

Local and landscape-scale biotic correlates of mistletoe distribution in Mediterranean pine forests

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Abstract

The study of the spatial patterns of species allows the examination of hypotheses on the most plausible ecological processes and factors determining their distribution. To investigate the determinants of parasite species on Mediterranean forests at regional scales, occurrence data of the European Mistletoe (*Viscum album*) in Catalonia (NE Iberian Peninsula) were extracted from forest inventory data and combined with different types of explanatory variables by means of generalized linear mixed models. The presence of mistletoes in stands of *Pinus halepensis* seems to be determined by multiple factors (climatic conditions, and characteristics of the host tree and landscape structure) operating at different spatial scales, with the availability of orchards of *Olea europaea* in the surroundings playing a relevant role. These results suggest that host quality and landscape structure are important mediators of plant-plant and plant-animal interactions and, therefore, management of mistletoe populations should be conducted at both local (i.e. clearing of infected host trees) and landscape scales (e.g. controlling the availability of nutrient-rich food sources that attract bird dispersers). Research and management at landscape-scales are necessary to anticipate the negative consequence of land-use changes in Mediterranean forests.

Key words: bird-mediated dispersal; Iberian Peninsula; land uses; landscape structure; *Pinus halepensis*; species distribution; *Viscum album*.

Resumen

Influencia de factores bióticos a escala local y de paisaje en la distribución del muérdago en pinares mediterráneos

El estudio de los patrones espaciales de las especies permite examinar hipótesis sobre los procesos ecológicos y factores más plausibles que determinan su distribución. Para investigar los determinantes de una especie parásita en bosques mediterráneos a escala regional, se combinaron datos sobre la presencia de muérdago (*Viscum album*) en Cataluña (NE de la Península Ibérica) extraídos del inventario forestal con diferentes variables explicativas por medio de modelos mixtos generalizados. La presencia de muérdago en masas de *Pinus halepensis* parece estar determinada por múltiples factores (condiciones climáticas, características del árbol hospedante, y estructura del paisaje) que operan a diferentes escalas espaciales, jugando los cultivos de *Olea europaea* un papel relevante. Los resultados sugieren que la calidad de los árboles hospedantes y la estructura del paisaje son importantes mediadores de las interacciones planta-planta y planta-animal y, por tanto, la gestión de las poblaciones de muérdago debería llevarse a cabo tanto a nivel local (es decir, cortando árboles hospedantes infectados) como de paisaje (por ejemplo, controlando la disponibilidad de hábitats ricos en nutrientes que atraen a las aves dispersantes). La investigación y gestión a escala de paisaje son necesarias para prevenir las consecuencias negativas de los cambios de uso del suelo en los bosques mediterráneos.

Palabras clave: dispersión mediada por aves; Península Ibérica; usos del suelo; estructura del paisaje; *Pinus halepensis*; distribución de especies; *Viscum album*.

Introduction

Understanding the processes responsible for the distribution of species is a long-standing question in ecology and a key element for developing principles for conservation management (Levin, 1992; Peterson and Parker, 1998). Processes in natural systems create distinctive patterns. The study of these patterns can, thus, help to infer hypotheses about the ecological processes and factors that shape the distribution of species. The identification of these determinants is, however, not trivial. Multiple factors are known to act across a hierarchy of spatial and temporal scales, and their resultant scale-dependent effects are responsible for the distribution of different species (Hortal *et al.*, 2010) and of the concomitant ecological relationships between them (García *et al.*, 2011).

Mistletoes provide an interesting example of a forest species whose occurrence is expected to be constrained by multiple factors, as a consequence of its complex life-habit. The term mistletoe does not refer to a lineage of plants, but a functional group of hemi-parasitic shrubs that obtain the water and minerals from their hosts (woody plants) via a specialized vascular attachment (Watson, 2001). As a consequence of this growth-form, mistletoes are less affected by large-scale abiotic conditions but depend on the availability of suitable host to establish and mature. The main dispersers of mistletoe seeds are birds, which play a prominent role in the transfer of seeds at both short and long-distances from the host tree (Zuber, 2004).

Because of these complex interactions (mistletoe-hosts vs. mistletoe-birds), the distribution of mistletoes is not necessarily and strictly tied to the distribution of the hosts (Watson, 2009a). Mistletoe presence is constrained at different spatial scales by a wide range of factors, including the abiotic limitations of temperature and water availability on mistletoe growth (Zuber, 2004), the biotic specificity regarding the host type and quality (de Buen *et al.*, 2002), and landscape-scale biotic factors influencing the abundance and movement of their main bird dispersers (García *et al.*, 2009; MacRaid *et al.*, 2010; Rodríguez-Cabal *et al.*, 2007). Abiotic conditions and host quality affect the availability of suitable habitats for mistletoe establishment (Watson, 2009b), while landscape properties—such as fruiting neighborhood (Carlo and Aukema, 2005), tree spatial distribution and size structure (Aukema, 2004; Kathleen, 1995)—influence the behavior of animal dispersers and modify seed deposition (Morales and Carlo, 2006).

