

REVIEW AND SYNTHESIS

Phylogenetic approaches for studying diversification

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Abstract

Estimating rates of speciation and extinction, and understanding how and why they vary over evolutionary time, geographical space and species groups, is a key to understanding how ecological and evolutionary processes generate biological diversity. Such inferences will increasingly benefit from phylogenetic approaches given the ever-accelerating rates of genetic sequencing. In the last few years, models designed to understand diversification from phylogenetic data have advanced significantly. Here, I review these approaches and what they have revealed about diversification in the natural world. I focus on key distinctions between different models, and I clarify the conclusions that can be drawn from each model. I identify promising areas for future research. A major challenge ahead is to develop models that more explicitly take into account ecology, in particular the interaction of species with each other and with their environment. This will not only improve our understanding of diversification; it will also present a new perspective to the use of phylogenies in community ecology, the science of interaction networks and conservation biology, and might shift the current focus in ecology on equilibrium biodiversity theories to non-equilibrium theories recognising the crucial role of history.

Keywords

Birth–death models, cladogenesis, diversity dynamics, extinction, speciation, stochastic biodiversity models.

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INTRODUCTION

Diversification – the balance between speciation and extinction – is central to one of the most fundamental questions in ecology: ‘How is biodiversity generated and maintained?’ Diversification is a key to understanding how biodiversity varies over geological time scales (Raup *et al.* 1973; Foote *et al.* 2007; Morlon *et al.* 2010; Quental & Marshall 2010, 2013; Ezard *et al.* 2011) and how it is distributed across the Earth’s surface (Rosenzweig 1995; Mittelbach *et al.* 2007; Weir & Schluter 2007; Rabosky 2009a; Wiens 2011; Jetz *et al.* 2012; Rolland *et al.* 2014), the tree of life (Alfaro *et al.* 2009; Rabosky 2009a) and ecological communities (Ricklefs 1987; Morlon *et al.* 2011b; Wiens *et al.* 2011). Diversification is a central component of major biodiversity theories, such as the neutral theory of biodiversity (Hubbell 2001) and the metabolic theory of ecology (Brown *et al.* 2004; Stegen *et al.* 2009). Diversification is also a primary predictor of three fundamental patterns in macroecology: the species abundance distribution, which describes how individuals are partitioned among species, the species–area relationship, which describes how species richness increases with geographical area, and the distance–decay relationship, which describes how community similarity declines with geographical distance (Rosenzweig 1995; Rosindell & Phillimore 2011). Diversification rates are thus some of the most important parameters in macroevolution, macroecology and community ecology.

While central to biodiversity research, diversification is particularly hard to study. Speciation and extinction processes typically happen on a scale of thousands to millions of years, and while estimating diversification rates from fossil data is feasible

for some groups such as planktonic foraminifers, planktonic diatoms, bivalves, gastropods and mammals (Raup *et al.* 1973; Foote *et al.* 2007; Ezard *et al.* 2011; Quental & Marshall 2013), it is not feasible for the majority of extant groups on Earth.

The paucity of the fossil record has encouraged the development of alternative approaches to study diversification, themselves inspired from palaeontological models (Raup *et al.* 1973; Hey 1992; Nee *et al.* 1994a,b). Phylogenies – branching trees that represent the evolutionary relationships among species – contain information about past diversification events. The phylogenetic trees of extant (present-day) species, referred to as ‘reconstructed phylogenies’ (Fig. 1), can be inferred using molecular data. In turn, these trees can be used along with various stochastic models to draw inferences about diversification and diversity dynamics. Since the early developments of Hey (1992) and Nee *et al.* (1992, 1994a,b), phylogenetic methods have become a prevailing approach for studying diversification (reviewed in Mooers & Heard 1997; Mooers *et al.* 2007; Ricklefs 2007; Pennell & Harmon 2013; Pyron & Burbrink 2013; Stadler 2013a) and such emphases are further supported by the ever-increasing availability of large scale, dated molecular phylogenies (Bininda-Emonds *et al.* 2007; Jetz *et al.* 2012).

The specific use of phylogenies for studying diversification remains scarce in ecology, despite the increasing importance that phylogenetic data have taken in this field over the last few years. In community ecology, phylogenies have mainly been used to approximate the ecological similarity of species (Webb *et al.* 2002; Cavender-Bares *et al.* 2009; Mayfield & Levine 2010); in the science of species’ interaction networks, they have been used to analyse the degree to which species’

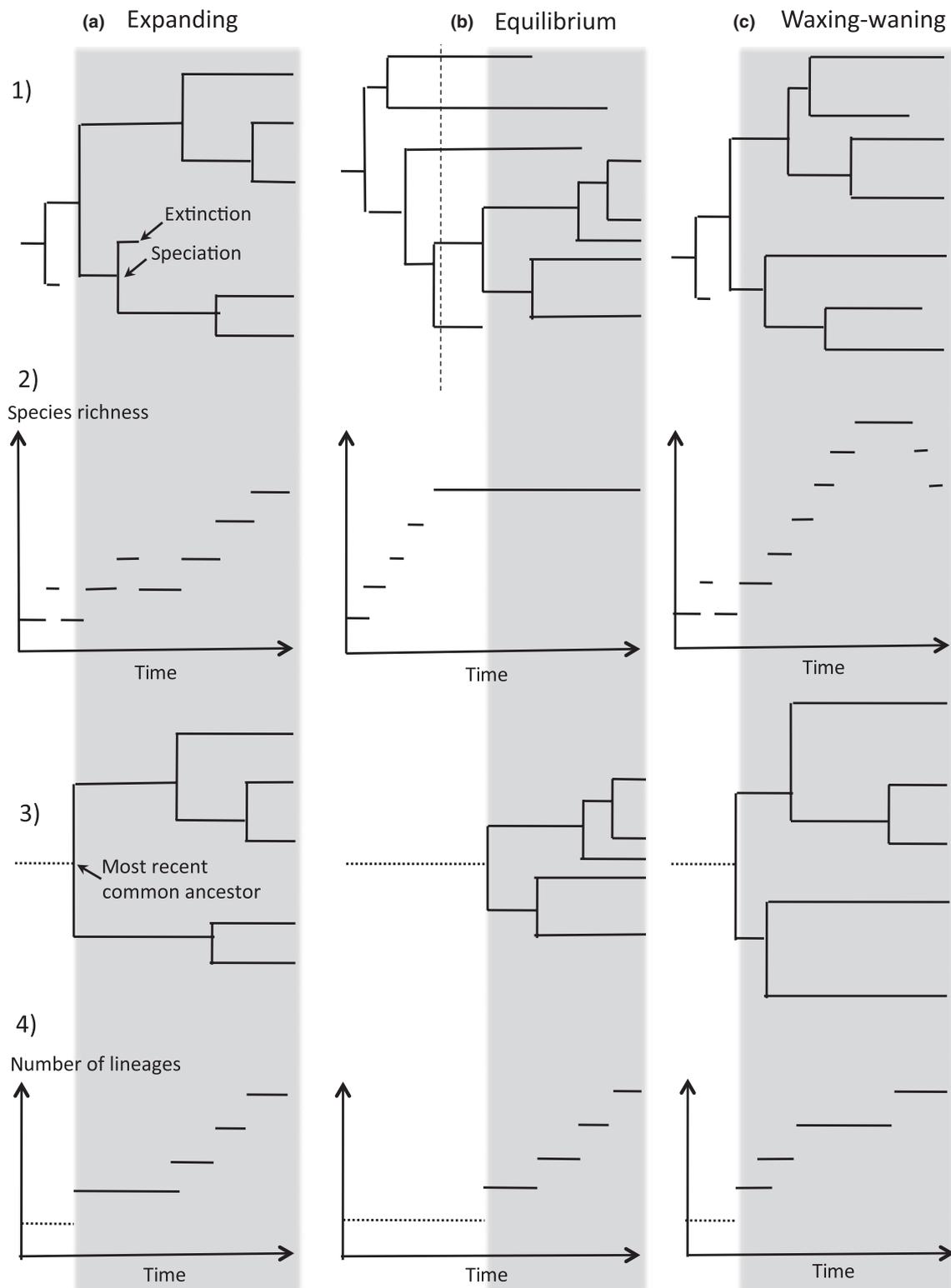


Figure 1 Analysing diversification with phylogenies. (1) Complete phylogenies representing the birth and death of species, (2) diversity-through-time plot, (3) reconstructed phylogeny and (4) lineage-through-time plot corresponding to scenarios of (a) expanding diversity, meaning that clades' richness increases over time, (b) equilibrium diversity, meaning that clades' richness stay constant over time and (c) waxing-waning diversity dynamics, meaning that clades' richness first increases and then decreases over time. The grey areas correspond to the time period going from the time of the most recent common ancestor in the reconstructed phylogeny to the present. Although the number of lineages in the reconstructed phylogeny always increases from 2 to present-day diversity (4), the corresponding diversity trajectory can be increasing (a), stable (b), or contain periods of diversity decline (c). In (b), starting from the time indicated with the dashed line, each extinction event is immediately followed by a speciation event, resulting in equilibrium dynamics.

