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Research

Ecological traps and species distribution models: a challenge for prioritizing areas of conservation importance

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Species distribution models analyse how species use different types of habitats. Their spatial predictions are often used to prioritize areas for conservation. Individuals may, however, prefer settling in habitat types of low quality compared to other available habitats. This ecological trap phenomenon is usually studied in a small number of habitat patches and consequences at the landscape level are largely unknown. It is therefore often unclear whether the spatial pattern of habitat use is aligned with the behavioural decisions made by the individuals during habitat selection or reflects actual variation in the quality of different habitat types. As species distribution models analyse the pattern of occurrence in different habitats, there is a conservation interest in examining what their predictions mean in terms of habitat quality when ecological traps are operating. Previous work in Belgium showed that red-backed shrikes *Lanius collurio* are more attracted to newly available clear-cut habitat in plantation forests than to the traditionally used farmland habitat. We developed models with shrike distribution data and compared their predictions with spatial variation in shrike reproductive performance used as a proxy for habitat quality. Models accurately predicted shrike distribution and identified the preferred clear-cut patches as the most frequently used habitat, but reproductive performance was lower in clear-cut areas than in farmland. With human-induced rapid environmental changes, organisms may indeed be attracted to low-quality habitats and occupy them at high densities. Consequently, the predictions of statistical models based on occurrence records may not align with variation in significant population parameters for the maintenance of the species. When species expand their range to novel habitats, such models are useful to document the spatial distribution of the organisms, but data on population growth rates are worth collecting before using model predictions to guide the spatial prioritization of conservation actions.

Keywords: behavioural maladaptation, ecological niche models, evolutionary trap, habitat preference, maladaptive habitat selection, niche-based models



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[Correction added on 25th September, 2020, after first online publication: Projekt

Deal funding statement has been added.]

Introduction

Species distribution models (SDMs) are widely used to examine the statistical dependence between species occurrence records and environmental conditions (Guisan and Zimmermann 2000, Franklin 2013, Guisan et al. 2017). Most techniques discriminate between the environmental conditions that are used by the species across the study area and those that are not used (Elith et al. 2006, Barbet-Massin et al. 2012). At the level of a spatial unit of analysis, the predictions derived from SDMs – hereafter referred to as the SDM outcomes – reflect the degree to which the local environmental conditions are similar to the conditions most frequently used by the species across the study area. Spatial variation in SDM outcomes is often proposed to assess the importance of different areas for the conservation of threatened species (Guisan et al. 2013, Lentini and Wintle 2015, Araújo et al. 2019).

Organisms may, however, use habitat types that are not necessarily the best options for their reproduction and survival. Deviation from ideal free distribution patterns may arise from a range of processes (Pulliam 2000, Hirzel and Le Lay 2008), including the limited availability of optimal conditions (Titeux et al. 2007), source–sink dynamics (Pulliam and Danielson 1991) or dispersal limitation (Pinto and MacDougall 2010). Previous studies have proposed different approaches to integrate these processes into the development and application of SDMs (Dormann et al. 2012, Schurr et al. 2012). Yet, the way to deal with novel conditions resulting from human-induced rapid environmental changes (Sih et al. 2011, Robertson et al. 2013) in SDM development has received little attention (Sánchez-Mercado et al. 2014). A number of studies have shown that novel conditions can become more attractive but provide lower fitness (reproduction or survival) to certain organisms than other available habitats – a phenomenon termed an ‘ecological trap’ (Schlaepfer et al. 2002, Robertson and Hutto 2006, Hale and Swearer 2016). These environmental changes are abrupt in evolutionary time and organisms may, therefore, be caught in habitats of low quality due to their behavioural preference during habitat selection (Van Dyck 2012, Robertson and Chalfoun 2016).

In their proposed framework to understand ecological traps, Robertson and Hutto (2006) underline that habitat preference should be measured as to reflect the behavioural decisions made by the individuals during habitat selection and cannot be reliably evaluated through the analysis of the density of occurrence records under particular environmental conditions. There are many situations in which this pattern of habitat use is not aligned with the behavioural decisions of the individuals (Railsback et al. 2003). For instance, inter-specific competition may interfere with habitat preference in determining the pattern of habitat use. With asymmetrical competition, a socially dominant competitor could displace a subordinate species from its preferred habitat (Sherry and Holmes 1988). In their recent study on the plains bison

Bison bison bison in Canada, Simon and Fortin (2019) showed that individuals were trapped in a spatially limited portion of the landscape, but with negative demographic consequences for the population over a much larger area.

These studies show that there is not necessarily a direct link between the behavioural decisions made by the individuals during habitat selection and their spatial distribution and relative density in habitat patches of varying quality. Yet, this link is seldom tested in studies on ecological traps because those that meet the criteria to demonstrate the existence of a trap often measure habitat preference and quality in a small number of geographically close habitat patches (Hale and Swearer 2016). A spatially explicit understanding of the link between habitat preference, habitat use and habitat quality is, therefore, needed to increase our ability to evaluate the consequences of ecological traps for the populations at the landscape level (Simon and Fortin 2019). This is the most relevant scale for the management of ecological traps (Hale and Swearer 2016) and also the scale at which SDMs approaches are typically applied to guide conservation actions. Therefore, there is a specific need to assess the significance of SDM outcomes when organisms are caught in an ecological trap. Although SDM outcomes will be directly determined by the spatial pattern of habitat use across the landscape, it is largely unknown what they mean in terms of habitat quality or habitat preference.

