The final publication is available at

https://doi.org/10.1111/avsc.12507

Additional Information

1   **Vegetation change over a period of 46 years in a Mediterranean mountain massif (Penyagolosa,**
2   **Spain).**

3   **Running title: Mediterranean vegetation change over time**

4

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1   **Abstract**

2   <u>Questions</u>

3   The Mediterranean mountain massifs are biodiversity hotspots threatened by climate change and
4   land use transformations among other factors. Did vegetation composition and alpha- and beta-
5   diversities change in mid and high-elevation Mediterranean ecosystems over the last 46 years? Can
6   these changes be explained by climate change or land use?

7   <u>Location</u>

8   Medium and high altitudes of the Penyagolosa Massif, Castellón, Eastern Spain.

9   <u>Methods</u>

10   In 2014, we re-surveyed 92 vegetation plots sampled in 1968, belonging to nine plant communities
11   distributed on basic and acid soils. We performed estimates of alpha- and beta-diversity,
12   multidimensional ordination of species composition, ecological characterization of species and non-
13   parametric tests to identify vegetation change over time.

14   <u>Results</u>

15   We observed different patterns of vegetation change depending on the plant community; an
16   increase in alpha-diversity, especially in high-altitude habitats; and a homogenisation of species
17   composition among plant communities. Seral communities and forests increased particularly in
18   locations on basic soils that used to be occupied by pastures and communities of degraded
19   successional stages. Higher Ellenberg indicator values of temperature and light, and loss of
20   temperate taxa, which are usually rare in the region, were found in the climax forest of high altitudes
21   and some acidophilous communities. However, altitudinal shifts of species distributions were
22   detected only in 8% of plant species, both upwards and downwards. An increase of nitrophily at
23   medium altitudes was also observed.

24   <u>Conclusions</u>

25   The results suggested that land use change related with abandonment of agro-sylvo-pastoral
26   systems was the major driving force of vegetation dynamics in most of the seral plant communities,
27   while thermophilisation was more evident in the high-altitude climax forest.

28

29   <u>Keywords:</u> Biodiversity; Climate change; Ecological indicator values; Land use; Long-term re-
30   surveys; Mediterranean mountain massif; Medium altitude; Plant community.

1 **Introduction**

2 The Mediterranean biome occupies only 2% of the world's emerged land, but contains 20% of the
3 known plant species in the world (Médail and Quézel, 1997). The Mediterranean Basin is considered
4 a plant biodiversity hotspot with a high proportion of endemic species (Médail and Myers, 2004).
5 However, biodiversity and ecosystem functioning are threatened by direct and indirect human
6 impacts. The Mediterranean Basin is profoundly altered as it has been inhabited by people of many
7 cultures for millennia. As a result, it is estimated that only 4.7% of its primary vegetation remains
8 unaltered (Geri *et al.*, 2010). The majority of vegetation has drastically changed in relation to human
9 forest management (i.e. deforestation for agriculture, grazing, and charcoal and firewood
10 production), which has led to soil erosion (Valladares, 2007). More recently, since the early 19th
11 century, the socio-economic changes have led to the rural exodus and abandonment of traditional
12 agro-sylvo-pastoral systems. One of the resulting effects is the extension of areas of forests and
13 seral communities following secondary successions. As a result, fuel load has increased, and
14 ecosystems and flora have become more uniform. In contrast, communities with reduced
15 vegetation cover have decreased, particularly pastures, which are some of the richest communities
16 in Mediterranean ecosystems (Médail and Quézel, 1997; Valladares, 2007).

17 In addition to these land use transformations, other drivers of long-term vegetation changes, such
18 as climate change or biological invasions, are acting in the Mediterranean Region with hardly
19 distinguishable effects (Clavero *et al.*, 2011). Global warming, which is predicted to alter
20 Mediterranean ecosystems in a way that is without precedent during the past 10 000 years (Guiot
21 and Cramer, 2016), may especially affect relic communities of high and cool mountain refugia, rich
22 in endemic species of a glacial or temperate origin (Ruiz-Labourdette *et al.*, 2012). Reduced
23 precipitation and less snow cover are also forecasted, which may affect hydrological processes and
24 river regimes (Nogués-Bravo *et al.*, 2008). Consequently, fire frequency is predicted to increase
25 (Mouillot *et al.*, 2002). In this context, the reduction in abundance of those species distributed in
26 cooler areas, followed by an increase in xerophilous and thermophilic species, is likely (Peñuelas,
27 2018). Furthermore, intensified agriculture, fertilizer production and fossil fuel combustion have
28 increased nitrogen deposition in ecosystems (Matson *et al.*, 2002), which may cause soil
29 acidification, and shifts in the composition of plants, soil microbes and fauna (Ochoa-Hueso *et al.*,
30 2011).

31 These different components of global change could have had interacting effects on biological
32 processes and biodiversity, with a magnitude that may vary among systems, biomes, and spatial and
33 temporal scales. It has been shown that land use changes can reverse, hide or exacerbate climate
34 change effects (Clavero *et al.*, 2011). All these multiple factors and their interrelations influence
35 species abundance and distribution, which can be used to monitor changes in biodiversity through
36 time (Magurran *et al.*, 2010).

37 In the Mediterranean area, most studies that have dealt with vegetation shifts over long time
38 periods have been based on comparisons made of aerial photographs and maps, which have been
39 available since the mid-20th century (Sanz-Elorza *et al.*, 2003; Geri *et al.*, 2010; Malavasi *et al.*, 2018).

1 These studies allow a detailed analysis of vegetation type migrations over time based on landscape
2 structure and predominant plant species. Nevertheless, floristic information about the past plant
3 communities, which is needed for in-depth analyses of the rarer species that may be affected by
4 both climate change and land use transformations, is mostly lacking.

5 Delimiting and using permanent plots is one of the most reliable methods to incorporate detailed
6 floristic composition into long-term changes of plant communities (Hédl *et al.*, 2017). However, only
7 a few permanent plots can be found in different regions and they generally span few decades.
8 Another approach consists in re-surveying vegetation plots from previous studies based on detailed
9 historical *relevés* (Magurran *et al.*, 2010). Although several issues have been raised about using this
10 methodology, such as relocation, observer, and seasonality bias, their effects can be minimized by
11 following the protocols used for sampling old plots as closely as possible (Chytrý *et al.*, 2014; Kapfer
12 *et al.*, 2017).

13 Many of these re-surveys have been performed in temperate areas of Europe, and climate change
14 has been identified as the main factor in vegetation shifts in not only alpine or subalpine habitats,
15 but also within lower altitudinal ranges (i.e. Lenoir *et al.*, 2010). However, in Mediterranean areas,
16 there are very few permanent plots available for vegetation comparison purposes and they usually
17 cover less than two decades (i.e. Fernández and Molero, 2013), and long-term comparisons made
18 from historical databases are scarce (i.e. Evangelista *et al.*, 2016; Frate *et al.*, 2018). These
19 comparative studies have focused mostly on summits at high altitudes, above 1900 m, where alpine
20 vegetation develops (Fernández and Molero, 2013; Jiménez-Alfaro *et al.*, 2014; Evangelista *et al.*,
21 2016). Thus, very few studies have dealt with Mediterranean low mountain massifs, which used to
22 be isolated and strongly affected by anthropogenic activities since ancient times, and which
23 constitute temperate-submediterranean microclimatic islands.

24 In order to better understand vegetation change in Mediterranean mountain massifs, we re-
25 surveyed a large data set that describes the medium- and high-altitude vegetation of the
26 Penyagolosa Massif (Spain), collected by Vigo in 1968 (Vigo, 1968). Nine vegetation communities
27 were included, developing on various soil types, different altitudes, and distinct successional stages.
28 Floristic changes were assessed in relation to environmental conditions. The following questions
29 were addressed: (i) has the vegetation changed over the past 46 years in this Mediterranean massif?
30 (ii) did the magnitude and patterns of vegetation changes differ between plant communities?, and
31 (iii) are these changes more related to land use transformations or to climate change?

