

Predicting the potential distribution of invasive ring-necked parakeets *Psittacula krameri* in northern Belgium using an ecological niche modelling approach

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Abstract The threat to biodiversity due to invasive alien species is considered second only to that of habitat loss. Given the large number of species that are currently invading ecosystems all over the world, we need to distinguish invaders with minor effects from those with large effects in order to prioritize management efforts. Ecological niche models can be used to predict the potential distribution of an invasive species from occurrence records and environmental data layers. We used the Ecological Niche Factor Analysis (ENFA), a presence-only predictive modelling approach, to describe the invasive ring-necked parakeets' realized niche and to identify areas suitable for the parakeet in northern Belgium. ENFA proved to be a robust and reliable modelling technique, able to gauge the ecological requirements of an invasive species without the need to include historical information on the starting point of the invasion. ENFA shows that the parakeets tend to occupy relatively rare habitats compared to the main environmental conditions in northern Belgium, although they show some tolerance for environmental conditions inside parks and forests. The general distribution of the ring-necked parakeet is governed primarily by the amount of older forest patches, parks

and built-up area in the landscape—reflecting the parakeets' need for suitable nesting cavities and its reliance upon urban areas to forage. Our resulting habitat suitability maps show that the parakeets have ample room to further increase their range in northern Belgium. Our results indicate some concern for increased competition between parakeets and the nuthatches, native cavity nesters known to suffer from competition with parakeets, as some regions known as nuthatch strongholds are highly likely to be invaded by the parakeets.

Keywords Biodiversity · Competition · Habitat suitability · Invasions · Presence-only modelling · Ring-necked parakeet

Introduction

Human activities such as exploration, colonization, trade and tourism have dramatically increased the diversity and scale of invasions by alien species (McNeely et al. 2001), and invasive alien species are now emerging as one of the major threats to biodiversity (Wilcove et al. 1998). They also pose a threat to human health (Vitousek et al. 1997) and cause considerable economic damage (Pimentel et al. 2005). Given the large number of species that are currently invading ecosystems all over the world, we need to distinguish invaders with minor effects from

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those with large effects in order to prioritize management efforts (Parker et al. 1999). However, in practice, management decisions on the need for action against a certain invasive species are often hampered by a lack of relevant ecological information such as the expected distribution and impact of the invasive species.

Predictive habitat models attempt to provide detailed predictions of distributions by relating presence or absence of a species to a set of environmental predictors that are likely to influence the suitability of the environment for the focal species (Guisan and Zimmerman 2000). For most of the available methods an accurate sampling of the presence/absence of the species is crucial (Hirzel et al. 2002). However, often absence data are not available, unreliable (most cryptic or rare species), or, as in the case of an invading alien species, absence data are of limited use because certain sites may be suitable but not yet reached by the invader (Hirzel et al. 2002). An alternative is modelling presence-only data. Methods that predict species distributions from presence-only data search for an environmental ‘envelope’ characterizing the areas in which the species is present and extrapolate to the remaining areas under study (Guisan and Zimmerman 2000). Examples of these alternative techniques, often called *profile* or *envelope methods* (Pearce and Boyce 2006), are Bioclimatic Prediction Systems, Support Vector Machines (SVM) and Ecological Niche Factor Analysis (ENFA) (Busby 1991; Guo et al. 2005; Hirzel et al. 2002).

The ENFA has proven to be a valuable tool for monitoring the potential spread of invasive alien or re-introduced species (Acevedo et al. 2007; Casinello et al. 2006; Hirzel et al. 2001, 2004). The ENFA builds on Hutchinson’s definition of an ecological niche (Hutchinson 1957), i.e. a hyper-volume in the multidimensional space of ecological variables (‘environmental space’) within which a species can maintain a viable population. ENFA is in fact a modified principal component analysis that computes habitat suitability (HS) maps by comparing the environmental response of the species to the environmental characteristics of the entire study area. Like a PCA, ENFA summarizes all predictor variables in a few independent factors, but in ENFA the extracted factors have a specific ecological relevance: the first factor is called the ‘marginality’ factor and

maximizes the difference between the species average and the average environmental conditions in the entire study area. This marginality factor describes how far the species optimum is from the mean environmental conditions in the study area. Subsequent factors (named ‘specialization’ factors) are then extracted successively by computing the direction that maximizes the ratio of the variance of the global distribution (i.e. the study area) to that of the species distribution. These specialization factors describe the narrowness of the species’ niche. A large part of the information is captured by a few of the first factors and the species distribution on these factors is then used to calculate a HS map for the whole study area (Hirzel et al. 2002).

In this paper we use ENFA to study the environmental factors that influence the spatial distribution of a rapidly spreading invasive species, the ring-necked parakeet (*Psittacula krameri*), and to produce HS maps that describe the potential geographic distribution of this invasive parakeet in northern Belgium (Flanders and the Brussels Capital region). Ring-necked parakeets are native to Africa and Asia (Forshaw 1978) and have established feral populations in at least 40 countries on five continents (Butler 2003, 2005, Strubbe unpubl.) due in large part to their popularity as pets. Despite the fact that ring-necked parakeets are widely introduced, the ecology of invasive populations remains largely unstudied. In Europe alone, there are currently more than 70 invasion propagules, with population sizes ranging from only a few tens to several thousands of individuals (Strubbe and Matthysen 2007; Strubbe unpubl.). The growing number and size of parakeet populations raises concerns for the loss of biodiversity and potential agricultural damage. Strubbe and Matthysen (2007) showed that in Belgium, ring-necked parakeets reach their highest breeding densities in urban and suburban forest fragments with abundant nesting cavities, and have an impact on native cavity nester species.

Ecological patterns and processes are scale-dependent (Levin 1992) and for predictive habitat modelling at the landscape level, the selection of scale is an important issue, as the spatial scale used may affect the accuracy of the predictions (Boyce 2006; Meyer and Thuiller 2006). The relationships between organisms and their environment can vary across spatial scales and different patterns can

emerge at different spatial scales (Mitchell et al. 2001). We therefore performed ENFA analyses at two different scales (i.e. extent of the study area) to study whether the same environmental factors emerge as driving the parakeet distribution, and how this influences ENFA model performance and predictive abilities. In particular we examined the effect of scale on the predicted HS maps of the Sonian Forest. This forest is located near Brussels on the edge of the current parakeet distribution and is the largest continuous forest remaining in Flanders and Brussels (>4000 ha). The Sonian forest is one of the strongholds of the nuthatch (*Sitta europaea*), a native cavity nester known to suffer from competition with parakeets (Strubbe and Matthysen 2007). We also included distance from the starting point of the invasion in our model to check whether model predictions are affected by the historical pattern of the invasion.

An ENFA model results in a continuous map expressing a range of environmental suitability for the target species. However, for conservation and species management practice, transforming these suitabilities into several habitat classes with a minimum of two (presence or absence) is more practical and reliable (Hirzel et al. 2006b; Liu et al. 2005). In order to identify the optimal thresholds required for this transformation, we explored the capabilities of the novel continuous Boyce index (Hirzel et al. 2006b) and compare it with a traditional approach, i.e. taking the 50% as threshold (Cramer 2003; Jimenez-Valverde and Lobo 2007; Liu et al. 2005). Comparing the amount of predicted suitable habitat across scales and threshold identifiers allows us to assess the robustness of ENFA as a predictive habitat model.

