

1 **Phylogenetic diversity and coevolutionary signals among trophic**
2 **levels change across a habitat edge**

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26 **Summary**

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

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

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

43 **4.** We found differences across trophic levels in how their phylogenetic diversity
44 responded to the habitat edge gradient. Plant and native parasitoid phylogenetic
45 diversity changed markedly across habitats, while phylogenetic variability of
46 herbivores (which were predominantly native) did not change across habitats, though
47 phylogenetic evenness declined in plantation interiors. Related herbivore species did
48 not appear to feed disproportionately on related plant species (i.e. there was no signal
49 of coevolution) even when considering only native species, potentially due to the high

50 trophic generality of herbivores. However, related native parasitoid species tended to
51 feed on related herbivore species, suggesting the presence of a coevolutionary signal
52 at higher trophic levels. Moreover, this signal was stronger in plantation forests,
53 indicating that this habitat may impose stresses on parasitoids that constrain them to
54 attack only host species for which they are best adapted.

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

58

59 **Introduction**

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

67 The phylogenetic information in a community can be summarized using
68 metrics analogous to the traditional measures of diversity, such as species richness
69 and evenness (Helmus *et al.* 2007; Schweiger *et al.* 2008; Cadotte *et al.* 2010),
70 thereby providing a fuller representation of community trait and functional diversity
71 than does taxonomic diversity alone (Srivastava *et al.* 2012). Phylogenetic diversity
72 has therefore been used to describe and understand community composition and
73 impacts on ecosystem processes, e.g. in plant communities it has been found to
74 increase biomass (Cadotte, Cardinale & Oakley 2008; Connolly *et al.* 2011) by

75 increasing niche complementarity. Furthermore, phylogenetic diversity of a lower
76 trophic level has been found to correlate positively with species richness of upper
77 trophic levels, by providing more habitat niches and/or more biomass (Dinnage *et al.*
78 2012).

79 Understanding how phylogenetic diversity changes in space and across trophic
80 levels may also allow the conservation of evolutionary information, an often-
81 neglected component of biodiversity (Vane-Wright 1992; Devictor *et al.* 2010;
82 Winter, Devictor & Schweiger 2013). In fact, recent research has found that climate
83 change and human disturbance can reduce the phylogenetic diversity of plant
84 communities (Knapp *et al.* 2008; Willis *et al.* 2008; Dinnage 2009), suggesting that
85 anthropogenic change might ‘select’ only certain closely-related species to
86 survive (Srivastava *et al.* 2012). Combined with the bottom-up effects of phylogenetic
87 diversity on higher trophic levels (Dinnage *et al.* 2012), this suggests that
88 phylogenetic approaches could help ecologists to predict the composition and
89 distributional responses of interrelated communities to global changes (Lavergne *et al.*
90 2010; Mouquet *et al.* 2012).

91 Similarly, combining phylogenetic information with species interaction
92 patterns, such as those of food webs, can indicate the degree to which phylogenies
93 shape interaction networks (Elias, Fontaine & van Veen 2013). Moreover, it could
94 also reveal the extent to which interacting organisms occupy corresponding positions
95 in their phylogenetic trees and how this is affected by environmental drivers. For
96 example, recent research has shown that genetically-similar consumers are more
97 likely to feed on genetically-similar prey when exposed to warmer temperatures
98 (Lavandero & Tylianakis 2013), suggesting that anthropogenic disturbances could

99 affect the strength of interactions among species and hence drive prey resource
100 specialization (Schemske *et al.* 2009; Lavandero & Tylianakis 2013).

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

109 We evaluate how phylogenetic composition at three different trophic levels is
110 affected by one of the greatest drivers of biodiversity loss: land-use change (Sala *et al.*
111 2000). Specifically, because habitat edges are a key factor influencing communities in
112 fragmented ecosystems (Ries *et al.* 2004), we measure changes to phylogenetic
113 relationships within quantitative plant-herbivore-parasitoid food webs across an edge
114 gradient between non-native plantation forests and native forest. We hypothesize that:

- 115 1) Phylogenetic diversity of plant communities will decrease across edges from
116 native to plantation forest, because disturbed monoculture plantations, and the
117 few species that naturally colonise them, should comprise a subset of the
118 species pool available in adjacent native forest. Further, we hypothesize that
119 this reduced niche availability (Dinnage *et al.* 2012) will cascade up to
120 herbivores and parasitoids.
- 121 2) Interactions among adjacent trophic levels will show phylogenetic congruence,
122 such that related consumer species feed on related resource species. This could
123 occur due to coevolution of interacting consumer-resource groups.

124 3) Moreover, because species in native forest have had more time to coevolve
125 than have assemblages recently created by mixing native and non-native
126 species, habitat edges and plantations of non-native trees will tend to have
127 fewer phylogenetically-congruent species interactions (i.e. weaker
128 coevolutionary signal) than native forests. Furthermore, generalist species are
129 more common in modified habitats and at habitat edges (Fagan, Cantrell &
130 Cosner 1999; Wimp *et al.* 2011), which could also weaken the signal of
131 consumer-resource coevolution.

132

133 **Methods**

134 **STUDY REGION AND SYSTEM**

135 Our study sites were located in the Nelson and Marlborough area (172°47'E to
136 173°53'E and 41°12'S to 41°33'S), New Zealand. The region is characterized by
137 remnant native southern beech forest (*Nothofagus spp.*, Fagaceae) interspersed within
138 plantation forests (mostly non-native *Pinusradiata* plantations), so that edges between
139 these two forest types are ubiquitous across the landscape (for more details on the
140 study region see Peralta *et al.* 2014). We selected eight sites, each characterised by an
141 edge gradient (ca. 1 km long) from native temperate forest into pine plantation forest.
142 All the plantation forests chosen were closed-canopy monocultures of *Pinusradiata*,
143 19-26 years old. The minimum distance between sites was at least 2.7 km (maximum
144 distance 94.6 km), i.e. nearly three times the distance between sampling plots within
145 an edge gradient.

