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

Stefano Chelli[1]*, Gianluigi Ottaviani[2], Enrico Simonetti[1], Camilla Wellstein[3], Roberto Canullo[1], Stefano Carnicelli[4], Anna Andreetta[4], Nicola Puletti[5], Sandor Bartha[6,7], Marco Cervellini[1,8], Giandiego Campetella[1]

[1] School of Biosciences and Veterinary Medicine, Plant Diversity and Ecosystems Management Unit, University of Camerino, Via Pontoni 5, I-62032 Camerino, MC, Italy.

[2] The Czech Academy of Sciences, Institute of Botany, 135 Dukelská, CZ-37982, Třeboň, Czech Republic.

[3] Faculty of Science and Technology, Free University of Bozen-Bolzano, Piazza Università 5, I-39100 Bozen, Italy.

[4] Department of Earth Sciences, University of Florence, Piazzale Cascine 15, I-50144 Firenze, Italy.

[5] CREA Research Centre for Forestry and Wood, Piazza Nicolini 6, I-38100 Trento, Italy.

[6] Institute of Ecology and Botany, MTA Centre for Ecological Research, H-2163 Vácrátót, Hungary.

[7] GINOP Sustainable Ecosystems Group, MTA Centre for Ecological Research, H-8237 Tihany, Klebelsberg Kuno u. 3. Hungary.

[8] Department of Biological, Geological, and Environmental Sciences, Alma Mater Studiorum, University of Bologna, I-40126 Bologna, Italy.

* Corresponding author: stefano.chelli@unicam.it

36

37

38

39

40 **ABSTRACT**

41 The study of plant trait-environment links is rarely focused on traits that inform on space occupancy

42 and resprouting (both affecting plant persistence), especially in forest understories. Traits that can

43 effectively capture such key functions are associated with clonality and bud banks. We hypothesized

44 that: 1) climate is the main driver of clonal and bud bank traits, 2) traits related to space occupancy

45 (e.g., greater lateral spread) are more important in more mesic, richer soils forests, and 3) traits

46 related to resprouting ability (e.g., larger bud bank) are more important in more intensively and

47 recently managed forests. We addressed these hypotheses by analysing a unique dataset that is

48 statistically representative of Italian forests heterogeneity and includes three biogeographic regions

49 (Alpine, Continental, Mediterranean). We recorded data for sixteen climatic, soil and management

50 variables. We calculated community weighted mean (CWM) values of seven clonal and bud bank

51 traits for the forest understory vegetation. We used i) redundancy analysis to assess trait-

52 environment relations, and ii) variance partitioning analyses to identifying the relative role of

53 different groups of abiotic variables on CWM variation of all traits combined together, as well as

54 clonal and bud bank traits taken separately. Climate alone had a pervasive effect in determining

55 patterns of clonal and bud bank traits in Italian forest understories, mainly related to the effects of

56 temperature extremes and seasonality. Unexpectedly, soil and management factors alone showed

57 marginal effects on clonal and bud bank traits. However, soil features influenced trait patterns when

58 joined with climate. Our results confirmed that, at the biogeographic scale, climate played a lion-

59 share role in determining persistence-related traits of forest-floor plants. At the local-scale, other

60 interplaying factors (e.g., management, soil variables) may come into play in shaping patterns of the

61 studied plant traits. This study stressed the importance of examining functional trait patterns along

62 complex environmental gradients.

63

64

65 **Keywords:** Clonality; Community weighted mean (CWM); Resprouting; Soil properties; Plant-

66 environment linkages; Trait-based ecology

67

68

69

70

71

72

73

74

1. Introduction

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

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

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-
158 forests.net/). For the entire country, the sampling strategy resulted in a dataset composed by 201
159 sampling areas (forest stands; Figure 1). In each forest stand, we sampled a 400 m² area within
160 which we recorded the plant species composition. We collected data on presence/absence and
161 coverage (%) for all understory vascular plants in each sampling area. The field sampling was done
162 during spring-summer 2006 following standard protocols (Allegrini et al., 2009; Canullo et al.,
163 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 (Andreetta 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 (m^2 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 Quested, 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

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

Redundancy Analysis (RDA) and Variance Partitioning

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

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

3. Results

3.1. Selection of explanatory variables

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

3.2. Relationship between CWM values and environmental variables

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

variation of most of the clonal and bud bank traits. Climate explained approximately between 65% and 75% of standardized variation (Fig. 3b) and it was related to clonal and bud bank traits that described space occupancy and resprouting abilities (hence persistence process; Klimešová et al., 2018). Our results were consistent with other large-scale studies based on plant functional traits informative on nutrient acquisition and use strategies (e.g., leaf economics traits; Laughlin et al., 2011). Temperature extremes, such as minimum temperature of the coldest month, had a pervasive effect on clonal traits. This signal can be interpreted as these traits being strongly affected, and filtered by temperature-related constraints, similarly to what revealed for other traits associated with resource acquisition and use along elevation gradients (Milla and Reich, 2011; Read et al., 2014; Ottaviani et al., 2019). Management and soil variables alone played a marginal role on trait patterns – unexpected result, especially for bud bank traits which were linked to disturbance regimes (Klimešová and Klimeš, 2007; Pausas and Keeley, 2014; VanderWeide and Hartnett, 2015).

