Research review

Adaptive radiation versus 'radiation' and 'explosive diversification': why conceptual distinctions are fundamental to understanding evolution

Author for correspondence:
Thomas J. Givnish
Tel: +1 608 262 5718
Email: givnish@wisc.edu

Thomas J. Givnish

Department of Botany, University of Wisconsin-Madison, Madison, WI 53706, USA

Summary

Adaptive radiation is the rise of a diversity of ecological roles and role-specific adaptations within a lineage. Recently, some researchers have begun to use 'adaptive radiation' or 'radiation' as synonymous with 'explosive species diversification'. This essay aims to clarify distinctions between these concepts, and the related ideas of geographic speciation, sexual selection, key innovations, key landscapes and ecological keys. Several examples are given to demonstrate that adaptive radiation and explosive diversification are not the same phenomenon, and that focusing on explosive diversification and the analysis of phylogenetic topology ignores much of the rich biology associated with adaptive radiation, and risks generating confusion about the nature of the evolutionary forces driving species diversification. Some 'radiations' involve bursts of geographic speciation or sexual selection, rather than adaptive diversification; some adaptive radiations have little or no effect on speciation, or even a negative effect. Many classic examples of 'adaptive radiation' appear to involve effects driven partly by geographic speciation, species' dispersal abilities, and the nature of extrinsic dispersal barriers; partly by sexual selection; and partly by adaptive radiation in the classical sense, including the origin of traits and invasion of adaptive zones that result in decreased diversification rates but add to overall diversity.

Introduction

Adaptive radiation – the rise of a diversity of ecological roles and attendant adaptations in different species within a lineage (Givnish, 1997) – is arguably one of the most important processes linking ecology and evolution. As exemplified by such groups as Darwin's finches (Lack, 1947; Grant & Grant, 2008), African rift-lake cichlids (Seehausen, 2006; Muschick *et al.*, 2012), Australian marsupials (Springer *et al.*, 1997; Nilsson *et al.*, 2010), Caribbean *Anolis* lizards (Losos, 2009; Wollenberg *et al.*, 2013) and Hawaiian honeycreepers (Lerner *et al.*, 2011), silverswords (Carlquist *et al.*, 2003), and lobeliads (Givnish *et al.*, 2009; Givnish & Montgomery, 2014), adaptive radiation is central to the origin of adaptations, the generation of biological diversity and the coexistence of closely related species.

Adaptive radiation is thought to be driven mainly by divergent selection caused by competition among closely related – and therefore, ecologically similar – species (Simpson, 1953; Givnish, 1997; Schluter, 2000). Adaptive radiation may be most likely in circumstances where alternative resources are underutilized by other species, as a consequence of mass extinction, of invasion of isolated islands, mountains or lakes by one or a few lineages, or through the evolution of a 'key innovation' (e.g. wings) that opens a new adaptive zone that can subsequently be partitioned ecologically (Simpson, 1953). Givnish (2010) argues that abundance may also be an important driver of ecological character displacement and, thus, of adaptive radiation in colonists of new or depopulated landscapes or adaptive zones, given that such abundance – together with the absence or rarity of other species competing for similar resources – would maximize selection for divergence in sympatry among related colonists. Initial divergence of colonizing populations in each other's absence might also arise if partially isolated islands or island-like areas offer strikingly different conditions. Such divergence, however, might not lead to daughter species that

can coexist locally without additional character displacement driven by competition in sympatry.

Of the early writers on adaptive radiation (Osborn, 1902; Huxley, 1942; Lack, 1947; Simpson, 1953; Carlquist, 1965; Mayr, 1970; Stebbins, 1974), only Simpson included what we might term explosive speciation in his concept of the process. However, even Simpson (1953) explicitly stated that a similar pattern of ecological divergence into a variety of adaptive zones, shaped by the same processes of competition and natural selection, might proceed gradually as well. This makes eminent sense: without any possibility of debate, the Australian marsupials would constitute an adaptive radiation whether they diverged in 1 Myr or (as in fact) 50 Myr (Nilsson *et al.*, 2010), and whether they constituted 23 surviving species or (as they actually do) 236 species (Wilson & Reeder, 2005). Without any possible debate, the striking functional, morphological and ecological divergence seen in Darwin's finches in the Galapagos marked them as an adaptive radiation (Grant & Grant, 2008) even before we knew that their 14 species diversified in only 2.3 Myr (Sato *et al.*, 2001), and despite the fact that they diversified at no higher rate than the coerebid tanagers of tropical America and the Caribbean from which they arose (Burns *et al.*, 2014). Without any possible debate, the unequaled range of nutrient-capture strategies seen in the genus *Brocchinia* identify it as an adaptive radiation, even though their species number only 20 and they took 14 Myr to diverge from each other, and are sister to the clade of all 3200 other species of bromeliads (Givnish *et al.*, 1997, 2014). Definitions of adaptive radiation that require accelerations of species diversification relative to sister groups will thus fail to identify Darwin's finches and *Brocchinia* as adaptive radiations; excluding such iconic examples of adaptive radiation makes such diversification-based definitions untenable.

Yet, over the last two decades, there has emerged a distressing tendency to conflate explosive species diversification with adaptive radiation. Guyer & Slowinski (1993) argued that a hallmark of adaptive radiation is that 'some organisms have features that allow them to speciate more prolifically or become extinct less frequently than organisms without these features', and then provided a quantitative test of whether individual phylogenies show a significant imbalance of proliferation rates that, in their view, would reveal a signature of adaptive radiation. Slowinksi & Guyer (1993) stated baldly that 'Traits believed to have caused increased diversification are usually termed 'key innovations' or 'key adaptations'', and then provided an additional test of whether a particular trait was consistently associated with elevated rates of net diversification among lineages.