146 Our study system comprised plant-herbivore and herbivore-parasitoid food
147 webs, as herbivory and parasitism are two common ecological processes in both
148 natural and managed systems. We focused on Lepidoptera larvae (caterpillars) as

149 herbivores because they can have a considerable impact on plant productivity
150 (MacLean 1984; Straw 1996), and their taxonomic diversity is known to increase with
151 plant phylogenetic diversity (Dinnage *et al.* 2012). At the same time, as relatively
152 specialized consumers, parasitoids can exert strong regulation over Lepidoptera
153 densities (Mills & Wajnberg 2008; Pennisi 2010), and thus represent important
154 biological control agents.

155

156 SAMPLING

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

169 Each plot was sampled once per month during the 2009-2010 and 2010-2011
170 southern-hemisphere summers (seven monthly samples in total). We pooled monthly
171 samples for each of the 32 sampling plots, because sampling dates were not
172 independent replicates of either forest type or location (edge vs. interior), which were
173 our variables of interest here. To estimate the plant biomass sampled, we counted the

174 number of leaves beaten per plant species on each transect and then multiplied this
175 number by the average leaf mass per species (Appendix S1).

176 We took all caterpillars to the lab to be identified to species or morphospecies,
177 and reared them under controlled-ambient conditions, until they either became adults
178 or parasitoids emerged. Once parasitoids emerged, we identified them to species or
179 morphospecies. For the morphospecies (hereafter ‘species’) of Lepidoptera and their
180 parasitoids, specimens were identified at least to genus level according to current
181 taxonomic classification, though some species are still undescribed (Appendix S1).
182 Specimens were identified based on their morphology, except for parasitoids, which
183 were also identified using molecular barcoding when species level identification was
184 not possible using only morphology (e.g., for males when keys apply only to females,
185 or for cryptic species). For molecular identification, specimens were sequenced for a
186 region of the mitochondrial cytochrome C oxidase subunit I (COI) gene (Appendix
187 S1), as used previously for parasitoid identification in other studies (Kaartinen *et al.*
188 2010).

189

190 PHYLOGENIES AND PHYLOGENETIC DIVERSITY METRICS

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

195 To determine the phylogenetic community composition of plants, herbivores
196 and parasitoids, we selected two metrics (Helmus *et al.* 2007) (Appendix S1). The
197 first metric, phylogenetic species variability (PSV), measures the phylogenetic
198 variability contained in a community, ranging from zero to one, and is highest when

199 species are equally distant to a common ancestor. The second metric, phylogenetic
200 species evenness (PSE), measures both phylogenetic and species evenness, and equals
201 PSV if all species have the same abundance (Helmus *et al.* 2007). We used Monte-
202 Carlo rarefaction for calculating both metrics with the phyloRarefy function (Bennet
203 2013) in R, so that differences in phylogenetic diversity would not be confounded by
204 differences in sampling effort between sites.

205

206 ANALYSES

207 *Phylogenetic diversity across a habitat edge gradient*

208 To test for differences in phylogenetic diversity at each trophic level across the
209 habitat edge gradient, we used generalized linear mixed-effects models (GLMMs)
210 with the lmer function of the lme4 package (Bates *et al.* 2014) in the R 3.0.2
211 environment (Team 2013). We used the phylogenetic diversity metrics for each
212 trophic level (i.e. plant, herbivore and parasitoid PSV and PSE) as response variables,
213 and forest type (native vs. plantation), location (edge vs. interior) and their interaction
214 as fixed predictors. We also incorporated sampling plot nested within site as random
215 factors to account for the non-independence of samples within a site. We used a
216 Gaussian error distribution, and checked for homoscedasticity and normality of
217 residuals in all cases. We began with a full model, which we then simplified by
218 removing interactions then main effects until no further reduction in residual
219 deviance was achieved, as measured by the Akaike Information Criterion (AIC).
220 Because parasitoid abundance can depend on the abundance of their host herbivores
221 (Fenoglio *et al.* 2012), we included herbivore abundance as a covariate in the
222 parasitoid models (Gotelli & Colwell 2001). For the same reason, we included plant

223 biomass as a covariate in the herbivore models. All the covariates were included first
224 in the model (i.e. before all the other fixed terms).

225 We then repeated these models, but used as response variables phylogenetic
226 diversity metrics (PSV and PSE), for plants and parasitoids, calculated only from
227 native species (Appendix S3). Herbivore phylogenetic metrics were calculated only
228 from native herbivore species, because the number of non-native herbivores was very
229 low and they were only located in a few sampling plots, so their impact on the
230 community was too small to warrant separate analysis.

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

235

236 *Phylogenetic congruence and coevolutionary signal across habitats*

237 To determine whether related species of consumers fed on related resource
238 species, we analyzed the degree of phylogenetic congruence in the plant-herbivore
239 and herbivore-parasitoid regional food webs. To accomplish this, we pooled all
240 samples from the 32 sampling plots to form a regional dataset (to maximize sample
241 size and detection of possible trophic links) defined by trophic level, and we used the
242 ParaFit test (Legendre, Desdevises & Bazin 2002) from the ape package (Paradis,
243 Claude & Strimmer 2004) in R. We performed four ParaFit tests, one for all the plant-
244 herbivore interactions, one for all the herbivore-parasitoid interactions, one for native
245 plant-herbivore interactions and one for native herbivore-parasitoid interactions. The
246 test included a phylogeny for each of the interacting trophic levels and a consumer x
247 resource species interaction matrix, comprising the feeding interactions we recorded

248 in our samples. The null hypothesis of the ParaFit test is that consumers utilize
249 resource species randomly with respect to the resource phylogenetic tree (Appendix
250 S1). Rejection of the null hypothesis indicates that interactions among trophic levels
251 are phylogenetically correlated. P-values were obtained by randomization of the
252 resource-consumer interactions (9,999 permutations) and comparison of the
253 randomized test statistic with that observed in our empirical food webs (Legendre,
254 Desdevises & Bazin 2002).

