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

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Title

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Short running title

Bird traits differ in invasions

Abstract

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

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

Keywords

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

Background

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

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

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

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

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

Methods

Data collection

Birds threatened by biological invasions

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

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

Alien birds

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

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

Species traits

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

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

Imputation of missing trait values using phylogeny

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

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

Statistical analysis

Axes simplification

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

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

Group dissimilarities in functional space

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

Trait-by-trait analysis

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

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

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

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

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

Results

Functional characterization of the impact of birds involved in biological invasions

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

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

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

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

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

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

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

Assessment of impact prediction for data deficient alien birds using traits

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

Discussion

Diverging functional strategies between IAS-threatened and alien birds

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

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

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

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

The importance of origin and eco-evolutionary history

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

The "two-sides-of-the-same-coin" hypothesis

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

Functional characterization of impact magnitude and mechanism

Impact magnitude

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

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

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

Impact mechanism

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

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

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

Using species traits to predict alien bird impact

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

Conclusion

Compared to previous studies focusing on the characteristics of either alien species or IAS-threatened species (26,27,35–37), this study takes advantage of a new morphological database (34) and approach (i.e., density distribution in a functional space) to evaluate the morphological, ecological and evolutionary differences between birds involved in biological invasions. Overall, morphological and life history traits allow us to distinguish the role of 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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Table 1: Correlation between ecological traits and the first three axes of principal coordinate analysis containing all birds involved in biological invasions (n = 850 unique species). Spearman coefficients and p-values are reported. Non-numeric traits (trophic level, foraging niche, region of origin) were converted into binary variables to compute the correlations. The strongest correlations (r < -0.4 or r > 0.4) and their associated significant p-values are shown in bold.

	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
Insessorial	**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

