

Identifying the factors that determine the severity and type of alien bird impacts

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Abstract

Aim: To identify traits related to the severity and type of environmental impacts generated by alien bird species, in order to improve our ability to predict which species may have the most damaging impacts.

Location: Global.

Methods: Information on traits hypothesized to influence the severity and type of alien bird impacts was collated for 113 bird species. These data were analysed using mixed effects models accounting for phylogenetic non-independence of species.

Results: The severity and type of impacts generated by alien bird species are not randomly distributed with respect to their traits. Alien range size and habitat breadth were strongly associated with impact severity. Predation impacts were strongly associated with dietary preference, but also with alien range size, relative brain size and residence time. Impacts mediated by interactions with other alien species were related to alien range size and diet breadth.

Main conclusions: Widely distributed generalist alien birds have the most severe environmental impacts. This may be because these species have greater opportunity to cause environmental impacts through their sheer number and ubiquity, but this could also be because they are more likely to be identified and studied. Our study found little evidence for an effect of per capita impact on impact severity.

KEYWORDS

alien birds, biological invasion, habitat breadth, impact, predation, range size

1 | INTRODUCTION

Recent years have seen some important advances in our understanding of the processes associated with biological invasions. In particular, the recognition that invasion is a multistage process has enabled the identification of traits that mediate the successful passage of species through different stages (Blackburn et al., 2011). For example, studies have shown that, for birds, the likelihood of transport and introduction

is higher for widespread and abundant species (Blackburn & Duncan, 2001) and that establishment is more likely for species with larger relative brain sizes (Sol, Duncan, Blackburn, Cassey, & Lefebvre, 2005). A recent study has also shown that bird species attain larger alien range sizes if they also have larger native range sizes, have been introduced more often and have longer residence times as aliens (Dyer et al., 2016).

However, less progress to date has been made regarding our understanding of the causes of variation in the impacts generated by

alien birds. This may be because, until recently, there has been no widely adopted standard method available to quantify and compare the impacts of alien species in general. However, this has changed with the advent of such methods as the Generic Impact Scoring System (GISS; Nentwig, Bacher, Pyšek, Vilà, & Kumschick, 2016) and the Environmental Impact Classification for Alien Taxa (EICAT) protocol (Blackburn et al., 2014; Hawkins et al., 2015). These methods enable us to categorize the impacts of alien species under a standard semi-quantitative framework, which can form the basis for analyses of the factors that influence the severity and type of alien bird impacts. A recent global assessment undertaken using the EICAT protocol showed that the severity of environmental impacts generated by alien birds varies substantially and that some species have relatively severe impacts (Evans, Kumschick, & Blackburn, 2016).

The number of bird species being introduced to new environments has increased rapidly over the last 50 years, driven by globalization and increasing economic development (Dyer, Cassey, et al., 2017; Seebens et al., 2017). Given that this trend is likely to continue (Levine & D'Antonio, 2003) and that the environmental impacts of some alien bird species can be severe, it would be useful to identify the factors that influence the severity and type of their impacts. This may help us to identify bird species that have the most damaging impacts as aliens, which in turn may enable timely management interventions to prevent or mitigate these impacts.

As far as we are aware, four studies have attempted to identify traits that may influence the severity of impacts generated by alien birds at the regional scale, three focussing on Europe (Kumschick, Bacher, & Blackburn, 2013; Kumschick & Nentwig, 2010; Shirley & Kark, 2009) and one on Australia (Evans, Kumschick, Dyer, & Blackburn, 2014). Two of these found larger-bodied birds to be associated with more severe impacts (Evans et al., 2014; Kumschick et al., 2013) suggesting that species with greater per capita resource requirements place greater demands on their new environment. Studies have also found measures of generalism to be linked with the impacts of alien birds, with habitat generalist species having more severe impacts in both Europe and Australia (Evans et al., 2014; Kumschick et al., 2013; Shirley & Kark, 2009), and diet generalist species having more severe impacts in Australia (Evans et al., 2014). Furthermore, species with large native geographic ranges (often used as a proxy for the breadth of environments that can be occupied by a species) were also found to have more severe impacts in Europe (Kumschick et al., 2013). This suggests that alien species able to exploit a wider range of environmental conditions have more opportunities to generate negative impacts.

A further three recent studies (Baker, Harvey, & French, 2014; Evans et al., 2016; Martin-Albarracín, Amico, Simberloff, & Nuñez, 2015) have categorized alien bird species in terms of their environmental impacts without explicitly testing for traits associated with impact severity or type. However, the results of these studies suggest further traits that might relate to variation in impact. For example, of the most damaging species identified in all three studies, approximately two-thirds were large-brained (relative to their body size). Further, relative brain size has been linked to higher rates of invasion

success amongst alien birds (Sol & Lefebvre, 2000) and to lower rates of avian mortality (Sol, Székely, Liker, & Lefebvre, 2007). Birds with larger brains may therefore have more severe impacts because they are better able to persist in new environments. Relative brain size has also been correlated with increased abundance in UK farmland birds (Shultz, Bradbury, Evans, Gregory, & Blackburn, 2005) and greater levels of ecological flexibility (Sol et al., 2005). Therefore, birds with larger brains may have more severe impacts on the environment by placing greater demands on resources. Evans et al. (2016) also found that predation impacts were more severe than those caused through other impact mechanisms. Thus, dietary preference may influence the severity of impacts associated with alien birds, with carnivorous species having more severe impacts.

