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Phylogenetic diversity and co-evolutionary signals among trophic levels change across a habitat edge

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Summary

1. Incorporating the evolutionary history of species into community ecology enhances understanding of community composition, ecosystem functioning and responses to environmental changes.

2. Phylogenetic history might partly explain the impact of fragmentation and land-use change on assemblages of interacting organisms and even determine potential cascading effects across trophic levels. However, it remains unclear whether phylogenetic diversity of basal resources is reflected at higher trophic levels in the food web. In particular, phylogenetic determinants of community structure have never been incorporated into habitat edge studies, even though edges are recognized as key factors affecting communities in fragmented landscapes.

3. Here, we test whether phylogenetic diversity at different trophic levels (plants, herbivores and parasitoids) and signals of co-evolution (i.e. phylogenetic congruence) among interacting trophic levels change across an edge gradient between native and plantation forests. To ascertain whether there is a signal of co-evolution across trophic levels, we test whether related consumer species generally feed on related resource species.

4. We found differences across trophic levels in how their phylogenetic diversity responded to the habitat edge gradient. Plant and native parasitoid phylogenetic diversity changed markedly across habitats, while phylogenetic variability of herbivores (which were predominantly native) did not change across habitats, though phylogenetic evenness declined in plantation interiors. Related herbivore species did not appear to feed disproportionately on related plant species (i.e. there was no signal of co-evolution) even when considering only native species, potentially due to the high trophic generality of herbivores. However, related native parasitoid species tended to feed on related herbivore species, suggesting the presence of a co-evolutionary signal at higher trophic levels. Moreover, this signal was stronger in plantation forests, indicating that this habitat may impose stresses on parasitoids that constrain them to attack only host species for which they are best adapted.

5. Overall, changes in land use across native to plantation forest edges differentially affected phylogenetic diversity across trophic levels, and may also exert a strong selective pressure for particular co-evolved herbivore–parasitoid interactions.

Key-words: co-evolution, food web, habitat fragmentation, ParaFit, phylogeny, phylomatic edge effects.

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Introduction

Ecologists are increasingly using information on the shared evolutionary history (i.e. phylogeny) of species to understand patterns in their distribution and abundance (Webb *et al.* 2002; Mouquet *et al.* 2012). Phylogenetic approaches have the benefit of linking phenotypic (i.e. trait) information with past evolutionary events (Cadotte *et al.* 2010; Srivastava *et al.* 2012), which, combined with information on contemporary ecology, provides insights into the mechanisms driving community structure (Cavender-Bares *et al.* 2009; Mouquet *et al.* 2012).

The phylogenetic information in a community can be summarized using metrics analogous to the traditional measures of diversity, such as species richness and evenness (Helmus *et al.* 2007; Schweiger *et al.* 2008; Cadotte *et al.* 2010), thereby providing a fuller representation of community trait and functional diversity than does taxonomic diversity alone (Srivastava *et al.* 2012). Phylogenetic diversity has therefore been used to describe and understand community composition and impacts on ecosystem processes; for example, in plant communities, it has been found to increase biomass (Cadotte, Cardinale & Oakley 2008; Connolly *et al.* 2011) by increasing niche complementarity. Furthermore, phylogenetic diversity of a lower trophic level has been found to correlate positively with species richness of upper trophic levels, by providing more habitat niches and/or more biomass (Dinnage *et al.* 2012).

Understanding how phylogenetic diversity changes in space and across trophic levels may also allow the conservation of evolutionary information, an often neglected component of biodiversity (Vane-Wright 1992; Devictor *et al.* 2010; Winter, Devictor & Schweiger 2013). In fact, recent research has found that climate change and human disturbance can reduce the phylogenetic diversity of plant communities (Knapp *et al.* 2008; Willis *et al.* 2008; Dinnage 2009), suggesting that anthropogenic change might 'select' only certain closely related species to survive (Srivastava *et al.* 2012). Combined with the bottom-up effects of phylogenetic diversity on higher trophic levels (Dinnage *et al.* 2012), this suggests that phylogenetic approaches could help ecologists to predict the composition and distributional responses of interrelated communities to global changes (Lavergne *et al.* 2010; Mouquet *et al.* 2012).