Here, we build on previous empirical evidence for the existence of an ecological trap to examine its consequences on the spatial distribution of the trapped organism at the landscape level and on the outcomes of SDMs developed with distribution data. Hollander et al. (2011) have previously shown a case of an ecological trap in the red-backed shrike *Lanius collurio*, a territorial, insectivorous, migratory bird species. Shrikes have long been selecting meadows and pastures in farmland areas to breed, but since the last few decades, forest management has created large clear-cuts with regrown vegetation in spruce plantation forests that offer novel habitat. Dominant males arrive in the clear-cut areas earlier than in the farmland habitat (Hollander et al. 2011) where they defend their territories less vigorously (Hollander et al. 2012). In contrast with this behavioural preference and in line with the ecological trap concept, reproductive performance (i.e. nest success, brood size and brood quality) is markedly lower in clear-cut areas than in traditional farmland habitat patches due to between-habitat differences in both food availability (Hollander et al. 2013, 2017) and nest predation (Hollander et al. 2015).

We used an independent structured dataset on shrike occurrence records to acquire data on habitat use across the same landscape as studied in Hollander et al. (2011). We examined whether the pattern of habitat use at the population level reflected the behavioural preference for clear-cut patches measured at the individual level (Hollander et al. 2011, 2012). We developed SDMs with the dataset on shrike occurrence records and we tested for differences in SDM outcomes between forest clear-cut and farmland sites where shrikes have established their nests. We then compared

these differences with the measures of reproductive performance reported in Hollander et al. (2011) that we used here as proxies for habitat quality in the two types of breeding sites. With these analyses, we assessed how the maladaptive behavioural decisions made by the birds during habitat selection are translated into a spatial pattern of habitat use and we evaluated the consequences of this pattern on the outcomes of SDMs developed with occurrence records. Our approach and results could contribute to framing the application scope for SDMs when species expand to novel habitats as a result of maladaptive habitat selection.

Material and methods

Study areas

Our study was conducted in south-eastern Belgium where agriculture and forestry created a mosaic landscape of farmland and forest. We selected the same two study areas of 400 km² each as in the work of Hollander et al. (2011) (Fig. 1). Farmland includes cultivated areas, meadows and pastures for livestock rearing, whereas forests are mostly plantations of Norway spruce *Picea abies* for timber production (Fig. 2). These forests are intensively managed through large-size clear-cutting in even-aged plantations.

Study species

The red-backed shrike *L. collurio* is a passerine bird that has a wide breeding range across the Western Palearctic (Lefranc and Worfolk 1997). When arriving from their overwintering sites in southern Africa, shrikes establish breeding territories in open habitats. Meadows and pastures with scattered and thorny hedges and bushes are the traditionally used habitat (Titeux et al. 2007), but regrown vegetation in forest clear-cut patches is a novel habitat for the species (Hollander et al. 2011).

Species occurrence records

We used red-backed shrike distribution data collected in the frame of the Breeding Bird Atlas of Wallonia (BBAW) project (Jacob et al. 2010) to build the SDMs. Fieldworkers recorded the presence of bird species in all habitat types within 40 km² atlas units. The total amount of time spent for data collection in an atlas unit typically ranged between 80 and 120 h. For species such as the red-backed shrike, fieldworkers were instructed to report the location of breeding sites with as much exhaustiveness as possible and in all occupied habitat types. Therefore, we assumed that the reported locations of breeding sites reflected the relative use of different habitat types by shrikes. Fieldworkers were asked to localise the breeding sites on printed maps at a scale of 1:10 000 and to provide an estimate of the spatial precision for each of these locations, i.e. 100, 200 or 500 m. Only the breeding sites reported on the map with an estimated spatial precision of 100 m were used to document the presence of the species because shrikes establish territories covering only 1–3 ha (Titeux et al. 2007).

Although the distribution data were collected between 2001 and 2008, we only used the breeding sites reported during the period 2004–2008 (Fig. 2) to ensure a reasonable temporal match with the data from Hollander et al. (2011) that we will further use to quantify reproductive performance (see below). Data collection spanned successive years during the atlas project and shrikes may use several times the same sites during their life. To avoid temporal replicates in the data, we removed any breeding site that was located within a 100-m distance from another site reported during a previous year.

