Diversification in evolutionary arenas – assessment and synthesis

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Abstract

Understanding how and why rates of evolutionary diversification vary is a central issue in evolutionary biology and ecology. The concept of adaptive radiation has attracted much interest, but is metaphorical and verbal in nature, making it difficult to quantitatively compare different evolutionary lineages or geographic regions. In addition, the causes of evolutionary stasis are relatively neglected. Here we review the central concepts in the evolutionary diversification literature and bring these together by proposing a general framework for estimating rates of diversification and quantifying their underlying dynamics, which can be applied across clades and regions and across spatial and temporal scales. Our framework describes the diversification rate (*d*) as a function of the abiotic environment (*a*), the biotic environment (*b*) and clade-specific phenotypes or traits (*c*); thus $d \sim a, b, c$. We refer to the four components (*a*–*d*) and their interactions collectively as the 'Evolutionary Arena'. We outline analytical approaches to this conceptual model that open up new avenues for research, and present a case study on conifers, for which we parameterise the general model. We also discuss three conceptual examples based on existing literature: the *Lupinus* radiation in the Andes in the context of emerging ecological opportunity and fluctuating fragmentation due to climatic oscillation; oceanic island radiations in the context of archipelago isolation and island formation and erosion; and biotically driven radiations of the Mediterranean orchid genus *Ophrys*. The results of the conifer case study are consistent with the long-standing scenario that large niches, lack of competition, and high-rates of niche evolution differentially promote diversification, but these results go further by quantifying the statistical interactions between variables representing these three drivers. The conceptual examples illustrate how using the synthetic Evolutionary Arena framework results in highlighting gaps in current knowledge, and thus help to identify future directions for research on evolutionary radiations. In this way, the Evolutionary Arena framework promotes a more general understanding of variation in evolutionary rates by making quantitative results comparable between case studies, thereby allowing new syntheses of evolutionary and ecological processes to emerge.

Key words: adaptive radiation, conifer phylogeny, evolutionary arena, macroevolutionary theory, model, phylogenetic comparative methods, species diversification, trait disparification

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"In reviewing the literature, we are struck that there is no one formula for developing a convincing hypothesis about diversification and its causes."

(Donoghue & Sanderson, 2015 p. 263)

I. INTRODUCTION

Biologists have long been fascinated by the circumstances under which evolutionary diversification, the interplay of speciation and extinction, is accelerated. Studies in recent decades on accelerated evolution of diversity – evolutionary radiation – have produced a proliferation of terminology and new statistical approaches. These developments in (macro-) evolution are largely based on the adaptive radiation paradigm (see Box 1; Osborn, 1902; Schluter, 2000; Simpson, 1944; Simpson, 1953), which is verbal and metaphoric, making quantitative comparisons of the trajectories and correlates of diversification between evolutionary lineages (species, clades), and among geographical regions, difficult. Here, we build on these theoretical foundations, and propose a conceptual framework for the study of diversification that also addresses the circumstances under which shifts in diversification rates or evolutionary stasis occur. It is not our aim to thoroughly review the literature on evolutionary radiations, rather we provide an overview of recent developments, concluding with a quantitative model that can in principle be applied in all systems, from cellular to global spatial scales and spanning ecological to evolutionary time frames.

(1) A short history of diversification theory

Darwin, in sharp contrast to early-nineteenth century dogma, envisioned evolution to be gradual, with small changes accumulating from generation to generation, eventually leading to species divergence. This gradualist view was soon challenged and seemingly contradicted by the fossil record, leading to the appreciation that rates of divergent evolution are uneven through time, sometimes generating species and ecomorphological diversity in evolutionary radiations (Osborn, 1902; Schluter, 2000; Stanley, 1979), while at other times demonstrating long-term stasis (Eldredge & Gould, 1972; Flegr, 2010; Gould & Eldredge, 1977) or decline in diversity (Rohde & Muller, 2005). The development of phylogenetic theory followed by the generation of massive DNA sequence datasets, increased computing power, and the proliferation of analytical methods (Altekar, Dwarkadas, Huelsenbeck *et al.*, 2004; Drummond, Ho, Phillips *et al.*, 2006; Felsenstein, 1973; Felsenstein, 1981; Huelsenbeck & Ronquist, 2001) have resulted in a vast accumulation of progressively higher quality phylogenies (Brassac & Blattner, 2015; Maddison, 1997), recognition of monophyletic groups, and estimates of the phylogenetic time-line of evolutionary radiations (Alfaro, Santini, Brock *et al.*, 2009; Magallón & Sanderson, 2001; Morlon, 2014; Nee, May & Harvey, 1994; Rabosky, 2014; Sanderson, 1997; Stadler, 2011; Stadler & Smrckova, 2016). These have revealed orders-of-magnitude differences in clade diversification rates, exemplified by *Amborella trichopoda*, an understory shrub endemic to New Caledonia, which is the only species of an angiosperm clade that is sister to, and therefore just as old as, the clade that contains all the other ca. 400,000 species of flowering plants (Albert, Barbazuk, dePamphilis *et al.*, 2013). Placing such salient diversification rate differences into a striking temporal context, Salzburger (2018, p. 705). recently noted that within "the time span that it took for 14 species of Darwin's finches to evolve on the Galapagos archipelago […], about 1,000 cichlid species evolved in Lake Malawi alone".

(2) Traits make a difference

Simpson (1944) emphasised the importance of **traits** (see Glossary, Box 2) and environments for understanding radiations, and postulated that most radiations are underpinned by **adaptation**. His adaptive radiation model envisioned diversification (phenotypic or taxonomic) to take place in **adaptive zones**. New adaptive zones may be generated, for example, by the evolution of new traits, or by climate change, or by the formation of novel landscapes, such as oceanic islands or human-

induced night-light environments around the globe (Arnold, Pfrender & Jones, 2001; de Vladar, Santos & Szathmary, 2017; Erwin, 1992; Hansen, Pienaar & Orzack, 2008; Simpson, 1953). The adaptive zone is a metaphor for the ways in which evolutionary innovations interact with environmental factors to modulate species diversification and trait **disparification** rates (Wiens, 2004b), and Simpson's concept of adaptive radiation underpinned and inspired a highly productive period of research on evolutionary radiations (e.g., Baldwin, 1997; Fryer, 1969; Hansen, 1997; Hansen *et al.*, 2008; Harmon, Losos, Davies *et al.*, 2010; Harmon, Schulte, Larson *et al.*, 2003; Hughes & Eastwood, 2006; Losos, 1994; Losos & Ricklefs, 2009; Nosil, Harmon & Seehausen, 2009; Sanderson & Donoghue, 1994; Seehausen, 2006; Stebbins, 1947; Wagner, Harmon & Seehausen, 2012).

The effects of functional traits on the diversification of lineages and species, combined with studying the temporal sequence of geographic movement and environmental change, estimated across a phylogenetic tree (Beaulieu & O'Meara, 2016; Felsenstein, 1985; Huelsenbeck, Rannala & Masly, 2000; Maddison, Midford & Otto, 2007; Meyer, Morrissey & Schartl, 1994; Paradis, 2005), has led to the recognition of **key innovations** (Hunter, 1998; Liem, 1973; Miller, 1949; Sanderson & Donoghue, 1994; Van Valen, 1971). Key innovations are exemplified by freezing tolerance in Antarctic fishes (Portner, 2002) and herbaceous life-history strategies for occupying seasonally freezing environments by flowering plants (Zanne, Tank, Cornwell *et al.*, 2014). In addition, phylogenetic comparative studies (Garamszegi, 2014; Harmon, 2019; Harvey & Pagel, 1991) have revealed the importance of **key events**, such as mass extinctions (e.g., of dinosaurs), climate change (e.g., late Miocene aridification), and orogeny (e.g., of the Andes and the New Zealand alps). Including a consideration of the genomic structure has led to the recognition that the connections between key innovations, key events, and diversification rate shifts can be complex, for example in context of hybridization and whole genome duplications in flowering plants (Landis, Soltis, Li *et al.*, 2018; Tank, Eastman, Pennell *et al.*, 2015), or African Rift Lake cichlids (Irisarri, Singh, Koblmüller *et al.*, 2018; Meier, Marques, Mwaiko *et al.*, 2017). Generally, however, it is the differential interaction between variable **intrinsic** (e.g., genome duplication) and **extrinsic** (e.g., climate change) factors that is thought to modulate diversification rates (for a general review on interactions in diversification see Donoghue & Sanderson, 2015; on the interplay of dispersal/biome shifts see Donoghue & Edwards, 2014; and on adaptive diversification see Glor, 2010; Stroud & Losos, 2016).

(3) Trait–environment interaction

The interaction between intrinsic (lineage specific) and extrinsic (environmental) factors provides the geographical and/or **ecological opportunity** for radiations to occur. Simpson (1953) summarised such opportunities in terms of three factors: (i) physical access to an environment, resulting from dispersal, or from the change of geo-ecological conditions in the region where a lineage already occurs; (ii) lack of effective competition in the environment, because no suitably adapted lineages already occur there; (iii) genetic capacity and adaptability of a lineage, which can be manifested in the evolution of key innovations. All three conditions have to be met for a successful adaptive radiation to start (Donoghue & Edwards, 2014).

The evolution of diversity can also result from geographical fragmentation promoting reproductive isolation. Isolation can result in stochastic divergence, i.e., genetic drift (Duret, 2002; Kimura, 1968; Pouyet, Mouchiroud, Duret *et al.*, 2017), leading to allopatric speciation. Repeated allopatric speciation can result in a "non-adaptive" radiation (Comes, Tribsch & Bittkau, 2008; Gittenberger, 1991; Verboom, Bergh, Haiden *et al.*, 2015). Such purely isolation-driven processes are contrasted to ecological speciation, which is driven by divergent selection pressures from the environment, implying that there will be (some) adaptation, and no (or less) random drift. Ecological speciation can result in repeated evolution of phenotypes and trait–environment interactions in adaptive radiations (trait utility; Schluter, 2000). However, in most radiations both ecological adaptation (natural selection) and geographic isolation (genetic drift) are involved (Gittenberger,

2004; Wiens, 2004a), although their relative contributions to diversification may vary between study systems.

In general, it is not the particular sequence of trait evolution (intrinsic) or access to a novel environment (extrinsic), but the establishment/evolution of the complementary state – either the establishment of an environment that fits a pre-evolved trait or an **exaptation**, or the evolution of the trait that is an adaptation to a pre-existing environment – that **triggers** a radiation (Bouchenak-Khelladi, Onstein, Xing *et al.*, 2015; Drummond, Eastwood, Miotto *et al.*, 2012; Kozak & Wiens, 2010; Nürk, Michling & Linder, 2018; Schwery, Onstein, Bouchenak-Khelladi *et al.*, 2015; Wagner *et al.*, 2012). Exploring the theoretical arguments that underpin such context-dependent radiations, Donoghue and Sanderson (2015) coined the term **synnovation** for interacting combinations of (several) innovative traits, and the term **confluence** to describe a sequential combination of a set of traits and events along phylogenetic lineages subtending radiations. Indeed, in recent years, the idea that accelerated diversification is the product of synnovations and confluences of multiple intrinsic and extrinsic factors has gained momentum (Arakaki, Christin, Nyffeler *et al.*, 2011; Guerrero, Rosas, Arroyo *et al.*, 2013; Harmon, Andreazzi, Débarre *et al.*, 2019; Linder & Bouchenak-Khelladi, 2017; Seehausen, 2015; Wagner *et al.*, 2012).

Here, we build on these insights into the interplay between intrinsic and extrinsic factors in driving diversification rate variation, as well as on conceptual developments in evolutionary radiation research. We aim to enrich and stimulate discussion about when and why rapid diversification occurs or does not occur. Advocating a multi-variable perspective on radiations, we formulate the 'Evolutionary Arena' framework (EvA) to encapsulate that perspective. By placing diversification in an explicit environmental context, we can search for and test trait correlates in concert with abiotic and biotic interactions involved in species diversification and trait disparification. These basic four components – diversification/disparification, intrinsic (clade-specific) traits, extrinsic abiotic and biotic factors – and their interactions can be compared between systems, thus offering scope to gain more general insights into the factors that underpin evolutionary diversification and disparification. Putting all four components together in the EvA framework encourages scientists to take into account the entirety of the evolutionary arena and the interactions among its players.

II. THE EVOLUTIONARY ARENA FRAMEWORK

The EvA framework incorporates the complexity of triggers, synnovations, and confluences associated with evolutionary radiations (Bouchenak-Khelladi *et al.*, 2015; Donoghue & Sanderson, 2015), allows for the integrated analysis of relative evolutionary radiation or stasis, and is amenable to application of phylogenetic comparative methods. In EvA the diversification (or disparification) rate of a focal lineage is a function of three components into which all macroevolutionarily relevant processes can be grouped and parameterised:

$$d \sim a, b, c$$

where *d* = **d**iversification or **d**isparification rate, *a* = **a**biotic environment, *b* = **b**iotic environment, and *c* = **c**lade-specific phenotypes or traits (Fig. 1).