Similarly, combining phylogenetic information with species interaction patterns, such as those of food webs, can indicate the degree to which phylogenies shape interaction networks (Elias, Fontaine & van Veen 2013). Moreover, it could also reveal the extent to which interacting organisms occupy corresponding positions in their phylogenetic trees and how this is affected by environmental drivers. For example, recent research has shown that genetically similar consumers are more likely to feed on genetically similar prey when exposed to warmer temperatures (Lavandero & Tylianakis 2013), suggesting that anthropogenic disturbances could affect the strength of interactions among species and hence drive prey resource specialization (Schemske *et al.* 2009; Lavandero & Tylianakis 2013).

Such congruence among interacting species' phylogenies can be expressed as the degree to which interactions are non-random with respect to their relatedness, which can be interpreted as a co-evolutionary signal within consumer–prey food webs (Brooks 1979; Legendre, Desdevises & Bazin 2002). This signal illuminates not only the evolutionary history of the system, but also the potential cascading effects of changes in the presence or abundance of species within the food web, such as those occurring after species loss (Stork & Lyal 1993; Moir *et al.* 2011), and can be used to predict novel consumer–resource interactions (Ives & Godfray 2006).

We evaluate how phylogenetic composition at three different trophic levels is affected by one of the greatest drivers of biodiversity loss: land-use change (Sala *et al.* 2000). Specifically, because habitat edges are a key factor influencing communities in fragmented ecosystems (Ries *et al.* 2004), we measure changes to phylogenetic relationships within quantitative plant–herbivore–parasitoid food webs across an edge gradient between non-native plantation forests and native forest. We hypothesize that

1. Phylogenetic diversity of plant communities will decrease across edges from native to plantation forest, because disturbed monoculture plantations, and the few species that naturally colonize them, should comprise a subset of the species pool available in adjacent native forest. Further, we hypothesize that this reduced niche availability (Dinnage *et al.* 2012) will cascade up to herbivores and parasitoids.
2. Interactions among adjacent trophic levels will show phylogenetic congruence, such that related consumer species feed on related resource species. This could occur due to co-evolution of interacting consumer–resource groups.
3. Moreover, because species in native forest have had more time to co-evolve than have assemblages recently created by mixing native and non-native species, habitat edges and plantations of non-native trees will tend to have fewer phylogenetically congruent species interactions (i.e. weaker co-evolutionary signal) than native forests. Furthermore, generalist species are more common in modified habitats and at habitat edges (Fagan, Cantrell & Cosner 1999; Wimp *et al.* 2011), which could also weaken the signal of consumer–resource co-evolution.

Materials and methods

STUDY REGION AND SYSTEM

Our study sites were located in the Nelson and Marlborough area (172°47′E to 173°53′E and 41°12′S to 41°33′S), New Zealand.

The region is characterized by remnant native southern beech forest (*Nothofagus* spp., Fagaceae) interspersed within plantation forests (mostly non-native *Pinus radiata* plantations), so that edges between these two forest types are ubiquitous across the landscape (for more details on the study region, see Peralta *et al.* 2014a). We selected eight sites, each characterized by an edge gradient (*c.* 1 km long) from native temperate forest into pine plantation forest. All the plantation forests chosen were closed canopy monocultures of *P. radiata*, 19–26 years old. The minimum distance between sites was at least 2·7 km (maximum distance 94·6 km), that is nearly three times the distance between sampling plots within an edge gradient.

Our study system comprised plant–herbivore and herbivore–parasitoid food webs, as herbivory and parasitism are two common ecological processes in both natural and managed systems. We focused on Lepidoptera larvae (caterpillars) as herbivores because they can have a considerable impact on plant productivity (MacLean 1984; Straw 1996), and their taxonomic diversity is known to increase with plant phylogenetic diversity (Dinnage *et al.* 2012). At the same time, as relatively specialized consumers, parasitoids can exert strong regulation over Lepidoptera densities (Mills & Wajnberg 2008; Pennisi 2010) and thus represent important biological control agents.

SAMPLING

We established four sampling plots per site (across the edge gradient): one in the native forest interior, one in the plantation forest interior and one at the edge of each forest type (i.e. 32 sampling plots in total) (Fig. S1, Supporting Information). The edge sampling plots were 10 m from the centre of the edge zone towards the forest interior (with the centre of the edge zone considered to be the last row of pine trees of the plantation forest), and the interior plots were 400–500 m from the centre of the edge zone or any other edge of the forest patch. In each sampling plot, we established a 50 × 2 m transect parallel to the edge. We identified all plant species along the transect, up to 2 m height, and beat them over white sheets to collect fallen caterpillars. Every 5 m along each transect (i.e. at 10 points), we also collected canopy samples of the nearest accessible tree by clipping off branches up to 9 m height and then beating them over the sheets.

