



Tansley insight

The ubiquity of alpine plant radiations: from the Andes to the Hengduan Mountains

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Summary

Alpine plant radiations are compared across the world's major mountain ranges and shown to be overwhelmingly young and fast, largely confined to the Pliocene and Pleistocene, and some of them apparently in the early explosive phase of radiation. Accelerated diversification triggered by island-like ecological opportunities following the final phases of mountain uplift, and in many cases enabled by the key adaptation of perennial habit, provides a general model for alpine plant radiations. Accelerated growth form evolution facilitated by perenniality provides compelling evidence of ecological release and suggests striking parallels between island-like alpine, and especially tropicalpine radiations, and island radiations more generally. These parallels suggest that the world's mountains offer an excellent comparative system for explaining evolutionary radiation.

I. Introduction

Alpine plant radiations – here defined as accelerated episodes of species and/or trait diversification (Sanderson, 1998), occurring in the alpine and subalpine (including tropicalpine) zones – have been documented in almost all the major mountain ranges of the world (Table 1), including the Andes (Hughes & Eastwood, 2006; Drummond *et al.*, 2012; Madriñán *et al.*, 2013; Luebert & Weigend, 2014; Nürk *et al.*, 2014), Rockies (Drummond *et al.*, 2012), the European Alpine System (Comes & Kadereit, 2003; Roquet *et al.*, 2013), the Qinghai-Tibetan plateau/Hengduan Mountains of the Himalaya (Favre *et al.*, 2014; Wen *et al.*, 2014), New Zealand (Winkworth *et al.*, 2005; Joly *et al.*, 2014), the East African rift valley mountains (Knox & Palmer, 1995; Gehrke &

Linder, 2009; Linder, 2014) and the New Guinea highlands (Brown *et al.*, 2006). In general these radiations are considered to be recent and rapid (Linder, 2008), and broadly associated with ecological opportunities afforded by the recent formation of alpine habitats during the Neotectonic Period of recent mountain uplift across the globe (Ollier, 2006). However, there have been few attempts to globally compare radiations across these different mountains and many questions surrounding alpine plant radiations remain. For example, how do radiations from different mountains compare in terms of age, species richness, and rates of diversification? Do alpine clades show higher rates of diversification than their lowland relatives? Are the multiple radiations documented from the high Andes – described as the 'world's fastest evolving biodiversity hotspot' (Madriñán *et al.*, 2013) – really

Table 1 Representative alpine plant radiations from some of the major mountain systems across the globe

Clade (Family)	Number of species	Crown age of clade (Myr)	Species diversification rate	Source
Andes: uplift history: initial uplift from the late Eocene, but generally considered that c. 50% of central Andean uplift occurred between 10 and 6 Myr ago; uplift earlier in the south and later in the northern Andes; first appearance of north Andean páramos c. 3.5 Myr (Gregory-Wodzicki, 2000; Ghosh <i>et al.</i> , 2006; Garziona <i>et al.</i> , 2008; Graham, 2009); radiations reviews: Sklenář <i>et al.</i> (2010); Madriñán <i>et al.</i> (2013); Luebert & Weigend (2014)				
<i>Lupinus</i> (Leguminosae)	81	1.19–3.5	1.56–5.21	Hughes & Eastwood (2006); Drummond <i>et al.</i> (2012)
<i>Hypericum</i> (Hypericaceae)	67	2.26–5.62	0.75–1.9	Nürk <i>et al.</i> (2014)
<i>Valeriana</i> (Valerianaceae)	55 ¹	< 5.0	0.8–1.34 ¹	Bell & Donoghue (2005); see also Moore & Donoghue (2007); Bell <i>et al.</i> (2012)
<i>Puya</i> (Bromeliaceae)	c. 190	5.9	??	Jabaily & Sytsma (2013); Madriñán <i>et al.</i> (2013)
<i>Calceolaria</i> (Calceolariaceae)	250	5.41 ²	0.99–2.45 ²	Cosacov <i>et al.</i> (2009); Madriñán <i>et al.</i> (2013)
<i>Gentianella</i> (Gentianaceae)	170	1.6–3.0	1.48–3.21	Von Hagen & Kadereit (2001)
<i>Espeletiineae</i> (Asteraceae)	120	2.42–5.92	0.69–1.69	Madriñán <i>et al.</i> (2013)
<i>Astragalus</i> (Leguminosae) ³	90	1.89	0.65–2.01	Scherson <i>et al.</i> (2008)
Western North American Rockies & Sierras: uplift history: concentrated from late Miocene onwards, the Sierra Nevada & Coast Ranges arising in the late Pliocene and Pleistocene (Axelrod, 1962; Farley <i>et al.</i> , 2001; Ollier, 2006); there appears to be a surprising dearth of well-documented plant radiations from the alpine zones of western North America.				
<i>Lupinus</i> (Leguminosae)	58	2.1–5.5	0.74–1.96	Drummond <i>et al.</i> (2012)
Perennial <i>Castilleja</i> (Orobanchaceae)	160	??	??	Tank & Olmstead (2008); D. Tank (unpublished data)
<i>Penstemon</i> (Plantaginaceae)	271	?diversification mainly Pleistocene	??	Wolfe <i>et al.</i> (2006)
New Zealand: uplift history: onset < 5 Myr ago in late Pliocene, but extensive and permanent alpine habitats only from 1.2 Myr ago to the present (Heenan & McGlone, 2013); radiations review: Winkworth <i>et al.</i> (2005)				
<i>Ourisia</i> (Plantaginaceae)	13	0.4–1.3	??	Meudt <i>et al.</i> (2009)
<i>Pachycladon</i> (Brassicaceae)	11	c. 1.0	0.35–2.19	Joly <i>et al.</i> (2014)
<i>Mysotis</i> (Boraginaceae)	35	Pliocene	??	Winkworth <i>et al.</i> (2002)
<i>Ranunculus</i> (Ranunculaceae)	16	5	??	Lockhart <i>et al.</i> (2001)
New Guinea: uplift history: main uplift during late Miocene and Pliocene (Chapell, 1974). No New Guinea alpine radiations appear to have been thoroughly documented so far, although there is compelling evidence for radiation in <i>Rhododendron</i> . Candidate genera with New Guinea alpine species flocks are <i>Hypericum</i> , <i>Gentiana</i> , <i>Ranunculus</i> , <i>Epilobium</i> , <i>Potentilla</i> , <i>Carex</i> , <i>Dimorphanthera</i> and <i>Vaccinium</i>				
<i>Rhododendron</i> section <i>Schistanthe</i> (formerly <i>Vireya</i>)	29 ⁴	< 10	??	Brown <i>et al.</i> (2006); Goetsch <i>et al.</i> (2011)
East Africa: uplift history: late Miocene/early Pliocene (Wichura <i>et al.</i> , 2010); radiations reviews: Gehrke & Linder (2009); Linder (2014)				
<i>Dendrosenecio</i> (Asteraceae)	11	c. 1.0	??	Knox & Palmer (1995)
<i>Alchemilla</i> (Afromilla clade) (Rosaceae)	c. 40	??	??	Gehrke <i>et al.</i> (2008)
<i>Hypericum</i> (Hypericaceae)	20	1.7–7.9	??	Meseguer <i>et al.</i> (2013)
Himalaya: uplift history: initial uplift from the mid to late Eocene; with parts of the Tibetan plateau at 4000 m by late Miocene, and more recent (early Pliocene) uplift of the Hengduan Mountains which are a hotspot of alpine Himalayan plant diversity today (Harrison <i>et al.</i> , 1992; Spicer <i>et al.</i> , 2003; Mulch & Chamberlain, 2006; Favre <i>et al.</i> , 2014); radiations reviews: Favre <i>et al.</i> (2014); Wen <i>et al.</i> (2014)				
<i>Delphinium</i> subg. <i>Delphiniastrum</i> + <i>Oligophyllum</i> (Ranunculaceae)	300	6.19–13.56	0.37–0.81	Jabour & Renner (2012)
<i>Delphinium</i> subg. <i>Aconitum</i> (Ranunculaceae)	250	4.35–11.45	0.42–1.11	Jabour & Renner (2012)
<i>Rheum</i> (Polygonaceae)	c. 55 ⁵	9.9–12.0	??	Sun <i>et al.</i> (2012)
<i>Ligularia</i> – <i>Cremanthodium</i> – <i>Parasenecio</i> complex (Asteraceae)	> 200	8.15–13.55	??	Liu <i>et al.</i> (2006)
<i>Rhodiola</i> (Crassulaceae)	60 ⁶	Late Miocene, but most spp Pliocene or younger	??	Zhang <i>et al.</i> (2014)
<i>Rhododendron</i> subg. <i>Hymenanthes</i> (Ericaceae)	215 ^{4,7}	3–5	??	Milne <i>et al.</i> (2010)
<i>Isodon</i> (Lamiaceae)	c. 70 ⁸	Diversification rate increase late Miocene/early Pliocene	??	Yu <i>et al.</i> (2014)