Materials and methods

Study area

We limited our study area to the northern part of Belgium (Flanders and the Brussels Capital Region) because standardized land-use and forest inventory maps (see below) were available for this part of the country. Furthermore, few current observations of ring-necked parakeets are known from the southern part of Belgium (Wallonia). The study area comprises 13,683 km² and with a human population

density of 508 individuals per square kilometer is one of the most densely populated regions in Europe. Forested areas cover only 13.4 % of the landscape.

Study species

In Brussels, three parakeet species have successfully established themselves. There are small populations of Monk Parakeet (*Myiopsitta monachus*, introduced in 1979, 125–250 bp) (De Schaetzen and Jacob 1985; Weiserbs and Jacob 2007) and Alexandrine Parakeet (*Psittacula eupatria*, introduced in 1998, 35–40 bp) (Scalliet 1999; Weiserbs and Jacob 2007; Weiserbs et al. 2000) but the most successful invader is the ring-necked parakeet. This species was first reported breeding in 1966 in Tervuren near Brussels, but the deliberate release of ca 40 parakeets of the Asiatic *borealis* subspecies by the Brussels Meli Zoo is generally considered the founder event of the Belgian population (Weiserbs and Jacob 2005). The population has grown to ±8000–8500 birds in 2006 (Weiserbs and Jacob 2007), and the increase fits an exponential model of population growth with an average annual growth rate of ca. 18% (Strubbe unpubl.). The parakeets have gradually increased their range which currently extends ca. ±40 km around the release site. A previous study based on point counts in 44 forests and parks showed that parakeet abundance is highest in urban and suburban forest fragments with abundant nesting cavities and also found evidence for a negative impact on native hole-nesting birds such as the nuthatch (Strubbe and Matthysen 2007).

Data origin

Parakeet distribution data

The presence data set consists of 447 detailed point locations of breeding parakeet pairs. 132 locations are available from surveys conducted for the Flemish breeding bird atlas (Vermeersch et al. 2004), the remaining 324 locations originate from local breeding bird inventory and monitoring projects, student master theses, personal communications by local ornithologists and personal observations (Bluekens 2002, pers. comm. A. Reygel, M. Louette, M. Segers, H. Papillon; Weiserbs et al. 2002). All these data were collected between 2002 and 2006.

Environmental descriptors

We extracted relevant ecological variables from two GIS databases: the Biological valuation map (BVM, Wils et al. 2004) and the forest reference layer (FRL). The BVM is a standardized survey and qualitative evaluation of the biotic environment of Flanders and the Brussels Capital Region, largely defined on the basis of vegetation, land use and small landscape elements. Since the BVM has more than 1000 unique vegetation/ land-use classes, we reclassified these into 15 relevant classes. Variables extracted from the BVM can be classified into (i) Forested habitat types [Beech (*Fagus sylvatica*), Oak (*Quercus sp.*), Poplar (*Populus sp.*), Ash (*Fraxinus excelsior*), other deciduous woodlands (including mixed woodlands and tree rows), deciduous woodlands (a combination of the 5 preceding types), parks, orchards and coniferous woodlands]; (ii) Anthropogenic habitats [open-space development (e.g. open residential areas), built-up areas, urban (combination of the two preceding types), agricultural fields and major roads]; and (iii) Other [water (rivers, ponds,...)]. The presence/absence of these classes were used as ecologically relevant variables that could act as determinants of the parakeets' distribution (hereafter called ecographical variables or EGVs) (Hirzel et al. 2002). The FRL is a detailed survey of all Flemish forest patches and provides information on forest age (young, middle aged, old and unequal aged forests) and crown openness (crown cover $< 1/3$, $1/3 < \text{cover} < 2/3$, $\text{cover} > 2/3$). Unfortunately, the FRL was not available for the Brussels Capital Region. Therefore, based on the BVM, we identified 190 forested or park-like sites in the Brussels Capital Region. Using recent aerial photographs available in Google Earth, we assessed the crown openness index of these areas according to the FRL guidelines. D.S. visited all these 190 sites to determine forest age. For the Brussels part of the Sonian Forest, detailed GIS data on forest age and crown openness were available from the forestry service. These data were then reclassified to match the classification of the FRL and resulting GIS maps were merged to create a FRL covering the whole study area. All EGVs were extracted at a raster resolution of 50×50 m.

Since little is known about the scale of ring-necked parakeets' habitat selection or its feeding ecology, we

used a multi-grain approach (Meyer 2007; Meyer and Thuiller 2006) to account for the fact that habitat selection can act at different spatial scales. Using a moving window algorithm (Hirzel et al. 2006a), we first converted the presence-absence EGVs mentioned above into continuous occurrence-frequency maps (range 0–100, Hirzel et al. 2006a), and we used two possible scales for these moving window calculations : (i) a radius of 700 m, based on the average home range size of 5 radio-tracked ring-necked parakeets (pers. comm. A. Shwartz, Tel Aviv, Israel); (ii) a larger radius of 2500 m, based on a preliminary telemetry study of breeding parakeets in the UK (only 1 male parakeet followed, Pithon 1998). A recent preliminary study on the habitat use of breeding parakeets in Brussels confirmed that they spend most of their daily foraging time within a few hundreds of meters from the nest, while occasionally foraging further afield. (Strubbe unpubl. data). As ring-necked parakeets are fast-flying, mobile birds that cover much larger distances on their daily flights to and from their communal roost sites (Kahl-Dunkel and Werner 2002), we also considered a long-range exploration scale (unlimited distance, Hirzel et al. 2004) by computing a distance map for each EGV, attributing to every cell the distance to the closest occurrence of that EGV. In summary, each presence-absence variable extracted from the BVM and the FRL generated three variables (each one at a different scale; i.e. 'multi-grain') except for the variables major roads, water and Ash *F. excelsior*. For the latter EGVs we only used the long-range exploration scale as the moving window operations yielded maps that were not continuous enough to be included in the ENFA analysis, i.e. the maps were made up of almost only two values. Moving window analyses were done with the CircAn module of Biomapper 3.2 (Hirzel et al. 2006a), the distance maps were prepared in ArcGis 9.1 (ESRI 2005).

We also considered several fragmentation indexes, as some observations suggest that ring-necked parakeets avoid large contiguous forest tracts (J.-P. Jacob and A. Weiserbs pers. comm., pers. obs.). For the EGV 'deciduous woodlands', we calculated two 'border length' statistics (radii 700 m and 2500 m, expressed as border length (m) per unit area). These border length statistics can be considered as measures of landscape fragmentation (Hirzel et al. 2006a). We also calculated the "in-and-out distance" for the EGV

‘deciduous woodlands’. This metric computes the distance to the edge of a deciduous woodland patch, whereby distances outside the patches are positive and distances inside the patches are negative (Hirzel et al. 2006a). Since the parakeets’ current distribution is heavily influenced by historical factors, in particular the location of the starting point of the invasion, we included the distance to the 1974 release site as a ‘release distance’ EGV (cf. Strubbe and Matthysen 2007). It should be noted that ecological niche models convert species presences from geographical space to environmental space, and predictions are then projected back into geographical space (Peterson 2001). Therefore release distance, while important for describing the current distribution in geographical space should have no meaning in environmental space. However, we added release distance to verify whether ENFA results may have been biased by the interplay between the historical expansion and the spatial configuration of relevant landscape elements whereby the importance of habitat factors that are common near the release site is inflated. In total, this resulted in 64 EGVs, and all these descriptors were standardized and normalized using the Box-Cox standardizing algorithm (Sokal and Rohlf 1981).