Characteristics of adaptive radiation

This view of adaptive radiation is problematic at several levels, in that it excludes several essential qualities of the phenomenon and includes some that are not truly characteristic of it. First, this view ignores entirely what were the core issues of adaptive radiation as viewed by Osborn, Huxley, Lack, Simpson, Carlquist, Mayr and Stebbins, namely: (1) an increase in the range of ecological roles collectively exhibited by members of a lineage (e.g. seed eating, fruit eating, gleaning insects from leaves, probing for insects under bark

in Darwin's finches); and (2) a corresponding increase in the diversity of traits associated with such roles (e.g. variations among species in beak size and shape). Second, it ignores whether traits associated with different ecological roles have actually been shown to be adaptations, through comparative, functional or population analyses, including convergence between ecologically analogous species in unrelated adaptive radiations (Givnish, 1997). Third, it ignores whether close relatives in a lineage compete with each other and exert selective pressure to drive divergence (Schluter, 2000). Fourth, it ignores the rate at which a lineage fills morphospace and whether, possibly, that rate decelerates through time (Givnish *et al.*, 2005; Jønsson *et al.*, 2012). Fifth, it ignores whether supposed 'key innovations' trigger the invasion of additional volumes of morphospace and ecospace, as Liem (1973) and others argued for the rise of pharyngeal jaws and how they allowed wide diversification in the morphology of external jaws and dietary choice in African rift-lake cichlids. Sixth, it ignores the extent to which species within a lineage overlap in geographic distribution, even though such overlap should be more likely in ecologically divergent species (Diamond, 1973; Schluter, 1996; Grant & Grant, 2006) and might occur little, if at all, in taxa undergoing speciation due to limited dispersal (Givnish, 1997; Patterson & Givnish, 2004; Kisel & Barraclough, 2010).

Seventh, it focuses on an aspect of adaptive radiation – acceleration of net species diversification compared with close relatives – that simply is *not* a defining characteristic (Givnish, 1997). Darwin's finches – the very apotheosis of adaptive radiation – fail to show any such acceleration compared with their immediate coerebid relatives (Burns *et al.*, 2014) despite exhibiting remarkable divergence in ecological roles and in beak and wing traits in morphospace (Jønsson *et al.*, 2012). *Brocchinia* shows a net rate of species diversification far *lower* than that of their sister group (all other bromeliads), despite having evolved more different means of obtaining mineral nutrients than any other genus of flowering plants (Givnish *et al.*, 1997). Finally, the Guyer-Slowinski view ignores the fact that several other processes and factors can accelerate speciation or slow extinction *without adaptive divergence*, notably through the facilitation of geographic speciation by: (1) limited dispersal (Mayr, 1970; Givnish, 1997, 1998, 2010; Kisel & Barraclough, 2010); (2) life in extensive cordilleras, archipelagoes, lake systems or submarine outcrops dissected by multiple natural barriers to gene flow and species dispersal (Mayr, 1970; Gentry & Dodson, 1987; Grant & Grant, 2008; Losos & Ricklefs, 2009; Givnish *et al.*, 2014; Wagner *et al.*, 2014); and (3) sexual selection (Seehausen *et al.*, 1997; Seehausen & Van Alphen, 1999; Podos & Nowicki, 2004; Grant & Grant, 2008). Fossorial rodents, plants with heavy seeds and brooding sea anemones all show extensive diversification without any evidence that selection for adaptive divergence as an important driver. *Navia* is by far the largest genus of bromeliads endemic to the tepuis of the Guayana Shield; its species differ little from each other in vegetative morphology or floral form, but it is one of only two bromeliad genera with naked seeds, bereft of any means of long-distance dispersal (Givnish, 1997).

The conflation of adaptive radiation (or simply 'radiation' as it is often put) with explosive diversification has become fairly

widespread (Sanderson & Donoghue, 1994; Heard & Hauser, 1995; Davies *et al.*, 2004; Klak *et al.*, 2004; Hughes & Eastwood, 2006; Arakaki *et al.*, 2011; Couvreur *et al.*, 2011; Drummond *et al.*, 2012; Linder *et al.*, 2014) – and indeed is captured in the very title of this symposium. The appeal of the Guyer-Slowinski perspective is that it provided the first steps toward quantitatively testing whether speciation, extinction or net diversification showed significant acceleration within a lineage, and whether particular traits were associated with that acceleration, all based on nothing more than a phylogeny and the distribution of the states of one or more characters across extant taxa. Such analyses are, I must emphasize, of enormous inherent interest, and the likelihood tests of Sanderson & Donoghue (1994) and the algorithms used in the programs such as GEIGER (Harmon *et al.*, 2008), MEDUSA (Alfaro *et al.*, 2009), BiSSE (Maddison *et al.*, 2007; FitzJohn *et al.*, 2009) and BAMM (Rabosky, 2014) are being widely, productively and increasingly used to test for variation in net diversification and its significant correlates. But progress in our ability to analyze variation in and the causes of diversification should be valued in its own right. Adaptive radiation is simply not explosive diversification.

Why should we care about this distinction? Nothing could be more pointless than a pedantic debate about definitions that goes nowhere. I would argue, however, that making a distinction between adaptive radiation and explosive diversification is fundamental to understanding evolution, and that failure to make such distinctions can blur such understanding and hinder progress.

Montane lupines

To illustrate this point, let us consider the supposed 'replicate adaptive radiations' and 'key innovations' in montane lineages of *Lupinus* (Fabaceae) studied by Drummond *et al.* (2012). Hughes & Eastwood (2006) had earlier shown that a monophyletic group of 81 Andean lupines had arisen in the last 2–4 Myr, and thus exhibited one of the highest rates of net species diversification known in plants. Hughes & Eastwood were careful to use the terms 'explosive plant species diversification' and 'radiation' rather than adaptive radiation, but also referred to 'key innovations', a term that has historically been used only in connection with adaptive radiation *per se*.

