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1 **Present conditions may mediate the legacy effect of past land-use changes on species richness and**
2 **composition of above- and below-ground assemblages**

3

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19

20 Running title: Forest continuity is mediated by stand maturity

21 **Summary**

22 1. In forest ecosystems, the influence of landscape history on contemporary biodiversity patterns has been
23 shown to provide a convenient framework to explain shifts in plant assemblages. However, very few studies
24 have controlled for present human-induced activities when analyzing the effect of forest continuity on
25 community structures. By cutting and removing trees, foresters substantially change stand ecological
26 conditions, with consequences on biodiversity patterns. Disentangling the effect of past and present human
27 activities on biodiversity is thus crucial for ecosystem management and conservation.

28 2. We explored the response of plant and springtail species richness and composition to forest continuity
29 (ancient vs recent) in montane forests, while controlling for stand maturity (mature vs overmature). We
30 established 70 sites in landscapes dominated by unfragmented ancient forests where we surveyed plants and
31 assessed springtails by analyzing environmental DNA.

32 3. Neither plant nor springtail species richness was influenced by forest continuity or by stand maturity.
33 Instead, site-specific characteristics, especially soil properties and canopy openness, were of major importance
34 in shaping above- and below-ground richness.

35 4. For plant and springtail species composition, the effect of forest continuity was mediated by stand maturity.
36 Thus, both plants and springtails showed a convergence in assemblage patterns with the increasing availability
37 of overmature stand attributes. Moreover, soil and stand-scale factors were evidently more important than
38 landscape-scale factors in shaping above- and below-ground species composition.

39 5. *Synthesis*. We clearly demonstrated that biodiversity patterns are more strongly influenced by present
40 human-induced activities than by past human-induced activities. In the Northern Alps where our study sites
41 were located, the colonization credit of most species has been paid off and the transient biodiversity deficit
42 usually related to forest continuity has moved toward equilibrium. These findings emphasize the necessity to
43 better control for local-scale factors when analyzing the response of biodiversity to forest continuity; we call
44 for more research into the effects of forest continuity in unfragmented mountain forests.

45

46 Key-words: ancient forest, community dynamics, dispersal, forest management, habitat quality, land-use

47 history, mountain forest, plant–soil interactions, secondary succession

48 **Introduction**

49 The influence of landscape history on contemporary biodiversity patterns is increasingly recognized as
50 a key factor that structures species assemblages today (Hermy & Verheyen 2007). Given that most of the
51 world’s terrestrial ecosystems have been more or less impacted by human actions (Newbold *et al.* 2015),
52 understanding legacies of the past may help to better understand present biodiversity patterns and predict the
53 future ecological impacts of on-going human practices on ecosystem services and functions (Vellend *et al.*
54 2013). In a context of continuing global biodiversity loss (Butchart *et al.* 2010), understanding the influence of
55 past and present human actions on ecosystems is of primary importance for conservation.

56 Forest ecosystems represent one third of Europe’s total land area (Forest Europe 2015). However,
57 European forest cover has fluctuated widely over the last centuries (Kaplan, Krumhardt & Zimmermann 2009).
58 After a long period of deforestation, forest cover has consistently increased since the mid-nineteenth century
59 (FAO 2015) and has nearly doubled in France (Mather, Fairbairn & Needle 1999). This reforestation has mainly
60 occurred on abandoned agricultural land, either through spontaneous recolonization or deliberate replanting.
61 Two types of forests have resulted: ancient forests, which have existed continuously for centuries, and recent
62 forests, which result from reforestation after a certain threshold date (Hermy & Verheyen 2007). This massive
63 land-use change has led researchers to develop the concept of “forest continuity”, also referred as “forest
64 ancientness” or “ancient woodland” (Flinn & Vellend 2005; Goldberg *et al.* 2007; Hermy & Verheyen 2007).
65 Forest continuity is thus defined as a minimum residence time of the wooded state since a threshold date,
66 which differs between countries in northwestern Europe due to the complex land use history and availability of
67 historical maps (e.g. 1600 or 1700 in GB; 1750 or 1800 in Germany; 1770–1800 in Belgium & Denmark; 1820 in
68 Sweden; 1820–1850 in France & Netherlands; Hermy and Verheyen, 2007).

69 Forest continuity has been shown to play a fundamental role in driving herbaceous plant assemblages
70 in temperate forests (Flinn & Vellend 2005; Hermy & Verheyen 2007). Two processes have been highlighted:
71 dispersal limitations due to poor ability of ancient-forest plant species to colonize recent forests (e.g. Verheyen
72 *et al.* 2003; Naaf & Kolk 2015) and recruitment limitations due to modifications in soil properties and
73 competitive interactions (e.g. Honnay *et al.* 2002a; Baeten, Hermy & Verheyen 2009). Given the influence of
74 forest continuity on primary producers it is therefore reasonable to assume that continuity has an indirect
75 effect on primary consumers and decomposers, especially for the less motile taxa. For example, it has been
76 shown that changes in plant communities between ancient and recent forests act indirectly on true bugs

77 (Gossner, Engel & Jessel 2008). Moreover, due to modifications in soil properties related to past land-use,
78 forest continuity can be expected to have direct effects on below-ground soil fauna. However, very few studies
79 to date have investigated these relationships (e.g. Assmann 1999; Buse 2012; Janssen *et al.* 2016).

80 Beyond past land-use effects, present human activities also impact forest biodiversity. Through
81 management practices, foresters substantially change stand ecological conditions, and this has consequences
82 on biodiversity (Paillet *et al.* 2010). Indeed, regardless of forest continuity, many forest taxa are influenced by
83 stand maturity attributes, e.g. dead-wood volume. This suggests that there is an additive effect of stand
84 maturity over forest continuity which, if not accounted for, may mask or reinforce the expected ecological
85 processes studied. However, very few studies have controlled for stand maturity when comparing ancient and
86 recent forests (but see, Kolb & Diekmann 2004; Kelemen, Kriván & Standovár 2014), making it difficult to
87 distinguish the effect of stand maturity from the effect of forest continuity *per se* (Nordén *et al.* 2014). To
88 properly disentangle the effect of past and present human activities and to subsequently improve conservation
89 strategies, this information is fundamental.