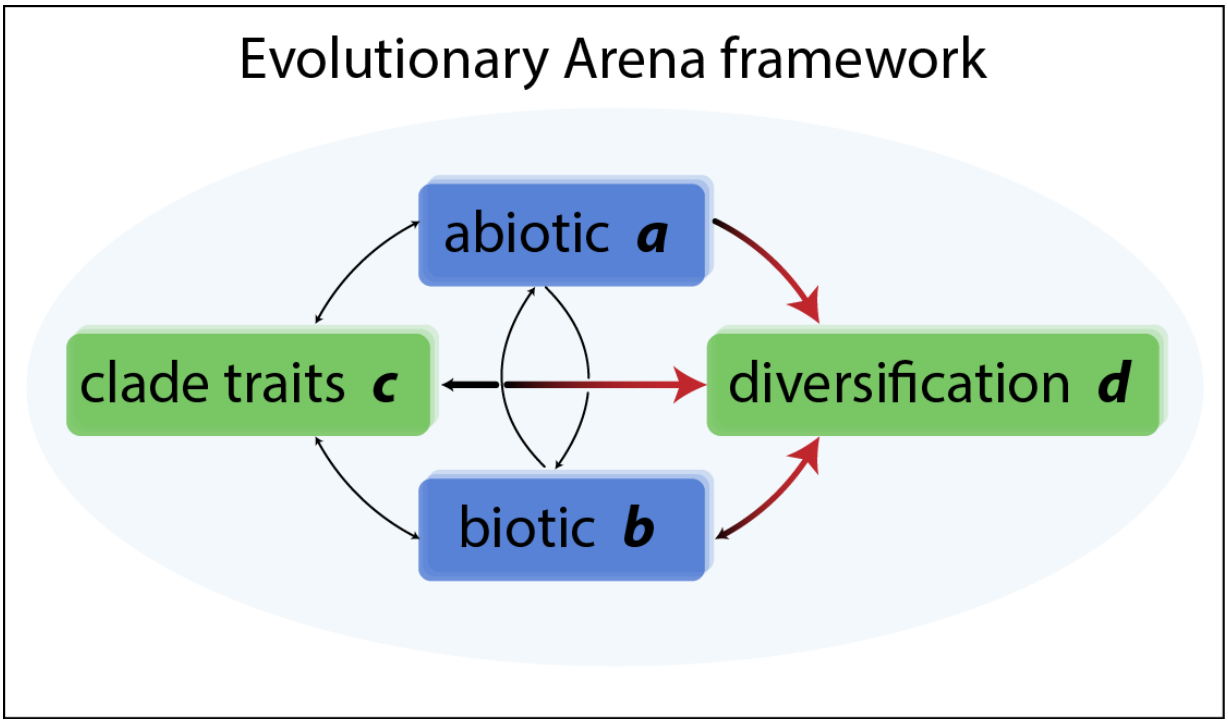

Figure 1. A conceptual visualisation of the Evolutionary Arena framework. The four components (boxes) are illustrated with interactions (arrows) among the components, with those influencing diversification rates (*d*) highlighted in red (larger arrows). We refer to the environment (abiotic (*a*) and the biotic (*b*) components; blue boxes) in combination with the traits (*c*) and diversification rate (*d*) of a biological lineage (green boxes) as the Evolutionary Arena. This framework is potentially dynamic, because interactions among the components allow for feedback, together shaping evolution. Note that, although all components can affect each other (positively or negatively; indicated by small black arrows), we focus here on the dependence of diversification on environmental (extrinsic biotic and abiotic) and clade-specific (intrinsic trait) factors.

These four components are:

d: diversification or *disparification rate* is the rate of evolution in the broadest sense and depends on the values of the *a*, *b*, and *c* components. *d* can be expressed by the rate of change in taxonomic diversity (number of species), interspecific morphological / phenotypic disparity, DNA nucleotide diversity and genetic differentiation (e.g., functional variation of expressed genes or metabolites), physiological diversity (e.g., photosynthetic modes), or niche diversity (e.g., diversity of ecological niches occupied) and differentiation (e.g., rate of ecological expansion). The instantaneous rate of diversification, defined as speciation minus extinction per unit time (Nee *et al.*, 1994), is the simplest expression of *d* and can be directly inferred from a dated species-level phylogeny (Alfaro *et al.*, 2009; Magallón & Sanderson, 2001; Morlon, 2014; Rabosky, 2006; Stadler, 2011; but see Henao Diaz, Harmon, Sugawara *et al.*, 2019; Rabosky, 2010). Disparification can be measured, for example, by (relative) evolutionary rate estimates (Boucher, Demery, Conti *et al.*, 2018; Butler & King, 2004; Felsenstein, 1985; Hansen, 1997; Pagel, 1999; Sakamoto & Venditti, 2018), the change in trait variance in a clade through time (Harmon *et al.*, 2003; Rolshausen, Davies & Hendry, 2018), or by transition rates between discrete character states (Huelsenbeck, Nielsen & Bollback, 2003). The diversification and/or disparification rate may be positive, resulting in an increase in diversity, or negative, resulting in a decrease in diversity.

a: abiotic environment incorporates abiotic factors, such as climate, soil, habitat variables, or

fragmentation of the species range. It can also include biotic elements, like vegetation types, which, as classes, cannot evolve. *a* can be measured as absolute values, e.g., area or niche space, or as the variance in these across space and time, for example, variance in mean annual precipitation, in number of vegetation types or soil types, physiographic heterogeneity, and the functional and structural connectivity. Ideally, the abiotic environment is described by processes that generate this environment, such as erosion or orogeny, or patterns of change, such as climate or vegetation change.

b: biotic environment captures the interactions of the focal lineage with all other species (including species both within and outside the clade and also including trophic interactions). The interaction(s) can be, for example, mutualistic (e.g. pollinators or dispersers, interspecific facilitation, or symbionts such as mycorrhiza), antagonistic (e.g., herbivores, diseases, interspecific competition, or hosts for parasites), or genetic (e.g., hybridization/introgression and horizontal gene transfer). These biotic interactions can also be indirect, if seen as part of the extended phenotype of the focal lineage (e.g., habitat modification such as niche construction, or grasslands increasing fire frequency). There is a rich theory surrounding biotic interactions (e.g., Red Queen hypothesis [Benton, 2009], niche construction [Laland, Matthews & Feldman, 2016]) suggesting they can have a powerful influence on diversification rates. The biotic environment is complex; both quantifying it and including it in analyses is challenging (Harmon *et al.*, 2019). Several recent studies indicate that inter-lineage competition (e.g., Pires, Silvestro & Quental, 2017; Silvestro, Antonelli, Salamin *et al.*, 2015) or interactions with possible dispersal agents (Onstein, Baker, Couvreur *et al.*, 2018) may modulate diversification rates.

c: clade-specific traits include the phenotypic characteristics of the focal species or lineage. Included here are, among others, physiological characteristics (e.g., variation in photosynthetic mode), anatomical or morphological traits, life history strategies, pollination strategies and dispersal modes. The phenotype (or the extended phenotype) is a manifestation, or function, of the genome (via the genotype–phenotype map, inasmuch as this is independent of the environment), or genome diversity (e.g., structural variation such as ploidy level variation, variation in genome size, or DNA nucleotide sequence variation) within the focal group. Therefore, this parameter should ultimately be genetically measurable.

The EvA framework thus encompasses three elements. These are, firstly, the environments or niches of the focal lineage decomposed into abiotic (*a*) and biotic (*b*) components; secondly, the traits of this lineage (component *c*) that interact with the environmental variables; and finally, the consequences of the environment and traits on the diversification rates (component *d*) of the focal lineage. Hence, the abiotic and biotic components establish the environmental context in which evolutionary diversification takes place. We refer to all interactions between the environmental context and the biological lineage and all emerging consequences as the Evolutionary Arena. Interactions between the biotic (*b*) and abiotic (*a*) components can lead to modifications of both (Fig. 1). This can be exemplified by ecosystem engineers modifying disturbance regimes (Jentsch & White, 2019; White & Jentsch, 2001), such as impacts of grass invasion on forests, increasing fire frequency and transforming the environments (Beerling & Osborne, 2006; Bond, Woodward & Midgley, 2005; Linder, Lehmann, Archibald *et al.*, 2018). Similar transformations have been proposed as consequences of mega-herbivore extinctions (component *b*) and climate change (component *a*), selecting for changes in fruit size (component *c*) (Onstein, Baker, Couvreur *et al.*, 2018). A further dynamic factor is provided by interactions between the diversification rate (*d*) and the predictor variables (*a, b, c*). Such feedback mechanisms can broadly be summarised by the concept of niche construction (Laland *et al.*, 2016; Laland, Odling-Smee & Feldman, 1999; Linder, Bykova, Dyke *et al.*, 2012; see also Thompson, 2005), and are exemplified by the Viking Syndrome described in reference to grasses (Linder et al 2018). The latter proposes that global grass success (in

species richness, environmental range, ecological dominance and geographical distribution) is due to the high invasiveness of grasses, which results from their high rate of dispersal (component *c*), effective establishment (component *c*), ecological flexibility (component *c*), and ability to transform environments by increasing the frequency of fire (component *a*) and the density of grazers (component *b*). These scenarios describe feedback systems where increased diversity and dominance of the diversifying clade increasingly modifies the abiotic and biotic environment.

(1) Extended analytical properties

The $d \sim a, b, c$ formulation of the EvA framework is general because it is simple and all-encompassing. The challenge faced in studies addressing evolutionary radiations is to disentangle the effects of the different components at different moments in time. Studies often assign the increase or decrease of diversification to particular factors that happen to have been investigated and quantified, disregarding the possible effects of other factors that may be driving or constraining diversification. The ultimate in understanding radiations and evolutionary stasis would be the joint estimation of all components at all times, but we cannot analyse an infinite number of variables. We argue that the complete EvA, as expressed by the abiotic and biotic environment, as well as the traits of organisms, should be considered when attempting to explain diversification rates. Thus, EvA can be summarised as a "formula for developing a convincing hypothesis about diversification and its causes" (Donoghue & Sanderson, 2015 p. 263) in which all components should be properly acknowledged. In this way, the EvA framework can provide key insights by comparing diversification between clades directly.

To make EvA operational requires parameterising it appropriately, which means making it more specific and detailed. Here, we describe four simple extensions to illustrate how the EvA framework can be enriched by more details to provide insights into different hypotheses in evolutionary diversification. We end this section by outlining general methodological approaches and possibilities for null hypothesis formulation.

1) *Direction of effects*: The three independent components *a*, *b*, and *c* can have a significant positive (+) or negative (-) effect on *d*, thus causing the diversification rate to increase or decrease, or even show a false absence of change as the summed end result of the three. This process of 'nullification', or less increase or decrease than expected, is sometimes ignored and interpreted as a lack of power by the factors influencing diversification. Statistical approaches comparing different systems could provide insights in cases in which diversification rates are higher or lower than expected.

2) *Complex conditions*: The framework can be expanded to include any *set of variables per component*. For example, the abiotic environment could be described by climatic factors such as mean annual precipitation, temperature, and by disturbance factors such as fire frequency. The set of variables selected depends on the hypothesis being tested. If, for example, the hypothesis is that *d* is related to the total variance in the abiotic environment *a*, then

$$a=\sum_{i=1}^{n} a_i,$$

where a_i is the ith variable of *a* (up to the last variable a_n) given as a measure of variance. Thus, the abiotic environment *a* (as well as the other components in EvA) can be decomposed into diverse measures.

3) *Rate shifts*: Explanations for shifts in diversification rates can be sought by testing for changes in the EvA component values. This can be done by including initial values at time *t* (ancestral) and the values after a time interval Δ*t* (derived), for example, at time *t*+Δ*t* after an event:

$$\Delta d = (a, b, c)_{t+\Delta t} - (a, b, c)_t$$

or simply:

$$\Delta d \sim \Delta a, \Delta b, \Delta c$$

If we, for example, hypothesise that geographic movement to a new region is a key event, the condition of *a* varies between *t* and *t*+Δ*t*.

4) *Interaction of components*. We can incorporate interactions between components, such as *ac*, *bc*, or *abc*:

$$d \sim a, b, c, ab, ac, bc, abc$$

This allows us to analyse whether the single components, or the interactions among them modulate the diversification rate, i.e., driving or constraining the evolution of diversity.

Such extensions to the EvA framework, if formulated appropriately in a specific context, can facilitate the direct testing of competing hypotheses about the diversification of a group, using standard model selection approaches (e.g., likelihood ratio tests for nested models, otherwise AIC or Bayes factors; Burnham & Anderson, 2002).

Phylogenetic pseudoreplication (Maddison & FitzJohn, 2015), which describes the non-independence of, or the autocorrelation among, species' traits due to shared ancestry, is a basic property of comparative analyses (Felsenstein, 1985). Phylogenetically independent contrasts (PIC; Felsenstein, 1985) and phylogenetic generalised least squares (PGLS; Grafen, 1989; Martins & Hansen, 1997) are methods for analysing comparative phylogenetic data by accounting for the covariances between traits resulting from shared phylogenetic history (Blomberg, Garland & Ives, 2003; Huey, Garland & Turelli, 2019; Pagel, 1994; Pagel, 1999; Revell, Harmon & Collar, 2008). These methods may be generally useful for exploring the relationships between components in the EvA framework (for examples, see Fig. 2). Although both methods can be thought of as "analogous to data transformations made to better approximate the assumptions of standard statistical tests" (Huey *et al.*, 2019, p 12), they, as well as most other phylogenetic comparative methods (but see, for example, Rolshausen *et al.*, 2018), implicitly assume a specific process underlying character change along the evolutionary lineage (i.e., a model of character evolution such as Brownian motion; Boucher *et al.*, 2018; Butler & King, 2004; Felsenstein, 1985; Hansen, 1997; Hansen & Martins, 1996; Khabbazian, Kriebel, Rohe *et al.*, 2016; Lande, 1976; Landis & Schraiber, 2017). The appropriate data transformation model in relation to the hypothesis being tested is a non-trivial question in comparative analyses (Uyeda, Zenil-Ferguson & Pennell, 2018); graphical models depicting hypothesized causal links (Höhna, Heath, Boussau *et al.*, 2014; Höhna, Landis, Heath *et al.*, 2016) might proof helpful here. On the other hand, the case of a singular, unreplicated event in the evolutionary history of a lineage challenges the statistical power of comparative phylogenetic methods (Felsenstein, 1985; Losos, 2011; Maddison & FitzJohn, 2015; Uyeda *et al.*, 2018). An approach to overcome this limitation might be the combined application of hypothesis testing and exploratory methods ('phylogenetic natural history') as outlined by Uyeda *et al.* (2018).

