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

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Summary

Recent decades have seen a decline of entire plant clades while other clades persist despite changing environments. We suggest that one reason why some clades persist is that species within these clades use similar habitats, because such similarity may increase the degree of co-occurrence of species within clades. Traditionally co-occurrence among clade members has been suggested to be disadvantageous because of increased competition and enemy pressure. Here, we hypothesize that increased co-occurrence among clade members promotes mutualist exchange, niche expansion or hybridization, thereby helping species avoid population decline from environmental change. We review the literature and analyse published data for hundreds of plant clades (genera) within a well-studied region and find major differences in the degree to which species within clades occupy similar habitats. We tentatively show that in clades for which species occupy similar habitats, species tend to exhibit increased co-occurrence, mutualism, niche expansion, and hybridization – and rarely decline. Consistently, throughout the geological past, clades whose species occupied similar habitats often persisted through long time-spans. Overall, for many plant species, the occupation of similar habitats among fellow clade members apparently reduced their vulnerability to environmental change. Future research should identify when and how this previously unrecognized eco-evolutionary feedback operates.

Key words: Assembly of present and fossil communities; Competition; Enemy pressure and mutualism of coexisting species; Conservation biology; Hybridization; Niche breadth, evolution and conservatism

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I. Entire clades decline while others persist; we suggest this might reflect an eco-evolutionary feedback between clade members occupying similar habitats, co-occurring locally and being less vulnerable to environmental change

Environmental change appears to threaten entire clades: changing environments are considered the principal cause of species decline (McKinney 1997), and declining species often are phylogenetically clustered (Purvis *et al.*, 2000; Sjöström & Gross, 2006; Thuiller *et al.*, 2005; Purvis, 2008 for a review, but see Davies *et al.*, 2011). Consequences of phylogenetic clustering may be the decline of entire branches of the phylogenetic tree (Vamosi & Wilson, 2008) and of phylogenetic diversities of regional biota (Eiserhardt *et al.*, 2014). Species in such declining clades might be vulnerable for two reasons. First, species within declining clades might share particular traits that make them less able to respond to environmental change (McKinney *et al.*, 1997). For instance, body size (Cardillo *et al.*, 2005; Davies *et al.*, 2011), life form (Sodhi *et al.*, 2008; Davies *et al.*, 2011), cold tolerance (Eiserhardt *et al.*, 2014), and fruit type (Sjöström & Gross, 2006) have been shown to be related to species decline and to characterize declining clades. However, explained variances remain low (*e.g.* Sodhi *et al.*, 2008) or trait relationships are inconsistent among clades (Sjöström & Gross, 2006), and opposite relationships have been reported in different studies (reviewed in McKinney, 1997). Second, species in declining clades might be vulnerable due to clade-level traits, such as species richness or phylogenetic age. Several studies have reported that species in species-poor clades have a higher risk of going extinct (Purvis *et al.*, 2001; Sjöström & Gross, 2006). However, several other studies report the opposite relationship of species in speciose clades suffering higher extinction risk (Schwartz & Simberloff, 2001; Davies *et al.*, 2011). In addition, Wang *et al.* (2013) reported that rare, putatively vulnerable species belong to phylogenetically young clades. However, also clade-level traits often explain only a limited portion of the variance in species rarity or decline (Wang *et al.*, 2013) and may be inconsistent among families (Sjöström & Gross, 2006; Davies *et al.*, 2011).

Here, we suggest a new perspective of how clade-level traits can affect the vulnerability of species: vulnerability of species within a clade may depend on whether these species occupy similar habitats. Species within some clades occupy surprisingly similar habitats, species within other clades surprisingly different habitats. Emblematic examples, for instance, are Potamogetonaceae or Cactaceae using almost exclusively submerged or dry habitats, respectively, versus Asteraceae or Poaceae, each of which use both very dry and very wet habitats. Individual clades in which species occupy particularly similar habitats have been recognized by Pearman *et al.* (2008), Donoghue (2008) and Olalla-Tarraga *et al.* (2011) and were systematically quantified by Lavergne *et al.* (2013). Such similar habitat use

among species within a clade may result from slow evolutionary divergence of occupied habitats among clade members (Wiens *et al.*, 2010; Losos, 2008; Kellermann *et al.*, 2012; see also Petitpierre *et al.*, 2012). Past evolutionary divergence of occupied habitats among species within a clade can be constrained by: (i), climatic, geographic and geologic factors, such as low spatial and temporal habitat heterogeneity within a given biogeographic region in which the clade diversified (Pennington *et al.*, 2004; Crisp *et al.*, 2009); or (ii), clade-specific factors, such as genetic or trait constraints (Alcantara *et al.*, 2014; Christin & Osborn, 2014; Johnson *et al.*, 2015; Siefert *et al.*, 2015), or constraints due to clade-specific biotic partners (Wise & Rausher, 2013; Yu & Nason, 2013). Similarity in habitat use among clade members, in turn, might increase the frequency of their local co-occurrence (Prinzing *et al.*, 2016). Eventually, local co-occurrence of fellow clade members, might either increase or decrease vulnerability of species to environmental change. Vulnerability may increase due to competitive replacement between clade members from abiotically suitable environments or enemy exchange. In contrast, vulnerability may decrease due to exchange of mutualists or increased intraspecific variability. We detail these hypotheses in the following sections.

We focus on similarity among clade members in terms of habitat conditions (habitat niche, Grubb 1977) quantified as the species' position along abiotic gradients such as soil moisture, pH, productivity, light availability and within-region gradients of temperature. In the hierarchical concept of Silvertown *et al.* (2006) the habitat use of a species corresponds to its beta niche. Two species using similar habitat conditions may co-occur in the same patch of a habitat, being spatially sufficiently proximate to interact. In contrast, larger-scale macroclimatic conditions used in the literature on "species distribution modelling" are less appropriate for our purpose as species within the same macroclimatic zone may still be spatially very far from each other and only share the same geographical range (gamma niche according to Silvertown, 2006). Inversely, the use of those smaller scale microenvironmental conditions that ultimately control whether two species interact or not— different microhabitats such as soil depths, different phenologies, different interacting predators or mutualists – (alpha niche, Silvertown, 2006) may also be less appropriate for our purpose. Species may use different microenvironmental conditions but nevertheless co-occur and initially interact within the same habitat patch. In fact, microenvironmental divergence or convergence among species may be a consequence rather than the cause of interactions among species co-occurring in a habitat patch.

In this study we develop the reasoning for each step of an eco-evolutionary feedback connecting similarity of habitat use among species within clades to co-occurrence among fellow-clade members and co-occurrence among clade members to their vulnerability to environmental change. We review the literature to provide evidence and, if unavailable, we re-analyse published accounts. We start with the implications from the ideas that seem to be mainstream in community ecology – that species suffer

from co-occurring with fellow clade members, and that such biotic pressure renders species more vulnerable to changing abiotic environments. We will then analyse and advocate the opposite view: that co-occurring with fellow clade members may render species less vulnerable to changing environmental conditions. We will finally review the existing evidence in favor of the overall relationship: between the degree to which species within clades occupy similar habitats and the risk of decline of species within these clades, both at present and in the fossil record. While this evidence remains tentative, it does permit to conclude that if species within a clade occupy similar habitats this increases the chance that these species (i) locally co-occur, (ii) locally help each other at least as much as they can impede each other, and (iii) persist under environmental change often even more than species in a clade in which habitat use is more variable. Past evolutionary constraints on habitat use of species within a clade might hence improve the present fate of the clade members and thereby of the entire clade, and this relationship might be mediated by interactions among locally co-occurring species.

II Definitions, and methods used to infer tentative evidence from published results

We focus throughout this review on angiosperms (flowering plants), as they currently represent the most diverse and dominant lineage of land plants. We use published data to study angiosperms from the Netherlands where uniquely detailed databases are available containing information at the species and community levels, as outlined below. For the entire regional species pool we accessed species-specific information on (i) habitat use along multiple environmental gradients (habitat positions and habitat breadths; Ozinga *et al.*, 2013, derived from the National Dutch Vegetation Database; Global Index of Vegetation-Plot Databases ID: EU-NL-001; Schaminée *et al.*, 2012), (ii) interactions with mycorrhizal mutualists (Hempel *et al.*, 2013), (iii) life histories (Ozinga *et al.*, 2005 based on information from the LEDA trait-database of Kleyer *et al.*, 2008) and their consequences on competitiveness (Grime 2001; Klotz *et al.*, 2002), (v) phylogenetic ages (Bartish *et al.*, 2016), (vi) hybrid status (Frank & Klotz, 1990; Jäger & Werner, 2005), and (vii) local co-occurrence (Prinzing *et al.*, 2016), again based on Dutch National Vegetation Database), the most complete regional vegetation database globally available, covering all habitat types across the Netherlands. Despite the unique data availability, restriction to the Netherlands has obvious shortcomings: the Netherlands have a low proportion of entirely natural habitats, and belong to a region of the world with limited overall richness of species and supraspecific clades. Also, the restricted surface of the Netherlands might imply that outside the Netherlands a given

species might co-occur with clade members that are not present in the Netherlands. However, most species in the Netherlands have similar co-occurring relatives elsewhere in Europe: in comparisons of specialist and generalist clades in the Dutch flora Ozinga *et al.* (2013) showed that the results were not biased by geographic sampling of lineages; that is, they did not depend on whether clades belonged to lineages that were well or poorly represented in the Netherlands. We provide additional examples of between-region-consistency below. Overall, a study on the Netherlands appears to be a good starting point, albeit analyses on other regions are desirable, should the data become available.