Each plot was sampled once per month during the 2009–2010 and 2010–2011 southern hemisphere summers (seven monthly samples in total). We pooled monthly samples for each of the 32 sampling plots, because sampling dates were not independent replicates of either forest type or location (edge vs. interior), which were our variables of interest here. To estimate the plant biomass sampled, we counted the number of leaves beaten per plant species on each transect and then multiplied this number by the average leaf mass per species (Appendix S1, Supporting Information).

We took all caterpillars to the laboratory to be identified to species or morphospecies, and reared them under controlled ambient conditions, until they either became adults or parasitoids emerged. Once parasitoids emerged, we identified them to species or morphospecies. For the morphospecies (hereafter 'species') of Lepidoptera and their parasitoids, specimens were identified at least to genus level according to current taxonomic classification, though some species are still undescribed (Appendix S1, Supporting Information). Specimens were identified based on their morphology, except for parasitoids, which were also identified using molecular barcoding when species-level identification was not possible using only morphology (e.g. for males when keys apply only to females, or for cryptic species). For molecular identification, specimens were sequenced for a region of the mitochondrial cytochrome *c* oxidase subunit I (COI) gene (Appendix S1, Supporting Information), as used previously for parasitoid identification in other studies (Kaartinen *et al.* 2010).

PHYLOGENIES AND PHYLOGENETIC DIVERSITY METRICS

We constructed an ultrametric phylogeny per trophic level. We used published phylogenies for plants (Webb & Donoghue 2005), and gene sequences obtained from GenBank (Benson *et al.* 2005) for herbivores or field samples for parasitoids (Appendix S1, Table S1, Supporting Information).

To determine the phylogenetic community composition of plants, herbivores and parasitoids, we selected two metrics (Helmus *et al.* 2007) (Appendix S1, Supporting Information). The first metric, phylogenetic species variability (PSV), measures the phylogenetic variability contained in a community, ranging from zero to one, and is highest when all species are equally distant to a common ancestor. The second metric, phylogenetic species evenness (PSE), measures both phylogenetic and species evenness, and equals PSV if all species have the same abundance (Helmus *et al.* 2007). We used Monte Carlo rarefaction for calculating both metrics with the phyloRarefy function (Bennet 2013) in R, so that differences in phylogenetic diversity would not be confounded by differences in sampling effort between sites.

ANALYSES

Phylogenetic diversity across a habitat edge gradient

To test for differences in phylogenetic diversity at each trophic level across the habitat edge gradient, we used generalized linear mixed-effects models (GLMMs) with the lmer function of the LME4 package (Bates *et al.* 2014) in the R 3.0.2 environment (R Core Team 2013). We used the phylogenetic diversity metrics for each trophic level (i.e. plant, herbivore and parasitoid PSV and PSE) as response variables, and forest type (native vs. plantation), location (edge vs. interior) and their interaction as fixed predictors. We also incorporated sampling plot nested within site as random factors to account for the non-independence of samples within a site. We used a Gaussian error distribution and checked for homoscedasticity and normality of residuals in all cases. We began with a full model, which we then simplified by removing interactions and then main effects until no further reduction in residual deviance was achieved, as measured by the Akaike Information Criterion (AIC). Because parasitoid abundance can depend on the abundance of their host herbivores (Fenoglio *et al.* 2012), we included herbivore abundance as a covariate in the parasitoid models (Gotelli & Colwell 2001). For the same reason, we included plant biomass as a covariate in the herbivore models. All the covariates were included first in the model (i.e. before all the other fixed terms).

We then repeated these models, but used as response variables phylogenetic diversity metrics (PSV and PSE), for plants and parasitoids, calculated only from native species (Appendix S3, Supporting Information). Herbivore phylogenetic metrics were calculated only from native herbivore species, because the

number of non-native herbivores was very low and they were only located in a few sampling plots, so their impact on the community was too small to warrant separate analysis.