Associations between diversification rates and the other components in the EvA framework can be tested using state-dependent speciation and extinction (SSE) models (such as BiSSE): a birth–death process where the diversification rates depend on the state of an evolving (binary) character (Maddison *et al.*, 2007), given a phylogeny and trait data. For complex components, the multistate SSE (MuSEE) model can be applied to accommodate several qualitative character states, or multiple (binary state) characters following Pagel (1994) for state recoding (FitzJohn, 2012). Although SSE model extensions for quantitative characters (QuaSEE; (FitzJohn, 2010) and geographic range evolution (GeoSEE; Goldberg, Lancaster & Ree, 2011) (to name just a few) have been developed, in the SSE model-family none is currently available for the likelihood calculation of a model considering both quantitative and qualitative variables (but see Felsenstein, 2012; Revell, 2014). This situation could be common under the EvA framework and represents a priority for method development.

Comparing a biologically meaningful and appropriately complex null hypothesis to the goodness-of-fit of alternative (H1) models is essential for detecting whether a character state-dependent model can explain more of the observed variation than could be expected under random diversification rates (Beaulieu, O'Meara & Donoghue, 2013; Caetano, O'Meara & Beaulieu, 2018). It has, for example, been shown for SSE models that the variation in the diversification rate observed in a phylogenetic tree is not necessarily explained by the focal factor (character) under study (Rabosky & Goldberg, 2015). False-positives can potentially result because the null hypotheses did not account for the possibility that diversification rates can be "independent of the character but not constant through time" (Harmon, 2019, p 215). Hidden state model (HSM) approaches (Beaulieu & O'Meara, 2016; Beaulieu *et al.*, 2013; Caetano *et al.*, 2018; Marazzi, Ané, Simon *et al.*, 2012), which incorporate unobserved ('hidden') factors as model parameters equivalent to observed ones, offer a solution to this fundamental problem. Comparing goodness-of-fit between 'hidden state' null models and those representing the focal factor(s) provides appropriately complex null hypotheses that can be used for testing differently parameterised EvA models, and thereby allows identification of "the meaningful impact of [the] suspected 'driver[s]' of diversification" (Caetano *et al.*, 2018, p 2308).

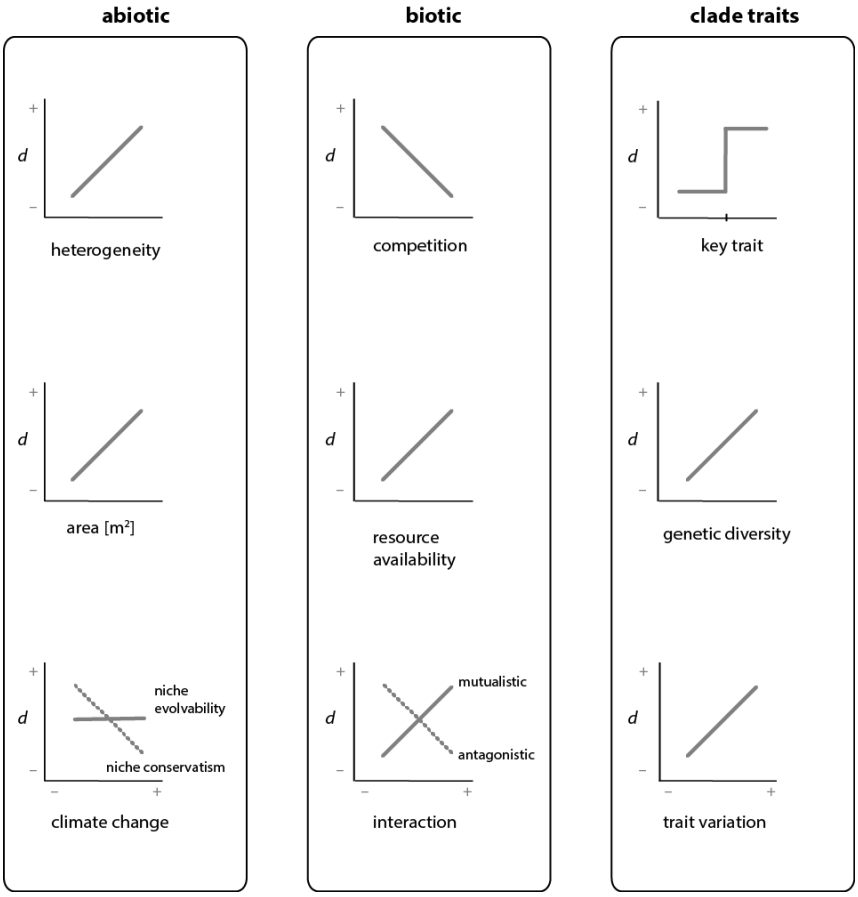

Figure 2. Possible effects on diversification rate (*d*) of selected variables grouped as abiotic (*a*), biotic (*b*), clade traits (*c*) components in the EvA framework. This illustrates how hypotheses that address ecological and evolutionary factors that cause differential rates of diversification can be developed. For 'key trait' the x axis is in time units (with a single evolutionary event of a key innovation causing accelerated diversification), for the other components it is a scale measure.

III. CASE STUDY: CONIFERS

We use a case study of conifer radiation to illustrate EvA implementation and component quantification. In contrast to the conceptual simplicity of the framework, obtaining data for all components across multiple lineages can be challenging. Here, we use published data on 455 conifer species (Larcombe, Jordan, Bryant *et al.*, 2018) that enable us to parameterise the $d \sim a, b, c$ framework. The conifers provide an excellent study clade for comparative analysis: the lineage is rich in species, geographically widespread, and well studied with excellent distribution data (Farjon,

2018) and with well-defined clades. Although conifers originated ca. 300 million years (Ma) ago, with the main clades thought to have diverged between the early Triassic (ca. 240 Ma) and mid-Cretaceous (ca. 100 Ma), most modern species arose in the Neogene or Quaternary (23 Ma–present; Leslie, Beaulieu, Rai *et al.*, 2012). We used the fossil-calibrated phylogeny of Leslie *et al.* (2012) to define 70 subclades with stem ages between 34 and 146 Ma using a cut-off at 33.9 Ma (the Eocene/Oligocene boundary) in order to focus on the variables which could explain Neogene–Quaternary diversification rate variation (Larcombe *et al.*, 2018). These subclades include up to 52 species each, with 29 of the 70 containing only one species.

The factors that contribute to *a*, *b* and *c* in the conifers model were derived from the output of a process-based niche model (Larcombe *et al.*, 2018). This niche modelling method is described in detail in Higgins, O'Hara, Bykova *et al.* (2012), and is based on a mechanistic model of plant growth, the 'Thornly Transport Resistance' model, which models resource acquisition, transport and allocation between roots and shoots, based on environmental information extracted from species distribution data (Higgins *et al.*, 2012). This produces two types of information for each species: 1) estimates of the geographic distribution of the potential niche of each species (i.e., a species distribution model [SDM]); and 2) estimates of the physiological parameters that describe the niche of each species. We used these metrics, and occurrence data and species richness per clade to parametrise $d{\sim}a, b, c$ as follows:

d = the diversification rates for each clade: calculated using the method-of-moments estimator of Magallón and Sanderson (2001) as $r_\varepsilon = \frac{1}{t} ln[n(1-\varepsilon) + \varepsilon]$, where r_ε is the net diversification rate assuming a relative extinction fraction ε = 0.9, *n* the number of extant species, and *t* the stem age of the clade.

a = abiotic environment, quantified by the clade niche size: the projected geographical range reflecting the potential niche of all species within the clades. This is calculated per clade as the number of ¼° grid cells across the globe that at least one species of the clade can occupy, based on the physiological SDM and corrected for clade species numbers (i.e., rarefied to the clade with the lowest diversity to remove sampling effects; Larcombe *et al.*, 2018). This means that if the score is small, the niche size of a clade is expected to be narrow, and if the score is large, the niche size of the clade is large so that the clade comprises ecologically more generalist species or the species in the clade might be specialised but different from one another. This clade-wise niche size is an appealing measure of *a* because it approximates the potential niche, consequently biotic interactions and effects of traits can be estimated separately. Figure 3 shows the combined potential niche for all 455 species in the dataset, i.e., the abiotic arena of the conifers.

b = competitive interactions estimated at the species level: we determine the expected competition for each species with all members within its clade (one of the 41 clades defined above) as the product of niche and geographic overlap between species. The metric underestimates competition because it excludes competitive processes with other clades and other indirect competitive processes (see discussion in Larcombe *et al.*, 2018). Geographic overlap is estimated based on the occurrence data. Niche overlap between each species pair was calculated using Schoener's niche overlap metric *D* (Schoener, 1968) based on the potential distributions from the SDM analysis. We then scaled these two numbers to range from 0 to 1 for each species pair and multiplied them to provide a competition index (Larcombe *et al.*, 2018). This means that if either score is zero, the competition score is zero, and if they have the same (potential) niche and the same (realized) range then the competition score is 1. The species-level estimates were averaged to provide clade level competition score. Critical for understanding the most recent diversification rates is the competition among species in the last few million years, assuming that our calculations based on the SDM account for the aspect that within-clade members having more similar traits with respect to resource acquisition than other species.

c = clade-specific rate of niche evolution: we used eleven physiological traits (see Supporting Information S1, Fig. S1) that were identified as being most important for defining the overall niche space of conifers (Larcombe *et al.*, 2018). Although an effectively limitless number of physiological traits could be defined, our method provides an objective selection criterion of ecologically appropriate measures. These eleven traits were fitted together in a multivariate Brownian motion model of evolution (Butler & King, 2004), and the diagonal elements of the resulting variance–covariance matrix for the traits in each clade represent the phylogenetic rate of evolution (O'Meara, Ane, Sanderson *et al.*, 2006). These were summed and scaled to provide a multidimensional niche evolution rate for each clade (Kozak & Wiens, 2010; Larcombe *et al.*, 2018; Title & Burns, 2015).

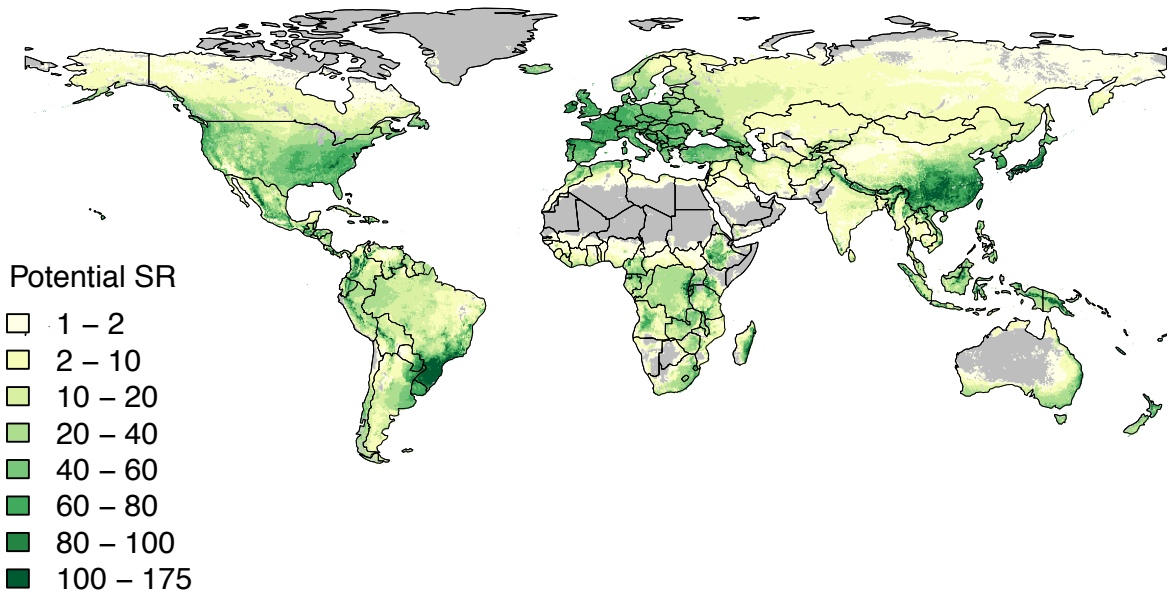

Figure 3. Projected potential species richness (SR) of conifers representing their abiotic arena. The abiotic arena of conifers is defined by geographic locations that can support one or more of 455 conifer species, based on projections from the process-based physiological niche model (the fundamental conifer niche). The projected potential SR (yellow-green shading) highlights areas that are suitable for conifer species. The abiotic arena alone does not always predict patterns of conifer diversity. For example, the eastern Congo is predicted to be climatically suitable for many species but in fact has relatively low conifer diversity. It is likely that clade-specific traits (*c*) and biotic interactions (*b*) limit the diversity in certain regions (see main text).

We fitted the conifers EvA model $\sqrt{d} \sim \ln(a) + b + \ln(c)$ by means of phylogenetic generalised least squares (PGLS), controlling for the non-independence between cases resulting from phylogenetic structure in the data using the R v3.5.3 (R Core Team, 2013) library 'phylolm' v2.6 (Ho & Ane, 2014). PGLS estimates the regression parameters of all variables (the scaled variables used to parameterise the components of EvA), adjusted for the phylogenetic signal in the model residuals. We accessed the standardised coefficients and calculated the variance explained by the model using the coefficient of determination (R^2) to measure goodness-of-fit, and also assessing partial R^2 (variance explained per predictor variable *a*, *b*, and *c*) using the R library 'rr2' v1.0.1 (Ives & Li, 2018; Ives, 2019). R scripts are available in Supporting Information S1.