Box 1 Data used in phylogenetic approaches for studying diversification

The different types of phylogenetic data that can be used for analysing diversification are illustrated in Fig. 2. The models applicable to each data type are listed in Table 1. Phylogenetic approaches for studying diversification focus on two main aspects of phylogenetic trees (Fig. 2): branching times, which require phylogenetic branch lengths to be in units relative to time (Fig. 2a–f); and topology, which does not have this requirement (Fig. 2g). The phylogeny is ideally dated, yielding biologically interpretable estimates of diversification rates, although this is not a strict requirement.

Species-level phylogenies (Fig. 2a) offer the most extensive set of possibilities for fitting diversification models. When diversification rates are homogeneous across lineages, all topologies are equally likely, such that the branching times (t_0, t_1, \dots, t_n) contain all the information relevant for analysing diversification. The stem age t_0 can be included in the analysis when available, in which case the diversification process should be conditioned on survival of a lineage from t_0 to the present in the likelihood computation. If only the crown age t_1 is available, the process should be conditioned on a speciation event at t_1 and survival of two lineages from t_1 to the present. Some diversification models (e.g. Models 3 and 9) require additional data, such as traits or palaeoenvironmental data.

Often only higher level phylogenies are available for species-rich groups (Fig. 2 b and c). Net diversification rates can be estimated from (stem or crown) clade age and species richness data (Fig. 2b), whereas speciation and extinction rates can both be estimated with a combination of branching times and species richness data (Fig. 2c).

Lineage-through-time plots (Fig. 2d, solid line) are a convenient way to visualise phylogenies and are widely used to describe phylogenetic tree shape, although plotting waiting times as a function of the time at which they end (Fig. 2d, dotted line) may in fact be a better approach (Hallinan 2012). Some authors have proposed approaches based on branch-length distributions, which represent the fraction of lineages in a given branch-length class (Fig. 2e) (Venditti *et al.* 2010).

Currently available approaches combining phylogenetic and fossil data need fossils to be placed on the phylogeny (fossil finds are represented by crosses in Fig. 2f). Thin dashed lines in Fig. 2f represent lineages with no extant descendants that are represented in the fossil record.

Several approaches use tree topology rather than branching times (Fig. 2g). Some of these approaches (e.g. Model 11) require additional data, such as abundance data (Jabot & Chave 2009).

interactions are conserved (Ives & Godfray 2006; Rezende *et al.* 2007); in conservation biology, they have been used to estimate the evolutionary uniqueness of species (Vane-Wright *et al.* 1991). In comparison, and despite the central role of diversification in several key ecological hypotheses, the use of diversification models in ecology is rare (but see Rabosky 2009b; Ricklefs 2010; Wiens 2011; Wiens *et al.* 2011).

Here, I review diversification models with the hope that it will stimulate a better integration of research in ecology and macroevolution (McInnes *et al.* 2011). I highlight important distinctions between various models, clarify the conclusions that can be drawn from each model, review empirical results and identify promising areas for future research.

These models can be classified into models where species are the unit of diversification, without any reference to individuals, population sizes, or geographical ranges (Fig. 1a, Models 1–10 below), and models where the dynamics of individuals, population sizes, or species ranges are considered explicitly (Models 11–13). The latter models are closer to models traditionally considered in ecology, where understanding the abundance and distribution of species has always been a central interest. The various models can further be classified with respect to whether diversification is assumed: (1) to be time constant (Models 1, 7, 8, 11) or to vary through time (Models 2–6, 9, 10, 12, 13), (2) to be homogeneous (Models 1–7) or to vary across lineages (8–13) and (3)

MODELS OF DIVERSIFICATION

Phylogenetic approaches to understanding diversification rely on a simple common principle: comparing empirical (reconstructed) phylogenies to (reconstructed) phylogenies obtained under various models of diversification. In practice, different types of phylogenetic data (Box 1 and Fig. 2) and different statistical approaches (Box 2) can be used for this comparison. Since the phylogenetic methods to study diversification were first proposed (Hey 1992; Nee *et al.* 1992, 1994a,b), a considerable number of models have been developed (Table 1).

to be instantaneous (Models 1–6, 8–13) or to be protracted (Model 7).

Model 1 – Homogeneous, time-constant diversification

In the simplest model, sometimes referred to as the ‘equal-rates’ model, diversification is modelled as a birth–death process in which species either give rise to new species or die, both with fixed rates (λ and μ respectively). λ and μ are homogeneous across species (i.e. all species have equal diversification rates). Under this model, λ is typically greater than μ (otherwise clade-wide extinction is fast) and clade diversity increases exponentially through time (Fig. 1a).

Under a pure birth (no extinction) model (Yule 1925), the increase in the number of reconstructed lineages with time –

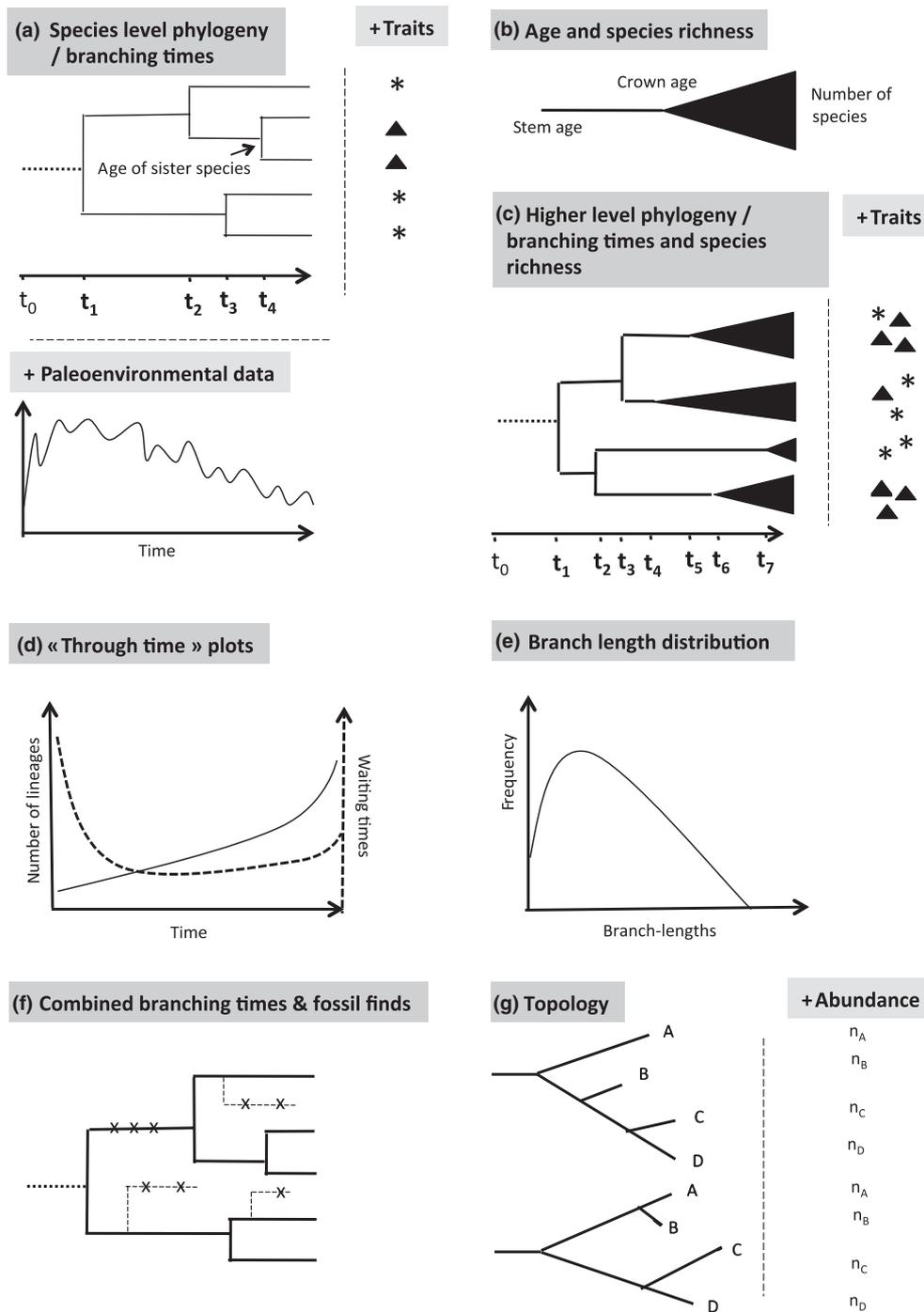


Figure 2 Illustration of data used in phylogenetic approaches for studying diversification. These various type of data and what they can be used for are detailed in Box 1. t_0, t_1, \dots, t_n represent branching times.

commonly visualised using lineage-through time (LTT) plot (Fig. 1d and Fig. 2d) – is linear on a semi-log scale, with a slope equal to the rate of speciation. Under a birth–death model, non-zero extinction results in an apparent acceleration in the accumulation of lineages towards the present, a signal known as the ‘pull of the present’ (Nee *et al.* 1994a). In principle, this upturn towards the present allows estimating extinction rates from reconstructed phylogenies, although the possibility of estimating extinction using phylogenies has been

called into question (Box 3) (Kubo & Iwasa 1995; Paradis 2004; Quental & Marshall 2010; Rabosky 2010).

