# Congruent responses of vascular plant and ant communities to pastoral land-use abandonment in mountain areas throughout different biogeographic regions

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## Abstract

**Background:** There is a long-term trend towards the abandonment of agro-pastoral activities in the mountain areas of Europe: the following encroachment process of semi-natural grasslands by shrubs is one of the main severe threats to the conservation of biodiversity in mountain environments. To better understand the impact of land abandonment, we analysed the reliability of plant functional groups, ant traits, and ant functional groups as indicators of land use changes. We carried out the research in Italy at four sites along a latitudinal/altitudinal gradient in three biogeographic regions (Mediterranean, Continental, Alpine). We identified three stages of a chronosequence at each site as representative of the plant succession in response to pastoral land-use abandonment.

**Results:** As expected, both the plant and ant assemblages considerably differed across sites at the species level and, within each site, among the three stages. This trend was found also using ant traits, functional groups of ants, and plant functional groups. Ant and plant communities were related in terms of composition and functionality. Harvester ants and ants with collective foraging strategy were associated with annual legumes and grasses (Therophytes); ants with a strictly individual foraging strategy with Phanerophytes. Ant traits and plant functional groups indicated significant differences among the three stages of the chronosequence. However, ant functional groups could not discriminate between the stages represented by secondary grasslands currently grazed and shrub-encroached grasslands ungrazed.

**Conclusion:** Despite some limitations of ant functional groups in explaining the succession stages of land abandonment, our results suggest that ants are a good surrogate taxon and might be used as bioindicators of land-use changes and ecosystem functioning. Furthermore, our findings indicate that the functional group approach should be applied to other European ecosystems. Finally, reducing the taxonomic complexity could contribute to developing predictive models to detect early environmental changes and biodiversity loss in mountain habitats.

**Keywords:** Biodiversity conservation, Bioindicators, Cross-taxon congruence, Functional groups, Land abandonment, Monitoring, Mountain pastures

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# Background

Agro-pastoral activities in mountain areas are crucial for maintaining the viability of rural traditions in Europe and are particularly relevant for resource and nature

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conservation (Gómez Sal and González García 2007). However, the abandonment of mountain environments due to socio-economic changes after the Second World War led to a drastic reduction of agro-pastoral activities and changed land uses (MacDonald et al. 2000; Tasser and Tappeiner 2002). Pastoral activities have shaped the landscape into a mosaic of plant communities supporting different levels of biodiversity and providing different ecosystem services (Yapp et al. 2010; Bagella et al. 2013; 2020; Pittarello et al. 2020). On the other hand, the cessation or the limitation of grazing management for several years has led to natural vegetation succession processes (Garbarino et al. 2013). Dwarf shrubs first, and trees later, were responsible for the encroachment of broad areas of semi-natural grasslands, which is considered one of the main threats to biodiversity conservation in mountain environments (Laiolo et al. 2004; Koch et al. 2015; Pittarello et al. 2016).

Identifying key taxonomic groups and possible relationships among them and land use patterns can help standardise efficient tools for biodiversity assessment and monitor the effects of land-use abandonment (Larrieu et al. 2018). Vascular plants are recognized as particularly suitable indicators in monitoring and conservation: they provide the physical structure for other organisms, including many habitat specialists distributed across broad environmental gradients, and are well known from a taxonomic point of view. For these reasons, vascular plants are traditionally considered one of the key surrogate taxonomic groups to select areas of concern in biodiversity conservation as they can reflect the diversity of other significant and less easily detectable taxa (Pharo et al. 2000; Burrascano et al. 2011; Bagella 2014; Bagella et al. 2014). However, many arthropod groups are considered good land-use change or abandonment indicators. Among them, ants are effective environmental indicators in almost all terrestrial habitats because of their wide range of climatic niches and their ability to cope with varying environmental conditions (Andersen and Majer 2004; Jiménez-Carmona et al. 2020). Besides, they play multiple roles in food webs: herbivores, decomposers, predators, parasites, seed dispersers, and pollinators (Hölldobler and Wilson 1990). As they are influenced by a more complex suite of environmental variables than plants, ants can provide useful information on short-term environmental changes in highly dynamic and vulnerable ecosystems (Zina et al. 2021).

Simple metrics as species richness have proved to be unreliable tools in biodiversity monitoring (Andersen and Majer 2004; Wan Hussin et al. 2012). Indeed, ecosystem processes are affected by the functional traits of organisms involved, and the taxonomic identity is not suitable to make functional comparisons among different biogeographical regions (Westoby et al. 2002; Garnier et al. 2004; Segar et al. 2013). Since functional traits mediate the response of organisms to the environment and influence ecosystem functioning (Chelli et al. 2019), they may help predict how communities might respond to landscape changes. Likewise, functional groups can be helpful and cost-effective to detect congruent and robust patterns of community structure between regions by transcending the effects of historical factors on species composition (Hoffmann 2010; Laureto et al. 2015). The definition of functional groups, based on specific traits depending on the aims and scale of the research (Smith and Huston 1989; Wilson 1999), has a long history in ecology, especially for plants (e.g. Raunkiaer 1934). The impact of pastoral land-use abandonment on vegetation has been investigated, and previous studies showed that plant traits provide insight on key processes driving vegetation changes (Prévosto et al. 2011). Plant functional groups were also successfully used for measuring the recovery of vegetation after cropland abandonment (Heydari et al. 2020). Ant functional groups have a relatively recent history (Andersen 1995). Although Andersen's scheme (1995) is still questionable outside Australia, it could be a useful generalisation in broad studies of functional trait variation in Europe (Gómez et al. 2003; Azcarate and Peco 2012; Satta et al. 2012; Verdinelli et al. 2017).

Despite the importance of ant-seed dispersal in conserving semi-open habitats of European pastures (Travers et al. 2020), information on ant-plant relationships for the European mountain areas is minimal (Hevia et al. 2016; Heuss et al. 2019). In addition, a multispecies approach can provide a better assessment of the overall diversity of an area, reflect more accurately changes in diversity caused by habitat modification, and provide more complete information for halting the biodiversity loss (Hevia et al. 2016). Therefore, we aimed to investigate the possibility of using very different taxa as bioindicators by analysing the effect of land abandonment on ant and plant communities in Italian mountain areas. For this purpose, we followed the space for time substitution approach (Pickett 1989) in different sites, characterised by a shared history of land-use, we identified three different stages of a vegetation succession following a pastoral land-use abandonment. Moreover, to examine the effect of geographical variation, we considered a biogeographic gradient, i.e. Mediterranean, Continental, and Alpine (EEA 2016). The specific objectives of the research were: (i) to analyse vascular plant and ant community patterns in response to pastoral land-use abandonment; (ii) to evaluate if vascular plant functional groups, ant traits, and ant functional groups were reliable indicators of the main changes of community composition, regardless of

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the biogeographic region, and (iii) to verify a possible overall cross-taxon congruence between ant and vascular plant communities, at the level of species and functional composition, and investigating whether ants can be used as surrogates of biodiversity of the studied taxa.

