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12

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63 **Abstract**

64 While mature forests are declining worldwide, tree plantations could provide habitats of
65 conservation value for forest-adapted species. However, to what degree the fauna in tree
66 plantations matches the diversity and composition of mature forest communities is still
67 debated. In this meta-analysis, we used beetle species (*Coleoptera*) as biodiversity indicators
68 to assess the conservation value (i.e. the log response ratio in species richness and abundance
69 and the Soerensen similarity) of tree plantations versus reference old-growth forests. We
70 tested the effects of biome, plantation age, tree species richness and origin, surrounding
71 habitat and the trophic position of the focal guild on the diversity and composition of beetle
72 communities.

73 Our results showed that tree plantations generally harboured communities with 47%
74 less individuals, 33% less species and a significantly distinct composition than old-growth
75 forests. In the case that tree plantations had a similar number of species or individuals as old-
76 growth forests, those plantations still displayed a 40% difference in species composition.
77 Beetle abundance was significantly lower in tropical/subtropical plantations and for
78 detritivorous species. We found no further significant drivers of beetle diversity and
79 community composition in tree plantations.

80 We conclude that, although tree plantations can provide crucial habitats for forest-
81 adapted species, they generally harbour less diverse and significantly different communities,
82 highlighting the conservation value of old-growth forests as biodiversity refuges. To properly
83 assess the conservation value of plantations in different taxa, we propose the use of species
84 composition instead of single diversity indices.

85

86 Introduction

87 Human land-use change has caused about two thirds of global biodiversity loss
88 (Newbold et al., 2015; Wilting et al., 2017) and is contributing to the extinction of species on
89 an unprecedented scale far beyond our planet's boundary of safe operating space (IPBES,
90 2019; Barnosky et al., 2011; Dunn et al., 2009; Wake and Vredenburg, 2008; Rockström et al.,
91 2009). Forests harbour the majority of terrestrial biodiversity (Secretariat of the Convention
92 on Biological Diversity, 2010) but between 1990 and 2020 about 420 million hectares of forest
93 was lost globally through deforestation (FAO and UNEP, 2020). Humid primary forests, as an
94 example, lost 5.9% of their area each year between 2002 and 2019 (Hansen et al., 2013,
95 Global Forest Watch, www.globalforestwatch.org).

96 If planted on degraded land, tree plantations might provide an important tool to
97 create secondary habitats and thereby minimize the loss of forest-adapted species. The
98 conservation value of tree plantations, however, is still under debate (Braun et al., 2017;
99 Bremer and Farley, 2010; Brockerhoff et al., 2008; Castaño-Villa et al., 2019; Liu et al., 2018;
100 Pirard et al., 2016). For instance, it is not yet clear to what extent the conservation value of
101 tree plantations differs between global biomes. At least in the tropics, tree plantations cannot
102 serve as a replacement for primary forest (Barlow et al., 2007; Gibson et al., 2011). The
103 conservation value of tree plantations depends on multiple factors that act both at the local
104 and at the landscape scale. At the local scale, the contribution of tree plantations to
105 biodiversity is greater when plantations include several tree species instead of being
106 monocultures (Liu et al., 2018) and when planted tree species are native rather than exotic
107 (Bremer and Farley, 2010). In addition, older plantations tend to harbour a higher biodiversity
108 than younger plantations (Crouzeilles et al., 2016; Mang and Brodie, 2015). At the landscape

109 scale, the success of tree plantations, as forest restoration measures, relies on the
110 configuration of the surrounding habitat. In particular, the distance to native forest remnants
111 negatively affects the plantation biodiversity (Kremer and Bauhus, 2020; Crouzeilles and
112 Curran, 2016).

113 To test the global effects of local and landscape variables on the conservation value of
114 tree plantations, a meta-analysis can be conducted to systematically summarize the large
115 body of published literature (Gurevitch et al., 2018; Koricheva et al., 2013). In a similar study,
116 Crouzeilles et al. (2016) used a global meta-analysis to show that the success of forest
117 restoration measures (albeit not specifically tree plantations) depends on the time elapsed,
118 the type of restored disturbances and the surrounding landscape. Although other meta-
119 analyses have studied the effects of tree plantations on biodiversity, these analyses were
120 either focused on other taxa (Bremer and Farley, 2010; Castaño-Villa et al., 2019), were more
121 regional (Mang and Brodie, 2015; Spake et al., 2015), or focussed exclusively on species
122 richness (Chaudhary et al., 2016; Mang and Brodie, 2015).

