Meta-analysis of tree diversity effects on the abundance, diversity and activity of herbivores' enemies

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Abstract

- The natural enemies hypothesis predicts that the abundance and diversity of antagonists such as predators and parasitoids of herbivores increases with the diversity of plants, which can lead to more effective top-down control of insect herbivores. However, although the hypothesis has received large support in agricultural systems, fewer studies have been conducted in forest ecosystems and a comprehensive synthesis of previous research is still lacking.
- We conducted a meta-analysis of 65 publications comparing the diversity, abundance or activity of various groups of natural enemies (including birds, bats, spiders and insect parasitoids) in pure vs. mixed forest stands. We tested the effects of forest biome, natural enemy taxon and type of study (managed vs experimental forest).
- We found a significant positive effect of forest tree diversity on natural enemy abundance and diversity but not on their activity. The effect of tree diversity on natural enemies was stronger towards lower latitudes but was not contingent on the natural enemy taxon.
- Overall, our study contributes substantially toward a better understanding of the "natural enemies hypothesis" in forest systems and provides new insights about the mechanisms involved. Furthermore, we outline potential avenues for strengthening forest resistance to the growing threat of herbivorous insects.

Keywords: Associational resistance ; Herbivory ; Meta-analysis ; Natural enemies ; Top-down control ; Tree diversity ; Pest control

Introduction

Forest ecosystems offer a wide variety of ecosystem services that benefit the economy and human wellbeing (Brockerhoff et al., 2017; de Groot et al., 2002). However, in the context of global change, forests are facing increasing threats including herbivory by native and invasive pest species (Grünig et al., 2020; Seidl et al., 2014). It is generally accepted that mixed forests are less vulnerable to insect herbivory than single-species forests (Jactel et al., 2021), a phenomenon commonly referred to as 'associational resistance' (Barbosa et al., 2009; Jactel et al., 2017; Letourneau et al., 2011) – though the opposite, 'associational susceptibility', may also occur (Schuldt et al., 2014; White & Whitham, 2000). Associational resistance is usually explained by two main mechanisms, driven by the presence of heterospecific neighboring trees: (i) a bottom-up effect (*sensu* Hunter & Price, 1992) on focal host accessibility, with insect herbivores being more likely to find and remain on hosts that are growing in dense single-species stands (the resource concentration hypothesis) and (ii) a top-down effect, corresponding to the control of herbivores population by their natural enemies, supposed to be more abundant in more diverse habitats *(the natural enemies hypothesis)*. The "natural enemies hypothesis" was first presented by Root (1973) and postulates that more diverse habitats provide predators and parasitoids with more abundant and predictable resources (*i.e. prey, breeding and nesting sites, refuge and shelter, etc.*) across spatial and temporal scales, increasing natural enemy abundance and diversity and thus leading to more efficient top-down control of herbivorous pest populations. This hypothesis is well-supported in agricultural systems where it has been shown that crops growing in mixture generally support higher level of predation of herbivores and suffer less loss from herbivory than crops growing in monoculture (Russell, 1989; Letourneau, 1987, Bianchi et al., 2006; Wan et al., 2020). On the other hand, the applicability of the natural enemies hypothesis in forests is still a matter of discussion (Staab & Schuldt, 2020), as studies are reporting positive (e.g. Esquivel-Gómez et al., 2017; Novais et al., 2017), neutral (e.g. Klapwijk & Björkman, 2018; Schuldt et al., 2008) or negative (e.g. Nixon & Roland, 2012) effects of tree diversity on insect parasitism or predation.