Table 1 (Continued)

Clade (Family)	Number of species	Crown age of clade (Myr)	Species diversification rate	Source
European Alpine System: uplift history: initial uplift in the early Tertiary, the period of major uplift 10–2 Myr ago with major ice sheets covering the Alps and Pyrenees through the Quaternary (Ager, 1975); radiations reviews: Comes & Kadereit (2003); Kadereit <i>et al.</i> (2004)				
<i>Androsace</i> (Primulaceae)	22	c. 7.0	0.62	Roquet <i>et al.</i> (2013)
<i>Globularia</i> (Globulariaceae)	23	< 2.4 Myr	3 independent European Alpine clades	Comes & Kadereit (2003)
<i>Primula</i> sect. <i>Auricula</i> (Primulaceae)	25	2.38	??	Zhang <i>et al.</i> (2004)
<i>Soldanella</i> (Primulaceae)	16	< 1 Myr	??	Comes & Kadereit (2003)

¹Páramo species only.

²The crown age applies to the genus as a whole, but the net species diversification rate to just the páramo subclade (Madrrián *et al.*, 2013).

³Clade F of Scherson *et al.* (2008).

⁴But not all are truly alpine species.

⁵Of the 60 species of *Rheum*, most are endemic to the Qinghai-Tibetan Plateau, with just a few across central/west Asia and Europe (Sun *et al.*, 2012).

⁶*Rhodiola* comprises 70 species in total with c. 10 non-Himalayan species nested within the large Himalayan radiation.

⁷Clade HA of Milne *et al.* (2010).

⁸Of the c. 100 species of *Isodon*, 70% occur in the Hengduan ranges of the Himalaya (Yu *et al.*, 2014).

exceptional compared with radiations in other mountains? Do the contrasting climates, degrees of isolation and rates of immigration in temperate and tropical mountains result in fundamentally different trajectories of radiation? What can we learn about the extrinsic and intrinsic triggers of plant radiations by comparing clades in alpine regions across the globe?

Available data (Table 1) confirm the ubiquity of rapid plant radiations across the world's mountains and the recency of the majority of these is striking. It seems clear that alpine radiations in Africa, Europe and New Zealand have in general generated fewer species than in the Andes and Himalaya which harbour the biggest alpine radiations. It is also apparent that the Andes and New Zealand are better studied than other regions in terms of documenting plant radiations. Most of the potentially largest alpine plant radiations, especially in the Himalaya, have yet to be documented, although there is much current activity to address this imbalance.

