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Identifying links between the biodiversity impacts and monetary costs of alien birds

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Abstract

1. Alien species can be damaging to native biodiversity, human well-being and the economy. Identifying the complete range of impacts they cause, and the ways that these impacts are connected, may inform the prioritisation of management actions to mitigate impacts.
2. Using datasets on the biodiversity impacts and monetary costs (damage and management costs) of alien birds, we aimed to establish whether species with the most severe biodiversity impacts also had the highest costs; whether types of biodiversity impact were associated with high costs; and whether specific factors associated with alien species are linked to both damaging biodiversity impacts and high costs.
3. We identified a positive relationship between a specific type of biodiversity impact (predation) and costs, possibly because predation by alien birds can be severely damaging to native species and therefore attracts management actions. However, predation impacts are likely to occur more frequently and to be easier to identify than some other impact mechanisms such as hybridisation and transmission of diseases, and they are therefore likely to be more frequently managed and hence to have costs.
4. We identified a specific species characteristic (generalism) to be associated with severe biodiversity impacts and high costs, probably because generalist species have greater opportunity to cause impacts, whether they be on biodiversity or the economy, or both. We also found widely distributed alien birds to be associated with high costs, probably because these species also have greater opportunity to cause impacts.

[Correction added on 16 August 2023, after first online publication: Affiliation 3 has been corrected to include IRD]

5. Management interventions that prevent the introduction of both predatory and generalist alien bird species, or that reduce their geographic distribution at early stages of invasions, may have significant biodiversity and economic benefits.

KEYWORDS
alien species, avian ecology, biological invasions, EICAT, InvaCost, invasive species, ornithology, predation, SEICAT, wildlife management

1 | INTRODUCTION

A species is considered to be alien when it has been introduced by people to regions of the world where it would not naturally occur (Blackburn et al., 2011). If an alien species has damaging impacts, it is considered to be invasive (IUCN, 2023). Invasive alien species are one of the five main causes of declining biodiversity across the globe, and they can adversely affect human well-being, in particular by hindering economic development and compromising human health (Díaz et al., 2019).

There are over 400 alien bird species with self-sustaining populations worldwide (Dyer et al., 2017), and some have unwanted impacts on nature and people (Evans et al., 2016, 2020). Impacts that affect nature include competition with native species for resources and predation of native species as a source of food (Martin-Albarracin et al., 2015). Impacts that affect people include the consumption of agricultural crops, damage to aircraft caused by bird strikes at airports, and fouling of public buildings and amenity spaces (Brochier et al., 2010). Damage and management costs associated with these impacts can be substantial. For example, in 2006/07, the Western Australian Government spent AU$2.45 million on a surveillance, research and control programme for common starlings (*Sturnus vulgaris*), which feed on soft fruit and are a threat to agriculture across the region (Roberts, 2006).

Comprehensive knowledge of the characteristics of these impacts is required to inform the prioritisation of management actions to deal with the most damaging alien species (Caffrey et al., 2014). Indeed, at the Fifteenth meeting of the Conference of the Parties to the Convention on Biological Diversity (COP 15), nations adopted 23 global targets for 2030, including Target 6 which requires the prioritisation of actions towards alien species with the most severe impacts (CBD Secretariat, 2022). Two frameworks and a database have recently been developed which aim to improve understanding of the biodiversity and socio-economic impacts of alien species, by enabling impact data to be categorised, quantified and standardised in a manner that facilitates direct comparisons of impacts by their severity and type. These are the Environmental Impact Classification for Alien Taxa (EICAT) (Blackburn et al., 2014), the Socio-economic Impact Classification for Alien Taxa (SEICAT) (Bacher et al., 2018) and the InvaCost database (Diagne, Leroy, Gozlan, Vaissière, Assailly, et al., 2020). Under EICAT, the environmental impacts of alien species are categorised by their type using 12 impact mechanisms (e.g. competition with native species and predation of native species) and by their severity using five impact categories (Minimal Concern [MC], Minor [MN], Moderate [MO], Major [MR] and Massive [MV]). Published guidelines (IUCN, 2020) provide a series of semi-quantitative impact scenarios which guide the assessment process. SEICAT uses data on the socio-economic impacts of alien species to assess how these impacts affect the well-being of people. Developed in tandem with EICAT, it adopts the same five impact categories (MC–MV). InvaCost is a living, publicly available database that provides a systematic, standardised methodology for the collection and treatment of data on the economic costs of alien species, enabling historical cost data in different currencies to be transformed to current, standardised values (Diagne, Leroy, Gozlan, Vaissière, Nuninger, et al., 2020).

EICAT has been used to undertake assessments of the biodiversity impacts of alien species from a range of taxonomic groups such as *Acacia* species (Jansen & Kumschick, 2022), rabbits and hares (Allmert et al., 2022) and birds (Evans et al., 2016). The results of the latter study informed research to identify factors that influence the severity of alien bird impacts (Evans, Kumschick, et al., 2018) and factors that make native birds vulnerable to these impacts (Evans et al., 2021). SEICAT has been used to improve understanding of the ways in which alien species from a range of taxonomic groups affect human well-being, including for example, marine fishes in the Mediterranean (Galanidi et al., 2018), gastropods in South Africa (Kesner & Kumschick, 2018) and birds globally (Evans et al., 2020). InvaCost has been used to describe and analyse the global economic costs associated with specific groups of alien species such as ants (Angulo et al., 2022), fish (Haubrock et al., 2022) and birds (Evans et al., n.d.), and to demonstrate that inaction to manage the impacts of alien species can result in spiralling costs (Ahmed et al., 2022). It has also been used to describe and analyse costs occurring in specific regions of the world (studies on costs have been published for 16 countries and 8 regions to date) (InvaCost, 2022), and to demonstrate that the global costs associated with alien species are grossly underestimated (Diagne et al., 2021).

Thus, EICAT, SEICAT and InvaCost provide useful datasets on alien species impacts. However, they each consider specific types of impact (biodiversity, human well-being and economic cost, respectively), so when used individually they do not provide information on the complete range of impacts caused by alien species. Combining data from EICAT, SEICAT and InvaCost may provide a more comprehensive understanding of these impacts. Indeed, identifying the complete range of biodiversity and socio-economic impacts caused by an alien species may better inform the prioritisation of management actions to mitigate its impacts.

Combining data from EICAT, SEICAT and InvaCost may also improve our knowledge of the links between biodiversity impacts and economic costs. Identifying statistical links may enable the prediction of biodiversity impacts or economic costs for species lacking data on either. Furthermore, as biodiversity and human well-being are linked through the provision of ecosystem services (Díaz et al., 2019), identifying connections between biodiversity and socio-economic impacts may inform a more holistic approach to the management of alien species.

To our knowledge, only a small number of studies have investigated relationships between the biodiversity impacts and socio-economic impacts of alien birds, and all at a regional scale, either in Europe (Kumschick & Nentwig, 2010; Kumschick et al., 2013, 2015; Shirley & Kark, 2009) or Australia (Evans et al., 2014). All adopted a similar method, undertaking a literature review to identify impacts and using a scoring system (Nentwig et al., 2010) to rank impacts by their severity and their type using a series of impact categories (e.g. environmental, economic and human health). None of these studies undertook any formal analysis using standardised data on economic costs. The results of these regional-scale studies indicate that some alien bird species are associated with both biodiversity impacts and socio-economic impacts. Indeed, alien bird species in Europe with damaging socio-economic impacts were found to also have damaging biodiversity impacts, although some alien bird species with minor socio-economic impacts also tended to have damaging biodiversity impacts (Kumschick et al., 2015).

