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Source: Journal of Vertebrate Biology, 71(22041)

Published By: Institute of Vertebrate Biology, Czech Academy of Sciences

URL: https://doi.org/10.25225/jvb.22041

Journal of Vertebrate Biology

Open Access

J. Vertebr. Biol. 2022, 71: 22041 DOI: 10.25225/jvb.22041

RESEARCH PAPER

Habitat use of the mistle thrush (*Turdus viscivorus*): the importance of urban areas and permanent crops

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Received 29 June 2022; Accepted 24 August 2022; Published online 4 October 2022

Abstract. The mistle thrush is a species that occurs in old-growth forests, especially coniferous forests, in hilly and mountain areas and avoids warm and dry areas and human settlements. Despite this, in recent decades, the mistle thrush has colonised Apulia, southern Italy's lowlands and coasts, in rural and urban contexts. This study investigates the habitat selection of this species in central Apulia, in both the breeding season and winter, by carrying out 301 point counts and 264 linear transects. Data were collected to build a Species Distribution Model (SDM) for each season with the MaxEnt algorithm and the regional land use map, selecting variables through the Akaike Information Criterion. Overlap in the suitability of both seasons was measured using Schoener's *D*. A total of 133 observations of mistle thrush were noted during the breeding season and 85 observations during winter. During the breeding season, the mistle thrush selected olive orchards, especially those near vineyards and urban areas, where it could find food and safe places to nest. In this period, however, it was also found in coniferous woodlands. The mistle thrush also used vineyards in winter, whereas it avoided urban areas in this period, possibly due to food scarcity. Non-irrigated arable lands were avoided all year round, whereas natural grasslands were only avoided during the winter. Irrigated arable lands positively affected the species. Furthermore, 60% of habitat characteristics were similar between the breeding and winter seasons. It is unclear what makes the mistle thrush shift its range southward and downslope. However, it is likely due to the general increase in forest cover, a positive rainfall trend in Central Italy during summer, and the absence of competition with similar species in central Apulia.

Key words: Turdidae, olive orchards, vineyards, MaxEnt, downslope shift, Mediterranean Basin

Introduction

The mistle thrush (*Turdus viscivorus* Linnaeus, 1758) is one of the six species of the genus *Turdus* that breed in Europe. A sedentary or partial migrant, the mistle thrush breeds from Europe and north-western Africa to South Siberia and Nepal, wintering in western and north-western Europe, in the Mediterranean Basin, in north Africa and east to central and southern Asia (Cramp 1988, del Hoyo et al. 2005). The species generally breeds in old-growth stands close to forest edges in coniferous and mixed forests but also orchards, plantations, park-like farmland, and gardens. It forages on nearby areas with low vegetation, such as short grassland, pastures, and arable lands (Cramp 1988, del Hoyo et al. 2005, Knaus 2020). It avoids warm and arid areas, with the highest densities in hilly or mountainous areas. Indeed, it mainly breeds at 900-1,600 m a.s.l. in Switzerland, at 1,200-2,000 m a.s.l. in Catalonia, and at 1,500-2,700 m a.s.l. in north Africa (del Hoyo et al. 2005, Knaus 2020). The European population is

estimated to stand at 9,720,000 mature individuals (min. 7,300,000, max. 13,600,000), of which most are found in the boreal forests of Fennoscandia and the mountains of western and central Europe (BirdLife International 2017). Despite the global population decreasing (BirdLife International 2016), the European population is considered stable, even if it suffered a moderate decline between 1980 and 2013 (BirdLife International 2015, 2021). Nonetheless, it is classified globally and in Europe as of Least Concern by the IUCN (BirdLife International 2015, 2016). The main threats are modern forestry practices (e.g. felling of old-growth forests), intensified grassland management, severe winter weather, and hunting pressure in areas such as Spain, where it is a game bird (BirdLife International 2016). The species is also classified as "Least Concern" in Italy, where an estimated 50,000-100,000 breeding pairs and an increasing population trend (Rondinini et al. 2013, BirdLife International 2015).

In Italy, the nominate *T. v. viscivorus* occurs in hilly and mountainous areas along the entire peninsula and on Sicily, with large gaps in the Po Valley, lowlands and coastal areas, whereas *T. v. deichleri* occurs in Sardinia. As in the rest of the European range, it breeds mainly between 600-700 m and 1,800-1,900 m a.s.l., inhabiting coniferous, broad-leaved and mixed forests with pastures and open areas, as well as in orchards and gardens (Brichetti & Fracasso 2008). Nonetheless, in recent decades, the species has unexpectedly colonised new areas in south-eastern Italy (e.g. Apulia region) (Knaus 2020); breeding in olive groves, orchards, and urban gardens, in lowlands and along the coasts (Liuzzi et al. 2013, Chiatante & Meriggi 2016), despite having been absent from much of this region at the end of the 20th century (Meschini & Frugis 1993).

The main aim of this research was to improve understanding of the mistle thrush's habitat use in central Apulia during both the breeding and winter seasons, where the species has extended its range and is now occurring in unusual habitats. Based on preliminary observations (Chiatante & Meriggi 2016) and the general ecology of the species (Cramp 1988, del Hoyo et al. 2005), the mistle thrush was expected to select olive orchards, vineyards, and urban areas in both the breeding season and in winter, whilst avoiding open landscapes, such as arable lands and grasslands, due to the lack of trees.

The relevance of the current research is multifaceted. Firstly, there are few studies directly aimed at understanding the ecology of this species in the Mediterranean Basin (Tellería et al. 2014, Lavabre et al. 2016), with this research being the first to investigate its ecology in southern Italy. Secondly, it is essential to understand what drives a forest species (EBCC 2019) to colonise agricultural and urban areas in a Mediterranean context. Indeed, in a period of climate warming, the general hypothesis is that ranges of numerous birds in the Northern Hemisphere are expected to shift northward and to higher altitudes (Pape Møller et al. 2010). The mistle thrush can be found listed among these species and, because of climate change, is predicted to disappear from many areas of the Mediterranean Basin by the late 21st century (Huntley et al. 2007). Although a lack of data between the end of the 20th century and the beginning of the 21st means that the causes of its expansion cannot be investigated, this research attempts to understand it. Additionally, few studies have investigated the ecology of common species, such as the mistle thrush. If preserving overall species-richness patterns is considered a valid conservation goal, then attention must be given to both common and rare species (Lennon et al. 2003).

Material and Methods

Study area

The study area is located in the central part of the Apulia region in south-eastern Italy (41°0′ N, 16°34′ E), corresponding to the Bari and Barletta-Andria-Trani provinces, covering an area of 5,406 km^2 (Fig. 1). Altitude ranges from sea level up to 679 m a.s.l. (Mt. Caccia), with 35% of the altitude ranging from sea level up to 200 m a.s.l. and 40% from 201 up to 400 m a.s.l. The climate is typically Mediterranean: along the coast and in the lowlands, the summers are warm, windy, and dry, whilst the winters are mild and rainy. During the winter, temperatures vary between 2-5 °C and 10-13 °C, whereas in summer, the minimum temperature ranges between 16-19 °C with a maximum of 28-30 °C. Precipitation, concentrated during the late autumn and winter, is scarce and in the form of rain. Average rainfall values vary between 27-28 mm in July and 67 mm in October. The landscape is mainly characterised by non-irrigated arable lands (especially cereal steppes) (32.4%) and olive groves (27.6%). Vineyards represent 8.7% of the surface area, followed by urban areas (8.5%), natural grasslands (7.5%), orchards (5.7%), and woodlands (4.5%). The study area comprises 51 municipalities with a total resident population of 1,648,744 (ISTAT 2019) and a population density of 304.98 persons/km^2.

