



New Phytologist Supporting information

Article title: **Benefits from living together? Clades whose species use similar habitats may persist due to eco-evolutionary feedbacks**

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The following Supporting Information is available for this article:

Notes S1 Habitat similarity among species within each of the angiosperm genera in the Netherlands

We provide an example of habitat use along multiple environmental gradients and its variation among species within each of the angiosperm genera in the Netherlands (from Ozinga *et al.*, 2013). We find that many of these genera exhibit minimal variation of the preferred habitats among their constituent species, while only a few show large variation, even after accounting for the present-day richness and the age of the genera (Fig. S1). This result appears to be true for the fossil record as well. Notes S3 provides an example of both strong and weak variation in habitat use through deep evolutionary time from the fossil record. Overall, clades appear to vary strongly in the degree to which their species occupy similar habitats.

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Notes S2 Relationship between competitiveness and habitat similarity within genera

Methods: The investment of species into competitiveness was inferred following Grime's CSR ecological plant strategy scheme (Grime, 1977; applied in Klotz *et al.*, 2002). Essentially, this system interprets multiple life history traits such as plant and seed size as indicative of competitiveness and ranks these traits along gradients of a three-way trade-off between competitiveness, stress tolerance and the capacity to use disturbed (ruderal) environments (C, S, or R). The CSR classifications ranks species as non-C (0), entirely C (1) or C combined with either stress tolerance or disturbance (0.5). We characterized genera by their means across species. Species possessing traits corresponding to competitiveness hence invest relatively more into competitiveness and less into the two other competing demands. Although the CSR scheme has been criticized (Grace, 1991), it has proven to be a good predictor of patterns of species coexistence in a given region and of environmental conditions (e.g. Carlyle *et al.*, 2010). Moreover, this scheme is the only one available to rank all species in our study region or in any other region according to their competitiveness.

Result: High similarity of habitats among species within plant genera decreases rather than increases competitiveness (Fig. S2). This relationship is independent of whether high habitat similarity corresponds to high co-occurrence among congeners (indicated by an unsigned residual co-occurrence in lower quartile, left graph) or whether habitat similarity is unrelated to co-occurrence (i.e. unsigned residual co-occurrence in higher quartile, right graph). An analysis including genus crown-age and species richness as covariables and treating residual co-occurrence as a continuous variable yields a non-significant interaction term 'habitat similarity × residual co-occurrence' ($t=-1.29$, $P=0.2$).

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Notes S3 Habitat similarity among related species in fossil plant–insect relationships

We are not aware of an example of habitat use by plants observed in the fossil record during the evolutionary history of a plant clade. There are, however, observations on long-term occupation of habitats involving insect herbivores. During the past two decades several studies of deep-time plant–insect associations have documented the persistence or lack thereof of specialized, tissue specific niches on particular plant-host taxa. These examinations have involved clades of gall wasps, wood-boring beetles and leaf-mining moths (Waggoner & Poteet, 1996; Labandeira *et al.*, 2001; Doorenweerd *et al.*, 2015, respectively), as well as instances of the ephemerality of such niches through their eradication by mechanisms such as plant-host switching and extinction, often involving leaf-miners (Labandeira, 1998; Winkler *et al.*, 2015). For insect herbivores a habitat roughly corresponds to a host plant species and the tissue types used on that host plant. The paleoecology of plant–insect associations therefore can contribute insight on habitat similarity among related species within clades, including between ancestors and descendants within lineages. There is evidence for habitat occupancy that is similar or dissimilar among ancestors and descendants within clades. One example of fossil evidence for phylogenetic similarity in habitat use among such relatives is found in lepidopteran leaf miners on oaks (Fagaceae: *Quercus*) from western North America that span several million years from the Middle Miocene to the present (Opler, 1973, 1974a). Within this study perhaps the best studied system are certain herbivores on *Quercus agrifolia* (coast live oak, encina), an oak species with a fossil record extending to the middle Miocene 12.5 million years ago (Mensing, 2005), as evidenced by megafloral occurrences (Axelrod, 1967, 1987) and stereotypical gall-wasp galls (Larew, 1992) indicating *Q. agrifolia*. *Quercus agrifolia* currently hosts four leaf-mining genera that form serpentine or blotch mines in internal leaf tissues: *Stigmella* (Nepticulidae), *Bucculatrix* (Bucculatricidae), *Lithocolletis* (Gracillariidae) and *Evippe* (Geometridae) (Opler, 1974b; Fig. S3A). Distinctive leaf mines (Labandeira *et al.*, 2007; Doorenweerd *et al.*, 2015) can be traced through modern *Q. agrifolia* to ancestral host species that are preserved as diagnostic, fossil leaf-mine morphotypes structurally identical to modern congeners. While there may have been host-switching among genera of other leaf miners and appearances and disappearances of other leaf miners on *Q. agrifolia*, these four genera exhibited deep-time persistence and continuity, and maintained habitat occupancy during an interval lasting from 12.5 to 5.3 million years ago (Opler, 1973) and to the present (Opler, 1974), in spite of profound environmental change, particularly from Pleistocene glaciation cycles.

