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1 **When origin, reproduction ability, and diet define the role of birds in invasions**

2

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8

9 **Title**

10 **When origin, reproduction ability, and diet define the role of birds in invasions**

11 **Abstract**

12 Introduced alien species can severely impact native biodiversity. While these impacts are well  
13 documented in the literature, they are usually studied through the lens of either the invasive  
14 alien species (IAS) or the native species that suffer from them but not both. A clear  
15 understanding of how both protagonists of biological invasions are characterized according to  
16 their impact is still lacking. Here, we analyzed the ecological strategies of 850 alien birds and  
17 IAS-threatened native birds. Using traits related to species morphology, life history, and  
18 ecology, we distinguished functional groups of birds based on their role in biological  
19 invasions. We then evaluated the functional characterization of these groups according to two  
20 impact magnitudes (high and low impact) and three invasion mechanisms (habitat effect,  
21 direct species effect, and indirect species effect). We found that alien birds and IAS-  
22 threatened native birds were functionally distinct: the former had mainland populations,  
23 deeper beaks, and larger clutches, while the latter were more insular endemic species with an  
24 insessorial foraging niche and animal-based diet. Impact magnitude was further correlated to  
25 generalist behavior for alien birds and insular endemism for IAS-threatened birds. By  
26 contrast, the impact mechanism was poorly explained by traits, except for native birds  
27 threatened by a direct species effect (e.g., predation), which were more insular endemic,  
28 larger, and with a longer beak than birds threatened by a habitat effect. By conjointly  
29 addressing the functional aspects of threatened and threatening diversity, this paper provides a  
30 new perspective on the global consequences of biological invasions.

31 **Keywords**

- 32 Aliens, birds, impact magnitude, impact mechanism, invasive species, native species,  
33 threatened species, traits

## 34 **Introduction**

35 Biological invasions are responsible for major ecological and socioeconomic impacts  
36 worldwide (Ricciardi et al. 2013, Diagne et al. 2021). Invasive alien species (IAS) have many  
37 ecological consequences on native ecosystems, ranging from negligible species disturbance to  
38 population extirpation or species extinction (Blackburn et al. 2004, Bellard et al. 2016a,  
39 Vanbergen et al. 2018). Their introduction is often accompanied by a panel of cascade effects  
40 on ecosystem processes and functions (Simberloff et al. 2013). Attempts to evaluate and  
41 classify IAS impacts have been widely developed, resulting in protocols that vary according  
42 to the studied taxa, spatial scales, habitat types, or objectives (González-Moreno et al. 2019).  
43 Among these initiatives, the Environmental Impact Classification for Alien Taxa (EICAT)  
44 classifies the ecological impacts of alien species in a standardized and objective manner  
45 (Blackburn et al. 2014, Hawkins et al. 2015). This protocol has been applied to a growing list  
46 of alien taxa, including birds (Evans et al. 2016), and was recently adopted by the  
47 International Union for Conservation of Nature (IUCN) to develop a reproducible and global  
48 framework to evaluate IAS impacts (IUCN 2020a). The IUCN Red List Threat Classification  
49 Scheme also provides another point of view for assessing the biodiversity impacted by IAS  
50 (IUCN 2020b). When taken together, the EICAT protocol and the IUCN Red List represent  
51 two powerful tools for studying the impacts of biological invasions at a global scale, as they  
52 focus on both aliens and native species threatened by IAS (hereafter, IAS-threatened species)  
53 (Bellard et al. 2016b, Van der Colff et al. 2020, Harfoot et al. 2021). Nevertheless, no study to  
54 date has conjointly characterized these impacts through the lens of both alien and IAS-  
55 threatened species.

56 Invasion success is mediated by various factors that interact with each other such as the  
57 characteristics of the recipient communities, invasion-related features, and species ecological  
58 traits (Pyšek et al. 2020). Morphological, life history, and ecological traits are indeed at the

59 core of global-scale studies aiming to explain the invasion success of species, namely  
60 mammals (Capellini et al. 2015), birds (Blackburn et al. 2009, Sol et al. 2012), amphibians  
61 and reptiles (Allen et al., 2017), fish (Ruesink 2005), and plants (van Kleunen et al. 2010).  
62 For instance, Sol et al. (2012) showed that despite the complex interactions between the life  
63 history traits and establishment success of alien birds, their traits contribute undeniably to  
64 explain the differences in alien performances: the low brood value and high relative brain size  
65 of birds enhance their establishment success. Furthermore, bird ecological traits such as  
66 habitat and diet breadth or alien range size are also correlated with their negative ecological  
67 impact (Shirley and Kark 2009, Evans et al. 2014, 2018a). More recently, large-scale studies  
68 evaluated the role of ecological traits in the vulnerability of IAS-threatened species, which are  
69 the other key participants in the dynamics of invasion (Leclerc et al. 2020, Bellard et al. 2021,  
70 Marino et al. 2021). Regarding impacting aliens, IAS-threatened species present specific traits  
71 that contribute to their vulnerability to biological invasions. For instance, Bellard et al. (2021)  
72 showed that water-level foragers and large-sized species are overrepresented among IAS-  
73 threatened birds. Indeed, many studies seek to explain invasion success by comparing the life  
74 history traits of threatened native species and successful alien species (Liu et al. 2017, Catford  
75 et al. 2019, Evans et al. 2021, Soares et al. 2021). However, these works focus on species that  
76 are generally threatened and not specifically threatened by IAS. As alien and native species  
77 present specific traits related to the impact that they cause or suffer from, we would expect an  
78 ecological divergence between species in terms of the different magnitudes or mechanisms of  
79 impact (Evans et al. 2018b, 2021).

80 Here, we present an overview of the association between morphological, life history, and  
81 ecological traits as well as the impact characteristics of birds involved in biological invasions.  
82 After compiling a trait database for both alien and IAS-threatened birds, we compared the  
83 distribution of birds within a functional space according to their impact magnitude or impact

84 mechanism. Our database benefits from the recent publication of a global compilation of  
85 morphological traits, which offers new perspectives for studies on bird functional diversity  
86 (Tobias et al. 2021). We expect for species characteristics to differ between alien species and  
87 IAS-threatened species as well within groups of different impact magnitudes or mechanisms.

88

## 89 **Methods**

### 90 **Data collection**

#### 91 *Birds threatened by biological invasions*

92 Birds at high risk of extinction because of biological invasions were selected from the IUCN  
93 Red List (IUCN 2020b). We identified species exposed to IAS using the IUCN Threats  
94 Classification Scheme (version 3.2), which provides a coherent categorization of threats to  
95 biodiversity (Salafsky et al. 2008). All species associated with the threats *8.1 Invasive non-*  
96 *native/alien species/diseases* or *8.4 Problematic species/diseases of unknown origin* (when we  
97 could determine the exotic origin of the named problematic species) were regarded as exposed  
98 to IAS. We focused on the subgroup of species at high risk of extinction from the vulnerable,  
99 endangered, and critically endangered categories in the IUCN Red List. From this pool of  
100 species (i.e., at high risk of extinction and threatened by IAS), we distinguished two  
101 magnitudes of impact. Birds with more than 50% of their total population experiencing a  
102 significant decline (slow, rapid, or very rapid) were classified as “highly impacted IAS-  
103 threatened birds,” whereas other birds (with less than 50% of their population experiencing  
104 fluctuations or no declines, as well as birds with unknown magnitude) were classified as  
105 “weakly impacted IAS-threatened birds.” We further collected the mechanism related to how  
106 the IAS impacts each species in the IUCN Stresses Classification Scheme (version 1.0). The  
107 mechanism was described using three binary variables for each species (Table S1): ecosystem

108 effect (set as 1 if the species is stressed by an ecosystem conversion/degradation or an indirect  
109 ecosystem effect and as 0 if not), direct species effect (set as 1 if the species is directly  
110 stressed by an effect on survival or reproduction; e.g., predation, species disturbance or  
111 reduced reproductive success), and indirect species effect (set as 1 if the species is stressed by  
112 competition, inbreeding, hybridization, or skewed sex ratio). This resulted in a total of 462  
113 birds at high risk of extinction due to biological invasion threats. These birds were associated  
114 with two different magnitudes as well as one, two, or three mechanisms of IAS impacts  
115 (Figure S1, (a)).

