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Confluence, synnovation, and depauperons in plant diversification

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Summary

We review the empirical phylogenetic literature on plant diversification, highlighting challenges in separating the effects of speciation and extinction, in specifying diversification mechanisms, and in making convincing arguments. In recent discussions of context dependence, key opportunities and landscapes, and indirect effects and lag times, we see a distinct shift away from single-point/single-cause 'key innovation' hypotheses toward more nuanced explanations involving multiple interacting causal agents assembled step-wise through a tree. To help crystalize this emerging perspective we introduce the term 'synnovation' (a hybrid of 'synergy' and 'innovation') for an interacting combination of traits with a particular consequence ('key synnovation' in the case of increased diversification rate), and the term 'confluence' for the sequential coming together of a set of traits (innovations and synnovations), environmental changes, and geographic movements along the branches of a phylogenetic tree. We illustrate these concepts using the radiation of Bromeliaceae. We also highlight the generality of these ideas by considering how rate heterogeneity associated with a confluence relates to the existence of particularly species-poor lineages, or 'depauperons.' Many challenges are posed by this re-purposed research framework, including difficulties associated with partial taxon sampling, uncertainty in divergence time estimation, and extinction.

I. Introduction

Species diversity is evidently not distributed evenly through time (Simpson, 1953) or across geography (Willis, 1922), taxonomy (Scotland & Sanderson, 2004), or phylogenetic history (Vargas & Zardoya, 2014). Nor is it distributed according to a simple random

model with a constant rate of speciation and extinction. This was shown first by comparison of simulated and real diversity curves in the fossil record (Raup *et al.*, 1973) and surveys of diversities of higher taxa with known fossil ages (Stanley, 1985); then in assays of phylogenetic tree shape and topology (Mooers & Heard, 1997), supported subsequently using phylogenetic trees with estimated

divergence times (Pybus & Harvey, 2000). Departures from a homogeneous diversification rate must lead to both unexpectedly species-rich and unexpectedly depauperate clades, but most work has focused on ‘radiations’, in which species richness significantly exceeds some background level (a Web of Science title search for ‘species-rich’ finds 354 citations, vs only 46 for ‘species-poor’). Indeed, the word ‘innovation,’ which is often used in connection with radiations, has a decidedly positive connotation, suggesting the *promotion* of diversity. Although this bias may have neglected some interesting patterns – and we draw attention here to the existence and causes of especially depauperate lineages – our focus is also squarely on plant radiations in the sense of increased diversification rate.

While we fully appreciate that the evolution of ‘disparity’ (in morphology, physiology, etc.) is of tremendous interest, and that it is central to the definitions of ‘adaptive radiation’ and ‘key innovation’ in the eyes of many authors (reviewed by Givnish, 1997; and unpublished; Sanderson, 1998; Losos & Mahler, 2010; Glor, 2010), we have chosen to concentrate here on the other major attribute that has figured prominently in these discussions, namely differential rates of diversification, which in turn are a function of the origin and extinction of species. This, we contend, is a worthy object of study in its own right, regardless of what views one holds on the definition of ‘adaptive radiation’. Of course, having decided to focus on diversification, it naturally becomes interesting to ask whether rapid diversification always, sometimes, or only rarely is associated with the evolution of significant disparity, and to try to identify any general circumstances where more or less disparity is associated with diversification. Note that we are not obliged to commit to any particular definition of ‘adaptive radiation’ to ask and to answer such questions clearly. In fact, as Olsen & Arroyo-Santos (2009) argued, invoking ‘adaptive radiation’ in this context may just distract attention from analyses of the underlying variables and, on the whole, may cause more trouble than it is worth.

Our main contention is that the study of radiations has matured faster than the terminology available to describe them. We believe more attention needs to be focused on what we term the *confluence* of a variety of interacting events and, as a step in this direction, we also introduce the term *synnovation* to highlight synergistic interactions among traits. Whereas *synnovation* and related terms focus on the promotion of diversification, the notion of confluence can just as well apply to factors resulting in species-poor lineages, or *depauperons*. Our hope is that these ideas will focus research in even more integrative directions, and will help to crystalize for broader audiences the great progress that our community has been making.

II. Lessons from the literature

As the analytical methods for studying diversification in a phylogenetic context have recently been thoroughly reviewed (e.g. Etienne & Haegeman, 2012; Stadler, 2013; Morlon, 2014), we motivate our proposals mainly based on lessons from empirical studies. The relevant literature is now so vast, however, that we highlight only selected studies that have figured prominently and

that help us to make some general observations. To focus our effort further, we primarily derive our inferences from studies of living plant species, with only brief consideration of fossil taxa.

We draw six take-home messages from our reading of the empirical literature. The first three are broadly related to testing radiation hypotheses and deriving convincing conclusions – they are more methodologically oriented. The last three are more biological and relate to our overall conception of the diversification problem. Together, we think these signal a major shift over the past few decades from an emphasis on simple causal hypotheses to more elaborate explanations involving multiple interacting agents (e.g. Drummond *et al.*, 2012; Wagner *et al.*, 2012).

1. Parsing speciation and extinction

The net diversification rate of a clade (r) is the difference between its rate of speciation (s), and extinction (e): that is, $r = s - e$. The nine possible combinations of changes in speciation and extinction rate are shown in Table 1, which emphasizes that radiations can be driven by increasing the speciation rate alone, by decreasing the extinction rate alone, or combinations of both. Many case studies have highlighted traits that are viewed as increasing speciation rate, for example, nectar spurs (Hodges & Arnold, 1995) or bilateral flower symmetry (Sargent, 2004). Others have highlighted traits that may drive radiation primarily by decreasing extinction rate, for example, latex production (Farrell *et al.*, 1991) or extrafloral nectaries (Marazzi & Sanderson, 2010).

The methodological challenge of inferring separate rates of speciation and extinction are well known (Nee, 2006; Rabosky, 2010), and we will note only that many studies are limited to estimating the net rate of diversification (e.g. Baldwin & Sanderson, 1998; Beaulieu & Donoghue, 2013). Instead, we draw attention to the likelihood that many individual factors influence speciation and extinction simultaneously, in the same direction or in opposite directions. For example, the evolution of chemical defenses in *Inga* (Fabaceae; Richardson *et al.*, 2001a; Kursar *et al.*, 2009) and *Protium* (Burseraceae; Fine *et al.*, 2014) might affect (in combination with other factors, such as habitat specialization) both speciation and extinction by increasing species range sizes and the coexistence of related species within communities. Such simultaneous effects also apply to geographic movements: entering a new area might increase the speciation rate by opening up new habitats

Table 1 Nine possible effects of a change along a phylogenetic tree on diversification

	Speciation rate	Extinction rate	Consequences for clade
Affects neither	–	–	Nothing happens
Affects one	Up	–	Speciation-driven radiation
	–	Down	Extinction-driven radiation
Affects both	Down	–	Slow death
	–	Up	Slow death
	Up	Up	Lots of turnover
	Down	Down	Little turnover
	Up	Down	Ultra-radiation
	Down	Up	Die horrible death

and also decrease extinction by release from predators or competitors.