Statistical methods

Ecological niche modelling and habitat suitability

ENFA analyses were performed using the BIOMAPPER software. ENFA was used to describe the parakeets’ niche and to identify the main environmental gradients that shape the spatial distribution of the ring-necked parakeet in Flanders and the Brussels Capital Region. The first factor extracted gives the *marginality coefficient*, which is defined as the standardized difference between the average conditions in areas with the species present, and those in the entire study area. This marginality ranges from -1 to $+1$ and indicates the rarity of the conditions selected by the parakeets within the study area. Positive or negative values show a species’ optimum to be higher (respectively lower) than the average conditions in the study area. All the subsequent factors (‘specialization’ factors) maximize the specialization, defined as the ratio of the species variance to the global variance. Successive factors explain the remaining specialization in decreasing amounts.

A high value of a specialization coefficient indicates a narrow niche breadth in comparison with available conditions. The *tolerance coefficient* is then defined as the inverse of the specialization, it ranges from 0 to 1 and can be used as an indicator of the species niche breadth (the closer to 0, the more specialized). As a large part of the information is accounted for by a few of the first factors, only those shown significant by comparison with Mac-Arthur’s Broken-stick distribution (Hirzel et al. 2002) are kept to compute the HS maps.

BIOMAPPER provides several algorithms for HS computations (Hirzel and Arlettaz 2003). We compared two algorithms on our parakeet data set: the median algorithm and the distance geometric mean algorithm. We compared these algorithms because data may be more suited to one algorithm than to another, and different algorithms can yield different HS maps (Braunisch and Suchant 2007; Hirzel and Arlettaz 2003). These algorithms assign a similarity coefficient (or HS, ranging from 0 to 100) between any location and the most suitable conditions. Note that these coefficients do not equal probabilities of occurrence, but that the suitability index is proportional to the probability of use (Hirzel et al. 2006b; Manly et al. 2002). The median algorithm makes the assumption that the best habitat is at the median of the species distribution on each factor, and that these distributions are symmetrical. The distance geometric mean algorithm makes no assumption about the shape of the species distribution. It is based on the density of observation points (parakeet presences) in the environmental space and it assumes that the higher the density of observations in the environmental space, the higher the suitability of the matching environmental conditions (Hirzel and Arlettaz 2003).

Competing models and scale issues

In order to explore which environmental characteristics best explain the spatial distribution of the parakeets in our study area, we created four datasets (A–D) with different combinations of the EGVs. Published data give contradictory information on preferred trees for breeding or feeding (Braun 2004; Butler 2003; Claes and Matthysen 2005; Franz 2007), therefore we tested models with the individual tree species as EGV or with all tree species lumped together as ‘deciduous woodlands’ in order to verify

which combinations were most appropriate. Several studies have found a relationship between parakeet presence and human habitations, and to check whether the parakeets discriminate between built-up city centers and open, residential areas or if they just prefer urban sites (Pithon 1998; Strubbe and Matthysen 2007), we ran models with several combinations of these habitat characteristics. Table 1 shows the EGVs for which the datasets differ. EGVs derived from the other variables (*F. excelsior*, parks, orchards, coniferous woodlands, agricultural fields, major roads, water, the EGVs extracted from the FRL and the ‘fragmentation’ EGVs) were used in all datasets. Each dataset (A–D) was fed two times to the ENFA algorithm, once including the EGV ‘release distance’, once without release distance. Thus, in total, we performed 8 ENFA analyses. In order to obtain HS maps, these 8 analyses were used as input for both the median algorithm and the distance geometric mean algorithm, yielding 16 competing HS maps.

In order to assess how variation in the extent of the study area changes the environmental factors driving the parakeet distribution, and how it influences the ENFA analysis and predictive model performance, we created a smaller study area (1487 km²) by intersecting the original study area with an oval encompassing all known parakeet breeding localities (see Fig. 2). We reran the four datasets described above (A–D) with this smaller area and this resulted in 16 competing small-scale HS maps. For simplicity, we will refer to the large scale study as the “Flanders” model (Flanders + Brussels Capital Region) while the small scale will be named the “Brussels” model (Brussels Capital Region and some parts of adjacent Flanders). Our major interest is to examine the effect of the scale used on the predicted

suitable habitat in the Sonian Forest. This 46.6 km² large, continuous forest is located at the south-southwestern edge of the parakeets’ current distribution, and is an important habitat for several native (cavity-nesting) species. At the Brussels scale, the Sonian Forest is a dominant landscape feature, accounting for more than 20% of all forests, although only 5.5% of all our parakeet breeding locations are located in it (= 24 pairs). At the Flanders scale, the Sonian Forest is much less important as it accounts for only 2.5% of all Flemish forests.

Model evaluation and reclassifying HS maps

In order to assess the statistical fit of a predictive habitat model, an extensive number of evaluation statistics have been developed (Jimenez-Valverde and Lobo 2007; Liu et al. 2005). However, most of these methods have been developed for presence/absence data, and crucially rely on a confusion matrix (a contingency table that counts how many presence and absence evaluation points occur in suitable and unsuitable areas). Presence-only models such as ENFA suffer from a lack of absence points, which causes all methods related to the confusion matrix to be flawed (Boyce et al. 2002). ENFA introduces the concepts of *Explained Specialization* (ExS, identical to the traditional “explained variance”) and *Explained Information* (ExI, a modified version of ExS that takes the marginality factor into account) (Hirzel et al. 2002) to indicate how the computed HS models explain the observed data. To assess the robustness and the predictive power of a HS model, ENFA uses the novel *continuous Boyce index* (Hirzel et al. 2006b), a threshold independent modification of the Boyce index (Boyce et al. 2002) which measures the relation between the observed and expected number of validation points for different HS values. The continuous Boyce index yields a smooth curve (Fig. 1) and the Boyce value ranges between 0 and 1 (the closer to 1, the better the model). The maximum value of the Boyce curve (called the F-value) shows how much the model differs from a random model (Fig. 1, Hirzel et al. 2006b) and the F-value can be used to further discriminate between competing models. By applying a k-fold cross-validation, k estimates of the continuous Boyce index are produced, allowing assessment of its central tendency and variance (Hirzel et al. 2006b).