A different mode emerges from the much older, component arthropod community (*sensu* Root, 1973), on Late Paleozoic *Psaronius* marattialean tree ferns. *Psaronius* occurs during the Late Carboniferous of the paleoequatorial Illinois and Appalachian basins, U.S.A. (Rothwell & Scott, 1983; Labandeira & Phillips, 1996, 2002; Labandeira *et al.*, 1997) and analogous habitats in European Euramerica (Rösler, 2000). Some of these associations continued throughout the Permian of North China and South China, paleocontinents that were being sutured to eastern Eurasia, forming Cathaysia (D’Rozario *et al.*, 2011; Fig. S3B). In the case of host *Psaronius chasei* and closely related species of the Illinois Basin, the collective evidence indicates significant convergence of insect consumer clades in habitat use. Independently garnered body-fossil insect data indicate considerable insect lineage turnover during this time interval, particularly at extinction events (Labandeira, 2005). As well, there is a parallel, more gradual pattern of replacement of the late Paleozoic insect fauna by the Modern fauna throughout the Permian (Labandeira, 2005). In the *Psaronius* component community, several functional feeding groups – distinctive, diagnosable, types of feeding, as analogous to leaf mining example mentioned above, were examined based on damage-type distinctiveness, a condition frequently detected in the fossil record (Labandeira, 2002; Labandeira *et al.*, 2007). These shifts in insect consumer clades occupying a particular habitat indicate low habitat similarity among ancestors and descendants.

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Notes S4 Species within clades occupying similar habitats: no consequences for the capacity to respond to environmental change

1. Suitable habitats remain available locally and can be tracked, particularly by species sharing similar habitats with their relatives.

Mechanism

Habitats have undergone periods of rapid and major shifts throughout the deep-time history of most clades. These rapid environmental shifts would be devastating for biotas that have slowly evolving habitat niches, provided that habitats can change equally across very large areas. Such a uniform change would preclude any rapid escape to more hospitable areas. However, the reality appears quite different.

Many landscapes in biomes ranging from tundra to tropical forests exhibit small-scale heterogeneity of abiotic environments at the scales of hundreds of meters or less (Scherrer & Körner, 2011). Biotic environments may vary at even a finer grain; for instance, provision for nectar production and pollination services (Thompson, 2004), or soil microbial activity (Bennett *et al.*, 2009; Jacquemyn *et al.*, 2014). For most species, large and continuous stretches of suitable environmental conditions are rare because they are overlain by spatially fine-grained habitat variation. Paradoxically, this fine-grained habitat heterogeneity can ensure that suitable environments remain accessible under large-scale (regional or continental) environmental change (Fig. S4). Large-scale changes might hence be compensated by small-scale redistribution. Indeed, this has been demonstrated for arthropods that redistribute among microhabitats on tree bark (Prinzing, 2005), or for thermophilous species inhabiting numerous extra-Mediterranean refugia during glacial stages of the Pleistocene (Schmitt & Varga, 2012). If tracking a suitable environment in space is impracticable, species may still respond to environmental changes by adaptive plasticity or maternal effects (Kuijper & Hoyle, 2015), or track suitable environments in time through a persistent seed bank in plants (Ozinga *et al.*, 2009) or hibernation in animals (Ultsch, 2006). Finally, even if environmental change operates at longer spatial or temporal scales, species may succeed in tracking environmental changes by long-distance dispersal. The fossil record provides rich examples of species that changed their ranges by tracking redistribution of their habitat-niche under Pleistocene climatic fluctuations (Lang, 1994).

