

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

3 **Abstract**

- 4 1. Associational resistance theory predicts that insect herbivory decreases with increasing
5 tree diversity in forest ecosystems. However, the generality of this effect and its underlying
6 mechanisms are still debated, particularly since evidence has accumulated that climate
7 may influence the direction and strength of the relationship between diversity and
8 herbivory.
- 9 2. We quantified insect leaf herbivory and leaf chemical defences (phenolic compounds) of
10 silver birch (*Betula pendula*) in pure and mixed plots with different tree species
11 composition across twelve tree diversity experiments in different climates. We investigated
12 whether the effects of neighbouring tree species diversity on insect herbivory in birch, *i.e.*
13 associational effects, were dependent on the climatic context, and whether neighbour-
14 induced changes in birch chemical defences were involved in associational resistance to
15 insect herbivory.
- 16 3. We showed that herbivory on birch decreased with tree species richness (*i.e.* associational
17 resistance) in colder environments but that this relationship faded as mean annual
18 temperature increased.
- 19 4. Birch leaf chemical defences increased with tree species richness but decreased with the
20 phylogenetic distinctiveness of birch from its neighbours, particularly in warmer and more
21 humid environments.
- 22 5. Herbivory was negatively correlated with leaf chemical defences, particularly when birch
23 was associated with closely related species. The interactive effect of tree diversity and
24 climate on herbivory was partially mediated by changes in leaf chemical defences.
- 25 6. Our findings confirm that tree species diversity can modify the leaf chemistry of a focal
26 species, hence its quality for herbivores. They further stress that such neighbour-induced
27 changes are dependent on climate and that tree diversity effects on insect herbivory are
28 partially mediated by these neighbour-induced changes in chemical defences.

29 7. Future studies should investigate i) which tree species traits, ii) how tree species
30 intermingling pattern and iii) to what extent climatic context ultimately affect associational
31 resistance in mixed forests.

32 **Keywords**

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

35 Introduction

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

47 Early attempts to explain associational resistance were mainly based on processes determined
48 by host plant density (*e.g.* the resource concentration hypothesis, Hambäck, Inouye,
49 Andersson, & Underwood, 2014), or mediated by natural enemies (*e.g.* the natural enemies
50 hypothesis, Moreira, Abdala-Roberts, Rasmann, Castagneyrol & Mooney, 2016) or by non-
51 host volatile chemical compounds (*e.g.* the semiochemical diversity hypothesis, Jactel,
52 Birgersson, Andersson, & Schlyter, 2011). Only recently, researchers have recognized that
53 associational resistance could also result from changes in host traits, such as nutritional quality
54 and production of anti-herbivores defences, induced by heterospecific neighbours (Moreira,
55 Abdala-Roberts, Parra-Tabla, & Mooney, 2014; Glassmire *et al.*, 2016; Castagneyrol *et al.*,
56 2018). Indeed, several reviews have shown that tree diversity can promote plant productivity
57 (Zhang, Chen, & Reich, 2012; Jactel *et al.*, 2018), which in turn could result in reduced
58 production of leaf chemical defences because of a trade-off between growth and defences
59 (Herms & Mattson, 1992; Endara & Coley, 2011). Consistently, increased tree diversity was
60 found to be associated with lower concentrations of leaf chemical defences, including
61 polyphenols, tannins, glycosids and alkaloids (Castagneyrol *et al.*, 2018; Muiruri *et al.*, 2019;
62 Rosado-Sánchez, Parra-Tabla, Betancur-Ancona, Moreira, & Abdala-Roberts, 2018; Walter *et*
63 *al.*, 2012).

64 Assuming that tree species traits involved in interactions with herbivores or in resource
65 acquisition are phylogenetically conserved, greater tree phylogenetic diversity should amplify
66 trait dissimilarity between species (Srivastava, Cadotte, MacDonald, Marushia, & Mirotnick,
67 2012) and hence, the magnitude of associational resistance mechanisms including the effect
68 of tree diversity on defences. In particular, greater plant functional diversity is expected to i)
69 extend resource concentration effects to herbivore species with wider diet breadth
70 (Castagneyrol *et al.*, 2014), ii) foster host-finding disruption due to the greater complexity of
71 the visual and chemical environments (Jactel *et al.*, 2011), and iii) increase resource use
72 complementarity between plant species resulting in higher growth and lower defence levels.
73 Consistently, the degree of phylogenetic or functional dissimilarity between focal plant
74 species and their heterospecific neighbours was found to affect associational effects on
75 herbivory, with greater impacts than plant species richness *per se* in most cases (Castagneyrol
76 *et al.*, 2014; Dinnage, 2013; Schuldt *et al.*, 2014; Yguel *et al.*, 2011).