Despite the above-mentioned studies examining the distribution patterns of mistletoes, there is a lack of knowledge on how the landscape structure shapes mistletoe-host and mistletoe-dispersers interactions over broad spatial extents (Bowen *et al.*, 2009). Recent studies highlight the relevance of landscape-scale factors in determining the distribution patterns of mistletoes (e.g. Bowen *et al.*, 2009; MacRaid *et al.*, 2010; Rodríguez-Cabal *et al.*, 2007), but few have assessed the relative role of landscape structure vs. other factors acting at multiple scales, such as climate and host characteristics. To determine the relative importance of different factors susceptible to influence the distribution of mistletoes at regional scales, we combine occurrence data of the European Mistletoe in a Mediterranean region (Catalonia, NE Iberian Peninsula) with several variables—climatic gradients, local characteristics of the host tree and forest plot, and availability of suitable habitats for mistletoes and dispersers at landscape scales—susceptible to influence it.

Methods

Study species and main dispersers

The European Mistletoe (*Viscum album* L.) has three widely distributed subspecies and one geographically restricted subspecies that differ in host specificity (Zuber and Widmer, 2009). In the Iberian Peninsula, the main hosts are pine (*Pinus halepensis* and *P. sylvestris*) and fir species (*Abies alba*), although mistletoes have been found parasitizing other hosts (such as birch and oak trees) (Lopez-Saez and Sanz de Bremond, 1992). Birds have been described as the main vectors of mistletoes seed dispersal. Berries may be an attractive food in wintertime (ripening starts from November to December) and birds feed on it and spread the seeds from February to March (Zuber, 2004).

In the NE Iberian Peninsula the main dispersers of mistletoes are frugivorous passerine birds of the genus *Turdus*, such as the Mistle Thrush (*Turdus viscivorus*) (Raül Aymí, personal communication) or Fieldfare (*Turdus pilaris*), although smaller species such as the Blackcap (*Sylvia atricapilla*) have also been associated with mistletoes' dispersal in Europe (Zuber, 2004). There is not a detailed study of the habitat preferences of these vectors, but they are known to inhabit open woodlands close to nutrient-rich food sources (such as cultivated fields) (Estrada *et al.*, 2004; Rey, 1995). The abundance of *S. atricapilla* has also been associated with orchards of *Olea europaea* in Andalusia (S Ibe-

rian Peninsula) (Rey, 1995), and *T. viscivorus* is also known to feed on Olive orchards in the South of the study area (Raül Aymí, personal communication).

Occurrence data

Occurrence data on the distribution of the European Mistletoe were extracted from the third Spanish National Forest Inventory (SNFI III; DGCN, 2007), which provides information on timber volume, species composition and sustainable development of forest resources at the plot level for the years 1997-2007. Plots correspond to circular areas of 25 m radius separated by 1 km distance. Each plot is divided into nested sub-plots of 5, 10, 15 and 25 m radius, where trees of different diameter are measured. In the innermost sub-plot (of 78.54 m²) all trees with diameter at breast height (DBH) ≥ 7.5 cm were sampled, whereas in the outer sub-plots (of 314.16, 706.86 and 1,963.5 m²) only bigger trees were sampled (DBH ≥ 12.5 , 22.5 and 42.5 cm, respectively). For all sampled trees in the plot the diameter at the breast height and the height of the tree were measured, as well as the presence/absence of *V. album*. Mistletoes abundance per sampled tree was not recorded, so we used presence/absences at the tree level for the analysis. The total number of plots considered in the analysis was 10,255; plots with incomplete data (i.e. missing information in some of the considered variables) were excluded to not bias the final results.

Preliminary analysis

To know the prevalence of the European Mistletoe in the study area, we calculated the number of parasitized sites and trees of different host species. The analyses show that 3.9 % of the sampled plots ($n = 10,255$) are occupied by mistletoes, with only 0.8 % of all sampled trees ($n = 205,157$) infected. The most affected host species is *P. halepensis* (11.6% of the plots with *P. halepensis* [$n = 2,839$] and 4.4% of sampled *P. halepensis* trees [$n = 29,032$] infected), followed by *P. sylvestris* (1.6% [$n = 3,004$] and 0.5% [$n = 43,200$], respectively) and *A. alba* (0.9% [$n = 225$] and 0.2% [$n = 3,772$], respectively) in minor proportions. We also plotted infected and non-infected sites on a geographic space, and found that *V. album* presents a main population on stands of *P. halepensis* in the South, and a smaller one on stands of *P. sylvestris* in the North (Fig. 1).

