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A forest canopy as a living archipelago:

why phylogenetic isolation may increase and age decrease diversity

Short title: Canopies as living archipelagos

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33 **ABSTRACT**

34 **Aim.** An individual tree resembles a living island, a small spatially distinct unit upon which colonizers maintain
35 populations. However, several differences exist compared to oceanic islands: a tree is relatively young, is
36 composed of numerous differently aged branches, may be phylogenetically isolated from neighbours, and
37 some of its colonizers are specific to particular tree lineages. We suggest that these specificities strongly
38 affect both alpha and beta-diversity within trees, including positive effects of isolation on the diversity of
39 generalists, and strengthening of the effect of isolation with tree age.

40 **Location.** Rennes, Bretagne, Western France

41 **Taxon.** Little-dispersive, generalist oribatid mites (Acari) and highly dispersive, specialist gall wasps
42 (Hymenoptera: Cynipidae) on oak (*Quercus* sp.) trees

43 **Methods.** We tested the effects of tree and branch age, tree and branch habitat-diversity, and tree
44 phylogenetic isolation on per-branch and per-tree alpha-diversity, and on within-tree beta-diversity of both
45 taxonomic groups

46 **Results.** For gall wasps, no variable explained diversity patterns at any level. In contrast, for oribatid mites we
47 found that high phylogenetic isolation of trees and high branch age increased alpha-diversity per tree and per
48 branch (in young trees) as well as turnover among branches. High tree age decreased alpha-diversity per
49 branch (in phylogenetically isolated trees) and increased turnover among branches. Increasing habitat
50 diversity increased alpha-diversity per tree, but decreased alpha-diversity per branch (in young trees).

51 **Main conclusions.** For mites, contrary to common expectation, we suggest that: (i) phylogenetically distant
52 neighbours are a source of immigration of distinct species; and (ii) with the increase of tree age, species-
53 sorting results in a few species colonizing and dominating their preferred patches. In gall wasps, strict
54 specialization on oaks, and efficient dispersal may render oak age or isolation unimportant. The positive
55 relationship between isolation and within-tree turnover is a new contribution to biogeography in general.

56 **Keywords.** alpha and beta-diversity; community assembly; gall wasps; island biogeography; living island;
57 oribatid mites; species turnover

58

59

60 INTRODUCTION

61 Studies on oceanic islands have provided key insights into the assembly and structuring of ecological
62 communities (Santos et al., 2016; Whittaker et al., 2017). Island properties have major effects on species
63 diversity. Islands with higher habitat diversity typically harbour larger numbers of species because they can
64 accommodate species with different habitat requirements (Fattorini et al., 2015; Hortal et al., 2009),
65 particularly habitat specialists. Larger islands tend to have higher species diversity, probably because the rate
66 of extinction relative to colonization is lower (MacArthur & Wilson, 1967). Spatially isolated islands typically
67 have lower species diversity, primarily because they can only be reached by few dispersers (MacArthur &
68 Wilson, 1967; Simberloff & Wilson, 1969; Hendrickx et al., 2009). Finally, there is evidence that, all else being
69 equal, young islands are occupied by less species due to little time available for their arrival (Whittaker et al.,
70 2008; Simberloff & Wilson, 1969; Cornell & Harrison, 2014), although opposing forces may also operate
71 (Whittaker et al., 2017).

72 Host organisms can be understood as living islands upon which entire communities, or even meta
73 communities, of colonizers can live or feed, surrounded by an unsuitable matrix of non-host organisms
74 (Gripenberg & Roslin, 2005, Gossner et al., 2009; Vialatte et al., 2010; Méndez-Castro et al., 2018; Patiño et
75 al., 2018). Many of the patterns and processes that occur on true islands can be transposed, with certain
76 limitations, to hosts (Santos et al., 2016). Similar to oceanic islands, hosts can vary in age. We may hence
77 hypothesize that alpha-diversity per host increases with host age, due to the accumulation of colonizers
78 through time (albeit assembly through local speciation will not occur). Alternatively, individual species may
79 become dominant through time, leading to a decline in species diversity (Table 1; hypotheses 1.1.1. and
80 1.1.2). Because hosts differ in habitat diversity, we may also hypothesize a positive relationship between
81 colonizers' alpha-diversity and within-host habitat diversity (Table 1; hypotheses 1.2) (e.g. Gripenberg &
82 Roslin, 2005; Lie et al., 2009).

83 There are obviously many differences between oceanic islands, and living host islands. Unlike oceanic
84 islands, phylogenetic relationships among hosts may influence the composition and diversity of colonizer
85 species. Hosts' physical or physiological characteristics control habitat conditions available to colonizers and
86 are often more different among distantly than among closely related host species (Revell et al., 2008).
87 Colonizers of an individual host may perceive neighbouring hosts from distantly related species as different
88 and unsuitable habitat. In this case, isolation should be measured as evolutionary differentiation and not as
89 spatial distance. Therefore, for host-specialized colonizers, the phylogenetically isolated host may be
90 surrounded by an unsuitable matrix (and may be unsuitable for specialist colonizers living on surrounding
91 hosts) (Yguel et al., 2011, 2014). As a consequence, phylogenetically isolated hosts have been shown to
92 harbour relatively depauperate colonizer communities (Table 1; hypothesis 1.3.1.; Vialatte et al., 2010; Yguel
93 et al., 2014; Grandez-Rios et al., 2015). Alternatively, we hypothesize that if habitat characteristics are only
94 moderately different among phylogenetically distant species (Revell et al., 2008; Gossner et al., 2009), or
95 colonizers are only moderately specialized on these characteristics, phylogenetic isolation of a host may have
96 the opposite effect. In this case, exchange among distantly related hosts remains possible and increases local
97 species diversity due to mass effects, i.e. due to strong immigration from adjacent patches including those of

98 different quality occupied by different species (Table 1; hypothesis 1.3., Brown & Kodric-Brown, 1977;
99 Mouquet & Loreau, 2003; Leibold et al., 2004; Gossner et al. 2009; Table 1). To our knowledge this alternative
100 hypothesis has not been tested so far.

