



CrossMark
click for updates

Research

Cite this article: Valente LM, Etienne RS, Phillimore AB. 2014 The effects of island ontogeny on species diversity and phylogeny. *Proc. R. Soc. B* **281**: 20133227. <http://dx.doi.org/10.1098/rspb.2013.3227>

Received: 18 December 2013

Accepted: 25 March 2014

Subject Areas:

evolution, ecology

Keywords:

island biogeography, volcanic ontogeny, phylogeny, radiation, endemism

Author for correspondence:

Luis M. Valente

e-mail: valente@uni-potsdam.de

Electronic supplementary material is available at <http://dx.doi.org/10.1098/rspb.2013.3227> or via <http://rspb.royalsocietypublishing.org>.

The effects of island ontogeny on species diversity and phylogeny

Luis M. Valente^{1,2}, Rampal S. Etienne³ and Albert B. Phillimore⁴

¹Department of Life Sciences, Imperial College London, Silwood Park Campus, Ascot SL5 7PY, UK

²Unit of Evolutionary Biology / Systematic Zoology, Institute of Biochemistry and Biology, University of Potsdam, Karl-Liebknecht-Strasse 24-25, Haus 26, D-14476 Potsdam, Germany

³Community and Conservation Ecology, Centre for Ecological and Evolutionary Studies, University of Groningen, PO Box 11103, Groningen 9700 CC, The Netherlands

⁴Institute of Evolutionary Biology, University of Edinburgh, Edinburgh EH9 3JT, UK

A major goal of island biogeography is to understand how island communities are assembled over time. However, we know little about the influence of variable area and ecological opportunity on island biotas over geological time-scales. Islands have limited life spans, and it has been posited that insular diversity patterns should rise and fall with an island's ontogeny. The potential of phylogenies to inform us of island ontogenetic stage remains unclear, as we lack a phylogenetic framework that focuses on islands rather than clades. Here, we present a parsimonious island-centric model that integrates phylogeny and ontogeny into island biogeography and can incorporate a negative feedback of diversity on species origination. This framework allows us to generate predictions about species richness and phylogenies on islands of different ages. We find that peak richness lags behind peak island area, and that endemic species age increases with island age on volcanic islands. When diversity negatively affects rates of immigration and cladogenesis, our model predicts speciation slowdowns on old islands. Importantly, we find that branching times of *in situ* radiations can be informative of an island's ontogenetic stage. This novel framework provides a quantitative means of uncovering processes responsible for island biogeography patterns using phylogenies.

1. Introduction

Oceanic archipelagos of volcanic origin, such as the Canaries, Galapagos and Hawaii have inspired fundamental theoretical developments in ecology and evolution, ranging from the nature of species–area relationships to the processes underpinning adaptive radiations (reviewed in [1]). The dynamic, transient nature of volcanic islands has long been recognized [2], but was not explicitly modelled in MacArthur & Wilson's [3] classic equilibrium theory of island biogeography (ETIB). Typical volcanic islands have a limited life span [4,5], and a major goal of recent island research has been to understand how species richness patterns and the processes governing community assembly change through time in such systems [6]. However, island biogeography lacks a quantitative framework to enable the study of how variable island area and ecological opportunity may influence diversity and phylogenetic patterns in isolated communities [7].

Volcanic island ontogeny begins with initial emergence from an underwater seamount, which is followed by a relatively short period of intense island-building, until maximum area and elevation are reached [4,8]. Islands then enter a slow erosional stage that leads to eventual island submergence [4,8]. Several verbal models integrating island ontogeny and ecological biogeography have been proposed (e.g. [5,6,9,10]). The most complete of these models is the general dynamic model (GDM) of oceanic island biogeography formulated by Whittaker *et al.* [6]. The GDM extended and updated the ETIB by incorporating new ideas on the geomorphic evolution of islands [4], *in situ* cladogenesis [11] and adaptive radiations [10]. The model's main proposition is that island diversity has an environmentally determined carrying capacity (K) that varies with island age as a result of ontogenetic changes in island area, elevational range, topographical complexity

and habitat diversity. According to the GDM, K should peak at or soon after the island has attained its maximum area and topographic complexity. K should then slowly decline as the island enters its erosional stage and loses area and elevational range, until the island submerges. Two key testable predictions arise from this verbal model: (i) total and endemic species richness should be a hump-shaped (unimodal) function of island age and (ii) island-wide (IW) rate of speciation should be highest at young to intermediate island ages until K has peaked. The GDM provides a good description of island species richness in many cases [6,12,13], with young archipelagos and highly dispersive taxa notable exceptions [14,15].

While speciation is a prominent feature of islands and is increasingly being incorporated into theoretical models, many of the empirical insights into insular radiation rely on taxonomy-based measures [6,16,17], such as the richness of single-island endemics, which has been shown to be very sensitive to taxonomic effort [18]. In the past decade, molecular phylogenies of insular taxa [19,20] have become increasingly common and the full extent of such data to inform us about the processes governing island biogeography is just starting to be explored [21,22]. A densely sampled time-calibrated molecular phylogeny of the populations/species on an island and their mainland counterparts has the potential to be informative about (i) whether an endemic species was likely to have arisen cladogenetically or anagenetically [23,24], (ii) the timing and rate of colonizations and subsequent migrations [25,26] and (iii) change in rates of insular diversification over time or with diversity [27]. One of the most sophisticated uses of phylogenetic information in island biogeography to date is Rabosky & Glor's [21] application of birth–death models to the phylogenetic branching times of *Anolis* lizards on Caribbean islands. They were able to show that rates of speciation have declined over time, with steeper decays taking place on smaller islands, providing strong evidence for controls of speciation consistent with the existence of an area-dependent K , as predicted by Whittaker *et al.* [7].

Despite the potential for phylogenies to introduce a temporal component into island biogeography, the field currently lacks an integrated quantitative framework that allows for the effects of process (immigration, extinction, speciation and island ontogeny) on pattern (e.g. richness, phylogeny) to be explored. While Chen & He [28] developed the first quantitative model to incorporate *in situ* speciation into the classic ETIB framework, their model did not incorporate the notion of a carrying capacity, the effects of island ontogeny on community composition or examine phylogenetic patterns. Here, we present a parsimonious, lineage-based simulation model that incorporates island ontogeny [6], immigration–extinction dynamics [3], phylogenetic birth–death models of *in situ* diversification [27,29] and diversity-dependence of species origination [30]. We model the effects of island ontogeny on community assembly processes by making per lineage rates of immigration, extinction and speciation area-dependent. We examine the expected effects of contrasting island ontogeny scenarios on the time series of IW biogeographic and speciation rates, as well as species richness, and test whether they follow a hump-shaped relationship with island age as predicted by the GDM. We explicitly model islands under conditions where species origination (immigration and speciation) rates are independent of the island's diversity and compare the shape of the resulting phylogenies with those that arise under a scenario where origination rates are diversity-dependent (DD) and decline with

increasing species richness, as would be expected for an island with a finite diversity carrying capacity [21]. We also provide a new set of expectations for the distribution of times of colonization and ages of species of different classes (immigrant, cladogenetic and anagenetic) for islands of different ontogenetic stages. Finally, we examine whether phylogenies of clades from islands at young life stages carry a signature of rapid radiation, and whether those from old life stages instead display declining speciation rates through time as posited by Whittaker *et al.* [6].