Environmental data

We selected 15 environmental variables (Table 1) that characterize the most important conditions for the reproduction of the study species in the region (Titeux et al. 2007,

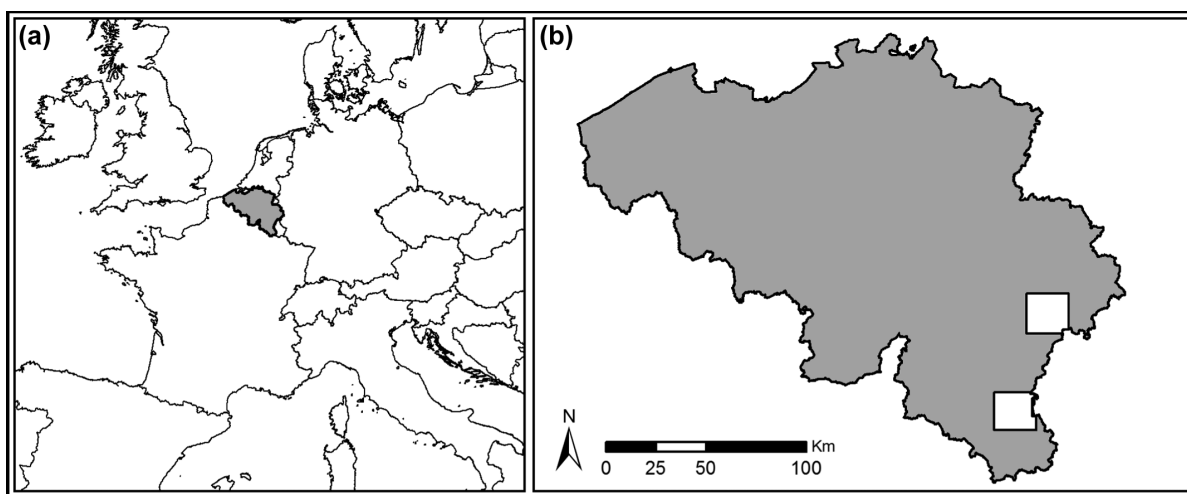


Figure 1. (a) Location of Belgium in NW Europe. (b) Location of the two study areas in SE Belgium.

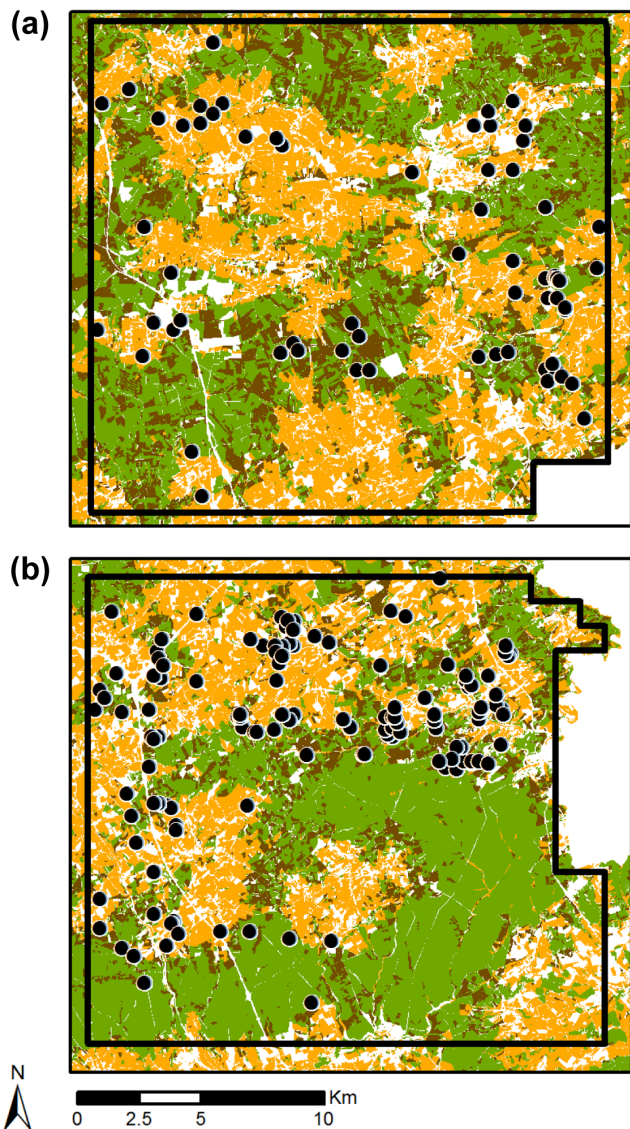


Figure 2. Breeding sites (black dots) of the red-backed shrike *Lanius collurio* in the northern (a) and southern (b) study areas (SE Belgium) during the period 2004–2008. Breeding sites were mapped according to a structured sampling scheme in the frame of the Breeding Bird Atlas of Wallonia (BBAW) project. The main land cover types are shown in the background: meadows and pastures (orange), mature plantation forest (green) and clear-cut patches (brown).

Aizpurua et al. 2015). These variables were constructed using readily available GIS layers and aerial photographs. All environmental variables were calculated within spatial units of 200×200 m sides – hereafter referred to as the 200-m resolution grid cells – covering the two study areas in order to approximately match the mean size of the shrike territories. These variables reflected the main vegetation types and landscape features that characterise the habitats used by shrikes in farmland and forest. All selected variables were only weakly correlated (Pearson correlation coefficients < 0.6).

