

The role of bird seed dispersers in determining forest species distribution patterns: a case study of *Viscum album* in Catalonia, Spain

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Seed dispersal by birds plays a crucial role in structuring landscape dynamics and supporting biodiversity. This animal-plant mutualism has been mostly studied in small scale extents, but the knowledge of landscape-wide processes is still scarce. Different biodiversity indicators can be used to study seed dispersal: the abundance of birds is related to the capacity of the frugivore assemblage to disperse seeds and influence the landscape structure; bird richness is related to the resilience of the assemblage to disturbances and change, and functional traits (e.g. dispersal mode or distance) are related to the actual capability of each species and individual to disperse seeds. In this study, we developed a set of general bird dispersal indicators based on species distribution models (SDMs) of bird dispersers to investigate, whether these indicators could explain the distribution patterns of *Viscum album* (European mistletoe) at different spatial scales in Catalonia, Spain. We used generalized linear mixed models to predict *V. album* distribution based on climatic conditions, bird dispersal indicators, and forest plot/host tree characteristics. To determine the dispersal range, we tested the indicators at different spatial resolutions. Results showed that different processes influence the distribution of *V. album* at the regional level (southern vs. northern parts of Catalonia). Richness of bird dispersal species explained best southern mistletoe distribution patterns, whereas the northern distribution of *V. album* could not be clearly linked with any dispersal indicator. These results suggest that on a landscape scale, different processes (present and historical) influence seed dispersal patterns of birds and consequently forest plant species distribution. Nevertheless, on top of the potential dispersal capability by birds, the heterogeneity of a landscape and the ecology of dispersers also needs to be considered in order to fully understand and predict the distribution patterns of *V. album*. Our approach, creating dispersal indicators based on SDMs of birds and using them to predict large scale plant species distribution, helped to shed light on the very complex process of seed dispersal at the landscape scale. This could open up new areas of study and aid the understanding of the ecological processes behind seed dispersal patterns at large spatial scales, thus guiding biodiversity management in a more efficient way.

Keywords: frugivory, biodiversity indicators, landscape structure, Iberian Peninsula, ecosystem services, animal-plant interaction;

1. Introduction

Birds provide a wide range of ecosystem services, including supporting, provisioning, regulating, and cultural services (Whelan et al. 2008). Especially through the provision of supporting services (i.e. pest control, scavenging, pollination, and seed dispersal; Whelan et al. 2008), they play an important ecological role in their ecosystems. Seed dispersal has been linked with all major drivers of biodiversity change, namely habitat fragmentation, overharvesting, biological invasions, and climate change (Pereira et al. 2010). For instance, seed dispersal by frugivorous birds has been

shown to influence landscape dynamics by structuring its heterogeneity and by promoting forest diversity (Jordano and Schupp 2000, García et al. 2011). In undisturbed habitats, this animal-plant mutualism drives plant gene flow and population dynamics, whereas in deforested land it can be critical for vegetation recovery (Kremen et al. 2007). Dispersal interactions have been extensively studied at the local scale, for example through studying the relationship between the attributes of a frugivore assemblage (e.g. species composition) and different components of dispersal like arrival or colonization rate of seeds (e.g. García and Martínez 2012) or by modelling dispersal interaction networks based on previously made observations of fruit consumption and seed deposition characteristics (e.g. García et al. 2018; Rodríguez-Pérez et al. 2017). However, the knowledge of landscape-wide processes related to seed dispersal by birds is still scarce. Indicators based on avian distribution data are a widespread tool to study environmental changes such as the impact of land abandonment on biodiversity or the status of biodiversity itself (e.g. Herrando et al. 2016; Gregory et al. 2005; Morelli et al. 2014), mainly due to high availability of freely accessible data (Engler et al. 2017). However, the use of bird-based indicators to study seed dispersal processes at large scales is a novel approach and requires the linkage of the knowledge of local dispersal processes to the distribution of birds as well as plant species at larger scales.

In general, seed dispersal processes can be divided into quantity and quality components (Jordano and Schupp 2000). Dispersal quantity describes the amount of seeds dispersed whereas dispersal quality refers to the probability of these seeds to be established within the landscape. Different biodiversity indicators (i.e. bird species abundance and richness) have been linked to the quantitative component of seed dispersal, whereas species specific traits can be related to both the quantitative and qualitative components (García et al. 2010, García and Martínez 2012, García 2016):

- (1) The abundance of birds has been shown to have a strong link with successful seed dispersal (García et al. 2018) and thus has been proposed to be a general coarse-grain indicator for dispersal processes (García et al. 2010). It indirectly reflects the habitat preferences of birds, as well as fruit availability (Telleria, Jose, L. et al. 2008; Donoso et al. 2017). Furthermore, quantitative dispersal factors (i.e. seed density and richness, visitation rate of dispersers, and interactions between bird species) are also correlated to this measure (Donoso et al. 2017, Carnicer et al. 2009, García et al. 2018, Jordano and Schupp 2000).

(2) Species richness provides a more qualitative measure of seed dispersal (García and Martínez 2012). The richer the frugivore assemblage, the higher the functional diversity of species traits and behavior. This results in more diverse diets and habitat uses of the dispersers, seed rain and eventually colonization and regeneration of plant species (Rodríguez-Pérez et al. 2017, García and Martínez 2012, García et al. 2018).

(3) Functional traits of birds related to their behavior and morphology determine whether a particular habitat and fruit resource is utilized or not and eventually, also serve to estimate the effectiveness of seed dispersal (quality component). These traits include the species diet (e.g. frugivorous vs. insectivorous), degree of specialization (generalists vs. specialists), dispersal mode (endozoochory vs. ectozoochory), and movement patterns. Whereas diet has been shown to depend more on fruit availability than on species specific preferences (García et al. 2013), dispersal mode and degree of specialization influence seed dispersal patterns as well as the quantity and quality of dispersed seeds (Jordano and Schupp 2000, Mellado and Zamora 2014a). In general, frugivore assemblages can be divided into three categories (Jordano and Schupp 2000): seed dispersers (SD), pulp consumer (PC) and pulp consumer-dispersers (PCSD). Studies have shown that the most effective dispersers by far are the ones that disperse seeds through endozoochory (SD), whereas PCSD only occasionally disperse seeds by carrying them to another tree to consume its pulp and PC very rarely contribute to seed dispersal. Within the group of SD, body size greatly determines the seed dispersal effectiveness of a species (Jordano & Schupp 2000). This is mostly related to the feeding rate, because bigger species (with bigger gape widths) can feed on more fruits in the same amount of time. Furthermore, more generalist species have been related to greater seed dispersal (García 2016), whereas the degree of specialization is inversely linearly correlated with body size (García et al. 2018). Hence, bigger dispersers are less specialized and disperse seeds more effectively. This is in line with the fact that bigger dispersers can handle fruits of all sizes, whereas small dispersers are limited to smaller fruit sizes. Thus, among multiple bird traits, body size can be used as indicator of seed dispersal capacity, as it has been proven to relate to dispersal distance (Morales et al. 2013), degree of specialization (García 2016, García et al. 2018, Carnicer et al. 2009, Jordano and Schupp 2000), as well as dispersal effectiveness (Mellado and Zamora 2014a).

To analyze the effectiveness of indicators, they need to be tested under different contexts. The European mistletoe (*Viscum album L.*) is a parasitic plant that is sessile in nature and relies completely on birds to disperse its seeds (Zuber 2004). These characteristics make it an ideal case study species to test the value of seed dispersal indicators at explaining plant species distributions at different spatial scales. Previous studies have linked *V. album* distribution to microclimatic conditions, distribution of host trees, forest cover and single tree structures, as well as to the seed dispersal patterns of birds and interactions with other organisms like seed predators (Roura-Pascual et al. 2012, Mellado and Zamora 2014a, Mellado and Zamora 2014b, Zamora and Mellado 2019). Additionally, the species has been shown to act as center of attraction for many dispersers, thus indirectly influencing the regeneration of other plant species and ultimately the heterogeneity of the landscape (Mellado et al. 2017, Hódar et al. 2018). Nevertheless, these studies were performed at small scales and thus knowledge about factors that influence the landscape-wide distribution of the species are still missing.

In this study, we aimed to develop a general set of bird seed dispersal indicators and test whether they can be used to explain dispersal processes at the landscape scale considering the distribution patterns of *V. album*. Indicators were based on species distribution models (SDMs) of birds and we tested different indicator types, considering abundance, species richness, and functional traits of birds. We sought to identify different regional dispersal processes by testing the indicators at different landscape scales related to the core distributions of *V. album*. The successful application of bird-based indicators to explain species distributions could open up new areas of study and aid the understanding of the ecological processes behind seed dispersal patterns at large spatial scales, thus guiding biodiversity management in a more efficient way.

2. Methods

2.1. Study area

The region under consideration was Catalonia, Spain. It covers ca. 32.000km² and is situated in the north-east of the Iberian Peninsula. During winter, wild fruits become a major diet component of many resident and over-wintering bird species in the region, thus providing an excellent study system for the application of seed-dispersal indicators.

2.2. Seed dispersal indicators

The main avian seed dispersers in the study area include non-migratory and migratory species, mainly of the genus *Turdus*, but also other species like *Erithacus rubecula* and *Sylvia atricapilla* which have been recorded to feed on fruits during winter months (Martínez et al. 2008; Garcia & Martinez 2012). Most of the species are legitimate seed dispersers (SD), whereas some are pulp consumers (PC) and pulp consumer-dispersers (PCSD). The species considered to be part of the indicators had to fulfill two criteria: (1) previous studies had to link the species to the dispersion of *V. album* and (2) there was enough evidence to rate species dispersal effectiveness. Using these criteria, we identified a total of 11 species related to *V. album* dispersal in the study area, with SD species being considered most effective at dispersing seeds (depending on their body weight), followed by PC and PCSD species (Table 1).

Table 1: List of species selected for inclusion in seed-dispersal indicators, ordered from most to least effective dispersers in relation to body weight and dispersal strategy (seed dispersers-SD, pulp consumer-PC or pulp consumer-dispersers-PCSD).