32

33 **Materials and Methods**

34 <u>Study area</u>

35 The Penyagolosa Massif is located in E Spain (Castellón), less than 50 km from the Mediterranean
36 Sea (Figure 1). The studied area includes a plain (from now on "the plain") of 9x2 km in the general
37 direction northeast by southwest, situated at 1100-1200 m a.s.l. Most of the agricultural activity in

the area occurs within this plain. The plain is surrounded by different mountains, and the highest peak is found in the south (Penyagolosa peak, 1814 m a.s.l., from now on "the peak"). The soils originated from calcareous parent rocks. However, some siliceous acid sediments are present on the mountains between calcareous layers. As a result of this geological configuration, a high diversity of habitats can be found in a relatively narrow area depending on altitude, orientation, slope, and soil type, ranging from sub-Mediterranean forests on brown soils to Mediterranean xerophilous plant communities. This high biodiversity justifies the consideration of the Massif as a Mediterranean hotspot, with an endemism rate of 10-20% (Médail and Quézel, 1997). It was declared a "Natural Park", which is the highest level of habitat conservation at a regional scale, in 2006.

In relation to climate, the Penyagolosa Massif is included in the Temperate bioclimate submediterranean variant (Miró *et al.*, 2016). Based on detailed climate change studies in the Valencia region, Miró *et al.* (2015) recorded, in the Penyagolosa Massif and in the 1948-2011 period, a warming rate of 1.1ºC for maximum temperature, 0.7ºC and 0.5ºC in the peak and the plain respectively for minimum temperature, and 0.9ºC and 0.7ºC in the peak and the plain respectively for mean temperature. Miró *et al.* (2016) also studied changes on the thermicity index $It=10(T+m+M)$ (T is the mean temperature, and m and M are the means of minimum and maximum temperatures of the coldest month respectively; Rivas-Martínez *et al.*, 2017). During the same period, the thermicity index has increased by 20 units in the peak and by 11 units in the plain. Consequently, in the Penyagolosa Massif, the area with a Lower Supratemperate thermotypic horizon has diminished by 60% and the area with Upper Supratemperate has almost disappeared (75%), while the area of the Upper Mesotemperate has increased (Miró *et al.*, 2016). Furthermore, Millán *et al.* (2005) recorded a reduction in the overall precipitation in the area.

During most of the 20th century, the land use of the Penyagolosa Massif developed around the "Mas" (big country house). Agriculture was carried out in small plots located mainly on the plain, but also on terraces. Stockbreeding (mostly sheep) was also an important activity. As a result, some forest areas were deforested to obtain summer and winter pasture fields. Forests were also used to extract lumber and firewood, especially from *Quercus* species (Roncero, 2005). However, in recent decades, most mountainous crop and pasture fields have been abandoned due to rural depopulation, and have been progressively colonised by *Quercus* and *Juniperus* species. In parallel to depopulation, afforestations with *Pinus* species and urbanisation around villages have increased. Although the number of forest fires has also increased since 1993 (first year with mapped data), there have been fewer than six forest fires in the Penyagolosa Natural Park, with a mean affected area of only 0.15 ha since then (Generalitat Valenciana, 2019).

Data set and re-sampling

The original data set included 110 phytosociological *relevés* performed on an area of about 100 m^2 at the medium (1100-1500 m) and high (1500-1800 m) altitudes of the Penyagolosa Massif by Vigo (1968). Not all the *relevés* performed in 1968 could be re-sampled because of inaccuracy of location data from the original plots. We also discarded plots in which vegetation suddenly and drastically

1 changed because of human activities (e.g. forest-breaks or plantation of logging forests). Finally, 92
2 re-sampled *relevés* belonging to nine associations, with at least five *relevés* in each association, were
3 selected (Figure 2). All the nomenclature was adapted following "The Plant List".

4 All the *relevés* were performed on 100 m^2 quasi-permanent plots. Re-location was possible from an
5 original 1:66 666 topographic map with 100 m contour lines and position and names of farm houses,
6 hills, ravines, fountains and other topographical features. Detailed descriptions of each plot, such as
7 altitude with a precision of 25 m, slope, aspect, place names, presence or distance to paths and farm
8 houses, and landscape photographs were also provided. Re-sampling was performed from May to
9 July in 2014. During both periods, the cover-abundance scale proposed by Braun-Blanquet (1964)
10 for estimating species proportions was used.

11 Data analysis

12 To quantify species composition change between 1968 and 2014, we performed three analyses:
13 compositional variability in terms of alpha- and beta-diversity; species composition change in
14 relation to their ecological indicator values and altitude; and "lost" and "new" species. Statistical
15 analyses were carried out using R (R Core Team, 2018) with RStudio (RStudio Team, 2016). The
16 "ggplot2" package (Warnes *et al.*, 2019) was used to create plots.

17 *Compositional variability between 1968 and 2014*

18 As the *relevés* were performed in quasi-permanent plots and there was some uncertainty in the
19 exact original plot area, the results of the analyses of the diversity of the species composition within
20 plant communities (alpha-diversity) have to be taken with caution. We calculated the Shannon-
21 Wiener index (*H*) (Shannon and Weaver, 1949) per plot using the "agricolae" R package (de
22 Mendiburu, 2019). We ran repeated-measures ANOVA to compare alpha-diversities in each plant
23 community between 1968 and 2014. To estimate beta-diversity within each community, Bray-Curtis
24 dissimilarity indices were calculated among *relevés* using species abundances. We then performed
25 a repeated-measures *t*-test to compare indices between 1968 and 2014. As a means to assess beta-
26 diversity considering all the *relevés* together (Anderson *et al.*, 2006), we computed the rate of
27 species composition homogenisation as a difference in multivariate homogeneity of dispersions
28 (variances) within all the samples from 1968 and those from 2014 (Anderson, 2006). To minimise
29 any bias due to different species numbers per sample, the Simpson index was used as a dissimilarity
30 measure. To establish possible significant differences in beta-diversity among years, the distances
31 of group members to the group centroid were subjected to ANOVA.

32 *Species composition change related to environmental variables*

33 As direct comparisons of climate parameters and nitrogen deposition were not possible because of
34 the lack of available comparable data between 1968 and 2014, we applied Ellenberg's indicator
35 system (Ellenberg *et al.*, 1992) to indirectly estimate differences in the environmental conditions to
36 each plant community between years. Ellenberg *et al.* (1992) ranked the vascular plant species of
37 Central Europe according to their occurrence optimum along key environmental niche axes. As most

1 of these indices did not fully fit into a Mediterranean climate, we used a modification of the
2 Ellenberg's plant classification established by Julve (1998-2019) and adapted for French flora, which
3 includes nearly 6000 species, of which nearly 4000 are Mediterranean and can be extrapolated to
4 North Italy and Spain (Tison *et al.*, 2014). Values were checked by the authors after examining the
5 ecological requirements of the species in Eastern Spain in the literature (De Bolòs and Vigo, 1984-
6 2001; Castroviejo, 1986-2012; López, 2006). The considered environmental axes followed a scale
7 from 1 to 9, including light (L, 1: hyper-sciophyte, 9: hyper-heliophyte); temperature (T, 1:
8 cryoromediterranean, 9: thermo-inframediterranean); continentality (C, 1: maritime, 9: hyper-
9 continental), atmospheric humidity (HA, 1: aero-xerophyte, 9: aero-hydrophyte); soil humidity (HE,
10 1: hyper-xerophyte, 9: seasonal amphibian plant); soil pH (R, 1: hyper-acidophyte, 9: hyper-
11 basophyte); soil nutrients (N, 1: hyper-oligotrophyte, 9: hyper-eutrophyte), soil texture (Tx, 1: clay,
12 9: slab), and soil organic matter (MO, 1: lithosol, 9: peat).

