

Why does diversification slow down?

Daniel Moen and H el ene Morlon

Center for Applied Mathematics,  cole Polytechnique, UMR 7641 CNRS, Route de Saclay, 91128 Palaiseau Cedex, France

Studies of phylogenetic diversification often show evidence for slowdowns in diversification rates over the history of clades. Recent studies seeking biological explanations for this pattern have emphasized the role of niche differentiation, as in hypotheses of adaptive radiation and ecological limits to diversity. Yet many other biological explanations might underlie diversification slowdowns. In this paper, we focus on the geographic context of diversification, environment-driven bursts of speciation, failure of clades to keep pace with a changing environment, and protracted speciation. We argue that, despite being currently underemphasized, these alternatives represent biologically plausible explanations that should be considered along with niche differentiation. Testing the importance of these alternative hypotheses might yield fundamentally different explanations for what influences species richness within clades through time.

Reconsidering the causes of diversification slowdowns

Understanding diversification dynamics (i.e., how and why speciation and extinction rates vary across time, space, and clades) has long interested evolutionary biologists [1]. Time-calibrated molecular phylogenies are increasingly used to characterize this diversification, particularly in groups with poor fossil records [1–3]. One emergent pattern is a slowdown of net diversification rates (see [Glossary](#)) over the histories of clades [2–4], typically linked to a slowdown in speciation rates. Such slowdowns been found with a variety of statistical methods ([Box 1](#)). A meta-analysis of 289 phylogenies spanning a variety of taxa found slowdowns in nearly 63% of clades [3]. Such slowdowns have strong implications for understanding the evolution of clades as well as global biodiversity patterns [5–7].

Why do many phylogenies show diversification slowdowns? Methodological biases can lead to such results and need to be controlled ([Box 2](#)). However, recent studies have avoided many biases and have still found strong support for slowdowns (e.g., [3,4,8]). Given that this appears to be a real and widespread pattern, studies now increasingly focus on the biological causes of diversification slowdowns ([Figures 1 and 2](#)). Many of these explanations are based on relatively old hypotheses put forward to explain diversifi-

cation dynamics from the fossil record (e.g., [9–12]). Renewed interest results from the widespread availability and promise of time-calibrated molecular phylogenies and diversification rate methods for evaluating these hypotheses. Many recent papers have emphasized the role of competition for limited resources, adaptive radiation, and ecological limits on the number of species within a clade (e.g., [2,4,5,8,13,14]). Here, we argue that current understanding of speciation, phenotypic evolution, and the fossil record suggests that, for many clades, alternative explanations are more likely to have produced the observed diversification slowdowns than are factors related to niche differentiation. Possibilities as diverse as the influence of geography on diversification [15], environment-driven pulses of high speciation rate [9], and a failure to keep pace with a changing environment [16] should be considered more thoroughly. In some cases, these hypotheses may be initially teased apart by estimating whether diversification rates vary with the number of species in the clade (also called ‘diversity dependence’) or instead through time ([Figure 1](#)). However, distinguishing among hypotheses within these broad categories may be difficult without additional information, such as data on geographic distributions or phenotypes. Therefore, we detail the conceptual basis of these hypotheses, suggest how they can be tested with different forms of data, and indicate directions for future research.

Hypotheses based on niche differentiation

The dominant explanation in the literature for diversification slowdowns is that they result from the influence of competition for limited resources or niches on diversification

Glossary

Adaptive radiation: the evolution of phenotypic and ecological diversity in a rapidly speciating clade [24].

Diversification rate slowdown: higher net diversification rate earlier rather than later during the history of a clade, with any functional form of decline (e.g., rates depend on time or species diversity).

Diversity-dependent diversification: diversification rates vary with the number of species in the clade through time [8,12,17] (sometimes also coined ‘density dependence’ by analogy with population dynamics). On its own, this does not imply that there is an ecological limit to the maximum number of species in a clade, or that diversification is associated with niche divergence.

Ecological limits: ecology-based limit on species diversity in a clade. Some papers have defined such limits as those imposed by a finite number of ecological niches (e.g., [18,22]); others have used the term less restrictively [5].

Net diversification rate: speciation rate minus extinction rate.

Niche filling: process by which species fill niche space as diversification proceeds. On its own, this does not imply that there is a limit to the maximum number of species in a clade.

Time-dependent diversification: diversification rates vary over time [60].

Waxing–waning: a pattern of diversification in which a clade first rises in diversity and then declines after reaching a peak in diversity.

Corresponding author: Moen, D. (moen@biologie.ens.fr).

Keywords: adaptive radiation; biogeography; diversification; ecological limits; extinction; speciation; wax–wane dynamics.

0169-5347/\$ – see front matter

  2014 Elsevier Ltd. All rights reserved. <http://dx.doi.org/10.1016/j.tree.2014.01.010>

Box 1. Ways to identify diversification slowdowns

Researchers have identified slowdowns in diversification rate using many metrics. Although we do not focus on computational details here, it is important to clarify what various metrics say about diversification and the factors that influence it.

Initial papers demonstrated slowdowns by showing concave lineage-through-time (LTT) plots [75], in which the accumulation of lineages on a phylogeny slowed through time. Later papers showed widespread evidence for speciation rate slowdowns by using the gamma statistic [2,4], a metric developed to identify departures from the constant rate pure-birth Yule model [76]. However, despite its common use, gamma contains insufficient information to distinguish many types of diversification dynamics, from diversity-dependent diversification (e.g., [4]) to waxing–waning dynamics [61]. Pigot *et al.* [15] proposed a metric that, although potentially overcoming some limitations of the gamma statistic, is also a summary statistic of net diversification that is limited in its ability to test the importance of speciation versus extinction rates.