Drummond *et al.* (2012) used a molecular phylogeny of *Lupinus* to identify multiple (adaptive) radiations in the New World, based on three significant accelerations of net species diversification in western North and South America, in Mexico and the Andes, and in lowland grassland and campos rupestres in eastern South America (primarily Brazil). Additional information suggested that the 'super-radiation' of *Lupinus* in the western Americas had nested within it three separate radiations in clades endemic to western North America, Mexico and the Andes. Evidence advanced regarding the nature of these diversifications as (adaptive) radiations included the diversity of growth forms in the montane clades, and the wide range of elevations and habitats occupied. The perennial iteroparous habit was identified as a 'key innovation' because it was consistently associated with accelerated rates of net diversification.

What's wrong with this picture? First, it is by no means clear that montane lupines actually constitute adaptive radiations in the historic sense: Where is the evidence that variation in growth form or life history has permitted different species to invade and dominate different kinds of habitat in the montane zone? Or that such phenotypic variation has allowed closely related species to coexist locally (e.g. see Rundell & Price, 2009)? Yes, the ability to invade higher elevations makes available a wide range of habitats that can be partitioned, but the numbers of species that arose after isolated elevational shifts could simply reflect geographic speciation within the montane zone (e.g. nonadaptive radiation *sensu* Gitzenberger, 1991; Givnish, 1997; Rundell & Price, 2009).

Second, the identification of the perennial habit as a 'key innovation' in montane lupines makes no sense. Perennial iteroparity (long life with repeated bouts of reproduction) was identified as a candidate key innovation using BiSSE, following the Guyer-Slowinski paradigm – the lineages with high rates of diversification all shared the perennial iteroparous habit, and not the annual semelparity (one time only reproduction) seen in other lupines. But this overlooks comparisons with other lineages: almost every clade at high elevations in the Andes, for example, consists of perennials, and yet probably none has as high a rate of diversification as lupines do, as so ably documented by Hughes & Eastwood (2006). Of course, a trait might be a key innovation in one ecological context, and not in another, depending on the range of ecological resources and competitors faced by different lineages; for many fish biologists, pharyngeal jaws appeared to be a key innovation in the African rift lakes, but not in the streams and rivers from which the highly diverse rift-lake cichlids arose (Fryer & Iles, 1972; Liem, 1973; Greenwood, 1984; see also Schweizer *et al.*, 2014 for nectarivory in parrots). It may be illuminating to view pharyngeal jaws instead as a background condition favoring adaptive radiation (*sensu* Bouchenak-Khelladi *et al.*, 2015; this volume), and see the immediate trigger for rift-lake cichlid diversification as instead being exceptional genomic variation and lability, given that rift-lake lineages display accelerated evolution of regulatory and coding sequences, insertions of transposable elements and novel microRNAs, and retention of ancient polymorphisms, possibly reflecting ancestral hybridizations (Brawand *et al.*, 2014). Such genomic traits provide rich material on which divergent selection has acted, but they are not key innovations *sensu* Simpson (1953) – they are not themselves the instrumentalities provided by phenotypic traits that allow invasion of new adaptive zones. How can perenniality be a key innovation, in the sense of triggering diversification, if it hardly ever does so across lineages *in the same environment*? Indeed, in California, annuals appear to be associated with much *higher* rates of diversification than perennials (Lewis, 1962, 1966; Raven & Axelrod, 1978; Givnish, 2010). Drummond *et al.* (2012) themselves note that perenniality might not be a key innovation, if codistributed traits instead drove diversification (Maddison *et al.*, 2007; Losos, 2011), or if perenniality evolved in response to factors other than elevation.

I would argue for a different explanation for lupine evolution in montane areas and campos rupestres. At high elevations in the tropics, where conditions are 'summer every day and winter every night', (Hedberg, 1964), nightly formation of ice crystals in the soil

militate strongly against the annual habit, for the simple reason that small seedlings are thrown out of the soil by frost heaves. At high elevations, that should select for perennials with vegetative spread that don't face the demographic bottleneck caused by seedling mortality. Infertile soils combined with intense fires should also work against seedlings and thus the annual habit, which might help account for the high incidence of perenniality in the campos rupestres of Brazil (and in bogs and pocosins worldwide).

Additional factors favor *Lupinus per se* in montane areas and campos rupestres. Cold soils, especially those recently derived from bedrock – as are likely to prevail at high elevations in the Rockies, Central America and the Andes – are likely to be N-limited, due to soil youth and the short time available for N fixation, cold inhibition of microbial decomposition and remineralization of N, and the relative abundance of phosphorus in the parent material (Vitousek & Farrington, 1997; Chadwick *et al.*, 1999; McNown & Sullivan, 2013). The N-fixing capability of lupines should therefore provide them with an ecological edge in many montane habitats, especially early in succession (e.g. see Morris & Wood, 1989). Fire also volatizes much of the N supply in fireswept ecosystems, giving N-fixers an advantage in such systems (e.g. campos rupestres) as well (Vitousek & Howarth, 1991; Leach & Givnish, 1996). So the N-fixing symbioses of *Lupinus* – unmentioned by Hughes & Eastwood (2006) and Drummond *et al.* (2012) – may be a key trait permitting invasion of montane zones and campos rupestres, whereas the perennial habit may have been strongly selected after invasion of such habitats.

Lupinus is marked by large seeds and (usually) short stature, a combination of traits likely to result in limited seed dispersal. N-fixation itself may favor large seeds, given its high start-up costs (Pate, 1985), accounting for the relatively large seeds seen in Fabaceae generally and in *Lupinus* specifically. Genetic studies have shown highly restricted gene flow in natural and agricultural lupine populations (Schaal, 1980; Hamblin *et al.*, 2005).