123 In our study, we focused on beetle species (*Coleoptera*) in forests and tree plantations,
124 because beetles account for 27% of the global insect richness (Stork et al., 2015) and are
125 widely used as indicator species (Audino et al., 2014; Rainio and Niemelä, 2003) for the effects
126 of environmental change (Cameron and Leather, 2012; Duelli and Obrist, 1998; Kotze et al.,
127 2011) and habitat fragmentation on biodiversity (Davies and Margules, 1998; Halme and
128 Niemelä, 1993; Niemelä, 2001; Spence et al., 1996). In forest ecosystems, beetles occupy
129 functional roles as defoliators, predators, xylophages and detritivores (Dajoz, 2000), making
130 them an ideal group to assess the conservation value of tree plantations across different
131 trophic levels (Nichols et al., 2007).

132 We conducted a global meta-analysis to compare the diversity and composition of
133 beetle communities in tree plantations and old-growth reference forests. We hypothesized
134 that tree plantations harbour beetle communities with lower species richness, abundance,
135 and of significantly different species composition. Since these differences could be related to
136 multiple factors including biome, plantation age, tree species richness and origin, matrix
137 habitat, and the trophic position of the focal beetles, we analysed each one of these effects
138 on our biodiversity responses. Specifically, we hypothesized that the differences between
139 tree plantations and reference forests increase from boreal to tropical biomes, and that these
140 differences are generally greater when plantations are younger, planted with non-native tree
141 species, planted in monocultures and established in a non-forest matrix with a large distance
142 to the next forest. We furthermore hypothesize that differences between plantations and
143 reference forests increase with the trophic level of the investigated species (from detritivores
144 and herbivores to predators). With this analysis, we provide the first global assessment on
145 the similarity and potential drivers of beetle communities in tree plantations as compared to
146 reference old-growth forests to assess their value as biodiversity conservation sites.

147

148 **Material and Methods**

149 *Literature search*

150 The primary literature for this meta-analysis was compiled on July 17, 2020 and
151 included the results of two literature searches. We searched the Web of Science on June 20,
152 2017 and July 17, 2020 with the same search terms that were used by Chaudhary et al. (2016):
153 TOPIC: (forest*) AND TOPIC: (impact OR effect OR influence OR role) AND TOPIC: (species
154 richness OR species diversity OR biodiversity) AND TOPIC: (natural* OR semi-natural* OR

155 primary OR manag* OR unmanag* OR virgin OR old-growth OR remnant* OR ancient* OR
156 silviculture OR cut* OR clearcut* OR felling OR clear-fell OR clearfell* OR select* cut* OR
157 thinning* OR coppice* OR logging OR unlogging* OR logged OR unlogged OR regeneration OR
158 plantation* OR planting* OR intensification OR old OR abandonment). We supplemented this
159 database with the first 1,000 results from two Google Scholar searches that we conducted on
160 October 11, 2017 and July 17, 2020 using the following search terms: (forest* OR afforest*
161 OR plantation*) AND (beetle* OR Coleoptera OR bug*). We restricted our database to
162 research articles, book chapters and proceeding papers and retrieved 19,654 publications.

163 We screened all titles and abstracts to only include those publications that i) were not
164 duplicates, ii) potentially measured the diversity of beetles in different forest types and iii)
165 established tree plantations on formerly non-forested areas. This screening yielded 521
166 publications. We screened the text of all articles and retained only those that reported beetle
167 species richness, abundance or community composition in tree plantations older than one
168 year and reference old-growth forests (consisting of pristine or unmanaged mature/old-
169 growth forests). This left us with 83 publications, published between 1989 and 2020, to be
170 included in our meta-analysis. The PRISMA diagram (Moher et al., 2010) of the literature
171 search and screening procedure is shown in Fig. S1.

