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1 **Title**

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

3 **Authors & affiliations**

4 Clara Marino^{1*}, Céline Bellard¹

5 ¹ Université Paris-Saclay, CNRS, AgroParisTech, Ecologie Systématique Evolution, 91405,

6 Orsay, France

7 * Corresponding author: clara.marino@universite-paris-saclay.fr

8 **Short running title**

9 **Bird traits differ in invasions**

10 **Abstract**

11 The ecological impacts of invasive alien species (IAS) are increasingly documented, however
12 they are usually studied through the lens of either the IAS or the affected species (IAS-
13 threatened species). A clear understanding of how both protagonists of biological invasions
14 are characterized is still lacking. We investigated the morphology, life-history, and ecology of
15 birds involved in biological invasions. Evaluating the distribution of 450 IAS-threatened birds
16 and 400 alien birds in a functional space, we found that both groups retained various
17 strategies. Aliens had larger clutches and were more likely to be herbivores than IAS-
18 threatened and worldwide birds, while IAS-threatened birds were more insular endemic from
19 Australia region than alien and worldwide birds. IAS-threatened species showed opposite
20 strategies to aliens regarding traits related to diet, origin, and reproduction. Further comparing
21 traits associated with impact magnitude, we found that even if aliens were mostly
22 herbivorous, those with high impact had more a generalist behavior and an animal-based diet
23 compared to aliens with low impact. By emphasizing differences relating to the distribution of

24 bird groups in a functional space, we opened new opportunities to identify the role of birds in
25 biological invasions.

26

27 **Keywords**

28 Aliens, birds, impact, traits, functional space, two-sides-of-the-same-coin hypothesis

29 **Background**

30 Biological invasions are responsible for major ecological and socioeconomic impacts
31 worldwide (1,2). Invasive alien species (IAS) have many ecological consequences on native
32 ecosystems, ranging from negligible species disturbance to population extirpation or species
33 extinction (3–5). Attempts to evaluate and classify IAS impacts have been widely developed,
34 resulting in protocols that vary according to the studied taxa, spatial scales, habitat types, or
35 objectives (6). Among these initiatives, the Environmental Impact Classification for Alien
36 Taxa (EICAT) classifies the ecological impacts of alien species in a standardized and
37 objective manner (7,8). This protocol has been applied to a growing list of alien taxa,
38 including birds (9), and was recently adopted by the International Union for Conservation of
39 Nature (IUCN) to develop a reproducible and global framework to evaluate IAS impacts (10).
40 The IUCN Red List Threat Classification Scheme also provides another point of view for
41 assessing the biodiversity impacted by IAS (11,12). When taken together, the EICAT protocol
42 and the IUCN Red List represent two complementary tools for studying the impacts of
43 biological invasions at a global scale (13) from species that successfully become introduced
44 (alien species) to species threatened by biological invasions in general (IAS-threatened
45 species).

46 Understanding what makes alien species successful or, in contrast, what renders native
47 species vulnerable to biological invasions is at the core of many studies (14–17). Specifically,
48 species traits have been identified as drivers of invasion success for alien species within a
49 variety of taxa, namely mammals (18), birds (19,20), amphibians and reptiles (21), fish (22),
50 and plants (23). For instance, the establishment success of alien birds is correlated with a high
51 body mass and strongly associated with a generalist profile in terms of diet and habitat (19).
52 Sol et al. (2012) showed that a low brood value and high relative brain size enhance also
53 establishment success of alien bird species. Species traits are also predictors of species'

54 vulnerability to global threats (24,25), and to biological invasions in particular (26,27).
55 Indeed, water-level foragers and large-sized species are overrepresented among IAS-
56 threatened birds, as well as habitat specialist species' (26). Altogether, those results suggest
57 that ecological and reproductive capacities helping to cope rapidly with a new environment
58 favor alien species in biological invasions. By contrast, traits conferring a high ecological
59 specialization and a “slow” life history are more often associated with species threatened by
60 IAS (26,27). This corroborates the assumption that traits contributing to species imperilment
61 should be opposed to those promoting alien success, also known as the “two-sides-of-the-
62 same-coin” hypothesis (28,29). Although validated for various taxonomic groups and scales
63 (vascular flora (28) and crayfishes (30) from north America; worldwide freshwater fish (15)
64 and legumes (29)), attempts to prove this hypothesis for terrestrial vertebrates such as birds or
65 reptiles were inconclusive (31–33). Nevertheless, in all cases, the alien species were opposed
66 to species that were imperiled regardless of the identity of the threats, whereas the features
67 conferring vulnerability were in fact highly threat-dependent (25,27). Therefore, one could
68 expect that alien species and IAS-threatened birds in general lie at opposite extremes of trait
69 values, both diverging from intermediate values encompassed by worldwide birds, but it has
70 never been explicitly tested.

71 The objective of this paper is twofold. First, we aim to explore how traits disentangle the role
72 of birds involved in biological invasions as alien birds or IAS-threatened birds, according to
73 their impact. Second, we propose to revisit the “two-sides-of-the-same-coin” hypothesis for
74 birds at global scale by comparing the traits of alien species and those of IAS-threatened
75 species with a control group of worldwide birds. We described 11 morphological, life history,
76 and ecological traits for both alien and IAS-threatened birds. Our database benefits from the
77 recent publication of a global compilation of morphological traits, which offers new
78 perspectives for studies on bird functional diversity (34). We thus investigated the distribution

79 of c.a. 400 alien birds and 450 IAS-threatened birds in a global avian functional space,
80 comparing their density on the axes of the space. We then conducted a trait-by-trait analysis
81 to better describe the functional properties of both groups, and we compared them to a control
82 group of worldwide birds described for the 11 traits. Finally, taking advantage of the EICAT
83 and IUCN Red List tools, we classified the impacts of both groups regarding their magnitude
84 (ranging from low to high impact) and the main mechanism they are associated with (e.g.,
85 direct species effect, indirect species effect, and habitat effect). Ecological traits like habitat
86 and diet breadth are positively correlated with the strength of alien birds ecological impacts
87 (35–37). Thus, we expect a gradient of traits between species at the extreme sides of the
88 continuum of impact (i.e., highly impacted IAS-threatened birds and alien birds with high
89 impact) and species with more moderate responses in biological invasions (i.e., weakly
90 impacted IAS-threatened birds and alien birds with low impact, Figure 1(a)).