Table 1 Ecographical variables that were used in only some of the four datasets

EGV	A	B	C	D
<i>F. sylvatica</i>			●	●
<i>Quercus</i> sp.			●	●
<i>Populus</i> sp.			●	●
Other deciduous woodlands			●	●
Deciduous woodlands	●	●		
Open-space development	●		●	
Built-up areas	●		●	
Urban		●		●

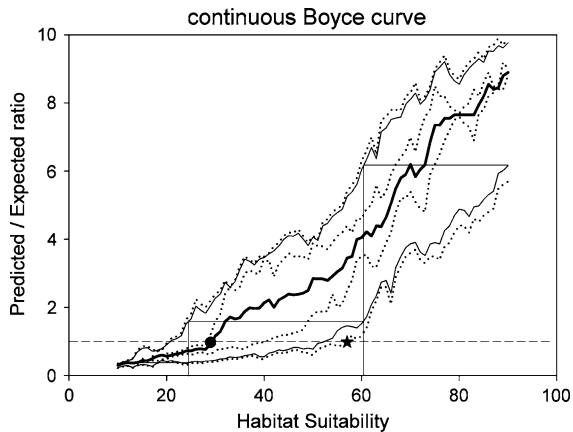


Fig. 1 Example of a continuous Boyce curve illustrating the delineation of habitat suitability classes. Dotted lines = individual Boyce curves, thick solid line = median of the individual Boyce curves, thin solid lines = 90% confidence intervals. Dashed line ($P/E = 1$): below this line the model predicts fewer presences than expected by chance, above the line the opposite. ● = median cuts the 1 line, * = ‘lowest’ Boyce curve cuts 1 line. Vertical lines indicate HS classes, based on the 90% confidence interval

Huberty’s rule was used to define the optimal number of cross-validations for our dataset.

The final step in our modeling was to transform the obtained HS maps (HS range 0–100) into a few meaningful and reliable classes (Hirzel et al. 2006b). A wide range of techniques has been created to reclassify continuous maps into several classes with a minimum of two (presence/absence), but most of these methods rely on a confusion matrix (Hirzel et al. 2006b; Liu et al. 2005), which makes them unsuitable for presence-only models (see above). The advantage of the continuous Boyce index is that it provides guidelines for choosing the number of HS classes and their boundaries that give the most consistent prediction of HS. The optimal number of classes can be found by looking at the 90% confidence interval around the continuous Boyce curve, with the goal of finding how many HS classes can be defined while minimizing their overlap (see Fig. 1). For invasive species management, information presented as presence/absence might be more practical than presented as suitability (Jimenez-Valverde and Lobo 2007; Liu et al. 2005). Therefore, we used three methods to choose a threshold to transform the suitability predictions into presence/absence. The first and most traditional approach was to consider areas with a HS below 50 as unsuitable

habitats, and the remaining areas as suitable. However, recent reviews criticized the 50% threshold as being one of the worst classifiers in almost all situations (Jimenez-Valverde and Lobo 2007; Liu et al. 2005). The other approaches are based on the continuous Boyce curve. We used the 90% confidence interval around the continuous Boyce curve to define non-overlapping HS classes (Hirzel et al. 2006b, see Fig. 1 for illustration). In the first Boyce method, we selected as threshold the point where the median of the k Boyce curves cuts the 1 line (see Fig. 1, circle), thus separating the areas where the species is found more or less frequently than expected by chance. In the second Boyce based method, we used the point where the lowest of the k Boyce curves cut the 1 line as threshold (see Fig. 1, star).

Results

Model evaluation statistics

Tables 2 and 3 show the model evaluation statistics for the ENFA analysis and HS computations at the different scales. By comparing the ENFA eigenvalues to MacArthur’s broken-stick distribution, we determined the number of significant factors to be used in the analyses. At the Flanders scale, 6–7 factors were retained, explaining 82–90% of the information (i.e. 100% of the marginality and 65–80% of the specialization). The Brussels scale models used 8–12 factors, explaining 79–82% of the information (100% of the marginality and 58–63% of the specialization). Huberty’s rule always yielded 8 cross-validations and by comparing the values of the continuous Boyce curves, it becomes clear that in almost all cases, the distance geometric mean algorithm attains a higher value, indicating a better model fit for this algorithm. The median algorithm performs better only for the datasets C and C rel. at the Brussels scale (see Table 3), but the differences with the geometric mean are small.

At both scales, datasets A & A release and B & B release perform the best (see Tables 2 and 3). The high values for ExS, ExI and the Boyce index indicate that these models are highly reliable (Hirzel et al. 2006b). At the Brussels scale, the models show a larger standard deviation, showing that these models are less robust than the models at the Flanders scale. Table 2 shows that, for the Flanders scale, the values

Table 2 ENFA evaluation statistics for Flanders for four different models (A–D) with or without release distance included (“rel”)

Model	#Factors	ExS	ExI	HS	B	SD	F
A	6	0.67	0.84	M	0.78	0.13	260
				G	0.97	0.03	350
B	6	0.72	0.86	M	0.82	0.12	475
				G	0.97	0.04	220
C	7	0.65	0.82	M	0.69	0.20	150
				G	0.81	0.29	100
D	7	0.70	0.85	M	0.60	0.22	80
				G	0.85	0.10	120
A rel	6	0.79	0.89	M	0.80	0.10	750
				G	0.96	0.05	360
B rel	6	0.80	0.90	M	0.79	0.11	620
				G	0.97	0.03	250
C rel	7	0.78	0.89	M	0.55	0.24	100
				G	0.84	0.08	110
D rel	7	0.80	0.90	M	0.39	0.27	120
				G	0.87	0.09	130

#F = number of retained factors, ExS = Explained specialization, ExI = Explained information, HS = Habitat suitability algorithm (M = median, G = distance geometric mean), B = Continuous Boyce index, SD = Standard deviation, F = Max. of Boyce curve (= deviation from randomness)

of the Boyce index and its SD are nearly equal for the models datasets A & A release and B & B release. To further discriminate between these models, we can use the maximum F-value. This value indicates how much a model deviates from randomness, and according to this criterion, model A and A-release perform the best. Following the same reasoning for the small scale, model B & B release perform the best, although the differences with A and A release are small. We will further only discuss the A & A release models because they correspond well with previous findings on the parakeets’ habitat selection (Strubbe and Matthysen 2007). Moreover, datasets B & B release yield largely the same important EGVs as A & A releases (details not shown).

Ring-necked parakeet niche description

Table 4 shows for the datasets A & A release which EGVs influence the spatial distribution of the ring-necked parakeet at both scales. Positive scores on marginality indicate that parakeets are more likely to

Table 3 ENFA evaluation statistics for Brussels for four different models (A–D) with or without release distance included (“rel”)

Data	#F	ExS	ExI	HS	B	SD	F
A	10	0.61	0.81	M	0.65	0.29	55
				G	0.81	0.24	50
B	8	0.58	0.79	M	0.73	0.20	70
				G	0.87	0.14	65
C	12	0.63	0.81	M	0.56	0.24	80
				G	0.49	0.29	50
D	9	0.58	0.79	M	0.53	0.26	55
				G	0.56	0.36	35
A rel	10	0.63	0.82	M	0.73	0.27	45
				G	0.84	0.20	45
B rel	9	0.63	0.82	M	0.76	0.19	60
				G	0.86	0.13	80
C rel	11	0.62	0.81	M	0.53	0.29	100
				G	0.51	0.33	40
D rel	10	0.62	0.81	M	0.47	0.34	50
				G	0.56	0.36	35

