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5 **CLIMATE IS THE MAIN DRIVER OF CLONAL AND BUD BANK TRAITS IN ITALIAN**
6 **FOREST UNDERSTORIES**

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ABSTRACT

The study of plant trait-environment links is rarely focused on traits that inform on space occupancy and resprouting (both affecting plant persistence), especially in forest understories. Traits that can effectively capture such key functions are associated with clonality and bud banks. We hypothesized that: 1) climate is the main driver of clonal and bud bank traits, 2) traits related to space occupancy (e.g., greater lateral spread) are more important in more mesic, richer soils forests, and 3) traits related to resprouting ability (e.g., larger bud bank) are more important in more intensively and recently managed forests. We addressed these hypotheses by analysing a unique dataset that is statistically representative of Italian forests heterogeneity and includes three biogeographic regions (Alpine, Continental, Mediterranean). We recorded data for sixteen climatic, soil and management variables. We calculated community weighted mean (CWM) values of seven clonal and bud bank traits for the forest understory vegetation. We used i) redundancy analysis to assess trait-environment relations, and ii) variance partitioning analyses to identifying the relative role of different groups of abiotic variables on CWM variation of all traits combined together, as well as clonal and bud bank traits taken separately. Climate alone had a pervasive effect in determining patterns of clonal and bud bank traits in Italian forest understories, mainly related to the effects of temperature extremes and seasonality. Unexpectedly, soil and management factors alone showed marginal effects on clonal and bud bank traits. However, soil features influenced trait patterns when joined with climate. Our results confirmed that, at the biogeographic scale, climate played a lion-share role in determining persistence-related traits of forest-floor plants. At the local-scale, other interplaying factors (e.g., management, soil variables) may come into play in shaping patterns of the studied plant traits. This study stressed the importance of examining functional trait patterns along complex environmental gradients.

Keywords: Clonality; Community weighted mean (CWM); Resprouting; Soil properties; Plant-environment linkages; Trait-based ecology

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75 **1. Introduction**

76 Understanding how vegetation responds to environmental variation is a longstanding, fundamental
77 goal in ecology (von Humboldt and Bonpland, 1807; Schimper, 1903). Trait-based approaches are
78 particularly suited to examine plant-environment relationships (Weiher et al., 1999; Violle et al.,
79 2007). Functional traits are morphological, phenological or eco-physiological features informative
80 on specific functions affecting plant performance, and they can mediate plant responses to changing
81 environments (Weiher et al., 1999; Violle et al., 2007; Chelli et al., 2019). Evidences are
82 accumulating explaining the relationships between functional traits and the environment in plant
83 communities at broad spatial scales (e.g., Qian et al. 2017; Le Bagousse-Pinguet et al., 2017;
84 Bruelheide et al., 2018; Vanneste et al., 2019). These studies showed that changing patterns of
85 communities' functional setting cannot be attributed to a single driver, but rather to a combination
86 of environmental factors (Simpson et al., 2016; Le Bagousse-Pinguet et al., 2017). Among these
87 environmental forces, climate showed a pervasive role acting as primary macro filter on the
88 functional structure of communities across biogeographical scales (Swenson and Weiser, 2010;
89 Vanneste et al., 2019; Wiczyński et al., 2019; but see Bruelheide et al., 2018). Soil properties can
90 also largely contribute to explaining trait variation at the community level (Simpson et al., 2016;
91 Pinho et al., 2018). On the contrary, the effect of management on plant community traits along
92 broad biogeographical gradients is still unexplored (Borgy et al., 2017). Previous results indicate
93 that management is an important factor determining forests dynamics, especially at the local scale
94 (Campetella et al., 2011; Vanneste et al., 2019).

95 Thus far, the study of plant-environment linkages focused mainly on traits informative on resource
96 acquisition and use strategies. These traits are associated with 1) aboveground organs, e.g., leaf-
97 height-seed scheme (Westoby, 1998), leaf and wood economics spectra Wright et al., 2004; Chave
98 et al., 2009), and 2) belowground resource acquisition strategies, investigating roots and
99 mycorrhizal associations (e.g., Freschet et al., 2017; Laliberté, 2017). Nevertheless, other key plant
100 functions related to different ecological dimensions, namely on-spot persistence, space occupancy,
101 and recovery after damage, remain largely neglected (Weiher et al., 1999; Klimešová et al., 2018;
102 Chelli et al., 2019). Traits that can effectively capture these understudied functions are those
103 associated with clonality (Klimešová et al., 2011, 2017) and bud bank (Klimešová and Klimeš,
104 2007; Pausas and Keeley, 2014).

105 Clonality increases plant capacity to explore the space surrounding the parent plant, and in highly

106 heterogeneous habitats it may give a competitive advantage (Oborny et al., 2000; Yu et al., 2008).
107 Ecologically, clonality is even more beneficial to plants when associated with bud banks (i.e., if the
108 clonal organ carries buds). This facilitates the development of adventitious roots and new shoots
109 from clonal spacers (e.g., rhizomes, stolons), and enables plants to resprout after disturbance
110 including frost and drought (Klimešová and Klimeš, 2007), grazing (VanderWeide and Hartnett,
111 2015), fire (Pausas et al., 2018), and logging (Canullo et al., 2011a). Therefore, being clonal in
112 conjunction with having a bud bank, may provide plants with effective strategies to cope with
113 changing environments, disturbances and management regimes.