II. Mountains as islands

Mountains have long been recognized as island-like systems (Carlquist, 1965, 1974; Hughes & Eastwood, 2006; Gehrke & Linder, 2009; Sklenář *et al.*, 2014) – so-called 'sky islands' – but the significance of this has not been fully explored in relation to the overall ubiquity of island-like evolutionary systems, and their prominence in studies of adaptive radiation (Losos & Ricklefs, 2009). Oceanic islands, and island-like systems including lakes, montane sky islands and valley systems share attributes of limited size, distinct boundaries, isolation, dispersal limitation, adaptive radiation and resulting high endemism. In particular, some mountain and lake systems, also share recency, and it is here that some of the most rapidly evolving radiations – of cichlid fish in African rift valley lakes (Wagner *et al.*, 2012), or Andean plants (Hughes & Eastwood, 2006; Madrrián *et al.*, 2013) – occur. Although recency (i.e. appearing in the Pliocene/Pleistocene

< 5 Myr ago), is indeed a global hallmark of most alpine habitats (Table 1), it is important to recognize the uncertainties surrounding the geological evidence for uplift and erosion histories, the great regional heterogeneity of these histories, especially for the Himalaya and the Andes, and the complexities associated with integration of uplift history and Pleistocene climate change in relation to the emergence and extent of alpine habitats (Heenan & McGlone, 2013; Favre *et al.*, 2014). These complexities bring obvious dangers of over-simplification, especially when correlating divergence times for montane plant radiations with mountain uplift histories. For example, initial uplift of the Himalaya and the Andes date back into the Eocene, but the timing of the later phases of uplift that are most relevant for understanding alpine radiations across different parts of the Himalaya and Andes remain debatable (Favre *et al.*, 2014; Luebert & Weigend, 2014). It is notable that the Hengduan Mountains, which harbour the greatest concentration of Himalayan plant diversity (Boufford, 2014), are thought to be more recent than the main Himalayan uplift (Favre *et al.*, 2014). Similarly, the recency of the northern Andean uplift compared with the southern and central Andes, is also associated with plant hyperdiversity in the páramo (Madrrián *et al.*, 2013; Luebert & Weigend, 2014). In this regard Heenan & McGlone's (2013) synthesis of geological, paleobotanical and historical climate evidence for New Zealand provides an impressive integrative model enabling more robust conclusions about the timing of the appearance, and likely extent, of alpine habitats in New Zealand over the last 5 Myr.

III. *Lupinus*: a model for alpine plant radiation

Over the last few years the legume genus *Lupinus* has emerged as a model system for investigating alpine plant radiations (Fig. 1) (Hughes & Eastwood, 2006; Drummond *et al.*, 2012). Application of methods for modelling rates of diversification across phylogenies (Silvestro *et al.*, 2011; Rabosky, 2014) favours a model of increased speciation rates to account for the very high rates of net

