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What factors increase the vulnerability of native birds to the impacts of alien birds?

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Biodiversity impacts caused by alien species can be severe, including those caused by alien birds. In order to protect native birds, we aimed to identify factors that influence their vulnerability to the impacts of alien birds. We first reviewed the literature to identify native bird species sustaining such impacts. We then assigned impact severity scores to each native bird species, depending on the severity of the impacts sustained, and performed two types of analyses. First, we used contingency table tests to examine the distribution of impacts across their severity, type and location, and across native bird orders. Second, we used mixed-effects models to test factors hypothesised to influence the vulnerability of native birds to the impacts of alien birds.

Ground-nesting shorebirds and seabirds were more prone to impacts through predation, while cavity-nesting woodpeckers and parrots were more prone to impacts through competition. Native bird species were more vulnerable when they occupied islands, warm regions, regions with climatic conditions similar to those in the native range of the invading alien species, and when they were physically smaller than the invading alien species. To a lesser extent, they were also vulnerable when they shared habitat preferences with the invading alien species.

By considering the number and type of native bird species affected by alien birds, we demonstrate predation impacts to be more widespread than previously indicated, but also that damaging predation impacts may be underreported. We identify vulnerable orders of native birds, which may require conservation interventions; characteristics of native birds that increase their vulnerability, which may be used to inform risk assessments; and regions where native birds are most vulnerable, which may direct management interventions. The impacts sustained by native birds may be going unnoticed in many regions of the world: there is a clear need to identify and manage them.

Keywords: alien species, EICAT, ornithology, seabirds, shorebirds, woodpeckers

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Introduction

Invasive alien species are one of the five direct drivers of anthropogenic change in nature with the greatest global impact on biodiversity (IPBES 2019). They cause profound structural changes to food webs and ecosystem function (Gandhi and Herms 2010, Simberloff et al. 2013), and are the most common threat associated with species extinctions worldwide since AD 1500 (Blackburn et al. 2019). Alien birds can have severe impacts on native species: for example, on Mauna Kea (Hawaii), competition with the Japanese white eye *Zosterops japonicus* has caused a collapse in the population of the Hawaii akepa *Loxops coccineus* (Freed et al. 2008). However, despite sometimes being severe, our understanding of the biodiversity impacts caused by alien birds is limited: impact data are only available for approximately 30% of alien bird species with self-sustaining populations worldwide (Evans et al. 2016, 2018a). Nevertheless, progress has been made in identifying traits associated with alien bird species that influence the severity of their impacts (Shirley and Kark 2009, Evans et al. 2014): these studies may help to identify damaging alien bird species and manage their impacts.

As these impacts result from interactions between alien and native species, it is likely that their severity is also influenced by the traits of impacted native species. Whilst alien birds affect native species from a range of taxonomic groups, many of their reported impacts are on native birds (Evans et al. 2016). Identifying the factors that influence the vulnerability of native birds to the impacts of alien birds may improve our impact prediction capabilities, potentially enabling the identification of vulnerable native bird species in regions where we lack impact data. A native species vulnerability assessment has yet to be undertaken for an entire taxonomic class of alien species, and thus remains a significant knowledge gap for invasion science. Here, we test three broad hypotheses in order to identify factors that influence the vulnerability of native birds to the impacts of alien birds.

First, the characteristics of native birds may influence their vulnerability to alien bird impacts (hypothesis H1). Native species that are taxonomically similar to the alien species they interact with may be prone to hybridisation impacts, and species with habitat or dietary requirements that are similar to those of their alien invader may be affected by competition for resources. Here, overlapping niches (a concept hypothesised to facilitate alien species impacts: Elton 1958) may result in damaging interactions between native and alien birds: this may be why native birds bear the brunt of many impacts generated by alien birds. Species with specialised habitat or dietary requirements may be vulnerable due to their reduced ability to adapt or disperse (sensu Clavel et al. 2011). Indeed, specialist bird species tend to be more severely affected by landscape fragmentation and disturbance than generalist bird species (Devictor et al. 2008), and more generally, specialist birds are more likely to be threatened with extinction than generalists (Şekercioğlu 2011). Thus, whilst alien species possessing traits associated with ecological flexibility have been found to be more damaging (in particular, habitat-generalist alien birds) (Kumschick et al. 2013, Evans et al. 2018b), we would expect native species possessing such traits to be less vulnerable. Small bird species (as measured by body mass) may be vulnerable due to their susceptibility to predation by larger alien birds, and to interference competition from larger alien birds with similar dietary and/or habitat requirements. Species with small native ranges may also be vulnerable due to their increased likelihood of extinction, and reduced opportunities for spatial refugia from threats.

Second, characteristics of the biotic environment may influence the severity of impacts sustained by native bird species (H2). In species-poor communities that are characterised by low levels of interspecific competition, native bird species may be less adept at competing with alien invaders (sensu Carlquist 1965). Conversely, native bird species from species-rich communities that are characterised by intense interspecific competition and predation may be less vulnerable, as these communities may be more resistant to invasions (Elton 1958, Case 1990, Levine and D'Antonio 2018). There may also be more niches for an alien bird to occupy in species-poor communities (including those on islands, which are often characterised by low levels of species richness) (Whittaker and Fernández-Palacios 2007). Native birds located within isolated ecosystems such as islands (sensu Itescu 2018) may also be vulnerable, as their limited exposure to other species in general may cause them to be naïve to the impacts of alien species (Caravaggi et al. 2018) and susceptible to pathogens and diseases introduced by alien birds to which they have had no previous exposure (Furlan et al. 2012, MacPhee and Greenwood 2013). More generally, it has been suggested that interactions involving native species that have little evolutionary experience of species similar to their alien invader are likely to be among the most damaging (Ricciardi and Atkinson 2004, Saul and Jeschke 2015). Similarly, invasion success has been hypothesised to be greater in areas with few species closely related to an alien invader, in comparison to areas that are rich in closely related species (Darwin's naturalization hypothesis) (Daehler 2001, Enders et al. 2018). Native birds located on islands may also be vulnerable because small, spatially restricted populations may be prone to extirpation, and because the chances of interactions between native and alien species are likely to increase on islands with a limited range of habitats. Indeed, many threatened birds are restricted to islands (Spatz et al. 2017, BirdLife International 2020a, b).