13 The effects of time on species composition were estimated firstly using the whole data set and then
14 separately for each plant community. The cover-abundance values of species were used to calculate
15 the Bray-Curtis dissimilarity index between the *relevés* from both study years. Based on these
16 dissimilarities, three-dimensional, non-metric multidimensional scaling (NMDS) was performed
17 using the function "metaMDS" of the "vegan" package (500 maximum iterations; 3 dimensions;
18 Oksanen *et al.*, 2019). Subsequently, the Ellenberg indicator values were fitted to the ordination
19 plot as vectors ("envfit" function). Also, to indirectly analyse the effects of time on environmental
20 conditions, we performed repeated-measures *t*-tests that compared mean Ellenberg values
21 between 1968 and 2014.

22 The significance of species composition change was tested by a non-parametric multivariate analysis
23 of variance (PERMANOVA), with 999 permutations and using the Bray-Curtis dissimilarity index
24 ("adonis" function). It is a permutational test that uses distance matrices of the species composition
25 of plots to find significant differences between years (Anderson, 2001).

26 To specifically analyse the potential effects of climate change in the Penyagolosa Massif that could
27 have occurred between 1968 and 2014, we studied the possible altitudinal migration of species. For
28 each species, altitude was recorded from the *relevés* where it was found, using a bin width of 25 m.
29 We only considered those species that were present in at least five *relevés* in each year (total of 170
30 species). Altitudes of the plots where each species was observed were weighted by their cover.
31 Weighted averages were then compared among years using weighted Student's *t*-test (Pasek *et al.*,
32 2018).

33 <u>"Lost" and "new" species</u>

34 We aimed to understand the biogeographical changes in the plant community composition between
35 1968 and 2014, and specifically if there have been gains or losses of rare vs. common species and
36 mediterranean vs. temperate species. We analysed the rarity on a regional scale and the chorology
37 of the "lost" and "new" species in each plant community, according to Mateo and Crespo (2009). A
38 species was considered "lost" when it was present in at least 25% of the *relevés* performed in 1968,
39 but was completely absent in 2014, and reciprocally for species considered "new". Rarity was

1　evaluated from 1 (very rare) to 5 (very abundant). The rarity values of the "lost" and "new" species
2　were compared by a Student's *t*-test (except in two communities that had less than four "lost"
3　species each). In relation to chorology, the species were grouped into three distribution areas: the
4　Eurosiberian (cold and temperate), the Mediterranean, and a wide range (Holarctic, sub-
5　cosmopolite and cosmopolite). A test of homogeneity, which compared the chorological origins of
6　"lost" and "new" species was performed by calculating a Pearson's chi-squared test.

7

8　**Results**

9　<u>Compositional variability between 1968 and 2014</u>

10　In the Penyagolosa Massif, species composition of the 92 relevés, independent of the community
11　they belong to, proved significantly to be more heterogeneous in the past than it is now, as indicated
12　by a longer mean distance to the group centroid in 1968 than in 2014 (ANOVA *p*-value<0.001)
13　(Figure 3). However, considering the plant communities one by one, the opposite occurred. Higher
14　values of beta-diversity among *relevés* within plant community were found in 2014 than in 1968,
15　and the differences were significant in all of them (repeated-measures *t*-test *p*-value<0.005) except
16　the forest communities *Deschampsio-Pinetum valentinum* (*p*-value=0.114) and *Violo-Quercetum*
17　*valentinae* (*p*-value=0.626) (Appendix S1). In summary, in the Penyagolosa Massif, results showed
18　that species composition of the *relevés* within community was more different in 2014 than in 1968,
19　but species composition of communities was more similar now than in the past, and that globally
20　there was a lower heterogeneity among *relevés* as a whole (higher homogenisation).

21　Parallel to this homogenisation, sampled vascular plant species number increased from 336 in 1968
22　to 373 in 2014 (Appendix S2). Alpha-diversity (*H*) gave no significant differences among years in any
23　studied plant community except in the two high-altitude communities (repeated-measures ANOVA
24　*p*-value=0.003 in *Pino-Juniperion sabinae* and 0.018 in *Poo-Festucetum hystricis*) and in *Saturejo-*
25　*Erinaceetum anthyllidis* (repeated-measures ANOVA *p*-value<0.001), where a significant increase in
26　alpha-diversity over time was noted (Appendix S3).

27　<u>Species composition change related to environmental variables</u>

28　PERMANOVA done with the whole data set showed significant differences in species composition
29　between 1968 and 2014 (*p*<0.005). However, NMDS analysis showed no clear patterns of
30　environmental shifts, suggesting more complex changes that may depend on plant community
31　(Figure 4). Consequently, different NMDS analyses were done in each plant community (Figure 5).
32　Plant species composition significantly changed in all communities, except in *Cephalanthero-*
33　*Quercetum pyrenaicae* (Appendix S4). Mean Ellenberg indices, used to track indirect environmental
34　conditions, also changed significantly between years depending on plant community (Appendix S5).

35

36

1

At the highest altitudes where only calcareous soils can be found, the forest *Pino-Juniperion sabinae* and the pasture *Poo-Festucetum hystricis* co-occurred. From 1968 to 2014, in both communities, the characteristic species have decreased their cover or even disappeared, while generalist species have increased. In *Pino-Juniperion sabinae*, the covers of *Juniperus sabina* (Ellenberg temperature index T=3) and *Pinus sylvestris* (T=3) dramatically reduced (from 75-100% of the area to less than 5% in most of the *relevés*). The more thermic *Pinus nigra* (T=6) and the cushion plant *Erinacea anthyllis* (T=2) have appeared instead (Appendix S6). According to the Ellenberg indices, both temperature and soil pH have increased, and soil organic matter content and texture have decreased. Conversely, in *Poo-Festucetum hystricis*, cushion plants (i.e. *Potentilla cinerea*, *Festuca hystrix*, and *Koeleria vallesiana*) have reduced their cover and been replaced with woody species, such as *Juniperus sabina*, *J. communis* and *Erinacea anthyllis* (Appendix S7). The Ellenberg indices of light and continentality have decreased, and that of soil nutrients has increased. We observed that the species compositions of both high-altitude communities were more similar in 2014 than in 1968 (Appendices S6 and S7). In particular, *Juniperus sabina*, *Pinus sylvestris*, and *Erinacea anthyllis* now have similar covers in both communities compared to 1968.

At medium altitudes and according to the Ellenberg indices, we observed an increase of nitrophily with time in all plant communities (Figure 5), which was significant in most of them (Appendix S5). Besides this common trait, different patterns of species composition change have occurred on basic and acid soils.

On acid soils, no significant species composition change was observed with time in the climax community *Cephalanthero-Quercetum pyrenaicae* (Appendix S8), although increased Ellenberg light index and decreased humidity indices were found. On the contrary, in the secondary *Pinus sylvestris* forests (*Deschampsio-Pinetum valentinum*), species composition significantly changed. The covers of *Pinus sylvestris* and *Quercus rotundifolia*, and those of deciduous *Malus sylvestris* and *Quercus faginea*, have increased since 1968 (Appendix S9). In contrast, the cover of some shrubs (i.e. *Calluna vulgaris* and *Erica scoparia*), and herbs (i.e. *Deschampsia flexuosa* and *Lathyrus linifolius*) have reduced. Along with these vegetation changes, Ellenberg index of organic matter decreased from 1968 to 2014. The more degraded successional stages corresponding to a shrub community (*Aveno-Callunetum*) and dense pastures (*Astragalo-Festucetum*) showed a loss of characteristic species and similar ecological change patterns with time. Ellenberg indices of light and soil pH increased, while organic matter index decreased. The characteristic species of *Aveno-Callunetum* were replaced with characteristic species of the more thermophilous phytosociological order *Lavanduletalia stoechidis* (i.e. *Erica arborea, Cistus populifolius, Thymus vulgaris*) (Appendix S10). In the pasture *Astragalo-Festucetum*, the loss of characteristic species was especially evident for *Nardo-Callunetea*, which indicates high humidity and high altitudes in the Mediterranean Region (Appendix S11). Pasture diversity has also diminished with time (i.e. Poaceae and *Trifolium* spp.).