90 We aimed to study the effect of forest continuity on vascular plants and springtails in mixed montane
91 forests, while controlling for stand maturity. Since forest continuity is expected to influence plant assemblages
92 and since plant assemblages determine resource inputs for the decomposer subsystem (Hansen 2000; Wardle
93 2006), variations in plant assemblages between ancient and recent forests may have important effects on
94 below-ground biota and the processes that they regulate (Wardle *et al.* 2004). Given the huge number of
95 diverse species and the fundamental role played by soil fauna in ecosystem functioning (Decaëns *et al.* 2006), it
96 appear essential to investigate the legacy effects induced by forest continuity on below-ground biodiversity.
97 Moreover, due to their small body size and the difficulties they have moving within the soil, most soil taxa are
98 likely to have poor dispersal abilities. As such, it has been showed that springtail diversity is affected by land-
99 use change and that species recovery in reforested sites may take more than 50 years, especially for poorly
100 dispersing species (Ponge *et al.* 2006). Moreover, springtails respond to modifications in soil conditions and
101 vegetation cover (Ponge *et al.* 2003; Korboulewsky, Perez & Chauvat 2016), two ecosystem alterations that
102 may result from past and present human-induced activities. Thus, a combined above- and below-ground
103 approach should enhance our understanding of the human impacts on biodiversity, and result in a better
104 orientation of conservation strategies (Wardle *et al.* 2004).

105 Specifically, we tested whether species richness and composition of herbaceous plants and springtails
106 responded to forest continuity and stand maturity. As it is likely that shifts in species richness and composition
107 result from a complex of different factors acting at different spatial scales (Siefert *et al.* 2012), we also tested
108 the relative influence of a set of soil, stand- and landscape-scale variables on plants and springtails. Landscape
109 variables were used to consider possible factors underlying the effect of forest continuity, e.g. related to
110 differences in the amount of habitats in the surrounding landscapes between ancient and recent forest sites.
111 Stand and soil variables were used to account for important local characteristics that may structure plant and
112 springtail communities, beyond the influence of stand maturity and forest continuity. Moreover, soil variables
113 helped us to control for possible remaining effects of past land-uses (e.g. Dupouey *et al.* 2002; Dambrine *et al.*
114 2007). Based on this scheme, we addressed the following two questions: (i) Are past human-induced activities
115 or are present human-induced activities more important in shaping herbaceous plant and springtail species
116 richness and composition? (ii) Among soil, stand and landscape, which factor has the greatest influence on
117 herbaceous plant and springtail species richness and composition?

118

119 **Materials and methods**

120 **Study area and experimental design**

121 The study was carried out in the French pre-Alps in the Vercors, Chartreuse and Bauges ranges (Fig. 1),
122 all of which are characterized by a limestone substratum and a temperate climate. The landscapes are mostly
123 forested (63%) and reforestation has mainly occurred above and below the persistent forest belt, as it has
124 elsewhere in European mountain areas (Kozak 2003; Gellrich *et al.* 2007). Moreover, due to physical
125 constraints and lack of logging roads, mountain forests has hitherto been less intensively managed than
126 lowland forests (Paillet *et al.* 2015). Therefore, compared to recent lowland forests, the recent montane forests
127 in the Northern Alps, i.e. forests that have existed since at least 1864, are mostly adjacent to ancient forests
128 and have the potential to develop towards stand structures similar to those found in ancient forests.

129 We sampled 70 sites located in montane beech-fir forests at an altitude of 800 – 1500 m. The
130 dominant tree species are European beech *Fagus sylvatica*, silver fir *Abies alba* and Norway spruce *Picea abies*.
131 Our stratified sampling design crossed forest continuity (ancient forests = 37; recent forests = 33) and stand
132 maturity (mature stands = 37; overmature stands = 33), resulting in 22 ancient-mature sites, 15 ancient-
133 overmature sites, 15 recent-mature sites and 18 recent-overmature sites. All selected sites were managed by

134 selective cutting at some point, i.e. stumps were measured at and around sites (see Appendix S3 & S4). To
135 ensure the independence among observations and avoid edge effects, all the sampling sites were established >
136 1 km away from any other sites, were located in ancient or recent forests > 5 ha in area, and were > 50 m from
137 the nearest stand edge.

138 **Forest continuity, stand maturity and soil characterization**

139 Forest continuity was characterized by crossing digitized and geo-referenced 1:40 000 État-Major
140 maps of France, charted in the middle of the 19th century, combined with up-to-date 1:10 000 vegetation maps
141 in a Geographic Information System managed with QGIS (QGIS Development Team 2015). Forest cover
142 overlapping in both maps was considered to indicate ancient forests, while current forest cover overlapping
143 with crops, pastures or meadows in the État-Major maps was considered to indicate recent forests. Around
144 each selected ancient and recent forest site (500 m radius), we controlled the État-Major maps using 1:5 000 or
145 1:2 500 cadastral plans drawn between 1809 and 1838 for the Vercors and the Chartreuse ranges (“Napoléonic
146 cadastre”) and between 1730 and 1738 for the Bauges range (“Sarde cadastre”). Past land-use in recent forest
147 sites was then accurately described (pastures: n = 17; meadows: n = 13; crops: n = 3). Moreover, to confirm the
148 continuity of the forest cover since the middle of the 19th century, we used aerial photographs taken in the
149 1950s, at and around each site.

150 Stand maturity was a priori approached by forest prospections (n = 117) and rapid stand attribute
151 measurements (diameter of the three largest trees, presence of large snags and/or of large coarse woody
152 debris). We then selected 70 stands in a way that ensures a balanced distribution of sites between ancient and
153 recent forests and a priori mature and overmature stands. In each selected stands, stand maturity was then
154 characterized on a 20 m radius plot and a 10 m radius subplot in which all standing trees and lying trunks were
155 recorded (for further details, see Janssen *et al.* 2016). Canopy openness was estimated with a spherical
156 densiometer from four points in the cardinal directions, 10 m away from the plot center. To distinguish
157 between mature and overmature stands (see Appendix S2), we used hierarchical cluster analysis (Ward
158 method) based on the three first axes of a principal component analysis (PCA) with a cumulative projected
159 inertia of 88.30% (ade4 package). PCA was conducted considering four environmental variables closely related
160 to stand maturity: volume of large coarse woody debris ($\varnothing > 30$ cm), number of large snags ($\varnothing > 30$ cm),
161 number of very large living trees ($\varnothing > 62.5$ cm) and tree microhabitat diversity (i.e. the number of microhabitat
162 types: cavities, sporophores of saproxylic fungi, ivy, sap runs, missing bark, cracks and shelter bark).

163 To characterize soil properties, we dug a soil pit > 50 cm in depth in the plot center. In each soil pit,
164 two soil samples were collected – at 0-10 cm (topsoil) and at 30-40 cm (subsoil) – and humus forms were
165 described. Each soil sample was analysed for pH (H₂O, NF ISO 10390), total C (NF ISO 10694), total N (NF ISO
166 13878) and available P content (Olsen method, NF ISO 11263). Subsoil samples were also analysed for clay, silt
167 and sand proportions. Soil analyses were performed by the INRA Soil Analysis Laboratory following procedures
168 of the French Standardization Association (i.e. AFNOR).