## Materials and methods
### Study sites and experimental design
The research was carried out in Italy at four sites located along a latitudinal/altitudinal gradient, in three biogeographic regions (Fig. 1; Table 1). On a physiognomic basis, we identified three dynamic stages of a chronosequence at each site (Table 1), representing the plant succession from pastoral use to abandonment. Stage 1 was represented by secondary grasslands currently grazed (grasslands dominated by grasses and other herbaceous species, e.g. forbs, legumes, etc.). Shrub-encroached grasslands ungrazed for 20–30 years (grasslands dominated by shrub and fern species, with a sporadic presence of trees. The herbaceous layer was mainly dominated by grasses and other herbaceous species, e.g. forbs, legumes, etc.) were the dominating vegetation in stage 2. Stage 3 was represented by woodlands, abandoned for at least 50 years (woodlands with a close canopy cover). The overstorey layer was dominated by tree species, whereas the understorey by shrubs or ferns. The understorey herbaceous layer had a low cover.

A number of 3 to 9 sampling units (hereafter 'plots') were established for each stage of each site for sampling vascular plants and ants, for 60 plots (Table 1). In Val Vogna, being located above the treeline, only stage 1 and stage 2 were represented.

### Data collection
Surveys on vascular plants (hereafter 'plants') were performed from May to July 2019, at the peak blooming period, to identify all species more easily. Along with four transects corresponding to four perpendicular radii of each plot, we applied the vertical point-quadrat method (Daget and Poissonet 1971) to assess the frequency of
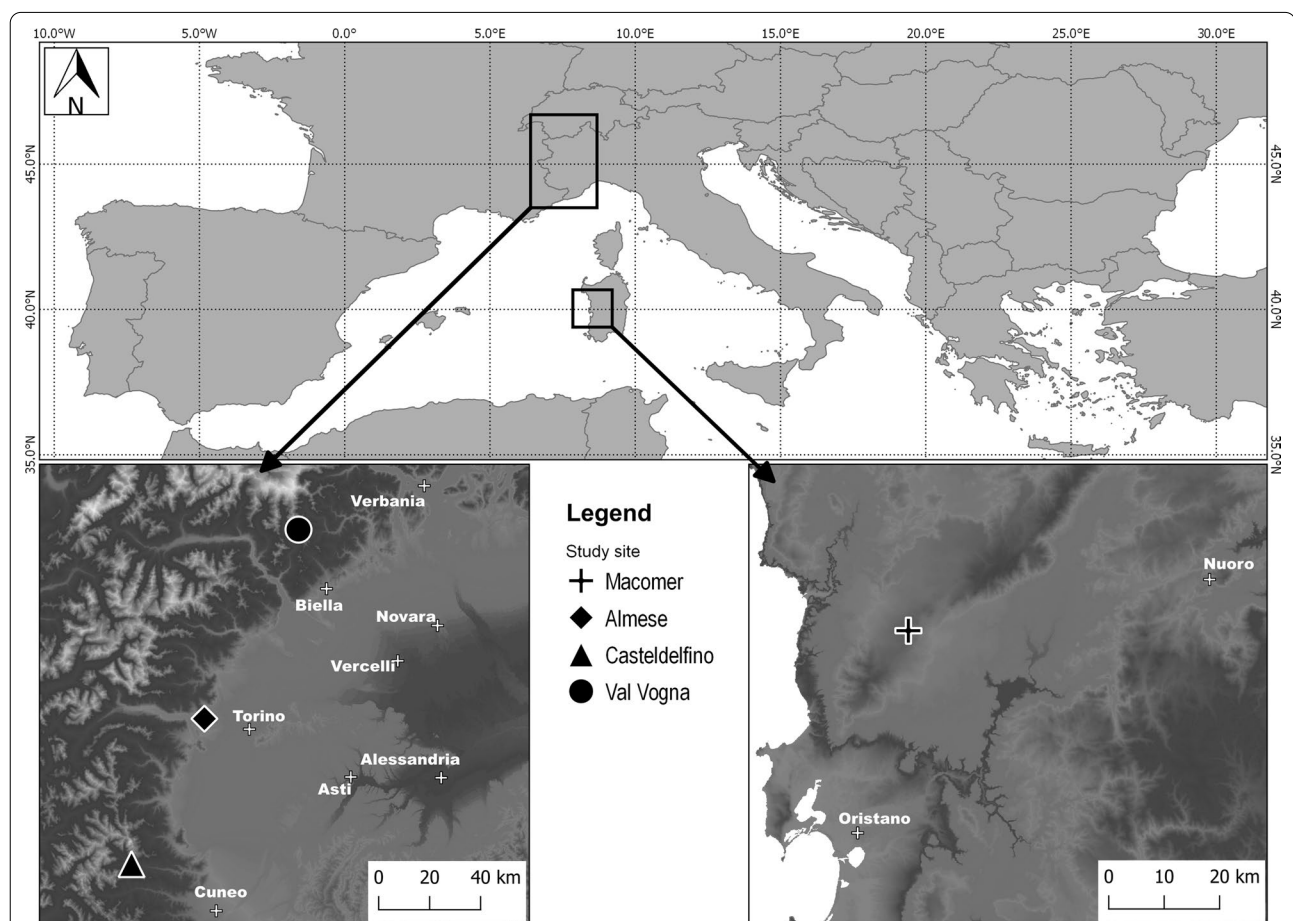


**Fig. 1** Map of the four study sites in Italy. Each site is in a specific biogeographic region: Mediterranean (Macomer), Continental (Almese), and Alpine (Casteldelfino and Val Vogna)