Third, abiotic factors may influence native species vulnerability (H3). Alien birds may be less likely to establish, and hence cause impacts, when introduced to regions characterised by extreme environmental conditions to which they are not adapted (sensu Chytrý et al. 2008). Native species that are adapted to these extreme conditions may be less vulnerable at these locations. This process of 'environmental filtering' (Kraft et al. 2015) also suggests that native species will be more vulnerable where the climatic conditions in the communities they inhabit are similar to those of the introduced alien birds' native habitat (Ricciardi et al. 2013, Enders et al. 2018). Indeed, climate matching has been shown to aid the

establishment (Redding et al. 2019) and spread (Abellán et al. 2017) of alien bird populations.

Here, we test the above hypotheses using a new global dataset on the severity and type of impacts sustained by native birds that have been caused by alien birds. Our approach is novel: it is the first study to apply impact severity scores calculated using the Environmental impact classification of alien taxa (EICAT) (Blackburn et al. 2014, IUCN 2020) to native species (they are usually assigned to alien species). This approach provides new insights regarding the vulnerability of native birds to the impacts of alien birds.

Material and methods

Data

We undertook a review to identify literature describing alien bird impacts on native birds (methods in the Supporting information), and compiled a list of the native bird species that have been recorded sustaining these impacts.

The EICAT has been developed to quantify and categorise the impacts of alien species (Blackburn et al. 2014). Under EICAT, an alien species is allocated to one of five impact categories depending on its most severe documented impacts to a native species across its entire alien range: minimal concern (MC – meaning that whilst the alien species interacted with a native species, it caused no discernible impacts); minor (MN – the alien species caused impacts that affected the performance of individual native species); moderate (MO – the alien species caused declining populations of one or more native species); major (MR – the alien species caused native species extirpations that would be reversible if the non-native species was removed); massive (MV – the alien species caused irreversible native species extinctions). An alien species is also categorised by the type of impacts it causes into one of 12 impact mechanisms: 1) competition, 2) predation, 3) hybridisation, 4) transmission of disease, 5) parasitism, 6) poisoning/toxicity, 7) bio-fouling or other direct physical disturbance, 8) grazing/herbivory/browsing, 9–11) chemical, physical or structural impact on ecosystem and 12) indirect impacts through interactions with other species.

EICAT scores are usually applied to categorise the impacts of alien species. Here, for the first time, we instead applied these EICAT scores to the impacted native species, based on the severity of the impacts they sustained. In so doing we created a dataset of native bird species with EICAT impact scores and impact mechanisms. For example, nest-site competition with an alien parakeet in Belgium has been found to cause declining populations of the Eurasian nuthatch *Sitta europaea* (Strubbe and Matthysen 2009): thus the Eurasian nuthatch was allocated to the MO impact category, and by the EICAT impact mechanism 'competition'. Some native bird species sustained impacts from multiple alien bird species: these were counted as separate impacts. Some species sustained impacts through two (or more) impact mechanisms (e.g. competition and predation): these were also counted as separate impacts.

To test our three hypotheses (H1–H3), and based on the factors discussed in the Introduction, we collected data on a series of variables (V1–V15) for each of the interacting native and alien bird species. These variables are summarised in Table 1; for data collection methods see the Supporting information.

Analysis

We carried out all our analyses using R ver. 4.0.0 (<www.r-project.org>). We used contingency table tests (χ^2 tests: the FunChisq package (Zhong and Song 2019)) to examine the distribution of impacts across their severity, type and location, and across native bird orders. First, we examined: 1) the association between the number of impacts sustained by native bird species from different orders, and the number of native bird species from different orders that may interact with alien birds globally; 2) the association between the number of impacts caused by alien bird species from different orders, and the number of native bird species that may interact with alien birds from different orders globally; and 3) the association between the number of impacts sustained by native bird species and different impact mechanisms. To calculate the number of native bird species that may interact with alien birds globally, we overlaid global range maps for all native birds (Birdlife International and Handbook of the Birds of the World 2019) with range maps for the alien bird species causing impacts (Dyer et al. 2017). Some native and alien bird species may interact at more than one location: these were counted as a separate interaction records. Nine native bird orders were analysed as separate groups, but due to small sample sizes, 13 orders were combined to produce one group titled 'Other orders'. Similarly, seven alien bird orders were analysed as separate groups, with five orders combined to produce one group titled 'Other alien orders'. Finally, two impact mechanisms were analysed as separate groups with three further mechanisms combined to produce one group titled 'Other mechanisms'.

Second, we examined the association between impact severity and a variety of potential drivers. Specifically, we compared the actual and expected number of 'weak', 'moderate' and 'severe' impacts that were: 1) sustained by native bird species from different orders, 2) associated with different impact mechanisms; and 3) recorded in different regions of the world. Native bird orders were grouped as previously described; regions were defined by continent (Africa, Asia, Australasia, western Europe, North (including Central) America) with islands of the Atlantic, Indian and Pacific oceans, Mediterranean Sea and Arabian Gulf combined to form one group titled 'Islands'. Each contingency table result includes an 'estimate', which is a value between 0 and 1, where 1 indicates complete mathematical dependence of the two variables, and 0 indicates complete independence.

We used mixed-effects models to test the variables we hypothesised to influence the vulnerability of native bird species to the impacts of alien birds. Due to low sample sizes amongst some of the five EICAT impact categories (e.g. MC

Table 1. The three hypotheses proposed regarding the factors that influence the vulnerability of native birds to the impacts of alien birds, and the variables used to test them.