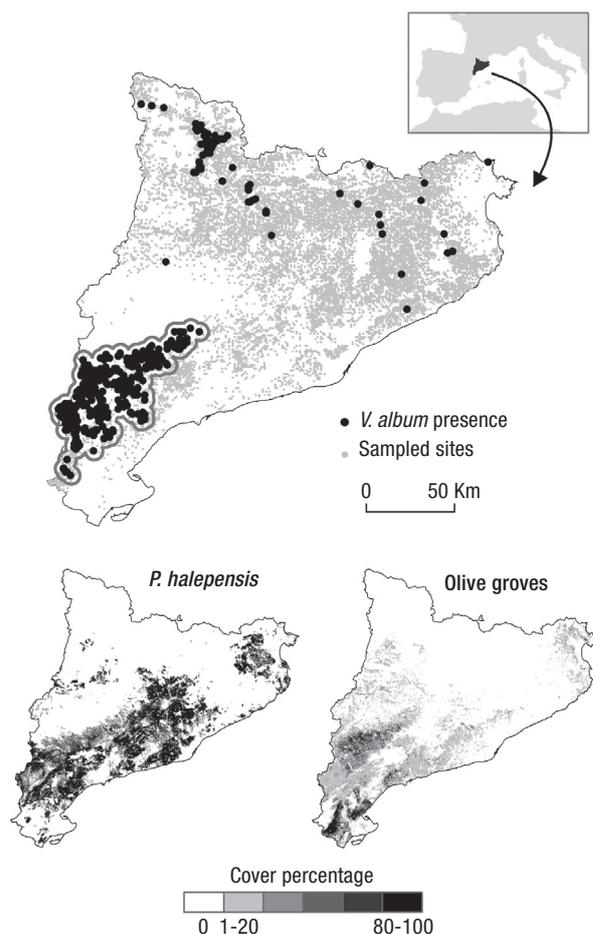


Figure 1. Distribution of *Viscum album* in Catalonia, and visualization of some explanatory variables related to the distribution of the main host species (*Pinus halepensis*) and nutrient-rich habitats for bird dispersors (Olive groves).

Explanatory variables

Data on the occurrence of mistletoes on the most parasitized host (i.e. *P. halepensis*) were complemented with various abiotic and biotic variables, which were selected based on plausible ecological hypothesis (Zuber, 2004). Abiotic variables refer to climatic conditions, while biotic determinants are related to host characteristics and habitat preferences of its main dispersors (see subsection *Study species and main dispersors*) at both local and regional scales (Table S1).

Climatic conditions.—Mistletoes are adapted to temperate climates, although cold areas can be inhabited if the temperature in summer is proportionally higher (Zuber, 2004). We thus expect to find a positive relationship between mean annual temperature (T_{AN} ;

tenth of °C) and mistletoes' occurrence. Other variables (such as annual precipitation and annual solar radiation) could indirectly influence the growth of mistletoes, but we limited the number of variables to those having a direct influence to reduce the number of combinations in the model selection procedure (see below). Data were extracted from the Climatic Atlas of Catalonia (Ninyerola *et al.*, 2000; 180 m × 180 m resolution).

Host tree.—The occurrence of mistletoes depends on suitable hosts that provide the resources necessary for their growth, but also on the number of times that the host has been visited by dispersers of mistletoe seeds. Host trees (*P. halepensis*) of a considerable size that have been in the region for a long period are, therefore, expected to have a higher deposition of seeds than younger trees (Aukema, 2004). We thus included two variables extracted from the SNFI III (DGCN, 2007): height (*H*; m) and diameter (*DN*; cm) of individual trees in each sampled plot, as surrogates of the host characteristics.

Forest plot.—The deposition of mistletoe seeds might not only depend on the characteristics of the host trees, but also on the characteristics of the neighboring trees that make a locality more or less attractive for bird dispersers. Frugivorous birds shift between habitats that provide different kinds of resources (e.g. cultivated fields for feeding vs. neighboring woodlands for cover), and thus open the ground for landscape effects on species occurrence patterns (García *et al.*, 2010). Two measures were thus included at the plot level: the density of trees (*dtree*; trees/ha) and the mean diameter of trees (*DN_m*; cm). Considering the nested structure of the SNFI III plots, *dtree* was calculated by first measuring the density of trees presenting a diameter between the range considered in each particular sub-plot and then summing up all the sub-plot densities. For example, the density of trees in the sub-plot of 10 m radius was calculated by counting the number of trees with a diameter between 12.5 and 22.5 cm and dividing it by the area of the sub-plot in hectares ($A_{10} = (\pi \cdot 10^2)/10,000 = 0.031$ ha).