But, in relation to our central argument below, we wish to emphasize that a sequence of phylogenetic events, concentrated along a series of branches in a phylogeny (Fig. 1), can have additive effects and collectively yield the variety of outcomes in Table 1. Thus, a trait that primarily decreases the extinction rate along one branch might be followed by an event that primarily increases the speciation rate, which might then trigger what we regard as a radiation. Such sequences of events delimit multiple regimes within a tree among which diversification rates can vary significantly. We return to this point below.

2. Specifying mechanisms

Surprisingly often, it remains unclear how a character or geographic movement is supposed to connect, mechanistically, to the diversification rate. In many cases an argument is made for the adaptive value of a trait, but not directly for how it would influence speciation and/or extinction. For example, the evolution of the vine habit is said to increase access to different light environments, and thereby to promote survival (Gianoli, 2004), but it is not entirely obvious how this would shift the diversification rate (the same applies to many other cases, for example, monocarp in *Agave* (Agavaceae); Good-Avila *et al.*, 2006). The dots need to be connected as clearly as possible, both to make a compelling

argument and to facilitate further tests. A particular mechanism can make specific testable predictions about the phylogenetic and/or geographic distribution of the trait of interest, and, perhaps more importantly, about the expected distribution of variation in the trait.

As an illustration, consider the seminal work by Hodges and colleagues on nectar spurs in the flowers of *Aquilegia* (Ranunculaceae; Hodges & Arnold, 1995; Hodges, 1997a,b). This clearly specified a mechanism that could increase the rate of speciation: a small difference in spur morphology might influence pollinator behavior and thereby function in pre-mating isolation. An expectation of this model is that sister species should often differ in spur characteristics and pollinator type. Although functional studies have demonstrated the plausibility of the mechanism, increasingly resolved phylogenetic trees for *Aquilegia* cast doubt on the role of spurs in driving speciation (Whittall & Hodges, 2007; Bastida *et al.*, 2010; Fior *et al.*, 2013). Shifts from bees to hummingbirds to hawkmoths have only rarely accompanied speciation events; instead they mark more inclusive clades within which a number of related species share the same basic spur morphology and pollinator type (Whittall & Hodges, 2007). Moreover, the parallel European radiation of *Aquilegia*, which took place within the same time frame as the North American radiation and yielded a similar number of species, entailed little differentiation in pollinators or spur morphology (Bastida *et al.*, 2010).

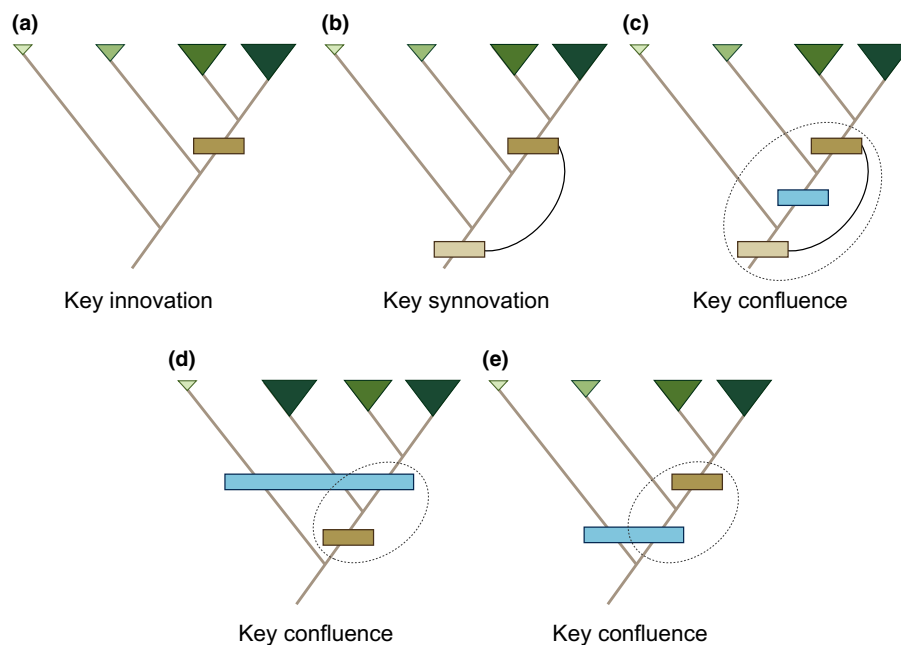


Fig. 1 Phylogenetic trees illustrating key innovation, key synnovation, and key confluence; triangle size and color represent clade diversity. (a) A 'key innovation' hypothesis in which the increased rate of diversification is attributed solely to the one marked character change (brown rectangle). (b) A 'key synnovation' hypothesis in which a pair of synergistically interacting characters (two brown rectangles) underlie a shift in diversification rate; note that the components of a synnovation need not have evolved on adjacent branches, but instead (as shown here) might be separated by some distance in the tree, creating a 'lag time' between the first innovation and the noteworthy increase in diversification. Note that elements of a synnovation (or confluence) might also be inferred to have arisen along a single branch (not shown). (c) A 'key confluence' hypothesis (stippled oval) in which an increased rate of diversification is attributed to the synergistic interaction of the marked synnovation (two brown rectangles) with an environmental/geographic factor (blue rectangle). (d) A key confluence involving an innovation (brown rectangle) followed by climate change (blue rectangle) affecting all of the lineages; here the radiation involves three major branches. (e) A key confluence involving the same innovation and climate change as in (d), but in the reverse order; here the radiation involves just two major branches.

In retrospect, a more likely general explanation for the rapid diversification of *Aquilegia* features geographic movements from Asia into North America and separately into Europe, and subsequent habitat differentiation in both areas, but especially in Europe in connection with recent climate changes (Bastida *et al.*, 2010; Fior *et al.*, 2013). Spurs may have played a less direct role in *Aquilegia* than in some other groups; for example, sister species in the orchid clade *Disa* do often differ in spur characteristics and pollinators (Johnson *et al.*, 1998).

Along these same lines, pollinator-driven diversification has been widely invoked to explain the radiation of angiosperms (Sargent, 2004; Kay & Sargent, 2009; van der Niet & Johnson, 2012; for contrasting results compare Schnitzler *et al.*, 2001 with Schiestl & Schluter, 2009). Specifically, bilaterally symmetrical flowers are viewed as restricting the direction of entry of pollinators with the potential for more precise pollen placement to decrease gene flow between incipient species (Neal *et al.*, 1998). Again, it follows that sister species in clades with bilateral flowers should often differ in the position of pollen deposition, and this could specifically be tested. The same applies to the number and arrangement of stamens, and their mode of operation; for example, the staminal lever in *Salvia* (Lamiaceae; Classen-Bockhoff *et al.*, 2004) and the beak of the galea in *Pedicularis* (Orobanchaceae; Ree, 2005; Eaton *et al.*, 2012). Directly in line with our central argument given in Section III, B. C. O'Meara *et al.* (unpublished) argue that it is the combination of bilateral corolla symmetry and reduced stamen number that triggers higher rates of speciation.

The point of the cases cited above is that, properly framed, it is not just the presence or absence of a state (e.g. bilateral symmetry), but the phylogenetic distribution of the variable(s) specifically related to speciation that matters (cf. the polymorphic 'modulators' of Bouchenak-Khelladi *et al.*, 2015). From this perspective, methods are needed to identify regions in a phylogeny that show the greatest lability in traits of interest (e.g. Marazzi *et al.*, 2012; Beaulieu *et al.*, 2013), which might allow us to test the proposition that heightened variability itself drives diversification (Ricklefs & Renner, 1994, 2000).