Species	Common name	Migratory status¹	Body weight (g)	Frugivorous type
<i>Turdus viscivorus</i>	Mistle thrush	R, OI	130	SD
<i>Turdus torquatus</i>	Ring ouzel	OM	120	SD
<i>Turdus pilaris</i>	Fieldfare	OM	110	SD
<i>Turdus merula</i>	Common blackbird	R, OI	100	SD
<i>Turdus philomelos</i>	Song thrush	R, OI	75	SD
<i>Turdus iliacus</i>	Redwing	OM	65	SD
<i>Erithacus rubecula</i>	European robin	R, OI	17	SD
<i>Sylvia atricapilla</i>	Eurasian blackcap	R, OI	17	SD
<i>Fringilla coelebs</i>	Chaffinch	R, OI	25	PC
<i>Parus major</i>	Great tit	R	17	PC
<i>Garrulus glandarius</i>	Eurasian jay	R	160	PCSD

¹R = resident, OI = overwintering individual, OM = overwintering migrant

2.3. Indicator selection

We sourced bird distribution data (i.e. distribution maps) from the Catalan Winter Bird Atlas 2006 – 2009 (CWBA; Herrando et al. 2011), which consists of species distribution models informing about the relative abundance of each species across Catalonia with a spatial resolution of 500 m (Appendix S1). For most species there was only one distribution map available, however if the distribution varied greatly over years, up to three maps were available. This was the case for two of the selected bird species (*T. iliacus* and *T. pilaris*), thus we only included the relative abundance of the year with the highest mean abundance. We combined the distribution maps of the species in Table 1 to generate four different bird dispersal indicators: (1) Disperser abundance, (2) Species Richness, (3) *Turdus spp.* Richness, and (4) Species Specialization (Table 2). To calculate the (4) Species Specialization indicator, we only considered SD species because they are the most effective dispersers and previous studies clearly established a linear relationship between body weight and degree of specialization (Jordano and Schupp 2000). To do so, we applied Community Weighted Mean (CWM) indices, weighting species with specific traits differently using body weight as surrogate. These type of indices have been shown to be more accurate in predicting ecosystem functioning than solely the aggregation of species-based (abundance or richness) indices (Gagic et al. 2015). Additionally, we estimated three different measures of each of the four indicators to test which one was able to explain *V. album* distribution best: mean values, mean values of the upper quantile (values > 75% percentile), and binary values of the upper quantile indicating presence and absence (P/A) of seed dispersal (values < 75% percentile = 0; values > 75% percentile = 1). Which species were included into which indicator, how the indicators were created, as well as indicator range values can be found in Table 2.

Table 2: List of indicators, included species, calculation process, and indicator range values. Basic relative abundance values range theoretically from 0 to 1, whereas 0 indicates no probability of occurrence and 1 total certainty of occurrence. The indicators are based on raster data of the Catalan Winter Bird Atlas 2006 – 2009 (Herrando et al. 2011), with a spatial resolution of 500 m.

Indicator	Species	Calculation Process	Indicator range
Abundance	All species	Sum relative abundance of species in each 500 m pixel and calculate the mean in each pixel	0 – 0.95

Species Richness	All species	Creation of binary data for each species in each 500 m pixel, with a threshold set to the upper quantile (> 75% percentile abundance value = present/1). Sum values in each pixel	0 – 10 Mean: 3.93
<i>Turdus spp.</i> Richness	<i>Turdus spp.</i>	Creation of binary data for each species in each 500 m pixel, with a threshold set to the upper quantile (> 75% percentile abundance value = present/1). Sum values in each pixel	0 – 6 Mean: 1.5
Specialization	Legitimate seed dispersers (SD)	Application of weighting scheme according to body weight (log(2) transformed) to each species (in each 500 m pixel): abundance value * body weight. Sum new values in each pixel and calculate the mean	0 – 0.95 Mean: 0.05

2.4. *Viscum album*

V. album is a mistletoe species native to many European regions (Zuber 2004). It specializes on parasitizing conifers, with pines being its major host tree. However, non-conifer tree species (e.g. *Quercus ilex* or *Quercus pubescens*), have also been reported to be host species. In Catalonia, two distinct regions of mistletoe distribution can be observed (Figure 1). In the South, the species is widely distributed and parasitizes mainly *Pinus halepensis*, whereas in the North its distribution is more scattered, with *Pinus sylvestris* as its main host tree. *V. album* produces white fleshy fruits during winter that remain available for frugivores until May (Zuber 2004). Due to this, it constitutes a major food source for resident and overwintering migrants, which in return disperse mistletoe seeds mainly in the period from February to March (Zuber 2004). The distribution of *V. album*, as well as forest related explanatory variables, were extracted from the third Spanish National Forest Inventory (SNFI III; DGCN 2007). Mistletoe presence/absence data was available at tree level in each measured plot (10647 plots across Catalonia). However, the majority of infestations occurred on only two species (*P. halepensis* 83% and *P. sylvestris* 14%), thus the analysis was conducted using the SNFI III plots where either one of these two species were present (9752 Plots).

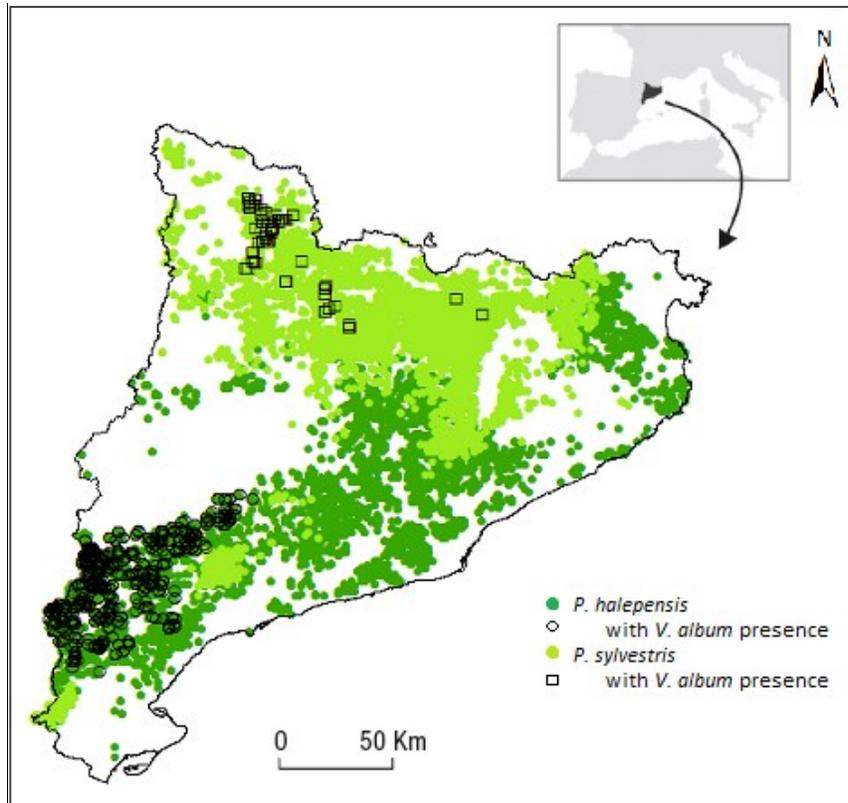


Figure 1: Distribution of host tree species and *Viscum album* in Catalonia according to the plots of the third Spanish National Forest Inventory (SNFI III; DGCN 2007)

2.5. Explanatory variables

The distribution of *V. album* does not solely depend on the presence of seed dispersers, but also on abiotic and biotic variables that are linked to the ecology of the species. We selected a set of variables potentially meaningful to explain *V. album* distribution related to climatic conditions, disperser presence, and forest plot and host tree characteristics (summary in Table 3):

Climatic conditions – *V. album* grows in temperate climate, whereas it is limited by minimum temperatures of the coldest month (-8°C , January) and minimum temperatures of the warmest month (15°C , July; Zuber 2004). Previous studies confirmed that mean annual temperature explains its distribution partially in the study region (Roura-Pascual et al. 2012). However, in the case of extreme weather conditions – extremely hot summers or cold winters – mild winters or hot summers can help the species to persist (Zuber 2004). Due to this, the annual range of temperature (Trange), which is the difference between the maximum temperature of the warmest period and the minimum temperature of the coldest period, is an even more suitable explanatory variable. We extracted this data from the WorldClim data base (Hijmans et al. 2005).

Disperser presence – Seed dispersal takes place at different spatial scales, depending on the dispersers under consideration, fruit availability, and landscape composition and structure (e.g. García et al. 2013; Donoso et al. 2017; Jordano and Schupp 2000). Due to this, we estimated indicator values at various spatial scales. In order to do so, we aggregated values of all indicators from the data source resolution (500 m) to larger resolutions and created four different square-sized buffers: 500 m, 1500 m, 2500 m, and 3500 m in length. Combined with the three different measures of each indicator, this resulted in 48 possible combinations (Ind; 4 indicator types x 3 measures x 4 buffers).

Forest plot/Host tree characteristics – Eventually, the occurrence of the mistletoe depends on suitable host trees and the chance of that tree being visited by dispersers. Hence, host trees bigger in size are prone to be infested more frequently due to two reasons: bigger trees are older and therefore exposed to possible infestations for a longer period of time (Aukema 2004) and bigger trees can act as important connection, resting, and vigilance points for potential dispersers (Herrera and García 2009; Martínez and García 2015). Thus, we included tree height (Ht) of individual trees in each sampled plot as surrogate for the suitability of the host tree. The overall maturity of the forest within each plot is also related to the above mentioned infestation probability. Due to this, we calculated a tree maturity index (Tmat), based on the diameter of each tree in the plot. To calculate the index, we only included the trees that were in the upper 10% of the diameter range (m) for the species across Catalonia, divided by the total number of host trees in the plot. For frugivorous birds, forests act as crucial food source and resting place (García et al. 2011). Due to this, the availability of forest as well as the diversity of resources within it play a major role in bird abundance. Nevertheless, birds' utilization of trees/forest patches outside large forest stands (e.g. in urban areas or agricultural land), as well as the ecotone-border effect, support the hypothesis that less dense forests are related to higher bird abundance (Herrando et al. 2011; Kark et al. 2007). Additionally, the establishment and growth of *V. album* also depends on solar radiation as it is a light demanding species. Hence, lower tree density also promotes mistletoe growth. We represented this hypothesis by considering the Forest canopy cover (FCC) as a predictor of *V. album* presence. Finally, available solar radiation and daily temperatures are also dependent on the aspect (A) of a plot, being southern aspects are generally warmer than northern ones in the study region, potentially representing another factor that explains the mistletoe's distribution. These variables were sourced from the third Spanish National Forest Inventory (DGCN 2007).

Table 3: Explanatory variables tested in *Viscum album* models. Data Source: CWBA = Catalanian Winter Bird Atlas (Herrando et al. 2011), SNFI III = Third Spanish National Forest Inventory (DGCN 2007).