172

173 *Data extraction*

174 From each of the 83 publications that met all inclusion criteria, we extracted the
175 following information necessary to calculate effect sizes: the mean, standard deviation and
176 number of replicates of the beetle measurements (species richness, abundance or species
177 composition) in tree plantations and in reference forests. In order to be consistent, we

178 favourably extracted species density estimates (i.e. per trap, sample or per area). When this
179 was not possible, we extracted species richness at the point of maximum effort on rarefaction
180 curves. We assumed that the sampling effort within published studies was generally sufficient
181 to capture the diversity and composition of the investigated beetle communities. If a study
182 measured beetle diversity in different years or plantations of different ages, we extracted the
183 necessary information for the youngest and the oldest plantation. If the necessary
184 information was not provided in texts or tables, we calculated them from raw data or
185 extracted them from figures using the ImageJ software (Rasband, 2015).

186 Where possible, we extracted additional information on the following variables that
187 we proposed to drive effect sizes (termed moderators): i) the location and biome of the study
188 sites (boreal, temperate, Mediterranean and tropical/subtropical), ii) the plantation age
189 (notion of youngest or oldest plantation in a study), iii) the richness of the planted tree species
190 (monocultures or mixtures), iv) the origin of the planted tree species (native, exotic or mixed),
191 v) the distance to the next mature forest (closer or farther than 500 m), vi) the matrix habitat
192 around the tree plantations (forest and/or plantations, mixture of forest and non-forest
193 habitats and non-forest habitats), vii) the trophic function of the surveyed beetles (predators,
194 herbivores, detritivores and 'others', which included unknown and mixed groups).

195

196 *Statistical Analyses*

197 Differences in beetle species richness and abundance between tree plantations and
198 reference old-growth forests were quantified with the log response ratio and its
199 corresponding variance estimate (eqn 1, Koricheva et al., 2013). Differences in community
200 composition were quantified with the Sørensen similarity index that could often only be

201 obtained from summarized species lists and was therefore not assigned with a variance
202 measure.

203

$$204 \quad \log \text{ response ratio} = \log\left(\frac{\bar{x}_{plant}}{\bar{x}_{ref}}\right); \text{ var} = \frac{sd_{plant}^2}{n_{plant} \bar{x}_{plant}^2} + \frac{sd_{ref}^2}{n_{ref} \bar{x}_{ref}^2}$$

205 **Eqn. 1.** Calculation of effect sizes (log response ratios) and effect sizes variances with \bar{x} : mean
206 diversity, sd: standard deviation, n: sample size, plant: tree plantations, ref: reference forests.

207

208 Due to the heterogeneity in the summarized studies, the obtained effect size weights
209 spanned up to five orders of magnitude and their application would have neglected any effect
210 of those studies with the highest effect size variances. To be able to include those studies with
211 a certain leverage, we rescaled all effect size weights so that they spanned only two orders of
212 magnitude (separately for the species richness and abundance data sets). For a high
213 proportion of effect sizes, we were unable to calculate the corresponding effect size
214 variances, due to missing sample sizes or standard deviations (90 out of 202 for species
215 richness and 108 out of 195 for abundance). To be able to include those incompletely
216 reported studies, we used a predictive mean matching algorithm to impute missing effect size
217 variances based on the reported ones. To account for the uncertainty in the imputed values,
218 we used a multiple imputation approach (Ellington et al., 2015; Idris et al.; Nakagawa, 2015;
219 Kambach et al., 2020) for which we created 100 separately imputed datasets, ran 100 analyses
220 and summarized the 100 results into uncertainty-adjusted model estimates.

221 We applied random-effect meta-analyses models (i.e. linear mixed-effects models
222 with a random term for every effect size to account for intrinsic variability) in order to

223 estimate average effect sizes of beetle species richness, abundance and community similarity
224 across all studies (grand means) and within data subsets (group means, e.g. within biomes,
225 Borenstein et al., 2010, Koricheva et al., 2013). Effect sizes were weighted by the inverse of
226 their corresponding variances. The Sørensen similarity index was analysed with unweighted
227 linear mixed-effects models. Between-study variance (τ^2) and the percentage of true
228 heterogeneity in effect sizes (I^2) were estimated with the Sidik-Jonkman estimator (Sidik and
229 Jonkman, 2005).

230 We expanded the mixed-effects models by adding the proposed moderators as linear
231 fixed effects. The significance of the moderators was determined with the Omnibus test of
232 moderators (against a χ^2 -distribution). Since most studies did not provide information on all
233 moderators, we refrained from constructing models that included all moderators at once and
234 instead ran separate models on those subsets of effect sizes for which the respective
235 moderator information was available. We tested the relationship between the Sørensen
236 similarity index and both species richness and abundance effect sizes using unweighted linear
237 models.