116

### 117 ***Alien birds***

118 Alien bird species with self-sustaining populations were extracted from the EICAT  
119 assessment results for alien birds (Evans et al. 2016). We used 119 species with information  
120 about the mechanism and magnitude of their impact. As with IAS-threatened species, we  
121 reclassified the mechanism of invasion using three binary variables (Table S1): ecosystem  
122 effect (set as 1 if the species impacts the ecosystem), direct species effect (set as 1 if the  
123 species directly impacts the survival or reproduction of native species), and indirect species  
124 effect (set as 1 if the species indirectly impacts native species). Alien birds were associated  
125 with one, two, or three impact mechanisms (Figure S1, (b)). We further coded the magnitude  
126 of the alien species impact based on the EICAT impact categories: species with minimal or  
127 minor impacts were classified as alien birds with low impact; and species with moderate,  
128 major, or massive impacts were classified as alien birds with high impact (IUCN 2020a).  
129 Species that were data deficient for the mechanism and magnitude of the impact (n = 256)  
130 were stored in the final alien database as “DD aliens” (data deficient aliens) (Figure S1, (c)).

131



## 132 ***Species traits***

133 We collected species-level traits for IAS-threatened and alien bird species (n = 863 unique  
134 species). These traits relating to morphology, lifestyle, and life history were shown to be  
135 important with regard to native species' vulnerability to biological invasions (Bellard et al.  
136 2021) as well as invasion success and impacts for aliens (Evans et al. 2018a). We extracted  
137 information about habitat breadth and island endemism from the IUCN database, about  
138 morphology (i.e., beak, tarsus, tail and wing morphology, body mass) and lifestyle (trophic  
139 level, foraging niche) from the AVONET database (Tobias et al. 2021), about volancy from  
140 Cooke et al. (2019), and about clutch size from the Amniote database (Myhrvold et al. 2015)  
141 (for a description of traits, see Table S2). Other species traits like relative brain size also play  
142 a role in bird invasion success (Sol et al. 2012). However, information about this trait mainly  
143 related to alien species (rate of completeness = 84%) with a very poor completeness for IAS-  
144 threatened birds (15%). This bias in the missing data prevents us from considering this trait in  
145 our analysis (Johnson et al. 2021). Our final database contained 11 traits that were not  
146 correlated with each other (Appendix 1 for trait selection). We ensured that the correct  
147 databases were merged correctly from different sources by verifying species synonyms. The  
148 *rl\_synonyms* function from the *rredlist* package (Chamberlain 2020) and the *synonyms*  
149 function from the *taxise* package (Chamberlain and Szocs 2013) were used for searches in the  
150 IUCN database and Integrated Taxonomic Information System, respectively. We removed 13  
151 species from the database due to inconsistencies in the taxonomy of the different databases.

152

## 153 ***Imputation of missing trait values using phylogeny***

154 Functional space computation requires fully informed trait databases. Although traits from the  
155 AVONET and IUCN databases were complete for the vast majority of the selected species,  
156 clutch size contained 28.3% of missing values for IAS-threatened and alien birds (Table S2).

157 To avoid an important loss of information regarding functional diversity, we imputed missing  
158 trait values using phylogeny. Closely related species tend to be more similar to each other,  
159 and thus by considering species phylogenetic relations, the performance of data imputation  
160 improves (Kim et al. 2018). We summarized the phylogenetic information using the first 10  
161 phylogenetic eigenvectors calculated from 1,000 trees obtained from [vertlife.org](http://vertlife.org) (Jetz et al.  
162 2012). Imputed values were generated with the *mice()* function from the *mice* package (van  
163 Buuren and Groothuis-Oudshoorn 2011) using the predictive mean matching method based on  
164 the traits and 10 phylogenetic eigenvectors. The imputation was performed on the 11 selected  
165 traits for all worldwide bird species ( $n = 11,124$ ). We then took as a complete dataset the  
166 median value for the 1,000 imputed datasets obtained from the 1,000 trees. To ensure the  
167 validity of data imputation, we performed data imputation on 100 artificially drilled datasets.  
168 They were obtained by selecting all species with complete trait values ( $n = 6,190$ ) and  
169 randomly generating the percentage of missing values that corresponded to each trait. We  
170 then evaluated the performance of data imputation by calculating the average normalized  
171 root-mean-square error (NRMSE) for numeric traits and the average sensitivity/specificity for  
172 binary traits on the 100 artificially drilled datasets (Table S2). Average NRMSE was below  
173 0.03 for all variables considered, thus indicating a very low error rate in the imputed missing  
174 data. Volancy was the only non-numeric variable to be imputed, showing a very high true  
175 positive rate (0.99) and a relatively good true negative rate (0.63). The final database for birds  
176 involved in biological invasions contained 850 species with fully informed traits, including  
177 456 IAS-threatened birds, 118 alien birds with information about their impact, and 290 DD  
178 aliens (note that 14 species were both alien and IAS-threatened species).

179

## 180 **Statistical analysis**

### 181 *Axis simplification*

182 Because the trait database contained different types of variables (e.g., numeric discrete,  
183 numeric continuous, categorical), we computed a functional space based on the principal  
184 component analysis (PCA) transformation of the raw traits following Mouillot et al. (2021).  
185 First, pairwise functional distances between the 850 bird species were calculated using the  
186 Gower dissimilarity index (Gower 1971) with the *daisy()* function from the *vegan* package  
187 (Oksanen et al. 2017). Second, principal coordinate analysis (PCoA) was applied to the  
188 distance matrix using the *pcoa()* function from the *ape* package (Paradis and Schliep 2019).  
189 We computed all our analyses based on the first three dimensions of the PCA, which  
190 represent 50% of variance explained.

191

### 192 ***Group dissimilarities in functional space***

193 *Functional space description.* To understand which ecological strategies were represented on  
194 the first four axes of the PCA, we computed the correlation between the studied traits and the  
195 four PCA axes. We used the *rcorr()* function from the *Hmisc* package (Harrell et al. 2021)  
196 after converting all the traits into numeric variables (e.g. categorical traits were converted into  
197 binary traits).

198 *Impact magnitude and mechanism.* We compared the ecological strategies of birds according  
199 to their role in biological invasions and their impact using raincloud plots (Allen et al., 2018).  
200 These plots enabled us to simultaneously depict the density and basic statistics of species  
201 repartition along the first functional space axes. For both alien and IAS-threatened birds, we  
202 first grouped species according to their impact magnitude (low and high) as well as their  
203 mechanism of impact: direct species effect, indirect species effect, and habitat effect  
204 (considering only species affected by one mechanism). We compared the distribution between  
205 groups along the axes using Kolmogorov-Smirnov (KS) tests, which were run independently  
206 for both alien species and IAS-threatened species. Finally, we evaluated the trait modalities or

207 values associated with the different groups of impact magnitudes and mechanisms. For each  
208 numeric trait, we compared the mean value of the different groups using ANOVA and post-  
209 hoc tests. For binary and categorical traits, we performed chi-squared tests of independence.

210

### 211 *Evaluation of trait usefulness to predict the impact status of data deficient aliens*

212 Our goal was to distinguish functional groups of birds based on their role in biological  
213 invasions and their impact on native systems. We thus evaluated the opportunity to classify  
214 data deficient (DD) species into alien species with high or low impact based on their position  
215 in the functional space. To this aim, we computed seven metrics to describe the position of  
216 each species in the functional space compared to the position of all species with an informed  
217 status. Metrics were either a minimal distance (to a species or group of species with known  
218 status) or a proportion of species within a buffer (Appendix 2, Table S3). Using each metric,  
219 we determined the predicted status of the 574 species with known status and evaluated the  
220 rate of predictions using contingency tables. We focused on evaluating the prediction for the  
221 group of “alien species with high impact.”