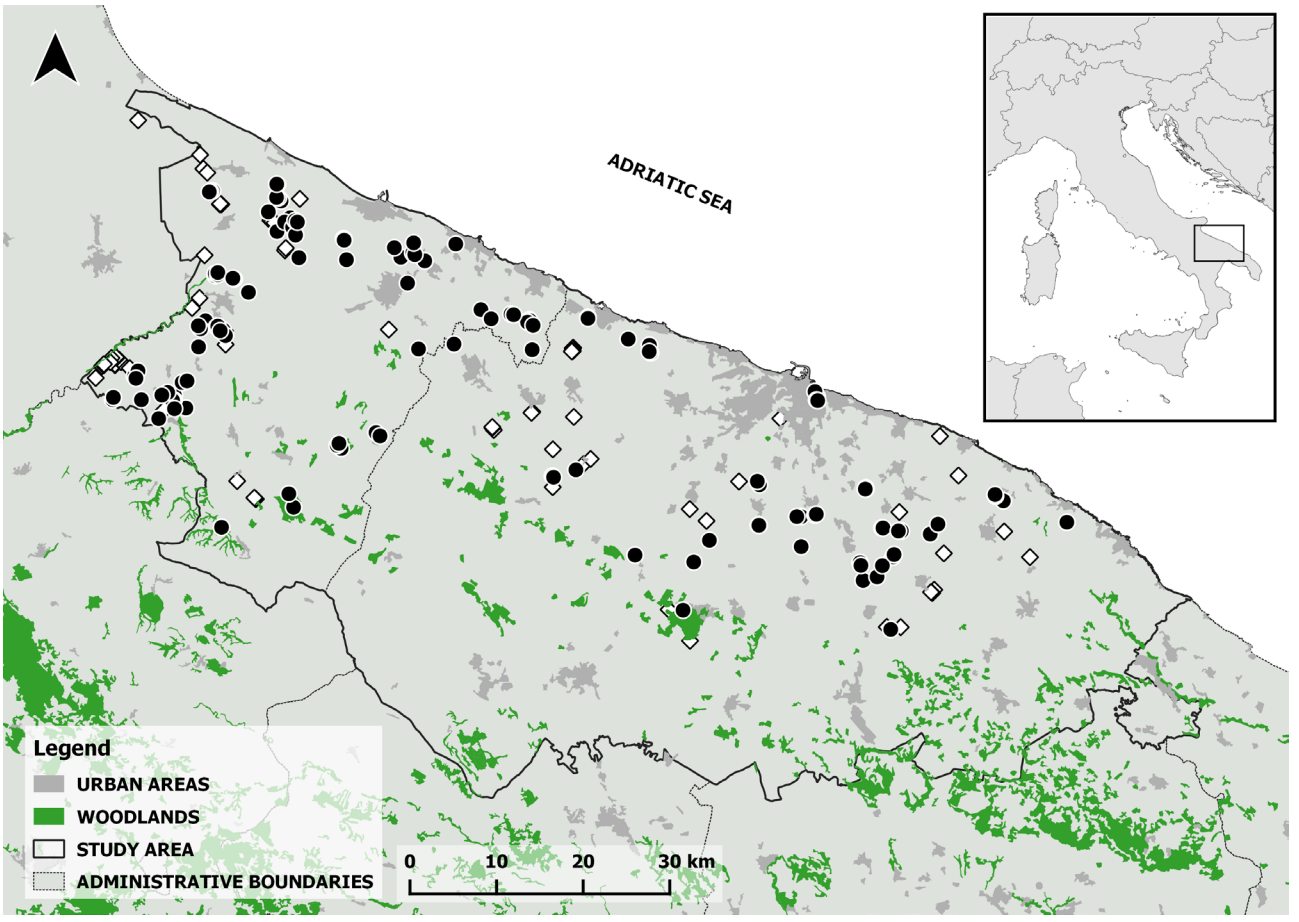

Fig. 1. The study area explored to investigate the habitat use of the mistle thrush in central Apulia (southern Italy). Black dots are mistle thrushes in the breeding season; white diamonds are mistle thrushes in winter.

Sampling design

A stratified random sampling design was used, with a proportional allocation of samples to guarantee the same sampling effort in each stratum (Krebs 1999). In this way, representativeness of the study area was ensured, and possible bias related to over- or under-sampling was reduced (Sutherland 2006). To this end, the study area was partitioned into 5,655 squares of 1 km^2. Homogeneous areas, referred to as Landscape Units (LU), were then identified by clustering similar squares with the help of k-means cluster analysis (see Appendix S1, Table S1, Fig. S1) (Legendre & Legendre 1998, Krebs 1999). For this purpose, the percentages of land use types were measured within each cell by a Geographic Information System (GIS) platform (QGIS v.3.14.16 "Pi") employing a regional land use map at the fourth level of CORINE land cover 1:5000 (2011 update, SIT – Regione Puglia; Table 1). Finally, the goodness of the LU classification was tested by the non-parametric Kruskal-Wallis test and Discriminant Function Analysis on the same environmental variables used for clustering (Legendre & Legendre 1998) (Table S2).

Fieldwork

Data were collected on the spatial distribution of the mistle thrush in both the breeding season and winter.

To collect data during the breeding season, the point count method with unlimited distance was used (Bibby et al. 2000, Sutherland et al. 2004) by carrying out 301 points randomly placed in the study area between April and May of the breeding season in 2012, according to the stratified sampling design (Table S3). Each point was surveyed once from dawn to 11:00 and lasted 10 minutes (Colwell & Coddington 1994, Chamberlain & Rolando 2014). In the surveys, the number of individuals counted, the number of singing males, and other breeding behaviours (e.g. nest building, mating, adult carrying food for young, etc.) were noted. However, searching for nests was not actively undertaken.

During the winter, counts were carried out along 264 transects for a total length of 185 km (mean per transect ± SD = 0.60 ± 0.33, min = 0.12, max = 0.26), which were randomly placed in the study area according

Table 1. Environmental variables used to investigate the habitat selection of the mistle thrush in central Apulia (southern Italy). Descriptive statistics of the environmental variables calculated for the study area are shown (values are measured in the 532 m grid), as well as the Variance Inflation Factor (VIF).

Environmental variable	Mean	±	SD	VIF
Urban areas (%)	7.9	±	17.2	1.80
Non-irrigated arable lands (%)	31.8	±	32.4	1.74
Irrigated arable lands (%)	0.7		6.4	1.14
Meadows (%)	0.9	±	5.4	1.06
Vineyards (%)	8.5	±	17.2	1.75
Orchards (%)	5.6	±	15.0	1.63
Olive groves (%)	27.1	±	32.5	1.77
Heterogeneous agricultural lands (%)	0.9	±	3.8	1.04
Broad-leaved woodlands (%)	2.87	±	11.0	1.30
Needle-leaved woodlands (%)	0.8	±	6.4	1.11
Natural grasslands (%)	7.4	±	16.5	1.76
Shrublands and Mediterranean scrubs (%)	1.0	±	4.9	1.09
Sparsely vegetated areas (%)	0.3	±	3.0	1.07

to the stratified sampling design (Bibby et al. 2000, Sutherland et al. 2004) (Table S3). Transects were walked once during December and January of the wintering seasons 2012-2013. In both periods, counts were conducted on calm days without persistent or heavy rain by recording all thrushes observed and heard. Moreover, when possible, the distances between the observer and birds were measured by a rangefinder (Leica Rangemaster 900 Scan). Data collection was not carried out outside these seasons (e.g. during summer or autumn migration).