#F = number of retained factors, ExS = Explained specialization, ExI = Explained information, HS = Habitat suitability algorithm (M = median, G = distance geometric mean), B = Continuous Boyce index, SD = Standard deviation, F = Max. of Boyce curve (= deviation from randomness)

occur in or near built-up areas, parks, old forests and unequal aged forests, while coniferous woodlands appear to be avoided as indicated by a negative marginality factor. Strong negative values were obtained for all variables related to agricultural fields, signifying that the parakeets tend to avoid agricultural areas. Negative values were also found for the in-and-out distance and, where included, the release distance, showing that parakeets are less likely to be found far from forest edges and that they are still more common close to their release site. A comparison of the marginality values of the individual EGVs at the Flanders and Brussels scale shows that there are only minor differences, suggesting that the same factors drive the parakeets’ distribution at both scales. Highest coefficients at the specialization factors were obtained for the in-and-out-distance and the release distance, as well as for the border length statistics. These high specialization coefficients correspond to a narrow niche relative to the conditions available for the parakeets. There is also some specialization for the percentages deciduous and coniferous woodlands,

Table 4 Correlations between the ENFA factors and the ecographical variables

Ecographical variable	Dataset A			Dataset A release			Dataset A			Dataset A release		
	Flanders			Flanders			Brussels			Brussels		
	MF ^a	SF ^b	SF ^b	MF ^a	SF ^b	SF ^b	MF ^a	SF ^b	SF ^b	MF ^a	SF ^b	SF ^b
	16%	22%	15%	41%	13%	12%	7%	11%	8%	7%	12%	10%
% Parks (2500 m)	+++	0	0	+++	0	0	+++	*	*	++	****	*
% Parks (50 m)	+++	*	***	+++	*	*	+++	0	*	+++	*	0
% Old forests (2500 m)	++	0	0	++	0	0	0	**	****	0	0	**
% Old forests (50 m)	+	**	***	+	**	***	++	0	*	++	0	0
% Middle aged forests (2500 m)	+	0	0	+	0	0	-	**	*	-	*	**
% Middle aged forests (50 m)	0	0	*	0	0	*	0	0	0	0	0	0
% Unequal aged forests (2500 m)	+	0	0	+	0	0	+	0	*	+	**	0
% Unequal aged forests (50 m)	++	*	*	++	*	0	+	*	0	+	0	*
% Young forests (2500 m)	+	0	0	+	0	0	0	*	0	0	*	*
% Young forests (50 m)	+	0	0	+	0	0	0	0	0	0	0	0
% Deciduous woodlands (2500 m)	+	**	*	+	**	0	-	****	*	-	*	****
% Deciduous woodlands (50 m)	0	***	*	0	***	**	0	**	*	0	0	**
% coniferous woodlands forests (2500 m)	-	0	0	-	0	0	-	****	****	-	**	****
% Coniferous woodlands forests (50 m)	-	*	***	-	0	***	0	0	*	0	*	0
% Orchards (2500 m)	0	0	0	0	0	0	-	**	*	-	*	**
% Orchards (50 m)	0	*	0	0	*	*	-	0	*	-	0	0
% Forest openness <1/3 (2500 m)	+	0	0	+	0	0	0	*	*	0	0	*
% Forest openness <1/3 (50 m)	+	*	0	+	*	0	+	0	0	+	0	0
% Forest openness 1/3 \diamond 2/3 (2500 m)	+	0	0	+	0	0	+	0	***	+	*	0
% Forest openness 1/3 \diamond 2/3 (50 m)	+	*	0	+	*	0	+	0	0	+	0	0
% Forest openness >2/3 (2500 m)	+	0	*	+	0	*	-	0	***	-	0	0
% Forest openness >2/3 (50 m)	0	*****	*****	0	*****	*****	+	0	*	+	0	0
% Built-up areas (2500 m)	++	0	0	+	0	0	++	*	**	++	*	*
% Built-up areas (50 m)	++	0	*	++	0	0	+	0	*	+	*	0
% Open-space development (2500 m)	0	0	0	0	0	0	0	0	*	0	*	0
% Open-space development (50 m)	0	0	0	0	0	0	-	0	*	-	0	0
% Agricultural fields (2500 m)	-	0	*	-	0	0	-	*	0	-	**	*
% Agricultural fields (50 m)	-	0	**	-	0	*	-	*	**	-	*	*
Border length (2500 m)	+	**	*	+	**	0	-	*****	*	-	***	*****
Border length (50 m)	0	*	****	0	*	*	0	**	*	0	0	**
Distance to parks	-	*	*	-	*	0	-	0	0	-	0	0
Distance to old forests	-	0	0	-	0	0	-	0	0	-	0	0
Distance to middle aged forests	-	0	0	-	0	0	-	0	0	-	0	0
Distance to young forests	-	0	*	-	0	0	0	*	0	0	0	*
Distance to unequal aged forests	-	0	0	-	0	0	-	0	0	-	0	0
Distance to deciduous woodlands	-	0	0	-	0	0	-	0	0	-	*	0
Distance to coniferous woodlands forests	+	0	0	+	0	0	++	*	**	+	*	*
Distance to orchards	0	0	0	0	*	*	+	0	*	+	*	0
Distance to Ash (<i>F. excelsior</i>)	0	0	*	0	0	0	+	0	*	+	***	0

Table 4 continued

Ecographical variable	Dataset A			Dataset A release			Dataset A			Dataset A release		
	Flanders			Flanders			Brussels			Brussels		
Distance to forest openness >1/3	–	0	0	–	0	0	–	0	0	–	0	0
Distance to forest openness 1/3 \diamond 2/3	–	0	0	–	0	0	–	0	0	–	0	0
Distance to forest openness >2/3	–	0	0	–	0	0	–	0	0	–	0	0
Distance to built-up areas	–	*	*	–	*	0	–	*	****	–	*	*
Distance to open-space development	+	*	0	+	*	0	+	0	**	+	*	0
Distance to agricultural fields	++	*	**	++	*	*	++	**	**	++	0	**
Distance to major roads	0	0	0	0	0	0	–	*	*	–	0	*
Distance to water	0	0	0	0	0	0	0	0	*	0	0	0
In-and-out distance	–	*****	**	–	*****	*****	–	*****	*	–	*	***
Release distance	x	x	x	–	0	*****	x	X	x	–	*****	0
Global marginality	2.89			3.10			2.28			2.39		
Global tolerance	0.41			0.32			0.56			0.54		

The percentages indicate the amount of specialization accounted for by the factor (only first three factors shown). MF is the marginality factor, which explains 100% of the marginality and some part of the specialization. SF are the specialization factors, which explain the remaining specialization in decreasing amounts

^a Marginality factor. The symbol + means that the parakeet was found in locations with higher values than average. The symbol – means the reverse. The greater the number of symbols, the higher the correlation. 0 indicates a very weak correlation.

^b Specialization factor. The symbol * means the parakeet was found occupying a narrower range of values than available. The greater the number of asterisks, the narrower the range. 0 indicates a very low specialization (Hirzel et al. 2002)

and at least at the Flanders scale a high specialization value is present for the percentage of forests with a crown cover larger than 2/3.