Inconsistencies in studies having tested the natural enemies in forest ecosystems may arise from multiple sources. Firstly, the natural enemies hypothesis, as it was initially presented, proposed that an increase in abundance and diversity of natural enemies would lead to greater top-down control of herbivores populations. However, relationships between abundance, diversity and actual biological control that natural enemies exert on insect herbivores in forests have not been examined thoroughly. Furthermore, different studies assessing the relevance of the natural enemies hypothesis have used different proxies for top-down control by natural enemies which could lead to different results due to methodological issues. For example, Esquivel-Gómez et al. (2017) found that the *richness* of spiders was significantly higher in mixed stands than in pure stands in a forest of south Mexico. On the contrary, Schuldt et al. (2008) found no effect of tree species mixing on the *abundance* of spiders in a deciduous forest of central Germany. Both studies assessed the response of natural enemies to tree diversity, but used different metrics (i.e. richness vs. abundance) which may have led to the difference in the results observed. In recent years, studies using direct measures of predation and parasitism while testing for an effect of tree diversity have increased (Abdala-Roberts et al., 2016; Bellone et al., 2020) but they cannot be directly compared to those measuring only predator abundance. Methodological issues can also arise from the type of study used to test the effect of tree diversity on natural enemies. Tree diversity experiments, where the number of tree species per area is manipulated (e.g in TreeDivNet, Paquette et al., 2018), are used increasingly because they allow for better, more controlled tests of the mechanisms behind natural enemy responses to tree diversity. However, these mainly recent experiments often include mixtures of rather low levels of tree diversity and they typically lack the features of mature forest such as deadwood and diverse microhabitats (Staab & Schuldt, 2020). Therefore, it was hypothesized that these different sources of heterogeneity in studies of natural enemies in mixed forests may make it difficult for clear patterns to emerge (Staab & Schuldt, 2020).

Second, experimental tests of the natural enemies hypothesis in specific locations fail to account for the effect of biogeographical gradients such as latitude, which is known to influence the biodiversity

of natural enemies and the strength of various biological interactions (Pennings & Silliman, 2005; Roslin et al., 2017). For example it has been shown that ectothermic arthropod predators such as spiders, ants or carabids are more active under warm climate (Becerra, 2015; Björkman et al., 2011).

Third, it has been found previously that the effect of tree diversity on natural enemies differed between taxa. An experiment conducted in Germany on 150 forest plots showed that the species richness of birds and bats was not related to tree diversity, while that of forest-dwelling predatory arthropods was (Penone et al., 2019). Therefore, discrepancies could exist between studies conducted in different forest biomes or focusing on different natural enemy taxa.

To assess the relevance of the natural enemies hypothesis in forests, we conducted a meta-analysis of 65 published studies from 1993 to 2020 that involved more than 200 case studies. We addressed methodological issues arising from the broad definition of the natural enemies hypothesis by testing whether the effect of tree diversity on natural enemies varied with the metrics used *(abundance, richness and activity)* and the type of study *(tree diversity experiment vs mature forest)*. We also evaluated the importance of the type of natural enemy *(birds, bats, arthropod predators vs. parasitoids)* as well as the forest biome *(tropical, temperate or boreal forest)* to account for the importance of ecological features and biogeographical gradients. Specifically, and albeit the potential effect of the metrics used to assess natural enemy responses to tree diversity, we predict that, following the work of Roslin et al. (2017), the strength of trophic interactions would be higher towards the tropics, which would result in stronger effect of tree diversity on natural enemies at lower latitudes. Additionally, we expect that more generalist natural enemies would benefit more from the diversity of forests, being able to exploit complementary host or prey resources.

Material & Methods

Data collection

We conducted an extensive literature search focusing on the effect of tree diversity on natural enemies (hereafter referred to as "NE") of herbivores. We searched the Web of Science and Scopus databases using the following combination of relevant keywords: [forest OR woodland OR "planted forest"] AND [tree NEAR (diversity OR richness OR composition OR gradients) OR (monoculture OR polyculture OR (pure OR mix*) NEAR stand)] AND [enem* OR predat* OR prey OR parasit* OR top-down OR control* OR bird* OR bat* OR chirop* OR spider* OR ant* OR carab* OR hoverfly OR syrph* OR ladybird OR ichneum* OR hymeno* OR dipter* OR "enemies hypothesis"] AND [diversity OR richness OR abundance OR density OR activity]. We limited the search to papers published in English, between 1950 and 2021. We then screened the title, abstract and full text when appropriate of each previously returned article and included them in the meta-analysis if they met the following criteria:

1. Studies focused on the activity (e.g., predation rate, predation attempts on prey models, percentage of parasitism), abundance or species richness or diversity of NE as a response variable (hereafter "NE response to tree diversity") in pure vs mixed forest stands or along a gradient of tree species richness or diversity.

2. Studies had to report the mean of the response variable, any measure of variability around means (standard deviation, standard error or 95% confident interval) and the sample size used in the study, or a correlation coefficient between one of the response variables and a gradient of tree species richness or diversity. Wherever necessary, we retrieved that information by digitizing the figures using WebPlotDigitizer version 4.2 (Rohatgi, 2019).