The model accounted for 64% of variation in diversification rates among the conifer clades (adjusted R^2 = 0.638). The predictor variables *a, b,* and *c* in the conifer EvA model differentially contributed to explaining *d* (table 1). The abiotic environment of clades (*a*) showed no relationship

to diversification rate (slope -0.003, $P = 0.89$). Competitive interactions (*b*) between the species in a clade show significant negative relationships to diversification (slope -0.581, $P < 0.001$), indicating a pattern consistent with diversity-dependent slowdowns in rates of species diversification. The rate of niche evolution (*c*) had a non-significant positive relationship to diversification rate (slope 0.166, $P = 0.36$).

Table 1. Estimated effects of abiotic environment (*a*), competitive interactions (*b*), and rate of niche evolution (*c*), on net diversification rate r_ε (*d*) across the conifer clades.

Source	Slope	Std. error	t value	*P*	% partial R^2
Abiotic environment (*a*)	-0.00264	0.14826	-0.01783	0.985	0.001
Competition (*b*)	-0.58138	0.12741	4.56292	<0.001	36.009
Rate of niche evolution (*c*)	0.16626	0.18091	0.91899	0.364	2.232
(Intercept)	0.60055	0.15967	3.76129	<0.001	—

The significantly negative effect of competition (*b*) on diversification (*d*) indicates higher diversification rates in clades where competition among species is low. This result is consistent with the concept of diversity-dependent diversification (Foote, 2000; Harmon & Harrison, 2015; Rabosky, 2013) and suggests that diversity-dependent relationships are more important among the conifers in regulating diversification rate than niche size (*a*) or rates of physiological trait evolution (niche evolution; *c*). However, the rates of niche evolution (*c*) among the conifer clades show a very similar, although inverse, pattern to that of competition (*b*) (Fig. 4). Estimates of a model accounting for interactions among predictor variables (results not shown due to lack of statistical power; see Supporting Information S1) indicated the two-way interaction *b*:*c* (competition interacting with rate of niche evolution) influencing diversification in the conifers, in line with findings by Larcombe *et al.* (2018), who showed that conifer evolution is jointly shaped by bounded and unbounded evolutionary processes (e.g., Harmon & Harrison, 2015). The two-way interaction *b:c* may subsequently enhance or relax diversity-dependent processes so as to promote or constrain diversification (Larcombe *et al.*, 2018). This is also consistent with the concept that spatial (or temporal) variation in trait disparity can result in variation in competitive pressure (Cornell, 2013; Marshall & Quental, 2016; McPeek, 2008). The interaction of competition and rate of niche evolution suggests that the fastest diversification in conifers is found when competition is low (increased ecological opportunity), which could be the result of fast trait/niche evolution (high adaptability of the lineage).

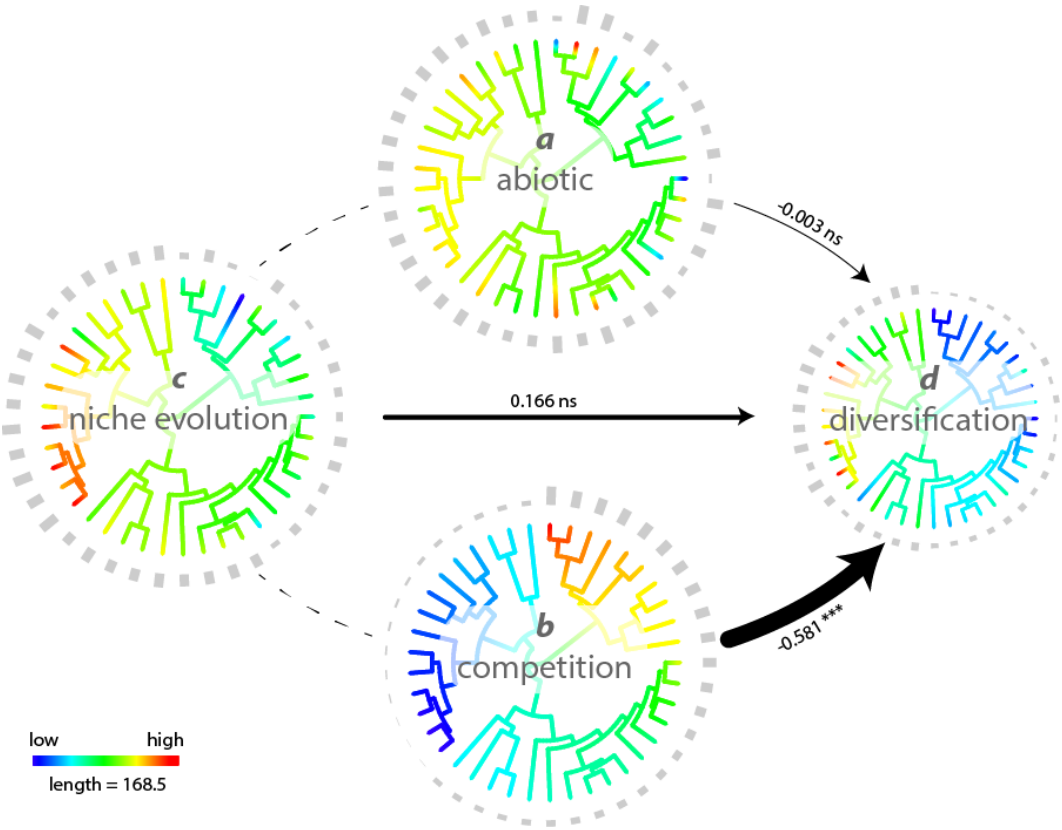

Figure 4. **Quantified EvA model for the conifers**. Coloured trees illustrate the distribution of abiotic environment (*a*), competitive interactions (*b*), rate of niche evolution (*c*), and diversification rates (*d*) across the conifer phylogeny with bars at tips detailing the values per clade and variable. The estimated effects on net diversification rates r_ε are indicated by arrows scaled to the standardised coefficients (slopes) also showing significant levels (ns, non-significant, ***, P <0.001). Colours on branches are rate estimates (obtained using the R package phytools' fastAnc function; Revell, 2012; see Supporting Information S1) and illustrate parameter distribution on the tree. When competition among species is low and the rate of niche evolution in a clade is pronounced, the diversification rate of that clade accelerates.

The case presented here shows the potential to infer general patterns using the EvA framework. However, it is in no way a full exploration of the approach, and more sophisticated analyses are likely to prove more informative. For example, our analysis assumes that rates for *d, b,* and *c* are fixed, which is an over-simplification. It could be interesting to repeat the analysis using species instead of clades, as this allows us to account for phylogenetic structure within the clades, ecologically highly variable species, and diversification stasis. However, there are issues interpreting tip-diversification rates. Methods are available to reconstruct ancestral sympatry and infer the effect of competition on trait divergence (Drury, Clavel, Manceau *et al.*, 2016; Nuismer & Harmon, 2015), and it might be possible to extend these methods to predict how competition impacts clade diversification. Methods that reconstruct and evolve ancestral states along phylogenies for *a, b,* and *c*, are also appealing (Uyeda *et al.*, 2018), and with increasing complexity of the EvA model, approaches such as hidden states will be important for rigorous testing against equivalently complex null hypotheses (Caetano *et al.*, 2018).

IV. CONCEPTUAL EXAMPLES

(1) *Lupinus* continental radiation

Among the most intensively investigated radiations are several in the tropical alpine environments of the high-elevation Andean grasslands. These environments emerged as a result of the most recent, Plio-Pleistocene uplift of the Andes, and consequently the radiations themselves are largely confined to the Pleistocene (Hughes & Atchison, 2015; Luebert & Weigend, 2014; Madriñán, Cortés & Richardson, 2013). These are exemplified by the diversification of *c.* 85 species of *Lupinus* (lupines, Leguminosae) within the last 1.2–3.5 Ma. The Andean *Lupinus* radiation has been attributed to a combination of intrinsic evolutionary (trait) innovation and extrinsic ecological opportunity (Drummond *et al.*, 2012; Hughes & Atchison, 2015; Fig. 5). The shift from an annual to a perennial life history (i.e., evolution of a clade-specific phenotype = *c* in EvA) is hypothesised to have acted as a key adaptation facilitating occupation of mesic montane habitats (Drummond *et al.*, 2012), as well as a key enabler of accelerated disparification of plant growth forms in the Andes (Nürk, Atchison & Hughes, 2019). This is because perennials have much greater cold tolerance than annuals, which is crucial for spreading into high-elevation ecosystems, and a fundamentally greater potential growth-form disparity than annuals (Nürk *et al.*, 2019; Ogburn & Edwards, 2015). At the same time, extrinsic ecological opportunities for diversification were available in the island-like high-elevation habitats that emerged during the last few million years due to Andean uplift (i.e., abiotic factor = *a* in EvA), prompting Hughes and Eastwood (2006) to refer to the Andean *Lupinus* clade as an example of "island-like radiation on a continental scale". In this example, the evolution of secondary perenniality, the shift from lowland to montane habitats, and the primary shift to higher rates of species diversification all coincide on the same branch of the phylogeny, presenting an example of a "key confluence" *sensu* Donoghue and Sanderson (2015). In the Andean *Lupinus* clade, *d* has been estimated as the rate of species diversification (Drummond *et al.*, 2012), phenotypic trait evolution or disparification of plant growth forms (Nürk *et al.*, 2019), and coding DNA sequence evolution (Nevado, Atchison, Hughes *et al.*, 2016). All of these estimates of *d* show accelerated rates across the western New World montane radiation when compared to the earlier diverging lineages of more slowly diversifying lowland western New World *Lupinus* annuals.

Lupinus thus provides an apparently straightforward example of a confluence of intrinsic innovation and extrinsic opportunity as the trigger for accelerated diversification of species and disparification of plant growth forms. This explanation assumes that ecological opportunity presented by empty sky island habitats and the means to take advantage of those opportunities (secondary perenniality) are driving diversification. However, treating the biotic environment (*b* in EvA) as zero, or empty of competition is clearly an over-simplification, given that there were apparently many plant radiations playing out during the Pleistocene across the high-elevation Andean grasslands, presumably in parallel with each other (Luebert & Weigend, 2014). The detailed order of timing of these radiations and their interactions remain unknown, just as interactions among sympatric and more or less contemporaneous radiations have been difficult to tease out more generally (Tanentzap, Brandt, Smissen *et al.*, 2015). The EvA framework draws attention to the fact that biotic factors have not been critically investigated beyond the simple idea of lack of competition in the newly emerged tropical alpine sky island habitat (Fig. 5).

A more detailed analysis might indicate what factors of these high-elevation habitats are important for the observed high rates of diversification. Indeed, it is aspects of the abiotic environment (*a* in EvA) that are most often put forward as the central explanation for the numerous rapid recent radiations in the high-elevation Andean grassland. Foremost amongst these aspects are: (i) the large continental-scale extent of the high-elevation Andes; (ii) the extreme physiographic heterogeneity; and (iii) the rapid fluctuation in the extent and connectivity between the north Andean páramo sky islands during the Pleistocene. Physiographic heterogeneity of the Andes, spanning steep and extended environmental gradients (e.g., temperature and rainfall), has long

been considered as a key factor driving diversification (Hughes & Eastwood, 2006) and indeed of diversification more generally (e.g., Rangel, Edwards, Holden *et al.*, 2018). It has also long been recognised that the area and connectivity of the high-elevation Andean grasslands have varied dramatically through the Pleistocene due to elevational shifts in vegetation zones and species distributions imposed by glacial–interglacial periods. However, it is only recently that area and connectivity have been modelled and quantified in sufficient detail through the Pleistocene (Flantua, O'Dea, Onstein *et al.*, 2019) to assess the potential of such an alpine 'flickering connectivity system' (Flantua & Hooghiemstra, 2018) to further enhance diversification (e.g., Nevado *et al.*, 2016). Such models demonstrate the need to quantify attributes of the abiotic environment (*a* in EvA) through time as well as the potential of such time-dependent models to make more realistic estimates of the impact on diversification rates (*d* in EvA). Moreover, considering the Andean *Lupinus* radiation in the light of the EvA framework highlights the lack of knowledge of the biotic interactions involved (*b* in EvA), indicating new research questions.

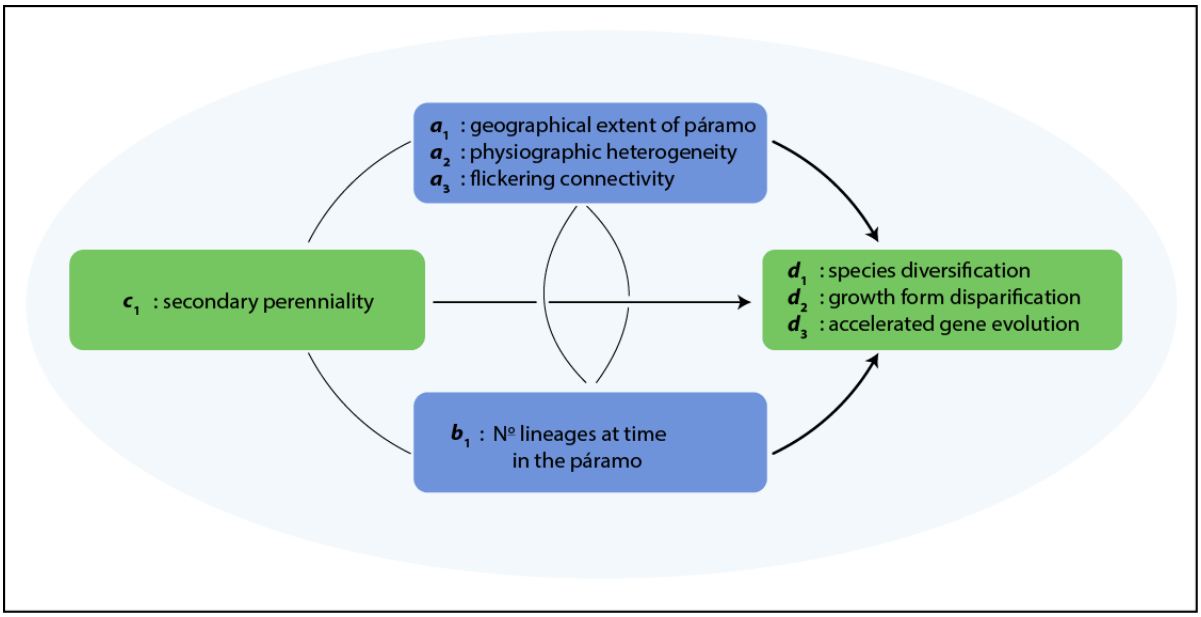

Figure 5. The EvA model for *Lupinus*: d_1 / d_2 / d_3 ~ (a_1, a_2, a_3), *b*, *c*.