As a baseline for comparison with the phylogenetic diversity metrics, we also tested for differences in species richness and abundance of each trophic level across the habitat edge gradient. For this purpose, we used GLMMs with the same predictors and random factors as explained above (Appendix S2, Supporting Information).

Phylogenetic congruence and co-evolutionary signal across habitats

To determine whether related species of consumers fed on related resource species, we analysed the degree of phylogenetic congruence in the plant–herbivore and herbivore–parasitoid regional food webs. To accomplish this, we pooled all samples from the 32 sampling plots to form a regional data set (to maximize sample size and detection of possible trophic links) defined by trophic level, and we used the ParaFit test (Legendre, Desdevises & Bazin 2002) from the ape package (Paradis, Claude & Strimmer 2004) in R. We performed four ParaFit tests, one for all the plant–herbivore interactions, one for all the herbivore–parasitoid interactions, one for native plant–herbivore interactions and one for native herbivore–parasitoid interactions. The test included a phylogeny for each of the interacting trophic levels and a consumer × resource species interaction matrix, comprising the feeding interactions we recorded in our samples. The null hypothesis of the ParaFit test is that consumers utilize resource species randomly with respect to the resource phylogenetic tree (Appendix S1, Supporting Information). Rejection of the null hypothesis indicates that interactions among trophic levels are phylogenetically correlated. *P*-values were obtained by randomization of the resource–consumer interactions (9999 permutations) and comparison of the randomized test statistic with that observed in our empirical food webs (Legendre, Desdevises & Bazin 2002).

Some consumer–resource interactions could contribute more to the phylogenetic congruence pattern and, hence, have a stronger signal of co-evolution than others. Therefore, after testing for overall congruence in the regional food web, we identified interactions between species that occupy corresponding positions in the phylogenies (i.e. those that contributed to the co-evolutionary signal) by using the ParaFitLink2 test (Legendre, Desdevises & Bazin 2002) (Appendix S1, Supporting Information). We tested whether the proportion of either total interactions (i.e. parasitism events) or unique consumer–resource links (i.e. trophic interactions among a pair of species) with a co-evolutionary signal changed across habitats. Each unique trophic interaction was defined as a resource–consumer combination (a given consumer species feeding on a given resource species). We used separate GLMMs for each response variable, with a binomial error distribution, and forest type, location (edge/interior), and the forest type × location interaction as predictors. We also included resource abundance as a covariate (entered first in the model, before the fixed terms) and plots nested within sites as random factors to account for their non-independence. We checked for overdispersion and performed model selection as explained in the first section of analyses.

Results

We constructed plant, herbivore and parasitoid phylogenies (Fig. S2, Supporting Information) based on 89, 39 and 36 taxa, respectively. We also determined between these taxa 5322 plant–herbivore interactions and 535 herbivore–parasitoid interactions across all forest types and edge vs. interior locations, which we used for determining phylogenetic diversity and testing phylogenetic congruence between consumer and resource species.

PHYLOGENETIC DIVERSITY ACROSS A HABITAT EDGE GRADIENT

Plant phylogenetic variability (PSV) was significantly higher in the edge of native forest than in the native forest interior ($t = 3{\cdot}31$, $P = 0{\cdot}005$), though this edge effect did not occur in the plantation forest (interaction term: $t = -4{\cdot}54$, $P < 0{\cdot}001$), when considering both native and non-native species (Table S4, Supporting Information, Fig. 1). However, when considering only native species, the native edge effect was marginally non-significant