77 Until now, studies on associational resistance have largely overlooked possible interactions
78 with abiotic factors (but see Walter *et al.*, 2012, Kambach, Kühn, Castagneyrol, & Bruelheide,
79 2016). Yet, climate has well documented effects on herbivore activity, abundance and
80 diversity, as well as on plant growth and the production of plant anti-herbivore defences,
81 including leaf phenolics. This was demonstrated through both experiments (*e.g.* Pineau *et al.*,
82 2017; Bauerfriend & Fischer, 2013) and observational studies along latitudinal and elevation
83 gradients (Kozlov, Lanta, Zverev, & Zvereva, 2015; Moreira *et al.*, 2018a; Moreira, Galman,
84 Francisco, Castagneyrol, & Abdala-Roberts, 2018b; Rodríguez-Castañeda, 2013; but see Moles,
85 Bonser, Poore, Wallis, & Foley, 2011; Anstett, Chen, & Johnson, 2016). Importantly, recent
86 studies showed an interplay between tree diversity and climatic conditions whereby climate
87 could alter the effect of tree diversity on ecosystem processes (Castagneyrol *et al.*, 2018; Jactel,
88 Poeydebat, Van Halder, & Castagneyrol, 2019; Ratcliffe *et al.*, 2017) and conversely, tree
89 diversity could buffer the adverse effect of extreme climatic events on trees (Jactel *et al.*,
90 2017). Being able to account for the effect of climate is therefore a major opportunity to
91 strengthen our understanding of the variability in the magnitude and direction of associational
92 effects in mixed forests.

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

95 chemical defences (phenolic compounds) in silver birch (*Betula pendula*) in plots with different
96 tree species composition across twelve locations with different climates. First, we addressed
97 the effects of tree species diversity on insect herbivory and leaf chemical defences in silver
98 birch, asking which of tree species richness, phylogenetic diversity or their combination best
99 explained both response variables. We hypothesized that tree diversity was associated with
100 lower herbivory (associational resistance) and lower chemical defence levels (due to higher
101 complementarity and growth-defence trade-off), and that these effects were stronger when
102 considering phylogenetic distinctiveness of the focal species instead of species richness,
103 considering that phylogenetic diversity accounts for niche differentiation. Second, we tested
104 whether diversity-herbivory and diversity-defences relationships depended on climate. Since
105 there is no consensus in the available literature, we had no particular directional hypothesis
106 regarding the influence of climate. Finally, we tested whether climate and diversity effects on
107 insect herbivory were mediated by changes in leaf chemical defences. Our study is one of the
108 first to investigate defence-mediated associational effects on insect herbivory in relation with
109 the climatic context. We aimed at building toward a more comprehensive understanding of
110 the interactive effects of tree species diversity and climate on forest resistance to insect pests.

111 **Material and Methods**

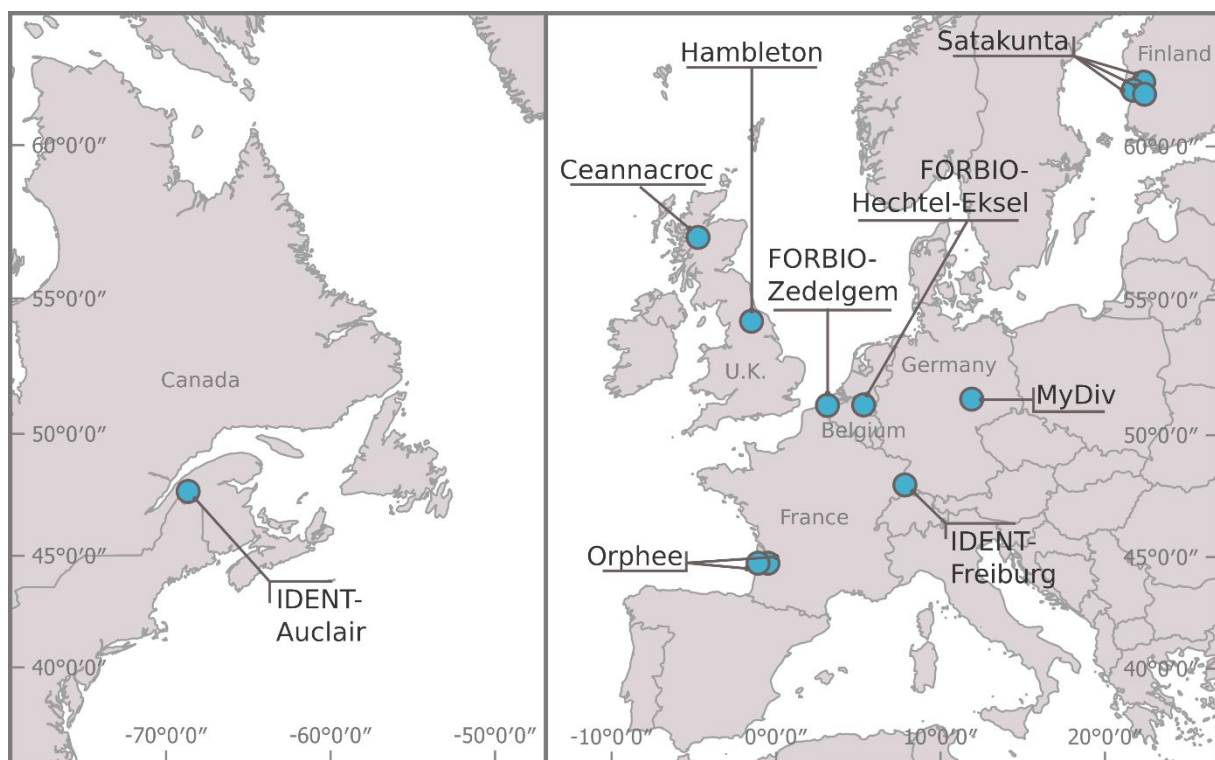
112 **Natural history**

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

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

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

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



134

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

136 Leaf collection and damage assessment

137 Fifty leaves per birch tree were haphazardly sampled in mid-July 2017 (2014 for the three
 138 Finnish sites). We assessed insect leaf herbivory as the overall percentage of leaf area
 139 removed by three common feeding guilds of insect herbivores: chewers, miners and
 140 skeletonizers. We assigned each leaf to one of seven classes of damage: (A) 0 % of leaf area
 141 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
 142 100%. To reduce unconscious bias in insect herbivory assessment, we split leaves from each