Three of these studies identified traits associated with alien birds that may influence the severity of their biodiversity and socio-economic impacts (Evans et al., 2014; Kumschick et al., 2013; Shirley & Kark, 2009), and a further study analysed and identified traits associated with more severe biodiversity impacts (at the global scale) but did not undertake analysis on socio-economic impacts (Evans, Kumschick, et al., 2018) (see Table 1 for a summary of these studies). At the regional scale (Europe and Australia), traits associated with generalism; e.g. the number of different habitats a species occupies (habitat breadth) or the number of different dietary items a species consumes (diet breadth) are consistently correlated with both more severe biodiversity impacts and socio-economic impacts, whilst traits associated with resource use (e.g. body mass and flock-forming species) are less conclusive (Evans et al., 2014; Kumschick et al., 2013; Shirley & Kark, 2009). They also indicate that the influence of some traits has been tested for biodiversity impacts (Evans, Kumschick, et al., 2018) but not for socio-economic impacts, including for example, several traits associated with the distribution of alien birds, such as alien range size (Table 1).

Here, we aim to use EICAT, SEICAT and InvaCost data to identify specific types of impacts and factors associated with alien birds that link their biodiversity impacts with their economic costs at the global scale. Based on the results of past studies, we expect to find that the more severe the biodiversity impact caused by an alien bird species, the greater its economic costs will be (hypothesis 1). Because some impact mechanisms (particularly predation) are associated with severe biodiversity impacts (Evans, 2021; Evans et al., 2016), we expect to find that these impact mechanisms are also associated with higher economic costs (hypothesis 2). Finally, also based on the results of past studies, we expect to find

TABLE 1 Results of published studies that have examined the influence of variables on the severity of the biodiversity impacts and socio-economic impacts of alien birds.

Predictor variable	Linked to more severe biodiversity impacts	Linked to more severe socio-economic impacts
Body mass	↑ (Evans et al., 2014; Kumschick et al., 2013); ↓ (Shirley & Kark, 2009); NS (Evans, Kumschick, et al., 2018)	↑ (Evans et al., 2014); NS (Kumschick et al., 2013; Shirley & Kark, 2009)
Sociality (flock-forming species)	↑ (Shirley & Kark, 2009)	NS (Shirley & Kark, 2009)
Habitat breadth	↑ (Evans et al., 2014; Evans, Kumschick, et al., 2018); NS (Kumschick et al., 2013; Shirley & Kark, 2009)	↑ (Evans et al., 2014; Kumschick et al., 2013; Shirley & Kark, 2009)
Diet breadth	↑ (Evans, Kumschick, et al., 2018); NS (Evans et al., 2014; Kumschick et al., 2013)	↑ (Evans et al., 2014); NS (Kumschick et al., 2013)
Native range size	↑ (Evans, Kumschick, et al., 2018; Kumschick et al., 2013); NS (Evans et al., 2014)	↑ (Evans et al., 2014; Kumschick et al., 2013)
The proportion of a species' diet comprising animal matter	NS (Evans, Kumschick, et al., 2018)	NT
Alien residence time	↑ (Evans, Kumschick, et al., 2018)	NT
Alien range size	↑ (Evans, Kumschick, et al., 2018)	NT
Relative brain size	NS (Evans, Kumschick, et al., 2018)	NT

Note: ↑ = positive relationship identified; ↓ = negative relationship identified; NS = variable tested but no significant relationship identified; NT = variable not tested in previous studies.

that specific factors such as species traits (e.g. body mass) are associated with both severe biodiversity impacts and high economic costs (hypothesis 3).

2 | MATERIALS AND METHODS

2.1 | Data on biodiversity impacts

Data on biodiversity impacts were taken from published global EICAT assessments (Evans et al., 2016) and additional unpublished assessments completed in 2021, which were undertaken in accordance with the EICAT guidelines (IUCN, 2020). From these EICAT assessments, we took each alien bird species' most severe impact score (MC–MV) and the mechanism associated with this impact (competition, predation, hybridisation etc.). For some of these species, no impact data were available to assess their impacts (i.e. no data describing their impacts were found during online literature reviews completed for the EICAT assessments). These species were categorised as being 'data deficient' (DD) under EICAT. In total, our dataset included 121 alien bird species with an EICAT score (MC–MV) and 296 species that were DD (417 species in total) (see Table S1, Supporting Information). We excluded the feral pigeon (*Columba livia*) from our analysis as the true alien range of this species is unknown. See Figure S1 for a flowchart of the methods.

2.2 | Data on economic costs

The total costs caused by each alien bird species were calculated by summing each available economic cost record for an alien bird species from the InvaCost database (v4.1). These records include costs associated with damage (e.g. to agriculture) and management (e.g. the eradication of an alien bird population due to its damaging biodiversity impacts). All costs have been converted in the database to US$ (2017 value). For complete information on InvaCost methodology and calculation methods, see Leroy et al. (2022). There are many 'costs' associated with both the biodiversity and socio-economic impacts of alien species that are difficult to monetise (e.g. the extinction of a native bird species caused by a predatory alien bird species on an island, which results in a direct decline in biodiversity and may affect local communities by causing negative perceptions of their surrounding environment). Thus, our analysis is of monetary costs (and hereafter, costs are referred to as 'monetary costs').

We then reviewed a global alien bird SEICAT assessment (Evans et al., 2020) to gather any additional information on monetary costs caused by alien birds that were not in the InvaCost database. SEICAT assessments incorporate a literature review for each alien species to identify data describing its socio-economic impacts, including cost data (where available). Thus, we did not use the actual published SEICAT impact scores (MC–MV) for each alien bird species but rather reviewed the literature gathered on socio-economic impacts during the SEICAT assessments to identify any data on costs.

The monetary costs of alien bird species with weak socio-economic impacts may not have been calculated or reported because they are likely to be low (and therefore perceived not to be an issue of concern). Indeed, invasion biology research tends to focus on species with the most severe impacts (Pyšek et al., 2008). Therefore, to identify alien bird species with low monetary costs, where an alien bird SEICAT assessment identified literature indicating that the monetary costs of an alien bird species were likely to be negligible, we assigned a value of US$0 to these species as a proxy for their actual monetary costs. For example, the little owl (*Athene noctua*) has been introduced to New Zealand with the aim of controlling other introduced bird species, where it appears to have few negative socio-economic impacts (and associated costs) (New Zealand Birds Online, 2013); this species was assigned a US$0 cost value (see Table S2, Supporting Information, for species allocated a US$0 cost value). We treated all alien bird species that were categorised as DD under SEICAT (i.e. species for which no data on socio-economic impacts were identified during SEICAT assessments) as being DD under InvaCost (i.e. species for which no data on monetary costs were available). In total, our dataset included 40 species with cost data (either an actual cost (22 species) or a $0 cost value (18 species)) and 378 species that were DD for costs (total = 417 species; the same 417 species assessed under EICAT) (see Table S1, Figure S1, Supporting Information).

Our cost calculations included costs associated with the control or eradication of alien bird species, even if these actions were undertaken to manage biodiversity impacts. We recognise that there is a direct link between biodiversity impact and monetary cost in these cases. Nevertheless, some alien bird species may have negligible biodiversity impacts that do not warrant control or eradication. Further, some alien species may be easier (and less costly) to control than others (e.g. flightless alien bird species such as the weka, or bird species with small alien populations). Therefore, control and eradication costs are likely to vary depending on the characteristics of the targeted alien bird species and the severity of its biodiversity impacts.