114 Clonal and bud bank traits-environment relationships have not been consistently studied across
115 species, growth forms, ecosystems, and biomes (Klimešová and Doležal, 2011; Wellstein and Kuss,
116 2011; Ye et al., 2014; Qian et al., 2017; Klimešová and Herben, 2015). For instance, along a
117 biogeographical gradient, Ye et al. (2014) found that clonal herbs, but non clonal woody species,
118 occurred more frequently in cold, dry or instable habitats (i.e., high temperature seasonality and
119 high precipitation seasonality). Also, most of the research dealing with clonal and bud bank traits
120 were carried out in temperate grasslands (e.g., Klimešová et al., 2014; Klimešová and Herben,
121 2015) and in fire-prone ecosystems (e.g., Pausas and Keeley, 2014; Pausas et al., 2018). Drivers of
122 clonal and bud bank traits patterns in forests and their understories in any biome remain greatly
123 unexplored. This is a relevant research gap, since forests are among the most widespread and
124 complex terrestrial ecosystems. The understory supports the vast majority of forest plant diversity
125 and plays a vital role in forest ecosystem functioning (e.g., soil processes, nutrient cycling and litter
126 decomposition Gilliam 2014; Landuyt et al., 2018).

127 Plants with short and persistently connected spacers are generally associated with drier and/or less
128 productive sites, while plants with long spacers and short-lived connections are often advantaged in
129 wetter and/or more productive sites (Halassy et al., 2005; Klimešová et al., 2011; Klimešová and
130 Herben, 2015). In relation to bud bank traits, belowground bud bank size tends to be smaller in dry
131 and hot habitats (Qian et al., 2017). Also, bud banks are generally strongly affected by disturbances,
132 especially in managed forests (Campetella et al., 2011; Canullo et al., 2011a), as bud banks can
133 assist overcoming severe damage (Herben et al., 2016).

134 Here, we aim to (1) identify trait-environment relationships of seven clonal and bud bank traits of
135 plants in the forest understory, and (2) quantify the relative contributions of climate, soil,
136 management in determining the community mean values of plant traits of the forest understories.
137 Italy was selected as model region for the research because (a) the country covers large latitudinal
138 and climatic gradients that include three biogeographic regions, i.e., Alpine, Continental,
139 Mediterranean, (b) Italy hosts a high number of plant species and forest types, (c) the country is
140 characterized by a long history of human exploitation of resources, e.g., wood and timber supply,

141 involving different management practices (see also Chelli et al. 2019), and (d) there is a high
142 diversity of soil types due to the great variety of pedogenetic processes (Costantini et al., 2013).
143 Given the range in within-country factors described above, we expected that: **(H1)** climate is the
144 main driver of traits associated with clonality and resprouting (macro-scale filter); **(H2)** traits
145 related to space occupancy ability (e.g., larger lateral spread) are more important in mesic, rich-soil
146 forests (habitat-scale filter); **(H3)** traits related to resprouting ability (e.g., perennial and larger
147 belowground bud bank) are more relevant in more intensively and recently managed forests
148 (habitat-scale filter).

149

150 **2. Materials and methods**

151 **2.1. Study area and sampling design**

152 The study area covered forested regions of Italy, estimated to be around 9 million hectares,
153 distributed in Mediterranean, Continental and Alpine biogeographic regions. The sampling design
154 was systematic and probabilistic (WGFB, 2011) and was based on a grid superimposed onto the
155 whole country with cells of 16 km x 16 km, with each corner of this grid being included as a sample
156 area if a forest larger than 1 ha was found there (after a field-check). This grid belongs to the
157 transnational network for monitoring the forest health status in Europe (ICP Forests: <http://icp-forests.net/>). For the entire country, the sampling strategy resulted in a dataset composed by 201
158 sampling areas (forest stands; Figure 1). In each forest stand, we sampled a 400 m² area within
159 which we recorded the plant species composition. We collected data on presence/absence and
160 coverage (%) for all understory vascular plants in each sampling area. The field sampling was done
161 during spring-summer 2006 following standard protocols (Allegrini et al., 2009; Canullo et al.,
162 2011b).

164

165 **2.2. Explanatory variables**

166 For each sampling area we recorded sixteen explanatory variables within three categories: climate,
167 soil, forest structure, management (Table 1). We obtained climate variables from the global
168 WorldClim database (first version; Hijmans et al., 2005); among the available parameters, we
169 selected six variables, related to temperature and precipitation variability (temperature seasonality,
170 precipitation seasonality) and extremes (maximum temperature of the warmest month, minimum
171 temperature of the coldest month, precipitation of the driest month, precipitation of the wettest
172 month). They were selected as they can influence both vegetative and regenerative functional traits
173 (e.g., Ye et al., 2014; Le Bagousse-Pinguet et al., 2017). In each sampling area, we measured four
174 soil variables according to standard procedures (Andretta et al., 2016; Table 1). The soil variables
175 chosen were indicative of soil nutrient status (topsoil available potassium (K)), nitrogen availability