More recent diversification rate methods use likelihood to directly infer the relation between diversification rates and other variables; their

flexibility enables one to estimate the way in which diversification slowdowns have occurred (e.g., slowdowns with time, species diversity, or environmental variables). Time-dependent models have been available since the earliest work on diversification methods [75,77], but have only recently been used to test temporal variation in speciation and extinction rates [60]. Models are now available in which discrete rate shifts can occur during the history of a clade and that can account for missing species ([66], see Box 2 for the consequences of ignoring incomplete sampling); these models can reveal long-term temporal trends, such as steady decline. Coalescent-based approaches can test explicit hypotheses about equilibrium dynamics and accommodate incomplete sampling [3]. Other models allow rate heterogeneity across lineages, negative net diversification rates, and incomplete sampling and can recover hump-shaped diversity curves through time ([62], waxing–waning dynamics). Truly diversity-dependent pure birth (no extinction) models [8] have now been expanded to accommodate non-zero extinction [17]. Finally, a recent model allows explicit tests of the effect of the environment on diversification, such as a pulse and later decrease in speciation rates due to climatic or geological events [70].

[2,8,13,17–19]. This explanation, which falls in the category of diversity-dependent explanations (Figure 1), is often related to adaptive radiation [4,14,20–23], because authors have hypothesized that speciation rate would slow down after the initial rapid speciation and as niches are filled (Figure 2; [4,20,21,24]). The idea of niche filling has been expanded further to suggest that there are a limited number of ecological niches within a clade, putting an ecological limit on clade diversity [5,17,21,22]. However, the ecological theory of adaptive radiation does not make the explicit prediction that slowdowns should follow radiations (but see [25]) or that there should be a hard limit to the number of ecological niches [24].

Box 2. Slowdowns in diversification rates resulting from methodological biases

Many biases in the methods used to estimate phylogeny and diversification rates can lead to apparent slowdowns in diversification rates. In many cases, these biases can be controlled, but some might be difficult to resolve. We briefly summarize these potential biases to refer readers to more extensive discussions of them.

Investigators have long recognized that insufficient taxonomic sampling will lead (on average) to more branching deeper in a phylogeny [76,77]. If one assumes that the missing species are a random sample, some procedures can account for this bias [3,4,28,62,66,76]. However, such approaches can be compromised if the number of missing species is unknown, and systematic sampling biases might exacerbate this problem [78]. Other biases might result from studying only large phylogenies, which are more likely than small phylogenies to show slowdowns just by chance [1,4,79].

Inaccurate estimation of phylogeny and branch lengths from DNA sequences can also lead to downstream biases when estimating diversification rates. Underparameterized substitution models [80], different methods for scaling molecular branch lengths into units of time [81], and the node-density effect [82] might all lead to greater amounts of branching deep in the phylogeny. Furthermore, deeper divergence times in gene trees than in their associated species tree could lead to biases toward deeper nodes in a phylogeny [13,19,83]. Finally, the difficulty of delimiting species or a failure to sample cryptic species can lead to fewer branching events near the tips of a phylogeny, resulting in a signal of a slowdown in diversification rate [4,13]. Both of these possibilities can at least be partially resolved by only analyzing an initial portion of the phylogeny so as to exclude the region that is most susceptible to these types of error (near the tips; e.g., [4,28]).

Interpretations of diversification slowdowns in terms of adaptive radiation are regularly made with little or no testing of ecological diversification and adaptation [4,20,23,26], the key components that distinguish adaptive from nonadaptive radiation [24]. In addition, given that few clades represent well-supported cases of adaptive radiation [24,26], it seems that too many clades show diversification slowdowns to assume (without testing) that such slowdowns indicate adaptive radiation and niche differentiation [6,27]. Although some studies of individual clades have shown strong support for early bursts of phenotypic evolution (i.e., those that might be expected in adaptive radiation [28–31]), a meta-analysis of an array of animal clades found support for an early burst model in only two out of 88 data sets [32].

In even classic cases of adaptive radiation, other factors might strongly influence diversification. For example,

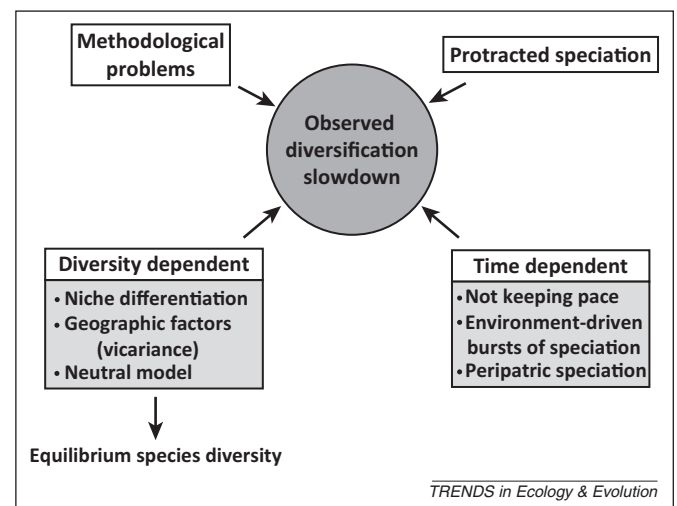


Figure 1. Conceptual diagram showing how various explanations for observed diversification slowdowns fall into broad categories. Potential methodological explanations are described in detail in Box 2. The explanations described in the main text fall into two broad categories: (i) diversity-dependent explanations, which can lead to equilibrium dynamics; and (ii) time-dependent explanations, which should not. Protracted speciation by itself is neither diversity-dependent nor time dependent, because rates of the initiation and completion of speciation are constant through time.