On basic soils, changes in Ellenberg soil pH index suggested acidification over time in all plant communities except *Salvio-Aphyllanthetum monspeliensis*. In 1968, the climax forest was *Violo-*

1 *Quercetum valentinae*, characterised by the presence of *Quercus faginea*, *Pinus nigra* and other
2 eurosiberian taxa. Nowadays, while the *Q. faginea* cover has not changed, *Q. rotundifolia* and *P.*
3 *sylvestris* are more abundant, and the covers of some sciophytes have been reduced [i.e. *Anemone*
4 *hepatica* (Ellenberg light index L=4, Ellenberg atmospheric humidity HA=5), and *Aquilegia vulgaris*
5 (L=6, HA=5)]. Some xerophilous species have appeared instead [i.e. *Brachypodium retusum* (L=8,
6 HA=3) and *F. paniculata* (L=7, HA=3)] (Appendix S12). Ellenberg index of atmospheric humidity has
7 decreased and that of light has increased correspondingly. Ellenberg index of organic matter has
8 also increased with time. The seral shrubland *Salvio-Aphyllanthetum monspeliensis* developed on
9 deep soils, where the characteristic species *Helichtrotichon pratense* and *Aphyllanthes*
10 *monspeliensis*, and *Brachypodium phoenicoides* used to predominate in 1968. The cover of all three
11 species has decreased with time, while the presence and/or cover of some trees (*Pinus sylvestris*
12 and *Quercus rotundifolia*) has increased instead (Appendix S13). Accordingly, Ellenberg temperature
13 index has decreased and that of continentality has increased. The open shrub community *Saturejo-*
14 *Erinaceetum anthyllidis* developed on very disturbed calcareous soils and rocky ridges.
15 Characteristic species like *Erinacea anthyllis*, *Potentilla cinerea*, and *Festuca hystrix,* among others,
16 predominated. These species, with high covers in 1968, occupied less than 25% of the sampled area
17 in 2014. In contrast, *Quercus rotundifolia* and *Pinus sylvestris* are now the predominant species in
18 some *relevés* (Appendix S14). Also, some characteristic species of *Salvio-Aphyllanthetum*
19 *monspeliensis*, which is closer to the climax forest in the process of ecological succession (Figure 2),
20 have appeared or increased, suggesting soil restoration. Accordingly, Ellenberg indices of soil
21 humidity and organic matter have increased, while those of light index and continentality have
22 lowered with time.

23 In order to establish possible species migration as a result of global warming, the changes in
24 altitudes of 170 species were estimated. Weighted Student's *t*-test was significant only for 23
25 species (14% of the total studied species), of which 14 (8.2%) migrated from lower to higher
26 altitudes and nine (5.3%) migrated from higher to lower altitudes (Appendix S15; Figure 6). The
27 pattern of migration was related to the altitudinal range that a given species occupied in 1968. Most
28 of the species that developed on the highest altitudes (above 1350 m) in 1968 migrated downwards,
29 and those from medium altitudes (1100 – 1350 m) migrated mostly upwards. In contrast, we could
30 not find any pattern of migration related to chorological origin (i.e. Mediterranean or Temperate)
31 or plant community.

32   "Lost" and "new" species

33 For each plant community, the number of "lost" species (present in the first survey but absent in
34 the second) ranged from three to 16 (Table 1). A higher number of "new" species (absent in the first
35 survey and appearing in the second) were observed, ranging from six to 27. Only in three plant
36 communities (*Cephalanthero-Quercetum pyrenaicae*, *Astragalo-Festucetum* and *Aveno-*
37 *Callunetum*) were significant differences found. In the three communities, proportion of species that
38 were rare or very rare, as well as those that had a temperate chorological origin, was higher among
39 the "lost" species (82.4% of rare and 85.3% of temperate species) than among the "new" ones

1 (25.5% and 21.8% respectively). We found specifically 13 very rare and mostly temperate species:
2 eleven of them were "lost" whereas only two were "new" in 2014 (Appendix s16).

3

4 **Discussion**

5 Our results showed the existence of vegetation change in the Penyagolosa Massif from 1968 to
6 2014. In most Mediterranean mountains, climate change and land use transformations have been
7 identified as the main drivers of change (Bodin *et al.*, 2013; Pausas and Millán, 2019). In the
8 Penyagolosa Massif, a fast warming trend has been detected especially since 1980 (Miró *et al.*,
9 2016), and is considered as one of the main threats for the survival of the temperate taxa that
10 account for 14% of the total flora of Penyagolosa (Fabregat and López, 2011). In the present study,
11 we also found great land use transformations over time, which is likely the result of the loss of
12 stockbreeding and farming activities during the last decades. Following a secondary succession,
13 species of forests and seral communities have expanded in the high-altitude pastures, in the
14 degraded successional communities on basic soils, and in the acidophilous *Pinus* forest. The increase
15 in wildlands was also observed in aerial photographs and satellite images made in the Penyagolosa
16 Massif (Valera, 2017). The percentage of area used for pastures and agriculture was reduced by half
17 and that of forests doubled during the period 1956-2017 (65%, 18% and 17% respectively in 1956
18 and 33%, 8% and 59% in 2017 respectively). In addition to these progressive ecological successions,
19 some reforestations with *Pinus nigra* and plantations of *Pinus sylvestris* timber forests were made,
20 especially after 1940 (Pérez, 2003). The afforestation of crop areas and pastures due to the
21 abandonment of farming activities is a common phenomenon in Western Mediterranean, such as
22 Corsica (San Roman Sanz *et al.*, 2013), Central Apennines (Malavasi *et al.*, 2018), and Southern
23 France (Sirami *et al.*, 2010). In the Penyagolosa Massif, climate change and land use transformations
24 may be interacting in several ways, as will be discussed below.

25 Considering all the plant communities as a whole, in agreement with most of the studies performed
26 in Europe, we found vegetation homogenisation with time, which followed the general trend of
27 increasing human activities in plains and the natural reforestation of abandoned mountain areas
28 (Geri *et al.*, 2010). However, homogenisation among plant communities has also been observed in
29 alpine European summits where global warming is the main driver of change, as anthropogenic
30 activities have been negligible in recent decades (Cannone and Pignatti, 2014). Therefore, although
31 land use transformations may be the main cause of the vegetation uniformity, climate change as a
32 complementary cause cannot be ruled out. The increase in beta-diversity among *relevés* within plant
33 community could be due to the fact that most *relevés* were performed on communities of transient
34 stages. Transient stages in secondary successions are usually characterized by the formation of
35 patches originated by different colonizing species that could have arrived or persisted at some
36 specific points. During the process of secondary succession, these patches may grow, coalesce and
37 break up until the establishment of climax communities (Zobel *et al.*, 1993).

38 Another effect of global warming in European mountains has been the upward shift in the upper
39 range limits of an increasing number of species (Stöckli *et al.*, 2011). This is a generalised pattern

1   that acts in the Mediterranean Basin (Pauli *et al.*, 2012) and in other Mediterranean areas, such as
2   California (Kelly and Goulden, 2008). Some of the predictions forthcoming decades made in Spanish
3   Baetic Mountains (Benito *et al.*, 2011), and in the Iberian Mountain range (Ruiz-Labourdette *et al.*,
4   2012), to which the Penyagolosa Massif belongs, fall in line with this general trend. However, we
5   only observed here altitudinal shifts in 13.5% of the total studied species. Of them, 8.2% generally
6   corresponded to species that occupied mid-altitudes in 1968 and that have migrated upwards, and
7   5.3% corresponded to high-altitude species that have migrated downwards. Our results agree with
8   Bodin *et al.* (2013). They analyzed shifts in plant species along an elevational gradient in Southeast
9   France, and found an upward shift of species at mid-elevations, which could be mostly due to
10   climate warming, and a non-significant or even a downward shift at high altitudes, which could be
11   due to gradual canopy closure following ecological successions in some communities that vary in
12   altitudes. These interactions of climate and land use changes may also have acted in the
13   Penyagolosa Massif.