(2) Island radiations

Radiations on volcanic oceanic islands (i.e., which arose *de novo* on the oceanic crust) pose an interesting problem as result of their typical lifecycle. In contrast to islands on the continental shelf, oceanic islands emerge following a volcanic eruption, grow rapidly in area, and then erode down to the sea level. Even though oceanic islands may show a flickering connectivity effect as a result of Pleistocene climate fluctuations (for example, lower glacial sea levels would have resulted in larger islands areas leaving an imprint on current biodiversity; Norder, Proios, Whittaker *et al.*, 2019; Simpson, 1974; Weigelt, Steinbauer, Cabral *et al.*, 2016), we here focus on the entire oceanic island lifecycle (Borregaard, Amorim, Borges *et al.*, 2017; Whittaker, Triantis & Ladle, 2008). This island lifecycle over around 10 million years is typically unimodal in its key properties, and so differs from a flickering model as described for the terrestrial high mountains of the Andes over the Pleistocene (Flantua & Hooghiemstra, 2018; Flantua *et al.*, 2019), which is multimodal. The island lifecycle is an ontogenetic geomorphological trajectory of area, elevation and habitat diversity – from island birth, through maturity, until island submergence. Consequently, this can be analysed as a continuous time series. The potential effects of this ontogeny on evolutionary processes have been described in the general dynamic model of island biogeography (Whittaker *et al.*, 2008), which provides a temporal framework for variations in island features (Lim & Marshall, 2017) such as area, topographical

complexity, isolation, and habitat diversity (*a* in EvA). The model has already been implemented using quantitative methods (Borregaard, Matthews & Whittaker, 2016; Valente, Etienne & Phillimore, 2014) and therefore can help define the temporal dimension of the abiotic arena in an insular EvA context.

In the EvA framework, oceanic islands offer a convenient conceptual aspect, in that the abiotic, geographical component of the Evolutionary Arena – the island or archipelago itself – is simple to define, as it has discrete boundaries and is isolated. While many classic studies have analysed insular diversification (*d* in EvA) in single monophyletic radiations (e.g., Hawaiian silverswords, Baldwin & Sanderson, 1998; Madagascan vangas, Jønsson, Fabre, Fritz *et al.*, 2012), another potential of islands is that entire communities resulting from multiple independent colonisation and sharing the same arena can be studied simultaneously, because the island definition is the same for all included taxa with similar dispersal capacity. For instance, by including all terrestrial birds of the Galápagos islands in the same model, Valente, Phillimore and Etienne (2015) were able to show that Darwin's finches have statistically exceptional rates of species diversification. The effect of the phenotype (*c* in EvA) can be considered on a lineage-specific basis (e.g., Givnish, Millam, Mast *et al.*, 2009) or, potentially, using a more powerful community-level multi-lineage approach, where the effects of given traits are assessed across multiple independent insular radiations within the same insular EvA model – for example, secondary woodiness (Nürk *et al.*, 2019). However, while methods for assessing diversity-dependent effects within single lineages (*b* in EvA) already exist (Rabosky & Glor, 2010; Valente *et al.*, 2015), we currently lack an approach for testing how the interaction of habitat heterogeneity, island size and present diversity can affect all lineages on an island-wide basis. For example, it is not clear exactly how diversity-dependence operates both among and within clades, or how speciation and endemism interact with ecological opportunity driven by topography, isolation and elevation (Román-Palacios & Wiens, 2018; Steinbauer, Field, Grytnes *et al.*, 2016). Here, EvA can provide a semantic framework for the integration of time-dependent models and multi-clade analyses, leading to a single coherent model for the evolution of diversity within island systems. The EvA framework makes explicit this research question.

(3) *Ophrys* biotically driven radiation

It is thought that biotic interactions (*b* in EvA) have been a dominant driver of the radiation of the Mediterranean orchid genus *Ophrys*, which has produced two parallel adaptive radiations within the last ~1 Ma. Both of these radiations are characterised by a shift to *Andrena* solitary bees as highly specific pollinator species, and by rapid phenotypic diversification of flowers (Breitkopf, Onstein, Cafasso *et al.*, 2015; Paulus & Gack, 1990). In this system, pollinators mediate strong reproductive isolation in the absence of any measurable post-pollination barriers to gene flow among closely related species (Sedeek, Scopece, Staedler *et al.*, 2014; Xu, Schlüter, Scopece *et al.*, 2011). Consequently, pollinators may drive speciation in these two parallel radiations. The high specificity of the pollinators in this system is due to the plants' chemical mimicry of the pollinator females' sex pheromones (i.e., phenotypic traits, *c* in EvA), which is predominantly mediated by alkenes (Schiestl, Ayasse, Paulus *et al.*, 1999; Schiestl, Ayasse, Paulus *et al.*, 2000; Xu, Schlüter, Grossniklaus *et al.*, 2012). A simple genetic basis underlies alkene biosynthesis, with only two loci being sufficient to completely change the pollinator-important alkene double-bond profile sensed by insects (Schlüter, Xu, Gagliardini *et al.*, 2011; Sedeek, Whittle, Guthörl *et al.*, 2016). Selection on alkene composition, and on loci putatively involved in their biosynthesis, is in stark contrast to the rest of the loci in the genome, where abundant polymorphisms are shared across closely related species (Sedeek *et al.*, 2014; Xu *et al.*, 2012). Simulations suggest that this simple trait architecture could lead to rapid pollinator-driven divergence (Xu & Schlüter, 2015). Overall, the available data suggest that, given the trait architecture of pollinator attraction, pollinators may be a key factor driving the *Ophrys* radiations. However, the relative importance of other factors remains unknown. For example, what is the potential contribution to phenotypic diversification (*d* in EvA) attributable

to the highly heterogeneous (dynamic) abiotic environment (*a* in EvA) providing habitats for plants and pollinators (*b* in EvA) during the last million years?

Potentially, proxies for all components are measurable here. Due to the extensive amount of allele sharing, and gene coalescence times frequently predating 'speciation' times (establishment of reproductive barriers), diversification (*d* in EvA) among very recent groups of *Ophrys* may best be assessed not by phylogenetic means, but by within-group pairwise estimates among closely related species, either in terms of genetic differentiation (e.g., F_{ST}) or phenotypic measurements. Among the abiotic measurables (*a* in EvA) would be estimates of habitat fragmentation (also, for example, estimates from biogeographic and niche modelling approaches) over the estimated age of target clades/species groups. Biotic interactions (*b* in EvA) can be represented as matrices of interactions at varying levels; in its simplest form, orchid species vs. pollinator species. Due to the occurrence of (i) parallel use of the same pollinators in different lineages and (ii) repeated use of the same pollinators by allopatric orchid species, such an interaction matrix could initially take the shape of a variance–covariance matrix as used in comparative analyses (O'Meara, 2012). Since the importance of different floral traits (including morphology and chemistry) for successful interaction with pollinators can be experimentally measured by quantifying insect responses (e.g., Xu *et al.*, 2012), such an interaction matrix may ultimately contain explicit likelihoods of plant/pollinator interactions (cf. pollination probabilities in Xu & Schlüter, 2015). Clade-specific intrinsic effects (*c* in EvA) essentially refer to the complexity of genetic/genomic change needed to effect a change in a relevant trait. This trait change would ideally be based upon mechanistic molecular knowledge that could then be quantified numerically. As a first step in this direction, it may be possible to construct a statistic that summarises trait–gene associations derived from genomic/transcriptomic data on gene polymorphisms and/or expression from phenotyped individuals. Overall, although the data to formally test the components of the EvA framework in the *Ophrys* example are not yet collected, doing so seems at least theoretically straightforward. Going beyond this example, EvA adds a comparative structure to these questions and provides a semantic bridge between micro- and macroevolution in systems where investigations span different levels, from populations to species and clades.

V. CONCLUSION

(1) The EvA framework provides a generalised structure with which to explore the modulators of diversification rates, in terms of the environment (biotic and abiotic) and the traits of the focal lineages. The framework is very flexible, facilitating the incorporation of both more detailed variables, interactions among the components, and changes in the direction of effect of these components. The EvA framework can be readily expanded to accommodate increasing levels of complexity.

(2) The EvA framework can be used to rank variables according to their relative influence on diversification rates, or to test for the interactions among variables. It can also be formulated as a hypothesis-testing framework, which can be used to test whether the likelihood of observing the data under a favourite particular model provides better fit than an appropriate null model, or to compare models of varying complexity. Applying these analyses within the EvA framework then allows us to identify the important components that account for differences in diversification rates.

(3) This framework encourages us to organise our knowledge of the factors regulating evolutionary radiations, evolutionary stasis and evolutionary decline of clades, and so facilitates the recognition of missing information. This encourages the search for more complete explanations of diversification rate shifts, particularly in the exploratory phases of research, rather than focusing on one conspicuous variable.

(4) It provides a very useful framework for comparing explanations of evolutionary diversification rate shifts between clades and regions. EvA components modulating diversification rate changes can

be compared verbally (e.g., Table 2), but if quantified a clearer result can be obtained, as shown for the conifers (Fig. 4). This should encourage a more comparative approach to exploring the phylogenetic and geographical variation in the correlates and drivers of diversification or extinction.

(5) The approach may be particularly useful in parameterising data-rich, broad-scale analyses comparing different systems, such as evolutionary radiations of clades across different regions (e.g., Wagner *et al.*, 2012), or between different clades within the same region (for example, the plant clade radiations in the north Andean páramos). It also provides a common terminology and currency for comparing diversification dynamics, potentially cutting a Gordian Knot in the conversation on where, when, why, and how radiations evolve.

(6) Using the EvA framework for comparative investigations of adaptive radiations may lead to substantial new insights into the variables which modulate the evolution of biotic diversity.

Table 2. Summary comparing factors grouped into the components of the EvAs for the four examples detailed above: worldwide conifers, Andean *Lupinus*, island radiations and Mediterranean *Ophrys*.

Case	***d***	***a***	***b***	***c***
Conifers	Net diversification rate	Geographical (niche) range (<1 % R^2)	Competition (36 % R^2)	Physiological traits (2.2 % R^2)
Lupinus	Speciation Disparification Genetic differentiation	Size of páramo Flickering connectivity Physiographical complexity	Competition	Perennial life history strategy → growth form diversity
Islands	Diversification	Island ontogeny Fragmentation (isolation)	Competition for island niches	Idiosyncratic
Ophrys	Speciation Phenotypic differentiation	Fragmentation of range	Pollinators	Floral traits, esp. odours Genetics

Radiations (Box 1)

Evolutionary radiation is a phase of accelerated proliferation of species and/or phenotypes, in the sense of significant increase in the diversification and/or disparification rate compared to background rates (without a shift, it is diversification). Evolutionary radiations may be grouped into:

Adaptive radiation: proliferation of species driven by the evolution of ecological and morphological (phenotypic) diversity that can be linked to adaptation to an environment. The environment may act as a modulator, facilitating rapid (potentially sympatric) speciation and/or slowing extinction. If not combined with shifts in diversification rates, the evolution of ecological and phenotypic disparity under background rates might be termed 'adaptive diversification'.

Geographic radiation: proliferation of species driven by enhanced opportunities for allopatric speciation (reproductive isolation resulting from spatial barriers) in a particular region (modified from Simões, Breitkreuz, Alvarado *et al.*, 2016).

These two categories of radiations are simplified: both adaptive and neutral processes likely play a role in modulating diversification rates in most radiations, but their relative contributions differ. For example, ecological factors may enhance the opportunity for reproductive isolation, and species divergence in adaptive radiations may additionally be promoted by spatial isolation (see main text, Trait–environment interaction).

Glossary (Box2)

Adaptation: a trait is an adaptation to a selective regime if it evolved in response to selection by that regime (Gould & Vrba, 1982)

Adaptive zone: a fitness peak in a set of related niches (the adaptive grid or macroevolutionary landscape) that a lineage occupies by virtue of a novel trait(s) that confer fitness in these niches.

Confluence: the sequential coming together of a set of traits (innovations and synnovations), environmental changes, and geographic movements along the branches of a phylogenetic tree (Donoghue & Sanderson 2015).

Disparification: increase in disparity in a clade through time. Here, disparity is the phenotypic variation (e.g., morphological differences) among taxa in a clade. Disparification is a characteristic of adaptive diversification.

Ecological opportunity: lineage-specific environmental conditions that contain both niche availability and niche discordance, favouring adaptation and promoting diversifying selection within the lineage (adapted from Wellborn & Langerhans, 2015).

Exaptation: a trait that has evolved for one use, and that is later useful for another usage (often but deceptively termed 'pre-adaptation'; adapted from de Vladar *et al.*, 2017; the original definition of Gould and Vrba (1982) is "features that now enhance fitness but were not built by natural selection for their current role").

Extrinsic factor: environmental factors such as abiotic and biotic niche parameters, not inherited genetically by the focal lineage.

Intrinsic factor: phenotypic (morphological, physiological) or genetic trait(s), inherited by the focal lineage.