Several of the 22 species with costs had either damage or management costs, but not both. This meant that the dataset of species was too small to undertake separate analysis of damage costs and management costs. We therefore combined damage and management costs for each species for the analysis.

Given the small number of alien bird species in our dataset, we acknowledge that the cost data we identified is unlikely to capture the complete range of monetary costs caused by alien birds. Indeed, our dataset is opportunistic, as the economic costs of alien species are not systematically studied, and therefore InvaCost only captures information on the costs of species that happen to be studied. Thus, our dataset represents a lower bound of costs associated with alien birds.

2.3 | Data on factors that may drive biodiversity impacts and monetary costs

We identified five broad hypotheses regarding the ways in which alien birds may cause biodiversity impacts and monetary costs

TABLE 2 Proposed hypotheses and their associated factors and variables.

Hypothesis	Factor	Predictor variable
H1: Resource use. Alien species with greater per capita resource requirements place greater demands on the environment, which may affect native biodiversity (e.g. overgrazing of native vegetation) or socio-economic interests (e.g. consumption of agricultural crops)	Size	V1: Body mass
	Whether alien bird species are solitary or flock-forming	V2: Sociality
H2: Generalism. Alien species with broad niches will have greater opportunity to cause impacts. For example, those occupying a wide range of habitats are likely to interact with a more diverse range of native species and assets of value to humans, increasing the chances that some of their impacts will be damaging to biodiversity or the economy. Habitat generalist alien birds have been found to have more severe impacts in Europe (Shirley & Kark, 2009) and Australia (Evans et al., 2014), and diet generalist alien birds have more severe impacts in Europe (Evans et al., 2014)	Habitat generalism	V3: Habitat breadth
	Diet generalism	V4: Diet breadth
	The size of an alien bird species native range (as an indicator of the breadth of environmental conditions a species may tolerate)	V5: Native range size
H3: Dietary preference. Specific diets of alien bird species are associated with specific types of impacts. For example, predatory alien birds (that eat animal matter) have been deliberately introduced to islands to control pest species (e.g. rats and insects) where they tend to have few reported economic impacts (perhaps because there are fewer opportunities for such impacts on islands) (Evans et al., 2020). However, they have reported biodiversity impacts on these islands (e.g. by preying on native birds) (Evans, 2021). Frugivorous alien birds may damage soft fruit, whilst seed-eating alien birds may damage crops (economic impacts), and both fruit and seed-eating alien birds may spread the seeds of alien plants (a biodiversity impact)	Diet preference (animal matter)	V6: The proportion of a species' diet comprising animal matter
	Diet preference (seeds and fruit)	V7: The proportion of a species' diet comprising seeds and fruit
H4: Distribution. Alien species that have more time to establish and spread may have more damaging impacts; those that are more widespread may have more damaging impacts, because they are likely to be more abundant and because they may have greater opportunity to cause impacts across the different types of habitats that they occupy	The length of time a species has been present as an alien	V8: Alien residence time
	The size of a species alien range	V9: Alien range size
H5: Ecological flexibility. Alien species that are better able to adapt to their new environment are more likely to thrive and cause impacts	Brain size (relative to body mass)	V10: Relative brain size

(H1–H5; Table 2). We collected data on a series of predictor variables associated with each of these hypotheses that are linked to specific factors associated with alien bird species (Table 2). See Data Sources for the sources of data for predictor variables. See Table S3, Supporting Information, for variable descriptions.

2.4 | Analysis—Linking severe biodiversity impacts with monetary costs; linking types of biodiversity impact with monetary costs

Our analysis of links between biodiversity impacts and monetary costs was restricted to species for which we had both an EICAT score and a cost value (40 species). Species categorised as DD under EICAT and/or InvaCost were excluded. Due to small sample sizes for certain EICAT impact categories (MR impacts, $n=3$; MV impacts, $n=1$), we converted EICAT data into a two-level variable: 'less severe' impacts (MC and MN impacts), $n=23$ species, and 'more severe' impacts (MO, MR and MV impacts), $n=17$ species. This divided impact severity such that 'less severe' impacts were those considered to be negligible (MC) or to affect the fitness of individuals of a native species (MN impacts), and 'more severe' impacts were those considered to be 'harmful' under EICAT because they cause declining populations of native species (MO impacts) and local or global species extinctions (MR and MV impacts, respectively). Costs were analysed as a continuous variable (US$).

As our dataset considers traits known to be influenced by phylogeny (e.g. body mass) and specific orders and families of alien birds are associated with specific types of impact (e.g. Anatidae with hybridisation), we expected our analysis to be influenced by phylogenetic autocorrelation. Following Evans et al. (2021), we used Birdtree.org (http://birdtree.org/) to download 100 randomly selected phylogenetic trees incorporating the 40 species in our dataset. We used *phylo.d* (Fritz & Purvis, 2010) in the *Caper* package in R (Orme et al., 2018) to calculate the D statistic (a measure of phylogenetic signal in a dataset) for each phylogenetic tree. We identified phylogenetic signal in severity of impact (average $D=0.4$) with a low probability of D resulting from no phylogenetic structure (average $p=0.03$) or Brownian phylogenetic structure (average $p=0.2$). To address this, we analysed our dataset using phylogenetic linear regression (regression analysis incorporating phylogenetic methods) (Revell, 2010) (the *phylolm* package in R) (Tung Ho & Ané, 2014) to account for potential phylogenetic relatedness among species.

We first compared the association between the severity of biodiversity impacts and monetary costs (phylogenetic linear regression using the *phylolm* package [and the *phylolm* function]) (Tung Ho & Ané, 2014), with biodiversity impact as a two-level predictor variable as previously described ('less severe' impacts and 'more severe' impacts), and costs as a continuous response variable). We then compared the association between different types of biodiversity impacts (using EICAT impact mechanism categories, e.g. competition, predation) and monetary costs. We divided each EICAT impact mechanism into a two-level predictor variable (e.g. competition impact = '1', no competition impact = '0'). Competition and predation impacts were analysed separately (competition impact, $n=13$ species, no competition impact, $n=27$ species; predation impact, $n=15$ species, no predation impact, $n=25$ species). Due to small sample sizes, impacts caused by other mechanisms (hybridisation, grazing, disease transmission, parasitism and structural impacts) were pooled to form a single group titled 'Other impact mechanisms' (impact, $n=17$ species, no impact, $n=23$ species). Costs were again analysed as a continuous response variable. We included all impacts caused by a species (not only a species' most severe impacts) when identifying the types of impacts they have. Where a species' impacts were associated with more than one impact mechanism, they were analysed for each of these mechanisms.

2.5 | Analysis—Identifying drivers of biodiversity impacts and monetary costs

We used the same 100 randomly selected phylogenetic trees, and phylogenetic linear regression (the *phylolm* function) (Tung Ho & Ané, 2014). We analysed each of the 10 predictor variables against (1) severity of biodiversity impact (a two-level response variable—'less severe' impacts and 'more severe' impacts using the *phyloglm* function), and (2) monetary cost (a continuous response variable using the *phylolm* function). The biodiversity impact analysis was similar in approach to that published by Evans, Kumschick, et al. (2018) (the results of this study are summarised in Table 1) but with a different set of alien bird species and a modified set of predictor variables. Undertaking the biodiversity impact analysis in this study, instead of using the results published in Evans, Kumschick, et al. (2018), enabled direct comparisons with the monetary cost analysis undertaken in this study.