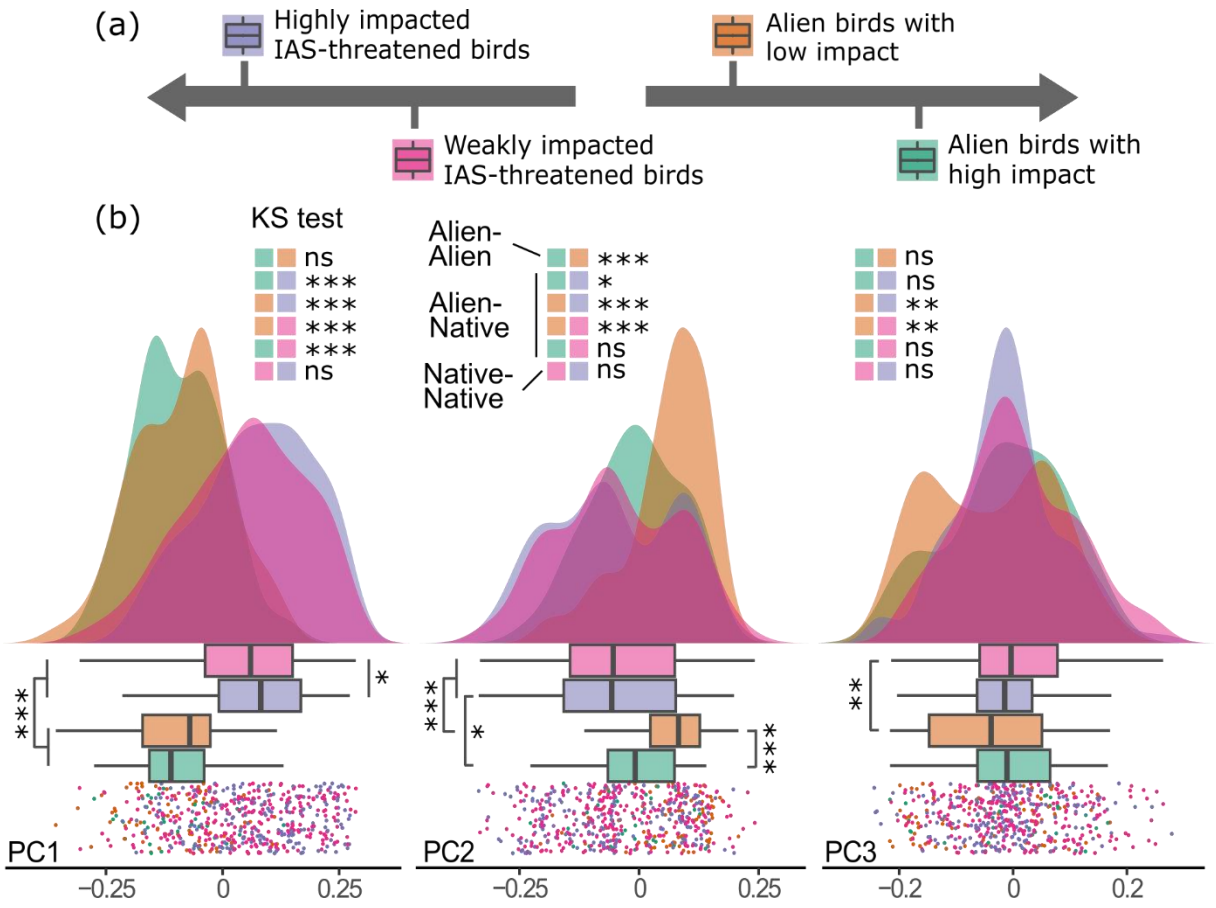


Figure 1. Functional characterization of birds and their impact in biological invasions. (a) Schematic overview of the considered groups and (b) distribution density of the four groups of birds involved in biological invasions (highly impacted IAS-threatened, weakly impacted IAS-threatened, alien with low impact, alien with high impact) in the first three axes of principal coordinate (PC) analysis. Boxplots are associated with the point distribution. Significant differences in mean values of axis between the groups are depicted with stars on both sides of the boxplots. At the top of each density plot, the Kolmogorov-Smirnov (KS) test in each axis compares the distributions 2-by-2 between groups (*** $p < 0.001$, ** $p < 0.01$, * $p < 0$ .05, ns = non-significant difference).

