

1 **Climate affects neighbour-induced changes in leaf chemical defences and tree**
2 **diversity-herbivory relationships**

3 Authors:

4 Charlotte Poeydebat^{1,2}, Hervé Jactel^{1,2}, Xoaquín Moreira³, Julia Koricheva⁴, Nadia Barsoum⁵,
5 Jürgen Bauhus⁶, Nico Eisenhauer^{7,8}, Olga Ferlian^{7,8}, Marta Francisco³, Felix Gottschall^{7,8},
6 Dominique Gravel⁹, Bill Mason¹⁰, Evalyne Muiruri⁴, Bart Muys¹¹, Charles Nock^{12,13}, Alain
7 Paquette¹⁴, Quentin Ponette¹⁵, Michael Scherer-Lorenzen¹³, Victoria Stokes¹⁰, Michael
8 Staab¹⁶, Kris Verheyen¹⁷ and Bastien Castagneyrol^{1,2}

9
10 Institutions and addresses:

11 ¹ INRAE, UMR 1202 BIOGECO, F-33610 Cestas, France

12 ² Université de Bordeaux, BIOGECO, UMR 1202, F-33400 Talence, France

13 ³ Misión Biológica de Galicia (MBG-CSIC), Apartado de correos 28, 36080 Pontevedra, Galicia,
14 Spain

15 ⁴ Department of Biological Sciences, Royal Holloway University of London, Egham, Surrey
16 TW20 0EX, United Kingdom

17 ⁵ Forest Research, Alice Holt Lodge, Farnham, Surrey, GU10 4LH, United Kingdom

18 ⁶ Chair of Silviculture, University of Freiburg, Tennenbacher Straße 4, 79106 Freiburg,
19 Germany

20 ⁷ German Centre for Integrative Biodiversity Research (iDiv) Halle-Jena-Leipzig, Deutscher
21 Platz 5e, 04103 Leipzig, Germany

22 ⁸ Institute of Biology, Leipzig University, Deutscher Platz 5e, 04103 Leipzig, Germany

23 ⁹ Département de biologie, Université de Sherbrooke, Sherbrooke, QC, Canada

24 ¹⁰ Forest Research, Northern Research Station, Roslin Midlothian EH25 9SY, United Kingdom

25 ¹¹ Division of Forest, Nature and Landscape, Department of Earth and Environmental Sciences,
26 KU Leuven, Leuven, Belgium

27 ¹² Department of Renewable Resources, University of Alberta, Edmonton, AB, Canada

28 ¹³ Faculty of Biology, Department of Geobotany, University of Freiburg, Schänzlestrasse 1,
29 Freiburg, Germany

30 ¹⁴ Centre for Forest Research, Université du Québec à Montréal, C.P. 8888, succ. Centre-ville,
31 Montreal, QC, Canada

32 ¹⁵ Faculty of Bioscience Engineering & Earth and Life Institute, Université catholique de
33 Louvain, 1348, Louvain-la-Neuve, Belgium

34 ¹⁶ Nature Conservation and Landscape Ecology, Faculty of Environment and Natural
35 Resources, University of Freiburg, Tennenbacher Straße 4, 79106 Freiburg, Germany

36 ¹⁷ Forest & Nature Lab, Department of Environment, Ghent University, Melle-Gontrode,
37 Belgium

38
39 Author for correspondence:

40 Charlotte Poeydebat, charlotte.poeydebat@zaclys.net

41

42 **Abstract**

- 43 1. Associational resistance theory predicts that insect herbivory decreases with increasing
44 tree diversity in forest ecosystems. However, the generality of this effect and its underlying
45 mechanisms are still debated, particularly since evidence has accumulated that climate
46 may influence the direction and strength of the relationship between diversity and
47 herbivory.
- 48 2. We quantified insect leaf herbivory and leaf chemical defences (phenolic compounds) of
49 silver birch (*Betula pendula*) in pure and mixed plots with different tree species
50 composition across twelve tree diversity experiments in different climates. We investigated
51 whether the effects of neighbouring tree species diversity on insect herbivory in birch, *i.e.*
52 associational effects, were dependent on the climatic context, and whether neighbour-
53 induced changes in birch chemical defences were involved in associational resistance to
54 insect herbivory.
- 55 3. We showed that herbivory on birch decreased with tree species richness (*i.e.* associational
56 resistance) in colder environments but that this relationship faded as mean annual
57 temperature increased.
- 58 4. Birch leaf chemical defences increased with tree species richness but decreased with the
59 phylogenetic distinctiveness of birch from its neighbours, particularly in warmer and more
60 humid environments.
- 61 5. Herbivory was negatively correlated with leaf chemical defences, particularly when birch
62 was associated with closely related species. The interactive effect of tree diversity and
63 climate on herbivory was partially mediated by changes in leaf chemical defences.
- 64 6. Our findings confirm that tree species diversity can modify the leaf chemistry of a focal
65 species, hence its quality for herbivores. They further stress that such neighbour-induced
66 changes are dependent on climate and that tree diversity effects on insect herbivory are
67 partially mediated by these neighbour-induced changes in chemical defences.
- 68 7. Future studies should investigate i) which tree species traits, ii) how tree species
69 intermingling pattern and iii) to what extent climatic context ultimately affect associational
70 resistance in mixed forests.

71 **Keywords**

72 Associational resistance, *Betula pendula*, biodiversity, leaf phenolics, mixed forests,
73 phylogenetic diversity, plant-insect interactions, TreeDivNet

74 **Introduction**

75 The influence of plant species diversity on plant-herbivore interactions is an old but still topical
76 question for ecologists (Castagneyrol, Kozlov, Poeydebat, Toigo, & Jactel, 2019; Siemann,
77 Tilman, Haarstad, & Ritchie, 1998). Ecological studies in forests have demonstrated that
78 increased tree species diversity generally leads to lower amount of damage caused by insect
79 herbivores, a phenomenon known as associational resistance (Barbosa *et al.*, 2009;
80 Castagneyrol, Jactel, Vacher, Brockerhoff & Koricheva, 2014; Iverson *et al.*, 2014). But several
81 other studies have also reported no change (Haase *et al.*, 2015) or even increased insect
82 herbivory when mixing tree species, *i.e.* associational susceptibility (Castagneyrol, Jactel, &
83 Moreira, 2018; Schuldt *et al.*, 2010). These inconsistent findings demonstrate the need for
84 improved understanding of ecological processes underlying tree diversity effects on insect
85 herbivory in forests.

86 Early attempts to explain associational resistance were mainly based on processes determined
87 by host plant density (*e.g.* the resource concentration hypothesis, Hambäck, Inouye,
88 Andersson, & Underwood, 2014), or mediated by natural enemies (*e.g.* the natural enemies
89 hypothesis, Moreira, Abdala-Roberts, Rasmann, Castagneyrol & Mooney, 2016) or by non-host
90 volatile chemical compounds (*e.g.* the semiochemical diversity hypothesis, Jactel, Birgersson,
91 Andersson, & Schlyter, 2011). Only recently, researchers have recognized that associational
92 resistance could also result from changes in host traits, such as nutritional quality and
93 production of anti-herbivores defences, induced by heterospecific neighbours (Moreira,
94 Abdala-Roberts, Parra-Tabla, & Mooney, 2014; Glassmire *et al.*, 2016; Castagneyrol *et al.*,
95 2018). Indeed, several reviews have shown that tree diversity can promote plant productivity
96 (Zhang, Chen, & Reich, 2012; Jactel *et al.*, 2018), which in turn could result in reduced
97 production of leaf chemical defences because of a trade-off between growth and defences
98 (Herms & Mattson, 1992; Endara & Coley, 2011). Consistently, increased tree diversity was
99 found to be associated with lower concentrations of leaf chemical defences, including
100 polyphenols, tannins, glycosids and alkaloids (Castagneyrol *et al.*, 2018; Muiruri *et al.*, 2019;
101 Rosado-Sánchez, Parra-Tabla, Betancur-Ancona, Moreira, & Abdala-Roberts, 2018; Walter *et*
102 *al.*, 2012).

103 Assuming that tree species traits involved in interactions with herbivores or in resource
104 acquisition are phylogenetically conserved, greater tree phylogenetic diversity should amplify
105 trait dissimilarity between species (Srivastava, Cadotte, MacDonald, Marushia, & Mirotnick,
106 2012) and hence, the magnitude of associational resistance mechanisms including the effect
107 of tree diversity on defences. In particular, greater plant functional diversity is expected to i)
108 extend resource concentration effects to herbivore species with wider diet breadth
109 (Castagneyrol *et al.*, 2014), ii) foster host-finding disruption due to the greater complexity of
110 the visual and chemical environments (Jactel *et al.*, 2011), and iii) increase resource use
111 complementarity between plant species resulting in higher growth and lower defence levels.
112 Consistently, the degree of phylogenetic or functional dissimilarity between focal plant species
113 and their heterospecific neighbours was found to affect associational effects on herbivory, with
114 greater impacts than plant species richness *per se* in most cases (Castagneyrol *et al.*, 2014;
115 Dinnage, 2013; Schuldt *et al.*, 2014; Yguel *et al.*, 2011).

116 Until now, studies on associational resistance have largely overlooked possible interactions
117 with abiotic factors (but see Walter *et al.*, 2012, Kambach, Kühn, Castagneyrol, & Bruelheide,
118 2016). Yet, climate has well documented effects on herbivore activity, abundance and diversity,
119 as well as on plant growth and the production of plant anti-herbivore defences, including leaf
120 phenolics. This was demonstrated through both experiments (*e.g.* Pineau *et al.*, 2017;
121 Bauerfriend & Fischer, 2013) and observational studies along latitudinal and elevation
122 gradients (Kozlov, Lanta, Zverev, & Zvereva, 2015; Moreira *et al.*, 2018a; Moreira, Galman,
123 Francisco, Castagneyrol, & Abdala-Roberts, 2018b; Rodríguez-Castañeda, 2013; but see Moles,
124 Bonser, Poore, Wallis, & Foley, 2011; Anstett, Chen, & Johnson, 2016). Importantly, recent
125 studies showed an interplay between tree diversity and climatic conditions whereby climate
126 could alter the effect of tree diversity on ecosystem processes (Castagneyrol *et al.*, 2018; Jactel,
127 Poeydebat, Van Halder, & Castagneyrol, 2019; Ratcliffe *et al.*, 2017) and conversely, tree
128 diversity could buffer the adverse effect of extreme climatic events on trees (Jactel *et al.*,
129 2017). Being able to account for the effect of climate is therefore a major opportunity to
130 strengthen our understanding of the variability in the magnitude and direction of associational
131 effects in mixed forests.

132 Using a unique network of tree diversity experiments ranging from temperate to boreal
133 biomes (TreeDivNet; Paquette *et al.*, 2018), we quantified insect leaf herbivory and leaf

134 chemical defences (phenolic compounds) in silver birch (*Betula pendula*) in plots with different
135 tree species composition across twelve locations with different climates. First, we addressed
136 the effects of tree species diversity on insect herbivory and leaf chemical defences in silver
137 birch, asking which of tree species richness, phylogenetic diversity or their combination best
138 explained both response variables. We hypothesized that tree diversity was associated with
139 lower herbivory (associational resistance) and lower chemical defence levels (due to higher
140 complementarity and growth-defence trade-off), and that these effects were stronger when
141 considering phylogenetic distinctiveness of the focal species instead of species richness,
142 considering that phylogenetic diversity accounts for niche differentiation. Second, we tested
143 whether diversity-herbivory and diversity-defences relationships depended on climate. Since
144 there is no consensus in the available literature, we had no particular directional hypothesis
145 regarding the influence of climate. Finally, we tested whether climate and diversity effects on
146 insect herbivory were mediated by changes in leaf chemical defences. Our study is one of the
147 first to investigate defence-mediated associational effects on insect herbivory in relation with
148 the climatic context. We aimed at building toward a more comprehensive understanding of
149 the interactive effects of tree species diversity and climate on forest resistance to insect pests.