91

92 **Methods**

93 **Data collection**

94 *Birds threatened by biological invasions*

95 Birds at high risk of extinction because of biological invasions were selected from the IUCN
96 Red List (11). We identified species exposed to IAS using the IUCN Threats Classification
97 Scheme (version 3.2), which provides a coherent categorization of threats to biodiversity (38).
98 All species associated with the threats *8.1 Invasive non-native/alien species/diseases* or *8.4*
99 *Problematic species/diseases of unknown origin* (when we could determine the exotic origin
100 of the named problematic species) were regarded as exposed to IAS. We focused on the
101 subgroup of species at high risk of extinction from the vulnerable, endangered, and critically
102 endangered categories in the IUCN Red List. From this pool of species (i.e., at high risk of

103 extinction and threatened by IAS), we distinguished two magnitudes of impact. Birds with
104 more than 50% of their total population experiencing a significant decline (slow, rapid, or
105 very rapid) were classified as “highly impacted IAS-threatened birds,” whereas other birds
106 (with less than 50% of their population experiencing fluctuations or no declines, as well as
107 birds with unknown magnitude) were classified as “weakly impacted IAS-threatened birds.”
108 We further collected the mechanism related to how the IAS impacts each species in the IUCN
109 Stresses Classification Scheme (version 1.0). The mechanism was described using three
110 binary variables for each species (Table S1): ecosystem effect (set as 1 if the species is
111 stressed by an ecosystem conversion/degradation or an indirect ecosystem effect and as 0 if
112 not), direct species effect (set as 1 if the species is directly stressed by an effect on survival or
113 reproduction; e.g., predation, species disturbance or reduced reproductive success), and
114 indirect species effect (set as 1 if the species is stressed by competition, inbreeding,
115 hybridization, or skewed sex ratio). This resulted in a total of 462 birds at high risk of
116 extinction due to biological invasion threats. These birds were associated with two different
117 magnitudes as well as one, two, or three mechanisms of IAS impacts (Figure S1, (a)).

118

119 ***Alien birds***

120 Alien bird species with self-sustaining populations were extracted from the EICAT
121 assessment results for alien birds (9). We used 119 species with information about the
122 mechanism and magnitude of their impact. As with IAS-threatened species, we reclassified
123 the mechanism of invasion using three binary variables (Table S1): ecosystem effect (set as 1
124 if the species impacts the ecosystem), direct species effect (set as 1 if the species directly
125 impacts the survival or reproduction of native species), and indirect species effect (set as 1 if
126 the species indirectly impacts native species). Alien birds were associated with one, two, or
127 three impact mechanisms (Figure S1, (b)). We further coded the magnitude of the alien

128 species impact based on the EICAT impact categories: species with minimal or minor impacts
129 were classified as alien birds with low impact; and species with moderate, major, or massive
130 impacts were classified as alien birds with high impact (10). Species that were data deficient
131 for the mechanism and magnitude of the impact (n = 256) were stored in the final alien
132 database as “DD aliens” (data deficient aliens) (Figure S1, (c)).

133

134 *Species traits*

135 We collected species-level traits for IAS-threatened and alien bird species (n = 863 unique
136 species), and for all birds in the world as a control group (n = 10,943). We collected five traits
137 related to morphology and life-history from the AVONET database (34): *tail length* (numeric)
138 and *hand-wing index* (i.e. a standardized biometric of wing) that are linked to locomotion,
139 dispersal abilities and territoriality (39), *beak length* and *beak depth* that are linked to resource
140 consumption and diet (40), and the *body mass*. We extracted *clutch size* (i.e. number of eggs
141 per clutch) for describing the reproductive rate of birds from the Amniote database (41).
142 Clutch size and body mass are linked to metabolic requirements, dispersal and reproductive
143 strategy of birds, which are key traits regarding vulnerability to invasions and invasion
144 success in other taxa (18,21,27). Finally, we combined five ecological traits. The *habitat*
145 *breadth* (i.e. the number of habitat types utilized by each species; 1, 2, 3, 4, 5+), the *insular*
146 *level* (1 = mainland endemics, 2 = species occurring on both island and mainland, 3 = insular
147 endemics) and the *region of origin* (Africa, Australia, Eurasia, North America, South
148 America, and Multiple) came from the IUCN database. The *trophic level* (herbivore,
149 omnivore, carnivore, scavenger) and the *foraging niche* (aerial, terrestrial, insessorial [i.e.,
150 perching on trees and vegetation], aquatic and generalist) came from AVONET. The habitat
151 breadth, trophic level and foraging niche are measures of bird ecological niche. The insular
152 level and region of origin depict different eco-evolutionary histories among birds. Overall,

153 these 11 traits relating to morphology, life history, lifestyle and evolutionary history were
154 shown to be important with regard to native species' vulnerability to biological invasions (26)
155 as well as invasion success and impacts for aliens (37). Traits were selected to be
156 complementary regarding bird ecology, with a good level of completeness and by keeping
157 variables that were not highly correlated with each other except for morphological ones (see
158 Appendix 1, Table S2 and Figure S1 for details on traits and their selection). We ensured that
159 the databases were merged correctly from different sources by verifying species synonyms.
160 The *rl_synonyms* function from the *rredlist* package (42) and the *synonyms* function from the
161 *taxise* package (43) were used for searches in the IUCN database and Integrated Taxonomic
162 Information System, respectively. We removed 13 species from the database due to
163 inconsistencies in the taxonomy of the different databases.

164

165 ***Imputation of missing trait values using phylogeny***

166 Functional space computation requires fully informed trait databases. Although traits from the
167 AVONET and IUCN databases were complete for the vast majority of the selected species,
168 clutch size contained 28.3% of missing values for IAS-threatened and alien birds (Table S2).
169 To avoid an important loss of information, we imputed missing trait values using phylogeny.
170 Closely related species tend to be more similar to each other, and thus by considering species
171 phylogenetic relations, the performance of data imputation improves (44). We summarized
172 the phylogenetic information using the first 10 phylogenetic eigenvectors calculated from
173 1,000 trees obtained from vertlife.org (45). Imputed values were generated with the *mice()*
174 function from the *mice* package (46) using the predictive mean matching method based on the
175 traits and 10 phylogenetic eigenvectors. The imputation was performed on the 11 selected
176 traits for all worldwide bird species (n = 10,943). We then took as a complete dataset the
177 median value for the 1,000 imputed datasets obtained from the 1,000 trees. To ensure the

178 validity of data imputation, we performed data inference on 100 artificially incomplete
179 datasets with randomly simulated missing values. They were obtained by selecting all species
180 with complete trait values ($n = 6,190$) and randomly generating the percentage of missing
181 values that corresponded to each trait. We then evaluated the performance of data imputation
182 by calculating the average normalized root-mean-square error (NRMSE) for numeric traits
183 and the average sensitivity/specificity for binary traits on the 100 artificially drilled datasets
184 (Table S2). Average NRMSE was below 0.03 for all variables considered, thus indicating a
185 very low error rate in the imputed missing data. The final database for birds involved in
186 biological invasions contained 850 species with fully informed traits, including 456 IAS-
187 threatened birds, 118 alien birds with information about their impact, and 290 DD aliens (note
188 that 14 species were both alien and IAS-threatened species).