We analysed each response variable separately (univariate analysis) and then all variables together, to identify variables with the strongest influence on biodiversity impact and monetary cost (multivariate analysis). We checked for multi-collinearity among variables using the *car* package (Fox & Weisberg, 2019), finding slight evidence for this (highest VIF value = 3.8; Table S4, Supporting Information). To address this, we removed two variables that were not found to be significant in univariate analysis (V2: Sociality and V10: Relative brain size). This reduced VIF values (all >3; Table S4, Supporting Information). During multivariate analysis, for the analysis of monetary costs (using the *phylolm function*), we used the *dredge* function in the *MuMIn* package (Bartoń, 2020) to undertake automated model simplification to identify the best-reduced model as ranked by AIC. For the analysis of biodiversity impacts (using the *phyloglm* function), we were unable to use the *dredge* function. So we reduced the model manually; after each run of the model, we removed the least significant variable, repeating this process to find the best model (as measured by AIC). This approach to model simplification follows that adopted for a related study which identified factors which influence the severity of the biodiversity impacts of alien birds (Evans, Kumschick, et al., 2018). Data for monetary cost, native and alien range size, alien residence time, body mass, brain size, diet preference (animal matter) and diet preference (seeds and fruit) were log-transformed. Plots to show the distribution of the raw data (including log transformations) are provided at Appendix A, Supporting Information. All analyses were conducted in R (version 4.1.2) (R Core Team, 2021).

3 | RESULTS

The global distribution of the most severe biodiversity impacts and monetary costs of the 40 alien bird species in our dataset is shown in Figure 1. A summary of these impacts and costs for each alien bird species is provided in Table S2, Supporting Information.

3.1 | Linking severe biodiversity impacts with monetary costs; linking types of biodiversity impact with monetary costs

We did not find a consistent association between severity of biodiversity impact and monetary cost, although relationships were identified for some of the 100 phylogenies analysed (Table 3). Alien bird species with reported predation impacts tended to have higher monetary costs (Table 3, Figure 2). No associations between other types of biodiversity impact (competition and 'other impact mechanisms') and monetary costs were identified (Table 3). Residual plots and model output summaries are provided in Appendix A, Supporting Information.

3.2 | Drivers of biodiversity impacts and monetary costs

In univariate analysis, positive relationships were identified for variables associated with generalism (hypothesis H2). Habitat generalist alien bird species had both more severe biodiversity impacts and higher monetary costs, while diet generalist alien bird species had more severe biodiversity impacts (and higher monetary costs for some of the phylogenies tested, though this effect was not significant on average) (Table 4). These were the only variables linked to both more severe biodiversity impacts and high monetary costs. Positive relationships were also identified

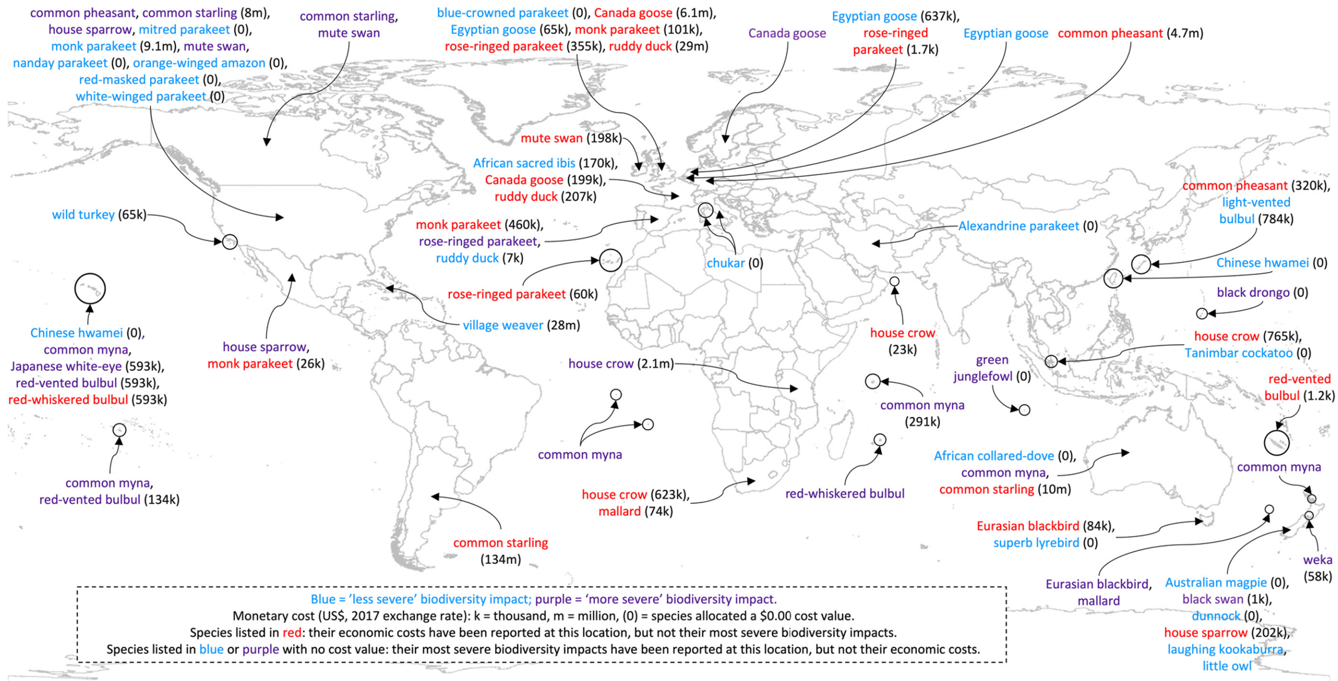

FIGURE 1 The global distribution of the biodiversity impacts and monetary costs associated with 40 alien bird species.

TABLE 3 The relationship between the total monetary costs of alien bird species and (1) the severity of their biodiversity impacts, (2) different types of biodiversity impact. All parameters in this table derive from phylogenetic linear regression using the *phylolm* package in R (Tung Ho & Ané, 2014) to account for potential autocorrelation among 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 provided in parentheses). Total sample size = 40 species. Significance codes: '***'$p < 0.001$ '**'$p < 0.01$ '*'$p < 0.05$.

Predictor variable	Estimated coefficient	Standard error	*p*
(1) Severity of biodiversity impact	1.55 (1–2)	0.71 (0.67–0.75)	0.05 (0.008**–0.14)
(2a) Competition impact (yes/no)	0.96 (0.62–1.2)	0.76 (0.6–0.85)	0.22 (0.14–0.31)
(2b) Predation impact (yes/no)	2.16 (1.79–2.48)	0.62 (0.54–0.68)	0.003** (<0.001***–0.01*)
(2c) Other impact mechanisms (yes/no)	0.11 (−0.12–0.4)	0.81 (0.61–0.91)	0.87 (0.66–0.99)

for variables associated with distribution (hypotheses H4). Alien bird species with larger alien ranges had higher monetary costs, and those that have been present for longer also had higher monetary costs (though not for all 100 phylogenies tested) (Table 4). No relationships were identified for any variables associated with other hypotheses; resource use, dietary preference and ecological flexibility (hypotheses H1, H3 and H5, respectively) (Table 4). For variables with significant relationships, the distribution of species by the severity of their biodiversity impacts and their monetary costs is shown in Figure 3.