169 **Environmental variables**

170 To model the response of plants and springtails to forest continuity and stand maturity, we used soil,
171 stand and landscape variables in addition to these two factors. Among a larger set of potential variables (see
172 Appendix S3 & S4 in Supporting Information), we selected nine uncorrelated and *a priori* biologically important
173 variables (Table 1 & see Appendix S5). Landscape variables – i.e. the distance to nearest forest edge
174 (Dist_Forest), land-use diversity (Alpha_LU, measured within a 500 m radius) and the forest proportion
175 (Prop_Forest, measured within a 500 m radius) – were measured in surrounding landscape at each sampling
176 site. Stand variables – i.e. mean canopy openness (Canop), the proportion of conifers (Tree_Compo) and the
177 number of diameter classes (5-cm) for standing trees (Tree_Struc) – were extrapolated from stand
178 measurements within each 20 m radius plot. Soil variables – i.e. the humus index (Ponge & Chevalier 2006)
179 (H_index), the pH (pH) and the total carbon/total nitrogen ratio (CN_ratio) – were derived from humus form
180 description and topsoil sample analysis.

181 **Plant survey**

182 Following the Braun-Blanquet abundance-dominance methodology, we surveyed all the vascular
183 plants within the 10 m radius circular subplot. To limit variation in plant species composition due to
184 environmental conditions, all the plots were established in ecologically similar sites (mesophilic and
185 neutrophilic) belonging to the alliance *Fagion sylvaticae*. Moreover, in order to characterize the entire ground-
186 layer plant community and account for plant phenology, two complete vegetation surveys were done: from
187 May to June 2014 for vernal species and from July to August 2014 for estival species. Finally, to limit biases
188 associated with observer effect, all surveys were performed by the first author (PJ).

189 **Springtail assessment**

190 Soil fauna studies often suffer from the inefficiency of sampling strategies and a strong taxonomic
191 deficit (André, Ducarme & Lebrun 2002). We therefore chose to use environmental DNA (eDNA) from the soil

192 core samples to characterize springtail communities. eDNA is an emerging approach for biodiversity studies
193 (Thomsen & Willerslev 2015) that has already proved its efficiency, e.g. for earthworms (Pansu *et al.* 2015).

194 In each site, two semi-circular 10 m radius plots were established. Within each semi-circular plot, 25
195 soil cores (10-cm depth) were collected in September 2015 and pooled together. To avoid cross-contamination,
196 the coring sampler was sterilized between sites by flame cleaning and, to avoid DNA degradation before
197 extraction, soil samples were dehydrated with silica gel. For each composite soil sample (n = 140), soil
198 extracellular DNA was isolated in November 2015 following Taberlet *et al.*'s (2012) protocol. Extraction was
199 performed with the NucleoSpin® Soil isolation kit (Macherey-Nagel, Düren, Germany); the lysis step was
200 skipped and the manufacturer's instructions were followed closely.

201 Springtail communities were assessed with a primer pair targeting a region of the 16S rRNA gene. For
202 each sample, three PCR replicates were carried out, resulting in 420 samples (see Appendix S1). Library
203 construction and sequencing for the samples (Illumina HiSeq 2500 platform, 2 x 100 bp, paired-end reads) were
204 carried out at Fasteris (Geneve, Switzerland). The DNA sequences read were then filtered and clustered into
205 molecular operational taxonomic units (MOTU) with the dedicated OBITools package and according to an
206 established workflow (Boyer *et al.* 2016). A complete description of data processing is proposed in Appendix
207 S1.

208 **Statistical analysis**

209 Analyses were performed with R version 3.2.2 (R Core Team 2016). We used presence/absence for
210 plants and for springtails as dependent variables in the following analysis. Based upon data exploration (Zuur,
211 Ieno & Elphick 2010), independent variables with a skewness >1 were log or log+1 transformed to approximate
212 normal distributions. For proportional data, logit transformation was applied (Warton & Hui 2011). We then
213 used two-way ANOVAs with type III sum of squares to test the significance of each environmental variable to
214 forest continuity, stand maturity and their interaction term (Table 1, see Appendix S3 & S4).

215 To determine whether plant or springtail richness was influenced by forest continuity and/or stand
216 maturity, we also used two-way ANOVAs with type III sum of squares. To verify hypothesis statements, we
217 developed 49 *a priori* candidate GLMs, plus a null model (see Appendix S6). We used Poisson regressions to
218 relate richness in plants and springtails to soil, stand and landscape variables; we considered a balanced
219 number of models to avoid biasing estimates toward a particular category of environmental variables. We
220 assessed multi-collinearity among explanatory variables with variance inflation factors (car package) and spatial

221 autocorrelation with Moran's correlogram in the model residuals among sampling sites (ncf package). To
222 identify the most parsimonious GLM, we used Akaike's information criterion corrected for small sample sizes
223 (AICc, Burnham & Anderson 2002). Moreover, we used model averaging to estimate parameter and associated
224 unconditional standard errors based on the subset of top ranking models for which the sum of the AICc weights
225 reached ≥ 0.95 (MuMIn package). To determine the relative importance of soil *versus* stand models, soil *versus*
226 landscape models and stand *versus* landscape models, we compared the sum of the AICc weights for three
227 categories of models: e.g. models that accounted for soil variables only, for stand variables only and models
228 that accounted for both types of variables (Burnham & Anderson 2002).

229 To determine if species composition was influenced by forest continuity and/or stand maturity, we
230 used multivariate GLMs. This approach has the advantage of being based on a GLM framework, which is
231 typically better able to handle the strong mean-variance relationship in abundance data (Warton, Wright &
232 Wang 2012). We fitted separate models to each species with a binomial distribution and summed across the
233 univariate response to estimate their multivariate response, i.e. assuming the independence of the species
234 response variables. The significance of the multivariate response was assessed with the PIT-trap method with
235 999 bootstrap resamples (mvabund package). We first assessed the effect of forest continuity and/or stand
236 maturity on plant and springtail composition and then performed a canonical analysis of principal coordinates
237 (CAP, Anderson & Willis 2003) with a Sørensen-Dice index, to provide a graphical representation of the
238 interaction. We then ran the 49 *a priori* models, plus the null model (see Appendix S6). To identify the most
239 parsimonious multivariate GLM, we used AICc. For each multivariate model, AICc was obtained by extracting the
240 log-likelihood and calculating the AICc of each univariate model, summing AICc values and standardizing the
241 sum by the number of observations. Model performance was evaluated according to the proportion of
242 deviance explained ($D^2 = (\text{null deviance} - \text{residual deviance}) / \text{null deviance}$), and the significance of each
243 independent variable was assessed using an analysis of variance on the full multivariate GLM. To determine the
244 relative importance of soil *versus* stand models, soil *versus* landscape models and stand *versus* landscape
245 models, we compared the sum of the AICc weights for the three categories of multivariate GLMs.