Linear transects were carried out during the winter and point counts during the breeding season for several reasons. First, multiple survey methods are used for detecting different species in different seasons, with specific methods being more effective than others (Bibby et al. 2000, Sutherland et al. 2004). In particular, it is more efficient to use transects during the winter because they offer a better chance to record birds, which can be advantageous because of the inconspicuous behaviour of birds in this season (Bibby et al. 2000, Wilson et al. 2000, Buckland et al. 2001). Point counts, widely used for counting birds (Ralph et al. 1995, Buckland 2006, Chamberlain & Rolando 2014), are often preferable to transects during the breeding season because of the territorial behaviour of birds (Bibby et al. 2000, Buckland et al. 2001). However, comparing the results from multiple survey methods can be challenging; each method has its own assumptions, and the probability of detecting a species varies between sampling methods and efforts (MacKenzie et al. 2006). Despite this, only the presence data of the species (see the paragraph "Species distribution modelling" below) collected with the method that guarantees the best detection was used.

Environmental variables

The spatial distribution of the mistle thrush was assessed using 13 variables related to land cover (Table 1). Specifically, data derived from the regional land use map at the fourth level of CORINE land cover 1:5000 was used (SIT – Regione Puglia). To accommodate the spatial ecology of the species, all variables were resampled to cells, of which the extent was based on the home range size of the species, as suggested by previous research. The mistle thrush usually moves in a radius of 300 m around the nest (28.3 ha) (Cramp 1988), corresponding to cells with a spatial resolution of 532 m; thus, all variables were resampled at this spatial resolution. The Variance Inflation Factor (VIF) was computed with a threshold of three to test collinearity and in order to remove highly correlated variables (Table 1) (Fox & Monette 1992, Zuur et al. 2010). The spatial analyses were computed by QuantumGIS v3.8.3 and by the software R v3.4.3 and related packages *raster* (Hijmans et al. 2014), *sp* (Pebesma & Bivand 2011) and *usdm* (Naimi 2017).

Species distribution modelling

In this study, Species Distribution Models (SDMs) were run by the MaxEnt algorithm (Phillips et al. 2006); a machine learning method that applies the principle of maximum entropy to predict the

potential distribution of species from presence-only data (Phillips & Dudík 2008, Elith et al. 2011). Indeed, it compares the environmental characteristics between occurrences and background points, representing the available environment. This method is helpful as, in many cases, it is difficult to assess the absence of a species when only presence data are available, especially when a survey design does not take repeated visits to the study sites into account. Indeed, at least three to five surveys should occur to determine with a reasonable margin for error the absence of a species at a site (Buckland et al. 1993, Tyre et al. 2003, MacKenzie et al. 2006). In other cases, as for most regions, systematic biological survey data tend to be sparse and/or limited in coverage, available only in herbarium records, museum specimens, and online databases. For this substantial data source, SDM methods are essential for modelling presence-only data (Elith et al. 2006, 2011). In addition, MaxEnt outperformed most alternative methods (Elith et al. 2006) and is particularly efficient for small sample sizes (Pearson et al. 2006, Wisz et al. 2008).

MaxEnt was run for both the breeding and wintering seasons, with only linear and quadratic features to ensure more ecologically realistic response curves (Bateman et al. 2012, Chiatante 2021) using 10,000 background points, with all other parameters set to default (maximum number of iterations = 5,000; convergence threshold = 10^{-5}; multiplier regularisation = 1) (Phillips & Dudík 2008, Elith et al. 2011). A problem with species distribution modelling is the spatial autocorrelation of occurrences, which would violate the assumption of data independence (Betts et al. 2006, Dormann et al. 2007). For this reason, to reduce bias, duplicate occurrence points in the same grid cell were removed so that only one point per grid cell was retained (Chou et al. 2020, Chiatante 2022). To obtain the most parsimonious model, the variables to retain were chosen by the corrected Akaike Information Criterion (AIC_c) (Akaike 1973, Burnham & Anderson 2002), as this method outperforms other generally applied criteria (Warren & Seifert 2011). However, two steps were necessary to build the most complex and parsimonious model. First, the variables selected were only those with an evident effect (therefore with some importance for the mistle thrush occurrence), with a pairwise comparison of the second-order Akaike Information Criterion (AIC_c; Akaike 1973) of two simple MaxEnt models: one with the intercept only and the other with each variable (Burnham et al. 2011). When the AIC_c value of the MaxEnt with the variable was lower than that with the intercept only, with a difference of at least two ($\Delta AIC_c \leq 2$), the variable was retained (Burnham & Anderson 2002, Warren & Seifert 2011). Once the number of variables was reduced, a priori set of models was built using all the combinations of the retained environmental variables (Chiatante 2021). The second-order Akaike Information Criterion (AIC_c) for each model was calculated, and the model with the lower AIC_c was selected as the best (Burnham & Anderson 2002, Warren & Seifert 2011). The regularisation multiplier parameter was set manually, for which default regularisation values may lead to overfitted models (Anderson & Gonzalez 2011, Radosavljevic & Anderson 2014). To reduce the complexity of the models and, therefore, the likelihood of over-parameterisation and the risk of model overfitting, models with different values for the regularisation multiplier were calibrated (default setting 0.01, 0.1, 0.5, 1.0, 1.5, 2.0, 3.0, 5.0), after which AIC_c values were used to select the most parsimonious models (Rodríguez-Ruiz et al. 2019, Chiatante 2022). The variable importance was assessed by both the percentage contribution and the permutation importance, which are criteria used to measure the contribution of each variable to the full model (Elith et al. 2011). Model accuracy was tested through the area under the curve of the Receiver Operating Characteristic (ROC) (Pearce & Ferrier 2000, Fawcett 2006).

Finally, the similarity between habitat suitability in the breeding season and winter was measured through Schoener's *D* (Schoener 1968), which was obtained by comparing the estimates of both MaxEnt models calculated for each grid cell of the study area (Warren et al. 2008, 2010). This measure was calculated through the following formula:

$$D_{(pX,\,pY)} = 1 - \frac{1}{2} \sum_{i} |p_{x,i} - p_{y,i}|$$

where $p_{X,i}$ and $p_{Y,i}$ are the normalised suitability scores for period X (the breeding season) and period Y (the winter) in grid cell i. This value ranges from 0, when there was no similarity, to 1, when all grid cells were estimated to be equally suitable for both periods. The reliability of this measure was tested by resampling the data 1,000 times with the bootstrap method and calculating the mean values and 95% confidence intervals (Legendre & Legendre 1998). The statistical analyses were carried out using the software R 3.4.3 (R Core Team 2019) and the packages *dismo* (Hijmans et al. 2011) and *ENMeval* (Muscarella et al. 2017).