More generally, Parker et al. (1999) hypothesize that an alien species' impact should be the product of its abundance, range size and per capita impact. If so, widespread and/or abundant alien bird species may have greater impacts on the environment because they are distributed more widely and in greater numbers. Bird species with longer residence times tend to have larger alien range sizes in comparison with more recent alien arrivals (Dyer et al., 2016) and may have had more time to cause impacts or be studied (Evans, Pigot, Kumschick, Şekercioğlu, & Blackburn, 2018). It is therefore sensible to account for the effects of residence time in understanding how intrinsic traits influence alien species impacts.

Taken together, the results of these studies suggest that impact severity is influenced by traits that are intrinsic to bird species. However, as these studies were either undertaken at a limited (regional) scale (Evans et al., 2014; Kumschick & Nentwig, 2010; Kumschick et al., 2013; Shirley & Kark, 2009) or did not formally analyse relationships between impacts and traits (Baker et al., 2014; Evans et al., 2016; Martin-Albarracín et al., 2015), we do not yet know whether the results apply to alien birds generally. Therefore, here we test a range of hypotheses (H) to identify the factors that influence the severity of impacts generated by alien birds. Based on the results of previous studies, we expect to find impacts to be more severe amongst species which: (H1) are large-bodied; (H2) are generalists; (H3) are carnivorous; (H4) have larger alien ranges; and (H5) have larger relative brain sizes. We include residence time as a covariate in our analyses to take into account the possibility that it increases the likelihood of alien bird impacts being observed (H6).

Whilst some studies have addressed relationships between bird species' traits and impact severity, to our knowledge, relationships between traits and the types of impacts generated by alien birds have yet to be formally examined. However, impact types have been found to vary across alien bird families (Martin-Albarracín et al., 2015) and orders (Evans et al., 2016). Furthermore, whilst related species tend to share a range of intrinsic characteristics, these traits often differ across orders and families (Bennet & Owens, 2002). We may therefore expect to find that specific physical traits and behavioural characteristics of alien birds are associated with specific types of impacts. Therefore, we additionally test the general hypothesis (H7) that different impact mechanisms are associated with different traits of alien bird species.

2 | METHODS

2.1 | Data

Our analysis is based on a global data set of alien bird impacts (Evans et al., 2016). This data set was generated by applying the EICAT protocol (Blackburn et al., 2014; Hawkins et al., 2015) to 415 bird species with alien populations identified in the recently published Global Avian Invasions Atlas (GAVIA; Dyer, Redding, & Blackburn, 2017). Completed in 2014, GAVIA represents the most comprehensive source of information on alien bird introductions worldwide. During the EICAT assessment (Evans et al., 2016), each bird species with an alien population was allocated to one of five categories based on the severity of its environmental impacts: Minimal Concern (MC); Minor (MN); Moderate (MO); Major (MR); Massive (MV). Each species was also allocated to one or more of the following 12 formal EICAT impact mechanisms depending on the type of impacts it generated: (1) Competition; (2) Predation; (3) Hybridization; (4) Transmission of disease to native species; (5) Parasitism; (6) Poisoning/toxicity; (7) Biofouling; (8) Grazing/herbivory/browsing; (9) Chemical, (10) Physical or (11) Structural impact on ecosystem; (12) Interaction with other alien species. Evans et al. (2016) identified alien bird impacts from nine of the 12 EICAT mechanisms (all except (6) Poisoning/toxicity; (7) Biofouling; and (9) Chemical impact on ecosystem). During the EICAT assessment, data on impacts were available for 119 of the 415 species, with the rest being categorized as Data Deficient (DD). A summary of the EICAT assessment results can be found in Evans et al. (2016) (Table S2).

We collated data on the following nine variables (here numbered v1 to v9) to test the hypotheses listed in Section 1:

H1: We tested whether larger species tend to have more severe impacts using data on adult body mass (g; v1) taken from Myhrvold et al. (2015).

H2: To test whether diet or habitat generalist species are more damaging, we calculated the number of major food types consumed by each species (diet breadth; v2) and the number of major habitat types occupied by each species in its native range (habitat breadth; v3) (for food and habitat types, see Appendix S2). This approach follows that adopted for two previous studies on the impacts of alien birds in Europe (Kumschick et al., 2013) and Australia (Evans et al., 2014) enabling direct comparisons to be made with the results of these studies.

To further assess the effect of generalism on impact severity, we used data on the size of a species' native breeding range (km²; v4) (as a proxy for the breadth or ubiquity of the environmental conditions that can be utilized by a species), taken from GAVIA (Dyer, Redding, et al., 2017).

H3: To examine the effect of carnivory on impact severity, we used proportional data on the types of food consumed by each species (Şekercioğlu, 2012), to calculate: the proportion of a species diet comprising animal matter (both vertebrate and invertebrate prey;

v5); and the proportion of a species diet comprising vertebrate prey (v6).

H4: To test whether widespread alien species have more severe impacts, we used alien range size data (km²; v7) taken from GAVIA (Dyer, Redding, et al., 2017). We would also predict that impacts should be more severe for abundant alien species. However, data on alien range abundance (either population size or density) are available for relatively few bird species, and therefore we did not pursue abundance analyses.

H5: To investigate whether alien birds with larger brains have greater impacts, brain size data (relative to body mass; v8) were taken from Sol et al. (2012). Where these data were unavailable (11 species), we calculated brain size data using averages for species from the closest taxonomic level within the Sol et al. (2012) data set. Thus, brain sizes for seven species were calculated using data from species of the same genus (dusky-headed parakeet (*Aratinga weddellii*), wandering whistling duck (*Dendrocygna arcuata*), black-rumped waxbill (*Estrilda troglodytes*), Spanish sparrow (*Passer hispaniolensis*), Chilean flamingo (*Phoenicopterus chilensis*), light-vented bulbul (*Pycnonotus sinensis*) and vinous-breasted starling (*Sturnus burmannicus*)); one using species of the same family (Madagascar turtle dove (*Nesoenas picturata*)); and three using species of the same order (Japanese bush warbler (*Cettia diphone*), red-fronted parakeet (*Cyanoramphus novaezelandiae*) and velvet-fronted nuthatch (*Sitta frontalis*)).