246

247 **Results**

248 Overall, 195 plant species were recorded on the 70 sites. Because overstory is directly influenced by
249 silviculture, we focused on understory species ($S = 157$; mean = 27; range 8-46), i.e. herbaceous plants

250 (therophytes, geophytes, hemicryptophytes and chamaephytes). The sequencing of springtail metabarcodes
251 generated 16 394 927 reads, which, after filtering, resulted in a total of 188 MOTUs (mean = 42; range 24-59)
252 (see Appendix S1).

253 **Variations in soil, stand and landscape variables in relation to forest continuity and stand maturity**

254 Soil, stand and landscape variables varied according to forest continuity and stand maturity
255 classification (see Appendix S3). Indeed, nearly all of the variables related to stand structural complexity and
256 dead-wood compartment increased from mature to overmature stands; while all the variables related to forest
257 proportion and distance to the edge increased from recent to ancient forests. On the other hand, soil variables
258 were not clearly related to forest continuity or to stand maturity. Only some weakly significant relationships
259 were found: topsoil C/N ratio and subsoil clay proportion increased from ancient to recent forests, while total
260 subsoil nitrogen increased from recent to ancient forests; humus index and total subsoil carbon increased from
261 overmature to mature stands; while subsoil clay proportion increased from mature to overmature stands.
262 However, total phosphorous and total nitrogen did not increase and pH did not become more basic in either
263 subsoil or topsoil when ancient and recent forests were compared, indicating the absence of a legacy effect
264 related to past land-use.

265 The interaction term between forest continuity and stand maturity was non-significant for almost all
266 the tested variables (see Appendix S4), indicating that these variables varied consistently between ancient and
267 recent forests, at a comparable level of maturity.

268 **Response of species richness to forest continuity, stand maturity and associated variables**

269 Two-way ANOVAs revealed no difference in plant or springtail richness between ancient and recent
270 forests, mature and overmature stands or between ancient-mature, ancient-overmature, recent-mature and
271 recent-overmature stands.

272 GLM results showed that plant and springtail richness were best predicted by the same most
273 parsimonious model (i.e. based on AIC_c), which accounted for soil and stand variables (Table 2). Observed
274 Moran's *I* for the top model's residuals was non-significant for both dependent variables, indicating that spatial
275 patterns had been accounted for by the environmental variables (see Appendix S7). The predictive value of this
276 model was high for plants (pseudo-R² = 73%) and low for springtails (pseudo-R² = 16%). Although this model
277 seems quite robust for explaining richness patterns, model selection uncertainty still remains since associated
278 AIC_c weight and evidence ratio were relatively low. We therefore used model averaging – the 7 top-ranked

279 plant models and 38 top-ranked springtail models – to draw inferences about the variables' influence on
280 richness. Plant and springtail richness increased with an increasing pH value (Table 3). Stand variables only
281 influenced plant richness, which increased with mean canopy openness and the proportion of conifers but
282 decreased with increasing number of tree diameter classes. Landscape variables did not influence either plant
283 or springtail richness.

284 Judging from the sum of AICc weights for GLMs, plant richness was more influenced by models
285 accounting for a combination of different environmental factors than was springtail richness (Fig. 2). Indeed,
286 for soil *versus* stand models, plant richness was better explained by models combining both types of variables
287 (sum of AICc weight, $\sum AICw = 0.87$), while springtail richness was more heterogeneous, though somewhat
288 better explained by soil models ($\sum AICw = 0.44$). When comparing soil *versus* landscape models, both plant and
289 springtail richness was better explained by soil models only ($\sum AICw$, range 0.56 – 0.67). Finally, when
290 comparing stand *versus* landscape models, plant richness was slightly better explained by models combining
291 both types of variables ($\sum AICw = 0.50$), while springtail richness was more heterogeneous, though better
292 explained by stand models ($\sum AICw = 0.41$).

293 **Response of species composition to forest continuity, stand maturity and associated variables**

294 Multivariate GLMs showed that the interaction term between forest continuity and stand maturity
295 was significant for both plant ($D^2 = 0.099$, $p = 0.001$) and springtail ($D^2 = 0.076$, $p = 0.021$) assemblages.
296 Variation in species composition between ancient and recent forests were thus different in mature and
297 overmature stands. Constrained ordination plots showed that plant and springtail species composition
298 converged from mature to overmature stands, regardless of forest continuity (Fig. 3). In others words,
299 dissimilarities among assemblages of species were more important between ancient and recent forests in
300 mature stands.

301 Multivariate GLMs results showed that variations in plant and springtail species composition were best
302 predicted by the same most parsimonious model (i.e. based on AICc), which accounted for soil variables only
303 (Table 4). However, compared to the full model (plants, $D^2 = 40\%$; springtails, $D^2 = 28\%$), this model explained a
304 relative low proportion of the variance. Moreover, model selection uncertainty remains for both dependent
305 variables since associated AICc weight and evidence ratio were low and since the null model was one of the ten
306 top-ranked models. Regarding the three most important variables influencing composition patterns (based on
307 the proportion of deviance explained), our results showed that plants were especially influenced by humus

308 index, the number of tree diameter classes and the proportion of coniferous; while springtails were especially
309 influenced by humus index, pH and canopy openness (Table 5).

310 Judging from the sum of AICc weights for multivariate GLMs, plant and springtail species composition
311 was more heterogeneous and models accounting for a combination of different environmental factors were of
312 relatively low importance (Fig. 4). Indeed, for soil *versus* stand models, plant assemblages were equally well
313 explained by both soil and stand models, while springtail assemblages were better explained by soil models
314 only ($\sum AICw = 0.54$). When comparing soil *versus* landscape models, both plant and springtail assemblages
315 ($\sum AICw = 0.57$ and $\sum AICw = 0.74$, respectively) were better explained by soil models. Finally, when comparing
316 stand *versus* landscape models, plants assemblages were equally well explained by stand and landscape
317 models, while springtail assemblages were better explained by stand models only ($\sum AICw = 0.68$).

318

319 **Discussion**

320 Our results clearly show that plant and springtail species richness and composition were more
321 influenced by present human-induced activities than by past human-induced activities. Moreover, no legacy
322 effect of past land-use were found for either soil or stand properties. Specifically, we highlighted the influence
323 of site-specific characteristics (i.e. soil properties) and present management practices (i.e. stand structure and
324 composition) in shaping above- and below-ground community structure. Landscape scale factors were not
325 important in explaining variations in plant and springtail species richness and composition. Furthermore, we
326 demonstrated that, in unfragmented montane forests dominated by ancient forests, the effect of forest
327 continuity is mediated by stand maturity and soil properties.