2. Material and methods

(a) Basic model

Our model considers a static mainland source pool with m species and an island with n species, with $n = 0$ at time $(t) = 0$. We adopted the straight-line immigration and extinction curve version of MacArthur & Wilson's ETIB [3], whereby at any given time each species on the mainland is equally likely to immigrate to the island, at a per lineage rate γ , and each species on the island is equally likely to go extinct, at a per lineage rate of μ . Immigration in our framework incorporates both dispersal (arrival) and successful establishment (colonization). Additionally, endemic species can be gained through *in situ* speciation via anagenesis or cladogenesis. Anagenetic speciation (where an island population diverges through time and becomes reproductively isolated from the mainland source population) occurs at a per lineage rate λ^a . Cladogenetic speciation (where one island species/population splits into two island endemic species) occurs at a per lineage rate λ^c . Species are classified as immigrant if they have populations on both island and mainland. Endemic species are those that are restricted to the island; they are classified as cladogenetic if their closest extant relative is endemic to the island, or as anagenetic if their closest extant relative is on the mainland.

(b) Diversity-dependence

We implemented our model in both a diversity-independent (DI) and DD setting. In the DI setting, there is no feedback of diversity on any of the per lineage parameters. The DD setting in comparison is intended to capture the effect of ecological limits and a carrying capacity [6,21]. Under DD, the number of niches on an island is limited and each new species requires a vacant niche. Therefore, the more species there are on the island, the lower are the chances that a successful colonization or cladogenesis event will take place. In the DD setting, we thus make per lineage rates of immigration and cladogenesis decline linearly with diversity [30]

$$\gamma_n = \max\left(0, \gamma_0 \left(1 - \frac{n}{K'}\right)\right) \quad (2.1)$$

and

$$\lambda_n^c = \max\left(0, \lambda_0^c \left(1 - \frac{n}{K'}\right)\right), \quad (2.2)$$

where n is island diversity; γ_0 and λ_0^c are, respectively, the initial per lineage rates of immigration and cladogenesis when island diversity is zero; γ_n and λ_n^c the per lineage rates of immigration and cladogenesis at n species. The K' parameter denotes the maximum number of niches on the island that could be attained in the absence of extinction [30]. Note that in the face of high levels of extinction, the dynamic equilibrium diversity may be substantially lower than K' . We left the rate of anagenesis (λ^a) DI, as we have no niche-based argument as to why diversity should further impede the rate of anagenetic speciation. We chose not to make extinction DD because phylogenetic analyses have provided little evidence for this type of feedback [27], but such a dependence could be easily incorporated into our simulation framework if it were deemed important in specific systems.

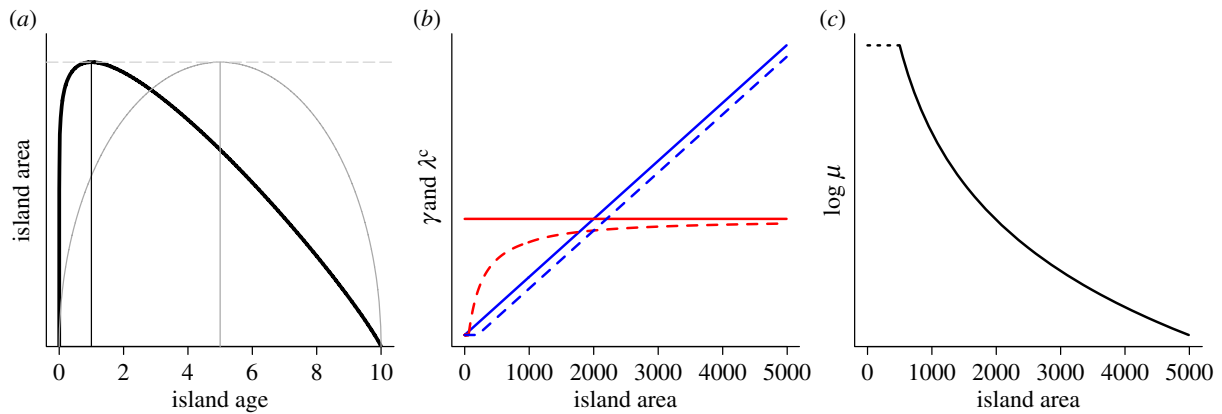


Figure 1. Effect of island ontogeny on initial model parameters. (a) Island area (A) trajectories in the three simulated ontogeny scenarios. Solid black, volcanic island ontogeny; solid grey, symmetrical area ontogeny; dashed grey, constant area ontogeny (null model). Island carrying capacity (K') is a proportion of A ($K' = 0.05A$) in the DD version, following the same curve as A but with lower amplitude. In the DI version, K' is infinite. Vertical lines indicate the island ages at which maximum A and K' are reached under the volcanic and symmetrical models. (b) Effect of island area on per lineage rates of immigration (γ , red) and cladogenesis (λ^c , blue) assuming 20 species are present ($n = 20$) and a mainland pool of 1000 species. Solid lines, DI version of the model; dashed lines, DD version. (c) Effect of island area on the initial rate of extinction (μ , log scale).

(c) Island ontogeny

We modelled the typical ontogeny of an oceanic island by allowing island area (A) to vary with island age t . We simulated islands under three contrasting island ontogeny scenarios (figure 1; electronic supplementary material): volcanic, symmetrical and constant area (null model). In the main text, we focus on the results of the volcanic ontogeny, but we report the full results of the other ontogenies in the electronic supplementary material.