Key event: events that modulates a shift in diversification rates.

Key innovation: new trait which facilitates the occupation of a new adaptive zone, or which breaks an evolutionary constraint; i.e. "phenotypes that allowed a species to interact with the environment in a novel way" (Stroud & Losos, 2016, p 508).

Phenotype: a set of features of an individual that stems from the interactions between genotype and environment.

Synnovation: interacting combination of traits with a particular consequence (Donoghue & Sanderson 2015).

Trait: a heritable attribute of biological lineages (individuals, populations, species, clades) that can be observed.

Trigger: Event or situation starting a radiation.

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References

ALBERT V. A., BARBAZUK, W. B., DEPAMPHILIS, C. W., DER, J. P., LEEBENS-MACK, J., MA, H., PALMER, J. D., ROUNSLEY, S., SANKOFF, D., SCHUSTER, S. C., SOLTIS, D. E., SOLTIS, P. S., WESSLER, S. R., WING, R. A., ALBERT, V. A., et al. (2013). The *Amborella* genome and the evolution of flowering plants. *Science* **342,** 1241089–1241089.

ALFARO M. E., SANTINI, F., BROCK, C., ALAMILLO, H., DORNBURG, A., RABOSKY, D. L., CARNEVALE, G. & HARMON, L. J. (2009). Nine exceptional radiations plus high turnover explain species diversity in jawed vertebrates. *Proceedings of the National Academy of Sciences of the United States of America* **106,** 13410–13414.

ALTEKAR G., DWARKADAS, S., HUELSENBECK, J. P. & RONQUIST, F. (2004). Parallel Metropolis coupled Markov chain Monte Carlo for Bayesian phylogenetic inference. *Bioinformatics* **20,** 407–415.

ARAKAKI M., CHRISTIN, P.-A., NYFFELER, R., LENDEL, A., EGGLI, U., OGBURN, R. M., SPRIGGS, E., MOORE, M. J. & EDWARDS, E. J. (2011). Contemporaneous and recent radiations of the world's major succulent plant lineages. *Proceedings of the National Academy of Sciences of the United States of America* **108,** 8379–8384.

ARNOLD S. J., PFRENDER, M. E. & JONES, A. G. (2001). The adaptive landscape as a conceptual bridge between micro- and macroevolution. *Genetica* **112,** 9–32.

BALDWIN B. G. (1997). Adaptive radiation of the Hawaiian silversword alliance: congruence and conflict of phylogenetic evidence from molecular and non-molecular investigations. In *Molecular evolution and adaptive radiation* (ed. T. J. Givnish and K. J. Sytsma), pp. 103–128. Cambridge University Press, UK, London.

BALDWIN B. G. & SANDERSON, M. J. (1998). Age and rate of diversification of the Hawaiian silversword alliance (Compositae). *Proceedings of the National Academy of Sciences of the United States of America* **95,** 9402–9406.

BEAULIEU J. M. & O'MEARA, B. C. (2016). Detecting hidden diversification shifts in models of trait-dependent speciation and extinction. *Systematic Biology* **65,** 583–601.

BEAULIEU J. M., O'MEARA, B. C. & DONOGHUE, M. J. (2013). Identifying hidden rate changes in the evolution of a binary morphological character: the evolution of plant habit in campanulid angiosperms. *Systematic Biology* **62,** 725–737.

BEERLING D. J. & OSBORNE, C. P. (2006). The origin of the savanna biome. *Global Change Biology* **12,** 2023–2031.

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,** 728–723.

BLOMBERG S. P., GARLAND, T. & IVES, A. R. (2003). Testing for phylogenetic signal in comparative data: behavioral traits are more labile. *Evolution* **57,** 717–745.

BOND W. J., WOODWARD, F. I. & MIDGLEY, G. F. (2005). The global distribution of ecosystems in a world without fire. *New Phytologist* **165,** 525–537.

BORREGAARD M. K., AMORIM, I. R., BORGES, P. A. V., CABRAL, J. S., FERNADEZ-PALACIOS, J. M., FIELD, R., HEANEY, L. R., KREFT, H., MATTHEWS, T. J., OLESEN, J. M., PRICE, J., RIGAL, F., STEINBAUER, M. J., TRIANTIS, K. A., VALENTE, L., et al. (2017). Oceanic island biogeography through the lens of the general dynamic model: assessment and prospect. *Biological Reviews* **92,** 830–853.

BORREGAARD M. K., MATTHEWS, T. J. & WHITTAKER, R. J. (2016). The general dynamic model: towards a unified theory of island biogeography? *Global Ecology and Biogeography* **25,** 805–816.

BOUCHENAK-KHELLADI Y., ONSTEIN, R. E., XING, Y., SCHWERY, O. & LINDER, H. P. (2015). On the complexity of triggering evolutionary radiations. *New Phytologist* **207,** 313–326.

871 BOUCHER F. C., DEMERY, V., CONTI, E., HARMON, L. J. & UYEDA, J. (2018). A general model for estimating
872 macroevolutionary landscapes. *Systematic Biology* **67,** 304–319.

873 BRASSAC J. & BLATTNER, F. R. (2015). Species-level phylogeny and polyploid relationships in *Hordeum*
874 (Poaceae) inferred by next-generation sequencing and *in silico* cloning of multiple nuclear loci.
875 *Systematic Biology* **64,** 792–808.

876 BREITKOPF H., ONSTEIN, R. E., CAFASSO, D., SCHLÜTER, P. M. & COZZOLINO, S. (2015). Multiple shifts to different
877 pollinators fuelled rapid diversification in sexually deceptive *Ophrys* orchids. *New Phytologist*
878 **207,** 377–389.

879 BURNHAM K. P. & ANDERSON, D. R. (2002). *Model selection and multimodel inference: a practical*
880 *information-theoretic approach*, 2nd edition. Springer Verlag, New York, Berlin, Heidelberg.

881 BUTLER M. A. & KING, A. A. (2004). Phylogenetic comparative analysis: a modeling approach for adaptive
882 evolution. *American Naturalist* **164,** 683–695.

883 CAETANO D. S., O'MEARA, B. C. & BEAULIEU, J. M. (2018). Hidden state models improve state-dependent
884 diversification approaches, including biogeographical models. *Evolution* **27,** 2308–2324.

885 COMES H. P., TRIBSCH, A. & BITTKAU, C. (2008). Plant speciation in continental island floras as exemplified by
886 *Nigella* in the Aegean Archipelago. *Philosophical transactions of the Royal Society of London.*
887 *Series B, Biological sciences* **363,** 3083–3096.

888 CORNELL H. V. (2013). Is regional species diversity bounded or unbounded? *Biological Reviews* **88,** 140-165.

889 DE VLADAR H. P., SANTOS, M. & SZATHMARY, E. (2017). Grand views of evolution. *Trends in Ecology & Evolution*
890 **32,** 324–334.

891 DONOGHUE M. J. & EDWARDS, E. J. (2014). Biome shifts and niche evolution in plants. *Annual Review of*
892 *Ecology, Evolution, and Systematics* **45,** 547–572.

893 DONOGHUE M. J. & SANDERSON, M. J. (2015). Confluence, synnovation, and depauperons in plant
894 diversification. *New Phytologist* **207,** 260–274.

895 DRUMMOND A. J., HO, S. Y. W., PHILLIPS, M. J. & RAMBAUT, A. (2006). Relaxed phylogenetics and dating with
896 confidence. *PLoS Biology* **4,** 699–710.

897 DRUMMOND C. S., EASTWOOD, R. J., MIOTTO, S. T. S. & HUGHES, C. E. (2012). Multiple continental radiations and
898 correlates of diversification in *Lupinus* (Leguminosae): testing for key innovation with incomplete
899 taxon sampling. *Systematic Biology* **61,** 443–460.

900 DRURY J., CLAVEL, J., MANCEAU, M. & MORLON, H. (2016). Estimating the effect of competition on trait
901 evolution using maximum likelihood inference. *Systematic Biology* **65,** 700–710.

902 DURET L. (2002). Evolution of synonymous codon usage in metazoans. *Current Opinion in Genetics &*
903 *Development* **12,** 640–649.

904 ELDREDGE N. & GOULD, S. J. (1972). Speciation and punctuated equilibria: an alternative to phyletic
905 gradualism. In *Models in Paleobiology* (ed. T. J. M. Schopf), pp. 82–115. Freeman, Cooper and
906 Company, San Francisco.

907 ERWIN D. H. (1992). A preliminary classification of evolutionary radiations. *Historical Biology* **6,** 133–147.

908 FARJON A. (2018). The Kew review: conifers of the world. *Kew Bulletin* **73,** 1–16.

909 FELSENSTEIN J. (1973). Maximum-likelihood estimation of evolutionary trees from continuous characters.
910 *American Journal of Human Genetics* **25,** 471–492.

911 FELSENSTEIN J. (1981). Evolutionary trees from DNA sequences: a maximum likelihood approach. *Journal of*
912 *Molecular Evolution* **17,** 368–376.

913 FELSENSTEIN J. (1985). Phylogenies and the comparative method. *American Naturalist* **125,** 1–15.

FELSENSTEIN J. (2012). A comparative method for both discrete and continuous characters using the threshold model. *American Naturalist* **179,** 145–156.

FITZJOHN R. G. (2010). Quantitative traits and diversification. *Systematic Biology* **59,** 619–633.

FITZJOHN R. G. (2012). Diversitree: comparative phylogenetic analyses of diversification in R. *Methods in Ecology and Evolution* **3,** 1084–1092.

FLANTUA S. G. A. & HOOGHIEMSTRA, H. (2018). Historical connectivity and mountain biodiversity. In *Mountains, climate and biodiversity* (ed. C. Hoorn, A. Perrigo and A. Antonelli), pp. 171–186. Wiley-Blackwell.

FLANTUA S. G. A., O'DEA, A., ONSTEIN, R. E. & HOOGHIEMSTRA, H. (2019). The flickering connectivity system of the north Andean páramos. *Journal of Biogeography***,** 10.1111/jbi.13607. bioRxiv: 10.1101/569681.

FLEGR J. (2010). Elastic, not plastic species: frozen plasticity theory and the origin of adaptive evolution in sexually reproducing organisms. *Biology Direct* **5,** 2-2.

FOOTE M. (2000). Origination and extinction components of taxonomic diversity: Paleozoic and post-Paleozoic dynamics. *Paleobiology* **26,** 578–605.

FRYER G. (1969). Speciation and adaptive radiation in African lakes. *SIL Proceedings, 1922-2010* **17,** 303–322.

GARAMSZEGI L. Z. (2014). *Modern phylogenetic comparative methods and their application in evolutionary biology*. Springer-Verlag, Berlin, Heidelberg.

GITTENBERGER E. (1991). What about non-adaptive radiation. *Biological Journal of the Linnean Society* **43,** 263–272.

GITTENBERGER E. (2004). Radiation and adaptation, evolutionary biology and semantics. *Organisms Diversity & Evolution* **4,** 135–136.

GIVNISH T. J., MILLAM, K. C., MAST, A. R., PATERSON, T. B., THEIM, T. J., HIPP, A. L., HENSS, J. M., SMITH, J. F., WOOD, K. R. & SYTSMA, K. J. (2009). Origin, adaptive radiation and diversification of the Hawaiian lobeliads (Asterales: Campanulaceae). *Proceedings of the Royal Society of London. Series B, Biological sciences* **276,** 407–416.

GLOR R. E. (2010). Phylogenetic insights on adaptive radiation. *Annual Review of Ecology, Evolution, and Systematics* **41,** 251–270.

GOLDBERG E. E., LANCASTER, L. T. & REE, R. H. (2011). Phylogenetic inference of reciprocal effects between geographic range evolution and diversification. *Systematic Biology* **60,** 451–465.

GOULD S. J. & ELDREDGE, N. (1977). Punctuated equilibria: the tempo and mode of evolution reconsidered. *Paleobiology* **3,** 115–151.

GOULD S. J. & VRBA, E. S. (1982). Exaptation – A missing term in the science of form. *Paleobiology* **8,** 4–15.

GRAFEN A. (1989). The phylogenetic regression. *Philosophical Transactions of the Royal Society of London Series B-Biological Sciences* **326,** 119–157.

GUERRERO P. C., ROSAS, M., ARROYO, M. T. K. & WIENS, J. J. (2013). Evolutionary lag times and recent origin of the biota of an ancient desert (Atacama-Sechura). *Proceedings of the National Academy of Sciences of the United States of America* **110,** 11469–11474.

HANSEN T. F. (1997). Stabilizing selection and the comparative analysis of adaptation. *Evolution* **51,** 1341–1351.

HANSEN T. F. & MARTINS, E. P. (1996). Translating between microevolutionary process and macroevolutionary patterns: The correlation structure of interspecific data. *Evolution* **50,** 1404–1417.

HANSEN T. F., PIENAAR, J. & ORZACK, S. H. (2008). A comparative method for studying adaptation to a randomly evolving environment. *Evolution* **62,** 1558–5646.

HARMON L. J. (2019). Phylogenetic comparative methods, version 1.4, pp. 234, https://lukejharmon.github.io/pcm/.

HARMON L. J., ANDREAZZI, C. S., DÉBARRE, F., DRURY, J., GOLDBERG, E. E., MARTINS, A. B., MELIÁN, C. J., NARWANI, A., NUISMER, S. L., PENNELL, M. W., RUDMAN, S. M., SEEHAUSEN, O., SILVESTRO, D., WEBER, M. & MATTHEWS, B. (2019). Detecting the macroevolutionary signal of species interactions. *Journal of Evolutionary Biology***,** Accepted Author Manuscript. doi:10.1111/jeb.13477.

HARMON L. J. & HARRISON, S. (2015). Species diversity is dynamic and unbounded at local and continental scales. *American Naturalist* **185,** 584–593.