328 **Richness patterns are obviously shaped by local factors**

329 Species richness was not directly influenced by stand maturity, let alone by forest continuity. This may
330 indicate the absence of past and present human-induced activities on current total above- and below-ground
331 richness. Previous studies also reported that forest continuity had no influence on total plant richness (e.g.
332 Hermy & Verheyen 2007; Sciama *et al.* 2009). For springtails, only one study has reported that richness
333 increases in ancient forests, as compared to very recently established forests (Heiniger *et al.* 2014). For stand
334 maturity, many studies have examined the influence of stand age on plant richness or have compared the plant
335 richness of managed *versus* unmanaged stands (as a proxy for stand maturity), but no clear trends have been
336 reported (Paillet *et al.* 2010; Duguid & Ashton 2013). Likewise, for springtails, while some studies state that

337 richness increases with stand age (e.g. Salamon, Scheu & Schaefer 2008; Chauvat *et al.* 2011b), others report a
338 non-significant increase or even a decrease (e.g. Addison, Trofymow & Marshall 2003; Chauvat, Zaitsev &
339 Wolters 2003). Overall our results are consistent with current knowledge and indicate that the classification
340 used, i.e. ancient *versus* recent and mature *versus* overmature, may be too coarse and heterogeneous to
341 properly reveal the underlying ecological processes involved. To disentangle the effect of forest continuity and
342 stand maturity on species richness, it therefore appears essential to move beyond simple categories to account
343 for related factors.

344 As compared to soil and stand scale factors, landscape scale factor performed poorly in explaining
345 richness patterns. This indicates that, at the spatial scale of our study, site-specific characteristics are of great
346 importance in shaping above- and below-ground species richness. However, this does not rule out the
347 possibility that richness patterns are better explained by other landscape factors at larger spatial scales.
348 Specifically, soil factors were powerful predictors of plant and springtail richness, while stand factors were
349 powerful predictors of plant richness only. Several studies have pointed out the importance of local-scale
350 factors for species richness (Wang *et al.* 2009; Zellweger *et al.* 2015; Bernhardt-Römermann *et al.* 2015). Light
351 availability is known to influence plant richness (Paillet *et al.* 2010; Bernhardt-Römermann *et al.* 2015), since
352 semi-open stands allow light- and shade-tolerant species to coexist. Moreover, through variations in closely
353 related resources, i.e. light, water and soil nutrients, overstory structure and composition influence understory
354 richness (Barbier, Gosselin & Balandier 2008). For example, the positive influence of the coniferous proportion
355 we found on plant richness may be related to an increase in soil water availability, given that the shift in
356 composition was driven by silver fir, a tree that prefers meso-hygrophilous soil conditions. For springtails, it has
357 been suggested that tree mixture, through the diversity of food resources supplied, may positively influence
358 species richness (Salamon & Alpehi 2009; Chauvat *et al.* 2011a). As previously stated (Korboulewsky *et al.*
359 2016), our results indicate that stand factors are of secondary importance and that springtail richness is
360 predominantly influenced by soil factors, especially pH (Salmon *et al.* 2006; Salamon *et al.* 2008). Apart from
361 forest-continuity and stand-maturity associated factors, it appears essential to account for soil factors to better
362 predict species richness. Our findings point out the importance of local resource availability and heterogeneity
363 in driving richness patterns of above- and below-ground taxa (Bartels & Chen 2010; Decaëns 2010).

364 **Species composition: the effect of forest continuity is mediated by stand maturity and local factors**

365 Species composition was not directly influenced by forest continuity. Indeed, plant and springtail
366 assemblages were closely related in both ancient and recent overmature stands, but strongly differed in
367 ancient and recent mature stands. This indicates that the effect of forest continuity was mediated by stand
368 maturity and thus that present human-induced activities may be of more importance than past ones in shaping
369 assemblages patterns. This surprisingly slight legacy effect is interesting given the large number of studies that
370 have demonstrated the influence of forest continuity on plant assemblages (review in Flinn & Vellend 2005;
371 Hermy & Verheyen 2007). However, most of the previous studies were conducted in rather similar ecological
372 conditions: lowland temperate forests encompassing fragmented and forest-poor landscapes and dominated
373 by recent forests (De Frenne *et al.* 2011). In the Northern Alps where our study plots were located, the
374 landscapes are mainly covered by unfragmented ancient forests, and reforestation has largely occurred next to
375 these ancient forests. Since fragmentation worsens dispersal limitations (Jamoneau *et al.* 2012) and since
376 colonization efficiency depends on habitat availability (De Frenne *et al.* 2011), forest-plant species have been
377 able to rapidly colonize recent forests in our study area. For springtails, Huhta and Ojala (2006) reported that
378 assemblages differed between 30-years-old birch plantations established on spruce forest soils and on arable
379 land. However, the authors found that soil properties differed with forest continuity and were key factors in
380 explaining differences in species composition. In our case, and contrary to numerous studies (e.g. Dupouey *et*
381 *al.* 2002; Dambrine *et al.* 2007), no legacy effect was found for soil properties. We therefore considered soil
382 habitat quality to be equivalent between the ancient and recent forests. Moreover, most of our recent forest
383 sites were established on former pastures or meadows. Since the legacy effect of past land-use is more
384 important on former croplands than on former grasslands (Koerner *et al.* 1997; Wulf 2004) and since remnant
385 population of forest species are better able to survive in grasslands (Wulf 2004; Burst *et al.* 2017),
386 recolonization of recent forests have probably been accelerated. This is especially true in mountain areas
387 where, as compared to lowland, a larger range of herbaceous forest species has the ability to grow in open
388 habitats (Schmidt, Kriebitzsch & Ewald 2011). We then inferred that the plant and springtail assemblages in our
389 study were not influenced by recruitment and dispersal limitations between ancient and recent forests and
390 that, therefore, forest continuity was of minor importance in shaping assemblages patterns. Instead, our
391 results underline the importance of stand maturity. Changes in stand characteristics with stand age or due to
392 forestry practices are well-known to influence both plant (e.g. Scheller & Mladernoff 2002; Amici *et al.* 2013;
393 Sabatini *et al.* 2014) and springtail communities (e.g. Addison *et al.* 2003; Chauvat *et al.* 2003; Salamon *et al.*

394 2008). Here, we document for the first time that stand maturity may mediate the effect of forest continuity by
395 leading to a convergence in assemblage patterns with the increasing availability of overmature stand
396 attributes. In recent forests, the effect of stand maturity may also reflect an increase in the residence time of
397 the wooded state from mature to overmature stands. This may have led to an increase of the recolonization
398 potential of forest species in recent-overmature stands but also to a greater recovery in environmental
399 conditions between ancient- and recent-overmature stands (e.g. Flinn & Marks 2007). Since stand maturity
400 may cause strong environmental filtering on biodiversity, and since stand maturity may interact with forest
401 continuity, controlling for habitat quality seems essential to demonstrate the effect of habitat continuity *per se*
402 (Nordén *et al.* 2014); especially in geographical areas where unfragmented forests dominate and where soil
403 properties have little or no legacy effect.