150 **Material and Methods**

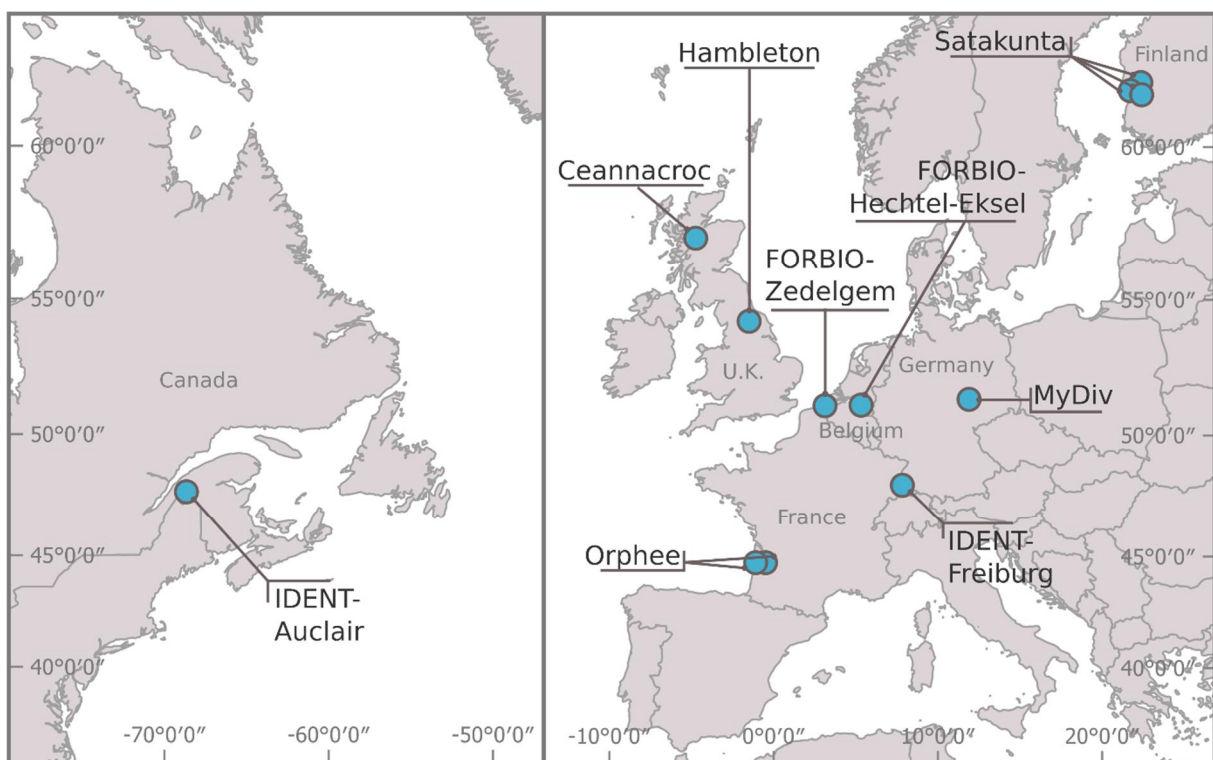
151 **Natural history**

152 The silver birch (*Betula pendula* Roth, Betulaceae) is a deciduous tree native to most of Europe
153 (Beck, Caudullo, de Rigo, & Tinner, 2016) that tolerates an extremely wide range of climatic
154 and edaphic conditions. In its native range, silver birch supports a large community of insect
155 herbivores, especially lepidopteran and hymenopteran (*i.e.* sawflies) leaf chewers and miners
156 (Beck *et al.*, 2016; Zúbrik, Kunca, & Csóka, 2013).

157 **Plot and tree selection in TreeDivNet experiments**

158 TreeDivNet consists of 27 long-term tree diversity experiments specifically designed to
159 investigate the effects of tree species diversity on forest functioning (Grossman *et al.*, 2018).
160 Because the experiments are globally distributed, TreeDivNet is particularly well suited to
161 explore how tree diversity effects on herbivory vary with climate. We collected data from
162 twelve sites belonging to six tree diversity experiments where silver birch was present (Fig. 1;
163 Supporting Information Table S1). These sites encompassed temperate and boreal biomes of

164 the northern hemisphere and spanned over 17 decimal degrees in latitude, covering about
165 half of the latitudinal span of silver birch (Beck *et al.*, 2016). At each site, we selected silver
166 birch monoculture plots and mixed species plots where silver birch was present. Tree species
167 richness in those mixtures ranged from two to six species (including silver birch) and included
168 broadleaved or coniferous species, or a mix of both. The species composition of mixture plots
169 varied among sites. At certain sites, species composition types were replicated in two to three
170 blocks. We randomly selected three to five birch trees in the core area of each experimental
171 plot (*i.e.* avoiding border trees to limit edge effects). The final dataset was derived from 564
172 trees planted in 157 plots.



173

174 *Figure 1. Map of the TreeDivNet experimental sites included in the study.*

175 **Leaf collection and damage assessment**

176 Fifty leaves per birch tree were haphazardly sampled in mid-July 2017 (2014 for the three
177 Finnish sites). We assessed insect leaf herbivory as the overall percentage of leaf area
178 removed by three common feeding guilds of insect herbivores: chewers, miners and
179 skeletonizers. We assigned each leaf to one of seven classes of damage: (A) 0 % of leaf area
180 removed, (B) 1 to 5%, (C) 6 to 15%, (D) 16 to 25%, (E) 26 to 50%, (F) 51 to 75%, and (G) 76 to
181 100%. To reduce unconscious bias in insect herbivory assessment, we split leaves from each

182 tree into two equal pools that were separately processed by two independent observers
183 unaware of leaf origin. Then, we aggregated insect herbivory estimates at the tree level by
184 averaging the median values of damage class of all leaves. In the case of the three Finnish sites
185 (Satakunta areas 1, 2 and 3), the methodology differed slightly but was still consistent (see
186 Muiruri *et al.*, 2019). On average, insect herbivores damaged 3.91% (\pm 2.60%) of leaf area
187 (damages ranged from 0.36 to 13.03% of leaf area; Supporting Information Table S2). We are
188 confident that we did not underestimate herbivory by overlooking missing leaves since leaves
189 did not start falling at the sampling time. The observed levels of insect herbivory were low and
190 comparable with those observed in other studies on silver birch (*e.g.* Castagneyrol *et al.*, 2018;
191 Kozlov *et al.*, 2015; Muiruri *et al.*, 2019).

192 **Phylogenetic isolation**

193 Given that tree species diversity effects on herbivores can be affected by phylogenetic
194 dissimilarity between the tree species in the mixture, we used phylogenetic information to
195 account for differences in tree species composition of mixed stands across the experiments
196 (Srivastava *et al.*, 2012). We used the *phylomatic* function from the *branching* package in R
197 (with tree R20120829; Chamberlain, 2018) to obtain an overall phylogenetic tree comprising
198 the overall pool of tree species (Supporting Information Fig. S2). Node ages down to family
199 level were derived from Magallón, Gómez-Acevedo, Sánchez-Reyes and Hernández-
200 Hernández (2015). Genus node ages were approximated by dividing the length of the edge
201 from the family node to the tip by two. The same was subsequently done for species nodes
202 considering edge length from the genus node to the tip. For each plot, we pruned the overall
203 phylogenetic tree to obtain a sub-tree corresponding to the pool of tree species present in the
204 plot.

205 Many metrics have been developed to characterize phylogenetic diversity of a pool of species
206 (Miller, Farine, & Trisos, 2017). Here, we computed Faith's total phylogenetic diversity (PD, *pd*
207 function in *picante* package; Kembel *et al.*, 2010), mean pairwise phylogenetic distance (MPD,
208 *mpd* function), mean phylogenetic distance between birch and associated species (β -MPD,
209 *comdist* function) and birch evolutionary distinctiveness (ED, *evol.distinct* function; Redding &
210 Mooers, 2006). PD and MPD are community-level phylogenetic diversity indices, whereas β -
211 MPD and ED are species-species indices representing the phylogenetic isolation of silver birch
212 from other tree species present in each plot. ED was eventually preferred to other

213 phylogenetic diversity metrics because it was less correlated with species richness (Supporting
214 Information Fig. S1).

215 **Climate data**

216 We extracted mean annual temperature and total annual rainfall averaged over the 1979-
217 2013 period (hereafter referred to as “temperature” and “rainfall” respectively) for each study
218 site using the Climatologies at High resolution for the Earth's Land Surface Areas dataset
219 (CHELSA; Karger *et al.*, 2017; Supporting Information Fig. S4a). In the ORPHEE experiment, half
220 of the plots were located in irrigated blocks sprinkled with 3 mm of water per night from May
221 to October. An annual surplus of 552 mm was thus added to the rainfall amount obtained
222 from the CHELSA database in these plots. To account for this additional irrigation treatment,
223 data collected in the ORPHEE experiment were considered as data from two distinct sites
224 (irrigated vs non-irrigated). Overall, our network of tree diversity experiments covered a 17°
225 latitudinal gradient and encompassed 10°C of variation in the mean annual temperature and
226 964 mm of variation in the annual rainfall.

227 **Leaf phenolics**

228 Leaf phenolics have been reported to confer resistance against insect herbivores in several
229 tree species including birch (Forkner, Marquis, & Lill, 2004; Moreira *et al.*, 2018b; Riipi *et al.*,
230 2005) and therefore represent a suitable proxy for assessing leaf chemical defences (or leaf
231 nutritional quality to herbivores). We quantified the concentration of phenolic compounds on
232 a subsample of five birch leaves - with little (<5%) or no damage - per tree, following a
233 procedure based on ultra-high performance liquid chromatography (as in Moreira *et al.*,
234 2018b; Visakorpi, Riutta, Martinez-Bauer, Salminen, & Gripenberg, 2019). Following drying (at
235 45°C during 72 hours) and grinding of leaves, we extracted phenolic compounds from 20 mg
236 of powdered dry leaf tissue with 1 mL of 70% methanol in an ultrasonic bath for 15 min,
237 followed by centrifugation (Moreira *et al.*, 2014). We then transferred the extracts to
238 chromatographic vials. Ultra-High-Performance Liquid-Chromatograph (UHPLC Nexera LC-
239 30AD; Shimadzu) equipped with a Nexera SIL-30AC injector and one SPD-M20A UV/VIS
240 photodiode array detector was used to perform the chromatographic analyses. The
241 compound separation was carried out on a Kinetex™ 2.6 µm C18 82-102 Å, LC Column 100 ×
242 4.6 mm, protected with a C18 guard cartridge. The flow rate was 0.4 mL min⁻¹ and the oven

243 temperature was set at 25°C. The mobile phase consisted of two solvents: water-formic acid
244 (0.05%) (A) and acetonitrile-formic acid (0.05%) (B), starting with 5% B and using a gradient to
245 obtain 30% B at 4 min, 60% B at 10 min, 80% B at 13 min and 100 % B at 15 min. The injection
246 volume was 3 µL. We identified four groups of phenolic compounds: flavonoids, ellagitannins
247 and gallic acid derivates (hydrolysable tannins), proanthocyanidins (condensed tannins) and
248 hydroxycinnamic acid (precursors to lignins). We quantified flavonoids as rutin equivalents,
249 condensed tannins as catechin equivalents, hydrolysable tannins as gallic acid equivalents,
250 and precursors to lignins as ferulic acid equivalents (Moreira *et al.*, 2018a, b). Quantification
251 of these phenolic compounds was achieved by external calibration using calibration curves at
252 0.25, 0.5, 1, 2, and 5 µg mL⁻¹. Total phenolic concentration was equal to 334.57 ± 107.48 mg
253 g⁻¹ of leaf dry matter on average and ranged from 13.51 to 775.08 mg g⁻¹ (Supporting
254 Information Table S3).

