire biodiversité endémique, offrant ainsi une contribution modeste, mais espérons-le significative, à la réflexion sur l'étude des ROAs.

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Annexe I : Cerca et al. (2023)

Résumé


Une caractéristique récurrente des archipels océaniques est la présence en leur sein de radiations adaptatives génératrices de clades endémiques riches en espèces, et pouvant offrir un formidable aperçu des liens entre écologie et évolution. Les développements récents en génomique évolutive ont contribué à résoudre certaines questions de longue date se situant à l'interface entre ces deux domaines. À l'aide d'une recherche bibliographique exhaustive, nous avons identifié des études portant sur 110 radiations adaptatives putatives provenant de 19 archipels océaniques différents, mais avons constaté l'absence d'étude de génomique évolutive pour la plupart de ces radiations. Notre revue de littérature révèle différentes lacunes dans les connaissances liées à l'absence d'approches génomiques, et identifie également un certain nombre de zones taxonomiques et géographiques sous-échantillonnées. Nous pensons qu'en comblant ces lacunes avec les données nécessaires, nous pourrions approfondir notre compréhension de l'adaptation, de la spéciation, ainsi que d'autres processus évolutifs.

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Opinion

Evolutionary genomics of oceanic island radiations

José Cerca ^{1,2,*} Darko D. Cotoras,^{3,4} Vanessa C. Bieker,¹ Rishi De-Kayne,⁵ Pablo Vargas,⁶ Mario Fernández-Mazuecos,^{7,8} Julia López-Delgado,⁹ Oliver White,¹⁰ Martin Stervander,¹¹ Anthony J. Geneva,¹² Juan Ernesto Guevara Andino,¹³ Joana Isabel Meier,¹⁴ Lizzie Roebke,^{15,16} Baptiste Brée,¹⁷ Jairo Patiño,¹⁸ Juan M. Guayasamin,^{19,21} María de Lourdes Torres,^{20,21} Hugo Valdebenito,^{21,22} María del Rosario Castañeda,²³ Jaime A. Chaves,^{24,19} Patricia Jaramillo Díaz,^{25,26} Luis Valente,^{15,16} Matthew L. Knope,²⁷ Jonathan P. Price,²⁷ Loren H. Rieseberg,²⁸ Bruce G. Baldwin,²⁹ Brent C. Emerson,³⁰ Gonzalo Rivas-Torres,^{31,33} Rosemary Gillespie,³² and Michael D. Martin¹

A recurring feature of oceanic archipelagos is the presence of adaptive radiations that generate endemic, species-rich clades that can offer outstanding insight into the links between ecology and evolution. Recent developments in evolutionary genomics have contributed towards solving long-standing questions at this interface. Using a comprehensive literature search, we identify studies spanning 19 oceanic archipelagos and 110 putative adaptive radiations, but find that most of these radiations have not yet been investigated from an evolutionary genomics perspective. Our review reveals different gaps in knowledge related to the lack of implementation of genomic approaches, as well as undersampled taxonomic and geographic areas. Filling those gaps with the required data will help to deepen our understanding of adaptation, speciation, and other evolutionary processes.

Island adaptive radiations as windows into ecological and evolutionary processes

Oceanic islands and archipelagos have played a pivotal role in our understanding of evolutionary and ecological processes [1–9]. This is due to several characteristics of oceanic islands, including (i) their isolation, which limits the dispersal of terrestrial organisms and often results in **disharmonic communities** (see [Glossary](#)); (ii) specific ecological conditions, including geomorphological features, strong climatic variation across small geographic areas, discrete patches of habitats, and irregular cycles of disturbances, which play a role in the creation of ecological opportunity for diversification; (iii) the possibility to estimate their geological age, which offers a well-defined temporal framework for studying and modeling evolutionary processes; and (iv) their frequent occurrence in fragmented, spatial groups (archipelagos) which provide natural evolutionary 'experiments' with replicates [10–16].

Island evolutionary biologists have generally focused on two adaptive phenomena: the island syndrome and **adaptive radiation** [17,18]. The island syndrome describes the repeated and often extreme phenotypic changes which frequently involve predictable changes, such as cases of gigantism (e.g., *Birgus* coconut crabs) or miniaturization (e.g., *Stegodon* dwarf elephants), that might result from **ecological release** [19–21]. Adaptive radiation [22] broadly refers to the rapid diversification of a single evolutionary lineage into multiple descendant species that are notably ecologically differentiated [7,23]. Theory predicts a fundamental role of trait utility in adaptive radiation as well as a clear correlation between phenotypic traits and ecological niche space

Highlights

Oceanic islands have long inspired biogeographers, ecologists, and evolutionary biologists. A common feature of these islands is the occurrence of adaptive radiations, where a lineage quickly diversifies to occupy different ecological niches. Adaptive radiations offer a natural experiment to understand how ecology drives phenotypic and genomic evolution.

Recently, the 'genomics revolution' has made a major contribution to the field of evolutionary biology by uncovering patterns, processes, and mechanisms of genomic evolution.

Although progress is being made, we find that the application of genomic tools to understand the evolution of oceanic island organisms is still in its infancy. In response to this, we discuss fundamental questions that will help to integrate evolutionary genomics and island biology.