Variable	Description	Range	Data Source
Annual Temperature Range (Trange)	Minimum winter temperature – maximum summer temperature	21.1 – 30.4 °C	WorldClim (Hijmans et al. 2005)
Dispersal Indicator (Ind)	Dispersal indicator + measure + buffer	Depending on indicator (see Table 2)	CWBA
Height (Ht)	Tree height of individual trees in each plot	1.9 – 28.5 m	SNFI III
Tree Maturity (Tmat)	Index of tree maturity at plot level	0 – 1	SNFI III
Forest Canopy Cover (FCC)	Canopy cover at plot level	5 – 100 %	SNFI III
Aspect (A)	Orientation of the plot	0 – 400 gon	SNFI III

2.6. Modelling approach

We examined the association of the bird dispersal indicators and the forest variables with the occurrence of *V. album* in the study area following a three-step analysis: whole Catalonia (landscape-wide analysis; I), northern and southern distribution (regional analysis; II), and regional interactions of dispersers and plot/tree characteristics (III). We decided to split the occurrence data into northern and southern distribution of *V. album*, because on the one hand, different host species can be distinguished in these two parts of the study area due to differences in climate and elevation and, on the other hand, different landscape structures and historical processes are involved in determining the presence or absence of *V. album*. Our aim of step III of the analysis was to further investigate how *V. album* could be linked with more local processes of specific preferences of seed dispersers regarding plot/tree characteristics. Identifying such preferences would aid the explanation of what habitat features are determining plant distribution. We modelled the occurrence of *V. album* as a function of all explanatory variables described in Table 3 using generalized linear mixed models (GLMMs). We tested for correlations between variables and only included low correlated variables in the model (Pearson's $R < 0.7$) to minimize potential

multicollinearity problems (Appendix S3.1). We assumed that the response variable followed a binomial distribution. The Spanish National Forest Inventory’s plot identity was included as a random factor, to account for the hierarchical structure of the data (non-independent data points at tree level within each plot). Starting from a fully saturated model (Zuur et al. 2009) including all basic variables (Trange + Ht + Tmat + FCC + A), we applied a backward stepwise regression to eliminate variables that do not contribute to the explanation of the data using a likelihood ratio test (cutoff p-value 0.05). We used the Akaike information criterion (AIC; Burnham and Anderson 2004) to compare models in the backward selection and to retain the most parsimonious model. Once the best model based on environmental predictors was identified (*basic model* from here on), we added to it each dispersal indicator, including each version of the indicator (type + measure + buffer; 48 combinations) at a time, to determine which indicator type and which indicator version produced the best signals. We applied this procedure to three different datasets (landscape-wide, South, and North), resulting in 144 fitted models including only linear terms (model structure: *basic model* + Ind). After checking model residuals to validate models (Appendix S3.2), we evaluated signal strength on the basis of the difference in AIC (Δ AIC) compared to the *basic model* of each dataset. Additionally, we calculated the deviance explained (Guisan and Zimmermann 2000) to assess the explanatory power of the model. We conducted the landscape-wide analysis (step I) to detect large scale trends, to evaluate the functionality of the indicator, and to have a basis for the comparison with regional processes in the South and North (step II). For step III, the analysis of regional interactions, we used the South and North regional model of the indicator with the biggest Δ AIC compared to the corresponding *basic model* as starting point. We fitted the models with interaction terms between indicators and *Forest plot/Host tree characteristics* variables of the corresponding *basic model* (model structure: forest/tree variable * Ind). To display interactions, we split each plot/tree variable into three categories based on lower (25%) and upper (75%) quantiles. Table 4 summarizes the modelling process, including the data used and the basic model structures. Analyses were carried out using the open source software R version 3.6.0 (R Core Team 2019). All GLMMs were fitted using the glmer function in the ‘lme4’ package in R (Bates et al. 2015).

Table 4: Summary of three-step analysis including model structure. The ‘basic model’ refers to the most parsimonious model based solely on environmental predictors.

Modelling Step	Model Structure	Scale
I	<i>V. album</i> ~ basic model + indicator ¹	Landscape-wide
II	<i>V. album</i> ~ basic model + indicator ¹	North OR South

III	<i>V. album</i> ~ selected variables * indicator ²	North OR South
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¹ We tested 48 different indicator versions resulting from the combination of each indicator type (Abundance, Species Richness, *Turdus spp.* Richness, or Specialization), measure (mean values, mean values of the upper quantile - values < 75% percentile -, and binary values of the upper quantile indicating presence and absence of seed dispersal - values < 75% percentile = 0; values > 75% percentile = 1), and buffer (500 m, 1500 m, 2500 m, 3500 m)

² The version of each indicator type that produced the best results (lowest AIC) is used to test for the importance of interactions

3. Results

The highest abundance and richness of bird-dispersal species was found in the southern and north-eastern part of the study area, whereas the highest values of the *Turdus spp.* Richness indicator and the Specialization indicator were found in the southern core distribution of *V. album* (Figure 2).

The deviance explained by mistletoe *basic models* (those excluding bird-dispersal indicators), was higher for the South regional model (13.1%), followed by the landscape-wide model (9.5%), and the North regional model (3%; Table 5). In general terms, the inclusion of indicators as model predictors slightly improved model-fit, contributing the most to explain mistletoe distribution in the South regional model. The overall best performing model in the South included the *Turdus spp.* Richness indicator. At the landscape-wide scale, the Species Richness indicator produced the most parsimonious model, and the Specialization indicator in the North regional model. However, only in the South the indicator improves model fit significantly (best model: $\Delta\text{AIC}35.61$), whereas landscape-wide (best model: $\Delta 7.43$) and in the North (best model: $\Delta 4.29$) the explanation power of the model including the indicator does not improve a lot regarding to the *basic models* (Table 5). This result is constant throughout all models of the three different scales (landscape-wide, South, and North). Regarding the indicator measure, indicator measures of binary values of the upper quantile indicating presence and absence of seed dispersal (values < 75% percentile = 0; values > 75% percentile = 1) contribute significantly to explain mistletoe distribution in the landscape-wide analyses, whereas measures using mean values performed best in the South and North regional models (Appendix S2).

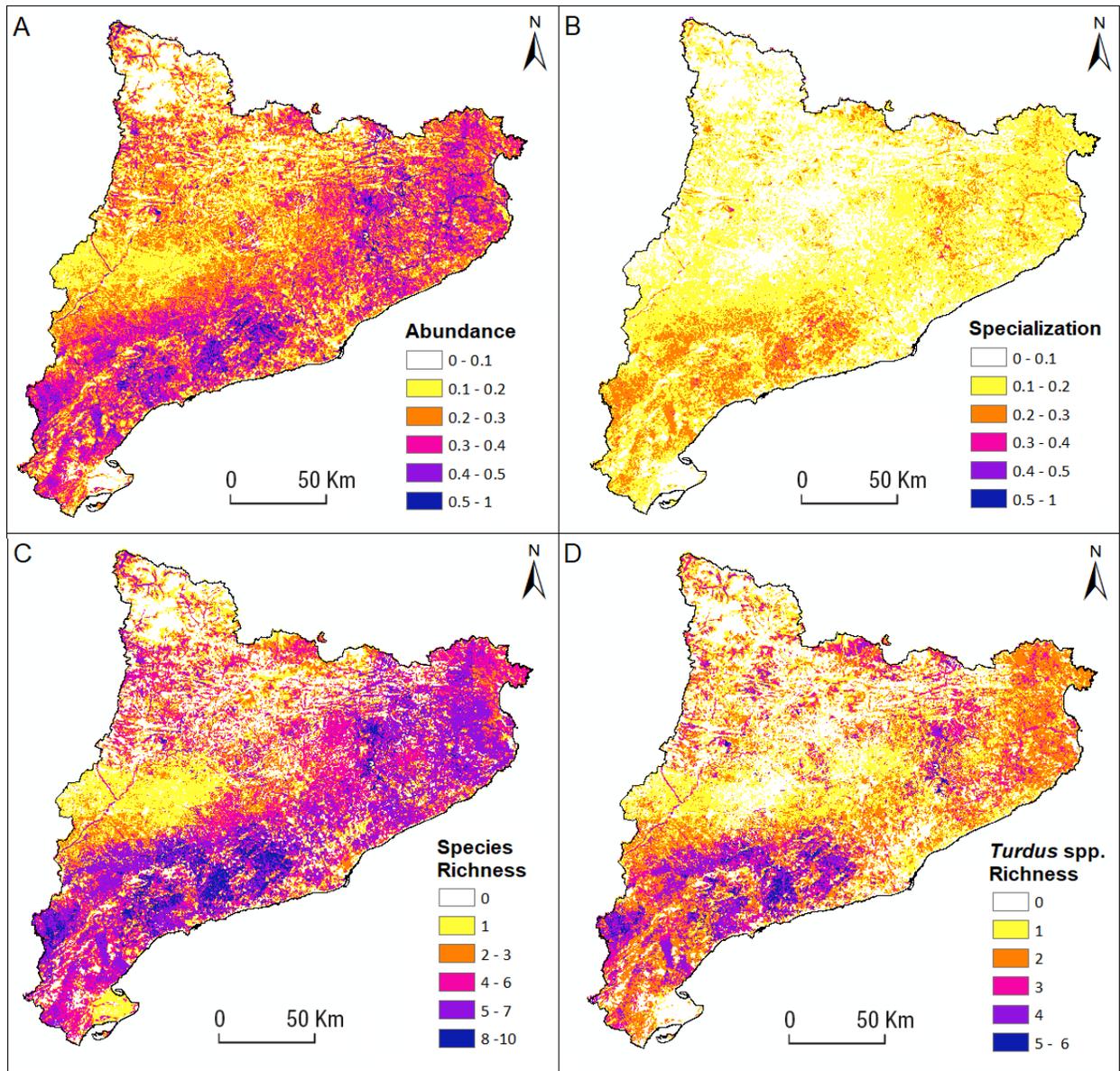


Figure 2: Maps of selected indicator types (basic resolution of 500 m, indicator measure: mean values)

Table 5: Most parsimonious model of each indicator according to AIC values. Scale indicates the scale of analysis (L = Landscape-wide, S = South, N = North), red values highlight the best performing indicator amongst all scales.

Scale	Model	AIC	Δ AIC	D ²
L	<i>V. album</i> ~ 1 (null model)	6224.7		
S	<i>V. album</i> ~ 1 (null model)	4953.3		
N	<i>V. album</i> ~ 1 (null model)	1233.5		
L	<i>V. album</i> ~ basic variables	5638.7	586.0	0.095
S	<i>V. album</i> ~ basic variables	4315.4	637.9	0.131
N	<i>V. album</i> ~ basic variables	1204.7	28.8	0.030
L	<i>V. album</i> ~ basic variables + Abundance	5636.1	2.6	0.096

S	<i>V. album</i> ~ basic variables + Abundance	4294.3	21.07	0.135
N	<i>V. album</i> ~ basic variables + Abundance	1202.5	2.26	0.033
L	<i>V. album</i> ~ basic variables + Specialization	5635.4	5.25	0.096
S	<i>V. album</i> ~ basic variables + Specialization	4289.5	25.93	0.136
N	<i>V. album</i> ~ basic variables + Specialization	1200.4	4.29	0.035
L	<i>V. album</i> ~ basic variables + Species Richness	5631.2	7.43	0.097
S	<i>V. album</i> ~ basic variables + Species Richness	4285.1	30.3	0.137
N	<i>V. album</i> ~ basic variables + Species Richness	1203.4	1.35	0.033
L	<i>V. album</i> ~ basic variables + <i>Turdus spp.</i> Richness	5636.5	2.14	0.096
S	<i>V. album</i> ~ basic variables + <i>Turdus spp.</i> Richness	4279.8	35.63	0.138
N	<i>V. album</i> ~ basic variables + <i>Turdus spp.</i> Richness	1201.9	2.82	0.034

D² = deviance explained (Guisan and Zimmermann 2000); ΔAIC = difference in the Akaike information criterion of each model to the null model or the model only including basic variables, respectively.