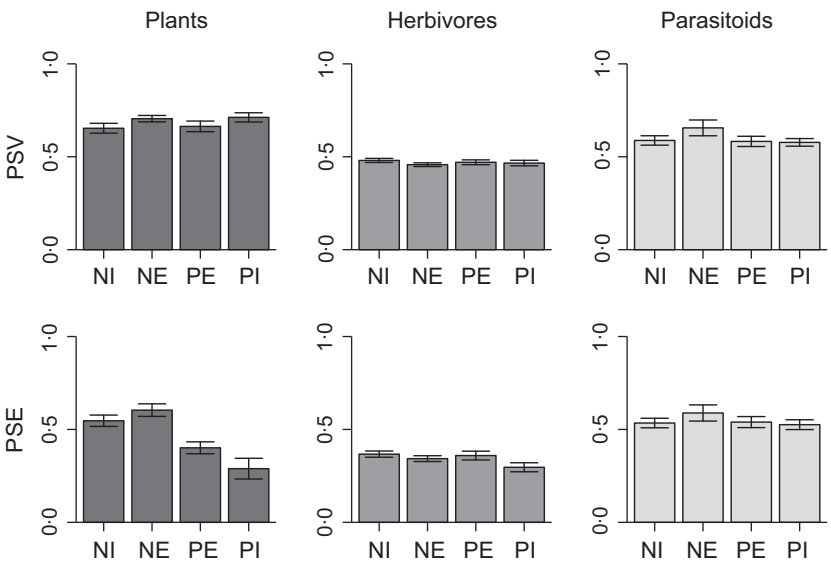

Fig. 1. Mean and SE phylogenetic diversity (including native and non-native species) of different trophic levels (plants, herbivores and parasitoids) across a habitat gradient from native forest interior (NI), through native edge (NE) and plantation edge (PE), to plantation forest interior (PI). PSV, phylogenetic species variability; PSE, phylogenetic species evenness.

($t = 2{\cdot}01$, $P = 0{\cdot}056$), though the negative forest type × edge interaction remained significant (interaction term: $t = -3{\cdot}58$, $P = 0{\cdot}003$) (Appendix S3, Table S3, Fig. S4, Supporting Information). Together, this suggests that differences in plant PSV between interior and edge locations in native forest were largely driven by the presence of distantly related non-native species.

Congruent with PSV, plant PSE was significantly higher in edge than in interior of both native and plantation forest (edge effect: $t = 2{\cdot}49$, $P = 0{\cdot}021$, forest type × edge interaction was removed from best-fitting model), but lower in interior plantation than in native forest interior ($t = -6{\cdot}77$, $P < 0{\cdot}001$) when including non-native plant species (Table S4, Supporting Information, Fig. 1). However, when only considering native plant species, plant PSE did not differ across forest types ($t = -1{\cdot}57$, $P = 0{\cdot}140$), and the edge vs. interior location term was not retained in the best-fitting model (Table S3, Fig. S4, Supporting Information). This suggests that the relative distribution of biomass among different lineages of native plants was relatively even across the habitat edge gradient, even though the addition of non-native species increased phylogenetic evenness at native forest edge (by introducing new species of relatively low, but even abundance), as it did with PSV. In plantation forest interiors, these non-native species were less evenly distributed, causing a decrease in PSE.

In contrast to plants, we found no differences in herbivore PSV across the habitat edge gradient (Table S4, Supporting Information, Fig. 1). However, herbivore PSE was lower in the plantation than in the native forest interior ($t = -2{\cdot}65$, $P = 0{\cdot}018$) and lower in the plantation interior than in the plantation edge (Table S4, Supporting Information, Fig. 1). No differences were found between edge and interior locations within the native forest ($t = -1{\cdot}20$, $P = 0{\cdot}252$) (Table S4, Supporting Information, Fig. 1). This suggests that even though plantations harbour more herbivore individuals than native forest interiors (Table S2, Fig. S3, Supporting Information), they nevertheless have less evenly distributed abundances between the different lineages.

For the parasitoids, we found that PSV did not change between edge and interior locations ($t = 1{\cdot}19$, $P = 0{\cdot}242$) nor was forest type retained in the best-fitting model (Table S4, Supporting Information, Fig. 1). However, when considering only native parasitoid species, we found that PSV was lower in interior forests than in edges ($t = 3{\cdot}50$, $P = 0{\cdot}002$) (Table S3, Fig. S4, Supporting Information), which suggests that the native parasitoid species present in habitat edges are distantly related.

Similarly to parasitoid PSV, parasitoid PSE did not change between edge and interior locations ($t = 1{\cdot}01$, $P = 0{\cdot}322$), nor was forest type retained in the best-fitting model when considering both native and non-native parasitoid species (Table S4, Supporting Information, Fig. 1). Nevertheless, when considering only native parasitoid species, parasitoid PSE was higher in edges compared to interior habitats ($t = 3{\cdot}51$, $P = 0{\cdot}002$) (Table S3, Fig. S4, Supporting Information). Furthermore, we found that parasitoid species richness both including and excluding non-native species did not change across a habitat edge gradient (Table S2, Fig. S3, Supporting Information) and that parasitism by native species was higher in plantation compared to native forest ($Z = 2{\cdot}49$, $P = 0{\cdot}013$), but did not change between edge and interior locations (Table S2, Supporting Information). This suggests that phylogenetic diversity captured changes in community composition that neither species richness nor abundance could detect.