Similar to the calculation of *dtree*, the mean diameter of trees (*DN_m*) was found by first calculating the basal area of all trees measured in the forest plot and then dividing it by the area of the sub-plot at which trees with that particular diameter were measured. The basal area of a tree corresponds to the cross-sectional area of a tree trunk at the breast height; it is calculated as: $BA_i = \pi \cdot (DN_i/2)^2$, where *DN_i* corresponds to the diameter of the trunk of tree *i*. However, to account for

the nested structure of the sampling design, we had to estimate the basal area of each tree per unit area. For example, the basal area of a tree with a diameter of 15 cm was divided by the area of the sub-plot of 10 m radius (i.e. 0.031 ha). Next we summed up the basal area per unit area of all trees and divided it by *dtree* to obtain the mean basal area per unit area of a tree in the plot (*BA_m*). Finally, we calculated the mean diameter of trees applying the formula $DN_m = ((BA_m/\pi)^{1/2}) \cdot 2$.

Landscape structure.—Besides the influence of local-scale correlates, landscape-scale variables associated with available hosts and bird dispersers are also susceptible to explain the patchy distribution of mistletoes at regional scales (MacRaidl *et al.*, 2010). Considering the host-specificity of the species and the potential foraging requirements of its main dispersers (see subsection *Study species and main dispersers*), we thus calculated the percentage of area covered by *P. halepensis* (*Phal*; %) and orchards of *O. europaea* (*Olive*; %) at 100, 250, 500 and 1000 m from the centre of the sampling unit. The different scales of analysis are used to examine the scale at which mistletoe dispersers forage and therefore deposit their previously ingested seeds. Short distances indicate that birds search for optimal habitats at small distances and the dispersal of seeds occurs at small scales, while long distances suggest that the deposition of mistletoe seeds in a certain host tree depends on the distribution of habitats present in a bigger surrounding area. Data on the distribution of *P. halepensis* was extracted from the SNFI III (DGCN, 2007), while data on Olive orchards from the Geographic Information System of Agricultural Plots (MAMRM, 2010; 1:10,000 scale).

Modeling approach

Because of the mistletoe-host specificity and the species' patchy distribution, we examined the occurrence of mistletoes on the main host species (*P. halepensis*) at two different spatial scales: Catalonia and core distributional area (i.e. areas at <5000m from the main pool of presence localities; Fig. 1, perimeter in grey). We regressed the presence/absence of mistletoes at the tree level with various explanatory variables using generalized linear mixed models. We assumed that the response variable followed a binomial distribution with its probability parameter being dependent on the explanatory variables. Plot identity was included as a random factor, accounting for the hierarchical

structure of the sampling design since trees within the same plot are not independent (Bolker *et al.*, 2009). Explanatory variables were standardized by subtracting the mean value of the variable in the study area from each individual value and dividing the difference by the standard deviation.

We examined all possible combinations of the seven explanatory variables (i.e. 127 models) and chose the best ones based on Akaike Information Criterion (AIC) (Quinn and Keough, 2002). The AIC measures the goodness of fit of a statistical model while taking into account the number of predictors included in the models (Akaike, 1974). Smaller values of AIC indicate better, more parsimonious, models. If many models have similar low AICs, we then calculated the difference in AICs between each model and the model presenting the lowest AIC and chose the one with the fewest number of variables. As a rough rule of thumb, Burnham and Anderson (2002) propose that models for which $\Delta AIC \leq 2$ receive substantial support and are considered when making inferences, models having $4 \leq \Delta AIC \leq 7$ have considerably less support, and models having $\Delta AIC \geq 10$ receive no support. A likelihood ratio test was also used to confirm that the selected model explained a similar amount of variance than more complex models with $\Delta AIC < 4$ and a significantly greater amount of variance than simpler models. The log-likelihood of the selected model was compared with the likelihood of these models using a χ^2 distribution with as many degree of freedom as the difference of variables used in both models. If $\Delta AIC < 4$ and the p -value did not drop significantly (> 0.05), then we chose the model with fewer variables (Lindsey, 2000).