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**Table 1** Coordinates, bedrock, topographic features, biogeographic region, and number of sampling units per each chronosequence stage of the four study sites located in Italy
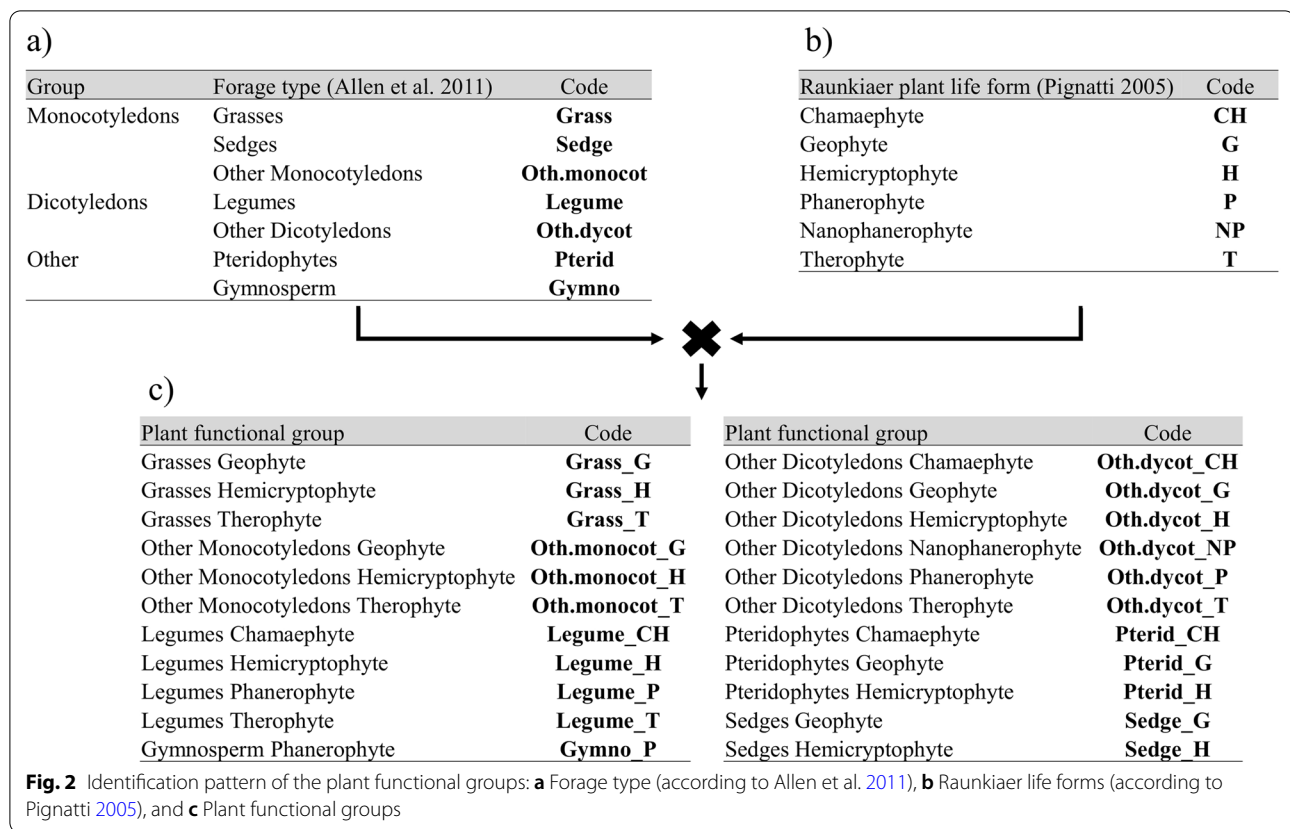
| | | Study sites | | | |
|---|---|---|---|---|---|
| | | **Macomer** | **Almese** | **Casteldelfino** | **Val Vogna** |
| Coordinates | | 40°14′05.9″N, 8°42′08.8″E | 45°06′25.2″N, 7°26′32.9″E | 44°35′14.0″N, 7°05′39.2″E | 45°46′51.5″N, 7°54′02.7″E |
| Bedrock | | Basalt | Serpentinite | Serpentinite | Gneiss |
| Elevation (m a.s.l.) | | 670 | 480 | 1380 | 1760 |
| Slope angle (degree) | | 5 | 21.2 | 26.3 | 18.6 |
| Altitudinal zonation | | Colline | Colline | Subalpine | Alpine |
| Biogeographic region | | Mediterranean | Continental | Alpine below the tree line | Alpine above the tree line |
| Chronosequence stage | | Number of sampling units | | | |
| | 1 | 9 | 3 | 3 | 3 |
| | 2 | 9 | 6 | 6 | 6 |
| | 3 | 9 | 3 | 3 | 0 |

occurrence of each plant species. Plot radius varied from 3 to 15 m, depending on the complexity of vegetation mosaic (Braun-Blanquet 1932). Plot size does not often influence patterns of vegetation composition (Otýpková and Chytrý 2006), and the variable sampling effort is considered suitable for analyses of changes that do not involve a comparison of alpha diversity (Chytrý and Otýpková 2003; Di Pietro et al. 2021). At regular intervals (12.5 cm to 50 cm, depending on the radius length), the plant species touching a vertical steel needle were identified and recorded (Perotti et al. 2018). Since the less frequent species are likely missed using this method, a complete list of plant species found within each circular plot was recorded. A schematic representation of the survey methodology is available in Additional file 1. Finally, in a 20 m radius buffer centred on the plot, the tree species percentage cover was detected from a photointerpretation of the most recent orthophotographs available from the Sardinian and Piedmont Region public repositories (Regione Piemonte 2018; Sardegna 2019). Nomenclature follows Pignatti et al. (2017).

The frequency of occurrence of each plant species recorded along the transects of each plot was converted to 100 measurements, i.e. species percentage cover (hereafter '%SC'). A %SC = 0.3 was attributed to all rare species (Pittarello et al. 2019).

Plant species were grouped into functional groups derived from their life form (Raunkiaer 1934) and forage type (Allen et al. 2011). Then, life forms following Pignatti (2005) (Fig. 2b) and forage types (Fig. 2a) were attributed to each plant species and combined to identify 22 plant functional groups (Fig. 2c). The sum of the %SC of the species belonging to each functional group was calculated afterwards for each plot.