Overall, even under major regional to global environmental shifts, suitable habitat environments often remain accessible (Fig. S4). Consequently, low variation of habitat niches and associated characters

among species may not prevent survival under changing environments, albeit some predicted climate changes may exceed observed migration capacities (Normand *et al.*, 2011). One might expect that clades whose species can track shifting environments have been able to conserve their ancestral niches (Prinzing, 2003). In such cases, similar habitat niches among related species within a clade would result from a particularly high capacity to track suitable patches of their preferred habitat, and not from a particularly low capacity for establishment in a new habitat niche.

Tentative evidence

We explored tentative evidence supporting the hypothesis that clades whose species use similar habitats succeed in tracking habitats. We used results from Ozinga *et al.* (2005) who had applied ordination techniques (DCA and CCA) to predict which habitat patches across fragmented Dutch landscapes are suitable for each single species of the Dutch flora. For some species, predictions matched observations better than for others, indicating that these species better tracked their habitat niches. The degree of habitat tracking was related to life-history traits of the species. Much of this interspecific variation of life-history traits could be explained by the capacity of species for long-distance dispersal (inferred from morphological characters), a long life span, and the existence of a persistent seed bank (Ozinga *et al.*, 2005). We averaged each of these three traits within genera; measured habitat similarity among species (section II); and found that none of the traits were correlated to the similarity of habitats among-species within genera (section II; unsigned $r < 0.21$, $P > 0.73$). Then we used a multiple regression analysis to explain the genus-means of the degree of habitat tracking by: (i) the genus-means of each of the three traits, (ii) the within-genus habitat similarity, and (iii) the interaction terms between habitat similarity and each of the three trait means. We found a significant positive interaction term between habitat similarity within genera and mean adult life-span ($df=144$, $t=2.1$ $P=0.040$, total R^2 of model=0.34): only for genera whose species occupy similar habitats, did high adult life-span improve habitat tracking (Fig. S5). Overall, for the same life span and capacity of long-distance dispersal, genera whose species share similar habitats did seem to have a higher capacity to track suitable habitat patches.

2. Any species carries the potential of evolving responses to present and future changing environments, even if species within clades have maintained similar habitats during the past.

Mechanism

If relatives within a clade occupy similar habitats this suggests slow or limited habitat differentiation in the past. Here, we argue that limited past differentiation does not necessarily prevent rapid innovation and habitat shift when the ancestral habitat niche entirely disappears (Armbruster & Baldwin, 1998). Specifically, we will explore possible mechanisms of how clades composed of species using similar habitats may have retained the potential to expand or change habitat niches with only limited genomic evolution.

Cryptic and epigenetic diversity maintains adaptive plasticity—Species within clades may, for instance, carry adaptations necessary for occupying a new habitat because of preadaptation or, more appropriately ‘exaptation’ (Gould & Vrba, 1982), particularly if physiological constraints imposed by the new habitat are similar to those of the old niche. Such preadaptation might involve multiple alleles available in polyploid species (Ainouche *et al.*, 2009), or epigenetically masked characters (Bossdorf *et al.*, 2008) that increase the robustness and survival of populations in changing environments (Angers *et al.*, 2010). Cryptic variation evidently has no effect on phenotypes within a given environmental background, but it potentially can be advantageous following environmental change (Hayden *et al.*, 2011, and references therein), ensuring a high potential for habitat-niche evolution even in populations and species with low genetic diversity (Richards *et al.*, 2012; Verhoeven & Preite, 2014). Expression of this hidden genetic variation may then be promoted by stressful environments (Hayden *et al.*, 2011). Collectively, these genetic mechanisms can increase *in situ* mean fitness under environmental changes and thus provide adaptation of a species to variable habitats, with almost no changes in its genetic composition. This would occur even if habitat niches have evolved relatively slowly in the past (Hoffmann & Sgrò, 2011).

Adaptation to variable environments through changes in metabolic pathways—Metabolism may be an important key toward understanding the capacity of species to quickly adapt to environmental change. Such rapid accommodation may occur even after long-term stasis in a habitat niche and under conditions of a conserved genetic background. On the one hand, a given metabolite may have functions that vary according to the habitat that the organism occupies, particularly for plant secondary compounds that may have versatile functions. For example, anthocyanins and monoterpenes are insect attractants in flowers while simultaneously possessing insecticidal and antimicrobial properties to protect vegetative

tissues (Wink, 2003). Alternatively, a given metabolic pathway may develop a new function. Recent findings reveal different mechanisms by which metabolic pathways respond to niche fluctuations. One group of mechanisms concerns genes or gene regulators driving the metabolome. Regulatory evolution may play important roles in short-term responses of species to environmental changes through, for instance, functional divergence of the transcription factors that regulate the metabolic pathways (Grotewold, 2005). In addition, mutations in regulatory loci alter the expression of functionally conserved proteins (Carroll, 2008; Fig. S4).