We focus here on clades at the level of genera and characterize the variation among species within genera. In the Netherlands these genera are mostly entirely monophyletic and, if not, almost monophyletic (Durka & Michalski, 2012). As a general tendency, species within angiosperm genera tend to use similar habitats notably in terms of pH, temperature and nitrogen (Prinzing *et al.*, 2001); to share many natural enemies (Schoonhoven *et al.*, 2005, Wardhaugh, 2014 on many phytophages feeding on only a single host genus); to share many mutualists (Armbruster, 2012 on preference of many pollinators for particular plant genera over others); and hybridizations are mostly within rather than between genera (*e.g.* Jäger & Werner, 2005). Each of these issues will be treated in the present review. Obviously, genera lack strict biological meaning as they differ in age and richness, and so we accounted for these characters in further analyses (see below for details on age estimations).

Specifically, we focused on variation of habitat use along abiotic gradients, which provides a context for the subsequent study of biotic consequences, notably of co-occurrences with and interactions among fellow clade members. Positions of species are known along gradients of light, temperature, soil moisture, pH and productivity from Ellenberg indicator values (Ellenberg, 1992). These species-specific indicator values are expert-knowledge classifications, ranging from 1–9 (or 1–12 for moisture), for the optimal occurrence of species along environmental gradients. Evidence for the accuracy of these indicator values has been provided by several studies reporting a close correlation between average indicator values and corresponding direct measurements of environmental variables (*e.g.* Hill *et al.*, 1997; Schaffers & Sykora, 2000; Diekmann, 2003; Ozinga *et al.*, 2013) and a very strong correlation between indicator values of the same species on different continents (Niinemets & Valladares, 2006). These values were adapted to the Netherlands and rendered more continuous using within-plot averages of indicator values for all plots in which a species was found (across 36853 plots, as in Ozinga *et al.*, 2013), but with practically identical results to those when using original indicator values. For a given species and a given gradient (*e.g.* pH) we then calculated the standard deviation across the local plot-means of all plots in which this species occurred (as in Ozinga *et al.*, 2013). This provided an estimate of the variation of occupied environments within that particular species along the gradient. This approach is much more differentiated and precise than many of the often-used

classifications based on numbers of habitat types occupied. We multiplied the values obtained for the different gradients to identify a volume of the habitat niche occupied by a given species and used this product as an integrative measure of within-species variation of habitat use (Ozinga *et al.*, 2013). We also characterized genera by calculating for each gradient the environmental position of a genus as the mean value across its constituent species, and the within-genus environmental variation as the standard deviation across its constituent species. Standard deviations along different niche axes were always positively correlated (mean $r=0.33$), and consequently we averaged for each genus the standard deviations for the different gradients. Low (mean) variation indicates that species within a genus use similar habitats.

Information on local co-occurrences were available from Prinzing *et al.* (2016). These authors quantified the frequency by which species locally encounter congeners using the Dutch National Vegetation Database (Hennekens *et al.*, 2010; Schaminée *et al.*, 2012) containing spatially explicit descriptions of species composition (presence/absence) in more than 350,000 small plots. For each species the average number of co-occurring congeners per plot is extracted and these per-species values are averaged within genera. (see Prinzing *et al.*, 2016 for detailed justification of this approach). Only genera occurring in multiple plots were considered. Interestingly, genera scoring high for co-occurrence in the Netherlands also score high in a distant region, South Africa (after partialing out differences in species richness between regions, Prinzing *et al.*, 2016).

Information on hybridization, mycorrhization and population trends came from a variety of sources. Information on hybridization was available from Frank & Klotz (1990), checked against Jäger & Werner (2005). These authors present “successful”, that is persistently established, hybrids accepted by botanists. More ephemeral hybridization that goes unnoticed to botanists are not relevant to our study here. Information on mycorrhization, life histories and consequences on competitiveness (*sensu* Grime, 2001) were available, respectively, from Hempel *et al.* (2013), from Ozinga *et al.* (2005 based on information in the LEDA trait-database; Kleyer *et al.*, 2008), and from Klotz *et al.* (2002). Information on population trends during the twentieth century were available from Ozinga *et al.* (2009). These authors used species occurrences in the Netherlands across a 1 km² grid during 1902–49 and during 1975–98. Specifically, a selection of nearly 25% of the grid cells with a high sampling intensity in both periods was used, supplemented by a correction factor for temporal differences in sampling intensity (Van der Meijden *et al.*, 2000). Our definition of decline corresponds to a regional application of IUCN red-list criteria (Ozinga *et al.*, 2009). Since trend data are sensitive to various sources of bias and to differences in spatial and temporal scale, we used a binary classification: species were labelled as declining if the number of grid-cell occurrences had declined by >25%.

Genera differ in age and hence time for divergence of habitat niche among species. Consequently, we controlled our analyses of habitat similarity within genera for differences in ages. To do so we used crown ages, *i.e.* the age of the most recent common ancestor of all species of a clade present in the study region (The Netherlands), or in other words, the age of the earliest diversification event among all the regional species within the clade. Crown ages should more realistically reflect the time for diversification of habitat niches within genera than stem age. High crown age of genera indeed was associated with somewhat increased variation of occupied environments, notably in terms of temperature, pH and nitrogen ($p < 0.05$), with graphical inspection showing that existing relationships are linear. Genus crown ages were inferred from a dated and finely resolved phylogeny covering a total of 557 genera. Details of the analyses for reconstruction of the dated phylogeny of Dutch angiosperm genera are provided in Hermant *et al.* (2012, their Appendix E) and in Bartish *et al.* (2016, their Appendix S3). In brief, these authors began their analyses by focusing on phylogenetic relationships at the level of all families, which can be represented by sequences of the same gene, *rbcL*, and then proceeded to genera within larger families and to particularly old genera (subtrees). Several genes from chloroplast genomes (cpDNA) and Internal Transcribed Spacers region of nuclear DNA (ITS) were used in these studies for phylogenetic reconstructions within the subtrees. The genes from cpDNA were selected and retrieved from GeneBank for maximal representation of the regional sample of species within the subtrees. For their dating analyses, the authors, similarly, first obtained age estimates for diversifications among all families, and then for subtrees in our sample. At the level of all families reconstructions were based on the same phylogeny and the same gene (*rbcL*) and established a set of reference nodes for calibration of the stem nodes of the subtrees. This approach ensures that age estimates for the stem and crown nodes of genera are comparable across families, since ages of all families are derived from the same basic node age estimates. If no phylogenetic information was available for intrageneric relationships, ages of the crown nodes were simply assessed as half of ages of the stem nodes of the corresponding genera. A dated tree in Newick format based on sequence relationships of all genera and about half of native angiosperms species represented in the Netherlands is available from the TreeBase ID: S13572. The tree is highly congruent with, but often more resolved than that of Durka & Michalski (2012) for the larger region of Europe. The tree is also congruent with that of Zanne *et al.* (2014). Zanne *et al.*'s tree covers some 10-15% of the global Angiosperm flora, which renders it less complete and representative of the Dutch genera than the complete tree that we used.

III. The interface between variation of habitat use within clades and the assembly of local communities: Clade members occupying similar habitats tend to locally co-occur

Within a region, species in some clades occupy very similar habitats as exemplified for the Netherlands in Supporting Information, Note S1 (Fig. S1). How does this affect local co-occurrence among these species? If we assume that competition leads to local replacement of species within clades (*e.g.* Webb *et al.*, 2002; Violle *et al.*, 2011) then we should expect clade members to never co-occur even if they have similar habitat requirements. If no such competition occurred, and if dispersal was unlimited and survival in a new habitat never possible, then we should expect local co-occurrence of clade members to depend entirely on the similarity of their habitat use: maximal co-occurrence among species in all clades of highest habitat similarity, minimal or no co-occurrence among species in all clades of lowest habitat similarity. To date, this relationship between habitat similarity among clade members and their local co-occurrence has to our knowledge only been studied by Prinzing *et al.* (2016, but see Sedio *et al.*, 2012 for a case study on a single clade, and Villabosos *et al.*, 2013 for comparing co-occurrences among clades). These authors used data on habitat use along individual environmental gradients and co-occurrences within genera of angiosperms and demonstrated that high co-occurrence among species is indeed found in genera in which species occupy similar habitats. Fig. 1 shows a more comprehensive analysis of their data accounting for multiple gradients (see section II), confirming that local co-occurrence within genera increases with within-genus similarity of habitat use. In other words, constraints during the evolutionary past leading to low variation in habitat use among species within a clade, partly control the - “microecological”- assembly of communities in local habitat patches (as suggested by Gerhold *et al.*, 2015). The pattern however shows some scatter, the reality is in between the extreme expectations outlined above: the effect of habitat similarity among clade members on co-occurrence might be overlaid by competition, dispersal limitation (Siefert *et al.*, 2015; Renwick & Rocca, 2015) or transient survival in unsuitable habitats.