(d) Effect of area on parameters

We treat area as a proxy for ecological opportunity, through its direct and indirect effects on altitudinal range, topography, habitat complexity and thus niche diversity [6]. In both DI and DD settings, we allow area to directly positively influence cladogenesis rates (but not immigration rates) and to negatively influence extinction rates (figure 1). We model a positive effect of area on opportunities for *in situ* allopatric or parapatric speciation by making the initial rate of cladogenesis the product of λ_0^c and A . We model a decline in the rate of per lineage extinction with area (figure 1) according to a truncated power law

$$\mu_t = \min\left(\mu_{\max}, \mu_{\min} \left(\frac{A_t}{A_{\max}}\right)^{-\log(\mu_{\min}/\mu_p) \log(A_p/A_{\max})}\right), \quad (2.3)$$

where μ_t is the rate of extinction at island age t , μ_{\min} is the minimum extinction rate on an island of maximum area and μ_p is the extinction rate at $A_p = pA_{\max}$, where $p = 0.1$. μ is capped at a maximum value $\mu_{\max} = 1000$ to avoid excessively elevated rates that drastically slow down simulations.

In the DD setting, we additionally model the influence of area on ecological opportunity by making K' proportional to area, which in turn influences γ (by reducing the probability of colonization, but not the probability of arrival) and λ^c (as per equations (2.1) and (2.2)).

(e) Simulations

We simulated under continuous time, starting at island birth (t_0) and ending at t_{end} . For each island ontogeny scenario (volcanic, symmetrical and constant area), we ran 1000 replicates of simulations with 16 combinations of parameter values in order to explore a wide range of the parameter space at low and high γ , μ , λ^a and λ^c (electronic supplementary material, table S1 and methods).

(f) Model output

For each simulation, we calculated the IW rates of immigration, extinction, anagenesis and cladogenesis, as well as the number of total, immigrant, anagenetic and cladogenetic species. We also calculated the number of radiations and the number of species per radiation.

In order to compare ages of colonization and species ages at different island stages (electronic supplementary material, methods), we extracted this information at t equal to 0.2, 0.5 and 0.9 proportions of t_{end} , representing, respectively, islands at young, mature and old stages.

We examined the shape of phylogenetic trees of island radiations at different proportions of t_{end} (0.05, 0.2, 0.5, 0.7 and 0.9), encompassing the stages where the island is growing and waning in size. We fitted different classes of widely used birth–death models of diversification [27] to the branch lengths of all the phylogenies with five or more species, in order to investigate whether we could detect changes in speciation and extinction rates over time. We fitted the following models: constant speciation rate with no extinction (pure birth model); constant speciation and extinction rates (birth–death model); exponentially declining speciation rate through time and constant extinction rate (SPVAR model); exponentially declining speciation rate through time and no extinction (SPVAR_μ0 model) and exponentially increasing extinction rate through time and constant speciation (EXVAR model) [27]. Models were fitted using existing functions within the R package LASER [31] with the exception of SPVAR_μ0, for which we modified the SPVAR model. For each clade, we calculated Akaike information criterion (AIC) weights for the five models—with a high AIC weight indicating a low relative AIC score for that model and thus high support. We then calculated the mean AIC weight for each of the models across all clades in an island and the fraction of simulations in which a model was the preferred (i.e. had the lowest AIC score) one for that island. We repeated the same procedure using small-sample corrected AIC (AICc) as a metric, with sample size equal to the number of branching times in each of the phylogenies. The results of the birth–death model fitting are consistent regardless of whether AIC or AICc were used as model-fit metrics, except that when using AICc the simplest model (pure birth) is favoured more often. Given that the two metrics give congruent results, we report the results using AIC, owing to uncertainty in determining the appropriate sample size for calculating AICc for models with declining speciation, and because AIC is the most commonly used metric in comparisons of models of diversification.

