CLIMATE IS THE MAIN DRIVER OF CLONAL AND BUD BANK TRAITS IN ITALIAN 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
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...
heterogeneous habitats it may give a competitive advantage (Oborný et al., 2000; Yu et al., 2008).

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

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

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

Here, we aim to (1) identify trait-environment relationships of seven clonal and bud bank traits of plants in the forest understory, and (2) quantify the relative contributions of climate, soil, management in determining the community mean values of plant traits of the forest understories. Italy was selected as model region for the research because (a) the country covers large latitudinal and climatic gradients that include three biogeographic regions, i.e., Alpine, Continental, Mediterranean, (b) Italy hosts a high number of plant species and forest types, (c) the country is characterized by a long history of human exploitation of resources, e.g., wood and timber supply,
involving different management practices (see also Chelli et al. 2019), and (d) there is a high
diversity of soil types due to the great variety of pedogenetic processes (Costantini et al., 2013).
Given the range in within-country factors described above, we expected that: (H1) climate is the
main driver of traits associated with clonality and resprouting (macro-scale filter); (H2) traits
related to space occupancy ability (e.g., larger lateral spread) are more important in mesic, rich-soil
forests (habitat-scale filter); (H3) traits related to resprouting ability (e.g., perennial and larger
belowground bud bank) are more relevant in more intensively and recently managed forests
(habitat-scale filter).

2. Materials and methods

2.1. Study area and sampling design

The study area covered forested regions of Italy, estimated to be around 9 million hectares,
distributed in Mediterranean, Continental and Alpine biogeographic regions. The sampling design
was systematic and probabilistic (WGFB, 2011) and was based on a grid superimposed onto the
whole country with cells of 16 km x 16 km, with each corner of this grid being included as a sample
area if a forest larger than 1 ha was found there (after a field-check). This grid belongs to the
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
sampling areas (forest stands; Figure 1). In each forest stand, we sampled a 400 m² area within
which we recorded the plant species composition. We collected data on presence/absence and
coverage (%) for all understory vascular plants in each sampling area. The field sampling was done
during spring-summer 2006 following standard protocols (Allegrini et al., 2009; Canullo et al.,
2011b).

2.2. Explanatory variables

For each sampling area we recorded sixteen explanatory variables within three categories: climate,
soil, forest structure, management (Table 1). We obtained climate variables from the global
WorldClim database (first version; Hijmans et al., 2005); among the available parameters, we
selected six variables, related to temperature and precipitation variability (temperature seasonality,
precipitation seasonality) and extremes (maximum temperature of the warmest month, minimum
temperature of the coldest month, precipitation of the driest month, precipitation of the wettest
month). They were selected as they can influence both vegetative and regenerative functional traits
(e.g., Ye et al., 2014; Le Bagousse-Pinguet et al., 2017). In each sampling area, we measured four
soil variables according to standard procedures (Andreetta et al., 2016; Table 1). The soil variables
chosen were indicative of soil nutrient status (topsoil available potassium (K)), nitrogen availability
(N/C; Rowe et al., 2011), regulation of nutrient availability (soil pH), and water holding capacity (effective soil volume) and all of the have been shown to potentially influence plant traits (e.g., Chen et al., 2019). In addition, at each forest sampling site we measured six variables related to forest management and structure (Table 1) – referred to management hereafter. Basal area (m$^2$ ha) – which is correlated with the total woody biomass, stand maturity and successional stage (Pinho et al., 2018 and references therein), total vegetation cover (including overstory), and litter cover. These three variables are recognized key biotic drivers determining microhabitat suitability to species, especially for forest understory vegetation, as these parameters can largely contribute to microclimatic buffering capacity (Kovács et al., 2017). We collected current land-use data related to deadwood removal, and total released deadwood. In particular, deadwood removal is linked to management practices aimed at avoiding the spreading of diseases, pests, or fires (Travaglini et al., 2007). Total released deadwood is widely considered a good proxy for disturbance intensity in managed forests, due to linkages with stand management gradients (Schall and Ammer, 2013; Puletti et al., 2017).

