

Assessing the potential impact of invasive ring-necked parakeets *Psittacula krameri* on native nuthatches *Sitta europaea* in Belgium

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Summary

1. Biological invasions are a major threat to biodiversity. Given the large number of invasive species, we need to be able to identify invaders with large effects in order to prioritize management efforts. Here, we present a framework using species distribution modelling to predict how abundance of native species will change as a result of competition with an invasive species using ring-necked parakeets *Psittacula krameri* and nuthatches *Sitta europaea* as a case study.

2. Ring-necked parakeets are widely introduced throughout Europe and compete with native cavity-nesters. Using the relationship between parakeet abundance and environmental variables in Brussels (Belgium), we predict parakeet abundance across Flanders. A competition coefficient, quantifying the parakeets' impact on nuthatches, was obtained by a regression on a data set of parakeet and nuthatch abundance. An estimate of the number of nuthatches that will be lost when parakeets have occupied all suitable sites was calculated by superimposing the abundance maps of the two species and applying the competition coefficient.

3. Our results predict a potential population of about 22 000 parakeet pairs, indicating that they could become one of the most numerous cavity-nesters in the region. Parakeet abundance is the highest in older, more fragmented forest in urban areas whereas nuthatches prefer larger, old and oak-dominated forests.

4. Our models indicate that throughout much of their range, and in a variety of habitats, parakeets and nuthatches will compete for nesting cavities, but as the competition strength is only moderate, the total impact of parakeets on nuthatch populations will be limited, with at most one-third of the population at risk.

5. *Synthesis and applications.* Species distribution models combined with empirical estimates of competition strength can be used as a general tool to make an assessment of the potential impact of established invasive species. Such information is required to make effective decisions on how to prioritize management effort and resources across the multitude of invasive species that currently threaten native ecosystems. For the ring-necked parakeet, our results indicate that there is no compelling evidence indicating that parakeets pose a threat large enough to justify an eradication campaign where they are currently present.

Key-words: biological invasions, boosted regression trees, cavity, competition, impact, species distribution modelling, threat

Introduction

Invasions of non-native species are among the leading threats to biodiversity and ecosystem functioning (Sala *et al.* 2000).

Given the large and growing number of species being introduced (Westphal *et al.* 2008), we need to quantify how species interactions will influence the abundance of native fauna. Furthermore, given that there are limited resources for the management of invasive species, it is essential to distinguish invaders with minor effects from those with large effects

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(Parker *et al.* 1999). Species distribution models (SDMs) are used increasingly to identify areas at risk of invasion, or to predict the range expansion of an established invader. For example, Peterson & Robins (2003) quantified the range overlap in the endangered northern spotted owl *Strix occidentalis* and its invasive competitor, the barred owl *Strix varia* in the USA, to show that the barred owl can persist in much of the spotted owl's distribution and may threaten its survival. Likewise, Heikkinen *et al.* (2007) showed that the distribution of woodpeckers was one of the important factors explaining the distribution of several owl species, as owls largely depend on woodpeckers to create suitable nesting cavities. Although these modelling attempts are promising, the integration of species interactions and SDM to quantitatively predict the impact of an invasion on native biota remains one of the biggest challenges facing invasion ecologists (Parker *et al.* 1999). Here, we illustrate a framework for predicting and quantifying the expected impact of an invasive species on a native species, using the invasion of the ring-necked parakeet *Psittacula krameri* Scopoli as a case study.

In Europe, ring-necked parakeets, which are native to Africa and Asia, have been widely introduced and have established at least 65 European populations (Lever 2005; Strubbe & Matthysen 2009a) with population sizes ranging from a few tens to several thousands (Strubbe & Matthysen 2007). In Belgium, parakeets were released in northern Brussels in 1974, and the population grew to 8000–8500 birds in 2006 (Weiserbs & Jacob 2007). Strubbe & Matthysen (2007, 2009b) examined the relationship between parakeet numbers and the abundance of several common native hole-nesting birds in 44 forest patches in Belgium and found a negative correlation between parakeet abundance and the number of nuthatches *Sitta europaea* L. present. Although nuthatches are small passerines, they prefer to breed in relatively large tree cavities, especially old woodpecker holes, which are also favoured by ring-necked parakeets (Butler 2003). Ring-necked parakeets start breeding at the end of February whereas nuthatches typically start laying eggs only during the second half of April, and this difference in timing of breeding enables parakeets to occupy nest sites first. The negative relationship between parakeet and nuthatch abundance is suggestive of competition for nesting cavities. A field experiment showed that blocking of parakeet breeding cavities led to a decrease in nuthatch breeding pairs, mainly caused by early cavity-takeovers by parakeets (Strubbe & Matthysen 2009b).

Strubbe & Matthysen (2009c) used the presence-only SDM technique ENFA (Hirzel *et al.* 2002) to relate a set of ± 450 point locations of breeding parakeets to a number of habitat variables. This analysis showed that parakeet distribution is governed primarily by the amount of older forest patches and human development in the landscape – reflecting the parakeets' need for suitable nesting cavities, and its reliance upon urban areas to forage. By assigning a habitat suitability index to each pixel in the study area (Hirzel *et al.* 2002), ENFA results show that in Flanders, there is ample suitable habitat available for parakeet colonization, and some known nuthatch strongholds are highly likely to be invaded by parakeets. Here, we extend these analyses by quantifying and predicting the

impact of competition for nest cavities between nuthatches and parakeets on nuthatch abundance. This is important, as information on the expected impact on native species is crucial for identifying priority invasive species to target for prevention and control, and for developing specific management objectives and actions.