176 (N/C; Rowe et al., 2011), regulation of nutrient availability (soil pH), and water holding capacity
177 (effective soil volume) and all of the have been shown to potentially influence plant traits (e.g.,
178 Chen et al., 2019). In addition, at each forest sampling site we measured six variables related to
179 forest management and structure (Table 1) – referred to management hereafter. Basal area ($\text{m}^2 \text{ ha}$) –
180 which is correlated with the total woody biomass, stand maturity and successional stage (Pinho et
181 al., 2018 and references therein), total vegetation cover (including overstory), and litter cover. These
182 three variables are recognized key biotic drivers determining microhabitat suitability to species,
183 especially for forest understory vegetation, as these parameters can largely contribute to
184 microclimatic buffering capacity (Kovács et al., 2017). We collected current land-use data related to
185 deadwood removal, and total released deadwood. In particular, deadwood removal is linked to
186 management practices aimed at avoiding the spreading of diseases, pests, or fires (Travaglini et al.,
187 2007). Total released deadwood is widely considered a good proxy for disturbance intensity in
188 managed forests, due to linkages with stand management gradients (Schall and Ammer, 2013;
189 Puletti et al., 2017).

190

191 **2.3. Clonal and bud bank traits**

192 We collected seven binary (i.e., presence/absence) clonal and bud bank traits (Table 2) from existing
193 literature (Canullo et al., 2011a; Campetella et al., 2011) and available databases (CLOPLA3;
194 Klimešová et al., 2017). These traits capture functional axes that have received less attention
195 (Ottaviani et al., 2017; Klimešová et al., 2018), namely space occupancy (i.e., clonality, fast lateral
196 spread; Table 2), ability to recover after disturbance (i.e., clonal growth organ position
197 belowground, bud protection, large bud bank, perennial bud bank belowground; Table 2), capacity
198 to share resources among ramets (long-term connection; Table 2) – all affecting plant persistence.
199 We assigned clonal and bud bank traits to all the understory species contributing to reach relative
200 cumulative coverage of 80% in each sampling area (Pakeman and Queded, 2007). Clonal and bud
201 bank attributes were available for 75% of the species. Traits were then weighted according to
202 species coverage at plot scale so to obtain community weighted mean values (hereafter referred to
203 as CWM, Garnier et al., 2004).

204

205 **2.4. Data analysis**

206 *Explanatory variables selection*

207 We carried out stepwise ordination in order to identify the most parsimonious set of single
208 explanatory variables for all traits together, and clonal and bud bank traits separately (Økland and
209 Eilertsen, 1994). Stepwise forward ordination is a procedure for selecting a subset of explanatory
210 variables from the set of all variables available for a constrained ordination. The goal was to reduce

211 the number of explanatory variables in the analysis, while maximizing the variation explained by
212 predictors (Blanchet et al., 2008).

213

214 *Redundancy Analysis (RDA) and Variance Partitioning*

215 We performed Redundancy Analysis (RDA) to observe correlations between explanatory variables
216 and traits, as CWM trait values were linearly related to environmental variables (Lepš and Šmilauer,
217 2003). RDA is a constrained Principle Components Analysis (PCA) so that the axes are linear
218 combinations of the environmental variables and is hence equivalent to a constrained multivariate
219 multiple regression. Finally, we used variance partitioning (Borcard et al., 1992) to identify the
220 contributions of different environmental groups (i.e., climate, soil, management) alone and in
221 combination to explain trait variation (as adjusted R^2). The stepwise-selected categorical variables
222 (i.e., only deadwood removal) have been decomposed using PCA (Appendix S1). The first
223 component of the PCA has been included in the RDA and in the variance partitioning analyses as a
224 continuous variable.

225

226 We performed all the statistical analyses in R environment, version 3.2.2 (R Development Core
227 Team, 2015) on incidence plots x traits matrix with community weighted mean data. The following
228 R packages were used: *vegan* (functions *ordistep*, *varpart* and *rda*) for stepwise ordination, variance
229 partitioning, and redundancy analysis; *stats* (function *prcomp*) for PCA (Borcard et al., 1992;
230 Blanchet et al., 2008; Legendre and Legendre, 2012).

231

232 **3. Results**

233 **3.1. Selection of explanatory variables**

234 The stepwise selection of explanatory variables resulted in the selection of 8 out of 16 variables
235 retained at $P \leq 0.05$ (Appendix S2). Minimum temperature of the coldest month had a significant
236 effect on all traits and clonal traits, while temperature seasonality and maximum temperature of the
237 warmest month influenced mainly bud bank traits. Precipitation of the wettest month exhibited a
238 significant relationship with all clonal and bud bank traits, and exerted a main effect on bud bank
239 traits. Only two soil variables contributed to the variation of traits: N/C and topsoil available K had
240 a marginal influence on all clonal and bud bank traits. Basal area and deadwood removal also were
241 selected to explain trait variation. Deadwood removal in particular showed the highest percentage
242 of variance explained for all, clonal and bud bank traits (Appendix S2).