222 All analyses were performed with R software (version 4.1.0) (R Core Team 2021).

223

## 224 **Results**

### 225 **Functional characterization of the impact of birds involved in biological invasions**

226 The first three axes of the PCA explained 50% of the total variance of the ecological traits of  
227 all birds involved in biological invasions. The PC1 axis showed the major contribution of the  
228 insular endemism, life history traits (i.e., body mass and clutch size) and traits related to  
229 resource consumption (i.e., beak depth, animal-based diet, insessorial foraging niche) (Table  
230 1). The negative part of PC1 was dominated by insular endemic species with an insessorial

231 foraging niche and animal-based diet, while the positive part was characterized by larger  
232 species with a deeper beak, larger clutch size, and mainland populations. The PC2 axis was  
233 mainly correlated to the trophic level with carnivore species on the negative side and  
234 herbivore species on the positive side of the axis. To a lesser extent, beak length was  
235 negatively correlated to this axis, while the insessorial trait was positively correlated. Finally,  
236 the foraging niche drove the PC3 axis, with the negative part associated with terrestrial  
237 species and the positive part with the insessorial strategy.

238 The distribution of alien birds (with high or low impact) significantly differed from the  
239 distribution of IAS-threatened birds (highly or weakly impacted) from PC1 to PC3 (Figure 1).  
240 Within-role comparisons showed that IAS-threatened birds were rather similarly distributed  
241 regardless of their impact magnitude except with PC1 (KS test,  $D = 0.16$ ,  $p = 0.009$ ). By  
242 contrast, the distribution of alien birds significantly differed in PC2 depending on their impact  
243 magnitude (KS-test,  $D = 0.35$ ,  $p = 0.003$ ), although the peak of the distribution was the same  
244 with the other axes. Considering the density distributions in PC1 and the traits correlated to  
245 this axis, highly impacted IAS-threatened birds were more insular endemic than weakly  
246 impacted IAS-threatened birds (confirmed using the single trait approach; Figure 2). On the  
247 opposite side of this axis, both alien groups were more associated with a larger clutch size,  
248 body mass, and beak depth.

249 Single trait analyses confirmed that morphological and life history traits do not allow us to  
250 disentangle the impact magnitude within IAS-threatened species or alien species (Figure 3).  
251 However, ecological traits showed intragroup differences for alien species: alien birds with a  
252 high impact were more carnivorous and omnivorous, while they also had a larger habitat  
253 breath (i.e., more generalists) compared to aliens with a low impact (Figure 2). Moreover,  
254 alien birds and IAS-threatened birds harbored distinct functional strategies (Figures 2, 3)  
255 regardless of their impact. Alien birds had a significantly longer tail length and larger clutch

256 size than IAS-threatened birds as well as a larger body mass compared to highly impacted  
257 IAS-threatened birds (Figure 3). They were also more generalist in terms of habitat use and  
258 were at lower trophic levels compared to species threatened by biological invasions (Figure  
259 3).

260 We pursued our analyses by disentangling the bird characteristics for each impact mechanism:  
261 direct species effect, indirect species effect, and ecosystem effect (Figure 4). Based on our  
262 previous results showing no major intragroup differences regarding impact magnitude, we  
263 considered only two groups: all alien birds and all IAS-threatened birds. IAS-threatened birds  
264 associated with a direct species effect diverged significantly from IAS-threatened birds  
265 associated with a habitat effect in the three axes (Figure 4, upper panel). Single trait analyses  
266 showed that species threatened by a direct effect were larger with a longer beak and a higher  
267 proportion of aquatic foragers compared to species threatened by habitat effect, as the latter  
268 were more insessorial. Moreover, directly impacted species were the only group among IAS-  
269 threatened species to contain non-flying birds and have twice as many endemic insular species  
270 as the group threatened by habitat effect. Alien birds with a direct impact on species differed  
271 strongly from the other mechanisms in PC2 (Figure 4, lower panel). They had a significantly  
272 higher trophic level and were more habitat generalists than other alien groups.

### 273 **Assessment of impact prediction for data deficient alien birds using traits**

274 When evaluating the ability to disentangle alien species with a high or low impact, we  
275 obtained a success rate ranging from 36.5% to 52.7% (Table S3). Focusing on the quality of  
276 prediction for the group “alien birds with high impact,” the true negative rate was high  
277 (specificity > 0.8), although we observed very few true positives, thus leading to low  
278 sensitivity for all the tested methods (from 0 to 0.5; Table S3).

279

## 280 **Discussion**

### 281 **Diverging functional strategies between IAS-threatened and alien birds**

282 Our results suggest that birds present diverging morphological, life history, and ecological  
283 strategies depending on their role in biological invasions. We found that alien birds had a  
284 larger clutch size, a longer tail length, and a larger proportion of herbivores, while they were  
285 also more habitat generalists than IAS-threatened birds (and more generally, than worldwide  
286 birds). Carnivorous birds were indeed less introduced and less successful at establishment in  
287 exotic places than herbivores and generalists (Jeschke and Strayer 2006). Alien and IAS-  
288 threatened birds are thus unlikely to enter into high competition for niche exploitation, as  
289 previously shown for insular communities (Soares et al. 2021). The finding that alien birds  
290 with a documented impact have large clutch sizes is in contradiction with previous works on  
291 birds (Sol et al. 2012). Indeed, contrary to other terrestrial vertebrates (Allen et al., 2017;  
292 Capellini et al., 2015), the “slow” life history of birds (i.e., small clutches and investment in  
293 future reproductive events) was known to favor the establishment of aliens (Sol et al. 2012).  
294 Nevertheless, it is important to note that establishment and impact are two different stages of  
295 invasion, which are likely to filter out species with different traits (see Bernery et al., in prep).  
296 Furthermore, introduced birds are a non-random sample of worldwide birds, with some  
297 families and characteristics like large body size being preferentially selected for hunting or pet  
298 trade (Duncan et al. 2003, Su et al. 2016). Thus, despite the apparent negative correlation  
299 between establishment success and high reproductive rate found in previous studies, the initial  
300 pool of transported birds might be biased toward large clutches compared to the global pool.  
301 This results in a generalist profile and faster reproductive rate for alien birds compared to  
302 natives and even worldwide birds. By contrast, IAS-threatened birds were more often insular  
303 endemic and flightless compared to introduced species and worldwide birds. These findings  
304 confirm the results of previous studies that highlight the peculiar strategies associated with

305 high vulnerability to biological invasions (Bellard et al. 2021). IAS-threatened birds are all the  
306 more vulnerable given that their ecological strategies are quite similar to those of extinct  
307 species (Fromm and Meiri 2021).

308 As a consequence, our findings lend support to the “two sides of the same coin” hypothesis,  
309 which suggests that the characteristics promoting alien success are the opposite to those that  
310 promote extinction risk (Bradshaw et al. 2008). Jeschke and Strayer (2008) and Blackburn  
311 and Jeschke (2009) found no evidence for this hypothesis when studying birds introduced into  
312 Europe and North America. However, they evaluated the characteristics of species at risk of  
313 extinction in general, whereas we focused on IAS-threatened species in particular.

314 Furthermore, considering traits together in a functional space and not individually might give  
315 a more complex and realistic view of species’ ecological strategies (Pakeman 2011). Our  
316 analysis of point distribution along the PC axes suggests that many ecological strategies are  
317 shared by alien and IAS-threatened birds. Nevertheless, we observed differences relating to  
318 the probability density distribution, which prove to be an efficient tool for studying similar but  
319 diverging groups of species (Carmona et al. 2016).