Materials and methods

ABUNDANCE MAPS

We obtained a data set of parakeet abundance at 48 sites from the Brussels metropolitan area (mean surface area of these forest patches: 31.8 ha, median: 15.5 ha). Thirty-seven sites were derived from point counts conducted by D.S. (first author) in forest patches during 2004–2006 (details in Strubbe & Matthysen 2007). Given that estimates from these point counts were highly correlated with actual breeding densities (see Strubbe & Matthysen 2007 for details), we could estimate the number of parakeet breeding pairs per hectare. Additional surveys were conducted at eight sites by D.S. in 2006 (Diederik Strubbe, unpublished data) and we also included three sites reported by (Weiserbs, Jacob & Rotsaert 2002).

Nuthatch abundance data comes from two sources. First, point counts were conducted in the same forest patches as the parakeets (see above) to give nuthatch abundances in 44 areas in the Brussels metropolitan region. Secondly, region-wide data on nuthatch abundance were taken from the Flemish Breeding Bird Atlas (Vermeersch *et al.* 2004). This atlas divides the region in a grid of 5×5 km and within each of these squares, exact point locations of breeding nuthatches were collected in eight randomly chosen 1-km grid cells. As we aim to predict parakeet and nuthatch abundance per forest patch, we only selected forest patches that were completely covered by surveyed grid cells. To create a region-wide nuthatch distribution model (see below), we did not include forest patches where parakeets are known to breed, as we wanted to obtain an estimate of nuthatch abundance independent of possible parakeet effects. Matthysen (1999) found that, in Flanders, nuthatch territory sizes were larger than 2 ha in 90% of all censuses, and therefore we did not consider patches smaller than 2 ha in our data set. This resulted in a data set of 3689 forests (mean surface area 13.1 ha, median 4.5 ha).

ENVIRONMENTAL PREDICTORS

We developed a series of environmental predictors to capture the known habitat requirements of both nuthatches and parakeets. We used two GIS data bases from the Flanders region: the Biological Valuation Map (BVM) and the Forest Reference Layer (FRL). The BVM is a standardized survey of the biotic environment, largely defined on the basis of vegetation, land use and small landscape elements. The FRL is a survey of all Flemish forests and provides information on forest age (young, middle aged, old and unequal-aged) and openness (canopy cover $< 1/3$, $> 1/3$ cover $< 2/3$, cover $> 2/3$). As the FRL is not available for the Brussels region, data were added from field surveys (see Strubbe & Matthysen 2009c for details). We only included forest patches that were at least 0.5 ha in size. Urban parks were considered as forest patches only when they were predominantly covered by trees, as indicated by the BVM. Patch metrics derived from these layers included tree species composition, forest age, forest surface area and a measure of forest openness. Tree species composition consists of the proportion of oak (*Quercus* spp.), beech

Fagus sylvatica L. and coniferous (*Pinus* spp.) trees in a forest patch. Parakeets have never been found nesting in coniferous trees (Butler 2003; C. J. Butler, pers. comm.), therefore they were considered as unsuitable habitat. All patch variables, except total surface forest area, were calculated for deciduous forests only. Coniferous forest was included in total surface forest area because parakeets prefer smaller, more fragmented forests, and an area of deciduous trees embedded in large coniferous forest might influence parakeets' behaviour (Pithon 1998; Butler 2003). As an indicator of cavity availability, we included the proportion of old forest and unequal-aged forest, as the latter often contain several old trees. Nuthatches favour closed forests whereas parakeets are thought to prefer more open, park-like forests (Forshaw 1978; Matthysen 1998). To account for this, we included the proportion of forest with a canopy closure $> 2/3$ as a measure of forest openness. Nuthatches prefer the forest interior (Matthysen 1998), whereas parakeets are thought to prefer forest edges (Pithon 1998), and therefore we also included the proportion of forest core area. For nuthatches, forest edge was defined as 50 m (according to Matthysen 1998) whereas, for parakeets, this was 52 m, based on the average distance to the forest edge of parakeets nesting in a large forest tract near Brussels (Diederik Strubbe, unpublished data). We also derived several landscape metrics such as the proportion of urban, suburban and forested area in a buffer around a forest patch. Buffer distance for ring-necked parakeets was 1033 m, based on the average maximum foraging distance from occupied nests obtained by a telemetry study on breeding parakeets (Diederik Strubbe, unpublished data). The nuthatch buffer distance was 80 m, based on the radius of a circular minimum nuthatch habitat of 2 ha (Matthysen 1999). As the parakeets' current distribution is heavily influenced by historical factors, in particular the location of the starting point of the invasion, we also calculated the distance to the 1974 release site. All GIS operations were conducted using ArcGIS 9.3 (ESRI 2008), and a summary of all variables used in the analyses can be found in Table S1. Note that all variables were extracted at the patch level, and that all analyses in this study were performed using the patches as the unit of analysis, not grid cells.