A second group of mechanisms concerns the possible recycling of enzymes in plant secondary metabolism. Plants maintain a 'silent metabolism' (Lewinsohn & Gijzen, 2009); that is, a hidden reservoir of metabolic capabilities through numerous but normally unused enzymes. Silent metabolism may result, for instance, from epistatic mutations having produced enzymes without any apparent endogenous substrate or function. These 'occult' enzymes may, in turn, evolve new pathways when expressed (Lewinsohn & Gijzen, 2009). Such enzyme repurposing would be facilitated by relaxed selection; that is, the removal of any selection pressure that would maintain the initial function of the enzyme (Ober, 2005; Lewinsohn & Gijzen, 2009). Such enzyme repurposing has been increasingly documented in bacteria, plants and animals and there now is evidence that this often plant-driven process is easily accomplished and has occurred independently in various lineages (Stefano & Kream, 2007; Bradbury *et al.*, 2014; Fig. S4). Many examples now have shown that the diversification of metabolism in plants often involves reusing previously evolved genetic material (Ober, 2005, Yang *et al.*, 2015). This 'silent metabolism' suggests that plants have evolved the means of maintaining potentially useful chemicals without the evolution of those chemicals (Lewinsohn & Gijzen, 2009). The above-described adaptive mechanisms involving the metabolome suggest ways by which species retain the capacity for habitat flexibility, even in clades that currently and likely in the past exhibited only little variation in occupation of habitat niches and in underlying genotypes (Lewinsohn & Gijzen, 2009; Hennion *et al.*, 2012).

Tentative evidence

It repeatedly has been shown that, despite limited variation of habitat-niche *positions* among species within clades, the habitat-niche *breadths* may vary strongly among related species (Brändle *et al.*, 2002). A given ancestral habitat-niche breadth of a species resulting from past ecological constraints does not prevent more recent niche expansion or contraction. Also, for a given habitat-related character, within-species dissimilarity is compatible with lack of among-species similarity. For instance, phylogenetic constraints on the absolute levels of metabolite composition do not prevent species from shifting the

relative composition of metabolites in response to habitat change (Hennion *et al.*, 2012). Such intraspecific responses to changing habitats have been demonstrated to result from heritable epigenetic variation (Zhang *et al.* 2013) and such epigenetic responses may be more important than genetic ones (Richards *et al.* 2012).

