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HAL Authorization

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

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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 demonstrate the complexity and context dependency of patterns and
65 mechanisms underlying associational resistance to insect herbivory in mixed forests.

66 **Keywords**

67 Associational effects, *Betula pendula*, evolutionary distinctiveness, leaf phenolics, mixed
68 forests, phylogenetic distinctiveness, plant-insect interactions, TreeDivNet

69 Introduction

70 The influence of plant species diversity on plant-herbivore interactions is an old but still topical
71 question for ecologists (Castagneyrol, Kozlov, Poeydebat, Toïgo, & Jactel, 2019; Haddad *et al.*,
72 2009; Root, 1973; Russell, 1989; Siemann, Tilman, Haarstad, & Ritchie, 1998). Ecological
73 studies have demonstrated that increased plant species diversity generally leads to lower
74 amount of damage caused by insect herbivores including in forests (Castagneyrol, Jactel,
75 Vacher, Brockerhoff & Koricheva, 2014; Iverson *et al.*, 2014; Jactel & Brockerhoff, 2007; Jactel,
76 Moreira, & Castagneyrol, in press; Letourneau *et al.*, 2011), a phenomenon known as
77 associational resistance (Barbosa *et al.*, 2009). But several other studies have also reported no
78 change (Cardinale *et al.*, 2011; Haase *et al.*, 2015) or even increased insect herbivory when
79 mixing tree species, *i.e.* associational susceptibility (Castagneyrol, Jactel, & Moreira, 2018;
80 Loranger *et al.*, 2014; Schuldt *et al.*, 2010). These inconsistent findings demonstrate the need
81 for improved understanding of ecological processes underlying tree diversity effects on insect
82 herbivory in forests.

83 Plant diversity can reduce insect herbivory through host density-dependent or host trait-
84 dependent processes. First, several studies established that plant diversity not only dilutes the
85 amount of resources available to a given herbivore (the resource concentration hypothesis,
86 Hambäck, Inouye, Andersson, & Underwood, 2014; Root, 1973), but also disrupt host-finding
87 processes through reduced host chemical and visual apparency (Barbosa *et al.*, 2009;
88 Castagneyrol, Giffard, Péré, & Jactel, 2013; Feeny, 1976; Jactel, Birgersson, Andersson, &
89 Schlyter, 2011; Zhang & Schlyter, 2004). Second, plant diversity effects on insect herbivory can
90 be indirectly driven by changes in plant chemical defences (*i.e.* indirect trait-mediated effects).
91 Several reviews have shown that tree diversity can promote plant productivity (Zhang, Chen,
92 & Reich, 2012; Liang *et al.*, 2016; Jactel *et al.*, 2018), which in turn could result in reduced
93 production of leaf chemical defences because of a trade-off between growth and defences
94 (Coley, Bryant, & Chapin, 1985; Herms & Mattson, 1992; Endara & Coley, 2011). Consistently,
95 increased tree diversity was found to be associated with lower concentrations of leaf chemical
96 defences, including polyphenols, tannins, glycosids and alkaloids (Castagneyrol *et al.*, 2018;
97 Muiruri *et al.*, 2019; Rosado-Sánchez, Parra-Tabla, Betancur-Ancona, Moreira, & Abdala-
98 Roberts, 2018; Walter *et al.*, 2012; but see Moreira, Abdala-Roberts, Parra-Tabla, & Mooney,
99 2014).

100 Assuming that tree species traits involved in interactions with herbivores or in resource
101 acquisition are phylogenetically conserved, greater tree phylogenetic diversity should amplify
102 trait dissimilarity between species (Srivastava, Cadotte, MacDonald, Marushia, & Mirotnick,
103 2012) and hence, the magnitude of associational resistance mechanisms including the effect
104 of tree diversity on defences. In particular, greater plant functional diversity is expected to i)
105 extend resource concentration effects to herbivore species with wider diet breadth
106 (Castagneyrol et al., 2014), ii) foster host-finding disruption due to the greater complexity of
107 the visual and chemical environments (the semiochemicals diversity hypothesis, Zhang &
108 Schlyter, 2004), and iii) increase resource use complementarity between plant species
109 resulting in even higher growth and lower defence levels. Consistently, the degree of
110 phylogenetic or functional dissimilarity between focal plant species and their heterospecific
111 neighbours was found to affect associational effects on herbivory, with greater impacts than
112 plant species richness *per se* in most cases (Castagneyrol et al., 2014; Dinnage, 2013; Jactel &
113 Brockerhoff, 2007; Ness, Rollinson, & Whitney, 2011; Schuldt et al., 2014; Yguel et al., 2011).

