

Commentary

Adaptation meets dispersal: legumes in the land of succulents

In his introduction to biogeography in the *Origin of Species*, Charles Darwin outlined the three ‘great facts’ of organismal distribution (Darwin, 1859). These add up to the following: the biotas of the major biogeographic regions of the world (at a continental scale) have distinct ‘affinities’ owing to the ‘bonds of inheritance’ from different ancestral inhabitants. Within each great realm, species became adapted to a similar set of environments (forests, grasslands, etc.), with the result that the occupants of these biomes differ from continent to continent. Darwin highlighted South America, Africa, and Australia, where ‘we shall find parts extremely similar in all their conditions, yet it would not be possible to point out three faunas and floras more utterly dissimilar.’ (p. 347). But, he hastened to add that there were also shared elements across realms: ‘The degree of dissimilarity will depend on the migration of the more dominant forms of life from one region into another having been effected with more or less ease, at periods more or less remote . . .’ (p. 350). Here he cited the northern forests of the Old and New Worlds, ‘where the land almost joins, and where, under a slightly different climate, there might have been free migration for the northern temperate forms . . .’ (p. 347). In the end, a balance is struck between *in situ* diversification and transcontinental dispersal.

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Against Darwin’s backdrop, the case highlighted by Gagnon *et al.* (pp. 1994–2008), in this issue of *New Phytologist*, stands out like a sore thumb. In a 225-species lineage of legumes (the *Caesalpinia* clade), they show that closely related plants have come to occupy a distinctive ‘succulent biome’ (with annual precipitation < 1200 mm) that is widely disjunct on separate continents (Schrire *et al.*, 2005; Oliveira-Filho *et al.*, 2013). These plants adapted to this habitat in one region and then spread to similar environments around the globe. Furthermore, this happened before surrounding plants on each continent managed to adapt to these harsh conditions. In other words, it was easier for the plants in this

lineage to move around, with their adaptations, than it was for other lineages to adapt *in situ*: it was ‘easier to move than to evolve’ (Donoghue, 2008). ‘Phylogenetic biome conservatism’ has been kicking around for some time (Crisp *et al.*, 2009), generating more or less skepticism (Edwards & Donoghue, 2013; Donoghue & Edwards, 2014). What Gagnon *et al.* (2019) have provided is a compelling real-world example, and one that (like all great studies) raises new questions of profound significance.

However, before we get to these, let us understand what Gagnon *et al.* (2019) actually did. First, they used a molecular phylogeny including *c.* 75% of the species in the clade to infer ancestral geographic areas and past movements. They determined that there were a minimum of 49 transcontinental movements over the past 55 million years. Second, they showed that occupation of the succulent biome was highly conserved as plants moved between continents. Of all the transcontinental movements, 27 of them were from a succulent biome on one continent to a succulent biome on another. Third, those biome shifts that did occur were associated with shifts in life-form. Species that occupy the ancestral succulent biome are trees and shrubs. Shifts into temperate environments were accompanied by the evolution of the suffrutescent (functionally, perennial herbaceous) habit, while those into savannas entailed the evolution of the liana (woody vine) habit. Finally, Gagnon *et al.* (2019) showed that dispersal events among succulent biomes have been spread rather evenly through time, with no major changes in the rate of diversification. The methods used by Gagnon *et al.* (2019) are not new. Instead, they applied a battery of existing comparative approaches (with acknowledged limitations) to explore a particular case in detail. The beauty of studies at this scale, with extensive species sampling, is the possibility of pinning down where and when particular evolutionary events took place. Attention to such details sets studies of ‘model clades’ apart from an increasing number of much larger but more superficial phylogenetical analyses (Donoghue & Edwards, 2019).

The mix of species in a particular biome is partially a function of the rate at which adaptations allowing occupancy evolve in the available lineages. In this case, the ancestors of the *Caesalpinia* clade evolved the deciduous habit and the ability to quickly produce new leaves after rain: ‘rapid burst post-dry season leaf flushing’ (RF). Deciduous leaves have evolved hundreds of times in plants, in relation to both drought and freezing (Edwards *et al.*, 2017). Legumes may be predisposed to the RF strategy because many have high leaf-nitrogen content (some facultatively, and independent of nitrogen fixation), and correspondingly high rates of photosynthesis. On this basis, McKey (1994) argued that legumes could more rapidly return the cost of producing short-lived leaves.

That is one side of the equation. The other side is dispersal, especially the rate of transcontinental movement. Legumes move around way better than you might imagine, or so it seems given

This article is a Commentary on Gagnon *et al.*, 2019: 1994–2008.