HARMON L. J., LOSOS, J. B., DAVIES, T. J., GILLESPIE, R. G., GITTLEMAN, J. L., JENNINGS, W. B., KOZAK, K. H., MCPEEK, M. A., MORENO-ROARK, F., NEAR, T. J., PURVIS, A., RICKLEFS, R. E., SCHLUTER, D., SCHULTE, J. A., SEEHAUSEN, O., et al. (2010). Early bursts of body size and shape evolution are rare in comparative data. *Evolution* **64,** 2385–2396.

HARMON L. J., SCHULTE, J. A., LARSON, A. & LOSOS, J. B. (2003). Tempo and mode of evolutionary radiation in iguanian lizards. *Science* **301,** 961–964.

HARVEY P. H. & PAGEL, M. D. (1991). *The comparative method in evolutionary biology*. Oxford University Press, Oxford, New York, Tokyo.

HENAO DIAZ L. F., HARMON, L. J., SUGAWARA, M. T. C., MILLER, E. T. & PENNELL, M. W. (2019). Macroevolutionary diversification rates show time dependency. *Proceedings of the National Academy of Sciences of the United States of America* **116,** 7403–7408.

HIGGINS S. I., O'HARA, R. B., BYKOVA, O., CRAMER, M. D., CHUINE, I., GERSTNER, E. M., HICKLER, T., MORIN, X., KEARNEY, M. R. & MIDGLEY, G. F. (2012). A physiological analogy of the niche for projecting the potential distribution of plants. *Journal of Biogeography* **39,** 2132–2145.

HO L. S. T. & ANE, C. (2014). A linear-time algorithm for Gaussian and non-Gaussian trait evolution models. *Systematic Biology* **63,** 397–408.

HÖHNA S., HEATH, T. A., BOUSSAU, B., LANDIS, M. J., RONQUIST, F. & HUELSENBECK, J. P. (2014). Probabilistic graphical model representation in phylogenetics. *Systematic Biology* **63,** 753–771.

HÖHNA S., LANDIS, M. J., HEATH, T. A., BOUSSAU, B., LARTILLOT, N., MOORE, B. R., HUELSENBECK, J. P. & RONQUIST, F. (2016). RevBayes: Bayesian phylogenetic inference using graphical models and an interactive model-specification language. *Systematic Biology* **65,** 726–736.

HUELSENBECK J. P., NIELSEN, R. & BOLLBACK, J. P. (2003). Stochastic mapping of morphological characters. *Systematic Biology* **52,** 131–158.

HUELSENBECK J. P., RANNALA, B. & MASLY, J. (2000). Accommodating phylogenetic uncertainty in evolutionary studies. *Science* **288,** 2349–2350.

HUELSENBECK J. P. & RONQUIST, F. (2001). MrBayes: Bayesian inference of phylogenetic trees. *Bioinformatics* **17,** 754–755.

HUEY R. B., GARLAND, T. & TURELLI, M. (2019). Revisiting a key innovation in evolutionary biology: Felsenstein's "phylogenies and the comparative method". *The American Naturalist***,** 000-000.

HUGHES C. E. & ATCHISON, G. W. (2015). The ubiquity of alpine plant radiations: from the Andes to the Hengduan Mountains. *New Phytologist* **207,** 275–282.

HUGHES C. E. & EASTWOOD, R. (2006). Island radiation on a continental scale: exceptional rates of plant diversification after uplift of the Andes. *Proceedings of the National Academy of Sciences of the United States of America* **103,** 10334–10339.

HUNTER J. P. (1998). Key innovations and the ecology of macroevolution. *Trends in Ecology & Evolution* **13,** 31–36.

IRISARRI I., SINGH, P., KOBLMÜLLER, S., TORRES-DOWDALL, J., HENNING, F., FRANCHINI, P., FISCHER, C., LEMMON, A. R., LEMMON, E. M., THALLINGER, G. G., STURMBAUER, C. & MEYER, A. (2018). Phylogenomics uncovers early hybridization and adaptive loci shaping the radiation of Lake Tanganyika cichlid fishes. *Nature Communications* **9,** 3159.

IVES A. & LI, D. (2018). rr2: an R package to calculate R^2s for regression models. *Journal of Open Source Software* **3,** 1028.

IVES A. R. (2019). R^2s for correlated data: phylogenetic models, LMMs, and GLMMs. *Systematic Biology* **68,** 234–251.

JENTSCH A. & WHITE, P. S. (2019). A theory of pulse dynamics and disturbance in ecology. *Ecology* **in press**.

JØNSSON K. A., FABRE, P. H., FRITZ, S. A., ETIENNE, R. S., RICKLEFS, R. E., JØRGENSEN, T. B., FJELDSÅ, J., RAHBEK, C., ERICSON, P. G. P., WOOG, F., PASQUET, E. & IRESTEDT, M. (2012). Ecological and evolutionary determinants for the adaptive radiation of the Madagascan vangas. *Proceedings of the National Academy of Sciences of the United States of America* **109,** 6620–625.

KHABBAZIAN M., KRIEBEL, R., ROHE, K. & ANÉ, C. (2016). Fast and accurate detection of evolutionary shifts in Ornstein-Uhlenbeck models. *Methods in Ecology and Evolution* **7,** 811–824.

KIMURA M. (1968). Evolutionary rate at the molecular level. *Nature* **217,** 624–626.

KOZAK K. H. & WIENS, J. J. (2010). Accelerated rates of climatic-niche evolution underlie rapid species diversification. *Ecology Letters* **13,** 1378–1389.

LALAND K. N., MATTHEWS, B. & FELDMAN, M. W. (2016). An introduction to niche construction theory. *Evolutionary ecology* **30,** 191–202.

LALAND K. N., ODLING-SMEE, F. J. & FELDMAN, M. W. (1999). Evolutionary consequences of niche construction and their implications for ecology. *Proceedings of the National Academy of Sciences* **96,** 10242–10247.

LANDE R. (1976). Natural selection and random genetic drift in phenotypic evolution. *Evolution* **30,** 314–334.

LANDIS J. B., SOLTIS, D. E., LI, Z., MARX, H. E., BARKER, M. S., TANK, D. C. & SOLTIS, P. S. (2018). Impact of whole-genome duplication events on diversification rates in angiosperms. *American Journal of Botany* **105,** 348–363.

LANDIS M. J. & SCHRAIBER, J. G. (2017). Pulsed evolution shaped modern vertebrate body sizes. *Proceedings of the National Academy of Sciences of the United States of America* **114,** 13224–13229.

LARCOMBE M. J., JORDAN, G. J., BRYANT, D. & HIGGINS, S. I. (2018). The dimensionality of niche space allows bounded and unbounded processes to jointly influence diversification. *Nature Communications* **9,** 4258.

LESLIE A. B., BEAULIEU, J. M., RAI, H. S., CRANE, P. R., DONOGHUE, M. J. & MATHEWS, S. (2012). Hemisphere-scale differences in conifer evolutionary dynamics. *Proceedings of the National Academy of Sciences of the United States of America* **109,** 16217–16221.

LIEM K. F. (1973). Evolutionary strategies and morphological innovations: cichlid pharyngeal jaws. *Systematic Zoology* **22,** 425–441.

LIM J. Y. & MARSHALL, C. R. (2017). The true tempo of evolutionary radiation and decline revealed on the Hawaiian archipelago. *Nature* **543,** 710–713.

LINDER H. P. & BOUCHENAK-KHELLADI, Y. (2017). Adaptive radiations should not be simplified: the case of the danthonioid grasses. *Molecular Phylogenetics and Evolution* **117,** 179–190.

LINDER H. P., BYKOVA, O., DYKE, J., ETIENNE, R. S., HICKLER, T., KUHN, I., MARION, G., OHLEMULLER, R., SCHYMANSKI, S. J. & SINGER, A. (2012). Biotic modifiers, environmental modulation and species distribution models. *Journal of Biogeography* **39,** 2179–2190.

LINDER H. P., LEHMANN, C. E. R., ARCHIBALD, S., OSBORNE, C. P. & RICHARDSON, D. M. (2018). Global grass (Poaceae) success underpinned by traits facilitating colonization, persistence and habitat transformation. *Biological Reviews* **93,** 1125–1144.

LOSOS J. B. (1994). Integrative approaches to evolutionary ecology - Anolis Lizards as model systems. *Annual Review of Ecology and Systematics* **25,** 467–493.

LOSOS J. B. (2011). Seeing the forest for the trees: the limitations of phylogenies in comparative biology. *American Naturalist* **177,** 709–727.

LOSOS J. B. & RICKLEFS, R. E. (2009). Adaptation and diversification on islands. *Nature* **457,** 830–836.

LUEBERT F. & WEIGEND, M. (2014). Phylogenetic insights into Andean plant diversification. *Frontiers in Ecology and Evolution* **2,** 27.

MADDISON W. P. (1997). Gene trees in species trees. *Systematic Biology* **46,** 523–536.

MADDISON W. P. & FITZJOHN, R. G. (2015). The unsolved challenge to phylogenetic correlation tests for categorical characters. *Systematic Biology* **64,** 127–136.

MADDISON W. P., MIDFORD, P. E. & OTTO, S. P. (2007). Estimating a binary character's effect on speciation and extinction. *Systematic Biology* **56,** 701–710.

MADRIÑÁN S., CORTÉS, A. J. & RICHARDSON, J. E. (2013). Páramo is the world's fastest evolving and coolest biodiversity hotspot. *Frontiers in Genetics* **4,** 1–7.

MAGALLÓN S. S. & SANDERSON, M. J. (2001). Absolute diversification rates in Angiosperm clades. *Evolution* **55,** 1762–780.

MARAZZI B., ANÉ, C., SIMON, M. F., DELGADO-SALINAS, A., LUCKOW, M. & SANDERSON, M. J. (2012). Locating evolutionary precursors on a phylogenetic tree. *Evolution* **66,** 3918–3930.

MARSHALL C. R. & QUENTAL, T. B. (2016). The uncertain role of diversity dependence in species diversification and the need to incorporate time-varying carrying capacities. *Philosophical transactions of the Royal Society of London. Series B, Biological sciences* **371,** 20150217.

MARTINS E. P. & HANSEN, T. F. (1997). Phylogenies and the comparative method: a general approach to incorporating phylogenetic information into the analysis of interspecific data. *American Naturalist* **149,** 646–667.

MCPEEK M. A. (2008). The ecological dynamics of clade diversification and community assembly. *The American Naturalist* **172,** E270–E284.

MEIER J. I., MARQUES, D. A., MWAIKO, S., WAGNER, C. E., EXCOFFIER, L. & SEEHAUSEN, O. (2017). Ancient hybridization fuels rapid cichlid fish adaptive radiations. *Nature Communications* **8,** 14363.

MEYER A., MORRISSEY, J. M. & SCHARTL, M. (1994). Recurrent origin of a sexually selected trait in *Xiphophorus* fishes inferred from a molecular phylogeny. *Nature* **368,** 539–542.

MILLER A. H. (1949). Some ecologic and morphologic considerations in the evolution of higher taxonomic categories. In *Ornithologie als Biologische Wissenschaft* (ed. E. Mayr and E. Schüz), pp. 84–88. Carl Winter.

MORLON H. L. N. (2014). Phylogenetic approaches for studying diversification. *Ecology Letters* **17,** 508–525.

NEE S., MAY, R. M. & HARVEY, P. H. (1994). The reconstructed evolutionary process. *Philosophical transactions of the Royal Society of London. Series B, Biological sciences* **344,** 305–311.

NEVADO B., ATCHISON, G. W., HUGHES, C. E. & FILATOV, D. A. (2016). Widespread adaptive evolution during repeated evolutionary radiations in New World lupins. In *Nature Communications*, vol. 7, pp. 1–9. Nature Publishing Group.

NORDER S. J., PROIOS, K., WHITTAKER, R. J., ALONSO, M. R., BORGES, P. A. V., BORREGAARD, M. K., COWIE, R. H., FLORENS, F. B. V., DE FRIAS MARTINS, A. M., IBÁÑEZ, M., KISSLING, W. D., DE NASCIMENTO, L., OTTO, R., PARENT, C. E., RIGAL, F., et al. (2019). Beyond the Last Glacial Maximum: island endemism is best

explained by long-lasting archipelago configurations. *Global Ecology and Biogeography* **28,** 184–197.

NOSIL P., HARMON, L. J. & SEEHAUSEN, O. (2009). Ecological explanations for (incomplete) speciation. *Trends in Ecology & Evolution* **24,** 145–156.

NUISMER S. L. & HARMON, L. J. (2015). Predicting rates of interspecific interaction from phylogenetic trees. *Ecology Letters* **18,** 17–27.

NÜRK N. M., ATCHISON, G. W. & HUGHES, C. E. (2019). Island woodiness underpins accelerated disparification in plant radiations. *New Phytologist*.

NÜRK N. M., MICHLING, F. & LINDER, H. P. (2018). Are the radiations of temperate lineages in tropical alpine ecosystems pre-adapted? *Global Ecology and Biogeography* **27,** 334–345.

O'MEARA B. C. (2012). Evolutionary inferences from phylogenies: a review of methods. *Annual Review of Ecology, Evolution, and Systematics* **43,** 267–285.

O'MEARA B. C., ANE, C., SANDERSON, M. J. & WAINWRIGHT, P. C. (2006). Testing for different rates of continuous trait evolution using likelihood. *Evolution* **60,** 922–933.

OGBURN R. M. & EDWARDS, E. J. (2015). Life history lability underlies rapid climate niche evolution in the angiosperm clade Montiaceae. *Molecular Phylogenetics and Evolution* **92,** 181–192.