IV. The mainstream hypotheses in community ecology imply that co-occurrence with fellow clade members is detrimental, but the evidence is equivocal.

Classically, community ecologists consider co-occurrence among species within clades as a disadvantage due to increased intensity of competition and enemy pressure. Such relationships would

imply a negative eco-evolutionary feedback between similarity in habitat niche within clades and the survival of species.

Competition pressure. Species suffering from high competition pressure might endure more from environmental change than species facing weak competition pressure. First, local competitors can limit access to declining abiotic resources (Martinez-Vilalta *et al.*, 2012). Second, competition among native species may facilitate establishment of introduced species (Gerhold *et al.*, 2011). In both cases, competition pressure would impose increased investment in competitiveness, implying a reduced investment in tolerance of a deteriorating environment (Grime, 2001). Multiple examples of trade-offs between investment into competitiveness and in the response to harsh environments are known, such as use of carbohydrates to tolerate drought versus use of carbohydrates for growth (Alpert, 2006); or early germination to escape competitors versus late germination to escape late frost (Ross & Harper, 1972), a case of the “ecological costs” of competitiveness (Koricheva, 2002). Such trade-offs between competitiveness and tolerance reflect to a large extent differences in the underlying functional traits that ensure these capacities (Adler *et al.*, 2014), which may incur a burden if the respective capacity is not needed (Kunstler *et al.*, 2015). The trade-off between competitiveness on one hand and tolerance of stressful environments (or the opportunistic use of temporally favourable environments) on the other often has been considered as the major axis along which plant life histories are differentiated, albeit the issue remains debated (Grime, 2001; Craine, 2005; Reich, 2014 for a syntheses).

Such high competition pressure may result from co-occurrence with fellow clade members, which, in turn, is promoted by similarity of habitat use (Fig. 1). Closely related species tend to be, on average, more ecologically similar than distantly related species (*e.g.* Burns & Strauss, 2011), and co-existing, closely related species might therefore compete strongly (Violle *et al.*, 2011). Increased competition among co-occurring related species might force such species to invest more energy in competitiveness and less in abiotic tolerance (Fig. 2).

However, co-occurrence of related species does not necessarily increase competition. Competition might be tempered due to character displacement among competitors (Dayan & Simberloff, 2005; see Section V.2). Moreover, recent studies investigating trait assembly under competition suggest that one possible outcome of competition is increased trait similarity and not trait dissimilarity (Scheffer & van Nes, 2006; Mayfield & Levine, 2010; Vergnon *et al.*, 2012; Tobias *et al.*, 2014). In that case similar, co-occurring, closely related species would not suffer from increased competition intensity, but profit from decreased competition asymmetry. Such decreased competition asymmetry makes the process of competitive exclusion slow enough to be offset by the many equalizing mechanisms that help prevent competitive exclusion. So there are two contrasting windows of opportunity for coexistence: being sufficiently different or being sufficiently similar (Scheffer & van Nes, 2006). Finally, similar

species may facilitate each other such as through shared effects on microclimates. Piston *et al.* (2015), for example, showed that the effects of cushion plants on closely related species changed from negative to positive as environmental conditions became more severe (see also Cavieres *et al.*, 2016). Hence, it is not clear whether or when co-occurring related species suffer more from competition than do other species, or whether and when such competition prevents these related species from responding to environmental change (Table 1).

To tentatively explore the evidence for an increased competition pressure on fellow clade members using similar habitats, we used the same genera as above (Fig. 1). We tested whether increased habitat similarity among relatives increased the investment of plants into competitiveness (inferred from the classification by Grime (2001) as explained in Note S2 and Fig. S2). We analysed the relationship for genera in which habitat similarity indeed corresponded to a high co-occurrence, and possibly high competition, that is genera with small unsigned residuals in the above relationship of co-occurrence versus habitat similarity (“small” being defined as the lowest quartile). We also analysed this relationship in genera for which co-occurrence corresponds minimally to habitat similarity, indicated by an unsigned residual co-occurrence in the highest quartile. An increase of competitiveness for genera whose species occupy similar habitats was not found in either of both groups. Indeed, the relationship of habitat variation to competitiveness was positive for both groups of genera (Note S2, Fig. S2). In a separate analysis we treated residual co-occurrence as a continuous variable and found the interaction term “habitat similarity x residual co-occurrence” as not significant ($t=-1.29$; $p>0.2$). Overall, habitat similarity and co-occurrence among fellow clade members does not appear to impose higher investment into traits that confer competitiveness.

Enemy pressure. The response to environmental change may be particularly difficult for organisms that suffer elevated pressure from natural enemies. For instance, Siemens *et al.* (2009) have demonstrated that mustards, which invest strongly in defence against natural enemies, have reduced capacity to respond to increasingly xeric abiotic environments. Below, we contend that such pressure from natural enemies might be higher in clades whose species use similar habitats than for species in other clades.

Closely related species belonging to the same clade are more likely than distantly related species to share or exchange enemies and diseases, including phytophagous insects, fungal pathogens and several invertebrate and vertebrate diseases (Daszak *et al.*, 2000; Brändle & Brandl, 2006; Watanabe *et al.*, 2014). The sharing of enemies among related host species appears to result from similarities in morphology, physiology, phenology, habitat use and range distribution among closely related hosts

(Brändle & Brandl, 2006). As explained above, related species using similar habitats tend to have a higher degree of co-occurrence. A host surrounded by closely related neighbors consequently may face an increased risk of infection by its neighbors' enemies and diseases (Daszak *et al.*, 2000; Gossner *et al.*, 2009; Vialatte *et al.*, 2010), increasing the damage caused by these enemies (Yguel *et al.*, 2011; Parker *et al.*, 2015) but also the enemy pressure suffered by the enemies themselves (Yguel *et al.*, 2014a). Such pressure from enemies may reduce the tolerance of the host to stresses such as environmental change (Siemens *et al.*, 2009) by triggering defences, which often may be costly (Strauss *et al.*, 2006). Enemy pressure also may cause a reduction of host population size, loss of genetic diversity (Dhondt *et al.*, 2006; Breed *et al.*, 2009), and finally, local extinction of host genotypes or species (McCallum & Dobson, 1995). Reduction in size of and diversity within populations may reduce their tolerance to environmental change.

Defence against enemies does, however, not automatically reduce the capacity to respond to changes of the habitat environment. The degree to which this happens may strongly depend on the type of defences (Fürstenberg-Hägg *et al.*, 2013) and the type of costs that these defences trigger within the specific environment studied (Koricheva, 2002). First, enemy defence may be of different types, and some types of defence may be more costly than others. Costs may be high in "quantitative" defences requiring, extensive tissues or large amounts of chemical compounds to reduce the edibility and digestibility of plant tissues, compared to "qualitative" defences requiring only small amounts of toxic compounds (Price, 1995). Moreover, "constitutive", permanently established defences (Brennan & Weinbaum, 2001a, 2001b) may be more costly in terms of resource allocation than "induced" defences produced only upon need (Kessler & Baldwin, 2001; Karban *et al.*, 1997; Zavala *et al.*, 2004), although opposite relationships exist for ecological costs (Cipollini *et al.*, 2003; Shudo & Iwasa, 2001). Defences of high-cost, quantitative or constitutive might hence constrain the capacity to respond to environmental change more than low-cost defences. However, some quantitative defences have been reported to increase also resistance against abiotic stress, such as tannins or waxes increasing resistance against both herbivory and desiccation (Jetter *et al.*, 2000; Brennan & Weinbaum, 2001a, 2001b).

Second, enemy defence may have different types of costs, some of which may be more constraining under habitat change, others less (Koricheva, 2002). These costs may be expressed in terms of energy allocation, as shown for mustards (Siemens *et al.*, 2009). Costs also may be expressed as the loss of opportunities, such as diapause during high enemy pressure at the cost of missing the opportunity to take up nutrients and overgrow competitors (Baldwin & Hamilton, 2000). Costs may, finally, be ecological (Gassmann & Hare, 2005; Van Velzen & Etienne, 2015), such as early budburst decreasing the pressure by late-season herbivores but increasing the risk from frost events. The latter type of cost,

for instance, may become less important under an increasingly warm climate. Overall, whether or not defence against enemies incurs a cost in terms of resistance to environmental change is highly context dependent. In particular cases, enemy pressure might even facilitate the response to changes in the abiotic environment.

While each of the individual mechanisms we invoked has been documented, we do not yet know their overall consequences (Table 1). Do species within a clade that use similar habitats currently suffer increased enemy pressure or alternatively invest more in defence against enemies? Does this trade-off handicap a species' response to environmental change? Currently, we are lacking the data needed to explore these questions. Meaningful analyses will require investigations characterizing the impact of enemies on plant hosts across an entire region involving large groups of hosts, as well as assessment of host investment in various modes of enemy defence. We admit that the above comparisons were among hosts that co-occur with similar, closely related as opposed to less similar and distantly related heterospecific hosts. Another scenario would be that all co-occurring plant hosts are conspecifics and hence phenetically very similar, which likely would incur even greater enemy pressure.