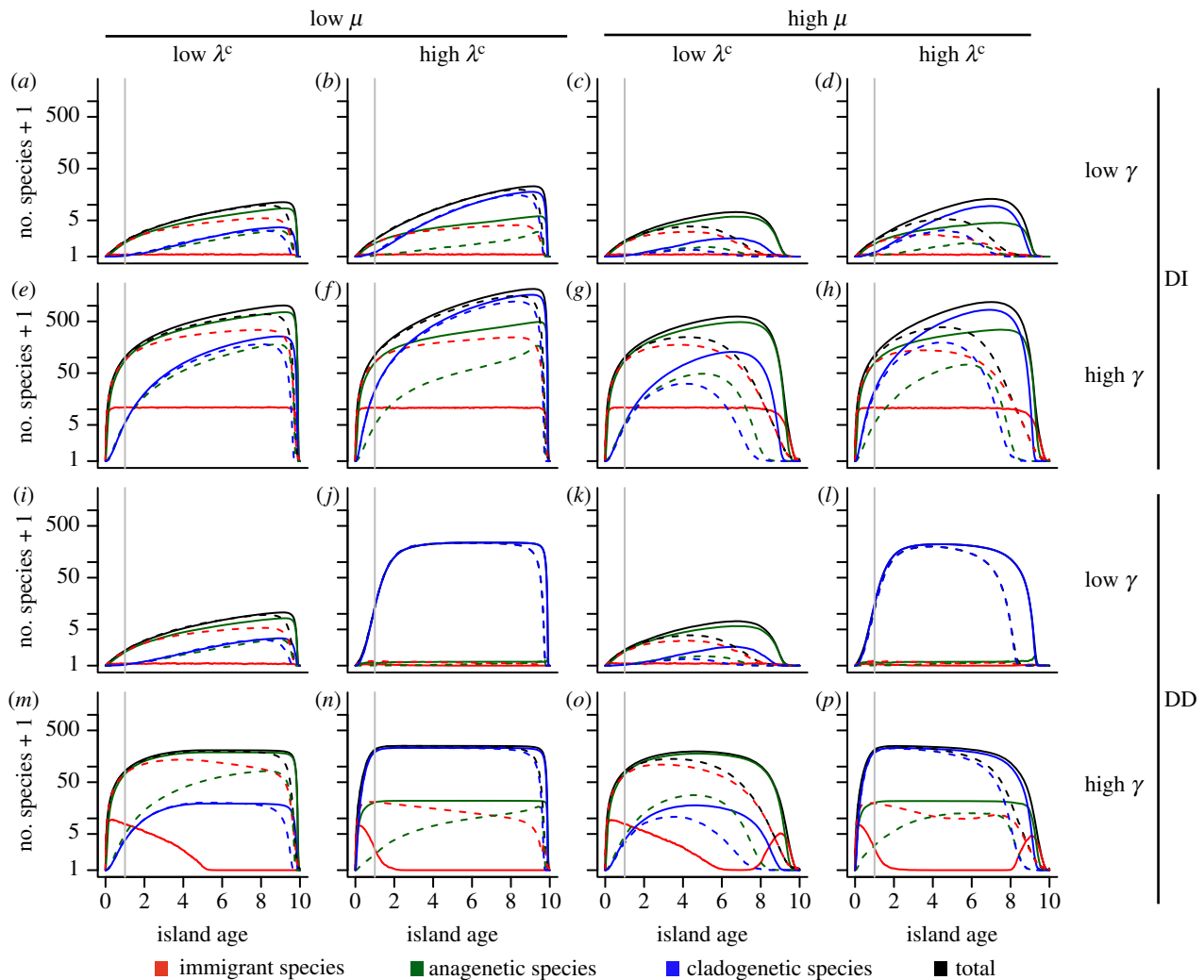


Figure 2. Time-series of total, immigrant, anagenetic and cladogenetic species richness for simulations of a volcanic island ontogeny. Each plot shows the results for a different combination of parameter values indicated in the outer axes. Low and high parameter values are given in the electronic supplementary material, table S1. Dashed lines, low rate of anagenesis; solid lines, high rate of anagenesis. γ , immigration rate; μ , extinction rate; λ^c , cladogenesis rate. DI, diversity-independent version ($a-h$), $K' = \infty$; DD, diversity-dependent version ($i-p$), $K' = 0.05$. Results are the medians for intervals of $t = 0.01$ over 1000 replicates. Vertical lines indicate the island ages at which maximum A and K' are reached.

The simulation model and subsequent analyses were implemented in R (R Development Core Team 2013), and code is available in the electronic supplementary material.

3. Results

(a) Island-wide rates

For volcanic islands, under DI, IW rates of immigration generally decline steadily through time (electronic supplementary material, figure S1). Under DD, this relationship is U-shaped in most cases, as at old ages declining island size promotes extinction and shifts the balance of inputs from cladogenesis back to immigration. The IW extinction rate generally increases with island age, under both DD and DI (electronic supplementary material, figure S1). The island age where maximum IW cladogenesis rate is achieved varies strongly under different scenarios (electronic supplementary material, figure S1). Under DI, maximum rates are reached in the second half of the island's life, whereas under DD, cladogenesis rates peak at early island ages. Under DD and high λ^c , two peaks in IW cladogenesis often occur, one in the first half of the island's life and a second,

shallower peak, in the second half. The IW rate of anagenesis has a moderately hump-shaped relationship with age, with the exception of the scenarios under DD, high γ and high λ^a , where two separate peaks in anagenesis occur (electronic supplementary material, figure S1). The later peak is due to an influx of immigrant species on old islands.

(b) Species richness

In the volcanic island scenario, total species richness is a clear hump-shaped function of island age when μ is high (figure 2). In such cases, under both DI and DD, total and endemic species richness peaks at intermediate island ages and generally after maximum area has been reached. By contrast, at low μ , species richness rises steadily until the very last stages of the island's life, when it drops very rapidly to zero as a result of the high IW rates of extinction and the depressed rates of cladogenesis and immigration that occur prior to complete island submergence.

Under low λ^c and high λ^a , the model predicts that volcanic islands become dominated by anagenetic species. When both λ^a and λ^c are low, islands become dominated by immigrant species. By contrast, under high λ^c , the majority of species