In their seminal paper, Nee *et al.* (1994a) adapted results from Kendall (1948) to derive a likelihood expression for phylogenetic branching times (Fig. 2) under equal rates models that inspired many advances in the field. Equal rates models are still widely used, serving in particular as null models of diversification. They are also at the base of one of the most popular methods for estimating diversification rates, the method-of-

moments, which allows estimating net diversification rates (speciation minus extinction) with only the age and species richness of clades (Fig. 2b) (Magallon & Sanderson 2001).

Model 2 – Time-varying diversification

While time-constant models are useful, there are many reasons why diversification rates can vary over the evolutionary history of a clade, including changes in the biotic and abiotic environments, diversity-dependent effects, or the combination of both. A straightforward and widespread approach to account for time variation in diversification rates is to assume a functional dependence of speciation and extinction rates with time (Nee *et al.* 1994b; Rabosky & Lovette 2008a; Morlon *et al.* 2011a; Stadler 2011; Hallinan 2012). Likelihood expressions of phylogenetic branching times for such models are available, for both continuous (e.g. linear, exponential; Rabosky & Lovette 2008a; Morlon *et al.* 2011a; Hallinan 2012) and discrete (referred to as the ‘discrete shift’ model; Stadler 2011; Hallinan 2012) forms of time variation. These time-dependent models allow a quantitative estimation of how diversification rates have varied through time. One can then estimate how species diversity itself varied through time (Box 4).

Time-dependent models are phenomenological models meant to describe how speciation and extinction rates vary over time. If time variation is detected, additional tests are needed to decide which processes, such as environmental drivers, diversity dependence, or other factors, are at play.

Model 3 – Environmental dependence

The main drivers of temporal variations in diversification rates are modifications in the abiotic (e.g. geographic, climatic) and biotic (e.g. access to food, intensity of predation)

environment. If some information about these environmental variables is known, for example, in the form of palaeoenvironmental data (e.g. a palaeotemperature curve or the diversity trajectory of an interacting species group, Fig. 2a), likelihood expressions for phylogenetic branching times can be derived that allow testing the effect of such environmental variation on diversification rates (Condamine *et al.* 2013). Similar to the approach used in time-varying diversification models, a functional dependence of diversification rates on the environment (or its variations) is assumed. It is then possible to test whether the environmental variation had a significant effect on diversification and to investigate the direction, magnitude and most likely functional form of this effect (Condamine *et al.* 2013). In this model, diversification rates can depend on time in addition to the measured environment.

Model 4 – Diversity dependence

Another potentially important source of time variation in diversification rates is the growth of the clade itself. As diversification proceeds and species accumulate, they fill geographical and niche space, potentially reducing opportunities for speciation and increasing extinction risk (Schluter 2000; Rabosky & Lovette 2008b; Pigot *et al.* 2010). This diversity-dependent effect is the evolutionary analogue of MacArthur and Wilson’s model of island biogeography, in which the immigration rate (as opposed to speciation) decreases and the extinction rate increases as the number of species on an island increases (MacArthur & Wilson 1963).

Directly testing the hypothesis that speciation rates decrease or that extinction rates increase as species pile-up necessitates the consideration of models in which speciation and extinction rates depend on the number of species alive at a given point in time (Nee *et al.* 1992; Rabosky & Lovette 2008b; Etienne

Box 2 Statistical approaches for comparing alternative models of diversification

Answering key questions about diversification using phylogenetic data often relies on comparing various models and selecting the one that best describes the data. For convenience, the phylogenetic data may be summarised by lineage-through-time plots (Fig. 2d) or summary statistics. Summary statistics are indices that capture the main properties of phylogenetic trees, that is, characteristics of their branching times (Fig. 2a), such as the γ statistic (Pybus & Harvey 2000) or topology (Fig. 2g).

Although fits to lineage-through-time plots or analyses based on summary statistics are still widely used, more powerful likelihood-based approaches are preferred when available. Indeed, alternative diversification scenarios can produce phylogenies with very similar shapes, meaning that using the most powerful statistical approaches (i.e. likelihood approaches) is crucial. Likelihood approaches consist of computing the probability of the observed data – in practice, a reconstructed phylogeny – given a model and a set of parameters, such as speciation and extinction rates. Models for which likelihoods are available can easily be compared to one another, provided consistent conditioning conditions and normalisation factors have been used for the likelihood computation (Stadler 2013b). Once normalised, likelihoods can be compared using likelihood ratio tests when the models are nested, the Akaike Information Criterion (Burnham & Anderson 2002) when they are not nested, Akaike weights if one wants to evaluate the probability of a model against a set of candidates (Burnham & Anderson 2002; Morlon *et al.* 2010), or Bayes factors when likelihoods are implemented in a Bayesian framework (Silvestro *et al.* 2011).

Analytical likelihood expressions are the most convenient in terms of implementation, computation time and flexibility. When they are not analytically tractable, likelihoods can sometimes be computed using pruning algorithms (Maddison *et al.* 2007; Etienne *et al.* 2012; FitzJohn 2012). Finally, when the likelihoods cannot be computed but the diversification process can be simulated efficiently, approximate bayesian computation (ABC) may be used (Jabot & Chave 2009; Rabosky 2009b). ABC approaches may take a more important role as models of increasing complexity are developed.

Table 1 Models of diversification used for phylogenetic inference

Model properties		Diversification rates										Method and Package (Box 2)	Reference
Extinction	Time variable	Environment dependent	Diversity dependent	Waxing-waning	Protracted speciation	Clade specific	Character dependent	Age dependent	Missing extant data	Required data (Box 1 and Fig. 2)			
Lineage-based <i>non-equilibrium dynamics</i>													
-	-	-	-	-	-	-	-	-	-	Branching times or age and species richness	Likelihood analytic	Yule (1925)	
Yes	-	-	-	-	-	-	-	-	Uniform	Branching times	Likelihood analytic	Nee <i>et al.</i> (1994b)	
Yes	-	-	-	-	-	-	-	-	Taxonomic	Branching times and species richness	Likelihood analytic	Rabosky <i>et al.</i> (2007)	
Yes	-	-	-	-	-	-	-	-	Taxonomic	Age and species richness	Moments analytic	Magallon & Sanderson (2001)	
Yes	-	-	-	-	-	-	-	-	Uniform dispersed clustered	Branching times	Likelihood analytic	Hohna <i>et al.</i> (2011)	
Yes	-	-	-	-	-	-	-	-	Uniform	Branching times and fossils	Likelihood analytic	Stadler (2010)	
Yes	-	-	-	-	-	-	-	-	-	Branching times and fossils	Likelihood analytic	Didier <i>et al.</i> (2012)	
Yes	Yes	-	-	-	-	-	-	-	-	Branching times	Likelihood analytic	Rabosky & Lovette (2008a)	
-	Discrete shifts	-	-	-	-	-	-	-	-	Branching times	Likelihood analytic	Rabosky (2006)	
Yes	Yes	-	-	Yes	-	Yes	-	-	Uniform clade specific	Branching times	Likelihood analytic	Morlon <i>et al.</i> (2011a)	
Yes + mass extinction	Discrete shifts	-	-	Yes	-	-	-	-	Uniform	Branching times	Likelihood analytic	Stadler (2011)	
Yes + mass extinction	Yes	-	-	Yes	-	-	-	-	Uniform	Branching times	Likelihood analytic	Hallinan (2012)	
Yes	Yes	-	-	-	-	Yes	-	-	Uniform clade specific	Branching times	Likelihood analytic	Silvestro <i>et al.</i> (2011)	
Yes	Yes	Yes	-	Yes	-	Yes	-	-	Uniform clade specific	Branching times and palaeoenvironmental data	Likelihood analytic	Condamine <i>et al.</i> (2013)	