V. We suggest that co-occurrence with fellow clade members is often beneficial and we present evidence

Contrary to what is implied by mainstream ecology, we suggest that co-occurrence among species within clades may also be advantageous and hence decrease their vulnerability to environmental change. We see two ways in how this may happen. First, fellow clade members using similar habitats may exchange mutualists, thus increasing their tolerance to environmental change. Second, fellow clade members using similar habitats compete and hybridize, thus increasing variation of the habitat niche within species and thereby the flexibility to environmental change. Below, we outline the possible mechanisms and the existing evidence.

V.1. Mutualist exchange

Similarity in habitat use among species within clades brings these species together within local patches of a particular habitat type (Fig. 1; Cavender-Bares *et al.*, 2009; Prinzing *et al.*, 2016). Co-occurring clade members might interact *positively* by sharing common mutualists and symbionts (Sargent *et al.*, 2011

for pollinators). Symbionts may help hosts to better tolerate harsh and changing environments. We will explore below how a symbiosis may be favoured if each of the partners shares similar habitat preferences with its fellow clade members, and how the symbiosis might, in turn, favour the hosts' response to environmental change (Fig. 2). We will do so exemplarily for a mutualism of particular importance: mycorrhiza. In terrestrial ecosystems, more than 80% of plant species live in symbiosis with mutualistic fungi and form mycorrhizae (Smith & Read, 2008). Mycorrhizal fungi provide soil nutrients to the plant, and in return the plant delivers carbohydrates to mycorrhizal fungi. Finally, mycorrhizal fungi have been shown to increase tolerance of their hosts to environmental changes (Courty *et al.*, 2010).

Given phylogenetic signal in habitat use, in mycorrhizal partnerships and in associated traits, related plants are likely to co-occur with related mycorrhizal species (Peay *et al.*, 2010; Anacker *et al.*, 2014). Co-occurrence might increase the probability that the same mycorrhizal fungal species are locally shared between related host species within a common mycorrhizal network (CMN). Such sets of interacting host and host-specific mycorrhiza species often will be nested within larger networks involving the same hosts interacting with non-specific mycorrhiza. But in some mycorrhizal interactions, such sets of specific host/fungal species may form distinct modules in the interaction web, rendering these modules potentially more essential for hosts (van der Heijden *et al.*, 2015). Such CMNs facilitate resource exchange between conspecific or non-conspecific neighbouring plants (Selosse *et al.*, 2006; Walder *et al.*, 2015), and seedling recruitment (Teste & Simard, 2008). In addition, CMNs might increase plant competitiveness (van der Heijden, 2002), and thereby promote selection for single plant species (Wilkinson, 1998). This selection would contribute to the maintenance of low-diversity plant communities (McGuire, 2007), and in particular of closely related species, i.e. species within clades using similar habitats. Within such a CMN, plants may invest more carbon in their fungal partners and become their major source of nutrients (Kiers *et al.*, 2011). Consequently, one may hypothesize that among multiple interacting plant species, CMNs promote and maintain a set of closely related mycorrhizal species and of closely related plant-host species, i.e. co-occurrence within clades. These sets of closely related species co-occur within the same patches of the same habitat-niche and exchange of mutualists may hence contribute to conservation of the habitat niches of these species.

From the arguments outlined above for a specific mutualism we hypothesize that co-occurring, closely related members of a clade of host plants might benefit from shared mutualists. Such shared mutualists may supply hosts with nutrients and are genetically highly variable thereby potentially increasing the hosts' tolerance to environmental changes (Johnson *et al.*, 2013). As a tentative test for our hypothesis we explored whether the effect of intra-genus co-occurrence on decline (as described in chapter II) depends on the degree to which the genera use mycorrhiza (taken from Hempel *et al.*,

2013 details in Fig. 3). We found a significant negative interaction: intra-generic co-occurrence reduces the proportions of declining species, but only in genera that have a high degree of mycorrhization and hence a strong potential to locally interact with congeners via shared CMNs (Fig. 3). This pattern is consistent with CMNs among co-occurring congeners decreasing their vulnerability to environmental change. However, whether such increased support of a co-occurring clade member by CMNs actually happens, remains to be tested in future studies (Table 1). In fact, these host plants that support mycorrhiza also may assume multiple risks. Mycorrhiza symbionts, for instance, may be functionally redundant and hence provide only a limited range of services to their hosts (Rineau & Courty, 2011; Courty *et al.*, 2016). Host plants may compete for these services provided by mycorrhizae (Walder *et al.*, 2012, 2015), which may also compete among each other (Maherali & Klironomos, 2007; Yguel *et al.*, 2014b). Consequently, plant–mycorrhizal interactions sometimes may destabilize entire communities (Bever *et al.*, 2010). Finally, mycorrhizae themselves may be susceptible to environmental change (Courty *et al.*, 2010). In the future, quantification of the benefits versus risks of co-occurring, related hosts exchanging mutualists will be important – not only for plants and mycorrhiza – but for all types of mutualist interactions. Should the benefits dominate this would provide an improved understanding of how the sharing of habitats among clade members may ultimately lead to better support of host individuals through mutualists, facilitating responses to environmental change.

V.2 Competition and hybridization increasing within-species variation of habitat use

Here we argue that similarity in habitat use among species within clades contributes to their local co-occurrence, which in turn, can trigger habitat expansion through character displacement or hybridization. Similar habitat-niches resulting in habitat-niche expansion is paradoxical, but might nevertheless be true and explain the lack of perfect niche convergence among related species (Losos, 2008), or the existence of a phylogenetic signal in habitat-niche position but not in niche breadth (Brändle *et al.*, 2002). A species in which the habitat niche remains flexible due to character displacement or hybridization might be better adaptable to environmental change (Fig. 2).

Character displacement among competitors. As explained above (Fig. 1), similar habitat use among clade members within a clade is the necessary prerequisite for their local co-occurrence. Co-occurrence with clade members may trigger not only ecological but also evolutionary interactions. One of these evolutionary interactions are character and niche shifts within each of the co-occurring clade members, resulting in character and niche displacement among species to reduce competition (Dayan & Simberloff, 2005; Stuart & Losos, 2013; Fig. 2). Such character and niche displacement may operate rapidly, within decades or less (Dayan & Simberloff, 2005). Indeed, we find evidence for character

displacement in communities composed of phylogenetically closely related species (Prinzing *et al.*, 2008; Gerhold *et al.*, 2011). These local character and niche shifts within species in response to co-occurring fellow clade members will increase the within-species variation of habitat-niches and of characters among localities. Increased variation between populations within species may increase the chance that some populations are amenable to coping with environmental change (Yoshimura & Jansen, 1996; Le Gac *et al.* 2012). Therefore, we hypothesize that similar habitat use among species within a clade may increase microevolutionary variation of characters and niches within the species of that clade (Silvertown *et al.* 2006). Such a result might increase the capacity of species to respond to niche-related changes (Fig. 2).

We tentatively tested whether congeneric species occupying similar habitats may increase their intraspecific habitat-niche variation through local interference. We used the published data presented in section II. We studied genera in which similar habitat use among species corresponds to local co-occurrence and such where it doesn't (*i.e.* low and high, respectively, unsigned residual co-occurrences). For the former we expect within-species variation in habitat niche to increase with an increasingly similar habitat use among species. We indeed found that within-species variation of the habitat niche of genera was influenced by a positive interaction term "among-species-similarity of habitat niche x residual-co-occurrence" ($t=2.5$, $p=0.014$, Fig. 4): habitat niches within species are particularly variable in those genera in which species occupy similar habitats and locally co-occur. This effect might be due to character displacement among relatives within genera. However, note that with the data at hand, we cannot exclude the possibility that increased within-species variation might also be the cause, rather than the consequence, of co-occurrence. Causalities among the co-occurrence of clade members, their niche variability and their response to environmental change require further investigation (Table 1).

Hybridization. The occupation of similar habitats by close relatives within a clade increases the probability of local co-occurrence of these species within patches of the same habitat (Fig. 1). Co-occurrence of relatives increases the likelihood of hybridization (Cavender-Bares *et al.*, 2009), and hybridization may, in turn, often increase evolutionary innovation within species (Aguille *et al.*, 2012; Abbott *et al.*, 2013; Fig. 2). Hybridization might trigger niche innovation as hybrids often show transgressive traits, exhibiting extremes compared to their parents due to either segregation of parental alleles in hybrids (Rieseberg & Willis, 2007), or to drastic genome reorganization modulating gene expression (Hill & Kotanen, 2001; Doyle *et al.*, 2008). For instance, the 150-year-old hybridization event between two *Spartina* species that co-occurred in patches of a shared, salt marsh habitat-niche has triggered structural and epigenetic changes in the newly formed allopolyploid *Spartina anglica* (Parisod *et al.*, 2009). These changes are associated with enhanced phenotypic plasticity and increased

invasiveness of the plant species within its salt-marsh niche, despite strong ongoing anthropogenic modification (Ainouche *et al.*, 2009). Finally, hybrids might avoid competition with their parent species by establishing themselves in a new niche, although more research is needed (Glennon *et al.*, 2014). Overall, similar habitat use among related species might accelerate microevolutionary variation of niches within species resulting from increased rates of hybridization. This microevolutionary variation may facilitate the response of extant species to changing environments. The response may happen very rapidly, on time scales of current global change, as in the example of *Spartina* above.