238

239 *Sensitivity and bias analyses*

240 Single studies could contribute multiple effect sizes, e.g., from multiple plantations or
241 forest types, multiple trophic groups, or multiple sampling methods. To test whether such
242 non-independence of effect sizes affected our results, we repeated all analyses with random-
243 effect meta-analysis models that incorporated a nested random effects structure in which
244 multiple plantations, forests, methods, and species groups were nested within the random
245 term of the study identity. We checked for potential bias in the log response ratios, due to

246 low sample sizes or high standard deviations, by calculating Geary's small-sample corrected
247 accuracy diagnostic (eqn 2, Geary, 1930, Lajeunesse, 2015). A value < 3 would indicate
248 potential a bias. We tested whether the inclusion of biased effect sizes or the weighting by
249 effect size variances affected our results by comparing them with the results obtained from
250 unweighted random-effects meta-analyses that included only those species richness and
251 abundance effect sizes with accuracy diagnostics ≥ 3 . Meta-analyses on biodiversity are
252 sensitive to the spatial scale of the biodiversity measurements (Chase et al., 2019; Spake et
253 al., 2021). We visually checked for relationships between the size of the sampling plots, the
254 number of replicates, the effect sizes and the respective effect size variances with co-
255 dependency as suggested in Spake et al. (2021). We furthermore checked for the potential
256 omission of nonsignificant effect sizes by visually inspecting funnel plots between effect sizes
257 and effect size variances in the species richness and abundance data sets. Finally, we checked
258 for geographic bias in the published literature by testing whether or not our meta-analysis
259 dataset covered the 20 countries that had the largest area of forest and plantation forest
260 (following the Global Forest Resources Assessment of the Food and Agriculture Organization
261 of the United Nations, 2020).

262 All analyses were calculated in R, version 4.0.2 (R Core Team, 2019), using the
263 following packages: *vegan* for similarity indices (Oksanen et al., 2019), *mice* for multiple
264 imputations (van Buuren and Groothuis-Oudshoorn, 2011), *metafor* for meta-analytical linear
265 models (Viechtbauer, 2010) and *ggplot2* for graphical representations (Wickham, 2009).

266

267

$$\frac{\bar{x}}{\text{sd}} \left(\frac{4n^{\frac{3}{2}}}{1 + 4n} \right) \geq 3$$

268 **Eqn. 2.** Geary's small-sample corrected accuracy diagnostic. Values < 3 indicate potential bias
269 in the log response ratio due to either a low mean value (\bar{x}), a low sample size (n) or a high
270 standard deviation (sd). Geary's diagnostic was calculated for tree plantations and reference
271 forests within the species richness and the abundance data sets.

272

273 **Results**

274 We obtained 202 effect sizes (i.e., individual comparisons between tree plantations
275 and reference old-growth forests) for beetle species richness, 195 effect sizes for beetle
276 abundance and 62 effect sizes for the Sørensen similarity index. The compiled 83 studies
277 represent findings from 92 forest sites that were globally distributed but sparse in the boreal
278 zone (Fig. 1).

279 Grand mean effect sizes of beetle species richness and abundance were significantly
280 negative (Fig. 2). In comparison to old-growth forests, tree plantations harboured, on average,
281 a 33% lower species richness (grand mean = -0.4) and a 47% lower abundance (grand mean =
282 -0.63) of beetles. The grand mean of the Sørensen similarity index was 0.58, indicating that
283 the community composition differed between tree plantations and the corresponding
284 reference forests (Fig. 2). Between-study variance was low for species richness ($\tau^2 = 0.04$),
285 high for beetle abundance ($\tau^2 = 0.88$) and low for the Sørensen similarity index ($\tau^2 = 0.002$).
286 The percentage of true heterogeneity was low for species richness ($I^2 = 1.3\%$), moderate for
287 beetle abundance ($I^2 = 32.8\%$) and low for the Sørensen similarity index ($I^2 = 0.2\%$).

288 Differences in species richness were not related to any of the proposed moderators
289 (Fig. 2). Differences in beetle abundance were moderated by the biome and the trophic level
290 of the investigated species (Fig. 2). Beetle abundance significantly decreased in tree

291 plantations in the tropics and subtropics and was significantly reduced for all detritivorous
292 and predatory but not for herbivorous species. Differences in community similarity were not
293 related to any of the proposed moderators (Fig. 2).