I would therefore assert that the combination of inherently low dispersal ability, short distances of overall gene flow, and life in extensive montane areas dissected by numerous natural barriers (e.g. valleys, ridges, drier or wetter than optimal areas) is what drives the exceptional rates of net diversification in *Lupinus* in montane areas, combined with adaptive radiation in elevational distribution (although the extent of elevational turnover of species in a given area vs horizontal turnover of species geographically remains undocumented). Furthermore, although a short, perennial herbaceous or shrubby habit combined with N-fixing ability almost surely helps permit invasion of montane areas, I would argue that these should not be seen as 'key innovations', in the sense of opening up a wide range of new ecological and adaptive possibilities, in the way that (for example) wings permitted not merely foraging in the air and nearby elevated surfaces, but also allowed specialization on foraging in those areas in different ways, involving substantial variation in wing size and shape. Rather, the combination of a short habit, perennial life history and N-fixing ability should provide a more-or-less one-dimensional advantage in a montane (or fireswept) landscape, with poor dispersal and the dissected nature of that landscape resulting in high diversification subsequently (see 'key landscape' concept of Givnish, 1997). Part of this perspective

incorporates what Drummond *et al.* (2012) call the 'montane mosaic', but they overlooked the role of limited dispersal and N fixation.

One additional piece of support for this explanation – based on making clear distinctions between adaptive radiation and geographic speciation, and between key innovations and limited gene flow – is that most montane *Lupinus* species are narrowly endemic to small areas, with very few co-occurring in any one area (C. Hughes, pers. comm.). Based on arguments given previously (see the Sixth point in the Introduction above), this pattern appears more likely to be a signature of geographic speciation coupled with limited dispersal ability. In essence, I would argue that montane lupine lineages are diverse not because they have evolved a rich variety of different ways of making a life in alpine landscapes, which would allow several of them to coexist locally (see Schweizer *et al.*, 2014), but instead because they have a number of traits that permit them – all essentially in the same way – to inhabit such areas, and because their low dispersal ability allows them to speciate rapidly and at small spatial scales in such landscapes (see also Givnish *et al.*, 2014). Although Hughes & Eastwood (2006) note a diversity of growth forms within Andean *Lupinus*, almost all of these are morphologically quite similar, and are built at or close to ground level, as expected in high-elevation herbs and subshrubs. Hughes & Eastwood (2006) note the absence of any physiological novelty that might account for the rapid diversification of *Lupinus* above the treeline (but see my comments above regarding the importance of N fixation). The extent of diversification due to adaptive radiation in elevation within Andean lupines – both in absolute terms and relative to that due to limited dispersal and geographic speciation – remains undocumented.

My argument is similar to that made by Ihlenfeldt (1994) and Klak *et al.* (2004) to account for the high diversification rate of the ruschioid Aizoaceae. Those authors hypothesized that the extremely limited movement of seeds via splash dispersal would lead to speciation at small spatial and temporal scales; genetic differentiation among populations at such small scales could also lead to selection for divergent adaptations to different kinds of microsites, leading to limited coexistence of species at small scales.

Similar arguments probably apply to many other systems. For example, the African rift-lake cichlids (c. 1000 of 1600 species worldwide in the family) have long been viewed as an exemplary case of adaptive radiation (Fryer & Iles, 1972; Liem, 1973; Greenwood, 1984; Meyer *et al.*, 1994; McMahan *et al.*, 2013), and they do show a remarkable interspecific breadth in external jaw morphology corresponding to great interspecific diversity in diet (Chakrabarty, 2005; Clabaut *et al.*, 2007), with extraordinary convergence among ecological analogues in different lakes (Kocher *et al.*, 1993). But ecologically diverse as rift-lake cichlids are, they exhibit no more than a few dozens of ways of making a living, not nearly enough to account for 1000 species. What accounts for the missing factor of 20 or more in diversity? It appears most likely that limited dispersal – caused by mouth-breeding and limitations of many populations to isolated rock outcrops, driven by heavy predation pressures and ultimately by the great depth of the lakes and hence their clarity in the shallow depths occupied by cichlids – amplifies diversification via geographic speciation within and

among lakes, resulting in communities of ecological analogs being replicated locally and regionally (Kocher *et al.*, 1993; Sturmbauer *et al.*, 2001; Seehausen, 2006; Wagner & McCune, 2009). Ole Seehausen (pers. comm.) notes that parallel ecological divergences within lakes are likely to characterize major regions of a lake rather than individual islands, and that a number of cases of apparent parallel adaptive radiations within lakes have been re-evaluated in terms of post-speciation gene flow. Numerous studies have shown very fine-scale spatial genetic structure in African rift-lake cichlids restricted to rocky outcrops (Danley & Kocher, 2001; Rico & Turner, 2002; Wagner & McCune, 2009; Seehausen & Wagner, 2014). The allopatry of many closely related species within some African rift lakes, and their divergence in color but rarely in other obvious traits related to diet or ecology, suggests a strong role of sexual selection in speciation at small scales (Salzburger, 2009; Mattersdorfer *et al.*, 2012; Tyers & Turner, 2013).