Hypotheses	Variable	Description
H1. Characteristics of native birds influence their vulnerability to the impacts of alien birds	V1: Phylogenetic distance	The similarity of the interacting native and alien species as measured by their phylogenetic distance
	V2: Habitat similarity	The proportion of broad habitat types occupied by a native species that are shared with its alien invader
	V3: Diet similarity	The proportion of a native bird species' diet that is shared with its alien invader
	V4: Habitat breadth	The number of major habitats occupied by the native species
	V5: Diet breadth	The breadth of a native bird species' diet
	V6: Body mass difference	The difference between the adult body mass (g) (log) of the native species and that of the alien species
	V7: Native range size	The native species' breeding range size (km^2) (log10)
H2. Characteristics of the biotic environment influence the vulnerability of native birds to the impacts of alien birds	V8: Native species richness	The number of different native bird species present within the country or region of impact
	V9: Eco-evolutionary experience	A measure of the native species' experience of the alien invader, and the alien species' experience of the native species
	V10: Island/continent	The broad location of impact: either island or continent
H3. Characteristics of the abiotic environment influence the vulnerability of native birds to the impacts of alien birds	V11, V12, V13, V14: Max. and min. av. monthly temp., and max. and min. av. monthly rainfall	Climatic conditions at the location of impact
	V15: Climatic similarity	A measure of the similarity of climatic conditions in the alien species' native range and the area of impact (the area in which impacts to a native bird species were recorded) (numbers closer to 0 = a more similar climate)

impacts = 1 native bird species), we converted these data to an ordinal response variable with three levels ('weak' = MC and MN; 'moderate' = MO; and 'severe' = MR and MV). Our dataset included variables known to have a strong phylogenetic signal (e.g. body mass), while previous studies have shown that certain orders of native birds are likely to be associated with specific impact mechanisms (e.g. Anatidae (waterfowl) with hybridisation) (Evans et al. 2016), and so we expected our results to be influenced by phylogenetic autocorrelation. To account for this, we downloaded 100 randomly selected phylogenetic trees from BirdTree.org (<https://birdtree.org/>), which incorporated all 208 native bird species in our dataset. Using phylogenetic trees necessitated the adoption of one impact record for each of the 208 native bird species in each phylogenetic tree: where a native bird species sustained impacts from more than one alien bird species (and therefore had more than one impact record and associated set of variables), we used the most severe impact record for that species for the analyses (i.e. the most severe of MC, MN, MO, MR and MV).

However, for 23 of the native bird species in our dataset (11%), their most severe impact was caused by more than one alien bird species, or occurred at more than one location (e.g. a species most severe impact was MN, but was sustained on Hawaii and also on the Seychelles). For these native bird species, we therefore had more than one most severe impact record and associated set of variables. To address this, for each of these 23 species, we randomly selected the most severe impact record to be included in the analyses, using a random name picker (<www.randomlists.com/name-picker?items=A%0AB>). We repeated this process ten times, creating ten separate datasets (a–j) of our 208 native bird species which included a different randomly selected most severe impact record for each of the 23 species. We analysed each of these ten datasets (a–j) separately. For a summary of the random selection results see the Supporting information.

We checked for multicollinearity amongst predictor variables using the car package (Fox and Weisberg 2011), finding evidence for multicollinearity between three climate variables (minimum average monthly temperature and maximum and minimum average monthly rainfall). We removed maximum average monthly rainfall, and this reduced multicollinearity amongst remaining variables (variance inflation factor (VIF) < 3 for all variables) (Supporting information). We used the MCMCglmm package (Hadfield 2010) to create linear mixed models using Bayesian Markov chain Monte Carlo methods, with a random effect to account for phylogenetic autocorrelation. We used ordinal trait distribution (family = ordinal) to analyse impact levels ('weak', 'moderate' and 'severe' impacts), a probit link function, including phylogenetic covariance between species as a random effect, and set flat, uninformative priors (following Evans et al. 2018a). We ran the models for 1 000 000 iterations, with a burn-in of 2500 iterations, which ensured adequate model convergence and mixing (effective sample sizes for all estimated parameters > 1000: cf. the Supporting information for diagnostic plots for all ten datasets). Following the first run of the model, we removed the least significant variable, and then re-ran the model, repeating this process until we identified

the best reduced model (defined as the model with the lowest deviance information criterion (DIC), which is a hierarchical modelling generalization of Akaike's information criterion (AIC); we used DIC, as this is the metric offered by the MCMCglmm package). We then used the dredge function in the MuMIn package (Bartoń 2018) to perform automated model selection on the reduced model (the minimum adequate model), ranking model combinations of fixed-effect terms by AIC to obtain relative importance values (RI) for each variable (the sum of the Akaike weights over all models for each variable) (here we used AIC, as this is the metric offered by the MuMIn package). We did not use the dredge function to perform automated model selection on all 14 variables in our dataset: dredging the large number of possible model combinations would be impractical due to the time it would take.

We used k-fold cross-validation to test the predictive ability of our models to successfully classify unseen data into the correct impact category. To further explore the predictive ability of our models, we compared categorisation using a χ^2 test (for all three impact categories: 'weak', 'moderate' and 'severe') (see the Supporting information for methods).

Results

The distribution of impact data across bird orders, impact severity and impact mechanisms are provided in the Supporting information, and the geographic distribution of impacts in Fig. 1. The 208 native bird species in our dataset are from 22 orders; impacts were caused by 58 alien bird species from 12 orders (Fig. 2). Some native bird species sustained impacts at different locations, by different alien bird species, and by more than one impact mechanism: there were 285 recorded impacts upon these 208 species. Approximately 65% of impacts were sustained by species from three orders: Passeriformes (perching birds) (37% of all impacts), Charadriiformes (shorebirds) (16%) and Anseriformes (waterfowl) (12%). On average, each alien bird species impacted four native bird species.

Recorded impacts were non-randomly distributed across native bird orders (Table 2 for a summary of all contingency table test results; Supporting information for the full test result). In particular, there were more impacts on Anseriformes (waterfowl) and Piciformes (woodpeckers) than expected, and fewer on species from 'Other orders', given the number of species from these orders which may interact with alien birds globally. Recorded impacts were also non-randomly distributed across alien bird orders (Table 2, Supporting information). In particular, more impacts were caused by Strigiformes (owls) than would be expected, given the number of native bird species that alien owls may interact with globally.