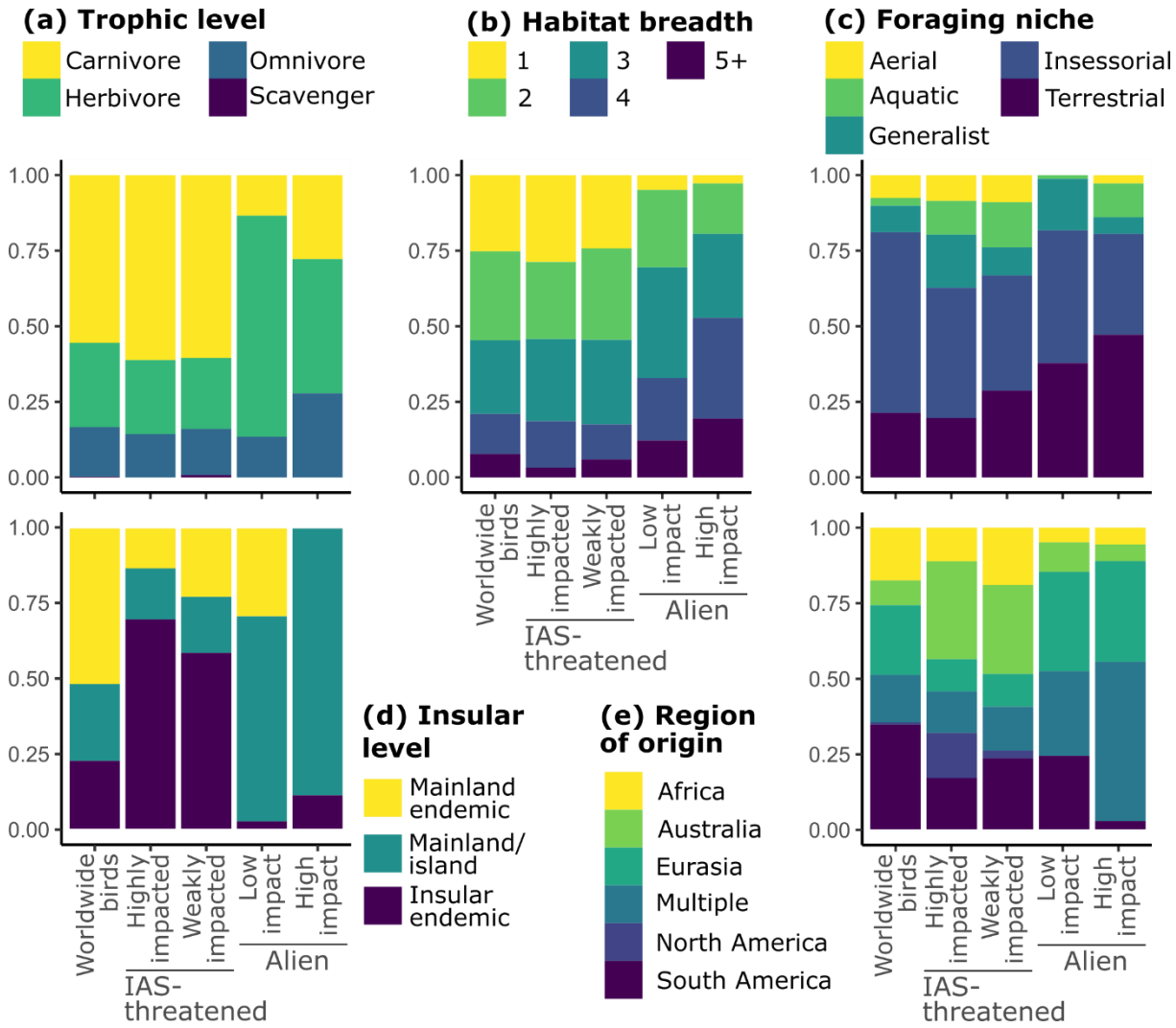


Figure 2. Proportions of trait modalities for IAS-threatened birds and alien birds according to their impact magnitude. X-axes represent the groups of birds along the continuum of impact in biological invasions as well as worldwide birds; Y-axes represent the proportion of each modality for each categorical trait.