## 320 **Functional characterization of impact magnitude and mechanism**

321 Differences in the impact magnitude of alien and IAS-threatened birds were weakly  
322 represented by the functional space. Trophic level and habitat breadth significantly differed  
323 between low and high impact magnitudes for alien birds, while insular endemism differed for  
324 highly or weakly impacted IAS-threatened birds. Regarding alien species, our results are in  
325 accordance with previous studies that assert the dominance of habitat and diet generalists  
326 within species with high impacts on native ecosystems (Shirley and Kark 2009, Kumschick et  
327 al. 2013, Evans et al. 2018a). Despite the close link between bird beaks and diet (Pigot et al.  
328 2020), morphological traits related to beak size and shape did not differ between alien birds  
329 with high or low impact. Moreover, the alien and native range sizes of introduced birds are



330 known to be positively correlated to the impact magnitude of alien birds (Evans et al. 2014,  
331 2018a). Given that bird dispersal ability, measured by the hand-wing index (HWI), is  
332 positively associated with species' geographical range size (Sheard et al. 2020), we expected  
333 to find a difference in HWI between aliens with high and low ecological impact. However,  
334 both groups showed similar values, suggesting that their dispersal ability is not determinant in  
335 the impact intensity of a species. Concerning IAS-threatened species, their impact magnitude  
336 is not linked to species traits except for insular endemism. This confirms previous studies that  
337 highlight the increased vulnerability of insular birds and other taxa compared to mainland  
338 ones regarding the biological invasion threat (Dueñas et al. 2021, Evans et al. 2021). This also  
339 illustrates that threatened species within the IUCN Red List present rather similar features  
340 independently of the scope and severity of the threat. Consequently, factors that induce  
341 significant and major population declines because of biological invasions are likely to be  
342 extrinsic (e.g., dependent on the invasion context, environment, or alien characteristics) and  
343 not intrinsically mediated by native species traits. Another possible explanation is that we did  
344 not take into account all the traits that may mediate the impact magnitude of IAS on native  
345 species. For instance, species with small range sizes are generally at a higher extinction risk  
346 than those with larger ranges and are thus more severely impacted by threats (Chichorro et al.  
347 2019). Nevertheless, it would be irrelevant to use this trait in our analyses, because IUCN  
348 threat categories are partly based on species range sizes, thus possibly leading to confounding  
349 effects (Mace et al. 2008). Finally, species are not usually at high risk of extinction because of  
350 a single threat but rather because of the joint effect of several threats (Capdevila et al. 2021).  
351 Thus, a previous perturbation (due to any major threat) can increase the vulnerability of a  
352 population to another perturbation (e.g., introduction of an alien species). Taking into account  
353 the exposure and resilience of IAS-threatened species to all threats combined could better help  
354 to address the differences in impact magnitude.

355 In the second part of the analysis, we tried to disentangle the characteristics of alien and IAS-  
356 threatened birds depending on the mechanism that they impact or are impacted by. We  
357 observed a clear difference in the profile of birds that are directly impacted by IAS (e.g.,  
358 predation) and those that are impacted through a habitat effect (e.g., change in vegetation or  
359 habitat degradation due to IAS). Compared to birds that are sensitive to habitat disturbance by  
360 IAS, birds prone to predation were larger, with a longer beak, frequently insular endemic, and  
361 possibly flightless, thus being the ideal naïve prey for alien predators (Carthey and Banks  
362 2014). For instance, the kiwi (*Apteryx spp.*), which presents this very profile, is highly  
363 predated by introduced mammals in New Zealand (McLennan et al. 1996). However, having  
364 all these characteristics of vulnerability does not necessarily mean that a native bird becomes  
365 prey. The large and flightless kagu (*Rhynochetos jubatus*), an endemic bird of New  
366 Caledonia, is not consumed by feral cats despite its clear victim profile (Palmas et al. 2020).  
367 This is possibly explained by its development of defensive behavior that has proven to be  
368 effective against cats. However, we did not consider this variable in our analyses. The kagu  
369 may nevertheless be predated by larger introduced mammals (e.g., feral dogs), which still  
370 make the species a prey threatened by direct mechanism. We expected that birds threatened  
371 by a habitat effect due to IAS would present characteristics similar to species threatened by  
372 habitat degradation in general: species with an invertebrate-based diet that require a large  
373 foraging space as well as habitat specialists that are more sensitive to habitat fragmentation  
374 (Sekercioglu 2007). Our results suggest that these birds, though more insessorial (i.e.,  
375 perching on trees and vegetation in general), are not more habitat specialist than species  
376 directly impacted by IAS, and they did not present a specific dispersal ability (measured by  
377 HWI or tail length). The differences observed between species impacted by habitat effect and  
378 direct species effect are thus better explained by the traits that make them vulnerable to  
379 predation rather than habitat change. Finally, our results confirmed that alien species that

380 directly impact native species have an animal-based diet (Evans et al. 2018a), even when  
381 considering predation, parasitism, and disease transmission mechanisms together as a direct  
382 species effect. These birds also had a wider habitat breadth than aliens with other mechanisms  
383 of impact, once again highlighting the real threat posed by generalist species when introduced  
384 into a new ecosystem (Loomans 2021).

385 For both aliens and IAS-threatened species, we characterized the impact type by pooling  
386 together the different mechanism categories (Table S1). We assumed that species directly  
387 impacted by species mortality, species disturbance, or reduced reproductive success shared  
388 common characteristics, although they might also have specific hidden traits associated with  
389 each of these mechanisms (this comment applies to the three impact mechanisms and the two  
390 groups of birds). Such pooling was necessary to perform density statistics along the functional  
391 space axes, the gain in statistical power compensating for the loss in precision. However, the  
392 pooling may also explain why we mostly detected ecological traits that differed between  
393 groups of different impact types as opposed to life history or morphological features.

#### 394 **Using species traits to predict alien bird impact**

395 Finally, the EICAT protocol is a powerful tool for assessing the impact of alien species.  
396 However, a large proportion of birds lack information regarding their ecological impact, while  
397 others are assessed with relative uncertainty (Probert et al. 2020). This absence of information  
398 is nevertheless not synonymous with an absence of impact, as the lack of data is a  
399 shortcoming to building relevant conservation policies at a global scale (Latombe et al. 2019).  
400 Moreover, many impacts take time to be reported or even noticed, given the time lag between  
401 the introduction of alien species, their spread, and their effect in new ecosystems (Rouget et  
402 al. 2016). Given the difficulty in capturing the impact potential before the actual reporting, we  
403 should instead focus on prevention to avoid ecologically costly invasions rather than on  
404 invasive species management, which proves to be much more efficient (Simberloff et al.

405 2013). We therefore evaluated the possibility of using species traits to infer the impact  
406 magnitude of DD alien birds. The prediction methods computed to detect alien birds with high  
407 impact did not perform very well. All tested metrics had a high specificity but a low  
408 sensitivity. This gap between sensitivity and specificity has already been observed in a  
409 method for creating invasive species watch lists (Faulkner et al. 2014). The simplicity of our  
410 prediction protocol combined with the low rate of alien birds with high impact in the  
411 functional space compared to non-impacting species can explain this poor sensitivity. Our  
412 results emphasize the importance of accounting for other factors that are crucial to invasion  
413 success (e.g., local context, introduction event-related features) and not only focusing on alien  
414 traits for predicting their potential impact (Redding et al. 2019). Furthermore, the functional  
415 and phylogenetic properties of the recipient community (e.g., ecological niche saturation,  
416 shared evolutionary history with introduced alien species) are likely to mediate the success of  
417 the establishment, spread, and thus impact of alien species (Jeschke and Heger 2018). For  
418 instance, in insular systems, impacts on biodiversity are higher in regions with more endemic  
419 species (Walsh et al. 2012). Other traits such as relative brain size that explains some  
420 cognitive adaptation in birds (Kaplan 2020) could have been useful in our analysis.  
421 Unfortunately, the lack of data for IAS-threatened birds did not allow us to include this trait.  
422 Even though birds are a widely documented taxon at a global scale (Etard et al. 2020),  
423 especially since the publication of the AVONET database, trait collection remains an ongoing  
424 challenge for performing global studies on functional diversity.

## 425 **Conclusion**

426 Compared to previous studies focusing on the characteristics of either alien species or IAS-  
427 threatened species (Shirley and Kark 2009, Evans et al. 2014, 2018a, Bellard et al. 2021,  
428 Marino et al. 2021), this study takes advantage of a new morphological database (Tobias et al.  
429 2021) and approach (i.e., density distribution in a functional space) to distinguish with better

430 accuracy the role of birds in biological invasions in terms of their impact magnitude and  
431 associated mechanisms. Overall, morphological and life history traits allow us to distinguish  
432 the role of birds in biological invasions as either invaders or victims, while their ecological  
433 characteristics are more related to the type of impact associated with IAS. Although this work  
434 is another step toward understanding and explaining the impacts of invasions, we still need to  
435 integrate the properties of the recipient environment, the introduction event, and the  
436 population features.

437

438

439 **Data availability statement**

440 The data and code that support our analyses are available from Zenodo (link to come after the  
441 acceptance of the paper). Data include species traits and groups (role in biological invasions  
442 and impact type).