294 The similarity in community composition between tree plantations and reference
295 forests was positively related to the similarity in species richness ($F_{1,60} = 30.1$, $p < 0.001$, Fig.
296 3) and abundance ($F_{1,59} = 14.3$, $p < 0.001$, Fig. 3). Plantations that harboured a similar species
297 richness or abundance as the old-growth forest sites were also more similar in species
298 composition. Following predictions from linear regressions, we found that plantations that
299 harboured a similar species richness and abundance as the old-growth forest sites showed,
300 on average, a Sørensen similarity of 0.63 for species richness and 0.61 for beetle abundance.

301 Adopting a nested random-effects structure did not improve the meta-analysis
302 models (log-likelihood did not change) and did not change the results of our analyses (Fig. S2).
303 Geary's accuracy diagnostic indicated that species richness effect sizes did not suffer from
304 bias (5 out of 112 effect sizes with an accuracy diagnostic > 3) but abundance effect sizes likely
305 did (28 out of 89 effect sizes with an accuracy diagnostic > 3). Unweighted random-effects
306 models across those effect sizes with an accuracy diagnostic ≥ 3 largely confirmed the results
307 from the multiple-imputation data sets (Fig. S3) but indicated some additional significant
308 moderators. Species richness was additionally related to the origin of the planted tree species.
309 Beetle abundance was additionally related to the origin of the planted tree species as well as
310 to the distance to the next forests and the type of habitat that surrounded the tree plantations
311 (Fig. S3). Co-dependency plots for the species richness dataset suggested a negative
312 relationship between plot size and sample size, between plot size and effect size and between
313 sample size and effect size variance (Fig. S4). For the beetle abundance dataset, the co-

314 dependency plots did not suggest such relationships (Fig. S5). The funnel plot for species
315 richness showed the expected pyramid pattern between effect sizes and effect size precision
316 (Fig. S6). Effect sizes with higher precision were thereby more narrowly distributed around
317 the grand mean effect size. The funnel plot for beetle abundance did not show such a
318 relationship between effect size value and effect size precision (Fig. S6).

319 We found a severe geographic bias in the published literature. We collated studies
320 from only nine out of the 20 countries with the largest area of forests and twelve out of the
321 20 countries with the largest amount of forest plantations (Fig. S7 and S8). In terms of forest
322 area, the top-three countries not included in our dataset were the Russian Federation, the
323 United States of America and the Democratic Republic of the Congo. In terms of forest
324 plantation area, the top-three countries not included were the United States of America,
325 Vietnam and the Republic of Korea.

326

327 **Discussion**

328 In this meta-analysis, we compiled 83 studies and synthesized the current state-of-
329 knowledge on the diversity and composition of beetle species (*Coleoptera*) in tree plantations
330 compared to reference old-growth forests. We applied imputation methods to guarantee the
331 inclusion of all available information. As expected, our results confirmed previous findings of
332 a generally lower biodiversity (Bremer and Farley, 2010; Brockerhoff et al., 2008; Castaño-
333 Villa et al., 2019; Crouzeilles et al., 2016) and a significantly different species composition
334 (Curran et al., 2014) in planted as compared to old-growth forests.

335 Surprisingly, most of our tested moderators were unrelated to the beetle community
336 in tree plantations. Only the biome and the trophic group of the investigated beetle guild

337 explained the differences in beetle abundance. Forest plantations tended to be especially
338 unsuited to conserve the biodiversity of tropical/subtropical forests. Although only significant
339 for beetle abundance, we found that the effect sizes of beetle species richness, abundance
340 and composition were all lowest in the tropical/subtropical biome, indicating that tropical
341 tree plantations cannot harbour the high diversity and complexity of microhabitats and biotic
342 interaction of tropical old-growth forests (Gibson et al., 2011). Aside from the tropics and
343 subtropics, we did not find further indications for a latitudinal or global gradient in the
344 compiled effect sizes.

345 Negative effects of tree plantations on beetle diversity were stronger for detritivorous
346 species. This might be attributed to a lower diversity and structural complexity of living and
347 dead plant material and thereby reduced diversity of habitat and food resources (Bremer and
348 Farley, 2010; Chumak et al., 2015; Spake et al., 2015). Different from the other trophic levels,
349 the number of herbivorous beetles was not reduced in tree plantations. Since the abundance
350 of beetle predators was significantly reduced in tree plantations, this might indicate that
351 plantations showed a lack of top-down control of herbivores. Old-growth forests might also
352 have a higher associational resistance against herbivores and pests than artificial tree
353 plantations (Jactel et al., 2020).

