RESEARCH PAPER

CrossMark

Beneath the mistletoe: parasitized trees host a more diverse herbaceous vegetation and are more visited by rabbits

José A. Hódar[1] (ORCID) · Alba Lázaro-González[1] · Regino Zamora[1]

Abstract

· *Key message* Parasitism by mistletoe increases the cover and diversity of herbaceous vegetation under the host tree and attracts the activity of rabbits in comparison to control trees. Thus, the effects on forest community go beyond the parasitized tree.

· *Context* Mistletoes are a diverse group of aerial hemiparasitic plants and are considered keystone species in forest ecosystems around the world. They produce nutrient-enriched litter, which exerts a substantial effect on soil-nutrient concentration, and the enriched nutrient patch alters the vegetation at the site as well as the associated fauna.

· *Aims* Our goal is to ascertain whether mistletoe (*Viscum album*) parasitism of pine forest of a Mediterranean mountain favors herbaceous vegetation and attracts mammalian herbivores.

· *Methods* We recorded in Sierra de Baza (SE Spain) the composition of the herbaceous vegetation under pines with and without mistletoe parasitism, and estimated the rabbit activity at the same sites by collecting their excrements.

· *Results* An effect on herbaceous vegetation, especially in grasses belonging to the family Poaceae, was reflected in a notable increase in soil cover, species richness, and species diversity beneath parasitized pines with respect to unparasitized ones. As a consequence, parasitized pines attract the activity of rabbits, as shown by a fivefold quantity of excrement with respect to control ones.

· *Conclusion* Parasitism by mistletoe, by creating patches of greater nutrient availability under the host canopy, extends its effects beyond the host tree to other members of the forest community, such as herbaceous plants and associated herbivorous animals, which in turn contribute to environmental heterogeneity with their activity.

✉ José A. Hódar
jhodar@ugr.es

[1] Grupo de Ecología Terrestre, Departamento de Ecología, Facultad de Ciencias, Universidad de Granada, 18071 Granada, Spain

1 Introduction

Plants and animals live in habitats that are heterogeneous, both in space and time (Wiens 2000). Field research has focused on the effect of heterogeneity in habitat quality on the distribution and abundance of organisms (Stewart et al. 2000); however, plants and animals are also able to initiate, maintain, and reinforce heterogeneous spatial patterns (Wiens 2000). Many processes of resource redistribution and concentration—some being abiotic such as changes in light patchiness, water runoff, and water availability, and others biotic such as litterfall, excrement accumulation in latrines, or food hoarding—create non-random patches of heterogeneous nutrient availability (Pickett et al. 2000). Among the biotic processes, plants can promote spatial heterogeneity by concentrating nutrients around themselves (Moro et al. 1997; Watson 2009) or

INRA SCIENCE & IMPACT   Springer

emitting particular secondary metabolites (Iason et al. 2005). Similarly, animals can do so by depositing excrement and/or foraging selectively in preferred patches (Willott et al. 2000; Bokdam 2001). Thus, the activity of plants and animals could modify spatial heterogeneity in nature.

A notable case of nutrient redistribution and concentration with strong effects on plant quantity and quality as food are parasitic plants (Watson 2009). Among these, mistletoes, a diverse group of aerial hemiparasitic plants, are considered keystone species in forest ecosystems around the world (Watson 2001). Recent studies with parasitic plants have shown their important role in regulating belowground processes by enhancing soil-nutrient availability and bolstering soil spatial heterogeneity (Quested et al. 2002; Fisher et al. 2013; Mellado et al. 2016). Mistletoes draw water and mineral resources from host plants, attaining higher concentrations of foliar nutrients than their hosts (Ehleringer and Marshall 1995; Bowie and Ward 2004), and they produce nutrient-enriched litter due to scant reabsorption prior to abscission (Pate et al. 1991; Quested et al. 2002) and the input of bird-derived debris (Mellado et al. 2016). Mistletoe litter often contributes large amounts of biomass to the forest floor, including leaves, flowers, and fruits (March and Watson 2007), which are rich in nutrients and have a high decomposition rate, enhancing soil-nutrient cycling (March and Watson 2010; Ndagurwa et al. 2016; Muvengwi et al. 2015). It has been shown that the volume of litter beneath a tree crown amasses with mistletoe infestation, increasing the overall litterfall (March and Watson 2007, 2010; Mellado et al. 2016), and thus the parasite may contribute to higher nutrient returns beneath host trees. Mistletoe litter contains lower C/N ratios (Mellado et al. 2016) and therefore decomposes faster and releases nutrients more rapidly than does the litter of co-occurring species, and may also stimulate the decomposition of more recalcitrant litter when mixed, for instance with those from the host plant (Quested et al. 2002). In this way, mistletoes can have a profound effect on soil-nutrient concentrations in terrestrial habitats, which may in turn affect the growth of neighboring plants (Quested et al. 2003; March and Watson 2010). In addition, mistletoes attract animal associates from a wide range of groups including mammals, birds, and insects, thereby augmenting diversity in environments where they occur (Watson 2009). According to the Dryad hypothesis (Watson 2009), mistletoe and parasitic plants are generally regarded as facilitators in low-productivity habitats, boosting heterogeneity in nutrient availability and productivity by shedding large quantities of enriched leaf litter (Watson 2015). The enriched nutrient patch alters the vegetation at the site as well as the associated fauna, and animal visitors may reinforce this nutrient increase by providing excrement, urine, or other animal remains (Van der Wal et al. 2004; Watson 2009; Mellado et al. 2016).