101 Also, unlike oceanic islands, host plants are composed of numerous young patches, which can be
102 characterized by within-patch alpha-diversity, and among-patch beta-diversity. We hypothesize that alpha-
103 diversity within these patches reflects that of the entire hosts, i.e. increases or decreases with host age or
104 host phylogenetic isolation as explained above (Table 1; hypotheses 2.1.1. and 2.1.2). Alternatively,
105 diversity within local patches may depend on patch characteristics rather than host characteristics. We
106 hypothesize that alpha diversity within patches will increase with patch age due to more time available for
107 species arrival (Table 1; hypothesis 2.2.1, Cornell & Harrison, 2014), and with the availability of more diverse
108 habitats for diverse specialists (Table 1; hypothesis 2.3.1., Hortal et al., 2009). However, according to the
109 area–heterogeneity trade-off hypothesis (Table 1; hypothesis 2.3.2, Kadmon & Allouche, 2007; Allouche et
110 al., 2012; but see Hortal et al., 2013 for criticisms), species diversity within patches decreases with habitat
111 diversity due to a reduction in the area available per habitat, constraining, in particular, habitat specialists. To
112 our knowledge, the importance of patch-level characters and host-level characters for patch-level alpha
113 diversity have not been compared so far. We finally formulate hypotheses on beta-diversity among patches
114 within hosts: it should increase with host age, because environmental heterogeneity within the hosts increases
115 or because species differently occupying these environments arrive through time and successively fill
116 available environments (Table 1; hypothesis 3.1). Such within-host beta-diversity may also increase with host
117 habitat diversity because more different habitats allow the establishment of more different species
118 communities (Table 1; hypothesis 3.2.1). Finally, we hypothesize that within host beta-diversity depends on
119 the host's phylogenetic isolation. If host lineages strongly sort colonizer species and phylogenetic isolation
120 impedes sorting, the few remaining colonizer species should spread across the host and, thus, reduce beta-
121 diversity among patches (Table 1; hypothesis 3.3.1.). Alternatively, if host lineages moderately sort colonizer
122 species and phylogenetic isolation permits spill over from neighbouring host lineages, the numerous species
123 might occur separate among patches of different environments (Table 1; hypothesis 3.3.2). To our
124 knowledge, so far, within-host (or within-island) beta-diversity has not been studied, let alone explained, and
125 the concept might even be new at the level of classical, oceanic islands.

126 Contrary to oceanic islands, the degree to which host characteristics affect the assembly of colonizer
127 communities might increase with the strength of the co-evolutionary relationships between hosts and
128 colonizers (Gossner et al., 2009; Yguel et al., 2014) and the degree of specialization of colonizers on
129 particular host species (above and Castagnyrol et al., 2014). For instance, tree crowns are abundantly
130 colonized by two groups of very small arthropods. First, oribatid mites (Acari: Oribatida) are only moderately
131 specialized on their hosts (Behan-Pelletier & Walter, 2000), and usually live and feed on detritus or cryptogam
132 upon trees. They are only indirectly dependent on tree traits (e.g. bark structure) that control the accumulation
133 of detritus or growth of cryptogams (e.g. Prinzing, 2003; Nash, 2008; for a review Walter & Proctor, 2013).
134 Such traits may show a moderate, albeit significant, phylogenetic signal, resulting in quantitative differences in
135 cryptogam cover among tree lineages (Rosell et al., 2014). Second, gall wasps (Hymenoptera: Cynipidae) are
136 highly specialized (Ambrus, 1974) to, for example, a single host genus. Indeed, gall wasps directly depend on

137 host anatomical and physiological traits that affect larval development (such as sclerotization), and many of
138 these traits show a strong phylogenetic signal (Stone et al., 2002; Hayward & Stone, 2005). We should hence
139 expect that phylogenetic isolation reduces diversity mostly in specialized groups such as gall wasps. In
140 addition, different groups of colonizers also differ in dispersal capacity. Oribatid mites are flightless and
141 depend on passive dispersal (e.g. by wind; Lehmitz et al., 2011, 2012) leading to low capacity to disperse to
142 new hosts (Jung and Croft 2001). Overall, low dispersal capacity combined with some moderate host
143 specialization in oribatid mites might lead to increased immigration of distinct species across short spatial
144 distances, from phylogenetically distant neighbours, through mass effect. Gall wasps, in contrast, can disperse
145 both passively and actively across large distances (Gilioli et al., 2013). High dispersal capacity might allow
146 finding host trees even if surrounded by phylogenetically distant neighbours.

147 We examine these hypotheses focusing on oribatid mites and oak gall wasps living on oak trees
148 (*Quercus* spp.) in closed forest canopy. We calculate diversity measures that integrate abundances per
149 species, as abundances provide more fine-grained information and are affected by dispersal limitation
150 (Simberloff 2009; Boulangéat et al. 2012). We first examine the relationships between alpha-diversity of mites
151 and gall wasps on the one hand, and microhabitat diversity, tree age, and phylogenetic isolation of the host
152 tree on the other hand. Second, we test whether these relationships also occur at the within-tree scale of
153 individual branches. Finally, we test whether among-branch species turnover of mite and gall wasp
154 communities within single trees is linked to microhabitats and ages of branches, and to age and phylogenetic
155 isolation of trees.

156

157 **MATERIALS AND METHODS**

158

159 **Selection of trees**

160 We sampled a temperate mixed forest located close to Rennes, Bretagne, France (48.11 N, -1.34 W) in
161 which oaks (*Quercus petraea* and *Q. robur*) grow surrounded by *Ilex aquifolium*, *Fagus sylvatica*, *Castanea*
162 *sativa*, *Ulmus minor*, *Alnus glutinosa*, *Sorbus torminalis*, *Corylus avellana*, *Carpinus betulus*, *Populus tremula*,
163 *Salix caprea*, *Abies alba*, *Rhamnus frangula*, *Tilia cordata*, *Betula pendula*, *Prunus avium*, *Malus sylvestris*
164 and *Pyrus pyraster*. We sampled from mid-August to mid-September 2006 (Vialatte et al., 2010; Yguel et al.,
165 2011 for details) studying nine distinct triplets - sets of three nearby (<150m) *Quercus* sp. trees - with each
166 triplet composed of either *Q. petraea* or *Q. robur*, two closely related species that can hybridize (Yguel et al.,
167 2014, note that individual trees had to be dropped from further analyses as explained below). Trees within a
168 triplet were chosen in order to maximize differences in tree circumference at breast height and phylogenetic
169 isolation to neighbours. Such an approach of spatially grouping ("blocking") and maximizing variation of
170 independent variables of interest (such as age) within groups has been recommended to partial out spatially
171 varying environmental impacts (Figure 1a; Legendre et al., 2004). Tree circumferences were used as a proxy
172 of age (as in Vialatte et al., 2010) and ranged from 60 to 277cm, corresponding to 80 to 180 years old
173 according to local forestry authorities (see Yguel et al., 2011). We did not consider younger, understory trees,
174 as such trees are often characterized by hosting a different fauna from adult trees (Gossner et al., 2009). For