### 2.3. Clonal and bud bank traits

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

### 2.4. Data analysis

#### Explanatory variables selection

We carried out stepwise ordination in order to identify the most parsimonious set of single explanatory variables for all traits together, and clonal and bud bank traits separately (Økland and Eilertsen, 1994). Stepwise forward ordination is a procedure for selecting a subset of explanatory 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
the variables identified by the stepwise selection was significant (P < 0.001; Fig. 2). The first axis accounted for 15.3% of the variability, and was primarily related to temperature variables and, to a lesser degree, soil parameters. The second axis explained only 1.7% of the total variability and it was primarily associated with precipitation and forest management. Along the first RDA axis, negative values were related to forest stands characterized by higher temperature seasonality and lower temperature of both the coldest and warmest month. They are mainly located in the Alpine and Continental biogeographic regions of Central and Northern Italy on nutrient poor soils. Forests in that grouping also were more mature (higher basal area) and the forest understory vegetation was characterized by a higher percentage of clonal species with belowground clonal organs, long-term connections among ramets, and higher resprouting abilities (large belowground bud bank; Fig. 2). Positive values on the first RDA axis were forest stands mainly located in the Mediterranean biogeographic region. Forests in that area had warmer climatic conditions and occurred on richer soils, with understory plants characterized by lower abilities to occupy space and resprout (Fig. 2). Because the second RDA axis accounted for very little of the overall variation in the data, it is difficult to draw conclusions regarding forest characteristics and clonal traits of the understory vegetation but several features are worth mentioning. For example, negative values on the second axis identified forest stands with higher precipitation in the wettest month and less intense management, i.e., with no deadwood removal. These forests were characterized by understory communities with fast lateral spread and perennial belowground bud bank (Fig. 2). Positive values described plots having opposed environmental conditions (i.e., more intensively managed and with lower precipitation in the wettest month), and distinguished by opposing trait patterns (i.e., slower lateral spread, and short-lived belowground bud bank).

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

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

4.3. Conclusions and future directions
The degree to which trait variation was explained by environmental variables (14.3%-16.0%) in this study was comparable to results of related studies in other forests (e.g., 9-31%, Vanneste et al., 2019). However, our research was based on a probabilistic sampling design (representative of the entire set of Italian forest types), and not on selected gradients (e.g., see Vanneste et al., 2019). This implied that we did not homogenize any of the environmental variables, so including a large environmental variability, that may be the main cause of the unexplained variance in the models. Yet, this was also one of the strongholds of this study: results emerging from environmental gradients are considered key to further the understanding of species and trait assembly in plant communities (e.g., von Humboldt and Bonpland, 1807; Schimper, 1903; Swenson and Weiser, 2010). At the biogeographic scale, climate confirmed its lion-share role in determining persistence-
related traits, as revealed for acquisition traits (e.g., Laughlin et al., 2011; Wieczynski et al., 2019). At the local-scale, other interplaying factors (e.g., management, soil variables) may come into play in shaping plant trait patterns. This evidence stresses the importance of implementing multiple-scale trait-based approaches (Hulshof and Swenson, 2010; Mokany and Roxburgh, 2010). The plant trait–environment links reported in our study were essentially produced by species turnover and/or changes in species cover values, and not by intraspecific variation. Therefore, we call for future studies to incorporate i) intraspecific (and, ideally, intra-clonal) trait variation, as it can play a fundamental role in plant community responses to changing environments (e.g., Hulshof and Swenson, 2010; Kichenin et al., 2013), and ii) traits capturing the widest possible functional spectrum (Weiher et al., 1999; Klimešová et al., 2018). This way, a more realistic and comprehensive understanding of community assembly and ecosystem functioning of forest understories could be effectively achieved.

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Supplementary material

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

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

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acquisition strategies increases during long-term ecosystem development. Nature Plants 1, 15050.
Table 1. Description of the explanatory variables with units, ranges, main references and notes.