BOOSTED REGRESSION TREES

Abundance predictions for parakeets and nuthatches were made using boosted regression trees (BRT; Friedman 2001; Elith, Leathwick & Hastie 2008). BRT is a relatively new technique in SDM, but it performs well because regression trees are able to fit complex nonlinear relationships and automatically handle interaction effects between predictors (Elith *et al.* 2006, 2008). BRT combine two algorithms: regression trees and boosting. Boosting means that regression trees are iteratively fitted to the data, gradually increasing emphasis on observations poorly modelled by the existing collection of trees (Schapire 2003). We used the statistical software *R* and the scripts provided by Elith *et al.* (2008) to find the optimal setting for the parameters required for BRT analysis, i.e. the learning rate (which determines the contribution of each tree to the growing model), the tree complexity (which controls whether interactions are fitted) and finally the number of trees. To balance model fit and predictive performance, we jointly optimized the number of trees, the learning rate and the tree complexity using a *k*-fold cross-validation procedure, whereby tree models are iteratively fit to a subset of the data (Hastie, Tibshirani & Friedman 2001). These subsets are randomly selected without replacement and this procedure introduces an element of stochasticity that improves model accuracy and reduces overfitting (Elith *et al.* 2008). After identifying the optimal model settings, we followed the model simplification procedure of

Elith *et al.* (2008), which proceeds by dropping the least important predictor, then re-fitting the model and sequentially repeating the process until the change in predictive deviance exceeds its original standard error. The parakeet abundance model was fitted assuming a Gaussian distribution because parakeet data were normally distributed (Shapiro–Wilk $W = 0.95$). Optimal BRT settings for this model were a tree complexity of two, a learning rate of 0.001 and 6150 trees.

Nuthatches were found breeding in only 554 of the 3689 surveyed patches, leading to a non-normal distribution (Shapiro–Wilk $W = 0.14$) and a high frequency of zero observations (85%). To accommodate this 'zero-inflation' (Welsh *et al.* 1996; Potts & Elith 2006), we used a hurdle model (Potts & Elith 2006) that consists of two steps: a presence–absence model is run with a Bernoulli (i.e. binomial) distribution and then an abundance model, in which all zeroes are excluded, is fitted with a (truncated) Poisson count distribution. The final model is obtained by multiplying both predictions, and can be interpreted as the predicted nuthatch abundance given a suitable habitat. Optimal settings for the presence–absence and abundance nuthatch model were a tree complexity of four and five, a learning rate of 0.01 and 0.005, and 2900 and 4000 trees respectively. We computed Moran's *I* correlograms (*R* package *spdep*; Bivand 2009) over a range of lag distances to check for spatial autocorrelation in the residuals of the BRT models. No significant spatial autocorrelation was detected (see Fig. S1).

Evaluation of model performance

We evaluated the predictive performance of the nuthatch presence–absence model by calculating the area under the receiver operating characteristic curve (*AUC*, Guisan & Thuiller 2005) using *R* package *ROCR* (Sing *et al.* 2005). An *AUC* value of 0.5 indicates random model performance and a value of one indicates occupied and unoccupied patches are perfectly distinguished. We evaluated abundance models by fitting a simple linear regression between the predicted and observed values (Potts & Elith 2006). The intercept term in the regression provides an indication of the bias, and the gradient of the fitted line provides an indication of the distribution of predictions over their numerical range compared with the spread of the observations. We used Pearson's and Spearman's correlation coefficients to assess the agreement between observed and predicted values (Potts & Elith 2006). All evaluation statistics were calculated using 10-fold cross-validation and the cross-validation procedures were run 50 times to ensure stable estimates of model evaluation statistics as recommended for small sample sizes (Elith *et al.* 2008).

Abundance predictions

We obtained region-wide predictions of nuthatch and parakeet abundance by applying the final BRT models to all patches with unknown abundances. For parakeet abundance, we set the distance to the 1974 release site to zero for all forest patches, as this variable reflects the progress of the invasion and we assume that, in the long term, parakeet abundance will not depend on the distance from the starting point of the invasion. As BRT does not provide confidence intervals, we estimated these by taking a bootstrap sample of the parakeet and nuthatch data, with a sample size equal to the input data set but selected randomly with replacement. A BRT was fitted to each sample, and once all predictions were made, we calculated the 5- and 95-percentile values as an estimate of the confidence intervals around our predictions (see Leathwick *et al.* 2006 for details).

COMPETITION

In order to assess the parakeets' impact on nuthatches, we first constructed a nuthatch habitat model using abundances from patches in the Brussels area. This habitat model contains all environmental variables that influence nuthatch abundance, and parakeet abundance was then added to this model (Fox & Luo 1996; Cruz, Rebelo & Crespo 2006). We used a Generalized Additive Mixed Model (GAMM, Wood 2006) with a Gaussian distribution for this analysis because GAMM allow nonlinear responses and a repeated measures design. To obtain the best nuthatch habitat model, we used a stepwise model selection procedure where variables are removed from the model if the associated d.f. is close to 1, when the plotted confidence band includes 0 everywhere and when dropping the variable does not cause a decline in the generalized cross-validation score (Wood 2006). We checked for interactions between parakeet abundance and any of the variables important in the nuthatch habitat model, but none were significant ($P > 0.05$). The regression coefficient describing the relationship between parakeet and nuthatch abundance was taken as the competition coefficient. We estimated the number of nuthatches that will be lost when parakeets have occupied all suitable sites by superimposing the abundance maps of each species and applying the competition coefficient using the following equation:

$$\begin{aligned} \text{NUTHATCH abundance}_{(\text{including parakeet effect})} = \\ \text{NUTHATCH abundance}_{(\text{independent of parakeet effect})} \\ - \text{competition coefficient} \times \text{parakeet abundance}_{(\text{predicted})}. \end{aligned}$$