Spatial pattern of habitat use

To estimate how red-backed shrikes use both habitat types, we first calculated the area that was potentially available for them in farmland (i.e. surface of meadows and pastures) and in forest (i.e. surface of clear-cut patches) across the study areas (Fig. 2). Second, we estimated the degree to which these potentially suitable areas were actually occupied by the shrikes. To do so, we overlaid the breeding sites from the shrike distribution data with aerial photographs (Table 1), we counted the number of sites located in farmland (meadows and pastures) and in forest (clear-cut patches), and we calculated for each habitat type separately the ratio between the number of breeding sites and the area potentially available for the shrikes. Breeding sites were not used in the calculations if their allocation to one of the two habitat types based on aerial photographs was uncertain.

Species distribution models

The 200-m resolution grid cells completely covered with mature forests or urban areas were excluded and SDMs were developed across the remaining areas where environmental conditions were not incompatible with the reproduction of the species (Titeux et al. 2007). SDMs were built with presence-absence modelling algorithms using the BIOMOD2 package (Thuiller et al. 2016) implemented in R (R Core Team): artificial neural networks (ANN), flexible discriminant analysis (FDA), generalized boosting models (GBM), generalized linear models (GLM) and multivariate adaptive regression splines (MARS).

For the shrike presence data, we used the 200-m resolution grid cells that contained the locations of breeding sites retained above (see Species distribution data) (number of grid cells: $n = 184$). As absence data are difficult to obtain in the frame of an atlas project, we selected pseudo-absences among the grid cells not included as presence data to reflect the environmental conditions that were available for shrikes across the study areas. We avoided as much as possible selecting pseudo-absences in areas potentially used by the species but not included as presence data. When producing the species presence data, we removed locations of breeding sites associated with a spatial precision of 200 or 500 m during the period 2004–2008, even if we knew that the species bred in these areas. Hence, we delineated circles with a radius of 200 or 500 m around these sites, respectively, and we assumed the presence of breeding shrikes somewhere in the grid cells intersecting these circles. We discarded these potentially occupied grid cells and we randomly selected pseudo-absence data among the remaining cells to cover 20% of the study areas ($n = 2927$). We used equal weighting for presences and pseudo-absences so that the whole set of presence data had the same weight as the set of pseudo-absence data in the SDMs. Such a large proportion of pseudo-absences but equally weighted to the presences was shown to produce the most accurate predictions based on simulations (Barbet-Massin et al. 2012).

Table 1. Environmental variables used to build the species distribution models for the red-backed shrike in Belgium. Each variable was calculated within 200-m resolution grid cells covering the two study areas (see Titeux et al. 2007 for detailed information on the relevance of each variable for breeding shrikes).

Variable	Source	Year	Units
Average orientation	DEM		°
Average slope	DEM		%
Topographic moisture index [†]	DEM		
Distance to closest urban area	COSW	2008	m
Surface of cultivated areas	COSW	2008	ha
Surface of meadows and pastures	COSW	2008	ha
Surface of semi-natural grasslands	COSW	2008	ha
Surface of broadleaved forest	MRW	1993	ha
Surface of coniferous forest	MRW	1993	ha
Surface of mixed forest	MRW	1993	ha
Surface of wetlands	COSW	2008	ha
Number of isolated trees and bushes	IGN	2009	
Total length of tree lines and hedgerows	IGN	2009	m
Surface of spruce plantation clear-cuts	Aerial pictures	2006–2010	ha
Dominant soil type ^{††}	CNSW	2007	

DEM: digital elevation model.

CNSW: 'Cartographie Numérique des Sols de Wallonie' – soil map of Wallonia (scale: 1:10 000).

COSW: 'Cartographie de l'Occupation du Sol en Wallonie' – land use map of Wallonia (scale: 1:10 000).

IGN: 'Institut Géographique National' – land use map of Belgium (scale: 1:10 000).

MRW: 'Ministère de la Région Wallonne' – land cover map of Wallonia (pixel resolution: 20 m).

Aerial pictures: 'Service Public de Wallonie (<<http://geoportail.wallonie.be>>)' – orthophotos 2006–2007 (resolution: 50 cm) and 2009–2010 (resolution: 25 cm).

[†] Topographic moisture index was calculated following Beven and Kirkby (1979).

^{††} Categorical variable.

For each algorithm, the models were calibrated 100 times using a random sample of 80% of the presence–absence data (calibration data) and were then evaluated against the remaining 20% of the data (evaluation data). The area under the curve (AUC) of a receiver-operating characteristic (ROC) plot was used as an overall measure of model predictive accuracy (Fielding and Bell 1997). AUC values range from 0 to 1 and measure the ability of the models to correctly discriminate between the environmental conditions that are used and not used by the species. AUC values below 0.6 are often considered as indicating models that fail to discriminate satisfactorily and values higher than 0.8 suggest a good to excellent discrimination ability (Swets 1988). In addition, the SDM outcomes were converted into binary predictions using the threshold that maximised the true skill statistics (TSS), i.e. the sum of sensitivity (proportion of presences correctly predicted) and specificity (proportion of pseudo-absences correctly predicted) minus one (Allouche et al. 2006, Jiménez-Valverde and Lobo 2007).