175 each focal tree, phylogenetic isolation was calculated according to Vialatte et al., (2010) as $[\sum(N_{\text{tree sp.}} \times$
176 $t_{\text{tree sp.}})/N_{\text{total trees}}]$. $N_{\text{tree sp.}}$ is the number of neighbours of a particular tree species directly in contact
177 with a focal tree's crown, $t_{\text{tree sp.}}$ is the phylogenetic distance (in MYBP) between the establishment of the
178 clade of the neighbouring species and the oaks, and $N_{\text{total trees}}$ is the number of trees (all species) in contact
179 with the focal tree's crown (Vialatte et al., 2010; Yguel et al., 2011, 2014; see Appendix S1 in Supporting
180 Information). A tree was considered to be in contact with the focal tree when they had their leaves in contact
181 (at least during wind), albeit barks remained separate. Phylogenetic distances were continuous (Appendix S1,
182 Tables S1-S6). For these trees in contact we also quantified the Simpson's species diversity (as $1-D$; $D =$
183 $\sum(\text{abundance of a species}/\text{total abundance})^2$). We finally quantified the distance to the closest oak (either *Q.*
184 *petraea* or *robur*, or their hybrids).

185

186 **Species and habitat sampling on branches and trees**

187 In each crown, six (for mites) and ten (for gall wasps), branches between 1.5 and 2m in length were
188 sampled using single-rope climbing and 6m branch cutters, in each of the three following strata: upper crown,
189 lower-shaded crown, lower sun-exposed crown (Figure 1b). Branches were aged by counting back from the
190 tip the shoot-growth branching points (identified by narrow winter growth marks). Branches were grouped into
191 branch tips (≤ 6 years) and the older parts (Figure 1c; the age range of which was recorded). Each branch
192 subsection was placed over a plastic tray and washed over its entire length with the help of a pressure
193 washer. The solution obtained for each branch was filtered using a coffee filter, which was dipped in alcohol.
194 Oribatid mite species (juvenile and adult individuals) were identified following Weigmann (2006). For gall
195 wasps, we measured branch length and recorded leaf galls, excluding bud galls, identifying species based on
196 gall morphology (Ambrus, 1974). Thus, we sampled bark for oribatids and for oribatid -specific habitat
197 conditions, and we sampled leaves for galls and gall-specific habitat conditions, resulting in two internally
198 consistent distinct sets of data and variables, that were analyzed separately.

199 We quantified alpha-diversity of gall wasps and mites per branch accounting for their abundance
200 distributions, which is useful when overall species richness is low. Specifically, we used the unit equivalent of
201 Simpson's diversity [calculated as $1-D$; $D = \sum(\text{abundance of a species}/\text{total abundance})^2$], using abundances
202 per branch. Simpson's index is largely independent of sample size (Rosenzweig 1995), contrary to species
203 numbers which would need to be rarified. To avoid potential under-sampling and zero-inflated data we only
204 considered branches and trees with Simpson's diversity > 0 . Alpha-diversity for the entire tree was calculated
205 as the Simpson's diversity ($1-D$) of the averaged abundances of each species on the entire tree ("per-tree
206 alpha-diversity"). Mite communities were strongly dominated by two species. Nevertheless high alpha-diversity
207 did not simply reflect these two species to have similar abundances (Appendix S1).

208 We also calculated within-tree turnover and nestedness-components of beta-diversity (Baselga, 2010)
209 using averaged values between each pair of branches of a tree based on a Bray-Curtis distance of the
210 occurrences of mites ('bray.part' function from 'betapart' package; Baselga & Orme, 2012). Our measure of
211 turnover is particularly unbiased by unequal sampling efforts resulting from unequal numbers of animals per
212 sample and particularly independent of nestedness (Barwell et al., 2015). We used pairwise turnover and

213 nestedness values to calculate average turnover and nestedness for each tree. But, we note that our
214 hypotheses refer to turnover.

215 Oribatid mites are usually associated with algae, fungi, moss or lichens, commonly feeding on these
216 organisms (Walter & Proctor, 2013, Prinzing, 2003). Consequently, the distribution of oribatids should depend
217 on the presence of these microhabitats. Therefore, we measured the coverage (%) per branch of algae,
218 mosses, crustose lichens, foliose lichens, and “mixed” (intermingled cryptogams). Again, we used the
219 Simpson’s metric to assess habitat diversity per branch and per tree. Habitat diversity per branch was
220 calculated as the Simpson’s diversity of habitat measurements on the branch. Habitat diversity per tree was
221 calculated as the Simpson’s diversity of the averaged per-branch measurements of each habitat variable. To
222 measure habitat composition and reduce data dimensionality, we also used the scaled and centered
223 percentages of each habitat variable to perform a Principal Components Analysis (PCA) using the Kaiser-
224 Guttman criterion for axis selection (‘vegan’ package in R; Dixon, 2003).

225 Gall wasp larvae feed on plant tissue. Consequently, the distribution of gall wasps should depend on
226 the composition of plant tissues. To identify habitat conditions of gall wasp larvae, we sampled ten leaves from
227 each stratum (upper crown, lower shaded crown, and lower exposed crown) of each tree (always the third leaf
228 from base of the branch) and cooled them until chemical analysis. We measured leaf C/N and Dry mass
229 contents according to standard protocols as detailed in Appendix S1. Habitat diversity of a tree was then
230 calculated as the average of standard deviations of C/N and dry mass. Note that such diversity of leaves as
231 habitats was not available at branch-scale contrary to the cryptogam measures.

232

233 **Explaining diversity**

234 We tested the hypotheses summarized in Table 1. In short, we statistically explained alpha-diversity per
235 tree as well as alpha-diversity per branch and beta-diversity per tree among branches by: ages, habitat
236 diversities and phylogenetic isolations and their interactions. For per-tree data we used ordinary multiple
237 regression analyses. For the more complex per-branch data nested within trees, we used mixed-effect
238 regression enriched by model averaging procedures. Variables were log transformed prior to the statistical
239 analyses, except for principal component axes. Independent variables were weakly correlated (unsigned
240 relationships mostly < 0.4; Appendix S1, Tables S3 and S6), indicating that multicollinearity was not an issue,
241 consistent with the high adjusted R^2 of our analyses. We also conducted a preliminary analysis to explore the
242 role of variables not accounted for by the hypotheses: spatial autocorrelation among studied trees, spatial
243 distance to the closest oak tree and species diversity of the ambient canopy. We found that these variables do
244 not relate to alpha diversities (Appendix S1).