114 The effects of climate on herbivore activity, abundance and diversity, as well as on plant growth
115 and the production of plant anti-herbivore defences, including leaf phenolics, are well
116 documented (Rodríguez-Castañeda, 2013; Jactel et al., 2019a; Kozlov, Lanta, Zverev, & Zvereva,
117 2015; Moreira et al., 2018a). It has been shown that increased temperature may result in
118 higher developmental rate and lower body mass of herbivorous insects (Pineau et al., 2017),
119 as well as in higher rate of consumption by herbivores due to higher metabolic losses
120 (Bauerfreund & Fischer, 2013). Most studies to date have reported an increase of herbivore
121 diversity and damage towards lower latitudes and elevations, which is generally interpreted as
122 a positive effect of temperature and precipitation on herbivory (Kozlov et al., 2015; Moreira,
123 Abdala-Roberts, Parra-Tabla, & Mooney, 2015; Wang et al., 2016; but see Moles, Bonser,
124 Poore, Wallis, & Foley, 2011; Anstett, Chen, & Johnson, 2016; Loughnan & Williams, 2018).
125 Besides, there is growing evidence that climate alters the chemistry of plants including trees
126 and, hence, their nutritional quality for herbivores. For example, leaf nutritional quality may
127 be reduced under drought conditions due to reduced leaf water and nitrogen contents, as well
128 as increased leaf content in defensive phenolic compounds including flavonoids and tannins
129 (Jactel et al., 2012; Moreira et al., 2018a; Mundim & Pringle, 2018 but see Gutbrodt, Dorn, &
130 Mody, 2012; Walter et al., 2012). Plant nutritional quality is also expected to vary with

131 temperature, with studies reporting a decrease of tree leaf phenolic content with increasing
132 temperature (Kuokkanen, Julkunen-Tiitto, Keinänen, Niemelä, & Tahvanainen, 2001; Moreira
133 et al., 2018a; Veteli, Kuokkanen, Julkunen-Tiitto, Roininen, & Tahvanainen, 2002).

134 The climate-dependency of associational effects has lately emerged as plausible explanation
135 for the observed variability in diversity-herbivory relationships. A recent study suggested that
136 the effects of tree species diversity on ecosystem functioning, including tree-insect
137 interactions, might be modulated by climatic conditions (Ratcliffe et al., 2017). Furthermore,
138 previous latitudinal and altitudinal studies have demonstrated that the strength and even the
139 direction of plant-herbivore interactions can change with climate (Abdala-Roberts, Moreira,
140 Rasmann, Parra-Tabla, & Mooney, 2016; Rodríguez-Castañeda, 2013; Roslin et al., 2017;
141 Schemske, Mittlebach, Cornell, Sobel, & Roy, 2009). To date, climatic factors have been largely
142 overlooked in studies on relationships between plant diversity and insect herbivory both at
143 local and large scales (but see Castagneyrol et al., 2018; Jactel, Koricheva, & Castagneyrol,
144 2019a; Jactel, Poeydebat, van Halder, & Castagneyrol, 2019b; Kambach, Kühn, Castagneyrol, &
145 Bruelheide, 2016; Walter et al., 2012).

146 Using a unique network of tree diversity experiments ranging from temperate to boreal
147 biomes (TreeDivNet; Paquette *et al.*, 2018), we quantified insect leaf herbivory and leaf
148 chemical defences (phenolic compounds) in silver birch (*Betula pendula*) in plots with different
149 tree species composition across twelve locations with different climates. First, we addressed
150 the effects of tree species diversity on insect herbivory and leaf chemical defences in silver
151 birch, asking which of tree species richness, birch phylogenetic distinctiveness or their
152 combination best explained both response variables. We hypothesized that tree diversity was
153 associated with lower herbivory (associational resistance) and lower chemical defence levels
154 (due to higher complementarity and growth-defence trade-off), and that these effects were
155 stronger when considering phylogenetic distinctiveness of the focal species instead of species
156 richness, because phylogenetic diversity accounts for niche differentiation. Second, we tested
157 whether diversity-herbivory and diversity-defences relationships depended on climate. Since
158 there is no consensus in the literature to date, we had no particular directional hypothesis
159 regarding the influence of climate. Finally, we tested whether climate and diversity effects on
160 insect herbivory were mediated by changes in leaf chemical defences. Our study is one of the
161 first to investigate defence-mediated associational effects on insect herbivory in relation with

162 the climatic context. We aimed at building toward a more comprehensive understanding of
163 the interactive effects of tree species diversity and climate on forest resistance to insect pests.

