

LETTER

Not all non-natives are equally unequal: reductions in herbivore β -diversity depend on phylogenetic similarity to native plant community

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Abstract

Effects of host plant α - and β -diversity often confound studies of herbivore β -diversity, hindering our ability to predict the full impact of non-native plants on herbivores. Here, while controlling host plant diversity, we examined variation in herbivore communities between native and non-native plants, focusing on how plant relatedness and spatial scale alter the result. We found lower absolute magnitudes of β -diversity among tree species and among sites on non-natives in all comparisons. However, lower relative β -diversity only occurred for immature herbivores on phylogenetically distinct non-natives vs. natives. Locally in that comparison, non-native gardens had lower host specificity; while among sites, the herbivores supported were a redundant subset of species on natives. Therefore, when phylogenetically distinct non-natives replace native plants, the community of immature herbivores is likely to be homogenised across landscapes. Differences in communities on closely related non-natives were subtler, but displayed community shifts and increased generalisation on non-natives within certain feeding guilds.

Keywords

Beta diversity, feeding guild, herbivore, host specificity, insects, managed landscapes, native plant, non-native plant, spatial scale.

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INTRODUCTION

Increased global trade and human movement of species influence the composition of biological communities worldwide through the introduction of non-native species into novel environments. Over time such introductions as well as associated extirpations of local species result in global homogenisation of biota (McKinney & Lockwood 1999). Biotic homogenisation is documented due to the introduction of plants (McKinney 2004; Qian & Ricklefs 2006), vertebrates (Rahel 2000; Winter *et al.* 2010) and invertebrate species (Shaw *et al.* 2010; Horsák *et al.* 2013), but non-native species may increase differentiation between localities as well (Sax & Gaines 2008; Shaw *et al.* 2010). Studies typically document the effect of novel species on diversity within the invaded trophic level (Legendre & De Cáceres 2013). However, the introduction of non-native species may trigger effects on other trophic levels that depend on the invaded trophic level for food or shelter (Tallamy 2004). For example, plant species play an essential role in ecosystems by supporting herbivorous insect populations that, in turn, support higher trophic levels (Marra *et al.* 1998; Burghardt *et al.* 2009).

In spite of the key role of insect herbivores, few studies describe the effect of non-native plant species on variation in herbivore community composition over space, or β -diversity (more studies examine point or α -diversity). One reason may be the difficulty in determining whether differences in β -diversity in herbivore populations are due to (1) increased richness per host, (2) higher host specificity or (3) changes

in host plant diversity (Lewinsohn *et al.* 2005; Novotny & Weiblen 2005). We overcome this challenge by utilising data collected within four replicated common gardens that controlled plant species richness, landscape structure and the relatedness of non-native species to the local plant community. By holding host plant α - and β -diversity constant, we are able to isolate changes in herbivore β -diversity due to plant origin at two spatial scales.

At local scales, the data set allows us to examine host specificity within native and non-native experimental gardens by comparing herbivore communities among tree species within a site. This reveals whether the higher site-level diversity previously reported within all four replicate gardens on native plants (Fig. 1; Burghardt & Tallamy 2013) is a product exclusively of higher herbivore richness per tree or also of higher differentiation of herbivores species among trees (host specificity).

At broader scales, it is important to understand whether herbivores that are able to use non-native plants represent a unique or redundant subset of species across sites. Knowing which occurs may allow predictions about whether the presence of non-native plant species leads to homogenisation or differentiation of herbivorous arthropods in un-manipulated plant communities (Harris *et al.* 2011).

One factor influencing whether an herbivore is able to use a novel host is how closely related the novel plant is to local natives (Pearse & Hipp 2009). If plants that are closely related share similar defensive compounds, insects adapted to local plants may be better able to circumvent the defences of closely related non-natives than the novel