More generally, limited dispersal and selection for adaptive divergence can interact synergistically and generate parallel adaptive radiations, as seen in cichlids in different African rift lakes (Kocher *et al.*, 1993), Caribbean *Anolis* on different islands (Jackman *et al.,* 1996), North American *Calochortus* (Patterson & Givnish, 2004) and Hawaiian lobeliads (Givnish *et al.*, 2009). For rift-lake cichlids, high water clarity also apparently drives strong sexual selection on male coloration, leading to more species in clearer lakes (Seehausen *et al.*, 1997). For rift-lake cichlids, it thus appears that parallel adaptive radiations, geographic speciation and sexual selection all help set high net rates of species diversification. I would argue that the rift-lake cichlid radiations may thus reflect the operation not merely of pharyngeal jaws as 'background' key innovations driving adaptive radiations in feeding ecology, but also of deep transparent lakes as key landscapes *sensu* Givnish (1997) as well, favoring restricted dispersal, and driving divergence in feeding ecology and visual divergence in traits related to mating.

Arguments along these lines can also be made for bromeliad diversification. Phylogenetic analyses indicate that epiphytism, the tank habit, hummingbird pollination and life in extensive tropical cordilleras (Andes, Serra do Mar) – all of which are closely coupled, spatially, ecologically and evolutionarily – all significantly accelerate net diversification (Givnish *et al.*, 2014). Epiphytism, the tank habit and the origin of hummingbird pollination apparently open new adaptive zones, in the sense that they make available a variable volume of ecospace that can be partitioned by differentially adapted species. Life in the montane zone of tropical cordilleras not only favors the origin of epiphytism, tanks, and hummingbird pollination: it also permits geographic speciation to proceed in parallel at several different points and in several different lineages at the same time. Even a trait such as CAM photosynthesis, which does not accelerate net diversification in bromeliads and thus would not be viewed as a diversifying influence in any of the models corresponding to the Guyer-Slowinski viewpoint, appears to have substantially elevated overall bromeliad diversity by adding the (low) diversity of lineages that were able to invade extremely dry regions, habitats and microsites that might otherwise not have been available (Givnish *et al.*, 2014). So bromeliad diversification appears to combine elements of adaptive radiation, geographic speciation and the

invasion of ecologically distinctive regions. Some traits are key innovations that open up a diverse range of ecological roles that can be partitioned by species differentially adapted to different portions of ecological space, even though some (like CAM) result in intrinsically lower rates of diversification. Other traits, such as life in montane habitats, appear instead to be 'evolutionary keys' that open up the invasion of ecologically rather monotonous real estate that can, however, lead to geographic speciation through the operation of natural extrinsic barriers to gene flow. Finally, there appear to be 'key landscapes' – for example, montane habitats and xeric habitats in the Andes – that appear to trigger the invasion of new adaptive zones (e.g. epiphytism, CAM photosynthesis) and accelerate speciation through geographic isolation with or without adaptive radiation (Givnish, 1997).

Cichlids and bromeliads

What might be the best way to accommodate the competing views of adaptive radiation as involving primarily ecological and adaptive divergence vs the tempo of species diversification? We might consider re-defining adaptive radiation as 'the rise of a diversity of ecological roles and associated adaptations within a lineage, accompanied by an unusually high level or rate of accumulation of morphological/physiological/behavioral disparity and ecological divergence compared with sister taxa or groups with similar body plans and life histories.' Such a definition would retain traditional components of adaptive radiation, while suggesting a way forward that includes tempo, not in species diversification, but in the rate of accumulation of disparity. The challenge with such a definition is that species are easily counted, in a more or less comparable fashion across contrasting lineages, whereas volumes of morphospace or ecospace are less easy to quantify – and it is most likely impossible to do so in a thorough fashion that is comparable across all organisms. But it is practical to make quantitative and objective comparisons of morpho- and ecospace volumes across at least some broadly similar groups of organisms, as demonstrated for Caribbean vs Central American *Anolis* lizards (Pinto *et al.*, 2008), and Hawaiian honeycreepers and Madagascar vangas vs other passerine birds (Losos & Ricklefs, 2009; Jønsson *et al.*, 2012). It would be a simple matter to go from such data to calculations of the rate of change in disparity. I recommend 'explosive speciation' or 'bursts of speciation' to describe substantial increases in the rate of speciation or net species diversification (= speciation – extinction), whether or not there is decisive evidence for a substantial increase in morpho- or ecospace occupied relative to comparable groups.

The moral of this story: If we are to understand the role of adaptive radiation in shaping evolution, it is crucial to avoid fuzzy definitions that blur the concepts of adaptive radiation and explosive diversification, and how each might be affected by geographic speciation, gene flow, sexual selection, key innovations, key landscapes and ecological keys. Why call a biological phenomenon a 'radiation' when what we really mean is an explosive diversification . . . or a true adaptive radiation? Why call a trait a key innovation when it is simply a lagging adaptation to the invasion of a particular set of conditions – or an ecological key that opens a landscape for geographic speciation? We can, of course, like

Humpty Dumpty in *Through the Looking Glass*, make words mean what we want them to mean. But it is far simpler to retain original, simple meanings so that we do not lose track of important distinctions as definitions (and perhaps concepts with them) morph into quite different things, dependent on transference and the interests of the moment. Let us remember that, after all, things did not work out all that well for Humpty Dumpty!

Acknowledgements

References

Alfaro ME, Santini F, Brock C, Alamillo H, Dornburg A, Rabosky DL, Carnevale G, Harmon LJ. 2009. Nine exceptional radiations plus high turnover explain species diversity in jawed vertebrates. *Proceedings of the National Academy of Sciences, USA* **106**: 13 410–13 414.

Arakaki M, Christin PA, Nyffeler R, Lendel A, Eggli U, Ogburn RM, Spriggs E, Moore MJ, Edwards EJ. 2011. Contemporaneous and recent radiations of the world's major succulent plant lineages. *Proceedings of the National Academy of Sciences, USA* **108**: 8379–8384.

Bouchenak-Khelladi Y, Renske E, Onstein RE, Xing Y, Schwery O, Linder HP. 2015. On the complexity of triggering evolutionary radiations. *New Phytologist* **207**: 313–326.