255 **Statistical analyses**

256 First, we used linear mixed models (LMM) to test for the effects of tree species richness and
257 birch phylogenetic distinctiveness on insect herbivory and leaf phenolic concentration (two
258 normally distributed response variables). To test whether tree species richness, phylogenetic
259 distinctiveness of birch or the combination of both best predicted the response variables, we
260 built three models for each response variable with either (i) tree species richness, (ii) birch
261 evolutionary distinctiveness (ED) or (iii) tree species richness and birch ED (main effects plus
262 interaction) as predictors. We calculated the Akaike Information Criterion corrected for small
263 sample size (AICc) of each model to identify the best model – with the lowest AICc - for a given
264 response variable (Burnham & Anderson, 2002; Johnson & Omland, 2004). If the AICc
265 difference between two models was less than two, they were considered equally likely. The
266 best herbivory and phenolic models were used in the subsequent analyses.

267 Second, we used LMMs to test for the effects of climate on insect herbivory and leaf phenolic
268 concentration. For each response variable, we used the full version of the best model(s) (with
269 the lowest AICc) from the first step to which we added temperature and rainfall main effects,
270 as well as all two- and three-ways interactions.

271 Third, we tested whether the variability in insect herbivory was accounted for by phenolic
272 concentration. Specifically, we included leaf phenolic concentration as a covariate in the full

273 model(s) from the second step. Two-ways interactions involving leaf phenolic concentration
274 and either temperature, rainfall or tree diversity were also included in the model(s) to test for
275 interactive effects. By comparing results of insect herbivory models without (second step) vs
276 with leaf phenolics (third step), we tested whether the effects of tree diversity and climate on
277 insect herbivory were mediated by changes in leaf chemical defences. That would be the case
278 if a significant effect of tree species diversity and/or climate on insect herbivory became non-
279 significant after including leaf phenolic concentration as a covariate.

280 In the last two steps, full models were simplified following a backward selection approach,
281 which consisted of sequentially dropping the terms with the lowest impact on model fit,
282 starting with the highest order interactions. Model simplification was done by using log-
283 likelihood tests based on a χ^2 distribution with significance threshold set at $\alpha = 0.05$.

284 In all models, we accounted for the hierarchical structure of data by using Plot nested within
285 Block, nested within Site, as a random factor (*i.e.* 1|Site/Block/Plot in R syntax). By doing so,
286 we accounted for the hierarchical structure of the data, as well as potential variance in the
287 response variables arising from uncontrolled factors such as site location within birch
288 distribution range, local soil properties, species pool, or tree planting density. Because of the
289 nature of the TreeDivNet network, these factors were confounded with the Site. To further
290 ensure that herbivory or defence patterns were not driven by uncontrolled factors at the site
291 level, we regressed the residuals of the final models against latitude and climatic conditions
292 (Supporting Information Fig. S5). We found no particular pattern in the residuals suggesting
293 that no 'hidden treatments' at site level (associated with their latitudinal position) might have
294 biased our test of diversity and climate effects.

295 In all models, predictors were scaled and centred, which made it possible to compare the
296 magnitude of the effects even when interaction terms were significant (Schielzeth, 2010).
297 Collinearity among all predictors was found to be weak enough to limit inflation of the
298 variance of estimated model parameters (variation inflation factors [VIFs] less than two).
299 Model parameters were estimated by restricted likelihood estimation and the significance (α
300 = 0.05) of the regression coefficients was tested with Student t-tests and Satterthwaite's
301 approximation for degrees of freedom. We evaluated model fit by calculating the percentage
302 of variance explained by fixed (R^2_m) and by fixed plus random effects (R^2_c) (Nakagawa &
303 Schielzeth, 2013).

304 Concentrations of all types of phenolic compounds were positively correlated with each other
305 (Supporting Information Fig. S6), which made it inappropriate to use all phenolic types as
306 predictors of insect herbivory in the same model (inflation of the variance of estimated model
307 parameters). We therefore ran separate models for each type of phenolics. Concentrations of
308 all types of phenolic compounds and concentrations of total phenolics co-varied with climate
309 and diversity predictors, *i.e.* direction of effects were consistent across phenolic types (Table
310 1; Supporting Information Table S4). We additionally summarized the information on phenols
311 using a principal component analysis (PCA) with the concentrations of the four individual
312 phenolic compounds (Supporting Information Fig. S7). The three first components of the PCA
313 altogether explained 92% of the variance and the points were well homogeneously
314 distributed. The first axis was associated with the concentrations of flavonoids and
315 hydrolysable tannins, the second axis with the concentration of condensed tannins and the
316 third with the concentration of lignin. Besides, PCA coordinates on the first three axes were
317 all positively correlated with the concentration of total phenolics (Supporting Information Fig.
318 S8). Based on these elements, we choose to present the results for total phenolic
319 concentration only in the main text.

320 All analyses were conducted in R (version 3.5.1; R Core Development Team, 2013) with the
321 following packages: lmerTest (Kuznetsova, Brockhoff, & Christensen, 2017), car (Fox &
322 Weisberg, 2018), and MuMIn (Barton, 2018).

323 **Results**

324 **Tree species diversity effects on insect herbivory and leaf phenolics**

325 We found no significant effect of species richness or birch evolutionary distinctiveness (ED)
326 *per se* on insect herbivory, and no interactive effect of the two diversity metrics either (Table
327 1a). The herbivory model with species richness and the herbivory model with birch ED had the
328 lowest AICc values, not differing by more than two units (Table 1a). These two models were
329 thus used in the subsequent analyses while the herbivory model with both diversity metrics,
330 which had a higher AICc value (Table 1a), was eliminated.

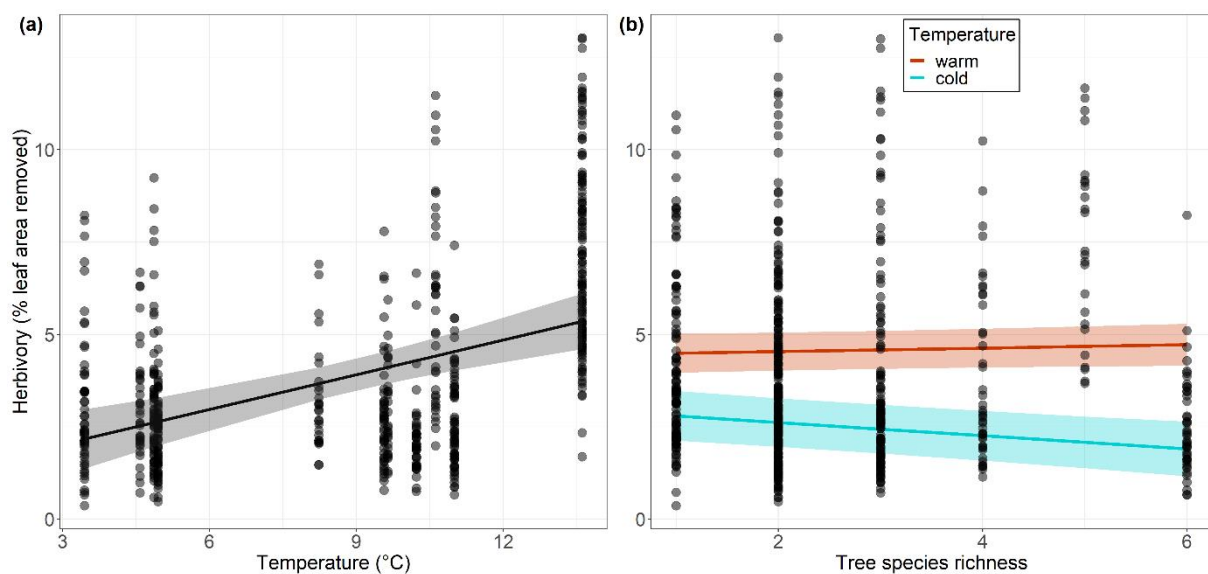
331 We found a significant negative effect of birch ED on leaf phenolic such that birch leaves were
332 less defended when birches were more phylogenetically distinct from their neighbours (Table
333 1b). In contrast, we found a significant and positive effect of tree species richness on leaf

334 phenolic concentration. The phenolics model with birch ED only had a lower AICc value than
335 the model with species richness only (Table 1b), but both of these models had higher AICc
336 values than the model with both diversity variables included (Table 1b). Hence, the best
337 phenolics model that was used in subsequent analyses was the model with both species
338 richness and birch ED.

339 Effects of climate and tree diversity on insect herbivory

340 We found that insect herbivory on birch leaves significantly increased with increasing
341 temperature (Fig. 2a; Table 2a) both in the model with tree species richness and in the model
342 with birch ED. Rainfall had no significant effect on insect herbivory.

343 The effect of tree species richness on insect herbivory was contingent upon temperature
344 (significant species richness \times temperature interaction; Table 2a). In particular, insect
345 herbivory decreased with increasing tree species richness at low temperatures but was not
346 affected by tree species richness at higher temperatures (Fig. 2b). In the final simplified model,
347 tree species richness and temperature collectively explained 22% of the variability in insect
348 herbivory ($R^2_m = 0.22$; $R^2_c = 0.59$). By contrast, there was no significant effect of the
349 interaction between birch ED and temperature or rainfall (Table 2a). Independent effects of
350 birch ED and temperature collectively explained 21% of the variability in insect herbivory (R^2_m
351 $= 0.21$; $R^2_c = 0.59$).



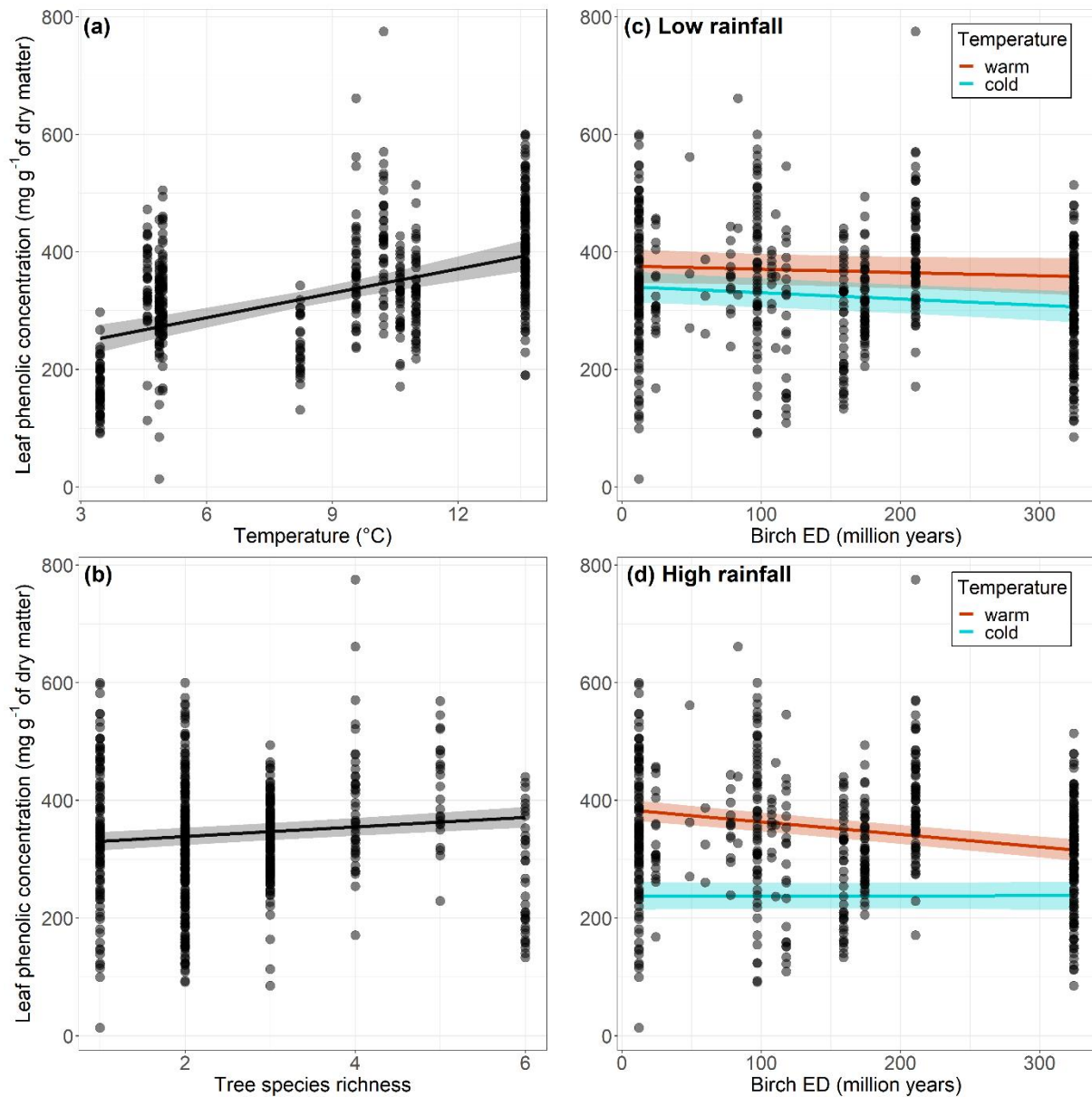
352

353 *Figure 2. Relationships (a) between insect herbivory on silver birch leaves and mean annual temperature*
354 *and (b) between insect herbivory and tree species richness for two contrasted temperature levels. The*