Approximately 69% of impacts were 'weak'; 27% were 'moderate' and 4% were 'severe'. Impact magnitudes were non-randomly distributed across native bird orders (Table 2, Supporting information). There were more 'severe' impacts on Columbiformes (pigeons and doves) and more 'moderate' impacts on Piciformes (woodpeckers) and Passeriformes (perching birds) than would be expected by chance.

The most impacts resulted from predation (52% of all impacts), followed by competition (33%) (Supporting

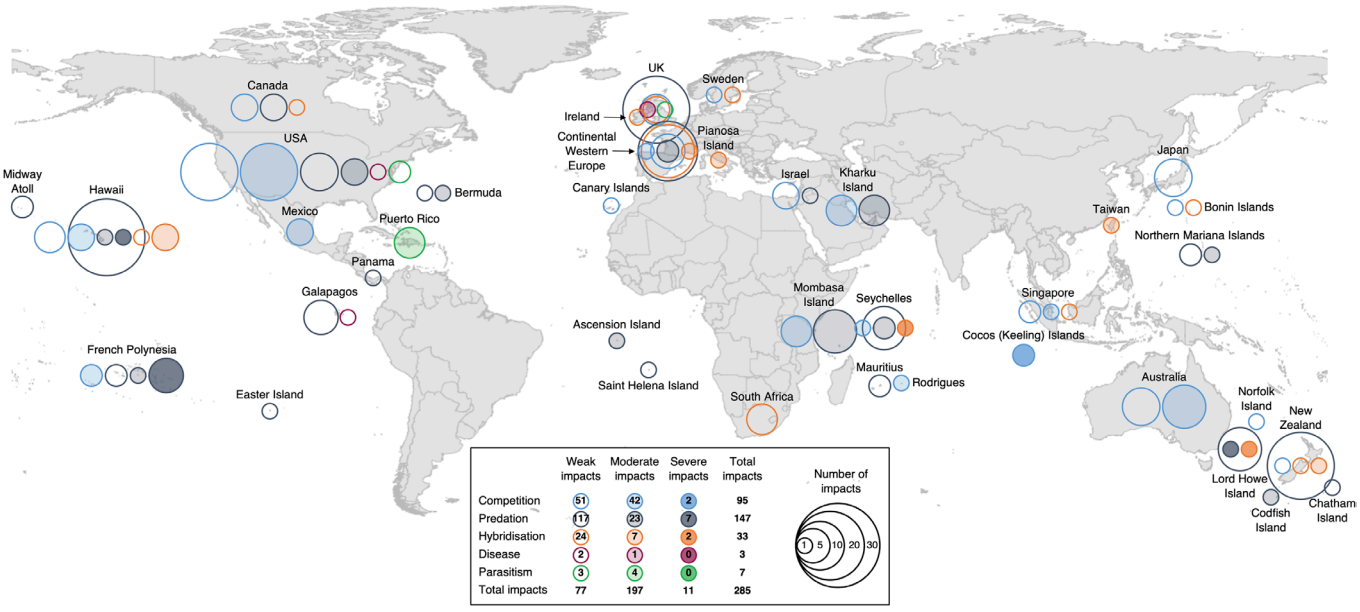


Figure 1. The global distribution of alien bird impacts on native birds. Total bird species = 208; total impacts to these species = 285.

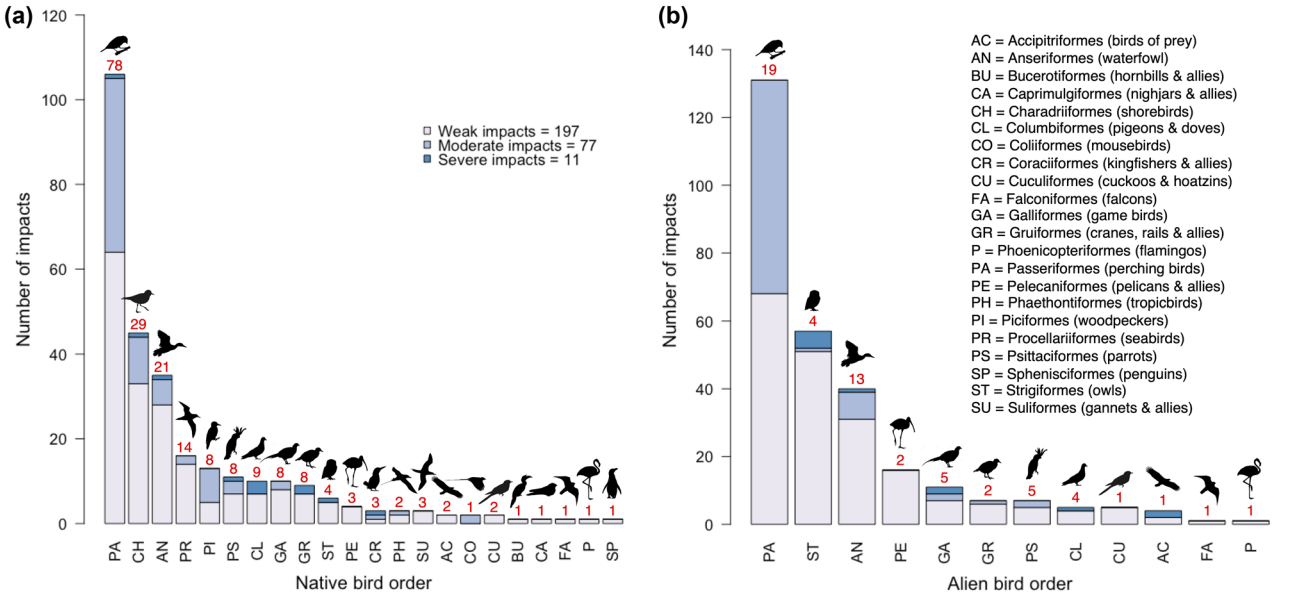


Figure 2. The number of impacts that are: (a) sustained by 208 native bird species from each of 22 orders; and (b) caused by 58 alien bird species from each of 12 orders. Total impacts = 285. The number of bird species in each order that have sustained impacts, and the number of alien bird species in each order that have caused impacts is indicated in red. All images used under the Public Domain Dedication 1.0 License, except: Coliiform (Enoch Joseph Wetsy (photo), John E. McCormack, Michael G. Harvey, Brant C. Faircloth, Nicholas G. Crawford, Travis C. Glenn, Robb T. Brumfield and T. Michael Keesey); Falconiform (Liftarn); Gruiform (T. Michael Keesey (vectorization) and HuttyMcphoo (photography)); Phaethontiform (Paul Baker (photo), John E. McCormack, Michael G. Harvey, Brant C. Faircloth, Nicholas G. Crawford, Travis C. Glenn, Robb T. Brumfield and T. Michael Keesey); Suliform (T. Michael Keesey (vectorization) and Larry Loos (photography)). These images are used under the Creative Commons Attribution 3.0 Unported License (<https://creativecommons.org/licenses/by-sa/3.0/legalcode>) and the Creative Commons Attribution-ShareAlike 3.0 Unported Licence (<https://creativecommons.org/licenses/by-sa/3.0/>).