The predictions of parakeet and nuthatch abundance and our estimate of the competition coefficient all have uncertainties (i.e. confidence intervals), and this leads to a number of possible scenarios of parakeet impact. We calculated variation in the parakeet impact using the mean, upper confidence intervals (CI) limit and lower CI limit associated with each abundance model and the competition coefficient. Note that the impact estimates we propose here are long-term impact forecasts, quantifying the number of nuthatches that could be lost when parakeets have reached the carrying capacity of all forest patches, which assumes that they will be able to disperse to all suitable patches (Guisan & Thuiller 2005).

Finally, we explored how the estimated nuthatch decline varies by habitat or region. For each forest patch, we first calculated the percentage of nuthatches lost according to a moderate impact scenario (i.e. mean values for predicted parakeet and nuthatch abundance and competition coefficient), and then ran a new BRT model with the percentage of nuthatches lost as dependent variable, and the habitat and landscape variables used for the nuthatch models as explanatory variables. We also calculated the actual number of nuthatches lost due to competition with parakeets, as impact in a given habitat may be proportionally high while the actual number of nuthatches lost can be small. To assess how impact estimates change along the range of values of the selected environmental variables, we divided these variables into three classes: low (<33%), medium (33–66%) and high (>66%). Forest size was classified as follows: small (<10 ha), medium (10–100 ha) or large (>100 ha).

Results

PREDICTIVE MODELS FOR PARAKEET AND NUTHATCH

The best parakeet model that explained 25.1% of the deviance had a Pearson's r of 0.63 and Spearman's r of 0.58, indicating

that predictions and observations were relatively similar in magnitude and similarly ordered. The intercept was -0.15 and slope 1.29 , indicating that model calibration was good (Potts & Elith 2006; Heinanen, Ronka & von Numers 2008). BRT automatically tests for interactions between predictor variables, but no interaction terms were retained in the final model, indicating that their inclusion did not increase the deviance explained by the model (Leathwick *et al.* 2006).

Parakeet abundance is highest in older forests (variable importance 29.4) in urban environments (37.3) while declining rapidly with increasing values for the amount of forest core (16.2) and forest surface area (8.5). Distance to the 1974 release site was selected as an important variable (8.6), showing that parakeet density declines with increasing distance from the release site (Fig. 1a and Fig S2). When applying BRT predictions to all forest patches, excluding the distance from the release site which was set to zero (see Materials and methods), we obtained a predicted abundance of 22 140 (9087–39 806) parakeet breeding pairs for the entire study area. This is a more than 10-fold increase compared with recent estimates of 480 to 1200 parakeet breeding pairs in the Brussels Capital Region (data 2000–2004, Weiserbs & Jacob 2007) and about 260–430 pairs in parts of adjacent Flanders (data 2000–2002, Vermeersch, Anselin & Devos 2006).

The presence-absence part of the nuthatch hurdle habitat model had an explained deviance of 82.5% and performed well in discriminating occupied and unoccupied patches when applied to data in the left-out partition (AUC : 0.952). According to this model, the probability of nuthatch presence increases with forest size (30.7) and is higher in patches that have at least some old (29.6) or unequal-aged trees (18.5, Fig. 1b). Nuthatches are more likely to be present in denser forests, as indicated by the positive relationship with the proportion of forest with a canopy closure $> 2/3$ (12.1). A greater number of oak trees (2.58) and a lower number of coniferous trees (1.58) positively influence nuthatch presence, although the contribution of these variables is low (Fig. S3). The BRT discovered two (weak) interactions: namely between forest size and the amount of core forest, and between forest size and the proportion of unequal-aged forests (see Fig. S4). The best nuthatch abundance model explained 69.3% of the deviance. Pearson's r was 0.64, Spearman's r equalled 0.75 and model calibration was reasonably good with an intercept of -0.80 and slope 1.18 . Forest size (67.5) and age (7.0) are again selected as predictors, but for nuthatch abundance, tree species composition is more important than in presence-absence modelling, as shown by the higher contributions of oak (8.4, positive) and coniferous (7.8, negative) forest (Fig. 1c). There is also some evidence for higher nuthatch abundance in forests with a larger core area (5.2, Fig. S5) and the BRT modelled two (weak) interactions, i.e. between forest size and the proportion of coniferous trees, and between forest size and the proportion of old trees (see Fig. S6). The nuthatch presence-absence and abundance model were merged using the hurdle method and applied to all forest patches, resulting in a predicted abundance of 4646 (2929–6776) breeding pairs. This agrees very well with the 4740 to 5750 pairs estimated in the