404 Compared to soil and stand scale factors, landscape scale factors performed poorly in explaining plant
405 and springtail species composition. This confirms the importance of site-specific characteristics in shaping
406 above- and below-ground communities. Although several studies have shown that ancient-forest species
407 distribution is influenced by landscape configuration and composition (Honnay *et al.* 2002b; De Frenne *et al.*
408 2011; Naaf & Kolk 2015), it has also been reported that, in unfragmented forests dominated by ancient forests,
409 local factors explain the larger part of species composition (Jamoneau *et al.* 2012). In the Northern-Alps,
410 species assemblages were indeed largely influenced by local factors. These findings are consistent with
411 previous studies showing the importance of soil pH and humus forms, stand composition and structure or
412 canopy openness in shaping both plant and springtail assemblages (e.g. Scheller & Mladernoff 2002; Salmon *et*
413 *al.* 2006, 2008; Sabatini *et al.* 2014; Korboulewsky *et al.* 2016). The importance of these local factors points out
414 the necessity to account for site specific characteristics and current human-induced activities when analyzing
415 the effects of forest continuity. Though it has been shown that tree species influences the recruitment of
416 ancient-forest species (Thomaes *et al.* 2014), that changes in canopy structure and composition induce a shift
417 in plant communities in ancient deciduous forests (Verheyen *et al.* 2012), and that several ancient-forest plant
418 species decrease in abundance with local disturbances (Naaf & Wulf 2011), very few studies have controlled for
419 stand factors when analyzing the effect of forest continuity on biodiversity. In unfragmented forests, this may
420 have led to premature conclusions on the relative effect of forest continuity on biodiversity.

421

422 **Conclusion**

423 In their review, Hermy and Verheyen (2007) stated that the impact of current management activities
424 on the distribution of ancient-forest species remained unclear. Through a dedicated sampling design, we
425 showed that i) the effect of forest continuity was mediated by stand maturity, and ii) that local factors are
426 extremely important in explaining biodiversity patterns. Specifically, we emphasize that, in the Northern Alps,
427 the colonization credit of most plant and springtail species has been paid off and that, as a result, the transient
428 biodiversity deficit usually related to forest continuity has moved toward equilibrium between ancient and
429 recent forests (Jackson & Sax 2010). Therefore, in unfragmented forest landscapes, above- and below-ground
430 species richness and composition clearly appear to be governed mostly by niche processes (see also Jamoneau
431 *et al.* 2012). This emphasizes the necessity to better control for soil and stand factors when analyzing the
432 response of biodiversity to forest continuity.

433 Finally, though it has been shown that fragmentation enhanced dispersal limitation (Honnay *et al.*
434 2002b; Jamoneau *et al.* 2012), most studies documenting the effect of forest continuity on biodiversity have
435 used sampling designs where recent forests were disconnected from ancient forests (Verheyen *et al.* 2003;
436 Kolb & Diekmann 2004; Sciama *et al.* 2009; Naaf & Kolk 2015). However, in cases where the extinction debt has
437 not yet been paid off, it may be difficult to disentangle the effect of fragmentation from the effect of forest
438 continuity *per se*. We show that in unfragmented forests, the legacy effect of past land-use is difficult to detect,
439 at least for patterns of species richness and composition. Caution must be exercised when drawing conclusions
440 about the effect of forest continuity based on the interpretation of plant assemblage shifts in similar ecological
441 conditions, i.e. lowland fragmented forests. Despite the fact that one third of Europe's land area is
442 mountainous and that 41 % of that area is covered by forests (EEA 2010), mountain forests have rarely been
443 studied through the lens of historical ecology. Ecological conditions similar to the ones in our study are likely to
444 occur in the Carpathians, the Central European Mountains, the Balkans, the Pyrenees and other areas in the
445 Alps (e.g. Kozak 2003; Gellrich *et al.* 2007; Dittrich *et al.* 2013). More research is therefore needed to better
446 understand the effect of forest continuity on biodiversity patterns in unfragmented mountain forests.

447

448 **Authors' contributions**

449 P.J., M.F., J.J.B. and C.B. conceived and designed the experiments. P.J., S.B., and P.T. performed the
450 experiments. P.J. analyzed the data and wrote the manuscript. All authors contributed critically to the drafts
451 and gave final approval for publication.

452

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459

460 **Data accessibility**

461 Data can be accessed through the Dryad Data Repository: <http://dx.doi.org/10.5061/dryad.6c886>
462 (Janssen et al. 2017).

463

464 **Reference**

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675

676 **Supporting information**

677 Additional supporting information may be found in the online version of this article:

678 **Appendix S1.** Springtail assessment by environmental DNA metabarcoding.

679 **Appendix S2.** Biplots showing site repartition along the two first axis of PCA, in relation to the four
680 environmental variables considered and site classification according to CAH results.

681 **Appendix S3.** Variation in contextual, soil, stand and landscape variables in relation to forest continuity and
682 stand maturity factors.

683 **Appendix S4.** Variation in contextual, soil, stand and landscape variables in relation to the interaction between
684 forest continuity and stand maturity factor.

685 **Appendix S5.** Correlation matrix of soil, stand and landscape variables used to model plant and springtail
686 species richness and composition in the French pre-Alps.

687 **Appendix S6.** Candidate models used to relate plant and springtail species richness and composition to soil,
688 stand and landscape variables, in the French pre-Alps.

689 **Appendix S7.** Moran's I correlogram on raw data and top model residuals used to predict plant and springtail
690 species richness in the French pre-Alps.

691

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694 issues arising from supporting information (other than missing files) should be addressed to the authors.

695 **Table 1.** Variations in soil, stand and landscape variables in relation to forest continuity and stand maturity factors in the French pre-Alps (p-value based on two-way
 696 ANOVAs, type III SS).