14   Our study also showed differentiated changes for each plant community depending mostly on the
15   altitude, soil type and successional stage. This different susceptibility to global warming and land
16   use transformations among communities is in agreement with some long-term studies performed
17   in Mediterranean mountains (Evangelista *et al.*, 2016; Frate *et al.*, 2018).

18   The communities developing in the highest altitudes accounted for most of the increasing alpha-
19   diversity, in agreement with Steinbauer *et al.* (2018), who found an accelerated increase in species
20   richness on alpine vegetation in 87% of the mountains across Europe as a result of global warming.
21   Here, we also found an increase of Ellenberg temperature index which may contribute to the
22   increased alpha-diversity in the climax *Pino-Juniperion sabinae*. Thermophilisation was also
23   observed over time in several high-altitude European summits (Gottfried *et al.*, 2012), including the
24   Mediterranean area (Evangelista *et al.*, 2016). However, in the Penyagolosa climax forest, only
25   generalist species increased, while characteristic species decreased. Similar patterns were observed
26   in Central Spanish summits, where land use changed only slightly and where an increase in
27   generalists was concurrent with a decline in dry grassland specialists (Jiménez-Alfaro *et al.*, 2014).

28   In the high-altitude pastures (*Poo-Festucetum hystricis*) an opposite trend occurred. Increased
29   alpha-diversity was also found, maybe because in Mediterranean ecosystems, species richness
30   usually fits in a "humped-back model" during secondary successions, reaching the highest diversity
31   few decades after abandonment (Bonet and Pausas, 2004). However, light index decreased with
32   time, and species composition change supported the occurrence of a colonisation of woody species
33   on abandoned pastures. As shrub canopy reduces radiation and temperature (Cuesta *et al.*, 2010)
34   umbrophilous species with cooler requirements may have been favoured underneath.

35   At medium altitudes, increased light Ellenberg index and decreased humidity index over time was
36   observed in the two *Quercus* climax forests, and in the most degraded community (*Aveno-*
37   *Callunetum*) and in pastures (*Astragalo-Festucetum*) on acid soils. Although the shifts of these
38   indices could be due to global warming, they could also partly be the result of the development of
39   some given stages during secondary successions. On this line, Jírová *et al.* (2012) showed that, when

1 shrubby grasslands developed instead of deciduous woodlands in karstic areas of central Europe
2 following a secondary succession, number of light-demanding and termophilous species increased.
3 In the acidophilous communities (except *Deschampsio-Pinetum valentinum*), the higher light
4 Ellenberg index and the lower humidity index could have caused the significant loss of rare and
5 temperate species, at the expense of an increase of commoner Mediterranean species. Thus, to
6 elucidate global warming effects, the analysis of "new" and "lost" species could prove particularly
7 important as many "lost" species are temperate species and may not be detected when studying
8 aerial photographs or dominant taxa. In contrast, in degraded successional stages on basic soils at
9 mid-altitudes, we observed a decrease in the Ellenberg indices of temperature and light and an
10 increase of humidity index, along with a similar expansion of species of forests and seral
11 communities than that observed in the high-altitude pastures. These results suggest a strong
12 influence of land use transformations over time, especially those related with secondary ecological
13 successions. Although the different global change components may impact species and plant
14 communities with complex patterns (Palombo *et al.*, 2013), our results suggest that rural
15 abandonment that increases wildlands may have been buffering the effects of global warming on
16 basic soils at mid-altitudes, as suggested by Pausas and Millán (2019) for the whole Mediterranean
17 area.

18 Besides the effect of climate change and land use transformations on long-term vegetation changes,
19 we also observed some shifts in the estimated edaphic parameters based on variations in Ellenberg
20 indices. The most evident was the increase in Ellenberg index of soil nutrients in most communities.
21 A higher nitrofily over time was also observed in the Apennines, probably as the result of a chronic
22 addition of N amounts (Evangelista *et al.*, 2016; Frate *et al.*, 2018). Also in the Montseny Mountains,
23 close to the Penyagolosa Massif, N load has been 15-17 kg.ha^{-1}.yr^{-1} during the last 3 decades, which
24 is within the critical range proposed for Mediterranean sclerophyllous forests (Aguillaume *et al.*,
25 2016). In this context, the plant species that have adapted to low N inputs are expected to be
26 replaced with nitrophilous species (Ochoa-Hueso *et al.*, 2011). Some causes of the increased
27 Ellenberg index of soil nutrients in the Penyagolosa Massif can be hypothesized. One possible cause
28 is the increase of soil nitrogen content as a direct effect of progressive secondary succession in most
29 of the studied Penyagolosa plant communities (van Hall *et al.*, 2017). Furthermore, reduced
30 overgrazing may have led to an expansion of herbs with better livestock feeding values and higher
31 nitrogen contents (Frate *et al.*, 2018). Some other edaphic changes observed here may be related
32 to land use changes. The abandonment of grazing systems may have resulted in diminished dung-
33 borne nutrient input leading to reduced organic matter and clay contents (Peco *et al.*, 2006), while
34 natural reforestation may have led to larger amounts of organic matter and lower pH in basic soils
35 (Chrenková et al., 2014; van Hall *et al.*, 2017), and to the recovery of the soil natural buffer capacity
36 and a rise in soil pH in acid soils (Mielniczuk, 1996).

37 Overall, our results suggest that land use change and global warming have been the major driving
38 forces of vegetation dynamics. The wide heterogeneity of vegetation changes observed among
39 different plant communities shows how difficult is to disentangle the complex impacts of global
40 change components on species and plant communities (Magurran *et al.*, 2010; Palombo *et al.*and

2013). In this context of climatic variability and socio-economic pressures on Mediterranean ecosystems, long-term time series of biodiversity, climate, and environmental parameters are considered to be very useful for extrapolating data into the future (Valladares, 2007). These studies may support local policies and management actions which can help reducing global change impacts. As an example, in Eastern Spain, policies of low-intensity fires, introduction of grazing animals, and re-vegetation of the lowlands in order to generate water condensation in mountains near the coast have been proposed (Pausas and Millán, 2019).

Acknowledgements

Author contributions

M.F. and H.M. conceived of the research idea; H.H., H.M., and M.F. collected data; A.G. performed statistical analyses; M.F. with contributions from H.M. and A.G., wrote the paper; all authors discussed the results and commented on the manuscript.

Data accessibility

Data are accessible in supplementary tables.

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19 **Tables with legends**

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Table 1. Differences in rarity and chorological origins between "lost" and "new" species in 2014. For rarity, all the data sets were normal and displayed homoscedasticity (Levene´s test), and p-values correspond to t-Student test. For chorological origins, p-values correspond to Pearson's chi-squared test, which was only performed for mediterranean and temperate taxa because of the low number of wide taxa. Asterisks show significant differences.