¹Department of Natural History, NTNU University Museum, Norwegian University of Science and Technology (NTNU), Trondheim, Norway

²Centre for Ecological and Evolutionary Synthesis (CEES), Department of Biosciences, University of Oslo, Oslo, Norway

³Department of Terrestrial Zoology, Senckenberg Research Institute and Natural History Museum, Senckenberganlage 25, 60325 Frankfurt am Main, Germany



occupation [24–26]. Adaptive radiations tend to occur on oceanic islands because they are located at the outer limit of the dispersal range of a given taxon [27]. Indeed, some of the most iconic examples of adaptive radiation are present on oceanic islands, such as the Hawaiian silversword radiation, which resulted in lianas, rosette plants, shrubs, cushion plants, and trees [28]. During the past ~3.5 million years they evolved outstanding variation in reproductive traits, floral architecture [28,29], and leaf morphology [29,30]. Equally prominent are the Galápagos finches, which collectively exploit many terrestrial habitats spanning from extremely arid, sun-exposed, coastal lava rock habitats to moist high-land *Scalesia* forests [31,32], and are renowned as a textbook example of adaptive radiation [33].

Advances in evolutionary genomics

The advent and development of high-throughput sequencing has transformed biology by opening new avenues of research that in turn provide new ways to tackle long-standing questions in evolution. These include resolving branches across the tree of life [34], uncovering the genetic basis of adaptation [35], and determining the evolution of genes and genomes across clades [36] (Box 1). In the context of adaptive radiation research, genomics has already contributed to the understanding of the genetic basis of adaptation and speciation [37], the role of hybridization in driving diversification [38,39], the genes underlying trait utility [40], and the genetic architecture of traits [41], among others.

Because some of the most celebrated adaptive radiations have occurred on oceanic islands, we set out to review evolutionary genomics on oceanic island adaptive radiations (Box 2) by asking what new insights have been gained by applying genomic sequencing to the study of speciation and diversification on oceanic islands. We found that there is currently both insufficient depth and diversity of genomic studies in the genomic studies of adaptive radiations on oceanic islands (Box 2 and Table S1 in the supplemental information online). Specifically, relatively few genomic studies have focused on understanding the fundamental factors that both promote and constrain adaptive radiations. We thus highlight the most substantial knowledge gaps regarding evolutionary genomics of adaptive radiations on islands through a set of outstanding questions (Box 3).

What is the basis of genetic variation underlying adaptive radiations on oceanic islands?

The extent of ecological and phenotypic diversity on oceanic island radiations represents an apparent evolutionary paradox. A high level of genetic variation is usually necessary to diversify eco-morphologically to a great extent [42], but a species colonizing an oceanic archipelago will typically suffer from founder effects (Figure 1) and, in many taxa, also inbreeding, ultimately leading to low levels of genetic variation. For example, it has been estimated that the original colonizing population of Galápagos finches comprised only 30 to 100 individuals [43]. In addition, recurrent local population extinctions driven by small area and environmental change can lead to further reductions in genetic variation (**population genetic diversity debt** [44]).

Our survey uncovered that hybridization and introgression are prevalent denominators on oceanic island adaptive radiations, and often drastically increase the levels of standing genetic variation in a species or population upon which natural selection acts [10,45,46]. Hybridization could lead to an increase in genetic variation in recently established island populations that would otherwise have little variation [10,45,47], thus counteracting the common negative effects of small population sizes and inbreeding depression [16]. Through hybridization, new phenotypes (intermediate or transgressive) may be formed. An example of transgressive phenotypes is the emergence of leaf phenotypes outside the range of variation across the parental species through

⁴Department of Entomology, California Academy of Sciences, 55 Music Concourse Drive, San Francisco, CA 94118, USA

⁵Institute of Evolutionary Biology, University of Edinburgh, Edinburgh EH9 3FL, UK

⁶Biodiversity and Conservation, Real Jardín Botánico, 28014 Madrid, Spain
⁷Departamento de Biología (Botánica), Facultad de Ciencias, Universidad Autónoma de Madrid, Calle Darwin 2, 28049 Madrid, Spain

⁸Centro de Investigación en Biodiversidad y Cambio Global, Universidad Autónoma de Madrid (CIBC-UAM), Calle Darwin 2, 28049 Madrid, Spain

⁹School of Biology, Faculty of Biological Sciences, University of Leeds, Leeds, UK

¹⁰Department of Life Sciences, The Natural History Museum, Cromwell Road, London, SW7 5BD, UK

¹¹Bird Group, Natural History Museum, Akeman Street, Tring, Hertfordshire HP23 6AP, UK

¹²Department of Biology and Center for Computational and Integrative Biology, Rutgers University–Camden, Camden, NJ, USA

¹³Grupo de Investigación en Biodiversidad Medio Ambiente y Salud (BIOMAS), Universidad de las Américas, Quito, Ecuador

¹⁴Department of Zoology, University of Cambridge, Downing Street, Cambridge CB2 3EJ, UK

¹⁵Naturalis Biodiversity Center, Darwinweg 2, 2333 CR Leiden, The Netherlands

¹⁶Groningen Institute for Evolutionary Life Sciences, University of Groningen, Box 11103, 9700, 5 CC Groningen, The Netherlands

¹⁷Université de Pau et des Pays de l'Adour (UPPA), Energy Environment Solutions (E2S), Centre National de la Recherche Scientifique (CNRS), Institut des Sciences Analytiques et de Physico-Chimie pour l'Environnement et les Matériaux (IPREM), 64000 Pau, France

¹⁸Island Ecology and Evolution Research Group, Instituto de Productos Naturales y Agrobiología (IPNA-CSIC), Calle Astrofísico Francisco Sánchez 3, 38206 La Laguna, Tenerife, Canary Islands, 38206, Spain

¹⁹Laboratorio de Biología Evolutiva, Instituto Biósfera, Colegio de Ciencias Biológicas y Ambientales, Universidad San Francisco de Quito (USFQ), Calle Diego de Robles y Avenida Pampite, Cumbayá, 170901 Quito, Ecuador

²⁰Laboratorio de Biotecnología Vegetal, Colegio de Ciencias Biológicas y

Box 1. Recent technical and methodological advances in genomics

As the field of genomics continues to change, progress is being made in terms of improving data quality and increasing the amount of data that can be obtained. These advances are made possible through improvements in sequencing machine chemistry, bioinformatic tools, and new theoretical models. Some recent and noteworthy advances in the field of genomics are given below.