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451

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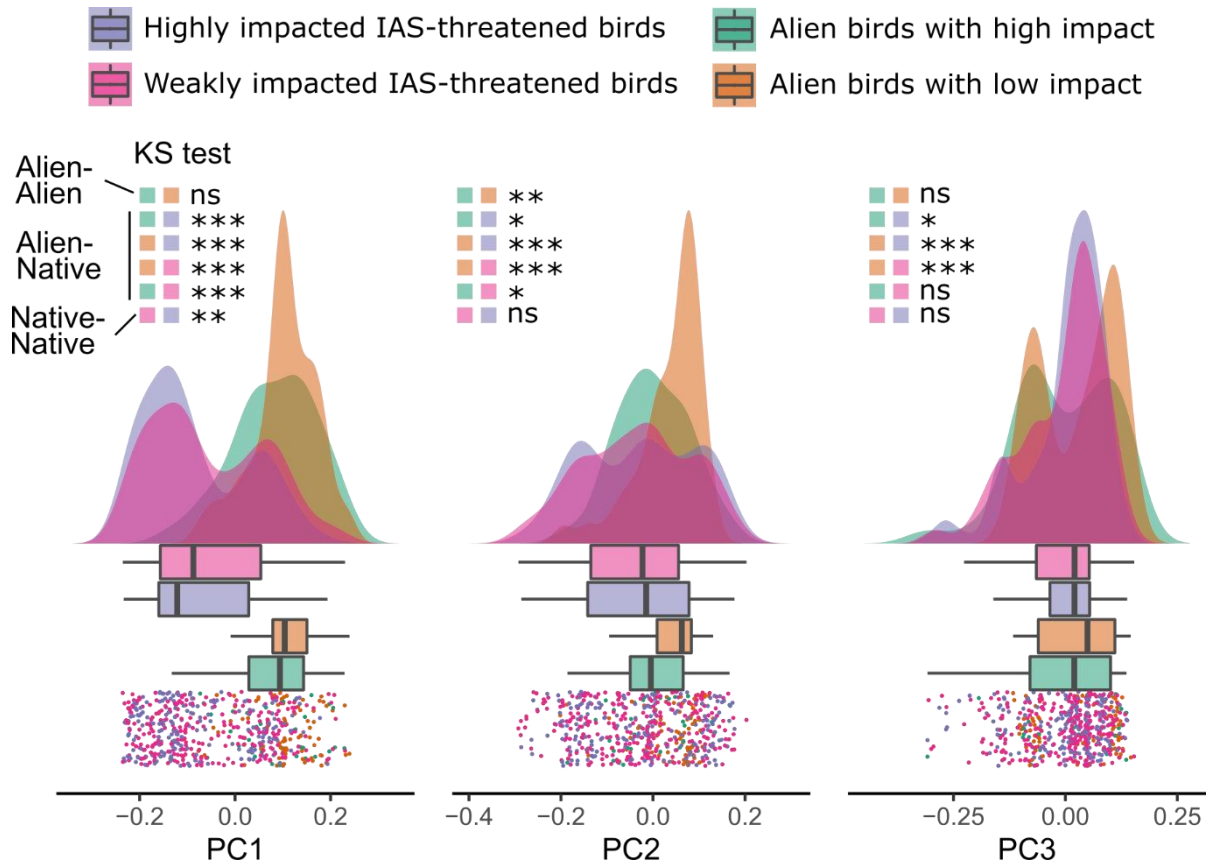
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609

610 **Table 1: Correlation between ecological traits and the first three axes of principal**  
611 **component analysis containing all birds involved in biological invasions** (n = 850 unique  
612 species). Spearman coefficients and p-values are reported. Non-numeric traits (trophic level,  
613 foraging niche) were converted into binary variables to compute the correlations. The  
614 strongest correlations ( $r < -0.4$  or  $r > 0.4$ ) and their associated significant p-values are shown  
615 in bold.

	<b>PC1 (22.2%)</b>		<b>PC2 (16.3%)</b>		<b>PC3 (11.3%)</b>	
	r	P	r	P	r	P
<b>Morphological traits</b>						
<b>Hand-wing index</b>	0.35	<0.001	-0.3	<0.001	0.16	<0.001
<b>Tail length</b>	0.34	<0.001	-0.21	<0.001	0.04	0.274
<b>Beak depth</b>	<b>0.46</b>	<b>&lt;0.001</b>	-0.15	<0.001	0.07	0.038
<b>Beak length</b>	0.32	<0.001	<b>-0.44</b>	<b>&lt;0.001</b>	-0.01	0.736
<b>Life history traits</b>						
<b>Body mass</b>	<b>0.47</b>	<b>&lt;0.001</b>	-0.4	<0.001	-0.24	<0.001
<b>Clutch size</b>	<b>0.43</b>	<b>&lt;0.001</b>	0.25	<0.001	-0.15	<0.001
<b>Ecological traits</b>						
<b>Insular endemism</b>	<b>-0.84</b>	<b>&lt;0.001</b>	0.06	0.101	-0.29	<0.001
<b>Volancy</b>	0.07	0.048	0.17	<0.001	0.25	<0.001
<b>Habitat breadth</b>	0.35	<0.001	-0.2	<0.001	0.06	0.077
<b>Trophic level</b>						
<b>Herbivore</b>	0.4	<0.001	<b>0.76</b>	<b>&lt;0.001</b>	0	0.921
<b>Omnivore</b>	0	0.923	0.07	0.058	-0.19	<0.001
<b>Carnivore</b>	<b>-0.42</b>	<b>&lt;0.001</b>	<b>-0.8</b>	<b>&lt;0.001</b>	0.16	<0.001
<b>Scavenger</b>	0.11	0.001	-0.07	0.047	-0.08	0.015
<b>Foraging niche</b>						
<b>Aerial</b>	-0.08	0.018	-0.3	<0.001	0.13	<0.001
<b>Aquatic</b>	0.13	<0.001	-0.4	<0.001	0.08	0.026
<b>Generalist</b>	0.02	0.564	-0.13	<0.001	0.11	0.001
<b>Insectorial</b>	<b>-0.42</b>	<b>&lt;0.001</b>	<b>0.46</b>	<b>&lt;0.001</b>	<b>0.61</b>	<b>&lt;0.001</b>
<b>Terrestrial</b>	0.38	<0.001	0	0.919	<b>-0.8</b>	<b>&lt;0.001</b>