H6: To determine whether impact severity is related to the length of time a species has been resident as an alien, we used data on the number of years since the first record of introduction for a species from GAVIA (Dyer, Redding, et al., 2017) as a measure of residence time (v9). The methods used to calculate residence times and native and alien range sizes are described in Dyer, Cassey, et al. (2017).

H7: To test whether the types of impacts generated by alien birds are influenced by their traits, we used data on all nine variables described above. During the EICAT assessment undertaken for birds (Evans et al., 2016), no impacts were allocated to three of the 12 EICAT mechanisms, and a further six EICAT mechanisms only received a small number of impact allocations (13 or fewer allocations for each mechanism). Therefore, these nine mechanisms were discounted from the analysis, which was restricted to the three remaining EICAT mechanisms: Competition (59 impact allocations), Predation (25) and Interaction with other alien species (18; for alien birds, this mechanism was found to relate solely to impacts associated with the dispersal of seeds of alien plants).

For competition impacts, we tested relationships with all variables except dietary preference. Birds with larger brains have been shown to possess higher levels of ecological flexibility (Sol et al., 2005). Therefore, because they are better able to exploit the resources available to them, we expect large-brained birds to be effective competitors. Larger birds may have an advantage over smaller species when it comes to competition for resources (Donadio & Buskirk, 2006; Morse, 1974; Peters, 1983). Generalist birds, more widespread species and those with longer residence times are more likely to have come into contact with and compete with other species.

For predation impacts, we tested for relationships with all variables except diet breadth. Orders and families of alien birds with large brains, including Strigiformes, Falconiformes (falcons) and Corvidae (crows and allies), were found to be associated with predation impacts by Evans et al. (2016). Predators are often large-bodied species (e.g., Accipitriformes (hawks, eagles and allies), Falconiformes and Strigiformes) (Evans et al., 2016; Therrien, Gauthier, Korpimäki, & Bêty, 2014). Predators are expected by definition to be carnivorous (e.g., Evans et al., 2016; Van Der Vliet, Schuller, & Wassen, 2008). Habitat generalists, more widespread species and those with longer residence times are more likely to have come into contact with and predated upon other species.

For interaction (alien seed dispersal) impacts, we tested relationships with habitat and diet generalism, range size and residence time, because these traits may influence the opportunity to generate impacts and also because more diverse diets may include fruits and seeds. We also tested for an effect of relative brain size, as the ecological flexibility of large-brained species suggests that they may be better at exploiting the resources available to them by having diverse diets that may include fruit and seeds.

2.2 | Analysis

We included in our analysis only those species for which we had data on all nine variables described above (113 species). Due to the relatively small size of our impact data set, impact severity data were converted into a two-level response variable: less severe impacts (those categorized as either **MC** or **MN** under the EICAT protocol) = 76 species; more severe impacts (those categorized as **MO**, **MR** or **MV**) = 37 species. This divided impacts such that less severe impacts are those that are negligible or only affect the fitness of individuals of native species and more severe impacts are those that, as a minimum, cause declines in populations of native species, or worse, cause local population extirpations or species extinctions. To test the effect of traits on the types of impacts generated by alien birds, for each species,

data on each EICAT impact mechanism were divided into a two-level response variable (e.g., for competition impacts: 0 = no competition impact; 1 = competition impact).

Our data set considers traits that are well known to show strong phylogenetic signal (e.g., body mass). Furthermore, different bird taxa have been shown to be associated with specific types of impact (e.g., Evans et al., 2016). We therefore expected to find evidence for phylogenetic autocorrelation in our analysis (sensu Münkemüller et al., 2012). To address this, we used Birdtree.org (<http://birdtree.org/subsets/>) to download 100 randomly selected phylogenetic trees incorporating the 113 species in our data set. We then tested for phylogenetic signal in impact severity, using the caper package in R (Orme, 2013) to calculate the *D* statistic (Fritz & Purvis, 2010) for each phylogenetic tree. We identified phylogenetic signal in impact severity in our data set (average *D* = 0.74; range 0.7–0.79) with a low probability of *D* resulting from either Brownian phylogenetic structure (average *p* < .001; range 0–0.005) or no phylogenetic structure (average *p* = .026; range 0.009–0.055). We therefore examined the relationships between each of the nine predictor variables and the severity and type of impacts generated by alien bird species using phylogenetic linear regression (the phylolm package in R: Ho & Ane, 2014) to account for potential phylogenetic relatedness amongst species.

We analysed each variable independently and then undertook multivariate analysis for all variables. After each run of the multivariate model, we removed the least significant variable, repeating the process until the simplified model contained only variables with significant terms (*p* < .05). We checked for multicollinearity amongst our nine predictor variables using the car package in R (Fox & Weisberg, 2011), but found no evidence of this (Appendix S1).

Data for body mass, relative brain size, native and alien range size and residence time were log transformed for analysis. All statistical analyses were undertaken using RSTUDIO version 0.99.893 (R Core Team, 2016).