355 *figure shows observed data (points) as well as model predictions (solid lines) and standard errors (shaded*
356 *areas). In panel (a), species richness was set at a median value to compute predictions. “Warm” and*
357 *“cold” temperature levels corresponded to 0.25 and 0.75 quartiles of the observed temperature range,*
358 *respectively.*

359 **Effects of climate and tree diversity on leaf phenolic concentration**

360 Leaf phenolic concentration significantly increased with increasing temperature and tended
361 to decrease with increasing rainfall but not significantly (Table 2b; Fig 3a). In addition, leaf
362 phenolic concentration significantly increased with species richness (Table 2b; Fig. 3b)
363 regardless of the climate (no significant interactions with rainfall or temperature). In contrast,
364 the effect of birch ED on leaf phenolic concentration was contingent upon temperature and
365 rainfall conditions (significant birch ED × temperature × rainfall interaction; Table 2b).
366 Specifically, leaf phenolic concentration decreased with increasing birch phylogenetic
367 distinctiveness independently of the temperature at low rainfall level (Fig. 3c), but decreased
368 more markedly with increasing phylogenetic distinctiveness of birch in warm conditions only
369 at high rainfall level (Fig. 3d). In the final simplified model, climate and tree species diversity
370 collectively explained 46% of the variability in phenolic concentration of birch leaves ($R^2_m =$
371 0.46 ; $R^2_c = 0.67$).



372

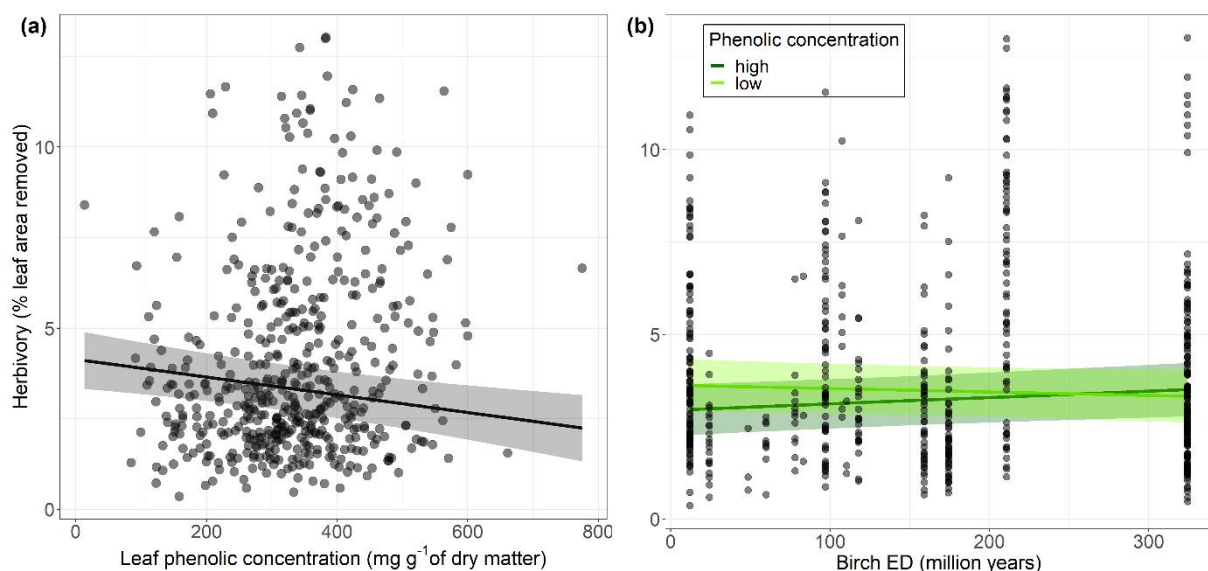
373 *Figure 3. Leaf phenolic concentration in birch leaves as a function of (a) temperature, (b) tree species*
 374 *richness and as a function of birch evolutionary distinctiveness (ED) for two contrasted levels of*
 375 *temperature under two contrasted levels of rainfall (c and d). The figure shows observed data (points)*
 376 *as well as model predictions (solid lines) and standard errors (shaded areas). “Warm” and “cold”*
 377 *temperature levels corresponded to 0.25 and 0.75 quartiles of the observed temperature range,*
 378 *respectively. “Low” and “high” rainfall levels corresponded to 0.25 and 0.75 quartiles of the observed*
 379 *rainfall range, respectively. The predictors that were not involved in the relationships shown were set at*
 380 *median values to compute predictions.*

381 **Indirect trait-mediated effects of tree diversity and climate on herbivory**

382 When we included leaf phenolic concentration as a covariate in the herbivory models – with
383 either species richness or birch ED - we found that insect herbivory decreased with increasing
384 leaf phenolic concentration in both cases (Table 3; Fig. 4a). In the two models, the positive
385 effect of temperature on insect herbivory remained significant (Table 3), which indicated that
386 the effect of temperature on insect herbivory was not mediated by leaf phenolics.

387 In the herbivory model with species richness, we found that the effect of species richness –
388 that was contingent upon temperature – became non-significant after including leaf phenolic
389 concentration as a covariate (Table 3), indicating that the effect of tree species richness on
390 insect herbivory was mediated by leaf phenolics. Temperature and leaf phenolic
391 concentration collectively explained 24% of the variability in insect herbivory ($R^2_m = 0.24$; R^2_c
392 $= 0.58$).

393 In the herbivory model with birch ED, we found that birch ED effect on insect herbivory was
394 contingent upon phenolic concentration in birch leaves (significant birch ED x phenolic
395 concentration interaction, Table 3). In particular, when birch leaves had low phenolic
396 concentration, insect herbivory decreased with increasing birch ED, while when birch leaves
397 had high phenolic concentration insect herbivory increased with increasing birch ED (Fig. 4b).
398 Temperature, birch ED and leaf phenolic concentration collectively explained 25% of the
399 variability in insect herbivory ($R^2_m = 0.25$; $R^2_c = 0.59$).



400

401 *Figure 4. Relationship (a) between insect herbivory and leaf phenolic concentration and (b) between*
402 *insect herbivory and birch evolutionary distinctiveness (ED) for different levels of leaf phenolic*

403 concentration. The figure shows observed data (points) as well as model predictions (solid lines) and
404 standard errors (shaded areas). “Low” and “high” phenolic concentration levels corresponded to 0.25
405 and 0.75 quartiles of the observed phenolic concentration range, respectively. The predictors that were
406 not involved in the relationships shown were set at median values to compute predictions.

407 **Discussion**

408 With this study, we showed that the effect of tree species diversity on insect herbivory on
409 silver birch leaves, *i.e.* associational effects, were climate-dependent and, in particular, varied
410 with temperature. Our findings also showed that tree species diversity modified chemical
411 defence levels in birch leaves and further suggested that such changes in leaf chemistry
412 induced by heterospecific neighbours were partly climate-dependent. Finally, we found that
413 associational effects were mediated by changes in defences under certain climatic conditions.
414 Below we discuss mechanisms underlying the observed patterns.

415 **Effects of tree diversity on insect herbivory are climate dependent**

416 We found no significant effects of either tree species richness or birch phylogenetic
417 distinctiveness *per se* on background levels of insect herbivory on birch. In fact, we found
418 evidence that tree diversity effects on herbivory were dependent on climate. This result could
419 partly explain the variable effects of tree diversity on herbivory previously reported in the
420 literature (Brezzi, Schmid, Niklaus, & Schuldt, 2017; Castagneyrol *et al.*, 2014; Jactel, Moreira,
421 & Castagneyrol, in press; Kambach *et al.*, 2016; Ratcliffe *et al.*, 2017; Schuldt *et al.*, 2010, 2014;
422 Vehviläinen, Koricheva, & Ruohomäki, 2007; Wein *et al.*, 2016) including in studies focusing
423 on birch trees (Castagneyrol *et al.*, 2018; Haase *et al.*, 2015; Muiruri *et al.*, 2019; Setiawan,
424 Vanhellefont, Baeten, Dillen, & Verheyen, 2014). Specifically, we provided evidence for
425 changes in associational effects along the mean annual temperature gradient: associational
426 resistance of birch to insect herbivory occurred in cold conditions whereas no associational
427 effects could be detected in warm conditions. The mitigation of associational resistance with
428 increasing temperature could be due to the higher proportion of generalist (*vs* specialist)
429 herbivore species in warmer regions (Forister *et al.*, 2015), that are less affected or even
430 benefit from plant diversity (Castagneyrol *et al.*, 2014). This finding might also be explained by
431 the greater abundance and activity of herbivores in warmer climate that may in turn lower
432 the resistance of mixed plant communities to herbivores. Supporting this view, associational

433 resistance to the bean beetle, *Callosobruchus maculatus*, was found to decrease with the
434 population density of this herbivore, likely because of conspecific avoidance behaviour
435 (Merwin, Underwood, & Inouye, 2017; but see Fernandez-Conradi, Jactel, Hampe, Leiva, &
436 Castagneryol, 2017). Higher herbivore density may also increase the probability for a host tree
437 to be located and attacked, simply because proportionally more individuals will pass through
438 the net of resistance mechanisms (*e.g.* resource concentration effect, host-finding disruption
439 or predation by natural enemies), resulting in lower apparent resistance to herbivores. In
440 support of this density-dependence hypothesis, our results showed that background insect
441 herbivory on birch leaves, although low, markedly increased with increasing mean annual
442 temperature (Kozlov *et al.*, 2015; Wang *et al.*, 2016). Several mechanisms have been proposed
443 to explain the positive effect of temperature on herbivory, including direct effects on
444 herbivores' developmental rate, winter survival and activity and indirect effects through
445 reduced plant nutritional quality inducing compensatory feeding (Bale *et al.*, 2002; Bauerfeind
446 & Fisher, 2013; Garibaldi, Kitzberger, & Ruggiero, 2011; Klapwijk, Ayres, Battisti, & Larsson,
447 2012).

448 We found no effect of rainfall on insect herbivory, neither directly nor through changes in the
449 herbivore response to tree diversity. Yet, drought-induced water stress is known to increase
450 tree susceptibility to defoliators (Carnicer *et al.*, 2011; Jactel *et al.*, 2012), and a previous study
451 reported an increase in insect herbivory on birch under drought (Castagneryol *et al.*, 2018).
452 We could not assess the effect of drought *per se* in the present study, and it is possible that
453 annual rainfall does not reflect water availability to trees because of site-specific topology or
454 edaphic conditions. Besides, ectophagous (skeletonizers and chewers) and endophagous
455 (miners) herbivores may respond inconsistently to rainfall conditions because they live on the
456 surface vs inside the leaves, which could also explain the absence of an overall response since
457 we pooled the two groups. Therefore, the lack of effect of rainfall on herbivory in the present
458 study should be interpreted with caution and this question should be further explored.