(continued)

Table 1. (continued)

Model properties												
Diversification rates												
Extinction	Time variable	Environment dependent	Diversity dependent	Waxing-waning	Protracted speciation	Clade specific	Character dependent	Age dependent	Missing extant data	Required data (Box 1 and Fig. 2)	Method and Package (Box 2)	Reference
-	-	-	Diverse-dependent speciation	-	-	-	-	-	-	Branching times	Likelihood analytic <i>Laser</i>	Rabosky & Lovette (2008b)
Yes	-	-	Diverse-dependent speciation and/or extinction	-	-	-	-	-	Uniform	Branching times	Likelihood algorithmic <i>DDD</i>	Etienne <i>et al.</i> (2012)
Yes	-	-	Diversity-dependent speciation and/or extinction	-	-	Yes	-	-	Uniform clade specific	Branching times	Likelihood algorithmic <i>DDD</i>	Etienne & Haegeman (2012)
-	-	-	-	-	Yes	-	-	-	-	Branching times	Likelihood analytic	Etienne & Rosindell (2012)
Yes	Yes	-	-	Yes	Yes	-	-	-	Uniform	Branching times	Likelihood analytic	Lambert <i>et al.</i> (2013)
Yes	-	-	-	-	-	Yes	-	-	Taxonomic	Branching times and species richness	Likelihood analytic <i>Laser Geiger</i>	Rabosky <i>et al.</i> (2007) and Alfaro <i>et al.</i> (2009)
Yes	-	-	-	-	-	-	Anagenetic binary state	-	-	Phylogeny and traits	Likelihood algorithmic <i>Diversitree</i> (<i>BISSE</i>)	Maddison <i>et al.</i> (2007)
Yes	Yes	-	-	Yes	-	Yes	Anagenetic binary states multiple characters	-	Uniform taxonomic	Phylogeny and traits	Likelihood algorithmic <i>Diversitree</i> (<i>BISSE</i>)	FitzJohn 2012;
Yes	Yes	-	-	Yes	-	Yes	Anagenetic binary states multiple characters	-	Uniform taxonomic	Phylogeny and traits	Likelihood algorithmic <i>Diversitree</i> (<i>MUSSE</i>)	FitzJohn (2012)
Yes	-	-	-	-	-	Yes	Anagenetic quantitative traits	-	Uniform	Phylogeny and traits	Likelihood algorithmic <i>Diversitree</i> (<i>QUASSE</i>)	FitzJohn 2012;
Yes	-	-	-	-	-	-	Anagenetic + cladogenetic binary state	-	Uniform taxonomic	Phylogeny and traits	Likelihood algorithmic <i>Diversitree</i> (<i>BISS-ness</i>)	Magnuson-Ford & Otto (2012)
Yes	-	-	-	-	-	-	Anagenetic + cladogenetic multiple states	-	Uniform	Phylogeny and traits	Likelihood algorithmic <i>Diversitree</i> <i>CLASSE</i>	Goldberg & Igić (2012)

(continued)

Table 1. (continued)

Model properties												
Diversification rates												
Extinction	Time variable	Environment dependent	Diversity dependent	Waxing-waning	Protracted speciation	Clade specific	Character dependent	Age dependent	Missing extant data	Required data (Box 1 and Fig. 2)	Method and Package (Box 2)	Reference
Yes	-	-	-	-	-	-	Geographic	-	Uniform	Phylogeny and geographical location	Likelihood algorithmic <i>Diversitree</i> (GeoSSE)	Goldberg <i>et al.</i> (2011)
-	Yes	-	-	-	-	-	-	Yes	-	Branch-length distribution	Analytic	Venditti <i>et al.</i> (2010)
Yes	-	-	-	-	-	-	-	Yes	-	Topology	Likelihood analytic	Keller-Schmidt <i>et al.</i> (2010)
Lineage-based <i>Equilibrium dynamics</i>												
Yes	-	-	-	-	-	-	-	-	-	Branching times	Likelihood analytic	Hey (1992)
Heritable extinction	Discrete shift	-	-	-	-	-	-	-	-	Branching times	<i>R code Morlon</i> Approximate Bayesian Computation	Rabosky (2009b)
Yes	Yes	-	-	-	-	-	-	-	Uniform	Branching times	Likelihood analytic <i>R code Morlon</i>	Morlon <i>et al.</i> (2010)
Individual-based <i>Neutral model</i>												
Yes	Yes	-	-	-	-	-	-	-	-	Topology and species abundance distribution	Approximate Bayesian Computation <i>R code Jabot</i>	Jaboyt & Chave (2009)

Each row in the table corresponds to a model of diversification. Columns specify the properties of the model, the data required for application of the model (Box 1 and Fig. 2), the statistical method used (Box 2) and reference to the original publication. The properties of the models follow the description from the main text. (-) indicates that the model does not accommodate the corresponding property (e.g., the model does not include extinction). The grey filling indicates that the model accommodates the corresponding property.

& Haegeman 2012; Etienne *et al.* 2012). In the absence of extinction, an analytical form of the likelihood of phylogenetic branching times can easily be derived (Rabosky & Lovette 2008b). In the presence of extinction, the likelihood can be computed using a pruning algorithm (Etienne & Haegeman 2012). In both cases, any functional form for the dependence of diversification rates on the number of species may be used, such as a linear or exponential variation in speciation and/or extinction rates as the number of species increase.

Model 5 – Equilibrium diversity

Under MacArthur and Wilson's model (1963), diversity reaches a 'dynamic equilibrium' where immigration and

extinction are balanced. Similarly, when *in situ* speciation (as opposed to immigration) plays a key role in the assembly of biotas, clades undergoing diversity-dependent diversification may eventually reach an equilibrium diversity, or 'diversity limit' (Raup *et al.* 1973; Hey 1992; Rabosky & Lovette 2008b; Rabosky 2009b; Morlon *et al.* 2010; Rabosky & Glor 2010; Etienne *et al.* 2012). This diversity limit is sometimes coined 'carrying capacity' and denoted K by analogy with terminology used in population dynamics.

The role of diversity limits and equilibrium processes in shaping patterns of species richness has mainly been analysed using diversity-dependent models (Model 4, Rabosky & Lovette 2008b; Etienne *et al.* 2012). This is a natural and useful approach. However, if hard limits on species diversity truly

Box 3 Can extinction rates and diversity declines be estimated using reconstructed phylogenies?

Nee *et al.* (1994a) wrote a paper entitled 'Extinction rates can be estimated from molecular phylogenies'. Two papers followed, one entitled 'Can extinction rates be estimated without fossils?' (Paradis 2004) and the other one 'Extinction rates should not be estimated from molecular phylogenies' (Rabosky 2010) both of which casted doubts on the possibility of estimating extinction rates from phylogenetic data (see also Kubo & Iwasa 1995). Finally, in a paper entitled 'Diversity dynamics: molecular phylogenies need the fossil record', Quental & Marshall (2010) argued that neither extinction rates, speciation rates, nor diversity declines can be properly estimated with only the molecular phylogenies of extant taxa. This box clarifies this debate.

First, although it might seem counterintuitive, extinction rates can in theory be estimated from reconstructed phylogenies (Nee *et al.* 1994a,b). Although a reconstructed phylogeny lacks all extinct species, branching times expected under a birth–death process are distinct from those expected under a pure birth process. This is well illustrated by the shape of lineage-through-time plots, which is linear under a pure birth process but curving upwards in the presence of extinction, a phenomenon known as the 'pull-of-the-present' (Nee *et al.* 1994a,b). Extinction rates can in principle be estimated using this upturn (Nee *et al.* 1994a,b; Ricklefs 2007). They can also be estimated from the likelihood of branching times, which has been confirmed by simulations (Paradis 2004; Morlon *et al.* 2010, 2011a).

Similarly, diversity declines over time can in theory be detected from reconstructed phylogenies. This is even more counterintuitive because the number of lineages in reconstructed phylogenies always increases (Ricklefs 2007; Quental & Marshall 2010; Wiens 2011). However, diversity declines leave distinctive branch-length patterns in reconstructed phylogenies, and simulations coupled with likelihood approaches have shown that diversity dynamics that include scenarios featuring periods of diversity decline can be accurately inferred (Morlon *et al.* 2011a).

Although theory and simulations show that extinction rates and diversity declines can be estimated from reconstructed phylogenies, this has proved difficult in practice. Instead of curving upward, empirical LTT plots tend to level off towards the present, and extinction rates estimated using likelihood approaches typically approach zero (Purvis 2008; Rabosky & Lovette 2008a). This is inconsistent with what we know from the fossil record, where extinctions are frequent (Foote *et al.* 2007; Quental & Marshall 2010, 2013; Pyron & Burbrink 2012). This bias in the estimation of extinction rates arises from deviations from the underlying model assumptions, for example, when the underlying assumption of rate homogeneity is violated (Rabosky 2010; Morlon *et al.* 2011a). This is problematic given that empirical data always violate theoretical models to some extent; however, it also means that proper estimates of extinction rates and diversity trajectories can be derived if a good enough model is used.