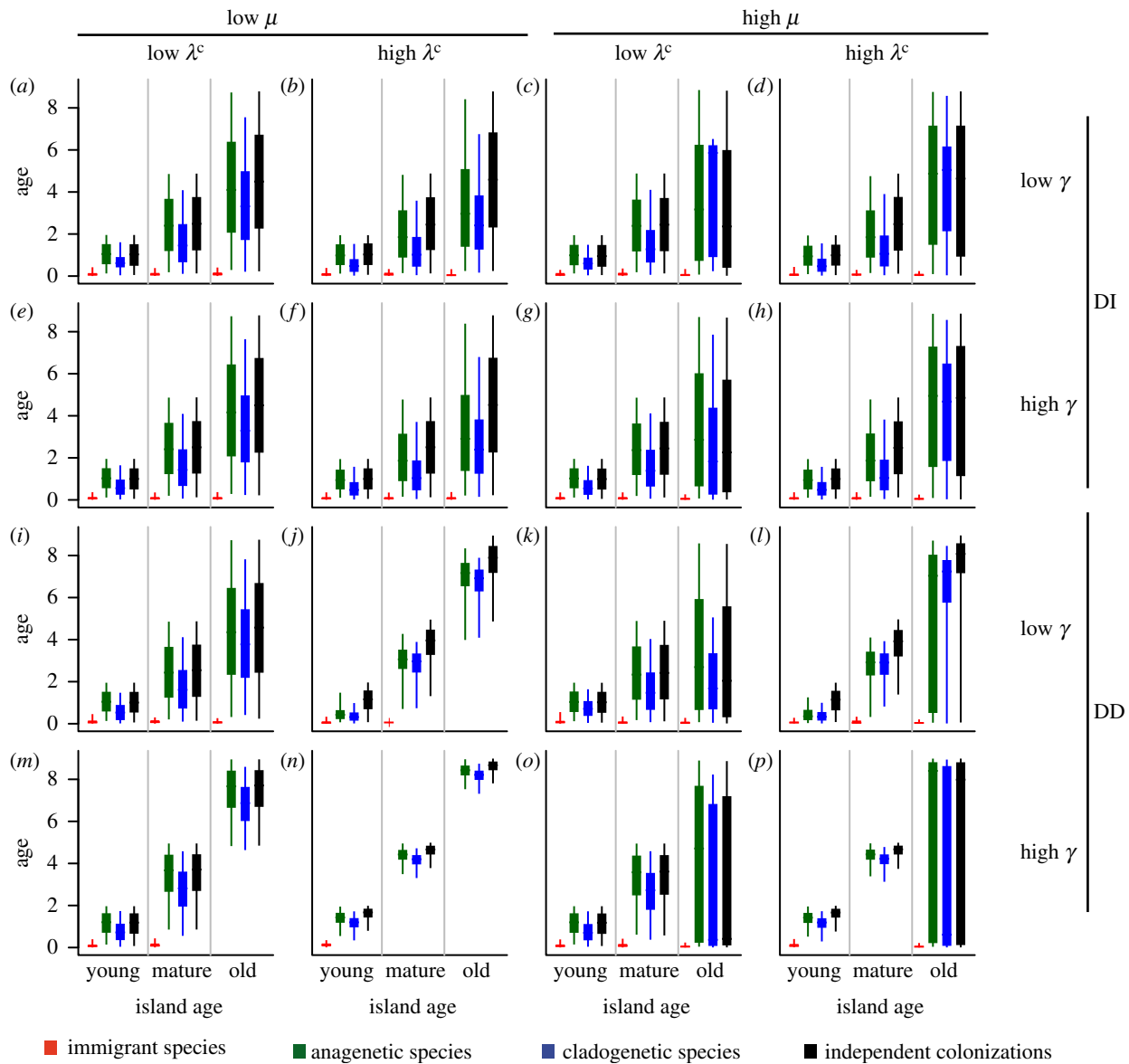


Figure 3. Distribution of ages of immigrant, anagenetic and cladogenetic species as well as of timings of colonization for young, mature and old island life stages for simulations of a volcanic area island ontogeny. Each plot shows the results for a different combination of parameter values indicated in the outer axes. Low and high parameter values are given in the electronic supplementary material, table S1. γ , immigration rate; μ , extinction rate; λ^c , cladogenesis rate. Simulations were run with high rates of anagenesis ($\lambda^a = 10$). DI (a–h), diversity-independent scenario ($K' = \infty$); DD (i–p), diversity-dependent scenario ($K' = 0.05$). Results are 0.25–0.75 (boxes) and 0.025–0.975 (vertical lines) quantiles over 1000 replicates. Median ages are shown with a horizontal line.

are of cladogenetic origin. A strong dominance of cladogenetic species is particularly visible under DD and high λ^c .

(c) Species ages and colonization times

The volcanic ontogeny model predicts that anagenetic species are on average older than cladogenetic and immigrant species, and that cladogenetic species are older than immigrant species (figure 3). Time since colonizations and ages of endemic species generally increase with island maturity. By contrast, there are no significant differences in the ages of immigrant species among the different island life stages.

(d) Phylogenetic tree shape and *in situ* radiations

For volcanic islands under DI, the pure birth model is preferred under most scenarios (figure 4). The model with declining speciation and zero extinction is preferred for a sizeable proportion of simulations, and this proportion increases with the age of the island at the time of establishment of an endemic

clade. Under DD, the pure birth model is preferred only at young and intermediate island ages or when λ^c is low, whereas the model with declining speciation and zero extinction is generally strongly preferred at late island ages. We find little support for models that include non-zero extinction, even under conditions where extinction rates are high. At the youngest island ages, under low λ^c or high μ , there are no clades of more than five species on which to fit the models.

In general, the model predicts a higher number of *in situ* radiations under DI but more species per radiation under DD (electronic supplementary material, tables S2–S4).

4. Discussion

(a) Island-wide rates and species richness

Our island biogeography model predicts that total and endemic richness should rise and fall with island age in volcanic islands (figure 2), providing quantitative support for one of

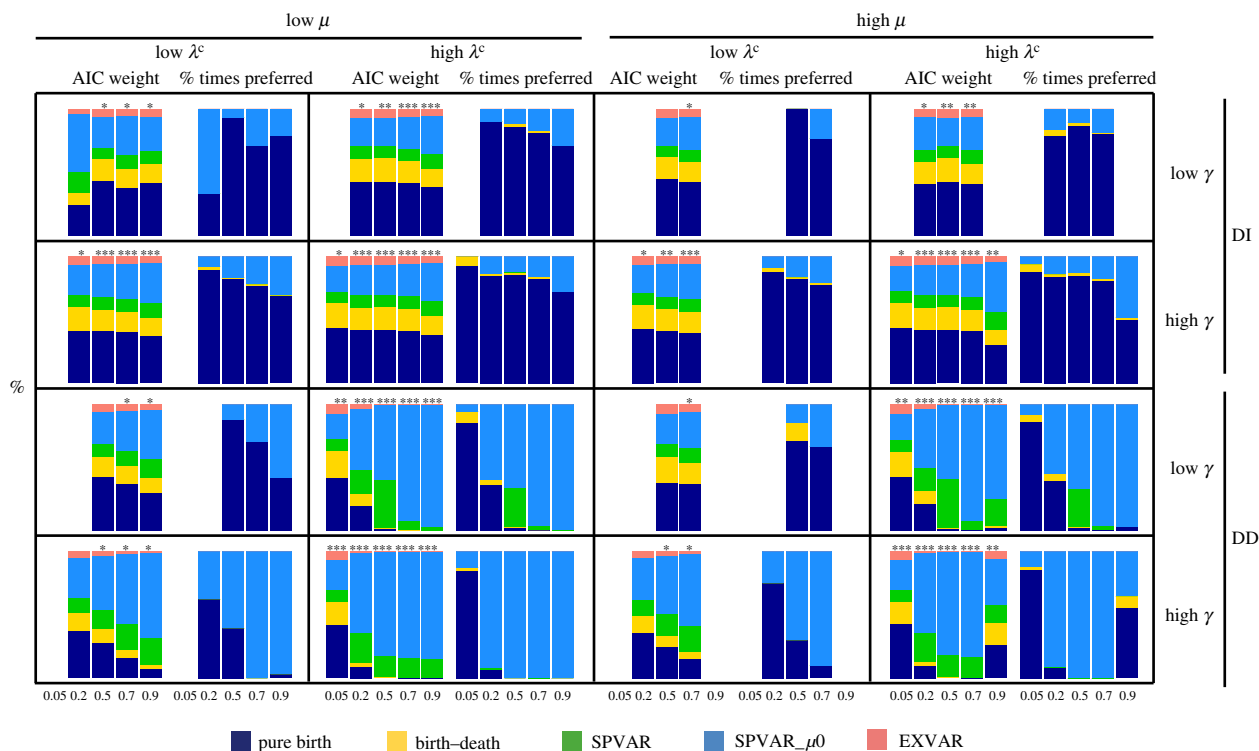


Figure 4. Diversification model fitting to phylogenies of island clades of volcanic ontogeny simulations. Each plot shows the results for a different combination of parameter values (electronic supplementary material, table S1). Vertical bars represent different island life stages—0.05, 0.2, 0.5, 0.7 and 0.9 proportions of total island age. For each parameter combination, the five bars on the left show AIC weights for each of the models at each life stage, and the five bars on the right show the proportion of times each model was preferred at each life stage. Asterisks above AIC weight bars represent number of clades used to fit models—no asterisk denotes more than 0 and less than 10; * denotes more than or equal to 10 and less than 100; ** denotes more than or equal to 100 and less than 1000; *** denotes more than or equal to 1000. If there were no clades with five or more species for a given life stage, no results are plotted. γ , immigration rate; μ , extinction rate; λ^c , cladogenesis rate. Simulations run with high rates of anagenesis ($\lambda^a = 10$).

the GDM's key predictions: an effect of island age on species richness when area and ecological opportunity follow the ontogenetic trajectory typical of volcanic islands [6]. However, in our simulations, species richness is only a smooth hump-shaped function of island age as predicted by Whittaker *et al.* [6] on islands with high background extinction. When extinction is low—as we might expect to be true of large tropical islands (e.g. Jamaica and Hawaii Island)—richness also rises and falls with age, but islands display a steady increase in diversity with time until a very late stage, when diversity collapses. In all scenarios, the peak in total species diversity shows a temporal lag with respect to the peak in island area and carrying capacity, revealing that maximal biodiversity is to be expected on islands that have already entered the erosive stage, in agreement with empirical evidence from taxonomic lists in a variety of archipelagos [12,13]. Importantly, we found that the species richness trajectory was highly variable, with different parameter sets often exhibiting contrasting shapes. This result suggests that the examination of species–area curves across islands of different ages and biogeographic contexts may be problematic, highlighting the importance of our framework as a potentially useful means of detecting key processes that cannot be identified via standard curve-fitting approaches.