The predictions obtained from the different modelling algorithms were combined using the ensemble forecasting procedure implemented in the BIOMOD2 package using only individual models with AUC values above 0.6 (i.e. with at least a fair ability to discriminate between conditions that are used and not used). This averaging procedure produced a prediction ranging between 0 and 1 in each grid cell (SDM outcomes). As we used pseudo-absences instead of fully reliable absences to build the SDMs, these predictions could not be interpreted as a true probability of occurrence of the

species, but they represented the extent to which the environmental conditions within the different grid cells were similar to the conditions most frequently used by the shrikes across the study area.

Reproductive performance

Although we did not use the data from Hollander et al. (2011) to build the SDMs, we used them to document shrike reproductive performance in the two distinct habitat types. During three consecutive years (2008–2010), Hollander et al. (2011) studied the reproductive performance of the red-backed shrikes in 118 sites in meadows and pastures (hereafter 'farmland': $n=58$) and in clear-cut patches (hereafter 'forest': $n=60$) across the two study areas. Hollander and colleagues searched for nests on a daily basis from mid-May to late July and nests were revisited throughout the season to determine 1) nest success (i.e. production of at least one fledgling), 2) brood size (i.e. number of nestlings older than 12 d) and 3) brood quality (i.e. average nestling body conditions). Brood quality was estimated from tarsus length, wing length (± 0.01 mm, digital callipers) and body mass (± 0.1 g, KERN laboratory balance) measured on 12-d old nestlings (range: 11–15 d). These three measures were combined into the first axis of a principal component analysis (PC1: explained variance = 89%, eigenvalue = 2.60, loadings: tarsus length = 0.58, body mass = 0.58, wing length = 0.57), which was averaged per nest (Hollander et al. 2017). We used these different measures of reproductive performance as proxies for habitat

quality in the two habitat types (Chalfoun and Martin 2007, Johnson 2007, Stephens et al. 2015).

Model predictions

We also used the data from Hollander et al. (2011) as an independent dataset to compare SDM outcomes and reproductive performance in the habitat types that are occupied by the species across the landscape (Pellissier et al. 2013, Thuiller et al. 2014, Jarnevich et al. 2015). We delineated 100-m radius circles around the 299 nest locations in the 118 sites where Hollander et al. (2011) measured shrike reproductive performance. This radius distance was set to match the geographical area covered by the territories of breeding shrikes around their nests. Temporal autocorrelation may arise from the establishment of shrike territories and nests in the same sites from one year to the other due to site fidelity. Hence, we selected the location of the oldest nest when there was at least a two-third overlap between the 100-m radius circles around two nest locations. As a result, we retained a reduced sample of shrike nest locations in farmland (meadows and pastures: $n=108$) and in forest (clear-cut areas: $n=116$). In addition, we randomly produced a similar number of locations ($n=115$) within the 200-m resolution grid cells used to select the pseudo-absences for the SDMs. We also delineated 100-m radius circles around these random locations to represent parts of the landscape where shrikes were assumed not to have established breeding territories. We calculated the area-weighted mean SDM outcomes among the grid cells intersecting each circle using the overlapping area between the circle and the grid cells as a weighting factor. We used a Kruskal–Wallis analysis to test for differences in the area-weighted mean SDM outcomes around the three types of locations, i.e. around the random locations reflecting the absence of shrike territories and around shrike nest locations in farmland and forest. A post hoc Mann–Whitney U-test analysis with multiple pairwise comparisons and Bonferroni correction was carried out to compare the three types of locations among each other.

Results

About 85% of the grid cells across the study areas were at least partly covered with potentially suitable vegetation for shrikes in farmland (meadows and pastures: 25 128 ha) or in forest (clear-cut patches: 6106 ha). From the shrike distribution data used to build the models, 72 breeding sites were located in meadows or pastures and 109 sites were located in forest clear-cut patches. Ten sites were located at the ecotone between the two habitat types and were not used in the calculations. On this basis, we estimated that shrikes used 0.3% of available areas in farmland and 1.8% in forest clear-cuts.

The AUC and TSS values obtained from the ensemble forecasting procedure were 0.81 and 0.46, respectively. The sensitivity and specificity values associated with the TSS were

0.71 and 0.76, indicating that 71% of presences and 76% of pseudo-absences in the evaluation data were correctly predicted by the SDMs. These values reflect a good ability of the SDMs to discriminate between the environmental conditions that were used and not used by shrikes for breeding across the study areas.

We compared SDM outcomes between the different habitat types used and not used by shrikes as reflected in the independent dataset from 2008 to 2010. Here, SDM outcomes differed significantly between the 100-m radius circles around the three types of locations, i.e. the random locations reflecting the absence of shrike territories and the shrike nest locations in farmland and forest (Kruskal–Wallis rank sum test, $\chi^2=199.45$, $p<0.0001$). The post hoc multiple comparisons showed that SDM outcomes were lower in randomly selected locations than around shrike nest sites in the forest or farmland habitats (Mann–Whitney U-test, all $p<0.001$). SDM outcomes were also higher around nests located in forest clear-cuts than around those established in farmland (U-value = -3.004 , $p=0.0013$, Fig. 3).