245

246 Alpha-diversity per tree

247 We tested the effects of tree crown’s age, its habitat diversity, and its phylogenetic isolation on the tree
248 crown’s alpha-diversity of mites and gall wasps. For both, we fitted independent multiple regressions using
249 Simpson’s diversity per tree as a response variable, and tree circumference, tree phylogenetic isolation, and

250 habitat diversity per tree as predictor variables. To account for possible changes in the effects of each
251 predictor variable at different values of the other predictors, we fitted three further models, each including one
252 of the following interactions: tree age : habitat diversity per tree, tree phylogenetic isolation : habitat diversity
253 per tree, and phylogenetic isolation : tree age (including all interaction terms together would lead to excessive
254 multicollinearity). We then chose the model with the lowest value of sample-size corrected Akaike's
255 Information Criteria (AICc) (Bunnefeld & Phillimore, 2012). In the mite dataset, after evaluating the residuals
256 (using probability and predicted-vs-residual plots), we removed a maximum of three outliers in order to
257 provide a better fit to our model. This procedure did not qualitatively change results, but adjusted R^2
258 increased from 0.294 to 0.689.

259

260 Explaining alpha-diversity per branch

261 We fitted mixed-effects regressions (Bunnefeld & Phillimore, 2012) to analyze how characteristics of
262 trees and branches explain species diversity at the within-tree scale. We used colonizer species Simpson's
263 diversity per branch as the response variable, and remind here that this variable is different from tree-level
264 alpha-diversity analyzed above: as tree-level diversity reflects the combined effect of branch-level diversity
265 and turnover among branches. As predictor variables we used tree age, tree phylogenetic-isolation, and either
266 branch age (for mites) or branch length (for gall wasps). Trees where the branches were collected were used
267 as random effects. As above, we also fitted three other models with the same variables, but including either of
268 the following interactions: tree age : branch age or length, tree phylogenetic isolation : branch age or length,
269 and tree phylogenetic isolation : tree age. We chose the models with the lowest values of AICc. To account for
270 the uncertainty in the selection of sets of variables in mixed effects models, we then conducted a
271 modelaveraging procedure. For both mites and gall wasps' models, we permuted the fixed-effect variables
272 found in the best mixed-effects model, fitting a new mixed-effects model for each subset ('dredge' function;
273 Bunnefeld & Phillimore, 2012; Bartoń, 2015). Next, we generated averaged models for mites and gall wasps
274 using subset models with $\Delta AICc < 2$ ('model.avg' function from 'MuMIn' R package; R version 3.4.2; R Core
275 Team, 2017; Burnham & Anderson, 2002; Bartoń, 2015). Importance values were calculated for each predictor
276 variable as the sum of Akaike weights of all models in which the variable appeared (Burnham & Anderson,
277 2002). After this procedure, mites had only one model with $\Delta AICc < 2$, so we interpreted results from this
278 mixed-model. Also, for mites we repeated this approach including as explanatory variables the log of habitat
279 diversity per branch and three axes of the PCA performed with the habitat variables (related to, respectively,
280 presence of uncovered branch and lack of algae; lack of crustose lichens and mosses; and the presence
281 of foliose lichen (Appendix S1, Tables S7-S9; equivalent per-branch data was not available for galls). In this
282 analysis we also included two additional interactions: tree age : habitat diversity per branch, and tree
283 phylogenetic isolation : habitat diversity per branch. We calculated averaged models again using the threshold
284 of $\Delta AICc < 2$. We only discuss results from this latter analysis for mites as it is the most complete. In all
285 model-averaging procedures, we included the marginal and conditional R^2 of subset models. These values
286 represent, respectively, the variance explained by only fixed and by fixed and random variables (calculated
287 with 'r.squaredGLMM' function; Nakagawa & Schielzeth, 2013).

288

289 Explaining beta-diversity among branches within tree crowns

290 We performed multiple linear regressions using as response variables the average turnover and
291 nestedness partitions of beta-diversity among branches of trees. We used tree age, tree phylogenetic
292 isolation, and habitat diversity per tree as predictor variables. We again tested for interactions by fitting models
293 including the following interactions: tree age : habitat diversity per tree, tree phylogenetic isolation : habitat
294 diversity per tree, and tree phylogenetic isolation : tree age. We chose models with the lowest AICc values.
295 For the mites dataset, after evaluating the residuals, we decided to remove three outliers (not the same as
296 mentioned previously) for the model using turnover as a response variable. This procedure did not
297 qualitatively change results, but adjusted R^2 increased from 0.53 to 0.66. Statistical representations of
298 interaction effects were visualized using 'visreg' R package (Breheny & Burchett, 2015).

299

300

301 **RESULTS**

302 A total of 25 mite species (including one undetermined) and 10 gall wasp species were recorded on 181
303 branches from 25 trees and 153 branches from 21 trees (Appendix S2, Tables S10 and S11). Mite abundance
304 varied from 40 to 1028 individuals per tree, with *Micreremus brevipes* (Michael, 1888) being the most
305 abundant. Gall wasp abundance varied from 6 to 414 individuals per tree, and *Neuroterus anthracinus* (Curtis,
306 1838) was the most abundant species.

307 **Alpha-diversity per tree**

308 For both mites and gall wasps, the best AICc model included no interactions (Table 2 throughout; for
309 galls Appendix S3). For mites, alpha-diversity increased with both increasing phylogenetic isolation (Figure
310 2a) and tree-level habitat diversity (Figure 2b). Tree age did not explain mite alpha-diversity. In the case of gall
311 wasps, the best AICc model did not explain variation in alpha-diversity ($F(3, 17)=1.098$; adjusted $R^2=0.014$;
312 $p=0.377$, Appendix S3).

313 **Alpha-diversity per branch**

314 For gall wasps, the best AICc model was the one with no interaction (Appendix S3). However, no
315 predictor was significant, explained variance was extremely low and none of the relationships was significant
316 (Table 3). For mites, the best AICc model included the interaction between phylogenetic isolation and tree age
317 (Table 2). In the additional model including information on branch habitat composition (PCA scores), the best
318 model included the interaction between tree age and branch habitat diversity (Appendix S3). When per-branch
319 habitat composition variables were not considered, mite diversity increased with phylogenetic isolation and
320 tree age on single branches. The significant interaction term between phylogenetic isolation and age indicated
321 that branches of more phylogenetically isolated trees had higher mite diversity when the tree was young, but
322 lower diversity when the tree was old (Table 1; Appendix S1, Figure S1). When including habitat composition
323 variables (Table 3), phylogenetic isolation increased mite diversity, while tree age and habitat diversity per
324 branch decreased mite diversity. The significant interaction between habitat diversity per branch and tree age

325 indicated that high habitat diversity decreased mite diversity in young and increased diversity in old trees
326 (Appendix S1, Figure S2). Branch age was in all models positively related to mite diversity (Table 3; Figure
327 2c).