Prior to this model selection process, we identified the radius of influence of the two landscape variables (percentage of cover of *P. halepensis* and Olive orchards, respectively). These variables were measured at different distances from the center of the sampling plot (100, 250, 500 and 1,000 m), and the most influential distance was identified by comparing the AIC of the univariate models generated at different distances from the center of the sampling plot. The distance giving the lowest AIC model was considered as the most appropriate to use in the model selection process with the other explanatory variables.

We evaluated the relative importance of explanatory variables included in the final selected model. For each variable we compared the deviance of the full model with the deviance of a model that excluded the target variable and also with the deviance of a model

constructed including only the target variable. The deviance can be regarded as a measure of lack of fit, with larger deviances indicating a poorer fit of the data. Highly relevant variables are, therefore, expected to increase the deviance when removed from the full model and present a similar deviance to the parsimonious model when considered alone. We preferred to examine the effect of explanatory variables through deviances than using the estimates of the models to avoid multicollinearity effects. Additionally, since generalized linear mixed models do not have a measure of model fitness (such as R-squared in linear regression), we calculated the explained variance of the final selected models as:

$$100 \times (\text{null deviance} - \text{residual deviance}) / \text{null deviance}$$

The null deviance corresponds to the worst possible model (only an intercept), while the residual deviance to the deviance of the model with the best possible fit (Zuur *et al.*, 2009). All the analyses were performed using the R package “lme4” (Bates and Maechler, 2009).

Results

The analyses aiming to identify the radius of influence of the landscape variables provided similar results at the two scales of analysis (Table S2). The percentage of area covered by *P. halepensis* is important at small distances (100 m for the analysis conducted in Catalonia, and 250 m in the southernmost core distribution), while the percentage of area in Olive orchards is relevant at the highest distance (1,000 m) at both scales of analysis (Table S2).

The most parsimonious model assessing the distribution of mistletoes in Catalonia includes all variables except the percentage of area covered with *P. halepensis* (Table 1a). It is important to note, however, that this model explains a similar amount of variance than the full model ($P > 0.05$), but a significantly different amount than simpler models ($P < 0.001$; Table 1a). When considering the southernmost core distribution, the most parsimonious model is the one including mean annual temperature, the diameter of the host tree, the mean diameter of the forest plots and percentage of area covered with orchards of Olive trees at 1,000 m (Table 1b). As previously, the variance explained in this models is similar to other models that also include the height of the host tree and the percentage of sur-

Table 1. Generalized linear mixed models explaining the distribution of *Viscum album* on *Pinus halepensis* at two different spatial scales: (a) Catalonia and (b) southernmost core distribution (Fig. 1). Only the best-subset models (those with a $\Delta AIC < 4$; abbreviated as BS) were presented, as well as the full model (F) and simpler models (S) generated by removing a different variable at a time from the parsimonious model (P, highlighted in bold). Each row corresponds to a different model. Columns third and fourth refer to the AIC analysis, while the other ones to the likelihood ratio test comparing each model with the most parsimonious one. See abbreviations of variables in the Methods

Models	Model type	AIC	ΔAIC	LogLik	χ^2	df	P
(a) Cat_{Phal}							
$T_{AN} + HT + dtree + DNm + Olive1000$	S	5,628.8	796.2	-2,807.4	798.2	1	< 0.001
$T_{AN} + DN + dtree + DNm + Olive1000$	S	5,577.3	744.7	-2,781.7	746.7	1	< 0.001
$T_{AN} + HT + DN + dtree + DNm$	S	5,313.1	480.5	-2,649.6	482.5	1	< 0.001
$T_{AN} + HT + DN + DNm + Olive1000$	S	4,910.4	77.8	-2,448.2	79.8	1	< 0.001
$T_{AN} + HT + DN + dtree + Olive1000$	S	4,879.6	47.0	-2,432.8	49.0	1	< 0.001
$HT + DN + dtree + DNm + Olive1000$	S	4,861.2	28.6	-2,423.6	30.6	1	< 0.001
$T_{AN} + HT + DN + dtree + DNm + Olive1000$	P	4,832.6	–	-2,408.3	–	–	–
$T_{AN} + HT + DN + dtree + DNm + Phla0100 + Olive1000$	BS/F	4,834.2	1.6	-2,408.1	0.42	1	0.52
(b) Core_{Phal}							
$T_{AN} + DNm + Olive1000$	S	4,727.9	304.3	-2,358.9	306.3	1	< 0.001
$T_{AN} + DN + DNm$	S	4,485.2	61.6	-2,237.6	63.5	1	< 0.001
$T_{AN} + DN + Olive1000$	S	4,434.5	10.9	-2,212.2	12.9	1	< 0.001
$DN + DNm + Olive1000$	S	4,428.8	5.2	-2,209.4	7.3	1	0.007
$T_{AN} + DN + DNm + Olive1000$	P	4,423.6	–	-2,205.8	–	–	–
$T_{AN} + HT + DN + DNm + Olive1000$	BS	4,424.7	1.1	-2,205.4	0.90	1	0.34
$T_{AN} + DN + DNm + Phla0250 + Olive1000$	BS	4,425.1	1.5	-2,205.6	0.49	1	0.48
$T_{AN} + HT + DN + DNm + Phla0100 + Olive1000$	BS	4,426.2	2.6	-2,205.1	1.39	2	0.50
$T_{AN} + HT + DN + dtree + DNm + Phla0100 + Olive1000$	F	4,733.1	309.5	-2,357.5	0	3	1