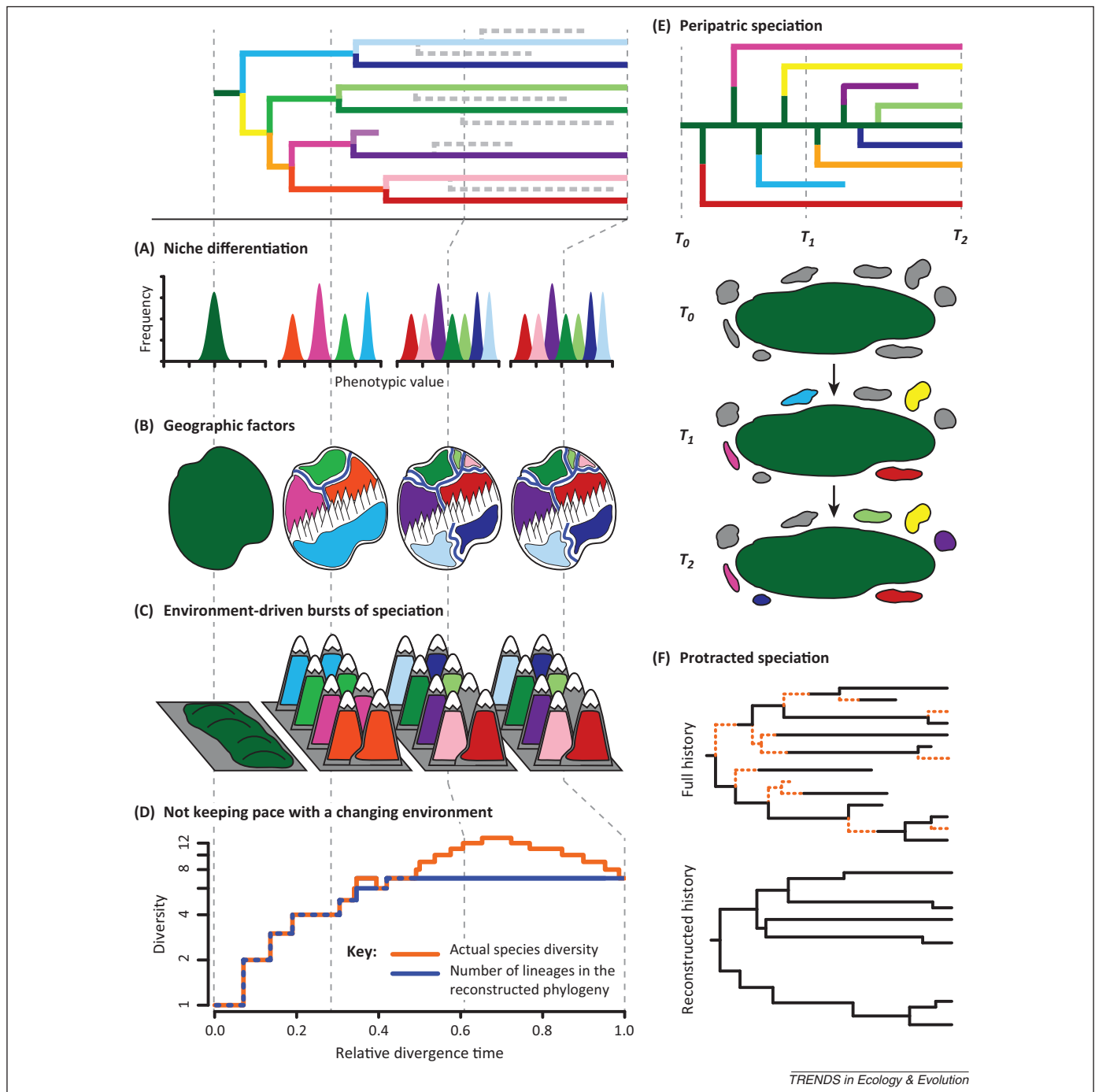


Figure 2. Different explanations for observed diversification slowdowns. At the top left is a hypothetical phylogeny with a diversification slowdown that could correspond to four biological explanations (A–D), whereas two explanations are more easily illustrated with their own phylogenies on the right (E,F). Colors correspond to the graphics below the phylogeny, as do time slices. One extinction event is represented in the middle of the phylogeny and by the absence of that species at the third time slice in (A–C). Broken gray branches represent additional branching and extinction events that only correspond to the bottom explanation (D). (A) In the case of niche differentiation, ecological and phenotypic diversification is expected to accompany speciation. In this hypothetical example, species diversify along a single phenotypic axis (e.g., that might correspond to resource use; the vertical axis is the frequency of individuals for a given phenotype). Speciation has slowed considerably by the third time slice because niche space has been filled. (B) The geographic model predicts that successive vicariance events affect relatively fewer species over time as their ranges become smaller, given limited range expansion. This leads to diversification slowdowns. Here, a mountain range and rivers divide geographic ranges to create new species. (C) In the case of environment-driven bursts of speciation, we expect significant geological or climatic events to lead to the rapid diversification of a group. In this example, initial mountain uplift leads to the isolation of four species at the second time slice, then those species subsequently speciate before the third time slice due to climatic specialization on different mountain slopes. (D) A clade might decline because its species cannot adapt to a changing biotic or abiotic environment. Under this scenario, a simple plot of the reconstructed lineages over time (blue) may show the slowdown but mask a more complex true history (orange). (E) Frequent peripatric speciation, wherein colonists from a large population give rise to new peripheral species that themselves fail to further speciate, may lead to slowdowns. In this case, the average rate of speciation for the entire clade decreases over time because most new species (e.g., those on small islands) do not speciate. (F) Protracted speciation might result in an underestimation of the branching events near the tips of a phylogeny, suggesting a slowing toward the present. The full history shows that protracted speciation (dotted orange lines) is a part of the entire history of a clade, but the failure to complete speciation only near the tips leads to an underestimation of branching events near the present in the reconstructed history.