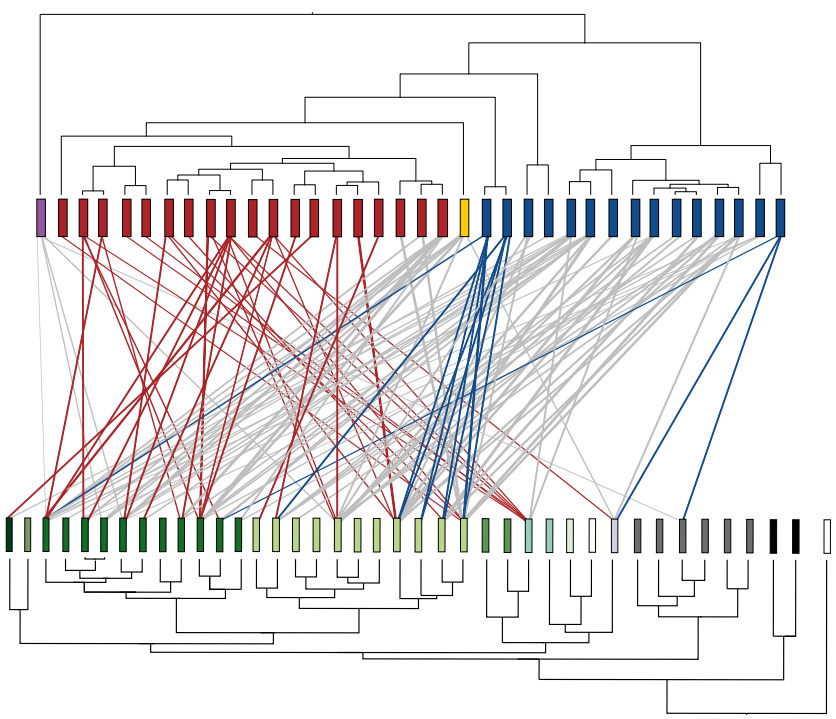

Fig. 2. Herbivore–parasitoid food web and phylogenetic congruence between native herbivore and parasitoid species (i.e. related native parasitoid species feed on related herbivore species). The top and bottom rectangles represent parasitoid and herbivore species, respectively, with different colours indicating different families. Links connecting herbivore and parasitoid species indicate a parasitism event. Coloured links are those between native parasitoid and herbivore species, coloured according to parasitoid family. Phylogenetic trees were constructed from two gene sequences, nuclear Wgl and mitochondrial cytochrome *c* oxidase subunit I (COI) for herbivores, and 28s ribosomal and mitochondrial COI for parasitoids.

PHYLOGENETIC CONGRUENCE

We found no evidence that closely related herbivore species tended to feed on closely related plant species ($P = 0{\cdot}421$, Fig. S5, Supporting Information), even when considering only native plant and herbivore species ($P = 0{\cdot}835$). Because this global test of congruence was not significant, only highly significant individual interactions should be considered for further testing changes in co-evolutionary signal across a habitat edge (Legendre, Desdevises & Bazin 2002), and none of the plant–herbivore interactions met this criterion.

On the other hand, when considering herbivore and parasitoid species (both native and non-native), more closely related parasitoid species did not tend to attack more closely related herbivore species ($P = 0{\cdot}256$, Fig. 2). However, closely related native parasitoid species tended to attack closely related herbivore species ($P = 0{\cdot}0004$, Fig. 2), which can be interpreted as a signal of co-evolution. We also found a significantly greater proportion of total native interactions with co-evolutionary signal, that is parasitism events by native parasitoids ($Z = 3{\cdot}23$, $P = 0{\cdot}001$), in plantation than in native forests (Table S5, Supporting Information, Fig. 3), although there were no differences in the proportion of unique native herbivore–parasitoid links with co-evolutionary signal across forest types ($Z = 1{\cdot}52$, $P = 0{\cdot}129$) (Fig. 3). This suggests that the frequency of native herbivore–parasitoid links that most contribute to the phylogenetic congruence of the food web (i.e. phylogenetic signal) can be affected by habitat fragmentation.