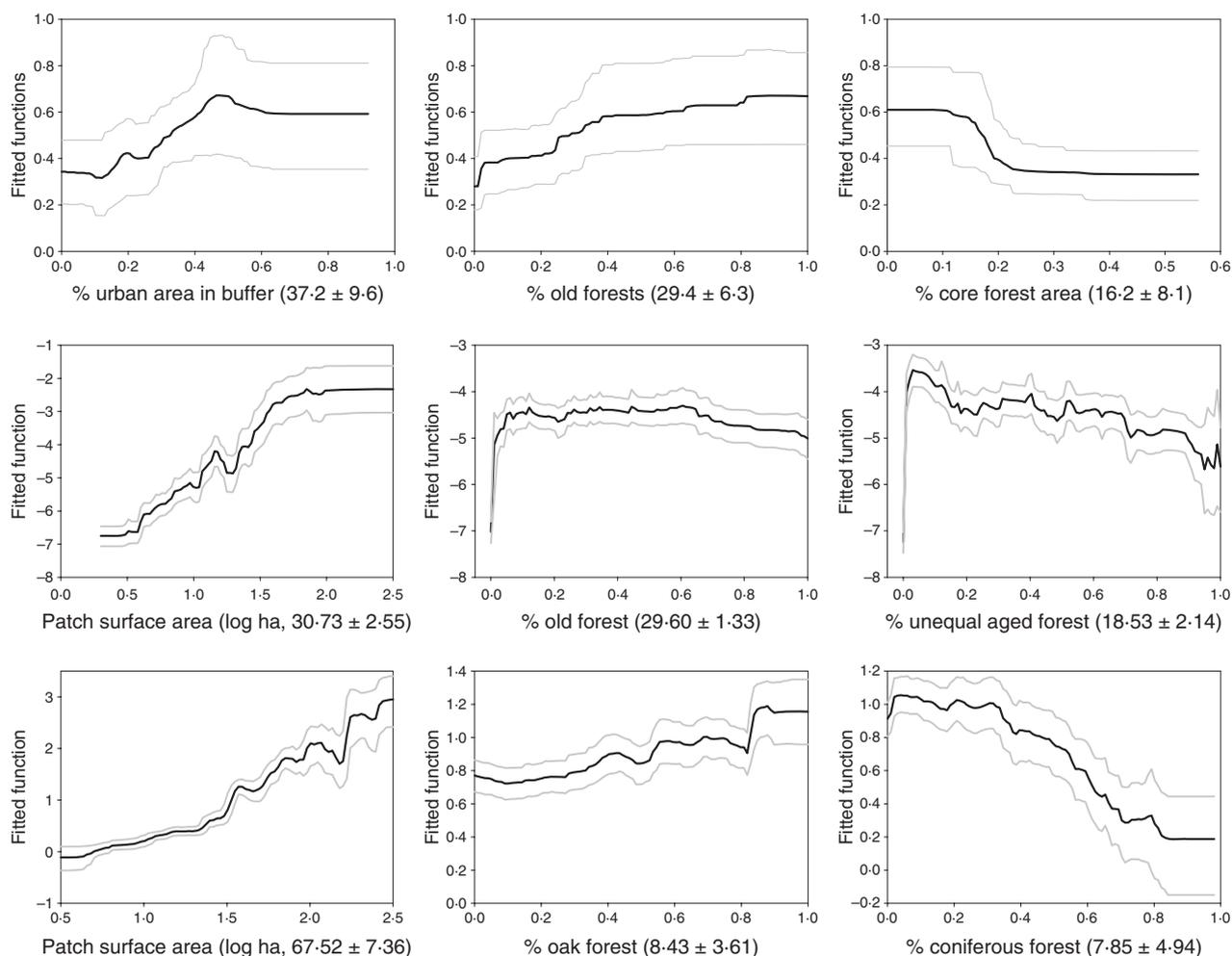


Fig. 1. Partial regression plots for the three most important variables predicting (a) parakeet abundance, (b) nuthatch distribution (presence-absence) and (c) nuthatch abundance. Grey lines indicate the 5–95% confidence intervals for the predicted values, estimated from predictions made from models fitted to bootstrap samples of the input data set. Percentage contributions of predictor variables (i.e. variable importance), and the standard deviation obtained by bootstrapping, are shown in parentheses.

Flemish and Brussels Breeding Bird Atlas (Vermeersch *et al.* 2006; Weiserbs & Jacob 2007). In order to obtain a clear visual representation of predicted parakeet and nuthatch abundance, we divided the country in 5×5 km Universal Transverse Mercator (UTM) squares and calculated the number of parakeet or nuthatch breeding pairs per UTM grid cell (Fig. 2).

COMPETITION

The GAMM analysis of the regional Brussels data set confirms that nuthatch abundance declines with parakeet abundance ($P = 0.0045$) in a linear way (significance of smooth term > 0.05 , Wood 2006). The competition coefficient associated with this slope (see Fig. S7) is -0.0229 (-0.0352 to -0.0106). Nuthatch abundance is largely governed by the same environmental predictors as found at the Flemish level. Abundance increases with the amount of oak forest, forest age (old and unequal-aged) and core forest area (Fig. S7). The positive relationship with the proportion of forest with canopy cover $> 2/3$ shows that, at the Brussels scale, nuthatches prefer

denser forests. R^2 of the model without parakeets is 0.53, after adding parakeets it is 0.56.