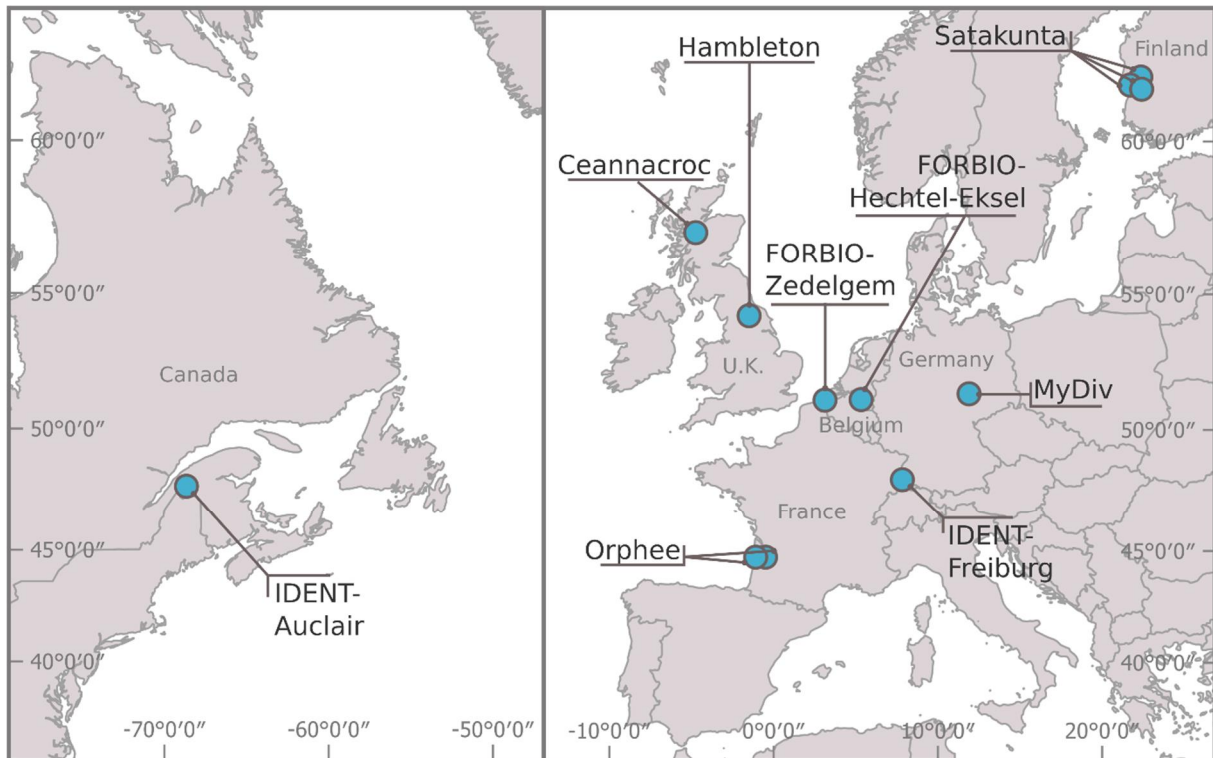
164 **Material and Methods**

165 **Natural history**

166 The silver birch (*Betula pendula* Roth, Betulaceae) is a deciduous tree native to most of Europe
167 (Beck, Caudullo, de Rigo, & Tinner, 2016) that tolerates an extremely wide range of climatic
168 and edaphic conditions. In its native range, silver birch supports a large community of insect
169 herbivores, especially lepidopteran and hymenopteran (i.e. sawflies) leaf chewers and miners
170 (Atkinson, 1992; Beck et al., 2016; Zúbrik, Kunca, & Csóka, 2013).

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

172 TreeDivNet consists of 27 long-term tree diversity experiments specifically designed to
173 investigate the effects of tree species diversity on forest functioning (Grossman et al., 2018;
174 Paquette et al., 2018; Verheyen et al., 2016). Because the experiments are globally distributed,
175 TreeDivNet is particularly well suited to explore how tree diversity effects on herbivory vary
176 with climate. We collected data from twelve sites belonging to six tree diversity experiments
177 where silver birch was present (Fig. 1; Supporting Information Table S1). These sites
178 encompassed temperate and boreal biomes of the northern hemisphere and spanned over 17
179 decimal degrees in latitude, covering about half of the latitudinal span of silver birch (Beck et
180 al., 2016). At each site, we selected silver birch monoculture plots and mixed species plots
181 where silver birch was present. Tree species richness in those mixtures ranged from two to six
182 species (including silver birch) and included broadleaved or coniferous species, or a mix of
183 both. The species composition of mixture plots varied among sites. At certain sites, species
184 composition types were replicated in two to three blocks. We randomly selected three to five
185 birch trees in the core area of each experimental plot (*i.e.* avoiding border trees to limit edge
186 effects). The final dataset was derived from 564 trees planted in 157 plots.



187

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

189 **Leaf collection and damage assessment**

190 Fifty leaves per birch tree were haphazardly sampled in mid-July 2017 (2014 for the three
 191 Finnish sites). We assessed insect leaf herbivory as the overall percentage of leaf area
 192 removed by three common feeding guilds of insect herbivores: chewers, miners and
 193 skeletonizers. We assigned each leaf to one of seven classes of damage: (A) 0 % of leaf area
 194 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
 195 100%. To reduce unconscious bias in insect herbivory assessment, we split leaves from each
 196 tree into two equal pools that were separately processed by two independent observers
 197 unaware of leaf origin. Then, we aggregated insect herbivory estimates at the tree level by
 198 averaging the median values of damage class of all leaves. In the case of the three Finnish sites
 199 (Satakunta areas 1, 2 and 3), the methodology differed slightly but was still consistent (see
 200 Muiruri et al., 2019). On average, insect herbivores damaged 3.91% (\pm 2.60%) of leaf area
 201 (damages ranged from 0.36 to 13.03% of leaf area; Supporting Information Table S2). We are
 202 confident that we did not underestimate herbivory by overlooking missing leaves since leaves
 203 did not start falling at the sampling time. The observed levels of insect herbivory were low and

204 comparable with those observed in other studies on silver birch (e.g. Castagneyrol et al., 2018;
205 Kozlov et al., 2015; Muiruri, Milligan, Morath, & Koricheva, 2015; Muiruri et al., 2019).

206 **Phylogenetic isolation**

207 Given that tree species diversity effects on herbivores can be affected by phylogenetic
208 dissimilarity between the tree species in the mixture, we used phylogenetic information to
209 account for differences in tree species composition of mixed stands across the experiments
210 (Srivastava et al., 2012). Many metrics have been developed to characterize phylogenetic
211 diversity of a pool of species (Miller, Farine, & Trisos, 2017). Here, we were primarily
212 interested in the phylogenetic contrast between *B. pendula* and associated species in the
213 mixtures. We therefore used evolutionary distinctiveness (ED), that is a species-specific metric
214 described by Redding and Mooers (2006), to estimate phylogenetic isolation of silver birch
215 from other tree species present in each plot.