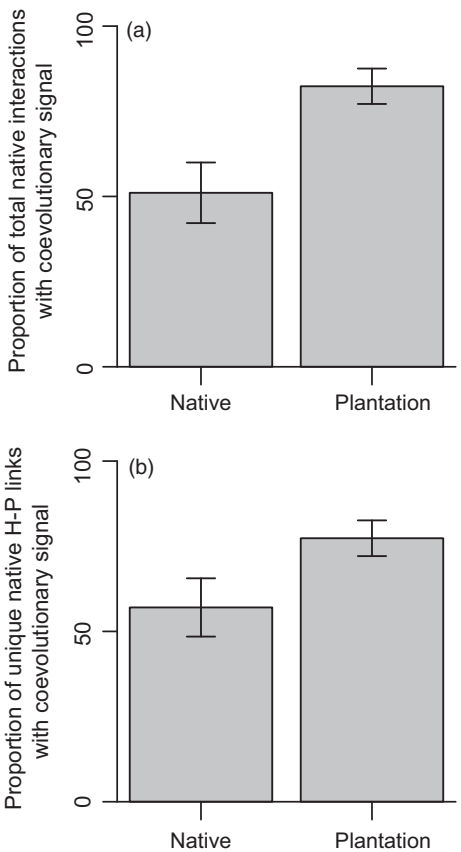

Fig. 3. Mean and SE of the (a) proportion of total native interactions (i.e. parasitism events, $N = 221$) with co-evolutionary signal and (b) proportion of unique native H-P (herbivore–parasitoid) links (i.e. pairwise trophic interactions, $N = 48$) with co-evolutionary signal, across forest types (native vs. plantation).

Discussion

Anthropogenic land-use change dramatically disrupts ecological and evolutionary relationships among organisms (Leimu *et al.* 2012). Here, we not only found that patterns of phylogenetic diversity varied significantly across the edge between managed and natural forests, but also that co-evolutionary signals changed in a manner that differed across trophic levels.

PHYLOGENETIC DIVERSITY ACROSS A HABITAT EDGE GRADIENT

Trophic levels differed in how their phylogenetic diversity responded to the edge gradient. For the plant community, we found that phylogenetic evenness (PSE) was lower in plantation interiors than in native forest interiors, although not when considering only native species. This was perhaps not surprising, given that plantation forests were composed mainly of one planted species (*P. radiata* in this case) and, even though there are usually few native plant species colonizing and inhabiting plantations (Keenan *et al.* 1997; Newmaster *et al.* 2006), our results suggest that the abundance of these native species is evenly distributed across clades in this managed habitat.

We also found that, as with PSE, plant phylogenetic variability (PSV, i.e. the variance of a hypothetical trait) was higher in the edge of native forest than in the interior, but this was only significant when including non-native species. Habitat edges are strongly affected by external dynamics and disturbance of the modified surroundings (Laurance 2002), which can create variable environmental conditions for plants and hence lead to higher variability of plant lineages that inhabit edges. In this case, this variability was driven by the addition of non-native species at the edges of native forest, which elevated the phylogenetic variability.

Despite the differences in PSV observed for plants, we did not observe any differences in herbivore phylogenetic variability, potentially due to lower herbivore trophic specialization (Pellissier *et al.* 2013), which would result in soft associations between specific plant and herbivore lineages and a more random distribution of herbivore lineages irrespective of the different plant communities. On the other hand, lower herbivore phylogenetic evenness in plantation interiors than in native forest could be explained by the high herbivore abundance in monoculture plantations (Jactel & Brockerhoff 2007), which are frequently dominated by few herbivore species.

Contrary to what we found for herbivores, both parasitoid phylogenetic variability and evenness were not affected by the edge gradient when considering both native and non-native species. However, when considering only native parasitoid species, parasitoid phylogenetic diversity was lower in forest interiors than in edges, suggesting that in habitat edges, ecological responses of species could be more different (Burns & Strauss 2011). In contrast to parasitoid phylogenetic diversity differences across habitats, parasitoid species richness did not change across the edge gradient. This suggests that by only looking at traditional diversity metrics, such as species richness, we might be overlooking other aspects of community composition, which could be particularly important if phylogenetic diversity provides a better representation of community traits and functional diversity (Srivastava *et al*. 2012).