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

272

273 **Results**

274 We constructed plant, herbivore and parasitoid phylogenies (Fig. S2) based on
275 89, 39 and 36 taxa respectively. We also determined between these taxa 5,322 plant-
276 herbivore interactions and 535 herbivore-parasitoid interactions across all forest types
277 and edge vs. interior locations, which we used for determining phylogenetic diversity
278 and testing phylogenetic congruence between consumer and resource species.

279

280 PHYLOGENETIC DIVERSITY ACROSS A HABITAT EDGE GRADIENT

281 Plant phylogenetic variability (PSV) was significantly higher in the edge of
282 native forest than in the native forest interior ($t = 3.31$, $P = 0.005$), though this edge
283 effect did not occur in the plantation forest (interaction term: $t = -4.54$, $P < 0.001$),
284 when considering both native and non-native species (Table S4, Fig. 1). However,
285 when considering only native species, the native edge effect was marginally non-
286 significant ($t = 2.01$, $P = 0.056$), though the negative forest type x edge interaction
287 remained significant (interaction term: $t = -3.58$, $P = 0.003$) (Appendix S3, Table S3,
288 Fig. S4). Together, this suggests that differences in plant PSV between interior and
289 edge locations in native forest were largely driven by the presence of distantly-related
290 non-native species.

291 Congruent with PSV, plant phylogenetic species evenness (PSE) was
292 significantly higher in edge than interior of both native and plantation forest (edge
293 effect: $t = 2.49$, $P = 0.021$, forest type x edge interaction was removed from best-
294 fitting model), but lower in interior plantation than in native forest interior ($t = -6.77$,
295 $P < 0.001$) when including non-native plant species (Table S4, Fig. 1). However,
296 when only considering native plant species, plant PSE did not differ across forest
297 types ($t = -1.57$, $P = 0.140$), and the edge vs. interior location term was not retained in

298 the best-fitting model (Table S3, Fig. S4). This suggests that the relative distribution
299 of biomass among different lineages of native plants was relatively even across the
300 habitat edge gradient, even though the addition of non-native species increased
301 phylogenetic evenness at native forest edge (by introducing new species of relatively
302 low, but even abundance), as it did with PSV. In plantation forest interiors, these non-
303 native species were less evenly distributed, causing a decrease in PSE.

304 In contrast to plants, we found no differences in herbivore PSV across the
305 habitat edge gradient (Table S4, Fig. 1). However, herbivore PSE was lower in the
306 plantation than in the native forest interior ($t = -2.65$, $P = 0.018$), and lower in the
307 plantation interior than in the plantation edge (Table S4, Fig. 1). No differences were
308 found between edge vs. interior locations within the native forest ($t = -1.20$, $P =$
309 0.252) (Table S4, Fig. 1). This suggests that even though plantations harbor
310 more herbivore individuals than native forest interiors (Table S2, Fig. S3), they
311 nevertheless have less evenly distributed abundances between the different lineages.

312 For the parasitoids, we found that PSV did not change between edge vs.
313 interior locations ($t = 1.19$, $P = 0.242$) nor was forest type retained in the best-fitting
314 model (Table S4, Fig. 1). However, when considering only native parasitoid species,
315 we found that PSV was lower in interior forests than edges ($t = 3.50$, $P = 0.002$) (Table
316 S3, Fig. S4), which suggests that the native parasitoid species present in habitat edges
317 are distantly related.

318 Similarly to parasitoid PSV, parasitoid PSE did not change between edge and
319 interior locations ($t = 1.01$, $P = 0.322$), nor was forest type retained in the best-fitting
320 model when considering both native and non-native parasitoid species (Table S4, Fig.
321 1). Nevertheless, when considering only native parasitoid species, parasitoid PSE was
322 higher in edges compared to interior habitats ($t = 3.51$, $P = 0.002$) (Table S3, Fig.

323 S4).Furthermore, we found that parasitoid species richness both including and
324 excluding non-native species did not change across a habitat edge gradient (Table S2,
325 Fig. S3), and that parasitism by native species was higher in plantation compared to
326 native forest ($Z = 2.49$, $P = 0.013$),but did not change between edge vs. interior
327 locations (Table S2). This suggests that phylogenetic diversity captured changes in
328 community composition that neither species richness nor abundance could detect.

329

330 PHYLOGENETIC CONGRUENCE

331 We found no evidence that closely-related herbivore species tended to feed on
332 closely-related plant species ($P = 0.421$, Fig. S5), even when considering only native
333 plant and herbivore species ($P = 0.835$). Because this global test of congruence was not
334 significant, only highly-significant individual interactions should be considered for
335 further testing changes in coevolutionary signal across a habitat edge (Legendre,
336 Desvignes & Bazin 2002), and none of the plant-herbivore interactions met this
337 criterion.