rounding landscape covered with *P. halepensis* separately and together ($P > 0.05$), but significantly different than simpler models ($P < 0.01$; Table 1b). When included in the most parsimonious models, the height of the host tree and the characteristics of the forest plot seem to have a negative influence on mistletoe distribution at the two scales of analysis, while the rest of the selected variables a positive one (Table 2).

According to the analysis of deviance used to identify the relative importance of variables, the most influential variables included in the parsimonious model developed in Catalonia are those variables related to the local characteristics of the host tree and the percentage of area covered with Olive orchards at landscape scales (Fig. 2a). When reducing the analysis to the southernmost core distribution of mistletoes, the most important variables seem to be the ones describing the characteristics of the host tree (Fig. 2b). To confirm that the relevance of Olive orchards in Catalonia is due to the influence of mistletoe dispersers and not to a spatial relationship with the host distribution, we calculated

the Pearson correlation coefficient between the percentage of Olive orchards at 1,000 m and the percentage of area in *P. halepensis* at 100 m. The correlation coefficient was positive but not high ($r = 0.25$, $P < 0.0001$), and this result suggest that the influence of Olive orchards can be considered a good surrogate of the distribution of bird dispersers at regional scales.

Discussion

Viscum album presents a patchy distribution in Catalonia, with two climatically-distinct populations. The main population in the South is located in a landscape dominated by orchards of *O. europaea*, with mistletoes parasitizing forest remnants of *P. halepensis* at the immediacy of the orchards. The smaller population grows on stands of *P. sylvestris* in the North, in a mountainous area with more extreme winter conditions. This capacity of the species to occur in a wide range of climatic conditions contrasts with the current

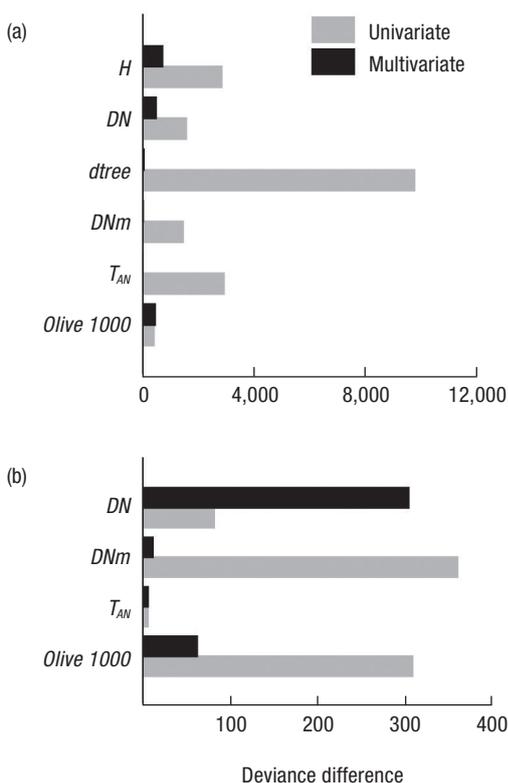


Figure 2. Relative influence of the explanatory variables included in the parsimonious models examining the distribution of *Viscum album* in Catalonia (a) and its southernmost core distribution (b). The bars indicate the difference in deviance (which represents the lack of fit of the model) between the parsimonious model and two additional models: the parsimonious model removing the target variable (black bars) and a model including the target variable alone (grey bars). The most influential variables are expected to present big black bars and small grey bars. See Methods for abbreviations of variables.

distribution of the species, which does not seem to occupy the entire potential range of the main host species (*P. halepensis*) even though the climatic conditions are suitable and the host is present. We hypothesize that this situation of partial range filling is mostly derived from dispersal constraints conditioned by large-scale landscape structure.