Ant sampling was performed at the same time as the vegetation survey. Four pitfall traps (7-cm-diameter, 11.8-cm-deep polypropylene vials), sunk into the soil and partially filled with a solution of water and monopropylene glycol (10/1; v/v), were placed at the corners of a 10-m side square centred on each vegetation plot. A scheme of each ant sampling unit is available in Additional file 1. After one week, all traps were removed and the ants were identified at the laboratory. The abundance of ant workers for each group of four traps (sampling unit) was transformed in presence-absence for subsequent statistical analyses. The specimens were identified to species level (see Additional file 1: S3 for the list of dichotomous keys available in the literature and used in this work), and the nomenclature follows AntWiki (2021). All the ant species were scored for ten traits (Table 2 and Additional file 1: S4), to characterise better the different dimensions of their functional niche (Arnan et al. 2014). The traits were obtained from databases present in the available literature (Seifert 2007; Arnan et al. 2012, 2014, 2017; Retana et al. 2015; Scupola 2018; Boet et al. 2020) and personal observations (see Table 2 and Additional file 1 for full details). In addition to the trait-based approach, we followed the functional group approach to reduce the complexity of ant taxonomy further. Ants were then classified following a global model of ant community dynamics, based on functional groups in relation to environmental stress (factors limiting ant productivity) and disturbance (factors removing ant biomass), proposed by Andersen (1995) for Australian ant communities: Subordinate Camponotini (Cm), Hot-climate Specialists (HCS), Cold-climate Specialists (CCS), Cryptic Species (Cr), Opportunists (Op), and Generalised Myrmicinae (GM). Such a functional group scheme could be

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**Fig. 2** Identification pattern of the plant functional groups: **a** Forage type (according to Allen et al. 2011), **b** Raunkiaer life forms (according to Pignatti 2005), and **c** Plant functional groups

adapted to European ant assemblages and provide a good understanding of functional community structure and responses to land-use changes at a biogeographical scale.

For each plot, the number of species belonging to each qualitative trait and functional group and the average values of quantitative traits were computed.

### Statistical analyses
#### Plants and ants as indicators
Non-metric multidimensional scaling (NMDS) was performed to examine the variation in the plant and ant community composition at the species level, across sites and chronosequence stage. Bray–Curtis measure was used to obtain all similarity matrices of plant %SC (Wildi 2010). Jaccard similarity index was used for ant presence absence data, as it is most suitable for the similarity calculation based on sparse binary data (Sanders et al. 2003).

Three NMDS analyses on plant and ant functional groups and ant traits were performed to test the hypothesis that community composition (and thus the placement of points on the ordination) is lacking in systematic structure across all study areas. Bray–Curtis similarity matrices were used for ordination analyses of all functional group data. As ant trait data derived from qualitative and quantitative traits, the dissimilarity matrix was

computed with a Gower distance on standardised values (Pavoine et al. 2009). Distance matrices and NMDS were computed using '*vegdist*' and '*metaMDS*' functions, respectively, in Vegan R-package (Oksanen et al. 2019) of R ver. 3.6.0 (www.r-project.org).

Three Permutational Multivariate Analyses of Variance (PERMANOVA), each followed by multiple comparisons, were carried out based on 999 permutations using the 'adonis2' function in the Vegan R-package. PERMANOVAs were performed to test for differences among the three stages. Distance matrices and data transformation used in PERMANOVA were the same adopted in the NMDS of each functional group or trait. In addition, multiple comparisons with Bonferroni *p*-values correction were carried out with the 'pairwise.perm.manova' function of RVAideMemoire R-package (Hervè 2020).

#### Cross-taxon congruence
Three Mantel tests with 999 permutations and Pearson correlation analyses were carried out on dissimilarity matrices to ascertain the multivariate correlation between ants and plants in terms of composition and functionality. The first Mantel test aimed at explaining the dependence of ants on vascular plant species. Jaccard distance and Bray–Curtis distance were used to compute

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**Table 2** List and description of the ant traits used in this study to analyse the response of ant communities to pastoral land use abandonment

| Trait | Data type | Measure* | Unit | Description |
|---|---|---|---|---|
| Worker size (WS) | Quantitative | Continuous | mm | Distance from the tip of the mandibles to the tip of the gaster |
| Worker polymorphism (WP) | Quantitative | Continuous | mm/mm | Mean worker size divided by worker size range |
| Colony size (CS) | Quantitative | Continuous | ln-transformed | Number of workers per colony |
| Diet (D) | Qualitative | Ordinal | 1 | Generalist (Gen) |
| | | | 2 | Mainly liquid feeder (LF) |
| | | | 3 | Predator/liquid feeder (PLF) |
| | | | 4 | Strictly predator (P) |
| | | | 5 | Seed harvester (SH) |
| Behavioural dominance (BD) | Qualitative | Binary | 1 | Dominant (Dom) |
| | | | 2 | Subordinate (Sub) |
| Diurnality (Di) | Qualitative | Binary | 1 | Not strictly Diurnal (nD) |
| | | | 2 | Strictly Diurnal (D) |
| Foraging strategy (FS) | Qualitative | Ordinal | 1 | Strictly group (FSG) |
| | | | 2 | Strictly collective (FSC) |
| | | | 3 | Both group and collective (FSGC) |
| | | | 4 | Strictly individual (FSI) |
| Number of nests per colony (nN) | Qualitative | Ordinal | 1 | Monodomy (Md) |
| | | | 2 | Both monodomy and polydomy (MPd) |
| | | | 3 | Polydomy (Pd) |
| Number of queens (nQ) | Qualitative | Ordinal | 1 | Monogyny (Mg) |
| | | | 2 | Both monogyny and polygyny (MPg) |
| | | | 3 | Polygyny (Pg) |
| Colony foundation (CF) | Qualitative | Ordinal | 1 | Dependent (Fd) |
| | | | 2 | Both dependent and independent (Fdi) |
| | | | 3 | Independent (Fi) |

*These traits can be continuous, ordinal or binary, and the data are treated differently before all multivariate analyses

the ant and vascular plants dissimilarity matrices, respectively. The second aimed at finding the relationship between ant traits and plant functional groups. As ant data derived from both qualitative and quantitative traits, the dissimilarity matrix was computed with a Gower distance on standardised values (i.e. the sum within each survey sum up to 1). The dissimilarity matrix for plant functional groups was calculated with Bray–Curtis distance. The third was carried out to test the dependence of ant functional groups on plant functional groups. Both dissimilarity matrices were computed with Bray–Curtis distance. Mantel tests were carried out using the '*mantel*' function in Vegan R-package (Oksanen et al. 2019).