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

153 **Phylogenetic isolation**

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

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

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

176 **Climate data**

177 We extracted mean annual temperature and total annual rainfall averaged over the 1979-
178 2013 period (hereafter referred to as “temperature” and “rainfall” respectively) for each study
179 site using the Climatologies at High resolution for the Earth's Land Surface Areas dataset
180 (CHELSA; Karger *et al.*, 2017; Supporting Information Fig. S4a). In the ORPHEE experiment, half
181 of the plots were located in irrigated blocks sprinkled with 3 mm of water per night from May
182 to October. An annual surplus of 552 mm was thus added to the rainfall amount obtained
183 from the CHELSA database in these plots. To account for this additional irrigation treatment,
184 data collected in the ORPHEE experiment were considered as data from two distinct sites
185 (irrigated vs non-irrigated). Overall, our network of tree diversity experiments covered a 17°
186 latitudinal gradient and encompassed 10°C of variation in the mean annual temperature and
187 964 mm of variation in the annual rainfall.

188 **Leaf phenolics**

189 Leaf phenolics have been reported to confer resistance against insect herbivores in several
190 tree species including birch (Forkner, Marquis, & Lill, 2004; Moreira *et al.*, 2018b; Riipi *et al.*,
191 2005) and therefore represent a suitable proxy for assessing leaf chemical defences (or leaf
192 nutritional quality to herbivores). We quantified the concentration of phenolic compounds on
193 a subsample of five birch leaves - with little (<5%) or no damage - per tree, following a
194 procedure based on ultra-high performance liquid chromatography (as in Moreira *et al.*,
195 2018b; Visakorpi, Riutta, Martinez-Bauer, Salminen, & Gripenberg, 2019). Following drying (at
196 45°C during 72 hours) and grinding of leaves, we extracted phenolic compounds from 20 mg
197 of powdered dry leaf tissue with 1 mL of 70% methanol in an ultrasonic bath for 15 min,
198 followed by centrifugation (Moreira *et al.*, 2014). We then transferred the extracts to
199 chromatographic vials. Ultra-High-Performance Liquid-Chromatograph (UHPLC Nexera LC-
200 30AD; Shimadzu) equipped with a Nexera SIL-30AC injector and one SPD-M20A UV/VIS
201 photodiode array detector was used to perform the chromatographic analyses. The
202 compound separation was carried out on a Kinetex™ 2.6 µm C18 82-102 Å, LC Column 100 ×
203 4.6 mm, protected with a C18 guard cartridge. The flow rate was 0.4 mL min⁻¹ and the oven

204 temperature was set at 25°C. The mobile phase consisted of two solvents: water-formic acid
205 (0.05%) (A) and acetonitrile-formic acid (0.05%) (B), starting with 5% B and using a gradient to
206 obtain 30% B at 4 min, 60% B at 10 min, 80% B at 13 min and 100 % B at 15 min. The injection
207 volume was 3 µL. We identified four groups of phenolic compounds: flavonoids, ellagitannins
208 and gallic acid derivates (hydrolysable tannins), proanthocyanidins (condensed tannins) and
209 hydroxycinnamic acid (precursors to lignins). We quantified flavonoids as rutin equivalents,
210 condensed tannins as catechin equivalents, hydrolysable tannins as gallic acid equivalents,
211 and precursors to lignins as ferulic acid equivalents (Moreira *et al.*, 2018a, b). Quantification
212 of these phenolic compounds was achieved by external calibration using calibration curves at
213 0.25, 0.5, 1, 2, and 5 µg mL⁻¹. Total phenolic concentration was equal to 334.57 ± 107.48 mg
214 g⁻¹ of leaf dry matter on average and ranged from 13.51 to 775.08 mg g⁻¹ (Supporting
215 Information Table S3).

216 **Statistical analyses**

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

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

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

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

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

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

256 In all models, predictors were scaled and centred, which made it possible to compare the
257 magnitude of the effects even when interaction terms were significant (Schielzeth, 2010).
258 Collinearity among all predictors was found to be weak enough to limit inflation of the
259 variance of estimated model parameters (variation inflation factors [VIFs] less than two).
260 Model parameters were estimated by restricted likelihood estimation and the significance (α
261 = 0.05) of the regression coefficients was tested with Student t-tests and Satterthwaite's
262 approximation for degrees of freedom. We evaluated model fit by calculating the percentage
263 of variance explained by fixed (R^2_m) and by fixed plus random effects (R^2_c) (Nakagawa &
264 Schielzeth, 2013).