189

190 **Statistical analysis**

191 *Axes simplification*

192 Because the trait database contained different types of variables (e.g., numeric discrete,
193 numeric continuous, categorical), we computed a functional space based on the
194 transformation of the raw traits following Mouillot et al. (2021). First, pairwise functional
195 distances between the 850 bird species were calculated using the Gower dissimilarity index
196 (48) with the *daisy()* function from the *vegan* package (49). Second, principal coordinate
197 analysis (PCoA) was applied to the distance matrix using the *pcoa()* function from the *ape*
198 package (50). We computed all our analyses based on the first three dimensions of the PCoA.
199 As morphological traits scaled with body mass (Figure S2), we computed a corrected PCoA
200 (hereafter, PCoA_c) with the same traits but all morphological measurements (i.e., hand-wing
201 index, tail length, beak depth and beak length) were corrected by the body mass (i.e., traits
202 were divided by the log-transformed body mass). Final results were similar to the PCoA (see

203 Figure S3), thus we only present in the main text the functional space with uncorrected traits,
204 that gave a simpler representation of bird morphology and ecological strategies. The results of
205 the PCoA_c are further discussed in the Supplementary material (Appendix 2, Table S3).

206

207 *Group dissimilarities in functional space*

208 To understand which ecological strategies were associated with the first three axes of the
209 PCoA, we computed the correlation between the studied traits and the three PCoA axes. We
210 used the *rcorr()* function from the *Hmisc* package (51) after converting all the traits into
211 numeric variables (e.g. categorical traits were converted into binary traits). We then compared
212 the ecological strategies of birds according to their role in biological invasions and their
213 impact using raincloud plots (Allen et al., 2018). These plots enabled us to simultaneously
214 depict the density and basic statistics of species distribution along the first functional space
215 axes. For both alien and IAS-threatened birds, we first grouped species according to their
216 impact magnitude (low and high) as well as their mechanism of impact: direct species effect,
217 indirect species effect, and habitat effect (considering only species affected by one
218 mechanism). We compared the distribution between groups along the axes using
219 Kolmogorov-Smirnov (KS) tests, which were run independently for both alien species and
220 IAS-threatened species. We also performed pairwise Wilcoxon tests (i.e. non-parametric t-
221 tests) to compare differences in mean values of axis between the groups.

222

223 *Trait-by-trait analysis*

224 Because some traits were correlated to each other, we conducted a trait-by-trait analysis to
225 compare the trait modalities or values associated with the different groups of impact
226 magnitudes and mechanisms, independently of each other. For each numeric and ordinal trait,

227 we compared the mean value of the different groups using ANOVA and post-hoc tests. As
228 morphological traits scaled with body size, all traits linked to body measurement were divided
229 by the log-transformed body mass. For categorical traits, we performed chi-squared tests of
230 independence. As we aim at exploring the “two-sides-of-the-same-coin” hypothesis, we also
231 compared the different groups with a control group of birds randomly picked among the
232 worldwide bird species. We created 100 control groups of 150 species, to keep a comparable
233 sample size in all groups, performed the tests for each group and summarized the statistics as
234 the mean estimate and the mean p-value obtained over the 100 control groups. For a
235 validation of the hypothesis *sensu* Blackburn & Jeschke (2009) (32), we expect the alien birds
236 to show an extreme value in a given trait, the IAS-T birds an opposite extreme value of this
237 trait, and the control group showing intermediate trait value, in average different from both
238 groups involved in biological invasions.

239

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

241 Our goal was also to distinguish functional groups of birds based on their role in biological
242 invasions and their impact on native systems. We thus evaluated the opportunity to classify
243 data deficient (DD) species into alien species with high or low impact based on their position
244 in the functional space. To this aim, we computed seven metrics to describe the position of
245 each species in the functional space compared to the position of all species with an informed
246 status. Metrics were either a minimal distance (to a species or group of species with known
247 status) or a proportion of species within a buffer (Appendix 3, Table S4). Using each metric,
248 we determined the predicted status of the 574 species with known status and evaluated the
249 rate of predictions using contingency tables. We focused on evaluating the prediction for the
250 group of “alien species with high impact.”

251 All analyses were performed with R software (version 4.1.0) (53). The data and the scripts
252 used for all the analyses are available online (54).

253

254 **Results**

255 **Functional characterization of the impact of birds involved in biological invasions**

256 The first three axes of the PCoA explained 62% of the total variance of the ecological traits of
257 all birds involved in biological invasions. The PC1 axis showed the major contribution of
258 insular endemism, life history traits (i.e., body mass and clutch size) and traits related to
259 resource consumption (i.e., beak depth, animal-based diet, insessorial foraging niche) (Table
260 1). The positive part of PC1 was dominated by insular endemic species with an insessorial
261 foraging niche, while the negative part was characterized by larger species - consequently
262 with a deeper and longer beak -, a higher dispersal ability, that occur in several habitats and
263 have mainland populations that originate from multiple regions. Note that the PCoA_c showed
264 distinct associations between axes and morphological traits, with species with longer beaks
265 when controlled by body mass being on the positive part of PC1 (Appendix 2, Table S3,
266 Figure S3). The PC2 axis was mainly correlated with trophic level with carnivore species on
267 the negative side and herbivore species on the positive side of the axis. Finally, foraging niche
268 and morphology drove the PC3 axis, with the negative part associated with terrestrial species
269 with high morphological measurements (e.g. large and long beak, long tail and a high hand-
270 wind index), and the positive part with insessorial strategy.