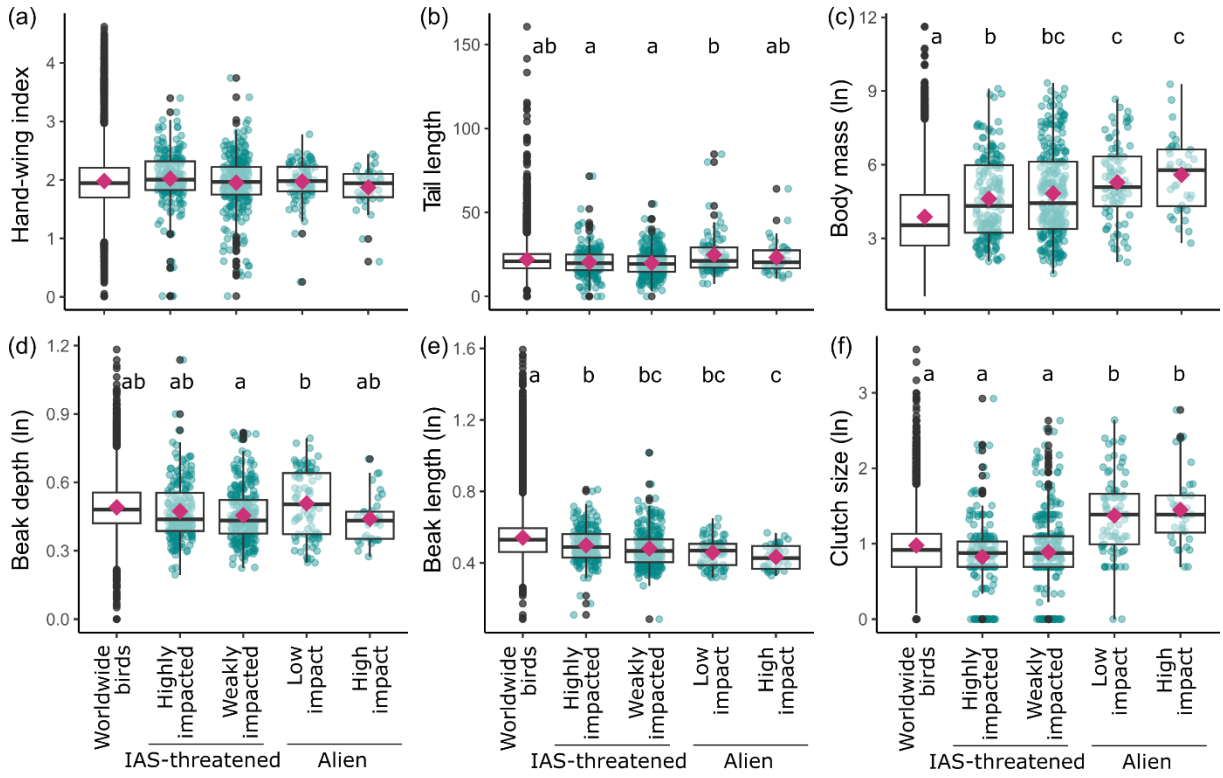
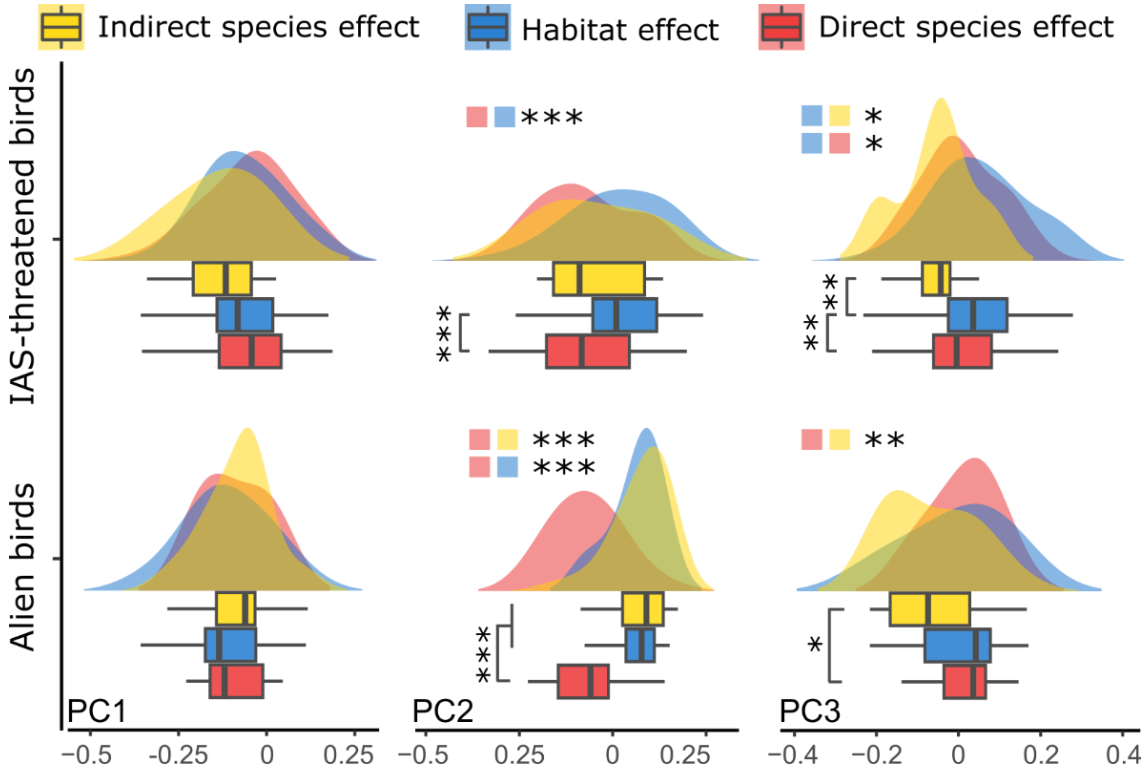


Figure 3. Relationships between species traits and impact magnitude for IAS-threatened birds and alien birds. X-axes represent the groups of birds along the continuum of impact in biological invasions as well as worldwide birds; Y-axes represent the morphological and life history numeric traits. Trait values were log-transformed for body mass, beak depth, beak length, and clutch size. Note that all traits linked to body measurement (i.e. hand-wing index, tail length, beak depth and, beak length) were corrected by body mass. Boxplots show the median and first and third quartiles, with outliers plotted individually in bold. Blue dots are raw values for unique species contained in each group. Pink diamonds represent the mean value for each trait. Significant differences between mean values are indicated with letters.



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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 (*** $p < 0.001$, ** $p < 0.01$, * $p < 0.05$).