In this study, we address these questions by focusing on mistletoe (*Viscum album* ssp. *austriacum* (Wiesb.)) parasitizing Black pines (*Pinus nigra* Arn.) on a Mediterranean mountain (SE Spain). Through its nutrient-rich litter and the accumulation of excrement from seed-dispersing birds, mistletoe enhances soil-nutrient availability beneath parasitized pines (Mellado et al. 2016), which could favor the growth of other plant species. Moreover, this parasite has a constant and uniform annual fruit production that makes parasitized trees constant food resources for frugivorous birds, thereby providing consistent sites for organic matter deposition in space and time (Mellado and Zamora 2015; Mellado et al. 2016).

In previous studies, we have measured the abundance of seeds moved by zoochory under the canopy of unparasitized and parasitized trees (Mellado and Zamora 2015) and soil-nutrient availability beneath the canopy of these same trees (Mellado et al. 2016). To fully understand the consequences of mistletoe parasitism in the whole forest community, here, we focus on herbaceous vegetation and a mammalian herbivore. Specifically, we test whether (1) plant communities beneath parasitized pines show a different cover and diversity of herbaceous vegetation with respect to control, and (2) whether parasitized pines promoted more occupancy by rabbits, in comparison to unparasitized pines.

2 Material and methods

2.1 Study site

The study was performed from autumn 2012 to summer 2013 in the Natural Park of Sierra de Baza (south-eastern Spain; 2°51′ W, 37°22′ N). The site is a mountain range with limestone rocks and calcareous soils, ranging between 1200 and 2269 m a.s.l. (Calar de Santa Bárbara, the highest peak). Climate is typically Mediterranean, with cold winters (snow cover above 1700 m lasts 2–4 months per year), precipitation concentrated in spring and autumn, and a pronounced summer drought (June–August). The main vegetation cover is pine woodlands, Aleppo (*Pinus halepensis* Mill.) and maritime pine (*P. pinaster* Ait.) at lower elevations, and Black (*P. nigra*) and Scots pine (*P. sylvestris* L.) from middle to high elevations. Pine woodlands are intermingled with oaks (*Quercus ilex* L.), maples (*Acer opalus* L. ssp. *granatense* Boiss.), and several fleshy-fruited shrubs, lianas, and trees, forming part of the plant community throughout the mountain (see Blanca and Morales 1991 for a detailed description of the Sierra de Baza vegetation). The mistletoe *Viscum album* ssp. *austriacum* is a hemiparasitic, dioecious epiphyte widely distributed across European coniferous forests. *Pinus nigra* and *P. sylvestris* constitute the most common host species in southern Spain and at the study site (Mellado 2016), where individual *V. album austriacum* can live for more than 30 years (Zuber 2004, *pers. obs*).

For this study, we selected 110 Black pines (hereafter focal trees), half of them parasitized by mistletoe and the other half unparasitized. Parasitized trees presented moderate to intense parasitic loads (20–40 and 50–80% of the host canopy covered by mistletoe, respectively), bearing at least one mistletoe > 30 years old (Mellado et al. 2016). Pines were selected to cover a large range of the mountain's heterogeneity, including stands with low (open) and high (closed) tree densities and three elevation levels (1350, 1650, and 1850 m). Trees were randomly selected and spatially paired (one parasitized and one unparasitized). Paired trees were of similar architecture, size (diameter at breast height [mean ± SE] 25.55 ± 1.31 cm), age (90–110 years old; see Herrero et al. 2013), and height (mean ± SE 6.87 ± 0.23 m). Paired trees were located 40 to 80 m apart to keep environmental contexts as similar as possible (e.g., climatic factors and composition of neighboring vegetation). The shrub cover beneath the tree canopy was similar between control and parasitized pines (Mellado and Zamora 2015; Mellado 2016).

2.2 Sampling herbaceous vegetation

The study took place between autumn of 2012 and summer of 2013 for three reasons. First, we were interested in herbaceous vegetation, which in Mediterranean ecosystems shows its growing peak during early spring, becoming dry later due to summer drought (Archibold 1995). Second, litterfall (leaves and fruits) from mistletoe falls to the soil mostly during winter, thus being available for consumption by herbivores and contributing to the nutrient return (Mellado et al. 2016; Ndagurwa et al. 2016). Finally, as a consequence of the previous points, most mammalian herbivores graze on herbs and grasses while available, shifting to a shrub-based diet when dry (summer) or unavailable (mid-winter) (Martínez 2009).