Model measure: at the landscape-wide scale the indicator using P/A (binary values of the upper quantile indicating presence and absence of seed dispersal ($0 < 75\% > 1$)) produced the most parsimonious model; South + North regional models were based on mean values; Buffer: all displayed results of models including indicators were based on the 3500 m buffer.

The models with the largest explanatory power amongst all scales and all indicators, were the ones including the indicator buffer of 3500 m. Bird-dispersal indicators were positively correlated to mistletoe presence in the landscape-wide and in the South regional models, whereas the North regional models suggested that a slightly negative relationship exists (Figure 3). However, coefficient estimates in the North have a high standard deviation and almost cross 0, thus suggesting combined with the small change in AIC, no effect of the indicator on mistletoe distribution in this region. On the contrary, a very clear trend to large scale influence of dispersers can be observed in the models of the Southern region (Figure 3B). Although in the South, all indicator buffers improve model fit significantly compared to the *basic model*, the bigger the buffer, the better the performance of the models (Appendix S2).

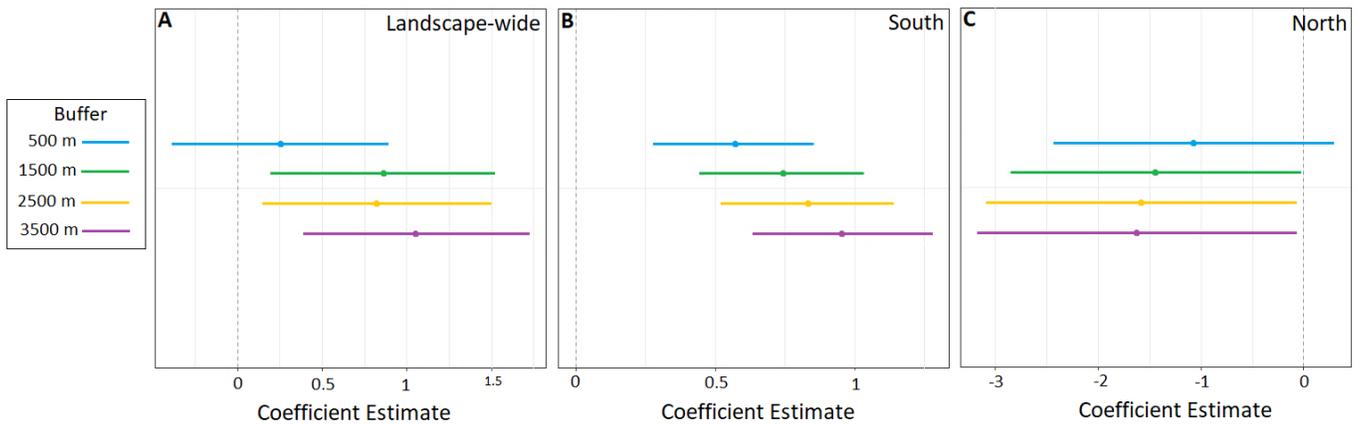


Figure 3: Coefficient estimates of all scales of analysis of the best performing indicators (Landscape-wide = Species Richness, South = *Turdus spp.* Richness, North = Specialization) at different buffer levels

Besides indicators, variables contributing most to landscape-wide models as well as to the South regional models were Temperature range (Trange), Height (Ht), Forest Canopy Cover (FCC), and Tree Maturity (Tmat). In the North regional models Trange, Ht, FCC, and Aspect (A) were most explanatory (Figure 4). Overall, Trange was positively correlated with the distribution of *V. album*, explaining the most of the model variation. Ht and A were also positively correlated to mistletoe presence, whereas FCC and Tmat were negatively related. The magnitude of variable coefficients in the North regional model was smaller than in the South regional and landscape-wide models. Due to this and due to the low explanatory power of indicators in the northern region, we focused the rest of the results section – modelling interactions between plot/tree characteristics and indicators (III) – on the South regional models, using the *Turdus spp.* Richness indicator as example.

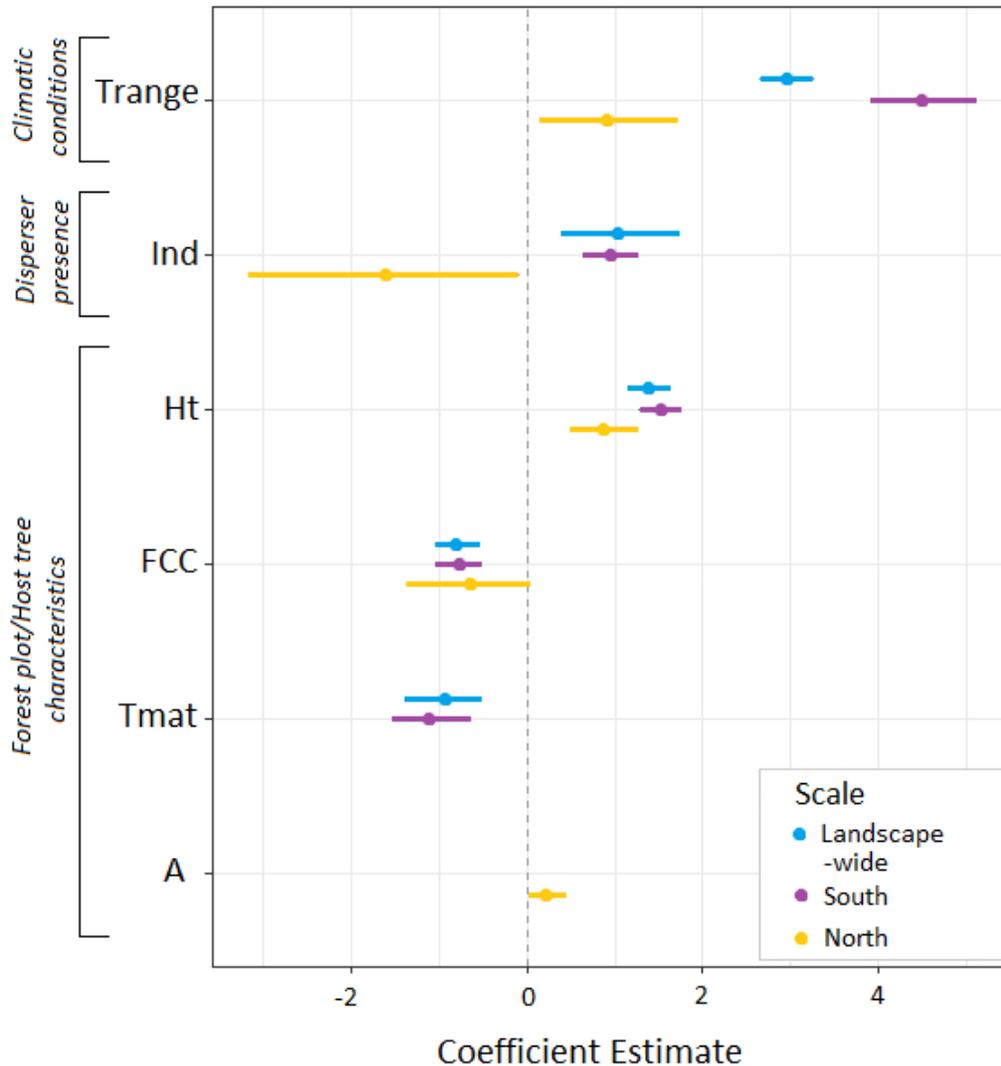


Figure 4: Coefficient estimates of all variables of best performing models including bird-dispersal indicators (Landscape = Species Richness, South = *Turdus spp.* Richness, North = Specialization). See table 3 for variables meaning.

Interaction models suggested an almost significant interaction between bird-dispersal indicator and FCC (Estimate: -0.355, p-value: 0.054) or tree height (Estimate: 0.232, p-value: 0.075), respectively. However, interactions between indicators and tree maturity did not produce significant results (Estimate: 0.107, p-value: 0.799). We summarized the variables into three categories based on quantiles (values < 25% = low, 25 – 50% = medium, > 75% = high) to further investigate interactions (Figure 5). *V. album* as well as disperser presence was proportionally higher at high trees and low forest canopy cover.

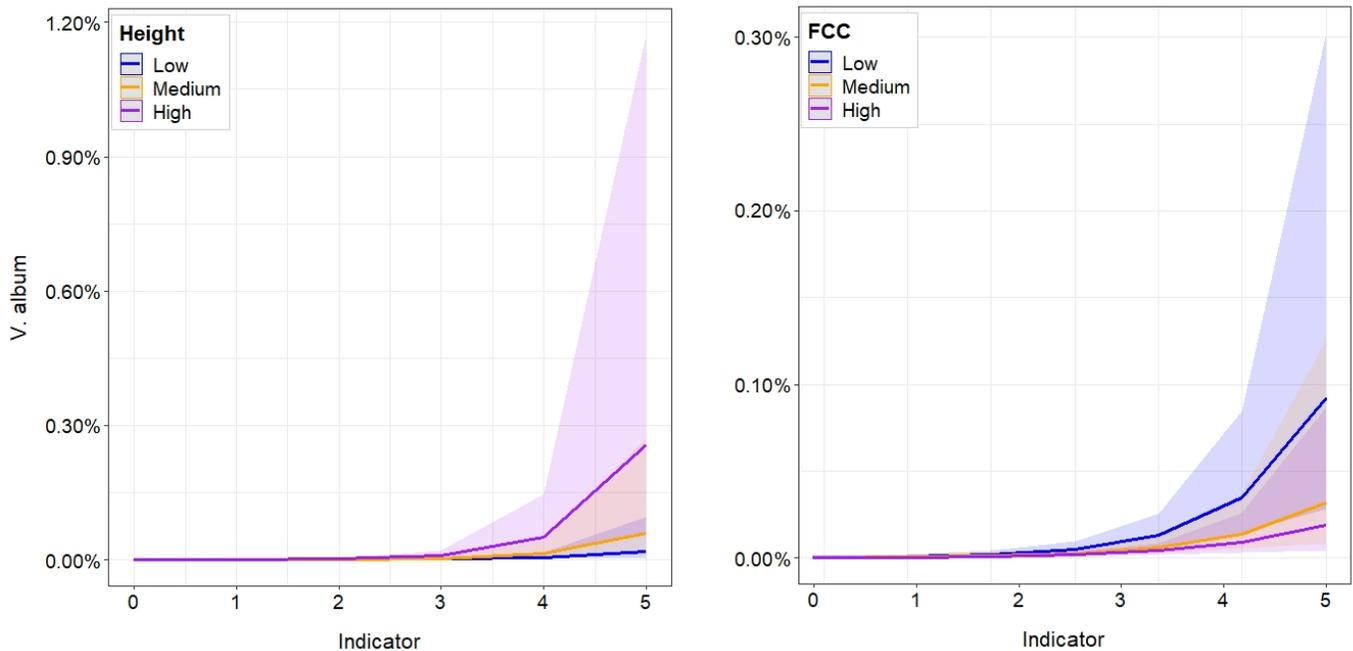


Figure 5: Interaction plots of the *Turdus spp.* Richness indicator (measure: mean values, buffer: 3500 m) and different levels of Height/FCC based on quantiles (values < 25% = low, 25 – 50% medium, > 75% = high)

4. Discussion

Our results have clearly shown that the landscape occurrence of a bird dispersed plant show a consistent association with bird indicators (abundance, richness, and specialization) mapped during winter when their dispersal potential is higher. Our results also highlighted the importance of considering different regional processes when investigating a very dynamic process such as seed dispersal at the landscape scale. Although landscape-wide models showed an association of seed-dispersal indicators and mistletoe distribution, it was difficult to capture a clear signal. On the one hand, this might be because a larger amount of data comes from the southern region and on the other hand, because different indicators did not equally explain the southern and northern species' distribution in the study area. A clear seed dispersal signal, no matter what indicator was considered, was observed in the southern region. However, signal strength in the Northern region was very weak or even non-existent.