354 Even though the differences between native/exotic and monospecific/mixed
355 plantations were not significant, we found that exotic and monospecific tree plantations
356 harbour beetle communities that have the potential to be less diverse and different from old-
357 growth forest (Bremer and Farley, 2010; Castaño-Villa et al., 2019). Thus, we tentatively
358 suggest that the establishment of exotic and/or monospecific plantations should be restricted
359 to only those areas where old-growth forests are scarce and highly fragmented and the

360 planting of native tree species is not an option (Berndt et al., 2008; Lugo, 1997; Pawson et al.,
361 2008). Previous findings indicate that the negative effects of exotic tree plantations might be
362 partially alleviated if the planted trees have native congeners (Gossner et al., 2009; Roques et
363 al., 2006) or traits that are similar to those from native tree species (Bertheau et al., 2009).
364 Planting mixtures of tree species might, in the long run, increase the vegetation complexity
365 and habitat heterogeneity; two factors that are positively related to the diversity of beetles
366 (Parisi et al., 2020; Lassau et al., 2005) as well as most animal taxa (Tews et al., 2004). A higher
367 diversity of tree species might also increase the amount and diversity of leaf litter, two
368 important drivers for the detritivore community (e.g. Attignon et al., 2004; Gessner et al.,
369 2010; Lassau et al., 2005), which we found to be the most difficult group to conserve in tree
370 plantations.

371 Our findings highlight that simple diversity indices (in our case, species richness and
372 abundance) cannot adequately reflect the compositional differences between plantations
373 and old-growth forests. Even if plantations achieved a similar richness and abundance of
374 beetle species, they still displayed a roughly 40% difference in the species composition. This
375 complements previous work showing that insect species richness recovers five times faster
376 after habitat restoration than the corresponding species composition (Curran et al., 2014).
377 Thus, research and management aiming at understanding and conserving forest biodiversity
378 must investigate not only the diversity but also the composition of focal groups and
379 communities.

380 Although we aimed at compiling an extensive dataset, the published literature missed
381 studies from some of the countries with the largest area of forests or forest plantations.
382 Especially studies from the Russian Federation, the United States of America, the Democratic

383 Republic of the Congo and from Vietnam are needed to evaluate the effects of tree
384 plantations on beetle communities. Furthermore, the data at hand is not sufficient to analyse
385 potentially important interactions between moderators (e.g. Jactel and Brockerhoff, 2007;
386 Cunningham and Murray, 2007; Meli et al., 2017; Spake et al., 2015; Jopp and Reuter, 2005;
387 Neumann et al., 2017; Kambach et al., 2016). The compiled studies differ in many aspects (e.g.
388 the management, tree density, previous land-use, disturbances, landscape configuration and
389 methodologies) whose effects could not be summarized in this meta-analysis.

390 In conclusion, we showed that tree plantations generally sustain beetle communities
391 that are not only less rich in species and individuals, but also compositionally different from
392 old-growth forests. Especially in tropical/subtropical sites and for detritivorous species, tree
393 plantations cannot conserve the diversity and composition of forest beetle communities.
394 Differences to old-growth forests were independent of the plantation age and inclusion of
395 exotic species as well as the proximity to the surrounding forest. We thus conclude that tree
396 plantations are unsuited and will likely not develop into adequate refuges for old-growth
397 forest species. Whether plantations of native tree mixtures that are allowed to develop into
398 structurally diverse forests (including mature trees, canopy gaps, dead plant material and
399 understory vegetation, Hartley, 2002; Irwin et al., 2014; Lindenmayer and Hobbs, 2004) might
400 indeed better conserve the biodiversity of old-growth forests yet remains to be reviewed.