In particular, diversity declines have been recovered from empirical phylogenies provided rate heterogeneity across lineages was accounted for (Morlon *et al.* 2011a). Accounting for rate heterogeneity required defining subclades hypothesised to follow their own diversity dynamics, different from that of the parent clade. In that particular study, subclades were defined based on taxonomy. To the extent that taxonomic groups represent groups with similar ecology and thus potentially comparable diversity dynamics, this partitioning provides a good first approach. Subclades could also be defined based on approaches for detecting clade-specific diversification (Model 8), for example, stepwise approaches similar to the one used in time-constant diversification models (Alfaro *et al.* 2009).

Conservation biologists probably want to know whether we can estimate human-driven extinction rates from reconstructed phylogenies. This is fundamentally different from estimating background extinction rates: on the scale of a phylogeny, recent or current extinctions are equivalent to a random (not necessarily uniform) sampling of the phylogeny at present. Regardless of whether anthropogenic extinction is uniform or not across the phylogeny, recent and current human-driven extinction rates cannot be estimated because sampling fractions (i.e. the fraction of extant species actually represented in the phylogeny) cannot be estimated from a reconstructed phylogeny (Morlon *et al.* 2010; Stadler 2013b). What can be estimated, however (bearing in mind the limitations highlighted above), are background extinction rates at present. To what extent these may be correlated with current extinction risks remains to be explored (Rolland *et al.* 2012; Condamine *et al.* 2013).

exist and operate on long time scales, the time spanned by the phylogenies we observe today may correspond to periods of equilibrium diversity rather than periods of diversity-dependent expansion (Fig. 1b). In addition, in diversity-dependent models at equilibrium, species turnover (i.e. the rate of species replacement) is fixed to $\lambda(K) = \mu(K)$, yet there is no *a priori* reason to expect that species turnover should be constant through time once a diversity limit has been reached. Species turnover may, for example, depend on environmental stability and/or experience periods of ‘turnover pulses’ (Rabosky 2009b).

Hey (1992) first proposed a model reproducing a scenario of strict equilibrium diversity: each extinction event is immediately followed by a speciation event, such that species richness remains constant over time (Fig. 1b, Hey 1992; Morlon *et al.* 2010). This differs from all models described so far, in which speciation and extinction events are decoupled, such that the total number of species varies stochastically over time (Fig. 1a and c, Nee *et al.* 1994a,b; Rabosky & Lovette 2008a,b; Stadler 2011; Morlon *et al.* 2011a). This model is not helpful for understanding a clade’s expansion because species richness is fixed over time. The model is, however, particularly relevant if clade’s expansion preceded the time spanned by the phylogeny (Fig. 1b), or happened early in this time period, as considered, for example, in Liow *et al.* (2010).

In Hey’s equilibrium model (1992), the turnover rate is constant over time. Morlon *et al.* (2010) extended this model to the case when the turnover rate varies over time. The authors derived a likelihood expression for phylogenetic branching times under this equilibrium model, as well as a comparable likelihood expression for non-equilibrium models. These developments provide a robust phylogenetic test of the hypothesis that diversity is at equilibrium, as well as a means to estimate species’ turnover and how it varies through time.

Model 6 – Waxing and waning of diversity

We know from the fossil record that clades wax and wane, that is clades decline in diversity after periods of expansion (Foote *et al.* 2007; Quental & Marshall 2010, 2013; Pyron & Burbrink 2012). Such waxing–waning diversity dynamics can easily be represented by time-varying models: any model with positive net diversification rate (i.e. more frequent speciation

than extinction) at the beginning of clade’s history followed by negative net diversification rate (i.e. more frequent extinction than speciation) will generate waxing–waning diversity dynamics (Fig. 1c). This happens if speciation rates decrease below extinction rates, extinction rates increase above speciation rates, or a combination of both.

Waxing–waning dynamics have not often been considered in phylogenetic analyses, because reconstructed phylogenies give the (potentially false) impression that species richness increases through time. As a consequence, inferring diversity declines from phylogenetic data alone has long been deemed impossible (Box 3) (Ricklefs 2007; Quental & Marshall 2010; Wiens 2011). Although inferring diversity declines remains a challenge that requires accounting for among-clade rate heterogeneity (Box 3), likelihood expressions corresponding to waxing–waning dynamics can be obtained from time-variable derivations (Nee *et al.* 1994b; Morlon *et al.* 2011a; Stadler 2011), and waxing–waning dynamics have been recovered from reconstructed phylogenies (Morlon *et al.* 2011a).

Model 7 – Protracted speciation

In species-based models, speciation is typically modelled as an instantaneous event. In reality, speciation requires reproductive isolation and may take several million years to complete (Avice *et al.* 1998). The duration of speciation (and its biogeographical correlates) can have a significant impact on species richness patterns such as the latitudinal diversity gradient (Weir & Schluter 2007). Accounting for the duration of speciation, or ‘protracted speciation’, substantially modifies the expected shape of reconstructed phylogenies (Purvis *et al.* 2009; Etienne & Rosindell 2012). The original derivation of likelihood expressions for phylogenetic trees under protracted speciation corresponded only to pure birth (no extinction) models (Etienne & Rosindell 2012); they have now been extended to include extinction (Lambert *et al.* 2013).

Model 8 – Clade-specific diversification

The difference in species richness across groups of organisms is often too large to be explained solely by stochastically driven variation. Detecting rate shifts, that is specific subclades

Box 4 Estimating diversity curves

While phylogenetic approaches to diversification focus on diversification rates, one might be interested in diversity itself and how it has varied through time. Historically, palaeobiologists have reported estimates of number of species or genera over geological time scales to identify periods of diversity expansion, decline or stability, and to test hypotheses about what controls diversity dynamics (Raup *et al.* 1973; Foote *et al.* 2007; Ezard *et al.* 2011). Similarly, diversity curves corresponding to various diversification scenarios may be reconstructed from phylogenetic information.

Under a birth–death model with parameters $\lambda(t)$ and $\mu(t)$ varying through time, the expected number of species at time t follows the differential equation $\frac{dN(t)}{dt} = [-\lambda(t) + \mu(t)]N(t)$ (time is measured from the present to the past). Imposing the condition $N(t) = N_0$, where N_0 is the present-day species richness of the clade, we find $N(t) = N_0 e^{\int_0^t (-\lambda(s) + \mu(s)) ds}$ which can be computed analytically or numerically depending on the functional forms of $\lambda(t)$ and $\mu(t)$ (see Morlon *et al.* 2010 for various examples and Morlon *et al.* 2011a for applications). It is also possible to compute diversity curves algorithmically under the diversity-dependent model of Etienne *et al.* (2012). These approaches have been used, for example, to compare diversity curves obtained from phylogenetic data to those obtained from the fossil record (Morlon *et al.* 2011a; Etienne *et al.* 2012).

in which diversification has been ‘abnormally’ fast or ‘abnormally’ slow, can help in understanding the potential causes of this heterogeneity. Rate shifts can be detected using clade richness distributions (Fig. 2c), tree topology (Fig. 2g) (Chan & Moore 2002) or branch-length distributions (Fig. 2e) (Shah *et al.* 2013). Two types of likelihood expressions are also available: the first assumes constant rates within subclades and can handle combined phylogenetic and species richness data (Fig. 2c) (Rabosky *et al.* 2007; Alfaro *et al.* 2009); the second necessitates species-level phylogenies (Fig. 2a) and allows time variation (Morlon *et al.* 2011a) or diversity dependence (Etienne & Haegeman 2012) within subclades.

These approaches of detecting rate shifts on phylogenetic trees do not require formulating an *a priori* hypothesis of why diversification rates vary across lineages. *A posteriori*, one can try to associate these shifts with specific events, including the colonisation of new geographical areas or the acquisition of new traits giving access to unexplored adaptive zones.

Model 9 – Character-dependent diversification

If there are *a priori* reasons to believe that specific characters (e.g. life-history or morphological traits, geographical locations) influence diversification, one can test for a correlation between the diversification rate and an ‘average’ trait of individual clades (Slowinski & Guyer 1993). Such an average may be obtained by taking a mean of trait values across extant species, or better an average over the full history of the clade based on ancestral trait values. However, ancestral reconstruction can be misleading when the potential impact of the trait on the diversification process is ignored (Maddison 2006). Recently developed approaches that directly model trait evolution and its impact on diversification are now available that are better suited to the problem.