Our study area spans three biogeographic regions and probably the large variability of climatic conditions across Italy may have contributed to climate being the key driver of trait patterns and further explaining why the local effects of soil and management factors were less important. However, soil features exerted a certain influence on traits when joined with climate (Le Bagousse-Pinguet et al., 2017). The results of this study indicate that key soil properties only had weak effects on traits (especially for clonal traits). This result contrasts with findings from other regions, where different functional traits were used, such as foliar economics traits (e.g., Bernard-Verdier et al., 2012; Ottaviani et al., 2016; Pinho et al., 2018). Different results between our study and others could be explained by that fact that soil features may be better linked to acquisitive function and traits (Zemunik et al., 2015; Simpson et al., 2016; Pinho et al., 2018). Also, clonal and bud bank traits could be relatedto trade-offs between different plant functions, namely resource acquisition *vs* persistence (Bellingham and Sparrow, 2000; Clarke and Knox, 2009; Klimešová et al., 2018) more than soil properties. Overall, our findings stress the need of including traits informative on different functions (e.g., resource acquisition, space occupancy, resprouting after disturbance) when aiming at disentangling plant-environment linkages comprehensively (Klimešová et al., 2018).

4.2. Trajectory of plant trait-environment links

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

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

377 **REFERENCES**
378 Allegrini, M.C., Canullo, R., Campetella, G., 2009. ICP-Forests (International Co-operative
379   Programme on Assessment and Monitoring of Air Pollution Effects on Forests): Quality
380   Assurance procedure in plant diversity monitoring. J. Environ. Monit. 11, 782–787.
381 Andreetta, A., Cecchini, G., Bonifacio, E., Comolli, R., Vingiani, S., Carnicelli, S., 2016. Tree or
382   soil? Factors influencing humus form differentiation in Italian forests. Geoderma 264, 195–204.
383 Bellingham, P.J., Sparrow, A.D., 2000. Resprouting as a life history strategy in woody plant
384   communities. Oikos 89: 409–416.
385 Bernard-Verdier, M., Navas, M.-L., Vellend, M., Violle, C., Fayolle, A., Garnier, E., 2012.

386 Community assembly along a soil depth gradient: contrasting patterns of plant trait convergence
387 and divergence in a Mediterranean rangeland. J. Ecol. 100, 1422–1433.

388 Blanchet, F.G., Legendre, P., Borcard, D., 2008. Forward selection of explanatory variables.
389 Ecology 89, 2623–2632.

390 Borcard, D., Legendre, P., Drapeau, P., 1992. Partialling out the spatial component of ecological
391 variation. Ecology 73, 1045–1055.

392 Borgy, B., Violle, C., Choler, P., Denelle, P., Munoz, F., Kattge, J., ... Van Bodegom, P.M., 2017.
393 Plant community structure and nitrogen inputs modulate the climate signal on leaf traits. Global
394 Ecol. Biogeogr. 26, 1138–1152.

395 Bruelheide, H., Dengler, J., Purschke, O., Lenoir, J., Jiménez-Alfaro, B., Hennekens, S. M., ... &
396 Kattge, J., 2018. Global trait–environment relationships of plant communities. Nature ecology &
397 evolution 2, 1906.

398 Campetella, G., Botta-Dukat, Z., Wellstein, C., Canullo, R., Gatto, S., Chelli, S., Mucina, L. Bartha,
399 S., 2011. Patterns of plant trait–environment relationships along a forest succession
400 chronosequence. Agr. Ecosyst. Environ. 145, 38–48.

401 Canullo, R., Campetella, G., Mucina, L., Chelli, S., Wellstein, C., Bartha, S., 2011a. Patterns of
402 clonal growth modes along a chronosequence of post-coppice forest regeneration in beech
403 forests of Central Italy. Folia Geobot. 46, 271–288.

404 Canullo, R., Starlinger, F., Granke, O., Fischer, R., Aamlid, D., Neville, P., 2011b. Assessment of
405 Ground Vegetation. Manual Part VII.1, 19 pp. UN\ECE ICP Forests Programme Coordinating
406 Centre, Hamburg.