459 **Levels of leaf defences are shaped by both tree diversity and climate**

460 Our results showed that tree diversity modifies leaf chemistry of focal birches – and hence
461 their quality for herbivores. Specifically, the concentration of leaf phenolics increased with
462 increasing tree species richness, but decreased with increasing birch evolutionary
463 distinctiveness, used as a proxy for birch functional distinctiveness in experimental plots

464 (Srivastava *et al.*, 2012). Positive effect of plant species diversity on plant chemical defences
465 have been previously reported in birch (Castagneyrol *et al.*, 2018; Muiruri *et al.*, 2019) and
466 other plant species (Bustos-Segura, Poelman, Reichelt, Gershenzon, & Gols, 2017; Kostenko,
467 Mulder, Courbois, & Bezemer, 2017; Moreira *et al.*, 2014). The underlying mechanisms
468 however are poorly understood and the opposing effects of species richness and functional
469 diversity suggest they are complex. On the one hand, defence induction in richer plant
470 community could arise in response to greater herbivory (Karban & Baldwin, 1997) due to
471 associational susceptibility. However, herbivore-mediation of species richness effects on
472 defences seems unlikely in our case since our results mainly report associational resistance
473 (Fig. 2b) and we found a negative association between herbivory and defence concentration
474 (Fig. 4a). On the other hand, it is plausible that the production of leaf phenolics reflected a
475 trade-off between growth and defences. Indeed, assuming that ecologically important traits
476 are phylogenetically conserved, increased allocation to growth in plots with functionally
477 dissimilar species (*e.g.* through complementarity or facilitation) could lead to a concomitant
478 reduction in defence investment (Bryant, Chapin, & Klein, 1983; Herms & Mattson, 1992). In
479 this sense, studies have reported that experimental manipulation of resource availability (*e.g.*
480 nutrients or water) can lead to concomitant and opposite modulations of growth and defence
481 production (Gutbrodt, Dorn, & Mody, 2012; Lange *et al.*, 2019). This process could be
482 particularly strong in birch, a fast-growing, resource-acquisitive species. Consistently, a recent
483 study found that tree species composition affected leaf chemistry in birch, with less defence
484 compounds in phylogenetically more diverse mixtures (Castagneyrol *et al.*, 2018).

485 A meta-analysis by Koricheva, Larsson, Haukioja and Keinänen (1998) supports the view that
486 tree diversity primarily affects the local abiotic conditions (specifically nutrient, water or light
487 availability) and that such effects subsequently shape plant secondary chemistry. In particular,
488 studies have demonstrated that crown illumination can affect leaf chemical composition, with
489 shading associated with lower carbohydrate and phenol concentrations in leaves of birch trees
490 (Henriksson *et al.*, 2003) and other species (Larsson, Wirén, Lundgren, & Ericsson, 1986; Mole,
491 Ross, & Waterman, 1988). The opposing effects of tree species richness and birch phylogenetic
492 distinctiveness on birch leaf phenolics could both relate to the relative heights or growth rates
493 of the trees present in the plots and the light available to birch trees. Indeed, birch is a fast-
494 growing, early successional species that is expected to be more shaded in monocultures or in

495 plots where it is present at high density (self-shading), than in mixtures where it is present at
496 lower density and mixed with slow-growing tree species. In our study, species richness
497 increase was correlated with the probability to include broadleaved species growing slower
498 than birch trees and with a reduction of birch proportion (Supporting Information Figs. S2 and
499 S3). Hence, the positive effect of species richness on leaf phenolic concentration in birch
500 leaves might be explained by a reduction of shading in species-richer mixtures. On the
501 opposite, the increase of birch phylogenetic distinctiveness was correlated with the
502 proportion of fast growing coniferous (vs broadleaved) neighbours such as larches or pines
503 (Supporting Information Figs. S2 and S3) that were generally taller than birch trees. The
504 decrease of leaf phenolic concentration with birch phylogenetic distinctiveness could
505 therefore result from lower light availability in plots where birch is more phylogenetically
506 isolated (mixed with a greater proportion of conifers). However, birches are able to adapt their
507 crown architecture to better compete with their neighbours for light acquisition (Lintunen &
508 Kaitaniemi, 2010), therefore potentially limiting the impact of neighbours on crown
509 illumination and leaf chemistry and explaining the relatively low phenolic concentration
510 changes observed along tree diversity gradients.

511 Because our study was not designed to determine the mechanisms underlying neighbour-
512 induced changes in leaf chemical defences, nor did it include tree growth or abiotic factors
513 measurements, our lines of arguments are mostly speculative. Few studies have explicitly
514 addressed the implication of growth-defence trade-offs in associational effects and they were
515 inconclusive (Moreira *et al.*, 2014; Rosado-Sánchez, Parra-Tabla, Betancur-Ancona, Moreira,
516 & Abdala-Roberts, 2017). Future studies should specifically investigate the role that tree
517 relative heights and architectures play in neighbour-induced changes of focal species
518 chemistry.

519 We found that the concentration of chemical defences increased with temperature, which
520 contrasts with the results of previous studies on oaks and birches in temperate and boreal
521 biomes (Kuokkanen, Julkunen-Tiitto, Keinänen, Niemelä, & Tahvanainen, 2001; Moreira *et al.*,
522 2018a). Although there is ample literature on the variation of plant defences along climatic
523 gradients, there is no consensus on the strength and direction of this relationship (Moles *et*
524 *al.*, 2011). Interestingly, we showed that climate also affected leaf phenolic concentration
525 indirectly by modulating the tree diversity-defences relationships. Specifically, decrease in

526 chemical defence levels of birch associated with greater tree phylogenetic diversity were
527 stronger in warm and humid conditions. This indicates that climate and tree species
528 composition jointly determined tree investment in chemical defences, likely through growth-
529 defence trade-offs.

530 **Do leaf chemical defences mediate effects of climate and diversity on insect herbivory?**

531 We found a negative relationship between leaf phenolic concentration and insect herbivory,
532 supporting the view that these secondary metabolites act as defences against herbivores (in
533 addition to being involved in other physiological processes; Forkner *et al.*, 2004; Harborne &
534 Williams, 2000).

535 We found evidence that the effect of temperature on leaf herbivory was independent of the
536 level of chemical defences. However, our results showed that the interactive effects of
537 temperature and tree species richness on insect herbivory were mediated by changes in leaf
538 chemical defence levels. This finding suggests that defence-mediated associational effects on
539 insect herbivory are also climate-dependent. In our case, such effects were only observed in
540 cold climates where chemical defences levels were low and where an increase in defences
541 may have a stronger effect on background insect herbivory levels.

542 We found that the effect of birch phylogenetic distinctiveness on herbivory varied with the
543 levels of chemical defences in birch leaves. Specifically, associational effects shifted from
544 resistance to susceptibility with the increase of leaf phenolics concentration. This finding
545 suggests that mechanisms involved in birch associational resistance against herbivores, other
546 than chemical defence, might have been at play (*e.g.* host-finding disruption, and resource
547 dilution), and that an undetermined factor was simultaneously controlling the concentration
548 of leaf chemical defences and interfering with these mechanisms. Forest structure, and more
549 specifically relative heights of tree species, may for instance influence at the same time (i) leaf
550 chemistry of a focal species by affecting crown illumination (Koricheva *et al.*, 1998) and the
551 synthesis of photo-protective flavonoids (Agati & Tattini, 2010) and (ii) the apparency of this
552 focal species to herbivores (Castagneyrol *et al.*, 2019; Damien *et al.*, 2016). In addition,
553 nutrient availability may affect growth of trees and the concentration of carbon-based
554 defences in leaves (Bryant *et al.*, 1983; Koricheva *et al.*, 1998). In turn, tree growth, as jointly
555 determined by tree diversity (the relative competitive ability of the species) and nutrient

556 availability, could affect apparency of the focal species to herbivores, as well as the abundance
557 and diversity of canopy arthropods (Stone, Gehring, & Whitham, 2010) with consequences for
558 multitrophic interactions.

559 **Conclusion**

560 By taking advantage of an international network of tree diversity experiments and a
561 standardized sampling protocol, we addressed the independent and interactive effects of tree
562 species diversity and climate on tree-herbivore interactions in temperate and boreal forests.
563 Altogether, our findings show that insect herbivory depends on a complex interplay between
564 tree species diversity and climatic conditions, and that diversity effects on insect herbivory are
565 partially mediated by neighbour-induced changes in leaf chemical defences. Our findings also
566 confirm that tree species diversity can modify leaf chemistry of a focal species – and hence its
567 quality for herbivores - but further suggest that such neighbour-induced changes are
568 dependent on climate. Nevertheless, our approach remains correlative in essence and the
569 ecological mechanisms underlying such patterns need to be further elucidated. We also
570 acknowledge that a limitation of this study is that we could not well control for the influence
571 of the position of the sites within the distribution range of birch (e.g. marginal or central), nor
572 for their spatial correlation, which could however influence tree-insect interactions through
573 local adaptation processes. Future studies should be specifically designed to investigate
574 whether diversity and climate interactively shape leaf chemistry of a focal host plant because
575 they jointly influence resource availability and their allocation to growth vs defences by trees.
576 Our study also supports the view that the phylogenetic or functional diversity of tree species
577 is complementary to species richness in predicting tree-herbivore relationships, likely because
578 it accounts for additional information relative to niche differentiation and functional
579 dissimilarities between tree species. Finally, our findings suggest that tree diversity effects on
580 herbivory levels should be viewed as a balance between multiple processes arising from
581 different attributes of tree diversity (inter-specific variation of different traits). Future
582 research should investigate which traits of tree species drive associational effects on herbivory
583 and address simultaneously multiple underlying mechanisms. For instance, it would be
584 particularly interesting to explore the role of forest structure and tree spatial arrangement in
585 associational effects, as it may be implied in both neighbour-induced changes in chemical
586 defences through effects on individual crown illumination, as well as in focal plant apparency.

587 Importantly, the climatic context in which plant-herbivore interactions occur should be
588 accounted for in future studies for a better understanding of the processes at play. By doing
589 so, the study of tree diversity effects on tree resistance to insect herbivores interactions will
590 move toward a more predictive framework.