Chromosome-resolved reference genomes

High-quality reference genomes are now becoming the standard of the field, and are obtained by combining long reads and contiguity-ligation sequencing. This has enabled the study of synteny, haplotype blocks, and rearrangements such as inversions and chromosomal fusions and fissions.

Detection and renewed interest in transposable elements (TEs)

TEs were previously difficult to study because they exist in high numbers along the genome and may comprise highly repeated regions. In practice, this meant that traditional sequencing approaches were unable to capture and reconstruct their extensive diversity, and early genomic methods would typically collapse TEs as high-coverage regions. The advent of high-quality long reads has allowed the identification and mapping of TEs, permitting reconstruction of their evolutionary history and impact on genome size and genes.

Determination of haplotype blocks and supergenes

Recent sequencing approaches and the development of methods to determine linkage between regions allow longer portions of the genome to be reconstructed, thus enabling detection of long portions of the genome that are inherited as a single block (**supergene**), which may have important evolutionary consequences.

Advances in the understanding of population genetics

The acquisition of a tremendous amount of genomic data has had an outstanding impact on population genomics because it has enabled the detection of **runs of homozygosity** along the genome, the inference of **ancestral recombination graphics**, the discovery of **barrier loci**, and distinction between introgression and incomplete lineage sorting.

Increased power to reconstruct phylogenies and the coalescence

Access to genomic data has spurred the development of new models to fully reconstruct relationships among species and populations. This includes genome-wide phylogenies and phylogenomic concordance factors [103].

Demographic histories

The use of genomic data to reconstruct demographic histories has enabled researchers to gain insight into population dynamics [104]. Recent advances in simulation models, which involves generating simulated data and comparing it to observed data, provide a powerful tool for understanding which factors may have played a significant role in shaping the evolutionary history of a lineage. These simulations can be intricate, and, by comparing them to empirical data, researchers are able to infer the probability of various demographic scenarios such as hybridization, population size fluctuations, and time of coalescence.

hybridization in the silverswords alliance, which enabled the exploitation of unoccupied ecological niches [48]. Hybridization can also lead to the evolution of intermediates, as shown in the *Argyranthemum* daisy radiation (Asteraceae, Canary Islands) in which two **homoploid hybrid species** occupy separate but intermediate geographic ranges of the parent species, with segregated ecological niches [49–51]. Two other examples are homoploid hybrids in the Hawaiian *Scaevola* naupaka radiation that occupy habitats intermediate relative to the dry and wet habitats of the parental species [52,53]. Finally, a direct consequence of hybridization might be introgression of a particular trait from one lineage to another, as was the case with muricate flowers in Hawaiian lobeliads (genera *Brighamia*, *Clermontia*, *Cyanea*, *Delissea*, *Lobelia* sect. *Galeatella*, *Lobelia* sect. *Revolutella*, and *Trematolobelia*) [54]. In this scenario, the introgression of functional alleles that facilitate the occupation of a vacant niche could result in phenotypic diversification and speciation.

What is the genetic basis of repeated evolution within adaptive radiations?

The repeated evolution of phenotypes or traits associated with the occupation of ecological niches offers a powerful approach for studying recurrent and potentially deterministic outcomes.

Ambientales, Universidad San Francisco de Quito (USFQ), Calle Diego de Robles y Avenida Pampite, Cumbayá, Quito, Ecuador

²¹Galapagos Science Center, Universidad San Francisco de Quito (USFQ) and University of North Carolina (UNC) at Chapel Hill, San Cristobal, Galapagos, Ecuador

²²Herbarium of Economic Botany of Ecuador (Herbario QUSF), Colegio de Ciencias Biológicas y Ambientales, Universidad San Francisco de Quito (USFQ), Calle Diego de Robles y Avenida Pampite, Cumbayá, Quito, Ecuador

²³Departamento de Ciencias Biológicas, Universidad ICESI, Cali 760031, Colombia

²⁴Department of Biology, San Francisco State University, San Francisco, CA 94132, USA

²⁵Estación Científica Charles Darwin, Fundación Charles Darwin, Santa Cruz, Galápagos, Ecuador

²⁶Department of Botany and Plant Physiology, University of Málaga, Málaga, Spain

²⁷Department of Biology, University of Hawai'i at Hilo, 200 West Kawaiili Street, Hilo, 96720, HI, USA

²⁸Department of Botany and Biodiversity Research Centre, University of British Columbia, Vancouver, BC, Canada

²⁹Jepson Herbarium and Department of Integrative Biology, 1001 Valley Life Sciences Building 2465, University of California, Berkeley, CA 94720-2465, USA

³⁰Island Ecology and Evolution Research Group, Instituto de Productos Naturales y Agrobiología (IPNA-CSIC), La Laguna, Spain

³¹Estación de Biodiversidad Tiputini, Colegio de Ciencias Biológicas y Ambientales, Universidad San Francisco de Quito (USFQ), Quito, Ecuador

³²Department of Environmental Science, Policy and Management, University of California, Berkeley, Berkeley, CA, USA

³³Universidad San Francisco de Quito (USFQ), Calle Diego de Robles y Avenida Pampite, Cumbayá, Quito, Ecuador

*Correspondence: jose.cerca@gmail.com (J. Cerca).