243

244 **3.2. Relationship between CWM values and environmental variables**

245 The RDA based on clonal and bud bank trait CWM values of Italian forest understories including

246 the variables identified by the stepwise selection was significant ($P < 0.001$; Fig. 2). The first axis
247 accounted for 15.3% of the variability, and was primarily related to temperature variables and, to a
248 lesser degree, soil parameters. The second axis explained only 1.7% of the total variability and it
249 was primarily associated with precipitation and forest management. Along the first RDA axis,
250 negative values were related to forest stands characterized by higher temperature seasonality and
251 lower temperature of both the coldest and warmest month. They are mainly located in the Alpine
252 and Continental biogeographic regions of Central and Northern Italy on nutrient poor soils. Forests
253 in that grouping also were more mature (higher basal area) and the forest understory vegetation was
254 characterized by a higher percentage of clonal species with belowground clonal organs, long-term
255 connections among ramets, and higher resprouting abilities (large belowground bud bank; Fig. 2).
256 Positive values on the first RDA axis were forest stands mainly located in the Mediterranean
257 biogeographic region. Forests in that area had warmer climatic conditions and occurred on richer
258 soils, with understory plants characterized by lower abilities to occupy space and resprout (Fig. 2).
259 Because the second RDA axis accounted for very little of the overall variation in the data, it is
260 difficult to draw conclusions regarding forest characteristics and clonal traits of the understory
261 vegetation but several features are worth mentioning. For example, negative values on the second
262 axis identified forest stands with higher precipitation in the wettest month and less intense
263 management, i.e., with no deadwood removal. These forests were characterized by understory
264 communities with fast lateral spread and perennial belowground bud bank (Fig. 2). Positive values
265 described plots having opposed environmental conditions (i.e., more intensively managed and with
266 lower precipitation in the wettest month), and distinguished by opposing trait patterns (i.e., slower
267 lateral spread, and short-lived belowground bud bank).

268

269 **3.3. Variance partitioning**

270 The amount of total variation explained by the three groups of variable-types (i.e., climate, soil,
271 management parameters) was 14.8% for all traits, 16.0% for clonal traits and 14.3% for bud bank
272 traits (Fig. 3a). Climate alone explained the largest proportion of the variation for all (9.9%), clonal
273 (10.4%) and bud bank traits (10.9%), amounting approximately between 65% and 75% of
274 standardized variation (Fig. 3b). Forest management and soil variables alone did not have strong
275 relationships with clonal and bud bank traits ($<1\%$, Fig. 3). The interaction between climate and soil
276 variables explained a limited variation of the trait groups (between 2.5% and 3.0%).

277

278 **4. Discussion**

279 **4.1. Climate as the main driver of clonal and bud bank traits in Italian forest understories**

280 Consistent with our prediction (H1), climate alone played a major role in controlling the CWM

281 variation of most of the clonal and bud bank traits. Climate explained approximately between 65%
282 and 75% of standardized variation (Fig. 3b) and it was related to clonal and bud bank traits that
283 described space occupancy and resprouting abilities (hence persistence process; Klimešová et al.,
284 2018). Our results were consistent with other large-scale studies based on plant functional traits
285 informative on nutrient acquisition and use strategies (e.g., leaf economics traits; Laughlin et al.,
286 2011). Temperature extremes, such as minimum temperature of the coldest month, had a pervasive
287 effect on clonal traits. This signal can be interpreted as these traits being strongly affected, and
288 filtered by temperature-related constraints, similarly to what revealed for other traits associated with
289 resource acquisition and use along elevation gradients (Milla and Reich, 2011; Read et al., 2014;
290 Ottaviani et al., 2019). Management and soil variables alone played a marginal role on trait patterns
291 – unexpected result, especially for bud bank traits which were linked to disturbance regimes
292 (Klimešová and Klimeš, 2007; Pausas and Keeley, 2014; VanderWeide and Hartnett, 2015).
293 Our study area spans three biogeographic regions and probably the large variability of climatic
294 conditions across Italy may have contributed to climate being the key driver of trait patterns and
295 further explaining why the local effects of soil and management factors were less important.
296 However, soil features exerted a certain influence on traits when joined with climate (Le Bagousse-
297 Pinguet et al., 2017). The results of this study indicate that key soil properties only had weak effects
298 on traits (especially for clonal traits). This result contrasts with findings from other regions, where
299 different functional traits were used, such as foliar economics traits (e.g., Bernard-Verdier et al.,
300 2012; Ottaviani et al., 2016; Pinho et al., 2018). Different results between our study and others
301 could be explained by that fact that soil features may be better linked to acquisitive function and
302 traits (Zemunik et al., 2015; Simpson et al., 2016; Pinho et al., 2018). Also, clonal and bud bank
303 traits could be related to trade-offs between different plant functions, namely resource acquisition vs
304 persistence (Bellingham and Sparrow, 2000; Clarke and Knox, 2009; Klimešová et al., 2018) more
305 than soil properties. Overall, our findings stress the need of including traits informative on different
306 functions (e.g., resource acquisition, space occupancy, resprouting after disturbance) when aiming
307 at disentangling plant-environment linkages comprehensively (Klimešová et al., 2018).