Future research needs to identify when the positive effects of hybridization on evolutionary innovation dominates over the possible negative effects (Table 1). Such negative effects include gene flow between incipient species resulting in genetic homogenization and eventually disappearance of limits between parent species; hybrid species replacing parent species; hybrids suffering from the merging of incompatible parental genomes, or genomes adapted to distinct environments (Burke & Arnold, 2001), generally leading to hybrid depression. The particular conditions under which hybridization triggers rather than suppresses evolutionary innovation have, to our knowledge, previously not been tested.

As a first step to understand the relationship between habitat similarity within clades and hybridization we tested whether occupation of similar habitats among congeneric species corresponds to an increased rate of hybridization, through an increased rate of co-occurrence (this evaluation used published data, as explained in section II). Indeed, we found hybridization to be higher in those genera whose species use similar habitat types, provided that this similarity in habitat use among congeners corresponds to an elevated co-occurrence, as demonstrated by low unsigned residual co-occurrences (Fig. 5, consistent with the observations of Prinzing *et al.*, 2016).

VI. There is tentative evidence for an eco-evolutionary feedback between habitat similarity among clade members, their co-occurrence, and their reduced vulnerability to environmental change.

V1.1 Relationship to present-day decline

Species in clades of high similarity in habitat use and high co-occurrence rarely decline. - We are not aware of any study that has related habitat similarity within extant clades to the tendency of their

constituent species to decline under ongoing environmental change. We hence compared within-genus similarity in habitat use (section II) to the per-genus proportion of species that declined during the twentieth century (from Ozinga *et al.*, 2009; section II). We found that genera composed of species occupying similar habitats tend to have a smaller percentage of declining species, even after accounting for the evolutionary age or species richness of the genera (Fig. 6a and 6b). This lack of decline in species that share similar habitats with congeners might be due to the benefits discussed above. Each of these benefits results from increased local co-occurrence among congeners sharing similar habitats. Indeed, this is the trend that we found that similar habitat use among species within genera corresponds to a low proportion of declining species provided that similar habitat use in itself corresponds to high local co-occurrence (*i.e.* unsigned residual co-occurrences are low): the interaction term *habitat-use similarity* \times *residual co-occurrence* is significantly positive ($t=2.48$, $p=0.014$, Fig. 6c). Tentatively, this indicates that, for angiosperms of the Netherlands, the use of similar habitats by congeners might reduce the risk of population decline through increasing the rate of co-occurrence. The mechanisms involved might include increased intra-specific niche variation, exchange of mutualists, an increased rate of hybridization, or other mechanisms. This conclusion is consistent with our above analyses, which generally confirmed the suggestion that use of similar habitats among congeners decreases vulnerability to environmental change.

In some clades, slow niche evolution in the past correlates to present decline, but the relationship generally is weak. - Little variation in habitat niches among relatives may, among others, results from constrained niche evolution in the past. It would hence be interesting to understand whether lineages that have undergone slow niche evolution in the past are favoured or handicapped today. We are aware of only a single study that systematically links the fate of species to the degree to which these species have retained their ancestors' niches. Lavergne *et al.* (2013) quantified the rate of past niche evolution in families of plants and birds, inferring niche from life history, climate distribution and trophic position. The authors then related rates of past niche evolution to present-day declines during 1970–90 and during 1990–2000. Overall, families whose species evolved slowly along two of three niche axes tended to decline more strongly during 1970-90 than families of faster niche evolution. However, this pattern had a major unexplained variation: some families had very slow niche evolution during the past and nevertheless their species are not declining today. Moreover, for the third niche axis, and for all three niche axes versus declines from 1990–2000, there was no relationship between the rate of past niche evolution and decline. Overall, there appear to be numerous cases where slow niche evolution does not render species more vulnerable to environmental change.

VI.2 Relationship to past lifespan in the fossil record

Paleoecological studies permit the documentation of similarity in habitat niches among relatives at long time intervals. Sometimes, such studies permit the tracking of evolution of habitat niches from ancestors to descendants (Note S3).

Clades of narrow abiotic ranges sometimes had short lifespan in the fossil record (“fossil lifespan” from here on). - The range of habitats occupied by entire clades has only rarely been systematically compared to the lifespans of these clades, and only for animals. Liow (2007) found that ostracode genera whose species each occupied a narrow bathymetric range, show decreased lifespans, but only in two out of nine datasets. Also from the plant fossil record several clades are known whose species occupied similar habitats, usually inferred from similar, specialized functional traits. Some of these clades suffered from environmental change such as specialized families in New Zealand during profound Miocene environmental changes (Lee *et al.*, 2001; Conran *et al.*, 2014), or specialized Antarctic clades under ice-cap engulfment of mountains 4 to 2 million years ago (Francis & Hill, 1996). Other clades, however, apparently did not suffer from major changes, such as 12 plant lineages in western North America chaparral from 48 to 11.5 million years that successfully survived within changing chaparral environments (Ackerly, 2004). Overall, habitat similarity within clades does not necessarily decrease clade longevity, although systematic quantitative overviews such as that of Liow are rare.

Clades of narrow host niches could have very long fossil lifespans. - We are aware of no example of habitat use by plants directly observed in the fossil record during the evolutionary history of a plant clade. There are, however, observations on habitat use by herbivores. For an insect herbivore, a habitat roughly corresponds to a host plant species and the types of tissues consumed on that host plant. In one example, species of several moth genera were mining foliar tissue of the oak *Quercus agrifolia* for more than 7 million years (Opler, 1973, 1974; Fig. S3A). In another example, the component community of arthropod herbivores and detritivores occupying the marattialean tree fern *Psaronius chasei*, from the Euramerican Late Pennsylvanian (Labandeira & Phillips, 2002) included both, detritivore and herbivore lineages persisting for up to 45 million years (D’Rozario *et al.*, 2011) as well as herbivore lineages entering and exiting the *Psaronius* host-plant (Fig. S3B). Both case studies indicate that some clades of insect herbivores were successfully specialized on and conserved the same “habitat type” (a tissue of a plant host) for several millions of years, despite major spatiotemporal shifts and profound changes in the ambient paleoenvironment that made other clades disappear.

VII. Conclusions and future directions

In conclusion, clade members occupying similar habitats do not necessarily suffer more from environmental change than clade members that occupy different habitats. Indeed, they may often suffer less. We do not suggest that habitat similarity among relatives within a clade alone permits reliable predictions of vulnerability of that clade to environmental change. Other factors such as the use of particularly endangered habitats, slow life histories, restricted range, or species-level ecological specialization likely are more important (reviewed in Pimm, 1991; Colles *et al.*, 2009). We do suggest, however, that there exists a detectable relationship between habitat similarity among species within clades and their vulnerability, and this relationship provides a new perspective for evolutionary ecology.

Specifically, if past evolutionary or biogeographic constraints on diversification of habitat use among species within a clade affect the species' present assembly into local communities, the species' microevolution and their extinction vulnerability, this would be a case of an eco-evolutionary feedback (see Post & Palkovacs, 2009; Mittelbach & Schemske, 2015, for conceptual development). One that has to our knowledge not been identified so far. We suggest that low evolutionary diversification of habitats within clades ultimately reduces the vulnerability of species. Such a phenomenon would explain why some clades in which habitat use was constrained in the evolutionary past have succeeded to persist in spite of past environmental change (Hermant *et al.*, 2012).

We conclude that clades whose species occupy similar habitats might decline less than other clades. We argue that species in such clades often co-occur and interact in a way that increases the species' capacity to respond to environmental change. However, there are cases where this conclusion does not appear to hold. Decline in plant species in South Africa, for instance, does not seem to vary among but within clades (Davies *et al.*, 2011). Also, many of the genera depicted in Fig. 4 a and Fig. 4b do not follow the overall relationship between habitat-similarity among congeners and decline. We see five possible levels at which our arguing may not hold in some cases.

First, occupation of similar habitat niches may not necessarily increase local co-occurrence within habitat patches. Local co-occurrence may be hindered for instance if habitat patches are ephemeral or dispersal among patches is limited. Fig. 4c (right) shows that genera whose species occupy similar habitats without co-occurring may decline just as much as genera whose species occupy dissimilar habitat niches.