Box 2. Adaptive radiations on oceanic islands

To evaluate the existence of broad patterns across studies of adaptive radiations on oceanic islands, we conducted a literature survey of >300 scientific articles (see supplemental information online). This search uncovered studies spanning 109 putative oceanic island adaptive radiations (see Figure 1 in main text and Table S1; a comprehensive set of criteria on how we classified the radiations is given in the supplemental information online). Across the oceanic island adaptive radiations identified, we found that specific taxonomic groups were substantially overrepresented, encompassing 55 different plant and 39 arthropod radiations. From these, Asteraceae/Compositae (asters, 17 radiations), Carabidae (ground beetles, six radiations), and Lamiaceae (mints, five radiations) had the highest reported number of oceanic island adaptive radiations (see Figure 2 in main text). Although some of these are among the most diverse lineages on continents, these organism groups are also particularly successful on islands. In terms of geography (Figure 1), the largest number of radiations are reported for Hawai'i (38 radiations), Canary Islands (21), and Galápagos (10).

Notably, most of the studied radiations have received little attention, and 51 of 109 radiations were investigated in a single paper, 38 in two to four papers, 12 in five to nine papers, and only eight in ≥ten papers. With 48 articles, the Galápagos finches were the most studied oceanic island adaptive radiation and accounted for ~15% of the literature surveyed (see Table S1 in the supplemental information online). The majority of the studies used DNA sequence data of single markers (131 articles), some form of morphological data (99 articles), or ecological data (81 articles). Only 48 (~15% of the entire set) studies employed some form of genomic-level data (e.g., RADseq, whole-genome resequencing, transcriptome, genome assemblies; see Table S1 in the supplemental information online).

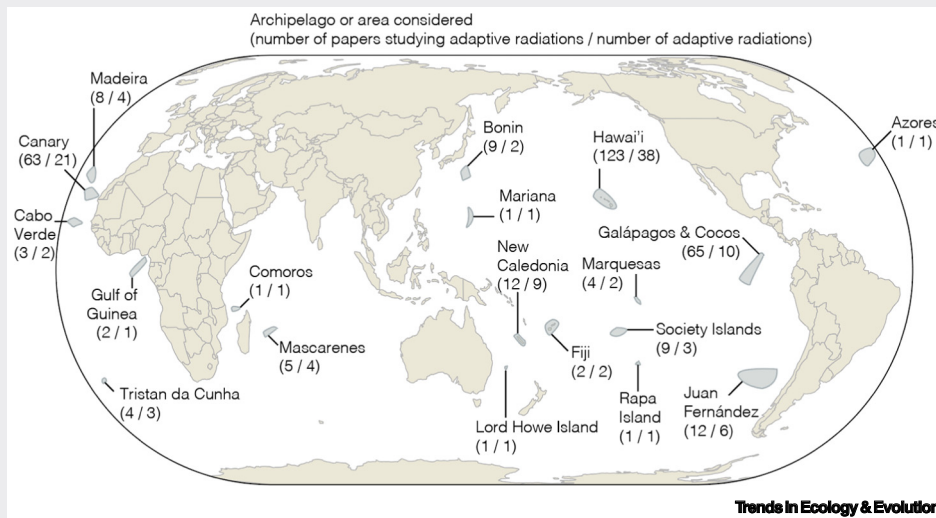


Figure 1. A global view of the number and distribution of adaptive radiations on islands. Numbers in parentheses give the number of articles studying adaptive radiation (left) and the number of adaptive radiations studied (right). The full dataset and criteria for establishing archipelagos are found in Table S1 in the supplemental information online. We retained New Caledonia because this continental island has been submerged, and therefore evolutionary and ecological processes occurred in a similar way to oceanic islands.

An important feature of oceanic island adaptive radiations is that species are, by definition, closely related, such that a common genomic and phenotypic background is likely, thus elevating prospects for the basis of repeated evolution. In addition, the diverse, discrete, and mosaic distribution of ecosystems on some islands can foster instances of repeated evolution of phenotypic traits and ecological occupation [55], thereby providing natural experiments to understand the genomic and ecological basis of traits associated with niche usage. Several studies identified in our literature search provided evidence of repeated evolution, including the Galápagos *Scalesia* radiation in which lobed-leaf morphologies evolved at least three times on different islands as a putative adaptive trait to arid conditions, whereas the tree habit evolved twice [56]. Similarly, evolutionary shifts to arid (xerophytes), humid (hygrophytes), and transition habitats (mesophytes)

Glossary

Adaptive radiation: the process in which multiple lineages diversify rapidly from a single ancestral lineage into a multitude of ecologically distinct forms.

Allopolyploid species: species with more than two haploid sets of chromosomes that are dissimilar and derived from different species.

Ancestral recombination graph: model used to represent coalescence and recombination events on a genome.

Barrier loci: loci that resist homogenization when gene flow occurs.

Convergent evolution: the evolution of similar and derived phenotypes from dissimilar ancestral phenotypes.

Diploidization: the process in which a polyploid genome reverts to a diploid condition.

Disharmonic communities: communities that have an uneven composition and distribution of taxonomic groups compared to a mainland source.

Ecological release: population-level niche expansions and shifts when a constraining interspecific interaction is reduced or removed.

Ecological versatility: the ability to occupy a set of disparate environments.

Homoploid hybrid speciation: when two species of the same ploidy level give rise to a hybrid species with the same ploidy level.

Parallel evolution: the evolution of similar and derived phenotypes from similar ancestral phenotypes.

Population genetic diversity debt: the genetic variation that will be lost following drift and/or natural selection.

Runs of homozygosity: contiguous regions of the genome in which an individual is homozygous across all sites.

Shared ancestral polymorphism: the ancestral genetic variation available in the genome.

Supergene: a group of genes that are inherited as a single genomic region and which jointly encode complex phenotypes.

Synteny: physical colocalization of genetic loci on the same chromosome within an individual or species.