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Fig. S1

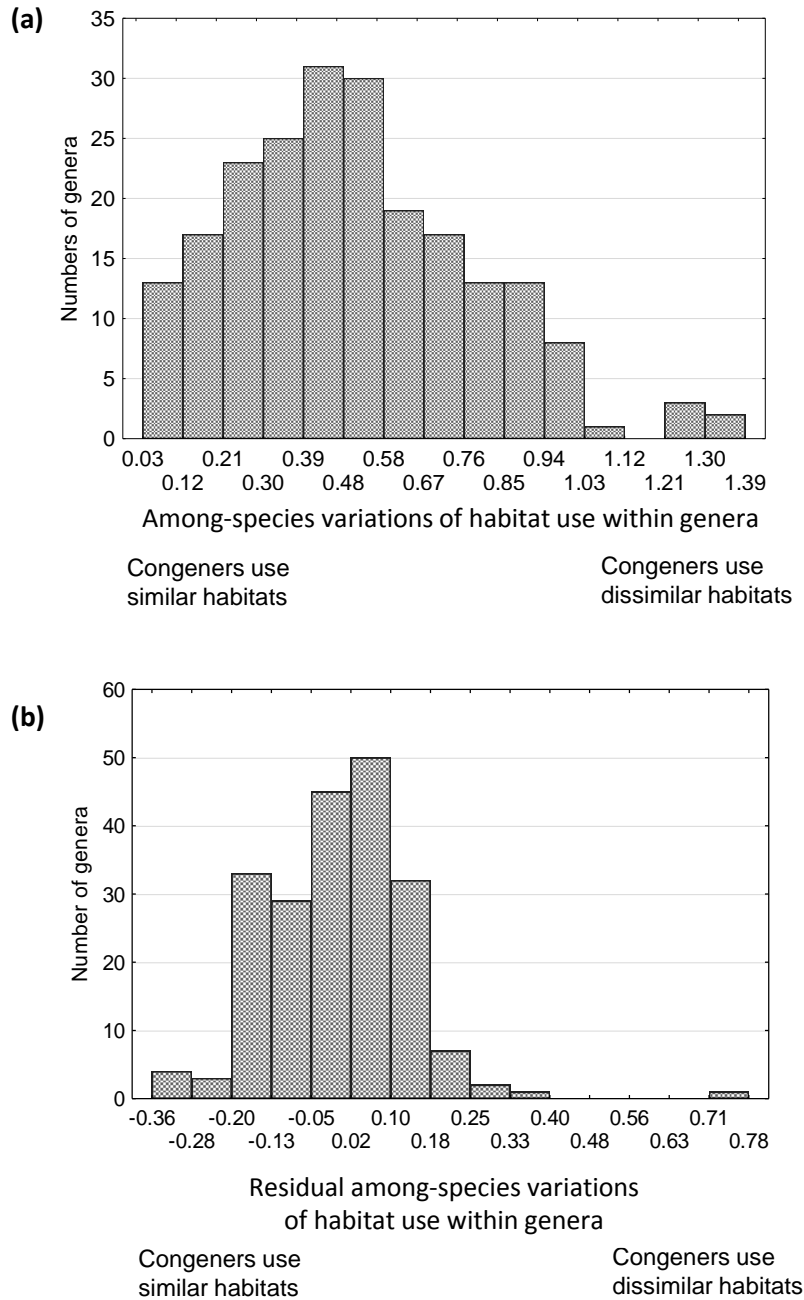


Fig. S1 An example of variation in habitats among species within different angiosperm genera, based on the flora of the Netherlands. For each species, positions along light, temperature, soil moisture, pH and soil productivity axes are taken from Ozinga *et al.* (2013) as explained in section II. Habitat variations among species within genera are calculated as the standard deviations separately for each environmental gradient (habitat-niche axis) and then are averaged across axes. The upper graph (a) shows raw values of within-genus variation, which differ by a factor of 30 among genera. The lower graph (b) shows residuals of within-genus variation after accounting for species richness and phylogenetic crown age of the genera (from Hermant *et al.*, 2012; see section II). See Notes S1 for further explanations.