phylogenetic analyses suggest that, in greater Antillean *Anolis* lizards, radiations on smaller islands (i.e., Jamaica and Puerto Rico) are ‘at or near equilibrium diversity’ [33]. If niche-based differences led to this equilibrium diversity, clades on the islands should also be at or near niche saturation. However, this does not seem to be the case. Decades of detailed ecological and evolutionary studies (summarized in [34]) have shown that the number of locally co-occurring and interacting *Anolis* species is represented by up to six distinct ecological types that are replicated across most islands (i.e., ecomorphs [34]). Yet clades on Jamaica and Puerto Rico have not reached these six ecomorphs, a clear case of ‘empty’ or ‘unused’ niches [35] (although it might be possible that smaller islands cannot support as many ecomorphs [34] or that the equilibrium number of occupied niches is below the maximum number of niches [11,36]). Moreover, there are multiple species of some ecomorphs (despite the absence of others) on each of these islands [34], and most *Anolis* speciation in the Greater Antilles (particularly on the largest islands) seems to have produced allopatric, ecologically equivalent sister species, at least in terms of resource competition [34,37]. These observations are not generally consistent with the hypothesis of ecological controls on species richness. Indeed, geographic constraints on diversification (see below) and niche divergence may interact to produce these slowdowns [33].

Another challenge to the idea that niche availability limits diversity is the infrequent occurrence of clades at a supposed limit ([3], but see [36]). This observation has been suggested to be due (in part) to the continuous evolution of key innovations, each of which enables subclades to break away from the dynamics of their parent clade and prevents reaching a limit to diversity [7]. However, even in this case, the broader parent clade should still show equilibrium dynamics [21]. Furthermore, the more general idea that bursts of diversification arise from greater niche availability early in the history of a clade has been suggested as unlikely for many clades [27]. Therefore, other possible causes of diversification slowdowns should be considered more thoroughly.

Underemphasized biological explanations for diversification slowdowns

Geography of diversification

Most speciation, particularly in animals, results from geographic isolation of populations with a lack of gene flow (i.e., allopatric speciation [38–42]). A common cause of such geographic isolation (and later speciation) is separation by a geographic barrier (i.e., vicariance [38]). These events are more likely to ‘miss’ small range sizes, such that vicariant speciation is most likely at intermediate to large range sizes [15,38,42]. Hence, as diversification proceeds and ranges are subdivided within a geographically bound group, per-species rates of speciation decline (Figure 2). In addition, extinction rates will increase as species range sizes (and, thus, population sizes) become smaller [38]. This geographic mode of diversification, which falls in the category of diversity-dependent explanations, could in principle lead to equilibrium diversity (Figure 1).

Recent studies lend support to the role of geography in explaining diversification slowdowns. First, Pigot *et al.* [15]

used a simulation model of geographic range evolution and cladogenesis to show that ecologically neutral speciation, extinction, dispersal, and range-size evolution can produce diversification slowdowns. In addition, studies of island species have shown that the probability of speciation increases with island size [43,44]. Finally, large, single-island assemblages show slowdowns, whereas clades in archipelagoes of small isolated islands show constant net diversification rates (i.e., spreading across islands leads to continual speciation opportunities [18]).

To produce diversification slowdowns, this explanation requires that range expansion after allopatric speciation is infrequent or delayed [15]. Such inhibition of range expansion on a macroevolutionary timescale can be linked to many factors unrelated to niche divergence, including low dispersal ability [45], conservatism in physiological traits [46], and reproductive interference [47]. These factors are unlikely to prevent range expansion over the full history of clades [45], but they will probably constrain ranges enough to slow the average rate of speciation in a group significantly. Thus, the geographic context of diversification alone can lead to diversification slowdowns without niche differentiation [8,15].

In some cases, niches might also be important when considering the influence of geography on slowdowns [36]. For example, competition between sister species with similar niches might prevent range expansion [45,48], limiting further allopatric speciation and slowing speciation rate in a clade. However, in this case, the maintenance of niche similarity (rather than niche divergence and the filling of a limited number of niches) is what leads to speciation rate slowdowns. In the case of hypotheses based on niche divergence, competition drives concomitant diversification of species and niches. When geography is important, competition impedes diversification and there should be little or no niche divergence associated with the slowdown.

Two additional models are similar to the geographic hypothesis as described above. First, Wang *et al.* [49] developed a neutral model of diversification in which average speciation rate declines over time because abundance decreases at speciation, such that species with high speciation rates are at a demographic disadvantage and tend to go extinct. This model is analogous to the geographic hypothesis, with abundance substituting for geographic range size. Second, frequent peripatric speciation might lead to diversification slowdowns. Under this model, one species with a large geographic range size gives rise to many small-ranged species that are unlikely to further speciate, leading to a linear increase in species over time instead of the exponential increase expected under standard birth–death models of diversification. Pigot *et al.* [15] found that the peripatric model led to slowdowns as long as geographic range size was relatively stable. *Zosterops lateralis*, a bird species complex that has repeatedly colonized multiple south Pacific islands from Australia and has led to many incipient species [40,50], may represent an empirical example of the peripatric model.

Environment-driven pulses of high speciation rate

Speciation rates might increase temporarily during periods of rapid environmental or geological change, then

decrease after the period ends (Figure 2 [26,51]). Such changes can lead to speciation via simple population isolation or the creation of an environmental gradient (e.g., climatic zonation along mountain slopes) along which speciation occurs due to climatic specialization [39]. Contrary to the previous hypotheses, where diversification slowdowns result from intrinsically negative diversity dependence (Figure 1), the slowdown here arises from the slowing of extrinsic factors that lead to speciation (such as vicariance events). This idea was introduced by Vrba [9] to describe diversification in the fossil record, calling it the ‘Turnover Pulse Hypothesis.’ In extant taxa, this possibility was suggested by Lovette and Bermingham [20], who found evidence for high speciation rates in *Dendroica* warblers close to a period of climate cooling and drying during the late Miocene 5–10 million years ago. Ricklefs [51] later noted that many passerine bird clades with diversification slowdowns originated during this same time period [4], as did many plant lineages in southern Africa [52]. Additionally, many Andean plant clades originated and diversified at a time of rapid uplift of the northern Andes [53,54]. In sum, evidence that environment-driven pulses of high speciation rate lead to diversification slowdowns is reasonable but largely anecdotal and awaits systematic testing.