In character-dependent diversification models, lineages are characterised by an evolving trait; they follow a birth–death process, in which speciation and extinction rates at any given time depend on the value of the trait at that time (Maddison *et al.* 2007; Goldberg *et al.* 2011; FitzJohn 2012; Goldberg & Igić 2012; Magnuson-Ford & Otto 2012). Given a phylogenetic tree and trait values characterising the extant species (Fig. 2a and c), likelihood values for these models can be computed using a pruning algorithm (Maddison *et al.* 2007).

Various versions of character-dependent diversification models exist, depending on whether the trait is discrete with two states, discrete with more than two states, or continuous (FitzJohn 2012), and depending on whether traits evolve only along phylogenetic branches (anagenesis), or also at cladogenetic events (i.e. speciation) (Goldberg *et al.* 2011; Goldberg & Igić 2012; Magnuson-Ford & Otto 2012). In all these models, diversification rates can depend on time in addition to the character state (Rabosky & Glor 2010; FitzJohn 2012).

Model 10 – Age dependence

A specific character that may influence species’ rates of speciation and extinction is their age: species may be more or less likely to go extinct or speciate the older they get (reviewed in Mooers *et al.* 2007). Species age is a non-inherited determinis-

tic trait, and thus cannot be modelled as a trait evolving stochastically along phylogenetic branches, as is done in the character-dependent approaches detailed above. Statistical tests of the age-dependent model are rare. The pure birth process with age-dependent speciation rate has been analysed in terms of topology (Fig. 2g) (Keller-Schmidt *et al.* 2010) and branch-length distribution (Fig. 2e) (Venditti *et al.* 2010). Likelihoods associated with branching times (Fig. 2a), however, are not yet available. A recent approach that allows computing likelihoods for a birth–death model with age-dependent death rates will soon be implemented (Lambert, personal communication).

Model 11 – The Neutral Theory of Biodiversity

The Neutral Theory of Biodiversity (NTB) of Hubbell (2001) is an individual-based model, in which two principal hypotheses are a metacommunity of constant size (often referred to as the zero-sum assumption) and an ecological equivalence between individuals (the neutrality assumption). When an individual dies in the metacommunity, with probability v , this individual is replaced by an individual from an entirely new species; that is, there is a speciation event (this form of speciation is typically referred to as the ‘point mutation’ mode of speciation, and v is the per individual speciation rate). Alternatively, with probability $1 - v$ the individual is replaced by an offspring from the metacommunity. Hence, each individual has at each time step an equal probability of giving rise to an entirely new species, and the probability for a species speciating is proportional to its abundance in the metacommunity. In the classic continent–island model, local communities (islands) are assembled through dispersal from the metacommunity (the continent); hence speciation happens in the metacommunity but not local communities; that is, there is no *in situ* speciation.

Several variations around this model exist, including models with a random fission mode of speciation (Davies *et al.* 2011), incipient species with abundance greater than one (Davies *et al.* 2011), protracted speciation (Rosindell *et al.* 2010) and *in situ* speciation (Rosindell & Phillimore 2011). The NTB yields predictions for phylogenetic patterns (Hubbell 2001; Jabot & Chave 2009; Davies *et al.* 2011). In particular, Jabot & Chave (2009) developed an Approximate Bayesian Computation approach (Box 2) that allows fitting the model to the topology of local phylogenies and associated local abundance (Fig. 2g). To date, the neutral model is the only model constructed at the level of individuals from which phylogenetic predictions have been analysed and that can be fitted to empirical data.

Model 12 – Geographical speciation

Pigot *et al.* (2010) developed another type of neutral model, a spatially explicit model that considers the geographical context of speciation and extinction. This model allows one to account for the fact that geographical isolation, which reduces gene flow between populations, often is an essential element of speciation. The authors did not consider individuals and their dynamics *per se*, but instead considered species range dynamics. Range boundaries evolve under a Brownian pro-

cess; extinction arises when range size drifts to zero, and speciation arises via vicariance or peripatry. In the vicariance scenario, geographical barriers are modelled by randomly dropping line segments onto the geographical space, and speciation happens whenever the geographical barrier splits a species's range. In the peripatric scenario, colonists disperse with a rate proportional to the perimeter (or area) of the range, and dispersal leads to speciation. Simulation analyses have revealed that the model can reproduce the range of topologies and branching times typically found in nature (Pigot *et al.* 2010). Approaches for fitting the model to data remain to be developed.

Model 13 – Ecological differentiation

McPeck (2008) proposed a metacommunity model covering speciation dynamics ranging from ecological equivalence (or neutrality) to ecological divergence. In this model, each patch in the metacommunity occupies a random position along an environmental gradient, and each species is characterised by its optimal position on the gradient. The dynamics of a given species in a given patch follows a logistic equation in which carrying capacity decreases as the species gets further away from its optimal position on the gradient. New species arise at a constant per-species rate with small abundances in each patch, and their characteristic (i.e. their optimal position on the gradient) is determined by a normal deviation from that of their progenitor. The magnitude of the deviation reflects the degree of ecological differentiation at the time of speciation. This model can reproduce the range of branching times typically found in nature (McPeck 2008); approaches for fitting this model to data remain to be developed.

EMPIRICAL TRENDS

Models of diversification are used to test various hypotheses about diversification and to estimate biologically relevant parameters such as speciation and extinction rates. Which models are supported and what have we learned from these various analyses?

Empirical pattern 1 – Diversification often slows down over time

There is extensive empirical evidence for significant deviations from the hypothesis of time constancy in diversification rates (i.e. deviations from Model 1). Empirical phylogenies tend to be more 'stemmy' (i.e. nodes accumulate early in the history of the clade) than phylogenies arising from constant rate birth–death models, which tend to be 'tippy' (i.e. nodes accumulate towards the present). As a result, empirical LTT plots typically do not display the pull of the present expected under a constant rate birth–death process (Box 3). The tendency of phylogenies to be stemmy can be measured with a summary statistic called γ , which takes negative values when phylogenies are more stemmy than expected under a constant rate pure birth model (Pybus & Harvey 2000). Phylogenies with negative γ values are prevalent in nature, suggesting that speciation rates decline through clades' histories (McPeck 2008; Phillimore & Price 2008).

Fits of time-variable models (Model 2) to empirical phylogenies have confirmed the ubiquity of this pattern: models with time-variable speciation rates are in general supported in comparison with time-constant models, and the trend is for a decline in speciation rates (Rabosky & Lovette 2008a; Morlon *et al.* 2010). This decline in speciation rate over time has often been interpreted as a diversity-dependent effect resulting from a saturation of niche space following adaptive radiations (Phillimore & Price 2008; Rabosky & Lovette 2008a; Etienne & Haegeman 2012), although various alternative biological and methodological explanations have recently been proposed (Moen & Morlon in press).

The consistent tendency for time declines in speciation rates was primarily reported for phylogenies representing 'small' clades (e.g. at or around the genus or family level, Phillimore & Price 2008; McPeck 2008; Rabosky & Lovette 2008a,b; Morlon *et al.* 2010). As phylogenies are constructed at much larger taxonomic scales, for example, for entire classes in the case of mammals (Bininda-Emonds *et al.* 2007) and birds (Jetz *et al.* 2012), new patterns emerge that suggest that the ubiquity of time declines does not hold at all taxonomic scales. For example, analysis of a phylogeny of all extant birds suggests an increase in diversification rates through time (Jetz *et al.* 2012). Understanding at which taxonomic scales rate declines are observed, and why, remains an avenue for future research.

Empirical pattern 2 – Diversification may (or may not) be diversity dependent

The recurrent signal of time decline in speciation rate across the tree of life (Empirical pattern 1) has often been interpreted in terms of diversity dependence, whereby speciation rates decline as species pile up (McPeck 2008; Phillimore & Price 2008; Rabosky & Lovette 2008a). However, fits of truly diversity-dependent models (Model 4) – as opposed to analyses based on the γ statistic (McPeck 2008; Phillimore & Price 2008) or on time-dependent models (Model 2) (Rabosky & Lovette 2008a) – remain scarce.

Even when true diversity-dependent models have been used (Rabosky & Lovette 2008b; Etienne & Haegeman 2012; Etienne *et al.* 2012), conclusions stemming from these analyses may be called into question (Moen & Morlon in press). Rabosky & Lovette (2008b) found support for pure-birth diversity-dependent models when compared to models with linear time decline in *Dendroica* warblers, but there is no guarantee that other forms of the time dependence would not actually provide a better fit. Etienne *et al.* (2012) found support for birth–death diversity-dependent models, but at least for one of the data sets they studied (the cetaceans), both the fossil record and time-dependent phylogenetic models suggest that species diversity in this group conforms to a waxing–waning curve rather than the logistic-like curve expected under diversity-dependent dynamics (Quental & Marshall 2010; Morlon *et al.* 2011a).