In spring 2013, we checked the soil under the pine canopy of all tagged trees. A square of 1 m² made with PVC tube was used to delimit the plots. The square was placed three times randomly beneath each pine canopy. We first recorded the percentage of surface area of bare soil, covered by rocks and covered by herbaceous vegetation within the plots. Then, we estimated the cover of every plant species in the plots according to a semi-quantitative scale (0 to 5, following the method proposed by Braun-Blanquet 1979), excepting shrubs (already studied in Mellado and Zamora 2015). Later, we converted the scores of the semi-quantitative scale of cover to percentage of plant cover in each plot (+ = 0.3%, 1 = 3%, 2 = 15%, 3 = 35%, 4 = 65%, 5 = 85%). All plants were identified to the lowest taxonomic level to test differences beneath parasitized and unparasitized pines in species richness, Shannon Index (as diversity), families cover (Poaceae, Fabaceae, and other families), and composition of herbaceous species. Plant nomenclature follows Blanca et al. (2011).

2.3 Estimating the occupancy under trees by rabbits

Several ungulate species live in Sierra de Baza, both wild (red deer *Cervus elaphus*, Spanish ibex *Capra pyrenaica*, wild boar *Sus scrofa*) and domestic (mixed herds of sheep *Ovis aries* and domestic goat *Capra hircus*) (CMAOT 2016). These species increase its browsing character during winter (Garin et al. 2001; Ferreira et al. 2013), and in reason of its body size, they sample the habitat on a coarse scale (Senft et al. 1987; Hódar and Palo 1997; Schaefer et al. 2008). Thus, we discarded them as a focus for this study. Conversely, we focus our attention on rabbit (*Oryctolagus cuniculus*). Rabbit is a small mammal with a restricted home range size (Soriguer 1981; Lombardi et al. 2007); thus, we consider it as an adequate species model to discriminate between individual trees depending on its parasitism by mistletoe. To examine the differential occupancy, we counted excrements beneath trees with and without mistletoe. Pellet count has been repeatedly used as an appropriated method to estimate density and/or habitat selection by rabbits (Lombardi et al. 2003; Santilli and Bagliacca 2010; Mutze et al. 2014).

At the beginning of autumn 2012, we checked the soil beneath the pine canopy of all tagged trees and cleaned away most of the recent excrement, whatever its source. Old excrement was in general easily recognizable, but in this way, we minimized the possibility of mistakes. At the end of winter (March–April 2013), we randomly delimited three 1-m² plots with the PVC square (as describe above) beneath each pine and collected all the excrement found. Clearly old excrements moved by abiotic factors (e.g., rain) were discarded. Initially, we distinguished whenever was possible between rabbit and hare (*Lepus granatensis*); however, hare was conspicuously scarce and restricted to the higher part of the mountain, so hereafter we considered together as rabbit. We kept the excrement specimens in cellophane bags, dried them in the laboratory for 48 h at 70 °C, and then weighed them.

2.4 Statistical analyses

All analyses were performed under the same structure, using tree condition (parasitized and unparasitized pines) as fixed factor and elevation (1350, 1650, and 1850 m), paired trees (1–55), and individual pines (1–110) as nested random ones. We used generalized linear mixed models (GLMM) assuming binomial error distribution to analyze the effects of tree conditions (parasitized or not) on percentage cover beneath pine canopies (bare soil, rock, and herbaceous vegetation) and Poisson error distribution and log-link function for total species richness of herbaceous vegetation. Herbaceous diversity (H') was tested using linear mixed model (LMM). Permutational multivariate analysis of variance (PERMANOVA), using the Bray-Curtis distance and 9999 permutations, was used to analyze significant differences on

plant species assemblages beneath parasitized and unparasitized pine trees. Individual significance by plant species on herbaceous community was analyzed using GLMMs with negative binomial error distribution, and square root transformation was required on community matrix.

For Fabaceae family cover, we applied a GLMM with negative binomial distribution and the log-link due to its absence from several samples, while Poaceae and other families cover were square-transformed, in order to meet assumptions of normality and homoscedasticity, and tested using LMM. The species richness by families was tested using GLMM with Poisson error distribution and log-link function.

To analyze preference of occupancy under parasitized or unparasitized pine trees across excrement records, we used a GLMM with negative binomial distribution due to high number of zeros. Data of rabbit presence/absence as well as amount of excrement recorded were averaged for the three plots of each pine tree, in order to reduce the number of empty samples, and therefore individual pine was removed from random factors.

All statistical analyses were conducted with the R software system Version 3.4.1 (R Development Core Team 2017). GLMMs and LMMs were carried out under *glmer*, *lmer*, and *glmer.nb* functions of *lmer4* packages, and the Shannon diversity index was calculated by *diversity* function. For PERMANOVA, we used only species above 0.5% of total cover on each plot and was performed under *adonis* function. *Diversity* and *adonis* functions were included in the *vegan* package.

Throughout the paper, means are expressed ± 1SE.

Data availability The datasets generated and/or analyzed during the current study are available in the Zenodo repository, https://doi.org/10.5281/zenodo.1311757 (Hódar et al. 2018).