401

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403

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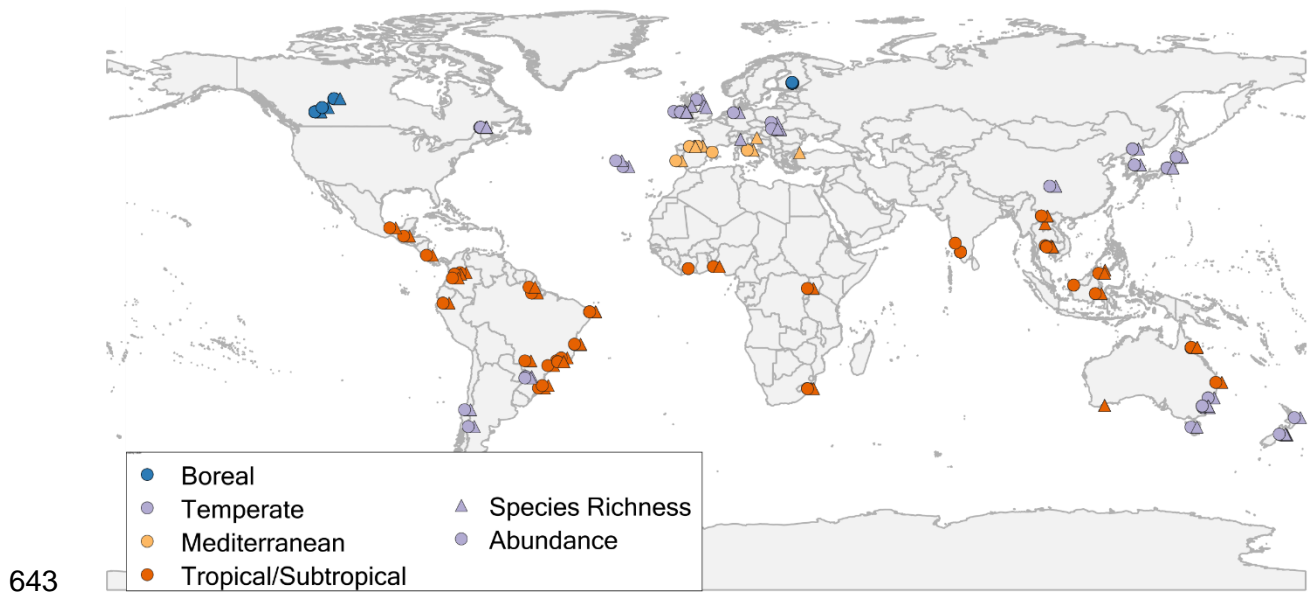
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644 **Fig. 1.** Geographical distribution of the studies included in this meta-analysis.

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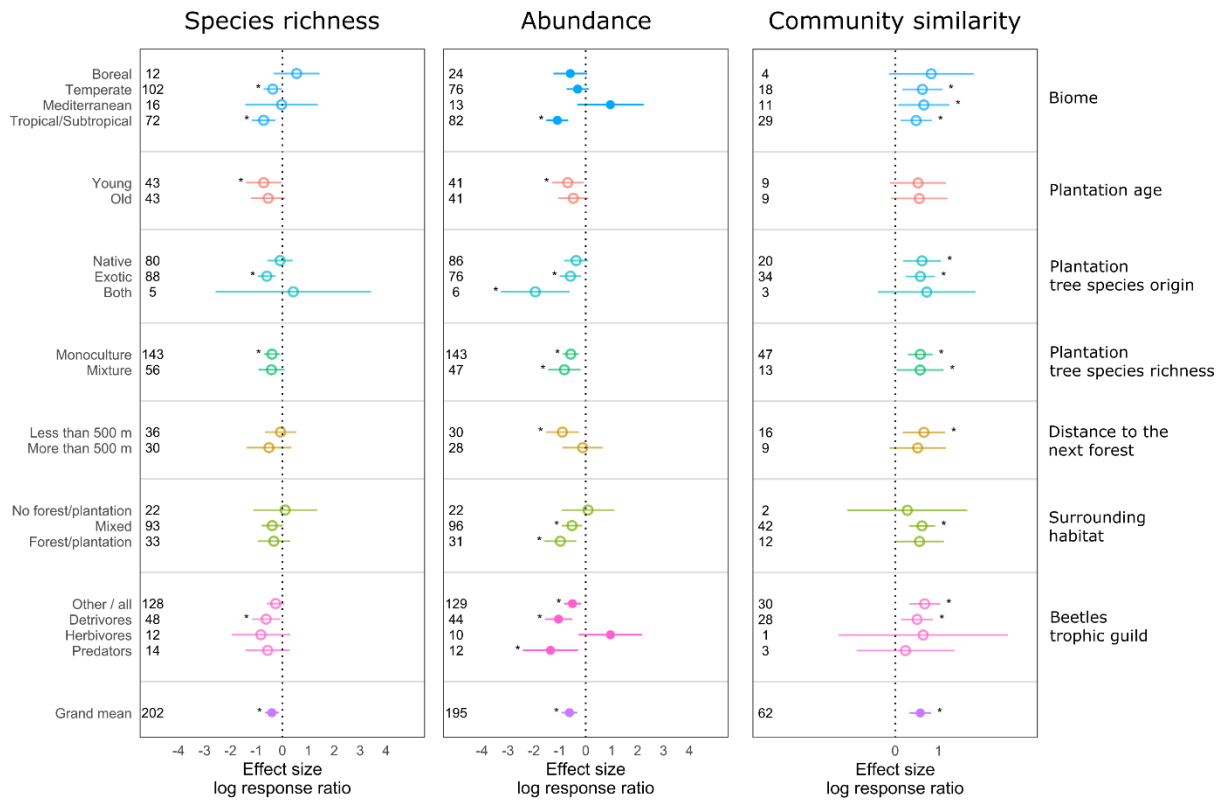
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658 **Fig. 2.** Forest plots showing the grand mean and subgroup mean effect sizes quantified as the
 659 log of mean beetle diversity in plantations divided by the mean diversity in reference forest
 660 sites. Closed dots indicate significant moderators (listed at the right side of the panel) or grand
 661 mean effects (shown at the bottom of each panel). Stars indicate significant subgroup mean
 662 effect sizes (listed at the left side of the panels) for which the approximated 95% confidence
 663 interval (horizontal lines) does not cross the dotted line of zero effect size.