<table>
<thead>
<tr>
<th>Group</th>
<th>Variable</th>
<th>Abbreviation</th>
<th>Unit</th>
<th>Range</th>
<th>Notes</th>
</tr>
</thead>
<tbody>
<tr>
<td>Climate</td>
<td>Temperature seasonality</td>
<td>T_season</td>
<td>CV (%)</td>
<td>51 – 75</td>
<td>Source: Hijmans et al. (2005), WorldClim</td>
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<td></td>
<td>Precipitation seasonality</td>
<td>P_season</td>
<td>CV (%)</td>
<td>7 – 64</td>
<td>Source: Hijmans et al. (2005), WorldClim</td>
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<td>Max temperature of the warmest month</td>
<td>max_T_warmest_m</td>
<td>°C</td>
<td>9.2 – 31.5</td>
<td>Source: Hijmans et al. (2005), WorldClim</td>
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<tr>
<td></td>
<td>Min temperature of the coldest month</td>
<td>min_T_coldest_m</td>
<td>°C</td>
<td>-10.5 – 7.1</td>
<td>Source: Hijmans et al. (2005), WorldClim</td>
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<td></td>
<td>Precipitation of the wettest month</td>
<td>P_wettest_m</td>
<td>mm</td>
<td>65 – 155</td>
<td>Source: Hijmans et al. (2005), WorldClim</td>
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<tr>
<td></td>
<td>Precipitation of the driest month</td>
<td>P_driest_m</td>
<td>mm</td>
<td>4 – 102</td>
<td>Source: Hijmans et al. (2005), WorldClim</td>
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<td>Soil</td>
<td>Soil pH</td>
<td>pH</td>
<td></td>
<td>4 – 8.6</td>
<td>Source: Andreetta et al. (2016)</td>
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<td></td>
<td>N/C</td>
<td>N_C</td>
<td>Na</td>
<td>0.05 – 0.19</td>
<td>Source: Andreetta et al. (2016)</td>
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<td>4.5 – 170</td>
<td>Good proxy of water holding capacity. Source: Andreetta et al. (2016)</td>
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<td>Biotic driver of vegetation.</td>
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<td>Litter cover</td>
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<td>Biotic driver of vegetation.</td>
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<td>Definition</td>
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<tr>
<td>Clonality</td>
<td></td>
<td></td>
<td></td>
<td>Ability to reproduce vegetative by means of clonal growth organs</td>
<td></td>
</tr>
<tr>
<td>Clonal growth organ belowground</td>
<td>Clonality</td>
<td>Clonality</td>
<td>Yes/no</td>
<td>Ability to reproduce vegetative by means of clonal growth organs</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Clonal growth organ belowground</td>
<td>CGO_below</td>
<td>Yes/no</td>
<td>The clonal growth organ is positioned belowground.</td>
<td></td>
</tr>
<tr>
<td>Clonal traits</td>
<td>Long-term connections</td>
<td>Conn_long</td>
<td>Yes/no</td>
<td>Persistence of connections among ramets &gt; 2 yrs</td>
<td></td>
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<tr>
<td></td>
<td>Fast lateral spread</td>
<td>Spread_fast</td>
<td>Yes/no</td>
<td>Clonal lateral spreading &gt; 0.25 m/yr</td>
<td></td>
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<tr>
<td></td>
<td>Bud protection</td>
<td>Bud_protection</td>
<td>Yes/no</td>
<td>Buds protected by specialized scale leaves</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Large bud bank</td>
<td>BB_large</td>
<td>Yes/no</td>
<td>Stem- and root-derived buds above- or belowground &gt;10</td>
<td></td>
</tr>
<tr>
<td>Bud bank traits</td>
<td>Perennial bud bank belowground</td>
<td>Perenn_BB_below</td>
<td>Yes/no</td>
<td>Persistence of belowground bud bearing organs &gt; 2 yrs</td>
<td></td>
</tr>
</tbody>
</table>
**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.
**Figure 2.** Redundancy analysis diagram showing the CWM trait values for the Italian forest understories constrained by the environmental variables identified by the stepwise selection procedure. Red labels indicate response variables (traits; see table 2 for abbreviations), whereas blue labels and arrows report predictors (variables related to climate, soil, structure and management; see table 1 and 2 for abbreviations).
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)

(b)