328 **Beta-diversity among branches**

329 For gall wasps, no interaction was included (Appendix S3), no predictor was significant and explained
330 variance was extremely low (both adjusted $R^2 < 0.05$, $p > 0.5$; Appendix S3). The best AICc model with
331 average turnover as a response variable was the one that included the interaction between phylogenetic
332 isolation and tree age for mites (Table 2). Specifically, for mites, turnover was higher in trees with high habitat
333 diversity and phylogenetic isolation (Table 2; Figure 2d). The significant interaction between tree age and tree
334 phylogenetic isolation indicated that mite turnover increased with tree age in phylogenetically non-isolated
335 trees, while decreased in isolated trees (Table 2; Appendix S1: Figure S3). The best AICc model with average
336 nestedness as a response variable did not contain this interaction between tree age and tree habitat diversity
337 for mites (Table 2; Appendix S3). Specifically, mite nestedness was higher in old than in young trees (Table 2).
338 Also, mite nestedness increased with tree age when trees provided low habitat diversity, but decreased when
339 trees were habitat diverse (Table 2; Appendix S1: Figure S4).

340

341 **DISCUSSION**

342 We characterized host trees as particular, living islands. We found that tree age, phylogenetic isolation,
343 and habitat diversity control alpha-diversity of colonizers on the entire living islands, as well as on and among
344 their individual branches (while other neighbourhood-related characteristics were not significant; Appendix
345 S1). Notably, such patterns only occurred for oribatid mites, which have poor dispersal ability and are less
346 specialized compared with gall wasps.

347 We found higher mite alpha-diversity on phylogenetically isolated host trees across the entire trees and
348 on each of their branches; This result is consistent with hypothesis 1.3.2, but contradicts 1.3.1. and what has
349 been observed before (reviewed by Grandez-Rios et al., 2015 for species richness as a measure of alpha-
350 diversity). We suggest that mite populations represent a different evolutionary situation from that found in
351 other taxa studied before. Mites do not feed on the tree itself and hence do not directly depend on tree traits
352 nor on their phylogenetic signal. However, mites depend indirectly on some tree traits, such as bark structure
353 and pH, that control cryptogam cover (Nash, 2008) and thus substrate and food of oribatids. Such bark traits
354 appear to show moderate but significant phylogenetic signal (e.g. Rosell et al., 2014), resulting in differences
355 in cryptogam covers among tree lineages. Consequently, distantly related trees should be preferred by
356 different mite species, while most mites could be able to survive on most tree species, even if they present
357 lower habitat quality for some of them (Behan-Pelletier & Walter, 2000 for a review). Arboreal mites are
358 frequently dispersed passively through wind (Lehmitz et al., 2011; Lehmitz et al., 2012) and a host
359 surrounded by distant relatives might hence be colonized by the mites preferring neighbouring hosts.
360 Consequently, species diversity should increase on evolutionarily isolated trees due to mass effects. The idea
361 that mass effects may contribute to local species richness under particular conditions is not new itself
362 (Mouquet & Loreau, 2003). Nevertheless, here we found evidence that for colonizers of hosts, such mass

363 effects can be particularly prominent in phylogenetically diverse host communities, and under intermediate (or
364 indirectly operating) phylogenetic signal of traits controlling the habitat quality of such hosts.

365 Two relationships were opposite at tree and at branch level. First, we found a positive relationship
366 between habitat diversity and mite alpha-diversity per tree, but a negative relationship per branch (consistent
367 with hypotheses 1.2.1. and 2.3.2, respectively, Table 1). An increase of species alpha diversity with habitat
368 diversity is intuitive as habitat specialists can better accommodate themselves at islands with a high variation
369 of resources and conditions available (Fattorini et al., 2015; Hortal et al., 2009). A decrease of species
370 diversity on branches with high habitat diversity, in contrast, might reflect the decreased area available for a
371 given suitable habitat. Second, we found that mite alpha-diversity per branch decreased with host-tree age (at
372 least when branches had low habitat diversity), but increased with branch age (consistent with hypotheses
373 2.1.2. and 2.2.1., respectively, Table 1). Older trees might increase the chance that those species that are
374 more efficient in colonizing a specific tree will dominate all branches of the crown sometime after arrival
375 (Badano et al., 2005; Lekevicius, 2009, for 'classical' islands). Overall, the local communities within, and the
376 species pool across a given host individual appear to be driven by opposing effects, in part perhaps because
377 the local communities are confined to very small modules (branches) where habitat surface might become a
378 limiting factor, and their filling by species takes time.

379 Tree characteristics influenced spatial turnover of mites among branches within trees. Precisely, mite
380 turnover increased with phylogenetic isolation (consistent with hypothesis 3.3.2., Table 1). A possible
381 explanation invokes again mass effects from phylogenetically distant neighbours that increase the pool of
382 species that colonize different branches (Badano et al., 2005; Lekevicius, 2009, for 'classical' islands).
383 Further, tree age gives time for habitat filtering by sorting specialists into their most suitable microhabitats
384 (tree branches) (consistent with hypothesis 3.2., Table 1). We are not aware of any study reporting the effect
385 of isolation and age of hosts or islands on the assembly of communities among patches within these hosts
386 or islands. There are, however, studies that describe the assembly within and among communities based on
387 the properties of landscape mosaics in which these communities are embedded (Hendrickx et al., 2009;
388 Chisholm et al., 2011). Assembly processes on individual hosts may hence be captured by concepts of
389 landscape ecology, albeit landscape ecologists have so far not accounted for the effect of the age of an entire
390 landscape or the degree of its isolation from other landscapes.