3. Convincing arguments

In reviewing the literature, we are struck that there is no one formula for developing a convincing hypothesis about diversification and its causes. Studies of individual clades, and even of individual evolutionary events, can sometimes be compelling, especially when these permit comprehensive sampling and explicit functional comparisons pivoting around an event of interest. Studies that test correlations across multiple clades and events (the stock-in-trade of phylogenetic comparative biology; but see Maddison & FitzJohn, 2015) can be highly useful, of course, in isolating the contribution of particular attributes in contrasting evolutionary backgrounds. In general, the most convincing cases bring together multiple lines of evidence (beyond phylogenetic trees and character reconstructions), including carefully designed functional studies and field experiments (Weber & Agrawal, 2012; cf. Wainwright *et al.*, 2012, for an exceptional zoological example).

Although multiple evolutionary instances are a distinct virtue, their convincingness depends on the veracity of the comparisons. Simple sister group comparisons typically lack the resolution to precisely identify where significant shifts in diversification occurred (e.g. possibly nested well within one of the two clades). Nectar spurs again provide an example. In addition to studying the single origin of spurs in *Aquilegia*, Hodges (1997a,b) compared the diversity of clades with spurs to that of their presumed sister groups without spurs, and found a positive relationship between spurs and diversity in most cases. However, the connection seems less convincing in light of recent phylogenetic work. For example, in *Halenia* (Gentianaceae) spurs evolved well before the major radiation of the group, which was probably driven instead by movement into neotropical mountains (von Hagen & Kadereit, 2003). Likewise, in *Impatiens* (Balsaminaceae) the spurred sepal considerably predated the rapid radiation that began in the Pliocene, perhaps driven more by seed dispersal traits (Janssens *et al.*, 2009).

The same applies to broad studies attempting to identify radiations and innovations using orders, families, etc., as terminals (e.g. Fiz-Palacios *et al.*, 2011; Ferrer & Good, 2012; Magallón *et al.*, 2015; D. Tank *et al.*, unpublished). The basic problem is that a large clade might be identified as a radiation when the actual diversification shift(s) took place within it (e.g. Sanderson & Donoghue, 1994), or perhaps in a more inclusive clade (e.g. Sanderson & Wojciechowski, 1996). This is a very real problem across angiosperms, where many of the exceptionally diverse named clades (e.g. Asteraceae, Poaceae, Orchidaceae, Cactaceae, Fabaceae, monocots, and angiosperms themselves) actually comprise ancient species-poor lineages subtending one or more nested radiations (Smith *et al.*, 2011).

4. Context dependence

The literature consistently shows that the influence of a trait on speciation or extinction (or both) is highly context dependent (de Queiroz, 2002; Donoghue, 2005). Geography and environment are often crucial. For example, fleshy, bird-dispersed fruits have been seen as a key innovation, with their effect on speciation mediated through increased long-distance dispersal and population isolation (e.g. Smith, 2001; Bolmgren & Eriksson, 2005; Biffin *et al.*, 2010), but such fruits may well have a different impact on diversification in mountain forests vs flat savannas. Seed dispersal by ants, often with the production of elaiosomes, probably reduces dispersal distances and gene flow, thereby increasing allopatric differentiation (Lengyel *et al.*, 2009), but myrmecochory may have its greatest impact on diversification in unpredictable, nutrient-limited, or fire-prone environments (Lengyel *et al.*, 2009). Klak *et al.* (2004) highlighted specialized hydrochastic capsules (which release only a few seeds at once, thereby extending dispersal through time) as driving the diversification of the ruschioid Aizoaceae in southern Africa, but these may increase the establishment of allopatric populations mainly in the context of the climatic uncertainty and edaphic heterogeneity of that area (Ellis *et al.*, 2006).

Temporal context is important too. A given landscape might or might not elicit a radiation, depending on when it is encountered, and on the diversity and structure of the biological community at

that time (Simpson, 1953; Donoghue & Edwards, 2014). For example, the radiation of a number of originally Laurasian, cold-adapted clades into the Andes of South America (e.g. *Valeriana* (Caprifoliaceae s.l.): Bell & Donoghue, 2005; *Lupinus* (Fabaceae): Hughes & Eastwood, 2006; *Astragalus* (Fabaceae): Scherson *et al.*, 2008) depended on their arrival at a time when suitable high-elevation environments were emerging and open for colonization. Similarly, the radiation in the Miocene of a variety of lineages that were pre-adapted to arid climates (C_4 grasses, Aizoaceae, etc.: Arakaki *et al.*, 2011) depended on the expansion of such environments in that period. Similarly, Ericaceae adapted to oligotrophic conditions (by virtue of small leathery leaves and specialized mycorrhizal associations) may have been pre-adapted to radiate into mountainous regions as these emerged (Schwery *et al.*, 2014).

Biotic context also matters. For example, radiations within leptosporangiate ferns depended on the presence of angiosperm-dominated forests (Schneider *et al.*, 2004). At a much smaller scale, hummingbirds were present when *Aquilegia* entered North America from Asia (Bastida *et al.*, 2010), and may have provided a 'bridge' there between bee and hawkmoth pollination (Whittall & Hodges, 2007). By contrast, hummingbirds were lost from Europe before the arrival of *Aquilegia*, and the radiation there proceeded with bees alone.

Recent studies feature even more complex context dependence. Kostikova *et al.* (2014) argued that in Polygonaceae the evolution of smaller seeds with specific dormancy and dispersal mechanisms lowered the extinction rate when lineages entered colder seasonal climates. In campanulid angiosperms, Beaulieu & Donoghue (2013) showed a correlation between the production of achene fruits and increased diversification rate, mainly driven by Asterales (with lesser effects in Apiales and Dipsacales), suggesting that this might have been attributable to the geographic spread of the Asteraceae out of South America (along with an increased rate of growth form evolution). In the Bromeliaceae case featured in Section III.6, Givnish *et al.* (2014) explored the effects of the evolution of several characters in the context of biotic interactions in different regions and habitats.

More attention is needed to the context that sympatry with close relatives creates. Increased diversification via allopolyploidy (e.g. *Tragopogon* (Asteraceae): Soltis *et al.*, 2012; *Persicaria* (Polygonaceae): Kim *et al.*, 2008) and homoploid hybrid speciation (e.g. *Helianthus* (Asteraceae): Yakimowski & Rieseberg, 2014) both depend on sympatry, and reinforcement involving recently diverged populations could generate diversity in some groups (e.g. *Costus* (Costaceae): Kay & Schemske, 2008; *Phlox* (Polemoniaceae): Hopkins & Rausher, 2012). Character displacement related to community composition (e.g. *Styloidium* (Styliaceae): Armbruster *et al.*, 1994) has recently been studied in several groups using measures of phylogenetic over-dispersion in local communities (*Burmeistera* (Campanulaceae): Muchhala & Potts, 2007; *Pedicularis*: Eaton *et al.*, 2012; *Iochroma* and relatives (Solanaceae): Muchhala *et al.*, 2014). It remains unclear, however, whether such sympatric divergence translates into increased diversification.