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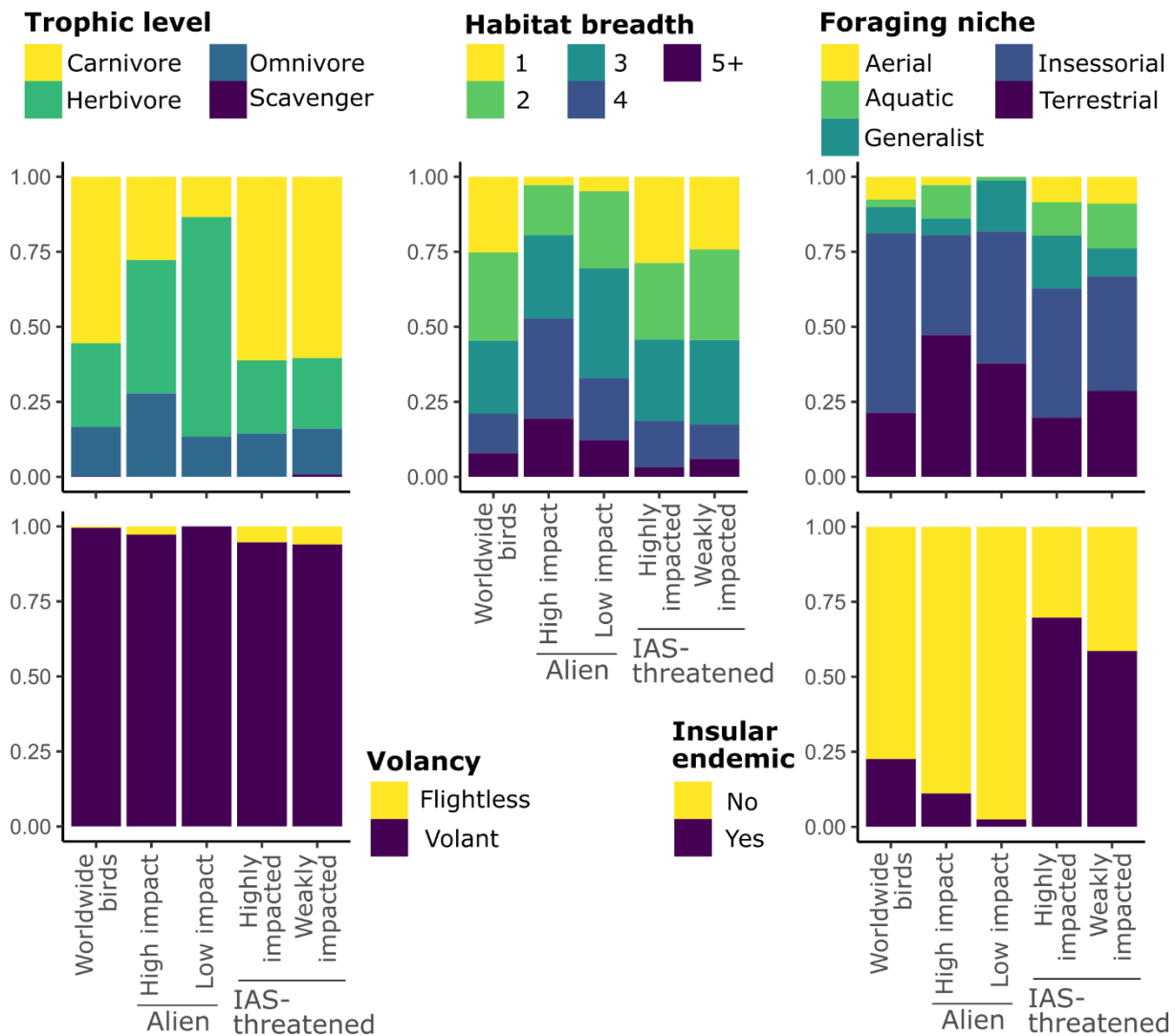


617

618 **Figure 1. Distribution density of the four groups of birds involved in biological invasions**  
 619 **(alien with high impact, alien with low impact, highly impacted IAS-threatened, weakly**  
 620 **impacted IAS-threatened) in the first three axes of principal component (PC) analysis.**

621 Boxplots are associated with the point distribution. At the top left of each plot, the  
 622 Kolmogorov-Smirnov (KS) test in each axis compares the distributions 2-by-2 between  
 623 groups (\*\* $p < 0.01$ , \*  $p < 0.05$ , ns = non-significant difference).

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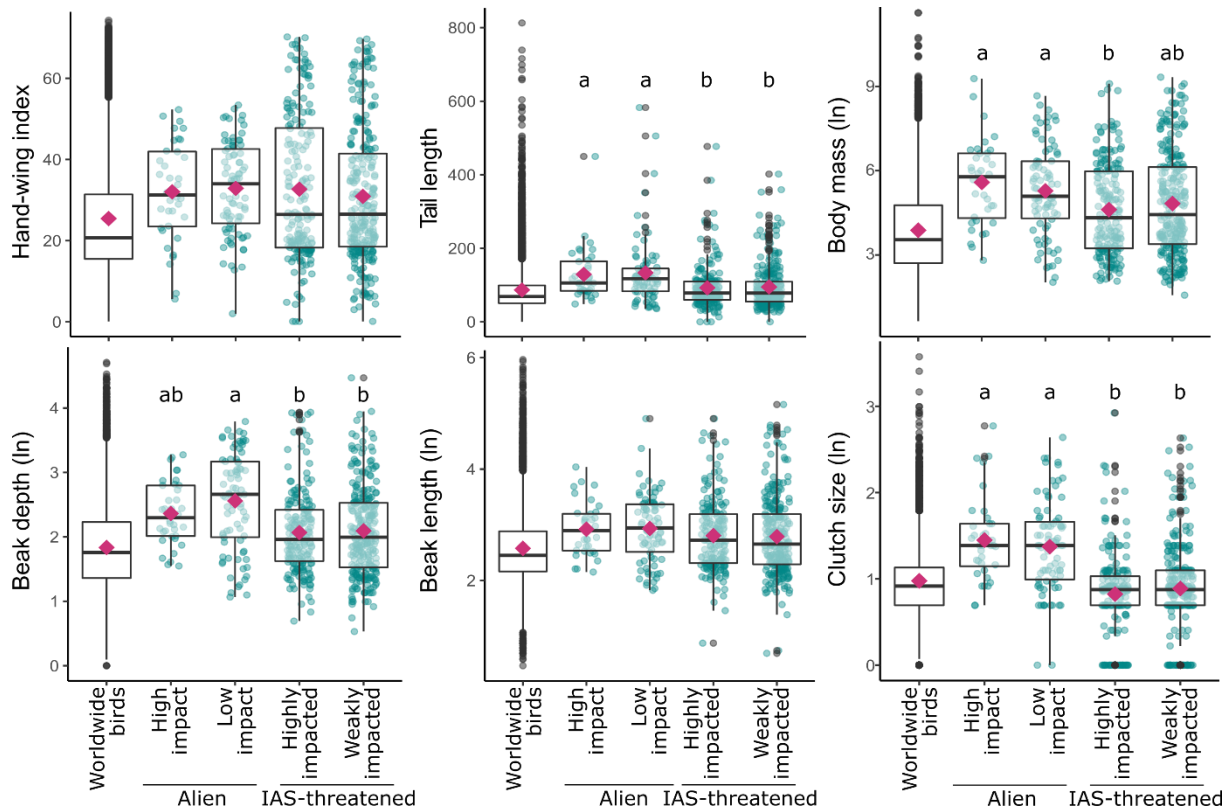
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**Figure 2. Proportions of trait modalities for alien and IAS-threatened birds according to their impact magnitude.** X-axes represent the groups of birds with different roles and impact magnitudes as well as worldwide birds; Y-axes represent the proportion of each modality for each ecological categorical or binary traits.



632

633 **Figure 3. Relationships between species traits and impact magnitude for alien and IAS-**

634 **threatened birds.** X-axes represent the groups of birds with different roles and impact

635 magnitudes as well as worldwide birds; Y-axes represent the morphological and life history

636 numeric traits. Trait values were log-transformed for body mass, beak depth, beak length, and

637 clutch size. Boxplots show the median and first and third quartiles, with outliers plotted

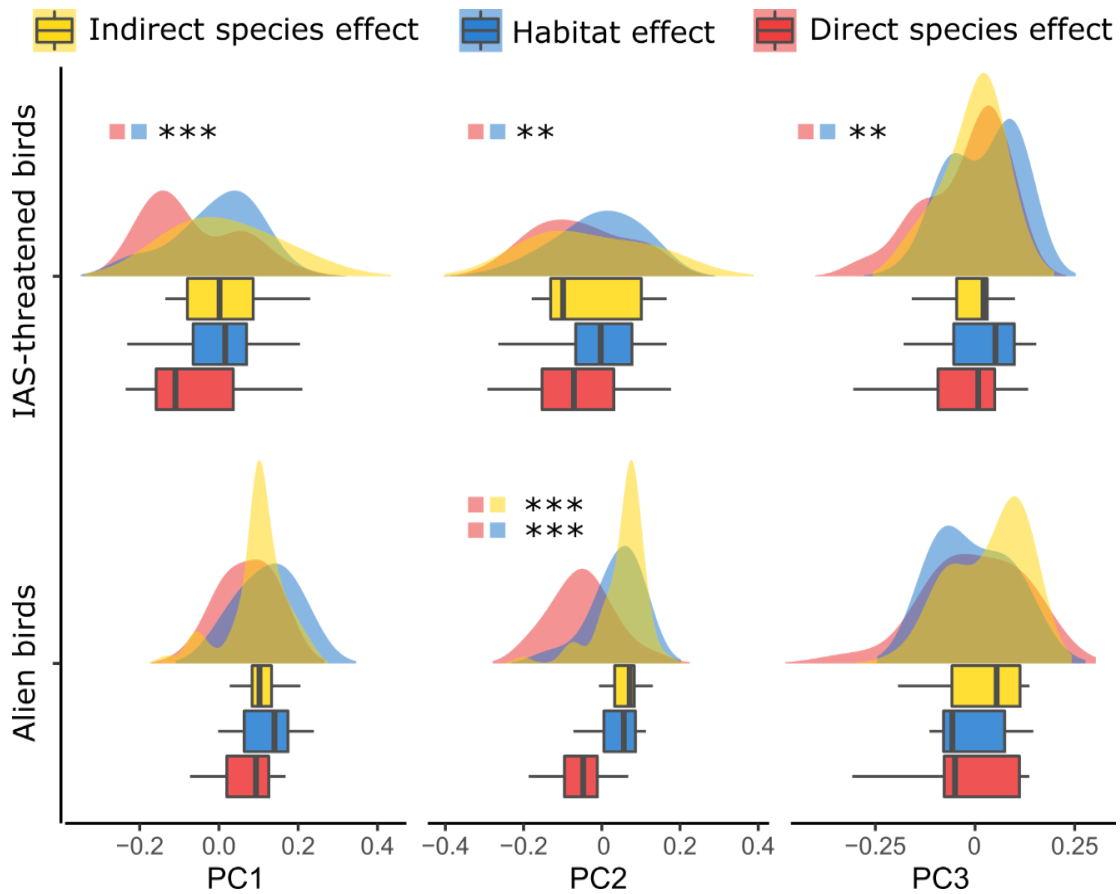
638 individually in bold. Blue dots are raw values for unique species contained in each group.