Fig. S2

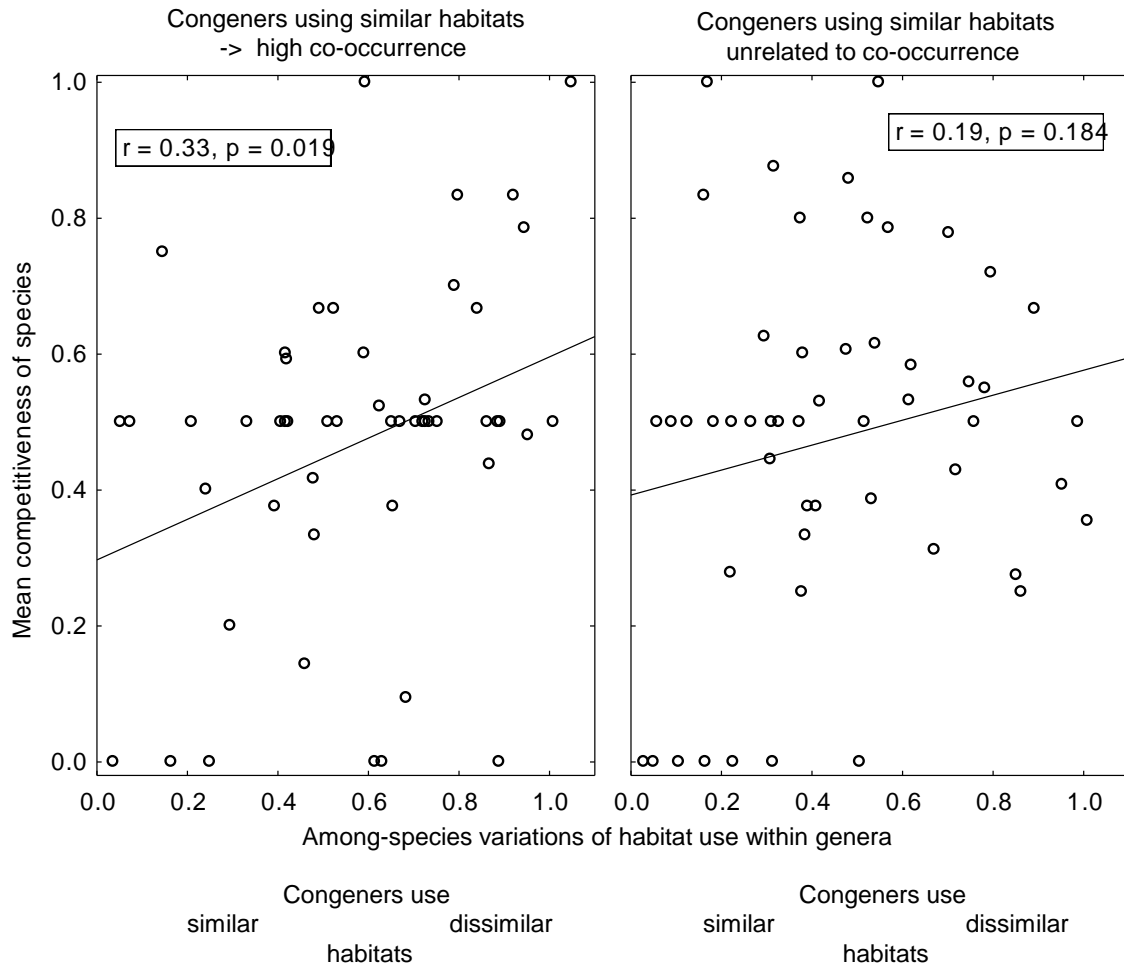


Fig. S2 Relationship between competitiveness and habitat similarity within genera. Genera in which habitat similarity corresponds to co-occurrence are analysed separately of genera that do not show this relationship. See 'Results' of Notes S2 for further explanations.