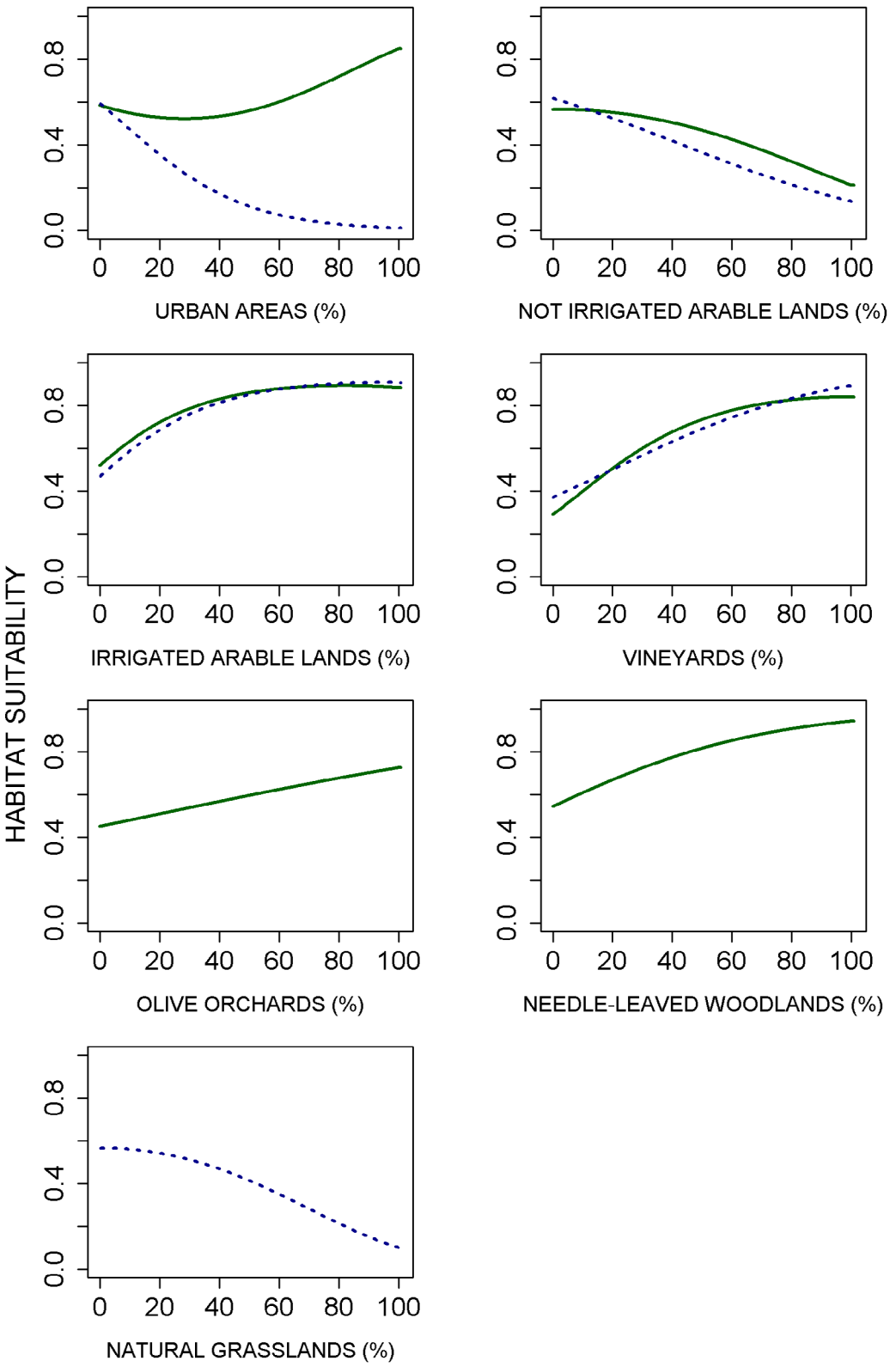

Fig. 2. Response curves of the variables included in the best MaxEnt model explaining the habitat use of the mistle thrush in central Apulia (southern Italy), in both the breeding season (solid line) and in winter (dotted line).

Results

During the breeding season, 133 observations of mistle thrush were noted. Among the 13 variables, only 10 were retained after the pairwise comparison with the null model (Table 2). The best MaxEnt model was composed of six variables. Among the most important (contribution greater than 5%) were vineyards, irrigated arable lands, and olive orchards, which positively affected the species (Table 3, Fig. 2).

Table 2. The AIC_c of the simple MaxEnt models, for both the wintering and breeding season of the mistle thrush in central Apulia (southern Italy), to compare with the AIC_c of the model with only the intercept. Variables retained for final MaxEnt models ($\Delta AIC_c \leq 2$) are in bold.

Environmental variable	AIC_c	ΔAIC_c
Breeding season (AIC_c null model = 2630.15)		
Urban areas (%)	**2,625.56**	**4.59**
Non-irrigated arable lands (%)	**2,561.89**	**68.25**
Irrigated arable lands (%)	**2,622.09**	**8.06**
Meadows (%)	**2,627.65**	**2.50**
Vineyards (%)	**2,539.68**	**90.47**
Orchards (%)	2,629.88	0.26
Olive groves (%)	**2,607.08**	**23.07**
Heterogeneous agricultural lands (%)	**2,627.69**	**2.46**
Broad-leaved woodlands (%)	**2,620.58**	**9.57**
Needle-leaved woodlands (%)	2,628.76	1.39
Natural grasslands (%)	**2,615.40**	**14.75**
Shrublands and Mediterranean scrubs (%)	2,628.89	1.25
Sparsely vegetated areas (%)	**2,627.30**	**2.85**
Wintering season (AIC_c null model = 1663.31)		
Urban areas (%)	**1,640.81**	**22.49**
Non-irrigated arable lands (%)	**1,625.99**	**37.31**
Irrigated arable lands (%)	**1,642.22**	**21.09**
Meadows (%)	1,663.71	–0.40
Vineyards (%)	**1,605.37**	**57.94**
Orchards (%)	**1,654.06**	**9.25**
Olive groves (%)	1,663.67	–0.36
Heterogeneous agricultural lands (%)	**1,660.26**	**3.05**
Broad-leaved woodlands (%)	**1,658.87**	**4.44**
Needle-leaved woodlands (%)	1,661.42	1.89
Natural grasslands (%)	**1,654.43**	**8.87**
Shrublands and Mediterranean scrubs (%)	1,661.50	1.81
Sparsely vegetated areas (%)	**1,660.11**	**3.19**

Conversely, non-irrigated arable lands negatively affected species occurrence (Fig. 2). Among the less important variables, urban areas and needle-leaved woodlands positively affected the mistle thrush (Fig. 2). The model accuracy was quite good (AUC = 0.858 ± 0.024) and the model predicted average suitability was equal to 0.356 ± 0.002 (SE) (Fig. S2).

During the winter, 85 observations of mistle thrush were noted. Among the 13 variables, only nine were retained after the pairwise comparison with the null model (Table 2). The best MaxEnt model was composed of five variables. Among the most important were vineyards and irrigated arable lands which positively affected the species (Table 3, Fig. 2). Contrarily, urban areas and non-irrigated arable lands negatively affected species occurrence (Fig. 2). Among the less important variables, natural grasslands negatively affected the mistle thrush (Fig. 2). The model accuracy was quite good (AUC = 0.750 ± 0.061) and the model predicted average suitability was equal to 0.333 ± 0.002 (SE) (Fig. S3).

Between the breeding season and winter, there was an average similarity of 0.600 ± 0.00009 (SE), with a minimum of 0.600 and a maximum of 0.601. Non-irrigated and irrigated arable lands, as well as vineyards, had similar effects on the mistle thrush in both periods (Fig. 2). Contrarily, urban areas had opposing effects between seasons (positive in the breeding, negative in the winter), whilst two land uses only affected the species during the breeding

Table 3. The best MaxEnt model for the mistle thrush in central Apulia (southern Italy). Estimates (β) of both linear and quadratic features are shown, as well their percent contribution and permutation importance.