The global marginality takes into account the marginality scores on all EGVs and gives a summary of how much the species habitat differs from the available conditions, indicating that the parakeets breed in relatively rare habitats compared to their availability in the study area. The global tolerance does the same with all the specialization factors and indicates a medium to small niche breadth (Table 4). A striking difference between the two scales is that, at the Flanders scale, adding the release distance to the dataset shows the parakeet to be even more marginal and specialized while it has almost no influence at the smaller Brussels scale. There is also a difference in the amount of specialization explained by the marginality factor which is larger at the Flanders scale (16–41%) compared to the Brussels scale (7%, Table 4).

Habitat suitability maps

The continuous Boyce index allowed the discrimination of five HS classes for all models except for the A-release at the Brussels scale, where only four

classes could be defined (Table 5). The threshold for highly suitable areas varies between 69 and 77, while the least suitable habitats are found below a threshold of 10–12. The different thresholds used to transform the suitability maps into predictions of presence–absence are also presented in Table 5. The traditional approach of using a value of 50 as threshold is clearly the strictest criterion while the first Boyce method (based on the point where the median Boyce curve cuts the 1 threshold, Fig. 1) is the most liberal.

When concentrating on dataset A at the Flemish scale, we see that the threshold for highly suitable areas lies at a HS value of 77, while the least suitable habitats are found below a threshold of 12. When translating these thresholds into percentage of forest surface (Table 6) we see that the majority of the forested habitats fall into the lowest HS class (64.1%), meaning that they are probably not suitable at all for ring-necked parakeets. Highly suitable areas are very rare as only a small percentage of the forests falls into the two highest HS classes. For an estimation of the parakeets' potential geographic distribution, we need to find a threshold to define a parakeet presence/absence map. We compared one subjective method, the often used 50% threshold,

Table 5 Habitat suitability (HS) classes and presence/absence thresholds for the Flemish and Brussels scale models

Scale		Habitat suitability classes					Presence/absence thresholds		
		1	2	3	4	5	classical	Boyce 1	Boyce 2
Flanders	A	0–12	13–30	31–62	62–76	77–100	50	15	23
	A release	0–11	12–28	29–49	50–68	69–100	50	14	20
Brussels	A	0–11	12–15	16–31	32–73	74–100	50	17	29
	A release	0–10		43405	19–69	70–100	50	15	28

The 90% confidence interval around the continuous Boyce curve was used to reclassify the ENFA HS maps (HS: 0–100) into non-overlapping HS classes (1 = least suitable, 5 = highly suitable). Boyce presence/absence thresholds indicate the areas where the parakeets are found more frequently than by chance (see Fig. 1)

Table 6 Percentages and km² indicating how much of the Flemish forests that fall into a certain HS class (HS classes: 1 = least suitable, 5 = highly suitable)

Flanders		Habitat suitability classes					Presence/absence thresholds		
		1	2	3	4	5	Classical	Boyce 1	Boyce 2
A	%	64.15	18.75	14.99	1.52	0.6	5.48	28.91	22.47
	km ²	1176	344	275	28	11	100	530	412
A release	%	71.27	15.07	8.01	4.46	1.18	5.4	22.76	18.59
	km ²	1306	276	147	82	22	99	417	341

Boyce presence/absence thresholds show the amount of Flemish forests where ring-necked parakeets are likely to occur more often than expected by chance alone

Table 7 Percentages of the Sonian Forest (a large forest tract near Brussels) where ring-necked parakeets are likely to occur according to models calculated at the Flanders and the Brussels scale

Scale		Presence/absence thresholds		
		Classical	Boyce1	Boyce2
Flanders	A	50.26	96.76	91.72
	A release	54.38	96.92	93.98
Brussels	A	21.74	80.63	50.62
	A release	14.72	80.89	45.52

Presence/absence thresholds determined following the continuous Boyce curve (see Fig. 1)

with two objective thresholds based on the continuous Boyce curve. The first Boyce based threshold lies at 15 (28.9% of forests are suitable) while the second Boyce threshold is somewhat stricter and yields a threshold value of 23 (= 22.5% suitable forest). The traditional 50% threshold delineates only 5.5% of the forests as suitable for parakeets (Tables 5 and 6).

If we now focus on the predicted parakeet distribution in the Sonian forest according to the Flemish and Brussels scale models, we see that with both models, the threshold criteria for selecting

presence/absence areas yield the same pattern. Again, the classical 50% threshold is the strictest method while the first Boyce index is the most liberal (presence/threshold at 15 for the Flemish model, at 17 for the Brussels model). When we transform these thresholds to percentages of suitable Sonian Forest, Table 7 shows that the Flemish scale models predict a much wider parakeet distribution than the Brussels scale models (50.2–96.7% for the Flemish models vs. 14.7–80.9% for the Brussels models). Models calculated at the Flemish scale predict almost the whole forest as suitable habitat whereas the Brussels scale models only indicate the forest edges, the north-eastern arm of the forest and a small part of the central forest as suitable for ring-necked parakeets.

In summary, our model indicates that, in northern Belgium, 100–530 km² forest is suitable as ring-necked parakeet breeding area (50% threshold vs. first Boyce index, Table 6). This corresponds to 0.74–3.9% of the total surface area of Flanders and Brussels, and to 5.4–28.9% of all forests (sum of all forested habitats = 1832 km²). The resulting HS map (Fig. 2) shows that there is ample suitable habitat for the parakeets to spread in, especially via the north-south axis from Brussels to the city of Antwerp. Along this axis, large

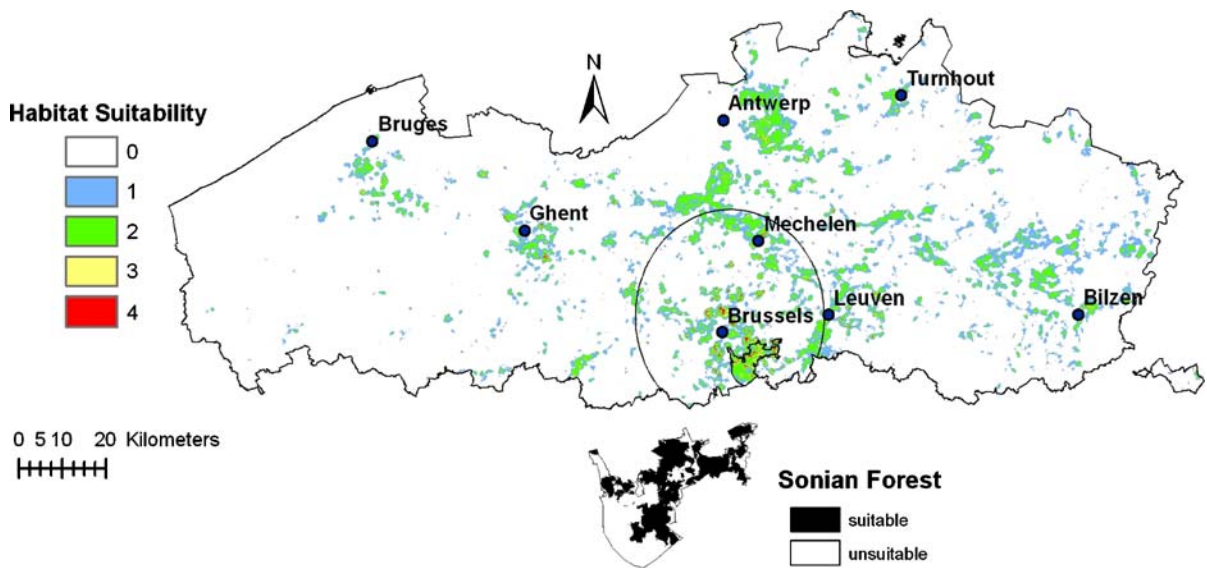


Fig. 2 Habitat suitability map for ring-necked parakeet. Habitat suitability is demonstrated by visualizing the five habitat suitability classes (0 = 64.1% of total forested area, 1 = 18.8%, 2 = 15.0%, 3 = 1.5%, 4 = 0.6%). Inset: habitat