information). Impact magnitudes were non-randomly distributed across impact mechanisms (Table 2, Supporting information). There were more 'moderate' competition impacts and fewer 'moderate' predation impacts than would be expected by chance.

Impact mechanisms were non-randomly distributed across native bird orders (Table 2, Supporting information). There were more predation impacts on Charadriiformes (shorebirds) and Procellariiformes (seabirds); more competition impacts on Piciformes (woodpeckers) and Psittaciformes (parrots); and more hybridisation impacts on Anseriformes (waterfowl) than would be expected by chance (all 24 impacts to Anseriformes in the 'Other mechanisms' category resulted from hybridisation). There were also more impacts through 'Other mechanisms' on Galliformes (game birds) than would be expected by chance.

The most impacts were recorded on oceanic islands (43% of all impacts); the fewest impacts were recorded in Africa (1.4%) (Fig. 1). Impact magnitudes were non-randomly distributed across regions (Table 2, Supporting information). There were more 'severe' impacts on islands, and more 'weak' impacts and fewer 'moderate' impacts in Europe than would be expected by chance.

Impact mechanisms were non-randomly distributed across regions (Table 2, Supporting information). There were more competition impacts in Asia, more predation impacts on islands and more impacts through 'Other mechanisms' in Africa and Europe (in Africa, all four of these impacts were for hybridisation; in Europe, 16 of these 18 impacts were for hybridisation).

For the minimum adequate models (as reduced by DIC), linear model inference revealed a positive relationship between V10 Island/continent and impact severity for all ten datasets analysed (Table 3, Fig. 3, Supporting information for full results). Automated model selection on the minimum adequate models revealed this variable to feature in the best model for all ten datasets; it also had a high average relative importance value (RI) (0.99) (Supporting information). A positive relationship with impact severity was also revealed for V6 Body mass difference and V11 Maximum average monthly temperature, and a negative relationship for V15 Climatic similarity; however these variables tended to have lower average RIs (0.64, 0.65 and 0.64, respectively). Nevertheless these variables did have a high RI (over 0.7) in some of the ten datasets analysed (V6 and V15 in four datasets; V11 in six). A positive relationship was also revealed for V2 Habitat similarity, but this variable had a low average RI (0.19).

Thus, when controlling for other variables, native birds tend to be more vulnerable to the impacts of alien birds when they occupy islands, regions characterised by warm climatic conditions, and climatic conditions that are similar to those

Table 2. Contingency table test results summary. Full results in the Supporting information.

Test description	Result description	χ^2	df	p	Est	Full results Supporting information
The association between the total number of native bird species within each order that may interact with alien bird species globally, and the actual and expected number of impacts sustained by native bird species from each order.	Recorded impacts were non-randomly distributed across native bird orders. There were more impacts on Anseriformes (waterfowl) and Piciformes (woodpeckers) than expected, and fewer on species from 'Other orders', given the number of species from these orders which may interact with alien birds globally.	69.4	9	***	0.01	Supporting information
The association between the total number of native bird species that may interact with alien bird species (with recorded impacts) from each order globally, and the actual and expected number of impacts caused by these alien bird species.	Recorded impacts were non-randomly distributed across alien bird orders. More impacts were caused by Strigiformes (owls) than would be expected, given the number of native bird species that alien owls may interact with globally.	105.5	7	***	0.02	Supporting information
The association between the actual and expected numbers of 'weak' (MC and MN), 'moderate' (MO) and 'severe' (MR and MV) impacts and each native bird order.	Impact magnitudes were non-randomly distributed across native bird orders. There were more 'severe' impacts on Columbiformes (pigeons and doves) and more 'moderate' impacts on Piciformes (woodpeckers) and Passeriformes (perching birds) than would be expected by chance.	49.6	18	***	0.14	Supporting information
The association between the actual and expected numbers of 'weak' (MC and MN), 'moderate' (MO) and 'severe' (MR and MV) impacts and each impact mechanism.	Impact magnitudes were non-randomly distributed across impact mechanisms. There were more 'moderate' competition impacts and fewer 'moderate' predation impacts than would be expected by chance.	49.9	8	***	0.21	Supporting information
The association between the actual and expected numbers of impacts for each impact mechanism and each native bird order.	Impact mechanisms were non-randomly distributed across native bird orders. There were more predation impacts on Charadriiformes (shorebirds) and Procellariiformes (seabirds); more competition impacts on Piciformes (woodpeckers) and Psittaciformes (parrots); and more hybridisation impacts on Anseriformes (waterfowl) than would be expected by chance.	170.5	18	***	0.26	Supporting information
The association between the actual and expected numbers of 'weak' (MC and MN), 'moderate' (MO) and 'severe' (MR and MV) impacts and each geographic region.	Impact magnitudes were non-randomly distributed across regions. There were more 'severe' impacts on islands, and more 'weak' impacts and fewer 'moderate' impacts in Europe than would be expected by chance.	66.5	10	***	0.22	Supporting information
The association between the actual and expected numbers of impacts for each impact mechanism and each geographic region.	Impact mechanisms were non-randomly distributed across regions. There were more competition impacts in Asia, more predation impacts on islands and more impacts through 'Other mechanisms' in Africa and Europe (in Africa, all four of these impacts were for hybridisation; in Europe, 16 of these 18 impacts were for hybridisation).	95.4	10	***	0.26	Supporting information

χ^2 = χ^2 value; df = degrees of freedom; p = p value (significance codes: '***' $p < 0.001$, '**' $p < 0.01$, '*' $p < 0.05$); Est = estimate (a value between 0 and 1, where 1 indicates complete mathematical dependence of the two variables, and 0 indicates complete independence).

in the invading alien species' native range, and when they are smaller than the invading alien species. To a lesser extent, they are also more vulnerable when their habitat preferences are similar to those of the invading alien species.