3 Results

3.1 Herbaceous vegetation

A total of 167 plant taxa were identified within the plots, most specimens being identified to the species level (Appendix
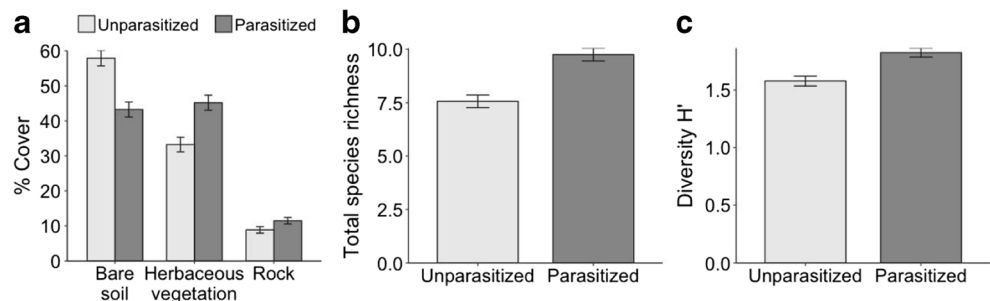
ESM1). The herbaceous vegetation (GLMM, $\chi^2 = 11.13$, $d.f. = 1$, $P < 0.001$) and rock cover (GLMM, $\chi^2 = 4.02$, $d.f. = 1$, $P = 0.045$) were significantly greater under parasitized pines in detriment to bare soil (GLMM, $\chi^2 = 16.08$, $d.f. = 1$, $P < 0.001$; Fig. 1a). Herbaceous plant assemblages beneath parasitized pines showed more species richness (GLMM, $\chi^2 = 14.56$, $d.f. = 1$, $P < 0.001$, Fig. 1b) and diversity (LMM, $\chi^2 = 10.18$, $d.f. = 1$, $P = 0.002$, Fig. 1c) than unparasitized ones. According to these results, their species composition was also significantly different between herbaceous communities under parasitized and unparasitized pine trees (PERMANOVA, *pseudo-F* = 4.32, $d.f. = 1$, $P < 0.001$). Individual species analysis reveals that these differences were due to 14 species, 13 of them more abundant beneath parasitized pines (four Poaceae, two Brassicaceae, three Caryophyllaceae, two Rubiaceae, and two Asteraceae), while only one specie (Fabaceae) was more abundant under unparasitized pines (Fig. 2).

Overall, plant species from Poaceae and Other families presented fuller cover (LMM$_{POACEAE}$, $\chi^2 = 13.66$, $d.f. = 1$, $P < 0.001$; LMM$_{OTHER}$, $\chi^2 = 6.35$, $d.f. = 1$, $P = 0.012$) and species richness (GLMM$_{POACEAE}$, $\chi^2 = 23.12$, $d.f. = 1$, $P < 0.001$; GLMM$_{OTHER}$, $\chi^2 = 8.31$, $d.f. = 1$, $P = 0.004$) under parasitized pines (Fig. 3), while Fabaceae showed no significant differences (GLMM$_{COVER}$, $\chi^2 = 0.57$, $d.f. = 1$, $P = 0.452$; GLMM$_{RICHNESS}$, $\chi^2 = 0.31$, $d.f. = 1$, $P = 0.581$).

3.2 Estimating the occupancy under trees by rabbit

Rabbit clearly prefers parasitized trees: The presence of rabbits under parasitized pines is much more frequent than under control ones (69 vs 25%, respectively; GLMM, z-value = 3.705, $d.f. = X$, $P < 0.000211$). Accordingly, the amount of excrement under parasitized pines is fivefold than those found under control ones (0.40 ± 0.03 vs 0.08 ± 0.07 g/m^2, respectively; GLMM, $\chi^2 = 10.89$, $d.f. = 1$, $P < 0.001$).

4 Discussion

Mistletoe clearly determines the cover and botanical composition of herbaceous vegetation beneath parasitized pines in

Fig. 1 Mean (± SE) of **a** percentage cover (bare soil, herbaceous vegetation, and rock cover), **b** species richness, and **c** Shannon diversity Index by square meter, beneath parasitized (dark-gray bars) and unparasitized (light-gray bars) pines
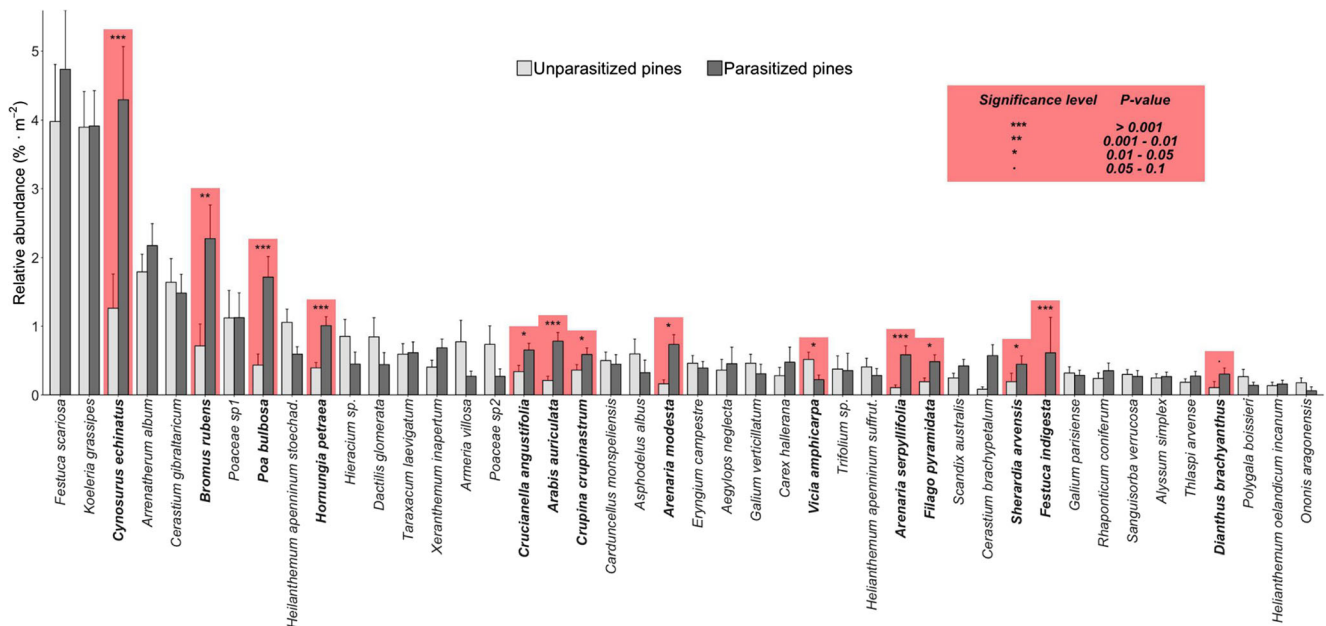
Fig. 2 Relative abundance by square meter of plant species (above 0.5% of total cover) presents on each plot sampled beneath parasitized (dark-gray bars) and unparasitized (light-gray bars) pines. Significant differences are highlighted by red rectangle