Fig. S3

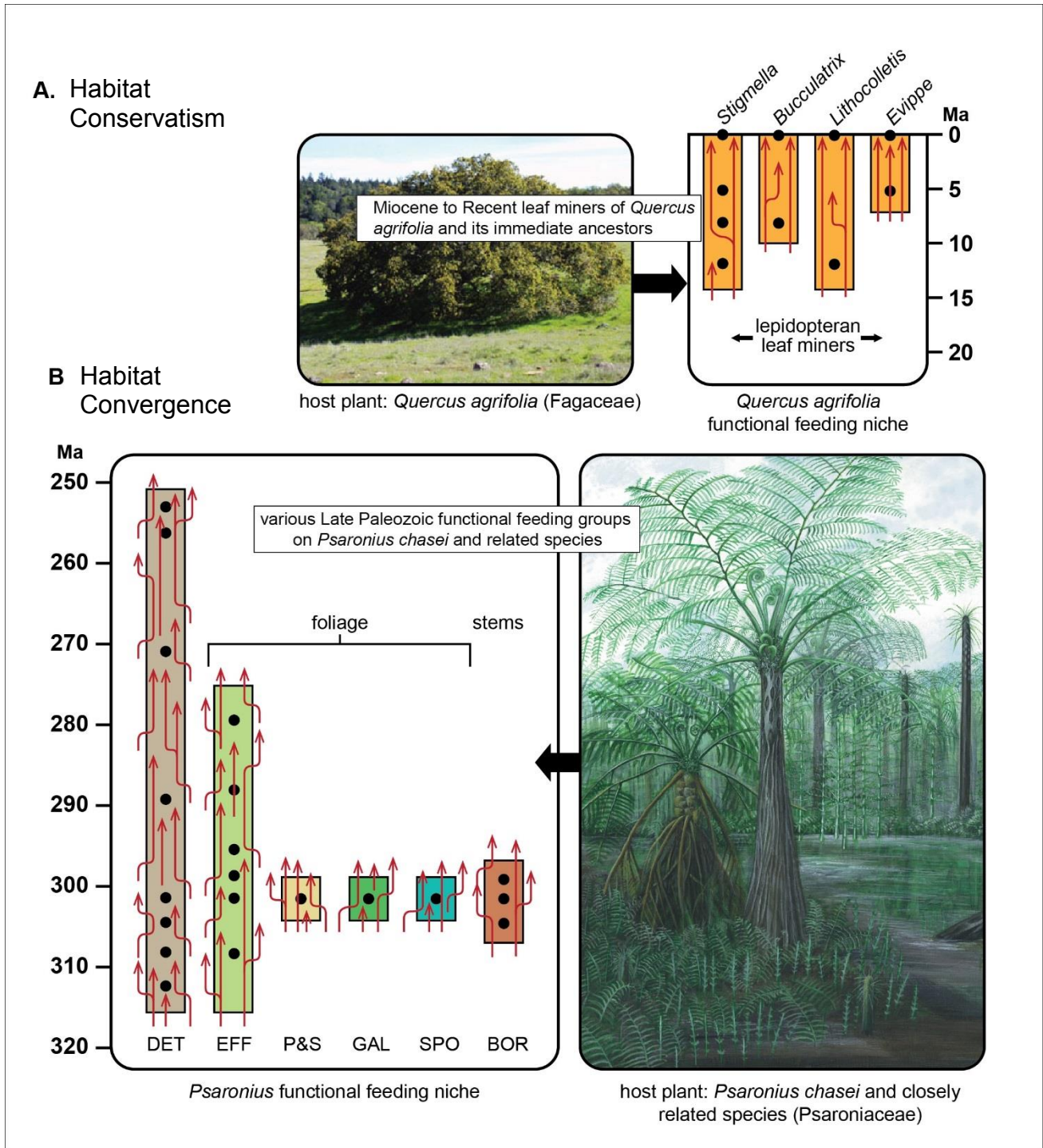


Fig. S3 Varying degrees of habitat similarity among ancestors and descendants in the fossil record of plant–insect interactions. Habitat conservatism between ancestors and descendants occurs in (A), and habitat convergence in (B). (A) *Quercus agrifolia* hosts four leaf-mining genera that have an antiquity from c. 12.5 to 5.3 million years, and continuing to the present, supporting a hypothesis of habitat-niche conservatism with low niche variation among species within genera. Each of the four leaf-mining feeding niches (distinctive mine morphotypes) houses only members of a single clade of (very) closely related species, likely a single species. (B) By comparison, the much older late Paleozoic *Psaronius chasei* and related species indicate significant entering, exiting and persistence of various unrelated insect consumer lineages that include detritivores (DET), external foliage feeders (EFF), piercer and suckers (P&S), gallers (GAL), spore and sporangia feeders (SPO), and pith borers (BOR). This pattern is consistent with the habitat convergence hypothesis that states high habitat variation among species within genera. Scales at left and right are given as millions of years (Ma); black dots indicate fossil occurrences; see Notes S3 text, Labandeira & Phillips (2002), and D’Rozario *et al.* (2011) for details. Reconstruction in (B) by Mary Parrish. See Notes S3 for further explanations.