216 We used the phylomatic function from the brranching package in R (with tree R20120829;
217 Chamberlain, 2018) to obtain an overall phylogenetic tree comprising the overall pool of tree
218 species (Supporting Information Fig. S1). Node ages down to family level were derived from
219 Magallón, Gómez-Acevedo, Sánchez-Reyes and Hernández-Hernández (2015). Genus node
220 ages were approximated by dividing the length of the edge from the family node to the tip by
221 two. The same was subsequently done for species nodes considering edge length from the
222 genus node to the tip. For each plot, we pruned the overall phylogenetic tree to obtain a sub-
223 tree corresponding to the pool of tree species present in the plot. Then, birch ED was
224 calculated using the evol.distinct function (equal splits method; Redding & Mooers, 2006;
225 Redding et al., 2008) from the picante package (Kembel et al., 2010) in R, as follows:

$$BirchED_{(T)} = 0.5^n \sum_{e \in S(T,R)} L_e$$

226

227 where T is the phylogenetic tree for the pool of tree species present in the plot, R the root of
228 the phylogenetic tree, e an edge along the path from the root of the tree to the *B. pendula* tip,
229 L the length of the edge e and n the number of nodes between the edge e and the *B. pendula*
230 tip. Low and high ED values correspond to low and high phylogenetic isolation, respectively.
231 Birch ED was positively correlated with species richness (see Supporting Information Fig. S2)

232 and ranged from 12.15 million years in birch monocultures (which corresponds to the length
233 of the edge from *B. pendula*-*Betula papyrifera* bifurcation to *B. pendula* tip) to 324.40 million
234 years in mixed plots where birch was associated with coniferous species only.

235 **Climate data**

236 We extracted mean annual temperature and total annual rainfall averaged over the 1979-
237 2013 period (hereafter referred to as “temperature” and “rainfall” respectively) for each study
238 site using the Climatologies at High resolution for the Earth's Land Surface Areas dataset
239 (CHELSA; Karger et al., 2017; Supporting Information Fig. S3a). In the ORPHEE experiment, half
240 of the plots were located in irrigated blocks sprinkled with 3 mm of water per night from May
241 to October. An annual surplus of 552 mm was thus added to the rainfall amount obtained
242 from the CHELSA database in these plots. To account for this additional irrigation treatment,
243 data collected in the ORPHEE experiment were considered as data from two distinct sites
244 (irrigated vs non-irrigated). Overall, our network of tree diversity experiments covered a 17°
245 latitudinal gradient and encompassed 10°C of variation in the mean annual temperature and
246 964 mm of variation in the annual rainfall.

247 **Leaf phenolics**

248 Leaf phenolics have been reported to confer resistance against insect herbivores in several
249 tree species including birch (Forkner, Marquis, & Lill, 2004; Lahtinen et al., 2004; Moreira,
250 Galmán, Francisco, Castagneyrol, & Abdala-Roberts, 2018b; Riipi et al., 2005) and therefore
251 represent a suitable proxy for assessing leaf chemical defences (or leaf nutritional quality to
252 herbivores). We quantified the concentration of phenolic compounds on a subsample of five
253 birch leaves - with little (<5%) or no damage - per tree, following a procedure based on ultra-
254 high performance liquid chromatography (as in Moreira et al., 2018b; Visakorpi, Riutta,
255 Martinez-Bauer, Salminen, & Gripenberg, 2019). Following drying (at 45°C during 72 hours)
256 and grinding of leaves, we extracted phenolic compounds from 20 mg of powdered dry leaf
257 tissue with 1 mL of 70% methanol in an ultrasonic bath for 15 min, followed by centrifugation
258 (Moreira et al., 2014). We then transferred the extracts to chromatographic vials. Ultra-High-
259 Performance Liquid-Chromatograph (UHPLC Nexera LC-30AD; Shimadzu) equipped with a
260 Nexera SIL-30AC injector and one SPD-M20A UV/VIS photodiode array detector was used to
261 perform the chromatographic analyses. The compound separation was carried out on a

262 Kinetex™ 2.6 µm C18 82-102 Å, LC Column 100 × 4.6 mm, protected with a C18 guard cartridge.
263 The flow rate was 0.4 mL min⁻¹ and the oven temperature was set at 25°C. The mobile phase
264 consisted of two solvents: water-formic acid (0.05%) (A) and acetonitrile-formic acid (0.05%)
265 (B), starting with 5% B and using a gradient to obtain 30% B at 4 min, 60% B at 10 min, 80% B
266 at 13 min and 100 % B at 15 min. The injection volume was 3 µL. We identified four groups of
267 phenolic compounds: flavonoids, ellagitannins and gallic acid derivates (hydrolysable tannins),
268 proanthocyanidins (condensed tannins) and hydroxycinnamic acid (precursors to lignins). We
269 quantified flavonoids as rutin equivalents, condensed tannins as catechin equivalents,
270 hydrolysable tannins as gallic acid equivalents, and precursors to lignins as ferulic acid
271 equivalents (Moreira et al., 2018a, b). Quantification of these phenolic compounds was
272 achieved by external calibration using calibration curves at 0.25, 0.5, 1, 2, and 5 µg mL⁻¹. Total
273 phenolic concentration was equal to 334.57 ± 107.48 mg g⁻¹ of leaf dry matter on average and
274 ranged from 13.51 to 775.08 mg g⁻¹ (see Table S3 in Supporting Information for more details).