Analysing all variables together, alien bird species with more severe biodiversity impacts tended to be diet generalists, whilst alien birds with higher monetary costs tended to have larger alien ranges (Table 5). The univariate relationship between habitat breadth and more severe biodiversity impacts was not recovered; nor were the univariate relationships between habitat and diet breadth and higher monetary costs, and alien residence time and higher monetary costs.

3.3 | Data deficiency

Most alien bird species in our dataset were data deficient for both biodiversity impacts and monetary costs ($n = 296$, 71% of all species) (Table S1, Supporting Information). Some species with reported biodiversity impacts were data deficient for monetary costs ($n = 81$, 19% of all species). No species that were data deficient for biodiversity impacts had data describing their monetary costs (Table S1, Supporting Information).

4 | DISCUSSION

4.1 | Linking severity and type of biodiversity impact with high monetary costs

The biodiversity impacts of alien birds are often difficult to monetise. For example, the alien Chinese hwamei (*Garrulax canorus*) hybridises with the native Taiwan hwamei (*Garrulax taewanus*) (Li

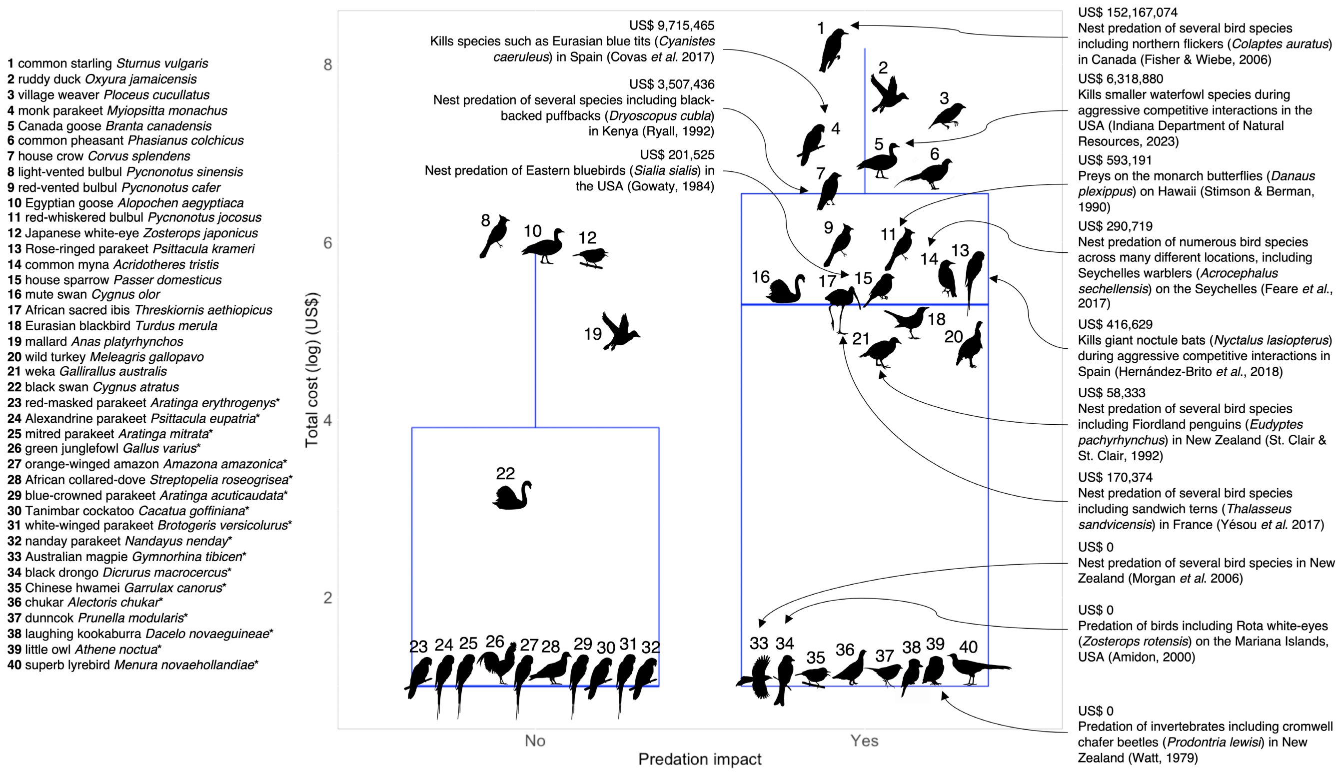

FIGURE 2 The total monetary costs caused by alien bird species as distributed by whether they do or do not have reported predation impacts. *y*-axis = the total monetary cost (logged) of an alien bird species (US$). Total costs (combined damage and management costs) and examples of predation impacts are provided for selected species. * = species assigned a US$0 cost value. Total species = 40. Bird species images were plotted manually over data points. Data points were distributed using jitter to prevent them from overlapping. Boxplots show the median and first and third quartiles (the 25th and 75th percentiles). All bird species images are used under the Public Domain Dedication 1.0 Licence, except: feral pigeon (Luc Viatour (source photo) and Andreas Plank); common starling (Gareth Monger); ruddy duck (Gabriela Palomo-Munoz); common myna (Maxime Dahirel); Eurasian blackbird (Anthony Caravaggi); weka (T. Michael Keesey (vectorisation) and HuttyMcphoo (photography)); and common peafowl (Cathy). These images are used under the Creative Commons Attribution 3.0 Unported Licence (https://creativecommons.org/licenses/by/3.0/), the Creative Commons Attribution-ShareAlike 3.0 Unported Licence (https://creativecommons.org/licenses/by-sa/3.0/) and the Creative Commons Attribution-NonCommercial-ShareAlike 3.0 Unported Licence (https://creativecommons.org/licenses/by-nc-sa/3.0/).

et al., 2010) in Taiwan, but this hybridisation appears to have no tangible costs. Our assessment does not, therefore, capture certain 'costs' caused by alien birds. Indeed, monetary costs only tend to be reported when biodiversity impacts are considered severe enough to warrant management. However, the biodiversity impacts of alien birds in general tend to be relatively minor and often go unmanaged (Evans et al., 2016). This may be why we did not identify a link between the severity of the biodiversity impacts caused by alien birds and high monetary costs. Indeed, the highest costs caused by alien birds tend to be associated with damage to assets of value (such as buildings and agricultural crops) rather than their biodiversity impacts (Evans et al., n.d.).

However, we did find predatory alien birds to be associated with monetary costs. The cost calculations for our analysis are of combined management and damage costs, and not all costs associated with predatory alien bird species arise due to the management of their predation impacts; some are the result of the damage they cause to assets of value (e.g. agriculture). Predatory alien birds may therefore be associated with costs in part because they tend to possess characteristics that provide them with greater opportunity to cause impacts (and not only through predation of native species). Indeed, the alien bird species in our dataset with reported predation impacts tend to be diet and habitat generalists (average diet and habitat breadth score = 4 and 5, respectively) when compared to species that do not have reported predation impacts (2.7 and 3.2, respectively); they also tend to have larger alien ranges (average = 3,690,419 km^2 vs. 165,077 km^2). Nevertheless, predation by alien birds can be damaging to native species (Evans, 2021; Evans et al., 2016), and due to the severity of these impacts, predatory alien birds may be targeted for management and thus be associated with monetary costs. For example, species in our dataset that have been managed due to their predation impacts include the African sacred ibis (*Threskiornis aethiopicus*), common myna (*Acridotheres tristis*), house crow (*Corvus splendens*) and weka (*Gallirallus australis*). Indeed, invasion biology research tends to focus on alien species with severe biodiversity impacts (Pyšek et al., 2008), and there may therefore be more studies to identify predation impacts in comparison to other impact mechanisms, and hence more schemes to

TABLE 4 The relationships between the biodiversity impacts and monetary costs caused by alien bird species and 10 predictor variables. All parameters in this table derive from phylogenetic linear regression using the *phylolm* package in R (Tung Ho & Ané, 2014) to account for potential autocorrelation among 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 provided in parentheses). Significant relationships ($p < 0.05$) are highlighted in bold. Total sample size = 40 species. Significance codes: '***' $p < 0.001$, '**' $p < 0.01$, '*' $p < 0.05$.