407 Chave, J., Coomes, D., Jansen, S., Lewis, S.L., Swenson, N.G., Zanne, A.E., 2009. Towards a
408 worldwide wood economics spectrum. Ecol. Lett. 12, 351–366.

409 Chelli, S., Marignani, M., Barni, E., Petraglia, A., Puglielli, G., Wellstein, C., …, Cerabolini, B.E.L.,
410 2019. Plant-environment interactions through a functional traits perspective: a review of Italian
411 studies. Plant Biosyst. DOI: 10.1080/11263504.2018.1559250

412 Chen, D., Ali, A., Yong, X.H., Lin, C.G., Niu, X.H., Cai, A.M., ... & Yu, F.H., 2019. A multi-species
413 comparison of selective placement patterns of ramets in invasive alien and native clonal plants to
414 light, soil nutrient and water heterogeneity. Sci. Tot. Environ. 657, 1568–1577.

415 Ciancio, O., Corona, P., Lamonaca, A., Portoghesi, L., Travaglini, D., 2006. Conversion of clearcut
416 beech coppices into high forests with continuous cover: a case study in central Italy. For. Ecol.
417 Manag. 224, 235–240.

418 Clarke, P.J., Knox, K.J.E., 2009. Trade-offs in resource allocation that favour resprouting affect the
419 competitive ability of woody seedlings in grassy communities. J. Ecol. 97, 1374–1382.

420 Costantini, E., Roberto, Barbetti, R., Fantappiè, M., L'Abate, G., Lorenzetti, R., Magini, S., 2013.

Pedodiversity. World soils book series. 105–178.

Freschet, G.T., Roumet, C., Treseder, K., 2017. Sampling roots to capture plant and soil functions. Funct Ecol, 31, 1506–1518.

Garnier, E., Cortez, J., Billès, G., Navas, M.L., Roumet, C., Debussche, M., Laurent, G., Blanchard, A., Aubry, D., Bellmann, A., Neill, C., 2004. Plant functional markers capture ecosystem properties during secondary succession. Ecology 85, 2630–2637.

Gilliam, F.S., 2014. The herbaceous layer in forests of eastern North America. Oxford University Press, New York.

Halassy, M., Campetella, G., Canullo, R., Mucina, L., 2005. Patterns of functional clonal traits and clonal growth modes in contrasting grasslands in the central Apennines, Italy. J. Veg. Sci. 16, 29–36.

Herben T., Chytry M., Klimešová J., 2016. A quest for species-level indicator values for disturbance. J. Veg. Sci. 27, 628–636.

Hijmans, R.J., Cameron, S.E., Parra, J.L., Jones, P.G., Jarvis, A., 2005. Very high resolution interpolated climate surfaces for global land areas. Int. J. Climatol. 25, 1965–1978.

Hulshof C.M., Swenson N.G., 2010. Variation in leaf functional trait values within and across individuals and species: an example from a Costa Rican dry forest. Funct. Ecol. 24, 217–23.

Iwasa, Y., Kubo, T., 1997. Optimal size of storage for recovery after unpredictable disturbances. Evol. Ecol. 11, 41–65.

Kichenin, E., Wardle, D.A., Peltzer, D.A., Morse, C.W., Freschet, G.T., 2013. Contrasting effects of plant inter□and intraspecific variation on community□level trait measures along an environmental gradient. Funct. Ecol. 27, 1254–1261.

Klimešová, J., Klimeš, L., 2007. Bud banks and their role in vegetative regeneration–a literature review and proposal for simple classification and assessment. Perspect. Plant. Ecol. 8, 115–129.

Klimešová, J., Doležal, J., 2011. Are clonal plants more frequent in cold environments than elsewhere? Plant Ecol. Div. 4, 373–378.

Klimešová, J., Doležal, J., Sammul, M., 2011. Evolutionary and organismic constraints on the relationship between spacer length and environmental conditions in clonal plants. Oikos 120, 1110–1120.

Klimešová, J., Malíková, L., Rosenthal, J., Šmilauer, P., 2014. Potential bud bank responses to apical meristem damage and environmental variables: matching or complementing axillary meristems? PloS one 9(2), e88093.

Klimešová, J., Herben, T., 2015. Clonal and bud bank traits: patterns across temperate plant communities. J. Veg. Sci. 26, 243–253.

Klimešová, J., Danihelka, J., Chrtek, J., Bello, F., & Herben, T. (2017). CLO□PLA: a database of

456   clonal and bud☐bank traits of the Central European flora. Ecology 98, 1179–1179.

457   Klimešová J, Martínková J, Ottaviani G, 2018. Belowground plant functional ecology: Towards an

458   integrated perspective. Funct. Ecol. 32, 2115–2126.