## Results
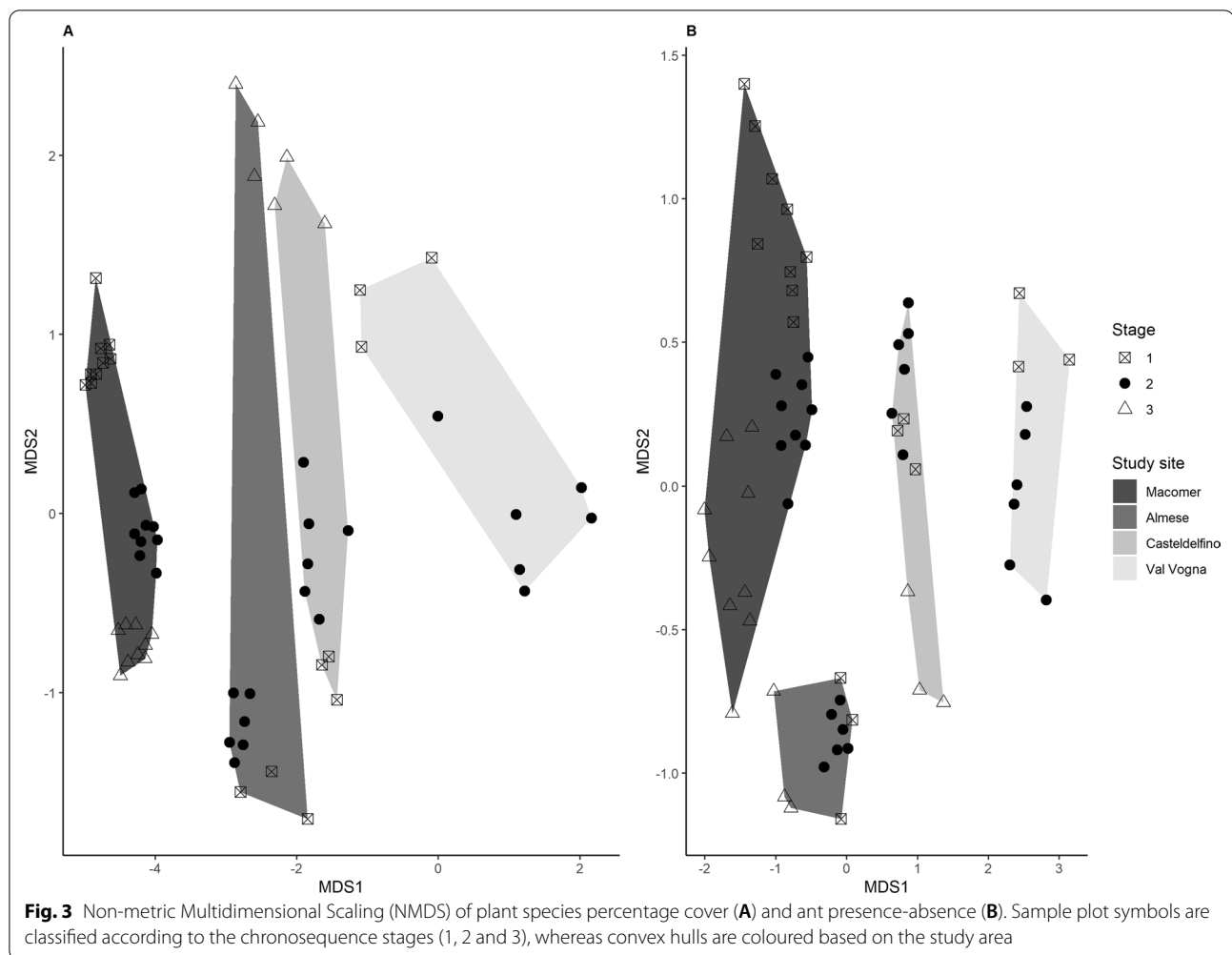### Plants and ants as indicators
Across the four study areas, 417 plant species (Additional file 1: S5) and 50 ant species (Additional file 1: S4) were found. NMDS provided a good ordination of plant and ant assemblages at the species level, as confirmed by low-stress values (0.14 and 0.10, respectively) (Fig. 3).

The four study sites were ordered and well separated along a biogeographic gradient (i.e. MDS1 axis), from the Mediterranean to Alpine. The three stages were well separated within the convex hull characterising each study site (i.e. along the MDS2 axis) from a taxonomic point of view.

The NMDS of plant functional groups proficiently discriminated amongst the three stages, and we also achieved consistent results when considering ant traits and functional groups (stressplot: 0.15, 0.21, and 0.18, respectively) (Fig. 4).

Furthermore, the PERMANOVA results confirmed the NMDS: the pairwise comparisons indicated significant differences amongst the three stages for both taxonomic groups, except for ant functional groups between stage 1 and stage 2 ($p$-value = 0.08) (Table 3).

Hemicryptophytes (grasses, legumes, and other dicotyledons) and Therophytes (both grasses and legumes) were mainly associated with stage 1 (Fig. 4A). Hemicryptophytes (both grasses and sedges) were associated with stage 2 as well, but a clear correspondence of

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**Fig. 3** Non-metric Multidimensional Scaling (NMDS) of plant species percentage cover (**A**) and ant presence-absence (**B**). Sample plot symbols are classified according to the chronosequence stages (1, 2 and 3), whereas convex hulls are coloured based on the study area

Nanophanerophytes (other dicotyledons) was also evident. Phanerophytes were strongly associated with stage 3.

The discrimination of the three stages by ants, both in terms of traits and functional groups, fairly reflected vegetation patterns. Indeed, the sequence of the three

stages, from 1 to 3, detectable through the convex hull centroids in the NMDS of vegetation, was observable in the NMDS plots of ant traits and functional groups as well (Fig. 4B). At the level of traits and functional groups for ants, data groupings were fairly well distinguishable

(See figure on next page.)