Using the same dataset as in Hollander et al. (2011), we showed that the three measures of shrike reproductive performance (i.e. nest success, brood size and brood quality) were lower in forest than in farmland (Fig. 4). Hollander et al. (2011) obtained similar results based on detailed quantitative analyses that included covariates to control for nuisance effects of additional factors. With the nest locations reported in this dataset, we plotted SDM outcomes around the nests against reproductive performance measured in the same nests, and we showed that brood quality was higher in farmland than in clear-cuts, whereas model predictions were higher for nests located in forest clear-cuts than for those established in farmland (Fig. 3).

Discussion

We built SDMs with structured shrike distribution data to estimate how model outcomes varied across a landscape where this bird occurred in two distinct habitat types. Based on independent behavioural data collected at the individual level, Hollander et al. (2011, 2012) demonstrated maladaptive habitat selection in the same study system: shrikes preferred establishing territories in clear-cut patches (forest habitat) but reproductive performance was higher in meadows and pastures (farmland habitat). Here, we showed that this behavioural preference translated into a higher density of shrikes in the trap than in the less attractive habitat. This spatial pattern of habitat use fed through to the outcomes of SDMs that were higher in the clear-cut patches than in meadows and pastures. If SDM outcomes were used to guide conservation planning for shrikes across the landscape (Lentini and Wintle 2015, Araújo et al. 2019), clear-cut patches in forest would be identified as priority areas even though farmland areas were of higher quality for the reproduction of the species.

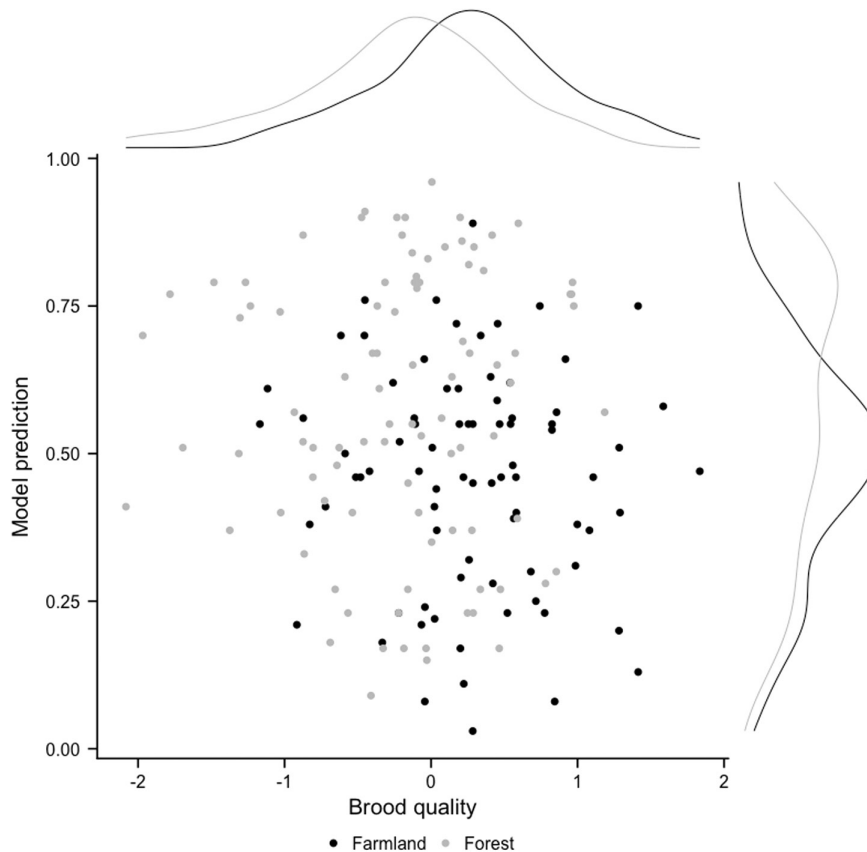


Figure 3. Scatter plot showing the relationship between the predictions derived from the species distribution models within the 100-m distance around the nest sites (model predictions) and the average nestling body conditions measured in the same nests (brood quality – data from Hollander et al. 2011). Nests established in farmland (meadows and pastures) and in forest (clear-cut areas) are represented in black and in grey, respectively. Estimated marginal probability density functions are shown along the two axes of the plot for each habitat type separately.

Shrikes occupy clear-cut patches in plantation forests in many parts of their breeding range (Lefranc and Worfolk 1997, Karlsson 2004, Lislevand 2012). This novel ecosystem is also used by other species, including birds (Stjernman et al. 2013), butterflies (Viljur and Teder 2016) and mammals (Bogdziewicz and Zwolak 2014). Although this habitat provides opportunities for some species associated with early successional vegetation stages (Paz Acuña and Estades 2011, Swanson et al. 2011, Žmihorski et al. 2016), it may act as an ecological trap for other organisms (Hollander et al. 2017). Beyond this specific ecosystem, an increasing amount of studies have documented cases of ecological traps in a variety of taxonomical groups and human-modified environments (Rotem et al. 2013, Hale and Swearer 2016, Robertson and Chalfoun 2016). Traps may also arise as an unintended consequence of habitat restoration (Hale and Swearer 2017), prescribed fires (Shochat et al. 2005) or invasive plant management (Carter et al. 2017). Therefore, the recommendations we will make go beyond the specific case of shrikes in plantation forests.