459   Kovács, B., Tinya, F., Ódor, P., 2017. Stand structural drivers of microclimate in mature temperate

460   mixed forests. Agr. Forest Meteorol. 234–235, 11–21.

461   Laliberté, E., 2017. Below-ground frontiers in trait-based plant ecology. New Phytol. 213, 1597–

462   1603.

463   Landuyt, D., Perring, M. P., Seidl, R., Taubert, F., Verbeeck, H., & Verheyen, K., 2018. Modelling

464   understorey dynamics in temperate forests under global change–Challenges and perspectives.

465   Perspect. Plant Ecol. 31, 44–54.

466   Laughlin, D.C., Fule, P.Z., Huffman, D.W., Crouse, J., Laliberte, E., 2011. Climatic constraints on

467   trait☐based forest assembly. J. Ecol. 99, 1489–1499.

468   Le Bagousse-Pinguet, Y., Gross, N., Maestre, F.T., Maire, V., de Bello, F., Fonseca, C.R., Kattge, J.,

469   Valencia, E., Leps, J.. Liancourt, P., 2017. Testing the environmental filtering concept in global

470   drylands. J. Ecol. 105, 1058–1069.

471   Legendre, P., Legendre, L., 2012. Numerical ecology, 3rd English edition. Elsevier Science BV,

472   Amsterdam.

473   Lepš, J., Šmilauer, P., 2003. Multivariate analysis of ecological data using CANOCO. Cambridge

474   university press.

475   Lohbeck, M., Poorter, L., Lebrija-Trejos, E., Martínez-Ramos, M., Meave, J.A., Paz, H., Pérez-

476   García, E., Romero-Pérez, E., Tauro, A., Bongers, F., 2013. Successional changes in functional

477   composition contrast for dry and wet tropical forest. Ecology 94, 1211–1216.

478   Milla, R., Reich, P.B., 2011. Multi-trait interactions, not phylogeny, fine-tune leaf size reduction

479   with increasing altitude. Ann. Bot. 107, 455–465.

480   Mokany K., Roxburgh S.H., 2010. The importance of spatial scale for trait–abundance relations.

481   Oikos 119, 1504–1514.

482   Oborny, B., Kun, Á., Czárán, T., Bokros, S., 2000. The effect of clonal integration on plant

483   competition for mosaic habitat space. Ecology 81, 3291–3304.

484   Økland, R.H., Eilertsen, O., 1994. Canonical correspondence analysis with variation partitioning:

485   some comments and an application. J. Veg. Sci. 5, 117–126.

486   Ottaviani, G., Martínková, J., Herben, T., Pausas, J. G., Klimešová, J., 2017. On Plant Modularity

487   Traits: Functions and Challenges. Trends Plant Sci. 22, 648–651.

488   Ottaviani, G., Marcantonio, M., Mucina, L. 2016. Soil depth shapes plant functional diversity in

489   granite outcrops vegetation of Southwestern Australia. Plant Ecol. Divers. 9, 263–276.

490   Ottaviani, G., Götzenberger, L., Bacaro, G., Chiarucci, A., de Bello, F., Marcantonio, M. 2019. A

491   multifaceted approach for beech forest conservation: environmental drivers of understory plant

492   diversity. Flora 256, 85–91.

493   Pakeman, R.J., Quested, H.M., 2007. Sampling plant functional traits: what proportion of the

494   species need to be measured? Appl. Veg. Sci. 10, 91–96.

495   Pausas, J.G., Keeley, J.E., 2014. Evolutionary ecology of resprouting and seeding in fire☐prone

496   ecosystems. New Phytol. 204, 55–65.

497   Pausas, J.G., Lamont, B.B., Paula, S., Appezzato-da-Glória, B., Fidelis, A., 2018. Unearthing

498   belowground bud banks in fire-prone ecosystems. New Phytol. doi: 10.1111/nph.14982

499   Pinho, B.X., Melo, F.P., Arroyo☐Rodríguez, V., Pierce, S., Lohbeck, M., Tabarelli, M., 2018.

500   Soil☐mediated filtering organizes tree assemblages in regenerating tropical forests. J. Ecol. 106,

501   137–147.

502   Puletti, N., Giannetti, F., Chirici, G., Canullo, R., 2017. Deadwood distribution in European forests.

503   J. Maps 13, 733–736.

504   Qian, J., Wang, Z., Klimešová, J., Lü, X., Kuang, W., Liu, Z., Han, X., 2017. Differences in below-

505   ground bud bank density and composition along a climatic gradient in the temperate steppe of

506   northern China. Ann. Bot. 120, 755–764.