To understand why two different populations of *V. album* can be distinguished in Catalonia, and why seed-dispersal signals are different between regions, it is important to consider the landscape structure of the study area. Extensive agricultural lands (crops) and urban areas separate the

southern and the northern *V. album* populations (Figure 6). The limited connectivity across the North-South geographical axis, combined with the change of the environmental gradients (hotter in the South and colder in the North), and the host species distribution, are important considerations of why dispersal processes could be limited over the region. The most important overall variable influencing the distribution of *V. album* was the annual range of temperature, which had a very strong positive influence on the occurrence of the species. Similar results have been found by Roura-Pascual et al. (2012), whereas they used the mean temperature as explanatory variable. Thus, climate warming, which is an ongoing observed trend in the Iberian Peninsula (Castro et al. 2005), could potentially open up new areas suitable for infestation currently too cold for species persistence, especially in the northern part of the study area (Zamora and Mellado 2019).

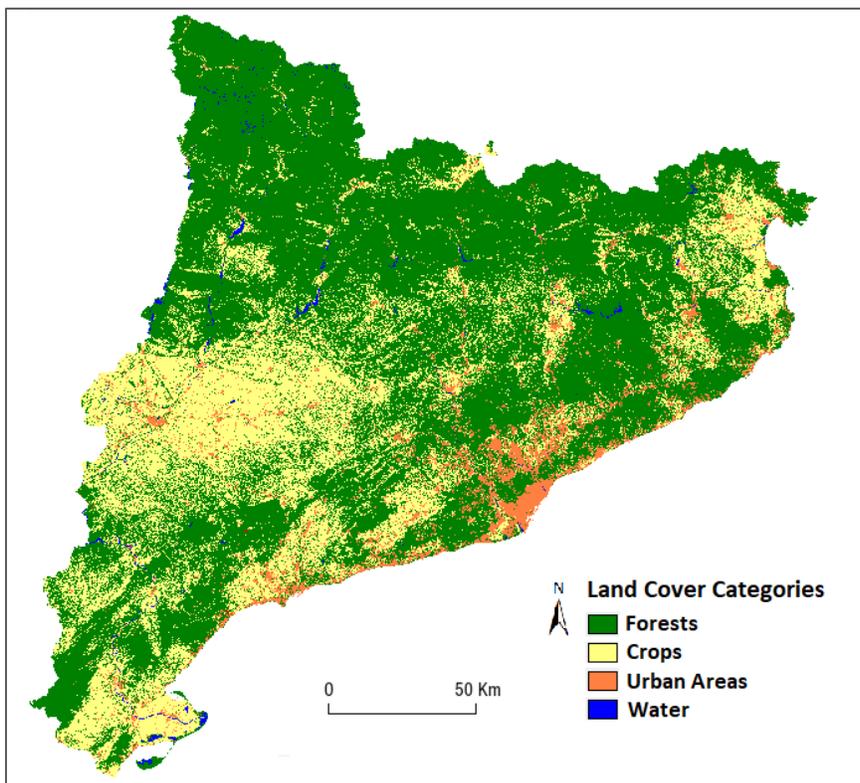


Figure 6: Land Cover Map of Catalonia (MCSC) according to the four main types (Data source: CREAM MCSC third edition, version 2 (images of 2005-2007))

Traditionally, species distribution models (SDMs) relate abiotic variables to the abundance or the presence/absence of species (Guisan and Thuiller 2005, Elith et al. 2006). The inclusion of biotic variables as predictors, such as the abundance of related species in terms of competition, inter-specific interaction or dispersal, is rare. Nevertheless, studies have shown that the inclusion of such

variables can considerably improve predictions (e.g. Meier et al. 2010; Giannini et al. 2013, Palacio and Girini 2018). Specifically modelling seed dispersal as biotic variable has been attempted before (e.g. Boulegeat 2012), however mainly by including dispersal as the potential ability of the plant species to disperse its seeds, not by explicitly including frugivore-dispersal-capacities. Nevertheless, obtaining data of actual seed dispersal processes, especially at large-scales, is very difficult (García 2016). We showed that the use of seed-dispersal bird species indicators can improve predictions of plant species distributions, as they serve as a good approximation to the actual dispersal processes.

In the southern part of Catalonia, quantitative and qualitative measures of dispersal, represented by disperser abundance, species richness and species specific specialization, all contributed to explain *V. album* distribution. However, the tested indicators did not perform equally well in predicting the presence/absence of the mistletoe. Disperser abundance had the lowest capability of prediction, followed by species specialization, species richness in general, and *Turdus spp.* Richness. Previous studies that investigated seed dispersal at local scales and modelled dispersal networks at regional scales, confirmed that disperser abundance is an important basic measure for dispersal processes but that species richness and species specific traits have a greater impact on seed dispersal density and richness (García et al. 2018, García and Martínez 2012, Rodríguez-Pérez et al. 2017). A rich frugivore assemblage, and thus high functional diversity, imply different behavior and habitat uses that lead to an increased variance in seed rain and potentially increased colonization probability. Main dispersers not only disperse mistletoe seeds, but also other plant species and thus play a major role in structuring biodiversity and regenerate degraded habitat (Mellado et al. 2017, Kremen et al. 2007). Due to this, it is an important consideration that not only the amount of individual dispersers present, but especially the variety in different species play a crucial role in this process (García and Martínez 2012, Fontaine et al. 2006). Besides clear evidence of the relationship of dispersers and mistletoe presence, we also showed that dispersal processes are a regional phenomenon. Although small-scale processes were not negligible, the clear trend of dispersal signals to large-scale extents (maximum when including information about potential dispersal processes within a buffer of 3500m around each forest plot) suggested that birds can disperse seeds far. Legitimate seed dispersers (SD) disperse seeds through endozoochory and have been linked to higher dispersal success (Jordano and Schupp 2000), whereas specific *Turdus spp.* have been shown to be able to disperse seeds over long distances (Martínez et al. 2008). The strong correlation of *Turdus spp.*

Richness with mistletoe distribution underlines this relationship of dispersal mode and dispersal distance. Despite that dispersal could take place over larger areas and the wide distribution of the main host tree – *P. halepensis* – would allow for a wider potential range of mistletoe infestation, the actual range of *V. album* in the southern region is limited to the south-west of the study area. The indicators helped to explain that not only the presence of the host tree, but large-scale dispersal constraints limit its distribution. A previous study confirmed that neighboring land use (i.e. the proximity to olive orchards) is an important characteristic to explain the presence of *V. album* (Roura-Pascual et al. 2012). Our work adds to this knowledge and suggests that this is due to the requirements of potential dispersers. The majority of the birds included into this study could be classified as generalists (after Mellado and Zamora 2014a), this is, species that utilize forested as well as non-forested lands. When comparing the location of infested trees in the southern region (Figure 1) with the proximity to crop land (Figure 6), this relationship is visualized. The ecology of dispersers potentially leads to a disproportionate establishment of mistletoe occupied areas (García and Ortiz-Pulido 2004), whereas the influence of local plot and tree characteristics on *V. album* in the South further emphasized this relationship. The height of a tree was positively related with mistletoe as well as dispersers' presence (showed through modelled interactions). This confirms our hypothesis that trees bigger in size are correlated with higher infestation probabilities over time, since they constitute attractive locations for birds which use them for resting and nesting, also providing vigilance opportunities. On the contrary, forest canopy cover as well as tree maturity showed a negative relationship with mistletoe presence. The negative influence of FCC and tree maturity could be related to dispersers' preference for less dense and mature forests (open woodlands) close to nutrient-rich habitats like olive-orchards. In addition, Gil-Tena et al. (2007) showed that excessive FCC (above 70%) might be detrimental to bird species richness. Our results implied a similar relationship according to the interaction of low FCC, *Turdus spp.* Richness, and mistletoe presence, as well as the high prediction power of the Species Richness indicators. Finally, the aspect of a plot did not aid to the explanation of mistletoe occurrence in the South. Due to the absence of major changes in elevation, the aspect in this part of the study area does not reflect a major change in environmental conditions. On the contrary, in the North, the mountain range of the Pyrenees runs from East to West, thus the differences between northern slopes (more humid) and southern slopes (drier) could be an important factor in explaining mistletoe occurrence. The fact that the aspect was included as explanatory variable in Northern regional models underlines this explanation.

In the North, all variables – including seed dispersal indicators – had very little explanatory power. In SDMs it is often assumed that biotic variables such as dispersal stay constant over time (Guisan and Thuiller 2005). However, the absence of the relationship of the presence of dispersers and the distribution of *V. album*, a frugivorous-dispersed species, indicate otherwise. Mistletoe plants can reach an age up to 30 years (Nierhaus-Wunderwald and Lawrenz 1997), thus processes that determined the present distribution of the mistletoe potentially no longer exist. Since the 1960s, severe socio economic changes have led to a change in landscape structure in the mountainous regions of Catalonia. Industrialized farming concentrated in flatter soils in the lowlands of the study area, whereas steeper areas became economically marginal which led to depopulation and abandonment of pasturelands (Cervera et al. 2019). Lost profitability of agricultural uses of productive soils and an increase of wood imports further drove this process. This abandonment of rural activities led to an expansion of forested land and thus might have decreased factors that favor the establishment of *V. album*. Open habitats including pastures, crops, and orchards that attracted birds in the past have been overtaken by young and homogenous forests (Cervera et al. 2019). Hence, it is possible that the current distribution of the mistletoe in the Northern part of Catalonia is not linked anymore to the distribution of main dispersers, currently limiting further dispersal of the plant. This change in dynamics could affect the ecological state of mountainous forests. Mistletoes have been proven to act as dispersal hotspots, thus influencing the heterogeneity of the forest by providing a stable food source for dispersers and by aiding seed dispersal of other species in the region (Mellado et al. 2016). Nevertheless, this link between historical dispersal processes and land use changes would need further investigation.