Our frequency histogram of possible scenarios indicates that parakeets will have a relatively small impact on nuthatches; in the most extreme scenario, about one-third of the nuthatch population would be lost (Fig. 3). In Fig. 4, we show predicted parakeet impact according to a moderate scenario (see Fig. S8, for the worst-case scenario). To examine whether the predicted parakeet impact varies among habitats, we calculated, per forest patch, the percentage of nuthatches lost according to the moderate impact scenario and used this as input for a new BRT analysis. The BRT model of predicted parakeet impact had an explained deviance of 77.7% and suggests that nuthatch loss will be proportionally higher in smaller, more fragmented and coniferous forests but lower in older and oak-dominated forest patches (see Fig. S9). However, when looking at the actual number of nuthatches lost (Fig. 5), differences in impact between habitats become less clear, as the number of nuthatch pairs lost is largely a function of their abundance in that habitat.

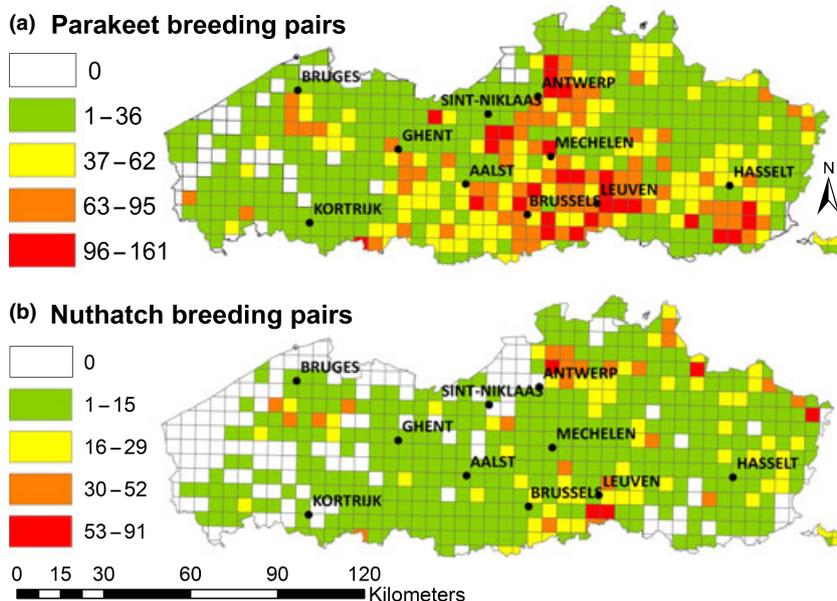


Fig. 2. Region-wide predicted parakeet (a) and nuthatch (b) abundances. Number of breeding pairs per 5×5 km UTM grid was obtained by summing the predicted parakeet or nuthatch abundances for each forest fragment within each grid cell.

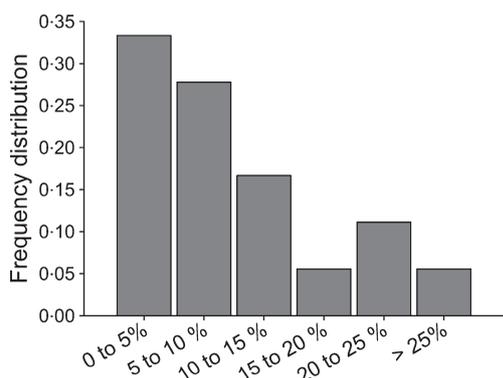


Fig. 3. Histogram of scenarios of predicted number of nuthatches that will be lost due to competition when parakeets have occupied all suitable areas.

Discussion

This study presents a framework for predicting population sizes of invasive and native species and shows how these can

be used to obtain high-resolution estimates of the intensity of competitive displacement. Using abundance data from the ring-necked parakeets' current range, our models predict a mean number of about 22 000 breeding pairs, indicating that parakeets could become one of the most numerous cavity-nesting birds in the region, particularly in comparison with similar-sized species such as the great spotted woodpecker *Dendrocopus major* L. or green woodpecker *Picus viridis* L. Parakeets will still be outnumbered by species such as jack-daw *Corvus monedula* L., stock dove *Columba oenas* L. and starling *Sturnus vulgaris* L. (Vermeersch *et al.* 2006; Weiserbs & Jacob 2007). Parakeets reach their highest abundance in older forests in urban areas, probably because older forests provide the parakeets with suitable nesting cavities whereas urban areas are generally characterized by an abundant food supply (Chace & Walsh 2006), possibly enhancing both parakeet survival and reproductive success (Robb *et al.* 2008). Older forests also favour nuthatches, but whereas parakeets are more abundant in smaller forest fragments, nuthatches prefer larger forests.

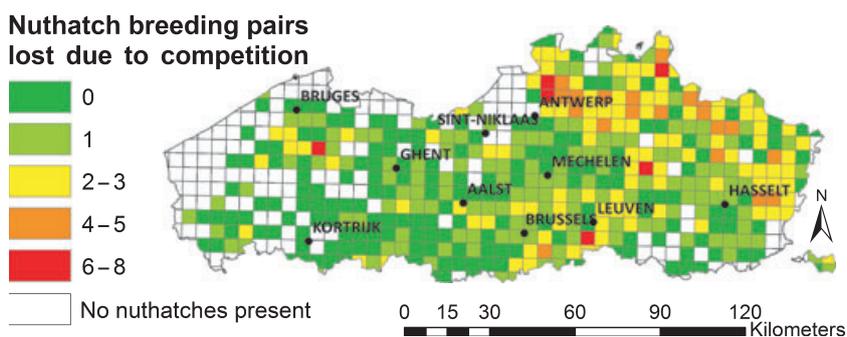


Fig. 4. Region-wide, long-term impact of parakeets on nuthatches according to a moderate scenario (mean values for both parakeet and nuthatch abundance, and competition strength). Number of breeding pairs lost per 5×5 km UTM grid was obtained by summing the predicted nuthatch losses for each forest fragment within each grid cell.