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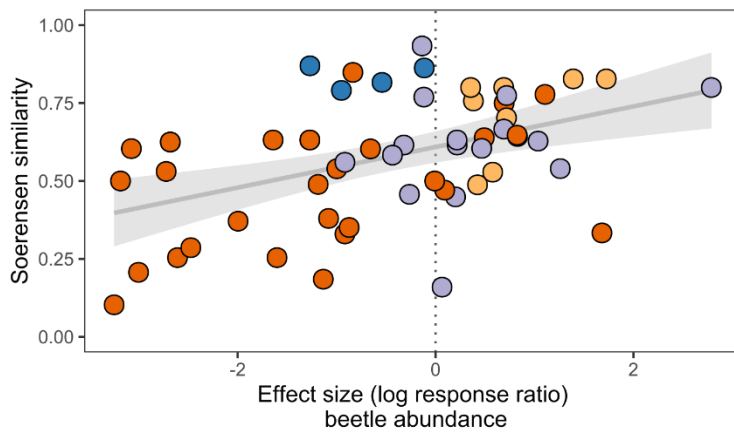
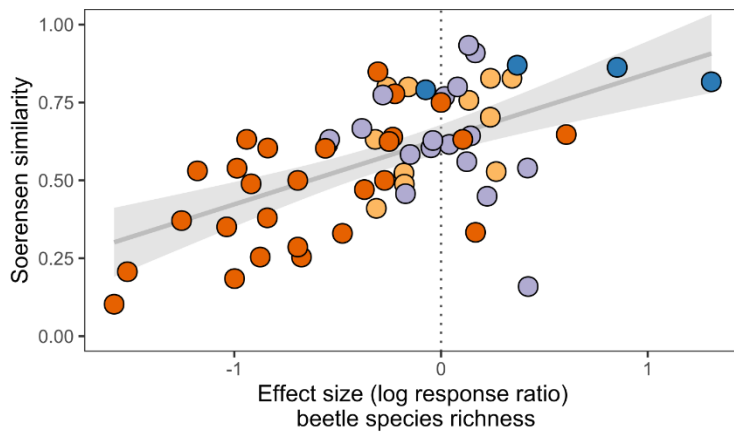
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Biome ● Boreal ● Temperate ● Mediterranean ● Tropical/Subtropical

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671 **Fig. 3.** The relationship between beetle species richness (top) and abundance (bottom) in tree
 672 plantations versus old-growth forests against the Soerensen similarity index. Each point
 673 represents one effect size. Single studies could contribute multiple effect sizes. Colouring
 674 refers to the biome in which a study was conducted.