PHYLOGENETIC CONGRUENCE AND CO-EVOLUTIONARY SIGNAL ACROSS HABITATS

The absence of congruence among the plant and herbivore phylogenies reinforced the idea that closely related herbivore species do not necessarily specialize on a phylogenetically limited range of plant species, but rather that they are more generalist in the resource lineages they use (but see Pellissier *et al*. 2013). This is also consistent with herbivory patterns previously observed on other large persistent plants (Fox 1981), where each plant species was eaten by a large array of herbivores. Fox (1981) proposed the term 'diffuse herbivory', to refer to the damage imposed by the herbivore assemblage on this type of plant, which should select for generalized plant defences that affect a diverse consumer guild. Such defences should not impose strong selective pressures on the herbivores, because their short generation times relative to long-lived plants would facilitate counter-adaptations. This suggests that plants respond to multiple herbivore species in both ecological and evolutionary time-scales, that is diffuse co-evolution (Janzen 1980; Fox 1981), rather than pairwise evolution where selection pressures exerted by a particular herbivore on a plant species are not affected by the presence/absence of other herbivore species (Hougen-Eitzman & Rausher 1994). It has been suggested that whether co-evolution is pairwise or diffuse depends on the trophic specialization of herbivores (Leimu & Koricheva 2006), and in the case of temperate forest Lepidoptera, it is not entirely surprising that we found no co-evolutionary signal between plants and herbivores.

In contrast to the plant–herbivore food web, we found significant phylogenetic congruence among interacting native herbivores (hosts) and native parasitoids, which can be understood from their life history. These endoparasitoids have an intimate relationship with their hosts, because their larval stage lives inside the host (Askew & Shaw 1986) and has to overcome its immune system (Vinson 1990). Therefore, close associations among host and parasitoid phylogenetic groups might well be expected. Furthermore, because both hosts and parasitoids have similarly short generation times, this may increase the possibility of detecting co-evolutionary changes (Bouletreau 1986), although non-native parasitoid species introduced in New Zealand may have not had enough time yet to co-evolve with herbivore species. Native herbivore–parasitoid combinations whose interactions contributed the most to the pattern of phylogenetic congruence were more abundant in plantations than in native forests. This stronger co-evolutionary signal in plantation forests suggests that parasitoids in disturbed habitats may only be able to utilize hosts that they have best evolved to attack. Analogously, climate warming has been shown to reduce the niche breadth plasticity of parasitoids (Lavandero & Tylianakis 2013), suggesting that different environmental changes could reduce the ability of parasitoid communities to suppress a broad range of host species and genotypes in natural systems and biological control programmes.

Conclusions

Overall, our results demonstrate that land-use change can alter not only species diversity, but also phylogenetic diversity and patterns of co-evolutionary relationships among species. These changes have potentially profound implications for ecosystem functioning and stability and may alter the relative ability of different trophic levels to adapt to change.

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Data accessibility

Data available from the Dryad Digital Repository http://doi.org/10.5061/dryad.t5557 (Peralta *et al*. 2014b).

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Supporting Information

Additional Supporting Information may be found in the online version of this article.

Appendix S1. Supplementary methods.

Appendix S2. Species richness and abundance across a habitat edge gradient.

Appendix S3. Phylogenetic diversity of native species.

Table S1. GenBank herbivore and parasitoid sequence accession numbers.

Table S2. Coefficient tables to determine changes in the species richness and abundance of plants, herbivores and parasitoids across a habitat edge gradient.

Table S3. Coefficient tables showing differences in phylogenetic diversity of native plants and parasitoids across a habitat edge gradient.

Table S4. Coefficient tables to determine changes in community phylogenetic diversity of different trophic levels across habitats.

Table S5. Coefficient tables for testing whether the proportion of total native interactions (i.e. parasitism events) and proportion of unique native herbivore–parasitoid links with co-evolutionary signal changed across forest types.

Fig. S1. Schematic diagram of each sampling site.

Fig. S2. Plant, herbivore and parasitoid phylogenies.

Fig. S3. Species richness and abundance of plants, herbivores and parasitoids across a habitat edge gradient.

Fig. S4. Phylogenetic diversity of native plants and parasitoids across a habitat edge gradient.

Fig. S5. Plant–herbivore food web.