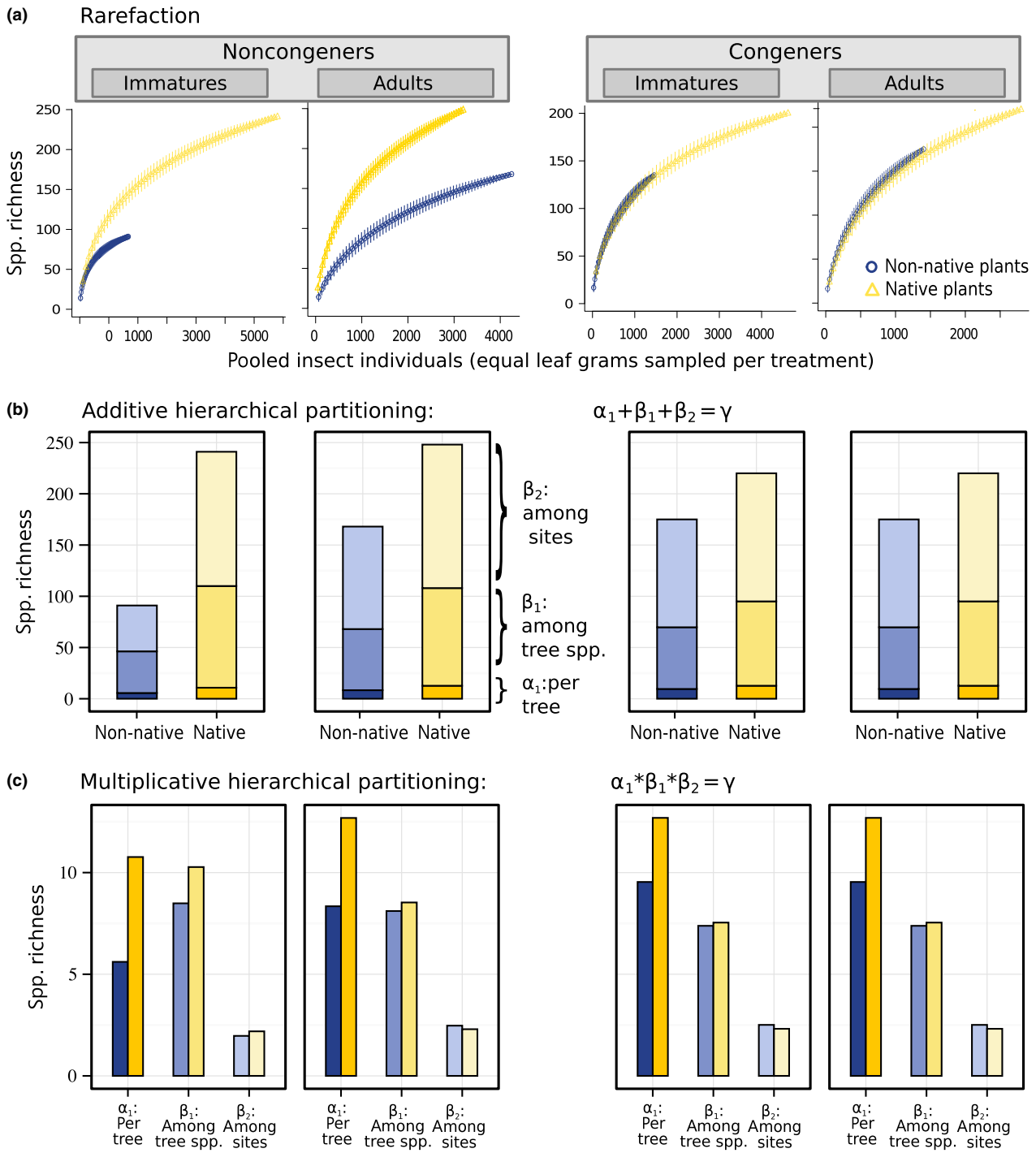


Figure 1 General diversity patterns: (a) Individual-based rarefaction curves with equivalent leaf grams sampled between treatments. This indicates that for the congeneric comparisons differences in species density between native (gold) and non-native (blue) plants are strictly abundance based (e.g. richness is lower because fewer individuals are collected for a given leaf biomass). The high abundance of adults on non-congeneric non-native gardens is primarily driven by the abundance of one species, *Corythucha cydoniae* (Fitch). (b) Additive hierarchical diversity partitioning into components for per tree α -diversity (darkest), among tree β_1 -diversity (middle hue) and among site β_2 -diversity (lightest). These components sum to the total γ -diversity of the treatment. (c) Multiplicative version isolating pure relative differentiation (e.g. β is independent of α). Here, β -diversity can be interpreted as the number of distinct units of the lower level partition and multiply to equal γ -diversity (e.g. for non-congeneric non-natives, six per tree*8 among tree *1.9 among site = 91 species).

defences of more distantly related species (Novotny & Bassett 2005; Cappuccino & Arnason 2006). Within these experimental gardens we are able to expand on this work to test

explicitly whether relatedness to the native community influences herbivore β -diversity patterns on non-native plants.

It is now well established that point-level measures such as herbivore damage, abundance and α -diversity are usually (although not always) lower on non-native plants (Simon 1986; Lewinsohn *et al.* 2005; Proches *et al.* 2008; Heleno *et al.* 2009; Burghardt *et al.* 2010; Bezemer *et al.* 2014). However, we are aware of no previous studies that address β -diversity of herbivores on native and non-native plants of varying relatedness to the native community with the approach or scale that we do here. Specifically we investigate whether (1) herbivore host specificity differs between native vs. non-native plants, (2) insects in non-native plant communities are a common subset across sites or a unique assemblage drawn from the local species pool at each site and (3) plant relatedness to the local species pool, herbivore life stage or herbivore feeding guild mediate these results. If non-native plants host more homogeneous herbivore communities across locations than do natives, then analyses of herbivore diversity on a single plant or sites are likely underestimating the negative impact of non-native plants on herbivore communities.

METHODS

Common gardens

Both congeneric and non-congeneric comparisons were replicated using randomised complete block protocol in four com-

mon gardens (at least 20 km apart) established in 2005–2006 at the University of Delaware Agricultural Experiment Station farms in Newark and Middletown, DE, at Flint Woods preserve in Centerville, DE and at Tyler Arboretum in Media, PA. Each garden was planted within 25 m of a mature woodland and was designed to control for scale of planting, fertilisation, watering regimen, as well as the size, architecture, habit, exposure, understory and spacing of the plants examined. Such variables typically make comparisons within areas in which non-native plants have become naturalised difficult. Within each site, eight saplings of each species in two distinct groupings separated by one metre were established for at least 1 year before sampling (see Fig. S1A in Supporting Information). By the end of the experiment trees were 2 m tall.

Congeneric comparison

To examine whether non-native plants that have close native relatives support the same β -diversity as natives, we planted one native and one non-native species from 13 woody plant genera representing 11 plant families (Table 1A). The genera were selected because they had locally abundant native and non-native congeneric members. We planted both members within two metres (Fig. S1A). If an insect was attracted to one congener, it had the opportunity to feed on the other as well.

Table 1 Plant species community composition in the (A) congeneric study (13 paired genera) and (B) non-congeneric study

Non-native species	Common name	Native species	Common name
(A) Congeneric comparison			
<i>Acer platanoides</i>	Norway maple	<i>Acer rubrum</i>	Red maple
<i>Betula pendula</i>	European white birch	<i>Betula nigra</i>	River birch
<i>Carpinus betulus</i>	European hornbeam	<i>Carpinus caroliniana</i>	American hornbeam
<i>Cornus kousa</i>	Kousa dogwood	<i>Cornus alternifolia</i>	Alternatleaf dogwood
<i>Ilex aquifolium</i>	English holly	<i>Ilex opaca</i>	American holly
<i>Juglans regia</i>	English walnut	<i>Juglans nigra</i>	Black walnut
<i>Prunus serrulata</i>	Korean cherry	<i>Prunus serotina</i>	Black cherry
<i>Rhododendron mucronulatum</i>	Korean rhododendron	<i>Rhododendron periclymenoides</i>	Pinxterbloom azalea
<i>Rosa multiflora</i>	Multiflora rose	<i>Rosa setigera</i>	Prairie rose
<i>Salix babylonica</i>	Weeping willow	<i>Salix nigra</i>	Black willow
<i>Tilia cordata</i>	Little-leaf linden	<i>Tilia americana</i>	Basswood
<i>Ulmus parvifolia</i>	Chinese elm	<i>Ulmus americana</i>	American elm
<i>Viburnum dilatatum</i>	Linden viburnum	<i>Viburnum dentatum</i>	Southern arrowwood
(B) Non-congeneric comparison			
<i>Ailanthus altissima</i>	Tree of heaven	<i>Acer rubrum</i>	Red maple
<i>Albizia julibrissin</i>	Silktree mimosa	<i>Celtis occidentalis</i>	Hackberry
<i>Berberis thunbergii</i>	Japanese barberry	<i>Fraxinus pennsylvanica</i>	Green ash
<i>Buddleja davidii</i>	Butterfly bush	<i>Juglans nigra</i>	Black walnut
<i>Cotoneaster lucidus</i>	Hedge cotoneaster	<i>Lindera benzoin</i>	Spicebush
<i>Elaeagnus umbellata</i>	Autumn olive	<i>Liquidambar styraciflua</i>	Sweetgum
<i>Forsythia x intermedia</i>	Forsythia	<i>Liriodendron tulipifera</i>	Tulip tree
<i>Ginkgo biloba</i>	Ginkgo	<i>Morus rubra</i>	Red mulberry
<i>Koeleruteria paniculata</i>	Goldenrain tree	<i>Nyssa sylvatica</i>	Black gum
<i>Lagerstroemia indica</i>	Crape myrtle	<i>Platanus occidentalis</i>	Sycamore
<i>Ligustrum obtusifolium</i>	Border privet	<i>Prunus serotina</i>	Black cherry
<i>Paulownia tomentosa</i>	Princess tree	<i>Quercus palustris</i>	Pin oak
<i>Pyrus calleryana</i>	Bradford pear	<i>Rhus copalina</i>	Winged sumac
<i>Poncirus trifoliata</i>	Hardy orange	<i>Salix nigra</i>	Black willow
<i>Rhamnus frangula</i>	Glossy buckthorn	<i>Ulmus americana</i>	American elm
<i>Syringa vulgaris</i>	Lilac	<i>Viburnum dentatum</i>	Southern arrowwood