Box 3. Study design for investigating the genomics of oceanic island adaptive radiations

One of the biggest advances brought by the 'genomics revolution' has been the convergence and integration of fields that relied on genetic data but have been traditionally distant, including phylogenetic systematics, population genetics, and functional genetics. Below we describe the ideal design for each of the questions identified.

What is the basis of genetic variation underlying adaptive radiations on oceanic islands?

To fully understand the origins, maintenance, and evolution of genetic variation, an ideal study design will include closely related outgroups such that phylogenetic reconstructions can be rooted and alleles can be polarized to find their ancestral state. The design will also benefit from a broad and geographically representative sampling of insular populations to fully identify and understand divergence and differentiation among populations. The characterization and quantification of unique genetic variation can be achieved by decomposing genetic variation, studying population structure, exploring changes of allelic frequencies along the genome, scans of selection, selective sweeps, and reconstructing the ancestral recombination graph. Introgression can be determined by establishing excess allele-sharing (e.g., Paterson's D or ABBA-BABA) and by demographic simulations that explicitly take hybridization into account.

What is the genetic basis of repeated evolution within adaptive radiations?

Lee and Coop [105] put together a comprehensive set of recommendations to distinguish the contribution of the three sources of repeated variation, namely *de novo* mutation, standing genetic variation, and introgression. Their recommendations involve the determination of long haplotypes and patterns of coalescence [105], and an experimental design will benefit from high-coverage data so that linkage can be estimated with confidence.

What is the genetic basis of repeated evolution across adaptive radiations?

The advent of chromosome-resolved genomes allows mapping of conserved (syntenic) and non-conserved regions of the genomes. By sequencing multiple genomes, and aligning and comparing them, one is able to understand which areas of the genome encompass broad genetic variation. Specifically, comparative genomic approaches permit the identification of general trends across large taxonomic lineages such as gene-family expansions (e.g., gene duplications) and contractions (gene losses), evidence of selection (dN/dS ratios), and mapping of gene features (synteny of genes, and TE locations). By functionally annotating genes using databases and model organism inferences, we are able to develop clear hypotheses about the causal links between features of the genome and their functions. These links should ideally be experimentally validated with functional genetic tools such as CRISPR and transcriptomic experiments. By determining sets of closely related genes in multiple genomes ('gene families') and studying their relatedness (the phylogeny of the gene family), one is able to understand expansions and contractions, and to determine the divergence of subgroups within the family.

When did the alleles underlying trait utility in adaptive radiations evolve?

Time-calibrated phylogenetic reconstructions allow an estimate of the divergence between lineages (species) to be obtained. If the allele of interest is present in a pair of species, it can be generally inferred that it pre-dates the divergence (speciation) event. The design benefits from including multiple outgroups to exclude scenarios of loss of a particular allele in a single outgroup. Determination of mutation rates, and simulations of the coalescent accounting for selective pressures and hybridization, can be used to obtain estimates for given alleles and haplotypes (Box 1).

What is the role of broad-scale genetic variation on oceanic island adaptive radiations?

Large-scale variation can be studied by comparing genomes from outgroups and radiations and by comparing lineages within radiations. Large-scale variation can also be putatively linked to ecological changes in some designs, although experiments such as CRISPR functional validation should be employed. Among-taxon comparisons can provide a window to conserved versus non-conserved genomic regions, whereas population-level whole-genome sequencing will complement this by informing on non-recombining blocks and on areas of the genome with excessive genomic divergence or differentiation. Novel techniques such as haplotagging hold great promise in determining large blocks under linkage at an affordable cost [106].

What is the prevalence of combinatorial effects on oceanic island adaptive radiations?

Combinatorial effects involve understanding whether hybridization and population divergence has catalyzed speciation and adaptation. The experimental design involves sequencing multiple individuals from different populations, testing for excess allele-sharing and genomic divergence, and performing demographic simulations with scenarios of where hybridization occurs.

have occurred repeatedly in Cape Verdean wall-rockets (*Diplotaxis*) [57,58]. In animals, several lineages of Hawaiian spiders show independent and repeated evolutionary origins of ecomorphs, notably stick spiders (genus *Ariamnes*) [59] and long-jawed spiders (genus *Tetragnatha*) [60]; in