Using k-fold cross-validation, our models showed a good level of discrimination, classifying impact records with a mean accuracy of 0.79 AUC (n = 100, SD = 0.016). The χ^2 tests showed a strong association between observed and predicted categories (mean χ^2 statistic = 37.3; mean p = 0.01).

Discussion

The severity, type and location of alien bird impacts, and the native bird species affected

Almost 70% of impacts sustained by native birds are 'weak'. This result is consistent with those of a previous global assessment of the environmental impacts of alien birds (Evans et al. 2016). Almost half of the many 'moderate' impacts sustained by Passeriformes (perching birds) were caused by the house

Table 3. The relationship between the severity of alien bird impacts sustained by native birds and predictor variables following model simplification, for the ten datasets analysed (a–j). The analysis was undertaken using the MCMCglmm package in R (Hadfield 2010). Results are the mean for 100 phylogenies. Total sample size for each dataset = 208 species.

Dataset	Intercept	V2 Habitat similarity	V6 Body mass difference	V10 Island/continent	V11 Max. av. monthly temp.	V15 Climatic similarity
a	< 0.001***	0.018*	0.042*	0.007**	< 0.001***	< 0.001***
b	< 0.001***	0.043*	0.025*	0.021*	< 0.001***	0.03*
c	< 0.001***	0.024*	0.038*	0.011*	< 0.001***	0.002**
d	< 0.001***	0.012*	0.012*	0.009**	< 0.001***	0.004**
e	< 0.001***	0.044*	0.068	0.024*	< 0.001***	0.026*
f	< 0.001***	X	0.034*	0.068	< 0.001***	0.056
g	< 0.001***	0.028*	X	0.01*	< 0.001***	0.001**
h	< 0.001***	0.041*	0.013*	0.017*	< 0.001***	0.04*
i	< 0.001***	0.01*	0.032*	0.009**	< 0.001***	0.002**
j	< 0.001***	0.054	0.041*	0.017*	< 0.001***	0.021*

Deviance information criterion (DIC): (dataset a) 245; (b) 250; (c) 246; (d) 238; (e) 252; (f) 252; (g) 248; (h) 245; (i) 245; (j) 251. All models: iterations = 2501: 999 991; thinning interval = 1; sample size = 99 750, each. X = variable did not feature in this model. Significance codes: '***' $p < 0.001$, '**' $p < 0.01$, '*' $p < 0.05$.

crow *Corvus splendens* and common myna *Acridotheres tristis*. These species compete with native birds for food, and also predate on their eggs and chicks. The combined effect of these two impact mechanisms has caused declining populations of native birds at several locations including Mombasa Island, Kenya (Ryall 1992).

The prevalence of predation impacts may arise because they are more straightforward to identify than impacts caused by other mechanisms (particularly hybridisation and disease transmission). Predation may also be more frequently recorded than mechanisms other than competition (which is likely to be a daily occurrence for many birds), because some alien birds (e.g. raptors) regularly prey on birds for food. Competition may be less frequently recorded than predation because it often involves specific interactions between a pair of native and alien species, whilst predation may affect a broad range of native birds: the barn owl *Tyto alba* impacts the most species in our dataset (27), all through predation. This result contrasts with that of Evans et al. (2016), who found competition to be the most frequently recorded impact mechanism. However, that assessment considered the most severe impact caused by an alien bird species, not the number of native species it affected. Here, taking into account the latter suggests predation is a greater threat to native birds than previously appreciated.

Nevertheless, we identified a relatively low number of 'moderate' predation impacts, which might suggest that native bird populations tend to withstand such impacts without adversely affecting their abundance. However, this may be because whilst it is relatively straightforward to observe predation impacts sustained by an individual native bird species (a 'weak' impact), and to determine that predation has extirpated a species from a region based on its conspicuous absence (a 'severe' impact), it may be more difficult to determine whether predation is having an impact on the overall recruitment of a native bird population (and hence causing a decline in that population: a 'moderate' impact). In contrast, we identified many 'moderate' competition impacts, half of which resulted from competition between breeding native and alien birds for nest cavities. Such impacts, which prevent native bird species from breeding, are likely to have implications for their population size, and may be relatively straightforward to identify (for example, through the abandonment of nest boxes across a study site). This is likely to be why Piciformes (woodpeckers and allies), which tend to be cavity-nesting, sustain both more 'moderate' impacts and more competition impacts than expected, and also more impacts in comparison to other native bird orders. Thus, our results suggest that 'moderate' competition impacts are more frequently reported than 'moderate' predation impacts: this may give a false impression of the severity of impacts caused by these two impact mechanisms.

All ten impacts on woodpeckers resulted from competition with cavity-nesting alien birds. Many countries in western Europe support large populations of cavity-nesting alien parrots (Menchetti and Mori 2014), particularly the rose-ringed parakeet *Psittacula krameri*, which has caused declining populations of the Eurasian nuthatch *Sitta europaea* in Belgium though nest-site competition (Strubbe and Matthysen 2009). The largest numbers of alien rose-ringed parakeets occur in the UK (> 30 000) (Pârâu et al. 2016). Whilst the impacts of alien species are context-dependent, it is possible that this species is causing as yet unquantified competition impacts on native (including endangered) cavity-nesting native bird species in the UK.

Impacts in Europe tended to be 'weak': many were recorded in the UK and resulted from predation by the little owl *Athene noctua*. This species is in rapid decline in the UK (UK Little Owl Project 2020) and unlikely to be a significant threat to native birds there. Many hybridisation impacts recorded in Europe were also 'weak'. Hybridisation with native bird species has been recorded for 18 alien waterfowl species in Europe, but this is a rare occurrence for most of these alien species and thus unlikely to have adverse impacts on native birds (Banks et al. 2008).