591 **References**

- 592 Agati, G., & Tattini, M. (2010). Multiple functional roles of flavonoids in photoprotection: Letters. *New*
593 *Phytologist*, 186(4), 786–793. doi: [10.1111/j.1469-8137.2010.03269.x](https://doi.org/10.1111/j.1469-8137.2010.03269.x)
- 594 Anstett, D. N., Chen, W., & Johnson, M. T. J. (2016). Latitudinal Gradients in Induced and Constitutive
595 Resistance against Herbivores. *Journal of Chemical Ecology*, 42(8), 772–781. doi: [10.1007/s10886-016-](https://doi.org/10.1007/s10886-016-0735-6)
596 [0735-6](https://doi.org/10.1007/s10886-016-0735-6)
- 597 Bale, J. S., Masters, G. J., Hodkinson, I. D., Awmack, C., Bezemer, T. M., Brown, V. K., ... Whittaker, J. B.
598 (2002). Herbivory in global climate change research: direct effects of rising temperature on insect
599 herbivores. *Global Change Biology*, 8(1), 1–16. doi: [10.1046/j.1365-2486.2002.00451.x](https://doi.org/10.1046/j.1365-2486.2002.00451.x)
- 600 Barbosa, P., Hines, J., Kaplan, I., Martinson, H., Szczepaniec, A., & Szendrei, Z. (2009). Associational
601 Resistance and Associational Susceptibility: Having Right or Wrong Neighbors. *Annual Review of*
602 *Ecology, Evolution, and Systematics*, 40(1), 1–20. doi: [10.1146/annurev.ecolsys.110308.120242](https://doi.org/10.1146/annurev.ecolsys.110308.120242)
- 603 Barton, K. (2018). MuMIn: Multi-Model Inference. R package version 1.42.1 (Version 1.42.1). Retrieved
604 from <https://CRAN.R-project.org/package=MuMIn>
- 605 Bauerfeind, S. S., & Fischer, K. (2013). Increased temperature reduces herbivore host-plant quality.
606 *Global Change Biology*, 19(11), 3272–3282. doi: [10.1111/gcb.12297](https://doi.org/10.1111/gcb.12297)
- 607 Beck, P., Caudullo, G., de Rigo, D., & Tinner, W. (2016). *Betula pendula*, *Betula pubescens* and other
608 birches in Europe: distribution, habitat, usage and threats. In J. San-Miguel-Ayanz, D. de Rigo, G.
609 Caudullo, T. Houston Durrant, & A. Mauri (Eds.), *European Atlas of Forest Tree Species* (pp. 70–73).
610 Luxembourg: Publication Office of the European Union.
- 611 Brezzi, M., Schmid, B., Niklaus, P. A., & Schuldt, A. (2017). Tree diversity increases levels of herbivore
612 damage in a subtropical forest canopy: evidence for dietary mixing by arthropods? *Journal of Plant*
613 *Ecology*, 10(1), 13–27. doi: [10.1093/jpe/rtw038](https://doi.org/10.1093/jpe/rtw038)
- 614 Bryant, J. P., Chapin, F. S., & Klein, D. R. (1983). Carbon/Nutrient Balance of Boreal Plants in Relation
615 to Vertebrate Herbivory. *Oikos*, 40(3), 357–368. doi: [10.2307/3544308](https://doi.org/10.2307/3544308)
- 616 Burnham, K. P., & Anderson, D. R. (2002). *Model selection and multi-modal inference: A practical*
617 *information theoretic approach* (Second edition, Vol. 2). New-York, NY: Springer.
- 618 Bustos-Segura, C., Poelman, E. H., Reichelt, M., Gershenzon, J., & Gols, R. (2017). Intraspecific chemical
619 diversity among neighbouring plants correlates positively with plant size and herbivore load but
620 negatively with herbivore damage. *Ecology Letters*, 20(1), 87–97. doi: [10.1111/ele.12713](https://doi.org/10.1111/ele.12713)
- 621 Carnicer, J., Coll, M., Ninyerola, M., Pons, X., Sanchez, G., & Penuelas, J. (2011). Widespread crown
622 condition decline, food web disruption, and amplified tree mortality with increased climate change-
623 type drought. *Proceedings of the National Academy of Sciences*, 108(4), 1474–1478. doi:
624 [10.1073/pnas.1010070108](https://doi.org/10.1073/pnas.1010070108)
- 625 Castagneyrol, B., Jactel, H., & Moreira, X. (2018). Anti-herbivore defences and insect herbivory:
626 Interactive effects of drought and tree neighbours. *Journal of Ecology*, 106(5), 2043–2057. doi:
627 [10.1111/1365-2745.12956](https://doi.org/10.1111/1365-2745.12956)

628 Castagneyrol, B., Jactel, H., Vacher, C., Brockerhoff, E. G., & Koricheva, J. (2014). Effects of plant
629 phylogenetic diversity on herbivory depend on herbivore specialization. *Journal of Applied Ecology*,
630 *51*(1), 134–141. doi: [10.1111/1365-2664.12175](https://doi.org/10.1111/1365-2664.12175)

631 Castagneyrol, B., Kozlov, M. V., Poeydebat, C., Toïgo, M., & Jactel, H. (2019). Associational resistance
632 to a pest insect fades with time. *Journal of Pest Science*, *93*(1), 427–437. doi: [10.1007/s10340-019-
633 01148-y](https://doi.org/10.1007/s10340-019-01148-y)

634 Chamberlain, S. (2018). brranching: Fetch 'Phylogenies' from Many Sources. R package version 0.3.0
635 (Version 0.3.0) [R]. Retrieved from <https://CRAN.R-project.org/package=brranching>

636 Damien, M., Jactel, H., Meredieu, C., Regolini, M., van Halder, I., & Castagneyrol, B. (2016). Pest
637 damage in mixed forests: Disentangling the effects of neighbor identity, host density and host
638 apparency at different spatial scales. *Forest Ecology and Management*, *378*, 103–110. doi:
639 [10.1016/j.foreco.2016.07.025](https://doi.org/10.1016/j.foreco.2016.07.025)

640 Dinnage, R. (2013). Phylogenetic diversity of plants alters the effect of species richness on invertebrate
641 herbivory. *PeerJ*, *1*, e93. doi: [10.7717/peerj.93](https://doi.org/10.7717/peerj.93)

642 Endara, M.-J., & Coley, P. D. (2011). The resource availability hypothesis revisited: a meta-analysis.
643 *Functional Ecology*, *25*(2), 389–398. doi: [10.1111/j.1365-2435.2010.01803.x](https://doi.org/10.1111/j.1365-2435.2010.01803.x)

644 Fernandez-Conradi, P., Jactel, H., Hampe, A., Leiva, M. J., & Castagneyrol, B. (2017). The effect of tree
645 genetic diversity on insect herbivory varies with insect abundance. *Ecosphere*, *8*(1), e01637. doi:
646 [10.1002/ecs2.1637](https://doi.org/10.1002/ecs2.1637)

647 Forister, M. L., Novotny, V., Panorska, A. K., Baje, L., Basset, Y., Butterill, P. T., ... Dyer, L. A. (2015). The
648 global distribution of diet breadth in insect herbivores. *Proceedings of the National Academy of
649 Sciences of the United States of America*, *112*(2), 442–447. doi: [10.1073/pnas.142304211](https://doi.org/10.1073/pnas.142304211)

650 Forkner, R. E., Marquis, R. J., & Lill, J. T. (2004). Feeny revisited: condensed tannins as anti-herbivore
651 defences in leaf-chewing herbivore communities of *Quercus*. *Ecological Entomology*, *29*(2), 174–187.
652 doi: [10.1111/j.1365-2311.2004.0590.x](https://doi.org/10.1111/j.1365-2311.2004.0590.x)

653 Fox, J., & Weisberg, S. (2018). *An R companion to applied regression* (Third Edition). Thousand Oaks,
654 CA: Sage Publications.

655 Garibaldi, L. A., Kitzberger, T., & Ruggiero, A. (2011). Latitudinal decrease in folivory within *Nothofagus*
656 *pumilio* forests: dual effect of climate on insect density and leaf traits? *Global Ecology and
657 Biogeography*, *20*(4), 609–619. doi: [10.1111/j.1466-8238.2010.00623.x](https://doi.org/10.1111/j.1466-8238.2010.00623.x)

658 Glassmire, A. E., Jeffrey, C. S., Forister, M. L., Parchman, T. L., Nice, C. C., Jahner, J. P., ... Dyer, L. A.
659 (2016). Intraspecific phytochemical variation shapes community and population structure for specialist
660 caterpillars. *New Phytologist*, *212*(1), 208–219. doi: [10.1111/nph.14038](https://doi.org/10.1111/nph.14038)

661 Grossman, J. J., Vanhellemont, M., Barsoum, N., Bauhus, J., Bruelheide, H., Castagneyrol, B., ...
662 Verheyen, K. (2018). Synthesis and future research directions linking tree diversity to growth, survival,
663 and damage in a global network of tree diversity experiments. *Environmental and Experimental
664 Botany*, *152*, 68–89. doi: [10.1016/j.envexpbot.2017.12.015](https://doi.org/10.1016/j.envexpbot.2017.12.015)

665 Gutbrodt, B., Dorn, S., & Mody, K. (2012). Drought stress affects constitutive but not induced herbivore
666 resistance in apple plants. *Arthropod-Plant Interactions*, *6*(2), 171–179. doi: [10.1007/s11829-011-
667 9173-0](https://doi.org/10.1007/s11829-011-9173-0)

668 Haase, J., Castagneyrol, B., Cornelissen, J. H. C., Ghazoul, J., Kattge, J., Koricheva, J., ... Jactel, H. (2015).
669 Contrasting effects of tree diversity on young tree growth and resistance to insect herbivores across
670 three biodiversity experiments. *Oikos*, *124*(12), 1674–1685. doi: [10.1111/oik.02090](https://doi.org/10.1111/oik.02090)

671 Hambäck, P. A., Inouye, B. D., Andersson, P., & Underwood, N. (2014). Effects of plant neighborhoods
672 on plant–herbivore interactions: resource dilution and associational effects. *Ecology*, *95*(5), 1370–
673 1383. doi: [10.1890/13-0793.1](https://doi.org/10.1890/13-0793.1)

674 Harborne, J. B., & Williams, C. A. (2000). Advances in flavonoid research since 1992. *Phytochemistry*,
675 *55*(6), 481–504. doi: [10.1016/S0031-9422\(00\)00235-1](https://doi.org/10.1016/S0031-9422(00)00235-1)

676 Henriksson, J., Haukioja, E., Ossipov, V., Ossipova, S., Sillanpaa, S., Kapari, L., & Pihlaja, K. (2003). Effects
677 of host shading on consumption and growth of the geometrid *Epirrita autumnata*: interactive roles of
678 water, primary and secondary compounds. *Oikos*, *103*(1), 3–16. doi: [10.1034/j.1600-
679 0706.2003.12306.x](https://doi.org/10.1034/j.1600-0706.2003.12306.x)

680 Herms, D., & Mattson, W. (1992). The Dilemma of Plants - to Grow or Defend. *Quarterly Review of*
681 *Biology*, *67*(3), 283–335. doi: [10.1086/417659](https://doi.org/10.1086/417659)

682 Iverson, A. L., Marín, L. E., Ennis, K. K., Gonthier, D. J., Connor-Barrie, B. T., Remfert, J. L., ... Perfecto, I.
683 (2014). REVIEW: Do polycultures promote win-wins or trade-offs in agricultural ecosystem services? A
684 meta-analysis. *Journal of Applied Ecology*, *51*(6), 1593–1602. doi: [10.1111/1365-2664.12334](https://doi.org/10.1111/1365-2664.12334)

685 Jactel, H., Birgersson, G., Andersson, S., & Schlyter, F. (2011). Non-host volatiles mediate associational
686 resistance to the pine processionary moth. *Oecologia*, *166*(3), 703–711. doi: [10.1007/s00442-011-
687 1918-z](https://doi.org/10.1007/s00442-011-1918-z)

688 Jactel, H., Gritti, E. S., Drössler, L., Forrester, D. I., Mason, W. L., Morin, X., ... Castagneyrol, B. (2018).
689 Positive biodiversity–productivity relationships in forests: climate matters. *Biology Letters*, *14*(4),
690 20170747. doi: [10.1098/rsbl.2017.0747](https://doi.org/10.1098/rsbl.2017.0747)

691 Jactel, H., Moreira, X., & Castagneyrol, B. (in press). Tree Diversity and Forest Resistance to Insect Pests:
692 Patterns, Mechanisms and Prospects. *Annual Review of Entomology*.