265 Concentrations of all types of phenolic compounds were positively correlated with each other
266 (Supporting Information Fig. S6), which made it inappropriate to use all phenolic types as
267 predictors of insect herbivory in the same model (inflation of the variance of estimated model
268 parameters). We therefore ran separate models for each type of phenolics. Concentrations of
269 all types of phenolic compounds and concentrations of total phenolics co-varied with climate
270 and diversity predictors, *i.e.* direction of effects were consistent across phenolic types (Table
271 1; Supporting Information Table S4). We additionally summarized the information on phenols
272 using a principal component analysis (PCA) with the concentrations of the four individual
273 phenolic compounds (Supporting Information Fig. S7). The three first components of the PCA
274 altogether explained 92% of the variance and the points were well homogeneously
275 distributed. The first axis was associated with the concentrations of flavonoids and
276 hydrolysable tannins, the second axis with the concentration of condensed tannins and the
277 third with the concentration of lignin. Besides, PCA coordinates on the first three axes were
278 all positively correlated with the concentration of total phenolics (Supporting Information Fig.
279 S8). Based on these elements, we choose to present the results for total phenolic
280 concentration only in the main text.

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

284 **Results**

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

286 We found no significant effect of species richness or birch evolutionary distinctiveness (ED)
287 *per se* on insect herbivory, and no interactive effect of the two diversity metrics either (Table
288 1a). The herbivory model with species richness and the herbivory model with birch ED had the
289 lowest AICc values, not differing by more than two units (Table 1a). These two models were
290 thus used in the subsequent analyses while the herbivory model with both diversity metrics,
291 which had a higher AICc value (Table 1a), was eliminated.

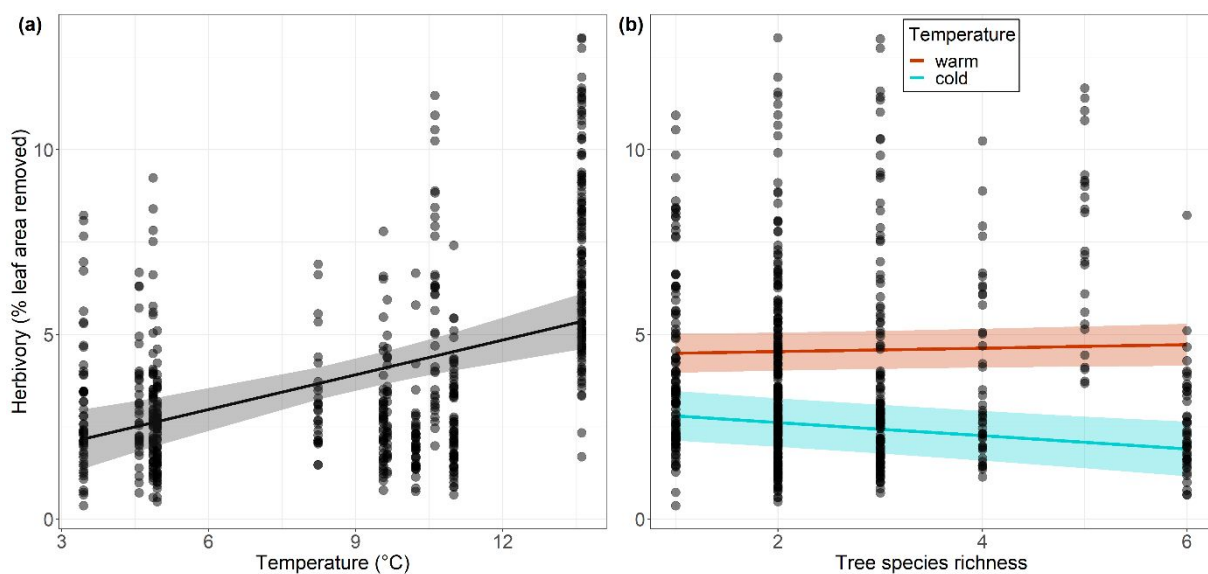
292 We found a significant negative effect of birch ED on leaf phenolic such that birch leaves were
293 less defended when birches were more phylogenetically distinct from their neighbours (Table
294 1b). In contrast, we found a significant and positive effect of tree species richness on leaf

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

300 **Effects of climate and tree diversity on insect herbivory**

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

304 The effect of tree species richness on insect herbivory was contingent upon temperature
 305 (significant species richness \times temperature interaction; Table 2a). In particular, insect
 306 herbivory decreased with increasing tree species richness at low temperatures but was not
 307 affected by tree species richness at higher temperatures (Fig. 2b). In the final simplified model,
 308 tree species richness and temperature collectively explained 22% of the variability in insect
 309 herbivory ($R^2_m = 0.22$; $R^2_c = 0.59$). By contrast, there was no significant effect of the
 310 interaction between birch ED and temperature or rainfall (Table 2a). Independent effects of
 311 birch ED and temperature collectively explained 21% of the variability in insect herbivory (R^2_m
 312 $= 0.21$; $R^2_c = 0.59$).