Our literature search yielded a total of 4666 candidate primary studies (last accessed in February 2021), of which we discarded 87% (4083 studies) that did not satisfy our inclusion criteria. We then completed our dataset by checking for any relevant articles present in the cited references of each article retained

after the first initial search or in recent reviews. A case study corresponded to any type of NE response to tree diversity, such that there could be more than one case study per primary study. We gave each primary study and case study a single ID. We finally gathered a dataset including 245 case studies from 65 primary studies that were published between 1993 and 2020 across 26 scientific journals (Fig. 1).

Calculating effect sizes

For each case study, we calculated Hedges' *d* effect size (Hedges & Olkin, 1985) as the standardized differences between NE responses to tree diversity in mixed vs. pure stands. Hedges' *d* was used because it can account for small sample sizes and uneven variance between control and treatment groups. A positive *d* value corresponds to a positive effect of tree diversity on NE, meaning that NE were more abundant, diverse or active in mixed stands as compared to pure stands. Negative *d* value indicate the opposite. When authors reported correlations between tree diversity and NE responses, we extracted Pearson's coefficient correlation and sample size from which we calculated Fisher's z-score. Positive value of Fisher's z mean that there is a positive correlation between the NE response variable and tree diversity. We then converted Fisher's *z* to Hedges' *d* (Koricheva et al., 2013). All effect sizes were calculated with the "metafor" package, using R version 3.6.1 (R Core Team, 2016; Viechtbauer, 2010).

Moderators

We modeled heterogeneity among effect sizes using three moderators (covariates).

Natural enemy response type

We first explored whether the type of response of NE to tree diversity was consistent across several methodological approaches. We categorized NE response as 'abundance', 'diversity' and 'activity'. Abundance was assessed using visual identification, trapping or other devices such as ultrasound detectors and included relative and absolute abundance of NE as well as mean number of NE per tree or per trapping device. NE diversity included species richness or Shannon index values. NE activity

referred to proportion of real or model hosts or prey that were missing, killed, or had evidence of parasitism or predation attempts.

Forest biome

For each primary article, we extracted the geographic coordinates of forest stands, from which we classified each system as 'boreal', 'temperate' or 'tropical' forest ecosystem.

Taxa of NE

We distinguished between three categories of NE: Birds and bats (predatory vertebrates), arthropods (generalist predatory invertebrates such as spiders, ants, carabids) and insect parasitoids (specialist predatory invertebrates). When such a classification could not be made from data reported by the authors of primary papers, we categorized NE as 'unspecified'. When multiple and undiscerned NE taxa were involved, NE were categorized as 'Multi-taxon'.

Type of study

For each study, we classified the forest in which the study was conducted as either "experimental forest", where the tree diversity gradient was experimentally manipulated (e.g. TreeDivNet), or "natural forest" for other cases.

Statistical analysis

We first calculated a grand mean effect size (Gurevitch & Hedges, 1999) across all studies to assess the effect of tree diversity on NE. This effect was considered significant if the 95% confidence interval around the grand mean effect size did not include zero. Following Cohen's guidelines (Cohen, 1988), an effect size of 0.2 or smaller is considered a 'small' effect size, 0.5 represents a 'medium' effect size and 0.8 or higher a 'large' effect size. We estimated consistency among studies by calculating between-study heterogeneity (τ^2 and associated Q statistics) as well as I^2, the standardized estimate of total heterogeneity ranging from 0 to 1 (Koricheva et al., 2013; Nakagawa et al., 2017). As we detected a large amount of residual heterogeneity in the grand mean effect size, we accounted for this using three moderators: NE response type, NE taxa and the forest biome.

We first addressed methodological issues by considering NE response type as a moderator, in interaction with NE taxa or forest biome. The interaction terms were not significant (NE response type × Biome: k = 247, Q_M = 0.50; P = 0.97; NE response type × NE taxa: k = 247, Q_M = 3.14, P = 0.53). We therefore tested each moderator separately. We reported the results of the omnibus test and interpreted the model coefficients and confidence intervals of each moderator level separately. We considered that model coefficient parameter estimates were significantly different from zero if the 95% CI around each effect size did not overlap zero.