693 Jactel, H., Petit, J., Desprez-Loustau, M.-L., Delzon, S., Piou, D., Battisti, A., & Koricheva, J. (2012).
694 Drought effects on damage by forest insects and pathogens: a meta-analysis. *Global Change Biology*,
695 *18*(1), 267–276. doi: [10.1111/j.1365-2486.2011.02512.x](https://doi.org/10.1111/j.1365-2486.2011.02512.x)

696 Jactel, H., Poeydebat, C., van Halder, I., & Castagneyrol, B. (2019). Interactive Effects of Tree Mixing and
697 Drought on a Primary Forest Pest. *Frontiers in Forests and Global Change*, *2*, 1–12. doi:
698 [10.3389/ffgc.2019.00077](https://doi.org/10.3389/ffgc.2019.00077)

699 Jactel, H., Bauhus, J., Boberg, J., Bonal, D., Castagneyrol, B., Gardiner, B., ... Brockerhoff, E. G. (2017).
700 Tree Diversity Drives Forest Stand Resistance to Natural Disturbances. *Current Forestry Reports*, *3*(3),
701 223–243. doi: [10.1007/s40725-017-0064-1](https://doi.org/10.1007/s40725-017-0064-1)

702 Johnson, J. B., & Omland, K. S. (2004). Model selection in ecology and evolution. *Trends in Ecology &*
703 *Evolution*, *19*(2), 101–108. doi: [10.1016/j.tree.2003.10.013](https://doi.org/10.1016/j.tree.2003.10.013)

704 Kambach, S., Kühn, I., Castagneyrol, B., & Bruehlheide, H. (2016). The Impact of Tree Diversity on
705 Different Aspects of Insect Herbivory along a Global Temperature Gradient - A Meta-Analysis. *Plos One*,
706 *11*(11), e0165815. doi: [10.1371/journal.pone.0165815](https://doi.org/10.1371/journal.pone.0165815)

707 Karban, R., & Baldwin, I. T. (1997). *Induced Responses to Herbivory*. Chicago: Chicago University Press.

708 Karger, D. N., Conrad, O., Boehner, J., Kawohl, T., Kreft, H., Soria-Auza, R. W., ... Kessler, M. (2017).
709 Data Descriptor: Climatologies at high resolution for the earth’s land surface areas. *Scientific Data*, *4*,
710 170122. doi: [10.1038/sdata.2017.122](https://doi.org/10.1038/sdata.2017.122)

711 Kembel, S. W., Cowan, P. D., Helmus, M. R., Cornwell, W. K., Morlon, H., Ackerly, D. D., ... Webb, C. O.
712 (2010). Picante: R tools for integrating phylogenies and ecology. *Bioinformatics*, *26*(11), 1463–1464.
713 doi: [10.1093/bioinformatics/btq166](https://doi.org/10.1093/bioinformatics/btq166)

714 Klapwijk, M. J., Ayres, M. P., Battisti, A., & Larsson, S. (2012). Assessing the impact of climate change
715 on outbreak potential. In P. Barbosa, D. K. Letourneau, & A. A. Agrawal (Eds.), *Insect outbreak revisited*
716 (pp. 429–450). Wiley-Blackwell.

717 Koricheva, J., Larsson, S., Haukioja, E., & Keinänen, M. (1998). Regulation of Woody Plant Secondary
718 Metabolism by Resource Availability: Hypothesis Testing by Means of Meta-Analysis. *Oikos*, *83*(2), 212–
719 226. doi: [10.2307/3546833](https://doi.org/10.2307/3546833)

720 Kostenko, O., Mulder, P. P. J., Courbois, M., & Bezemer, T. M. (2017). Effects of plant diversity on the
721 concentration of secondary plant metabolites and the density of arthropods on focal plants in the field.
722 *Journal of Ecology*, *105*(3), 647–660. doi: [10.1111/1365-2745.12700](https://doi.org/10.1111/1365-2745.12700)

723 Kozlov, M. V., Lanta, V., Zverev, V., & Zvereva, E. L. (2015). Global patterns in background losses of
724 woody plant foliage to insects. *Global Ecology and Biogeography*, *24*(10), 1126–1135. doi:
725 [10.1111/geb.12347](https://doi.org/10.1111/geb.12347)

726 Kuokkanen, K., Julkunen-Tiitto, R., Keinänen, M., Niemelä, P., & Tahvanainen, J. (2001). The effect of
727 elevated CO₂ and temperature on the secondary chemistry of *Betula pendula* seedlings. *Trees*, *15*(6),
728 378–384. doi: [10.1007/s004680100108](https://doi.org/10.1007/s004680100108)

729 Kuznetsova, A., Brockhoff, P. B., & Christensen, R. H. B. (2017). lmerTest Package: Tests in Linear Mixed
730 Effects Models. *Journal of Statistical Software*, *82*(13), 1–26. doi: [10.18637/jss.v082.i13](https://doi.org/10.18637/jss.v082.i13)

731 Lange, E. S., Kyryczenko-Roth, V., Johnson-Cicalese, J., Davenport, J., Vorsa, N., & Rodriguez-Saona, C.
732 (2019). Increased nutrient availability decreases insect resistance in cranberry. *Agricultural and Forest*
733 *Entomology*, *21*(3), 326–335. doi: [10.1111/afe.12335](https://doi.org/10.1111/afe.12335)

734 Larsson, S., Wirén, A., Lundgren, L., & Ericsson, T. (1986). Effects of Light and Nutrient Stress on Leaf
735 Phenolic Chemistry in *Salix dasyclados* and Susceptibility to *Galerucella lineola* (Coleoptera). *Oikos*,
736 *47*(2), 205–210. doi: [10.2307/3566047](https://doi.org/10.2307/3566047)

737 Lintunen, A., & Kaitaniemi, P. (2010). Responses of crown architecture in *Betula pendula* to
738 competition are dependent on the species of neighbouring trees. *Trees*, *24*(3), 411–424. doi:
739 [10.1007/s00468-010-0409-x](https://doi.org/10.1007/s00468-010-0409-x)

740 Magallón, S., Gómez-Acevedo, S., Sánchez-Reyes, L. L., & Hernández-Hernández, T. (2015). A
741 metacalibrated time-tree documents the early rise of flowering plant phylogenetic diversity. *New*
742 *Phytologist*, *207*(2), 437–453. doi: [10.1111/nph.13264](https://doi.org/10.1111/nph.13264)

743 Merwin, A. C., Underwood, N., & Inouye, B. D. (2017). Increased consumer density reduces the
744 strength of neighborhood effects in a model system. *Ecology*, *98*(11), 2904–2913. doi: [10.1002/ecy.200](https://doi.org/10.1002/ecy.200)

745 Miller, E. T., Farine, D. R., & Trisos, C. H. (2017). Phylogenetic community structure metrics and null
746 models: a review with new methods and software. *Ecography*, *40*(4), 461–477. doi:
747 [10.1111/ecog.02070](https://doi.org/10.1111/ecog.02070)

748 Mole, S., Ross, J. A. M., & Waterman, P. G. (1988). Light-induced variation in phenolic levels in foliage
749 of rain-forest plants. I. Chemical Changes. *Journal of Chemical Ecology*, *14*(1), 1–21. doi:
750 [10.1007/BF01022527](https://doi.org/10.1007/BF01022527)

751 Moles, A. T., Bonser, S. P., Poore, A. G. B., Wallis, I. R., & Foley, W. J. (2011). Assessing the evidence for
752 latitudinal gradients in plant defence and herbivory. *Functional Ecology*, *25*(2), 380–388. doi:
753 [10.1111/j.1365-2435.2010.01814.x](https://doi.org/10.1111/j.1365-2435.2010.01814.x)

754 Moreira, X, Abdala-Roberts, L., Parra-Tabla, V., & Mooney, K. A. (2014). Positive Effects of Plant
755 Genotypic and Species Diversity on Anti-Herbivore Defenses in a Tropical Tree Species. *PLoS ONE*, *9*(8),
756 e105438. doi: [10.1371/journal.pone.0105438](https://doi.org/10.1371/journal.pone.0105438)

757 Moreira, X, Castagneyrol, B., Abdala-Roberts, L., Teran, J. C. B.-M. y, Timmermans, B. G. H., Bruun, H.
758 H., ... Tack, A. J. M. (2018). Latitudinal variation in plant chemical defences drives latitudinal patterns
759 of leaf herbivory. *Ecography*, 41(7), 1124–1134. doi: [10.1111/ecog.03326](https://doi.org/10.1111/ecog.03326)

760 Moreira, X, Galman, A., Francisco, M., Castagneyrol, B., & Abdala-Roberts, L. (2018). Host plant
761 frequency and secondary metabolites are concurrently associated with insect herbivory in a dominant
762 riparian tree. *Biology Letters*, 14(12), 20180281. doi: [10.1098/rsbl.2018.0281](https://doi.org/10.1098/rsbl.2018.0281)

763 Moreira, X., Abdala-Roberts, L., Rasmann, S., Castagneyrol, B., & Mooney, K. A. (2016). Plant diversity
764 effects on insect herbivores and their natural enemies: current thinking, recent findings, and future
765 directions. *Current Opinion in Insect Science*, 14, 1–7. doi: [10.1016/j.cois.2015.10.003](https://doi.org/10.1016/j.cois.2015.10.003)

766 Muiruri, E. W., Barantal, S., Iason, G. R., Salminen, J., Perez-Fernandez, E., & Koricheva, J. (2019). Forest
767 diversity effects on insect herbivores: do leaf traits matter? *New Phytologist*, 221(4), 2250–2260. doi:
768 [10.1111/nph.15558](https://doi.org/10.1111/nph.15558)

769 Nakagawa, S., & Schielzeth, H. (2013). A general and simple method for obtaining R² from generalized
770 linear mixed-effects models. *Methods in Ecology and Evolution*, 4(2), 133–142. doi: [10.1111/j.2041-
771 210x.2012.00261.x](https://doi.org/10.1111/j.2041-210x.2012.00261.x)

772 Paquette, A., Hector, A., Castagneyrol, B., Vanhellefont, M., Koricheva, J., Scherer-Lorenzen, M., &
773 Verheyen, K. (2018). A million and more trees for science. *Nature Ecology & Evolution*, 2(5), 763–766.
774 doi: [10.1038/s41559-018-0544-0](https://doi.org/10.1038/s41559-018-0544-0)

775 Pineau, X., David, G., Peter, Z., Sallé, A., Baude, M., Lieutier, F., & Jactel, H. (2017). Effect of
776 temperature on the reproductive success, developmental rate and brood characteristics of *Ips*
777 *sexdentatus* (Boern.): Temperature effect on *I. sexdentatus* brood. *Agricultural and Forest Entomology*,
778 19(1), 23–33. doi: [10.1111/afe.12177](https://doi.org/10.1111/afe.12177)

779 R Core Development Team. (2013). *R: A language and environment for statistical computing*. Vienna,
780 Austria: R Foundation for Statistical Computing. Retrieved from <http://www.R-project.org/>

781 Ratcliffe, S., Wirth, C., Jucker, T., van der Plas, F., Scherer-Lorenzen, M., Verheyen, K., ... Ohse, B. (2017).
782 Biodiversity and ecosystem functioning relations in European forests depend on environmental
783 context. *Ecology Letters*, 20(11), 1414–1426. doi: doi.org/10.1111/ele.12849

784 Redding, D. W., & Mooers, A. O. (2006). Incorporating evolutionary measure into conservation
785 prioritization. *Conservation Biology*, 20(6), 1670–1678. doi: [10.1111/j.1523-1739.2006.00555.x](https://doi.org/10.1111/j.1523-1739.2006.00555.x)

786 Riipi, M., Kause, A., Haukioja, E., Ossipov, V., Ossipova, S., & Pihlaja, K. (2005). Variable responses of
787 folivorous sawflies to leaf quality of mountain birch. *Canadian Journal of Forest Research*, 35(1), 189–
788 198. doi: [10.1139/x04-166](https://doi.org/10.1139/x04-166)

789 Rodríguez-Castañeda, G. (2013). The world and its shades of green: a meta-analysis on trophic
790 cascades across temperature and precipitation gradients. *Global Ecology and Biogeography*, 22(1),
791 118–130. doi: [10.1111/j.1466-8238.2012.00795.x](https://doi.org/10.1111/j.1466-8238.2012.00795.x)

792 Rosado-Sánchez, S., Parra-Tabla, V., Betancur-Ancona, D., Moreira, X., & Abdala-Roberts, L. (2017).
793 Tree species diversity alters plant defense investment in an experimental forest plantation in southern
794 Mexico. *Biotropica*, 50(2), 246–253. doi: [10.1111/btp.12527](https://doi.org/10.1111/btp.12527)

795 Rosado-Sánchez, S., Parra-Tabla, V., Betancur-Ancona, D., Moreira, X., & Abdala-Roberts, L. (2018).
796 Effects of tree species diversity on insect herbivory and leaf defences in *Cordia dodecandra*. *Ecological*
797 *Entomology*, 43(6), 703–711. doi: [10.1111/een.12648](https://doi.org/10.1111/een.12648)