TABLE 1 The relationships between the severity of impacts generated by alien birds and predictor variables. All parameters in this table derive from phylogenetic linear regression using the phylolm package in R (Ho & Ane, 2014) to account for potential autocorrelation amongst species due to their phylogenetic relatedness. Results are the mean values for 100 phylogenies (lower and upper confidence limits (2.5% and 97.5%) are also provided in parentheses). Significant relationships (*p* < .05) are highlighted in bold. Total sample size = 113 species

Predictor variable	Estimate	Std. Error	<i>p</i>
Alien range size	0.062 (0.041–0.077)	0.017 (0.015–0.019)	.001** (<.001***–.006**)
Body mass	0.236 (0.108–0.392)	0.162 (0.139–0.182)	.180 (.021*–.503)
Brain size	0.017 (–0.061–0.090)	0.126 (0.117–0.139)	.798 (.483–.988)
Diet breadth	0.116 (0.084–0.157)	0.033 (0.029–0.035)	.003** (<.001***–.009**)
Diet preference (animal matter)	0.003 (0.001–0.004)	0.003 (0.002–0.003)	.368 (.155–.669)
Diet preference (vertebrates)	0.014 (0.010–0.018)	0.007 (0.006–0.007)	.047* (.007**–.139)
Habitat breadth	0.118 (0.091–0.150)	0.027 (0.024–0.030)	.002** (<.001***–<.009**)
Native range size	0.170 (0.109–0.237)	0.047 (0.041–0.054)	.007** (<.001***–.030*)
Residence time	0.204 (0.107–0.309)	0.066 (0.051–0.078)	.008** (<.001***–.042*)

Estimate = estimated coefficient; Std. Error = standard error; Significance codes: ****p* < .001; ***p* < .01; **p* < .05.

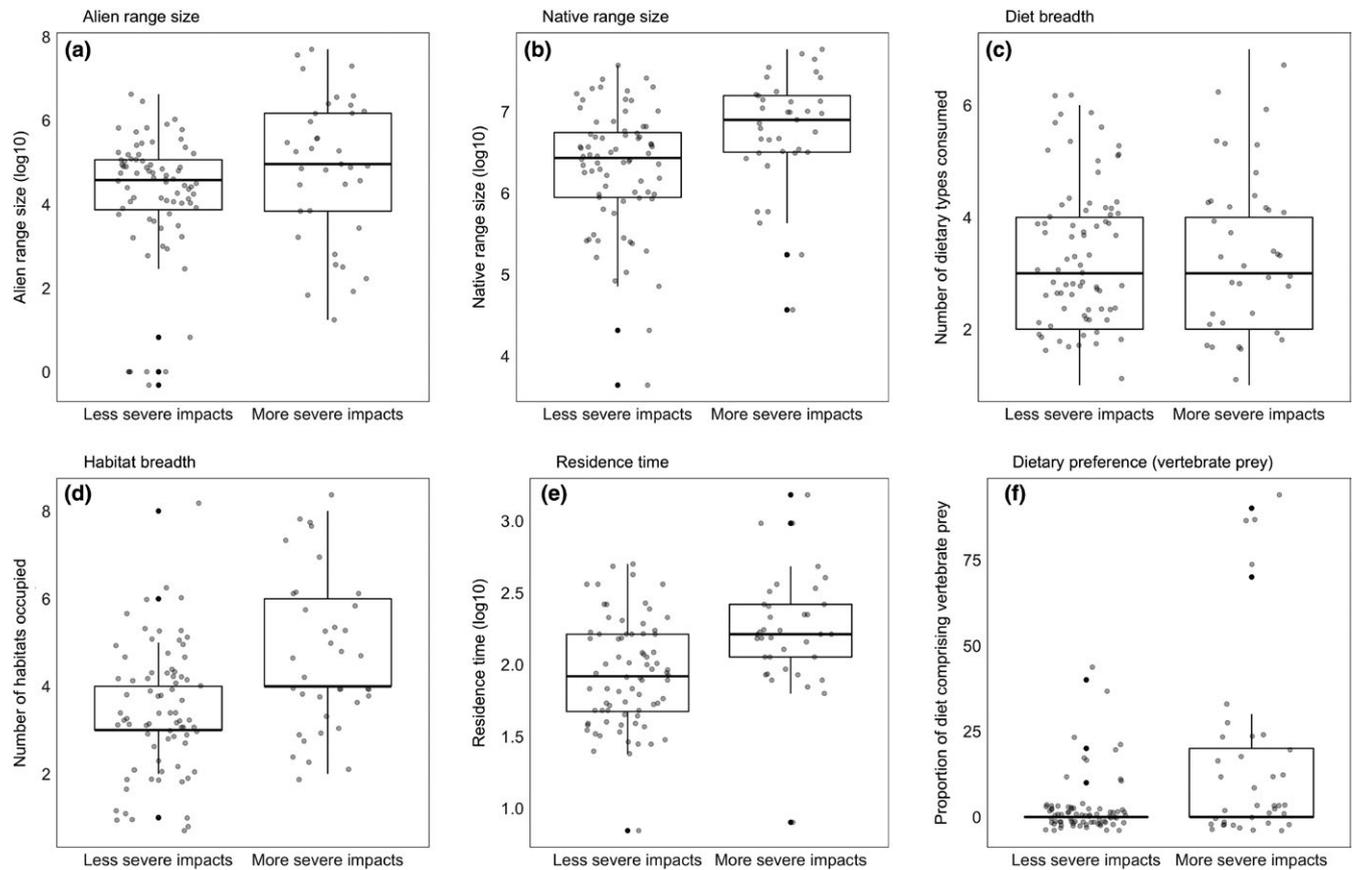


FIGURE 1 The distribution of alien bird species generating “less severe” and “more severe” impacts for (a) Alien range size (km^2); (b) Native range size (km^2); (c) Diet breadth (number of dietary types consumed); (d) Habitat breadth (number of habitats occupied); (e) Residence time (number of years since first introduction); (f) Dietary preference (proportion of diet comprising vertebrate prey). Species with less severe impacts: $n = 76$, species with more severe impacts: $n = 37$. Jitter used to add random noise to data to prevent overplotting