We ran each model using the *rma.mv* function of the "metafor" package and accounted for potential non-independence between case study by including Case ID nested within Study ID as random factors. The use of multiple comparisons to the same control was controlled by using a variance-covariance matrix among effect sizes.

Preliminary analyses testing for an effect of study type (experimental vs natural forest) showed that this factor did not significantly affect NE responses to tree diversity (Q_M = 0.005, P = 0.94) and therefore was not included in the following results section.

Finally, we used several complementary approaches (funnel plot, leave-one out meta-analysis, Rosenberg fail-safe number and cumulative meta-analysis) to evaluate the robustness and sensitivity of our results to several sources of bias (see supplementary material 2)

Results

Of the 245 cases studies we analyzed, 159 were associated with arthropods (56 of which were associated with parasitoids), 56 with birds, 16 with bats and 14 with mixed or unidentified NE. NE abundance and richness were assessed 112 and 85 times respectively, while only 48 cases studies assessed NE activity. Studies were mostly conducted in temperate forest (n = 30), followed by tropical (n = 25) and boreal forests (n = 10).

199 The grand mean effect size (± 95% CI) was significantly positive (0.41 ± [0.17, 0.65], sample size: k =
200 245, indicating that, overall, NE responded moderately and positively to tree diversity in forest (Fig.
201 2A. However, there was a large and significant amount of total heterogeneity (τ^2 = 1.76, Q_T = 2899.32,
202 P < 0.001), mainly attributed to between-study heterogeneity (I^2 = 0.91).
203 We found a significant effect of the metric (i.e. abundance, diversity or activity) used to characterize
204 NE response to tree diversity (Q_M = 8.34, P = 0.015, k = 247). Both NE abundance (0.46 ± [0.14, 0.79])
205 and diversity (0.68 ± [0.36, 1.01]) were significantly higher in mixed than in pure forests, while NE
206 activity did not significantly influence NE response to tree diversity (-0.16 ± [-0.61, 0.30]) (Fig. 2B).
207 We found a significant effect of the forest biome in which studies took place (Q_M = 19.64, P = 0.04, k =
208 247). Mean effect size was large, positive and significantly different from zero in tropical forests (1.43
209 ± [0.72, 2.14]) but non-significant in temperate forests (0.08 ± [-0.09, 0.95]) and in boreal forests (-0.16
210 ± [-0.84, 0.50]) (Fig. 2C).
211 Model coefficient parameter estimates were positive for birds/bats (0.77 ± [0.05, 1.49]) and
212 arthropods (excluding parasitoids) (0.68 ± [0.10, 1.25]), almost null for parasitoids (0.09 ± [-0.78,
213 0.97]) and negative for "mixed" taxa (-0.56 ± [-1.76, 0.64]). However, the identity of the NE taxon did
214 not influence NE response to tree diversity in forest (Q_M = 2.11, P = 0.54, k = 247).
215 Finally, we found no significant two or three-way interaction between NE response type, forest biome
216 and NE taxa.

217 Discussion

218 Our meta-analysis provides the first quantitative and up-to-date assessment of the effect of tree
219 species diversity on natural enemies of insect herbivores in forest ecosystems. Overall, NE abundance
220 and diversity were higher in mixed than in pure forests, but not their activity, thus providing positive
221 although partial support to the natural enemies' hypothesis in forest. This also suggest that increasing
222 forest tree diversity may not automatically lead to stronger top-down control of herbivores by natural

223 enemies and this is corroborated by the large amount of between-study heterogeneity found in our
224 quantitative meta-analysis. Those findings are also consistent with recent studies assessing the effect
225 of tree diversity on natural enemies in forest (reviewed by Staab & Schuldt, 2020) and indicates that
226 this hypothesis may not apply universally in forests. However, we were able to identify some key
227 factors explaining the variation in response of NE to tree diversity in forest.