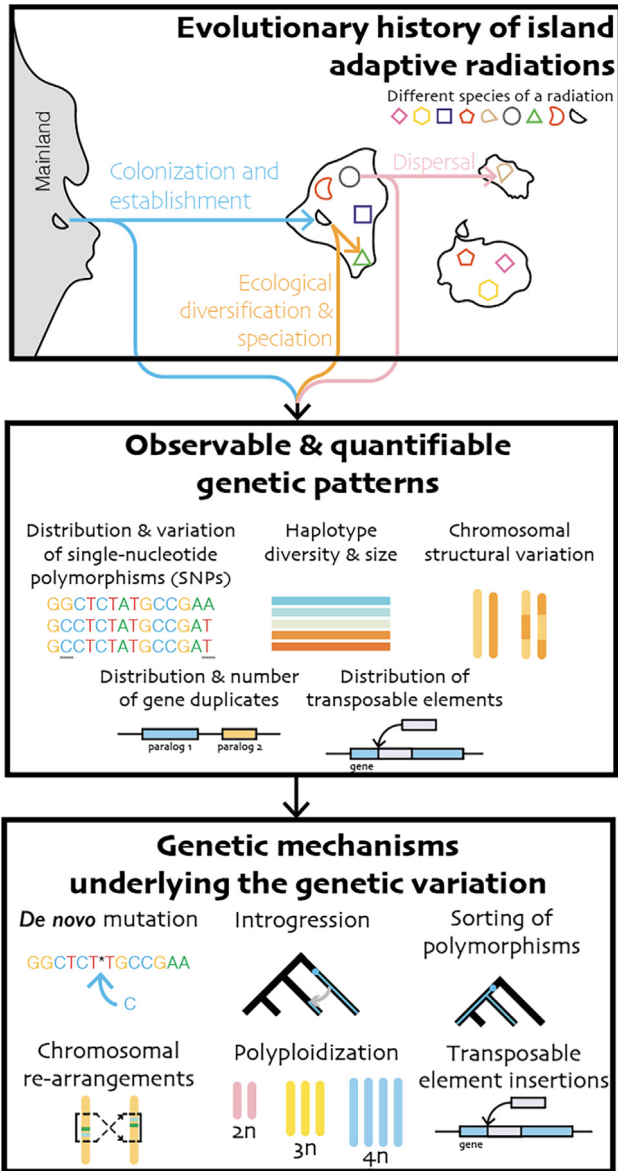


Figure 1. Evolutionary history, observable genomic patterns, and mechanisms of an adaptive radiation. The top panel shows a graphical representation of one possible trajectory of an adaptive radiation involving colonization, establishment, *in situ* speciation and ecological diversification, and subsequent dispersal. The middle panel displays some possible types of genetic patterns that can be observed and quantified to disentangle the contributions and impacts of the different processes (SNPs, haplotype diversity and size, chromosomal variation, distribution and number of gene duplicates and transposable elements). The bottom panel highlights possible genomic mechanisms that can be inferred from the genomic patterns from the intermediate box (mutation, hybridization, ancestral polymorphism, rearrangements, polyploidization, transposable element insertions).

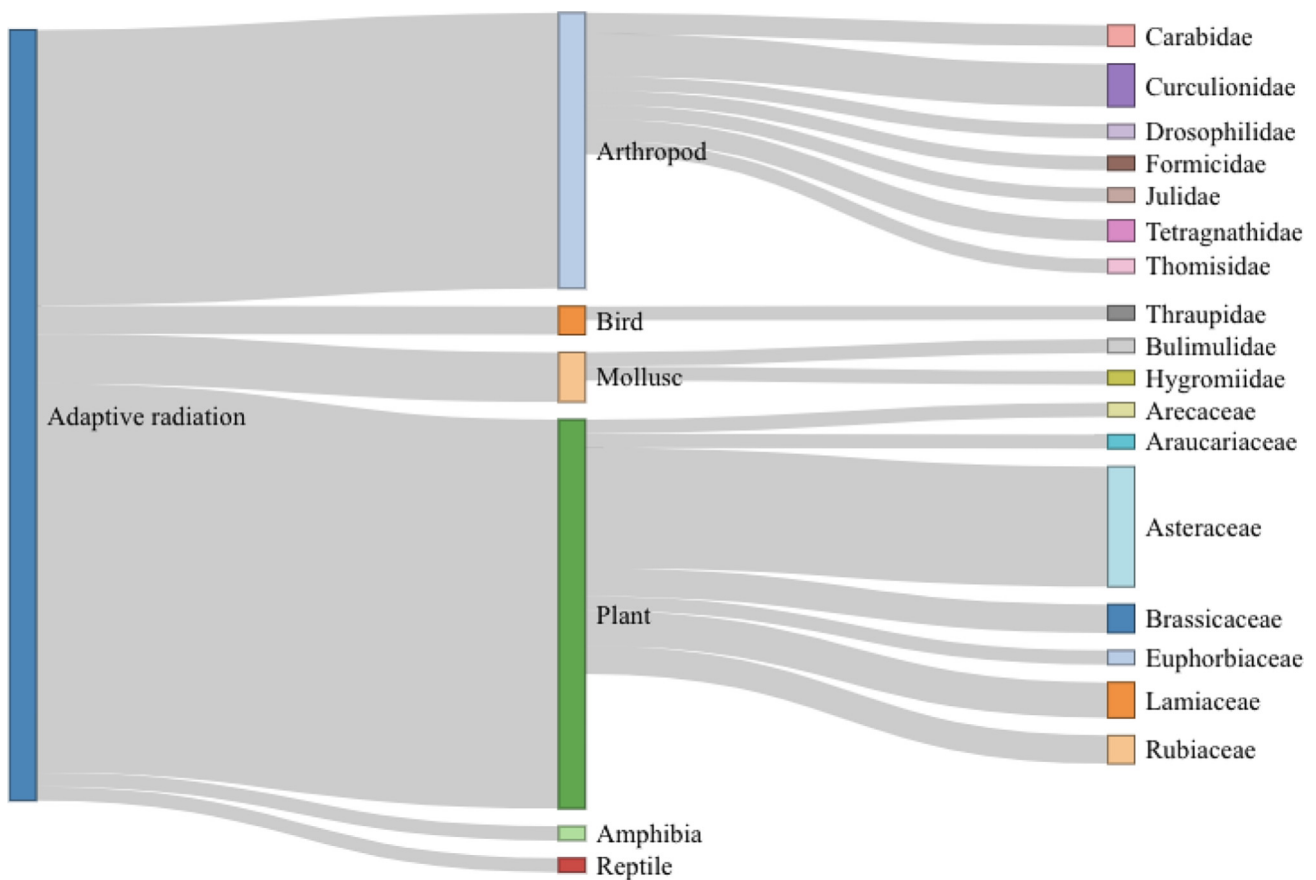
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both lineages, taxa with similar niche and phenotype have evolved from different ancestors within the radiation.