Niche filling and competitive interactions among related species within communities are invoked to explain diversity-dependent

slow-downs in diversification (Raup *et al.*, 1973; Rabosky, 2009, 2014), though a number of other processes could be responsible (Etienne & Rosindell, 2012; Moen & Morlon, 2014), and some models predict the opposite (Emerson & Kolm, 2005). Vamosi & Vamosi (2010, 2011) argued that trait evolution can change these dynamics, by increasing either the geographic area available for further diversification or the carrying capacity of a region. For example, they suggested that bilaterally symmetrical flowers could increase diversification by allowing the co-existence of a larger number of closely related species.

5. Key opportunities and key landscapes

Context dependence implies that significant radiations can occur in the absence of evolutionary changes, simply, for example, by the movement of a lineage into a new region that provides more of the same environment, in a more 'open' state. This is the sense in which 'key opportunity' has been used (e.g. Moore & Donoghue, 2007). This is distinguishable from 'key landscape' in the sense of Givnish (1997, unpublished), which refers to a landscape that promotes diversification across multiple lineages. Island archipelagos provide the classic case, but continental mountain chains act similarly (see Drummond *et al.*, 2012; Hughes & Atchison, 2015). Some radiations in these settings are of an adaptive type, with shifts into multiple habitats and life forms, for example, silverswords (*Dubautia* and relatives, Asteraceae; Baldwin, 1997; Baldwin & Sanderson, 1998) and *Bidens* (Asteraceae; Knope *et al.*, 2012) in Hawaii; *Lobelia* (Lobeliaceae) and relatives in Africa and Hawaii (Knox & Palmer, 1998; Givnish *et al.*, 2009); *Aeonium* (Crassulaceae) and *Sonchus* (Asteraceae) in the Macronesian islands (Kim *et al.*, 1996; Jorgensen & Olesen, 2001); and *Espeletia* (Asteraceae) in the mountains of South America (Monasterio & Sarmiento, 1991). Others are at the 'nonadaptive' (Gittenberger, 1991; Givnish, 1997; Rundell & Price, 2009) end of the spectrum, with niche conservatism and climate change promoting isolation and subsequent divergence in allopatry but with little niche or morphological differentiation (Wiens, 2004).

There has been great interest in documenting unusually high rates of diversification in particular areas, including the Mediterranean basin (Valente *et al.*, 2010a,b), the páramo of the Andes (Madrinán *et al.*, 2013), the Qinghai-Tibetan plateau (Wen *et al.*, 2014), and the Cape Floristic Province in South Africa (Richardson *et al.*, 2001b; Klak *et al.*, 2004; Linder & Hardy, 2004; Sauquet *et al.*, 2009). These have undoubtedly been hotspots of diversification for many plant groups, but it is important to note that in each of these regions there are a wide range of outcomes among clades, and this distribution of outcomes deserves study in its own right. That is, there are plant groups that have radiated little if at all in these areas (e.g. for the Cape flora, Warren & Hawkins, 2006), alongside multiple iconic radiations – for example, *Erica* (Ericaceae), *Pelargonium* (Geraniaceae), Restionaceae, and Iridaceae in the Cape region of South Africa (Goldblatt & Manning, 2002; Linder, 2003); Proteaceae in Mediterranean hotspots of the Southern Hemisphere (Sauquet *et al.*, 2009); *Dianthus* (Caryophyllaceae) in Mediterranean Europe (Valente *et al.*, 2010b); *Espeletia*, *Lupinus*, *Puya* (Bromeliaceae), and

Valeriana in páramo (Madriñán *et al.*, 2013); Aizoaceae in succulent Karoo (Klak *et al.*, 2004); and *Pedicularis*, *Rhododendron* (Ericaceae), and *Sausurea* (Asteraceae) in the Hengduan Mountains of the eastern Himalayas (Boufford, 2014; Wen *et al.*, 2014). Explanations range from enhanced speciation as a function of spatial heterogeneity to decreased extinction as a result of relative temporal stability (e.g. Jansson & Davies, 2008; Linder, 2008). Such comparisons will be especially useful when specific predictions can be tested, for example, concerning area sizes, ages, and physical connectivities (Donoghue & Edwards, 2014).

Geographic area, by itself, has been noted as a correlate of diversity in angiosperm families, suggesting density dependence and an important role for expansion into new territory, which might be enhanced by certain traits (e.g. herbaceous habit; Vamosi & Vamosi, 2010, 2011; or perennial habit permitting expansion into montane territory; Drummond *et al.*, 2012; Hughes & Atchison, 2015). Increased vein density within angiosperms (Boyce *et al.*, 2009; Brodribb & Feild, 2010) could be viewed as providing a competitive edge (enhanced water flow and photosynthesis) and promoting occupation of more territory. A similar argument might be made for a positive feedback between higher growth rates and the production of easily decomposed leaf litter and higher fertility soils (Berendse & Scheffer, 2009). Geographic expansion might result from evolutionary transition into new biomes (Donoghue, 2008; Crisp *et al.*, 2009; Donoghue & Edwards, 2014), and such shifts do appear to have promoted diversification in some cases (e.g. Verboom *et al.*, 2003, 2009; Sauquet *et al.*, 2009; Koenen *et al.*, 2013; Onstein *et al.*, 2014).

6. Lag times, enablers, and indirect effects

Not infrequently, the evolution of a trait of interest seems to be situated near a point in a phylogeny identified as a significant radiation – but not right at that point (e.g. Smith *et al.*, 2011). If the attribute in question had anything to do with the radiation, it must have exerted an indirect effect. It was necessary, perhaps, but not sufficient.

Cactaceae provide an example. They started out in warm semi-arid environments with inducible CAM photosynthesis in their leaves (Edwards & Donoghue, 2006). The early evolution of delayed bark formation and stomata on the stems enabled an increase in stem succulence, which set the stage for the vascularization of the cortex in the Cactoideae and their radiation into even drier and colder habitats (Edwards & Donoghue, 2006). Subsequent shifts in growth form and pollination further elevated diversification rates in several lineages (Arakaki *et al.*, 2011; Hernandez-Hernandez *et al.*, 2014). In such cases, it is hard to pin the cause of the radiation on any single attribute (Donoghue, 2005); instead, as we develop at length in Section III, several factors apparently came together to promote diversification in a step-wise fashion.

C₄ photosynthesis in grasses (Poaceae) is a case of an apparent lag-time. Spriggs *et al.* (2014; see also Bouchenak-Khelladi *et al.*, 2009, 2014) showed an association between the evolution of C₄ within the PACMAD clade and higher rates of diversification.

They argued that the initial effect might have been to increase the competitive ability and survival of C₄ plants in hot, arid, open environments, but that there was a ‘delayed rise’ within C₄ lineages, such that increased diversification only set in later when climates changed and grassland environments spread.

Extrafloral nectaries (EFNs) might also have promoted diversification indirectly. Ant-attracting EFNs are correlated with a higher diversification rate in *Senna* (Fabaceae; Marazzi & Sanderson, 2010), in which they may have increased individual fitness and the potential for dispersal into new areas. The persistence of plants with EFNs might have allowed them to radiate later with the ecological opportunities afforded by uplift of the Andes (Marazzi & Sanderson, 2010). EFNs in *Viburnum* (Adoxaceae), which, in combination with domatia, maintain protective mite populations (Weber *et al.*, 2012), have also been correlated with a higher diversification rate (Weber & Agrawal, 2014; Spriggs *et al.*, 2015). Here, too, the initial effect may have been to increase individual fitness, and potentially range size, thereby increasing the likelihood of a later rise in speciation rate.