Overall, our findings suggest that the distribution of *V. album* in stands of *P. halepensis* is attributable to long-term responses of the species to the availability of suitable host plants (mistletoe-host interactions) and to the availability of habitats influencing the presence of bird dispersers at landscape scales (mistletoe-dispersers interactions). These patterns have been found for other mistletoes species but over much smaller spatial extents (García *et al.*, 2009). Climatic conditions

and neighboring forest plots had a relatively small influence, while the characteristics of the host tree and the presence of favorable habitats for its dispersers at landscape scales had the highest relevance. The percentage of area covered with Olive orchards—used a surrogate of dispersers’ abundance (Rey, 1995)—played a prominent role when examining the occurrence of the species in Catalonia, but the characteristics of the host tree—especially the diameter of the tree—appeared as the most relevant variable when considering the southernmost core distribution with a more homogeneous distribution of the Olive orchards. Differences in mistletoe abundances between southwestern and northeastern forests of *P. halepensis* could, thus, be primarily linked to the unequal distribution of habitats suitable for the most important dispersers of mistletoes across Catalonia.

As expected, the diameter of the host tree had a local positive influence: the bigger the diameter, the more probable was to find the species. Trees with big diameters tend to present big canopies and have been in the area for long time, which increases the chances of arrival and establishment of mistletoes seeds dispersed by birds (Aukema, 2004). On the contrary, the density and the mean diameter of forest plots had a negative but minor influence at both scales of study. The prefer-

Table 2. Fixed effects in the most parsimonious generalized linear mixed model explaining the distribution of *Viscum album* on *Pinus halepensis* at two different spatial scales: (a) Catalonia and (b) southernmost core distribution (Fig. 1). *z*-statistics and corresponding *P*-values test the null hypothesis that the parameter estimate is equal to 0 in that particular model. The explained variance (see Methods) of the model developed in Catalonia is 31%, while the explained deviance of the model developed in the southernmost core distribution is 8%

Fixed effects	Estimate	SE	<i>z</i> -value	<i>P</i>
(a) Cat _{Phal}				
<i>T_{AN}</i>	8.8	2.1	4.1	< 0.001
<i>HT</i>	-1.3	0.4	-3.3	0.001
<i>DN</i>	110.3	7.1	15.6	< 0.001
<i>dtree</i>	-907.9	125.7	-7.2	< 0.001
<i>DNm</i>	-45.9	8.1	-5.6	< 0.001
<i>Olive1000</i>	18.0	1.2	14.4	< 0.001
(b) Core _{Phal}				
<i>T_{AN}</i>	5.4	2.0	2.7	< 0.01
<i>DN</i>	103.7	6.2	16.7	< 0.001
<i>DNm</i>	-24.8	7.3	-3.4	< 0.001
<i>Olive1000</i>	7.0	0.9	8.1	< 0.001

ence of mistletoes for low density forests with trees of small diameter could be linked to the habitat requirements of its main bird dispersers, which tend to inhabit open woodlands close to nutrient-rich habitats (see subsection *Study species and main dispersers*). However, this interpretation needs further support, as methodological limitations inherent to the hierarchical sampling design may decrease the correlation between tree or plot characteristics and mistletoe occurrence. For example, the use of a limited gradient of tree diameters could hinder the detection of mistletoes in small trees. Similarly, the indices used to characterize the thickness and age of the forest plots (i.e. density and mean diameter of trees) could be insufficient and therefore limit the predictive power of these attributes in front of other variables (such as the characteristics of the host tree and the presence of favourable habitats for dispersers).

In any case, the relatively low importance of forest plot attributes in determining the dispersion of mistletoe seeds as measured in this study seems supported by the absence of the percentage of area covered in *P. halepensis* from the models. Birds track habitats for fruits and seeds more than suitable habitats for nesting. The unexpected negative influence of the host's height on the distribution of mistletoes in Catalonia can be due to the highest occurrence of mistletoes on *P. halepensis* (see subsection *Preliminary analysis*), which present a lower height than other suitable mistletoe host trees (i.e. *P. sylvestris* and *A. Alba*). Nevertheless, the absence of this variable from the model describing the southernmost distribution of mistletoes indicates that this variable plays a negligible role. These results suggest that, although suitable hosts (i.e. big pines) may condition mistletoe presence on local pine woodlands, the regional patterns of mistletoe occurrence seem to be unaffected by the large-scale distribution of hosts but driven by the availability of fruit-rich habitats that attract bird dispersers.