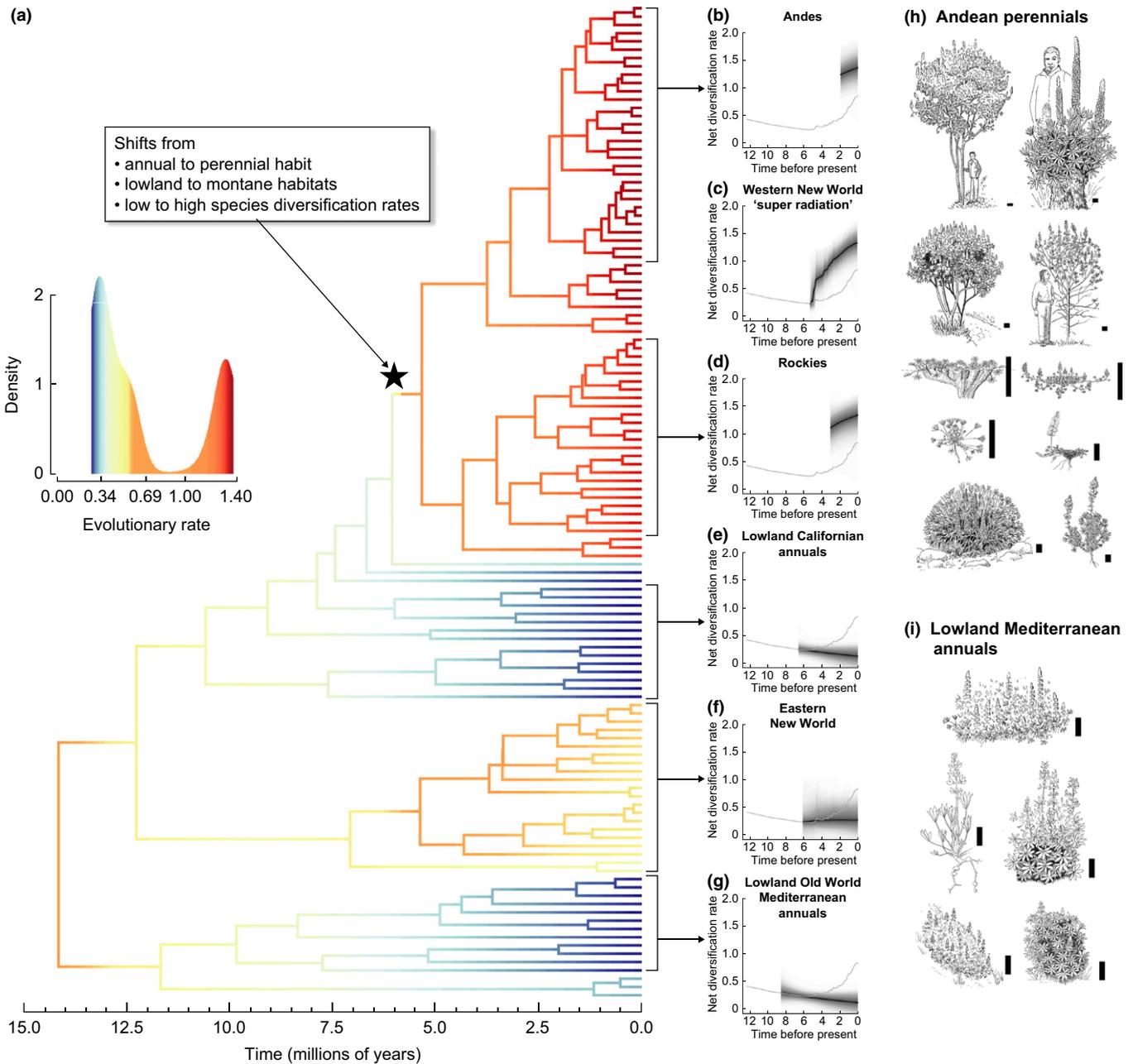


Fig. 1 The genus *Lupinus* (Leguminosae) as a model illustrating the key parameters of alpine plant radiations: evolutionary adaptation, ecological opportunity, ecological release, and accelerated rates of species and trait diversification. (a) Time-calibrated phylogeny of *Lupinus* (from Drummond *et al.*, 2012) with branches coloured by net rate of species diversification (evolutionary rate) across the tree estimated using Bayesian Analysis of Macroevolutionary Mixtures (BAMM; Rabosky, 2014). The diversification rate shift marked by a star corresponds to the primary rate shift found by Drummond *et al.* (2012) and is consistently found with high overall probability under all most probable distinct rate configurations explored by BAMM. The diversification rate shift subtends a large montane western New World 'super radiation' with nested parallel radiations in the Rockies and Andes (Drummond *et al.*, 2012). This rate shift coincides with postulated shifts from annual to perennial growth form and from lowland to montane habitats in western North America (Drummond *et al.*, 2012), suggesting a close association between these transitions and accelerated rates of species diversification. This congruence points towards a combination of evolutionary adaptation (perenniality) and ecological opportunity (availability of new alpine habitats) as likely enablers or triggers of radiation. (b–g) Curves of net diversification rate through time across the whole genus (in grey), and clade-specific trajectories in black with associated clades indicated by brackets, for the Andes (b), Rockies (d), lowland Californian annuals (e), eastern New World – a mix of annuals and perennials, lowland and montane (f) and lowland Old World Mediterranean annuals (g); the additional rates-through-time plot (c) is for the whole western New World super-radiation clade subtended by the diversification rate shift marked by a star. Note that net diversification rates in (b), (c) and (d) are increasing towards the present, with no evidence of any rate slowdowns, suggesting that these are examples of the early explosive phases of radiation. (h, i) Variation in plant growth forms for representative subsets of high-elevation Andean perennials (h) and lowland Mediterranean climate annuals (i) (bars, 5 cm) showing the accelerated disparification in growth forms enabled by perenniality associated with the Andean radiation (Hughes & Eastwood, 2006) compared with the more uniform and constrained variation associated with the lowland annual growth form. This pattern is likely attributable to ecological release associated with reduced interspecific competition in the recently formed island-like high-elevation grassland habitats of the Andes (Hughes & Eastwood, 2006).

species diversification for the large western New World *Lupinus* 'super-radiation' and the Andean and Rocky Mountain radiations nested within it (Drummond *et al.*, 2012; Koenen *et al.*, 2013). These reconstructions show that diversification rates are still accelerating in the Andes and Rockies (Fig. 1), suggesting that these radiations are examples of the explosive early phase of radiation before the onset of any diversity-dependent rate slowdown (Rabosky, 2013). Such high speciation rates are in line with those predicted under an ephemeral speciation model, whereby speciation is very common and rapid, but the majority of produced species do not persist, but instead go extinct or are reabsorbed into parental forms (Rosenblum *et al.*, 2012; Rabosky, 2013). By contrast, Roquet *et al.* (2013) found evidence for declining rates of diversification towards the present for the European alpine radiation of *Androsace*, in line with classical adaptive radiation trajectories in which both early bursts of rapid diversification and subsequent diversification rate slowdowns are observed (Gavrilets & Losos, 2009; Yoder *et al.*, 2010). It remains to be seen how robust these results are when fully sampled phylogenies become available, and to what extent other young alpine radiations also show high, and still accelerating diversification rates.

IV. Perenniality and life-form disparification

A close association between the shift from annual to perennial habit and the shift from lowland to montane habitats is an emerging common feature of plant clades that include alpine species and species radiations, and is well documented in western New World *Lupinus* (Fig. 1) (Drummond *et al.*, 2012), Arabideae (Karl & Koch, 2013), Delphinieae (Jabbour & Renner, 2012), *Androsace* (Roquet *et al.*, 2013), North American *Castilleja* (Tank & Olmstead, 2008), and Gentianinae (Favre *et al.*, 2010). In this regard the many convergent occurrences of extreme perenniality represented by long-lived cushion plants in alpine habitats are especially notable (Roquet *et al.*, 2013; Aubert *et al.*, 2014). The apparent generality of this shift to longer lifecycles associated with montane occurrence and radiations is striking and suggests that perenniality could have played a general role as a key adaptation, enabling lineages to take advantage of ecological opportunities associated with the recent availability of alpine habitats to rapidly diversify (Drummond *et al.*, 2012). Shifts from herbaceous annual habit to perennial woodiness are also a common feature of oceanic island plant radiations (Carlquist, 1965; Böhle *et al.*, 1996) again suggesting strong parallels between island and island-like alpine radiations.