**Fig. 4** NMDS of plant functional groups (**A**), ant traits (**B**), and ant functional groups (**C**). Convex hulls and centroids of the distribution of grouped data Labels codes (centred on scores): **A** Grass_G: Grasses Geophytes; Grass_H: Grasses Hemicryptophytes; Grass_T: Grasses Therophyte; Gymno_P: Gymnosperm Phanerophytes; Legume_CH: Legumes Chamaephyte; Legume_H: Legumes Hemicryptophyte; Legume_P: Legumes Phanerophyte; Legume_T: Legumes Therophyte; Oth.dycot_CH: Other Dicotyledons Chamaephyte; Oth.dycot_G: Other Dicotyledons Geophyte; Oth.dycot_H: Other Dicotyledons Hemicryptophyte; Oth.dycot_NP: Other Dicotyledons Nanophanerophyte; Oth.dycot_P: Other Dicotyledons Phanerophyte; Oth.dycot_T: Other Dicotyledons Therophyte; Oth.monocot_G: Other Monocotyledons Geophyte; Oth.monocot_H: Other Monocotyledons Hemicryptophyte; Oth.monocot_T: Other Monocotyledons Therophyte; Pterid_CH: Pteridophytes Chamaephyte; Pterid_G: Pteridophytes Geophyte; Pterid_H: Pteridophytes Hemicryptophyte; Sedge_G: Sedges Geophyte; Sedge_H: Sedges Hemicryptophyte. **B** D: diurnal; nD: not strictly diurnal; FSG: strictly group foraging strategy; FSC: strictly collective foraging strategy; FSGC: both group and collective foraging strategy; FSI: strictly individual foraging strategy; Mg: monogyny; MPg: both monogyny and polygyny; Pg: polygyny; Md: monodomous; MPd: monodomous and polydomous; Pd: polydomous; Fd: dependent; Fdi: both dependent and independent; Fi: independent; Sub: subordinate; Dom: dominant; CS: colony size; WS: worker size; WP: worker polymorphism; Gen: generalist; LF: mainly liquid feeder; PLF: predators/liquid feeder; P: strictly predator; SH: seed harvester. **C** Op: opportunists; Cr: cryptic species; Cm: subordinate camponotini; GM: generalised myrmicinae; CCS: cold climate specialists; HCS: hot climate specialists
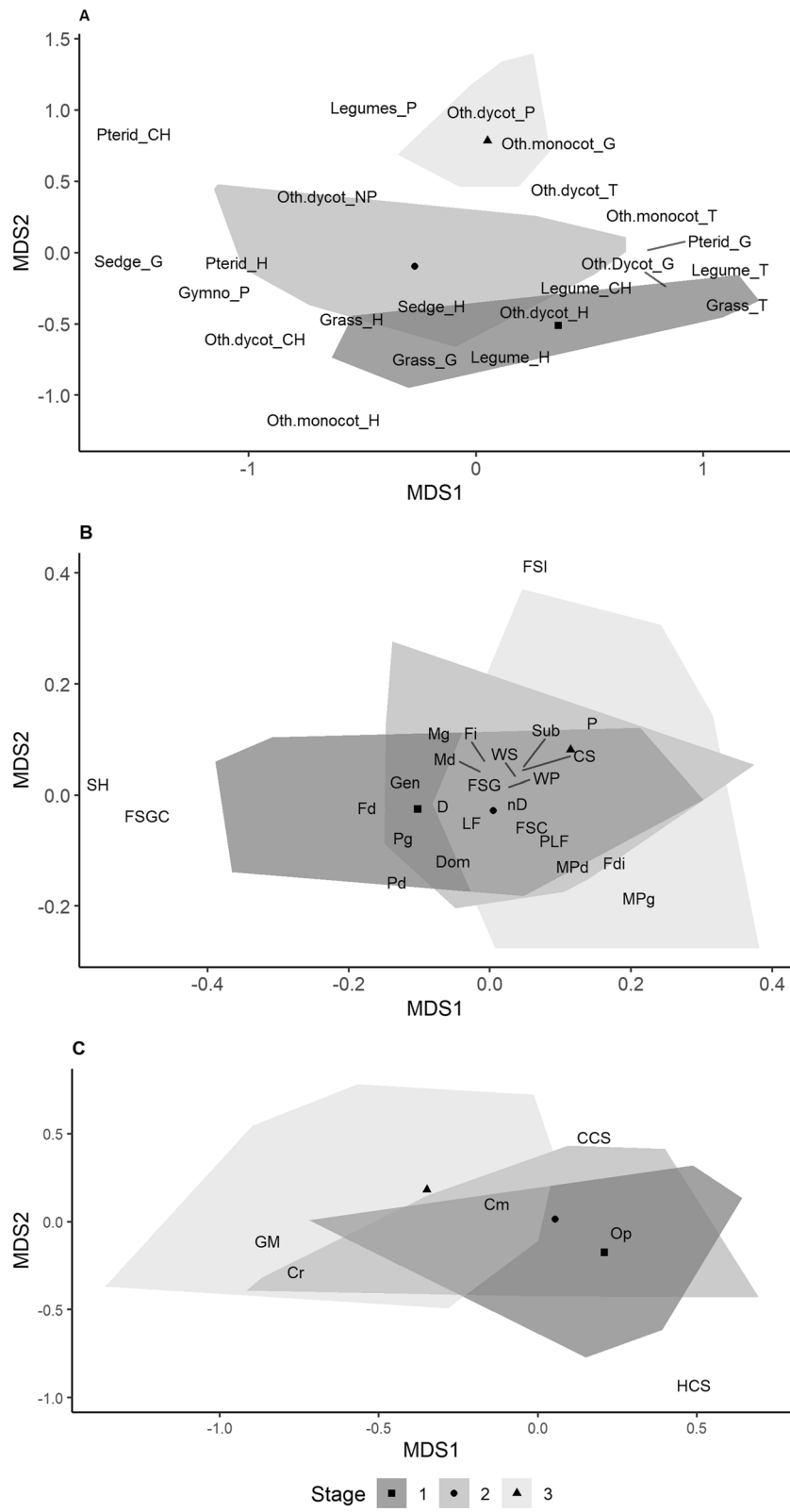
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**Fig. 4**  (See legend on previous page.)

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**Table 3** Results of PERMANOVA and pairwise comparisons with Bonferroni *P*-value adjustments on the three stages based on plant functional groups, ant traits, and ant functional groups, respectively

| | Df | SumOfSqs | $R^2$ | F | Pr (>F) | Stage* | | |
|---|---|---|---|---|---|---|---|---|
| | | | | | | 1 | 2 | 3 |
| Plant functional groups | 2 | 4.97 | 0.3 | 15 | *** | a | b | c |
| Ant traits | 2 | 0.34 | 0.2 | 5.9 | *** | a | b | c |
| Ant functional groups | 2 | 1.29 | 0.2 | 6.2 | *** | a | a | b |

* Data within a row followed by the same letter do not differ at $P \geq 0.05$

within each phase, although the positions of plots in the multivariate space were partially overlapped. Stage 1 was characterised by seed harvester ants with a group and collective foraging strategy. Conversely, the woodlands of stage 3 harboured above all species with an individual foraging strategy. NMDS did not separate stages 1 and 3 from stage 2, which was characterised by an intermediate combination of ant traits. In terms of ant functional groups, the NMDS results showed a distribution of all sampling units similar to that obtained from the trait data (Fig. 4C). Cold-climate Specialists increased from stage 1 to 3, whereas Hot-climate Specialists followed the opposite trend. Stage 2 differed from stage 1 mainly for a higher contribution of Cold Climate Specialists and less importance of Hot Climate Specialists. Stage 3 was characterised by the absence of Hot Climate Specialists and the higher relative contribution of Cryptic Species.