		N	Rarity						p-value	Chorological origin			p-value
			1	2	3	4	5	Mean±SD		M	T	W	
Poo-Festucetum hystricis (P-F)	lost	13	1	4	3	5	0	2.75±1.00	0.522	7	4	2	0.48
	new	22	0	9	5	5	3	3.00±1.03		19	2	1	
Pino-Juniperion (P-J)	lost	6	0	4	1	1	0	2.50±0.84	0.1	5	1	0	0.85
	new	25	0	6	9	5	5	3.31±1.09		15	5	5	
Salvio-Aphyllanthetum monspeliensis (S-A)	lost	10	0	4	4	2	0	2.80±0.79	0.164	7	3	0	0.85
	new	6	0	0	4	2	0	3.33±0.52		4	1	1	
Cephalanthero-Quercetum pyrenaicae (C-Q)	lost	9	2	7	0	0	0	1.78±0.44	0.010*	0	8	1	<0.001*
	new	17	1	5	7	3	1	2.88±0.99		11	4	2	
Astragalo-Festucetum (A-F)	lost	16	6	6	2	2	0	2.06±1.00	<0.001*	2	14	0	<0.001*
	new	27	1	5	12	6	3	3.19±1.00		18	7	2	
Saturejo-Erinaceethum anthyllidis (S-E)	lost	3	0	1	2	0	0	2.67±0.58	-	3	0	0	-
	new	18	3	6	7	2	0	2.44±0.92		12	4	2	
Violo-Quercetum valentinae (V-Q)	lost	3	0	2	1	0	0	2.33±0.58	-	3	0	0	-
	new	8	2	1	2	1	2	3.00±1.60		5	1	2	
Aveno-Callunetum (A-C)	lost	9	4	3	1	1	0	1.89±1.05	0.002*	1	7	1	0.0015*
	new	11	0	2	3	3	3	3.64±1.12		9	2	0	
Deschampsio-Pinetum valentinum (D-P)	lost	11	1	6	3	1	0	2.36±0.54	0.26	3	7	1	1
	new	9	2	6	0	0	1	2.11±0.90		1	6	2	

N: number of species. Rarity 1: very rare, 2: rare; 3: intermediate abundance; 4: common; 5. very common. Chorological origins M: Mediterranean; T: Temperate (including paleotemperate, eurosiberian, euroasiatic, and atlantic species); W: wide distribution. Rarity and chorological origins were assessed according to Mateo and Crespo (2009).

1   **Figures with legends**

2   Figure 1. Location of the 92 re-surveyed *relevés* in the Penyagolosa Massif. Green area corresponds
3   to the limits of the Penyagolosa Natural Park.

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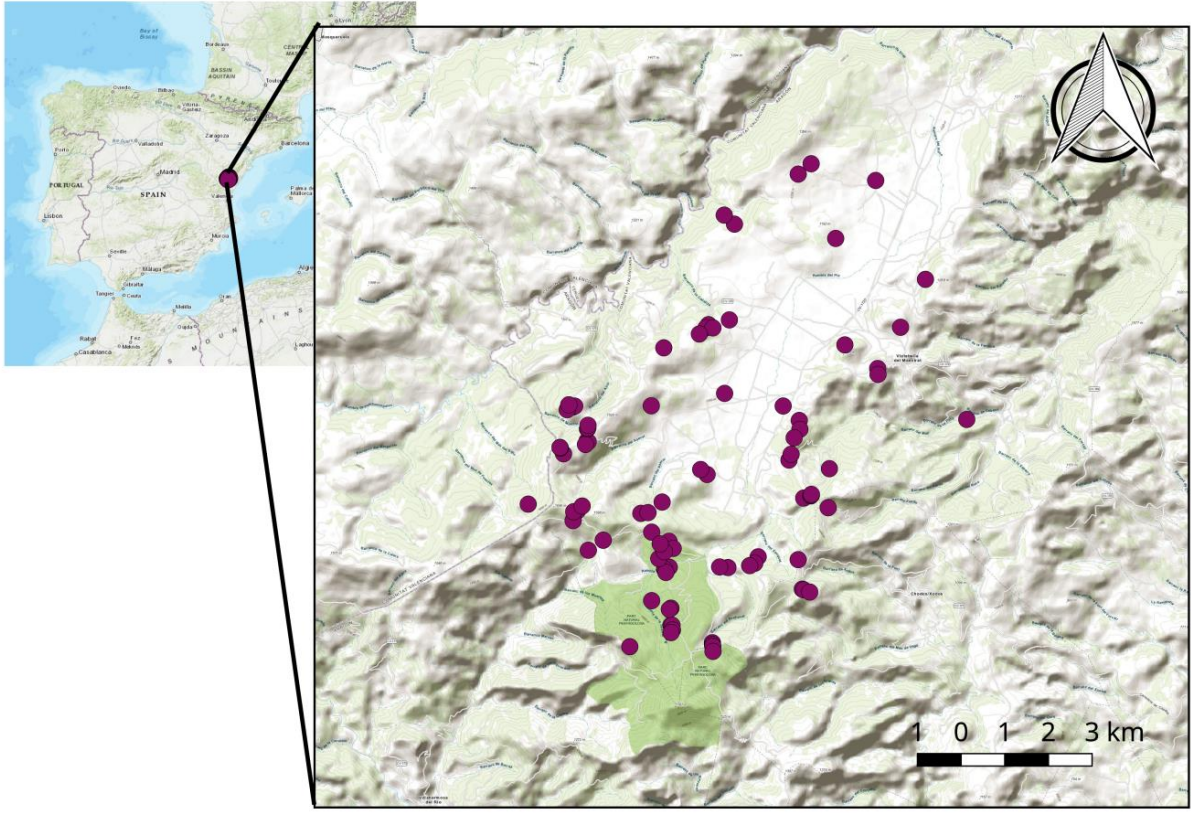
Figure 2. Studied vegetation communities in the medium and high altitudes of the Penyagolosa

Massif. Spatial and temporal relationships are shown. Numbers in brackets indicate the number of