275 **Statistical analyses**

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

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

291 Third, we tested whether the variability in insect herbivory was accounted for by phenolic
292 concentration. Specifically, we included leaf phenolic concentration as a covariate in the full
293 model(s) from the second step. Two-ways interactions involving leaf phenolic concentration
294 and either temperature, rainfall or tree diversity were also included in the model(s) to test for
295 interactive effects. By comparing results of insect herbivory models without (second step) vs
296 with leaf phenolics (third step), we tested whether the effects of tree diversity and climate on
297 insect herbivory were mediated by changes in leaf chemical defences. That would be the case
298 if a significant effect of tree species diversity and/or climate on insect herbivory became non-
299 significant after including leaf phenolic concentration as a covariate.

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

304 In all models, we accounted for the hierarchical structure of data by using Plot nested within
305 Block, nested within Site, as a random factor (i.e., 1|Site/Block/Plot in R syntax). By doing so,
306 we also accounted for any variance explained by uncontrolled parameters (e.g., experimental
307 design, soil properties). In all models, predictors were scaled and centred, which made it
308 possible to compare the magnitude of the effects even when interaction terms were
309 significant (Schielezeth, 2010). Collinearity among all predictors was found to be weak enough
310 to limit inflation of the variance of estimated model parameters (variation inflation factors
311 [VIFs] less than two). Model parameters were estimated by restricted likelihood estimation
312 and the significance ($\alpha = 0.05$) of the regression coefficients was tested with Student t-tests
313 and Satterthwaite's approximation for degrees of freedom. We evaluated model fit by
314 calculating the percentage of variance explained by fixed (R^2_m) and by fixed plus random
315 effects (R^2_c) (Nakagawa & Schielzeth, 2013). All analyses were conducted in R (version 3.5.1;
316 R Core Development Team, 2013) with the following packages: lmerTest (Kuznetsova,
317 Brockhoff, & Christensen, 2017), car (Fox & Weisberg, 2018), and MuMIn (Barton, 2018).

318 Concentrations of all types of phenolic compounds were positively correlated with each other
319 (Supporting Information Fig. S4), which made it inappropriate to use all phenolic types as
320 predictors of insect herbivory in the same model (inflation of the variance of estimated model
321 parameters). Concentrations of all types of phenolic compounds and concentrations of total

322 phenolics co-varied with climate and diversity predictors, *i.e.* direction of effects were
323 consistent across phenolic types (Table 1; Supporting Information Table S4). Based on this, we
324 choose to present results for total phenolic concentration only.

325 **Results**

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

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

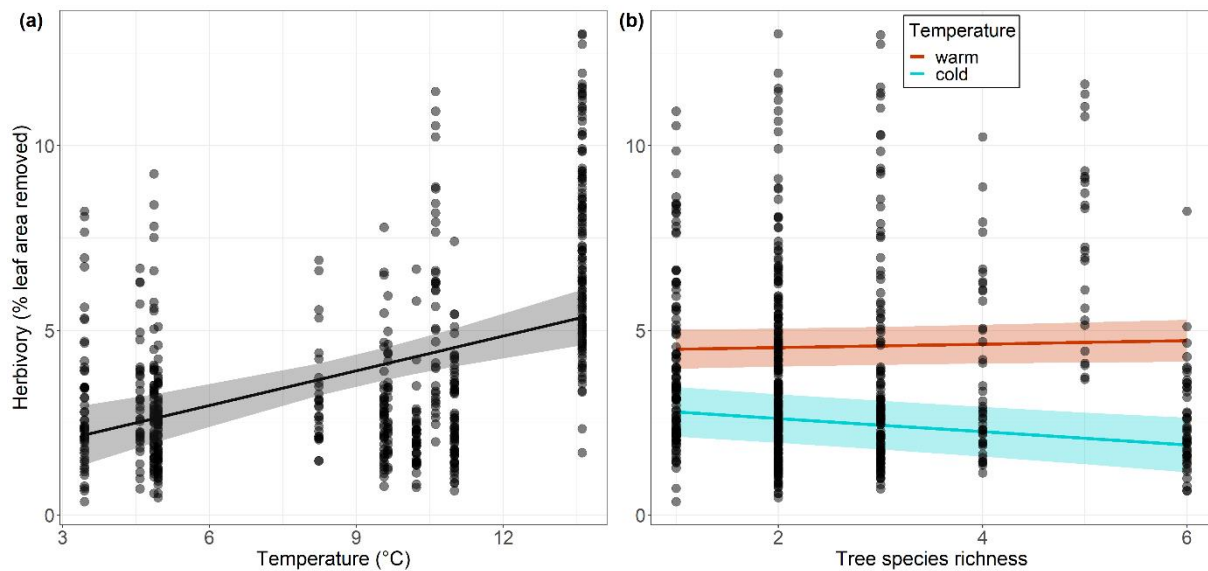
333 We found a significant negative effect of birch ED on leaf phenolic such that birch leaves were
334 less defended when birches were more phylogenetically distinct from their neighbours (Table
335 1b). In contrast, we found a significant and positive effect of tree species richness on leaf
336 phenolic concentration. The phenolics model with birch ED only had a lower AICc value than
337 the model with species richness only (Table 1b), but both of these models had higher AICc
338 values than the model with both diversity variables included (Table 1b). Hence, the best
339 phenolics model that was used in subsequent analyses was the model with both species
340 richness and birch ED.