507   R Core Team, 2015. R: A language and environment for statistical computing. R Foundation for

508   Statistical Computing, Vienna, Austria. URL https://www.R-project.org/

509   Read, Q.D., Moorhead, L.C., Swenson, N.G., Bailey, J.K., Sanders, N.J., Fox, C., 2014. Convergent

510   effects of elevation on functional leaf traits within and among species. Funct. Ecol. 28, 37–45.

511   Rowe, E.C., Emmett, B.A., Smart, S.M., Frogbrook, Z.L., 2011. A new net mineralizable nitrogen

512   assay improves predictions of floristic composition. J. Veg. Sci. 22, 251–261.

513   Rubio, A., Escudero, A., 2003. Clear-cut effects on chestnut forest soils under stressful conditions:

514   lengthening of time-rotation. For. Ecol. Manag. 183, 195–204.

515   Sammul, M., Kull, K., Niitla, T., Möls, T., 2004. A comparison of plant communities on the basis of

516   their clonal patterns. Evol. Ecol. 18, 443–467.

517   Schall, P., Ammer, C., 2013. How to quantify forest management intensity in Central European

518   forests. Eur. J. For. Res. 132, 379–396.

519   Schimper, A.F.W., 1903. Plant-geography upon a physiological basis. Clarendon Press, Oxford, UK.

520   Simpson, A.H., Richardson, S.J., Laughlin, D.C., 2016. Soil–climate interactions explain variation

521   in foliar, stem, root and reproductive traits across temperate forests. Global Ecol. Biogeogr. 25,

522   964–978.

523   Swenson, N.G., & Weiser, M.D., 2010. Plant geography upon the basis of functional traits: an

524   example from eastern North American trees. Ecology 91, 2234–2241.

525   Travaglini, D., Barbati, A., Chirici, G., Lombardi, F., Marchetti, M., Corona, P., 2007. ForestBIOTA

526   data on deadwood monitoring in Europe. Plant Biosyst. 141, 222–230.

527   VanderWeide, B.L., Hartnett, D.C., 2015. Belowground bud bank response to grazing under severe,

528   short-term drought. Oecologia 178, 795–806.

529   Vanneste, T., Valdés, A., Verheyen, K., Perring, M. P., Bernhardt-Römermann, M., Andrieu, E., ... &

530   De Frenne, P., 2019. Functional trait variation of forest understorey plant communities across

531   Europe. Basic Appl Ecol 34, 1–14.

532   Violle, C., Navas, M.L., Vile, D., Kazakou, E., Fortunel, C., Hummel, I., Garnier, E., 2007. Let the

533   concept of trait be functional! Oikos 116, 882–892.

534   von Humboldt, A., Bonpland, A., 1807. Essay on the Geography of Plants. Paris.

535   Vojtkó, A.E., Freitag, M., Bricca, A., Martello, F., Moreno, J,. Küttim, C.M., Kun, K., de Bello, F.,

536   Klimešová, J., Götzenberger, L., 2017. Clonal vs leaf-height-seed (LHS) traits: which are filtered

537   more strongly across habitats? Folia Geobot. 52, 269–281.

538   Weiher, E., van der Werf, A., Thompson, K., Roderick, M., Garnier, E., Eriksson, O., 1999.

539   Challenging Theophrastus: a common core list of plant traits for functional ecology. J. Veg. Sci.

540   10, 609–620.

541   Wellstein, C., Kuss, P., 2011. Diversity and frequency of clonal traits along natural and land-use

542   gradients in grasslands of the Swiss Alps. Folia Geobot. 46, 255–270.

543   Westoby, M., 1998. A Leaf-height-seed (LHS) plant ecology strategy scheme. Plant Soil 199, 213–

544   227.

545   WGFB, 2011. The BioSoil Forest Biodiversity field manual, version 1.0/1.1/1.1a for the field

546   assessment 2006-07. In: JRC – Inst. for Environment and Sustainability (ed) Evaluation of

547   BioSoil Demonstration Project: Forest Biodiversity. Publications Office of the European Union,

548   Luxembourg, pp 81-102. doi:10.2788/84823

549   Wieczynski, D.J., Boyle, B., Buzzard, V., Duran, S.M., Henderson, A.N., Hulshof, C.M., Kerkhoff,

550   A.J., McCarthy M.C., Michaletz, S.T., Swenson, N.G., Asner, G.P., Bentley, L.P., Enquist, B.J.,

551   Savage, V.M., 2019. Climate shapes and shifts functional biodiversity in forests worldwide.

552   PNAS 116, 587–592.

553   Wright, I.J., Reich, P.B., Westoby, M. Ackerly, D.D., Baruch, Z., Bongers, F., ..., Flexas, J., 2004.

554   The worldwide leaf economic spectrum. Nature 428, 821–827.

555   Ye, D., Hu, Y., Song, M., Pan, X., Xie, X., Liu, G., Ye, X., Dong, M., 2014. Clonality-climate

556   relationships along latitudinal gradient across China: adaptation of clonality to environments.