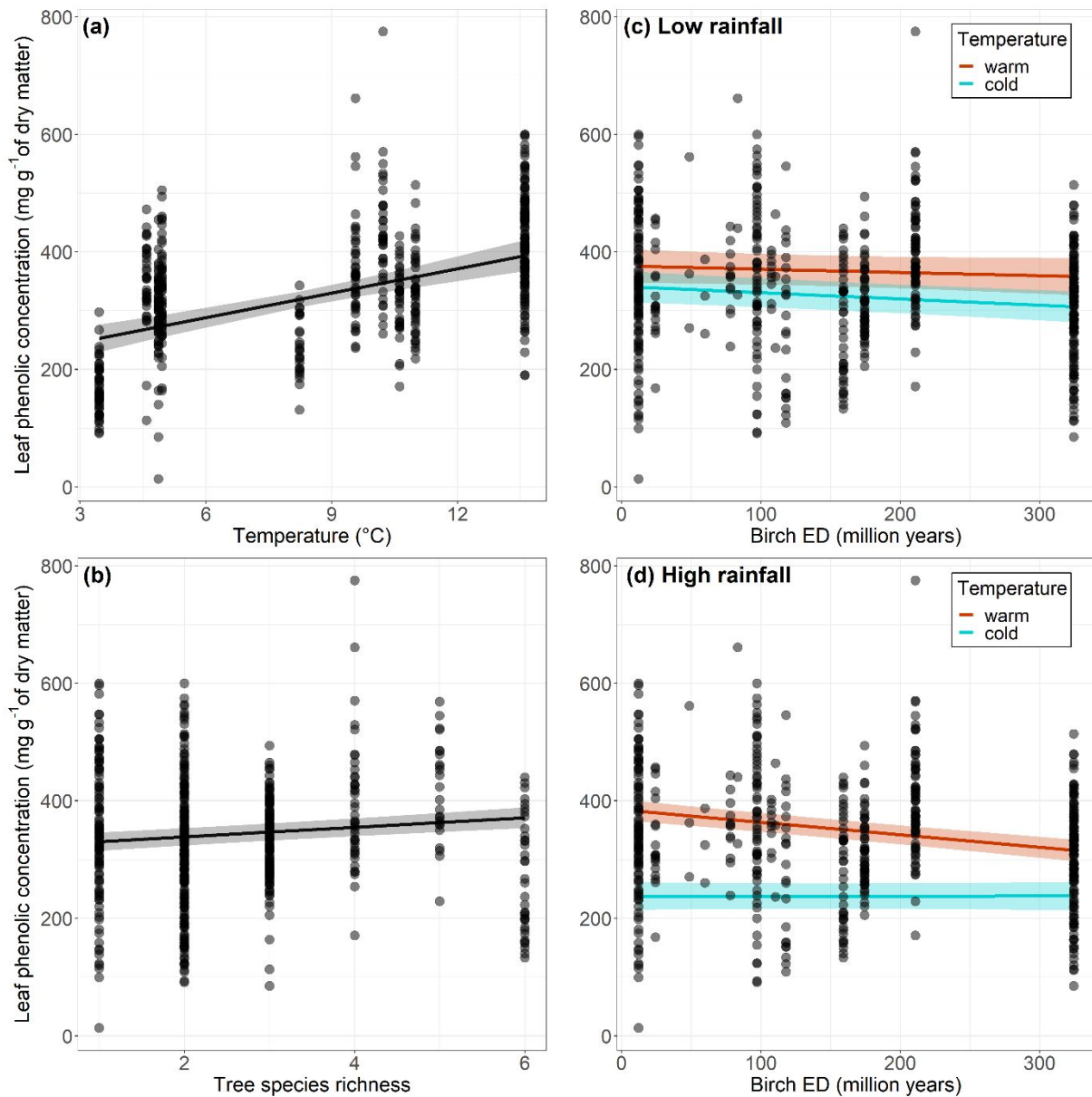


313

314 **Figure 2.** Relationships (a) between insect herbivory on silver birch leaves and mean annual
315 temperature and (b) between insect herbivory and tree species richness for two contrasted
316 temperature levels. The figure shows observed data (points) as well as model predictions (solid
317 lines) and standard errors (shaded areas). In panel (a), species richness was set at a median
318 value to compute predictions. “Warm” and “cold” temperature levels corresponded to 0.25 and
319 0.75 quartiles of the observed temperature range, respectively.

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

321 Leaf phenolic concentration significantly increased with increasing temperature and tended
322 to decrease with increasing rainfall but not significantly (Table 2b; Fig 3a). In addition, leaf
323 phenolic concentration significantly increased with species richness (Table 2b; Fig. 3b)
324 regardless of the climate (no significant interactions with rainfall or temperature). In contrast,
325 the effect of birch ED on leaf phenolic concentration was contingent upon temperature and
326 rainfall conditions (significant birch ED × temperature × rainfall interaction; Table 2b).
327 Specifically, leaf phenolic concentration decreased with increasing birch phylogenetic
328 distinctiveness independently of the temperature at low rainfall level (Fig. 3c), but decreased
329 more markedly with increasing phylogenetic distinctiveness of birch in warm conditions only
330 at high rainfall level (Fig. 3d). In the final simplified model, climate and tree species diversity
331 collectively explained 46% of the variability in phenolic concentration of birch leaves ($R^2_m =$
332 0.46; $R^2_c = 0.67$).