Failure to keep pace with a changing environment

An inability to keep pace with a changing biotic or abiotic environment may lead to diversification slowdowns (Figure 2) [16,55]. This hypothesis is distinct in that slowdowns may result in an actual decline in diversity after a period of expansion rather than lead to equilibrium diversity (Figure 2), a pattern sometimes called ‘waxing–waning dynamics’. This scenario falls in the category of time-dependent explanations (Figure 1), with diversification slowing down such that net diversification rates switch from positive (corresponding to increasing diversity) to negative (corresponding to decreasing diversity) over the history of a clade. This could be due to speciation rates decreasing below extinction rates, extinction rates increasing above speciation rates, or both. Under this scenario, clades in both the expanding and the declining phase will show diversification slowdowns, thus potentially explaining the ubiquity of the pattern.

In terms of evidence, we know from the fossil record that most taxa go extinct [56], and recent paleontological studies have further shown that many genera symmetrically rise and fall in diversity [16,57], including groups that have extant representatives [16]. Recent studies have suggested that a changing environment leads to the downfall of entire clades, particularly if they cannot tolerate abiotic environmental changes or if other expanding clades outcompete them [16,58]. Ricklefs [51] proposed a scenario of coevolutionary interactions between pathogens and their hosts that may fit this model. He suggested that initial speciation rate in a host clade is high due to initial pathogen resistance (the ‘escape and radiate’ hypothesis of Ehrlich and Raven [59]), but then rates would subsequently decline due to pathogens overcoming the resistance and limiting further diversification. The decline phase of a host clade could lead to eventual extinction, as we discuss here, or it may lead to net diversification rates of zero until additional

pathogen resistance evolved. This model remains to be tested.

Waxing–waning dynamics were not initially thought to apply to observed diversification slowdowns (for example, those inferred via negative gamma values; Box 1; [56]) because recent extinctions would erase the signal of earlier speciation slowdowns [60]. However, Quental and Marshall [61] demonstrated that clades in decline could in fact show negative gamma values. Waxing–waning dynamics have rarely been inferred from phylogenies, but this results from a past lack of serious consideration because reconstructed phylogenies give the impression that species richness only increases through time [1,61]. However, a study of modern whales illustrated that diversity declines can be recovered from reconstructed phylogenies ([62], see also [55]). Further studies will be necessary to determine the importance of waxing–waning dynamics for empirical phylogenies.

Protracted speciation

Under many speciation concepts, there is an expected lag time between the initial divergence of populations and when they have achieved reproductive isolation or when gene flow completely stops [39,63,64]. However, the time at which sister species are inferred to have split in a phylogeny will date to the original population split, not the ‘completion’ of speciation. Consequently, the presence of incipient species in a clade (and the failure to include them as distinct species in the phylogeny) will exclude the most recent branching points of a phylogeny. This concept, referred to as ‘protracted speciation’ [63,64], may partly explain slowing diversification rates through time [65] because branching events near the tips will be excluded.

Protracted speciation is distinct from other hypotheses in that it only applies to a certain portion of the history of a group (i.e., near the present). This is a strength of the explanation because there is no reason for the present day to be a special time at which most clades show slowdowns [56,65], and indeed protracted speciation should only (and always) be applicable in the present day [65]. By contrast, the explanation is somewhat limited in that the process will have no applicability to deep-time slowdowns. Many analyses have found slowdowns after removing the most recent branch lengths (e.g., [4,28]), and such slowdowns cannot be explained by protracted speciation.

Identifying the biological causes of slowdowns in diversification rates: ways forward

Novel phylogenetic diversification methods are increasingly making subtle differences among models differentiable (e.g., [3,8,17,19,62,66,67]). Yet it has become clear that similar branching patterns in phylogenies can be the product of distinct biological scenarios [3,27], and that comparing model fit alone often might not tease apart these scenarios [17,68]. As such, here we propose ways to test the ecological, phenotypic, and geographic corollaries of these hypotheses, in addition to suggesting further needs in modeling diversification.

Testing diversification scenarios

Many current alternatives to niche-divergence hypotheses have seen few explicit tests using diversification models.

This is largely due to two reasons. First, few explicit inference approaches are available to compare directly the models of diversification discussed herein. For example, approaches do not exist to compare the model of peripatric speciation or the neutral model of Wang *et al.* [49] to other models, such as constant rates, time-dependent diversification, and diversity-dependent diversification. Even rigorously testing among these latter models is still not common (Box 1). However, at least simply testing for diversity dependence versus time-variable diversification rates may eliminate some hypotheses (Figure 1), with additional data serving to further differentiate hypotheses (see below).

Second, many hypotheses simply have been under recognized. Waxing–waning dynamics can now be tested [55,62], as well as protracted speciation [65]. Tools are also available to evaluate the hypothesis that common environmental factors have led to bursts in speciation. To do so, one could simply first determine a priori events that might have led to high speciation rates in a group, and then examine support for a model that allows a diversification rate shift at the time of the events (e.g., [69]). Alternatively, for a more complex history of diversification, one could use paleontological environmental data, specify a functional response of diversification rates to the environmental factors hypothesized to have had a strong influence (e.g., rates of speciation increase during periods of geological activity or climatic change), and infer the likelihood support of this relation [70].