### Cross-taxon congruence
In plants and ants, the patterns of species composition revealed by NMDS were characterised by a gradual change along the ordination axes from secondary grasslands over woodlands, i.e. across the chronosequence stages following the pastoral land-use abandonment. The comparison of community similarity matrices performed using the overall dataset showed a strong and significant relationship between the two taxa at the species level (Mantel $r = 0.75$, $p < 0.001$). However, such a relationship between community structures was moderate at the functional level. Mantel test performed on similarity matrices obtained from ant traits and plant functional groups showed moderate relationships between the two taxa (Mantel $r = 0.36$, $p < 0.001$). A direct correspondence between ants and vascular plants was also confirmed at the functional group level, although the cross-taxon congruence was weaker (Mantel $r = 0.25$, $p < 0.001$).

### Discussion
#### Plants and ants as indicators
At the species level, plant and ant communities showed a consistent pattern related to the biogeographic region.

Stage 1 was the expression of secondary grasslands with a dominance of herbaceous species maintained by grazing livestock (Kahmen et al. 2002; Diaz et al. 2007). Secondary grasslands showed a strong differentiation, particularly at the opposite biogeographic positions, with different plant species: *Dasypyrum villosum* and *Avena barbata* in the Mediterranean site and *Festuca rubra* subsp. *commutata* and *Poa alpina* in the Alpine area above the treeline. At the two intermediate sites, species of secondary grasslands were mainly from the *Festuco-Brometea* class (Ciaschetti et al. 2020). The dynamic processes of grassland encroachment (stage 2) led to different communities depending on the biogeographical region of location (Bagella and Caria 2011). We found *Pteridium aquilinum* subsp. *aquilinum* in the Mediterranean, *Rubus ulmifolius* in the Continental, *Prunus spinosa* in the Alpine areas below the tree line and *Rhododendron ferrugineum* above the tree line. Woodlands vegetation (stage 3) was characterised by a floristic composition gradually more mesophilous (e.g. from *Quercus ichnusae* to *Fagus sylvatica*).

The ant communities in grasslands (stage 1) were typical of open habitats (Seifert 2007; Lentini and Verdinelli 2012; Scupola 2018; Verdinelli et al. 2017). In the Mediterranean region *Tapinoma simrothi*, *Messor ibericus*, *Aphaenogaster spinosa* commonly occurred in open grasslands, whereas in the Continental region *Pheidole pallidula* and other omnivorous species were frequent. In the Alpine regions, the community was represented by species seeking food both in the herbaceous and arboreal layers (Seifert 2007) and that were also well adapted to mountain area grasslands (Scupola 2018), with *Lasius alienus* and *Formica fusca* below the tree line and the boreal *Formica lemani*, *Myrmica sulcinodis* and *Manica rubida* above the tree line. At the stage 2 within the Alpine region, temporary parasitic and/or dulotic species (e.g. *F. exsecta* and *F. lugubris*) were sampled. Species commonly found under the trees or in shaded habitats of stage 3, such as *Aphaenogaster ichnusa* and *Myrmecina graminicola*, were shared with stage 2 as probably favoured by the abundance of shrubs and tall grasses (Verdinelli et al. 2017; AntWiki 2021).

In the Mediterranean area, annual legumes and grasses were dominant, as annual species are more tolerant to dry environments due to their fast growth rates and early and prolific seed set (Grime 1974). In Continental and Alpine areas Hemicryptophytes (mainly legumes, grasses, and sedges) are more abundant (Körner 2003) and grazing favoured their persistence (Illa et al. 2006). Stage 2 was defined by plant species typical of an early abandonment process, including tall and/or woody species (Pykälä 2005), which characterise the natural dynamic processes to dwarf shrub- and tree-dominated communities (Kesting et al. 2009). In the Mediterranean site we found tall Pteridophyte Hemicryptophyte species. Instead, in Continental and Alpine sites we found Nanophanerophyte dicotyledons. Stage 3 was entirely separated from stage 1 and stage 2, as the dominant species were Phanerophytes. Indeed, trees were sporadic in stages 1 and 2 as Phanerophytes are generally less frequent in grazing systems (Illa et al. 2006; Komac et al. 2013).

Also, ant traits and functional groups were good indicators of the time stages. Changes in ground cover may be important in determining the number of species able to use disturbed environments (Andersen 2019; Carvalho et al. 2020). These changes can have wide-ranging ecosystem effects given the role of ants as ecosystem engineers and their impact on many ecosystem functions (Folgarait 1998). The direct trophic relationship between ants and plants was clear in stage 1. Indeed, the seed diet, the collective foraging strategy, and other traits are associated with open habitats (Retana et al. 2015). Hot-climate Specialists include thermophilic taxa and specialist seed harvesters (Morton and Davidson 1988), whose occurrence was likely due to the combination of soil type and vegetation cover, which are the main drivers of ant assemblages (Bestelmeyer and Wiens 2001; Ríos-Casanova et al. 2006). Shrub-encroached grasslands offer moderate soil surface temperatures and substrate for potential prey and liquid food (i.e. extrafloral nectar and/or honeydew). These conditions favoured the Cold-climate Specialists and Cryptic Species (small to minute species, predominantly myrmicines and ponerines, that nest and forage primarily within soil, litter, and rotting logs), as a result of the decreasing insolation and increasing moisture (Arnan et al. 2012). The similarities between ant and plant communities' successional pathways are also remarkable in stage 3. Cold-climate Specialists and Cryptic Species increased their relative frequency in woodlands, where the thermal influence of canopy cover is stronger, and the insolation at ground level is minimal (Andersen 1995, 1997; Zina et al. 2021).