re-sampled *relevés* for each association. Indications of transition processes are extracted from Vigo
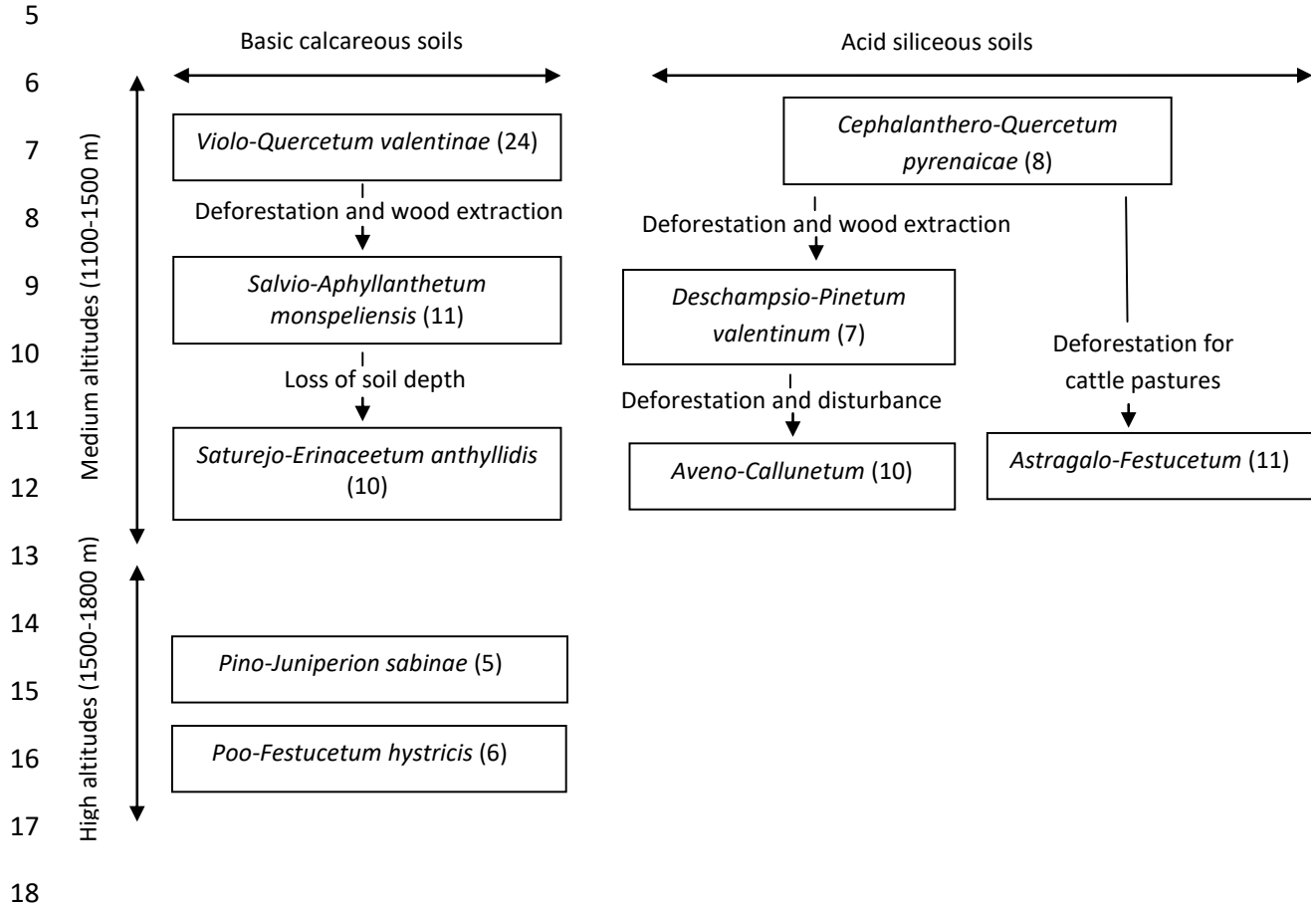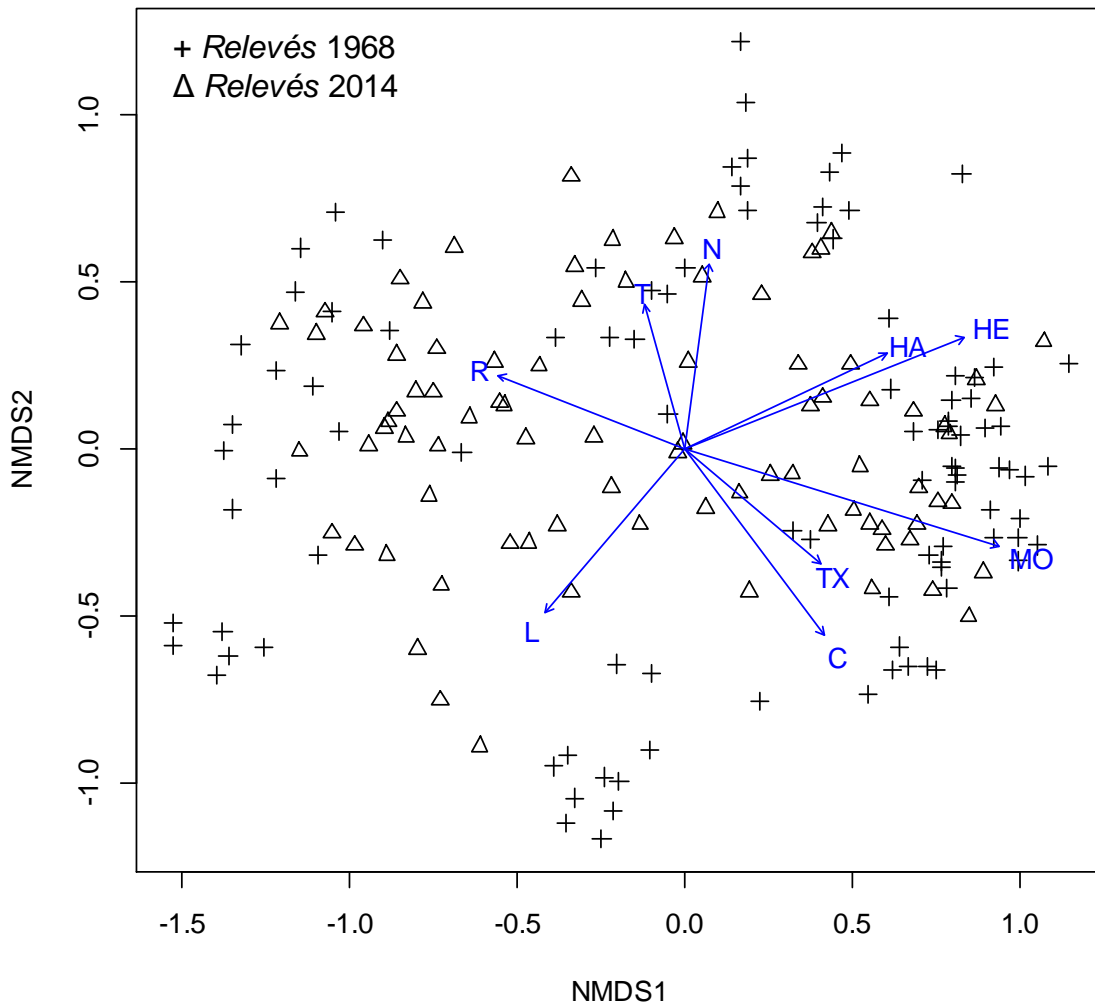
(1968).

1   Figure 3. Boxplots of the distances to centroid for each year (2014 and 1968), which represent the
2   community heterogeneity between new and old vegetation samples. Boxplots show medians,
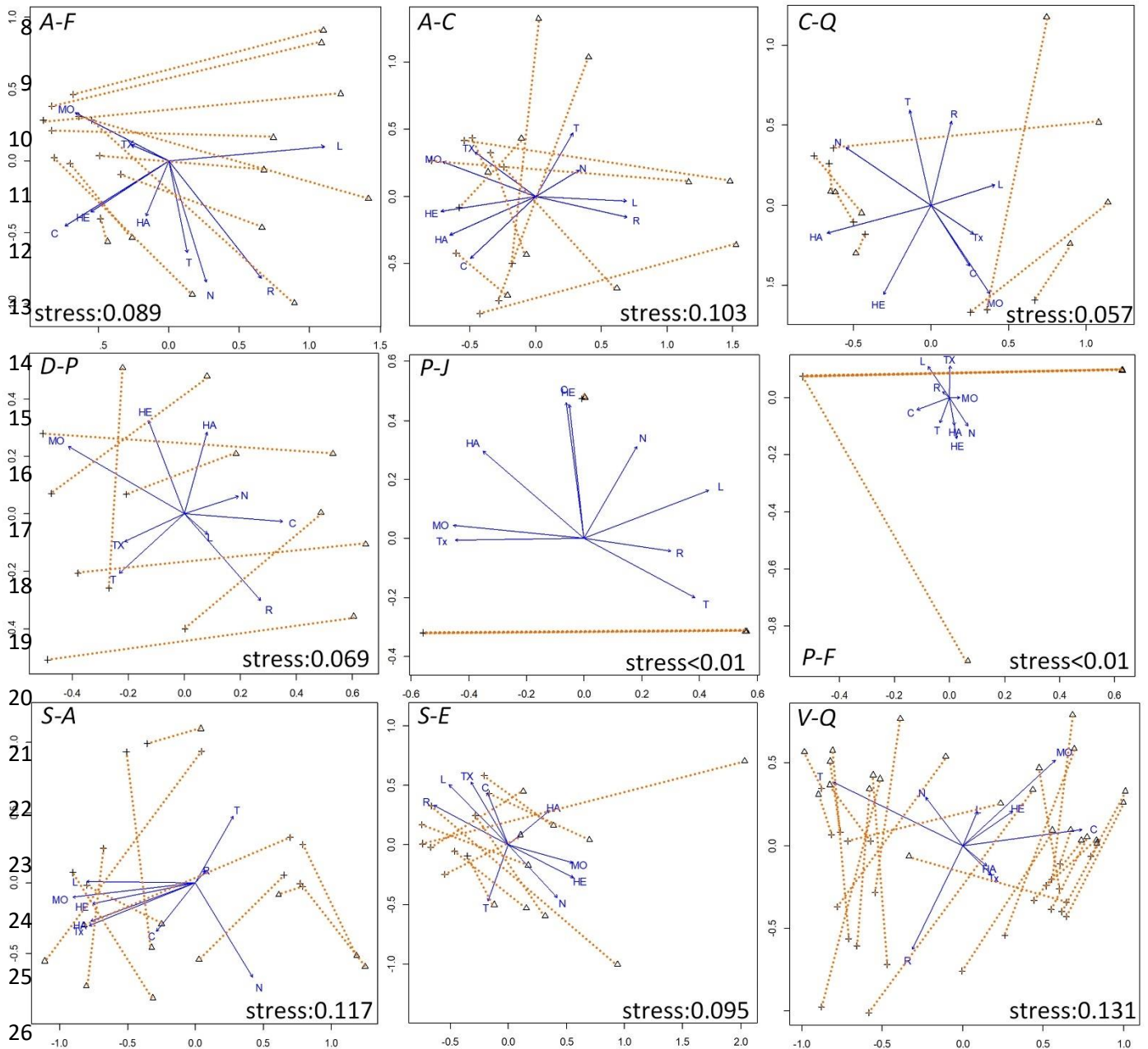3   interquartile and min-max ranges.