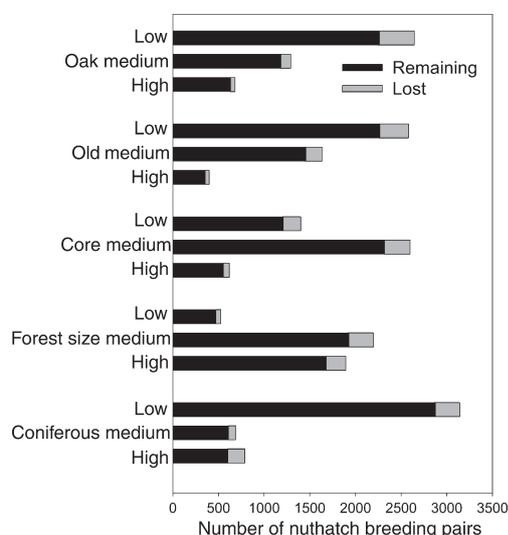


Fig. 5. Predicted numbers of nuthatch breeding pairs in relation to different habitat variables, and predicted losses due to parakeet competition under a moderate impact scenario (see text). Forest size was deemed small when < 10 ha, medium when between 10 and 100 ha and large when > 100 ha. Other variables refer to % coverage of the forest patch, and are classified as follows: low (< 33%), medium (33–66%) and high (> 66%).

Nuthatch abundance is also influenced by the tree species composition, showing that the factors driving nuthatch distribution differ from the ones determining abundance. Coniferous trees are known low-quality habitats for nuthatches whereas rough-barked trees, such as oaks, provide nuthatches with a rich insect supply (Matthysen 1998). Despite these differences in preferred habitats, a visual comparison between the predicted region-wide nuthatch and parakeet abundance indicates that parakeet and nuthatch distributions largely overlap. Nuthatch rich areas can be found around Antwerp and south of Brussels and Leuven, and it is in these regions that parakeets are expected to reach their highest densities. Eastwards, there is also ample habitat for the parakeet to spread into, with high predicted abundances around the cities of Leuven and south of Hasselt. Westward, where open landscapes dominate, there is less suitable habit and moderately high parakeet abundances are only found around the cities of Ghent and Bruges. However, in spite of this overlap in distribution and the high predicted parakeet abundances, the total impact on nuthatches will probably only be small, and in a worst-case scenario, about one-third of the nuthatch population would be at risk. A more moderate scenario, i.e. taking the mean values for both parakeet and nuthatch abundance and competition strength, indicates a loss of 11% of the nuthatches. This is because the competition coefficient, which quantifies the parakeets' impact on nuthatches, is only moderate. This probably follows from the fact that nuthatches are smaller than parakeets and can, as a last resort, use cavities that are too small for parakeets. This flexibility in nest site choice may allow coexistence, or at least help to limit the competitive impact of parakeets (Strubbe & Matthysen 2009b).

The spatial distribution of a moderate scenario parakeet impact indicates that competition will occur not only in the

Antwerp and Brussels areas, but also in the east and north-eastern part of the region, in habitats where neither parakeets nor nuthatches are predicted to be very abundant. This is probably because the (north) east is dominated by coniferous trees, which are generally of a lower habitat quality. Forest patches dominated by coniferous trees have a low initial carrying capacity of nuthatches, most probably due to low abundance of both food and nest sites. As our competition model assumes a linear impact of parakeets independently of habitat, even a very low parakeet density can be predicted to lead to complete disappearance of nuthatches. Parakeet impact can thus be proportionally higher in coniferous forests, but in absolute numbers the number of nuthatch pairs lost per habitat type is largely related to nuthatch abundance in that habitat, and the loss of nuthatch breeding pairs in the north-east follows from the fact that this is the most forested region of the country. In the Antwerp region, a large number of small forests are present, whereas the regions south of Brussels and Leuven harbour the regions' largest remaining forest areas. This could explain the higher parakeet impact in Antwerp compared with Brussels and Leuven, as differences in preferred habitats between parakeets and nuthatches cause parakeet impact to be lower in older, bigger forests with a large amount of core habitat.

In this study, we estimated nuthatch loss due to competition with parakeets by linearly extrapolating the parakeet impact observed in the Brussels metropolitan area. Our forecast assumes that the current, sampled abundance of parakeets and nuthatches is a reliable indicator of their habitat requirements, and that the future abundance can be predicted from habitat quality. The latter assumption might be violated if the overall population has source-sink or metapopulation dynamics. Indeed, in Flanders, Matthysen (1999) found that nuthatch abundance was lower in forest fragments compared with large forests, and suggested that this was not due to differences in habitat quality but reflects a lower juvenile survival due to increasing hazards of dispersing across an unfavourable habitat matrix (e.g. urban areas). When parakeets invade forest patches and occupy available nesting cavities, they reduce the carrying capacity for nuthatches (Strubbe & Matthysen 2009b). Hence, dispersing nuthatches might be forced to visit more potentially suitable fragments in order to find a suitable vacant territory. The increased mortality associated with this extra dispersal could theoretically lead to a larger loss of nuthatches than predicted by our models. However, with at most one-third loss of nuthatch carrying capacity, this is unlikely.