Non-congeneric comparison

On a spatially distinct plot (Fig. S1b), we compared β -diversity across 16 species of native woody plants common in northern Delaware and 16 species of non-native woody landscaping plants that are either invasive or commonly used locally as landscape plants (Table 1B). The non-native species used in this comparison had no native congeners in or near the study area. The goal for species selection was to compare a group of non-native species to a group of native species that could represent ornamental plantings in a typical suburban yard in the Mid-Atlantic US. This criterion limited the potential pool of species; however, it also ensured the direct application of results to landscape management. Native species represented 16 plant families while non-natives represented 14 families. The spatial design was similar to the congener gardens except that species were arrayed randomly (Fig. S1b). Statistics for phylogenetic signal determined that the native and non-native species selected were distributed randomly across a phylogenetic tree consisting of all study species (see Supporting Information for detailed methods).

Arthropod collection

Herbivores were sampled twice in 2007 and 2008 (June and August) to capture both spring flush and late summer feeders. We sampled four trees on each sample date (the plants were sampled non-destructively, but the insects were sampled destructively). Each four-tree unit was sampled once in a year by vacuuming insects from plant foliage for an equal time interval using a reverse leaf blower (Craftsman gasoline blow/vac, Item # 7179469, Brook *et al.* 2008), then meticulously searching the targeted leaves and stems for any remaining insects (Wagner 2005). We counted and collected voucher specimens of internal feeders (gallers and leaf miners). Insects were stored in 80% ethanol. We counted the leaves vacuumed and collected a subset of 100 leaves from each species, which were dried and weighed to standardise by leaf biomass sampled.

Arthropod classification

Each arthropod was identified to genus and species when possible using chaetotaxy (Stehr 1987; Triplehorn *et al.* 2005), images (Wagner 2005), specialist identification and the University of Delaware Insect Museum collection. Where specific identifications were not possible, a morphospecies approach was utilised. We classified foliar herbivore species into feeding guilds as primarily (1) leaf chewers, (2) mesophyll feeders, (3) phloem suckers, (4) xylem suckers or (5) internal feeders such as gallers and miners (see Burghardt & Tallamy 2013; Table A1). These classifications are similar to those used by (Novotny *et al.* 2010). Our mesophyll feeder group is analogous to their 'leaf sucker' group and our internal feeder group includes both their 'leaf miner' and 'galler' groups. Individuals were classified as immature or adult. Utilising a combination of identification approaches may introduce bias into the data, which we minimised by focusing our species-level identification effort within groups where morphospecies

approaches were likely to artificially inflate diversity. One concern was inflation of lepidopteran larval morphospecies due to poor documentation of morphological changes across larval instars. Therefore, some early instars were linked to older instars using DNA bar-coding through the Biodiversity Institute of Ontario (Ratnasingham & Hebert 2007). These individuals were linked to known species in the database at >99.5% similarity. As a result a greater proportion of immature species (69–72%) were identified to species vs. morphospecies than adults (45–50%); however, identification proportion did not vary by more than 4.5% between treatments and comparisons.

Metrics

α -diversity (the mean diversity of a subunit) and γ -diversity (the global diversity across all sites of the experimental treatment) are both inventory diversity measures with the differentiation between the two accounting for β -diversity. Recent debate on the best way to define and analyse this differentiation (Anderson *et al.* 2011) emphasises the importance of clarity on the part of authors about the definitions used. Here, our goal is not to contribute to the debate about the best single measure. Instead we use a variety of approaches to illustrate patterns and test specific hypotheses. Because of the controlled replicated nature of our study across space, we determine β -diversity through a variation (vs. gradient) approach (Anderson *et al.* 2011). After first quantifying basic patterns through hierarchical additive and multiplicative diversity partitioning (Crist *et al.* 2003; Jost 2007), we focus on three distinct components of community differentiation: host specificity, species redundancy and compositional dissimilarity. Throughout this paper we refer to the variation in herbivore composition among tree species within a garden at a site as *host specificity* (local scale; e.g. differences in multi-tree β_{SIM} measures within gardens). We refer to those differences in herbivore communities among sites *within* a plant origin treatment as *species redundancy* (regional scale; e.g. differences across sites within plant origin group by measuring dispersion from the group centroid; V4a in (Anderson *et al.* 2011)). Lastly, we refer to differences in herbivore composition across sites between plant origin groups as *compositional dissimilarity* (regional scale; e.g. whether the location of native and non-native group centroids is different; e.g. V2 and V3 in (Anderson *et al.* 2011)). The compositional dissimilarity measure is conceptually different from the diversity partitioning and local-scale analysis because the communities on non-native and native plants are compared to one another directly within the analysis. This allows hypothesis testing about whether the species on non-natives are similar to those on native plants.

Statistical analysis

Hierarchical diversity partitioning

To show general patterns, total γ -diversity per treatment was partitioned into additive (absolute magnitude of β diversity) and multiplicative components (pure relational differentiation) representing per tree α -diversity, among tree β -diversity and among site β -diversity using the *adipart* and *multipart*

functions in the *vegan* package (Crist *et al.* 2003; Jost 2007; Chao *et al.* 2012).

Host specificity

To determine whether arthropod communities are similarly distinct across non-native tree species and across native tree species, we calculated multiple-unit (here, multiple-tree species) total Sorenson dissimilarity values (β_{SOR}) for arthropod communities on the native and non-native trees within each site ($n = 4$; Fig. 2a). This total was decomposed into a multi-tree turnover component or host specificity (β_{SIM}) and a nestedness component (β_{SNE} - accounts for differences in β -diversity created by one community existing as subset of another community, Baselga & Orme 2012). Multi-unit dissimilarities were chosen over mean pairwise dissimilarities due to recent work demonstrating that pairwise dissimilarities misrepresent shared arthropod species occurring across more than two tree species (Baselga 2010). In order to determine whether dissimilarities consistently differed between native and non-native gardens we used a two-way ANOVA with origin as a fixed effect and site as a blocking factor ($n = 4$). β_{SIM} results were also compared to mean pairwise Raup-Crick dissimilarity ($\beta_{\text{r-c}}$) which uses a probabilistic null model approach to condition out the effect of species richness (a known feature of the data set see Fig. 1, Chase *et al.* 2011). This analysis was performed separately for the immature and adult arthropod communities. The R package *betapart* was used to decompose

β -diversity values (Baselga & Orme 2012). Jaccard's dissimilarity produced qualitatively similar results to Sorenson's so only the latter is presented. All multi-tree β -diversity measures were calculated for each site on species data pooled across the sample dates for each tree species.