3 | RESULTS

Univariate analysis revealed positive relationships ($p < .01$) between impact severity and five predictor variables (native and alien range size, diet and habitat breadth and residence time): bird species had more severe impacts if they had larger native and alien ranges, broader habitat and dietary preferences and longer residence times (Table 1). These relationships were significant for all 100 phylogenies used. We also found a positive relationship ($p < .05$) between impact severity and dietary preference (the proportion a species diet comprising vertebrate prey); this effect was significant on average, but not over all the phylogenies analysed (Table 1). The distribution of species with less severe impacts (MC or MN) and more severe impacts (MO, MR or MV) for these variables is shown in Figure 1 (these plots do not account for potential phylogenetic relatedness of the species in our data set). We found no relationships between impact severity and body mass, relative brain size or the proportion of a species diet comprising animal matter (invertebrate and vertebrate prey) (Table 1), albeit that a positive relationship to body mass was observed over some of the phylogenies used.

Following model simplification, multivariate analysis indicated that birds generating more severe impacts have larger alien ranges (on

average approximately 20 times the size of those for species with less severe impacts) and occupy a greater breadth of habitats in their native range (an average of 4.7 habitats for species with more severe impacts versus 3.4 for species with less severe impacts; Table 2). The positive univariate relationships between impact severity and native range size, diet breadth, diet preference (the proportion of a species diet comprising vertebrate prey) and residence time were not recovered when controlling for other predictors.

We did not find evidence in support of any consistent relationships between competition impacts and predictor variables in either univariate or multivariate analysis, albeit that negative effects of alien range size, body mass, relative brain size and diet breadth were recovered for some of the phylogenies used (Table 3).

Univariate analysis revealed positive relationships ($p < .001$) between predation impacts and alien range size and dietary preference (the proportion of a species diet comprising animal matter) (Table 3). We also found positive relationships ($p < .05$) (though inconsistent across phylogenies) between predation impacts and brain size, dietary preference (the proportion of a species diet comprising vertebrate prey) and residence time (Table 3). Multivariate analysis for predation impacts revealed a positive relationship ($p < .001$) with dietary preference (the proportion of a species diet comprising animal matter),

TABLE 2 Multivariate analysis showing significant relationships ($p < .05$) following model simplification, between the severity of impacts generated by alien birds and predictor variables. All parameters in this table derive from phylogenetic linear regression using the *phylolm* package in R (Ho & Ane, 2014) to account for potential autocorrelation amongst species due to their phylogenetic relatedness. Results are the mean for 100 phylogenies (lower and upper confidence limits (2.5% and 97.5%) are also provided in parentheses). Total sample size = 113 species

Predictor variable	Estimate	Std. Error	<i>p</i>
Alien range size	0.054 (0.039–0.064)	0.016 (0.014–0.018)	.002** (<.001***–.007**)
Habitat breadth	0.108 (0.080–0.138)	0.026 (0.023–0.029)	.003** (<.001***–.003**)

Estimate = estimated coefficient; Std. Error = standard error; Significance codes: *** $p < .001$; ** $p < .01$; * $p < .05$.

which was recovered across all 100 phylogenies used. This analysis also identified positive effects of alien range size, relative brain size and residence time, along with a negative effect of native range size, albeit that these relationships were not recovered across all phylogenies used (Table 4).

Univariate analysis did not reveal any significant relationships between interaction (alien seed dispersal) impacts and predictor variables (Table 3). However, in multivariate analysis, a consistent negative relationship ($p < .01$) with alien range size was identified, along with a positive relationship ($p < .05$) with diet breadth (Table 4).

4 | DISCUSSION

Due to increasing globalization and international trade, the number of animals and plants being introduced to new environments has increased markedly over the last century (Hulme, 2009; Perrings et al., 2002). Studies suggest this development is set to continue (Levine & D'Antonio, 2003) that we have yet to reach a global saturation point for alien introductions (Seebens et al., 2017) and that birds are no exception to this trend (Dyer, Cassey, et al., 2017). Given that the environmental impacts of some alien birds can be severe, causing declines in populations of native species, and in some cases, contributing to native species extinctions (Evans et al., 2016), it is important that we develop and implement a full range of measures to identify and manage their impacts (Kumschick et al., 2015). Regional studies in Europe and Australia (Evans et al., 2014; Kumschick & Nentwig, 2010; Kumschick et al., 2013) have linked the impacts of alien birds to the traits that they possess. Here, we extend this research by identifying traits that correlate with alien bird impacts on a global scale. Of the variables tested, we find that alien range size and habitat breadth are strongly associated with impact severity—it is widely distributed generalist alien birds that have the most severe environmental impacts.