338 On the other hand, when considering herbivore and parasitoid species (both
339 native and non-native), more closely-related parasitoid species did not tend to attack
340 more closely-related herbivore species ($P = 0.256$, Fig. 2). However, closely related
341 native parasitoid species tended to attack closely related herbivore species ($P =$
342 0.0004 , Fig. 2),which can be interpreted as a signal of coevolution. We also found a
343 significantly greater proportion of total native interactions, i.e. parasitism events by
344 native parasitoids ($Z = 3.23$, $P = 0.001$),in plantation than in native forests (Table S5,
345 Fig. 3), although there were no differences in the proportion of unique native
346 herbivore-parasitoid links with coevolutionary signal across forest types ($Z = 1.52$, $P =$
347 0.129) (Fig. 3). This suggests that the frequency of native herbivore-parasitoid links

348 that most contribute to the phylogenetic congruence of the food web (i.e. phylogenetic
349 signal) can be affected by habitat fragmentation.

350

351 **Discussion**

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

357

358 PHYLOGENETIC DIVERSITY ACROSS A HABITAT EDGE GRADIENT

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

368 We also found that, as with phylogenetic species evenness (PSE), plant
369 phylogenetic variability (PSV, i.e. the variance of a hypothetical trait) was higher in
370 the edge of native forest than in the interior, but this was only significant when
371 including non-native species. Habitat edges are strongly affected by external
372 dynamics and disturbance of the modified surroundings (Laurance 2002), which can

373 create variable environmental conditions for plants and hence lead to higher
374 variability of plant lineages that inhabit edges. In this case, this variability was driven
375 by the addition of non-native species at the edges of native forest, which elevated the
376 phylogenetic variability.

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

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

397

398 PHYLOGENETIC CONGRUENCE AND COEVOLUTIONARY SIGNAL
399 ACROSS HABITATS

400 The absence of congruence among the plant and herbivore phylogenies
401 reinforced the idea that closely-related herbivore species do not necessarily specialise
402 on a phylogenetically-limited range of plant species, but rather that they are more
403 generalist in the resource lineages they use (but see Pellissier *et al.* 2013). This is also
404 consistent with herbivory patterns previously observed on other large persistent plants
405 (Fox 1981), where each plant species was eaten by a large array of herbivores. Fox
406 (1981) proposed the term ‘diffuse herbivory’, to refer to the damage imposed by the
407 herbivore assemblage on this type of plant, which should select for generalized plant
408 defenses that affect a diverse consumer guild . Such defenses should not impose
409 strong selective pressures on the herbivores, because their short generation times
410 relative to long-lived plants would facilitate counter-adaptations. This suggests that
411 plants respond to multiple herbivore species in both ecological and evolutionary
412 timescales, i.e. diffuse coevolution (Janzen 1980; Fox 1981), rather than pairwise
413 evolution where selection pressures exerted by a particular herbivore on a plant
414 species are not affected by the presence/absence of other herbivore species (Hougen-
415 Eitzman & Rausher 1994). It has been suggested that whether coevolution is pairwise
416 or diffuse depends on the trophic specialization of herbivores (Leimu & Koricheva
417 2006), and in the case of temperate forest Lepidoptera, it is not entirely surprising that
418 we found no coevolutionary signal between plants and herbivores.

419 In contrast to the plant-herbivore food web, we found significant phylogenetic
420 congruence among interacting native herbivores (hosts) and native parasitoids, which
421 can be understood from their life history. These endoparasitoids have an intimate
422 relationship with their hosts, because their larval stage lives inside the host (Askew

423 &Shaw 1986) and has to overcome its immune system (Vinson 1990). Therefore,
424 close associations among host and parasitoid phylogenetic groups might well be
425 expected. Furthermore, because both hosts and parasitoids have similarly short
426 generation times, this may increase the possibility of detecting coevolutionary
427 changes (Bouletreau 1986), although non-native parasitoid species introduced in New
428 Zealand may have not had enough time yet to coevolve with herbivore species. Native
429 herbivore-parasitoid combinations whose interactions contributed the most to the
430 pattern of phylogenetic congruence were more abundant in plantations than in native
431 forests. This stronger coevolutionary signal in plantation forests suggests that
432 parasitoids in disturbed habitats may only be able to utilise hosts that they have best
433 evolved to attack. Analogously, climate warming has been shown to reduce the niche
434 breadth plasticity of parasitoids (Lavandero & Tylianakis 2013), suggesting that
435 different environmental changes could reduce the ability of parasitoid communities to
436 suppress a broad range of host species and genotypes in natural systems and
437 biological control programmes.

438

439 CONCLUSIONS

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

445

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459

460 **Supporting Information**

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

462 **Appendix S1.** Supplementary methods.

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

464 **Appendix S3.** Phylogenetic diversity of native species.

465 **Table S1:** GenBank herbivore and parasitoid sequence accession numbers.

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

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

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

472 **Table S5:** Coefficient tables for testing whether the proportion of total native
473 interactions (i.e. parasitism events) and proportion of unique native herbivore-
474 parasitoid links with coevolutionary signal changed across forest types.
475 **Fig.S1:** Schematic diagram of each sampling site.
476 **Fig. S2:** Plant, herbivore and parasitoid phylogenies.
477 **Fig.S3:** Species richness and abundance of plants, herbivores and parasitoids across a
478 habitat edge gradient.
479 **Fig. S4:** Phylogenetic diversity of native plants and parasitoids across a habitat edge
480 gradient.
481 **Fig. S5:** Plant-herbivore food web.