Three mechanisms have been suggested to underlie repeated evolution, **parallel evolution**, or **convergent evolution** during radiations of oceanic island biota: hybridization (introgression), **shared ancestral polymorphism**, and *de novo* mutation [61,62]. Vizueta *et al.* [63] found identical amino acid shifts in different lineages of *Dysdera* spiders (Canary Islands), suggesting *de novo* evolution of dietary phenotypes. In Galápagos *Hogna* wolf spiders, introgression underlies parallel evolution [64,65]. In the woody Hawaiian *Metrosideros*, a rich pool of ancestral genetic variation and the reassortment of this variation have likely fueled the radiation [66]. Despite these important insights, the prevalence and relative importance of these mechanisms remain mostly unexplored.

What is the genetic basis of repeated evolution across adaptive radiations?

Our literature review revealed that particular taxonomic groups have repeatedly and extensively radiated across multiple archipelagos, but that not much research has been done to compare the genetic basis of repeated phenotypic evolution across radiations (Figure 2). The repeated occurrence of adaptive radiations in taxa from the same higher taxonomic group offers a powerful approach for understanding to what extent intrinsic factors facilitate radiations. Among intrinsic factors, we consider both the underlying genomic basis and the phenotypic traits themselves. Noticeably, the groups radiating frequently on islands are not always from taxa that are the most globally diverse. For example, Orchidaceae is one of the most species-rich plant families, but orchids are underrepresented as adaptive radiations on remote islands, likely because their dependence on mycorrhiza and specialized floral biology limits establishment [67,68]. The tendency of some groups to adaptively radiate on islands could indicate that particular families have an appropriate set of traits to disperse, establish, and speciate in relatively isolated environments [7,10,62], and that members of these families have capabilities to quickly adapt and fill ecological niches. As an example, the basis of **ecological versatility** for Curculionidae (snout weevils) is associated with their capacity to feed on different plant hosts [69–72], whereas a 'weedy' life history might benefit radiation in the Asteraceae. The high potential for particular traits



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Figure 2. Overall number of hypothetical adaptive radiations presented by taxon. The 109 adaptive radiations identified in our review of the literature (bar to the left) are organized by major taxa (bars in the middle). On the right we display families in which two or more adaptive radiations were found. The size of the bar indicates the number of radiations within each. The supplemental information online provides details of how we scored the hypothetical radiations. Specifically, the dataset collected is found in Table S1 and a thorough description on scoring the adaptive radiations is provided in the supplemental information.

to repeatedly evolve [55], such as variation in beak morphology in birds, seems to be commonplace in multiple radiations.

The tendency to radiate may involve a combination of ecological, phenotypic, and genomic factors. For now, the paucity of comparative genomic studies (Box 2) revealed by our literature search makes it difficult to identify the underlying genetic basis that is responsible for the diversification, although this remains a central aspect of understanding the process of radiation. The combination of high-quality genomes and comparative genomics will likely provide answers to this question and open new avenues of research.

When did the alleles underlying trait utility in adaptive radiations evolve?

Trait utility, together with common ancestry, rapid speciation, and phenotype–environment correlation, is one of the four criteria outlined to diagnose the adaptive nature of a radiation, and it characterizes trait performance or fitness in different environments [22]. Some phenotypic variation of particular traits, such as leaves in plants and beaks in birds, seem to underlie repeated changes across oceanic island adaptive radiations, and this may be facilitated by particular genomic architectures [41]. Genomic data allow the age of genetic variants to be estimated, and there is accumulating evidence for the role of 'ancestral genetic variation' in producing new phenotypes [38,66,73]. For instance, there is a 240 000 bp long haplotype encompassing the *ALX1* homeobox gene in Galápagos finches. This gene is associated with beak morphology, which finches use to feed on different seeds (trait utility), and the variation within the haplotype pre-dates the origin of the radiation [40,73–75].

What is the role of broad-scale genetic variation on oceanic island adaptive radiations?

Because of its convenience and power, the field of population genomics has traditionally focused on understanding how the frequencies of SNPs vary between populations and over time. However, our understanding of phenotypic traits and local adaptation remains incomplete until we are able to make sense of the broad-scale variation that is increasingly being uncovered as novel technologies emerge (Box 1). We found evidence that the following five types of broad-scale genetic variation have contributed to oceanic adaptive radiations.

- (i) Transposable elements (TEs): these are DNA sequences that proliferate along the genome, thus having an impact on genome size and cell economy, and can directly interfere with genes [76,77]. When TEs jump within a genic region they can lead to frameshifts, to the creation of a pseudogene, or to the movement of genes. Instability caused by founder events, inbreeding, and environmental stresses typical of oceanic island adaptive radiations could suppress TE regulation (i.e., the genome shock hypothesis) [78]. This could lead to an upsurge of TE insertions, especially when combined with low effective population sizes which decrease the efficacy of selection in purging deleterious mutations [78]. The adaptive radiation of Caribbean *Anolis* lizards (in a mixture of continental and oceanic islands) has an unusual accumulation of TEs within *HOX* clusters [79,80], which is hypothesized to be associated with increased phenotypic variation [80]. However, compared to closely related lineages, the Hawaiian *Tetragnatha kauaiensis* [81], the Macaronesian *Dysdera silvatica* [82,83], and the Galápagos *Scalesia atractyloides* [84] show no evidence of TE proliferation.
- (ii) Gene duplication: this can lead to the formation of new phenotypes – one of the copies could acquire novel functions (neofunctionalization) or both copies can become specialized, resulting in two separate genes contributing to the function of the original ancestral gene (subfunctionalization) [79]. All these phenomena also take place in the continent, although they appear to act faster on islands. As an example, evidence from the silverswords shows

that the floral genes *ASAP1* and *ASAP3* are duplicates, likely resulting from allopolyploidization (**allopolyploid species**) [85]. In addition, the genomes of the spiders *T. kauaiensis* (Hawai'i) and *D. silvatica* (Macaronesia) contain evidence for gene-family expansions associated with sensory perception of taste, chemosensory ability, and metabolism [81,82].