ONSTEIN R. E., BAKER, W. J., COUVREUR, T. L. P., FAURBY, S., HERRERA-ALSINA, L., SVENNING, J. C. & KISSLING, W. D. (2018). To adapt or go extinct? The fate of megafaunal palm fruits under past global change. *Proceedings of the Royal Society of London. Series B, Biological sciences* **285,** 20180882.

OSBORN H. F. (1902). The law of adaptive radiation. *The American Naturalist* **36,** 353–363.

PAGEL M. (1994). Detecting correlated evolution on phylogenies: a general method for the comparative analysis of discrete characters. *Proceedings of the Royal Society of London. Series B, Biological sciences* **225,** 37–45.

PAGEL M. (1999). Inferring the historical patterns of biological evolution. *Nature* **401,** 877–884.

PARADIS E. (2005). Statistical analysis of diversification with species traits. *Evolution* **59,** 1–12.

PAULUS H. F. & GACK, C. (1990). Pollinators as prepollinating isolation factors: evolution and speciation in *Ophrys* (Orchidaceae). *Israel Journal of Botany* **39,** 43–79.

PIRES M. M., SILVESTRO, D. & QUENTAL, T. B. (2017). Interactions within and between clades shaped the diversification of terrestrial carnivores. *Evolution* **71,** 1855–1864.

PORTNER H. O. (2002). Climate variations and the physiological basis of temperature dependent biogeography: systemic to molecular hierarchy of thermal tolerance in animals. *Comparative Biochemistry and Physiology a-Molecular and Integrative Physiology* **132,** 739–761.

POUYET F., MOUCHIROUD, D., DURET, L. & SEMON, M. (2017). Recombination, meiotic expression and human codon usage. *Elife* **6,** e27344.

R CORE TEAM. (2013). R. R foundation for statistical computing, available from http://www.R-project.org, Vienna, Austria.

RABOSKY D. L. (2006). Likelihood methods for detecting temporal shifts in diversification rates. *Evolution* **60,** 1152–1164.

RABOSKY D. L. (2010). Extinction rates should not be estimated from molecular phylogenies. *Evolution* **64,** 1816–1824.

RABOSKY D. L. (2013). Diversity-dependence, ecological speciation, and the role of competition in macroevolution. *Annual Review of Ecology, Evolution, and Systematics, Vol 44* **44,** 481–502.

RABOSKY D. L. (2014). Automatic detection of key innovations, rate shifts, and diversity-dependence on phylogenetic trees. *PloS One* **9,** e89543.

RABOSKY D. L. & GLOR, R. E. (2010). Equilibrium speciation dynamics in a model adaptive radiation of island lizards. *Proceedings of the National Academy of Sciences of the United States of America* **107,** 22178–22183.

RABOSKY D. L. & GOLDBERG, E. E. (2015). Model inadequacy and mistaken inferences of trait-dependent speciation. *Systematic Biology* **64,** 340–355.

RANGEL T. F., EDWARDS, N. R., HOLDEN, P. B., DINIZ, J. A. F., GOSLING, W. D., COELHO, M. T. P., CASSEMIRO, F. A. S., RAHBEK, C. & COLWELL, R. K. (2018). Modeling the ecology and evolution of biodiversity: biogeographical cradles, museums, and graves. *Science* **361,** eaar5452.

REVELL L., HARMON, L. & COLLAR, D. (2008). Phylogenetic signal, evolutionary process, and rate. *Systematic Biology* **57,** 591–601.

REVELL L. J. (2012). phytools: an R package for phylogenetic comparative biology (and other things). *Methods in Ecology and Evolution* **3,** 217–223.

REVELL L. J. (2014). Ancestral character estimation under the threshold model from quantitative genetics. *Evolution* **68,** 743–759.

ROHDE R. A. & MULLER, R. A. (2005). Cycles in fossil diversity. *Nature* **434,** 208–210.

ROLSHAUSEN G., DAVIES, T. J. & HENDRY, A. P. (2018). Evolutionary rates standardized for evolutionary space: perspectives on trait evolution. *Trends in Ecology & Evolution* **33,** 379–389.

ROMÁN-PALACIOS C. & WIENS, J. J. (2018). The Tortoise and the Finch: testing for island effects on diversification using two iconic Galápagos radiations. *Journal of Biogeography* **45,** 1701–1712.

SAKAMOTO M. & VENDITTI, C. (2018). Phylogenetic non-independence in rates of trait evolution. *Biology Letters* **14,** 20180502.

SALZBURGER W. (2018). Understanding explosive diversification through cichlid fish genomics. *Nature Reviews Genetics* **19,** 705–717.

SANDERSON M. J. (1997). A nonparametric approach to estimating divergence times in the absence of rate constancy. *Molecular Biology and Evolution* **14,** 1218–1231.

SANDERSON M. J. & DONOGHUE, M. J. (1994). Shifts in diversification rate with the origin of Angiosperms. *Science* **264,** 1590–1593.

SCHIESTL F. P., AYASSE, M., PAULUS, H. F., LÖFSTEDT, C., HANSSON, B. S., IBARRA, F. & FRANCKE, W. (1999). Orchid pollination by sexual swindle. *Nature* **399,** 421–422.

SCHIESTL F. P., AYASSE, M., PAULUS, H. F., LÖFSTEDT, C., HANSSON, B. S., IBARRA, F. & FRANCKE, W. (2000). Sex pheromone mimicry in the early spider orchid (*Ophrys sphegodes*): patterns of hydrocarbons as the key mechanism for pollination by sexual deception. *Journal of Comparative Physiology A* **186,** 567–574.

SCHLUTER D. (2000). *The ecology of adaptive radiation*. Oxford University Press, Oxford, New York.

SCHLÜTER P. M., XU, S., GAGLIARDINI, V., WHITTLE, E. J., SHANKLIN, J., GROSSNIKLAUS, U. & SCHIESTL, F. P. (2011). Stearoyl-acyl carrier protein desaturases are associated with floral isolation in sexually deceptive orchids. *Proceedings of the National Academy of Sciences of the United States of America* **108,** 5696–5701.

SCHOENER T. W. (1968). The Anolis lizards of Bimini: resource partitioning in a complex fauna. *Ecology* **49,** 704–726.

SCHWERY O., ONSTEIN, R. E., BOUCHENAK-KHELLADI, Y., XING, Y. W., CARTER, R. J. & LINDER, H. P. (2015). As old as the mountains: the radiations of the Ericaceae. *New Phytologist* **207,** 355–367.

SEDEEK K. E. M., SCOPECE, G., STAEDLER, Y. M., SCHÖNENBERGER, J., COZZOLINO, S., SCHIESTL, F. P. & SCHLÜTER, P. M. (2014). Genic rather than genome-wide differences between sexually deceptive *Ophrys* orchids with different pollinators. *Molecular Ecology* **23,** 6192–6205.

SEDEEK K. E. M., WHITTLE, E., GUTHÖRL, D., GROSSNIKLAUS, U., SHANKLIN, J. & SCHLÜTER, P. M. (2016). Amino acid change in an orchid desaturase enables mimicry of the pollinator's sex pheromone *Current Biology* **26,** 1505–1511.

SEEHAUSEN O. (2006). African cichlid fish: a model system in adaptive radiation research. *Proceedings of the Royal Society of London. Series B, Biological sciences* **273,** 1987–1998.

SEEHAUSEN O. (2015). Process and pattern in cichlid radiations - inferences for understanding unusually high rates of evolutionary diversification. *New Phytologist* **207,** 304–312.

SILVESTRO D., ANTONELLI, A., SALAMIN, N. & QUENTAL, T. B. (2015). The role of clade competition in the diversification of North American canids. *Proceedings of the National Academy of Sciences of the United States of America* **112,** 8684–8689.

SIMÕES M., BREITKREUZ, L., ALVARADO, M., BACA, S., COOPER, J. C., HEINS, L., HERZOG, K. & LIEBERMAN, B. S. (2016). The evolving theory of evolutionary radiations. *Trends in Ecology & Evolution* **31,** 27–34.

SIMPSON B. B. (1974). Glacial migrations of plants: island biogeographical evidence. *Science* **185,** 698–700.

SIMPSON G. G. (1944). *Tempo and mode in evolution*. Columbia University Press, New York.

SIMPSON G. G. (1953). *The major features of evolution*. Columbia University Press,, New York.

STADLER T. (2011). Inferring speciation and extinction processes from extant species data. *Proceedings of the National Academy of Sciences of the United States of America* **108,** 16145–16146.

STADLER T. & SMRCKOVA, J. (2016). Estimating shifts in diversification rates based on higher-level phylogenies. *Biology Letters* **12,** 20160273.

STANLEY S. M. (1979). *Macroevolution – Pattern and process*. WH Freeman & Co, San Francisco, CA, USA.

STEBBINS G. L. (1947). Evidence on rates of evolution from the distribution of existing and fossil plant species. *Ecological Monographs* **17,** 149–158.

STEINBAUER M. J., FIELD, R., GRYTNES, J. A., TRIGAS, P., AH-PENG, C., ATTORRE, F., BIRKS, H. J. B., BORGES, P. A. V., CARDOSO, P., CHOU, C. H., DE SANCTIS, M., DE SEQUEIRA, M. M., DUARTE, M. C., ELIAS, R. B., FERNANDEZ-PALACIOS, J. M., et al. (2016). Topography-driven isolation, speciation and a global increase of endemism with elevation. *Global Ecology and Biogeography* **25,** 1097–1107.

STROUD J. T. & LOSOS, J. B. (2016). Ecological opportunity and adaptive radiation. *Annual Review of Ecology, Evolution, and Systematics* **47,** 507–532.

TANENTZAP A. J., BRANDT, A. J., SMISSEN, R. D., HEENAN, P. B., FUKAMI, T. & LEE, W. G. (2015). When do plant radiations influence community assembly? The importance of historical contingency in the race for niche space. *New Phytologist* **207,** 468–479.

TANK D. C., EASTMAN, J. M., PENNELL, M. W., SOLTIS, P. S., SOLTIS, D. E., HINCHLIFF, C. E., BROWN, J. W., SESSA, E. B. & HARMON, L. J. (2015). Nested radiations and the pulse of angiosperm diversification: increased diversification rates often follow whole genome duplications. *New Phytologist* **207,** 454–467.

THOMPSON J. N. (2005). *The geographic mosaic of coevolution –Interspecific interactions*. University of Chicago Press, Chicago, IL.

TITLE P. O. & BURNS, K. J. (2015). Rates of climatic niche evolution are correlated with species richness in a large and ecologically diverse radiation of songbirds. *Ecology Letters* **18,** 433–440.

UYEDA J. C., ZENIL-FERGUSON, R. & PENNELL, M. W. (2018). Rethinking phylogenetic comparative methods. *Systematic Biology* **67,** 1091–1109.

VALENTE L. M., ETIENNE, R. S. & PHILLIMORE, A. B. (2014). The effects of island ontogeny on species diversity and phylogeny. *Proceedings of the Royal Society of London. Series B, Biological sciences* **281,** 20133227.

VALENTE L. M., PHILLIMORE, A. B. & ETIENNE, R. S. (2015). Equilibrium and non-equilibrium dynamics simultaneously operate in the Galápagos islands. *Ecology Letters* **18,** 844–852.

1228 VAN VALEN L. (1971). Adaptive zones and the orders of Mammals. *Evolution* **25,** 420–428.

1229 VERBOOM G. A., BERGH, N. G., HAIDEN, S. A., HOFFMANN, V. & BRITTON, M. N. (2015). Topography as a driver of
1230 diversification in the Cape Floristic Region of South Africa. *New Phytologist* **207,** 368–376.

1231 WAGNER C. E., HARMON, L. J. & SEEHAUSEN, O. (2012). Ecological opportunity and sexual selection together
1232 predict adaptive radiation. *Nature* **487,** 366–370.

1233 WEIGELT P., STEINBAUER, M. J., CABRAL, J. S. & KREFT, H. (2016). Late Quaternary climate change shapes island
1234 biodiversity. *Nature* **532,** 99–102.

1235 WELLBORN G. A. & LANGERHANS, R. B. (2015). Ecological opportunity and the adaptive diversification of
1236 lineages. *Ecology and Evolution* **5,** 176–195.

1237 WHITE P. S. & JENTSCH, A. (2001). The search for generality in studies of disturbance and ecosystem
1238 dynamics. In *Progress in Botany*, vol. 62. *Progress in Botany* (ed. K. Esser, U. Lüttge, J. W. Kadereit
1239 and W. Beyschlag), pp. 399–450. Springer, Berlin, Heidelberg.

1240 WHITTAKER R. J., TRIANTIS, K. A. & LADLE, R. J. (2008). A general dynamic theory of oceanic island
1241 biogeography. *Journal of Biogeography* **35,** 977–994.

1242 WIENS J. J. (2004a). Speciation and ecology revisited: phylogenetic niche conservatism and the origin of
1243 species. *Evolution* **58,** 193–197.

1244 WIENS J. J. (2004b). What is speciation and how should we study it? *American Naturalist* **163,** 914–923.

1245 XU S. & SCHLÜTER, P. M. (2015). Modeling the two-locus architecture of divergent pollinator adaptation:
1246 how variation in *SAD* paralogs affects fitness and evolutionary divergence in sexually deceptive
1247 orchids. *Ecology and Evolution* **5,** 493–502.

1248 XU S., SCHLÜTER, P. M., GROSSNIKLAUS, U. & SCHIESTL, F. P. (2012). The genetic basis of pollinator adaptation in
1249 a sexually deceptive orchid. *PLoS Genetics* **8,** e1002889.

1250 XU S., SCHLÜTER, P. M., SCOPECE, G., BREITKOPF, H., GROSS, K., COZZOLINO, S. & SCHIESTL, F. P. (2011). Floral
1251 isolation is the main reproductive barrier among closely related sexually deceptive orchids.
1252 *Evolution: International Journal of Organic Evolution* **65,** 2606–2620.