III. New terms, new possibilities

The preceding review highlights the emergence in the literature of more complicated explanations for radiations involving multiple interacting causal agents. Traits can have multiple effects on speciation and extinction, and might elicit a particular outcome only in a certain context. A trait might evolve at one point in a phylogeny, but only influence diversification later, when other traits or external conditions have changed. Although it appears that synergistic interactions of factors are the norm, this is not reflected in the terms in wide use to describe radiations. We could try to retrofit the older ‘key innovation’ terminology, but, by its very nature, this tends to narrow the search to one causal event at one point in time. Instead, we suggest that some standardization of older terms and the introduction of several new ones – explained with the help of Fig. 1 – might help to crystalize the emerging outlook, stimulate new research, and convey our community’s new understanding to a broader audience.

1. Apomorphy and innovation

The most general technical term in use for a character (intrinsic to the organism, heritable, and passed down through the tree) that arises anywhere in a phylogeny is ‘apomorphy’ (Hennig, 1966). When does an apomorphy qualify as an ‘innovation’? One possibility is to simply equate apomorphy and innovation and use the words interchangeably. However, given the existence of the two terms, and the tendency in the literature to view ‘innovation’ as a special case of ‘apomorphy’, we suggest that innovation be used when it is posited (hypothesized initially, and then hopefully tested) that an apomorphy possesses some specific characteristic or downstream consequence of interest. We purposely leave this open ended, in recognition of the fact that there are multiple possible consequences of potential interest to biologists. Of course, this invites specialized terms for particular classes of innovations, some of which we highlight here.

2. Precursor, enabler, and key innovation

One possible consequence of interest is the acquisition of novel character identity (e.g. the origin of a new, individualized body part), in which case the term ‘novelty’ would be appropriate (Wagner, 2014). Another possible downstream consequence of interest is an increase in the probability of origin of some other character of interest, in which case we suggest the term ‘precursor’ (Marazzi *et al.*, 2012). Yet another possibility is an innovation that promotes the exploration of new designs or serves to increase the generation of disparity, in which case we suggest the term ‘enabler’ (Donoghue, 2005). Of course, the consequence of most direct relevance here is a shift in the rate of diversification. By our reading of the literature, the term ‘key innovation’ has most often been used for a trait that significantly increases the diversification rate. We are aware of no term for the opposite effect, namely for a trait that decreases the diversification rate, but we think such a term would be useful (see Section IV).

Of course, it is possible for an innovation to have more than one of the effects we have highlighted (and ours is not an exhaustive list). For example, an apomorphy might act as a precursor and as an enabler at the same time, and a precursor or an enabler could also increase the diversification rate. With respect to increased diversification, one possibility would be to consistently use the word ‘key’ as a modifier. Thus, a trait that promoted origins of another trait *and* also promoted diversification would be a ‘key precursor’. Similarly, a ‘key enabler’ would be a trait hypothesized to increase both disparity *and* diversification. We appreciate that associating the word ‘key’ with diversification is arbitrary, but we suspect this probably reflects common usage and would be least disruptive.

3. Synnovation

So far, we have tried only to clarify the meaning (proposed usage) of existing terms. We note, however, that these all refer to single apomorphies/innovations – they are focused on single evolutionary events, happening at single points in a tree (or, if replicated, each instance localized in this way). Our main point is that this is insufficient, at least for productive discussions of shifts in diversification. We need, in addition, to be thinking about combinations of characters that interact synergistically with one another to produce effects of interest. As an attempt to encourage such thinking (and, as necessary, the development of new methods) we introduce the term ‘synnovation’ (‘synergy’ + ‘innovation’) to refer to two or more interacting apomorphies that together have some property or downstream consequence of interest (including, but not limited to, those noted above for single apomorphies). Of most direct relevance here are characters that interact with one another to increase the diversification rate, for which we would (in parallel with ‘key innovation’) use ‘key synnovation’. As we stressed above, it will be critical to specify the nature of hypothesized interactions and their joint consequences for diversification.

From the earliest discussions of the key innovation concept, it has been noted that the attributes that have an impact on diversification may have been built up sequentially. Cracraft (1990), for example, provided a compelling example in his analysis

of the flight apparatus in birds, a complex set of interacting traits assembled in a series of steps in a region of the phylogeny extending from dinosaurs to modern birds. In plants, Donoghue (2005) provided a concrete example of an enabler (overtopping growth resulting in a trunk and side branches), and one of the new designs that it facilitated (megaphyllous leaves), together promoting diversification within monilophytes (in leptosporangiate ferns) and lignophytes (in seed plants).

4. Confluence

Until now, we have been talking about single apomorphies or interacting combinations of apomorphies that have specific properties or consequences of interest. However, when it comes to diversification, it is evident from the literature on context dependence that this is still insufficient. Many shifts in diversification seem to entail additional, extrinsic factors, such as migration into new territories (e.g. Moore & Donoghue, 2007) and/or environmental shifts such as climate change (e.g. Arakaki *et al.*, 2011). We need, therefore, a more encompassing term that accommodates the coming together of innovations or synnovations with biogeographic movements and/or environmental changes. For this we suggest the very general and widely understood term ‘confluence’ (as in the phrase ‘a confluence of events’). In this context, confluence refers to the assembly of a set of attributes – including innovations, synnovations, environments, and geographic territories – that together yield some consequence of interest. We imagine that this assembly generally takes place sequentially, through a region of a phylogenetic tree, although shifts in some of the elements might be inferred along the same phylogenetic branch. Where the specific consequence of interest is an increase in the diversification rate, we would, for consistency, use the phrase ‘key confluence’. Examples along these lines have increased in the literature, and have become increasingly explicit, such as the ‘multi-tiered scenario’ of Drummond *et al.* (2012) to explain the ‘super radiation’ of *Lupinus* in terms of morphological innovation (perennial habit) and the occupation of montane environments. We suppose that confluences also underlie most significant decreases in diversification too (see Section IV).

5. Indirect effects revisited

Several recent developments (and terms), mentioned briefly above, are consistent with the spirit of our proposals, and help to clarify our viewpoint. Weber & Agrawal (2014) highlighted traits having an ‘indirect effect’ on diversification, where subsequent changes in context set off one or more increases in diversification rate (see also Marazzi & Sanderson, 2010). Similarly, Spriggs *et al.* (2014) highlighted ‘lag times’ or ‘delayed shifts’ between the origin of a trait and an increase in the diversification rate. These cases highlight context dependence and the need for additional characters and/or environmental changes to spark diversification. In our terms, they point to a confluence of events, played out over some period of time, including character combinations (synnovations) and extrinsic changes of various sorts. Under these circumstances, which we

take to be the norm, no single factor is the driver and every component of the confluence has an indirect effect.