Additional data beyond phylogenies per se

Given that examining the phylogeny alone might not be powerful enough to distinguish among hypotheses [3,17,68], incorporating other data into phylogenetic diversification analysis, such as population size, traits, range size and overlap, and fossils would be useful and needs to be developed [56,70]. More simply, all hypotheses have other predictions beyond diversification *per se* and such predictions should be tested. For example, the most basic necessity for testing the influence of niche divergence on diversification is data on traits that affect competition among species within a clade (e.g., [28–31,68]), yet these data are not often presented. More refined statistical approaches that directly link the tempo of species diversification to the tempo of phenotypic evolution will also help in this endeavor [30,31]. Furthermore, information on range overlap is necessary to distinguish between geographic- and niche divergence-based causes of slowdowns, and explicitly considering this might often be simple. For example, even if the species in a given clade show niche divergence, if they do not occur in the same geographic area then there was probably little role for ecological differentiation in species diversification [6]. Alternatively, the widespread co-occurrence of closely related species might indicate little importance for geographic factors, because slowdowns are not likely to be due to geographic factors under high rates of secondary range overlap [15]. Hence, a simple, initial test might be one that analyzes the link between the phylogenetic relatedness and co-occurrence of species.

The geographic vicariance hypothesis suggests that, within a geographic area (e.g., a continent), sister clades (those of the same age) should show an inverse relation between species diversity in that area and average range size, and as far as we know this has not yet been tested. Alternatively, one could test the theoretical result that larger range sizes are those that are more likely to be bisected by vicariance to produce daughter species [38], as done by Price [42]. The geographic peripatric model similarly yields testable predictions, such as an uneven distribution of range sizes across species [15] and a highly imbalanced phylogeny (due to many small-ranged species ‘budding off’ a large-ranged species; Figure 2). Finally, given that the geographic models (both vicariant and peripatric) focus on range dynamics in general, understanding the determinants of range boundaries and expansion (e.g., [45]) would help resolve whether this model applies to a given clade.

Paleontological data can also offer a rich source of additional evidence [56]. Indeed, early hypotheses about the dynamics of macroevolutionary diversification came from the fossil record (e.g., [11,12]), although most such studies did not include ecological data, which limits their ability to provide support for the various hypotheses we outline above. However, ecological data are available for some fossil taxa (e.g., [71,72]) and morphology can be used as a proxy for ecological data for many fossils [73]. Such data can be combined with fossil-estimated speciation and extinction rates to test how niche filling is associated with diversification rates. Geographic range data of fossils can similarly test the importance of geography on diversification rates. As a good example of such approaches, Ezard *et al.* [74] combined morphological, depth habitat, and paleoclimatic data with a complete phylogeny (i.e., including all extinct species) of the macroperforate planktonic foraminifera to test which factors influenced their diversification during the Cenozoic. Finally, waxing and waning can be directly tested with origination and extinction rates over time in paleontological data [16], as can environment-driven bursts of speciation [9].

Concluding remarks

Many clades show diversification slowdowns. This pattern might be driven by many biological factors. No one hypothesis will apply to all groups that show a signal of declining diversification rates, and some clades might experience multiple factors that lead to diversification slowdowns. We simply argue here that the importance of the dominant explanation (that based on niche divergence) might be largely overstated. Other biological factors can explain why many groups show decreasing diversification rates through time, but much work remains to be done to distinguish among them. This will necessitate considering both the phylogenetic and nonphylogenetic predictions of various hypotheses and testing the underlying assumptions.

Acknowledgments

We thank F. Condamine, H. Doll, J. Green, J. Losos, A. Phillimore, A. Pigot, T. Quental, J. Rolland, J. Rosindell, J. Wiens, and an anonymous reviewer for insightful criticisms and helpful suggestions for this paper.