Although much emphasis has been placed on insular woodiness, or montane perenniality, and how to explain these phenomena, equally striking is the rapid appearance of diverse life forms associated with plant radiations on islands and island-like montane systems. *Lupinus* again provides a good example with small trees, large woody shrubs, herbaceous acaulescent clump-forming perennials, pachycaul stem rosettes and dwarf mat-forming perennials all represented within the Andean radiation (Fig. 1h) (Hughes & Eastwood, 2006). Similarly diverse life forms occur in Andean *Hypericum* (Nürk *et al.*, 2014), *Valeriana* (Eriksen, 1989) and *Draba* (Pfitsch, 1994), tropicalpine systems more generally

(Carlquist, 1974; Hedberg & Hedberg, 1979), and the New Zealand alpine *Brachyglottis* alliance (Wagstaff & Breitwieser, 2004). The parallels between mountains and true island systems, which also demonstrate this syndrome of accelerated life-form diversification (Carlquist, 1965; Böhle *et al.*, 1996), are once again striking. This accelerated disparification of plant growth forms – the rapid occupation of potential growth form morphospace enabled by perenniality – associated with both island and alpine plant radiations provides compelling evidence for ecological release driven by ecological opportunity that has been the dominant explanation for adaptive (island) radiation (Gavrilets & Losos, 2009; Yoder *et al.*, 2010). However, it remains to be seen to what extent life-form disparification in mountains is predominantly a tropicalpine phenomenon and whether it is driven by release from environmental constraints in the peculiarly stable environments on oceanic islands and tropicalpine mountains (Carlquist, 1965, 1974), or from reduced interspecific competition in recently emerged island-like alpine habitats, or a combination of both. What does seem clear is that combinations of intrinsic key evolutionary adaptation (perenniality) and extrinsic ecological opportunity are key explanations for alpine plant radiations, as found for radiations more widely (Wagner *et al.*, 2012).

V. A comparative system for understanding evolutionary radiation

The world's mountains offer a promising comparative system for investigating plant radiations, and especially recent rapid radiations, of which there appear to be many, with similar potential to elucidate the extrinsic environmental/ecological and intrinsic evolutionary factors that drive radiation, explored to great effect for cichlid fish radiations in lakes (Wagner *et al.*, 2012). Although no comparative analyses have yet been carried out for alpine plant radiations, it seems likely that some of the analogous features of mountains identified as extrinsic drivers of fish diversity in lakes – depth, area, incident solar radiation and age (Wagner *et al.*, 2012) – will also be important in determining the size of ecological opportunities and the resources made available, and hence explaining alpine plant radiation, its scale and rate. For example, the greater areas of alpine habitats in the Andes and Himalaya, where high overall species richness and radiations of 50 to 100+ plant species have been documented, contrasts with the smaller areas and more modest floras and species radiations (5–40 species) in the mountains of New Zealand, East Africa and New Guinea (Linder, 2014; Sklenář *et al.*, 2014) (Table 1). Height of mountains is perhaps less relevant than depth of lakes, given that plant growth has an upper elevation limit, although even here the greater fish diversity in littoral as opposed to pelagic lake habitats might argue for using lake circumference as a better proxy of resource availability than area (Wagner *et al.*, 2012). By extension, length of treeline and treeline-based area models (Körner *et al.*, 2011; Paulsen & Körner, 2014) can be used to quantify the extent of alpine habitats. Of course area, circumference and depth/height are overly simplistic proxies for resource availability or overall physiographic (topographic and habitat) heterogeneity, which is a key predictor of both overall species diversity (Kreft & Jetz, 2007) and the dense packing

of narrowly restricted endemic species that make up many alpine radiations (Hughes & Eastwood, 2006). Inclusion of rugosity or ruggedness as a factor in mountain definition and quantification (Körner *et al.*, 2011; Drummond *et al.*, 2012) may go some way to accounting for this heterogeneity. It is striking that the Andes and the Hengduan Mountains, which encompass some of the most deeply dissected physiographies and the steepest and most extended environmental gradients on the planet, represent two of the hottest plant diversity hotspots (Kreft & Jetz, 2007; López-Pujol *et al.*, 2011; Boufford, 2014) and likely harbour the most spectacular alpine plant radiations (Table 1) (Madriñán *et al.*, 2013; Favre *et al.*, 2014). Another key factor potentially dictating the dynamics, rate and extent of alpine radiations is glaciation history. In tropical/subtropical mountains glaciations prompted simple vertical displacements of vegetation zones whereby alpine and montane forest habitats likely remained in adjacent valleys throughout the distribution range across the whole of the Pleistocene (Hooghiemstra & Van der Hammen, 2004). By contrast, much more dramatic displacements to lower and geographically distant and isolated refugia are implicated for temperate mountains such as the Alps and Rockies (Gavin *et al.*, 2014). Such contrasting histories will be key in explaining differences in alpine plant radiations across the globe, for example the relatively species-poor radiations in the European Alpine System (Table 1). Integration of the full gamut of extrinsic environmental factors alongside species diversification, trait and niche evolution reconstructions will be needed to better understand the predictors of alpine radiation.

VI. Future perspectives

It is clear that there are a large number of plant radiations in mountains, and especially in the alpine zones of the Andes and Himalaya, offering ample and fertile territory for deeper analysis. However, it is also clear that understanding and quantifying alpine plant radiations is hampered by lack of monographic taxonomic accounts (including plant functional trait data), of robust and well-sampled phylogenies, and of detailed diversification analyses for many clades (Table 1). Species delimitation and/or wider taxonomic issues, including generic delimitation and lack of robust infrageneric classifications, bedevil diversification analyses of every species-rich alpine plant group. There are few phylogenies with adequate taxon sampling to establish the monophyly, number and extent of radiations with confidence (i.e. the possibility that species flocks in some mountains, such as the East African Mountains, the European Alpine System and the Himalaya may be made up of several small congeneric radiations rather than single large ones which appear to be more prevalent in the Andes), let alone resolve species relationships and hence geotemporal trajectories of diversification. Indeed, lack of phylogenetic resolution remains the tell-tale hallmark of radiation. Recent studies using genome-scale data to resolve species relationships among closely related Himalayan *Pedicularis* (Orobanchaceae) (Eaton & Ree, 2013) and Lake Victoria cichlid fish (Wagner *et al.*, 2013) have provided unprecedented resolution within these prominent radiations. These studies, so far sampling just small subclades or subsets of species, provide important pointers for resolving even the youngest and

fastest radiations with denser taxon sampling. We can look forward in the near future to bigger and better phylogenies that employ near-complete taxon sampling and large gene sets for a larger sample of lineages containing alpine radiations. Better phylogenies for large clades which span multiple mountain systems and multiple radiations (such as *Draba* and other Brassicaceae, Campanulaceae, Gentianaceae, Hypericaceae, *Alchemilla* (Rosaceae), *Senecio* and other Asteraceae), will be especially instructive for understanding the drivers of alpine plant radiations across the globe.