Across-site compositional dissimilarity

Due to lack of replication at the regional scale we were unable to use the same statistical approach to assess β -diversity across sites as we did for host specificity. Instead, we first assessed differences in community composition between native and non-native plants across sites to determine whether species composition is more attributable to plant origin or dominated by site effects (e.g. the local species pool; Fig. 2b). We used an unconstrained ordination technique, principal coordinates analysis (PCoA), to visualise dissimilarities between the species composition of arthropod communities. Dissimilarity matrices between gardens were calculated using pairwise Sorenson dissimilarity (β_{SOR}) again decomposed into a turnover component (β_{SIM}) and a nestedness component (β_{SNE}). β_{SIM} results were again compared to Raup-Crick dissimilarity ($\beta_{\text{r-c}}$) (Chase *et al.* 2011). Lastly we utilised the abundance-based Morista-Horn dissimilarity ($\beta_{\text{m-h}}$) using cubed root abundances, which was recently determined to be most robust metric in cases of under-sampling or detection bias (Beck *et al.* 2013). These measures were calculated on species data pooled across the sample dates and tree species within each site.

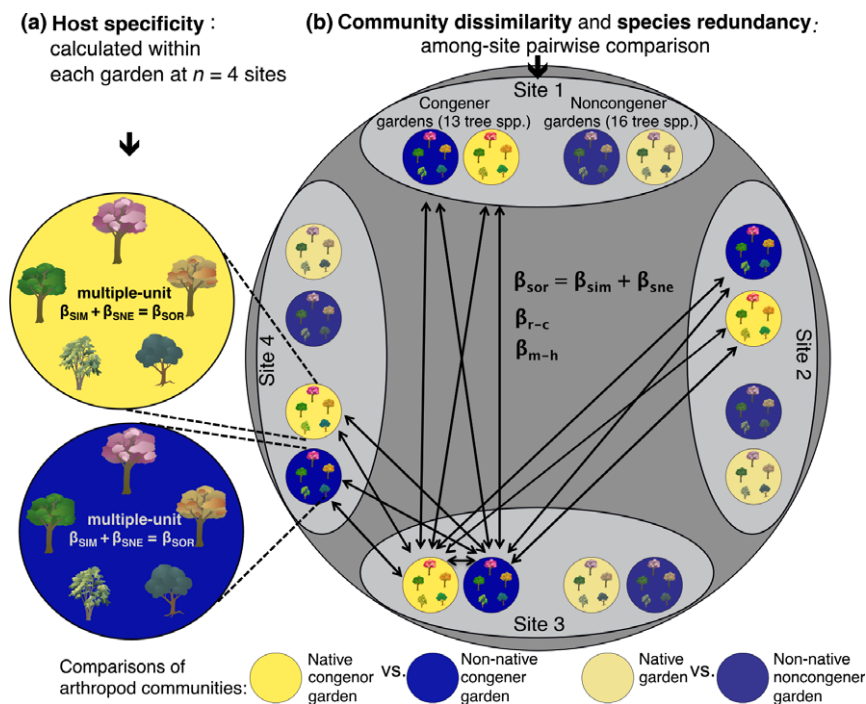


Figure 2 Schematic of β -diversity calculations performed at the spatial scale of (a) within site (a multiple-tree β -diversity index decomposed into nestedness and turnover components (host specificity) is calculated individually for each garden within each site) and (b) among sites (all pairwise dissimilarities between sites and gardens are calculated but not shown here for clarity). For the latter, PCoA was used to visualise differences in species composition between gardens. PERMANOVA and BETADISPER were then used to formally test whether community composition and dispersion differed between native and non-native plant-based arthropod communities. Gardens are simplified representations (e.g. each congeneric garden contains eight trees of 13 tree genera each (one native, one non-native in each genus); non-congeneric gardens (eight trees of 16 non-native species without a close native relative in the study area and are compared to a garden of 16 native species).

A PERMANOVA model with origin and site as factors tested whether plant origin, local site effects or both best explained compositional dissimilarity between sites. We report PERMANOVA results here to best match the unconstrained graphical representation of data; however, the results are qualitatively the same using a constrained distance-based redundancy approach (db-RDA). The R package *vegan* was used to calculate PCoAs, dissimilarity matrices, PERMANOVA, variance partitioning (varpart) and distance-based RDA (R Development Core Team 2009; Oksanen *et al.* 2012). There has been a debate about whether PERMANOVA is a robust technique when data exhibit heterogeneous dispersions; however, a recent study demonstrated that the technique is robust for balanced designs such as this (Anderson & Walsh 2013).

Across-site species redundancy

Next, we used BETADISPER within the *vegan* package (Oksanen *et al.* 2012) to conduct a permutational test comparing the homogeneity of dispersion from group centroid in multivariate space between native and non-native sites (Anderson *et al.* 2006). This analysis is analogous to Levene's test for homogeneity of variances in univariate statistics, capturing a different aspect of β -diversity than PERMANOVA by determining whether there are differences between groups in the amount of dissimilarity within groups (e.g. dispersion around group median; Anderson *et al.* 2006). A group with a smaller dispersion of sites across multivariate space can be interpreted as supporting a more redundant arthropod community across sites. We repeated this analysis for each feeding guild.

RESULTS

In total, within the congeneric comparison we sampled 53 004 dry grams of native leaves and 52 419 dry grams of non-native leaves, as well as 62 236 dry grams of native leaves and 64 023 dry grams of non-native leaves in the non-congeneric comparison. We identified 17 410 herbivores from 328 immature species and 252 adult species. Individual-based species rarefaction curves showed that species density was always higher on native gardens but that was driven by richness and abundance differences in non-congeneric gardens and only abundance-based differences in congeneric gardens (equal plant biomass was sampled within each treatment; Fig. 1a). In addition, native gardens always had higher additive β -diversity partitions both among trees and among sites indicating a greater absolute magnitude of β -diversity (Fig. 1b). However, β components in additive partitioning still depend on α -diversity (Chao *et al.* 2012); when this dependence was removed using multiplicative diversity partitioning which isolates pure relative differentiation, only the immature insect community on non-native plants without close native relatives shows a general pattern of lower relative differentiation (Fig. 1c).