Environmental variable	Estimate linear feature	Estimate quadratic feature	Percent contribution	Permutation importance
Breeding season				
Urban areas	–1.791	3.176	1.9	5.7
Non-irrigated arable lands	0.000	–1.584	27.0	13.0
Irrigated arable lands	4.982	–3.043	6.7	6.0
Vineyards	5.035	–2.483	54.8	57.7
Olive groves	1.168	-	6.5	11.3
Needle-leaved woodlands	2.628	-	3.0	6.3
Winter				
Urban areas	–4.887	-	8.6	6.6
Non-irrigated arable lands	–1.821	–0.512	19.8	40.2
Irrigated arable lands	5.041	–2.637	20.0	13.5
Vineyards	2.636	-	50.0	39.6
Natural grasslands	0.000	–2.448	1.6	0.0

season (olive groves and needle-leaved woodlands, both positively) and one only had an effect during the winter (natural grasslands, negatively).

Discussion

This research aimed to explore the habitat selection of the mistle thrush in a recently colonised area of southern Italy, where it is found in lowland and coastal areas, in intensively cultivated agroecosystems, and in urban areas. In order to achieve the aims set out by the current study, linear transects in winter and point counts were used in the breeding season. As previously mentioned, no issues arose through the use of this method due to the fact that only occurrence data, not abundances were analysed, and due to the fact that the MaxEnt algorithm was built fundamentally to model presence-only data, collected using many techniques and without a survey design (Elith et al. 2006, 2011).

As expected, olive orchards and vineyards positively affected the species during the breeding season. Despite orchards generally being indicated as possible breeding habitats (Cramp 1988, del Hoyo et al. 2005, Knaus 2020), the mistle thrush was not found in olive orchards of Spain (Rey 1993, Castro-Caro et al. 2014, Morgado et al. 2020), Greece (Solomou & Sfougaris 2015), or north-eastern Algeria (Bouam et al. 2017) during the breeding season. Nevertheless, olive orchards could play a role in the ecology of the species in Sicily (La Mantia et al. 2014), despite the fact that the species finds a suitable habitat in those areas where there has been a significant increase in forests, reforestation and bushes at the expense of pastures and arable lands (La Mantia et al. 2014). Contrarily, the results of this study showed that in central Apulia, olive orchards are important during the breeding season, possibly because as scarce woodlands, they offer nesting sites, especially in lowland areas. In addition, olive orchards grow with a planting scheme that is not dense, which favours the species, which tends to avoid dense vegetation (Cramp 1988). Indeed, as forests become denser, the potential habitat for this species generally decreases (Versluijs et al. 2020). Moreover, as a ground feeder, the mistle thrush selects areas with low vegetation, such as grasslands and arable lands, where it can find food with ease (Cramp 1988, Knaus 2020). In the study site, olive orchards are ploughed and weeded regularly, offering the mistle thrush perfect places to forage. Despite mistle thrushes also being observed in olive orchards during the winter, in this season, this habitat is not clearly selected. In the Mediterranean Basin, numerous species of birds from central and northern Europe use olive orchards in winter, including species of *Turdus*, especially the song thrush (*Turdus philomelos*) (Rey 1993, Chiatante & Meriggi 2016). Indeed, these species have a mainly frugivorous diet during the winter and olives represent an important food source for them (Cramp 1988, del Hoyo et al. 2005). Nonetheless, the mistle thrush was not found in olive orchards during the winter in Spain (Rey 1993, 2011), selecting mainly wild olive shrublands (Rey 1993), further attesting to the avoidance of olive orchards in this season.

This avoidance may be due to competition with song thrushes or other frugivorous species, that are more abundant than mistle thrushes, which leads to a shift toward more available habitats, such as vineyards. On the other hand, the possibility of a lower detectability of the species during the winter cannot be excluded.

This study shows the importance of vineyards for the mistle thrush, both during the breeding season and in the winter. The mistle thrush also occurs in vineyards in northern Italy (Assandri et al. 2016), western France (Barbaro et al. 2017) and northern Spain (Puig-Montserrat et al. 2017, Rollan et al. 2019) during the breeding season, although with very low abundances (Barbaro et al. 2021). Nevertheless, at least in northern Italy, the mistle thrush does not nest in vineyards (Assandri et al. 2017b). However, in central Apulia, the same situation observed in northern Italy with the congeneric song thrush in apple orchards and vineyards could occur. Indeed, in northern Italy, song thrushes nest in apple orchards (Brambilla et al. 2013) and do not avoid intensive vineyards; on the contrary, an apparent process of "spillover" seems to occur because the species tends to colonise vineyards adjacent to apple orchards (Assandri et al. 2017a). In addition, song thrushes also nest in vineyards (Assandri et al. 2017b). In this way the mistle thrush may nest in olive orchards in the current study area, in particular in those adjacent to vineyards where the species could also nest, although breeding behaviours that suggested the presence of nests in vineyards were not observed in this study. Furthermore, vineyards could also be selected because of food availability. Indeed, in the study area, they are frequently ploughed all year long, providing many ground invertebrates, which are very important to the species' diet, especially during the breeding season (Cramp 1988, del Hoyo et al. 2005). It is already known that the species selects vineyards both in northern Italy (Assandri et al. 2016) and northern Spain (Rollan et al. 2019) during the winter. As in the breeding season, during the winter, vineyards could be used for feeding, with ploughing providing invertebrates and the presence of unharvested grapes being advantageous as they are a readily available seasonal food source.

Results of this study show the positive effects of needle-leaved woodlands (old reforestations composed mainly by *Pinus* spp. and *Cupressus* spp.) on the mistle thrush during the breeding season. This is in agreement with the widely accepted knowledge that the probability of the species' occurrence increases with the increasing amount of this kind of forest (del Hoyo et al. 2005, Brichetti & Fracasso 2008, Knaus 2020).

The current study demonstrated that during the breeding season the species also selected urban areas. Generally, the species does not live too close to human settlements, but in parts of the range in question (especially in Western and Central Europe), it has recently overcome its reluctance to inhabit urban parks and gardens (Cramp 1988, Knaus 2020). Generally, urban environments provide more stable and predictable food supplies, higher temperatures, and lesser temperature variability (Gil & Brumm 2014). Food may be more readily available in the proximity of humans and urban habitats may be colonised because of a reduction in the abundance of predators (Gil & Brumm 2014). All these advantages could explain the colonisation of urban areas by the mistle thrush in central Apulia. Indeed, garden lawns and shrubberies offer ideal feeding and nesting conditions. Similarly, in England, the mistle thrush colonises urban areas and villages, with higher densities in urban areas (1.8 ind./km^{-2}) than in rural ones (0.8 ind./km^{-2}) (Mason 2000). The mistle thrush also occurs in French (Clergeau et al. 2001) and Polish cities (Kopij 2019), and in Italy, it seems that this species is positively affected by the presence of roads (Morelli et al. 2015). Nevertheless, it was found that urban environments negatively affect the species during the winter. It is likely that this is not related to urbanisation *per se*, but to food availability, microhabitat preferences, and direct and indirect human activity (Tryjanowski et al. 2015). Indeed, changes in food availability in urban areas are probably key mechanisms that lead to changes in avian community structure (Shochat et al. 2004, 2006). Considering that in winter the mistle thrush consumes more fruits than in summer, and that fruit is scarce in winter in urban areas, the species may prefer to live in rural areas, in order to avoid the loss of energy brought about when moving between cities and the countryside, where it can find food. This is particularly true if we consider how birds are subjected to increased energy loss due to lower temperatures in winter, leading to a need to avoid areas of food shortage and to reduce energy expenditure (Hutto 1985, Caraco et al. 1990, Sherry et al. 2005, Diggs et al. 2011). Conversely, food availability during the breeding season (especially in the form of invertebrates) is higher everywhere and energy loss in this period is negligible, causing some mistle thrushes to move toward urban areas for nesting, in order to find a safe and favourable environment to raise their broods.