Brawand D, Wagner CE, Li YI, Malinsky M, Keller I, Fan S, Simakov O, Ng AY, Lim ZW, Bezault E *et al*. 2014. The genomic substrate for adaptive radiation: genomes of five African cichlid fish. *Nature* **513**: 375–381.

Burns J, Shultz AJ, Title PO, Mason NA, Barker FK, Klicka J, Lanyon SM, Lovette IJ. 2014. Phylogenetics and diversification of tanagers (Passeriformes: Thraupidae), the largest radiation of Neotropical songbirds. *Molecular Phylogenetics and Evolution* **75**: 41–77.

Carlquist S. 1965. *Island life*. New York, USA: Natural History Press.

Carlquist S, Baldwin BG, Carr GD, eds. 2003. *Tarweeds and silverswords: evolution of the Madiinae (Asteraceae)*. St Louis, MO, USA: Missouri Botanical Garden Press.

Chadwick OA, Derry LA, Vitousek PM, Huebert BJ, Hedin LO. 1999. Changing sources of nutrients during four million years of ecosystem development. *Nature* **397**: 491–497.

Chakrabarty P. 2005. Testing conjectures about morphological diversity in cichlids of Lakes Malawi and Tanganyika. *Copeia* **2005**: 359–373.

Clabaut C, Bunje PME, Salzburger W, Meyer A. 2007. Geometric morphometric analyses provide evidence for the adaptive character of the Tanganyikan cichlid fish radiations. *Evolution* **61**: 560–578.

Couvreur TLP, Forest F, Baker WJ. 2011. Origin and global diversification patterns of tropical rain forests: inferences from a complete genus-level phylogeny of palms. *BMC Biology* **9**: 44.

Danley PD, Kocher TD. 2001. Speciation in rapidly diverging systems: lessons from Lake Malawi. *Molecular Ecology* **10**: 1075–1086.

Davies TJ, Barraclough TG, Chase MW, Soltis PS, Soltis DE, Savolainen V. 2004. Darwin's abominable mystery: insights from a supertree of the angiosperms. *Proceedings of the National Academy of Sciences, USA* **101**: 1904–1909.

Diamond JM. 1973. Distributional ecology of New Guinea birds. *Science* **179**: 759–769.

Drummond CS, Eastwood RJ, Miotto STS, Hughes CE. 2012. Multiple continental radiations and correlates of diversification in *Lupinus* (Leguminosae): testing for key innovations with incomplete taxon sampling. *Systematic Biology* **61**: 443–460.

FitzJohn RG, Maddison WP, Otto SP. 2009. Estimating trait-dependent speciation and extinction rates from incompletely resolved phylogenies. *Systematic Biology* **56**: 701–710.

Fryer G, Iles TD. 1972. *The cichlid fishes of the Great Lakes of Africa: their biology and evolution*. Edinburgh, UK: Oliver and Boyd.

Gentry AH, Dodson CH. 1987. Diversity and biogeography of neotropical vascular epiphytes. *Annals of the Missouri Botanical Garden* **74**: 205–233.

Gitzenberger E. 1991. What about non-adaptive radiation? *Biological Journal of the Linnean Society* **43**: 263–272.

Givnish TJ. 1997. Adaptive radiation and molecular systematics: aims and conceptual issues. In: Givnish TJ, Systma KJ, eds. *Molecular evolution and adaptive radiation*. New York, NY, USA: Cambridge University Press, 1–54.

Givnish TJ. 1998. Adaptive radiation of plants on oceanic islands: classical patterns, molecular data, new insights. In: Grant P, ed. *Evolution on islands*. New York, NY, USA: Oxford University Press, 281–304.

Givnish TJ. 2010. Ecology of plant speciation. *Taxon* **59**: 1326–1366.

Givnish TJ, Barfuss MHJ, Van Ee B, Riina R, Schulte K, Horres R, Gonsiska PA, Jabaily RS, Crayn DM, Smith JAC *et al*. 2014. Adaptive radiation, correlated and contingent evolution, and determinants of net species diversification in Bromeliaceae. *Molecular Phylogenetics and Evolution* **71**: 55–78.

Givnish TJ, Millam KC, Theim TT, Mast AR, Patterson TB, Hipp AL, Henss JM, Smith JF, Wood KR, Sytsma KJ. 2009. Origin, adaptive radiation, and diversification of the Hawaiian lobeliads (Asterales: Campanulaceae). *Proceedings of the Royal Society B: Biological Sciences* **276**: 407–416.

Givnish TJ, Montgomery RA. 2014. Common-garden studies on adaptive radiation of photosynthetic physiology among Hawaiian lobeliads. *Proceedings of the Royal Society B: Biological Sciences* **281**: 20132944.

Givnish TJ, Pires JC, Graham SW, McPherson MA, Prince LM, Patterson TB, Rai HS, Roalson ER, Evans TM, Hahn WJ *et al*. 2005. Repeated evolution of net venation and fleshy fruits among monocots in shaded habitats confirms *a priori* predictions: evidence from an *ndh*F phylogeny. *Proceedings of the Royal Society B: Biological Sciences* **272**: 1481–1490.

Givnish TJ, Sytsma KJ, Smith JF, Hahn WJ, Benzing DH, Burkhardt EM. 1997. Molecular evolution and adaptive radiation in *Brocchinia* (Bromeliaceae: Pitcairnioideae) atop tepuis of the Guayana Shield. In: Givnish TJ, Sytsma KJ, eds. *Molecular evolution and adaptive radiation*. New York, NY, USA: Cambridge University Press, 259–311.

Grant PR, Grant BR. 2006. Evolution of character displacement in Darwin's finches. *Science* **313**: 224–226.