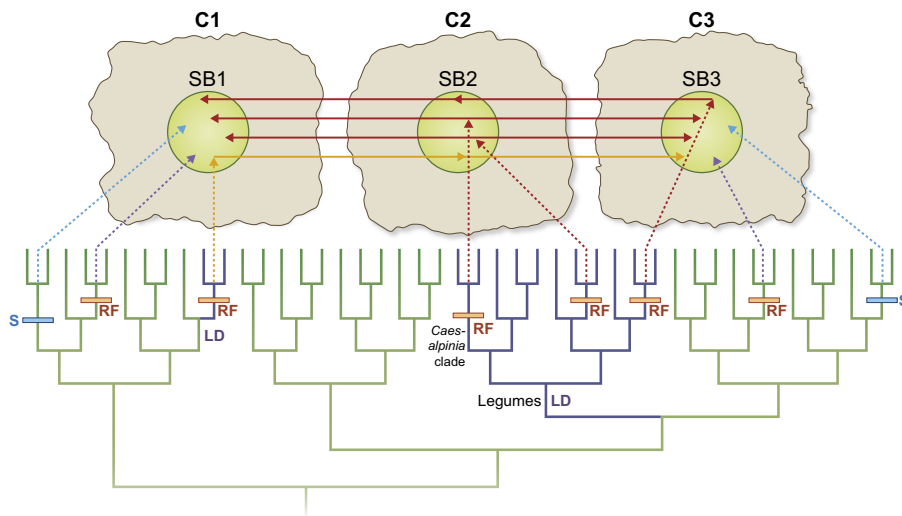


Fig. 1 Adaptation plus dispersal can foster a transcontinental 'metacommunity'. See text for details. C, continent; LD, long distance; RF, rapid flushing; S, succulent; SB, succulent biome. Dotted lines represent movement into the succulent biome; solid lines represent transcontinental dispersal.

their far-flung distributions (Raven & Polhill, 1981). If legumes can readily evolve RF, and if they are also good dispersers, it stands to reason that they could move between succulent biomes. This makes sense, but it would be nice to know more about the actual dispersal of these species. Browsing the illustrations in the monograph of the group (Gagnon *et al.*, 2016), my sense is that most of them have fairly normal-looking legume fruits (like pea pods), but some are woody and indehiscent, some have gnarly spines, some have wings, and one small pantropical group even has pods that drift on ocean currents. It would be good to know how these map onto the phylogeny. In the meantime, there is a bit of a conundrum. It has been shown in other studies that legumes in patches of seasonally dry tropical forest in South America are quite isolated from one another (Särkinen *et al.*, 2012) and show little sign of gene flow. This does not square well with the notion that these plants are great movers. Maybe, as Gagnon *et al.* (2019) suggest, their wide distribution is more a function of the stability of these environmental conditions over very long time periods – eventually you can get anywhere!

For me, the revelation in this case is the transcendent significance of how the two key parameters – adaptation and dispersal – evolve in relation to one another. Fig. 1, inspired by Gagnon *et al.* (2019), attempts to illustrate this interaction and its consequences. Three continents are depicted (C1–C3), each with a succulent biome in the center (SB1–SB3). Rapid flushing (RF) evolves multiple times as a strategy that allows persistence in this environment. A number of these origins take place within the legumes (including in the *Caesalpinia* clade), and these have a propensity from the outset for long-distance (LD) dispersal (presumably legumes would spread just as widely in other biomes, e.g. savannas, rain forests). Entry into the succulent biome evolves in another LD clade here, but also in clades that lack LD dispersal (and therefore impart a degree of continental 'affinity'). The key is that only the clades with RF plus LD spread to succulent biomes on other continents. The result is that the legumes in the succulent biome function as a somewhat connected 'metacommunity' (Lavin *et al.*, 2004). Of course, multiple lineages of leaf- and stem-succulent plants (S) also (eventually) evolved into the succulent biome.

It is where adaptation and dispersal meet in evolution that we see an outcome unanticipated by Darwin. Is it just chance that these are correlated? Perhaps. But, perhaps RF and dispersal/establishment reflect an underlying attribute. For example, high nitrogen metabolism could be a factor that promotes both. Is this situation unique, or are there other examples? Wetlands might be another case. Aquatic plants have evolved over 200 times in the vascular plants (Cook, 1999), often accompanied by the evolution of asexual reproductive mechanisms that promote LD dispersal (Philbrick & Les, 1996). Indeed, one finds many of the same aquatic clades on every continent – Alismataceae, Lemnoideae, Potamogetonaceae, and Menyanthaceae, to name a few.

I cannot resist one last irony highlighted by Gagnon *et al.* (2019), namely that a succulent biome full of legumes may have existed long before succulents themselves joined the party. The *Caesalpinia* clade was radiating, presumably in scattered dry environments, way back in the Eocene, but the major clades of succulent plants did not come on the scene until the Miocene (Arakaki *et al.*, 2011). The implication is that there was a nonanalog vegetation type back then, with one of the major strategies (rapid flushing) present, but the other (stem succulence) missing. Such quirks may turn out to be the norm in biome assembly. For example, tropical rainforest habitats may have existed before the Cretaceous (Davis *et al.*, 2005), but without some of today's iconic residents, including legumes themselves!

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