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Research article

Disparate relatives: Life histories vary more in genera occupying intermediate environments

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ABSTRACT

Species within clades are commonly assumed to share similar life history traits, but within a given region some clades show much greater variability in traits than others. Are variable clades older, allowing more time for trait diversification? Or do they occupy particular environments, providing a wider range of abiotic or biotic opportunities for the establishment and maintenance of diverse trait attributes? Does environmental opportunity increase trait variability across all species, or is it specific to species belonging to the same clade, increasing only within-clade trait variability? We studied the variability of six life-history traits (initiation of flowering, duration of flowering, plant life span, seed mass, stress tolerance, type of reproduction) within 383 angiosperm genera from Central Europe distributed along six abiotic gradients. We compared patterns of within-genus variability to those present in the entire dataset, independent of genus membership. We found that trait variability differed strongly between genera, but did not depend on their age. Trait variability was higher within genera occupying intermediate positions along regional abiotic environmental gradients, compared with patterns across the entire dataset (and unbiased by geographical sampling, family membership or species richness). Increasing trait variability within genera reflected increasing independence of traits from the abiotic environment. We conclude that intermediate abiotic environments play an important role in maintaining and possibly generating the striking diversity of life history traits present within certain clades. They may do so by relaxing the abiotic constraints on the evolution and maintenance of species traits within clades.

Introduction

Clades within a region differ in their species richness but also in their trait variability, and high species richness does not equal high trait variability (Losos and Miles, 2002; Adams et al., 2009). The trait variability within a clade can be measured as the standard deviation of attributes of a given trait across its constituent species. High variability of traits in some clades may undermine the common tenet that clade membership can be used as a proxy for traits (Webb et al., 2002). While the factors driving species diversity of clades within a region have been extensively studied (e.g. Bowker et al., 2010; Kozak and Wiens, 2010), those driving the trait variability within clades have received much less attention (e.g. Harmon et al., 2010 for variation in animal body size). It has been suggested that increased contemporary trait variability within some clades might be due to their greater age, allowing a greater period of time over which divergence could occur (Moles et al., 2005; Ackerly and Nyffeler, 2004) (Hypothesis 1 in Table 1 and Fig. 1, note that all hypotheses referred to here are summarized together in Table 1). However, increased contemporary trait variability within clades may also be influenced by the environments occupied by the clades' constituent species. We know that local biotic interactions or environmental filters may affect both the diversity of clades and of traits realized within local communities (e.g. Helmus et al., 2007a), but we do not know whether, across an entire region, clades occupying particular environments show more variable traits than those occupying others.

Among the best-studied factors influencing plant traits are abiotic stress (e.g. freezing) and competitive interactions (Grime, 1977). These factors generally vary inversely along most abiotic gradients, as stress is suggested to become more intense and competitive interactions less important toward the extremes of

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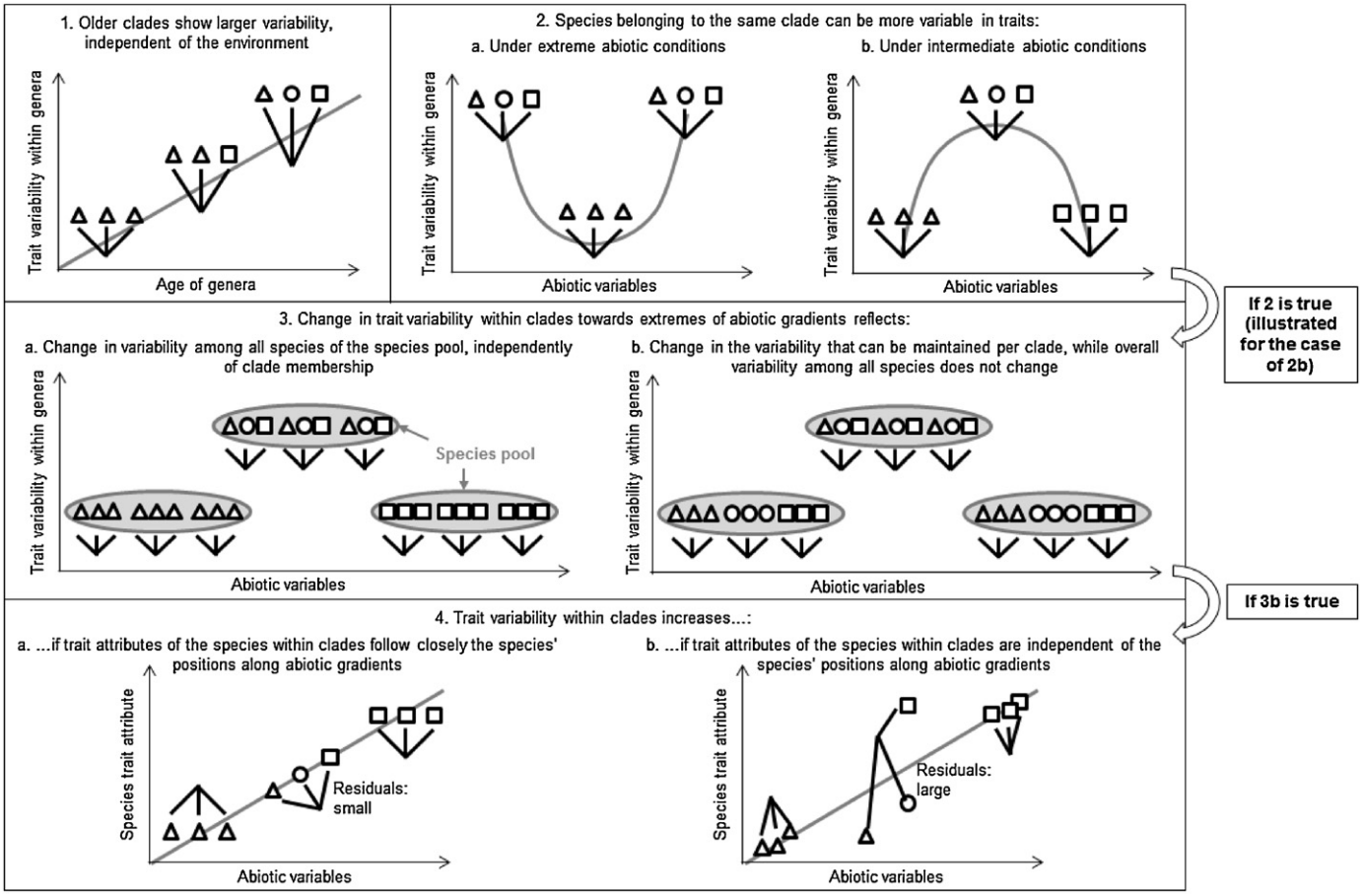