Grant PR, Grant BR. 2008. *How and why species multiply– the radiation of Darwin's finches*. Princeton, NJ, USA: Princeton University Press.

Greenwood PH. 1984. African cichlids and evolutionary theories. In: Echelle AA, Kornfield I, eds. *Evolution of fish species flocks*. Orono, ME, USA: University of Maine Press, 141–154.

Guyer C, Slowinski JB. 1993. Adaptive radiation and the topology of large phylogenies. *Evolution* **47**: 253–263.

Hamblin J, Barton J, Sanders M, Higgins TJV. 2005. Factors affecting the potential for gene flow from transgenic crops of *Lupinus angustifolius* L. in Western Australia. *Australian Journal of Agricultural Research* **56**: 613–618.

Harmon LJ, Weir JT, Brock CD, Glor RE, Challenger W. 2008. GEIGER: investigating evolutionary radiations. *Bioinformatics* **24**: 129–131.

Heard SB, Hauser DL. 1995. Key evolutionary innovations and their ecological mechanisms. *Historical Biology* **10**: 151–173.

Hedberg O. 1964. *Features of Afroalpine plant ecology*. Uppsala: Almqvist & Wiksen.

Hughes C, 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, USA* **103**: 10 334–10 339.

Huxley J. 1942. *Evolution: the modern synthesis*. New York, NY, USA: Harper and Brothers.

Ihlenfeldt H-D. 1994. Diversification in an arid world: the Mesembryanthemaceae. *Annual Review of Ecology and Systematics* **25**: 521–546.

Jackman T, Losos JB, Larson A, de Queiros K. 1996. Phylogenetic studies of convergent adaptive radiations in Caribbean *Anolis* lizards. In: Givnish TJ, Sytsma KJ, eds. *Molecular evolution and adaptive radiation*. New York: Cambridge University Press, 535–557.

Jønsson KA, Fabre PH, Fritz SA, Etienne RS, Ricklefs RE, Jørgenson TB, Fjeldså J, Rahbek C, Ericson PGP, Woog F et al. 2012. Ecological and evolutionar determinants for the adaptive radiation of the Madagascaran vangas. *Proceedings of the National Academy of Sciences, USA* **109**: 6620–6625.

Kisel Y, Barraclough TG. 2010. Speciation has a spatial scale that depends on levels of gene flow. *American Naturalist* **175**: 316–334.

Klak C, Reeves G, Hedderson T. 2004. Unmatched tempo of evolution in Southern African semi-desert ice plants. *Nature* **427**: 63–65.

Kocher TD, Conroy JA, McKaye KR, Stauffer JR. 1993. Similar morphologies of cichlid fish in Lakes Tanganyika and Malawi are due to convergence. *Molecular Phylogenetics and Evolution* **2**: 158–165.

Lack D. 1947. *Darwin's finches.* Cambridge, UK: Cambridge University Press.

Leach MK, Givnish TJ. 1996. Ecological determinants of species loss in prairie remnants. *Science* **273**: 1555–1558.

Lerner HRL, Meyer M, James HF, Hofreiter M, Rleischer RC. 2011. Multilocus resolution of phylogeny and timescale in the extant adaptive radiation of Hawaiian honeycreepers. *Current Biology* **21**: 1838–1844.

Lewis H. 1962. Catastrophic selection as a factor in speciation. *Evolution* **16**: 257–271.

Lewis H. 1966. Speciation in flowering plants. *Science* **152**: 167–172.

Liem KF. 1973. Evolutionary strategies and morphological innovations: cichlid pharyngeal jaws. *Systematic Zoology* **22**: 425–441.

Linder HP, Rabosky DL, Antonelli A, Wuest RO, Ehlemuller R. 2014. Disentangling the influence of climatic and geological changes on species radiations. *Journal of Biogeography* **41**: 1313–1325.

Losos JB. 2009. *Lizards in an evolutionary tree: ecology and adaptive radiation of anoles.* Berkeley, CA, USA: University of California Press.

Losos JB. 2011. Convergence, adaptation, and constraint. *Evolution* **65**: 1827–1840.

Losos JB, Ricklefs RE. 2009. Adaptation and diversification on islands. *Nature* **457**: 830–836.

Maddison WP, Midford PE, Otto SP. 2007. Estimating a binary character's effect on speciation and extinction. *Systematic Biology* **56**: 701–710.

Mattersdorfer K, Koblmueller S, Sefc KM. 2012. AFLP genome scans suggest divergent selection on colour patterning in allopatric colour morphs of a cichlid fish. *Molecular Ecology* **21**: 3531–3544.

Mayr E. 1970. *Populations, species, and evolution.* Cambridge, MA, USA: Belknap Press.

McMahan CD, Chakrabarty P, Sparks JS, Smith WL, Davis MP. 2013. Temporal patterns of diversification across global cichlid biodiversity (Acanthomorpha: Cichlidae). *PLoS ONE* **8**: e71162.

McNown RW, Sullivan PF. 2013. Low photosynthesis of treeline white spruce is associated with limited soil nitrogen availability in the Western Brooks Range, Alaska. *Functional Ecology* **27**: 672–683.

Meyer A, Montero C, Spreinat A. 1994. Evolutionary history of the cichlid fish species flocks of the East African great lakes inferred from molecular phylogenetic data. *Advances in Limnology* **44**: 409–425.

Morris WF, Wood DM. 1989. The role of lupine in succession on Mount St. Helens: facilitation or inhibition? *Ecology* **70**: 697–703.

Muschick M, Indermaur A, Salzburger W. 2012. Convergent evolution within an adaptive radiation of cichlid fishes. *Current Biology* **22**: 2362–2368.

Nilsson MA, Churakov G, Sommer M, Tran NV, Zemann A, Brosius J, Schmitz J. 2010. Tracking marsupial evolution using archaic genomic retrotransposon insertions. *PLoS Biology* **8**: e1000436.