The shape of the relationship between IW rates of speciation and age varies greatly between scenarios with and without diversity-dependence in rates of immigration and cladogenesis (electronic supplementary material, figures S1–S3). Under DI, cladogenesis and anagenesis are a hump-shaped

function of island age, peaking long after the maximum area is attained and declining only as species and immigrant diversity dwindle. By contrast, under DD, cladogenesis and anagenesis rates display peaks that either occur in the period immediately following island emergence or shortly after maximum carrying capacity is achieved. These results agree with the prediction of the GDM that cladogenesis should be predominant on younger islands [6]. Interestingly, secondary peaks in speciation rates also occur at late ontogenetic stages under DD, which are caused by a release of ecological niches driven by depressed species richness on submerging islands as a result of elevated rates of extinction λ^c with declining area, and reduced rates of cladogenesis and immigration with declining carrying capacity.

(b) Lineage branching times

Molecular phylogenetic data from a variety of endemic and immigrant island taxa is rapidly accumulating. For example, Papadopulos *et al.* [19] were able to estimate the times of colonization and *in situ* speciation of a significant proportion of the vascular flora of Lord Howe Island through the application of molecular dating methods to both island taxa and their extant mainland relatives. Parent *et al.* [32] and Illera *et al.* [33] compiled molecular estimates of ages of colonization for the terrestrial fauna of the Galapagos and the avifauna of Macaronesia, respectively. In our simulations, we have generated expectations that may guide interpretation of such datasets of colonization and speciation ages of island taxa in the context

of volcanic ontogeny (figure 3; electronic supplementary material, figures S6 and S7). We found that the distribution of species and colonization ages obtained from phylogenies of extant species is informative about island ontogenetic stage and can provide insights into whether species diversity has a negative feedback on the rate of cladogenesis.

Our model predicts that immigrant species are younger than endemic taxa regardless of island ontogeny, in agreement with phylogenetic patterns in Caribbean avian communities from islands with varied geomorphic histories [34]. The age of non-endemic species varies little with ontogeny, revealing that estimates of the time of colonization of non-endemic species carry little information about an island's geomorphic stage. By contrast, we found that the age of island endemics is expected to increase with island age in islands with variable area, a result that is consistent with a higher proportion of ancient taxa on older oceanic islands [10,35].

Adaptive radiations, such as the Galapagos finches [32] and Hawaiian *Tetragnatha* spiders [10] are important features of the biota of remote volcanic islands. Whittaker *et al.* [6] posited that if islands have a time-variable carrying capacity, radiations should be more frequent at young ages in the period leading up to island maturity, while rates of diversification should decline at older ages as erosion reduces island area and previously available niches become filled. In strong agreement with this hypothesis, our simulations of islands with volcanic ontogeny and a finite diversity carrying capacity (DD, figure 4) reveal that phylogenies exhibit a signature of radiation when sampled from young islands but one of slowdown in speciation rates when sampled from mature to old islands, as would be expected if *in situ* radiations were more prevalent at early ages when niche availability is maximal [21,36]. Although alternative processes may explain slowdowns in rates of speciation from phylogenies [37,38], our study reveals that if negative feedbacks of diversity operate, declines in speciation rates should be detectable from phylogenetic trees of radiations from islands that are declining in size. Yet, although elevated rates of extinction occurred on intermediate to old islands in our simulations, models with non-zero extinction were only selected in a minority of phylogenies, confirming that a signal of past extinction events may be difficult to detect from extant island data [7], as it is from molecular phylogenies in general [27].

While we found a striking difference between phylogenies from recently emerged and old islands in simulations with diversity-dependence, such differences were absent from islands simulated under diversity-independence, for which unsurprisingly the preferred model at all island ages was one with constant speciation (figure 4). Recent studies have found evidence that equilibrium controls of diversity may be widespread [39] and that a model with no ecological limits to species richness is unlikely to apply to island systems [21,40], even to those with large areas such as Madagascar [41]. We therefore believe that the DD version of our model is the most biologically realistic implementation. An important mechanism through which a negative feedback of diversity on community assembly rates may operate is through geographical incumbency, where the diversification of primary colonists inhibits the ultimate diversity of closely related secondary colonizers [42,43]. Indeed, niche pre-emption effects on rates of immigration and speciation have been reported from a variety of insular environments and taxa [44,45].

(c) Model development and parameter estimation

Our model provides a flexible framework to study island community assembly and can easily be extended to a variety of island ontogenetic trajectories, such as insular environments of non-volcanic origin (e.g. land-bridge islands, continental fragments and lakes) or islands where volcanic activity may create new habitats at older ages, potentially enabling late bursts of speciation [15]. Asymmetry in rates of immigration could also be incorporated, mimicking biological variation in dispersal kernels (e.g. spore- versus seed-dispersed plants [14]) or distributional changes in source populations owing to the temporal sequence of island formation in archipelago settings [15]. In addition, the effect of biotic interactions on rates of speciation and extinction could also be modelled and may potentially lead to more idiosyncratic patterns of community assembly [6].

Our model is lineage-based and has been designed to be fitted to real phylogenetic and phylogeographical datasets from island taxa that include the times of colonization of the ancestors of endemic species and immigrant populations, as well as the branching times of *in situ* radiations. Phylogenetic trees from a variety of island radiations are already available, but the relationships between island taxa with their relatives from the mainland or nearby landmasses are often unknown, because such estimates require well-sampled phylogenies of taxa from outside the focal area of study [19]. Although accurate estimation of timings of colonization is data-demanding, increasingly complete tree-of-life resources are rapidly becoming available (e.g. [46]) that can guide the identification of the closest relatives of island species or populations, thus reducing sampling effort.