391 Contrary to the findings regarding oribatids, the assembly of gall wasps does not seem to be driven by
392 the characteristics of hosts we have evaluated here (Table 1). Contrary to oribatids, gall wasps are good
393 dispersers that present high host-specialization and that can even alter their habitats by inducing the growth
394 of plant tissue (Stone et al., 2002; Hayward & Stone, 2005). These contrasting ecological characters
395 might at least partly explain why gall wasps are less dependent on characters of their living islands and their
396 neighbourhoods than mites (Figure 3). The fact that species from both ecological groups were sampled on the
397 same trees, and with sample sizes in similar orders of magnitude, strengthens our confidence that the
398 observed differences do not stem from methodological biases. Based on the same experiment as the present
399 study, Yguel et al. (2011, 2014) found that the alpha-diversity of chewing phytophages (mainly Lepidoptera)
400 was lower on phylogenetically isolated host trees. Notably, lepidopterans have intermediate (between oribatids

401 and gall wasps) degrees of host-specialization and dispersal capacities (for Lepidoptera in the present study
402 system; Yguel et al., 2011). Therefore, lepidopterans on phylogenetically distant neighbours may be less
403 capable of colonizing a focal tree than are oribatid mites, and lepidopterans from spatially distant but
404 phylogenetically proximate host trees might be less capable of finding focal trees than are gall wasps (Figure
405 3). Similar effects of host phylogenetic isolation that was found for gall wasps might also occur in chalcidoid
406 wasps (Yguel et al., 2014). Overall, a given character of a host – being surrounded by distantly related
407 neighbours – may have opposite effects on colonizer organisms that differ in host specialization and dispersal
408 ability. We stress however that this conclusion resides on a single taxon per type of colonizer biology. Further
409 confirmations for other taxa are needed.

410 We are aware that our study may present some limitations. Sampling was done during the end of
411 summer, so identified patterns might not fully reflect the effects of tree characteristics on the assembly of
412 colonizers. This is especially important for gall wasps, which might produce smaller generations and smaller
413 galls during spring than in summer (Hayward & Stone, 2005). Also, sampling was restricted to peripheral
414 branches, leaving out major branches, deadwood and trunks, with their deeply fissured bark and thick, three-
415 dimensional cryptogam cover harbouring different species of oribatid mites in high abundances. We hence do
416 not pretend to characterize the entire oribatid fauna of a tree, but only that of one relatively young structure,
417 comparable among trees of all ages. Finally, our sample size is limited, albeit this would not explain any
418 observed significant effects. Moreover, our major results are relatively solid (e.g. with non-significant effects
419 with $p > 0.05$, adjusted R^2 up to 0.689, and partly based on averaging across numerous models; see Table 2),
420 which increases our confidence in the conclusions taken from them.

421 Our results suggest that, unless colonizers can easily reach and manipulate host trees, forest trees can
422 function as living islands. However, these living islands present specificities, such as phylogenetic isolation
423 from neighbours and rapid growth of individual patches, which can in turn determine the assembly of their
424 colonizers. Phylogenetically isolated trees may, for the studied mites, have increased diversity consistent with
425 mass effects from distantly related neighbour hosts, while old trees have decreased colonizer diversity within
426 patches, consistent with sorting of organisms into their preferable patches through time. Distinct
427 metacommunity perspectives (mass effects and species sorting) may explain how trees as living islands
428 influence the assembly of their colonizers. While assembly may be driven by isolation, age and habitat
429 diversity as on true islands, the processes invoked here are partly different from those on true islands.
430 Specifically, we suggest that the level of insularity is controlled also by the biology of the colonizers
431 themselves, insularity being highest for colonizers that disperse little and depend directly on host traits that
432 show strong phylogenetic signal.

433

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550 **Table 1.** Summary of studied alternative hypotheses on the effects of host-tree and branch characteristics on colonizer faunas, in a spatially
 551 contiguous forest canopy of adult, similar sized trees. The “+” and “-” mean, respectively, expected positive or negative relationships between
 552 predictor and response variables. Hypotheses corroborated for oribatids are in bold. No hypothesis was corroborated for gall wasps.

	Response variable	Predictor variable	Alternative Hypothesis 1	Alternative Hypothesis 2
1.1.	Alpha-diversity per host	Age of host	+ the older the host the more likely a colonization occurred.	- the older the host the more likely it is dominated by particular species.
1.2.		Habitat diversity of host	+ the more diverse the habitats the larger the niche space.	None.
1.3.		Host phylogenetic isolation of host	- if relevant host characteristics for colonizers are phylogenetically strongly conserved or colonizers are highly specialized. Then isolated hosts will be hard to reach for the species that can live there (ecological sorting, impeded by isolation).	+ if relevant host characteristics for colonizers are phylogenetically moderately conserved or colonizers are only moderately specialized, then isolated hosts will receive species from neighbouring, phylogenetically distant hosts (mass effect, facilitated by isolation).
2.1.	Alpha-diversity per patch within host	Age and phylogenetic isolation of hosts	+ age and phylogenetic isolation may increase species richness in the hosts (explained above) and hence in its constituent patches.	- age and phylogenetic isolation may decrease species diversity in the host (explained above) and hence in its constituent patches.
2.2.		Patch age and its interaction with host characteristics	+ more time available for the arrival of species in older patches within hosts - provided that host age and phylogenetic isolation ensure a large species pool.	None.
2.3.		Habitat diversity per patch and its interaction with host characteristics	+ more habitats will be available for species with different niches - provided that host age and phylogenetic isolation ensure a large species pool.	- the area available per habitat will also decrease, constraining in particular habitat specialists.
3.1.	Within-host beta-diversity	Age of host	+ because environmental heterogeneity within hosts increases or because species differently occupying these environments arrive through time.	None.
3.2.		Habitat diversity of host	+ more habitats will be available for different species with different niches.	None.
3.3.		Phylogenetic isolation of host	- if host lineages strongly sort colonizer species and phylogenetic isolation impedes sorting, the few remaining colonizer species may spread across the host and reduce turnover among patches	+ if host lineages moderately sort colonizer species and phylogenetic isolation permits spill over from neighbouring host lineages.

Table 2. Effects of age and phylogenetic isolation on alpha-diversity, turnover and nestedness of mites in crowns of host trees (using multiple regression analysis with best subset search based on delta AICc<2). Alpha-diversity response variables were (1) tree-level species Simpson’s diversity [F(3,20)=16.54; adjusted R²=0.689; p-value<0.001], and (2) branch-level species Simpson’s diversity (observations=181; groups=25; Marginal R²=0.152; Conditional R²=0.201; see Table 2 for analyses including habitat covariables). Beta-diversity response variables were: (3) average mite turnover [F(4, 17)=11.19; adjusted R²=0.66; p-value<0.001], and (4) average mite nestedness [F(4, 20)=3.619; adjusted R²=0.304; p-value=0.022] among branches of each tree. Significant p-values are in bold. Equivalent analyses for gall wasps were all non-significant with R²<0.015. Variables were ln+1-transformed, except for PC axes.