Empirical pattern 3 – Diversification may (or may not) be adaptive

Time declines in speciation rates have been interpreted not only as a signal of diversity dependence but also as a signal of ecological speciation and adaptive radiations (Schluter 2000;

McPeck 2008; Phillimore & Price 2008; Rabosky & Lovette 2008a,b). Under this hypothesis, speciation rates decline as species fill niche space, reducing ecological opportunities. This interpretation is disputable (Moen & Morlon in press). For example, slowdowns have often been detected in clades with complex biogeography, in which species are not co-occurring and thus not competing for niche space (McPeck 2008; Phillimore & Price 2008). In this case, it seems that other explanations for diversification slowdowns are needed. Recent studies have shown that geographical speciation (Model 12), environment-driven bursts of speciation (Model 3), declining diversity (Model 6) and protracted speciation (Model 7) can explain the shape of empirical trees, without invoking ecological differentiation between species (Moen & Morlon in press).

Empirical pattern 4 – Diversity does not follow long-term equilibrium dynamics

Under diversity-dependent diversification, clades are typically headed to equilibrium dynamics. They will eventually reach an upper bound in species richness, commonly referred to as ‘carrying capacity’ by analogy with population dynamics (Rabosky & Lovette 2008b; Etienne & Haegeman 2012; Etienne *et al.* 2012). This upper bound may be determined by the amount of space available to species, the number of niches they can occupy, or the total number of individuals in the clade. Macroecological studies that aim to explain levels of species richness (e.g. across latitudes) by current environmental correlates such as temperature, productivity or geographical area implicitly assume that species richness has reached a carrying capacity imposed by these ecological limits and has then followed long-term equilibrium dynamics.

However, even if diversity-dependent diversification is widespread, clades may not follow long-term equilibrium dynamics. First, clades may be too young to have reached an equilibrium, or they may have reached this equilibrium only recently (Rabosky & Glor 2010); second, equilibrium dynamics may never be achieved if the carrying capacity changes over time, for example, as a response to changing environmental conditions (Quental & Marshall 2013). Phylogenetic tests of equilibrium diversity models (Model 5) suggest that the time spanned by phylogenies typically does not correspond to equilibrium dynamics (Hey 1992; Mooers *et al.* 2007; Morlon *et al.* 2010). Indeed, LTT plots corresponding to Hey’s model are not realistic (Hey 1992); while they are more so when turnover rates are allowed to vary through time, equilibrium models remain typically less likely than birth–death models (Morlon *et al.* 2010, 2012). Hence, the species richness we see today likely does not result from long-term equilibrium dynamics.

Empirical pattern 5 – Many clades may be declining in diversity

Diversification slowdowns may lead to speciation rates falling below extinction rates, or equivalently extinction rates increasing above speciation rates, ultimately leading to diversity declines rather than equilibrium dynamics. Diversity declines are widespread in the fossil record (Foote *et al.* 2007;

Quental & Marshall 2010, 2013; Pyron & Burbrink 2012), and there is increasing evidence that many phylogenetic patterns currently interpreted as a signature of diversity dependence and ecological limits may in fact correspond to diversity declines (Quental & Marshall 2010; Pyron & Burbrink 2012). Further empirical applications of waxing–waning models (Model 6) (Morlon *et al.* 2011a; Pyron & Burbrink 2012) are clearly needed.

Empirical pattern 6 – Diversification is generally not homogeneous across lineages

There is empirical evidence for wide deviations from the hypothesis of rate homogeneity across lineages. Equal rates model (i.e. Model 1) typically produces phylogenies more balanced than empirical trees; that is, the sizes of model sister clades tend to be more similar than in nature (Mooers & Heard 1997). Fits of clade-specific diversification models (Model 8) to empirical phylogenies have confirmed heterogeneities in the speed at which species diversify: models with multiple shifts in diversification rates at the base of some clades are typically supported in comparison with equal rate models, corresponding to both acceleration and slowdowns in diversification (Rabosky *et al.* 2007; Alfaro *et al.* 2009; Morlon *et al.* 2011a; Jetz *et al.* 2012). Accounting for rate heterogeneity is crucial to obtain meaningful estimates of diversification rates (Rabosky 2010; Morlon *et al.* 2011a). Indeed, extinction rate estimates can be drastically inflated (Rabosky 2010) or deflated (Morlon *et al.* 2011a) when rate heterogeneity is not accounted for.

The finding that diversification rates vary widely from one clade to the other is often interpreted in terms of species selection and ecological differences across clades, and has encouraged the search for ecological correlates of diversification (see Empirical pattern 8). This interpretation should be taken with caution, however; neutral models such as the NTB of Hubbell (2001) and the geographical speciation model of Pigot *et al.* (2010) can indeed both generate trees with as much imbalance as empirical trees (Empirical pattern 7) (Jabot & Chave 2009; Pigot *et al.* 2010; Davies *et al.* 2011).

Empirical pattern 7 – Neutral models can reproduce some observed shapes of phylogenetic trees

Neutral models, which assume an ecological equivalence among species, can generate trees with levels of imbalance in agreement with empirical trees (Jabot & Chave 2009; Pigot *et al.* 2010; Davies *et al.* 2011). In Hubbell’s NTB model with the point mutation or fission mode of speciation (Model 11), phylogenetic imbalance arises from stochastically driven differences in population sizes because the probability for a species to diversify is proportional to its population size (Jabot & Chave 2009; Davies *et al.* 2011). The protracted version of this model (Rosindell *et al.* 2010) should maintain this property, although this has not yet been directly tested.

Simulations suggest that Hubbell’s neutral model with point mutation or fission mode of speciation generate phylogenetic trees that are much more tipy than empirical trees, and thus

fails to explain empirical branching times (Davies *et al.* 2011). By accounting for the fact that speciation takes time to complete, the protracted version of this model (Rosindell *et al.* 2010) generates trees which branch-length pattern in the recent past is closer to empirically observed patterns (Etienne & Rosindell 2012). However, preliminary simulation studies suggest that protractedness is not enough to obtain realistic branch-length patterns over the full length of phylogenetic trees (J. Rosindell & R. S Etienne, pers. comm.).

The results detailed above pertain to neutral equilibrium dynamics. There are reasons to believe that a non-equilibrium version of the model would lead to realistic branching times. For example, the model of Pigot *et al.* (2010, Model 12) generates trees with realistic branching times, and this model is also neutral and has a geographical formulation that leads to dynamics of population sizes, speciation and extinction similar to Hubbell's neutral model. This is explained by non-equilibrium dynamics whereby a rapid decline in species' average range size at the beginning of clades' history results in a reduction in speciation rates through time. A non-equilibrium version of Hubbell's model initiated with a single abundant species would similarly result in a rapid decline in species' average population size that would induce a slowdown in speciation rate and lead to realistic branching times in phylogenies.

That neutral models can generate trees similar to empirical trees does not imply that empirical trees were generated by neutral processes. Rather, it implies that a phylogenetic tree alone typically does not contain enough information to evaluate the effect of species differentiation on diversification; additional information, for example, linked to the species characteristics, is needed to understand the importance of species' ecological differences in driving differences in diversification rates (Empirical pattern 8).

Empirical pattern 8 – Both biotic and abiotic factors influence long-term diversity dynamics

The factors influencing diversification have been analysed through the paradigm of the Red Queen and Court Jester hypotheses respectively, referring to biotic and abiotic drivers (Benton 2009). Analysing the influence of biotic and abiotic factors on diversification typically requires palaeoenvironmental or trait data in addition to a phylogenetic tree.

Empirical applications of the environmental model (Model 3) (Condamine *et al.* 2013) – which allows an analysis of the influence of abiotic and biotic palaeoenvironmental conditions on diversification – remain to be explored (see Cantalapiedra *et al.* 2013), but previous fossil analyses suggest that environmental conditions have had a strong influence on diversity dynamics (Ezard *et al.* 2011).

Empirical applications of character-dependent diversification models (Model 9) (Maddison *et al.* 2007; FitzJohn 2012) have shown that diversification rates vary as a function of both intrinsic factors, such as species' mode of reproduction (Goldberg & Igić 2012) or diet (Price *et al.* 2012), and extrinsic factors, such as geography (Rabosky & Glor 2010; Goldberg *et al.* 2011; Rolland *et al.* 2014). Such questions had traditionally been analysed at small temporal and taxonomic scales,

and character-dependent diversification analyses have allowed the expansion of their scope by evaluating the long-term effect of species characteristics on the tempo of diversification of whole clades (but see Davis *et al.* 2013 for limitations). Overall, these analyses have demonstrated a major role of species' ecology on long-term diversity dynamics.