All SDM techniques contain a number of inherent assumptions, such as the assumption of equilibrium with the environment. This assumption is violated when the species being modelled has not occupied or fully saturated suitable habitat and could result in an underestimation of the species' range or abundance. SDMs also do not consider dispersal limitations and thus assume that the species occurs at all locations where the habitat is suitable. This can result in an overestimation of the species' range, as dispersal barriers or poor dispersal abilities can prevent the establishment of species in a suitable habitat (reviewed in Guisan & Thuiller 2005). However, despite these limitations, our results about the distribution of and the

interaction between parakeets and nuthatches can probably be generalized to most of the lowlands of the European Atlantic biogeographical region (i.e. Flanders, the Netherlands and parts of the UK, Germany and France). These areas share a climate that has equable temperatures with mild winters and relatively cool summers, land use is generally intensive and natural habitats are often fragmented (Hopkins & Buck 1995). In this region, nuthatches are typical birds of mature broadleaved forests (reviewed in Matthysen 1998), and studies from several countries indicate that ring-necked parakeets mainly colonize human-dominated habitats (UK: Pithon 1998; Butler 2003; the Netherlands: Van Diek 2005; Germany: Braun 2009; France: Clergeau, Vergnes & Delanoue 2009). In Mediterranean Europe, the milder climate might allow parakeets to invade more natural habitats, which makes it more difficult to estimate the magnitude of parakeet impact. Recent studies suggest that most of continental Europe is too cold to be colonized by parakeets (Shwartz *et al.* 2009; Strubbe & Matthysen 2009a).

Our results suggest that it is unlikely that ring-necked parakeets will cause severe declines of native nuthatches. In this way, the parakeet invasion may be comparable with the invasion of north-America by the European starling *S. vulgaris* L. Starlings were introduced to New York City in 1890 and have become one of the most abundant birds of the USA. Although, there is a multitude of local studies claiming competition between starlings and native birds, a country-wide analysis of long-term bird survey data failed to support the hypothesis that starlings have a severe impact on native birds (Koenig 2003). However, even though ring-necked parakeets have been widely introduced throughout Europe (Lever 2005; Strubbe & Matthysen 2009a), their distribution is still fairly localized and probably far from reaching its potential distribution, as shown for the region studied in this article. Thus, we cannot exclude the possibility that as the species further expands its range, it will have a more severe impact on some rare and threatened cavity-nesters such as wryneck *Jynx torquilla* L. In these cases, it might be necessary to closely monitor the breeding cavities of the native hole-nester, and possibly take measures to protect them from the parakeets. For example, in Mauritius, where the introduced ring-necked parakeet hinders conservation efforts for the threatened endemic echo parakeet *Psittacula equis*, ring-necked parakeets are removed from cavities suitable for echo parakeets (Jones 1980, J. Malham, pers. comm.).

To our knowledge, this is one of the few studies using SDMs to quantify the impact an invasive species is expected to have on native biota. Our results suggest that simple overlays of predicted species distributions to identify areas where an invasive species is likely to negatively impact native species might yield an exaggerated estimate of the potential impact, as range overlap may be large whereas the strength of competitive interactions can be only moderate. For several taxonomic groups, notably birds but also some fish (Arismendi *et al.* 2009), crayfish (e.g. Cruz *et al.* 2006) or insects [e.g. ladybirds (Coccinellidae), Evans 2004], data on native and invasive species distribution and abundance are not too difficult to collect, or

are often available in national or regional biodiversity atlases or monitoring projects. We argue that the modelling framework proposed here could be used as a general tool to make an assessment of the (distribution of) potential impact of established invasive species. Such a tool would be extremely valuable, given limited resources available to manage invasive species. For example, if we can quantitatively determine that an invasive species will have relatively minor effects, then we can invest fewer resources in its control (though continued assessment of effect would be prudent). Further, by mapping the predicted impact of invasive species we can determine if there are certain regions that are particularly susceptible or important for native species and concentrate management efforts accordingly.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Fig. S1. Moran's I correlogram of residuals from the Boosted Regression Trees (BRT) models.

Fig. S2. Partial regression plots showing all variables influencing parakeet abundance.

Fig. S3. Partial regression plots showing all variables influencing nuthatch distribution.

Fig. S4. Interactions between predictor variables for nuthatch distribution.

Fig. S5. Partial regression plots showing all variables influencing nuthatch abundance.

Fig. S6. Interactions between predictor variables for nuthatch abundance.

Fig. S7. Partial GAM plots showing variables influencing nuthatch abundance in Brussels.

Fig. S8. Spatial distribution of impact on nuthatches according to a worst-case scenario.

Fig. S9. Parakeet impact on nuthatches in different habitat types.

Table S1. Summary of the variables used to model parakeet and nuthatch abundance

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