Predictor variables	Estimate	SE	t value	p-value
PER-TREE MITE ALPHA-DIVERSITY				
(Intercept)	-0.362	0.120	-3.025	0.007
phylogenetic isolation	0.093	0.015	6.322	<0.001
tree age	-0.005	0.042	-0.123	0.904
tree habitat diversity	1.055	0.211	4.999	<0.001
PER-BRANCH MITE ALPHA-DIVERSITY				
(Intercept)	-0.587	0.236	-2.487	0.014
tree age	0.877	0.315	2.78	0.011
phylogenetic isolation	0.211	0.063	3.324	0.003
branch age	0.076	0.025	3.055	0.003
phylogenetic isolation: tree age	-0.241	0.091	-2.648	0.015
WITHIN-TREE MITE TURNOVER AMONG BRANCHES				
(Intercept)	-1.326	0.222	-5.963	<0.001
log(phylogenetic isolation + 1)	0.366	0.063	5.811	<0.001
log(tree age + 1)	1.645	0.300	5.483	<0.001
log(tree habitat diversity + 1)	0.577	0.181	3.182	0.005
log(phylogenetic isolation + 1):log(tree age + 1)	-0.497	0.090	-5.498	<0.001
WITHIN-TREE MITE NESTEDNESS AMONG BRANCHES				
(Intercept)	-0.260	0.386	-0.673	0.509
phylogenetic isolation	0.010	0.017	0.603	0.554
tree age	0.871	0.383	2.275	0.034
tree habitat diversity	1.301	0.817	1.593	0.127
tree age: tree habitat diversity	-2.055	0.863	-2.381	0.027

Table 3. Effects of habitat variables, and (as in Table 2) age and phylogenetic isolation on Simpson’s alpha-diversity of mites and gall wasps in crowns of host trees. Averaged models of parameter estimates, each based on five models (averaged marginal $R^2=0.166$; averaged conditional $R^2=0.220$), and three (averaged marginal $R^2=0.002$; averaged conditional $R^2=0.131$) subset models. Variables were ln+1-transformed, except for PC axes.

Predictor variable	Importance	Estimate	SE	Adjusted		
				SE	z value	p-value
PER-BRANCH MITE ALPHA-DIVERSITY WITH PER-BRANCH HABITAT VARIABLES						
(Intercept)		0.256	0.13	0.131	1.957	0.05
phylogenetic isolation	1	0.042	0.014	0.015	2.808	0.005
branch age	1	0.067	0.026	0.026	2.57	0.01
tree age	1	-0.251	0.114	0.12	2.089	0.037
branch habitat diversity	1	-0.733	0.25	0.252	2.91	0.004
tree age:branch habitat diversity	1	0.9	0.314	0.317	2.841	0.005
PC2	0.59	-0.007	0.008	0.008	0.833	0.405
PC3	0.29	0.003	0.007	0.007	0.423	0.673
PC1	0.12	<0.001	0.003	0.003	0.136	0.892
PER-BRANCH GALL WASP ALPHA-DIVERSITY						
(Intercept)		0.322	0.041	0.042	7.712	<0.001
tree age	0.248	0.008	0.026	0.028	0.296	0.767
branch length	0.203	<0.001	0.006	0.006	0.156	0.876

FIGURES

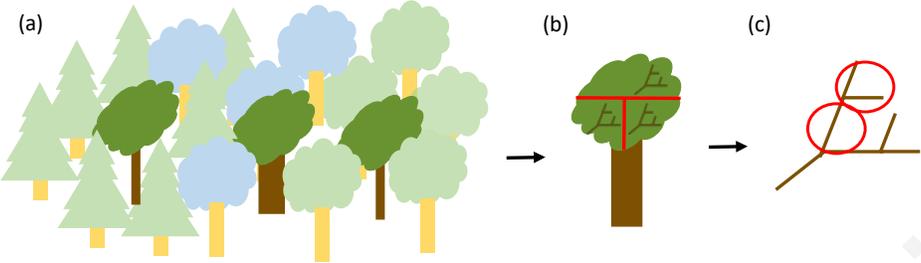


Figure 1.