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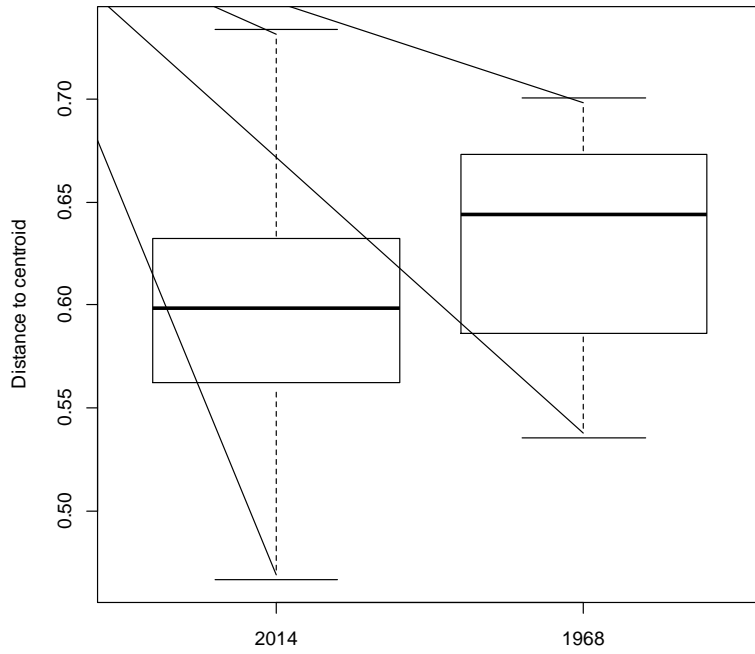
Figure 4. NMDS diagram showing species composition change between old (1968) and new (2014)

2   sampling in mid and high-altitudes of Penyagolosa Massif, with fitted Ellenberg indicator values. C:

3   continentality; HA: atmospheric humidity; HE: soil humidity; L: light; MO: Organic matter; N: soil

4   nutrients; R: soil pH; S: salinity; T: temperature; Tx: soil texture. Stress value: 0.147.

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Figure 5. NMDS diagrams of the two first axes (x-axis: NMDS1 and y-axis: NMDS2) showing species composition change for each plant community between old (1968) and new (2014) sampling, with fitted Ellenberg indicator values. Dotted lines relate original and re-surveyed *relevés* on each individual plot. Stress values are indicated in each diagram. C: continentality; HA: atmospheric humidity; HE: soil humidity; L: light; MO: Organic matter; N: soil nutrients; R: soil pH; T: temperature; Tx: soil texture. For abbreviations of plant communities, see Table 1.
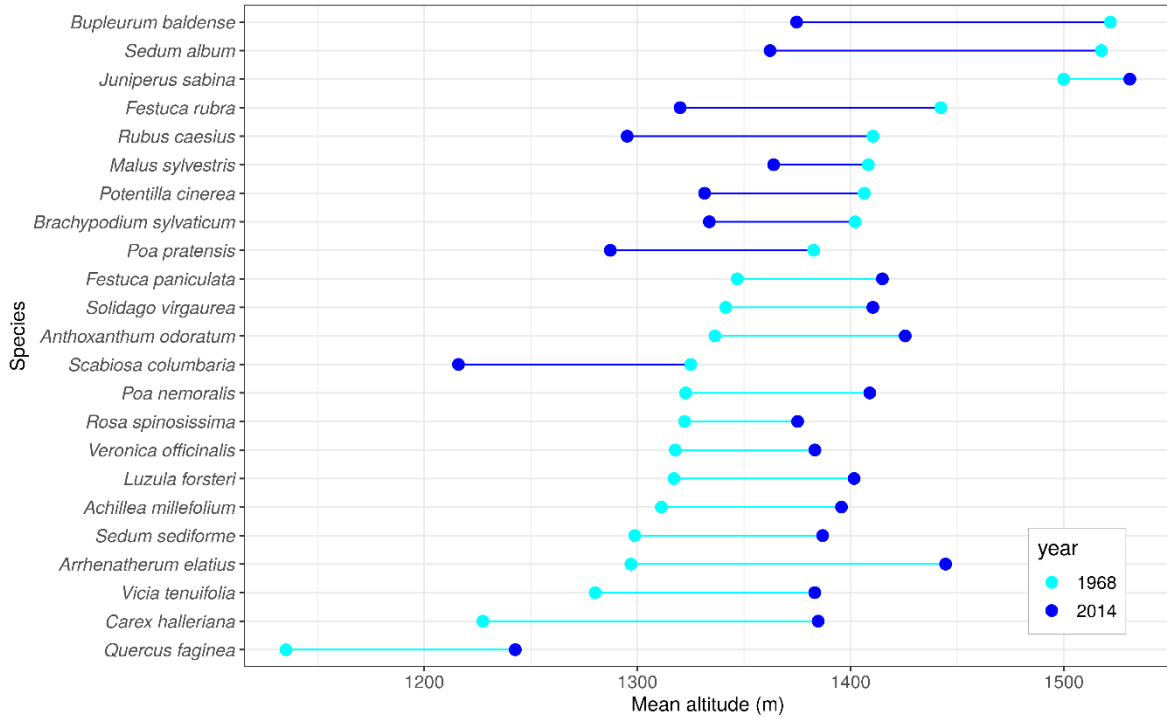
Figure 6. Weighted mean altitude for 1968 and 2014 of the species which appeared in at least 5
2 *relevés* in each year and which showed significant differences between years (weighted Student's *t*-
3 tests). Color of segments is light when weighted mean altitude has increased and dark when it has
4 decreased from 1968 to 2014.

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1   **List of appendices**

2   Appendix S1. Analysis of beta-diversity among *relevés* within communities.

3   Appendix S2. List of the species found in Peñagolosa Mountains in 1968 and 2014 grouped by
4   botanical families.

5   Appendix S3. Analysis of alpha-diversity (Shannon-Wiener index) within communities.

6   Appendix S4. Significance of species composition change using a non-parametric multivariate
7   analysis of variance (PERMANOVA), with 999 permutations and the Bray-Curtis dissimilarity index.

8   Appendix S5. Analysis of Ellenberg indices among *relevés* within communities.

9   Appendix S6. Relevés of *Pino-Juniperion sabinae*.

10   Appendix S7. Relevés of *Poo-Festucetum hystricis*.

11   Appendix S8. Relevés of *Cephalanthero-Quercetum-pyrenaicae*.

12   Appendix S9. Relevés of *Deschampsio-Pinetum valentinum*.

13   Appendix S10. Relevés of *Aveno-Callunetum*.

14   Appendix S11. Relevés of *Astragalo-Festucetum*.

15   Appendix S12. Relevés of *Violo-Quercetum valentinae*.

16   Appendix S13. Relevés of *Salvio-Aphyllanthetum*.

17   Appendix S14. Relevés of *Saturejo-Erinaceetum*.

18   Appendix S15. Altitudinal distribution of the covers/abundances of those species that showed a
19   significant elevational shift from 1968 to 2014 (weighted Student's *t*-test).

20   Appendix S16. List of "lost" and "new" species found in each plant community in 2014.