333

334 **Figure 3.** Leaf phenolic concentration in birch leaves as a function of (a) temperature, (b) tree

335 species richness and as a function of birch evolutionary distinctiveness (ED) for three

336 contrasted levels of temperature under three contrasted levels of rainfall (c and d). The figure

337 shows observed data (points) as well as model predictions (solid lines) and standard errors

338 (shaded areas). “Warm” and “cold” temperature levels corresponded to 0.25 and 0.75 quartiles

339 of the observed temperature range, respectively. “Low” and “high” rainfall levels corresponded

340 to 0.25 and 0.75 quartiles of the observed rainfall range, respectively. The predictors that were

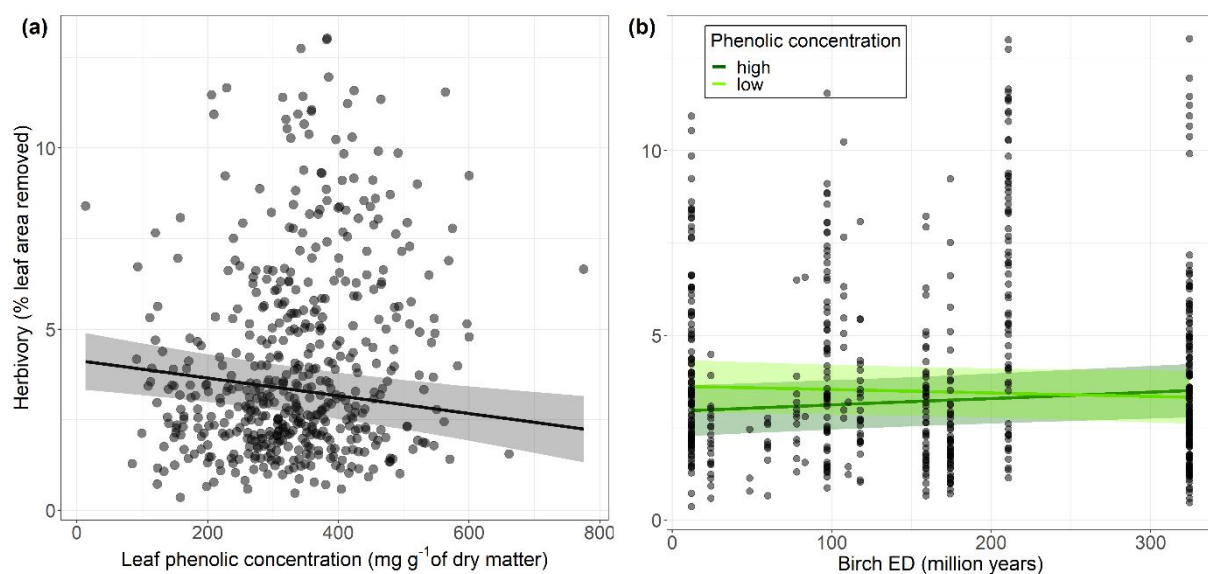
341 not involved in the relationships shown were set at median values to compute predictions.

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

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

348 In the herbivory model with species richness, we found that the effect of species richness –
 349 that was contingent upon temperature – became non-significant after including leaf phenolic
 350 concentration as a covariate (Table 3), indicating that the effect of tree species richness on
 351 insect herbivory was mediated by leaf phenolics. Temperature and leaf phenolic
 352 concentration collectively explained 24% of the variability in insect herbivory ($R^2_m = 0.24$; R^2_c
 353 $= 0.58$).

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



361

362 **Figure 4.** Relationship (a) between insect herbivory and leaf phenolic concentration and (b)
363 between insect herbivory and birch evolutionary distinctiveness (ED) for different levels of leaf
364 phenolic concentration. The figure shows observed data (points) as well as model predictions
365 (solid lines) and standard errors (shaded areas). “Low” and “high” phenolic concentration levels
366 corresponded to 0.25 and 0.75 quartiles of the observed phenolic concentration range,
367 respectively. The predictors that were not involved in the relationships shown were set at
368 median values to compute predictions.

369 Discussion

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

377 Effects of tree diversity on insect herbivory are climate dependent

378 We found no significant effects of either tree species richness or birch phylogenetic
379 distinctiveness *per se* on background levels of insect herbivory on birch. In fact, we found
380 evidence that tree diversity effects on herbivory were dependent on climate. This result could
381 partly explain the variable effects of tree diversity on herbivory previously reported in the
382 literature (Brezzi, Schmid, Niklaus, & Schuldt, 2017; Castagneyrol *et al.*, 2014; Jactel, Moreira,
383 & Castagneyrol, in press; Kambach *et al.*, 2016; Ratcliffe *et al.*, 2017; Schuldt *et al.*, 2010, 2014;
384 Vehviläinen, Koricheva, & Ruohomäki, 2007; Wein *et al.*, 2016) including in studies focusing
385 on birch trees (Castagneyrol *et al.*, 2018; Haase *et al.*, 2015; Muiruri *et al.*, 2019; Setiawan,
386 Vanhellefont, Baeten, Dillen, & Verheyen, 2014). Specifically, we provided evidence for
387 changes in associational effects along the mean annual temperature gradient: associational
388 resistance of birch to insect herbivory occurred in cold conditions whereas no associational
389 effects could be detected in warm conditions. The mitigation of associational resistance with