228 Consistent with the predictions of the natural enemies hypothesis, we confirm that the abundance and
229 diversity of NE are higher in mixed species forests. Two main non-exclusive mechanisms may explain
230 this pattern. First, diverse forests are expected to host more stable populations of herbivores
231 throughout the year (Lawton & Strong, 1981; Siemann et al., 1998; Vehviläinen et al., 2007) and are
232 thus more likely to provide natural enemies with abundant and various prey and hosts, allowing them
233 to maintain stable populations. In addition, more diverse habitats can offers a better supply of
234 complementary food such as pollen or nectar which can improve the fitness of natural enemies and
235 lead to higher abundance (Cappuccino et al., 1999; Russell, 1989) as well as more microhabitats for
236 nesting or resting (Asbeck et al., 2019; Batáry et al., 2014), and shelter against adverse conditions. In
237 turn, tree diversity had no overall effect on NE activity. One possible ecological explanation could be
238 that intraguild competition, which arises when natural enemies filling the same ecological niche co-
239 occur and share the same prey population (Finke & Denno, 2003; Rosenheim, 1998), or when intraguild
240 predation (e.g. super predators or hyperparasitoids) weakens top-down control of host or prey, even
241 though the abundance or richness of natural enemies increases in mixed forests. For example, Sanders
242 et al. (2011) found that increasing spider richness did not influence prey control and that the overall
243 outcome strongly depends on the interference between the predators species involved. Another
244 explanation could be that, just as host trees are more difficult to locate and colonize by herbivorous
245 insects in mixed forests because they are physically or chemically hidden by their heterospecific
246 neighbours (Jactel et al. 2021), prey may be more difficult to find by their predators in more complex
247 forests (Nell et al., 2018; Tarbox et al., 2018). Lastly, it is technically much more difficult to properly

248 estimate predation or parasitism of forest insect herbivores than to estimate NE abundance. We could
249 retrieve only 15 papers on NE activity and most of them were based on the use of sentinel caterpillars
250 (38% of all methods used to assess NE activity). There is therefore a need for more studies assessing
251 concomitantly natural enemy abundance/richness and activity in order to properly understand the link
252 between NE abundance and richness and the actual biological control they exert on herbivores.

253 Natural enemy responses to tree diversity were stronger towards lower latitudes. In a recent review,
254 Staab & Schuldt (2020) already pointed out that latitude and climate could be an important factor
255 shaping NE response to tree diversity in forest and, because tree diversity is much higher in tropical
256 than in temperate and boreal forests, it could have stronger effects on natural enemies. Additionally,
257 previous work highlighted an increase in natural enemy activity or abundance with decreasing latitude
258 (Roslin et al., 2017; Zvereva et al., 2020). Many natural enemies of herbivores are ectothermic
259 arthropods such as spiders, wasps, carabids or ants, and temperature is known to be a key abiotic
260 factors affecting their metabolism and activity (Deutsch et al., 2008; Zvereva & Kozlov, 2006). As such,
261 higher activity of natural enemies, associated with higher overall tree species diversity and stronger
262 trophic interactions for all NE taxa in tropical forests (Gaston, 2000; Hargreaves et al., 2019; Hillebrand,
263 2004), may explain why the natural enemies responses to tree diversity was stronger in tropical forests
264 than in temperate or boreal forests.
265 Finally, we found no significant difference of natural enemy responses to tree diversity between NE
266 taxa. Several studies suggest that natural enemy responses to tree diversity are species-specific
267 (Ampoorter et al., 2020; Riihimäki et al., 2005; Staab & Schuldt, 2020; Wan et al., 2020), and some
268 species may not respond to tree diversity, even though the overall effect is positive. For example,
269 Kaitaniemi et al. (2007) found that abundance of predatory ants was higher in mixed forests stands
270 and lead to higher predation of the European pine sawfly, but the abundance of other predators such
271 as spiders and predatory heteropterans did not change between mixed and pure stands. Additionally,
272 the natural enemies hypothesis predicts that generalist natural enemies may benefit more from an

273 increase in tree diversity than specialists, as generalists would be able to make better use of the greater
274 number of alternative prey and host species found in mixed habitats. For example, Legault et al. (2018)
275 found that tree diversity had a positive effect on the generalist parasitoid of the spruce budworm
276 *Apanteles fumiferanae* but did not affect parasitism rate by the specialist parasitoid *Glypta*
277 *fumiferanae.* Consequentially, and given the fact that NE responses to tree diversity can be closely
278 linked to NE identity, it is not surprising that no overall pattern have been found. Finally, it is important
279 to note that studies using multi-taxon approaches to test the responses of different natural enemies
280 to tree diversity under standardized methods were rare (only 6 studies among the 65 included in the
281 meta-analysis). The availability of more such multi-taxon studies would help to unfold global patterns
282 that may otherwise remain unexplored.