271 The distribution of alien birds (with high or low impact) significantly differed from the
272 distribution of IAS-threatened birds (highly or weakly impacted) from PC1 to PC3 (Figure
273 1(b) and Figure S3(b)). Intra-group comparisons for impact type showed that IAS-threatened
274 birds were rather similarly distributed regardless of their impact magnitude except with PC1

275 were they showed a slight difference in mean axis value but not in their density of distribution
276 (Wilcoxon test, $W = 27,908$, $p = 0.049$; KS test, $D = 0.10$, $p = 0.23$). By contrast, the
277 distribution of alien birds significantly differed in PC2 depending on their impact magnitude
278 (Wilcoxon test, $W = 848$, $p < 0.001$; KS-test, $D = 0.41$, $p < 0.001$), although their distributions
279 were similar on the other axes. Considering the density distributions in PC1 and the traits
280 correlated with this axis, highly impacted IAS-threatened birds were more insular endemic
281 and less mainland endemic than weakly impacted IAS-threatened birds (confirmed using the
282 single trait approach; Figure 2, (d)). On the opposite side of this axis, both alien groups were
283 more associated with a high number of used habitat, larger body mass, and thus higher
284 morphological measurements, but see results from Figure S3 and Table S3 when
285 morphological measurements are controlled by body mass.

286 We also conducted a single trait analyses to compare the proportion of traits modalities within
287 the different groups. Morphological and life history traits did not allow us to disentangle the
288 impact magnitude within IAS-threatened species or alien species (Figure 3). However,
289 ecological traits showed intragroup differences for alien species: alien birds with a high
290 impact were more carnivorous and omnivorous, had a larger habitat breath (i.e., more
291 generalists) and originated more from multiple regions when comparing with aliens with a
292 low impact, that contained more mainland endemic species (Figure 2). Moreover, alien birds
293 and IAS-threatened birds harbored distinct functional strategies (Figures 2, 3) regardless of
294 their impact. Alien birds had a significantly longer tail length (controlled by body size) and
295 larger clutch size than IAS-threatened birds with the control group of worldwide birds
296 showing intermediate results (Figure 3, (b-f)).

297 Moreover, alien birds showed a larger body mass compared to highly impacted IAS-
298 threatened birds but both groups showed a significant larger body mass compared to the
299 control group of worldwide birds (Figure 3, (c)). Alien birds were also more generalist in

300 terms of habitat use and were at lower trophic levels compared to species threatened by
301 biological invasions and the control group of worldwide birds (Figure 2, (a-b)). Regarding the
302 region of origin, IAS-threatened birds originated more from Australia region, while alien
303 birds came more from Eurasia and multiple regions (Figure 2, (e)).

304 We pursued our analyses by disentangling the bird characteristics for each impact mechanism:
305 direct species effect, indirect species effect, and ecosystem effect (Figure 4). Based on our
306 previous results showing no major intragroup differences regarding impact magnitude, we
307 considered only two groups: all alien birds and all IAS-threatened birds. IAS-threatened birds
308 associated with a direct species effect diverged significantly from IAS-threatened birds
309 associated with a habitat effect in the second and third axes (Figure 4, upper panel). Single
310 trait analyses showed that species threatened by a direct effect were larger with a longer beak
311 and a higher proportion of aquatic foragers compared to species threatened by habitat effect,
312 as the latter were more insessorial. Moreover, directly impacted species had twice as many
313 endemic insular species as the group threatened by habitat effect. Alien birds with a direct
314 impact on species differed strongly from the other mechanisms in PC2 (Figure 4, lower
315 panel). They had a significantly higher trophic level and were more habitat generalists than
316 other alien groups.

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

318 When evaluating the ability to disentangle alien species with a high or low impact among the
319 alien species that were data deficient regarding their impact magnitude, we obtained a success
320 rate ranging from 37.2% to 53.6% (Table S4). Focusing on the quality of prediction for the
321 group “alien birds with high impact,” the true negative rate was high (specificity > 0.75),
322 although we observed very few true positives, thus leading to low sensitivity for all the tested
323 methods (from 0.19 to 0.72; Table S4).

324

325 **Discussion**

326 **Diverging functional strategies between IAS-threatened and alien birds**

327 Our results suggest that birds present diverging morphological, life history, and ecological
328 strategies depending on their role in biological invasions. Considering traits together in a
329 functional space and not only individually enabled a more complex and realistic view of
330 species' ecological strategies (55).

331 *Diet and reproduction as intrinsic factors for distinguishing alien from IAS-threatened birds*

332 Exploring traits of alien birds with impact and IAS-threatened birds, we found that aliens had
333 a larger proportion of herbivores, a larger clutch size, and a longer tail length, while they were
334 also more habitat generalist than IAS-threatened birds (and more generally, than worldwide
335 birds). Birds with a plant-based diet were indeed more introduced and more successful at
336 establishment in exotic places than carnivorous birds (56). Given the discrepancies between
337 the trophic strategies of aliens and IAS-threatened birds, both groups are unlikely to enter into
338 high competition for resource exploitation (17). As a consequence, the competition between
339 native and introduced birds is probably not as deleterious for native species as other
340 mechanisms due to IAS (e.g., predation, habitat degradation). Our result showing larger clutch
341 sizes for alien birds with impact is in discordance with previous works (20). Contrary to other
342 terrestrial vertebrates (18,21), the “slow” life history of birds (i.e., small clutches and
343 investment in future reproductive events) was known to favor the establishment of aliens (20).
344 Nevertheless, as establishment and impact are two separate stages of invasion, they are likely
345 to filter out species with different traits (57). Furthermore, introduced birds are a non-random
346 sample of worldwide birds, with some families and characteristics like large body size (and
347 thus “slow” reproductive rates) being preferentially selected for hunting or pet trade (58,59).

348 Thus, despite the apparent negative correlation between establishment success and high
349 reproductive rate found in previous studies, the initial pool of transported birds might be
350 biased toward large clutches compared to the global pool. This leads to a generalist profile
351 and faster reproductive rate for alien birds compared to IAS-threatened and even worldwide
352 birds. Our results further demonstrated that alien birds with and without impact are also a
353 non-random sample of worldwide birds, with specific traits (e.g., having shorter beaks and
354 longer tails for larger body sizes, being more herbivore and habitat generalist than worldwide
355 birds; Figure 2, 3).