Local host specificity analysis

In phylogenetically distinct non-native plant communities, we found lower host specificity (β_{SIM}) within communities of

immature arthropods. That is, when we sampled a non-native plant, the arthropod community on that plant was likely to be more similar to arthropods sampled on other non-native plants than when we compared arthropod assemblages on two native plants (Fig. 3, Table S1). Interestingly, non-natives did have a higher nestedness (β_{SNE}) component than natives leading to a small overall difference in total β_{SOR} . The adult community patterns were qualitatively similar but not significantly different (but see Fig. S4). In contrast, when non-native species had a nearby native plant in the same genus, relative host specificity of non-native plants was similar to their native counterparts. The β_{SIM} results were confirmed through a comparison with Raup-Crick distance-based results ($\beta_{\text{r-c}}$), which utilises a null modelling approach to resample communities, thus conditioning out the effect of sample size and α -diversity on β -diversity (see Fig. S4).

Among site analysis

In general, non-native plants unrelated to the native community supported immature herbivore communities that consisted of a redundant subset of the herbivore species found on the native plants across sites (Fig. 4). Adult insects on these same non-native plants represented a different community than on the natives but were not more redundant across space. In contrast, non-native plants that are closely related to the native community had virtually identical adult herbivore communities to their native counterparts. Immature insects on these plants did represent a different community composition than that on native plants, but species were equally redundant across sites. Site effects were strongest in the congeneric comparison and adult communities. The use of an abundance-based distance, $\beta_{\text{m-h}}$, simply served to further magnify the differences between treatments (Fig. 4). β_{sim} results were again recapitulated by the null model-based $\beta_{\text{r-c}}$ measure (Fig. S4).

Immature insects on non-congeneric plants

The community on non-native plants was different than the community on native plants and was not site dependent (Fig. 4, Table S2, variance partitioning: origin = 0.52, site = 0.06). However, this biological distinctiveness is attributable to differences in nestedness (β_{snc}) between treatments, as demonstrated by the lack of significant effect of plant origin when the β_{sim} and $\beta_{\text{r-c}}$ measures were used to isolate turnover (Fig. 4, Fig. S4, Table S2). Here, the herbivore community on non-natives is entirely subsumed within the native community indicating that the community of immature herbivores on non-native plants consists of a redundant and depauperate subset of the species that occur on native plants.

Adult insects on non-congeneric plants

Herbivore communities are distinct on non-natives and are attributable to both plant origin and site based on both β_{SOR} and $\beta_{\text{m-h}}$ (Fig. 4, Table S2, variance partitioning: origin = 0.14, site = 0.32). When abundance is considered,

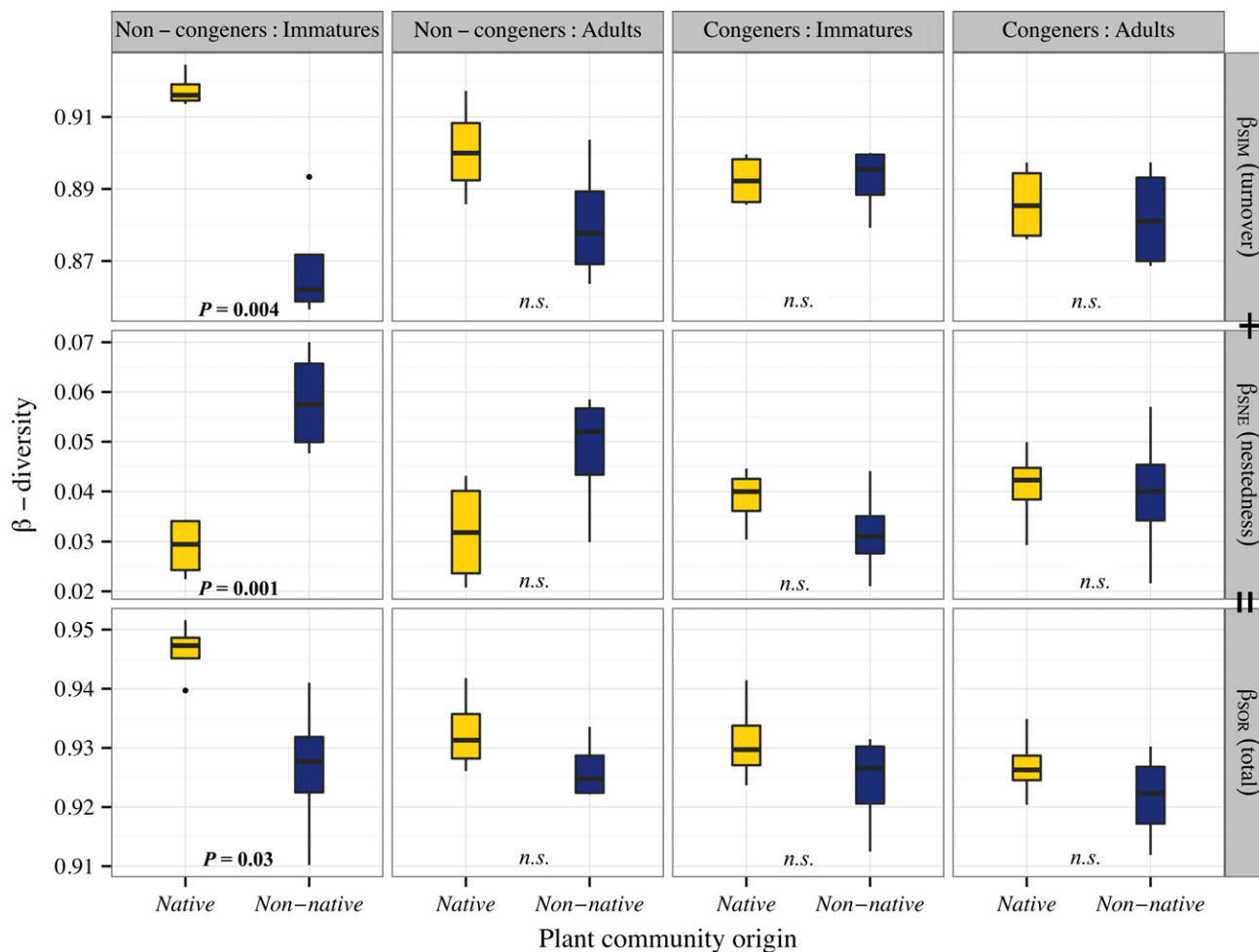


Figure 3 Box-plots of multi-tree β -diversity values calculated within each site to examine host specificity of arthropods between tree species within each garden. A total β -diversity measure (β_{SOR}) decomposed into a nestedness (β_{SNE}) and turnover (β_{SIM}) component was calculated across tree species within each site for native and non-native species separately ($n = 4$). Host specificity (or species replacement from host to host) is represented by the β_{SIM} component. A paired t -test (ANOVA with site as a pairing factor) was then used to determine if native and non-native species exhibited the same patterns (P -values, also see Table S1). Note that y -axis ranges are not the full range possible (e.g. 0–1). The β_{SIM} result was confirmed with a probabilistic null modelling approach (Raup-Crick distance), which conditions out the effect of sample size and α -diversity on β -diversity (Fig. S4).

species redundancy across sites was significantly higher on non-native plants.