Motivated by Simpson's (1953) discussion of the physical, ecological, and evolutionary factors necessary for the occupation of a new adaptive zone (Glor, 2010; cf. the model of Donoghue & Edwards, 2014 for a shift into a new biome), Bouchenak-Khelladi *et al.* (2015) categorized variables as 'background' (present before the start of a radiation), 'triggers' (contemporaneous with a radiation), or 'modulators' (arising after a radiation). They found variation across several plant radiations in whether intrinsic or extrinsic variables (or both) provided backgrounds, triggers, or modulators. The order did not seem to matter as much as eventually attaining the right combination (although we imagine order being important in other cases; Fig. 1d,e). Fully consistent with our outlook, all of this implies that radiations are complex, unfold over time, and involve a confluence of intrinsic and extrinsic events. Where we differ perhaps is with respect to their statement that 'each radiation should be triggered by a single variable'. Instead, we are arguing for the importance of synnovations (multiple interacting traits) and confluences (including extrinsic variables), with diversification and its causes distributed through a region of a tree (Donoghue, 2005).

6. A worked example

To illustrate the use of these terms, we have chosen Bromeliaceae as an example, focusing especially on the excellent work of Givnish *et al.* (2014), who carried out an extensive series of analyses using a phylogeny for 90 of the *c.* 3140 neotropical species (Fig. 2). Several other recent studies have also dealt with Bromeliaceae, sometimes yielding contrasting results as a consequence of differences in scope, sampling, and methodology (Quezada & Gianoli, 2011; Silvestro *et al.*, 2014; Bouchenak-Khelladi *et al.*, 2015). Our aim is not to solve evolutionary problems within Bromeliaceae, just to illustrate how we would apply the terms discussed above in a real case.

Some background on Bromeliaceae is necessary. First, although CAM photosynthesis may have been connected to rapid diversification within the Bromelioideae (Silvestro *et al.*, 2014; see also Quezada & Gianoli, 2011), Givnish *et al.* (2014) found that CAM was probably not a driver across Bromeliaceae as a whole; not all CAM Bromeliaceae radiated, and Tillandsioideae radiated without CAM (at least initially). Second, the 'tank' habit is so closely linked phylogenetically with the evolution of epiphytism in Bromeliaceae (Givnish *et al.*, 2014; Silvestro *et al.*, 2014) that it is difficult to tease apart their individual effects; they may have acted in concert to promote species richness. Third, in Bromelioideae the evolution of 'entangled seeds' preceded the evolution of epiphytes; the order is unclear in Tillandsioideae, but it is possible that entangled seeds of some type (sticky or comose) were necessary for the evolution of epiphytism. Fourthly, geographic movements seem to have been important – from Guyana into the Andes, from the Andes into the lower elevation Atlantic rainforests of Brazil in Bromelioideae, and probably multiple movements into Central America and the Caribbean in the mostly higher elevation Tillandsioideae.

In our terminology, a confluence, involving both intrinsic and extrinsic factors, drove diversification in both the Bromelioideae and the Tillandsioideae (Fig. 3). In both cases the confluence appears to have involved a specific synnovation composed of entangled seeds, epiphytism, and the closely connected tank condition (Fig. 2). In the Bromelioideae these seem to have evolved in this order, suggesting the possibility that entangled seeds acted as an enabler; in Tillandsioideae the order is still unclear. Whether CAM should also be included in the synnovation is unclear. In the Bromelioideae its evolution predated the rest of the synnovation, whereas in Tillandsioideae CAM evolved within the radiation (a modulator in the sense of Bouchenak-Khelladi *et al.*, 2015). Importantly, in both the Bromelioideae and the Tillandsioideae it appears that movement into new regions and habitats played an important role, and must therefore be considered elements of the confluence along with the synnovation. One wonders in such a case (and could potentially test) whether the order of assembly of a synnovation alters the pattern of diversification, or whether all that matters is that the elements of the confluence eventually come together (cf. Bouchenak-Khelladi *et al.*, 2015). In any case, all of these elements worked in combination to elevate species richness – causation is not attributable to any one of them in isolation.

In this example, the comparison of the two major radiations within Bromeliaceae suggests that a similar synnovation independently influenced both. The details of this synnovation hypothesis could be tested internally by further resolution of Bromeliaceae phylogeny, but also potentially by designing relevant functional experiments to better understand the interaction among the component characters. Various break-downs, or modifications, of the synnovation in derived clades could also present research opportunities (e.g. Galley & Linder, 2007; Humphreys *et al.*, 2011). It is also possible to look outside of Bromeliaceae for 'the same' or very similar key synnovations and confluences, and such comparisons might suggest the addition or subtraction of elements to achieve even greater generality.

Leptosporangiate ferns and orchids provide obvious outside comparisons. In ferns, the evolution of epiphytism also appears to have been associated with increased diversification (Schuettelpelz & Pryer, 2009); it may have originated in several clades well before multiple diversification shifts were promoted by the rapid spread of angiosperm-dominated rainforests. In orchids, epiphytism is also probably associated with higher diversity, where, tellingly, it has been portrayed as 'a suite of key innovations' (Gravendeel *et al.*, 2004). Silvera *et al.* (2009) argued that CAM photosynthesis was a drought avoidance mechanism that stimulated the evolution of epiphytism, and that epiphytism, in turn, promoted higher rates of speciation into a wider range of habitats, especially with the spread of tropical rainforests. Overall, these comparisons suggest that synnovations involving epiphytism generally also involve some enabling character changes (e.g. seed dispersal or drought avoidance) and subsequent environmental changes that opened new territory and habitats. Although CAM is clearly not necessary for the radiation of epiphytes (e.g. in Tillandsioideae), it is so often associated that it may have been an important part of the synnovation in multiple cases. In general, the identification of similar synnovations/confluences elsewhere in a phylogeny, and