5. Conclusion

We showed that bird-seed dispersal indicators based on different measures of biodiversity can be used, in combination with other factors that determine the successful establishment of *Viscum album* (e.g. climatic conditions and forest/host tree characteristics), to investigate distribution patterns of this plant species at regional and landscape scales. The direct inclusion of birds distribution data into modelling the plant geographical distribution patterns helped to determine the potential importance of seed dispersal processes compared to factors affecting its establishment at the local scale (e.g. seed positioning) and can be used to study regional differences in dispersal

processes. However, we also showed that plant species distribution is not only dependent on the presence and the ability of dispersers, but to a large extent it can be limited by landscape heterogeneity and connectivity. Different components of dispersers' biodiversity (abundance, richness, and species specialization) can have a different effect on quantitative and qualitative components of the dispersal process and related ecosystem functions (García et al. 2010, García and Martínez 2012, García 2016). Thus, identifying the relative importance of each of these components through dispersal-indicators could improve the understanding of large-scale plant species distribution and help to effectively manage biodiversity. Especially in human-modified landscapes, the knowledge of seed dispersal processes can be applied to slow-down habitat degradation and biodiversity decline or to accelerate the recovery of degraded areas (McConkey et al. 2012). Our approach, creating dispersal indicators based on SDMs of birds and using them to predict plant species distribution, makes the seed dispersal process more accessible. Future studies could use such indicators to assess species dynamics over time or to model future plant species distributions using predictions of birds' distributions into future forest conditions.

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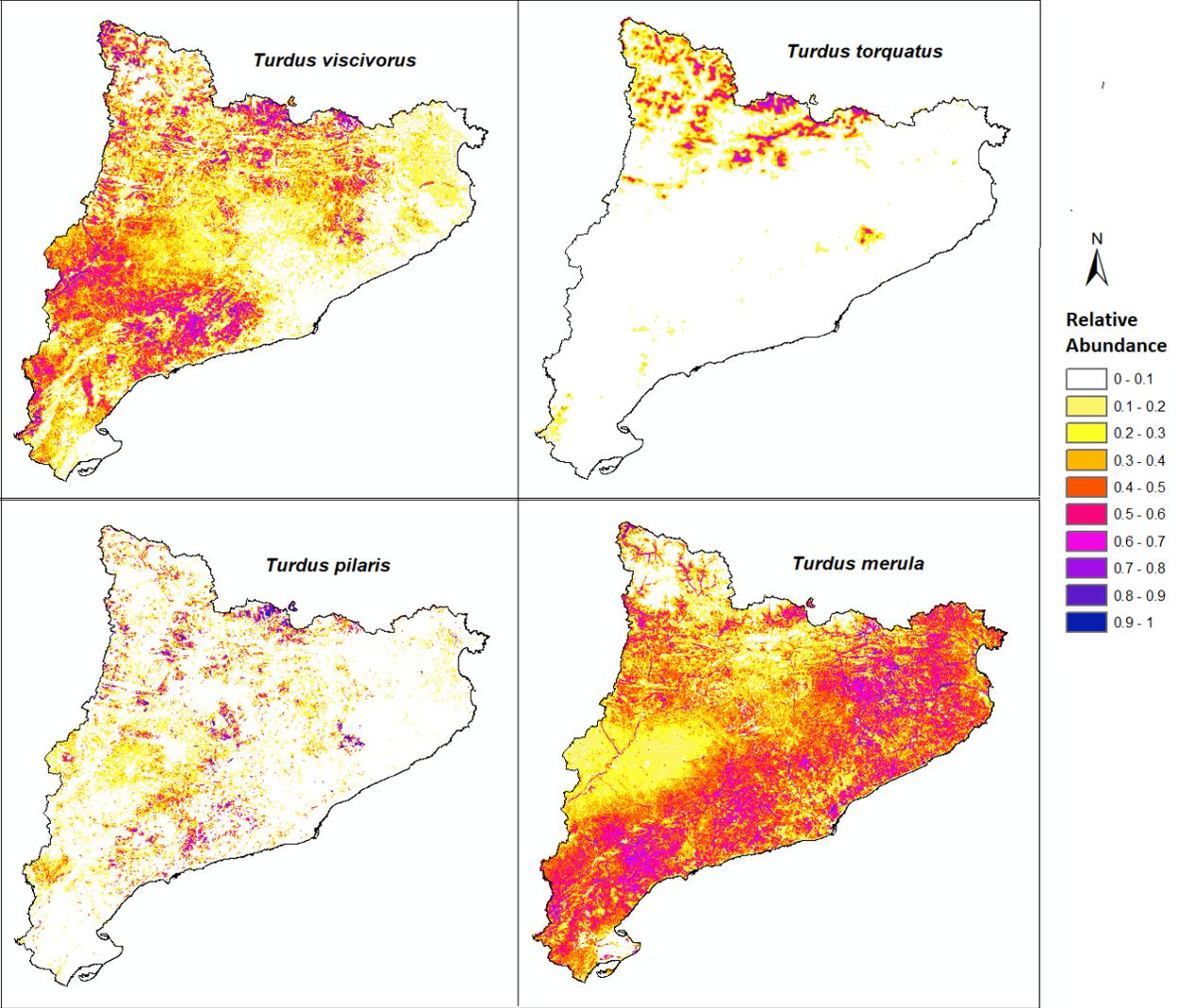
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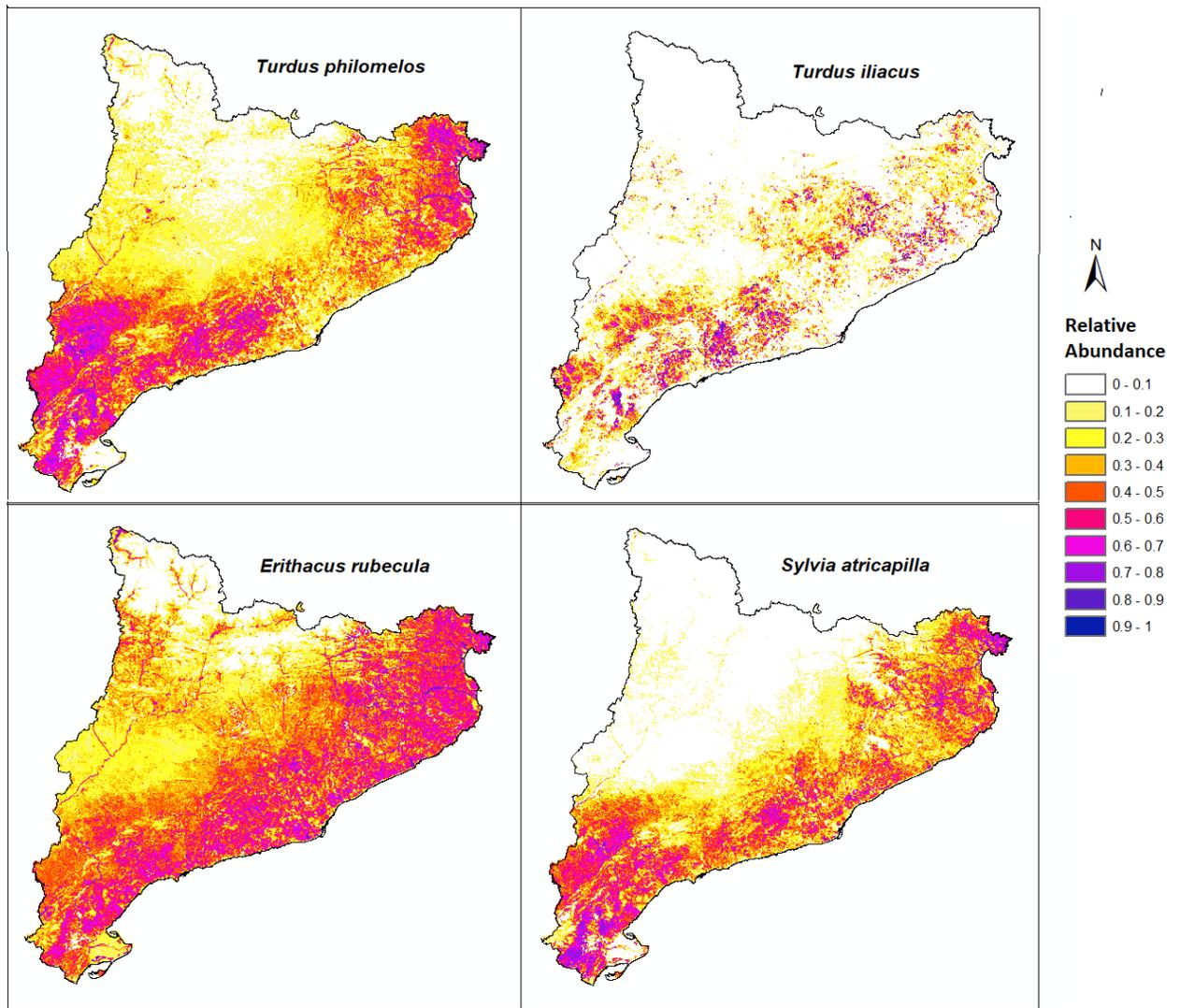
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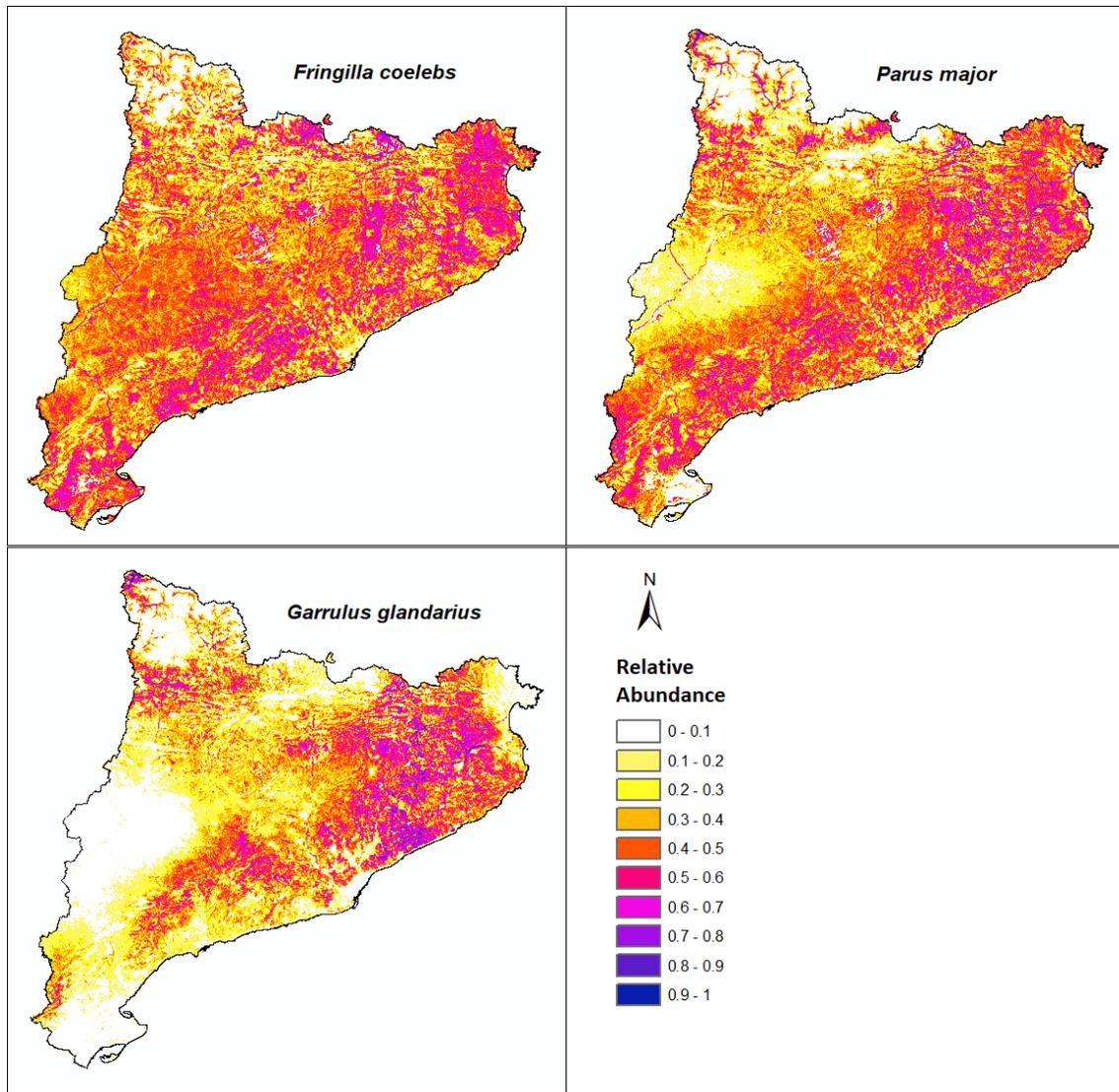
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Appendix