comparison to unparasitized ones. The most noteworthy results are a general increase in plant cover, species richness (especially in Fam. Poaceae), and diversity. In line with these, plant species composition shows also differences, where several grass species clearly responded to the presence of mistletoe in trees by

Fig. 3 Mean (± SE) of herbaceous cover (above) and species richness (below) by square meter of **a** Fabaceae, **b** Poaceae, and **c** other families of herbs, beneath parasitized (dark-gray bars) and unparasitized (light-gray bars) pines

increasing its abundance with respect to control trees, as revealed by individual species analysis (Fig. 2).

There are at least two different, non-mutually exclusive, possibilities to explain why grasses are especially favored. First, they are highly responsive to fertilization. A recent work (Mellado et al. 2016) performed exactly in the same pines used by us clearly demonstrated that mistletoe increased the amount, quality, and diversity of organic matter input beneath the host canopy, directly through its nutrient-rich litter and indirectly through a reduction in host litterfall and an increase in bird-derived debris. As a result, the spaces beneath parasitized pines became an enriched hotspot. Parasitized pines show a higher NPK soil availability than did control pines (Mellado et al. 2016; see also Ndagurwa et al. 2016), and this fertilization stimulates the development of Poaceae more than, for example, Fabaceae (Grünzweig and Körner 2003). Moreover, N-fixing species such as Fabaceae are more responsive to an exclusive increase in P (Stöcklin and Körner 1999; Stöcklin et al. 1998) than NPK together (Grünzweig and Körner 2003), and even a unique increase of N does not benefit their growth (Xia and Wan 2008; Huang et al. 2015) or can lower abundance and richness of N_2-fixing species in a herbaceous community (Suding et al. 2005). Thus, legumes can lose their advantage with respect to other non-N_2-fixing species under N fertilization (Suding et al. 2005). Second, rabbits, by showing a preference for grazing under parasitized pines, can spread seeds in their excrement during their foraging activity (Malo and Suárez 1995; Dellafiore et al. 2010). Poaceae is the staple food for rabbits, especially during winter (see below), and consequently seeds from this family will be preferentially dispersed. Furthermore, Poaceae are in general
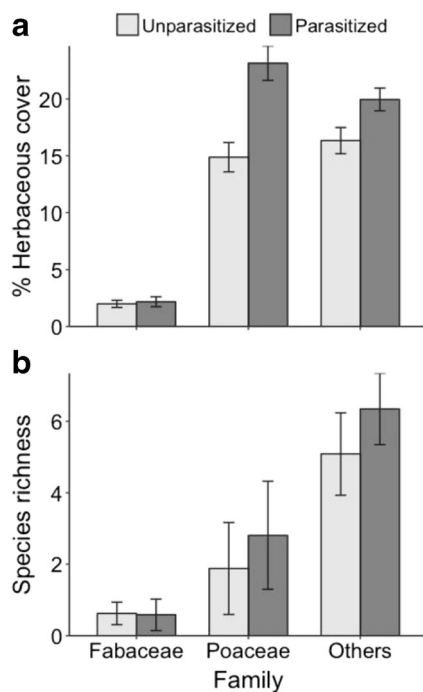
more resistant to grazing than are Fabaceae or other forbs, thus reinforcing the pattern.

The greater herbaceous cover, richness, and diversity under parasitized pines were notable in afforested pine woodlands. Pine plantations are widespread in Mediterranean environments, and due to the characteristics of most of them (low tree diversity, high density, lack of vegetation heterogeneity) sometimes have been considered "green deserts" unuseful to restore the natural biodiversity (Chirino et al. 2006; Bremer and Farley 2010). A study in the nearby Sierra Nevada mountain range (Gómez-Aparicio et al. 2009) showed that pine plantations in fact bore lower total plant richness and H′ index values than native stands, especially when compared with deciduous broadleaf forests, but that this negative effect appeared only for herbaceous species, and not for woody species. This result was attributed to the high tree density of plantations in comparison to native fragments, which in turn implies dimmer understory light, usually responsible of low herbaceous richness and cover. Mistletoe parasitism, by increasing nutrient availability and heterogeneity (Mellado et al. 2016) as well as light penetration to the understory (Mellado 2016), ameliorates the environment for the growth of herbaceous vegetation. In this context, the role of the mistletoe facilitating diversity and heterogeneity should be considered as a positive factor for the naturalization of the artificial stands of pine plantations.