482

483 **References**

484 Askew, R.R. & Shaw, M.R. (1986) *Parasitoid communities: their size, structure and*
485 *development*. Academic Press, London.
486 Bates, D., Maechler, M., Bolker, B. & Walker, S. (2014) lme4: Linear mixed-effects
487 models using Eigen and S4. R package version 1.0-6. [http://CRAN.R-](http://CRAN.R-project.org/package=lme4)
488 [project.org/package=lme4](http://CRAN.R-project.org/package=lme4).
489 Bennet, J.D. Phylogenetic
490 rarefaction. [https://github.com/DomBennett/EcoDataTools/wiki/Phylogenetic-](https://github.com/DomBennett/EcoDataTools/wiki/Phylogenetic-Rarefaction)
491 [Rarefaction](https://github.com/DomBennett/EcoDataTools/wiki/Phylogenetic-Rarefaction)
492 Benson, D.A., Karsch-Mizrachi, I., Lipman, D.J., Ostell, J. & Wheeler, D.L. (2005)
493 GenBank. *Nucleic Acids Research*, **33**, D34-D38.
494 Bouletreau, M. (1986) *The genetic and coevolutionary interactions between*
495 *parasitoids and their hosts*. Academic Press, New York.

496 Brooks, D.R. (1979) Testing the context and extend of host-parasite coevolution.
497 *Systematic Zoology*,**28**, 299-307.

498 Burns, J.H. & Strauss, S.Y. (2011) More closely related species are more ecologically
499 similar in an experimental test. *Proceedings of the National Academy of*
500 *Sciences of the United States of America*,**108**, 5302-2507.

501 Cadotte, M.W., Cardinale, B.J. & Oakley, T.H. (2008) Evolutionary history and the
502 effect of biodiversity on plant productivity. *Proceedings of the National*
503 *Academy of Sciences of the United States of America*,**105**, 17012-17017.

504 Cadotte, M.W., Davies, T.J., Regetz, J., Kembel, S.W., Cleland, E. & Oakley, T.H.
505 (2010) Phylogenetic diversity metrics for ecological communities: integrating
506 species richness, abundance and evolutionary history. *Ecology Letters*,**13**, 96-
507 105.

508 Cavender-Bares, J., Kozak, K.H., Fine, P.V.A. & Kembel, S.W. (2009) The merging
509 of community ecology and phylogenetic biology. *Ecology Letters*,**12**, 693-715.

510 Connolly, J., Cadotte, M.W., Brophy, C., Dooley, A., Finn, J. & Kirwan, L. (2011)
511 Phylogenetically diverse grasslands are associated with pairwise interspecific
512 processes that increase biomass. *Ecology*,**92**.

513 Devictor, V., Mouillot, D., Meynard, C., Jiguet, F., Thuiller, W. & Mouquet, N.
514 (2010) Spatial mismatch and congruence between taxonomic, phylogenetic
515 and functional diversity: the need for integrative conservation strategies in a
516 changing world. *Ecology Letters*,**13**, 1030-1040.

517 Dinnage, R. (2009) Disturbance alters the phylogenetic composition and structure of
518 plant communities in an old field system. *PLoS one*,**4**, e7071.

519 Dinnage, R., Cadotte, M.W., Haddad, N.M., Crutsinger, G.M. & Tilman, D. (2012)
520 Diversity of plant evolutionary lineages promotes arthropod diversity. *Ecology*
521 *Letters*,**15**, 1308-1317.

522 Elias, M., Fontaine, C. & van Veen, F.J.F. (2013) Evolutionary history and ecological
523 processes shape a local multilevel antagonistic network. *Current Biology*,**23**,
524 1355-1359.

525 Fagan, W.F., Cantrell, R.S. & Cosner, C. (1999) How habitat edges change species
526 interactions. *The American Naturalist*,**153**, 165-182.

527 Fenoglio, M.S., Srivastava, D., Valladares, G., Cagnolo, L. & Salvo, A. (2012) Forest
528 fragmentation reduces parasitism via species loss at multiple trophic levels.
529 *Ecology*,**93**, 2407-2420.

530 Fox, L.R. (1981) Defense and dynamics in plant-herbivore systems. *American*
531 *Zoologist*,**21**, 853-864.

532 Gotelli, N.J. & Colwell, R.K. (2001) Quantifying biodiversity: procedures and pitfalls
533 in the measurement and comparison of species richness. *Ecology Letters*,**4**,
534 379-391.

535 Helmus, M.R., Bland, T.J., Williams, C.K. & Ives, A.R. (2007) Phylogenetic
536 measures of biodiversity. *The American Naturalist*,**169**, E68-E83.

537 Hougen-Eitzman, D. & Rausher, M.D. (1994) Interactions between herbivorous
538 insects and plant-insect coevolution. *The American Naturalist*,**143**, 677-697.

539 Ives, A.R. & Godfray, H.C.J. (2006) Phylogenetic analysis of trophic associations.
540 *The American Naturalist*,**168**, E1-E14.

541 Jactel, H. & Brockerhoff, E.G. (2007) Tree diversity reduces herbivory by forest
542 insects. *Ecology Letters*, **10**, 835-848.