798 Schielzeth, H. (2010). Simple means to improve the interpretability of regression coefficients:
799 Interpretation of regression coefficients. *Methods in Ecology and Evolution*, 1(2), 103–113. doi:
800 [10.1111/j.2041-210x.2010.00012.x](https://doi.org/10.1111/j.2041-210x.2010.00012.x)

801 Schuldt, A., Assmann, T., Bruelheide, H., Durka, W., Eichenberg, D., Härdtle, W., ... Purschke, O. (2014).
802 Functional and phylogenetic diversity of woody plants drive herbivory in a highly diverse forest. *New*
803 *Phytologist*, 202(3), 864–873. doi: [10.1111/nph.12695](https://doi.org/10.1111/nph.12695)

804 Schuldt, A., Baruffol, M., Böhnke, M., Bruelheide, H., Härdtle, W., Lang, A. C., ... Assmann, T. (2010).
805 Tree diversity promotes insect herbivory in subtropical forests of south-east China. *Journal of Ecology*,
806 98(4), 917–926. doi: [10.1111/j.1365-2745.2010.01659.x](https://doi.org/10.1111/j.1365-2745.2010.01659.x)

807 Setiawan, N. N., Vanhellefont, M., Baeten, L., Dillen, M., & Verheyen, K. (2014). The effects of local
808 neighbourhood diversity on pest and disease damage of trees in a young experimental forest. *Forest*
809 *Ecology and Management*, 334, 1–9. doi: [10.1016/j.foreco.2014.08.032](https://doi.org/10.1016/j.foreco.2014.08.032)

810 Siemann, E., Tilman, D., Haarstad, J., & Ritchie, M. (1998). Experimental Tests of the Dependence of
811 Arthropod Diversity on Plant Diversity. *The American Naturalist*, 152(5), 738–750. doi:
812 [10.2307/2463851](https://doi.org/10.2307/2463851)

813 Srivastava, D. S., Cadotte, M. W., MacDonald, A. A. M., Marushia, R. G., & Mirotchnick, N. (2012).
814 Phylogenetic diversity and the functioning of ecosystems. *Ecology Letters*, 15(7), 637–648. doi:
815 [10.1111/j.1461-0248.2012.01795.x](https://doi.org/10.1111/j.1461-0248.2012.01795.x)

816 Stone, A. C., Gehring, C. A., & Whitham, T. G. (2010). Drought negatively affects communities on a
817 foundation tree: growth rings predict diversity. *Oecologia*, 164(3), 751–761. doi: [10.1007/s00442-010-](https://doi.org/10.1007/s00442-010-1684-3)
818 [1684-3](https://doi.org/10.1007/s00442-010-1684-3)

819 Vehvilainen, H., Koricheva, J., & Ruohomaki, K. (2007). Tree species diversity influences herbivore
820 abundance and damage: meta-analysis of long-term forest experiments. *Oecologia*, 152(2), 287–298.
821 doi: [10.1007/s00442-007-0673-7](https://doi.org/10.1007/s00442-007-0673-7)

822 Visakorpi, K., Riutta, T., Martinez-Bauer, A. E., Salminen, J.-P., & Gripenberg, S. (2019). Insect
823 community structure covaries with host plant chemistry but is not affected by prior herbivory. *Ecology*,
824 e02739. doi: [10.1002/bes2.1561](https://doi.org/10.1002/bes2.1561)

825 Walter, J., Hein, R., Auge, H., Beierkuhnlein, C., Löffler, S., Reifenrath, K., ... Jentsch, A. (2012). How do
826 extreme drought and plant community composition affect host plant metabolites and herbivore
827 performance? *Arthropod-Plant Interactions*, 6(1), 15–25. doi: [10.1007/s11829-011-9157-0](https://doi.org/10.1007/s11829-011-9157-0)

828 Wang, X.-F., Liu, J.-F., Gao, W.-Q., Deng, Y.-P., Ni, Y.-Y., Xiao, Y.-H., ... Jiang, Z.-P. (2016). Defense pattern
829 of Chinese cork oak across latitudinal gradients: influences of ontogeny, herbivory, climate and soil
830 nutrients. *Scientific Reports*, 6, 27269. doi: [10.1038/srep27269](https://doi.org/10.1038/srep27269)

831 Wein, A., Bauhus, J., Bilodeau-Gauthier, S., Scherer-Lorenzen, M., Nock, C., & Staab, M. (2016). Tree
832 Species Richness Promotes Invertebrate Herbivory on Congeneric Native and Exotic Tree Saplings in a
833 Young Diversity Experiment. *PLOS ONE*, 11(12), e0168751. doi: [10.1371/journal.pone.0168751](https://doi.org/10.1371/journal.pone.0168751)

834 Yguel, B., Bailey, R., Tosh, N. D., Vialatte, A., Vasseur, C., Vitrac, X., ... Prinzing, A. (2011). Phytophagy
835 on phylogenetically isolated trees: why hosts should escape their relatives. *Ecology Letters*, 14(11),
836 1117–1124. doi: [10.1111/j.1461-0248.2011.01680.x](https://doi.org/10.1111/j.1461-0248.2011.01680.x)

837 Zhang, Y., Chen, H. Y. H., & Reich, P. B. (2012). Forest productivity increases with evenness, species
838 richness and trait variation: a global meta-analysis: *Diversity and productivity relationships*. *Journal of*
839 *Ecology*, 100(3), 742–749. doi: [10.1111/j.1365-2745.2011.01944.x](https://doi.org/10.1111/j.1365-2745.2011.01944.x)

840 Zúbrik, M., Kunca, A., & Csóka, G. (2013). *Insects and diseases damaging trees and shrubs of Europe*
841 (N.A.P. Editions).

842

843

Tables

844

Table 1. Effects of tree species diversity on (a) insect herbivory and (b) leaf phenolic concentration. Comparison of models with species richness, birch evolutionary distinctiveness (ED) or both diversity metrics as predictors. Bold predictors have a significant effect. AICc*: best (lowest) AICc.

845

Predictors	Standardized estimate \pm sd	df	t-value	P-value	R^2_m (R^2_c)	AICc	Random intercept effects (Variance \pm sd)		
							Site	Block:Site	Plot:Block:Site
a) Herbivory									
w/ Sp. richness									
Intercept	3.81 \pm 0.53	11.28	7.24	<0.001	0.00 (0.57)	2322.47*	3.10 \pm 1.76	0.25 \pm 0.50	0.46 \pm 0.68
Species richness	-0.03 \pm 0.09	143.74	-0.34	0.737					
w/ Birch ED									
Intercept	3.81 \pm 0.53	11.28	7.25	<0.001	0.00 (0.57)	2322.57*	3.10 \pm 1.76	0.25 \pm 0.50	0.46 \pm 0.68
Birch ED	0.01 \pm 0.09	122.90	0.11	0.916					
w/ Sp. Richness and Birch ED									
Intercept	3.75 \pm 0.53	11.42	7.12	<0.001	0.00 (0.57)	2328.52	3.07 \pm 1.75	0.25 \pm 0.50	0.45 \pm 0.67
Species richness	0.01 \pm 0.10	140.37	0.11	0.916					
Birch ED	0.16 \pm 0.13	128.18	1.20	0.231					
Sp. richness x Birch ED	0.27 \pm 0.17	135.56	1.56	0.121					
b) Phenolics									
w/ Sp. richness									
Intercept	332.29 \pm 23.67	10.09	14.04	<0.001	0.00 (0.65)	5819.74	5930 \pm 77	0 \pm 0	1663 \pm 41
Species richness	4.35 \pm 4.67	146.67	0.93	0.353					
w/ Birch ED									
Intercept	331.80 \pm 23.68	10.09	14.01		0.02 (0.65)	5810.79	5953 \pm 77	0 \pm 0	1446 \pm 38
Birch ED	-15.05 \pm 4.71	126.40	-3.19	0.002					
w/ Sp. Richness and Birch ED									
Intercept	332.00 \pm 23.87	10.26	13.91	<0.001	0.03 (0.65)	5798.61*	5997 \pm 77	0 \pm 0	1375 \pm 37
Species richness	10.74 \pm 4.90	141.50	2.19	0.030					
Birch ED	-19.33 \pm 6.87	147.95	-2.82	<0.006					
Sp. richness x Birch ED	-0.43 \pm 8.98	156.27	-0.05	0.962					

846

847 **Table 2.** Effects of tree diversity, temperature and rainfall on (a) insect herbivory and (b) leaf phenolic
 848 concentration. Predictors that were excluded from the final model during simplification are not shown.
 849 **Bold predictors have a significant effect.**

Predictors	Standardized estimate \pm sd	df	t-value	P-value	R ² _m (R ² _c)
a) Herbivory					
w/ Sp. richness					0.22 (0.59)
Intercept	3.81 \pm 0.43	10.35	8.93	<0.001	
Species richness	-0.05 \pm 0.09	142.59	-0.551	0.582	
Temperature	1.21 \pm 0.46	10.26	2.64	0.024	
Sp. richness x Temperature	0.19 \pm 0.09	135.27	2.14	0.034	
Variance \pm sd					
Site	1.95 \pm 1.40				
Block:Site	0.25 \pm 0.50				
Plot:(Block:Site)	0.41 \pm 0.64				
w/ Birch ED					0.21 (0.59)
Intercept	3.82 \pm 0.42	10.34	9.05	<0.001	
Temperature	1.21 \pm 0.45	10.24	2.68	0.023	
Variance \pm sd					
Site	1.91 \pm 1.38				
Block:Site	0.25 \pm 0.50				
Plot:(Block:Site)	0.45 \pm 0.67				
b) Phenolics w/ Sp. Richness and Birch ED					0.46 (0.67)
Intercept	327.30 \pm 13.30	6.89	24.62	<0.001	
Species richness	11.47 \pm 4.39	148.33	2.61	0.010	
Birch ED	-13.37 \pm 5.16	140.89	-2.59	0.011	
Temperature	53.06 \pm 14.32	6.82	3.71	0.008	
Rainfall	-31.14 \pm 13.33	6.83	-2.34	0.053	
Birch ED x Temperature	-8.84 \pm 4.89	124.77	-1.81	0.073	
Birch ED x Rainfall	-5.15 \pm 4.75	131.52	-1.09	0.280	
Temp. x Rainfall	29.79 \pm 12.72	6.72	2.34	0.053	
Birch ED x Temp. x Rainfall	-13.22 \pm 4.15	121.02	-3.19	0.002	
Variance \pm sd					
Site	1586.60 \pm 39.82				
Block:Site	0.00 \pm 0.00				
Plot:(Block:Site)	993.60 \pm 31.52				

850
 851
 852
 853

854 **Table 3.** Effects of leaf phenolic concentration on insect herbivory as a covariate of tree diversity,
 855 temperature and rainfall. Predictors that were excluded from the final model during simplification are
 856 not shown. Bold predictors have a significant effect.

Predictors	Standardized estimate \pm sd	df	t-value	P-value	R ² _m (R ² _c)
Herbivory w/ Sp. Richness					0.24 (0.58)
Intercept	3.96 \pm 0.43	9.30	9.20	<0.001	
Temperature	1.41 \pm 0.45	9.57	3.15	0.011	
Phenolics	-0.29 \pm 0.12	466.99	-2.39	0.017	
Variance \pm sd					
Site	1.77 \pm 1.33				
Block:Site	0.30 \pm 0.55				
Plot:(Block:Site)	0.42 \pm 0.65				
Herbivory w/ Birch ED					0.25 (0.59)
Intercept	3.99 \pm 0.44	9.29	9.11	<0.001	
Birch ED	0.02 \pm 0.10	111.88	0.22	0.826	
Temperature	1.41 \pm 0.46	9.54	3.11	0.012	
Phenolics	-0.25 \pm 0.12	476.63	-2.04	0.042	
Birch ED x Phenolics	0.23 \pm 0.10	285.52	2.42	0.016	
Variance \pm sd					
Site	1.84 \pm 1.36				
Block:Site	0.31 \pm 0.55				
Plot:(Block:Site)	0.35 \pm 0.59				

857

858