308

309 **4.2. Trajectory of plant trait-environment links**

310 Our findings that more mesic and colder forests hosted understory communities with higher clonal
311 and resprouting abilities was in line with previous studies (Ye et al., 2014; Vojtkó et al., 2017),
312 partially supporting H2. However, these forests were also poorer in soil nutrients, thus contrasting
313 the second part of our hypothesis, in which we predicted higher importance of traits related to space
314 occupancy ability in more mesic, richer soils forests. Drier, warmer forests plots were characterized
315 by understory communities exhibiting both reduced abilities to occupy space and to resprout,

316 possibly due to tradeoffs between different functions, i.e., persistence *vs* acquisition (see
317 Bellingham and Sparrow, 2000; Clarke and Knox, 2009; Klimešová et al., 2018). The results
318 suggest that in poorer environments, space occupancy and resprouting ability could be constrained
319 by limiting resources available to support plant growth. The evidence of prevailing clonal strategies
320 in cold forests contribute also to the open debate about the dominance of clonality in cold
321 environments as an effective strategy under constraining conditions (Klimešová and Doležal, 2011).
322 We found that less disturbed forests were distinguished by understory communities having
323 perennial belowground bud bank. This result was contrary to the prediction of greater importance
324 of traits related to bud bank-resprouting ability in more disturbed stands (H3). Bud banks are known
325 to act as a buffer against disturbance (see Klimešová and Herben, 2015, and references therein). Our
326 results may be related to the severity of disturbance as clonal plants may have not been able to build
327 sufficient storage of carbohydrates for resprouting when the disturbances are severe (Iwasa and
328 Kubo, 1997). This could be the case of recently coppiced forests in which stands were exposed to
329 more severe drought, frost, and soil erosion (Ciancio et al., 2006). These abiotic limitations and
330 processes can generate a cascade of detrimental effects on bulk density or porosity and depletion of
331 the soil organic matter and other nutrients (Rubio and Escudero, 2003). Under these circumstances,
332 the prevalence of seed regeneration is more likely to occur than vegetative reproduction (Klimešová
333 and Herben, 2015), and such regeneration from seeds is usually negatively correlated with
334 resprouting capacity (Bellingham and Sparrow, 2000). Additionally, in less disturbed forests,
335 understories showed higher space occupancy ability (i.e., fast lateral spread). This increased
336 mobility probably reflected an effective strategy responding to the higher spatio-temporal
337 patchiness of light in late successional forests (foraging ability, Sammul et al., 2004; Canullo et al.,
338 2011a).

339

340 **4.3. Conclusions and future directions**

341 The degree to which trait variation was explained by environmental variables (14.3%-16.0%) in this
342 study was comparable to results of related studies in other forests (e.g., 9-31%, Vanneste et al.,
343 2019). However, our research was based on a probabilistic sampling design (representative of the
344 entire set of Italian forest types), and not on selected gradients (e.g., see Vanneste et al., 2019). This
345 implied that we did not homogenize any of the environmental variables, so including a large
346 environmental variability, that may be the main cause of the unexplained variance in the models.
347 Yet, this was also one of the strongholds of this study: results emerging from environmental
348 gradients are considered key to further the understanding of species and trait assembly in plant
349 communities (e.g., von Humboldt and Bonpland, 1807; Schimper, 1903; Swenson and Weiser,
350 2010). At the biogeographic scale, climate confirmed its lion-share role in determining persistence-

351 related traits, as revealed for acquisition traits (e.g., Laughlin et al., 2011; Wiczyński et al., 2019).
352 At the local-scale, other interplaying factors (e.g., management, soil variables) may come into play
353 in shaping plant trait patterns. This evidence stresses the importance of implementing multiple-scale
354 trait-based approaches (Hulshof and Swenson, 2010; Mokany and Roxburgh, 2010). The plant trait–
355 environment links reported in our study were essentially produced by species turnover and/or
356 changes in species cover values, and not by intraspecific variation. Therefore, we call for future
357 studies to incorporate i) intraspecific (and, ideally, intra-clonal) trait variation, as it can play a
358 fundamental role in plant community responses to changing environments (e.g., Hulshof and
359 Swenson, 2010; Kichenin et al., 2013), and ii) traits capturing the widest possible functional
360 spectrum (Weiher et al., 1999; Klimešová et al., 2018). This way, a more realistic and
361 comprehensive understanding of community assembly and ecosystem functioning of forest
362 understories could be effectively achieved.

363

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371

372 **Supplementary material**

373 **Appendix S1.** PCA of the stepwise selected categorical variable “deadwood removal”.

374 **Appendix S2.** Effects of each climate, soil, and management variables for all traits, clonal traits and
375 bud bank traits.

376

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566 **Table 1.** Description of the explanatory variables with units, ranges, main references and notes.