References

- 1 Ricklefs, R.E. (2007) Estimating diversification rates from phylogenetic information. *Trends Ecol. Evol.* 22, 601–610
- 2 McPeck, M.A. (2008) The ecological dynamics of clade diversification and community assembly. *Am. Nat.* 172, E270–E284
- 3 Morlon, H. *et al.* (2010) Inferring the dynamics of diversification: a coalescent approach. *PLoS Biol.* 8, e1000493
- 4 Phillimore, A.B. and Price, T.D. (2008) Density-dependent cladogenesis in birds. *PLoS Biol.* 6, 483–489
- 5 Rabosky, D.L. (2009) Ecological limits and diversification rate: alternative paradigms to explain the variation in species richness among clades and regions. *Ecol. Lett.* 12, 735–743
- 6 Wiens, J.J. (2011) The causes of species richness patterns across space, time, and clades and the role of ‘ecological limits’. *Q. Rev. Biol.* 86, 75–96
- 7 Cornell, H.V. (2013) Is regional species diversity bounded or unbounded? *Biol. Rev.* 88, 140–165
- 8 Rabosky, D.L. and Lovette, I.J. (2008) Density-dependent diversification in North American wood warblers. *Proc. R. Soc. B* 275, 2363–2371
- 9 Vrba, E.S. (1985) Environment and evolution: alternative causes of the temporal distribution of evolutionary events. *S. Afr. J. Sci.* 81, 229–236
- 10 Sloss, L.L. (1950) Rates of evolution. *J. Paleontol.* 24, 131–139
- 11 Walker, T.D. and Valentine, J.W. (1984) Equilibrium models of evolutionary species diversity and the number of empty niches. *Am. Nat.* 124, 887–899
- 12 Raup, D.M. *et al.* (1973) Stochastic models of phylogeny and the evolution of diversity. *J. Geol.* 81, 525–542
- 13 Weir, J.T. (2006) Divergent timing and patterns of species accumulation in lowland and highland neotropical birds. *Evolution* 60, 842–855
- 14 Burbrink, F.T. *et al.* (2012) Evidence for determinism in species diversification and contingency in phenotypic evolution during adaptive radiation. *Proc. R. Soc. B* 279, 4817–4826
- 15 Pigot, A.L. *et al.* (2010) The shape and temporal dynamics of phylogenetic trees arising from geographic speciation. *Syst. Biol.* 59, 660–673
- 16 Quental, T.B. and Marshall, C.R. (2013) How the Red Queen drives terrestrial mammals to extinction. *Science* 341, 290–292
- 17 Etienne, R.S. *et al.* (2012) Diversity-dependence brings molecular phylogenies closer to agreement with the fossil record. *Proc. R. Soc. B* 279, 1300–1309
- 18 Fritz, S.A. *et al.* (2012) Diversification and biogeographic patterns in four island radiations of passerine birds. *Evolution* 66, 179–190
- 19 Pyron, R.A. and Burbrink, F.T. (2013) Phylogenetic estimates of speciation and extinction rates for testing ecological and evolutionary hypotheses. *Trends Ecol. Evol.* 28, 729–736
- 20 Lovette, I.J. and Bermingham, E. (1999) Explosive speciation in the New World *Dendroica* warblers. *Proc. R. Soc. B* 266, 1629–1636
- 21 Etienne, R.S. and Haegeman, B. (2012) A conceptual and statistical framework for adaptive radiations with a key role for diversity dependence. *Am. Nat.* 180, E75–E89
- 22 Kennedy, J.D. *et al.* (2012) Ecological limits on diversification of the Himalayan core Corvoidea. *Evolution* 66, 2599–2613
- 23 Scantlebury, D.P. (2013) Diversification rates have declined in the Malagasy herpetofauna. *Proc. R. Soc. B* 280, 20131109
- 24 Schluter, D. (2000) *The Ecology of Adaptive Radiation*, Oxford University Press
- 25 Gavrillets, S. and Vose, A. (2005) Dynamic patterns of adaptive radiation. *Proc. Natl. Acad. Sci. U.S.A.* 102, 18040–18045
- 26 Lieberman, B.S. (2012) Adaptive radiations in the context of macroevolutionary theory: a paleontological perspective. *Evol. Biol.* 39, 181–191
- 27 Rabosky, D.L. (2009) Heritability of extinction rates links diversification patterns in molecular phylogenies and fossils. *Syst. Biol.* 58, 629–640
- 28 Harmon, L.J. *et al.* (2003) Tempo and mode of evolutionary radiation in Iguanian lizards. *Science* 301, 961–964
- 29 Jönsson, K.A. *et al.* (2012) Ecological and evolutionary determinants for the adaptive radiation of the Madagascan vangas. *Proc. Natl. Acad. Sci. U.S.A.* 109, 6620–6625
- 30 Mahler, D.L. *et al.* (2010) Ecological opportunity and the rate of morphological evolution in the diversification of Greater Antillean anoles. *Evolution* 64, 2731–2745
- 31 Weir, J.T. and Mursleen, S. (2013) Diversity-dependent cladogenesis and trait evolution in the adaptive radiation of the auks (Aves: Alcidae). *Evolution* 67, 403–416
- 32 Harmon, L.J. *et al.* (2010) Early bursts of body size and shape evolution are rare in comparative data. *Evolution* 64, 2385–2396
- 33 Rabosky, D.L. and Glor, R.E. (2010) Equilibrium speciation dynamics in a model adaptive radiation of island lizards. *Proc. Natl. Acad. Sci. U.S.A.* 107, 22178–22183
- 34 Losos, J.B. (2009) *Lizards in an Evolutionary Tree: Ecology and Adaptive Radiation of Anoles*, University of California Press
- 35 Losos, J.B. (1992) The evolution of convergent structure in Caribbean *Anolis* communities. *Syst. Biol.* 41, 403–420
- 36 Rabosky, D.L. (2013) Diversity-dependence, ecological speciation, and the role of competition in macroevolution. *Annu. Rev. Ecol. Evol. Syst.* 44, 481–502
- 37 Losos, J.B. *et al.* (2006) Adaptation, speciation, and convergence: a hierarchical analysis of adaptive radiation in Caribbean *Anolis* lizards. *Ann. Mo. Bot. Gard.* 93, 24–33
- 38 Rosenzweig, M.L. (1995) *Species Diversity in Space and Time*, Cambridge University Press
- 39 Coyne, J.A. and Orr, H.A. (2004) *Speciation*, Sinauer Associates
- 40 Price, T.D. (2008) *Speciation in Birds*, Roberts & Company
- 41 Phillimore, A.B. *et al.* (2008) Sympatric speciation in birds is rare: insights from range data and simulations. *Am. Nat.* 171, 646–657
- 42 Price, T.D. (2010) The roles of time and ecology in the continental radiation of the Old World leaf warblers (*Phylloscopus* and *Seicercus*). *Philos. Trans. R. Soc. Lond. B* 365, 1749–1762
- 43 Losos, J.B. and Schluter, D. (2000) Analysis of an evolutionary species-area relationship. *Nature* 408, 847–850
- 44 Kisel, Y. and Barraclough, T.G. (2010) Speciation has a spatial scale that depends on levels of gene flow. *Am. Nat.* 175, 315–334
- 45 Pigot, A.L. and Tobias, J.A. (2013) Species interactions constrain geographic range expansion over evolutionary time. *Ecol. Lett.* 16, 330–338
- 46 Kozak, K.H. and Wiens, J.J. (2006) Does niche conservatism promote speciation? A case study in North American salamanders. *Evolution* 60, 2604–2621
- 47 Gröning, J. and Hochkirch, A. (2008) Reproductive interference between animal species. *Q. Rev. Biol.* 83, 257–282
- 48 Price, T.D. and Kirkpatrick, M. (2009) Evolutionary stable range limits set by interspecific competition. *Proc. R. Soc. B* 276, 1429–1434
- 49 Wang, S. *et al.* (2013) Speciation rates decline through time in individual-based models of speciation and extinction. *Am. Nat.* 182, E83–E93
- 50 Moyle, R.G. *et al.* (2009) Explosive Pleistocene diversification and hemispheric expansion of a ‘great speciator’. *Proc. Natl. Acad. Sci. U.S.A.* 106, 1863–1868
- 51 Ricklefs, R.E. (2010) Evolutionary diversification, coevolution between populations and their antagonists, and the filling of niche space. *Proc. Natl. Acad. Sci. U.S.A.* 107, 1265–1272
- 52 Verboom, G.A. *et al.* (2009) Origin and diversification of the Greater Cape flora: ancient species repository, hot-bed of recent radiation, or both? *Mol. Phylogenet. Evol.* 51, 44–53
- 53 Hughes, C. and Eastwood, R. (2006) Island radiation on a continental scale: exceptional rates of plant diversification after uplift of the Andes. *Proc. Natl. Acad. Sci. U.S.A.* 103, 10334–10339
- 54 Antonelli, A. *et al.* (2009) Tracing the impact of the Andean uplift on Neotropical plant evolution. *Proc. Natl. Acad. Sci. U.S.A.* 106, 9749–9754
- 55 Pyron, R.A. and Burbrink, F.T. (2012) Extinction, ecological opportunity, and the origins of global snake diversity. *Evolution* 66, 163–178
- 56 Quental, T.B. and Marshall, C.R. (2010) Diversity dynamics: molecular phylogenies need the fossil record. *Trends Ecol. Evol.* 25, 434–441
- 57 Foote, M. (2007) Symmetric waxing and waning of marine invertebrate genera. *Paleobiology* 33, 517–529
- 58 Benton, M.J. (2009) The Red Queen and the Court Jester: species diversity and the role of biotic and abiotic factors through time. *Science* 323, 728–732
- 59 Ehrlich, P.R. and Raven, P.H. (1964) Butterflies and plants: a study in coevolution. *Evolution* 18, 586–608
- 60 Rabosky, D.L. and Lovette, I.J. (2008) Explosive evolutionary radiations: decreasing speciation or increasing extinction through time? *Evolution* 62, 1866–1875