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References

- Ager DV. 1975. The geological evolution of Europe. *Proceedings of the Geological Society* 86: 127–154.
- Aubert S, Boucher F, Lavergne S, Renaud J, Choler P. 2014. 1914–2014: a revised worldwide catalogue of cushion plants 100 years after Hauri and Schröter. *Alpine Botany* 124: 59–70.
- Axelrod DI. 1962. Post-Pliocene uplift of the Sierra Nevada, California. *Bulletin of the Geological Society of America* 73: 183–198.
- Bell CD, Donoghue MJ. 2005. Phylogeny and biogeography of Valerianaceae (Dipsacales) with special reference to the South American valerians. *Organisms Diversity and Evolution* 5: 147–159.
- Bell CD, Kutscher A, Arroyo MTK. 2012. Phylogeny and diversification of Valerianaceae (Dipsacales) in the southern Andes. *Molecular Phylogenetics and Evolution* 63: 724–737.
- Böhle U-T, Hilger HH, Martin WF. 1996. Island colonization and evolution of the insular woody habit in *Echium* L. (Boraginaceae). *Proceedings of the National Academy of Sciences, USA* 93: 11 740–11 745.
- Boufford DE. 2014. Biodiversity hotspot: China's Hengduan Mountains. *Arnoldia* 72: 24–35.
- Brown GK, Nelson G, Ladiges PY. 2006. Historical biogeography of *Rhododendron* section *Vireya* and the Malesian archipelago. *Journal of Biogeography* 33: 1929–1944.
- Carlquist S. 1965. *Island life. A natural history of the islands of the World*. New York, NY, USA: Natural History Press.
- Carlquist S. 1974. *Island biology*. New York, NY, USA: Columbia University Press.
- Chapell JMA. 1974. Geology of coral terraces, Huon Peninsula, New Guinea: a study of Quaternary movements and sea level changes. *Bulletin of the Society of Geology of America* 85: 553–570.
- Comes HP, Kadereit JW. 2003. Spatial and temporal patterns in the evolution of the flora of the European Alpine System. *Taxon* 52: 451–462.
- Cosacov A, Sérisc AN, Sosa V, De-Nova JA, Nylander S, Cocucci A. 2009. New insights into the phylogenetic relationships, character evolution, and phylogeographic patterns of *Calceolaria* (Calceolariaceae). *American Journal of Botany* 96: 2240–2255.
- 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.
- Eaton DAR, Ree RH. 2013. Inferring phylogeny and introgression using RADseq data: an example from flowering plants (*Pedicularis*: Orobanchaceae). *Systematic Biology* 65: 689–706.
- Eriksen B. 1989. Valerianaceae. In: Harling G, Andersson L, eds. *Flora of Ecuador*, vol 34. Arlöv, Sweden: Berlings, 1–59.