		Biodiversity impact			Monetary cost		
Hypothesis	Predictor variable	Estimated coefficient	Standard error	*p*	Estimated coefficient	Standard error	*p*
H1: Resource use	V1: Body mass	−0.005 (−0.07–0.28)	0.49 (0.46–0.51)	0.93 (0.59–0.1)	−0.56 (−0.91–−0.18)	1.07 (1–1.14)	0.62 (0.4–0.87)
	V2: Sociality	−0.13 (−0.19 – −0.07)	0.31 (0.3–0.32)	0.68 (0.53–0.82)	0.61 (0.44–0.8)	0.45 (0.4–0.51)	0.2 (0.08–0.34)
H2: Generalism	V3: Habitat breadth	0.5 (0.48–0.54)	0.22 (0.22–0.23)	**0.02*** (**0.02***–**0.03***)	0.56 (0.46–0.68)	0.2 (0.19–0.21)	**0.009**** (**0.002****–**0.02***)
	V4: Diet breadth	0.82 (0.77–0.87)	0.33 (0.32–0.34)	**0.01*** (**0.01***–**0.02***)	0.6 (0.39–0.72)	0.31 (0.27–0.35)	0.07 (**0.02***–0.17)
	V5: Native range size	0.55 (0.33–0.71)	0.45 (0.42–0.48)	0.23 (0.1–0.44)	0.91 (0.57–1.11)	0.57 (0.45–0.63)	0.12 (0.08–0.21)
H3: Dietary preference	V6: Proportion animal matter	0.48 (0.18–0.57)	0.91 (0.88–0.94)	0.6 (0.52–0.85)	−0.07 (−0.89–0.88)	1.53 (1.3–1.79)	0.8 (0.5–0.99)
	V7: Proportion seeds and fruit	−0.45 (−0.69–−0.04)	0.95 (0.91–0.99)	0.64 (0.46–0.97)	2.28 (1.76–2.68)	1.64 (1.46–1.82)	0.17 (0.12–0.27)
H4: Distribution	V8: Alien residence time	1.37 (1.15–1.59)	0.9 (0.86–0.93)	0.13 (0.08–0.19)	2.11 (1.37–2.53)	0.81 (0.68–0.9)	**0.02*** (**0.002****–0.05)
	V9: Alien range size	0.44 (0.36–0.49)	0.29 (0.28–0.3)	0.13 (0.1–0.21)	0.96 (0.8–1.11)	0.27 (0.25–0.29)	**0.001**** (**<0.001*****–**0.004****)
H5: Ecological flexibility	V10: Relative brain size	−0.47 (−0.5–−0.43)	0.27 (0.27–0.28)	0.09 (0.06–0.11)	−0.61 (−0.94–−0.37)	0.8 (0.75–0.89)	0.46 (0.26–0.64)

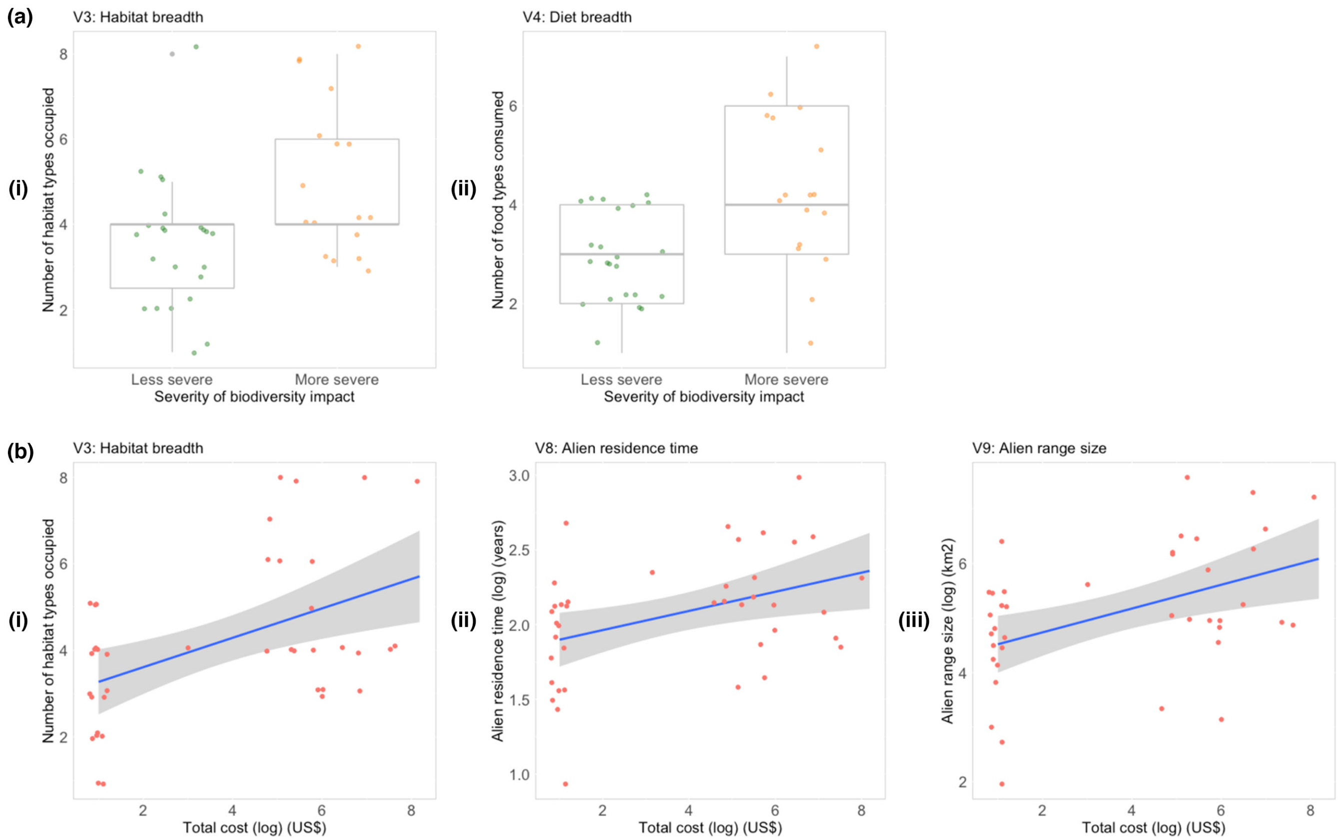

FIGURE 3 (a) The severity of the biodiversity impacts caused by alien bird species as distributed by their: (i) habitat breadth and (ii) diet breadth. (b) The total monetary costs caused by alien bird species as distributed by their: (i) habitat breadth, (ii) alien residence time and (iii) alien range size. *x*-axis (a) = the severity of the biodiversity impacts caused by an alien bird species. 'Less severe' = impacts categorised as MC under EICAT (alien bird species with no discernible impacts) and impacts categorised as MN under EICAT (impacts that affect the fitness of individuals of a native species), $n = 23$. 'More severe' = alien species with impacts categorised as MO, MR and MV under EICAT (population level impacts that are defined as being 'harmful' under EICAT), $n = 17$. *x*-axis (b) = the total monetary cost caused by an alien bird species (US$). Total species = 40. Boxplots in (a) show the median and first and third quartiles (the 25th and 75th percentiles), with outliers plotted on grey. Trend lines in (b) are the simple linear fit of the relationship between the variables used in the analysis.