The mistletoe footprint translates to herbivorous animals, by increasing growth and diversity of understory herbaceous plants (March and Watson 2007). Rabbits are small-bodied mammals with a limited home range (ca. 1 Ha in Soriguer 1981; 0.5–2 Ha in Lombardi et al. 2007), for which an intense use of understory of parasitized trees is easy to record. Rabbits might prefer grazing under parasitized pines because grasses, mainly Poaceae, are more abundant in these pines with respect to control, as a result of increased amounts of litter and excrement and thus more vigorous microbial mineralization activity (Mellado 2016). Poaceae respond better to this kind of fertilization than do other groups of forbs (Grünzweig and Körner 2003), increasing its biomass and presumably its nutrient content, while rabbits clearly prefer foods having higher nutrient contents (Somers et al. 2008). Furthermore, Poaceae are the staple food for rabbits during winter (Soriguer 1988; Martins et al. 2002; Kontsiotis et al. 2015). Another reason why rabbits could be attracted to parasitized pines is the mistletoe litterfall. Mistletoe is a nutritive plant for herbivores: Rodrigáñez (1949) and González-González and González-Doncel (1999) refer to mistletoe as an important livestock food source, searched for by shepherds, who cut them down to feed to the animals. Thus, for small mammals with a restricted home range, such as rabbits, it should be easy to track the natural fall of mistletoe leaves from the parasitized pines within its home range, quickly consuming them.

The role of mistletoe as a generator of environmental heterogeneity has previously been identified by shaping the spatial deposition pattern of zoochorous seeds in the forest, which may be reflected in the future configuration of the woody-plant community (Mellado and Zamora 2015), as well as in greater soil availability and spatial heterogeneity (Mellado et al. 2016). The present study, however, is the first to show that the impact of parasite litter on the understory extends to other members of the forest community such as herbaceous plants and associated herbivorous animals, which in turn can contribute to reinforce the environmental heterogeneity with their activity. This effect is especially important in Mediterranean environments, where, due to afforestation trends during recent decades, large areas are covered by pine plantations characterized by a homogeneous spatial structure and monospecific composition. In this context, mistletoe can provide more habitat and resources for other herbaceous plant species to become established, fostering plant diversity in the pine forest.

5 Conclusion

In conclusion, the effects promoted by mistletoe go beyond the host tree, affecting the whole herbaceous plant community beneath the parasitized tree and their herbivorous consumers. The increase of diversity and heterogeneity could even be considered as a positive factor for the naturalization of the artificial stands of pine plantations, widespread in Mediterranean environments. These findings strengthen the idea of mistletoes as ecosystem engineers alter the microenvironment of soil and create patches of increased nutrient availability under the host canopy, while as keystone species, they alter species composition of the herbaceous community and the activity of grass-eating mammals such as rabbits (Jones et al. 1994; Watson 2001), expanding their long-lasting effects to other organisms of the forest community.

Compliance with ethical standards

Conflict of interest   The authors declare that they have no conflict of interest.

References

Archibold OW (1995) Ecology of world vegetation. Chapman & Hall, London

Blanca G, Morales C (1991) Flora del Parque Natural de la Sierra de Baza. Universidad de Granada, Granada

Blanca G, Cabezudo B, Cueto M, Salazar C, Morales-Torres C (eds) (2011) Flora vascular de andalucía oriental. Universidades de Almería, Granada

Bokdam J (2001) Effects of browsing and grazing on cyclic succession in nutrient-limited ecosystems. J Veg Sci 12:875–886

Bowie M, Ward D (2004) Water and nutrient status of the mistletoe *Plicosepalus acaciae* parasitic on isolated Negev Desert populations of *Acacia raddiana* differing in level of mortality. J Arid Environ 56: 487–508

Braun-Blanquet J (1979) Fitosociología: bases para el estudio de las comunidades vegetales. Blume, Madrid

Bremer LL, Farley KA (2010) Does plantation forestry restore biodiversity or create green deserts? A synthesis of the effects of land-use transitions on plant species richness. Biodivers Conserv 19:3893–3915

Chirino E, Bonet A, Bellot J, Sánchez JR (2006) Effects of 30-year-old Aleppo pine plantations on runoff, soil erosion, and plant diversity in a semi-arid landscape in south eastern Spain. Catena 65:19–29

CMAOT, Consejería de Medio Ambiente y Ordenación del Territorio (2016) Memoria de actividades cinegéticas de la temporada 2015–2016. Instituto Andaluz de Caza y Pesca Continental, Andalucía

Dellafiore CM, Gallego-Fernández JB, Muñoz-Vallés S (2010) The rabbit (*Oryctolagus cuniculus*) as a seed disperser in a coastal dune system. Plant Ecol 206:251–261