557   PloS one, 9(4), e94009.

558   Yu, F., Wang, N., He, W., Chu, Y., Dong, M., 2008. Adaptation of rhizome connections in drylands:

559   increasing tolerance of clones to wind erosion. Ann. Bot. 102, 571–577.

560   Zemunik, G., Turner, B. L., Lambers, H., & Laliberté, E. (2015). Diversity of plant nutrient-

561   acquisition strategies increases during long-term ecosystem development. Nature Plants 1,

562   15050.
563

564

565   **TABLES**

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+/Kg	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.

567

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
	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
Clonal traits	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_below	Yes/no	Persistence of belowground bud bearing organs > 2 yrs

570

571

FIGURES

Figure 1. Map showing the location of the 201 plots in Italy (left panel). On the right, the most

abundant types are represented: 1 alpine coniferous forest; 2 beech forest; 3 deciduous oak forest; 4

evergreen Mediterranean maquis.
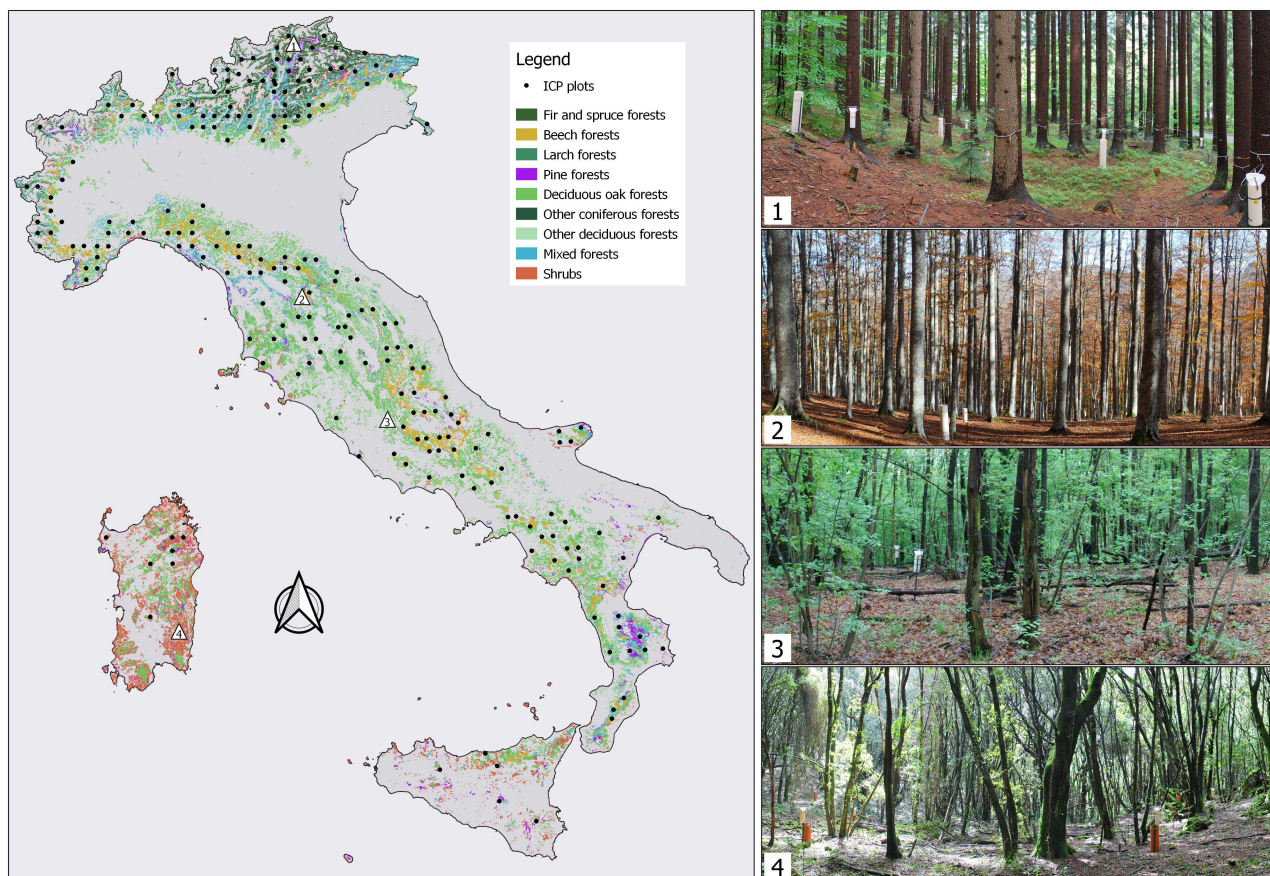
576

577

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
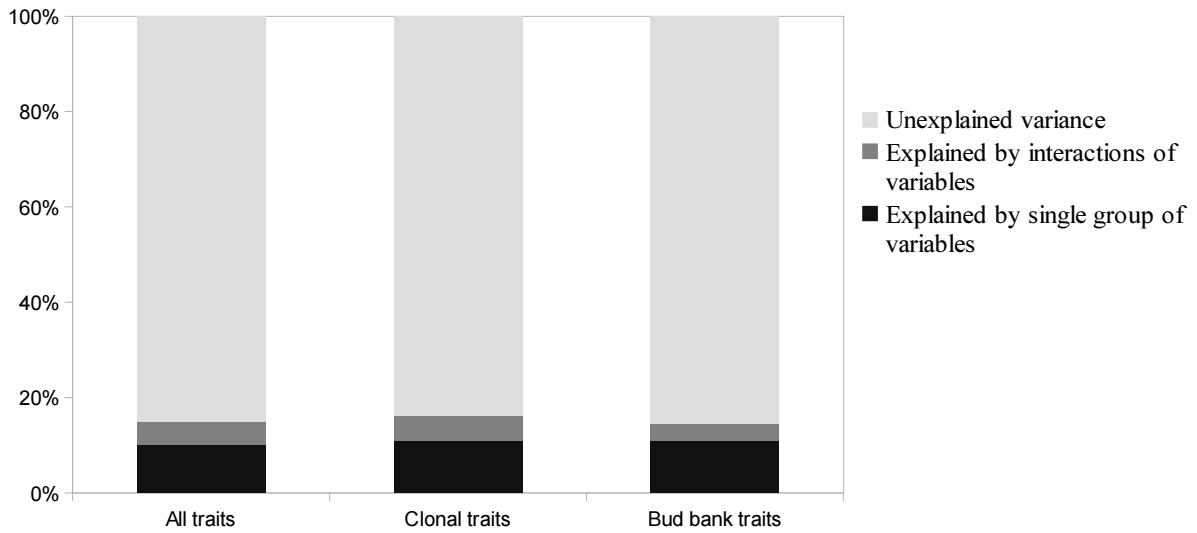582   management; see table 1 and 2 for abbreviations).
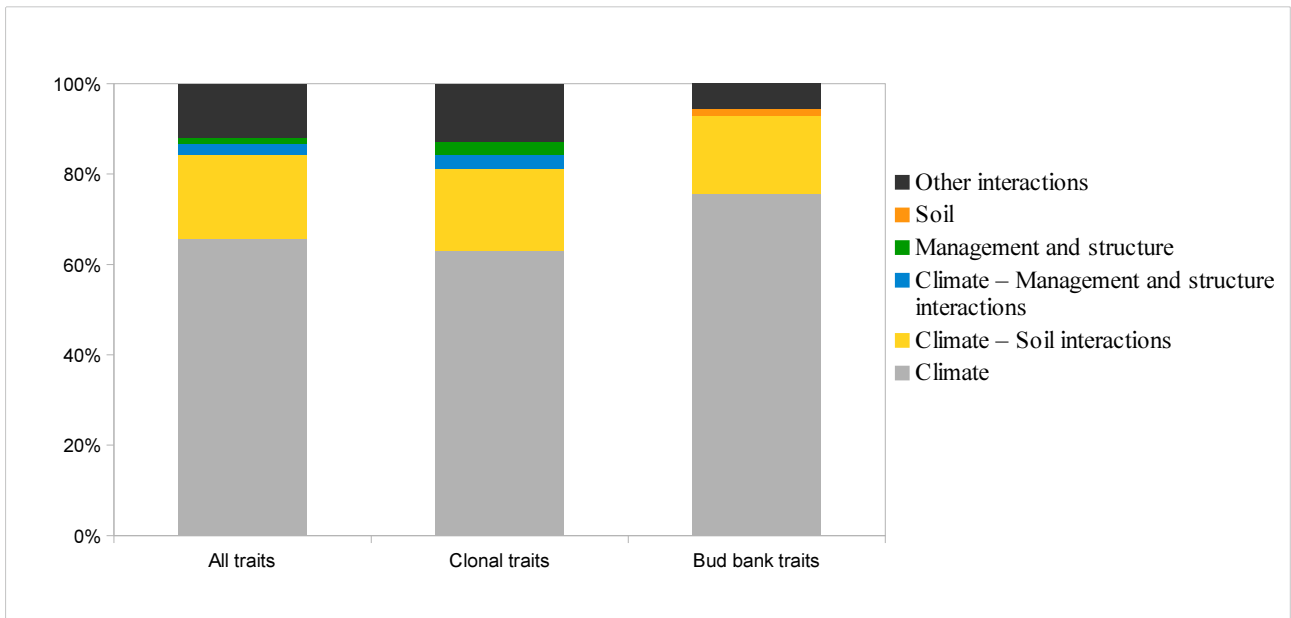