Second, co-occurrence among clade members may not trigger the interactions that increase the capacity to respond to environmental change but rather those that have the opposite effect. Recruitment of mutualists, for instance, may not be favoured by co-occurring clade members if mutualists are highly generalist and can interact with any clade – or if mutualists are specialized to a single plant species. Hybridization may not be favoured if species reproduce vegetatively. Inversely, competition may be favoured in undisturbed and productive habitats (Grime, 2001; Huston, 2014). Herbivore pressure may be favoured by co-occurring clade members if herbivores are specialists of that clade, and if the herbivores are little controlled by their enemies, e.g. in sites of intermediate productivity or high fragmentation (Fretwell, 1987; Kruess & Tschardtke, 1994).

Third, co-occurrence among clade members may not only be the cause of interactions but also their result. Members of a given clade might co-occur because they can't stand the asymmetric competition from other clades, because they are the sole to persist the local predation pressure, because they have been co-dispersed by mutualists, because they have a broad niche, or because they are hybrids having retained their parent species' habitat preferences.

Fourth, interactions among clade members that in theory favour the capacity to respond to environmental change may in practice be little important. Support from mutualists, for instance, may be required mainly under nutrient poor conditions. Variation of habitat niches may be required only if environmental change affects habitats rather than, for instance, the ecotoxicological conditions or the disturbance regime within habitats.

Finally, the current vulnerability of species to environmental change also might be independent of the similarity of habitat use among relatives within clades, an aspect that we did not develop in this study. Specifically, species may be able to track environmental change in space or time or by shifts in metabolomic composition or function (the chemical processing of metabolites). We detail these aspects in Note S4 and Fig. S4. We explore whether and how clade members using similar habitats track small-scale environmental change in space and time and stress that the phenotypic, epigenetic and metabolic mechanisms behind the capacity of species to shift and expand environmental optima remain to be identified (Fig. S5).

Overall, there might be distinct situations under which the mechanisms we suggest may not apply, but rather those we suggest as “implications from mainstream ecology”, or there is no relationship at all. Future research should systematically test whether such situations may explain why sometimes our conclusion does not hold. The situation of co-occurrence among clade members as a consequence, rather than a cause, of interactions could be excluded by assembling co-occurring clade members experimentally. To some degree this has already been done unconsciously in numerous diversity

experiments, which could now be meta-analysed. This future research should include regions that are larger, or more species rich or more pristine than the Netherlands. Research should also account for the effect of co-occurrence among clade members on ecosystem functioning, such as more efficient decomposition of plant litter (Pan *et al.*, 2015). Ultimately this future research will help us to understand eco-evolutionary questions: Which ecological situations have favoured the persistence of “specialist” clades composed of species occupying similar habitats, thereby contributing to the frequently reported pattern of niche conservatism (Wiens, 2010, phylogenetic signal sensu; Losos, 2008)? Which ecological situations have contributed to the persistence of generalist species within these “specialist” clades?

Addressing these questions requires a combination of expertise from ecological, evolutionary and molecular biology, integrating macroevolutionary patterns with local interactions among species in ecosystems. We recommend pursuit of a feedback perspective rather than a unidirectional perspective in which macroevolutionary patterns are given priority to explain local processes or the inverse (Cornell & Lawton, 1992; Ricklefs, 2004). We hope that this review will assist in improving the integration of often disconnected disciplines by joint study of global macroevolutionary patterns and local interactions among and microevolution within species. Integration of these fields implies integration of varied data and we recommend profiting from extensive published databases that are becoming available for an increasing number of regions of the globe, covering local community assembly across the tree of life.

VIII. References

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Figure legends

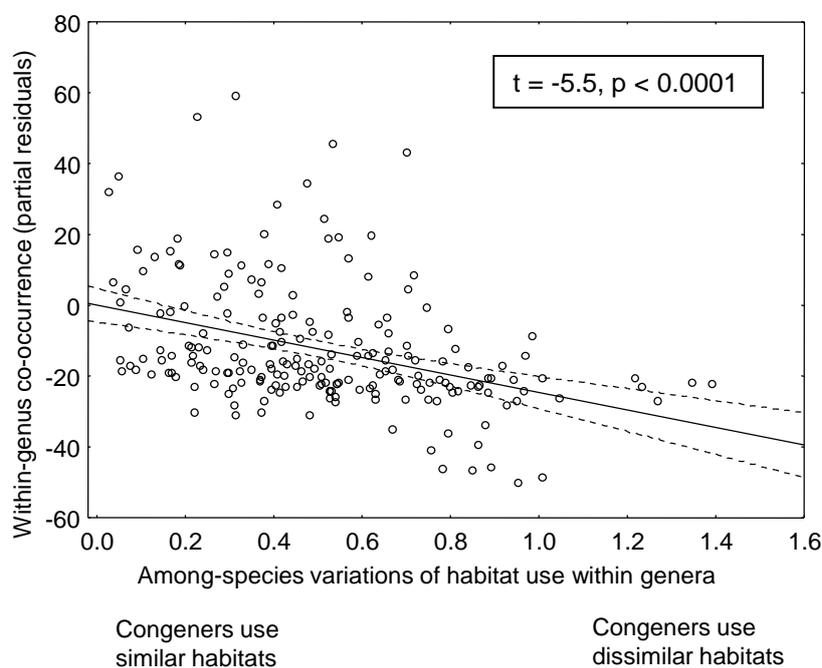


Fig. 1 Co-occurrence among species within a genus is high in those genera in which species use similar habitats, that is in genera of low variation in habitat use (multiple regression, $df=201$, $t=-5.5$, $p<0.0001$). Data points are angiosperm genera studied in the Netherlands. The within-genus co-occurrence is the number of fellow-congeners with which an average species will co-occur on an average plot (from Prinzing *et al.*, 2016). Within-genus co-occurrence is given as partial residuals from an analysis accounting for confounding effects of other variables increasing the chance for co-occurrence: (i) genus–species richness, (ii) genus crown age (e.g. Perret *et al.*, 2007), and (iii) mean intraspecific variation in habitat use (from Ozinga *et al.*, 2013; Hermant *et al.*, 2012, as explained in section II). Here and elsewhere we verified normality and homogeneity of residuals graphically and ensured robustness to exclusion of possible outliers. This negative relationship is phylogenetically independent: it was found in 13 out of 15 angiosperm orders.

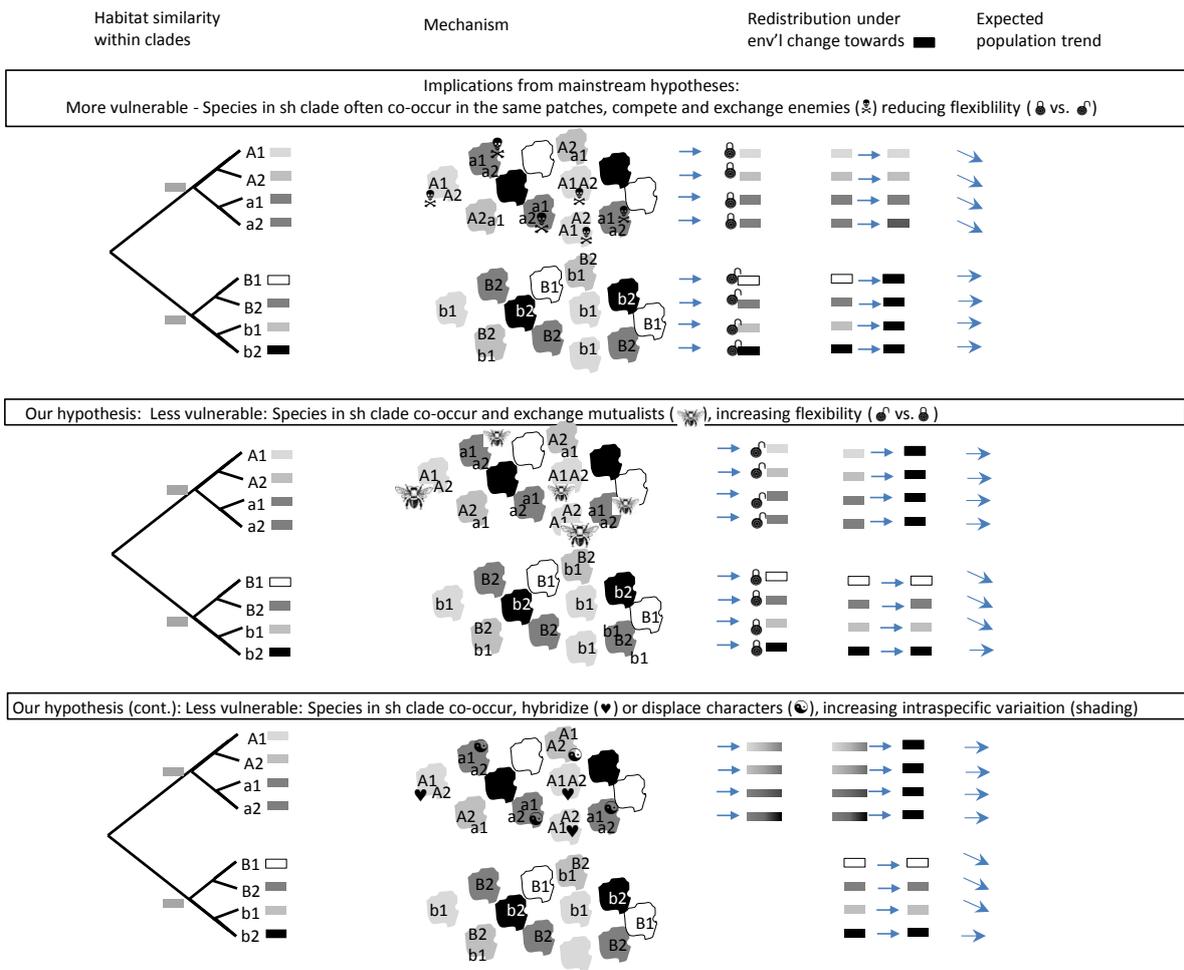


Fig. 2 Scheme summarizing the hypotheses regarding the consequences of similarity in habitat use among clade members: increases in vulnerability of species to current environmental change (more vulnerable, "implications from mainstream hypothesis"), decrease in vulnerability (less vulnerable, "our hypothesis"). Species in the upper of the two clades, occupy similar habitats (sh = similar habitat-use clade), in contrast to species in the lower clade. Shades of grey correspond to the environments used; for example, different moisture conditions.