Fig. S4

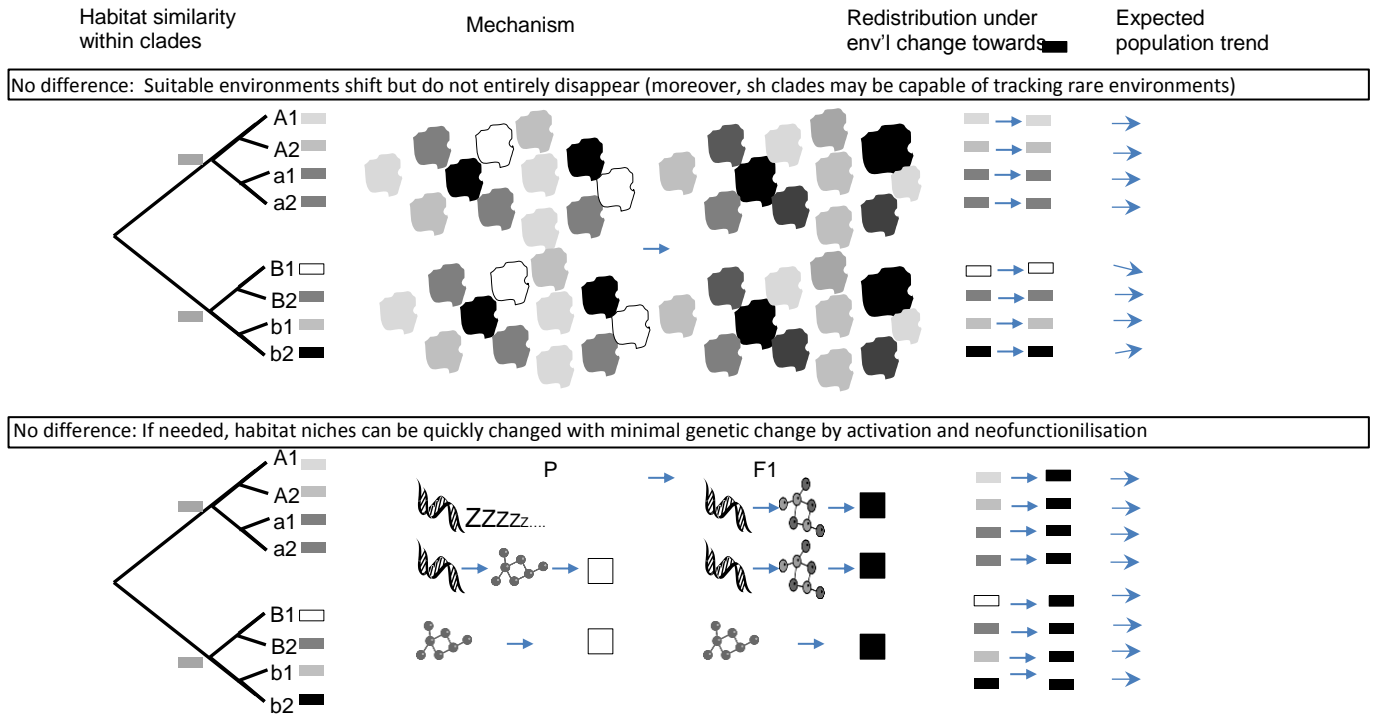


Fig. S4 Scheme summarizing the scenarios in which similarity in habitat use among closely related species has no consequences on the vulnerability of species to present environmental change. Species in the upper of the two clades, occupy similar habitats (sh = similar habitat use clade), contrary to species in the lower clade. Shades of grey correspond to environments used, such as different moisture conditions. See Notes S4 for further explanations.

Fig. S5

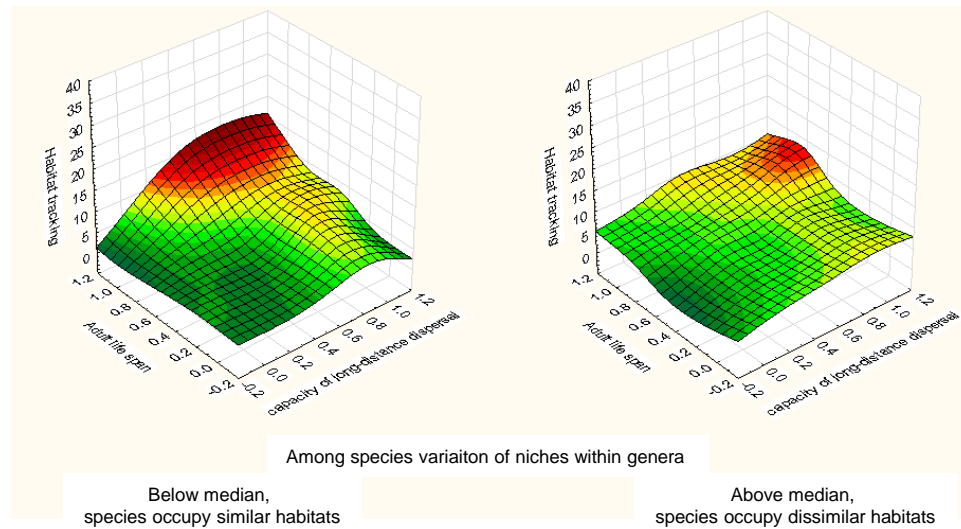


Fig. S5 Habitat tracking (z, colours) as a function of the capacity of long-distance-dispersal (x) and of adult life span (y). Analyses based on within-genus averages of data from Ozinga *et al.* (2005). Separate analyses for genera whose species each use similar or dissimilar habitats (as in Fig. S4). Note that genera of high adult life span and long-distance dispersal have relatively high capacity of habitat tracking – provided that the species in that genus use similar habitats. Note that an analysis across the full data set treating habitat similarity as a continuous variable yields a significant interaction term ‘habitat similarity × adult life span’ ($P=0.04$, see text for details). Everything else being equal, habitat tracking is higher in genera whose species occupy similar habitats.