Immature insects on congeneric plants

Plant origin and site effects also explained the community of immature insects on congeneric non-natives (Fig. 4, Table S2, variance partitioning: origin = 0.20, site = 0.35). Native plants hosted a significantly different community of herbivores than non-native plants through changes in turnover among sites (β_{sim}). No difference in species redundancy between the native and non-native plants was detected.

Adult insects on congeneric plants

The adults on congeneric non-native plants were largely indistinguishable from those on native congeners (Fig. 4, Table S2, variance partitioning: origin = 0.04, site = 0.47). Instead, arthropod communities on non-native plants were driven by

the local species pool, and were just as biologically distinct across sites as native communities (non-significant dispersion difference).

Differential feeding guild responses

The guild analysis reinforced the pattern that immature herbivores are most sensitive to plant origin, particularly if non-natives do not have close native relatives. Every guild but xylem feeders were sensitive to plant origin in at least one comparison, and the analysis revealed more redundant communities on non-natives within many guilds where we did not see a significant difference in the overall analysis. We only present the $\beta_{\text{r-c}}$ results here due to the advantage of controlling for α -diversity differences (Fig. 5), but comparison with the β_{SOR} and $\beta_{\text{m-h}}$ results (Fig. S2 and S3) reveal similar (although not identical) patterns. Regardless of dissimilarity chosen, plant origin is playing a large role in differentiating these communities.

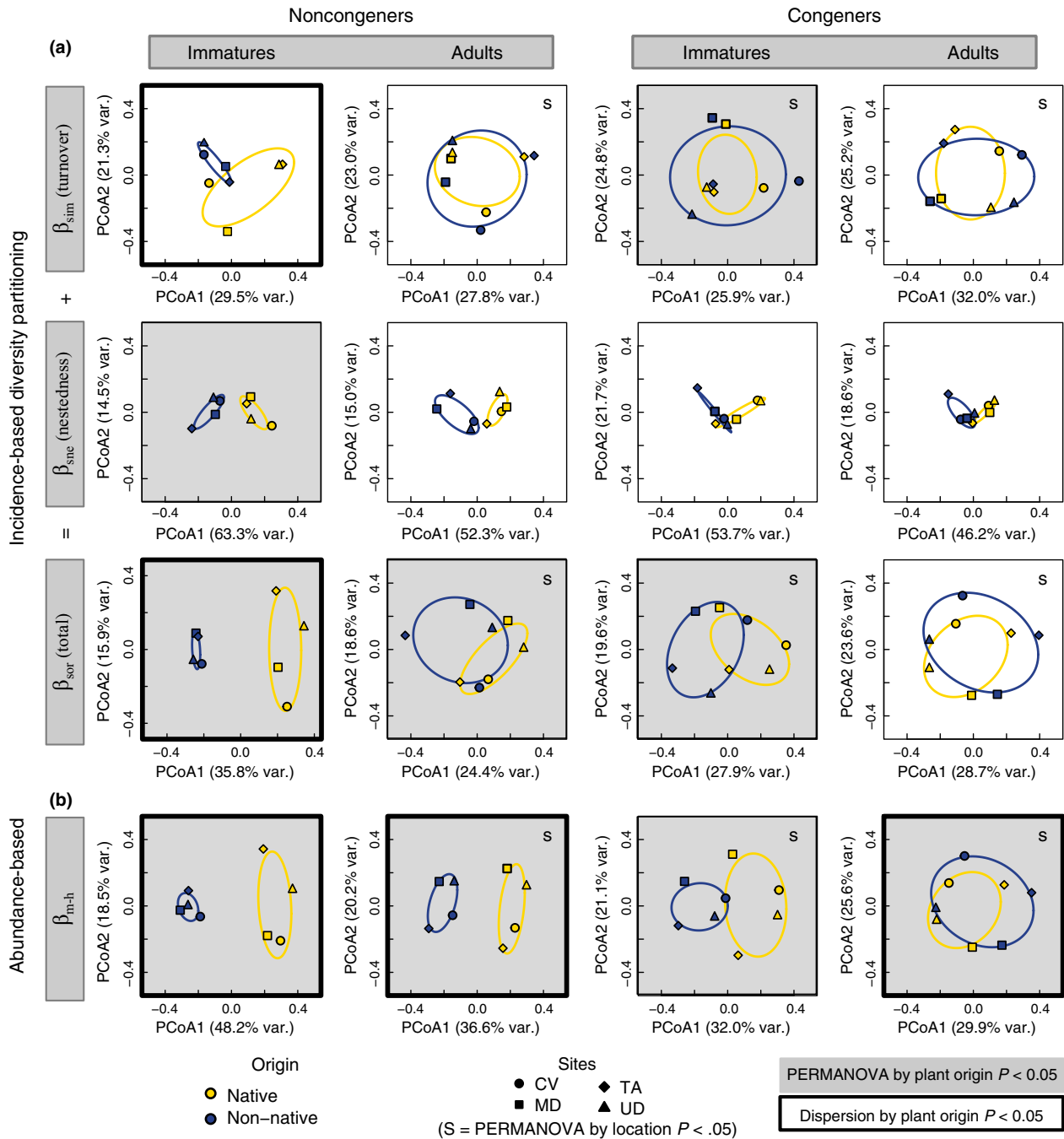


Figure 4 PCoA ordination (unconstrained) of the arthropod communities found across sites within native (gold) and non-native (blue) gardens using both (a) An incidence-based approach which partitions total Sorenson dissimilarity (β_{sor}), into a turnover-based component (β_{sim}) and nestedness-based component (β_{sne}) and (b) Abundance-based Morista-Horn dissimilarity (β_{m-h}). Shading represents a significant effect of plant origin in PERMANOVA which tests whether the group centroid of arthropod communities on native and non-native plant species differs in multivariate space (e.g. different community composition) and a darkened black border which indicates a significant effect of origin using BETADISPER which tests whether the dispersion of a treatment from its median are different between groups (e.g. different relative species redundancy across space). The β_{sim} result was recapitulated with a null modelling approach using the Raup-Crick distance, which conditions out the effect of sample size and α -diversity (Fig. S4).