TABLE 5 Multivariate analysis showing significant relationships following model simplification (the best reduced model as ranked by AIC). All parameters in this table derive from phylogenetic linear regression using the *phylolm* package in R (Tung Ho & Ané, 2014) to account for potential autocorrelation among species due to their phylogenetic relatedness. Total sample size = 40 species. Significance codes: '***' $p < 0.001$, '**' $p < 0.01$, '*' $p < 0.05$. ~ = variable did not feature in model.

		Biodiversity impact			Monetary cost		
Hypothesis	**Predictor variable**	**Estimated coefficient**	**Standard error**	***p***	**Estimated coefficient**	**Standard error**	***p***
H2: Generalism	V3: Habitat breadth	0.42	0.23	0.07	~	~	~
	V4: Diet breadth	0.81	0.35	0.02*	~	~	~
H3: Dietary preference	V7: Proportion seeds and fruit	~	~	~	2.51	1.36	0.07
H4: Distribution	V9: Alien range size	~	~	~	0.89	0.28	0.003**

manage predation impacts. Several other species in our dataset have attracted research to assess the effect of their predation impacts; e.g. the common starling (Fisher & Wiebe, 2006) and the little owl (*Athene noctua*) (Hayden, 2004).

However, because some alien bird species prey on other species to survive, predation impacts are likely to occur more frequently than impacts associated with some other mechanisms, such as hybridisation and transmission of diseases, and thus there may be more management schemes (with costs) to control and eradicate them. Furthermore, predation impacts may be easier to identify than impacts caused through other mechanisms, such as competition, hybridisation and the transmission of diseases (Evans et al., 2021;

Tompkins & Jakob-Hoff, 2011), and some predatory alien birds are relatively large species (though not always, see Figure 2) that prey on smaller bird species (Evans, 2021), and their size may make them easier to identify and control. Thus, due to the relatively high frequency of occurrence of predation impacts, and the relative ease of the identification of predation impacts and management of (some) predatory alien birds, they are more likely to be associated with monetary costs than other impact mechanisms. Interventions to stop the introduction of predatory alien birds may prevent frequent (and potentially severe) biodiversity impacts and unwanted monetary costs associated with schemes to manage them.

4.2 | Identifying factors associated with biodiversity impacts and monetary costs

Our results suggest that certain factors afford alien birds greater opportunity to cause deleterious effects, whether they be on biodiversity or the economy, or both. Habitat and diet generalists are more likely to have impacts than specialist species restricted to a limited range of environments and food types. This may be because they have greater opportunity to cause impacts, as they are likely to interact with a broader range of native species and to come into contact with a wider range of assets of value to humans. Indeed, the species in our dataset with broad environmental tolerances also tend to be able to occupy urban environments, where they may cause biodiversity impacts in parks and gardens and affect assets of value such as buildings. All but one of the eight species with the greatest habitat breadth in our dataset (occupying six or more broad habitat types) have severe biodiversity impacts and monetary costs >$0.

Variables associated with the geographic distribution of alien species (alien residence time, and in particular, alien range size) were also predictors of monetary costs. This is likely to be because widespread species have a greater opportunity to cause deleterious effects on both biodiversity and the economy and in different ways at different locations (see Figure 1). For example, the common myna has one of the largest alien ranges in our dataset (>2,300,000 km^2; the median for all species in our dataset = 114,864 km^2). It has reported monetary costs on French Polynesia and Seychelles (Evans et al., n.d.) and reported competition impacts in Australia (Grarock et al., 2012) and predation impacts in Israel, and on Seychelles, Cook Islands, Saint Helena, Ascension Island, Hawaii, Mauritius and Midway Atoll (it is known to prey on at least 16 native bird species from five orders) (Evans, 2021). Alien bird species present for longer time periods have had more time to establish and spread. For example, the African sacred ibis was introduced to France in the 1970s, and its population spread along the Atlantic Coast over several decades before the implementation of a costly eradication programme to address its unwanted impacts, which included predation of native birds (Yésou et al., 2017).

Because generalist and widespread alien bird species have a greater opportunity to cause deleterious effects (on either biodiversity or the economy), they are also more likely to be subject to control or eradication measures, which can be costly. Indeed, over half of the 10 species in our dataset with the greatest habitat breadth and longest alien residence times have reported costs associated with their management. These costs are likely to increase as the distributional extent of an alien species' increases and it becomes more difficult to control or eradicate. The unsuccessful eradication of approximately 1 million house crows in Zanzibar (Tanzania), undertaken to address deleterious effects on both biodiversity and the economy (ZABISO, 2020), has so far cost approximately US$1.5 million (van Ham et al., 2013); the successful eradication of a small population of house crows (<30) on Socotra Island (Yemen) cost US$20,500 (Suleiman & Taleb, 2010).

Our results suggest that timely management interventions, sensu (Hulme et al., 2009), to limit the distributional extent of alien bird species (particularly generalist species and those that prey on native species) may have important benefits for both biodiversity and the economy. It may be too late to efficiently address the impacts of some widespread, generalist, predatory alien bird species such as the ring-necked parakeet (*Psittacula krameri*) in the UK, as these efforts are now likely to be costly (Ahmed et al., 2022). However, there may be opportunities to do so for recent alien bird incursions, and for those occurring in the future (alien species' numbers are predicted to rise considerably by 2050, including numbers of alien bird species) (Seebens et al., 2021). In the UK, for example, climate change may be assisting the establishment of the red-billed leiothrix (*Leiothrix lutea*) (Broughton et al., 2022).

We identified a negative (though non-significant) trend between relative brain size and both severity of biodiversity impact and monetary cost. This is likely due to the presence of several parrot species in our dataset, which are large-brained and tend to have minor biodiversity impacts and low (or no) reported monetary costs. That said, two parrot species in our dataset do have high reported monetary costs (the ring-necked parakeet and the monk parakeet [*Myiopsitta monachus*]), and the ring-necked parakeet also has 'more severe' biodiversity impacts; e.g. by preying on native bat species in Spain (Hernández-Brito et al., 2018). Notably, these are the two parrot species in our dataset with the largest alien ranges, longest alien residence times and greatest habitat breadth scores (all variables associated with severe biodiversity impacts and/or monetary costs).