Alien range was found to be the strongest predictor of impact severity, with positive relationships found during both univariate and multivariate analyses (Tables 1 and 2, Figure 1). This result was suggested by the equation proposed by Parker et al. (1999) whereby the impact of an alien species depends on its alien geographic range size, abundance and per capita impact. Of the 37 species causing the most severe impacts globally (MO, MR or MV), 26 have comparatively large alien ranges of over 30,000 km². This suggests that widely distributed

alien birds have greater opportunity to cause environmental impacts, increasing the chances that some of these impacts will be severe. For example, the common myna (*Acridotheres tristis*) is a widely distributed alien species (alien range = c.2.3 million km²) that generates a range of environmental impacts. In Australia, it competes with native birds including the crimson rosella (*Platycercus elegans*) (Grarock, Tidemann, Wood, & Lindenmayer, 2012); in Tahiti, it predated upon the eggs of the Tahiti flycatcher (*Pomarea nigra*) (Blanvillain, Salducci, Tutururai, & Maeura, 2003); and in Hawaii, it spreads the seeds of the alien lantana (*Lantana camara*) (Lever, 2005). We also found a positive association between alien range size and predation impacts in both univariate and multivariate analysis (Tables 3 and 4). On average, alien bird predation impacts have been found to be more severe than for other impact mechanisms (Evans et al., 2016), which may in part explain why alien range size is associated with impact severity.

Habitat generalism was also found to be positively associated with impact severity in both univariate and multivariate analysis, and across all the phylogenetic hypotheses analysed (Tables 1 and 2, Figure 1). Alien bird species have more severe impacts if they occupy a broader range of habitats in their native range. Previous studies have found habitat generalism to be associated with more severe alien bird impacts in Europe (Kumschick & Nentwig, 2010; Kumschick et al., 2013; Shirley & Kark, 2009) and Australia (Evans et al., 2014), and here we confirm this result globally. Of those species causing more severe impacts (MO, MR or MV), more than 75% are habitat generalist species occupying four or more of the 10 habitat types identified for analysis. The effect of habitat breadth is likely to arise because habitat generalist birds are able to survive in a broader range of environments and therefore have more opportunity to generate impacts. Habitat generalist species with documented impacts include the swamp harrier (*Circus approximans*), which is implicated in the extinction of the Polynesian imperial pigeon (*Ducula aurorae wilkesii*) and the extirpation of blue lorikeet (*Vini peruviana*) populations on Tahiti (Shine, Reaser, & Gutierrez, 2003). Univariate analysis also identified relationships between impact severity and other measures of generalism (native range size and diet breadth: Table 1, Figure 1), albeit that these did not retain their effects in multivariate analysis.

Our analyses suggest that the extent of an alien bird species distribution (both in terms of range size and diversity of habitats occupied) increases the likelihood that it has more severe documented environmental impacts. Given that distributional extent is generally correlated with abundance in native (Gaston & Blackburn, 2000; but see

TABLE 3 Univariate analysis showing relationships between the types of impacts generated by alien birds and predictor variables. All parameters in this table derive from phylogenetic linear regression using the *phylolm* package in R (Ho & Ane, 2014) to account for potential autocorrelation amongst species due to their phylogenetic relatedness. Results are the mean for 100 phylogenies (lower and upper confidence limits (2.5% and 97.5%) are also provided in parentheses). Significant relationships ($p < .05$) are highlighted in bold. Nine of the 12 formal EICAT impact mechanisms were discounted from the analysis because they either had low numbers of impacts allocated to them or none: Hybridization (13 allocated impacts), Grazing/herbivory/browsing (10), Transmission of disease to native species (seven), Parasitism (one), Chemical impact on ecosystem (one), Structural impact on ecosystem (one), Poisoning/toxicity (none), Biofouling (none) and Physical impact on ecosystem (none). Sample size: Competition = 59 allocated impacts; Predation = 25 allocated impacts; Interaction with other alien species (alien seed dispersal) = 18 allocated impacts

EICAT impact mechanism	Predictor variable	Estimate	Std. Error	p
Competition	Alien range size	-0.034 (-0.091 to -0.001)	0.019 (0.017-0.021)	.205 (<.001***-.862)
	Body mass	-0.177 (-0.401 to 0.090)	0.173 (0.146-0.208)	.337 (.020*-.874)
	Brain size	-0.225 (-0.447 to -0.069)	0.133 (0.123-0.153)	.148 (.003**-.601)
	Diet breadth	-0.053 (-0.117 to -0.020)	0.036 (0.032-0.043)	.193 (.004**-.578)
	Habitat breadth	0.017 (-0.008 to 0.060)	0.031 (0.027-0.036)	.596 (.102-.946)
	Native range size	-0.041 (-0.097 to -0.009)	0.053 (0.047-0.062)	.488 (.080-.878)
	Residence time	0.024 (-0.010 to 0.054)	0.074 (0.055-0.095)	.738 (.470-.958)
Predation	Alien range size	0.053 (0.033 to 0.075)	0.012 (0.010-0.013)	<.001*** (<.001***-.002)
	Body mass	0.131 (0.075 to 0.184)	0.113 (0.093-0.131)	.259 (.151-.439)
	Brain size	0.206 (0.140 to 0.273)	0.085 (0.071-0.098)	.022* (.003**-.057)
	Diet preference (animal matter)	0.009 (0.007 to 0.011)	0.002 (0.002-0.002)	<.001*** (<.001***-<.001***)
	Diet preference (vertebrates)	0.010 (0.008 to 0.011)	0.005 (0.004-0.005)	.040* (.015*-.074)
	Habitat breadth	-0.001 (-0.009 to 0.007)	0.020 (0.016-0.024)	.865 (.658-.985)
	Native range size	-0.026 (-0.043 to -0.012)	0.035 (0.028-0.041)	.462 (.265-.726)
Residence time	0.103 (0.052 to 0.171)	0.047 (0.035-0.056)	.049* (.002**-.168)	
Interaction (alien seed dispersal)	Alien range size	-0.025 (-0.038 to -0.015)	0.012 (0.010-0.014)	.057 (.004**-.187)
	Brain size	-0.047 (-0.064 to -0.028)	0.086 (0.074-0.099)	.583 (.467-.745)
	Diet breadth	0.037 (0.023 to 0.050)	0.023 (0.019-0.026)	.121 (.055-.233)
	Habitat breadth	-0.003 (-0.011 to 0.005)	0.020 (0.016-0.023)	.822 (.617-.994)
	Native range size	0.023 (0.002 to 0.044)	0.034 (0.028-0.040)	.521 (.239-.910)
Residence time	0.008 (-0.003 to 0.020)	0.047 (0.036-0.057)	.857 (.717-.983)	

Estimate = estimated coefficient; Std. Error = standard error; Significance codes: *** $p < .001$; ** $p < .01$; * $p < .05$.