Immature insects on non-congeneric plants

Communities of chewers, mesophyll, phloem and internal feeders on non-native plants were more redundant across sites than communities on native plants. Except for phloem-feeders, these groups also harboured dissimilar communities on non-natives vs. natives (Fig. 5, Table S3).

Adult insects on non-congeneric plants

Differences within the adult communities were concentrated within mesophyll and phloem-feeders. Their communities on non-native plants were composed of compositionally distinct but more redundant species across sites (Fig. 5, Table S3).

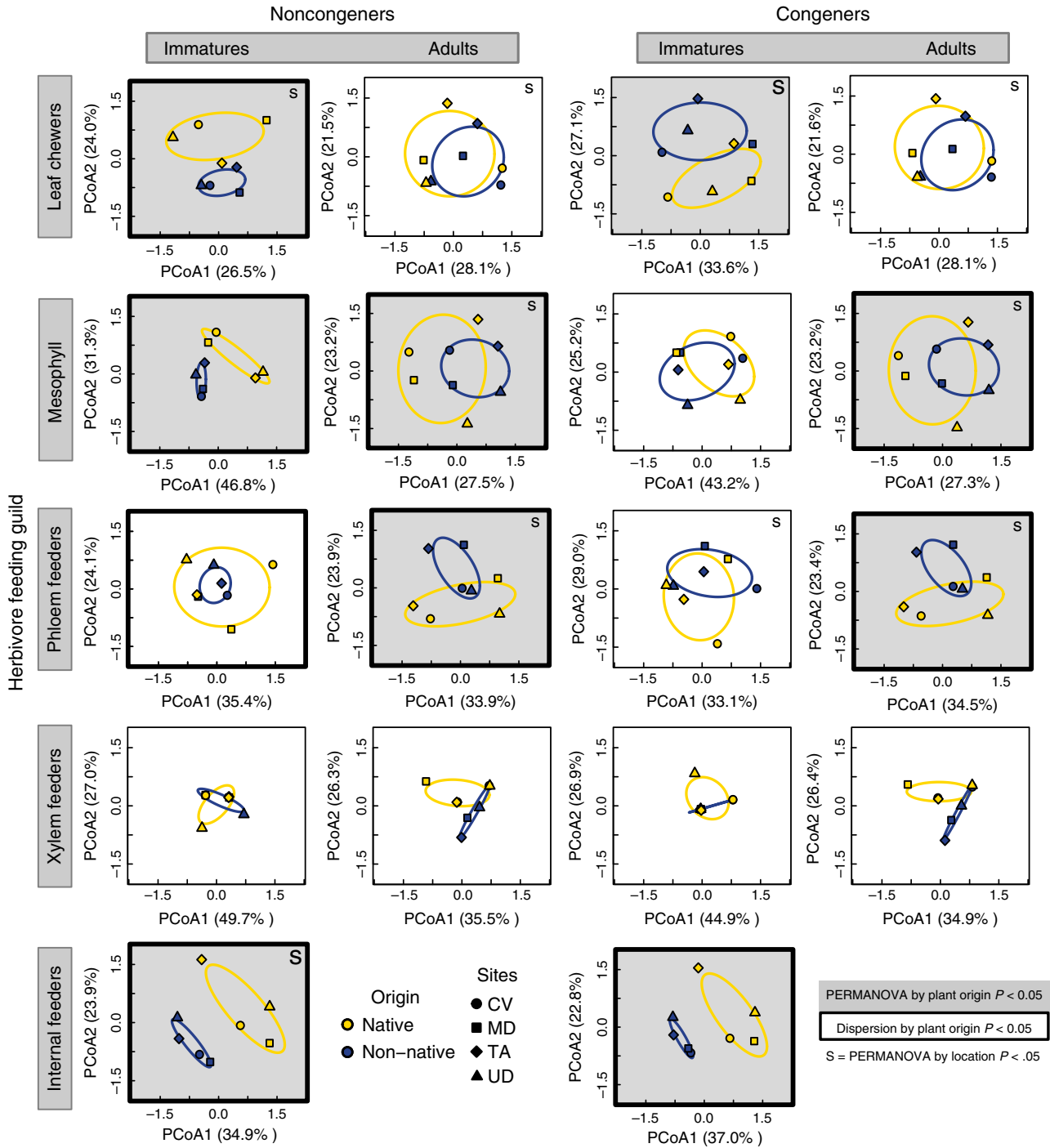


Figure 5 PCoA ordination (unconstrained) of each feeding guild community using the Raup–Crick dissimilarity (β_{rc}) calculated across sites within native and non-native gardens. This dissimilarity uses a null model approach to condition out the impact of α -diversity on dissimilarity, a known aspect of the data set (Chase *et al.* 2011). Shading represents a significant effect of plant origin in PERMANOVA which tests whether the group centroid of arthropod communities on native and non-native plant species differs in multivariate space (e.g. different community composition) and a darkened black border which indicates a significant effect of origin using BETADISPER which tests whether the dispersion of a treatment from its median are different between groups (e.g. species redundancy across space).

Immature insects on congeneric plants

Chewing insects were compositionally different on non-natives, but had equal species redundancy. Non-native plants also hosted a different and more redundant internal feeder community than did natives (Fig. 5, Table S3).

Adult insects on congeneric plants

Similar to the adult communities on non-congeneric plants, differences were concentrated within mesophyll and phloem-feeders, with compositionally distinct but more generalised species across sites on non-natives compared to natives (Fig. 5, Table S3).

DISCUSSION

This study adds to the evidence that non-native trees and shrubs are not the ecological equivalent of natives in their support of higher trophic levels. We have demonstrated that, in addition to decreasing arthropod abundance and species richness (Burghardt & Tallamy 2013), non-native plants produce different patterns of herbivore compositional dissimilarity and species redundancy across sites as well as host specificity between tree species. This suggests that commonly used point diversity measures may not be capturing the full impact of non-natives on insect diversity. Our study also adds necessary and important nuance to the discussion. Not all non-natives are equally unequal to native plants, and not all feeding guilds are affected the same way. Non-native plant species that are unrelated to any native species support more depauperate and generalised communities of herbivores than non-native species that have a close native relative within the local community. Immature insects are more negatively affected than adults. This insight will help inform the debate about the ecological value of the non-native plants comprising novel ecosystems (Hobbs *et al.* 2006, Davis *et al.* 2011, Schlaepfer *et al.* 2011), particularly in terms of the degree to which they do or do not support local food webs.