543 Janzen, D.H. (1980) When is it coevolution? *Evolution*,**34**, 611-612.

- 544 Kaartinen, R., Stone, G.N., Hearn, J., Lohse, K. & Roslin, T. (2010) Revealing secret
545 liaisons: DNA barcoding changes our understanding of food webs. *Ecological*
546 *Entomology*,**35**, 623–638.
- 547 Keenan, R., Lamb, D., Woldring, O., Irvine, T. & Jensen, R. (1997) Restoration of
548 plant biodiversity beneath tropical tree plantations in Northern Australia.
549 *Forestry Ecology and Management*,**99**, 117-131.
- 550 Knapp, S., Kühn, I., Schweiger, O. & Klotz, S. (2008) Challenging urban species
551 diversity: contrasting phylogenetic patterns across plant functional groups in
552 Germany. *Ecology Letters*,**11**, 1054-1064.
- 553 Laurance, W.F. (2002) Hyperdynamism in fragmented habitats. *Journal of Vegetation*
554 *Science*,**13**, 595-602.
- 555 Lavandero, B. & Tylianakis, J.M. (2013) Genotype matching in a parasitoid-host
556 genotypic food web: an approach for measuring effects of environmental
557 change. *Molecular Ecology*,**22**, 229-238.
- 558 Lavergne, S., Mouquet, N., Thuiller, W. & Ronce, O. (2010) Biodiversity and climate
559 change: integrating evolutionary and ecological responses of species and
560 communities. *Annual Review of Ecology, Evolution and Systematics*,**41**, 321-
561 350.
- 562 Legendre, P., Desdevises, Y. & Bazin, E. (2002) A statistical test for host-parasite
563 coevolution. *Systematic Biology*,**51**, 217-234.
- 564 Leimu, R. & Koricheva, J. (2006) A meta-analysis of genetic correlations between
565 plant resistances to multiple enemies. *The American Naturalist*,**168**, E15-E37.
- 566 Leimu, R., Muola, A., Laukkanen, L., Kalske, A., Prill, N. & Mutikainen, P. (2012)
567 Plant-herbivore coevolution in a changing world. *Entomologia Experimentalis*
568 *Et Applicata*,**144**, 3-13.

569 MacLean, D.A. (1984) Effects of spruce budworm outbreaks on the productivity and
570 stability of balsam fir forests. *The Forestry Chronicle*,**60**, 273-279.

571 Mills, N.J. & Wajnberg, E. (2008) *Optimal foraging behaviour and efficient*
572 *biological control methods*. Blackwell Publishing Ltd, Oxford, UK.

573 Moir, M.L., Vesk, P.A., Brennan, K.E.C., Keith, D.A., McCarthy, M.A. & Hughes, L.
574 (2011) Identifying and managing threatened invertebrates through assessment
575 of coextinction risk. *Conservation Biology*,**25**, 787-796.

576 Mouquet, N., Devictor, V., Meynard, C.N., Munoz, F., Bersier, L.F., Chave, J.,
577 Couteron, P., Dalecky, A., Fontaine, C., Gravel, D., Hardy, O.J., Jabot, F.,
578 Lavergne, S., Leibold, M., Mouillot, D., Münkemüller, T., Pavoine, S.,
579 Prinzing, A., Rodrigues, A.S.L., Rohr, P.R., Thébault, E. & Thuiller, W.
580 (2012) Ecophylogenetics: advances and perspectives. *Biological Reviews*,**87**,
581 769-785.

582 Newmaster, S.G., Bell, F.W., Roosenboom, C.R., Cole, H.A. & Towill, W.D. (2006)
583 Restoration of floral diversity through plantations on abandoned agricultural
584 land. *Canadian Journal of Forest Research*,**36**, 1218-1235.

585 Paradis, E., Claude, J. & Strimmer, K. (2004) APE: analyses of phylogenetics and
586 evolution in R language. *Bioinformatics*,**20**, 289-290.

587 Pellissier, L., Ndiribe, C., Dubuis, A., Pradervand, J.N., Salamin, N., Guisan, A. &
588 Rasmann, S. (2013) Turnover of plant lineages shapes herbivore phylogenetic
589 beta diversity along ecological gradients. *Ecology Letters*,**16**, 600-608.

590 Pennisi, E. (2010) The little wasp that could. *Science*,**327**.

591 Peralta, G., Frost, C.M., Rand, T.A., Didham, R.K. & Tylianakis, J.M. (2014)
592 Complementarity and redundancy of interactions enhance attack rates and
593 spatial stability in host-parasitoid food webs. *Ecology*,**95**, 1888-1896.

594 Ries, L., Fletcher, R.J.J., Battin, J. & Sisk, T.D. (2004) Ecological responses to habitat
595 edges: mechanisms, models and variability explained. *Annual Review of*
596 *Ecology, Evolution and Systematics*,**35**, 491-522.

597 Sala, O.E., Chapin, F.S., Armesto, J.J., Berlow, E., Bloomfield, J., Dirzo, R., Huber-
598 Sanwald, E., Huenneke, L.F., Jackson, R.B., Kinzig, A., Leemans, R., Lodge,
599 D.M., Mooney, H.A., Oesterheld, M., Poff, N.L., Sykes, M.T., Walker, B.H.,
600 Walker, M. & Wall, D.H. (2000) Global biodiversity scenarios for the year
601 2100. *Science*,**287**, 1770-1774.

602 Schemske, D.W., Mittelbach, G.G., Cornell, H.V., Sobel, J.M. & Roy, K. (2009) Is
603 there a latitudinal gradient in the importance of biotic interactions? *Annual*
604 *Review of Ecology, Evolution and Systematics*,**40**, 245-269.

605 Schweiger, O., Klotz, S., Durka, W. & Kühn, I. (2008) A comparative test of
606 phylogenetic diversity indices. *Oecologia*,**157**, 485-495.

607 Srivastava, D.S., Cadotte, M.W., MacDonald, A.M., Marushia, R.G. & Mirotnick,
608 N. (2012) Phylogenetic diversity and the functioning of ecosystems. *Ecology*
609 *Letters*,**15**, 637-648.