Novosolov et al., 2017) and alien birds (Blackburn, Gaston, & Duncan, 2001), we would also expect to see a relationship between impact severity and abundance, were sufficient data available to analyse it. We find less evidence for a likely effect of per capita impact. Notably, there is no effect of body mass on impact severity in univariate or multivariate analysis (Tables 1 and 2), or indeed on the likelihood that species impose deleterious predation, competition or interaction impacts on their new environment (Tables 3 and 4). Body mass is positively associated with per capita resource requirements across species (Peters, 1983), but the effect of this variation may be minor compared to the effects of variation in the numbers of alien individuals exploiting native resources.

The tendency for the impacts of alien birds to be more severe on islands when compared to continents (Evans et al., 2016) may also partly explain the positive effect of range size on impact severity. All nine bird species that have caused native species extirpations and extinctions (MR or MV impacts) have done so on islands. Of the 26 species

with large alien ranges (>30,000 km²), nearly 60% cause impacts on islands. These species include the red-whiskered bulbul (*Pycnonotus jocosus*; 76,111 km²) which, through predation, is considered to be responsible for the disappearance of large spiders of the genus *Neophilina* on Mauritius (Diamond, 2009; Linnebjerg, Hansen, Bunbury, & Olesen, 2010) and the barn owl (*Tyto alba*; alien range = 36,947 km²), which, through competition, is implicated in the extinction of the Lord Howe Island boobook (*Ninox novaeseelandiae albaria*) (Garnett, Szabo, & Dutson, 2011). Therefore, alien range size may also be correlated with impact severity because widely distributed alien birds are more likely to have been introduced to islands.

However, the strong positive relationship between alien range size and impact severity may arise because widely distributed alien birds are more likely to have their impacts identified and recorded. A recent study (Evans et al., 2018) found alien range size to be a strong predictor of the availability of impact data for alien birds, with more data available for species with larger alien ranges. Larger alien range size

TABLE 4 Multivariate analysis showing significant relationships ($p < .05$) following model simplification, between predation and interaction (alien seed dispersal) impacts and predictor variables. All parameters in this table derive from phylogenetic linear regression using the `phylolm` package in R (Ho & Ane, 2014) to account for potential autocorrelation amongst species due to their phylogenetic relatedness. Results are the mean for 100 phylogenies (lower and upper confidence limits (2.5% and 97.5%) are also provided in parentheses). Sample size: Predation = 25 allocated impacts; Interaction with other alien species (alien seed dispersal) = 18 allocated impacts

EICAT impact mechanism	Predictor variable	Estimate	Std. Error	p
Predation	Alien range size	0.031 (0.013 to 0.044)	0.013 (0.011–0.015)	<.001*** (<.001***–.218)
	Brain size	0.119 (0.079 to 0.164)	0.074 (0.065–0.082)	<.001*** (<.001***–.251)
	Diet preference (animal matter)	0.008 (0.006 to 0.009)	0.002 (0.002–0.002)	<.001*** (<.001***–<.001***)
	Native range size	–0.042 (–0.064 to –0.018)	0.033 (0.028–0.038)	<.001*** (<.001***–.574)
	Residence time	0.077 (0.028 to 0.129)	0.055 (0.046–0.063)	<.001*** (<.001***–.618)
Interaction (alien seed dispersal)	Alien range size	–0.037 (–0.052 to –0.025)	0.013 (0.010–0.014)	.009** (<.001***–.045*)
	Diet breadth	0.063 (0.039 to 0.084)	0.024 (0.020–0.027)	.015* (.001**–.062)

Estimate = estimated coefficient; Std. Error = standard error; Significance codes: *** $p < .001$; ** $p < .01$; * $p < .05$.

may increase the likelihood that a species is introduced to regions of the world that are hotspots of invasive species research. For example, more than half of the alien bird species identified as causing the most severe impacts globally (MR or MV impacts) do so in Australia or New Zealand. Both of these countries have been severely affected by the impacts of alien species (see Allen & Lee, 2006; Invasive Animals CRC, 2017). It is possible that a climate of heightened awareness and sensitivity to the impacts of alien species, within a developed region with capacity for alien species research, has resulted in the careful scrutiny of alien species impacts in these regions. The impacts of alien birds may not necessarily be higher there than elsewhere, but rather be more likely to be studied.