- (iii) Haplotype blocks: these are non-recombining portions of the genome that are inherited together [86,87] and function as blueprints for complex phenotypes [86]. They are being identified in an increasing number of organisms with the help of genomic data, which enable reconstruction of linkage along the genome. The only evidence of haplotype blocks we are aware of on oceanic adaptive radiations comes from the Galápagos finches, in which beak development genes are suggested to be overrepresented in these blocks [75].
- (iv) Chromosomal rearrangements: these include translocations, fusions, agmatoploidy, dysploidy, inversions, and fissions that might result in new genetic combinations by changing linkage patterns or by separating genes from their regulatory elements [86,88], and often underlie haplotype blocks. In animals, the most studied group comprises >100 species of subgenus *Drosophila* from Hawai'i and displays a strong pattern of inversion polymorphism. **Syntenic** analyses of the *S. atractyloides* genome revealed strong associations between gene-rich regions and inversions [84].
- (v) Polyploidy: this phenomenon has been suggested as an important mechanism for ecological versatility and phenotypic evolution in plants [89]. We detected a high incidence of polyploidy in radiating plant lineages, in line with previous more comprehensive research showing that many endemic plants on islands are polyploids (80% of Hawaiian endemics [90] and >60% of Juan Fernández endemics [91]). It has been suggested that the colonizing ancestors of many of these lineages may already have been ancestral polyploids [92] and that elevated ploidy might act as a catalyst of ecological versatility through the 'two heads think better than one' analogy. Empowered by two (sub)genomes, the colonizing lineage has more genes and more alleles, which can translate into a potentially more efficient response to novel ecological conditions [85,92]. Although this is plausible, polyploidization could also have the opposite effect by inhibiting responses to selection if an advantageous allele is recessive and masked by the remaining alleles [93]. *S. atractyloides* is a tetraploid species, and it has been speculated that **diploidization** in this lineage slowed down as a result of insular adaptation [84].

What is the prevalence of combinatorial effects on oceanic island adaptive radiations?

The combinatorial synthesis postulates that when ancient genetic variation is brought together by hybridization, it might catalyze speciation processes [38]. This synthesis emerged from the growing recognition of the role of hybridization in increasing the genetic variability of lineages [38,73,94], which opposes the long-standing view that hybridization has a negative effect on biodiversity [4] and that hybrids are 'evolutionary noise' [95]. An important consideration of the combinatorial synthesis is the time-window wherein hybridization occurs: if the hybridizing species have diverged only minimally, hybridization might have no effect [96] or even lead to lineage fusion, as reported for the Galápagos tortoises [97], whereas with higher levels of species divergence introgression may not be possible or could result in sterile progeny owing to the build-up of reproductive barriers. Combinatorial events occur between these two periods, and it is likely that the temporal duration of this window is taxon- or lineage-specific.

Combinatorial effects may occur on oceanic islands through a combination of introgression and changes of allelic frequencies owing to genetic drift. Genetic drift has a potentially important role because the possibility of inter-island allopatric establishment and the regular cycles of disturbance and change within islands (e.g., volcanic, erosional, topographic) lead to population

fragmentation with random changes in allelic frequencies. Fragmented and to some degree genetically diverged populations could become locally adapted, and secondary contact between these may catalyze combinatorial processes [10,98]. For example, in Hawai'i, ecosystems are fragmented by lava flows, creating mosaic ecosystem patches (kīpuka). Because ecological succession may take place across decades or centuries, kīpuka remain semi-isolated, and organisms with low dispersal abilities, such as arthropods or some plants, might be confined to particular kīpuka and undergo divergence [96,98]. On the island of Lanzarote in the Canary Islands, these same volcanically isolated patches are referred to as 'islotos'. In this same group of islands, climatic oscillations may change the ratio and the source of colonizing species, and thereby lead to cycles of secondary contact with continental species [44,99,100]. Some of the features and patterns recognized in the combinatorial synthesis are shared with the 'surfing syngameon hypothesis' [44,99], which postulates that secondary contact from the mainland or other islands followed by gene flow has generated genetic diversity in some regions in the Canary Islands. An integration of the combinatorial synthesis and the surfing syngameon may be warranted [101].

Concluding remarks: the future of genomic research on oceanic island adaptive radiations

The study of evolutionary genomics on oceanic island adaptive radiations is in its infancy, but has tremendous potential to inform us about ecology and evolution. The diversity and variation observed in these radiations can provide complementary insights to the outstanding body of work of adaptive radiation research, but which has been limited to a handful of biological systems. However, before this is possible, the gap between evolutionary genomics and island biology needs to be addressed. To this end, we have postulated a set of genomic questions that are connected to the evolution of island radiations (see [Outstanding questions](#)).

Considering the threats to island biotas, such as tourism, habitat loss, habitat fragmentation, introduced diseases, and invasive species [102], among many others, opportunities to study biodiversity on islands are likely to diminish rapidly unless current trends are reversed through accelerated conservation efforts.

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Declaration of interests

The authors declare no conflicts of interest.

Supplemental information

Supplemental information associated with this article can be found, in the online version, at <https://doi.org/10.1016/j.tree.2023.02.003>.

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Outstanding questions

What is the basis of genetic variation underlying adaptive radiations on oceanic islands?

What is the genetic basis of repeated evolution within adaptive radiations?

What is the genetic basis of repeated evolution across adaptive radiations?

When did the alleles underlying trait utility in adaptive radiations evolve?

What is the role of broad-scale genetic variation on oceanic island adaptive radiations?

What is the prevalence of combinatorial effects on oceanic island adaptive radiations?

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LABORATOIRE :
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(IPREM)

CONTACT

Baptiste Brée
Baptiste.bree.pro@gmail.com