Osborn HF. 1902. The law of adaptive radiation. *American Naturalist* **36**: 353–363.

Pate JS. 1985. Economy of symbiotic nitrogen fixation. In: Givnish TJ, ed. *On the economy of plant form and function.* New York, NY, USA: Cambridge University Press, 299–325.

Patterson TB, Givnish TJ. 2004. Geographic cohesion and parallel adaptive radiations in *Calochortus* (Calochortaceae): evidence from a cpDNA sequence phylogeny. *New Phytologist* **161**: 253–264.

Pinto G, Mahler DL, Harmon LJ, Losos JB. 2008. Testing the island effect in adaptive radiation: rates and patterns of morphological diversification in Caribbean and mainland *Anolis* lizards. *Proceedings of the Royal Society B: Biological Sciences* **275**: 2749–2757.

Podos J, Nowicki S. 2004. Beaks, adaptation, and vocal evolution in Darwin's finches. *BioScience* **54**: 501–510.

Rabosky DL. 2014. Automatic detection of key innovations, rate shifts, and diversity-dependence on phylogenetic trees. *PLoS ONE* **9**: 389543.

Raven PH, Axelrod DI. 1978. Origin and relationships of the California flora. *University of California Publications in Botany* **72**: 1–139.

Rico C, Turner GF. 2002. Extreme microallopatric divergence in a cichlid species from Lake Malawi. *Molecular Ecology* **11**: 1585–1590.

Rundell RJ, Price TD. 2009. Adaptive radiation, nonadaptive radiation, ecological speciation and nonecological speciation. *Trends in Ecology and Evolution* **24**: 394–399.

Sanderson MJ, Donoghue MJ. 1994. Shifts in diversification rate with the origin of angiosperms. *Science* **264**: 1590–1593.

Salzburger W. 2009. The interaction of sexually and naturally selected traits in the adaptive radiations of cichlid fishes. *Molecular Ecology* **18**: 169–185.

Sato A, Tichy H, O'hUigin C, Grant PR, Grant BR, Klein J. 2001. On the origin of Darwin's finches. *Molecular Biology and Evolution* **18**: 299–311.

Schaal BA. 1980. Measurement of gene flow in *Lupinus texensis.* *Nature* **284**: 450–451.

Schluter D. 1996. Ecological causes of adaptive radiation. *American Naturalist* **148**: S40–S64.

Schluter D. 2000. *The ecology of adaptive radiation.* Oxford, UK: Oxford University Press.

Schweizer M, Güntert M, Seehausen O, Leuenberger C, Hertwig ST. 2014. Parallel adaptations to nectarivory in parrots, key innovations and the diversification of the Loriinae. *Ecology and Evolution* **4**: 2867–2883.

Seehausen O. 2006. African cichlid fish: a model system in adaptive radiation research. *Proceedings of the Royal Society B: Biological Sciences* **273**: 1987–1998.

Seehausen O, Van Alphen JJ. 1999. Can sympatric speciation by disruptive sexual selection explain rapid evolution of cichlid diversity in Lake Victoria? *Ecology Letters* **2**: 262–271.

Seehausen O, Van Alphen JJ, Witte F. 1997. Cichlid fish diversity threatened by eutrophication that curbs sexual selection. *Science* **277**: 1808–1811.

Seehausen O, Wagner CE. 2014. Speciation in freshwater fishes. *Annual Reviews of Ecology, Systematics, and Evolution* **45**: 621–651.

Simpson GG. 1953. *The major features of evolution.* New York, NY, USA: Columbia University Press.

Slowinksi JB, Guyer C. 1993. Testing whether certain traits have caused amplified diversification: an improved method based on a model of random speciation and extinction. *American Naturalist* **142**: 1019–1024.

Springer MS, Kirsch JAW, Chase JA. 1997. The chronicle of marsupial evolution. In: Givnish TJ, Sytsma KJ, eds. *Molecular evolution and adaptive radiation.* New York, NY, USA: Cambridge University Press, 129–162.

Stebbins GL. 1974. *Flowering plants: evolution above the species level.* Cambridge, MA, USA: Belknap Press.

Sturmbauer C, Baric S, Salzburger W, Ruber L, Verheye E. 2001. Lake level fluctuations synchronize genetic divergences of cichlid fishes in African lakes. *Molecular Biology and Evolution* **18**: 144–154.

Tyers AM, Turner GF. 2013. Signal and preference divergence among populations of the non-endemic basal Lake Malawi cichlid fish *Astatotilapia calliptera* (Perciformes: Cichlidae). *Biological Journal of the Linnean Society* **110**: 180–188.

Vitousek PM, Farrington H. 1997. Nutrient limitation and soil development: experimental test of a biogeochemical theory. *Biogeochemistry* **37**: 63–75.

Vitousek PM, Howarth RW. 1991. Nitrogen limitation on land and in the sea: how can it occur? *Biogeochemistry* **13**: 87–115.

Wagner CE, Harmon LJ, Seehausen O. 2014. Cichlid species-area relationships are shaped by adaptive radiations that scale with area. *Ecology Letters* **17**: 583–592.

Wagner CE, McCune AR. 2009. Contrasting patterns of spatial genetic structure in sympatric rock-dwelling cichlid fishes. *Evolution* **63**: 1312–1326.

Wilson DE, Reeder DM, eds. 2005. *Mammal species of the world.* Baltimore, MD, USA: Johns Hopkins University Press.

Wollenberg KC, Wang IJ, Glor RE, Losos JB. 2013. Determinism in the diversification of Hispaniolan trunk-ground anoles (*Anolis cybotes* species complex). *Evolution* **67**: 3175–3190.