- 61 Quental, T.B. and Marshall, C.R. (2011) The molecular phylogenetic signature of clades in decline. *PLoS ONE* 6, e25780
- 62 Morlon, H. *et al.* (2011) Reconciling molecular phylogenies with the fossil record. *Proc. Natl. Acad. Sci. U. S. A.* 108, 16327–16332
- 63 Avise, J.C. and Walker, D. (1998) Pleistocene phylogeographic effects on avian populations and the speciation process. *Proc. R. Soc. Lond. B* 265, 457–463
- 64 Rosindell, J. *et al.* (2010) Protracted speciation revitalizes the neutral theory of biodiversity. *Ecol. Lett.* 13, 716–727
- 65 Etienne, R.S. and 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
- 66 Stadler, T. (2011) Mammalian phylogeny reveals recent diversification rate shifts. *Proc. Natl. Acad. Sci. U. S. A.* 108, 6187–6192
- 67 Morlon, H. (2014) Phylogenetic approaches for studying diversification. *Ecol. Lett.* <http://dx.doi.org/10.1111/ele.12251>
- 68 Machac, A. *et al.* (2013) Ecological causes of decelerating diversification in carnivoran mammals. *Evolution* 67, 2423–2433
- 69 Condamine, F.L. *et al.* (2012) What causes latitudinal gradients in species diversity? Evolutionary processes and ecological constraints on swallowtail biodiversity. *Ecol. Lett.* 15, 267–277
- 70 Condamine, F.L. *et al.* (2013) Macroevolutionary perspectives to environmental change. *Ecol. Lett.* 16, 72–85
- 71 Bush, A.M. and Bambach, R.K. (2011) Paleoeologic megatrends in marine Metazoa. *Ann. Rev. Earth Planet. Sci.* 39, 241–269
- 72 Novack-Gottshall, P.M. (2007) Using a theoretical ecospace to quantify the ecological diversity of Paleozoic and modern marine biotas. *Paleobiology* 33, 273–294
- 73 Roy, K. and Foote, M. (1997) Morphological approaches to measuring biodiversity. *Trends Ecol. Evol.* 12, 277–281
- 74 Ezard, T.H.G. *et al.* (2011) Interplay between changing climate and species' ecology drives macroevolutionary dynamics. *Science* 332, 349–351
- 75 Harvey, P.H. *et al.* (1994) Phylogenies without fossils. *Evolution* 48, 523–529
- 76 Pybus, O.G. and Harvey, P.H. (2000) Testing macro-evolutionary models using incomplete molecular phylogenies. *Proc. R. Soc. B* 267, 2267–2272
- 77 Nee, S. *et al.* (1994) The reconstructed evolutionary process. *Philos. Trans. R. Soc. Lond. B* 344, 305–311
- 78 Cusimano, N. and Renner, S.S. (2010) Slowdowns in diversification rates from real phylogenies may not be real. *Syst. Biol.* 59, 458–464
- 79 Pennell, M.W. *et al.* (2012) Trees of unusual size: biased inference of early bursts from large molecular phylogenies. *PLoS ONE* 7, e43348
- 80 Revell, L.J. *et al.* (2005) Underparameterized model of sequence evolution leads to bias in the estimation of diversification rates from molecular phylogenies. *Syst. Biol.* 54, 973–983
- 81 Rüber, L. and Zardoya, R. (2005) Rapid cladogenesis in marine fishes revisited. *Evolution* 59, 1119–1127
- 82 Webster, A.J. *et al.* (2003) Molecular phylogenies link rates of evolution and speciation. *Science* 301, 478
- 83 Burbrink, F.T. and Pyron, R.A. (2011) The impact of gene-tree/species-tree discordance on diversification-rate estimation. *Evolution* 65, 1851–1861