390 increasing temperature could be due to the higher proportion of generalist (*vs* specialist)
391 herbivore species in warmer regions (Forister *et al.*, 2015), that are less affected or even
392 benefit from plant diversity (Castagneyrol *et al.*, 2014). This finding might also be explained by
393 the greater abundance and activity of herbivores in warmer climate that may in turn lower
394 the resistance of mixed plant communities to herbivores. Supporting this view, associational
395 resistance to the bean beetle, *Callosobruchus maculatus*, was found to decrease with the
396 population density of this herbivore, likely because of conspecific avoidance behaviour
397 (Merwin, Underwood, & Inouye, 2017; but see Fernandez-Conradi, Jactel, Hampe, Leiva, &
398 Castagneryol, 2017). Higher herbivore density may also increase the probability for a host tree
399 to be located and attacked, simply because proportionally more individuals will pass through
400 the net of resistance mechanisms (*e.g.* resource concentration effect, host-finding disruption
401 or predation by natural enemies), resulting in lower apparent resistance to herbivores. In
402 support of this density-dependence hypothesis, our results showed that background insect
403 herbivory on birch leaves, although low, markedly increased with increasing mean annual
404 temperature (Kozlov *et al.*, 2015; Wang *et al.*, 2016). Several mechanisms have been proposed
405 to explain the positive effect of temperature on herbivory, including direct effects on
406 herbivores' developmental rate, winter survival and activity and indirect effects through
407 reduced plant nutritional quality inducing compensatory feeding (Bale *et al.*, 2002; Bauerfeind
408 & Fisher, 2013; Garibaldi, Kitzberger, & Ruggiero, 2011; Klapwijk, Ayres, Battisti, & Larsson,
409 2012).

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

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

422 Our results showed that tree diversity modifies leaf chemistry of focal birches – and hence
423 their quality for herbivores. Specifically, the concentration of leaf phenolics increased with
424 increasing tree species richness, but decreased with increasing birch evolutionary
425 distinctiveness, used as a proxy for birch functional distinctiveness in experimental plots
426 (Srivastava *et al.*, 2012). Positive effect of plant species diversity on plant chemical defences
427 have been previously reported in birch (Castagneyrol *et al.*, 2018; Muiruri *et al.*, 2019) and
428 other plant species (Bustos-Segura, Poelman, Reichelt, Gershenzon, & Gols, 2017; Kostenko,
429 Mulder, Courbois, & Bezemer, 2017; Moreira *et al.*, 2014). The underlying mechanisms
430 however are poorly understood and the opposing effects of species richness and functional
431 diversity suggest they are complex. On the one hand, defence induction in richer plant
432 community could arise in response to greater herbivory (Karban & Baldwin, 1997) due to
433 associational susceptibility. However, herbivore-mediation of species richness effects on
434 defences seems unlikely in our case since our results mainly report associational resistance
435 (Fig. 2b) and we found a negative association between herbivory and defence concentration
436 (Fig. 4a). On the other hand, it is plausible that the production of leaf phenolics reflected a
437 trade-off between growth and defences. Indeed, assuming that ecologically important traits
438 are phylogenetically conserved, increased allocation to growth in plots with functionally
439 dissimilar species (*e.g.* through complementarity or facilitation) could lead to a concomitant
440 reduction in defence investment (Bryant, Chapin, & Klein, 1983; Herms & Mattson, 1992). In
441 this sense, studies have reported that experimental manipulation of resource availability (*e.g.*
442 nutrients or water) can lead to concomitant and opposite modulations of growth and defence
443 production (Gutbrodt, Dorn, & Mody, 2012; Lange *et al.*, 2019). This process could be
444 particularly strong in birch, a fast-growing, resource-acquisitive species. Consistently, a recent
445 study found that tree species composition affected leaf chemistry in birch, with less defence
446 compounds in phylogenetically more diverse mixtures (Castagneyrol *et al.*, 2018).

447 A meta-analysis by Koricheva, Larsson, Haukioja and Keinänen (1998) supports the view that
448 tree diversity primarily affects the local abiotic conditions (specifically nutrient, water or light
449 availability) and that such effects subsequently shape plant secondary chemistry. In particular,
450 studies have demonstrated that crown illumination can affect leaf chemical composition, with
451 shading associated with lower carbohydrate and phenol concentrations in leaves of birch trees

452 (Henriksson *et al.*, 2003) and other species (Larsson, Wirén, Lundgren, & Ericsson, 1986; Mole,
453 Ross, & Waterman, 1988). The opposing effects of tree species richness and birch phylogenetic
454 distinctiveness on birch leaf phenolics could both relate to the relative heights or growth rates
455 of the trees present in the plots and the light available to birch trees. Indeed, birch is a fast-
456 growing, early successional species that is expected to be more shaded in monocultures or in
457 plots where it is present at high density (self-shading), than in mixtures where it is present at
458 lower density and mixed with slow-growing tree species. In our study, species richness
459 increase was correlated with the probability to include broadleaved species growing slower
460 than birch trees and with a reduction of birch proportion (Supporting Information Figs. S2 and
461 S3). Hence, the positive effect of species richness on leaf phenolic concentration in birch
462 leaves might be explained by a reduction of shading in species-richer mixtures. On the
463 opposite, the increase of birch phylogenetic distinctiveness was correlated with the
464 proportion of fast growing coniferous (*vs* broadleaved) neighbours such as larches or pines
465 (Supporting Information Figs. S2 and S3) that were generally taller than birch trees. The
466 decrease of leaf phenolic concentration with birch phylogenetic distinctiveness could
467 therefore result from lower light availability in plots where birch is more phylogenetically
468 isolated (mixed with a greater proportion of conifers). However, birches are able to adapt their
469 crown architecture to better compete with their neighbours for light acquisition (Lintunen &
470 Kaitaniemi, 2010), therefore potentially limiting the impact of neighbours on crown
471 illumination and leaf chemistry and explaining the relatively low phenolic concentration
472 changes observed along tree diversity gradients.