| Group | Variable | Abbreviation | Unit | Range | Notes |
|--------------------------|--------------------------------------|------------------|-----------------------------------|--------------|-----------------------------------------------------------------------|
| Climate | Temperature seasonality | T_season | CV (%) | 51 – 75 | Source: Hijmans et al. (2005), WorldClim |
| | Precipitation seasonality | P_season | CV (%) | 7 – 64 | Source: Hijmans et al. (2005), WorldClim |
| | Max temperature of the warmest month | max_T_warmest_m | °C | 9.2 – 31.5 | Source: Hijmans et al. (2005), WorldClim |
| | Min temperature of the coldest month | min_T_coldest_m | °C | -10.5 – 7.1 | Source: Hijmans et al. (2005), WorldClim |
| | Precipitation of the wettest month | P_wettest_m | mm | 65 – 155 | Source: Hijmans et al. (2005), WorldClim |
| | Precipitation of the driest month | P_driest_m | mm | 4 – 102 | Source: Hijmans et al. (2005), WorldClim |
| Soil | Soil pH | pH | | 4 – 8.6 | Source: Andreetta et al. (2016) |
| | N/C | N_C | Na | 0.05 – 0.19 | Source: Andreetta et al. (2016) |
| | Topsoil available K | Soil_aval_K | cmol+/K g | 0.01 – 7 | Unpublished data |
| | Effective soil volume | Soil_volume | cm | 4.5 – 170 | Good proxy of water holding capacity. Source: Andreetta et al. (2016) |
| Structure and management | Total vegetation cover | Tot_veg_cov | % | 40 – 100 | Biotic driver of vegetation. |
| | Litter cover | Litter_cover | % | 2 – 100 | Biotic driver of vegetation. |
| | Basal area | Basal_area | m ² /ha | 2.8 – 69 | Related to the total woody biomass |
| | Current land-use | Current_landuse | Classes | 4 categories | Unmanaged, managed >10yrs ago, managed within 10 yrs, unknown. |
| | Total released deadwood | Total_deadwood | m ³ /400m ² | 0 – 15 | Good proxy of disturbance intensity. |
| | Deadwood removal | Deadwood_removal | Classes | 5 categories | Yes, partly, accumulation in piles, no, unknown. |

568 **Table 2.** Plant clonal and bud bank traits, with acronyms used in the study, unit (binary,
 569 presence/absence), and definitions.

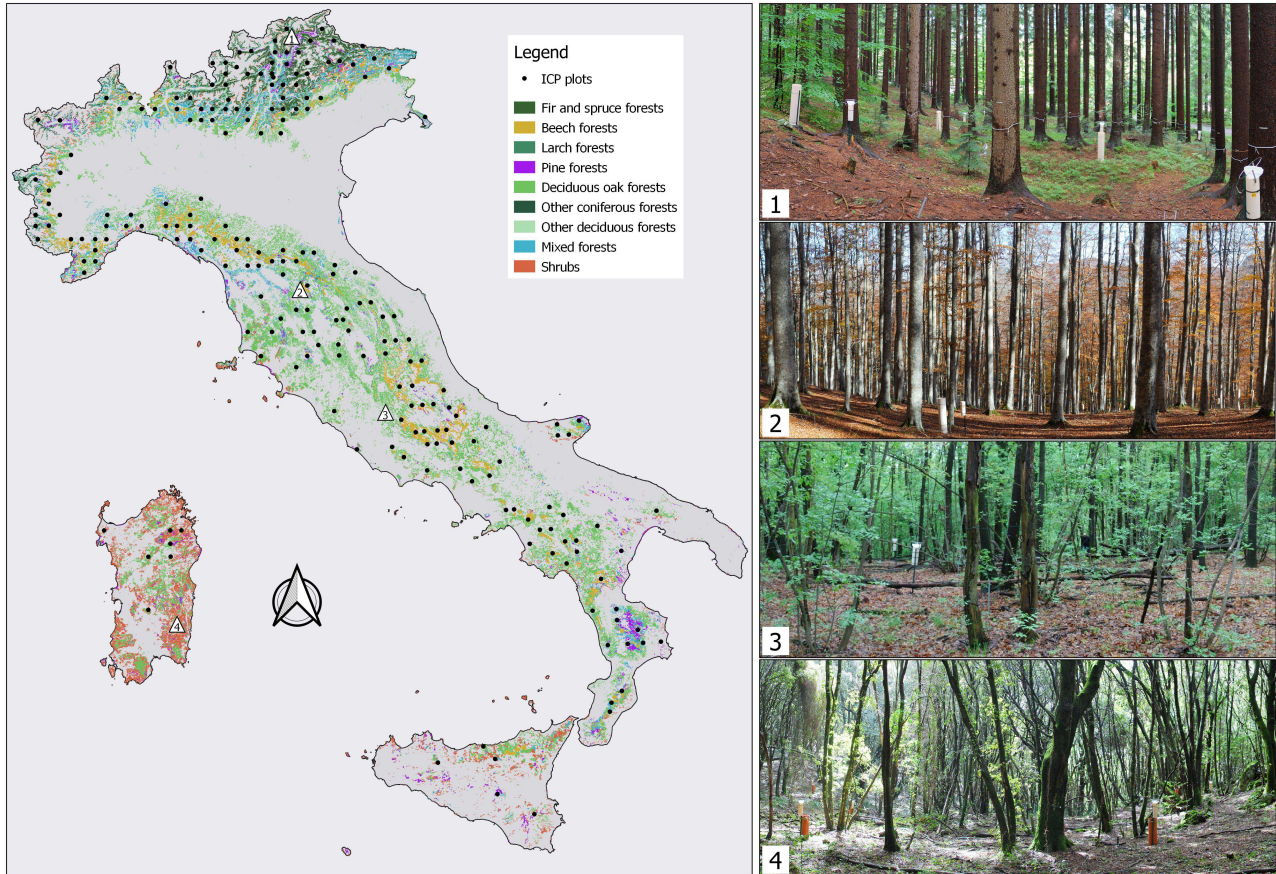
| Group | Plant trait | Abbreviation | Unit | Definition |
|-----------------|---------------------------------|---------------------|-------------|------------------------------------------------------------------|
| Clonal traits | Clonality | Clonality | Yes/no | Ability to reproduce vegetative by means of clonal growth organs |
| | Clonal growth organ belowground | CGO_below | Yes/no | The clonal growth organ is positioned belowground. |
| | Long-term connections | Conn_long | Yes/no | Persistence of connections among ramets > 2 yrs |
| | Fast lateral spread | Spread_fast | Yes/no | Clonal lateral spreading > 0.25 m/yr |
| | Bud protection | Bud_protection | Yes/no | Buds protected by specialized scale leaves |
| Bud bank traits | Large bud bank | BB_large | Yes/no | Stem- and root-derived buds above- or belowground >10 |
| | Perennial bud bank belowground | Perenn_BB_be low | Yes/no | Persistence of belowground bud bearing organs > 2 yrs |