639 Pink diamonds represent the mean value for each trait. Significant differences between mean

640 values are indicated with letters.

641





642

643 **Figure 4. Distribution density of the impact mechanism groups for IAS-threatened and**

644 **alien birds in the first three axes of the PCA.** Means of the distributions were compared

645 using the Kruskal-Wallis test on coordinates along each axis and with a post-hoc test for 2-by-

646 2 comparisons (\*\*\*)  $p < 0.001$ , \*\*  $p < 0.01$ , \*  $p < 0.05$ ).

647

648 **Supplementary material**

649 **Title: When origin, reproduction ability, and diet define the role of birds in invasions**

650

651 This file contains:

652 - Appendix 1 to 2

653 - Tables S1 to S3

654 - Figures S1

655 - References (included also in the main text)

656

657

658 **Appendix 1**

659 Collecting traits from AVONET, IUCN, Amniote and Cooke databases lead to a total of 17  
660 traits that were related to bird morphology, ecology and their life-history (Table S1). First, we  
661 regressed each trait against all other using linear models and computed variance inflation factors  
662 (VIF; *vif* function from *car* package (Fox and Weisberg 2011)). We then removed the trait that  
663 had the highest summed VIF values in all regressions, and redo the procedure while VIF values  
664 were above 3. We ended up with a total of 11 variables that were not inter-correlated, resulting  
665 mostly on the removal of morphological traits (e.g., Beak width, Tarsus length, Wing length,  
666 Kipps distance) that were highly correlated between them. VIF values for all remaining  
667 variables were thus below 3.

668 **Appendix 2**

669 We tested a set of metrics to predict data deficient alien impact magnitude on species that had  
670 information on their impact. For each species in the distance matrix with known status (n=574),  
671 we computed seven metrics (Table S3) that are either a minimal distance (to a species or a group  
672 of species with informed impact) or a proportion of species within a buffer. We then attributed,  
673 using each of the seven metrics, a predicted impact status to the 574 species based on their  
674 distance with all species within the space (573 species used as predictors for each species). For  
675 minimal distance metrics, we attributed to each species the status corresponding to the closest  
676 impact group (i.e. the group that had the minimal metric value). For relative proportion metrics,  
677 we attributed the status of the impact group that were the most represented (i.e. the group that  
678 had the maximal metric value). Finally, we evaluated the prediction strength of each metric by  
679 computing success rate (i.e. the ratio between the number of correctly predicted species and the  
680 total number of species to predict). We further calculated the sensitivity and specificity of each  
681 metric for the group “alien species with high impact” because it was the group of interest as we  
682 aimed to predict the potentiality of alien birds to have major impact on native systems.

683 **Table S1. Classification of impact mechanisms for alien and native bird species.** Native  
 684 bird impacts came from IUCN Stresses Classification Scheme (version 1.0); alien bird impacts  
 685 were defined by (Evans et al. 2016) and we reported in light grey the exact definitions they used  
 686 in their Table 1.

<i>Impact mechanisms used in our study</i>	<i>IUCN impact mechanisms for IAS-threatened birds</i>	<i>EICAT impact mechanisms for alien birds</i>
<i>Habitat effect</i>	1.1 Ecosystem conversion 1.2 Ecosystem degradation 1.3 Indirect ecosystem effects	<b>8. Grazing/herbivory/browsing</b> Grazing, herbivory or browsing by the alien taxon leads to deleterious impact on native plant species. <b>9. Chemical impact on ecosystem</b> The alien taxon causes changes to the chemical biotope characteristics of the native environment; nutrient and/or water cycling; disturbance regimes; or natural succession, leading to deleterious impact on native taxa. <b>11. Structural impact on ecosystem</b> The alien taxon causes changes to the structural biotope characteristics of the native environment; nutrient and/or water cycling; disturbance regimes; or natural succession, leading to deleterious impact on native taxa. <b>12. Interaction with other alien species</b> The alien taxon interacts with other alien taxa (e.g. through pollination, seed dispersal, habitat modification), facilitating deleterious impact on native species. These interactions may be included in other impact classes (e.g. predation, apparent competition) but would not have resulted in the particular level of impact without an interaction with other alien species.
<i>Direct species effect</i>	2.1 Species mortality 2.2 Species disturbance 2.3.7 Reduced reproductive success	<b>2. Predation</b> The alien taxon predate on native taxa, either directly or indirectly (e.g. via mesopredator release), leading to deleterious impact on native taxa. <b>4. Transmission of disease to native species</b> The alien taxon transmits diseases to native taxa, leading to deleterious impact on native taxa. <b>5. Parasitism</b> The alien taxon parasitizes native taxa, leading directly or indirectly (e.g. through apparent competition) to deleterious impact on native taxa.
<i>Indirect species effect</i>	2.3.1 Hybridization 2.3.2 Competition 2.3.3 Loss of mutualism 2.3.4 Loss of pollinator 2.3.5 Inbreeding 2.3.6 Skewed sex ratios	<b>1. Competition</b> The alien taxon competes with native taxa for resources (e.g. food, water, space), leading to deleterious impact on native taxa. <b>3. Hybridization</b> The alien taxon hybridizes with native taxa, leading to deleterious impact on native taxa.

687

688 **Table S2. Traits collected for functional space computing.** Traits in grey and italic were  
689 removed before functional space computation because they were highly correlated with other  
690 traits in the database.

<b>Trait*</b>	<b>Source</b>	<b>Variable type</b>	<b>% of missing values†</b>	<b>Data imputation performance#</b>
<b>Morphology</b>	(Tobias et al. 2021)			
<i>Beak length (culmen)</i>		<i>Numeric</i>	/	
Beak length (nares)‡		Numeric	2.5 %	0.008 ± 0.002
<i>Beak width</i>		<i>Numeric</i>	/	
Beak depth‡		Numeric	2.6 %	0.008 ± 0.001
<i>Tarsus length</i>		<i>Numeric</i>	/	
<i>Wing length</i>		<i>Numeric</i>	/	
<i>Kipps distance</i>		<i>Numeric</i>	/	
<i>Secondary one</i>		<i>Numeric</i>	/	
Hand-wing index		Numeric	3.0 %	0.025 ± 0.001
Tail length		Numeric	2.5 %	0.013 ± 0.002
<b>Life history</b>				
Body mass‡	(Tobias et al. 2021)	Numeric	3.7 %	0.002 ± 0.002
Clutch size‡	(Myhrvold et al. 2015)	Numeric	28.3 %	0.030 ± 0.001
<b>Ecology</b>				
Trophic level	(Tobias et al. 2021)	Categorical	0 %	/
Foraging niche	(Tobias et al. 2021)	Categorical	0 %	/
Habitat breadth	(IUCN 2020)	Numeric	0 %	/
Volancy	(Cooke et al. 2019)	Binary	7.7 %	Sensibility 0.998 ± 0.002 Specificity 0.627 ± 0.294
Insular endemism	(IUCN 2020)	Binary	0 %	/

691

692 **\*Traits description** (only for traits used in the functional space computation):

- 693 - *Beak length (nares)*: “Length from the anterior edge of the nostrils to the tip of the  
694 beak”. Beak length is related to resource use (Pigot et al. 2020).  
695 - *Beak depth*: “Depth of the beak at the anterior edge of the nostrils”. Beak depth is related  
696 to resource use (Pigot et al. 2020).