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

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

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

351 interaction between birch ED and temperature or rainfall (Table 2a). Independent effects of
 352 birch ED and temperature collectively explained 21% of the variability in insect herbivory (R^2_m
 353 = 0.21; $R^2_c = 0.59$).



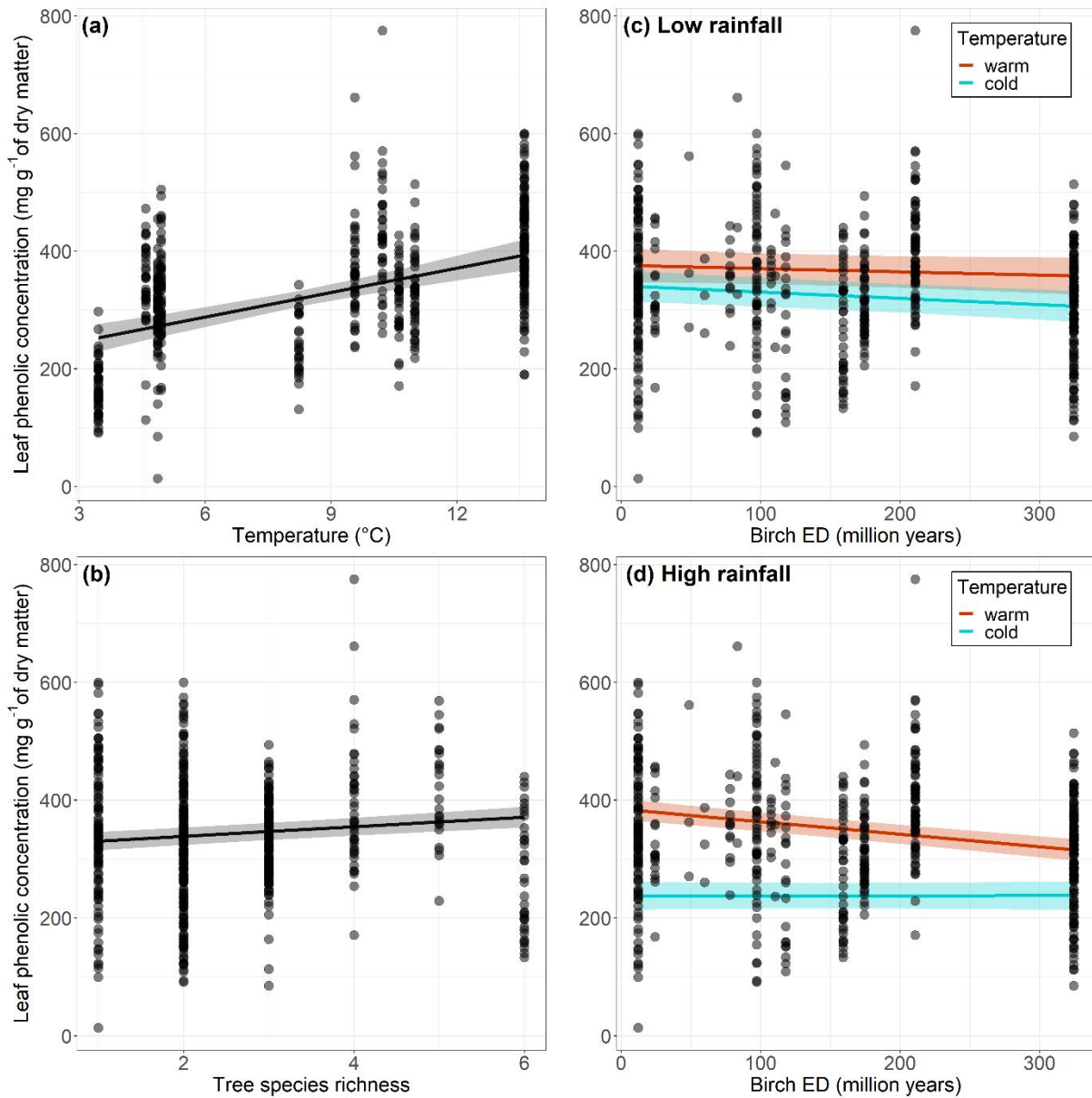
354

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

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

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

372 collectively explained 46% of the variability in phenolic concentration of birch leaves ($R^2_m =$
 373 0.46; $R^2_c = 0.67$).