Variables	Description	Ancient	Recent	p-value	Mature	Overmature	p-value
		Mean (\pm SD)	Mean (\pm SD)		Mean (\pm SD)	Mean (\pm SD)	
Soil variables							
H_index	Humus index (based on humus form)	2.68 (\pm 1.36)	2.91 (\pm 1.68)	0.7146	3.19 (\pm 1.39)	2.33 (\pm 1.53)	0.0006
pH	pH-H ² O (topsoil)	6.31 (\pm 1.03)	6.40 (\pm 0.88)	0.8580	6.45 (\pm 1.08)	6.24 (\pm 0.81)	0.3799
CN_ratio	Total carbon / total nitrogen ratio (topsoil)	17.49 (\pm 2.34)	17.71 (\pm 2.70)	0.0453	18.12 (\pm 2.46)	17.00 (\pm 2.45)	0.9617
Stand variables							
Canop	Mean canopy openness (%)	10.47 (\pm 5.24)	10.27 (\pm 5.46)	0.7436	8.65 (\pm 3.82)	12.31 (\pm 6.09)	0.0061
Tree_Compo	Coniferous proportion	75.77 (\pm 14.19)	75.51 (\pm 17.82)	0.2164	72.37 (\pm 16.29)	79.33 (\pm 14.80)	0.0063
Tree_Struc	Number of diameter classes of standing trees	11.97 (\pm 1.76)	12.61 (\pm 2.09)	0.5805	11.08 (\pm 1.01)	13.61 (\pm 1.85)	0.0001
Landscape variables							
Alpha_LU	Land-use diversity (500 m radius)	2.51 (\pm 1.04)	3.03 (\pm 0.98)	0.0317	2.89 (\pm 1.10)	2.61 (\pm 0.97)	0.5744
Dist_Forest	Distance to forest edge in meters	226 (\pm 111.77)	139 (\pm 86.31)	0.0043	174 (\pm 105.00)	197 (\pm 113.71)	0.4129
Prop_Forest	Forest proportion (500 m radius)	92.32 (\pm 10.81)	87.00 (\pm 13.30)	0.0043	86.30 (\pm 13.99)	93.74 (\pm 8.57)	0.3190

697 **Table 2.** The 5 among 50 top-ranking models (see Appendix S6) predicting plant and springtail richness in the
698 French pre-Alps, as assessed with Akaike's information criterion corrected for small sample size (AIC_c). Number
699 of estimated parameters including the intercept (k), AIC_c, the difference in AIC_c (Δ AIC_c), AIC_c weight (W),
700 adjusted R² and evidence ratio (ER), i.e. Akaike weight of the top-ranked model/Akaike weight of the second
701 top-ranked model, are provided.

No.	Candidate model	k	AIC _c	Δ AIC _c	W	R ²	ER
Plant richness							
23	pH Tree_Struc Tree_Compo Canop	5	501.3	0.000	0.641	0.728	5.7
14	Tree_Struc Tree_Compo Canop	4	504.8	3.486	0.112	0.704	1.9
28	H_index pH CN_ratio Tree_Struc Tree_Compo Canop	7	506.1	4.779	0.058	0.728	1.5
38	Tree_Struc Tree_Compo Canop Alpha_LU	5	507.0	5.629	0.038	0.705	1.0
36	Tree_Struc Tree_Compo Canop Prop_Forest	5	507.0	5.684	0.037	0.705	1.0
Springtail richness							
23	pH Tree_Struc Tree_Compo Canop	5	470.3	0.000	0.090	0.156	1.0
2	pH	2	470.4	0.057	0.088	0.069	1.1
4	H_index pH	3	470.7	0.363	0.075	0.094	1.5
6	pH CN_ratio	3	471.6	1.225	0.049	0.083	1.0
37	Tree_Struc Tree_Compo Canop Dist_Forest	5	471.6	1.247	0.048	0.140	1.1

702 **Table 3.** Importance (Imp.), average coefficients (Estimate) and confidence intervals (95% CI) for each variable
 703 predicting plant and springtail richness in the French pre-Alps. The 95% confidence interval of coefficients in
 704 bold excluded 0.

Parameter	Plant richness			Springtail richness		
	Imp.	Estimate	(95% CI)	Imp.	Estimate	(95% CI)
H_index	0.09	-0.001	(-0.111; 0.099)	0.28	-0.040	(-0.119; 0.038)
pH	0.72	0.060	(0.010; 0.111)	0.32	0.044	(0.005; 0.085)
CN_ratio	0.06	-0.030	(-0.405; 0.338)	0.27	-0.090	(-0.391; 0.204)
Canop	1.00	0.247	(0.152; 0.342)	0.37	-0.060	(-0.140; 0.013)
Tree_Compo	1.00	0.115	(0.065; 0.166)	0.40	0.026	(-0.015; 0.069)
Tree_Struc	1.00	-0.710	(-1.031; -0.395)	0.55	0.227	(-0.023; 0.477)
Alpha_LU	0.04	-0.020	(-0.138; 0.090)	0.12	0.035	(-0.061; 0.131)
Dist_Forest	0.03	-0.001	(-0.090; 0.069)	0.27	0.062	(-0.006; 0.131)
Prop_Forest	0.03	0.007	(-0.034; 0.048)	0.13	-0.001	(-0.048; 0.029)

705

706 **Table 4.** The 5 among 50 top-ranking models (see Appendix S6) predicting variation in plant and springtail
707 species composition in the French pre-Alps, as assessed with Akaike's information criterion corrected for small
708 sample size (AIC_c). Number of estimated parameters including the intercept (k), AIC_c, the difference in AIC_c (Δ
709 AIC_c), AIC_c weight (W), proportion of deviance explained (D²) and evidence ratio (ER), i.e. Akaike weight of the
710 top-ranked model/Akaike weight of the second top-ranked model, are provided.

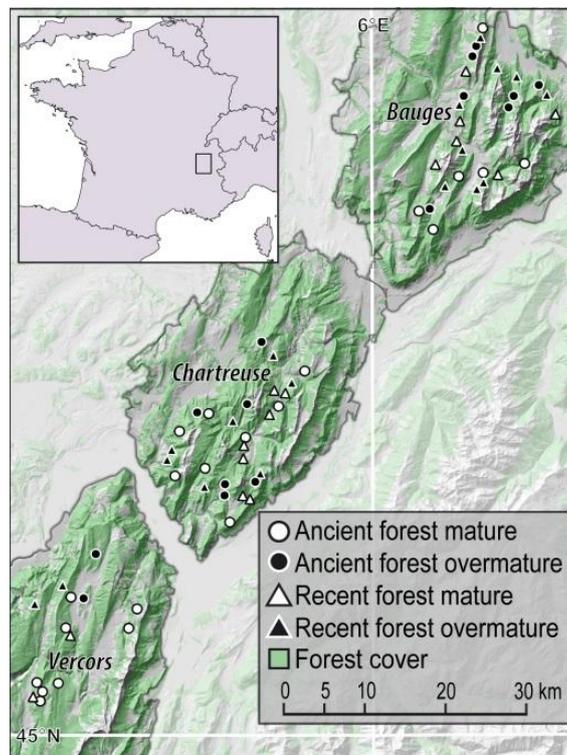
No.	Candidate model	k	AIC _c	Δ AIC _c	W	D ²	ER
Plant assemblages							
1	H_index	2	101.2	0.0	0.050	0.056	1.14
3	CN_ratio	2	101.5	0.2	0.044	0.053	1.01
24	Tree_Struc Tree_Compo Canop CN_ratio	5	101.5	0.3	0.043	0.209	1.05
5	H_index CN_ratio	3	101.6	0.4	0.041	0.102	1.02
12	Tree_Struc Canop	3	101.7	0.4	0.040	0.102	1.13
Springtail assemblages							
1	H_index	2	150.1	0.0	0.136	0.045	1.08
4	H_index pH	3	150.2	0.1	0.124	0.084	1.38
2	pH	2	150.9	0.8	0.090	0.039	1.01
50	Null	1	150.9	0.8	0.088	0.000	1.96
5	H_index CN_ratio	3	152.3	2.1	0.045	0.070	1.02