S1: Maps of relative abundance of each species selected for the indicators based on species distribution models of the Catalan Winter Bird Atlas 2006 -2009 (Herrando et al. 2011)







S2: Complete results of null models, *basic models* and all 144 model versions including indicators

Model abbreviations:

- Basic model = model including only climatic and forest plot/host tree characteristics variables;
- M_500/M_1500/M_2500/M_3500 = models including indicators based on mean values and on 500/1500/2500/3500 m buffers;
- Q_500/Q_1500/Q_2500/Q_3500 = models including indicators based on mean values of the upper quantile (values > 75% percentile) and on 500/1500/2500/3500 m buffers;

- PA_500/PA_1500/PA_2500/PA_3500 = models including indicators based on binary values of the upper quantile indicating presence and absence (P/A) of seed dispersal (values < 75% percentile = 0; values > 75% percentile = 1) and on 500/1500/2500/3500 m buffers;

Df = Degrees of Freedom; Δ AIC = difference in the Akaike information criterion of each model to the null model or the *basic model*, respectively; D² = deviance explained (Guisan and Zimmermann 2000);

LANDSCAPE-WIDE							
		Abundance			Specialization		
Model	Df	AIC	Δ AIC	D ²	AIC	Δ AIC	D ²
Null model	2	6224.68	/	/	6224.68	/	/
Basic model	6	5638.66	586.02	0.0954	5638.66	586.02	0.0954
M_500	7	5640.43	-1.77	0.0955	5640.67	-2.00	0.0955
M_1500	7	5640.48	-1.81	0.0955	5640.63	-1.97	0.0955
M_2500	7	5640.56	-1.90	0.0955	5640.57	-1.91	0.0955
M_3500	7	5640.66	-2.00	0.0955	5640.28	-1.62	0.0956
Q_500	7	5640.45	-1.78	0.0955	5638.46	0.21	0.0958
Q_1500	7	5640.40	-1.74	0.0955	5640.67	-2.00	0.0954
Q_2500	7	5640.66	-1.99	0.0955	5640.54	-1.88	0.0955
Q_3500	7	5639.88	-1.22	0.0956	5640.66	-1.99	0.0955
PA_500	7	5640.38	-1.72	0.0955	5638.09	0.57	0.0959
PA_1500	7	5639.92	-1.25	0.0956	5635.59	3.08	0.0963
PA_2500	7	5636.30	2.36	0.0962	5636.62	2.05	0.0961
PA_3500	7	5636.07	2.60	0.0962	5635.42	3.25	0.0963

		Species Richness			<i>Turdus spp.</i> Richness		
Model	Df	AIC	Δ AIC	D ²	AIC	Δ AIC	D ²
Null model	2	6224.68	/	/	6224.68	/	/
Basic model	6	5638.66	586.02	0.0954	5638.66	586.02	0.0954
M_500	7	5640.35	-1.68	0.0955	5639.12	-0.46	0.0957
M_1500	7	5640.13	-1.47	0.0956	5639.04	-0.38	0.0958
M_2500	7	5640.11	-1.44	0.0956	5638.63	0.03	0.0958
M_3500	7	5639.68	-1.02	0.0956	5637.54	1.12	0.0960
Q_500	7	5639.41	-0.74	0.0957	5638.26	0.40	0.0959
Q_1500	7	5640.20	-1.54	0.0956	5640.66	-2.00	0.0955
Q_2500	7	5640.39	-1.72	0.0955	5640.50	-1.83	0.0955
Q_3500	7	5640.20	-1.54	0.0956	5639.48	-0.82	0.0957

PA_500	7	5640.06	-1.39	0.0956	5640.54	-1.87	0.0955
PA_1500	7	5634.13	4.53	0.0965	5637.39	1.28	0.0960
PA_2500	7	5635.03	3.63	0.0963	5636.99	1.67	0.0961
PA_3500	7	5631.24	7.43	0.0970	5636.52	2.14	0.0962

SOUTH REGIONAL MODELS							
		Abundance			Specialization		
Model	Df	AIC	Δ AIC	D ²	AIC	Δ AIC	D ²
Null model	2	4953.29	/	/	4953.29	/	/
Basic model	6	4315.40	637.89	0.131	4315.40	637.89	0.131
M_500	7	4310.17	5.23	0.132	4307.03	8.37	0.133
M_1500	7	4303.44	11.95	0.133	4299.37	16.03	0.134
M_2500	7	4300.07	15.33	0.134	4295.83	19.57	0.135
M_3500	7	4294.33	21.07	0.135	4289.47	25.93	0.136
Q_500	7	4314.32	1.08	0.131	4308.92	6.48	0.132
Q_1500	7	4311.95	3.45	0.132	4303.21	12.18	0.133
Q_2500	7	4309.86	5.54	0.132	4299.93	15.47	0.134
Q_3500	7	4300.05	15.35	0.134	4291.85	23.55	0.136
PA_500	7	4313.61	1.79	0.131	4307.55	7.85	0.132
PA_1500	7	4312.26	3.14	0.132	4302.32	13.08	0.134
PA_2500	7	4303.94	11.46	0.133	4306.02	9.38	0.133
PA_3500	7	4304.08	11.32	0.133	4303.60	11.80	0.133

		Species Richness			<i>Turdus spp.</i> Richness		
Model	Df	AIC	Δ AIC	D ²	AIC	Δ AIC	D ²
Null model	2	4953.29	/	/	4953.29	/	/
Basic model	6	4315.40	637.89	0.131	4315.40	637.89	0.131
M_500	7	4307.08	8.32	0.133	4301.97	13.43	0.134
M_1500	7	4296.37	19.03	0.135	4291.81	23.59	0.136
M_2500	7	4291.98	23.42	0.136	4286.67	28.73	0.137
M_3500	7	4285.10	30.30	0.137	4279.77	35.63	0.138
Q_500	7	4308.83	6.57	0.132	4300.75	14.65	0.134
Q_1500	7	4302.02	13.38	0.134	4297.67	17.73	0.134
Q_2500	7	4298.63	16.77	0.134	4296.54	18.86	0.135
Q_3500	7	4287.40	28.00	0.137	4293.88	21.52	0.135
PA_500	7	4310.81	4.59	0.132	4309.44	5.96	0.132
PA_1500	7	4300.39	15.01	0.134	4301.25	14.15	0.134

PA_2500	7	4302.98	12.42	0.133	4299.93	15.47	0.134
PA_3500	7	4295.96	19.44	0.135	4297.08	18.32	0.135

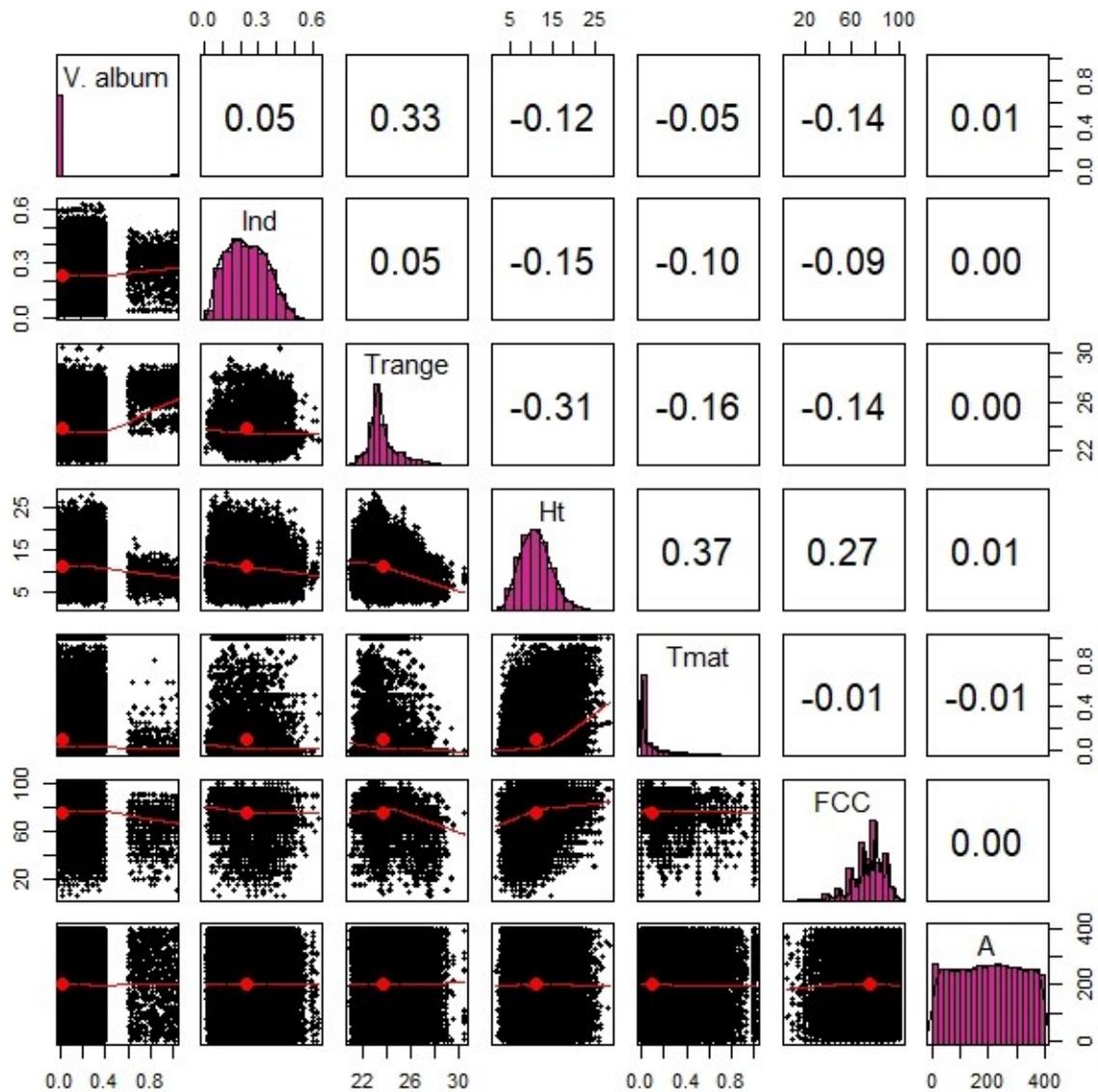
NORTH REGIONAL MODELS							
Abundance					Specialization		
Model	Df	AIC	Δ AIC	D ²	AIC	Δ AIC	D ²
Null model	2	1233.52	/	/	1233.52	/	/
Basic model	6	1204.72	28.79	0.0299	1204.72	28.79	0.0299
M_500	7	1204.77	-0.05	0.0315	1203.51	1.21	0.0325
M_1500	7	1202.98	1.75	0.0330	1201.06	3.66	0.0345
M_2500	7	1202.80	1.93	0.0331	1200.50	4.22	0.0350
M_3500	7	1202.46	2.26	0.0334	1200.43	4.29	0.0350
Q_500	7	1206.39	-1.67	0.0302	1205.76	-1.04	0.0307
Q_1500	7	1205.85	-1.13	0.0306	1205.18	-0.46	0.0312
Q_2500	7	1206.60	-1.88	0.0300	1205.31	-0.58	0.0311
Q_3500	7	1206.70	-1.98	0.0299	1205.65	-0.93	0.0308