4.3 | Comparing our results to past studies

Although our dataset is relatively small (40 species; approximately one-third of the 116 species identified as having environmental impacts worldwide) (Evans et al., 2016), the biodiversity impacts and monetary costs in our dataset are broadly distributed across the globe. In another global study (Evans, Kumschick, et al., 2018), factors associated with the distributional extent of alien birds (alien range size and alien residence time) were found to be predictors of more severe biodiversity impacts. Our study is the first to test the influence of these factors on the socio-economic impacts (monetary costs) of alien birds, and we confirm that distributional extent not only drives more severe biodiversity impacts but also high monetary costs. Our results for generalism support the findings of previous studies, which have found habitat and diet breadth to be predictors of more severe biodiversity impacts at the global scale (Evans, Kumschick, et al., 2018) and habitat breadth to be a predictor of more severe biodiversity and socio-economic impacts at the regional scale (Evans et al., 2014; Kumschick et al., 2013; Shirley & Kark, 2009). However, our study was the first to use cost data, and it demonstrates that generalism is specifically linked with higher costs (as opposed to broadly defined socio-economic impacts). Indeed, using data on costs, our study is the first to try to link the severity and type of biodiversity impacts caused by alien birds with their monetary costs. In so doing, our study demonstrates that predation impacts are more likely to be associated with monetary costs when compared to other mechanisms.

Two regional studies found body mass to be associated with more severe biodiversity impacts and socio-economic impacts in Europe (Evans et al., 2014; Kumschick et al., 2013), but we did not identify any significant relationships with body mass at the global scale. For biodiversity impacts, this may be because analysis undertaken in the two regional studies did not include data on island impacts (as many islands occupied by alien birds are located outside of Europe). Biodiversity impacts caused by alien birds tend to be particularly severe on islands (Evans, 2021; Evans et al., 2021), and some of these impacts (in our dataset) are caused by relatively small alien bird species such as the red-vented bulbul (*Pycnonotus cafer*). With regard to monetary costs, there are several relatively small alien bird species in our dataset that have costs by causing agricultural damage in low-income regions, such as the village weaver (*Ploceus cucullatus*) in the Dominican Republic; there are many low-income regions outside of Europe. The contrasting results of these regional studies and our global study suggest that alien bird risk assessments should account for scale. For example, our results may not be as relevant to biodiversity risk assessments for alien bird incursions within mainland Europe, where no islands are present.

4.4 | Data deficiency and impact prediction

Most alien bird species in our dataset do not have reported biodiversity impacts or monetary costs. It has been concluded that alien bird species with no reported biodiversity impacts that have large alien ranges and/or long alien residence times are likely to have minor biodiversity impacts because if these impacts were severe, they would have been noticed and reported (Evans, Pigot, et al., 2018). On this basis, we suggest that alien bird species with these traits that have no reported monetary costs are genuinely likely to have low monetary costs (those that can be monetised). However, as the impacts of alien species tend to be context dependent (Pyšek et al., 2020), and human development influences the availability of impact data across different regions of the world (Evans & Blackburn, 2020), we cannot rule out that some alien bird species with no reported costs do actually have monetary costs particularly in less developed regions. Indeed, the economic impacts of alien species are often felt most acutely by the rural poor, where they affect agricultural activities and food security (Perrings, 2005), but alien species tend to be less studied in these regions (Bellard & Jeschke, 2015).

Many species ($n=81$) with reported biodiversity impacts are data deficient for monetary costs. Nevertheless, these species tend to have relatively small alien ranges when compared to alien bird species with reported monetary costs (Figure S2, Supporting Information). As we found alien range size to be positively correlated with monetary cost, it is possible that some of these species will have low monetary costs. Nevertheless, some of the 81 species that are data deficient for monetary costs have relatively large alien ranges, such as the house finch (*Haemorhous mexicanus*) (see Figure S2, Supporting Information). As alien range size is positively correlated with cost, species like this may have monetary costs that (as far as we are aware) have not been published.

Four predatory alien bird species (raptors) that have been introduced to oceanic islands to control rats and insect pests have severe biodiversity impacts by preying on native species, but they are data deficient for monetary costs; the Australian masked-owl (*Tyto novaehollandiae*), barn owl (*Tyto alba*), great horned owl (*Bubo virginianus*) and swamp harrier (*Circus approximans*) (Figure S2, Supporting Information). Their predation impacts may be difficult to value, and their opportunity to cause negative socio-economic impacts on islands may be limited, as there may be fewer assets of value to affect, and thus their costs may be low (Vaissière et al., 2022). This may be why two other species with severe biodiversity impacts on islands have a cost value of US$0 (the green junglefowl (*Gallus varius*) and black drongo (*Dicrurus macrocercus*) (Figure S2, Supporting Information). This absence of cost data for raptors on islands may appear to counter our result regarding the positive association between predation and monetary costs. However, the Australian masked-owl is to be eradicated from Lord Howe Island (Australia) due to the severity of its biodiversity impacts (O'Dwyer & Carlile, 2016), and barn owls are being managed in Hawaii due to their biodiversity impacts (Bean, 2013; Raine et al., 2019). These management actions will be costly, but as far as we are aware, these costs have not been published. Thus, severe predation impacts on islands may also drive monetary costs. This may also appear to counter our result regarding the positive association between alien range size and monetary cost (as being on islands, these alien raptor species have small alien ranges; Figure S2, Supporting Information). However, costs incurred managing alien raptors on islands are likely to be relatively low compared to damage and management costs associated with broadly distributed alien bird species at mainland locations (Evans et al., n.d.).

5 | CONCLUSIONS

By combining data on the biodiversity impacts, socio-economic impacts and monetary costs of alien birds, we identify links between their biodiversity impacts and monetary costs. Our results indicate that management interventions to prevent the introduction of both predatory and generalist alien bird species, or that reduce their geographic distribution at early stages of invasions, may have significant biodiversity and economic benefits. We missed the opportunity to efficiently manage some alien bird species which are now widespread and abundant across many regions of the world; we need not miss these opportunities for future alien bird invasions, which are predicted to increase in number in the future (Seebens et al., 2021). Whilst we lack data on the monetary costs associated with many alien bird species, we predict that some of these species are likely to have low monetary costs. Nevertheless, our results lead us to conclude that species with no reported costs but with large alien ranges and/or predation impacts should be further studied as potential candidates for high monetary costs.

AUTHOR CONTRIBUTIONS

Thomas Evans and Franck Courchamp conceived the study; Thomas Evans designed the methodology, collected and analysed the data and led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

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CONFLICT OF INTEREST STATEMENT

The authors declare that they have no conflicting interests.

DATA AVAILABILITY STATEMENT

Data used for the analysis in this study are available from the Dryad digital repository: DOI: https://doi.org/10.5061/dryad.dz08kps35 (Evans et al., 2023).

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Table S1. The number of alien bird species with and without data describing their biodiversity impacts and monetary costs.

Table S2. Summary of each alien bird species' most severe biodiversity impact and total monetary costs.

Table S3. Predictor variable descriptions.

Table S4. Variance Inflation Factor values for predictor variables.

Figure S1. Methods flowchart.

Figure S2. (a) The most severe biodiversity impact caused by each alien bird species that is data deficient (DD) for monetary costs (i.e. has no reported costs). (b) The alien range size of each alien bird species that has a biodiversity impact and a monetary cost value ('Species with costs') compared with the alien range size of each alien bird species that has a biodiversity impact but that is DD for monetary costs ('Species DD for costs').

Appendix A: Figure A1. Plots showing the distribution of data before and after being log transformed.

Figure A2. Residual plot and density plot for the biodiversity impact mechanism found to influence monetary costs (predation).
Figure A3. Residual plots and density plots for multivariate analysis: (a) biodiversity impacts, and (b) monetary costs.
Table A1. Root Mean Squared Errors (RMSE).
Model output summaries.

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