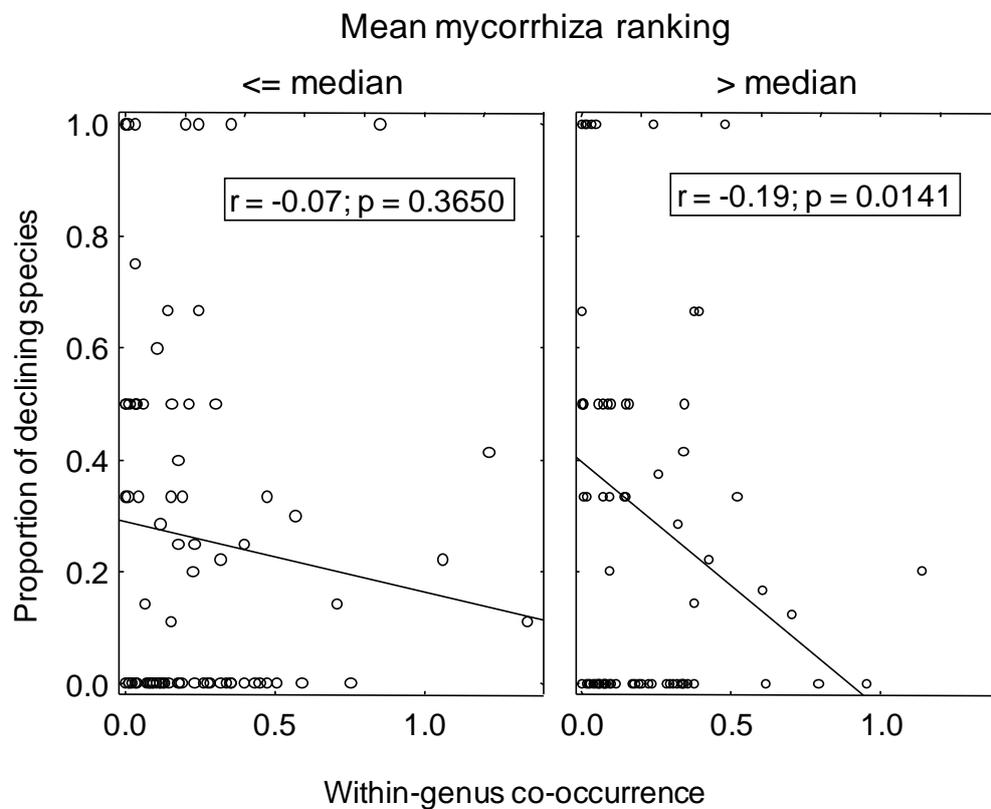


Fig. 3 A high degree of intra-genus co-occurrence (as in Fig. 1) corresponds to a low proportion of declining species within a genus, provided its species are colonized by mycorrhiza (above median mycorrhization rank, right graph, vs. left graph). Decline or non-decline of species was recorded during the twentieth century (from Ozinga *et al.*, 2009). Mycorrhization was extracted for each species from Hempel *et al.* (2013) as 0, 1 or 0.5 (only “non-mycorrhized”, only “mycorrhized”, both) and averaged within genera (median of averages = 0.8). An analysis treating the mycorrhization of species within genera as a continuous variable yields a significant interaction term “co-occurrence x mycorrhization” ($t=1.996$, $p=0.046$, 3 extreme outliers excluded).

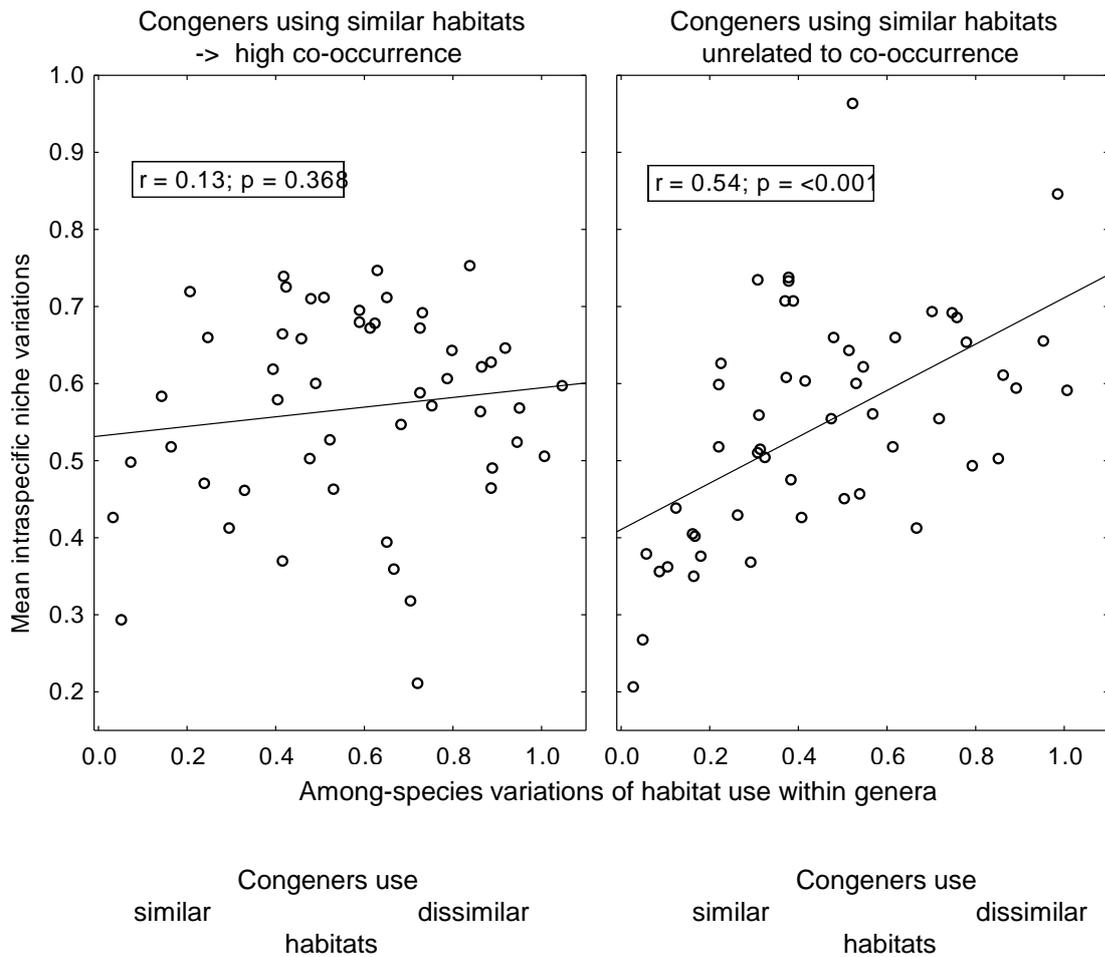


Fig. 4 Genera in which species use similar habitats show low within-species habitat variation (from Ozinga, 2013), except if high habitat similarity corresponds to high within-genus co-occurrence (right vs. left graph: highest and lowest quartile of unsigned residual co-occurrences). The co-occurrence among congeners that occupy similar habitats consequently leads to a *relative* increase of within-species habitat variation. An analysis including genus crown-age and species richness as covariables and treating residual co-occurrence as a continuous variable yields a significant interaction term “habitat similarity x residual co-occurrence” ($t=2.5, p=0.014$).