Likelihood methods for use with the branching times of molecular phylogenies exist and can readily be applied to understand the processes affecting insular biotas. For instance, clade-based methods allow for the estimation of DD or otherwise time-varying rates of diversification (e.g. [27,30,47]). The GeoSSE method [48] allows for implementation of a model closer in spirit to the approach of MacArthur & Wilson [3], as it allows for the insular community to be the focal unit and permits the estimation of (constant) rates of speciation within and between regions, as well as dispersal between regions and extinction. While these methods can provide valuable insights, neither is a good fit to the processes we include in our model. Hence, island biogeography lacks a means of estimating key parameters from data. We hope that our simple island-centric model will spur developments that allow parameters to be estimated from data, either in a likelihood framework or via the application of approximate Bayesian computation. Such a framework would allow the field of island biogeography to undergo a transition from being largely focused on pattern description to be in a position to infer the processes that govern oceanic community assembly in relation to island age, area and isolation. For instance, to what extent are remote islands of different ages at or close to a diversity equilibrium? And how do per lineage rates of immigration, speciation and extinction covary with island isolation, area and age?

Acknowledgements. We thank Alex Pigot, Alex Papadopulos, Paulo Borges, Marcial Escudero, Vincent Savolainen, Yael Kisel, Ralph Tiedemann, the CESAB 'ISLANDS' working group, and one anonymous reviewer for advice and discussions.

Funding statement. This work was funded by a Marie Curie Intra-European Fellowship (IEF 273066 'Birdisland') and an Alexander von Humboldt Postdoctoral Fellowship to L.M.V. A.B.P. was funded by a NERC advanced fellowship (Ne/I020598/1).

References

- Losos J, Ricklefs R. 2010 *The theory of island biogeography revisited*. Princeton, NJ: Princeton University Press.
- Darwin C. 1842 *The structure and distribution of coral reefs: being the first part of the geology of the voyage of the Beagle, under the command of Capt. Fitzroy R.N. during the years 1832 to 1836*. London, UK: Smith, Elder and Company.
- MacArthur RH, Wilson EO. 1967 *The theory of island biogeography*. Princeton, NJ: Princeton University Press.
- Price JP, Clague DA. 2002 How old is the Hawaiian biota? Geology and phylogeny suggest recent divergence. *Proc. R. Soc. Lond. B* **269**, 2429–2435. (doi:10.1098/rspb.2002.2175)
- Paulay G. 1994 Biodiversity on oceanic islands: its origin and extinction 1. *Am. Zool.* **34**, 134–144. (doi:10.1093/icb/34.1.134)
- Whittaker RJ, Triantis KA, Ladle RJ. 2008 A general dynamic theory of oceanic island biogeography. *J. Biogeogr.* **35**, 977–994. (doi:10.1111/j.1365-2699.2008.01892.x)
- Whittaker RJ, Triantis KA, Ladle RJ. 2010 A general dynamic theory of oceanic island biogeography: extending the MacArthur–Wilson theory to accommodate the rise and fall of volcanic islands. In *The theory of island biogeography revisited* (eds JB Losos, RE Ricklefs), pp. 88–115. Princeton, NJ: Princeton University Press.
- Jackson TA. 2013 A review of volcanic island evolution and magma production rate: an example from a Cenozoic island arc in the Caribbean. *J. Geol. Soc. Lond.* **170**, 547–556. (doi:10.1144/jgs2011-166)
- Stuessy TF. 2007 Evolution of specific and genetic diversity during ontogeny of island floras: the importance of understanding process for interpreting island biogeographic patterns. In *Biogeography in a changing world* (eds MC Ebach, RS Tangney), pp. 117–132. Boca Ratón, FL: CRC Press.
- Gillespie R. 2004 Community assembly through adaptive radiation in Hawaiian spiders. *Science* **303**, 356–359. (doi:10.1126/science.1091875)
- Losos JB, Schluter D. 2000 Analysis of an evolutionary species–area relationship. *Nature* **408**, 847–850. (doi:10.1038/35048558)
- Cameron RAD, Triantis KA, Parent CE, Guilhaumon F, Alonso MR, Ibáñez M, de Frias Martins AM, Ladle RJ, Whittaker RJ. 2013 Snails on oceanic islands: testing the general dynamic model of oceanic island biogeography using linear mixed effect models. *J. Biogeogr.* **40**, 117–130. (doi:10.1111/j.1365-2699.2012.02781.x)
- Bunnefeld N, Phillimore AB. 2012 Island, archipelago and taxon effects: mixed models as a means of dealing with the imperfect design of nature's experiments. *Ecography* **35**, 15–22. (doi:10.1111/j.1600-0587.2011.07078.x)
- Patiño J, Guilhaumon F, Whittaker RJ, Triantis KA, Gradstein SR, Hedenäs L, González-Mancebo JM, Vanderpoorten A. 2013 Accounting for data heterogeneity in patterns of biodiversity: an application of linear mixed effect models to the oceanic island biogeography of spore-producing plants. *Ecography* **36**, 904–913. (doi:10.1111/j.1600-0587.2012.00020.x)
- Borges PAV, Hortal J. 2009 Time, area and isolation: factors driving the diversification of Azorean arthropods. *J. Biogeogr.* **36**, 178–191. (doi:10.1111/j.1365-2699.2008.01980.x)
- Emerson BC, Kolm N. 2005 Species diversity can drive speciation. *Nature* **434**, 1015–1017. (doi:10.1038/nature03450)
- Rosindell J, Phillimore AB. 2011 A unified model of island biogeography sheds light on the zone of radiation. *Ecol. Lett.* **14**, 552–560. (doi:10.1111/j.1461-0248.2011.01617.x)
- Gray A, Cavers S. 2014 Island biogeography, the effects of taxonomic effort and the importance of island niche diversity to single-island endemic species. *Syst. Biol.* **63**, 55–65. (doi:10.1093/sysbio/syt060)
- Papadopoulos AST, Baker WJ, Crayn D, Butlin RK, Kynast RG, Hutton I, Savolainen V. 2011 Speciation with gene flow on Lord Howe Island. *Proc. Natl Acad. Sci. USA* **108**, 13 188–13 193. (doi:10.1073/pnas.1106085108)
- Lerner HRL, Meyer M, James HF, Hofreiter M, Fleischer RC. 2011 Multilocus resolution of phylogeny and timescale in the extant adaptive radiation of Hawaiian honeycreepers. *Curr. Biol.* **21**, 1838–1844. (doi:10.1016/j.cub.2011.09.039)
- Rabosky DL, Glor RE. 2010 Equilibrium speciation dynamics in a model adaptive radiation of island lizards. *Proc. Natl Acad. Sci. USA* **107**, 22 178–22 183. (doi:10.1073/pnas.1007606107)
- Emerson BC, Gillespie RG. 2008 Phylogenetic analysis of community assembly and structure over space and time. *Trends Ecol. Evol.* **23**, 619–630. (doi:10.1016/j.tree.2008.07.005)
- Stuessy TF, Jakubowsky G, Gomez RS, Pfosser M, Schluter PM, Fer T, Sun B-Y, Kato H. 2006 Anagenetic evolution in island plants. *J. Biogeogr.* **33**, 1259–1265. (doi:10.1111/j.1365-2699.2006.01504.x)
- Kisel Y, Barraclough TG. 2010 Speciation has a spatial scale that depends on levels of gene flow. *Am. Nat.* **175**, 316–334. (doi:10.1086/650369)
- Johnson KP, Adler FR, Cherry JL. 2000 Genetic and phylogenetic consequences of island biogeography. *Evolution* **54**, 387–396. (doi:10.1111/j.0014-3820.2000.tb00041.x)
- Cornuault J, Warren BH, Bertrand JAM, Milá B, Thébaud C, Heeb P. 2013 Timing and number of colonizations but not diversification rates affect diversity patterns in hemsporidian lineages on a remote oceanic archipelago. *Am. Nat.* **182**, 820–833. (doi:10.1086/673724)
- Rabosky DL, Lovette IJ. 2008 Explosive evolutionary radiations: decreasing speciation or increasing extinction through time? *Evolution* **62**, 1866–1875. (doi:10.1111/j.1558-5646.2008.00409.x)
- Chen X-Y, He F. 2009 Speciation and endemism under the model of island biogeography. *Ecology* **90**, 39–45. (doi:10.1890/08-1520.1)
- Nee S, May RM, Harvey PH. 1994 The reconstructed evolutionary process. *Phil. Trans. R. Soc. Lond. B* **344**, 305–311. (doi:10.1098/rstb.1994.0068)
- Etienne RS, Haegeman B, Stadler T, Aze T, Pearson PN, Purvis A, Phillimore AB. 2012 Diversity-dependence brings molecular phylogenies closer to agreement with the fossil record. *Proc. R. Soc. B* **279**, 1300–1309. (doi:10.1098/rspb.2011.1439)
- Rabosky D. 2006 LASER: a maximum likelihood toolkit for detecting temporal shifts in diversification rates from molecular phylogenies. *Evol. Bioinform. Online* **2**, 247–250.
- Parent CE, Caccione A, Petren K. 2008 Colonization and diversification of Galápagos terrestrial fauna: a phylogenetic and biogeographical synthesis. *Phil. Trans. R. Soc. Lond. B* **363**, 3347–3361. (doi:10.1098/rstb.2008.0118)
- Illera JC, Rando JC, Richardson DS, Emerson BC. 2012 Age, origins and extinctions of the avifauna of macaronesia: a synthesis of phylogenetic and fossil information. *Q. Sci. Rev.* **50**, 14–22. (doi:10.1016/j.quascirev.2012.07.013)
- Cadena CD, Ricklefs RE, Jiménez I, Bermingham E. 2005 Ecology: is speciation driven by species diversity? *Nature* **438**, E1–E2; discussion E2. (doi:10.1038/nature04308)
- Parent CE, Crespi BJ. 2006 Sequential colonization and diversification of Galapagos endemic land snail genus *Bulimulus* (Gastropoda, Stylommatophora). *Evolution* **60**, 2311–2328. (doi:10.1111/j.0014-3820.2006.tb01867.x)
- Etienne RS, Haegeman B. 2012 A conceptual and statistical framework for adaptive radiations with a key role for diversity dependence. *Am. Nat.* **180**, E75–E89. (doi:10.1086/667574)
- Pigot AL, Phillimore AB, Owens IPF, Orme CDL. 2010 The shape and temporal dynamics of phylogenetic trees arising from geographic speciation. *Syst. Biol.* **59**, 660–673. (doi:10.1093/sysbio/syq058)
- Etienne RS, Rosindell J. 2012 Prolonging the past counteracts the pull of the present: protracted speciation can explain observed slowdowns in diversification. *Syst. Biol.* **61**, 204–213. (doi:10.1093/sysbio/syr091)
- Rabosky DL. 2013 Diversity-dependence, ecological speciation, and the role of competition in macroevolution. *Annu. Rev. Ecol. Evol. Syst.* **44**, 481–502. (doi:10.1146/annurev-ecolsys-110512-135800)
- Gillespie RG. 2013 Adaptive radiation: convergence and non-equilibrium. *Curr. Biol.* **23**, R71–R74. (doi:10.1016/j.cub.2012.11.052)
- Scantlebury DP. 2013 Diversification rates have declined in the Malagasy herpetofauna. *Proc. R. Soc. B* **280**, 20131109. (doi:10.1098/rspb.2013.1109)