In general, at local scales we found similar relative host specificity (β_{SIM}) between native and non-native gardens. Therefore, the higher diversity of arthropods previously reported on natives within a site (Burghardt & Tallamy 2013) is best explained by differences in per tree richness of arthropods rather than differences in host specificity. The exception was immature arthropod communities on phylogenetically distinct non-natives; here, β_{SIM} of herbivores was higher on native plants indicating higher host specificity. However, non-natives had higher component of β -diversity due to nestedness (β_{SNE}) than natives resulting in only a small, though still statistically significant, difference in total β_{SOR} . This suggests that species replacement plays a larger role in structuring communities on natives, with a larger role attributed to species loss among trees in non-native communities (Baselga 2010). Though the relative differences are small (e.g. ~5% lower host specificity on non-native plants Fig. 3, Fig. S5, Fig. S6), this analysis suggests that at local scales the community of immatures on phylogenetically distinct non-natives is more generalised across hosts in addition to having lower per host richness.

At broader spatial scales, plant origin and site together consistently explained ~50–60% of the variation found within insect communities, but the proportion attributed to each factor varied markedly across experiments. Plant origin was much more important in determining the immature insect communities on phylogenetically distinct non-native plants while site effects determined the adult community on non-native congeners. Approximately equivalent effects of site and plant origin were found within adult communities on non-congeners and immature communities on congeners.

Regionally, decomposing total dissimilarity (β_{SOR}) within the non-congeneric comparison revealed that the compositional distinctness between native and non-native immature communities was attributable to differences in nestedness (β_{SNE}) between native and non-native gardens. In contrast, isolating species

turnover among sites (β_{SIM}) removed the effect of plant origin on community distinctness, but species redundancy remained much higher on non-native species compared to natives across sites. Therefore, the species of herbivores found on phylogenetically distinct non-native plants are a subset of generalists from the native community that are found across all sites. This shift towards more generalised communities has also been found across space on non-natives within a few herbaceous plant species (Zwölfer 1988; Novotny *et al.* 2003), and herbivores more quickly colonise a non-native with native congeners than one with no local close relatives (Bürki & Nentwig 1997).

One important distinction highlighted by our results is the difference between the absolute magnitude of differentiation differences (e.g. diversity excess *sensu*, Chao *et al.* 2012) and pure relative differentiation measures. These concepts are exemplified by additive hierarchical diversity partitioning (Fig. 1b) and multiplicative partitioning (Fig. 1c) respectively. The general pattern within our data set is a much higher absolute magnitude of differences between non-native and native plants on all gardens at all scales, with more subtle differences in relative differentiation limited to the immature insect community on non-congeneric plants. We emphasise that we did not do any hypothesis testing with this approach, but it illustrates the patterns within the data set that lead to our results. Because both the among tree host specificity and among site species redundancy (to a lesser degree) analyses are calculated within each treatment independently and the relative patterns are statistically compared, they are more analogous to the pure relative differentiation measure and show similar, subtler differences (Fig. 1c). Interestingly, with these same data broken down by feeding guild we detected decreased species redundancy on non-natives within at least one guild in all comparisons even with this more relative measure (Fig. 5). In contrast, the community dissimilarity analysis among sites explicitly involves calculating similarity between native and non-native sites as well as within (e.g. community overlap), highlighting a different type of differentiation. Here, differences between gardens are ubiquitous.

This pattern of greater utilisation by herbivores of non-native congeners as compared to phylogenetically distinct non-natives fits closely with the concept of 'ecological fitting' contributing to host use patterns within communities (Janzen 1985). Here, many of the insect species we collected on non-native plants have not necessarily evolved to use these non-native species, but are expanding their host range to include those non-natives that happen to have traits that already fit the adaptations of local herbivores (Agosta 2006; Harvey *et al.* 2010). Because these traits (such as phytochemistry) are phylogenetically conserved, we see patterns in host use that favour expansion onto congeneric non-natives with close native relatives rather than onto those without. If this proves to be a general rule it would reduce the negative impact of non-native congeners on herbivore communities.

Differences in species composition across sites were driven by differential sensitivity of herbivore feeding guilds to plant origin, revealing shifts towards more generalised communities within comparisons where they that were not detected in the overall analysis. Within communities of immature insects, chewing herbivores and internal feeders were most sensitive

(with additional mesophyll and phloem-feeders effects on non-congeneric plants). Chewing herbivores and internal feeders on native and non-native plants also showed the largest differences in abundance within the experiment (Burghardt & Tallamy 2013). This is not surprising because it is difficult for chewers to avoid plant defences without developing specialised physiological adaptations (Rosenthal & Janzen 1979). Moreover, internal feeders have developed highly specialised relationships with plants and are previously known to colonise novel hosts slowly (Strong *et al.* 1984).

Unexpected, however, was (1) the strong impact of plant origin on the composition and redundancy of adult mesophyll and phloem feeder communities and (2) the lack of impact on adult chewing insects. Variation in specialisation within guilds and life stages may account for this. For example, on tropical tree species, larval chewers exhibit much higher specialisation than adult chewers possibly because non-mobile larvae are typically confined to one plant resource (Novotny *et al.* 2010), or because immatures consume orders of magnitude more leaf tissue than adults and therefore are more sensitive to plant defences. While Novotny and coworkers did not separate adult and immature individuals, the same study also demonstrated high specialisation in mesophyll feeders, and some specialisation within phloem-feeders, which is consistent with our results as is their finding of low specialisation in xylem feeders which showed no impact of non-natives in our study.

Combined with our previous abundance results (Burghardt & Tallamy 2013), it is clear that immature insects are most vulnerable to the replacement of native host plants, particularly with non-native plants that are unrelated to local native plants. These results suggest that when phylogenetically distinct non-native plants replace native plant communities, the community of arthropod herbivores is likely to be homogenised as a few species of generalists replace species of specialists across landscapes. It is also likely that all herbivorous feeding guilds except for xylem feeders will be negatively impacted in some way. In contrast, once they have reached adulthood, insects appear to be less sensitive to changes in host plant origin, particularly when they encounter a non-native with close native relatives. It is important to note that even though adult herbivores appear to use non-native plants relatively frequently, reduced use by immatures indicates that many of the adults we collected in this study completed their immature development on nearby native plant species. In our experiments, native trees were plentiful, but if communities lack native plants for immature development, adult communities of insect herbivores may become impoverished as well.

Managing novel ecosystems requires the balanced consideration of the impact of non-natives on numerous biophysical and community processes. Given the results of this study and the importance of insect herbivores to higher trophic levels (Tallamy 2004), we suggest that regardless of the trophic level of a novel species, one priority of such management should be the maintenance of whole food-web integrity and complexity.

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AUTHORSHIP

D.W.T. conceived the experiment; K.T.B. and D.W.T. collected the data; K.T.B. conceived the analytic approach and questions, identified arthropods and wrote the first draft of the manuscript with D.W.T. contributing substantially to revisions.

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