Many SDM techniques based on presence and pseudo-absence data discriminate between the environmental

conditions that are most used by the species and those that are less frequently occupied or not used at all (Guisan and Zimmermann 2000, Barbet-Massin et al. 2012, Guisan et al. 2017). SDM approaches are indeed designed to directly reflect the spatial pattern of habitat use across the landscape. Predictive accuracy estimates such as the ones we obtained here usually provide support to the use of SDM outcomes for conservation applications because these values are considered to reflect a good discrimination ability of the models (Swets 1988, Allouche et al. 2006). With our case study on an ecologically trapped bird, we showed that SDMs may successfully identify the environmental conditions and geographical areas that are most used by the species, but these areas may not be the most suitable ones for the organism's fitness. There was a mismatch between SDM outcomes and habitat quality because habitat use (i.e. higher densities in the forest habitat) was aligned with the maladaptive behavioural decisions made by the individuals during habitat selection (i.e. preference for the forest habitat). We encourage a broader application of SDM approaches and a thorough evaluation of model outcomes in other study systems where ecological traps have been identified, or where they are likely, because

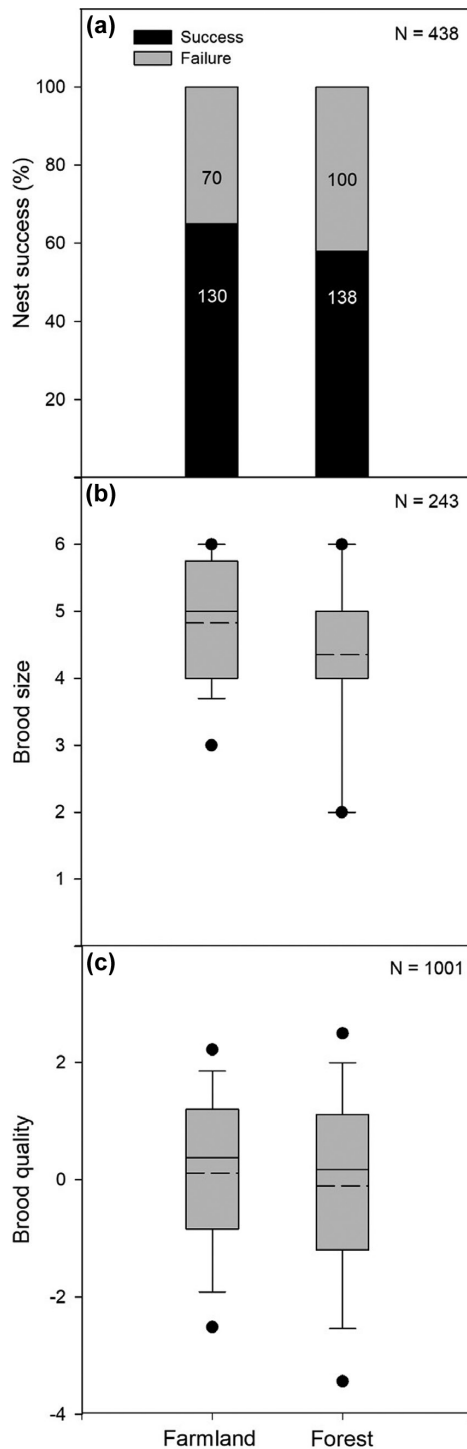


Figure 4. Reproductive performance of red-backed shrikes in the farmland (pastures and meadows) and the forest (clear-cut areas) habitats (data from Hollander et al. 2011) in SE Belgium. (a) Proportion of breeding attempts associated with nest success (black) and failure (grey). (b-c) Box-and-whisker plots and quartile distribution ($\perp$ and $\top$: 5th and 95th percentiles, $\bullet$: outlying values, ---: mean value, —: median value) for brood size (i.e. number of nestlings older than 12 d per nest) and brood quality (i.e. average nestling body conditions per nest). The number of nests (for nest success and brood size) or nestlings (for brood quality) is indicated in the panels.

habitat use may deviate from habitat preference in many situations (Sherry and Holmes 1988, Robertson and Hutto 2006). This will be needed to increase our understanding of the link between habitat preferences, habitat use and habitat quality at the landscape level when organisms show maladaptive habitat selection.

Species are frequently reported to breed under novel conditions that emerged as a result of human-induced rapid environmental changes (Sih et al. 2011), but detailed knowledge is often lacking on the fitness or demographic consequences of this shift in habitat use. In this context, SDMs based on distribution data will remain an important tool to document the spatial distribution of the organisms relative to the environmental conditions. However, this pattern may potentially result from an ecological trap and densely occupied habitat types in the landscape are therefore not necessarily the most important ones for the conservation of the species. Hence, SDM outcomes should not be used to prioritise conservation options amongst different areas or habitat types. Identifying such spatial priorities is key to implement specific actions aiming for the long-term persistence of the species (Strimas-Mackey and Brodie 2018), but both theoretical and empirical studies have shown that the attractiveness of a trap habitat may have significant to even detrimental consequences for populations (Delibes et al. 2001, Kristan 2003, Simon and Fortin 2019). Hence, focusing protection on habitats that act as an ecological trap may have undesirable consequences for the conservation of these species.