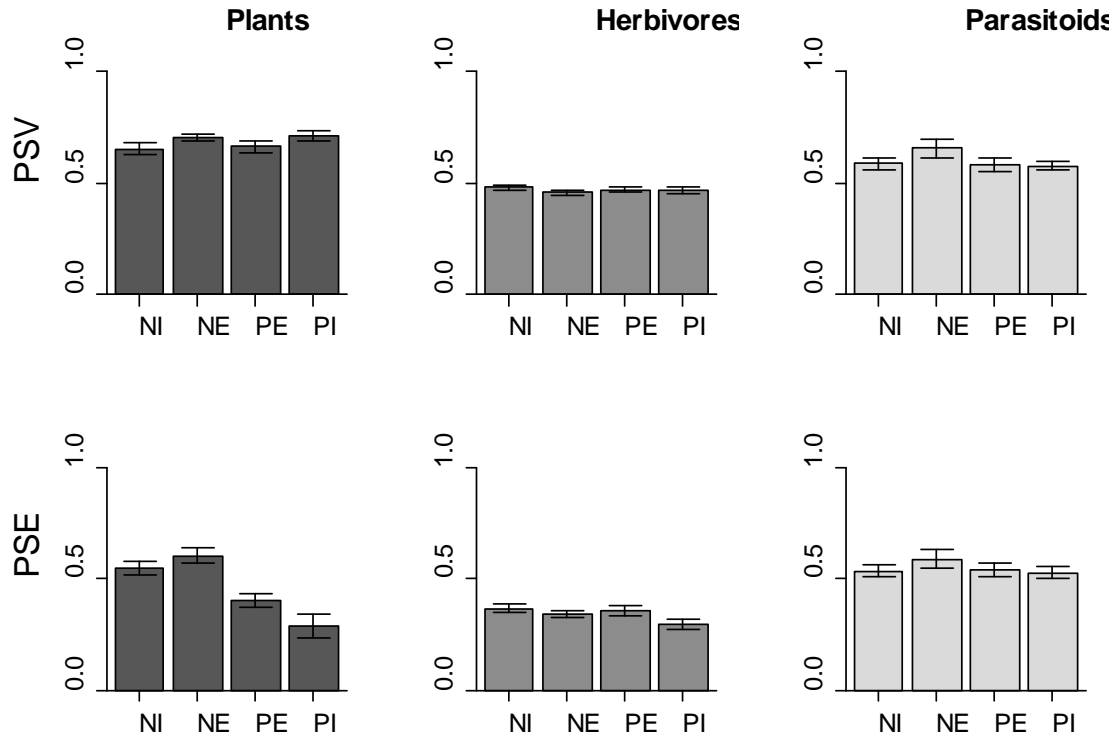
610 Stork, N.E. & Lyal, C.H.C. (1993) Extinction or 'co-extinction' rates? *Nature*,**366**,
611 307.

612 Straw, N.A. (1996) The impact of pine looper moth, *Bupalus piniaria* L. (Lepidoptera;
613 Geometridae) on the growth of Scots pine in Tentsmuir forest, Scotland.
614 *Forest Ecology and Management*,**87**, 209-232.

615 Team, R.C. (2013) R: A language and environment for statistical computing. . (ed.
616 R.F.f.S. Computing). Vienna, Austria.

617 Vane-Wright, R.I. (1992) Systematics and global biodiversity strategy. *Antenna*,**16**,
618 49-56.

- 619 Vinson, S.B. (1990) How parasitoids deal with the immune system of their host: An
620 overview. *Insect Biochemistry and Physiology*,**13**, 3-27.
- 621 Webb, C.O., Ackerly, D.D., McPeck, M.A. & Donoghue, M.J. (2002) Phylogenies
622 and community ecology. *Annual Review of Ecology and Systematics*,**33**, 475-
623 505.
- 624 Webb, C.O. & Donoghue, M.J. (2005) Phylomatic: tree assembly for applied
625 phylogenetics. *Molecular Ecology Notes*,**5**, 181-183.
- 626 Willis, C.G., Ruhfel, B., Primack, R.B., Miller-Rushing, A.J. & Davis, C.C. (2008)
627 Phylogenetic patterns of species loss in Thoreau's woods are driven by climate
628 change. *Proceedings of the National Academy of Sciences of the United States*
629 *of America*,**105**, 17029-17033.
- 630 Wimp, G.M., Murphy, S.M., Lewis, D. & Ries, L. (2011) Do edge responses cascade
631 up or down a multi-trophic food web? *Ecology Letters*,**14**, 863-870.
- 632 Winter, M., Devictor, V. & Schweiger, O. (2013) Phylogenetic diversity and nature
633 conservation: where are we? *Trends in Ecology & Evolution*,**28**, 199-204.
- 634



635

636 **Fig.1:** Mean and SE phylogenetic diversity (including native and non-native species)