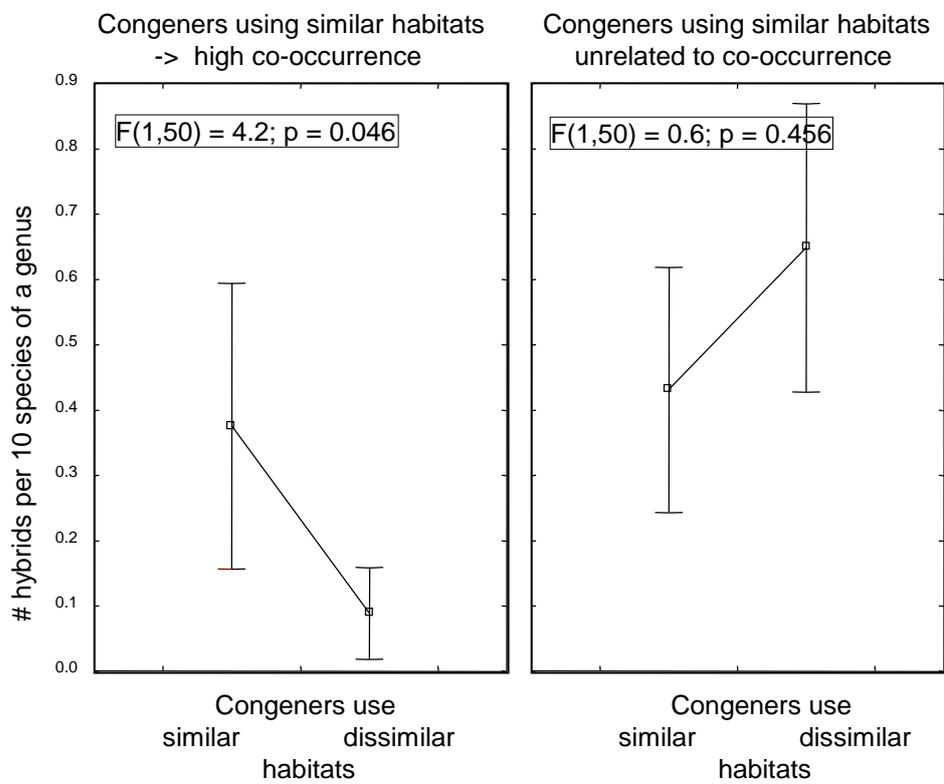


Fig. 5 The relative number of hybrids is high for genera in which species use similar habitats (i.e. below-median habitat variation), provided that using similar habitats corresponds to high intra-generic co-occurrence (left vs. right graph; i.e. unsigned residual co-occurrence in lower quartile and in upper quartile). Hybrids are taken from Frank & Klotz (1990) and Jäger & Werner (2005); the similarity in habitat use and co-occurrence as in Fig. 1 and explained in section II. Clade members using similar habitats consequently increase the probability of hybridization. Note that analyses using an interaction term and a continuous gradient of niche variation are impossible due to numerous zero values in the dependent variable.

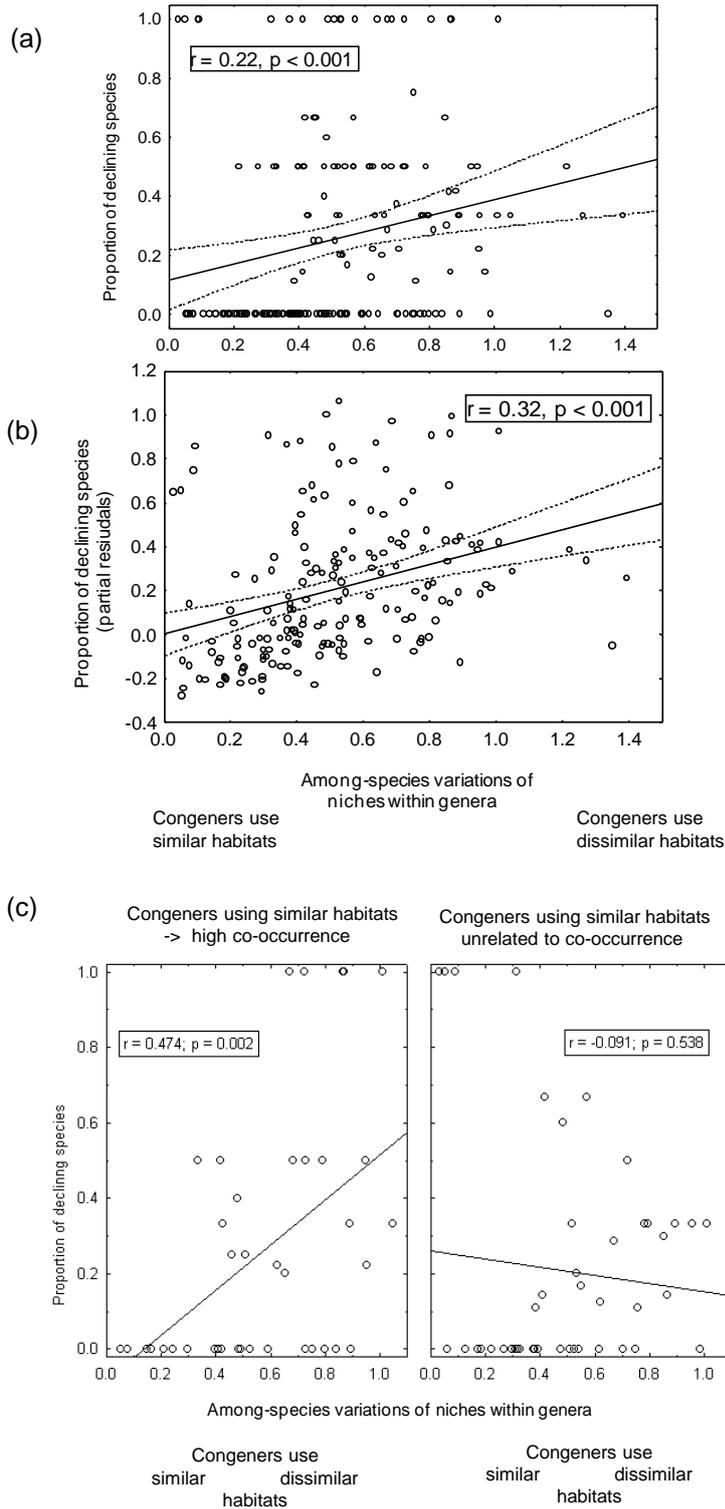


Fig. 6 Genera in which species use similar habitats show a low proportion of declining species during the twentieth century (from Ozinga *et al.*, 2009). (a), Simple relationship ($r=0.22$, $p<0.001$); (b), Partial residuals from a multiple regression analysis accounting for multiple covariables that might influence

within-genus variation of habitats or fates of species (species richness, phylogenetic age, mean within-species variation of habitats) ($r=0.32$, $p<0.001$). Note that this relationship is phylogenetically independent: it was found in 14 out of 15 orders. (c). The above relationship is particularly strong for genera in which similar habitat use corresponds to high intra-generic co-occurrence but disappears if similar habitat use does not correspond to co-occurrence (left vs. right graph, unsigned residual co-occurrence in lower and higher quartile, respectively). An analysis including genus crown-age and species richness as covariables and treating residual co-occurrence as a continuous variable yields a significant interaction term "similarity in habitat use x residual co-occurrence" ($t=2.48$, $p=0.014$). The term remains significant ($t=2.14$, $p=0.034$) after including mean niche positions as covariables, which are variables classically used to explain species decline.

Supporting Information

Additional supporting information may be found in the online version of this article

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

Note S2 Relationship between competitiveness and niche variation within genera

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

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

Fig. S1 An example of variation in habitats among species within different angiosperm genera, based on the flora of The Netherlands.

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' for further explanations.

Fig. S3 Varying degrees of habitat similarity among ancestors and descendants in the fossil record of plant–insect interactions

Fig. S4 Scheme summarizing the scenarios in which similarity in habitat use among species within clades has no consequences on the vulnerability of species to present environmental change.

Fig. S5 Habitat tracking as a function of the capacity of long-distance-dispersal, adult life span and habitat similarity within genera.

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Table 1 Several questions that need to be resolved to understand whether species within clades using similar habitats facilitates or impedes response to present environmental change.

Mainstream hypotheses imply that co-occurrence with fellow clade members is detrimental and increases vulnerability to environmental change.

Competition

When is competition in nature particularly intense among fellow clade members using similar habitats?

Does competition with fellow clade members using similar habitats limit the distribution of species? Does this limitation increase vulnerability to environmental change?

Do fellow clade members using similar habitats invest more into competitiveness? Does this limit investments into responses to environmental change?

Natural enemies

Do fellow clade members using similar habitats suffer more from natural enemies than other species? Does this increase vulnerability to environmental change?

Do fellow clade members using similar habitats invest more into defence against natural enemies? Does this limit alternative investments into responses to environmental change? Which types of defences are particularly costly?

We hypothesize that co-occurrence with fellow clade members is often beneficial and reduces vulnerability to environmental change.

Mutualism

Do fellow clade members using similar habitats profit particularly strongly from mutualists?

Do fellow members of host clades using similar habitats compete for mutualists? Inversely, do the mutualists compete with fellow clade members for hosts?

Do the costs of the competitive interactions outweigh the benefits for the mutualist?

Character displacement

Is there local character displacement among clade members if they use similar habitats?

Does intra-specific variation of characters increase the flexibility to environmental change?

Hybridization

Do fellow clade members using similar habitats exhibit higher rates of hybridization, and can this be explained by high intra-clade co-occurrence?

Do hybrids better tolerate environmental change?