283 Conclusion and future work

284 Our results indicate that natural enemy abundance and richness respond positively to an increase in
285 tree diversity in forests, providing at least partial support for the natural enemies hypothesis in forest
286 ecosystems. However, considering that tree diversity does not seem to influence natural enemy
287 activity consistently, it is not yet clear how this effect of tree diversity will affect the ability of natural
288 enemies to exert biological control of herbivore populations. While mixed forests might sustain more
289 abundant and diverse communities of natural enemies, more attention is needed to further
290 understand how this could lead to stronger biotic interactions with their hosts or prey. We therefore
291 recommend that studies assessing NE abundance or richness as a proxy of biological control includes
292 accurate measures of NE activity as well, in order to reach a better understanding of the mechanisms
293 involved in the natural enemies hypothesis in forests.
294 Finally, we suggest that more attention is given to studies involving multiple taxa of NE and, ideally
295 that more standardized methods are applied to different species of NE. Otherwise predicting global
296 responses of natural enemies' communities to tree diversity will remain challenging.

Declaration of Competing Interests

None.

Data accessibility

Data and supplementary material are available online from the Data INRAE repository: https://doi.org/10.15454/KS8TLS

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Figures

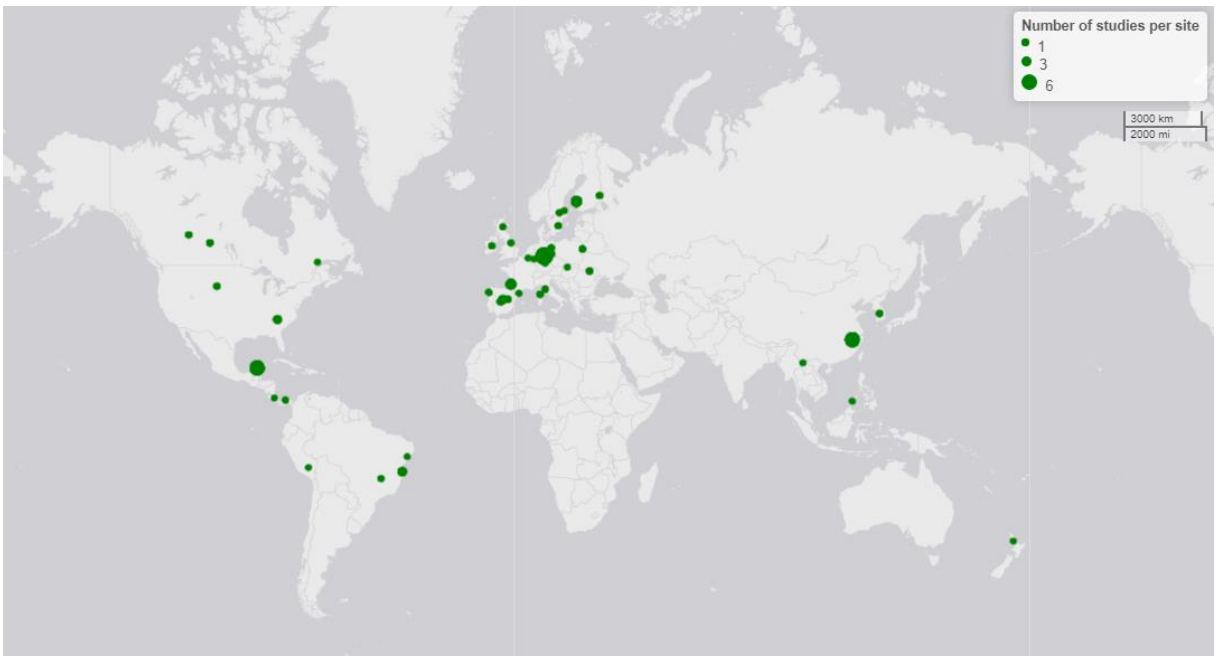

Figure 1. Map of study sites of the 65 articles included in the meta-analysis. Dot sizes are proportional to the number of studies conducted at the same study site.