EXPANDING THE SCOPE OF PHYLOGENETIC APPROACHES TO DIVERSIFICATION

The set of available models to study diversification has drastically expanded in the last few years. Below, I discuss the limited performance and identifiability of these models, as well as potential avenues for improvement. I highlight future directions at the interface with ecological research, focusing on unified models, phylogenetic community ecology and species interaction networks. Diversification models also have applications in conservation research that have already been detailed elsewhere (Rolland *et al.* 2012; Condamine *et al.* 2013; see also Box 3).

Developing unified diversification models

The quest for unified models is central to ecological research (McGill 2010). Interestingly, of the 10 'unified theories of ecology' identified by McGill (2010), only one – the neutral theory of biodiversity – incorporates diversification. Given that this specific theory ignores adaptive diversification and species interactions, it seems that a lot of work remains to be done in this direction. A first step would consist in unifying diversification models. The current approach consists in selecting the 'best' diversification model out of a set. This yields an oversimplified view of diversification in which a single process, such as environmental or diversity dependence, supposedly explains clades' evolution (Pyron & Burbrink 2013; Stadler 2013a). To make matters worse, likelihoods for different models available in different packages are not always comparable because different normalisation factors or conditioning have been used (Stadler 2013b). Developing a framework under which models can be meaningfully compared would be a good first step. An even bigger step will consist in integrating different processes, such as environmental dependence, diversity dependence, protracted speciation, character dependence, geographical speciation and ecological differentiation, into a single unified model. Finally, the Holy Grail would be to connect this unified diversification model with unified models stemming from ecology. This might shift the current focus in ecology on equilibrium biodiversity theories (MacArthur & Wilson 1963; Hubbell 2001) to non-equilibrium theories recognising the crucial role of history (Ricklefs & Schluter 1993).

Analysing the performance of diversification models

As models become more inclusive, more complex, and thus also parameter heavy, the question of their performance becomes crucial (Pyron & Burbrink 2013). Yet, compared to the tremendous progress that has been made in the development of new models and techniques for studying diversification, efforts to investigate the individual and comparative

performance of these methods fall short. Davis *et al.* (2013) analysis of character-dependent models (Model 9) is one of the rare examples of a thorough performance analysis. More studies in this direction, as well as a better appreciation of limitations by empiricists, would be highly beneficial (Losos 2011).

Three of the main factors that limit inference are tree size, missing species and phylogenetic uncertainty. Focusing on large trees has drawbacks – such as biasing the study of biodiversity to that of species-rich clades and increasing the odds that the data violates assumptions such as rate homogeneity across lineages – but the analysis of small trees is challenged by limited statistical power. Missing species are problematic not only because they reduce sample size but also because their number is uncertain (Pyron & Burbrink 2013) and because they are typically not uniformly distributed on the tree (Stadler 2013a). Finally, phylogenetic reconstruction is subject to various sources of uncertainties, including topological and dating uncertainties, which directly affect diversification analyses but are rarely accounted for. These various limitations could be better accounted for by systematically reporting confidence intervals around parameter estimates, running diversification analyses on a posterior Bayesian distribution of trees, and testing the robustness of the results to various potential biases. In addition to these precautions, paying particular attention to results arising from phylogenetic analyses is necessary. For example, when an extinction rate of zero is obtained for a clade that obviously has experienced historical extinction, this suggests that the data violate some of the model assumptions strongly enough to put a warning on the confidence we can reasonably put in the results arising from this model, and that more efforts should be made to select a better adapted model (Morlon *et al.* 2011a; Box 3).

A related issue concerns the identifiability of the different models: many diversification models are difficult to distinguish from one another under conditions common to empirical phylogenies. We already know, for example, that neutral models and ecological models can reproduce the shape of phylogenetic trees equally well (McPeck 2008; Pigot *et al.* 2010), and that very different diversification scenarios can have similar likelihood support (Morlon *et al.* 2010). Exploring model identifiability under empirically realistic scenarios is an important avenue for future research. In addition, in a unified inclusive model such as the one proposed above, Bayesian implementations will be needed to sample the full parameter space and to identify alternative combinations of parameters providing a good fit to the data (Silvestro *et al.* 2011; Stadler 2013a).

Integrating phylogenetic data with other sources of data

Ultimately, we will need to increase the power of discrimination among models by developing inferences based on phylogenetic and additional data. The value of such data integration is well illustrated by the numerous insights we have gained from inferences based on joint phylogenetic and trait or geographical data. Most current empirical applications of character-dependent models analyse one character at a time. Applications of multiple trait models (FitzJohn 2012) would further increase our power of inference and would

allow the quantification of the relative importance of various characteristics of species on diversification, in addition to assessing the correlated evolution of these multiple traits (Pennell & Harmon 2013).

Other ecological data, such as abundance, range size, or potentially number of subspecies could be used in combination with phylogenies to increase our statistical power of inference. This will require developing inference tools associated with models constructed at the level of individuals, ranges, or subspecies, as well as collecting or compiling abundance, range size or subspecies data at the global scale. For example, global-scale relative abundances will help distinguishing scenarios of equilibrium vs. non-equilibrium neutral models, whereas relative abundances at the community scale are useful for inferring parameters on the equilibrium neutral model (Jabot & Chave 2009).

The integration of historical (fossil and palaeoenvironmental) data into phylogenetic approaches would greatly improve our inferences, as already detailed in several recent papers (Quental & Marshall 2010; Condamine *et al.* 2013; Fritz *et al.* 2013; Pennell & Harmon 2013; Slater & Harmon 2013; Stadler 2013a). Phylogenetic models that allow the integration of palaeoenvironmental data are now available (Condamine *et al.* 2013). The extent to which such analyses will provide new and important insights depends on the availability of relevant palaeoenvironmental data. Most current palaeoenvironmental reconstructions concern global-scale averages across the Cenozoic (e.g. Zachos *et al.* 2008), but reconstructions in the regions or continents where clades evolved would be more relevant. Deeper time reconstructions would also be particularly useful.

Connecting with phylogenetic community ecology

Phylogenetic community ecology consists in comparing the phylogenetic structure of local communities to random draws from a regional phylogeny (Webb *et al.* 2002; Cavender-Bares *et al.* 2009; Mayfield & Levine 2010). In the absence of a mechanistic model of diversification and community assembly, random draws provide a reasonable set of null local communities with which to compare empirical communities. However, substituting mechanistic models of diversification and community assembly to random draws would improve the approach in at least three ways: first, such models would provide explanations for (and gather information from) the shape of regional phylogenies; second, they could account for the effect of dispersal limitation and thus potentially solve the well-known problem of scale dependence in community phylogenetics (Cavender-Bares *et al.* 2009); third, they would allow a statistically more powerful comparison between expectations and data, for example based on likelihoods rather than on summary statistics such as the phylogenetic diversity of a community. While such models have already started to be considered (Hubbell 2001; McPeck 2008; Stegen *et al.* 2009; Pigot *et al.* 2010), very few have been used to provide predictions for spatial patterns of phylogenetic diversity (Morlon *et al.* 2011b), or sufficiently developed to be fitted to empirical data (Jabot & Chave 2009 is one exception in the context of the neutral theory). Models inspired from island biogeography (Rosindell & Phillimore 2011), the metacommunity framework (McPeck

2008), or the metabolic theory of biodiversity (Stegen *et al.* 2009) could serve as the basis for the development of mechanistic models for phylogenetic community ecology.

Modelling phylogenetic webs of life

Although species evolve and diversify in a complex network of species interactions, current models of diversification typically ignore species interactions. Inference approaches based on joint phylogenetic and species interaction data allow testing the degree to which species interactions are evolutionarily conserved (Ives & Godfray 2006; Rezende *et al.* 2007), but do not allow analysing the effect of species interactions on diversification. This results in a tremendous lack of knowledge concerning the role of natural enemies, mutualism and more generally coevolution in explaining clade diversification (Ricklefs 2010). Along with efforts to collect network and phylogenetic data at larger scales, phylogenetic comparative methods for studying the evolution of interaction networks are needed to analyse these phylogenetic webs of life. Research in this direction has already started, but has so far been focused on trait evolution rather than diversification (Ingram *et al.* 2012).

CONCLUSION

Phylogenies have become a cornerstone of biodiversity research. They will continue to play an increasing role for understanding the ecological processes influencing diversification, dispersal, coexistence and ultimately species richness patterns. Tremendous progress has been made in the last decade in both the development of phylogenetic models for understanding diversification and the integration of phylogenetic biology with ecology. The biggest advance in this ongoing integration may yet have to come, and will rest on our ability to embrace the use of diversification models in community ecology, the science of interaction networks and conservation biology.

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