We found no impact data for many less-developed regions (Fig. 1), including hotspots for threatened and endemic native birds such as Indonesia (Johnson and Stattersfield

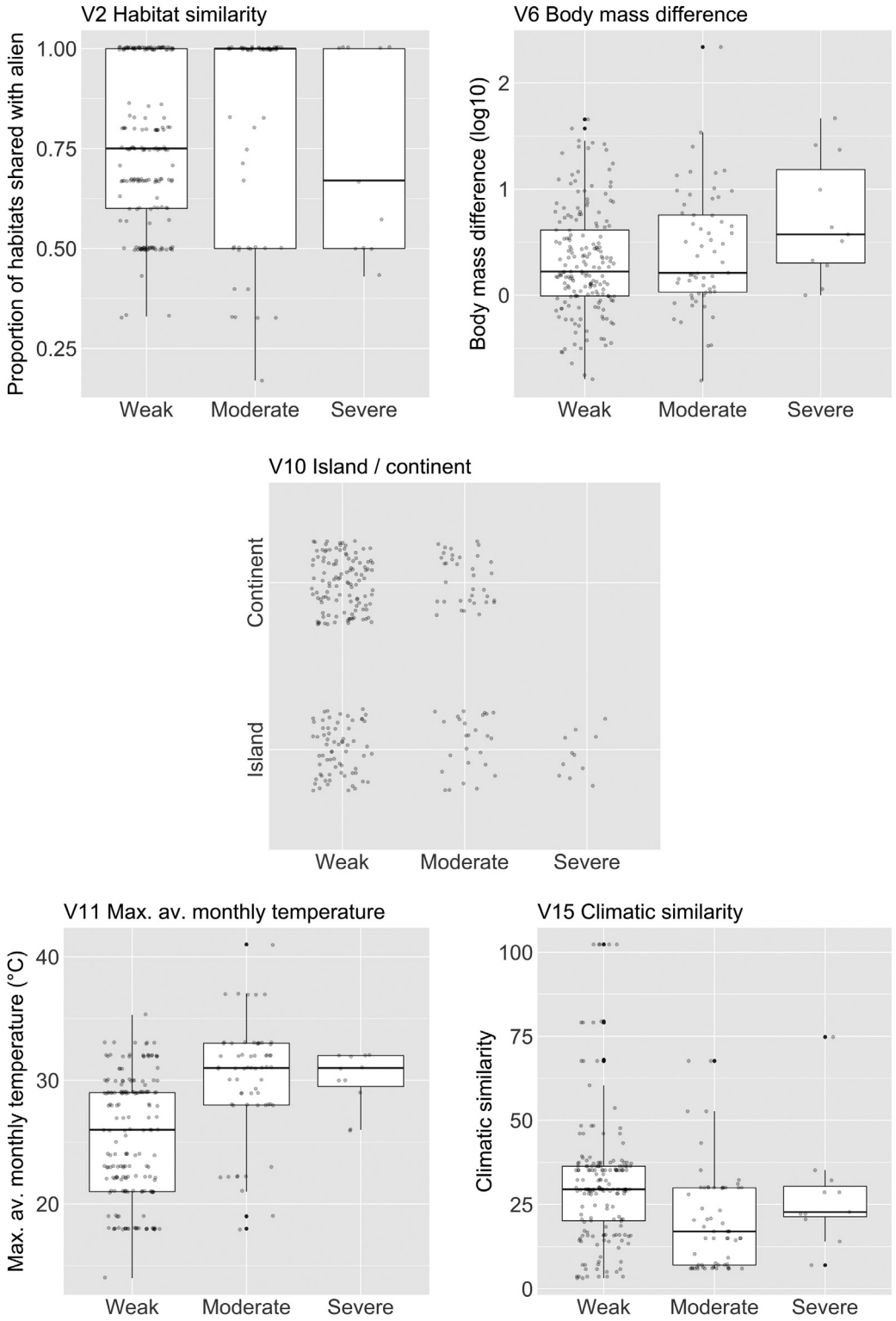


Figure 3. The relationship between the severity of alien bird impacts sustained by native birds and: V2, the proportion of habitat types occupied by a native bird species that are also occupied by the impacting alien bird species; V6, the difference in body mass (log10) between the impacted native bird species and impacting alien bird species; V10, the location of impact – either island or continent; V11, the maximum average monthly temperature at the location of impact; V15, the similarity of climatic conditions in the impacting alien species' native range and the area of impact. Total sample size = 285 impacts. X-axis = impact severity (weak, moderate or severe impact). Jitter used to add random noise to the data to reduce the number of overlapping data points. Boxplots show the median and first and third quartiles (the 25th and 75th percentiles), with outliers plotted individually in bold.

1990), which also supports alien birds known to severely impact native birds elsewhere (e.g. the common myna). In regions like these, impacts on native birds may be going unnoticed (Evans and Blackburn 2020, Evans 2021). This may be because research on the impacts of alien species, and ecological research more generally, is biased towards developed regions of the world (Bellard and Jeschke 2016, Nuñez et al. 2019).

What factors increase vulnerability?

Variables relating to all three of the hypotheses we posed were found to influence vulnerability. However, native birds located on islands (a characteristic of the abiotic environment) are particularly vulnerable. All 11 'severe' impacts occurred on islands, and seven resulted from predation. Approximately 27% of the alien bird species in our dataset are predators which have been deliberately introduced to islands, often to control 'pest' species (particularly the black rat *Rattus rattus* and insects). Thus, islands not only support many threatened native bird species (Szabo et al. 2012), but they have also been the focus of deliberate predatory alien bird introductions. This may explain the prevalence of impacts caused by alien Strigiformes (owls) and of predation impacts sustained by Charadriiformes (shorebirds) and Procellariiformes (seabirds). Shorebird and seabird species often nest on the ground and in open habitats, leaving them vulnerable to predation and islands are important breeding grounds for shorebirds and seabirds (Great Barrier Reef Marine Park Authority 1997, Birds Australia 2010). Many shorebird and seabird species are threatened with extinction (Thomas et al. 2006; Dias et al. 2019) and experiencing population declines globally (North American Bird Conservation Initiative Canada 2019). As seabird species tend to be characterised by slow life-histories, predation can limit their population growth (Roos et al. 2018). Given the potential for underreporting of 'moderate' predation impacts, further research is needed to identify and manage such impacts to shorebirds and seabirds (Evans 2021). Where feasible and necessary, eradications should be undertaken (Veitch et al. 2019): this would significantly reduce the global threat posed by alien birds to native birds.