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572 **FIGURES**

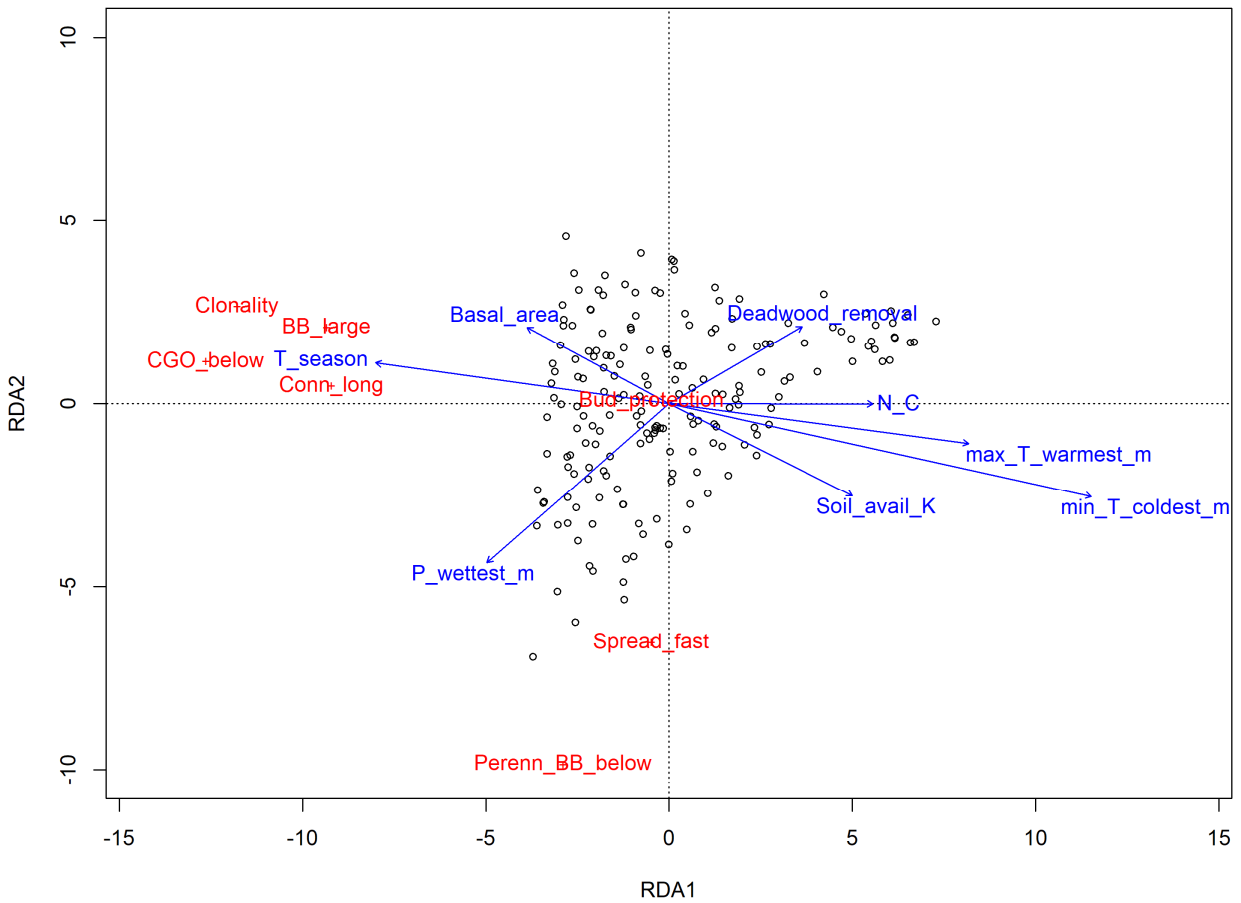
573 **Figure 1.** Map showing the location of the 201 plots in Italy (left panel). On the right, the most
574 abundant types are represented: 1 alpine coniferous forest; 2 beech forest; 3 deciduous oak forest; 4
575 evergreen Mediterranean maquis.



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578 **Figure 2.** Redundancy analysis diagram showing the CWM trait values for the Italian forest
579 understories constrained by the environmental variables identified by the stepwise selection
580 procedure. Red labels indicate response variables (traits; see table 2 for abbreviations), whereas
581 blue labels and arrows report predictors (variables related to climate, soil, structure and
582 management; see table 1 and 2 for abbreviations).