- Farley KA, Rasmus ME, Bogue SW. 2001. Post-10 Myr uplift and exhumation of the Northern Coast Mountains, British Columbia. *Geology* 29: 99–102.
- Favre A, Päckert M, Pauls SU, Jähmig SC, Uhl D, Michalak I, Mueller-Riehl AN. 2014. The role of the uplift of the Qinghai-Tibetan plateau for the evolution of Tibetan biotas. *Biological Reviews*. doi: 10.1111/brv.12107.
- Favre A, Yuan Y-M, Kupfer P, Alvarez N. 2010. Phylogeny of subtribe Gentianinae (Gentianaceae): biogeographic inferences despite limitations in temporal calibration points. *Taxon* 59: 1701–1711.
- Garzone CN, Hoke GD, Libarkin JC, Withers S, MacFadden B, Eiler J, Gosh P, Mulch A. 2008. Rise of the Andes. *Science* 320: 1304–1307.
- Gavin DG, Fitzpatrick MC, Gugger PF, Heath KD, Rodríguez-Sánchez F, Dobrowski SZ, Hampe A, Hu FS, Ashcroft MB, Bartlein PJ *et al.* 2014. Climate refugia: joint inference from fossil records, species distribution models and phylogeography. *New Phytologist* 204: 37–54.
- Gavrilov S, Losos JB. 2009. Adaptive radiation: contrasting theory with data. *Science* 323: 732–737.
- Gehrke B, Bräuchler C, Romoleroux K, Lundberg M, Heubl G, Erikson T. 2008. Molecular phylogenetics of *Alchemilla*, *Aphanes* and *Lachemilla* (Rosaceae) inferred from plastid and nuclear intron and spacer DNA sequences, with comments on generic classification. *Molecular Phylogenetics and Evolution* 47: 1030–1044.
- Gehrke B, Linder HP. 2009. The scramble for Africa: pan-temperate elements on the African high mountains. *Proceedings of the Royal Society B* 276: 2657–2665.
- Ghosh P, Garzone CN, Eiler JM. 2006. Rapid uplift of the Altiplano revealed through ¹³C-¹⁸O bonds in paleosol carbonates. *Science* 311: 511–515.
- Goetsch LA, Craven LA, Hall BD. 2011. Major speciation accompanied the dispersal of *Vireya* Rhododendrons (Ericaceae, *Rhododendron* sect. *Schistanthe*) through the Malayan archipelago: evidence from nuclear gene sequences. *Taxon* 60: 1015–1028.
- Graham A. 2009. The Andes: a geological overview from a biological perspective. *Annals of the Missouri Botanical Garden* 96: 371–385.
- Gregory-Wodzicki KM. 2000. Uplift history of the central and northern Andes: a review. *Geological Society of America Bulletin* 112: 1091–1105.
- Harrison TM, Copeland P, Kidd W, Yin A. 1992. Raising Tibet. *Science* 255: 367–380.
- Hedberg I, Hedberg O. 1979. Tropical-alpine life-forms of vascular plants. *Oikos* 33: 297–307.
- Heenan PB, McGlone MS. 2013. Evolution of New Zealand alpine and open-habitat plant species during the late Cenozoic. *New Zealand Journal of Ecology* 37: 105–113.
- Hooghiemstra H, Van der Hammen T. 2004. Quaternary ice-age dynamics in the Colombian Andes: developing an understanding of our legacy. *Philosophical Transactions of the Royal Society B* 359: 173–181.
- Hughes CE, Eastwood RJ. 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.
- Jabaily RS, Sytsma KJ. 2013. Historical biogeography and life-history evolution of Andean *Puya* (Bromeliaceae). *Botanical Journal of the Linnean Society* 170: 201–224.
- Jabbour F, Renner S. 2012. A phylogeny of Delphinieae (Ranunculaceae) shows *Aconitum* is nested within *Delphinium* and that late Miocene transitions to long life cycles in the Himalayas and southwest China coincide with bursts in diversification. *Molecular Phylogenetics and Evolution* 62: 928–942.
- Joly S, Heenan PB, Lockhart PJ. 2014. Species radiation by niche shifts in New Zealand's rockresses (*Pachycladon*, Brassicaceae). *Systematic Biology* 63: 192–202.
- Kadereit JW, Griebeler EM, Comes HP. 2004. Quaternary diversification in European alpine plants: pattern and process. *Philosophical Transactions of the Royal Society B* 359: 265–274.
- Karl R, Koch MA. 2013. A worldwide perspective on crucifer speciation and evolution: phylogenetics, biogeography and trait evolution in tribe Arabideae. *Annals of Botany* 112: 983–1001.
- Knox EB, Palmer JD. 1995. Chloroplast DNA variation and the recent radiation of the giant senecios (Asteraceae) on the tall mountains of eastern Africa. *Proceedings of the National Academy of Sciences, USA* 92: 10349–10353.
- Koenen EJM, de Vos JM, Atchison GW, Simon MF, Schrire BD, de Souza ER, de Queiroz LP, Hughes CE. 2013. Exploring the tempo of species diversification in legumes. *South African Journal of Botany* 89: 19–30.
- Körner C, Paulsen J, Spheeris EM. 2011. A definition of mountains and their bioclimatic belts for global comparisons of biodiversity data. *Alpine Botany* 121: 73–78.
- Kreft H, Jetz W. 2007. Global patterns and determinants of vascular plant diversity. *Proceedings of the National Academy of Sciences, USA* 104: 5925–5930.
- Linder HP. 2008. Plant species radiations: where, when, why? *Philosophical Transactions of the Royal Society B* 363: 3097–3105.
- Linder HP. 2014. The evolution of African plant diversity. *Frontiers in Ecology and Evolution* 2: 38.
- Liu J-Q, Wang Y-J, Wang A-L, Hideaki O, Abbott RJ. 2006. Radiation and diversification within the *Ligularia*–*Cremanthodium*–*Parasenecio* complex (Asteraceae) triggered by uplift of the Qinghai-Tibetan Plateau. *Molecular Phylogenetics and Evolution* 38: 31–49.
- Lockhart PJ, McLenachan PA, Havell D, Glenny D, Huson D, Jensen U. 2001. Phylogeny, radiation, and transoceanic dispersal of New Zealand alpine buttercups: molecular evidence under split decomposition. *Annals of the Missouri Botanical Garden* 88: 458–477.
- López-Pujol J, Zhang F-M, Sun H-Q, Ying T-S, Ge S. 2011. Centres of plant endemism in China: places for survival or speciation? *Journal of Biogeography* 38: 1267–1280.
- Losos JB, Ricklefs RE. 2009. Adaptation and diversification on islands. *Nature* 457: 830–836.
- Luebert F, Weigend M. 2014. Phylogenetic insights into Andean plant diversification. *Frontiers in Ecology and Evolution* 2: 27.
- Madriñán S, Cortés AJ, Richardson JE. 2013. Páramo is the world's fastest evolving and coolest biodiversity hotspot. *Frontiers in Genetics* 4: 1–7.
- Meseguer AS, Aldasoro JJ, Sanmartín I. 2013. Bayesian inference of phylogeny, morphology and range evolution reveals a complex evolutionary history in *St. John's wort* (*Hypericum*). *Molecular Phylogenetics and Evolution* 67: 379–403.
- Meudt HM, Lockhart PJ, Bryant D. 2009. Species delimitation and phylogeny of a New Zealand plant species radiation. *BMC Evolutionary Biology* 9: 111.
- Milne RI, Davies C, Prickett R, Inns LH, Chamberlain DF. 2010. Phylogeny of *Rhododendron* subgenus *Hymenanthes* based on chloroplast DNA markers: between-lineage hybridisation during adaptive radiation? *Plant Systematics and Evolution* 285: 233–244.
- Moore BR, Donoghue MJ. 2007. Correlates of diversification in the plant clade Dipsacales: geographic movement and evolutionary innovations. *American Naturalist* 170: S28–S55.
- Mulch A, Chamberlain CP. 2006. Earth science: the rise and growth of Tibet. *Nature* 439: 670–671.
- Nürk NM, Scheriau C, Madriñán S. 2014. Explosive radiation in high Andean *Hypericum* – rates of diversification among New World lineages. *Frontiers in Genetics* 4: 1–14.
- Ollier CD. 2006. Mountain uplift and the Neotectonic period. *Annals of Geophysics* 49: 437–450.
- Paulsen J, Körner C. 2014. A climate-based model to predict potential treeline position around the globe. *Alpine Botany* 124: 1–12.
- Pfitsch WA. 1994. Morphological and physiological radiation in páramo *Draba*. In: Rundel PW, Smith AP, Meinzer FC, eds. *Tropical and alpine environments: plant form and function*. Cambridge, UK: Cambridge University Press, 151–165.
- Rabosky DL. 2013. Diversity-dependence, ecological speciation, and the role of competition in macroevolution. *Annual Reviews of Ecology, Evolution and Systematics* 44: 481–502.
- Rabosky DL. 2014. Automatic detection of key innovations, rate shifts, and diversity-dependence on phylogenetic trees. *PLoS ONE* 9: e89543.
- Rouget C, Boucher FC, Thuiller W, Lavergne S. 2013. Replicated radiations of the alpine genus *Androsace* (Primulaceae) driven by range expansion and convergent key innovations. *Journal of Biogeography* 40: 1874–1886.
- Rosenblum EB, Sarver BAJ, Brown JW, Des Roches S, Hardwick KM, Hether TD, Eastman JM, Pennell MW, Harmon LJ. 2012. Goldilocks meets Santa Rosalia: an ephemeral speciation model explains patterns of diversification across time scales. *Evolutionary Biology* 39: 255–261.
- Sanderson MJ. 1998. Reappraising adaptive radiation. *American Journal of Botany* 85: 1650–1655.
- Scherson RA, Vidal R, Sanderson MJ. 2008. Phylogeny, biogeography, and rates of diversification of New World *Astragalus* (Leguminosae) with an emphasis on South American radiations. *American Journal of Botany* 95: 1030–1039.