356 *The importance of origin and eco-evolutionary history*

357 We found that IAS-threatened birds were more often insular endemic compared to alien and
358 worldwide birds. Facilitated niche shifts during invasion due to high constraints in their native
359 range (60,61) was not an important factor here associated with insular endemic species that
360 become successful invaders. One exception in our database was the New Zealand weka
361 (*Gallirallus australis*), a flightless rail that has been introduced on several islands of New
362 Zealand where it predates on endemic threatened species, but which is also threatened in its
363 native island by invasive alien mammals (e.g. rats) (62). Moreover, IAS-threatened birds
364 present similar ecological strategies as documented extinct species (e.g., large, insular
365 endemic and flightless (63)). We also demonstrated that IAS-threatened birds originated more
366 from the Australian region while alien birds came more from Eurasia and multiple regions.
367 The Australian region with surrounding islands like Indonesia, Papua New Guinea and New
368 Zealand is known for hosting a large portion of endemic insular threatened and extinct birds
369 globally (64). Regarding alien birds, their introduction history is strongly marked with the
370 spread of Eurasian species following the era of European colonization (65).

371 *The “two-sides-of-the-same-coin” hypothesis*

372 Although we found diverging functional strategies for alien and IAS-threatened species, our
373 findings lend poor support to a revisited “two-sides-of-the-same-coin” hypothesis, positing
374 that the characteristics promoting alien success are at the extreme opposite to those that
375 promote vulnerability to IAS, as in previous studies on birds (32,33). Compared to worldwide
376 birds, alien and IAS-threatened species do not show significant deviations in terms of traits
377 except for insular level or region of origin. Moreover, alien birds also showed a significantly
378 longer tail length (controlled by body size) and larger clutch size than IAS-threatened birds.
379 However, the control group of worldwide birds showed intermediate results that were not
380 statistically different from one group or the other.

381 **Functional characterization of impact magnitude and mechanism**

382 *Impact magnitude*

383 Density plot analysis and trait-by-trait analysis did not reveal strong differences among alien
384 neither IAS-threatened birds regarding impact magnitude (except for alien birds on PC2 in
385 Figures 1 and S3, Figure 2 (a,b,d). Specifically, both analyses revealed that trophic level and
386 habitat breadth significantly differed between low and high impact magnitudes for alien birds,
387 while insular level differed for highly or weakly impacted IAS-threatened birds. Alien birds
388 with high impact were more from multiple regions suggesting they might have a native range
389 with broader eco-evolutionary conditions compared with alien birds with low impact. Our
390 results are in accordance with previous studies that assert the dominance of habitat and diet
391 generalists within alien species with high impacts on native ecosystems (35,37,66).

392 Morphological traits did not explain the impact magnitude among groups of birds, neither the
393 bird dispersal ability, measured by HWI and tail length.

394 Concerning IAS-threatened species, their impact magnitude was not linked to species traits
395 except for insular level. This confirms previous studies that highlight the increased
396 vulnerability of insular birds and other taxa compared to those with mainland populations

397 regarding the biological invasion threat (14,67). Consequently, factors that induce significant
398 and major population declines because of biological invasions are likely to be extrinsic (e.g.,
399 dependent on the invasion context, environment, alien characteristics, or the combination of
400 threats involved). Another possible explanation is that we did not take into account important
401 traits that may mediate the impact magnitude of IAS on native species. For instance, species
402 with small range sizes are generally at a higher extinction risk than those with larger ranges
403 (24). Because IUCN threat categories are partly based on species range sizes, using this trait
404 in our analysis could possibly lead to confounding effects (68).

405 *Impact mechanism*

406 In the second part of the analysis, we tried to disentangle the characteristics of alien and IAS-
407 threatened birds depending on the mechanism that they impact or are impacted by. We
408 observed a difference in the profile of IAS-threatened birds that are directly impacted (e.g.,
409 predation by IAS) and those that are impacted through a habitat effect (e.g., change in
410 vegetation or habitat degradation due to IAS). Compared to birds that are sensitive to habitat
411 disturbance by IAS, birds prone to predation were larger, frequently insular endemic and
412 terrestrial, thus being the ideal naïve prey for alien predators (69). For instance, the kiwi
413 (*Apteryx spp.*), which presents this very profile, is highly predated by introduced mammals in
414 New Zealand (70). However, having all these characteristics of vulnerability does not
415 necessarily mean that a native bird becomes prey. The large and flightless kagu (*Rhynochetos*
416 *jubatus*), an endemic bird of New Caledonia, is not consumed by feral cats despite its clear
417 “victim” profile (71). This is possibly explained by its development of defensive behavior that
418 has proven to be effective against cats. The kagu may nevertheless be predated by larger
419 introduced mammals (e.g., feral dogs), which still make the species a prey threatened by
420 direct mechanism.

421 We expected that birds threatened by a habitat effect due to IAS would present characteristics
422 similar to species threatened by habitat degradation: species with an invertebrate-based diet
423 that require a large foraging space as well as habitat specialists that are more sensitive to
424 habitat fragmentation (72). Our results suggest that these birds, though more insessorial (i.e.,
425 perching on trees and vegetation in general), are not more habitat specialist than species
426 directly impacted by IAS, and they did not present a specific dispersal ability. However,
427 insessorial life-style renders species sensitive to the removal of trees either by humans or by
428 non-native species. For instance, the Rufous Flycatcher (*Myiarchus semirufus*) is a tree-
429 perching bird endemic of the Northern Peru preferring large trees for nesting, and is
430 threatened by the increasing presence of goats (*Capra hircus*) that prevent tree growth by
431 grazing (73).

432 Finally, our results confirmed that alien species that directly impact native species have an
433 animal-based diet compared to aliens with other mechanisms of impact (37). They also had a
434 wider habitat breadth, once again highlighting the threat posed by generalist species when
435 introduced into a new ecosystem (74). For both aliens and IAS-threatened species, we
436 characterized the impact type by pooling together the different mechanism categories (Table
437 S1). We assumed that species directly impacted by species mortality, species disturbance, or
438 reduced reproductive success shared common characteristics, although they might also have
439 specific hidden traits associated with each of these mechanisms (this comment applies to the
440 three impact mechanisms and the two groups of birds). Such pooling was necessary to
441 perform density statistics along the functional space axes, the gain in statistical power
442 compensating for the loss in precision. However, the pooling may also explain why we mostly
443 detected ecological traits that differed between groups of different impact types as opposed to
444 life history or morphological features.