suitability of the Sonian Forest, calculated at the Brussels scale and booleanized according to the 2nd Boyce index (threshold value = 29). Oval shows the area encompassing all known parakeet presence points (the “Brussels” scale model)

future populations can be expected around the city of Mechelen (halfway between Brussels and Antwerp) and in the southern and eastern part of the Antwerp metropolitan area. To the east, highly suitable areas are scarcer and the best areas are located in the regions surrounding the smaller cities of Leuven (± 20 km east of Brussels) and Turnhout (± 30 km east of Antwerp). In the western part of the country, more suitable areas are only found around the provincial capitals of Ghent and, to a lesser extent, Bruges, the capital of the forest-poor West-Vlaanderen province. If we visually compare our best HS map (i.e. dataset A, distance geometric algorithm) to the HS maps yielded by the other datasets and algorithms, we see that roughly the same areas are predicted as suitable, the major difference is the HS value given to the areas. The maps resulting from the median algorithm tend to predict high overall suitabilities, while the distance geometric mean maps are more variable in the HS values given.

Discussion

Model evaluation and selection

Based on the evaluation statistics presented in Tables 2 and 3, datasets A & A release and B & B

release gave the best model fit. It is difficult to discriminate between these datasets as they have comparable explanatory and predictive power. The main difference between these two datasets lies in the classification of urban habitats. Dataset A discriminates between built-up areas and open-space development (e. g. residential areas) whereas dataset B groups these two categories into one ‘urban’ class. We chose datasets A & A release for further consideration and analysis because the results of this dataset correspond best with an earlier study on the ring-necked parakeets’ habitat selection (Strubbe and Matthysen 2007). Table 4 shows that according to dataset A, ring-necked parakeets are found breeding in habitats surrounded by a relatively high amount of built-up area, while open-space development has no particular importance. The same pattern was found by Strubbe and Matthysen (2007) using another parakeet dataset and method (point counts and multiple regression) in the same general study area.

For all models, except the models C & C release at the Brussels scale, the distance geometric mean outperformed the median algorithm in our datasets. The median algorithm assumes that the factor distributions are unimodal and roughly symmetrical, therefore strong deviations from normality in these distributions will cause the median algorithm to yield

invalid HS predictions. If the species habitat distribution shows asymmetry or multimodality, this will be reflected by the marginality factor (Hirzel and Arlettaz 2003), and a plot of the observed parakeet habitat distribution against the marginality factor shows that the distribution is indeed asymmetrical (skewness = 2.38, kurtosis = 5.94). This skewness is probably the reason behind the better performance of the distance geometric mean algorithm.

The high values of the Boyce index for the A & A release models (Tables 2 and 3) indicate highly reliable maps with a high predictive power (Hirzel et al. 2006b). These results should however be treated with some caution, as we are dealing with an invasive species, which may not yet have fully occupied its fundamental niche. Our niche factor analysis therefore represents an estimate of the parakeets' realized niche, in the study areas and environmental conditions being considered (Philips et al. 2006). If the realized and fundamental niche differ, it is simply impossible for any modeling algorithm to describe the species' full fundamental niche because the information is just not present in the presence-only dataset (Philips et al. 2006). In the case of invading species, it is possible that a species may behave as a specialist in the early stages of a colonization, while becoming more generalist as the population expands (Hilden 1965; Sol et al. 1997). In other words, the results presented here could be an underestimation of the parakeets potential distribution, as the possibility exists that the parakeets will start inhabiting areas with environmental conditions suitable but not yet encountered, or not yet used by the parakeets.

In order to discriminate between the effects of habitat choice and historical factors such as the starting point of the invasion, we took into account the distance to the historical release site (Strubbe and Matthysen 2007). The global marginality and tolerance values in Table 4 show that adding distance to the release site has an influence only at the Flanders scale. It causes the parakeet to be even more marginal and specialized (i.e. a higher global marginality and a lower global tolerance), with a strong increase in the amount of specialization explained by the marginality factor (16–41%). This is most probably due to the fact that release distance is highly correlated with parakeet presence at the Flanders scale, because the parakeets have not yet reached areas far away from their release site. The Brussels scale study area was

designed to encompass all known parakeet breeding locations (see Fig. 2), hence it is not unexpected that release distance has only a minor effect on global marginality and specialization at this scale (Table 4). More importantly, at both scales, the release distance has no effect on the marginality scores of the individual EGVs and only little effect on the specialization scores. Adding the release distance does not cause major shifts in the marginality and specialization values of the individual EGVs. This indicates that the EGVs identified by ENFA are genuinely important for the parakeets, and we conclude that ENFA is able to gauge the ecological requirements of an invasive species without the need to include historical information on the starting point of the invasion. Adding the release distance to the datasets does not constitute an improvement to the ENFA analysis and the release distance dataset will not be discussed any further.

In order to examine how variation in the extent of the study area influences our model prediction, we ran all models at two different scales (Brussels and Flanders). At both scales, the spatial distribution of the parakeets is driven by the same EGVs (Table 4, see below (Section “Ring-necked parakeet niche description”) for interpretation of these EGVs). The differences in the absolute marginality and tolerance values between the two scales are trivial as they are due to the fact that these indexes depend on the global set chosen as reference, so that a species might appear extremely marginal or specialized on the scale of a whole country, but much less so on a subset of it (Hirzel et al. 2002). Inspection of the potential distribution maps produced by the Flanders (Fig. 2) and Brussels (not shown) scale models shows the same general features arising, except for the Sonian Forest—our area of main interest. Irrespective of the threshold criterion used to convert the continuous HS maps into a number of reliable HS classes, the Flemish scale models predict a much wider parakeet distribution than those at the Brussels scale (Table 7). The Flemish scale models predict almost the whole forest as suitable, although monitoring projects, breeding bird atlases (Weiserbs and Jacob 2007) and a survey conducted by D.S. failed to find breeding parakeets in the forest interior. This indicates that the Flemish scale models considerably overestimate the potential amount of suitable habitat in the Sonian Forest, especially the forest interior zones. This could result from a violation of the assumption of