Ehleringer JR, Marshall JD (1995) Water relations. In: Press MC, Graves JD (eds) Parasitic plants. Chapman and Hall, London, pp 125–140

Ferreira LMM, Celaya R, Benavides R, Jáuregui BM, García U, Santos AS, García RR, Rodrigues MAM, Osoro K (2013) Foraging behaviour of domestic herbivore species grazing on heathlands associated with improved pasture areas. Livest Sci 155:373–383

Fisher JP, Phoenix GK, Childs DZ, Press MC, Smith SW, Pilkington MG, Cameron DD (2013) Parasitic plant litter input: a novel indirect mechanism influencing plant community structure. New Phytol 198:222–231

Garin I, Aldezábal A, García-González R, Aihartza JR (2001) Composición y calidad de la dieta del ciervo (*Cervus elaphus* L.) en el norte de la península ibérica. Anim Biodivers Conserv 24:53–63

Gómez-Aparicio L, Zavala MA, Bonet FJ, Zamora R (2009) Are pine plantations valid tools for restoring Mediterranean forests? An assessment along abiotic and biotic gradients. Ecol Appl 19:2124–2141

González-González G, González-Doncel I (1999) Algunos residuos forestales y madereros en la alimentación del ganado. Invest Agrar-Sist R Sist R 1:349–373

Grünzweig JM, Körner C (2003) Differential phosphorus and nitrogen effects drive species and community responses to elevated CO_2 in semi-arid grassland. Funct Ecol 17:766–777

Herrero A, Rigling A, Zamora R (2013) Varying climate sensitivity at the dry distribution edge of *Pinus sylvestris* and *P. nigra*. For Ecol Manag 308:50–61

Hódar JA, Palo RT (1997) Feeding by vertebrate herbivores in a chemically heterogeneous environment. Écoscience 4:304–310

Hódar JA, Lázaro-González A, Zamora R (2018) Beneath the mistletoe: parasitized trees host a more diverse herbaceous vegetation and are more visited by rabbits (Version v1) [Dataset]. Zenodo. https://doi.org/10.5281/zenodo.1311757

Huang W, Zhou G, Deng X, Liu J, Duan H, Zhang D, Chu G, Liu S (2015) Nitrogen and phosphorus productivities of five subtropical tree species in response to elevated CO_2 and N addition. Eur J For Res 134:845–856

Iason GR, Lennon JJ, Pakeman RJ, Thoss V, Beaton JK, Sim DA, Elston DA (2005) Does chemical composition of individual Scots pine trees determine the biodiversity of their associated ground vegetation? Ecol Lett 8:364–369

Jones CG, Lawton JH, Shachak M (1994) Organisms as ecosystem engineers. Oikos 69:373–386

Kontsiotis VJ, Bakaloudis DE, Merou T, Xofis P (2015) Trophic ecology of the European wild rabbit *Oryctolagus cuniculus* on the Mediterranean island of Lemnos, Greece. Ecol Res 30:683–691

Lombardi L, Fernández N, Moreno S, Villafuerte R (2003) Habitat-related differences in rabbit (*Oryctolagus cuniculus*) abundance, distribution, and activity. J Mammal 84:26–36

Lombardi L, Fernández N, Moreno S (2007) Habitat use and spatial behaviour in the European rabbit in three Mediterranean environments. Basic Appl Ecol 8:453–463

Malo JE, Suárez F (1995) Herbivorous mammals as seed dispersers in a Mediterranean dehesa. Oecologia 104:246–255

March WA, Watson DM (2007) Parasites boost productivity: effects of mistletoe on litterfall dynamics in a temperate Australian forest. Oecologia 154:339–347

March WA, Watson DM (2010) The contribution of mistletoes to nutrient returns: evidence for a critical role in nutrient cycling. Austral Ecol 35:713–721

Martínez T (2009) Role of various woody species in Spanish Mediterranean forest and scrubland as food resources for Spanish ibex (*Capra pyrenaica* Schinz) and Red Deer (*Cervus elaphus* L.). In: Rigueiro-Rodríguez A, McAdam J, Mosquera-Losa MR (eds) Agroforestry in Europe. Current status and future prospects. Springer, New York, pp 233–254

Martins H, Milne JA, Rego F (2002) Seasonal and spatial variation in the diet of the wild rabbit (*Oryctolagus cuniculus* L.) in Portugal. J Zool 258:395–404

Mellado A (2016) Ecological interactions mediated by the European mistletoe, *Viscum album subsp. austriacum*, in Mediterranean forests—an integrated perspective. PhD thesis, University of Granada, Granada

Mellado A, Zamora R (2015) Spatial heterogeneity of a parasitic plant drives the seed-dispersal pattern of a zoochorous plant community in a generalist dispersal system. Funct Ecol 30:459–467

Mellado A, Morillas L, Gallardo A, Zamora R (2016) Temporal dynamic of parasite-mediated linkages between the forest canopy and soil processes and the microbial community. New Phytol 211:1382–1392

Moro MJ, Pugnaire FI, Haase P, Puigdefábregas J (1997) Effect of the canopy of *Retama sphaerocarpa* on its understorey in a semiarid environment. Funct Ecol 11:425–431