Irrigated arable lands positively affected the mistle thrush in both winter and during the breeding season. During the breeding season, the mistle thrush feeds mostly on invertebrates, including earthworms (Cramp 1988, del Hoyo et al. 2005) and it was demonstrated that its abundance is related to their abundance (Martay & Pearce-Higgins 2020). In addition, in other thrushes (namely common blackbird *Turdus merula* and song thrush), there is also evidence that wet soils enhance reproductive success (Miller et al. 2017) and survival (Robinson et al. 2007), a fact that could also be true for the mistle thrush. In this way, the selection of irrigated arable lands when compared to non-irrigated lands is likely due to the high availability of earthworms. In addition, irrigated arable lands could also be important due to direct water availability, essential during the dry and hot summers typical of the study area. This fact is consistent with the occurrence of the species near water in North Africa (del Hoyo et al. 2005). Conversely, non-irrigated arable lands and grasslands are avoided by the mistle thrush, a factor especially true in the study area, which is both very large and treeless, and therefore unfavourable for the species (Cramp 1988). However, at the boundaries of its range, it has been found to occupy treeless sites, nesting in walls or on the ground (Cramp 1988).

The colonisation of the lowlands and coast in this Mediterranean area by the mistle thrush is somehow unexpected, especially due to the hot and dry climate. Indeed, the range of the mistle thrush is expected to shift northward and upward, disappearing from many areas of the Mediterranean Basin (Huntley et al. 2007, Pape Møller et al. 2010). In general, southward and downward shifts of ranges occur in birds (Lenoir et al. 2010, Tingley et al. 2012, DeLuca & King 2017) as a direct consequence of habitat modifications and human-induced disturbances, or following natural disturbances (Lenoir et al. 2010). Moreover, Lenoir et al. (2010) argued that the species shifting downwards are ones that had been limited by competition with other species at the downslope edge of their ranges and that some characteristics of the downslope shifters may give them a competitive advantage as their competitors change with a warming climate. Furthermore, downward shifts could be caused by changes in non-temperature environmental gradients, such as temporal increases in precipitation (Tingley et al. 2012). However, what drives this southward and downward shift in Apulia remains unclear and the current hypotheses are relatively speculative. In Italy, forest cover has increased in recent decades (Rete Rurale Nazionale 2019) and there has been a positive trend (+26%) in summer precipitation (Toreti et al. 2009, Fioravanti et al. 2021). In this context therefore, the mistle thrush's shift may be favourable to the species, taking advantage also of the absence of a potential competitor, as suggested by Lenoir et al. (2010). Indeed, the common blackbird, a generalist and competitive species, is absent or very scarce as a breeder in the area (Liuzzi et al. 2013), being a negligible limitation factor for the expansion of the mistle thrush toward the south.

Acknowledgements

I would like to thank Pietro Chiatante for his help in the fieldwork. I would like to thank Laura Bohin for the linguistic revision.

Data Availability Statement

The datasets generated during and/or analysed during the current study are available from the corresponding author on a reasonable request.

Literature

Akaike H. 1973: Information theory as an extension of the maximum likelihood principle. In: Petrov B.N. & Csaki F. (eds.), Second international symposium on information theory. *Akadémiai Kiadó, Budapest, Hungary: 267–281.*

Anderson R.P. & Gonzalez I., Jr. 2011: Species-specific tuning increases robustness to sampling bias in models of species distributions: an implementation with Maxent. *Ecol. Model. 222: 2796–2811.*

Assandri G., Bogliani G., Pedrini P. & Brambilla M. 2016: Diversity in the monotony? Habitat traits and management practices shape avian communities in intensive vineyards. *Agric. Ecosyst. Environ. 223: 250–260.*

Assandri G., Bogliani G., Pedrini P. & Brambilla M. 2017a: Assessing common birds' ecological requirements to address nature conservation in permanent crops: lessons from Italian vineyards. *J. Environ. Manag. 191: 145–154.*

Assandri G., Giacomazzo M., Brambilla M. et al. 2017b: Nest density, nest-site selection, and breeding success of birds in vineyards: management implications for conservation in a highly intensive farming system. *Biol. Conserv. 205: 23–33.*

Barbaro L., Assandri G., Brambilla M. et al. 2021: Organic management and landscape heterogeneity combine to sustain multifunctional bird communities in European vineyards. *J. Appl. Ecol. 58: 1261–1271.*

Barbaro L., Rusch A., Muiruri E.W. et al. 2017: Avian pest control in vineyards is driven by interactions between bird functional diversity and landscape heterogeneity. *J. Appl. Ecol. 54: 500–508.*

Bateman B.L., VanDerWal J., Williams S.E. & Johnson C.N. 2012: Biotic interactions influence the projected distribution of a specialist mammal under climate change. *Divers. Distrib. 18: 861–872.*

Betts M.G., Diamond A.W., Forbes G.J. et al. 2006: The importance of spatial autocorrelation, extent and resolution in predicting forest bird occurrence. *Ecol. Model. 191: 197–224.*

Bibby C.J., Burgess N.D., Hill D.A. & Mustoe S.H. 2000: Bird census techniques. *Academic Press, London, UK.*

BirdLife International 2015: *Turdus viscivorus*: the IUCN Red List of Threatened Species 2015: e.T22708829A60195505. *https://www.iucnredlist.org/*

BirdLife International 2016: *Turdus viscivorus*: the IUCN Red List of Threatened Species 2016: e.T22708829A87878799. *https://www.iucnredlist.org/*

BirdLife International 2017: European birds of conservation concern: populations, trends and national responsibilities. *BirdLife International, Cambridge, UK.*

BirdLife International 2021: European Red List of Birds. *Publications Office of the European Union, Luxembourg.*

Bouam I., Bachir A.S. & Katayama N. 2017: Variation in bird assemblages along an agricultural intensification gradient: a case study of olive orchards in North-Eastern Algeria. *Ornithol. Sci. 16: 147–157.*

Brambilla M., Martino G. & Pedrini P. 2013: Changes in song thrush *Turdus philomelos* density and habitat association in apple orchards during the breeding season. *Ardeola 60: 73–83.*

Brichetti P. & Fracasso G. 2008: Italian Ornithology, vol. 5, Turdidae-Cisticolidae. *Oasi Alberto Perdisa Editore, Bologna, Italy.*

Buckland S.T. 2006: Point-transect surveys for songbirds: robust methodologies. *Auk 123: 345–357.*

Buckland S.T., Anderson D.R., Burnham K.P. & Laake J.L. 1993: Distance sampling: estimating abundance of biological populations. *Chapman & Hall, London, UK.*

Buckland S.T., Anderson D.R., Burnham K.P. et al. 2001: Introduction to distance sampling: estimating abundance of biological populations. *Oxford University Press, Oxford, UK.*

Burnham K.P. & Anderson D.R. 2002: Model selection and multimodel inference: a practical information-theoretic approach. *Springer, New York, USA.*

Burnham K.P., Anderson D.R. & Huyvaert K.P. 2011: AIC model selection and multimodel inference in behavioral ecology: some background, observations, and comparisons. *Behav. Ecol. Sociobiol. 65: 23–35.*

Caraco T., Blanckenhorn W.U., Gregory G.M. et al. 1990: Risk-sensitivity: ambient temperature affects foraging choice. *Anim. Behav. 39: 338–345.*