583
584

585
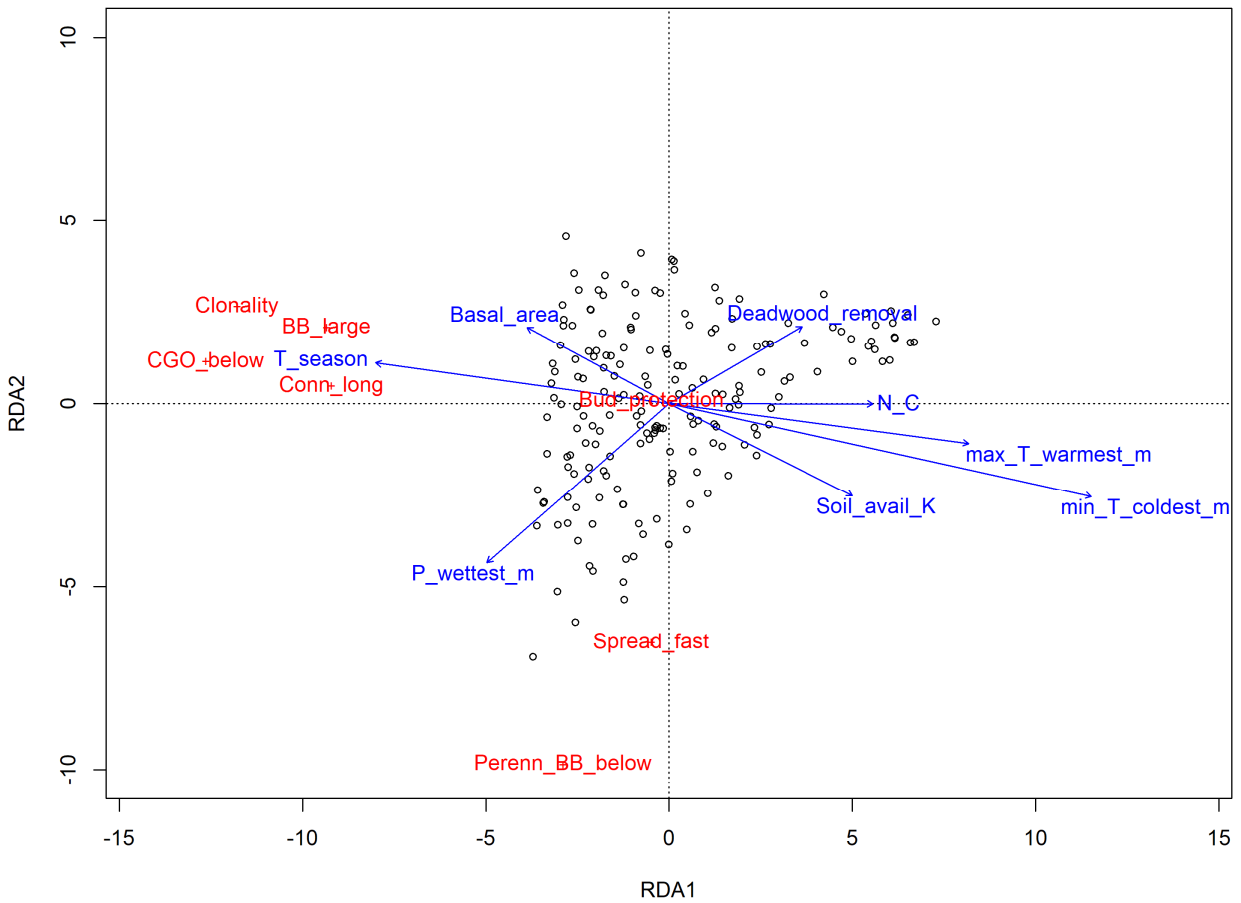
Figure 3. Variance partitioning (% of adjusted R^2) explained by climate, soil, forest management

and structure variable types (and their interactions) for the CWM of all traits, clonal and bud bank

traits in the Italian forest understories. a) explained *vs* unexplained variance; b) focus on explained

variance (standardized at 100%).

a)

591

592   **b)**

593

594

595

596

597