Mutze G, Cooke B, Lethbridge M, Jennings S (2014) A rapid survey method for estimating population density of European rabbits living in native vegetation. Rangel J 36:239–247

Muvengwi J, Ndagurwa HG, Nyenda T (2015) Enhanced soil nutrient concentrations beneath-canopy of savanna trees infected by mistletoes in a southern African savanna. J Arid Environ 116:25–28

Ndagurwa HGT, Ndarevani P, Muvengwi J, Maponga TS (2016) Mistletoes via input of nutrient-rich litter increases nutrient supply and enhance plant species composition and growth in a semi-arid savanna, Southwest Zimbabwe. Plant Ecol 217:1095–1104

Pate JS, True KC, Kuo J (1991) Partitioning of dry-matter and mineral nutrients during a reproductive cycle of the mistletoe *Amyema linophyllum* (Fenzl.) Tieghem parasitizing *Casuarina obesa* Miq. J Exp Bot 42:427–439

Pickett STA, Cadenasso ML, Jones CG (2000) Generation of heterogeneity by organisms: creation, maintenance and transformation. In: Hutchings MJ, John EA, Stewart AJA (eds) The ecological consequences of environmental heterogeneity. British Ecological Society-Blackwell, Oxford, pp 33–52

Quested HM, Press MC, Callaghan TV, Cornelissen JHC (2002) The hemiparasitic angiosperm *Bartsia alpina* has the potential to accelerate decomposition in sub-arctic communities. Oecologia 130:88–95

Quested HM, Press MC, Callaghan TV (2003) Litter of the hemiparasite *Bartsia alpina* enhances plant growth: evidence for a functional role in nutrient cycling. Oecologia 135:606–614

R Development Core Team (2017) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna. URL http://www.R-project.org/

Rodrigáñez C (1949) Prados arbóreos. Publicaciones del Ministerio de Agricultura, Servicio de Capacitación y Propaganda, n° 3. Madrid, 190 pp

Santilli F, Bagliacca M (2010) Habitat use by the European wild rabbit (*Oryctolagus cuniculus*) in a coastal sandy dune ecosystem of Central Italy. Hystrix 21:57–64

Schaefer JA, Morellet N, Pépin D, Verheyden H (2008) The spatial scale of habitat selection by red deer. Can J Zool 86:1337–1345

Senft RL, Coughenour MB, Bailey DW, Rittenhouse LR, Sala OE, Swift DM (1987) Large herbivore foraging and ecological hierarchies. Bioscience 37:789–799

Somers N, D'Haese B, Bossuyt B, Lens L, Hoffmann M (2008) Food quality affects diet preference of rabbits: experimental evidence. Belg J Zool 138:170–176

Soriguer RC (1981) Biología y dinámica de una población de conejos (*Oryctolagus cuniculus* L.) en Andalucía Occidental. Doñana Acta Vertebr 8:1–379

Soriguer RC (1988) Alimentación del conejo (*Oryctolagus cuniculus* L. 1758) en Doñana, SO. España. Doñana Acta Vertebr 15:141–150

Stewart AJA, John EA, Hutchings MJ (2000) The world is heterogeneous: ecological consequences of living in a patchy environment. In: Hutchings MJ, John EA, Stewart AJA (eds) The ecological consequences of environmental heterogeneity. British Ecological Society-Blackwell, Oxford, pp 1–8

Stöcklin J, Körner C (1999) Interactive effects of elevated CO_2, P availability and legume presence on calcareous grassland: results of a glasshouse experiment. Funct Ecol 13:200–209

Stöcklin J, Schweizer K, Körner C (1998) Effects of elevated CO_2 and phosphorus addition on productivity and community composition of intact monoliths from calcareous grassland. Oecologia 116:50–56

Suding KN, Collins SL, Gough L, Clark C, Cleland EE, Gross KL, Milchunas DG, Pennings S (2005) Functional-and abundance-based mechanisms explain diversity loss due to N fertilization. Proc Natl Acad Sci U S A 102:4387–4392

Van der Wal R, Bardgett RD, Harrison KA, Stien A (2004) Vertebrate herbivores and ecosystem control: cascading effects of faeces on tundra ecosystems. Ecography 27:242–252

Watson DM (2001) Mistletoe—a keystone resource in forests and woodlands worldwide. Annu Rev Ecol Evol Syst 32:219–249

Watson DM (2009) Parasitic plants as facilitators: more dryad than Dracula? J Ecol 97:1151–1159

Watson DM (2015) Disproportionate declines in ground-foraging insectiorous birds after mistletoe removal. PLoS One 10:e0142992

Wiens JA (2000) Ecological heterogeneity: an ontogeny of concepts and approaches. In: Hutchings MJ, John EA, Stewart AJA (eds) The ecological consequences of environmental heterogeneity. British Ecological Society-Blackwell, Oxford, pp 9–31

Willott SJ, Miller AJ, Incoll LD, Compton SG (2000) The contribution of rabbits (*Oryctolagus cuniculus* L.) to soil fertility in semi-arid Spain. Biol Fertil Soils 31:379–384

Xia J, Wan S (2008) Global response patterns of terrestrial plant species to nitrogen addition. New Phytol 179:428–439

Zuber D (2004) Biological flora of Central Europe: *Viscum album* L. Flora 199:181–203