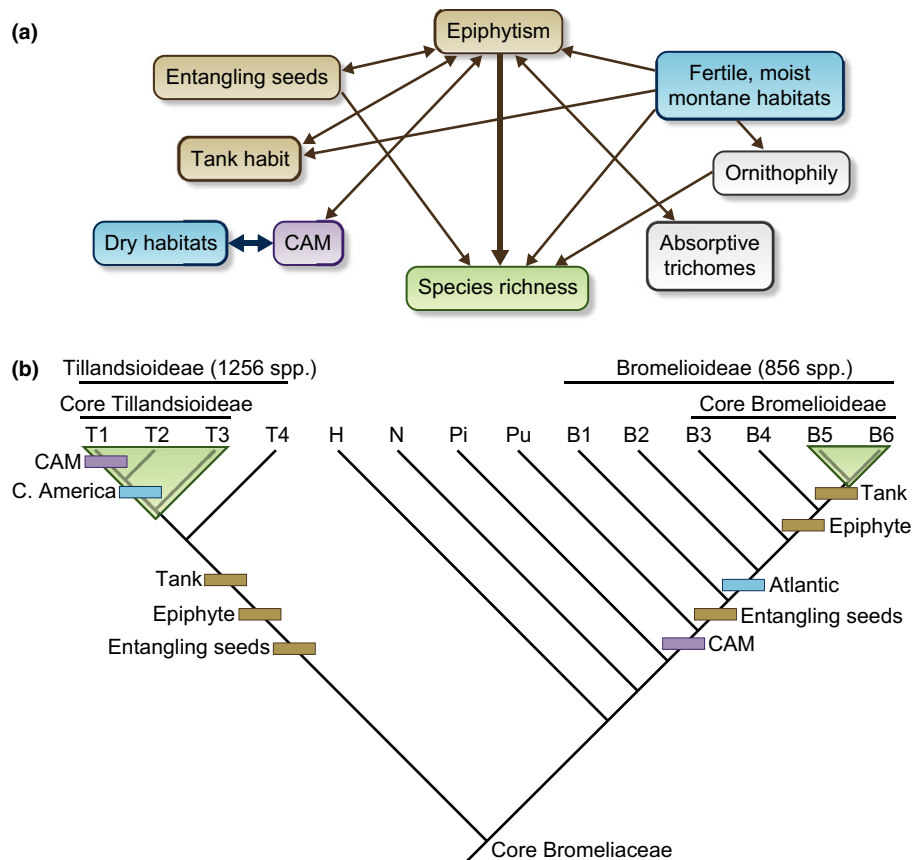


Fig. 2 Synnovation and confluence in the radiation of Bromeliaceae. (a) The set of variously interrelated factors analyzed by Givnish *et al.* (2014) in relation to species richness (modified from their Fig. 1). Brown boxes mark characters considered part of the replicated synnovation in (b); blue boxes mark biogeographic/ environmental factors considered part of the confluence. Characters in white boxes are not considered part of the synnovation in (b); CAM photosynthesis (purple box) is not consistently associated with diversification in Bromeliaceae (see main text). (b) A simplified version of phylogenetic relationships in core Bromeliaceae (excluding the more distantly related Brochinioideae and Lindmanioideae) derived from Givnish *et al.* (2014) (H, Hechtioideae; N, Navioideae; Pi, Pitcairnioideae; Pu, Puyoideae; T1–T4, major lineages within Tillandsioideae; B1–B6, major lineages within Bromelioideae). Givnish *et al.* (2014) identified significant radiations (shown as green triangles) corresponding to what we label ‘Core Tillandsioideae’ and within what we label ‘Core Bromelioideae’. The ‘key confluence’ in both lineages includes a synnovation composed of entangled seeds, epiphytism, and the closely associated tank habit (brown rectangles), along with geographic movement (blue rectangles) opening up new territory (movement to the Atlantic rain forest in Bromelioideae; movements into Central America and the Caribbean within Tillandsioideae).

tests of their joint effects on diversification, are areas in need of methodological attention.

IV. Rate heterogeneity and depauperons

The most likely signal of any confluence of processes affecting diversification is heterogeneous rates of speciation and extinction in time, in space, and across phylogeny. The prospects for accurately reconstructing highly heterogeneous diversification histories remain uncertain, however, not least because of the impacts of extinction through time, and the difficulty of accounting for these impacts in clades with a poor fossil record (Nagalingum *et al.*, 2011; Quental & Marshall, 2011). Fortunately, after nearly a century of modeling diversification (Yule, 1924; Kendall, 1949; Strathmann & Slatkin, 1983; Raup, 1985; Stanley, 1985; Slowinski & Guyer, 1989; Gilinsky & Good, 1991; Nee *et al.*, 1992, 1994; Nee, 2006), substantial progress has been made on statistical inference in the context of these models using likelihood and

Bayesian approaches (Morlon *et al.*, 2011; Etienne & Haegeman, 2012; Rabosky *et al.*, 2013).

Strong inferences about rate heterogeneity are essential to explain radiations and their causes, but this also applies more broadly to other diversity patterns in the tree of life. Rather than dwelling entirely on radiations, we turn to another pattern in which the lexicon developed above may well be relevant: the flip side of evolutionary radiations – significantly depauperate lineages, or ‘depauperons’ (Strathmann & Slatkin, 1983; Magallón & Sander-son, 2001; Renner, 2004; Ricklefs, 2005; Ricklefs *et al.*, 2006) (Fig. 3). ‘Living fossils’ are a special case (Darwin, 1859: p. 107), long recognized by their combination of low rates of both diversification and morphological evolution (Eldredge & Stanley, 1984; Cloutier, 1991; Yoshida, 2002; Lloyd *et al.*, 2012; but see Schopf, 1984 for a critique and an attempt to dissect the relationship between these rates). Phylogenetic analyses suggest that depauperons are common. *Amborella trichopoda*, as sister to the remaining 250 000+ angiosperms, is the poster child

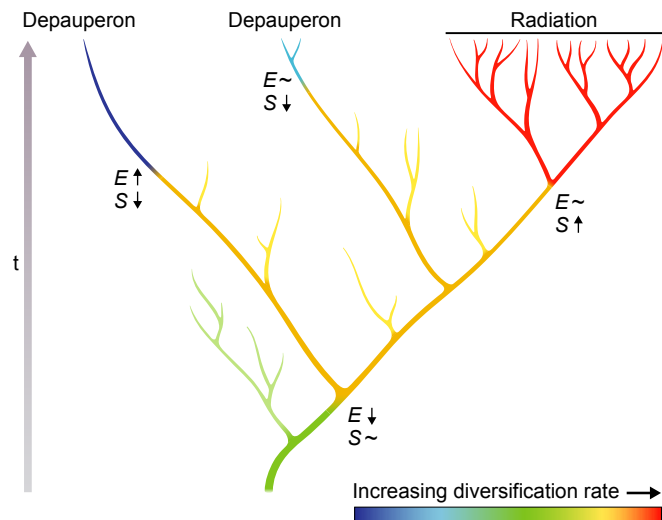


Fig. 3 One possible scenario (in addition to the one described by Strathmann & Slatkin, 1983; see main text) for the existence of 'depauperons', with diversification rate represented by different branch colors. Extinction rate (E) goes down near the base of the entire clade (yellow branches), while speciation rate (S) stays the same; the subclade on the right (red branches) undergoes a radiation as speciation rate goes up and extinction rate stays the same; in both depauperons (blue branches) speciation rate goes down, but the extinction rate stays the same in the middle one and goes up on the left.

for a plant depauperon, but there are many others (e.g. Osmundaceae (22 spp.) sister to the remaining 9000 species of leptosporangiate ferns; *Acorus* (2–4 spp.) sister to the remaining 60 000 monocots; Anomochlooideae (4 spp.) sister to the remaining 12 000 Poaceae; Apostasioideae (16 spp.) sister to the remaining 22 000 Orchidaceae; Anthionemeae (70 spp.) sister to the remaining 3700 Brassicaceae; Barnadesioideae (94 spp.) sister to the remaining 23 000 Asteraceae). Even crude tests (e.g. the sister group test of Slowinski & Guyer, 1989) in these cases lead to clear statistical rejection of homogeneous rate models in favor of heterogeneous rate models with different diversification rates in the depauperon and its sister group. Mangroves provide an example with high replication, the repeated origin (perhaps 21 times) of this lifestyle yielding depauperons with a collective diversification rate just 1/4 that of angiosperms as a whole (Ricklefs *et al.*, 2006).