Before using SDM outcomes to guide such conservation actions for species that have recently expanded their distribution to novel environments, there is a need to evaluate the degree to which these newly occupied conditions contribute to the reproduction of the species. Even if this is much more time consuming than relying on distribution data only, more comprehensive data linked to the vital rates of the populations under study should be analysed to provide a proximate underpinning of the relative quality of the different habitat types occupied by the species (Chalfoun and Martin 2007, Johnson 2007, Pellissier et al. 2013, Thuiller et al. 2014). If such an assessment indicates that part of the population has shifted to a novel ecosystem where at least some aspects of the vital rates of the populations are considerably reduced compared to the previously occupied sites, the precautionary principle should be applied until further information is collected on the strength of this potential trap and its prevalence in the landscape. In such a case, SDM outcomes should not be used to prioritize areas for the long-term persistence of the species but should be limited to document its spatial distribution, because the pattern of habitat use may poorly reflect actual variation in habitat quality underlying the vital rates of the populations.

The impacts of an ecological trap at the population level depend on the attractiveness of the trap compared to the traditionally used habitat(s), the relative availability of the different habitat types occupied across the landscape, and the fitness consequences of the trap (Hale and Swearer 2016, Sánchez-Clavijo et al. 2016). A variety of methods have been

proposed to assess the consequences of maladaptive habitat selection on population dynamics through a separate modelling of habitat attractiveness and quality (Delibes et al. 2001, Donovan and Thompson III 2001, Fletcher et al. 2012, Hale et al. 2015). However, most of the proposed approaches are theoretical models and/or are not spatially explicit (Sánchez-Clavijo et al. 2016), which limits their use to identify spatial priorities for conservation management. Mechanistic modelling approaches that explicitly relate spatial distribution data to individual behavioural traits simulate how population-level patterns emerge from the interactions between individuals and from variation in individual behaviour (DeAngelis and Mooij 2005). These techniques have the potential to deal with the behavioural motivation of the individuals to select among habitats varying in attractiveness. Individual-based models have been developed to evaluate the effect of maladaptive habitat selection on the spatial distribution and population dynamics of virtual species in simulated landscapes (Sánchez-Clavijo et al. 2016) but similar developments with real-world data are lacking.

Quantifying the attractiveness of different habitat types occupied by a particular species may demand considerable field and experimental work (Robertson and Hutto 2006, Pärt et al. 2007, Hollander et al. 2012). For that reason, dealing with the potential mismatch between habitat attractiveness and quality in the modelling process itself is probably mainly achievable at relatively small spatial scales. Alternative approaches that may be applied at larger scale include the use of vital rates of the populations as response variables in the development of the SDMs. Suárez-Seoane et al. (2017) used a correlative SDM approach to evaluate the spatial variations in the breeding success of the Great Bustard in Spain. They found large areas where the predictions of models based on breeding occurrence and on breeding success disagreed, indicating a considerable mismatch between the spatial distribution of the species and the important areas for its reproduction and long-term persistence. The authors proposed their approach as a suitable compromise between purely mechanistic models and correlative SDM methods based on distribution data that can be easily applied to guide the implementation of large-scale conservation strategies supporting population maintenance. Recent initiatives that integrate spatial information about key demographic parameters at large spatial scales and across a range of species will therefore provide useful information for the development of such modelling approaches (Robinson et al. 2014).

The ecological trap concept is also relevant at scales that encompass the entire distribution range of a species. A number of species have been shown to track changing climate conditions and shift their range of distribution (Lenoir and Svenning 2015, Scheffers et al. 2016). These distributional changes are often assumed to reflect adaptive behavioural responses to changing climatic conditions. However, the fitness consequences of such behavioural flexibility have received little attention. Recent studies have suggested that

individuals may encounter traps when moving and experiencing novel conditions (Hale et al. 2016). Range shifts are the results of moving individuals ('disperser' phenotypes, Debeffe et al. 2014) that may be more likely to face traps than other phenotypes. Hence, this process may affect a biased sample of individuals and induce changes in the frequency distribution of personalities or other phenotypes, with potentially significant conservation consequences. Although SDMs are increasingly used to predict range shifts and to identify future spatial conservation priorities under climate change (Franklin 2013, Araújo et al. 2019), most modelling approaches and studies largely ignore potential maladaptive responses of the organisms when they track suitable climate conditions. To the best of our knowledge, approaches that integrate ecological and evolutionary processes into the modelling framework (Thuiller et al. 2013, Briscoe et al. 2019) have not yet explicitly considered the potential interaction between range shift and ecological traps under changing climate. We encourage novel research at the crossroad between species distribution modelling, ecological traps and environmental change impact assessment across a range of spatial scales and species of different taxonomic groups.

Data availability statement

Shrike occurrence records used to build the species distribution models were collected in the frame of the Breeding Bird Atlas of Wallonia (BBAW) project (Jacob et al. 2010) and are available upon request (info@observations.be). All shrike reproductive performance data used in the analysis are available from the Dryad Digital Repository: <<https://doi.org/10.5061/dryad.j6q573n8f>> (Titeux et al. 2019).

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