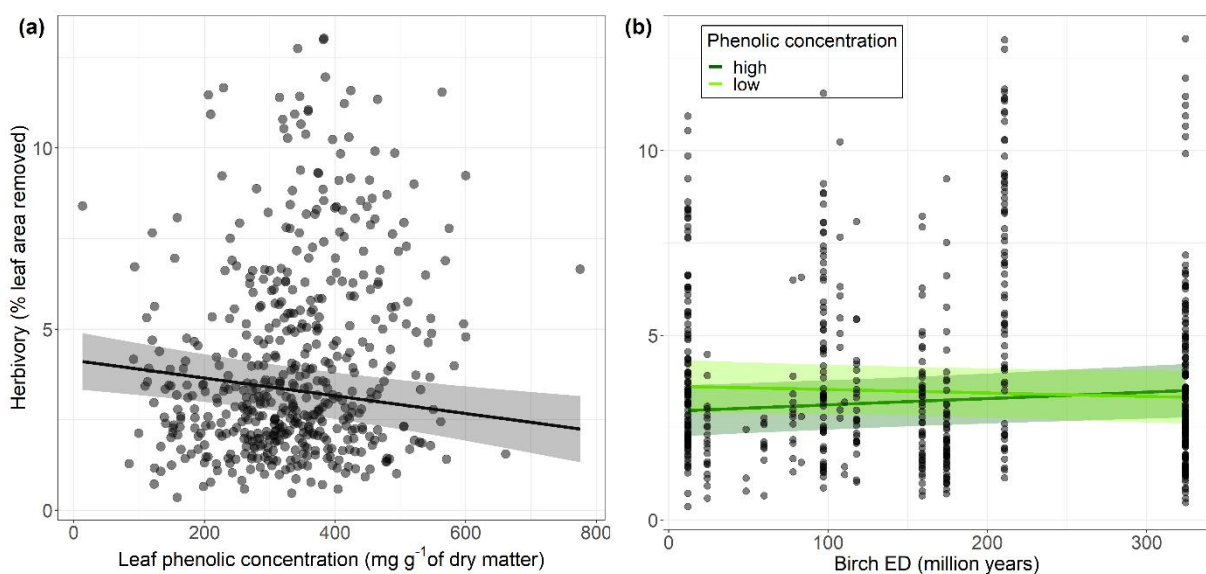
374
 375 *Figure 3. Leaf phenolic concentration in birch leaves as a function of (a) temperature, (b) tree species*
 376 *richness and as a function of birch evolutionary distinctiveness (ED) for two contrasted levels of*
 377 *temperature under two contrasted levels of rainfall (c and d). The figure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

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

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

389 In the herbivory model with species richness, we found that the effect of species richness –
390 that was contingent upon temperature – became non-significant after including leaf phenolic
391 concentration as a covariate (Table 3), indicating that the effect of tree species richness on
392 insect herbivory was mediated by leaf phenolics. Temperature and leaf phenolic
393 concentration collectively explained 24% of the variability in insect herbivory ($R^2_m = 0.24$; R^2_c
394 = 0.58).

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



402

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

409 **Discussion**

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

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

418 We found no significant effects of either tree species richness or birch phylogenetic
419 distinctiveness *per se* on background levels of insect herbivory on birch. In fact, we found
420 evidence that tree diversity effects on herbivory were dependent on climate. This result could
421 partly explain the variable effects of tree diversity on herbivory previously reported in the
422 literature (Brezzi, Schmid, Niklaus, & Schuldt, 2017; Castagneyrol et al., 2014; Jactel et al., in
423 press; Kambach et al., 2016; Ness et al., 2011; Ratcliffe et al., 2017; Schuldt et al., 2010, 2014,
424 2015; Vehviläinen, Koricheva, & Ruohomäki, 2007; Wein et al., 2016) including in studies
425 focusing on birch trees (Castagneyrol et al., 2018; Haase et al., 2015; Muiruri et al., 2015, 2019;
426 Setiawan, Vanhellefont, Baeten, Dillen, & Verheyen, 2014). Specifically, we provided
427 evidence for changes in associational effects along the mean annual temperature gradient:
428 associational resistance of birch to insect herbivory occurred in cold conditions whereas no
429 associational effects could be detected in warm conditions. The mitigation of associational
430 resistance with increasing temperature could be due to the higher proportion of generalist (*vs*
431 specialist) herbivore species in warmer regions (Forister et al., 2015), that are less affected or
432 even benefit from plant diversity (Castagneyrol et al., 2014; Jactel & Brockerhoff, 2007). This
433 finding might also be explained by the greater abundance and activity of herbivores in warmer

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

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

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

462 Our results showed that tree diversity modifies leaf chemistry of focal birches – and hence
463 their quality for herbivores. Specifically, the concentration of leaf phenolics increased with
464 increasing tree species richness, but decreased with increasing birch evolutionary

465 distinctiveness, used as a proxy for birch functional distinctiveness in experimental plots
466 (Srivastava et al., 2012). Positive effect of plant species diversity on plant chemical defences
467 have been previously reported in birch (Castagneyrol et al., 2018; Muiruri et al., 2019) and
468 other plant species (Bustos-Segura, Poelman, Reichelt, Gershenzon, & Gols, 2017; Kostenko,
469 Mulder, Courbois, & Bezemer, 2017; Moreira et al., 2014; Mraja, Unsicker, Reichelt,
470 Gershenzon, & Roscher, 2011). The underlying mechanisms however are poorly understood
471 and the opposing effects of species richness and functional diversity suggest they are complex.
472 On the one hand, defence induction in richer plant community could arise in response to
473 greater herbivory (Karban & Baldwin, 1997) due to associational susceptibility. However,
474 herbivore-mediation of species richness effects on defences seems unlikely in our case since
475 our results mainly report associational resistance (Fig. 2b) and we found a negative association
476 between herbivory and defence concentration (Fig. 4a). On the other hand, it is plausible that
477 the production of leaf phenolics reflected a trade-off between growth and defences whereby
478 increased allocation to growth in plots with functionally dissimilar species (*e.g.* through
479 complementarity or facilitation) leads to a concomitant reduction in defence investment
480 (Bryant, Chapin, & Klein, 1983; Herms & Mattson, 1992). In this sense, studies have reported
481 that experimental manipulation of resource availability (*e.g.* nutrients or water) can lead to
482 concomitant and opposite modulations of growth and defence production (Gutbrodt et al.,
483 2012; Lange et al., 2019). This process could be particularly strong in birch, a fast-growing,
484 resource-acquisitive species. Consistently, a recent study found that tree species composition
485 affected leaf chemistry in birch, with less defence compounds in phylogenetically more
486 diverse mixtures (Castagneyrol et al., 2018).