The contrast between models needed to explain a species-rich clade and the persistence of a species-poor clade helps illustrate some of the challenges of inferring rate heterogeneity. Although species-rich clades are by no means 'easily' explained in real cases, mathematically they are not challenging: they require a shift to a high net diversification rate sustained over a long enough period of time. An increase in the rate parameter of a simple Yule model with high constant speciation and no extinction suffices. By contrast, as Strathmann & Slatkin (1983) first pointed out, it is much harder to explain the persistence of species-poor clades on long time-scales. A low net diversification must be combined with the lowest biologically realistic extinction rates, recognizing that the latter will presumably never be zero. Contrary to expectation, over a long enough time-scale most of these clades will simply go extinct. It is highly improbable, for many combinations of low extinction rates and low (but higher) speciation rates, that a clade *both* survives a long time *and* leaves a small number of descendants.

Faced with this conundrum and *yet also* the existence of a large number of small and ancient animal phyla, Strathmann & Slatkin (1983) postulated an explicitly heterogeneous diversification model that initially generates a large number of species, but then is followed by much lower speciation rates (and nonzero extinction). They described both episodic and more gradual versions of this heterogeneity, the latter assuming a density-dependent decrease in speciation rate over time. They found that present-day depauperons must represent a small number of surviving lineages from a once much larger pool of closely related species, none of whom survived to the present. In other words, there must have been distinct diversification regimes at different points in history.

Other sequences of processes could also produce depauperons. For example, in the 'taxon pulse' of Erwin (1985), a clade starts diversifying in an ancestral environment, but then moves and radiates in a derived environment, perhaps cycling through this sequence several times, while each time suffering high extinction in the ancestral environment(s) (Fig. 3). Not only are depauperons repeatedly generated, but the signal of evolutionary history is repeatedly degraded and eventually lost in such a process. The 'dying embers' scenario in *Viburnum* (Spriggs *et al.*, 2015) might be an example – it may have started out in the tropics, then moved and radiated in temperate and boreal areas, but experienced elevated extinction in the ancestral tropical environment.

In a complete lexicon we would be concerned about the entire shape of the tree of life, and develop relevant terms related to both increases and decreases in diversity. Confluence is neutral with respect to direction; that is, we can say that a confluence of events caused radiation or extinction at some rate. On the 'increase' side we have 'innovation' for individual traits leading to increase, and now 'synnovation' for a combination of traits underlying radiation. On the 'decrease' side we lack comparable terms.

V. Obstacles to identifying synnovation, confluence, and depauperons

Unfortunately, better terminology does not make inference in the face of rate heterogeneity any easier. In the interest of 'full disclosure', we briefly note just three especially difficult problems that can introduce error and bias into such inferences: partial taxon sampling (and sample size in general: Nee *et al.*, 1994; Cusimano & Renner, 2010; Höhna *et al.*, 2011; Wertheim & Sanderson, 2011), divergence time estimation in the absence of a molecular clock (Britton, 2005; Revell *et al.*, 2005; dos Reis *et al.*, 2014), and extinction, sometimes informed by the fossil record (Quental & Marshall, 2011), but often not (Nee *et al.*, 1994; Magallón & Sanderson, 2001; Nee, 2006; Ricklefs, 2007; Purvis, 2008; Crisp & Cook, 2009; Rabosky, 2010; Morlon *et al.*, 2011).

In synnovation and confluence, several distinct events – trait origins, shifts in speciation and extinction rate, ecological changes and dispersal – probably occurred over some time interval (not all at once at a single point on a tree). Their discovery thus relies on time calibrations, and, especially for confluences involving both intrinsic and extrinsic features, on absolute ages that depend on fossil calibrations. Problems with absolute age estimation are well known

(Ronquist *et al.*, 2012), but improvements are foreseeable, perhaps combining better vetting of fossil calibrations (e.g. Parham *et al.*, 2012a,b; Wilf & Escapa, 2014) and better relaxed clock models that incorporate biological causes of molecular rate variation (e.g. Worobey *et al.*, 2014). The localization of events to a window in time is also often limited by the resolution afforded by a single edge of a phylogenetic tree (although cf. stochastic mapping, e.g. Huelsenbeck *et al.*, 2003; Revell, 2013). Think of the long angiosperm stem edge, for example. We may need to be satisfied with localizing trait changes and diversification shifts to wide time intervals, and testing for statistical overlap between several broad regions in the phylogeny.

As an illustration of these problems, consider the depauperon case. First, with respect to sampling, depauperons are easily overlooked, as the celebrated example of *Amborella* attests, while endless candidates for species-rich clades have been proposed and debated. Although some have passed muster and others have not, analyses of these clades have not suffered quite as much from partial taxon sampling. Second, sample size is a severe problem. Even with precise divergence times, the accuracy of speciation and extinction rate estimates and the power of tests for differences in rate between the depauperon and the rest of the tree are inherently limited. For example, the difference between two sister groups with one and 10 species is not significant according to either a Slowinski–Guyer (SG) test, which ignores divergence times, or a likelihood ratio test, which requires exact divergence times. But if the clades have 100 and 1000 taxa, the likelihood test indicates a highly significant difference; without the additional knowledge provided by divergence times, the SG test still fails to detect any difference.

Finally, the detection of depauperons amidst a background of higher average rates and occasional rapid radiations exemplifies the difficulties that extinction poses for inference. Rate heterogeneity involving early radiation followed by declining speciation rates can explain the persistence of depauperons, but only as a lingering small sample from an originally much larger population of clades that went extinct (see Fig. 3). As a consequence, finding a robust association between any single depauperon and its traits, ecology, etc. (e.g. Ricklefs, 2006) is highly subject to sampling error.

VI. Conclusions

A shift is well underway in studies of plant radiations, from simple ‘innovation’ hypotheses to increasingly complicated ‘synnovation’ and ‘confluence’ hypotheses. Our intention in coining these new terms is to draw attention to these emerging objects of study, namely the particular sequences and combinations of traits, and environments, and geographic movements, assembled over time, that have interacted to produce both the major increases and the major decreases in diversification that we observe throughout the tree of life.

We can imagine strongly contrasting responses to these proposals. One response – the one we hope for – would view the new terms as facilitating a welcome shift away from the ‘single-point, single-cause’ mindset that has dominated radiation discussions until recently. A less charitable response would reject these

terms as unnecessary, or perhaps even counterproductive, as they give the appearance of trying to salvage an initial causal hypothesis in the face of disappointment over the lack of a perfect correlation. Why not, one might ask, just reject the initial key innovation hypothesis as unfounded and formulate/test a new one? The problem with this response is that it encourages the continued search for single events at single points. If we are right, most such hypotheses will fail, and this will not be especially productive. It will be more productive, we think, to shift the frame of reference and focus attention directly on identifying and testing the effects of specific combinations of attributes, and searching for generalities of this sort across multiple clades.

Regardless, as our explanations inevitably, and more explicitly, become increasingly complex, we will need better tools to identify and analyze synnovations and confluences of all sorts, and the heterogeneity in rates that accompany them. In the end, success will probably require the integration of phylogenies with many other data sources – that is, trees by themselves can only go so far. Geography and climate are key elements, of course, and we need to directly integrate historical biogeography and functional experiments. This will yield a much richer and more useful field of study. However, as we proceed, it is increasingly important to acknowledge and try to accommodate the inevitable uncertainties noted above, and other fundamental methodological issues facing our community (e.g. Maddison & FitzJohn, 2015). These are, and will remain, extremely difficult inference problems. We would be well advised to remain skeptical, bearing in mind that even our best methods can only partially compensate for various inadequacies.

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