445 **Using species traits to predict alien bird impact**

446 Ultimately, the EICAT protocol is a powerful tool for assessing the impact of alien species.
447 However, a large proportion of birds lacks information regarding their ecological impact,
448 while others are assessed with high uncertainty (75), which is not synonymous with an
449 absence of impact (76). Impacts take time to be reported or even noticed, given the time lag
450 between the introduction of alien species, their spread, and their effect in new ecosystems
451 (77). We therefore evaluated the possibility of using species traits to infer the impact
452 magnitude of DD alien birds. The prediction methods computed to detect alien birds with high
453 impact did not perform well. All tested metrics had a high specificity but a low sensitivity.
454 This gap between sensitivity and specificity has already been observed in a method for
455 creating invasive species watch lists (78). The simplicity of our prediction protocol combined
456 with the low number of alien birds with high impact (n=39) in the functional space compared
457 to non-impacting species (n=535) can explain this poor sensitivity. This result also
458 emphasizes the importance of accounting for other factors that are crucial to invasion success
459 (e.g., local context, introduction event-related features, 79). Furthermore, the functional and
460 phylogenetic properties of the recipient community (e.g., ecological niche saturation, shared
461 evolutionary history with introduced alien species, relative brain size) are likely to mediate
462 the success of alien species (80,81).

463

464 **Conclusion**

465 Compared to previous studies focusing on the characteristics of either alien species or IAS-
466 threatened species (26,27,35–37), this study takes advantage of a new morphological database
467 (34) and approach (i.e., density distribution in a functional space) to evaluate the
468 morphological, ecological and evolutionary differences between birds involved in biological
469 invasions. Overall, morphological and life history traits allow us to distinguish the role of
470 birds in biological invasions as either alien or IAS-threatened, lending low support to the

471 “two-sides-of-the-same-coin” hypothesis. Conversely, ecological traits were better factors to
472 explain the type of impact associated with aliens and IAS-threatened species.

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483

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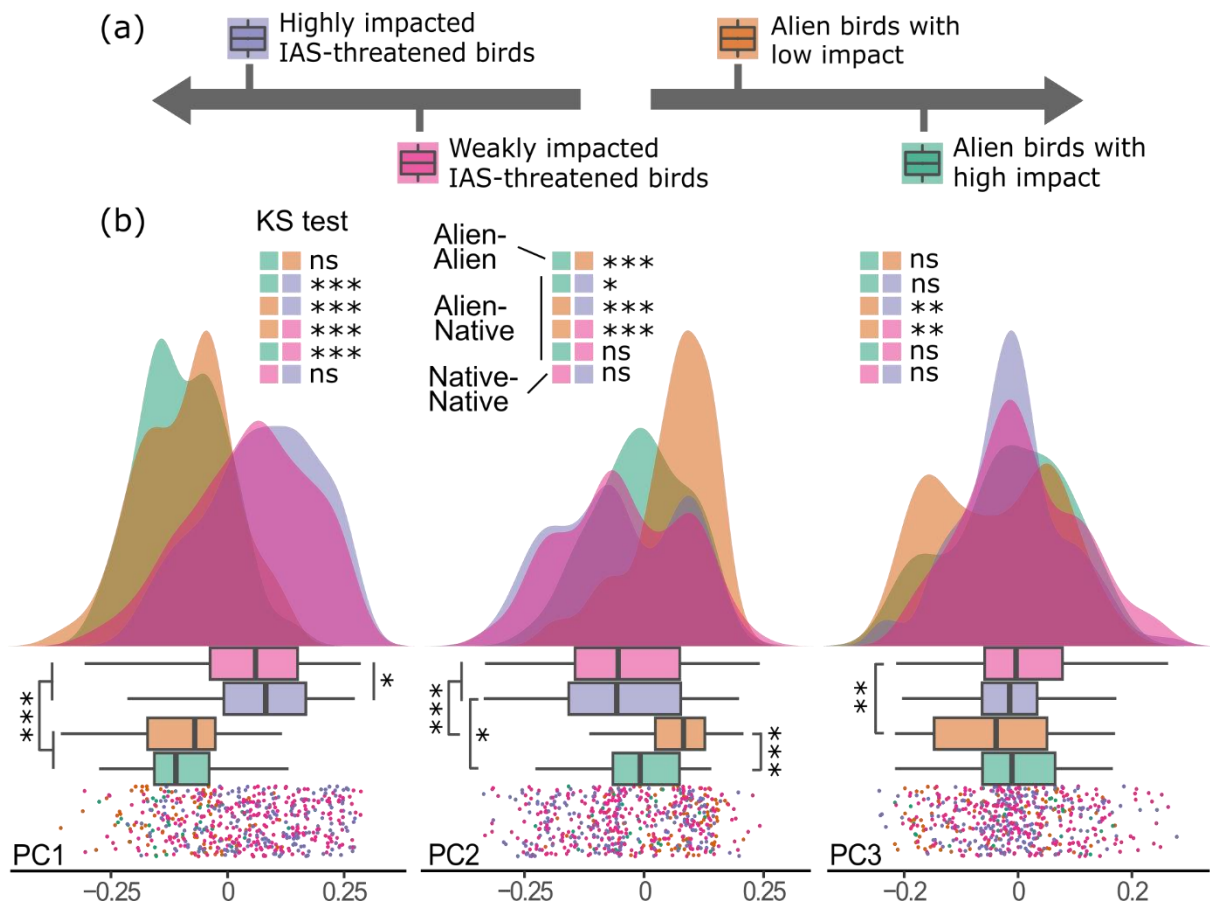
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689 **Table 1: Correlation between ecological traits and the first three axes of principal**
690 **coordinate analysis containing all birds involved in biological invasions** (n = 850 unique
691 species). Spearman coefficients and p-values are reported.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

695

	PC1 (25.1%)		PC2 (22.8%)		PC3 (14.6%)	
	r	P	r	P	r	P
Morphological traits						
Hand-wing index	-0.43	<0.001	-0.30	<0.001	-0.44	<0.001
Tail length	-0.38	<0.001	-0.15	<0.001	-0.39	<0.001
Beak depth	-0.49	<0.001	-0.05	0.133	-0.56	<0.001
Beak length	-0.42	<0.001	-0.36	<0.001	-0.45	<0.001
Life history traits						
Body mass	-0.61	<0.001	-0.28	<0.001	-0.33	<0.001
Clutch size	-0.39	<0.001	0.36	<0.001	0.11	0.001
Ecological traits						
Insular level	0.59	<0.001	-0.31	<0.001	-0.18	<0.001
Habitat breadth	-0.46	<0.001	-0.19	<0.001	0.04	0.249
Trophic level						
Herbivore	-0.26	<0.001	0.78	<0.001	-0.38	<0.001
Omnivore	0.02	0.61	0.05	0.112	0.37	<0.001
Carnivore	0.27	<0.001	-0.82	<0.001	0.10	0.004
Scavenger	-0.12	0.001	-0.05	0.177	0.01	0.777
Foraging niche						
Aerial	-0.01	0.845	-0.31	<0.001	-0.03	0.329
Aquatic	-0.22	<0.001	-0.37	<0.001	-0.27	<0.001
Generalist	-0.04	0.206	-0.14	<0.001	0.13	<0.001
Inessorial	0.60	<0.001	0.31	<0.001	-0.49	<0.001
Terrestrial	-0.44	<0.001	0.15	<0.001	0.59	<0.001
Region of origin						
Africa	0.08	0.026	0.13	<0.001	0.21	<0.001
Australia	0.33	<0.001	-0.08	0.028	-0.10	0.003
Eurasia	-0.13	<0.001	0.17	<0.001	0.12	<0.001
North America	0.21	<0.001	0.01	0.683	-0.08	0.014
South America	0.13	<0.001	0.14	<0.001	-0.05	0.166
Multiple	-0.50	<0.001	-0.34	<0.001	-0.11	0.001