**Cross-taxon congruence**

Even though the plant and ant community composition differed among sites, the two groups responded to pastoral land-use abandonment in a similar way, both at taxonomic and functional levels. This finding was coherent with the general principle that cross-taxon congruence is strengthened at a large scale (Westgate et al. 2014). Although climatic or biogeographic gradients generally favour a conformity of species numbers at large spatial scales, the strong congruence of community similarities between ants and plants was an interesting outcome of the present study. The impact of grazing abandonment on biodiversity has been investigated extensively in different ecosystems worldwide, but the effects on ants and plants have been usually treated separately. In Mediterranean grasslands, past evidence suggests that grazing abandonment harms biodiversity, and this view is mainly based on studies focused on vegetation (Peco et al. 2005, 2006). Mountain grazing abandonment in alpine areas can promote the establishment of vegetation characterised by few species and negatively affect biodiversity (Cislaghi et al. 2019). However, grazing involves different trophic levels (Filazzola et al. 2020), organisms and ecosystems (Maghniaa et al. 2017; Mannu et al. 2018, 2020), and the impact of grazing on biodiversity can be negative or positive. For example, grazing decreased the ant species richness in American and Australian rangelands (Woinarski et al. 2002; Boulton et al. 2005). In temperate rangelands, livestock grazing maintained grassland structure by suppressing woody encroachment and increased ant species richness (Schmidt et al. 2012). In Mediterranean grasslands, grazing abandonment increased the functional and species ant diversity (Azcárate and Peco 2012). In our study, we observed that ant and vascular plant community composition varied in a similar way in response to pastoral land-use abandonment. According to Radnan and Eldridge (2017), grazing in secondary grasslands favoured Hot Climate Specialists. However, the same authors showed that grazing had stronger effects on ants than any increase in shrub cover, as ant and plant communities can respond to pastoral land abandonment in an idiosyncratic way (Német et al. 2016). Although plants are considered poor surrogates of invertebrate biodiversity (Andersen and Majer 2004), our result shows that ants and plants can provide a congruent representation of biodiversity. This finding confirms what has been reported in recent studies involving plant communities, ant communities and other arthropods (Ford et al. 2012; Corcos et al. 2021; Zina et al. 2021). Ant communities might be classified according to structural attributes that parallel those adopted in vegetation science (Andersen 1995), and used as surrogates in biodiversity studies. However, the moderate level of cross-taxon congruence we found at the level of functional groups suggests the need for further investigations

to develop new and comprehensive ant metrics suitable for pastoral mountain areas.

## Conclusions

Our attempt to compare the community pattern of plants and ants in mountain areas of different biogeographic regions in response to the abandonment of pastoral land use provided encouraging results. Pastoral land use is one of the main driving forces that caused a change of species composition from secondary grasslands to woodlands in the two taxa: the abandonment promoted the woody species colonisation and the conversion of the original grassland ant community. Cross-taxa relationships confirmed this result. Although we did not test congruency within each chronosequence stage or biogeographic region, the analyses of the entire dataset showed that ant communities mirrored the plant species and functional groups at taxonomic and functional levels. The functional groups explain a good proportion of trait variation among species. They allow going beyond the taxonomic barriers and can be a valuable tool in cost-effective ecological surveys. Although the cross-taxon congruence was moderate at the functional group level, the results underline the reliability of ants as bioindicators of land changes and ecosystem functioning. This result is important because it could greatly facilitate biodiversity monitoring and conservation. Due to their role in food webs and ecosystem functioning, ants can provide a more fine-grained and dynamic view of ecosystems than plants. An in-depth study of the main drivers of ant community composition would certainly be a notable improvement in understanding how their structure and function vary in response to land use. However, simplified ant monitoring systems should be developed to meet the needs of land managers. Finally, our findings indicate that the functional group approach and the reduction of the taxonomic complexity could contribute to developing predictive models to detect early environmental changes and biodiversity loss in mountain habitats.

## Abbreviations

%SC: Species percentage cover; Grass_G: Grasses Geophytes; Grass_H: Grasses Hemicryptophytes; Grass_T: Grasses Therophyte; Gymno_P: Gymnosperm Phanerophytes; Legume_CH: Legumes Chamaephyte; Legume_H: Legumes Hemicryptophyte; Legume_P: Legumes Phanerophyte; Legume_T: Legumes Therophyte; Oth.dycot_CH: Other Dicotyledons Chamaephyte; Oth.dycot_G: Other Dicotyledons Geophyte; Oth.dycot_H: Other Dicotyledons Hemicryptophyte; Oth.dycot_NP: Other Dicotyledons Nanophanerophyte; Oth.dycot_P: Other Dicotyledons Phanerophyte; Oth.dycot_T: Other Dicotyledons Therophyte; Oth.monocot_G: Other Monocotyledons Geophyte; Oth.monocot_H: Other Monocotyledons Hemicryptophyte; Oth.monocot_T: Other Monocotyledons Therophyte; Pterid_CH: Pteridophytes Chamaephyte; Pterid_G: Pteridophytes Geophyte; Pterid_H: Pteridophytes Hemicryptophyte; Sedge_G: Sedges Geophyte; Sedge_H: Sedges Hemicryptophyte; D: Diurnal; nD: Not strictly Diurnal; FSG: Strictly group foraging strategy; FSC: Strictly collective foraging strategy; FSGC: Both group and collective foraging strategy; FSI: Strictly individual foraging strategy; Mg: Monogyny; MPg: Both monogyny and polygyny; Pg: Polygyny; Md: Monodomous; MPd: Monodomous and polydomous; Pd: Polydomous; Fd: Dependent; Fdi: Both dependent and independent; Fi: Independent; Sub: Subordinate; Dom: Dominant; CS: Colony size; WS: Worker size; WP: Worker polymorphism; Gen: Generalist; LF: Mainly liquid feeder; PLF: Predators/liquid feeder; P: Strictly predator; SH: Seed harvester; Op: Opportunists; Cr: Cryptic species; Cm: Subordinate camponotini; GM: Generalised myrmicinae; CCS: Cold climate specialists; HCS: Hot climate specialists.

## Supplementary Information

The online version contains supplementary material available at https://doi.org/10.1186/s13717-022-00379-9.

> **Additional file 1. Appendix S1.** Schematic representation of surveys on vascular plants through the vertical point-quadrat method along four transects corresponding to four perpendicular radii of a circular plot. **Appendix S2.** Scheme of ant sampling design: four pitfall traps, 10 m distant from each other, were sunk into the soil and centred on each vegetation plot. **Appendix S3.** Ant dichotomous key reference list. **Appendix S4.** Ant species collected during the survey per each stage. Ant functional groups (FG): Subordinate Camponotini (Cm), Hot-climate Specialists (HCS), Cold-climate Specialists (CCS), Cryptic Species (Cr), Opportunists (Op), Specialised Predators (SP), and Generalised Myrmicinae (GM). Ant traits: Worker size (WS), Worker polymorphism (WP), Colony size (CS), Diet (D), Behavioural dominance (BD), Diurnality (Di), Foraging strategy (FS), Number of nests per colony (nN), Number of queens (nQ), Colony foundation (CF). For ant traits in species for which no data are reported in the literature, ten workers per species were randomly selected and measured for determining the WS; the mean thereof was used as a value for each species. **Appendix S5.** List of plant species found across the study sites associated with their Raunkiaer plant life form (Pignatti 2005), Forage type (Allen et al. 2011), Plant functional group, and the occurrence in the stages of the chronosequence. The latter is the combination of the life form and the forage type. Plant species nomenclature follows Pignatti et al. (2017).

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## Declarations

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