Seed dispersal by frugivorous animals is responsible for the distribution of various plant species (Zamora *et al.*, 2010), and in particular of mistletoes (Aukema, 2004; García *et al.*, 2009). There is not scientifically-proven evidence of the influence of birds on the distribution of mistletoes in our study area, but the importance of the percentage of area covered with Olive orchards suggests that the occurrence of mistletoes on *P. halepensis* could be highly influenced by the ecology of its main dispersers. *T. viscivorus* and other relevant species would feed on nutrient-rich food

sources close to woodlands, favoring the dispersion of mistletoe seeds between nearby forest when tracking fruits of higher nutritional value (such as Olive trees). As a consequence of large-scale fruit resource tracking, frugivorous birds would promote disproportionate seed dispersal and establishment on mistletoe occupied areas surrounded by Olive orchards (García and Ortiz-Pulido, 2004; Wenny and Levey, 1998). However, the influence of bird-dispersers has only been examined indirectly through the availability of Olive orchards and other variables related to the presence of fruit rich habitats (such as soil productivity) could better explain the effect of birds on the distribution of mistletoes. Further studies would be necessary to confirm the neighboring effect of Olive orchards on the European Mistletoe.

The existence of this neighboring effect would presuppose that patches affect each other in a positive or negative way, depending on: (i) the spatial arrangement of patches in a heterogeneous landscape, and (ii) the kind of organism considered and their movement abilities (Chust *et al.*, 2003; Wiens, 1989). The negative consequences of these effects on forest health -due to the creation of new parasite foci or the long-term re-infestation of once colonized hosts- contrasts with the positive restoration effects that zoochorous dispersion exerts when leading to seed transfer from higher-quality patches to low-diversity, homogeneous pine plantations (Zamora *et al.*, 2010), or from mature forests to deforested, degraded habitats (García *et al.*, 2010). These both positive and negative effects of plant-animal interactions have potential consequences for the functioning of forest ecosystems and, consequently, the relevance of the landscape structure should be explicitly considered when studying the dynamics of organisms —and mistletoes in particular— at regional scales.

It is important to note, however, that it was possible to evaluate the distribution of *V. album* in stands of *P. halepensis* because the mistletoe-disperser components of the landscape that explain the establishment of mistletoes interaction are still present. A similar analysis was attempted to examine the northernmost distribution of mistletoes in stands of *P. sylvestris* (not included in this study, but statistically verified), but it did not give conclusive results. A potential hypothesis for these results is that past land-uses, not the current nearby habitats, determined the distribution of the European Mistletoe. Mediterranean landscapes have undergone severe changes in the last decades, as a consequence of socio-economic changes and the high

influence of humans. This effect has been relatively important in mountainous regions (such as in the northernmost distributional area of the European Mistletoe), where the abandonment of traditional rural activities has promoted the progression of forest at the expenses of open habitats. We think that these dynamics might have masked the influence of past land-use practices (such as grasslands or cultivated fields) that favored the establishment of *V. album* in the past.

Conclusions

Our study raises some hypothesis about the role of landscape structure as an important driver of plant-plant and plant-animal interactions. Landscapes correspond to heterogeneous geographic areas composed of multiple interacting components, from natural terrestrial and aquatic systems to human-dominated environments. The occurrence and spatial arrangement of these components determine the establishment/maintenance of certain biotic interactions and, therefore, of the involved species (mistletoes, their host plants and their bird dispersers). The recognition of these landscape-scale biological correlates is important to identify the elements responsible for the distribution of organisms, but also to design efficient management strategies to prevent (or at least mitigate) the negative consequences of land-use changes and the expansion of pest species in natural ecosystems (Norton and Reid, 1997). This is especially important in a context of global change, where Mediterranean forests are expected to be heavily vulnerable to extreme climatic events and outbreaks of undesired species. The presence of parasite species, such as mistletoes, could be enhanced under extreme conditions and have an increasingly strong impact on trees.

In this sense, our results suggest two important aspects to consider when managing the biological biodiversity of woodland ecosystems. First, the preservation of biological diversity cannot be done regarding species as isolated entities. The clearing of infected hosts controls the spread of *V. album* at local scales (patch level), but it does not ensure an efficient management of the pest at regional scales (landscape level). Second, the factor responsible for the distribution of *V. album* at regional scales seems to be the distribution of suitable habitats (i.e. nutrient-rich food sources such as Olive orchards) for its main dispersers. Therefore, when the aiming to reduce the occurrence of mistletoes, it is

necessary to both control the number of infected host trees of a certain size at local scales and the availability of nutrient-rich fruits (such as Olives orchards) through planned pickings at regional scales. It is, thus, necessary to encourage research at landscape scales where multiple interactions can be evaluated and management measures can be adopted to minimize—or at least contain—the negative consequences of future changes in the distribution of Mediterranean forests.

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Supplementary data

Table S1. Summary of the explanatory variables used in the study.

Table S2. Models examining the influence of landscape-related variables at different distances from the sampling plot.

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