696

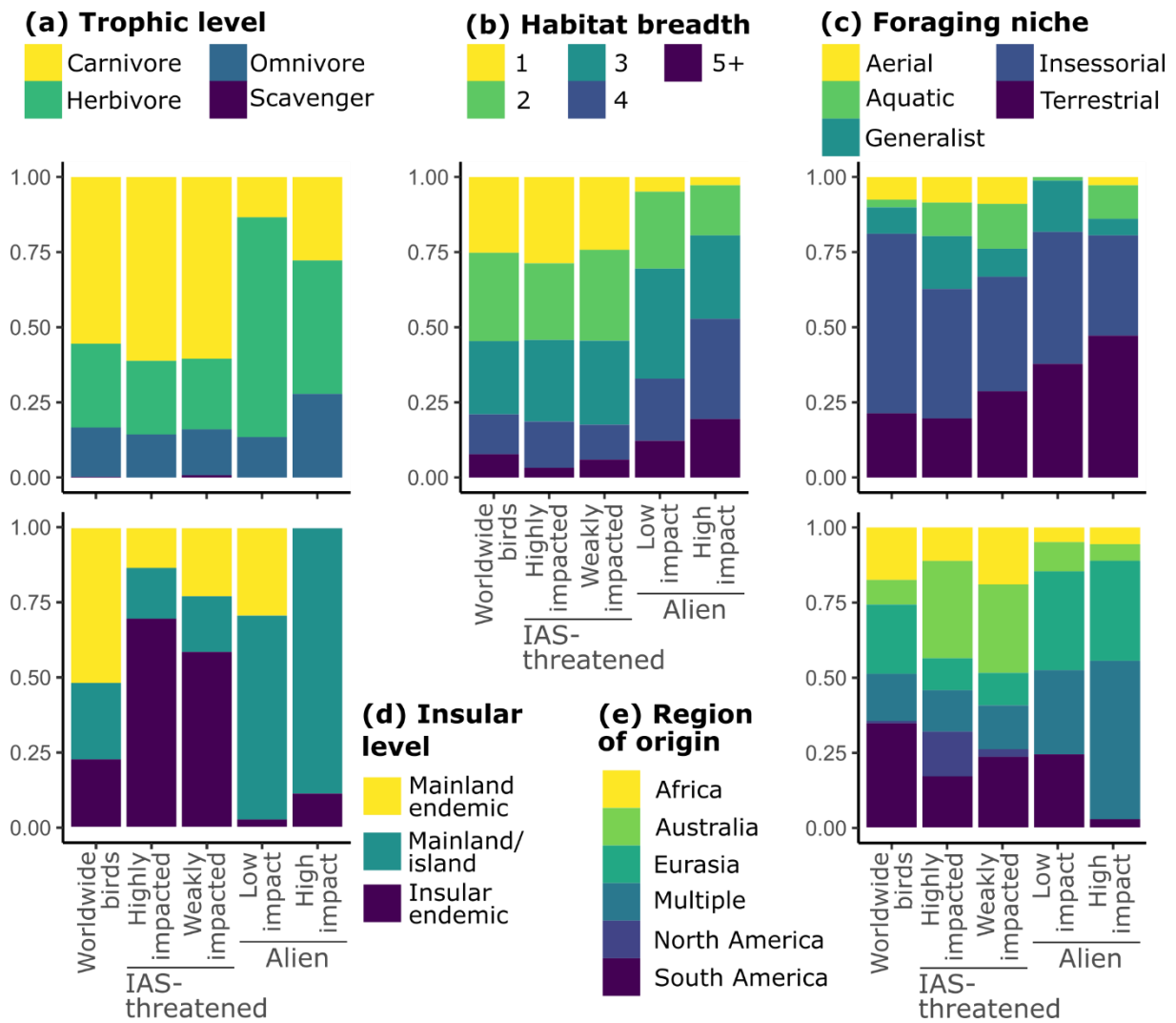


697

698 **Figure 1. Functional characterization of birds and their impact in biological invasions.**

699 (a) Schematic overview of the considered groups and (b) distribution density of the four
700 groups of birds involved in biological invasions (highly impacted IAS-threatened, weakly
701 impacted IAS-threatened, alien with low impact, alien with high impact) in the first three axes
702 of principal coordinate (PC) analysis. Boxplots are associated with the point distribution.
703 Significant differences in mean values of axis between the groups are depicted with stars on
704 both sides of the boxplots. At the top of each density plot, the Kolmogorov-Smirnov (KS) test
705 in each axis compares the distributions 2-by-2 between groups (*** $p < 0.001$, ** $p < 0.01$, *
706 $p < 0.05$, ns = non-significant difference).

707



708

709 **Figure 2. Proportions of trait modalities for IAS-threatened birds and alien birds**