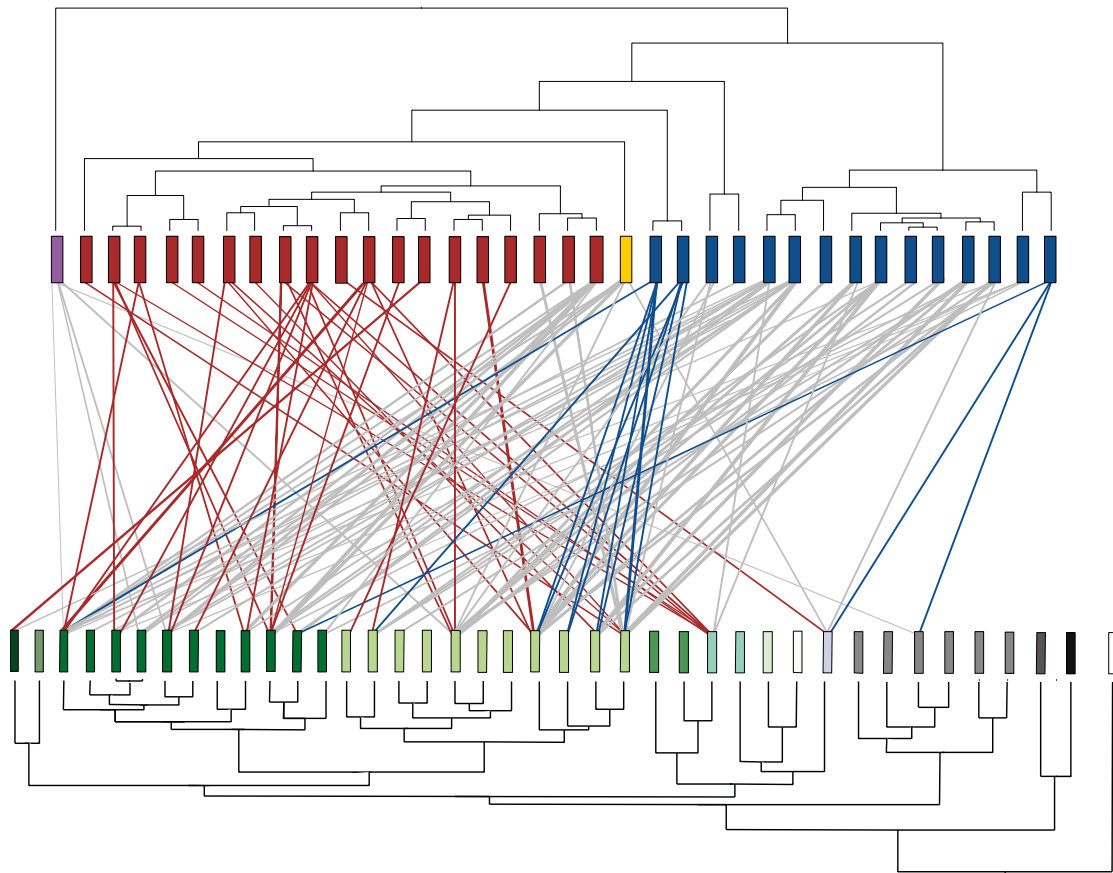
637 of different trophic levels (plants, herbivores, parasitoids) across a habitat gradient

638 from native forest interior (NI), through native edge (NE) and plantation edge (PE), to

639 plantation forest interior (PI). PSV = Phylogenetic species variability, PSE =

640 Phylogenetic species evenness.

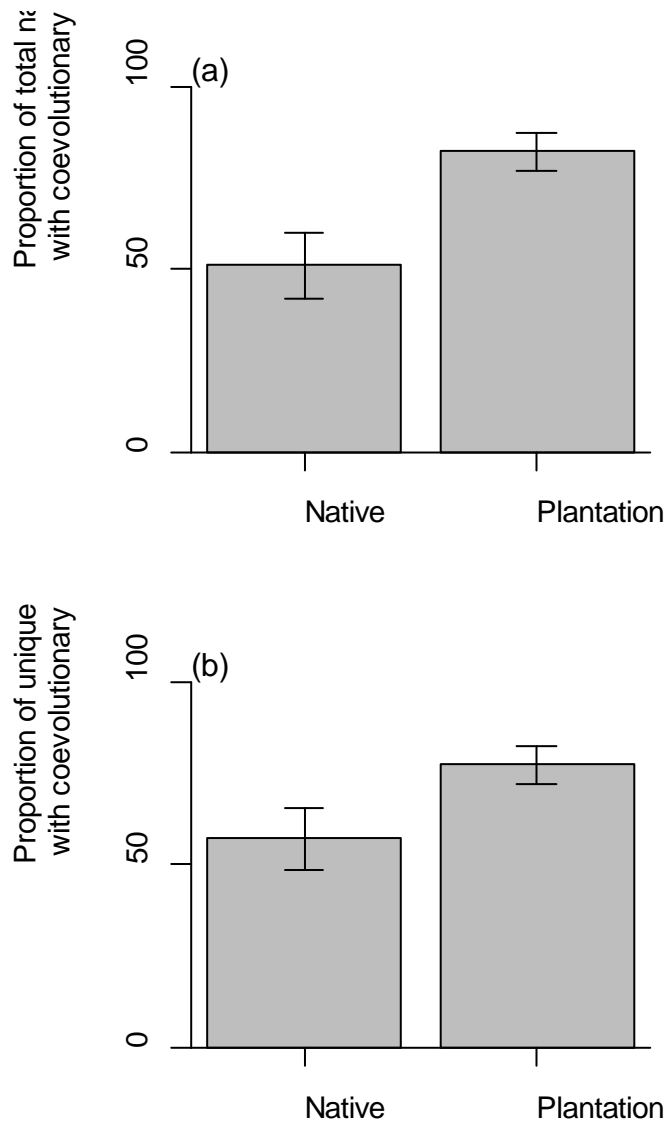
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643 **Fig. 2:** Herbivore-parasitoid food web and phylogenetic congruence between native
 644 herbivore and parasitoid species (i.e. related native parasitoid species feed on related
 645 herbivore species). The top and bottom rectangles represent parasitoid and herbivore
 646 species respectively, with different colours indicating different families. Links
 647 connecting herbivore and parasitoid species indicate a parasitism event. Coloured links
 648 are those between native parasitoid and herbivore species, coloured according to
 649 parasitoid family. Phylogenetic trees were constructed from two gene sequences,
 650 nuclear Wgl and mitochondrial COI for herbivores and 28s ribosomal and
 651 mitochondrial COI for parasitoids.

652



653

654 **Fig.3:** Mean and SE of the (a) proportion of total native interactions (i.e. parasitism
655 events, N = 221) with coevolutionary signal, and (b) proportion of unique native H-P
656 (herbivore-parasitoid) links (i.e. pairwise trophic interactions, N = 48) with
657 coevolutionary signal, across forest types (native vs. plantation).