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

481 We found that the concentration of chemical defences increased with temperature, which
482 contrasts with the results of previous studies on oaks and birches in temperate and boreal

483 biomes (Kuokkanen, Julkunen-Tiitto, Keinänen, Niemelä, & Tahvanainen, 2001; Moreira *et al.*,
484 2018a). Although there is ample literature on the variation of plant defences along climatic
485 gradients, there is no consensus on the strength and direction of this relationship (Moles *et*
486 *al.*, 2011). Interestingly, we showed that climate also affected leaf phenolic concentration
487 indirectly by modulating the tree diversity-defences relationships. Specifically, decrease in
488 chemical defence levels of birch associated with greater tree phylogenetic diversity were
489 stronger in warm and humid conditions. This indicates that climate and tree species
490 composition jointly determined tree investment in chemical defences, likely through growth-
491 defence trade-offs.

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

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

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

504 We found that the effect of birch phylogenetic distinctiveness on herbivory varied with the
505 levels of chemical defences in birch leaves. Specifically, associational effects shifted from
506 resistance to susceptibility with the increase of leaf phenolics concentration. This finding
507 suggests that mechanisms involved in birch associational resistance against herbivores, other
508 than chemical defence, might have been at play (*e.g.* host-finding disruption, and resource
509 dilution), and that an undetermined factor was simultaneously controlling the concentration
510 of leaf chemical defences and interfering with these mechanisms. Forest structure, and more
511 specifically relative heights of tree species, may for instance influence at the same time (i) leaf
512 chemistry of a focal species by affecting crown illumination (Koricheva *et al.*, 1998) and the

513 synthesis of photo-protective flavonoids (Agati & Tattini, 2010) and (ii) the apparency of this
514 focal species to herbivores (Castagneyrol *et al.*, 2019; Damien *et al.*, 2016). In addition,
515 nutrient availability may affect growth of trees and the concentration of carbon-based
516 defences in leaves (Bryant *et al.*, 1983; Koricheva *et al.*, 1998). In turn, tree growth, as jointly
517 determined by tree diversity (the relative competitive ability of the species) and nutrient
518 availability, could affect apparency of the focal species to herbivores, as well as the abundance
519 and diversity of canopy arthropods (Stone, Gehring, & Whitham, 2010) with consequences for
520 multitrophic interactions.

521 **Conclusion**

522 By taking advantage of an international network of tree diversity experiments and a
523 standardized sampling protocol, we addressed the independent and interactive effects of tree
524 species diversity and climate on tree-herbivore interactions in temperate and boreal forests.
525 Altogether, our findings show that insect herbivory depends on a complex interplay between
526 tree species diversity and climatic conditions, and that diversity effects on insect herbivory are
527 partially mediated by neighbour-induced changes in leaf chemical defences. Our findings also
528 confirm that tree species diversity can modify leaf chemistry of a focal species – and hence its
529 quality for herbivores - but further suggest that such neighbour-induced changes are
530 dependent on climate. Nevertheless, our approach remains correlative in essence and the
531 ecological mechanisms underlying such patterns need to be further elucidated. We also
532 acknowledge that a limitation of this study is that we could not well control for the influence
533 of the position of the sites within the distribution range of birch (e.g. marginal or central), nor
534 for their spatial correlation, which could however influence tree-insect interactions through
535 local adaptation processes. Future studies should be specifically designed to investigate
536 whether diversity and climate interactively shape leaf chemistry of a focal host plant because
537 they jointly influence resource availability and their allocation to growth vs defences by trees.
538 Our study also supports the view that the phylogenetic or functional diversity of tree species
539 is complementary to species richness in predicting tree-herbivore relationships, likely because
540 it accounts for additional information relative to niche differentiation and functional
541 dissimilarities between tree species. Finally, our findings suggest that tree diversity effects on
542 herbivory levels should be viewed as a balance between multiple processes arising from
543 different attributes of tree diversity (inter-specific variation of different traits). Future

544 research should investigate which traits of tree species drive associational effects on herbivory
545 and address simultaneously multiple underlying mechanisms. For instance, it would be
546 particularly interesting to explore the role of forest structure and tree spatial arrangement in
547 associational effects, as it may be implied in both neighbour-induced changes in chemical
548 defences through effects on individual crown illumination, as well as in focal plant apparency.
549 Importantly, the climatic context in which plant-herbivore interactions occur should be
550 accounted for in future studies for a better understanding of the processes at play. By doing
551 so, the study of tree diversity effects on tree resistance to insect herbivores interactions will
552 move toward a more predictive framework.

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805 **Tables**

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

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					

809 **Table 2.** Effects of tree diversity, temperature and rainfall on (a) insect herbivory and (b) leaf phenolic
 810 concentration. Predictors that were excluded from the final model during simplification are not shown.
 811 **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				

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816 **Table 3.** Effects of leaf phenolic concentration on insect herbivory as a covariate of tree diversity,
 817 temperature and rainfall. Predictors that were excluded from the final model during simplification are
 818 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				

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