- 697 - *Hand wing index*: Kipp’s distance (“length from the tip of the first secondary feather to  
698 the tip of the longest primary”) corrected for wing size (“length from the carpal joint  
699 (bend of the wing) to the tip of the longest primary on the unflattened wing”). It is a  
700 standardized biometric of bird dispersal (Sheard et al. 2020)
- 701 - *Tail length*: “Distance between the tip of the longest rectrix and the point at which the  
702 two central rectrices protrude from the skin, typically measured using a ruler inserted  
703 between the two central rectrices”. Tail length is also linked to bird dispersal abilities  
704 and flight capacities.
- 705 - *Body mass*: body mass as a species average, including male and female specimens.
- 706 - *Clutch size*: mean number of eggs per clutch.
- 707 - *Trophic level*: categories are based on the relative importance of the different items  
708 consumed by each species, with a 70% threshold. The trait is coded by four categories:  
709 herbivore (diet based on >70% plants), carnivore (diet based on >70% live animals),  
710 scavenger (diet based on >70% carrions) and omnivore (multiple trophic level diet).
- 711 - *Foraging niche*: it represents the preferred foraging stratum of each species (Primary  
712 lifestyle variable in AVONET), coded as “Generalist” if none was dominant. The trait  
713 is coded by five categories: aerial, terrestrial, insessorial, aquatic and generalist.
- 714 - *Habitat breadth*: categories represent the number of habitat types utilized by each  
715 species. Habitat types are based on the IUCN Habitats Classification Scheme (version  
716 3.1). 12 habitats were considered: forest, savannah, shrubland, grasslands, wetlands,  
717 rocky areas, caves and subterranean habitats, desert, coastal marine areas, artificial,  
718 introduced vegetation, other. The habitat breadth was coded using five ordered  
719 categories, ranging from one to ‘five or more’ used habitats.
- 720 - *Volancy*: the trait is coded as binary, taking one if the species is volant and zero if the  
721 species is flightless.

722 - *Insular endemism*: the trait is coded as binary, taking one if the species is insular  
723 endemic and zero if it has a mainland population.

724 † Percentage of missing values are for the 850 IAS-threatened and alien bird species. All traits  
725 in AVONET were complete, but for some species, trait values were inferred from a closely  
726 related species. For applying a consistent method of data imputation over the traits coming from  
727 different data sources, we replaced the inferred values in AVONET by missing values.

728 # For numeric variables, the reported performance is the mean NRSME, corresponding to the  
729 RMSE normalized by the values range, of the 100 datasets imputed  $\pm$  standard deviation.  
730 Performance is high for low values of NRMSE. For binary variables, the performance is  
731 reported by the sensitivity and the specificity. Sensitivity is the probability that the trait is  
732 predicted to be present when it is actually present, specificity is the probability of obtaining the  
733 absence of a trait when it is actually absent. Performance is high when both metrics are close to  
734 1. The performance was not assessed for metrics that had a complete coverage (no missing  
735 values) for the 850 considered bird species.

736 ‡ These traits were log-converted before functional space computation.

737

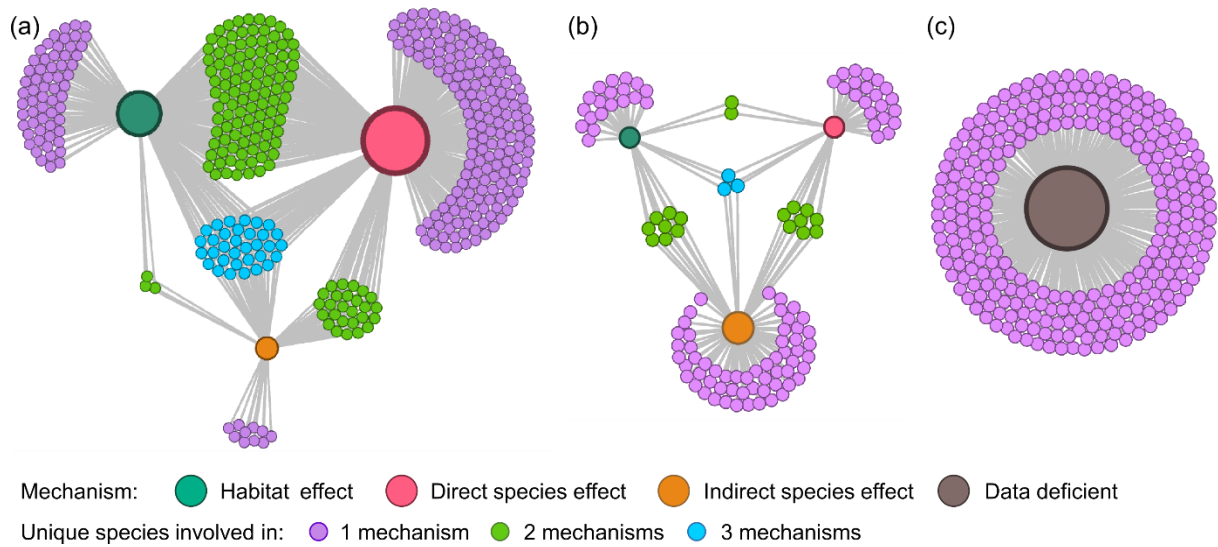


738 **Table S3. Methods for evaluating species impact status and corresponding success rates.**

<i>Definition</i>	<i>Success rate*</i>	<i>TP</i>	<i>TN</i>	<i>FP</i>	<i>FN</i>	<i>Sensitivity</i>	<i>Specificity</i>
<b>Minimal distance metrics</b>							
Minimal distance to each group	52.7%	9	505	33	27	0.25	0.94
Mean distance to each group	36.5%	11	432	106	25	0.31	0.80
Mean distance to each group within a buffer b1	41.2%	18	449	89	18	0.50	0.83
Mean distance to each group within a buffer b2	42.8%	18	461	77	18	0.50	0.86
<b>Relative proportion metrics</b>							
Proportion of species from each group within the 10 closest neighbors, corrected by the observed proportion of each group in the total space	44%	10	502	36	26	0.28	0.93
Proportion of species from each group within a buffer b1, corrected by the observed proportion of each group in the total space	44%	3	507	31	33	0.08	0.94
Proportion of species from each group within a buffer b1, corrected by the observed proportion of each group in the total space	37%	0	508	30	36	0.0	0.94

739 \*Success rate is the ratio between the number of correctly predicted species across all groups  
740 (IAS-threatened highly impacted, IAS-threatened weakly impacted, alien with high impact,  
741 alien with minor impact) and the total number of species to predict. TP, TN, FP, FN, Sensitivity  
742 and Specificity refer to the evaluation of prediction rate for the group “alien species with high  
743 impact”. TP, TN, FP, FN are the number of species that are true positive, true negative, false  
744 positive and false negative respectively (on the total of 574 species) for the group alien with  
745 high impact. Sensitivity is the probability that the species is predicted to be alien with high  
746 impact when it is actually an alien with high impact (also called true positive rate,  $sensitivity =$   
747  $\frac{TP}{TP+FN}$ ). Specificity is the probability to predict another status than alien with high impact when  
748 it is actually no the species status (also called true negative rate,  $specificity = \frac{TN}{TN+FP}$ ).

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750

751 **Figure S1.** Graphical representation of species–mechanism interactions for (a) IAS-threatened

752 birds (n = 411) and (b-c) alien birds (n = 402) with a quantified impact (b, n = 119) or data

753 deficient (c, n = 283) linked to the three mechanisms of impact. Colors represent either the type

754 of impact mechanism or the number of mechanism involved. Node size is proportional to their

755 degree (i.e., number of interactions). Networks were created using Gephi 0.9.2

756 (<https://gephi.org>).

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