With regard to impact mechanisms, the effect of alien geographic range size on data availability may also explain its positive relationship with predation impacts, but not its negative relationship with interaction (alien seed dispersal) impacts (Table 4). The average alien range size for species with interaction impacts in our data set is approximately five times smaller than that for all alien bird species. Almost a quarter of the birds with seed dispersal impacts have alien ranges restricted solely to islands, including the silvereye (*Zosterops lateralis*; Tahiti and Kiribati), the Japanese bush warbler (*Cettia diphone*; Hawaii) and the smooth-billed ani (*Crotophaga ani*; the Galapagos Islands). It seems unlikely that alien birds only disperse alien plant seeds on islands, but it is possible that this dispersal has larger negative effects on islands where the native flora is depauperate, and where extinctions may have disproportionately removed native seed dispersers. Szabo, Khwaja, Garnett, and Butchart (2012) found avian bird extinctions to be most severe on islands, with specific foci for extinctions including the Hawaiian Islands, Mascarene Islands and French Polynesia. Island ecosystems are considered to be particularly vulnerable to the loss of seed dispersal agents, because of their often highly asymmetric seed dispersal networks (Schleuning, Böhning-Gaese, Dehling, & Burns, 2014). For example, in Hawaii, a recent study showed that patterns of seed dispersal have been significantly altered following the eradication of native frugivores. In their absence, alien species do not serve

as functional replacements, instead dispersing the seeds of an invasive alien plant and fewer seeds of native plants (90% of seeds being from two ubiquitous species) (Pejchar, 2015). Seed dispersal impacts were also found to be positively associated with diet breadth. This may be because alien birds with catholic diets are more likely to consume seeds and berries, and thus more likely to become seed dispersal agents.

Predation impacts were found to be most strongly associated with the amount of animal matter (both invertebrate and vertebrate) consumed by a species, a relationship that is recovered in both univariate and multivariate analysis and across all 100 phylogenies used in the analysis (Tables 3 and 4). This relationship is unsurprising as predation is, by definition, the consumption of animal matter. However, predation impacts were more strongly associated with species consuming both vertebrates and invertebrates than for species whose diet consists solely of vertebrate prey (Tables 3 and 4). This suggests that predation impacts are not confined just to “classic” carnivores such as owls, hawks and falcons, but that more catholic or omnivorous bird species may be a threat to native faunas. For example, the diet of the African sacred ibis (*Threskiornis aethiopicus*) includes insects, amphibians, reptiles, fish and small mammals (BirdLife International, 2016a), and this species is on the list of invasive alien species of European Union concern (European Commission, 2016). The impacts of omnivorous alien birds can be severe—for example, the great kiskadee (*Pitangus sulphuratus*) and the red-whiskered bulbul are both reported to have eradicated invertebrates (Department of Environment and Natural Resources (Bermuda), 2017; Diamond, 2009; Linnebjerg et al., 2010). The impacts of alien birds on invertebrates may be underestimated, as species extinctions in these groups are not widely reported, and the threat status of invertebrate species is often poorly understood in comparison with other taxa (Bland et al., 2017). The impacts of catholic species may also explain why diet breadth was found to be a strong indicator of impact severity in univariate analysis (Table 1), albeit not when controlling for other variables (Table 2).

We also identified positive relationships between predation impacts and relative brain size and residence time in multivariate analysis, although these relationships were not recovered for all 100 phylogenies used (Table 4). Predatory birds such as owls and crows tend to be large-brained (in our data set, these species include the Australian masked owl (*Tyto novaehollandiae*) and the American crow (*Corvus brachyrhynchos*)). Being long-lived (Rowe, 2008), birds of prey often have relatively slow life histories, and possibly require longer time periods, when compared to other bird orders, to establish populations and cause impacts. However, if the latter effect was true, we might expect to find an effect of body mass on predation impacts, as larger bird species also tend to be longer lived (Peters, 1983). Therefore, residence time may be associated with predation impacts because alien birds with longer residence times are more likely to be noticed and recorded. We also find a counter-intuitive negative relationship between predation impacts and native range size in multivariate analysis (Table 4). The reason for this is not immediately obvious, but some alien birds with predation impacts have restricted native ranges. For example, the weka (*Gallirallus australis*) has a native range of 36,830 km² (200 times smaller than the average native range size), on the east coast of the North Island of New Zealand. It was translocated to its alien range because of declining population numbers (BirdLife International, 2016b).

5 | CONCLUSIONS

This study represents one of the first formal analyses of alien species impacts undertaken using data generated by an EICAT assessment (Evans et al., 2016). It demonstrates that EICAT data can be used to provide useful insights regarding the factors that drive the severity and type of impacts generated by alien species. Our findings of expected relationships, such as that between predation impacts and the consumption of animal matter, are reassuring of the ability of our analyses to detect robust associations between impacts and traits. Taken together, our results indicate that it is widely distributed generalist alien birds that cause the most severe impacts to the environment. In contrast, our analyses find little evidence for an effect of per capita impact on impact severity. The effects of alien range size and generalism may arise because these species have greater opportunity to cause environmental impacts through their sheer numbers, but we cannot rule out an effect of the likelihood that the impacts of such species are identified and studied. Should the former be the case, this study provides support for the improvement of risk assessments and other procedures to minimize the global distribution of alien birds.

The results of this study may also assist in predicting which species (including those which currently do not have alien populations, and those alien species currently categorized as **DD** under EICAT) may have damaging impacts. For example, the New Caledonian crow (*Corvus moneduloides*) is a **DD** species and is a habitat and diet generalist (being reported to occupy forest, shrubland, grassland and artificial terrestrial habitats,

and being omnivorous; BirdLife International, 2016c). It belongs to a family of birds found to be associated with more severe impacts (Corvidae; Evans et al., 2016) and is present as an alien on an island (Maré, Loyalty Islands), where the impacts of alien birds have been found to be more acute (Evans et al., 2016). We would predict, on the basis of our analyses, that the impacts of this species are going unnoticed.

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DATA ACCESSIBILITY

Data available from University College London (UCL) open-access repository: <<https://doi.org/10.14324/000.ds.10040947>> (Evans et al., 2018).

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BIOSKETCH

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SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article.

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