Castro-Caro J.C., Barrio I.C. & Tortosa F.S. 2014: Is the effect of farming practices on songbird communities landscape dependent? A case study of olive groves in southern Spain. *J. Ornithol. 155: 357–365.*

Chamberlain D. & Rolando A. 2014: The effects of a settling-down period on estimates of bird species richness and occurrence from point counts in the Alps. *Bird Study 61: 121–124.*

Chiatante G. 2021: Habitat requirements of the masked shrike *Lanius nubicus* in the southern Balkans. *Bird Study 68: 198–210.*

Chiatante G. 2022: Spatial distribution of an assemblage of an endemic genus of birds: an example from Madagascar. *Afr. J. Ecol. 60: 13–26.*

Chiatante G. & Meriggi A. 2016: The importance of rotational crops for biodiversity conservation in Mediterranean areas. *PLOS ONE 11: e0149323.*

Chou E., Kershaw F., Maxwell S.M. et al. 2020: Distribution of breeding humpback whale habitats and overlap with cumulative anthropogenic impacts in the Eastern Tropical Atlantic. *Divers. Distrib. 26: 549–564.*

Clergeau P., Jokimäki J. & Savard J.-P.L. 2001: Are urban bird communities influenced by the bird diversity of adjacent landscapes? *J. Appl. Ecol. 38: 1122–1134*.

Colwell R.K. & Coddington J.A. 1994: Estimating terrestrial biodiversity through extrapolation. *Philos. Trans. R. Soc. Lond. B 345: 101–118.*

Cramp S. 1988: Handbook of the birds of Europe, the Middle East and North Africa. Tyrant flycatchers to thrushes, vol 5. *Oxford University Press, Oxford, UK.*

del Hoyo J., Elliot A. & Sargatal J. 2005: Handbook of the birds of the world. Cuckoo-shrikes to thrushes, vol. 10. *Lynx Edicions, Barcelona, Spain.*

DeLuca W.V. & King D.I. 2017: Montane birds shift downslope despite recent warming in the northern Appalachian Mountains. *J. Ornithol. 158: 493–505.*

Diggs N.E., Marra P.P. & Cooper R.J. 2011: Resource limitation drives patterns of habitat occupancy during the nonbreeding season for an omnivorous songbird. *Condor 113: 646–654.*

Dormann C.F., McPherson J.M., Araújo M.B. et al. 2007: Methods to account for spatial autocorrelation in the analysis of species distributional data: a review. *Ecography 30: 609–628.*

EBCC 2019: Final species classification for 2019 update in Europe and its biogeographical regions. *European Bird Census Council, Beek-Ubbergen, the Netherlands.*

Elith J., Graham H.C., Anderson P.R. et al. 2006: Novel methods improve prediction of species' distributions from occurrence data. *Ecography 29: 129–151.*

Elith J., Phillips S.J., Hastie T. et al. 2011: A statistical explanation of MaxEnt for ecologist. *Divers. Distrib. 17: 43–57.*

Fawcett T. 2006: An introduction to ROC analysis. *Pattern Recognit. Lett. 27: 861–874.*

Fioravanti G., Fraschetti P., Lena F. et al. 2021: Gli indicatori del clima in Italia nel 2020. *ISPRA, Rome, Italy.*

Fox J. & Monette G. 1992: Generalised collinearity diagnostics. *J. Am. Stat. Assoc. 87: 178–183.*

Gil D. & Brumm H. 2014: Avian urban ecology: behavioural and physiological adaptations. *Oxford University Press, Oxford, UK.*

Hijmans R.J., van Etten J., Mattiuzzi M. et al. 2014: Package *raster*: geographic data analysis and modeling. *www.cran.r-project.org*

Hijmans R.J., Phillips S.J., Leathwick J.R. & Elith J. 2011: Package *dismo*: species distribution modeling. *www.cran.r-project.org*

Huntley B., Green R.E., Collingham Y.C. & Willis S.G. 2007: A climatic atlas of European breeding birds. *Lynx Edicions, Barcelona, Spain.*

Hutto R.L. 1985: Habitat selection by nonbreeding, migratory land birds. In: Cody M.L. (ed.), Habitat selection in birds. *Academic Press, Orlando, USA: 455–476.*

ISTAT 2019: Popolazione residente 2018. *Istituto Nazionale di Statistica, Rome, Italy.*

Knaus P. 2020: *Turdus viscivorus* mistle thrush. In: Keller V., Herrando S., Voříšek P. et al. (eds.), European breeding bird atlas 2: distribution, abundance and change. *European Bird Census Council & Lynx Edicions, Barcelona, Spain: 710–711.*

Kopij G. 2019: The effect of urbanisation on population densities of forest passerine species in a Central European city. *Ornis Hung. 27: 207–220.*

Krebs C.J. 1999: Ecological methodology. *Benjamin Cummings, Menlo Park, USA.*

La Mantia T., Bonaviri L. & Massa B. 2014: Ornithological communities as indicators of recent transformations on a regional scale: Sicily's case. *Avocetta 38: 67–81.*

Lavabre J.E., Gilarranz L.J., Fortuna M.A. & Bascompte J. 2016: How does the functional diversity of frugivorous birds shape the spatial pattern of seed dispersal? A case study in a relict plant species. *Philos. Trans. R. Soc. Lond. B 371: 20150280.*

Legendre P. & Legendre L. 1998: Numerical ecology. *Elsevier, Amsterdam, the Netherlands.*

Lennon J.J., Koleff P., Greenwood J.J.D. et al. 2003: Contribution of rarity and commonness to patterns of species richness: richness patterns and rarity/commonness. *Ecol. Lett. 7: 81–87.*

Lenoir J., Gégout J.-C., Guisan A. et al. 2010: Going against the flow: potential mechanisms for unexpected downslope range shifts in a warming climate. *Ecography 33: 295–303.*

Liuzzi C., Mastropasqua F. & Todisco S. 2013: Avifauna pugliese...130 anni dopo. *Edizioni Favia, Bari, Italy.*

MacKenzie D.I., Nichols J.D., Royle A.J. et al. 2006: Occupancy estimation and modeling: inferring patterns and dynamics of species. *Elsevier, Boston, USA.*

Martay B. & Pearce-Higgins J.W. 2020: Opening a can of worms: can the availability of soil invertebrates be indicated by birds? *Ecol. Indic. 113: 106222.*

Mason C.F. 2000: Thrushes now largely restricted to the built environment in eastern England. *Divers. Distrib. 6: 189–194.*

Meschini E. & Frugis S. 1993: Atlante degli uccelli nidificanti in Italia. *Ric. Biol. Selvag. 20 (Suppl.): 1–344.*

Miller M.W., Leech D.I., Pearce-Higgins J.W. & Robinson R.A. 2017: Multi-state, multi-stage modeling of nest-success suggests interaction between weather and land-use. *Ecology 98: 175–186.*

Morelli F., Jerzak L., Pruscini F. et al. 2015: Testing bird response to roads on a rural environment: a case study from Central Italy. *Acta Oecol. 69: 146–152.*

Morgado R., Santana J., Porto M. et al. 2020: A Mediterranean silent spring? The effects of olive farming intensification on breeding bird communities. *Agric. Ecosyst. Environ. 288: 106694.*

Muscarella R., Galante P.J., Soley-Guardia M. et al. 2017: Package *ENMeval*: automated runs and evaluations of ecological niche models. *www.cran.r-project.org*

Naimi B. 2017: Package *usdm*: uncertainty analysis for species distribution models. *www.cran.r-project.org*