normality of the predictors that is required by the ENFA, as the EGV in-and-out distance, which measures the distance to forest edge, is actually not normally distributed. In Flanders, forests are relatively scarce and fragmented, causing forest interior to be a (very) rare habitat. The non-normal distribution of the distance to a forest edge, combined with the tendency of profile methods such as ENFA to yield overoptimistic predictions (Engler et al. 2004; Zaniwski et al. 2002), apparently causes our Flemish-scale models to overpredict the suitable habitat of the Sonian Forest. At the more limited Brussels scale, the distribution of the distance to forest edges is also not normal, but to a lesser extent than at the Flemish scale, and indeed a lower HS is predicted for most of the Sonian Forest. This leads us to the conclusion that, at least for the Sonian Forest, the Brussels scale model yields a more accurate prediction than the Flemish scale models, even though it has a lower Boyce index and higher standard deviation (Table 2 and 3, Boyce index and S.D. for Flemish model = 0.91 ± 0.03 vs. 0.81 ± 0.24 for the Brussels model). The first Boyce method predicts around 80 % of the Sonian Forest as suitable habitat, while the second Boyce index identifies only $\pm 50\%$ of the forest as suitable. A recent telemetry study in the Sonian Forest found breeding parakeets not further than ± 500 m from the forest edge (Strubbe unpubl.), while the longest distance reported is ± 750 m (Vermeersch et al. 2004, pers. comm. M. Louette). The band of suitable forest edge predicted by the second Boyce index corresponds more to these findings than the (broader) zone identified by the first Boyce index and we conclude that the second Boyce index probably yields the most accurate prediction. The inset of Fig. 2 shows the suitable parts of the Sonian Forest according to the second Boyce index. Suitable areas are mainly found at the forest edges, or in the north-eastern arm of the forest, where some parts are managed as parks or arboreta. One part of the central Sonian Forest is also shown as suitable for parakeets, most probably because there are some ponds and castle domains present over there, which fragment the forest.

Ring-necked parakeet niche description

The high values of the marginality coefficient indicate that the ring-necked parakeet breeds in areas differing strongly from the mean environment, while the specialization coefficients indicate a medium niche

breadth (Table 4). Ring-necked parakeets require habitats with sufficient cavities for nesting and these are typically found only in city parks and older forests, an uncommon habitat type in the Flanders and Brussels regions (Van Der Aa 2007). However, the intermediate degree of specialization indicates that the parakeets show some tolerance for environmental conditions inside parks and forests, and this could be related to the parakeets generalist foraging behavior (see below, Forshaw 1978; Python 1998).

The spatial distribution of the parakeets is heavily influenced by EGVs representing the availability of suitable nesting cavities (parks, old forests, and also unequal aged forests, as these forests often contain several old trees). Breeding densities of cavity-nesting birds are often limited by a scarcity of suitable nest sites (Newton 1994; Newton 1998), and this seems also true for most Psittaciformes (Collar 1997; Forshaw 1978), many of which are obligate secondary cavity nesters. Strubbe and Matthysen (2007) found that the density of ring-necked parakeets breeding in a forest patch was directly correlated with the density of potential nest sites. In Flanders, 55% of the forests are younger than 40 years and the forests are characterized by a lack of old trees and standing dead wood (Dumortier et al. 2005), causing the Flemish forests to be considerably reduced in cavity availability compared with old natural forests (McComb and Noble 1981; Wesolowski 2006). It is thus reasonable to assume that cavity availability will be an important factor, governing the future distribution and abundance of the ring-necked parakeet in northern Belgium. Ring-necked parakeets are known as birds of open, deciduous woodlands (Cramp 1985), and their avoidance of coniferous woodlands could be due to a lack of suitable nest sites in these forests (Newton 1994, 1998). Another important EGV is the amount of built-up area surrounding a parakeet breeding site. This probably relates to increased food availability, as in urban areas food is often provided via bird feeders. Ring-necked parakeets are flexible foragers (Cramp 1985; Dhindsa and Saina 1994; Franz and Krause 2003; Python 1998) and they are known to use these feeders throughout the year, but mostly in winter and during the breeding season (Dewinck 2005; Python 1998). Increased food supply through the use of bird feeders can lead to higher survival (Brittingham 1991; Jansson et al. 1981) and breeding performance (Martin 1987; Reynolds et al. 2003) and subsequent

higher breeding densities. The avoidance of areas dominated by agricultural fields and the indifference towards orchards shows that the ring-necked parakeet will probably not settle in these habitats, at least not during the breeding season.

Future ring-necked parakeet distribution in northern Belgium

Our resulting HS map shows that the ring-necked parakeet has ample room for further spread in northern Belgium (Fig. 2). As most (highly) suitable habitats are found along the urbanized north-south axis from Brussels to Antwerp, we expect the ring-necked parakeets to first colonize the areas north of Brussels. This view is supported by a recent study (Vermeersch et al. 2006), reporting an increase in parakeet range size towards the north, although exact locations of breeding pairs are not yet known. Recently, a small roost site (± 35 birds) was discovered in the northeastern part of the Antwerp metropolitan area. In western direction, the parakeets have not yet reached the suitable areas around Ghent, but they do breed in Aalst, halfway Ghent and Brussels. The parakeets may have more difficulties reaching the isolated areas of highly suitable habitat around Bruges, Turnhout and Bilzen, as suitable 'stepping stone' patches are rarer in these areas. However, ring-necked parakeets are mobile birds that cover large distances on their daily flights to and from their roost sites and there are regular observations of (small groups of) parakeets from several parts of northern Belgium so we expect them to eventually reach most suitable sites. A recent breeding bird atlas (Weiserbs and Jacob 2007) estimates the number of parakeet breeding pairs in the Brussels Capital Region to be 480–1.200. Our model shows that there is ± 26 km² suitable parakeet habitat in the Brussels Capital Region, and when we use a middle value of 800 pairs, this corresponds with ± 31 breeding pairs per km². In our model this corresponds with ± 26 km² suitable parakeet habitat, or ± 31 breeding pairs per km². If we extrapolate this number to the estimated amount of potential suitable habitat in Flanders (Table 6), the expected number of parakeet breeding pairs in northern Belgium is in the order of magnitude of 10.000–15.000 pairs. This extrapolation indicates that the ring-necked parakeets has the potential to become one of the most numerous (cavity-nesting)

birds, and these results indicate some concern for increased competition between parakeets and the native nuthatches, as known nuthatch strongholds such as the regions south and east of Antwerp (Matthysen 1998) are highly likely to be invaded by the parakeets.

Conclusions

This study shows that the ring-necked parakeet has not yet colonized all suitable habitats in northern Belgium, and that future parakeet population growth and expansion can be expected. The availability of habitats with ample nesting cavities and close to built-up areas are the main factors driving the distribution of the ring-necked parakeet in northern Belgium. Our predictions show that the ring-necked parakeet may be able to colonize 22.5–28.9% of all forested habitats in our study area. This equals 34–45% of all parks and deciduous woodlands, the main habitat type of the nuthatch. To assess the effect of the parakeet on native hole-nesters in a quantitative way, similar HS maps should be produced for native hole-nesters at risk for competition with the parakeets. By overlaying predictive maps of parakeets and native species, we will be able to identify the zones where competition will be most severe and to estimate the impact on the overall population of native species. This study also tackles some of the methodological challenges associated with ENFA. We show that the novel continuous Boyce index is a useful tool for presence-only model selection and performance evaluation, and we also highlight the difficulty of reclassifying continuous distribution maps into a number of relevant classes or presence/absence maps, particularly in the case of presence-only models.

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