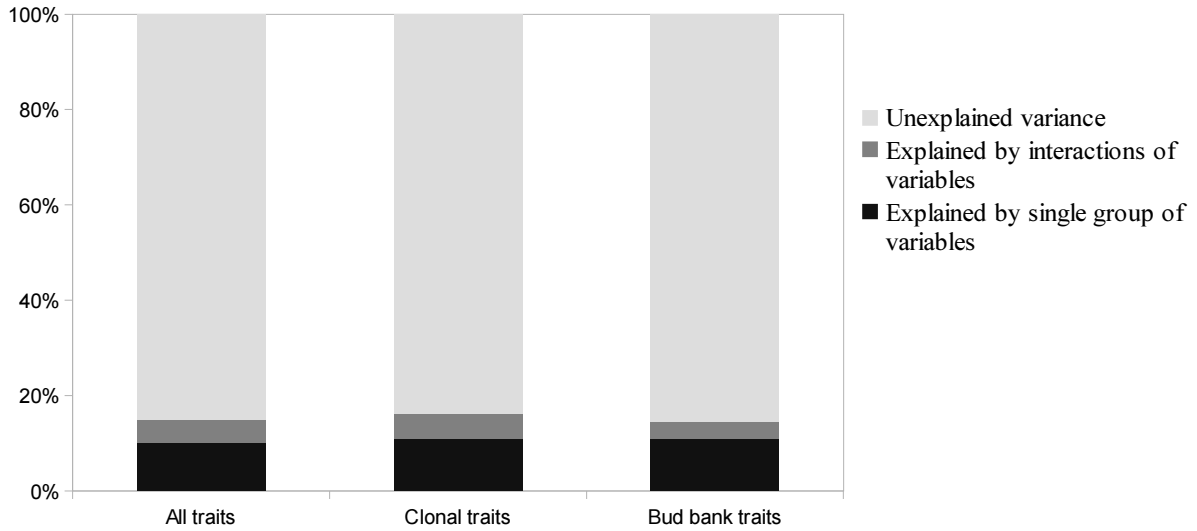
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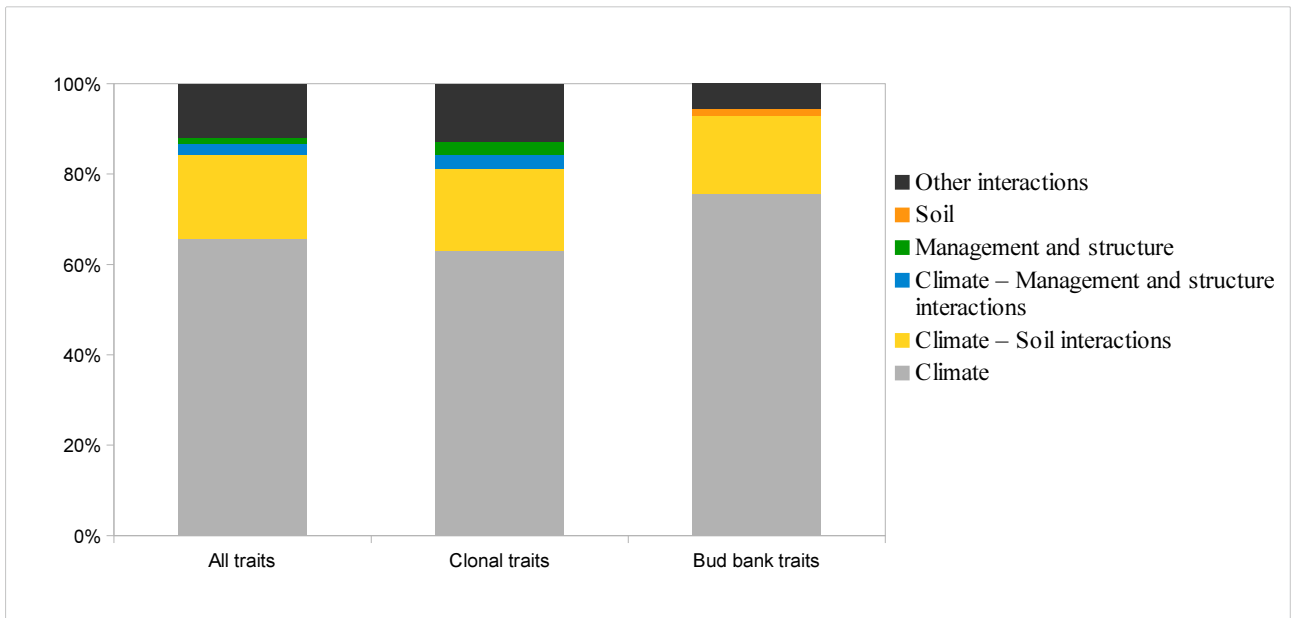
586 **Figure 3.** Variance partitioning (% of adjusted R^2) explained by climate, soil, forest management
587 and structure variable types (and their interactions) for the CWM of all traits, clonal and bud bank
588 traits in the Italian forest understories. a) explained vs unexplained variance; b) focus on explained
589 variance (standardized at 100%).

590 **a)**



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592 **b)**



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