Accepted manuscript

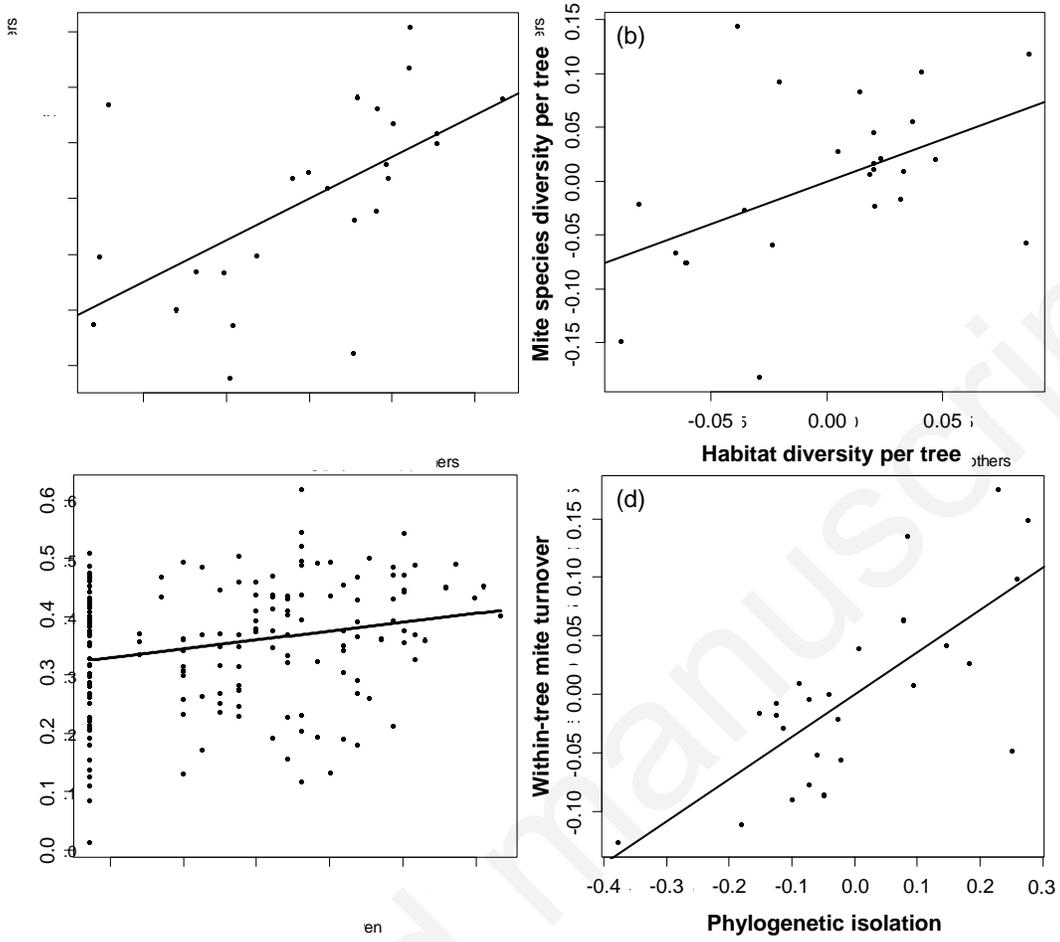


Figure 2.

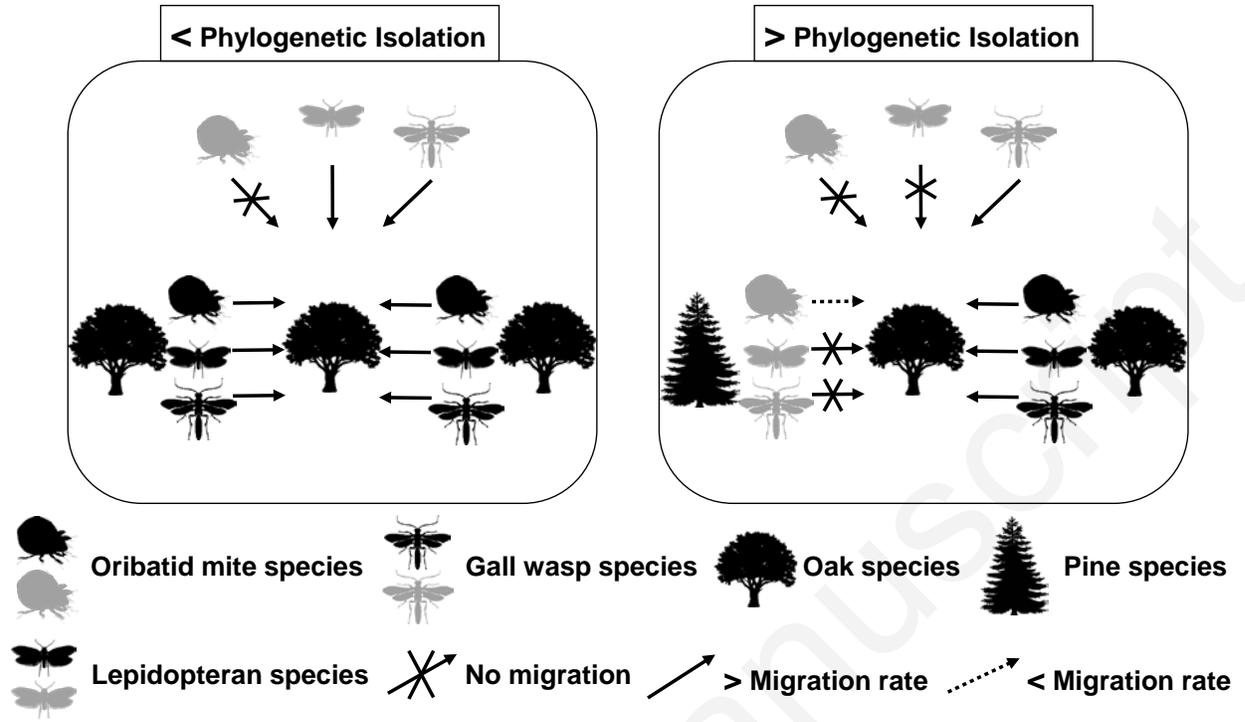


Figure 3.

FIGURE LEGENDS

Figure 1. Sampling scheme established in a temperate mixed forest located close to Rennes, Bretagne, France (48.11 N, -1.34 W): (a) Triplet of oaks (dark trees) varying in age (trunk width) and phylogenetic distance of neighbours (trees of other colours and shapes). (b) Three strata within an oak crown (upper, lower shaded, lower more exposed). (c) younger and older branches within strata. Oak trees belong to *Quercus petraea* and *Q. robur* species. Neighbour trees also belonged to the following species: *Ilex aquifolium*, *Fagus sylvatica*, *Castanea sativa*, *Ulmus minor*, *Alnus glutinosa*, *Sorbus torminalis*, *Corylus avellana*, *Carpinus betulus*, *Populus tremula*, *Salix caprea*, *Abies alba*, *Rhamnus frangula*, *Tilia cordata*, *Betula pendula*, *Prunus avium*, *Malus sylvestris* and *Pyrus pyraeaster*.

Figure 2. Partial residual plots showing the effects of (a) tree phylogenetic isolation and (b) habitat diversity per tree on mite alpha-diversity per tree, (c) of branch age on mite species diversity per branch, and (d) of phylogenetic isolation on within-tree mite turnover. Partial residual presents the response of a given dependent variable to a given predictor variable while accounting for the effects of other predictor variables in the multiple regression models (see Table 2). Variables were ln+1-transformed.

Figure 3. Observed effect of host phylogenetic isolation on the assembly of different groups of colonizers. A phylogenetically isolated host (right) may present higher species diversity of oribatid mites due to immigration, even at low rate, of new species (grey) from distantly related host neighbours, while there is no long-distance immigration from distant closely related host trees (long-distance immigration is represented on top of figure). On the other hand, host phylogenetic isolation may have no effects on gall wasps due to their high dispersal and habitat manipulation capacities, which allow them to colonize across large distances any tree individual to which they are specialized. Finally, the diversity of lepidopterans may be negatively affected by phylogenetic isolation of a focal tree because lepidopterans on neighbouring trees cannot use the

focal tree nor can they manipulate its nutritional quality (as suggested by Yguel et al., 2011, 2014). Lack of colonization from distantly related neighbours is not compensated by increased immigration across large distances from closely related host trees. Silhouettes of oribatids (by B. Lang) and gall wasps (by M. Broussard), and lepidopterans (uncredited image) and pines (uncredited image) from <http://phylopic.org>, respectively under licenses of <http://creativecommons.org/licenses/by/3.0/>, and <http://creativecommons.org/publicdomain/mark/1.0/>.

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