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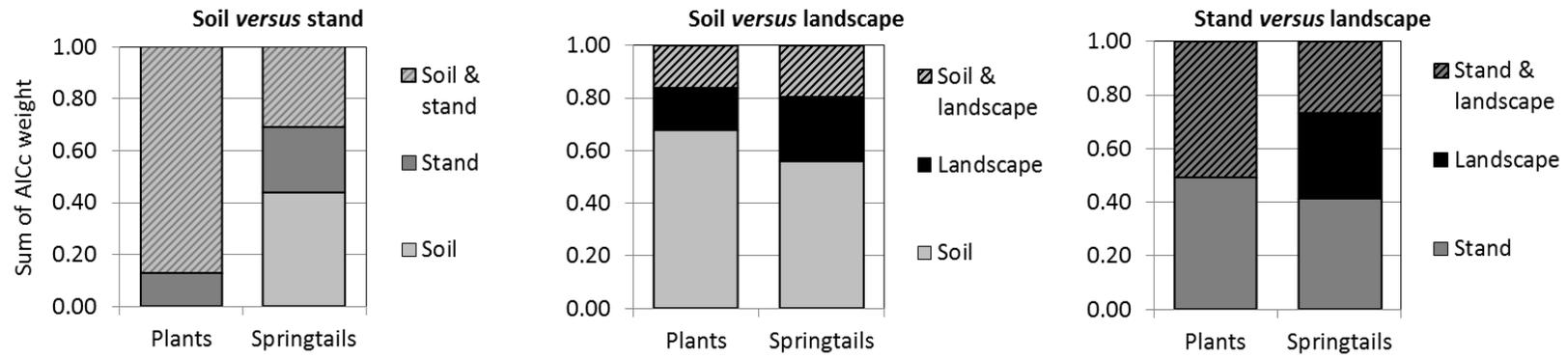
712 **Table 5.** Importance (Imp.), proportion of deviance explained (D^2) and significance for each variable of the full
 713 model predicting variation in plant and springtail species composition in the French pre-Alps.

Var.	Plant assemblages			Springtail assemblages		
	Imp.	D^2	p-value	Imp.	D^2	p-value
H_index	0.3596	0.056	0.001	0.4445	0.045	0.001
pH	0.3119	0.041	0.007	0.3766	0.039	0.001
CN_ratio	0.3583	0.048	0.001	0.2253	0.025	0.085
Canop	0.3703	0.048	0.001	0.1242	0.035	0.002
Tree_Compo	0.3351	0.049	0.001	0.1161	0.025	0.137
Tree_Struc	0.3656	0.052	0.001	0.1454	0.030	0.011
Alpha_LU	0.1415	0.025	0.009	0.0811	0.021	0.349
Dist_Forest	0.1935	0.040	0.001	0.0798	0.025	0.095
Prop_Forest	0.1792	0.035	0.001	0.1028	0.031	0.003

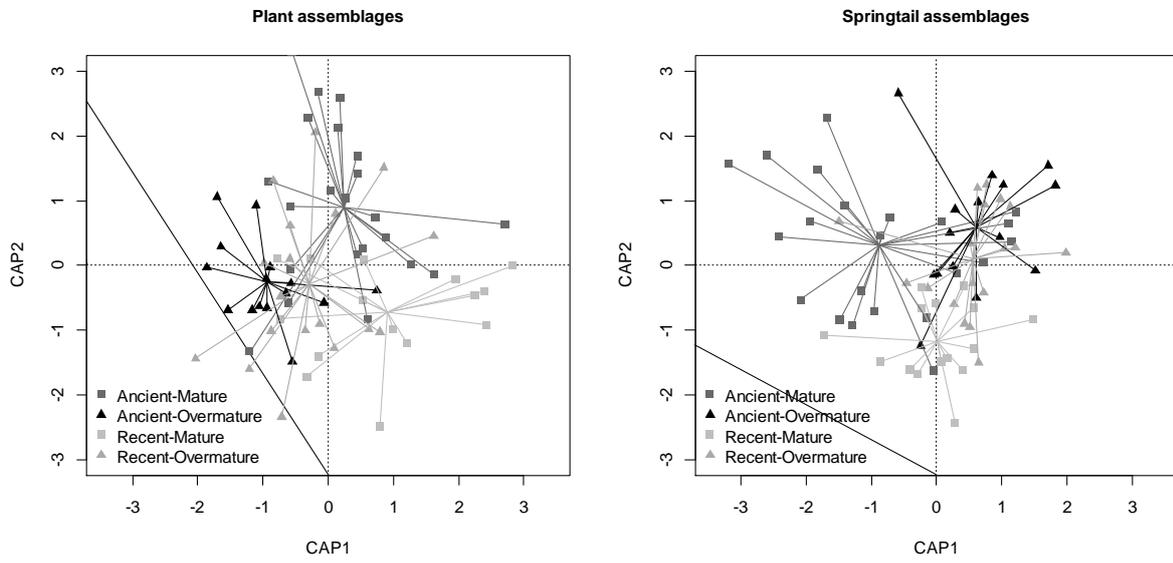
714 **Fig. 1.** Study area and distribution of sampling sites among ancient and recent forests and mature and
715 overmature stands in the French pre-Alps.



716 **Fig. 2.** Relative influence of parameters related to soil, stand and/or landscape on plant and springtail richness in the French pre-Alps. Sums of AIC_c weights are provided for
 717 models based exclusively on (i) soil and/or stand variables; (ii) soil and/or landscape variables; (iii) stand and/or landscape variables.



718 **Fig. 3.** Constrained canonical analysis of principal coordinates of plant and springtail species composition in
719 relation to the interaction between forest continuity and stand maturity.



720 **Fig. 4.** Relative influence of parameters related to soil, stand and/or landscape on plant and springtail species composition in the French pre-Alps. Sums of AIC_c weights are
 721 provided for models based exclusively on (i) soil and/or stand variables; (ii) soil and/or landscape variables; (iii) stand and/or landscape variables.