Fig. 1. Illustration of the different hypotheses explaining variation of trait variability within clades across a region. White circles, triangles and squares illustrate different attributes of the same trait for different species. Species belong to different clades (three species per clade). In 1, trait variability within clades only depends on the age of the clades, and older clades show larger variability (Hypothesis 1, Table 1). In 2, trait variability within clades depends on the opportunities to establish and maintain diverse trait attributes in a given environment. In 2a, trait variability is increased under extreme abiotic conditions (Hypothesis 2a, Table 1). In 2b, trait variability is increased under intermediate abiotic conditions (Hypothesis 2b, Table 1). We assume for the next part of this Figure that Hypothesis 2 is valid and we illustrate for the case of Hypothesis 2b. In 3a, environmental opportunity operates equally across all species and incumbent clades reflect this overall trait variability (Hypothesis 3a, Table 1). In 3b, environmental opportunity is specific to species belonging to the same clade (for instance due to interaction with closely related competitors or with specialized pollinators or phytophages), and thus it affects only within-clade trait variability (Hypothesis 3b, Table 1). We assume for the next part of this Figure that Hypothesis 3b is valid (and again illustrate it for increased trait variability under intermediate abiotic conditions). In 4a, the main driver of increased trait variability within clades may be the increased phenotypic response of their constituent species to the abiotic gradients (Hypothesis 4a, Table 1). In this case, increased trait variability corresponds to increasing correlation, i.e. decreasing residuals, between species traits and abiotic variables. In 4b, the main driver of increased trait variability may be the independence of phenotypes from the abiotic constraints, instead phenotypes may respond to biotic factors increasing in intensity or diversity in intermediate abiotic environments (Hypothesis 4b, Table 1). In this case, increased trait variability corresponds to decreasing correlation, i.e. increasing residuals, between species traits and abiotic variables. The data obtained support Hypotheses 2b, 3b and 4b.

gradients (Welden and Slauson, 1986). Also, the number of potentially interacting species generally declines toward these extremes (Michalet et al., 2006; Bartish et al., 2010). Both abiotic stress and competition (and other biotic interactions) may foster as well as limit trait variability through strong directional selection pressures (Swenson and Enquist, 2007; Pfennig, 2009) as well as through ecological sorting (Helmus et al., 2007a). Overall, if the environment influences trait variability within clades, we may expect that trait variability will become either more or less important toward the extremes of abiotic gradients (Hypothesis 2a and 2b, respectively, in Table 1 and Fig. 1).

Extreme abiotic environments may influence trait variation in one of the two ways. First, these environments may change trait variability among all species, independent of clade membership, by providing a particularly wide range of abiotic or biotic opportunities, and hence for species that differ strongly in traits (Ackerly and Cornwell, 2007) (Hypothesis 3a in Table 1 and Fig. 1). The establishment and maintenance of a particularly large overall range of trait attributes among all species will then be reflected by an increased trait variability of species within clades. Second, extreme abiotic environments may influence the variability within clades by affecting only that which can be maintained per clade, with overall variability across all species not changing (Hypothesis 3b in Table 1 and Fig. 1). In fact environmental opportunity might be specific to species belonging to the same clade. For instance, particular environments may provide many closely related competitors, or many phytophages or pollinators specialized on a given incumbent plant clade (DiMichele et al., 2004; Pfennig, 2009). Interactions with these species will promote the establishment and maintenance of a particularly large variability of trait attributes within each clade occupying these environments, without increasing trait variability across the entire species pool.

If environmental opportunity operates indeed within clades (above Hypothesis 3b), then the main driver of increased trait variability in clades in particular sections of abiotic gradients within a region may be the increased phenotypic response of their