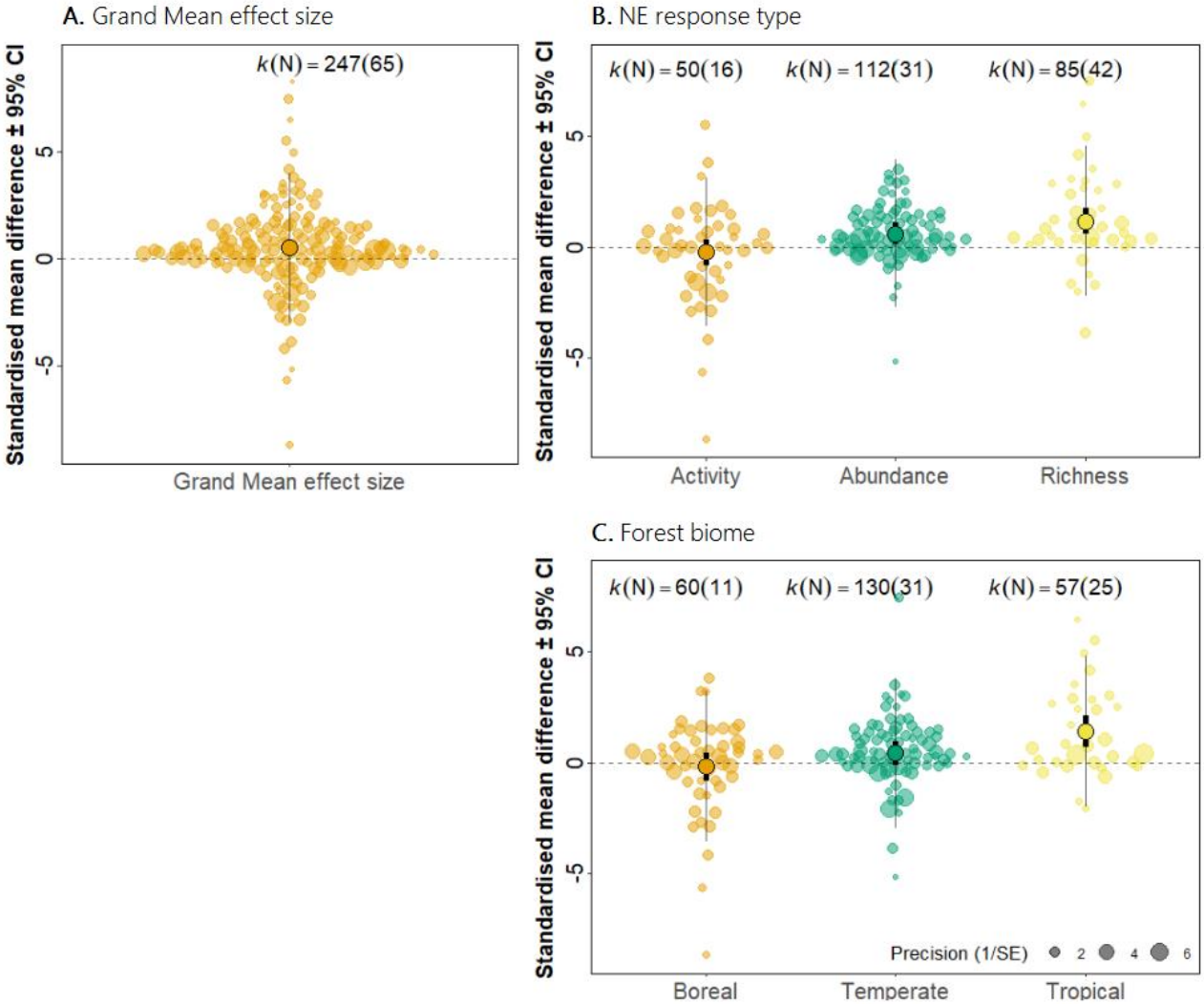

Figure 2. Summary of tree diversity effects on natural enemies (NE). (a) Grand mean effect size. (b) Effect of NE responses type. (c) Effect of the forest biome. Dots and error bars represent model parameter estimates and corresponding 95% confidence intervals. Black circled dots represent the mean effect size for each moderator. Vertical thick lines represent the 95% confidence interval. Thin vertical lines represent the prediction interval, which is the expected range of true effects in similar studies. K (n) represent the number of case studies (K) and the number of primary studies (n) for each moderator level.