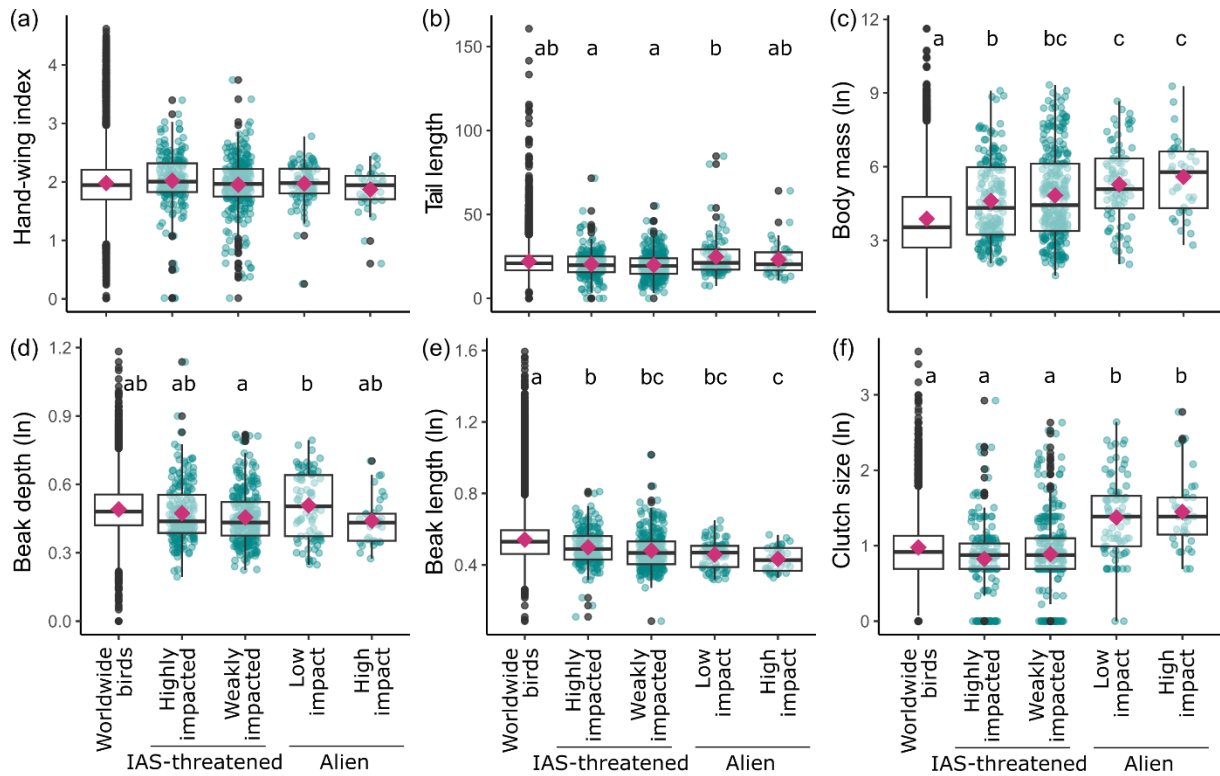
710 **according to their impact magnitude.** X-axes represent the groups of birds along the

711 continuum of impact in biological invasions as well as worldwide birds; Y-axes represent the

712 proportion of each modality for each categorical trait.

713

714



715

716 **Figure 3. Relationships between species traits and impact magnitude for IAS-threatened**

717 **birds and alien birds.** X-axes represent the groups of birds along the continuum of impact in

718 biological invasions as well as worldwide birds; Y-axes represent the morphological and life

719 history numeric traits. Trait values were log-transformed for body mass, beak depth, beak

720 length, and clutch size. Note that all traits linked to body measurement (i.e. hand-wing index,

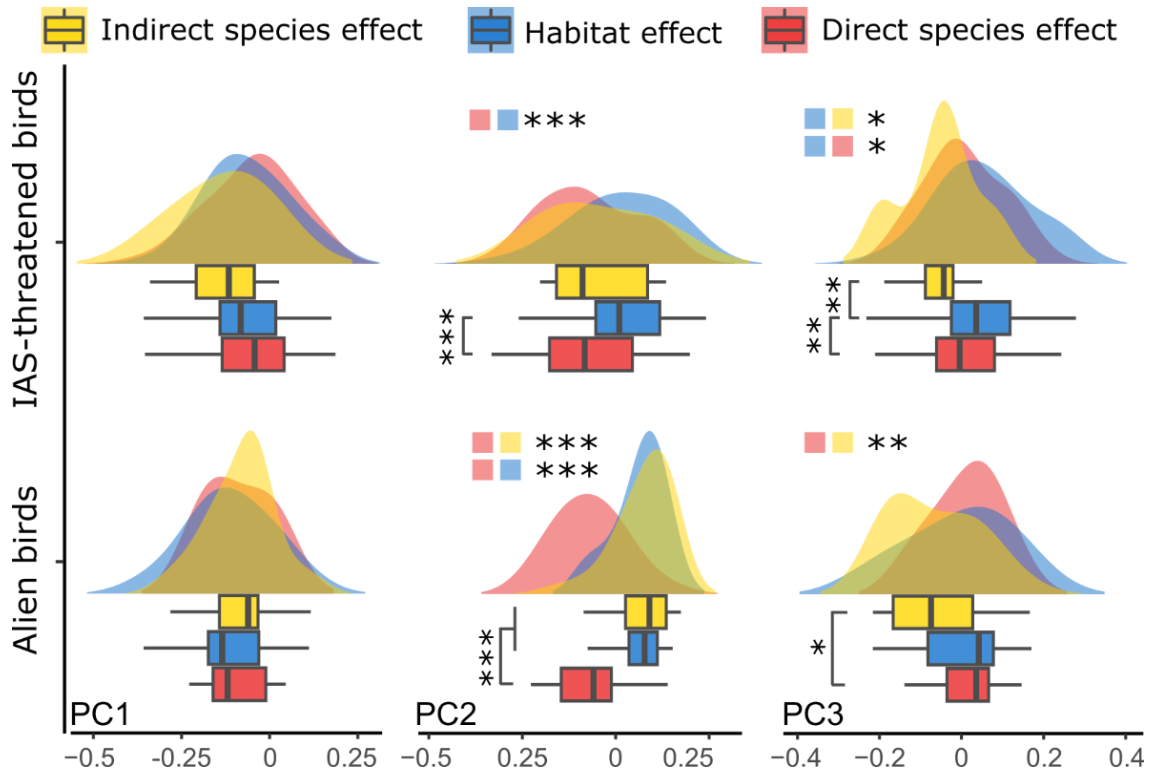
721 tail length, beak depth and, beak length) were corrected by body mass. Boxplots show the

722 median and first and third quartiles, with outliers plotted individually in bold. Blue dots are

723 raw values for unique species contained in each group. Pink diamonds represent the mean

724 value for each trait. Significant differences between mean values are indicated with letters.

725



726

727 **Figure 4. Distribution density of the impact mechanism groups for IAS-threatened birds**

728 **and alien birds in the first three axes of the PCoA.** Significant differences in mean values

729 of axis between the groups are depicted with stars on the left of the boxplots. At the top of

730 each density plot, the Kolmogorov-Smirnov (KS) test in each axis compares the distributions

731 2-by-2 between groups (***) $p < 0.001$, ** $p < 0.01$, * $p < 0.05$).