42. Silvertown J, Francisco-Ortega J, Carie M. 2005 The monophyly of island radiations: an evaluation of niche pre-emption and some alternative explanations. *J. Ecol.* **93**, 653–657. (doi:10.1111/j.1365-2745.2005.01038.x)
43. Schenk JJ, Rowe KC, Steppan SJ. 2013 Ecological opportunity and incumbency in the diversification of repeated continental colonizations by muroid rodents. *Syst. Biol.* **62**, 837–864. (doi:10.1093/sysbio/syt050)
44. Lee WG, Tanentzap AJ, Heenan PB. 2012 Plant radiation history affects community assembly: evidence from the New Zealand alpine. *Biol. Lett.* **8**, 558–561. (doi:10.1098/rsbl.2011.1210)
45. Fabre P-H, Moltensen M, Fjeldså J, Irestedt M, Lessard JP, Jønsson KA. 2013 Multiple waves of colonization by monarch flycatchers (*Myiagra*, Monarchidae) across the Indo-Pacific and their implications for coexistence and speciation. *J. Biogeogr.* **41**, 274–286. (doi:10.1111/jbi.12202)
46. Jetz W, Thomas GH, Joy JB, Hartmann K, Mooers AO. 2012 The global diversity of birds in space and time. *Nature* **491**, 444–448. (doi:10.1038/nature11631)
47. Morlon H, Parsons TL, Plotkin JB. 2011 Reconciling molecular phylogenies with the fossil record. *Proc. Natl Acad. Sci. USA* **108**, 16 327–16 332. (doi:10.1073/pnas.1102543108)
48. Goldberg EE, Lancaster LT, Ree RH. 2011 Phylogenetic inference of reciprocal effects between geographic range evolution and diversification. *Syst. Biol.* **60**, 451–465. (doi:10.1093/sysbio/syr046)