- Silvestro D, Schnitzler J, Zizka G. 2011. A Bayesian framework to estimate diversification rates and their variation through time and space. *BMC Evolutionary Biology* 11: 311.
- Sklenář P, Dušková E, Balslev H. 2010. Tropical and temperate: evolutionary history of the Páramo flora. *Botanical Review* 77: 71–108.
- Sklenář P, Hedberg I, Cleef AM. 2014. Island biogeography of tropical alpine floras. *Journal of Biogeography* 41: 287–297.
- Spicer RA, Harris NBW, Widdowson M, Herman AB, Guo S, Valdes PJ, Wolfe JA, Kelley SP. 2003. Constant elevation of southern Tibet over the past 15 million years. *Nature* 421: 622–624.
- Sun Y, Wang A, Wan D, Wang Q, Liu J. 2012. Rapid radiation of *Rheum* (Polygonaceae) and parallel evolution of morphological traits. *Molecular Phylogenetics and Evolution* 63: 150–158.
- Tank DC, Olmstead RG. 2008. From annuals to perennials: phylogeny of subtribe Castillejininae (Orobanchaceae). *American Journal of Botany* 95: 608–625.
- Von Hagen KB, Kadereit JW. 2001. The phylogeny of *Gentianella* (Gentianaceae) and its colonization of the southern hemisphere as revealed by nuclear and chloroplast DNA sequence variation. *Organisms Diversity and Evolution* 1: 61–79.
- Wagner CE, Harmon LJ, Seehausen O. 2012. Ecological opportunity and sexual selection together predict adaptive radiation. *Nature* 487: 366–369.
- Wagner CE, Keller I, Wittwer S, Selz OM, Mwaiko S, Greuter L, Sivasundar A, Seehausen O. 2013. Genome-wide RAD sequence data provide unprecedented resolution of species boundaries and relationships in the Lake Victoria cichlid adaptive radiation. *Molecular Ecology* 22: 787–798.
- Wagstaff SJ, Breitwieser I. 2004. Phylogeny and classification of *Brachyglottis* (Senecioneae, Asteraceae): an example of a rapid species radiation in New Zealand. *Systematic Botany* 29: 1003–1010.
- Wen J, Zhang J-Q, Nie Z-L, Zhong Y, Sun H. 2014. Evolutionary diversifications of plants on the Qinghai-Tibetan Plateau. *Frontiers in Genetics* 5(4): 1–16.
- Wichura H, Bousquet R, Oberhansli R, Strecker MR, Trauth MH. 2010. Evidence for middle Miocene uplift of the East African Plateau. *Geology* 38: 543–546.
- Winkworth RC, Grau J, Robertson AW, Lockhart PJ. 2002. The origins and evolution of the genus *Mysotis* L. (Boraginaceae). *Molecular Phylogenetics and Evolution* 24: 180–193.
- Winkworth RC, Wagstaff SJ, Glenny D, Lockhart PJ. 2005. Evolution of the New Zealand mountain flora: origins, diversification and dispersal. *Organisms Diversity and Evolution* 5: 237–247.
- Wolfe AD, Randle CP, Datwyler SL, Morawetz JJ, Aguedas N, Diaz J. 2006. Phylogeny, taxonomic affinities, and biogeography of *Penstemon* (Plantaginaceae) based on ITS and cpDNA sequence data. *American Journal of Botany* 93: 1699–1713.
- Yoder JB, Clancey E, Des Roches S, Eastman JM, Gentry L, Godsoe W, Hagey TJ, Jørgensen D, Oswald BP, Robertson J *et al.* 2010. Ecological opportunity and the origin of adaptive radiations. *Journal of Evolutionary Biology* 23: 1581–1596.
- Yu X-Q, Maki M, Drew BT, Paton AJ, Li H-W, Zhao J-L, Conran JG, Li J. 2014. Phylogeny and historical biogeography of *Isodon* (Lamiaceae): rapid radiation in south-west China and Miocene overland dispersal into Africa. *Molecular Phylogenetics and Evolution* 77: 183–194.
- Zhang J-Q, Meng S-Y, Allen GA, Wen J, Rao G-Y. 2014. Rapid radiation and dispersal out of the Qinghai-Tibetan Plateau of an alpine plant lineage *Rhodiola* (Crassulaceae). *Molecular Phylogenetics and Evolution* 77: 147–158.
- Zhang L-B, Comes HP, Kadereit JW. 2004. The temporal course of Quaternary diversification in the European high mountain endemic *Primula* section *Auricula* (Primulaceae). *International Journal of Plant Sciences* 165: 191–207.



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