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

496 growing, early successional species that is expected to be more shaded in monocultures or in
497 plots where it is present at high density (self-shading), than in mixtures where it is present at
498 lower density and mixed with slow-growing tree species. In our study, species richness
499 increase was correlated with the probability to include broadleaved species growing slower
500 than birch trees and with a reduction of birch proportion (Supplementary Materials Figs S1
501 and S2). Hence, the positive effect of species richness on leaf phenolic concentration in birch
502 leaves might be explained by a reduction of shading in species-richer mixtures. On the
503 opposite, the increase of birch phylogenetic distinctiveness was correlated with the
504 proportion of fast growing coniferous (vs broadleaved) neighbours such as larches or pines
505 (Supplementary Materials Figs S1 and S2) that were generally taller than birch trees. The
506 decrease of leaf phenolic concentration with birch phylogenetic distinctiveness could
507 therefore result from lower light availability in plots where birch is more phylogenetically
508 isolated (mixed with a greater proportion of conifers). However, birches are able to adapt their
509 crown architecture to better compete with their neighbours for light acquisition (Lintunen &
510 Kaitaniemi, 2010), therefore potentially limiting the impact of neighbours on crown
511 illumination and leaf chemistry and explaining the relatively low phenolic concentration
512 changes observed along tree diversity gradients.

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

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

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

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

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

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

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

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

560 **Conclusion**

561 By taking advantage of an international network of tree diversity experiments and a
562 standardized sampling protocol, we addressed the independent and interactive effects of tree
563 species diversity and climate on tree-herbivore interactions in temperate and boreal forests.
564 Altogether, our findings show that insect herbivory depends on a complex interplay between
565 tree species diversity and climatic conditions, and that diversity effects on insect herbivory are
566 partially mediated by neighbour-induced changes in leaf chemical defences. Our findings also
567 confirm that tree species diversity can modify leaf chemistry of a focal species – and hence its
568 quality for herbivores - but further suggest that such neighbour-induced changes are
569 dependent on climate. Nevertheless, our approach remains correlative in essence and the
570 ecological mechanisms underlying such patterns need to be further elucidated. In particular,
571 future studies should be specifically designed to investigate whether diversity and climate
572 interactively shape leaf chemistry of a focal host plant because they jointly influence resource
573 availability and their allocation to growth vs defences by trees. Our study also supports the
574 view that the phylogenetic or functional diversity of tree species is complementary to species
575 richness in predicting tree-herbivore relationships, likely because it accounts for additional
576 information relative to niche differentiation and functional dissimilarities between tree
577 species. Finally, our findings suggest that tree diversity effects on herbivory levels should be
578 viewed as a balance between multiple processes arising from different attributes of tree
579 diversity (inter-specific variation of different traits). Future research should investigate which
580 traits of tree species drive associational effects on herbivory and address simultaneously
581 multiple underlying mechanisms. For instance, it would be particularly interesting to explore
582 the role of forest structure and tree spatial arrangement in associational effects, as it may be
583 implied in both neighbour-induced changes in chemical defences through effects on individual
584 crown illumination, as well as in focal plant apparency. Importantly, the climatic context in
585 which plant-herbivore interactions occur should be accounted for in future studies for a better
586 understanding of the processes at play. By doing so, the study of tree diversity effects on tree
587 resistance to insect herbivores interactions will move toward a more predictive framework.

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596

597 Author contributions

598 BC and HJ designed the study. HJ, NB, JB, NE, OF, FG, DG, JK, BMa, EM, BMu, CN, AP, QP, MSL,
599 VS, MS, KV and BC collected data. XM and MF performed phenolics analysis. CP computed
600 extra data, extracted climatic data and run the analysis. CP, BC, HJ, XM and JK wrote the first
601 draft. All co-authors contributed substantially to subsequent revisions.

602

603 Data availability

604 Data are available from the Data INRAe repository: <https://doi.org/10.15454/SHCUXW>.

605

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Tables

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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.

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					

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933 **Table 2.** Effects of tree diversity, temperature and rainfall on (a) insect herbivory and (b) leaf phenolic
 934 concentration. Predictors that were excluded from the final model during simplification are not shown.
 935 **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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940 **Table 3.** Effects of leaf phenolic concentration on insect herbivory as a covariate of tree diversity,
 941 temperature and rainfall. Predictors that were excluded from the final model during simplification are
 942 not shown. Bold predictors have a significant effect.

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

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