Species Richness					<i>Turdus spp.</i> Richness		
Model	Df	AIC	Δ AIC	D ²	AIC	Δ AIC	D ²
Null model	2	1233.52	/	/	1233.52	/	/
Basic model	6	1204.72	28.79	0.0299	1204.72	28.79	0.0299
M_500	7	1205.81	-1.09	0.0307	1205.49	-0.77	0.0309
M_1500	7	1204.00	0.72	0.0321	1202.69	2.03	0.0332
M_2500	7	1203.71	1.02	0.0324	1201.90	2.82	0.0338
M_3500	7	1203.37	1.35	0.0327	1202.15	2.57	0.0336
Q_500	7	1205.91	-1.19	0.0306	1205.70	-0.98	0.0307
Q_1500	7	1205.16	-0.44	0.0312	1205.10	-0.37	0.0312
Q_2500	7	1206.04	-1.32	0.0305	1204.68	0.05	0.0316
Q_3500	7	1206.64	-1.92	0.0300	1204.26	0.46	0.0319

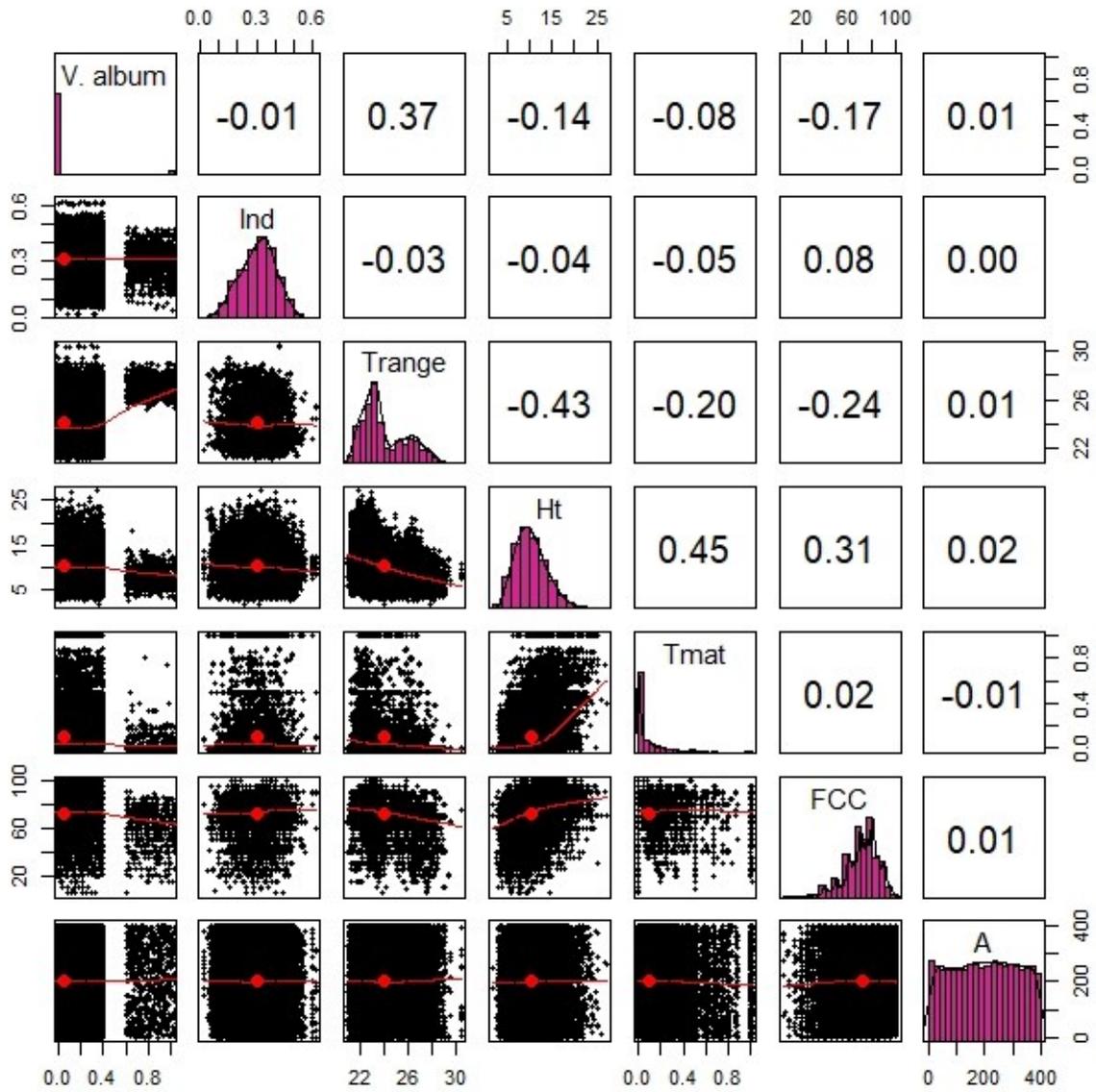
S3: Model validation plots

S3.1. Pearson's correlations between predictor variables. To represent the indicator variable, we include the Abundance indicator at 500 m resolution, as all other indicator types, measures, and buffers are based on this one and thus, correlation is related.

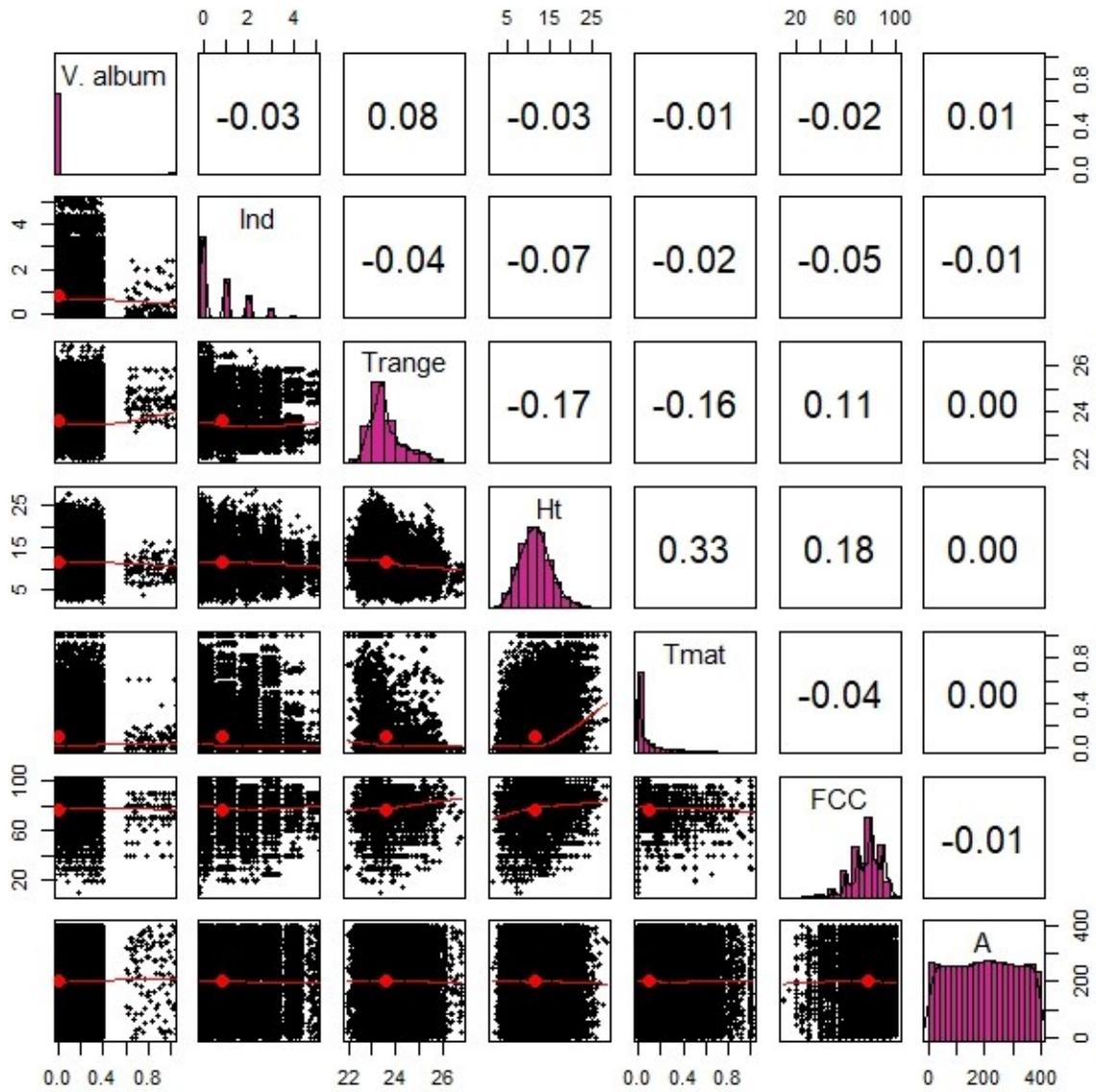
Landscape-wide correlation plot



Southern distribution correlation plot



Northern distribution correlation plot



S3.2. Model residuals created with the 'DHARMA' package (Hartig 2019). Plots correspond to best performing models including indicators at buffer level of 3500 m (Landscape = Species Richness, South = *Turdus spp.* Richness, North = Specialization).