As the size of an island decreases, native bird vulnerability increases (Supporting information, Evans 2021). The 11 'severe' impacts in our dataset occurred on islands with an average size of 283 km^2. These species extirpations and extinctions were caused by competition, predation and hybridisation, suggesting that on smaller islands, native birds may be vulnerable to 'severe' impacts from a range of impact mechanisms, which may therefore affect a range of native bird species (not only those prone to predation such as seabirds and shorebirds). Indeed, the six 'severe' impacts recorded on islands < 100 km^2 (average size $= 12$ km^2) were sustained by Anseriformes (waterfowl), Columbiformes (pigeons and doves), Charadriiformes (shorebirds), Gruiformes (cranes, rails and allies) and Strigiformes (owls). This may be because small islands support small native bird populations which are prone to extirpation when sustaining different types of impacts (Spatz et al. 2017). It may also be because smaller islands tend to support a limited range of habitats, increasing the likelihood that these habitats are shared by native and alien birds, which raises the chances of native/alien interactions.

Two variables of the abiotic environment influence vulnerability: thus environmental filtering (sensu Kraft et al. 2015) not only influences the establishment (Redding et al. 2019) and spread (Abellán et al. 2017) of alien birds, but also the severity of their impacts (at least on birds). Increased vulnerability in warmer regions is a result, to some extent, driven by 'severe' impacts recorded on tropical islands (Fig. 1). However, 71% of 'moderate' impacts on continents occur within regions with a maximum average monthly temperature of 28°C or higher. Warmer regions are generally more biodiverse (Rohde 1992) and thus may offer a greater variety of species to impact upon. They may also provide more hospitable conditions for alien birds to establish (Walther et al. 2009), suggesting that climate change may increase the vulnerability of native birds to the impacts of alien birds. This is also likely to be why climatic similarity increases the vulnerability of native birds: alien bird populations are more likely to establish (and thus be more abundant and widespread) in regions with similar climatic conditions to those found in their native range, and this may increase the chances of damaging native/alien interactions.

Two characteristics of native bird species also increase vulnerability. A recent study undertaken using EICAT data found no relationship between the severity of impacts caused by alien birds and their body mass (Evans et al. 2018b). However, that study considered the most severe impact caused by each alien bird species, and not the breadth of native bird species that they impacted. Here, by taking the latter into account, we reveal that native birds that are smaller than their alien counterpart tend to be more vulnerable. Indeed, all but one 'severe' impact was sustained by a native bird that was smaller than the impacting alien bird. This result is to some extent driven by the seven 'severe' predation impacts in our dataset, which were caused by large raptor species. However, being smaller than other bird species may be disadvantageous when competing for resources: 79% of the 42 'moderate' competition impacts were sustained by native birds that were smaller than the impacting alien bird. This result contrasts with the general finding that larger-bodied species tend to be more at risk from extinction, including larger-bodied birds (Gaston and Blackburn 1995, Bennett and Owens 1997). Native birds also tend to be more vulnerable when more of the habitats that they may occupy may also be occupied by invading alien birds, although the influence of this variable was weak. Nevertheless, to some extent this suggests that native birds restricted to a limited range of habitats (habitat-specialists) may be particularly vulnerable if these habitats are also occupied by alien birds. This may be why 64% of the 14 impacts sustained by strict

habitat-specialist bird species in our dataset (species occupying one broad habitat type alone) were 'moderate' or 'severe', whilst only 24% of the 34 impacts sustained by species occupying six or more habitat types were 'moderate' or 'severe'. Maintaining a diversity of functioning habitats within an ecosystem may therefore be an important strategy to mitigate the impacts of alien species.

Conclusion

This study is the first native species vulnerability assessment to be undertaken using impact data for an entire taxonomic class of alien species. By considering the breadth of native bird species that are affected by alien birds, we shed new light on the impacts they sustain, revealing predation to be more widespread than indicated by previous studies. Our results also suggest that damaging predation impacts may be underreported. Due to their susceptibility to predation, shorebirds and seabirds sustain a disproportionate number of predation impacts. Woodpeckers tend to sustain damaging impacts, most likely due to their predisposition for competition with alien birds for nest cavities, which are a limiting resource. It is possible that cavity-nesting bird species are sustaining as yet unquantified impacts resulting from widespread cavity-nesting alien parrots incursions across Europe (particularly the large, expanding population of the rose-ringed parakeet in the UK).

We found variables associated with all three of our hypotheses to increase the vulnerability of native birds to the impacts of alien birds. In particular, native birds are more vulnerable when they occupy islands, and their vulnerability increases as island size decreases. Native birds are also more vulnerable in warmer regions, and in regions where climatic conditions are similar to those found in the invading alien species' native range. Thus, environmental filtering, which has been found to influence the establishment and spread of alien birds, also influences the severity of their impacts. Climate change may be increasing the vulnerability of native birds to the impacts of alien birds.

Native bird species that are smaller than their alien counterpart are also more vulnerable, probably because they are more susceptible to impacts through both predation and competition. They also tend to be more vulnerable when more of the habitats that they occupy may also be occupied by their alien counterpart. This suggests that habitat-specialist native birds may be particularly vulnerable to the impacts of alien birds, and habitat generalists less so. Maintaining a diversity of functioning habitats within an ecosystem may therefore be an important strategy to mitigate the impacts of alien species.

Data availability statement

Data available from the Dryad Digital Repository: <http://dx.doi.org/10.5061/dryad.6wwpzgmxg> (Evans et al. 2021).

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