Pape Møller A., Fiedler W. & Berthold P. 2010: Effects of climate change on birds. *Oxford University Press, Oxford, UK.*

Pearce J. & Ferrier S. 2000: Evaluating the predictive performance of habitat models developed using logistic regression. *Ecol. Model. 133: 225–245.*

Pearson R.G., Raxworthy C.J., Nakamura M. & Townsend Peterson A. 2006: Predicting species distributions from small numbers of occurrence records: a test case using cryptic geckos in Madagascar. *J. Biogeogr. 34: 102–117.*

Pebesma E. & Bivand R. 2011: Package *sp*: classes and methods for spatial data. *www.cran.r-project.org*

Phillips S.J., Anderson R.P. & Schapire R.E. 2006: Maximum entropy modeling of species geographic distributions. *Ecol. Model. 190: 231–259.*

Phillips S.J. & Dudík M. 2008: Modeling of species distributions with Maxent: new extensions and a comprehensive evaluation. *Ecography 31: 161–175.*

Puig-Montserrat X., Stefanescu C., Torre I. et al. 2017: Effects of organic and conventional crop management on vineyard biodiversity. *Agric. Ecosyst. Environ. 243: 19–26.*

R Core Team 2019: R: a language and environment for statistical computing. *R Foundation for Statistical Computing, Vienna, Austria.*

Radosavljevic A. & Anderson R.P. 2014: Making better Maxent models of species distributions: complexity, overfitting and evaluation. *J. Biogeogr. 41: 629–643.*

Ralph C.J., Sauer J.R. & Droege S. 1995: Monitoring bird populations by point counts. *Pacific Southwest Research Station, Forest Service, U.S. Department of Agriculture, Albany, USA.*

Rete Rurale Nazionale 2019: RaF Italia 2017-2018. Rapporto sullo stato delle foreste e del settore forestale in Italia. *Compagnia delle Foreste S.r.l., Arezzo, Italy.*

Rey P.J. 1993: The role of olive orchards in the wintering of frugivorous birds in Spain. *Ardea 81: 151–160.*

Rey P.J. 2011: Preserving frugivorous birds in agro-ecosystems: lessons from Spanish olive orchards: frugivorous birds in agro-ecosystems. *J. Appl. Ecol. 48: 228–237.*

Robinson R.A., Baillie S.R. & Crick H.Q.P. 2007: Weather-dependent survival: implications of climate change for passerine population processes. *Ibis 149: 357–364.*

Rodríguez-Ruiz J., Mougeot F., Parejo D. et al. 2019: Important areas for the conservation of the European roller *Coracias garrulus* during the non-breeding season in southern Africa. *Bird Conserv. Int. 29: 159–175.*

Rollan À., Hernández-Matías A. & Real J. 2019: Organic farming favours bird communities and their resilience to climate change in Mediterranean vineyards. *Agric. Ecosyst. Environ. 269: 107–115.*

Rondinini C., Battistoni A., Peronace V. & Teofili C. 2013: Lista Rossa IUCN dei Vertebrati Italiani. *Comitato Italiano IUCN e Ministero dell'Ambiente e della Tutela del Territorio e del Mare, Rome, Italy.*

Schoener T.W. 1968: The *Anolis* lizards of Bimini: resource partitioning in a complex fauna. *Ecology 49: 704–726.*

Sherry T.W., Johnson M.D. & Strong A.M. 2005: Does winter food limit populations of migratory birds? In: Greenberg R. & Marra P.P. (eds.), Birds of two worlds. *Johns Hopkins University Press, Baltimore, USA: 414–425.*

Shochat E., Lerman S.B., Katti M. & Lewis D.B. 2004: Linking optimal foraging behavior to bird community structure in an urban-desert

landscape: field experiments with artificial food patches. *Am. Nat. 164: 232–243.*

Shochat E., Warren P.S., Faeth S.H. et al. 2006: From patterns to emerging processes in mechanistic urban ecology. *Trends Ecol. Evol. 21: 186–191.*

Solomou A.D. & Sfougaris A.I. 2015: Bird community characteristics as indicators of sustainable management in olive grove ecosystems of Central Greece. *J. Nat. Hist. 49: 301–325.*

Sutherland W.J. 2006: Ecological census techniques: a handbook. *Cambridge University Press, Cambridge, UK.*

Sutherland W.J., Newton I. & Green R. 2004: Bird ecology and conservation: a handbook of techniques. *Oxford University Press, Oxford, UK.*

Tellería J.L., Carrascal L.M. & Santos T. 2014: Species abundance and migratory status affects large-scale fruit tracking in thrushes (*Turdus* spp.). *J. Ornithol. 155: 157–164.*

Tingley M.W., Koo M.S., Moritz C. et al. 2012: The push and pull of climate change causes heterogeneous shifts in avian elevational ranges. *Glob. Change Biol. 18: 3279–3290.*

Toreti A., Fioravanti G., Perconti W. & Desiato F. 2009: Annual and seasonal precipitation over Italy from 1961 to 2006. *Int. J. Climatol. 29: 1976–1987.*

Tryjanowski P., Sparks T.H., Biaduń W. et al. 2015: Winter bird assemblages in rural and urban environments: a national survey. *PLOS ONE 10: e0130299.*

Tyre A.J., Tenhumberg B., Field S.A. et al. 2003: Improving precision and reducing bias in biological surveys: estimating false-negative error rates. *Ecol. Appl. 13: 1790–1801.*

Versluijs M., Hekkala A.-M., Lindberg E. et al. 2020: Comparing the effects of even-aged thinning and selective felling on boreal forest birds. *Forest Ecol. Manag. 475: 118404.*

Warren D.L., Glor R.E. & Turelli M. 2008: Environmental niche equivalency versus conservatism: quantitative approaches to niche evolution. *Evolution 62: 2868–2883.*

Warren D.L., Glor R.E. & Turelli M. 2010: ENMTools: a toolbox for comparative studies of environmental niche models. *Ecography 33: 607–611.*

Warren D.L. & Seifert S.N. 2011: Ecological niche modeling in Maxent: the importance of model complexity and the performance of model selection criteria. *Ecol. Appl. 21: 335–342.*

Wilson R.R., Twedt D.J. & Elliott A.B. 2000: Comparison of line transects and point counts for monitoring spring migration in forested wetlands. *J. Field Ornithol. 71: 345–355.*

Wisz M.S., Hijmans R.J., Li J. et al. 2008: Effects of sample size on the performance of species distribution models. *Divers. Distrib. 14: 763–773.*

Zuur A.F., Ieno E.N. & Elphick C.S. 2010: A protocol for data exploration to avoid common statistical problems: data exploration. *Methods Ecol. Evol. 1: 3–14.*

Supplementary online material

Appendix S1. Landscape classification for data collection.

Table S1. Landscape Units defined by cluster analysis and used to randomly allocate sampling point counts.

Table S2. Land use classes with significant differences between the landscape units obtained by the cluster analysis (Kruskal-Wallis test).

Table S3. The Landscape Units (LU), their surfaces (km^2), number of point counts, length of transects and their density carried out during the breeding season and winter.

Fig. S1. Landscape Units defined by cluster analysis and used to schedule the sampling design.

Fig. S2. The predicted spatial distribution of the mistle thrush in central Apulia (southern Italy) during the breeding season.

Fig. S3. The predicted spatial distribution of the mistle thrush in central Apulia (southern Italy) during the winter.

(https://www.ivb.cz/wp-content/uploads/JVB-vol.-71-2022-Chiatante-G.-Appendix-1-Table-S1-S3-Fig.-S1-S3.pdf)