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Prominent role of invasive species in avian biodiversity loss

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ABSTRACT

The rise of extinction rates associated with human activities has led to a growing interest in identifying extinction-prone taxa and extinction-promoting drivers. Previous work has identified habitat alterations and invasive species as the major drivers of recent bird extinctions. Here, we extend this work to ask how these human-driven impacts differentially affect extinction-prone taxa, and if any specific driver promotes taxonomic homogenization of avifauna. Like most previous studies, our analysis is based on global information of extinction drivers affecting threatened and extinct bird species from the IUCN Red List. Unlike previous studies, we employ a multivariate statistical framework that allows us to identify the main gradients of variation in extinction drivers. By using these gradients, we show that bird families with the highest extinction risk are primarily associated with threats posed by invasive species, once species richness and phylogeny are taken into account. As expected, the negative impact of invasive species was higher on island species, but our results also showed that it was particularly high in those species with small distribution ranges. On the other hand, mainland species and island species with large ranges tended to be affected by habitat destruction. Thus the impacts of invasive species promote the process of taxonomic homogenization among islands and between islands and continents. Consequently, introduced species may increase biotic homogenization not only directly, as generally believed, but also indirectly through their disproportional impact on endemic species imperilment.

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1. Introduction

Concern over the dramatic rise of extinction rates associated with human activities has led to a growing interest in identifying both extinction-prone taxa and the drivers of extinction (Didham et al., 2007; Sodhi et al., 2008). As human impacts are unlikely to diminish in the near future, identifying such imperilment situations is essential for defining management priorities and predicting future trends. Previous work has revealed that the risk of extinction associated with particular extinction drivers varies across taxa in a non-random fashion (Hughes, 1999; Owens and Bennett, 2000). In birds, for example, extinction risk caused by direct persecution and introduced predators is higher in species with larger body size and longer generation times, whereas extinction risk derived from habitat loss are related to habitat specialization and small body size (Owens and Bennett, 2000). Here, we extend this previous work to ask how different drivers impact taxa particularly

prone to extinction and the consequences that this can have for biotic homogenization.

Research on the current extinction crisis is at present greatly facilitated by the existence of the IUCN red list project, the world's most comprehensive inventory of the global conservation status of plant and animal species (Rodrigues et al., 2006). The IUCN red list provides a valuable resource for investigating the consequences of human activities on biodiversity loss and homogenization (e.g. Owens and Bennett, 2000), but most previous research on the impacts of extinction drivers has been limited to the production of "threat rankings" (e.g. Wilcove et al., 1998; Gurevich and Padilla, 2004; Clavero and García-Berthou, 2005) at least for two reasons. First, previous works have recorded extinction drivers as categorical variables, mainly coded as presence/absence, which limits the range of possible statistical analyses (e.g. Hughes, 2004). Second, most extinction events and imperilment situations imply more than one extinction driver (e.g. Gurevich and Padilla, 2004), a fact that makes it difficult to analyze the incidence of any individual extinction driver. These limitations can be overcome through the use of multivariate statistics to generate gradients of extinction drivers that can be treated as continuous variables, thus facilitating later analyses.

Using information on threats from the IUCN, we employ a multivariate statistical framework to generate continuous gradients of extinction drivers for all threatened bird species. These extinction

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driver gradients are used to address two issues. First, we ask whether different drivers have produced differential impacts on bird families that differ in their overall extinction risk. We address this question by analyzing the relationship between these gradients and the fraction of species of each avian family that are at risk of extinction. The clustering of species extinctions within higher taxa accelerates biodiversity loss, since those groups could be lost faster than if extinction occurred at random (McKinney, 1997). Therefore, if a certain extrinsic driver was disproportionately implicated in the declines of species belonging to highly threatened families, its potential role on global biodiversity loss would be larger than that of threat causes affecting “safer” families. Ultimately, the extinction of supra-specific taxa implies the loss of any biological character specific to those evolutionary lineages, with important consequences for the impoverishment of the world’s biota (Myers, 1997; Webb et al., 2001).

The second question we ask is whether human-related drivers of species decline contribute unequally to the process of taxonomic homogenization, one of the components of biotic homogenization (Olden and Rooney, 2006). Homogenization patterns are determined by the identities of species involved in extinction and invasion events affecting local biotas (Olden and Poff, 2003; Olden and Rooney, 2006). The selective extinction of species with restricted ranges (e.g. Manne et al., 1999) should promote the loss of distinctiveness in local species composition, reducing β diversity and contributing to the global process of taxonomic homogenization (McKinney and Lockwood, 1999; Olden and Rooney, 2006). We consequently examine whether particular extinction drivers may threaten selectively restricted-range species, thus promoting taxonomic homogenization.

2. Materials and methods

2.1. Data collection

Birds are a particularly appropriated taxon for analyses of extinction risk because they represent one of the few taxa for which all endangered species and drivers of decline are reasonably well-known (Rodrigues et al., 2006; Butchart, 2008). We utilized information on extrinsic drivers of species decline affecting the 1341 threatened bird species from the 2006 IUCN Red List of Threatened Species (henceforth the Red List) (www.iucnredlist.org). The Red List considers threatened species those classified as vulnerable (VU), endangered (EN), critically endangered (CR), and extinct (EX) (IUCN, 2001). Extinct species are those having gone extinct in the last 500 years (historical extinctions), and we included in this category some species thought to be extinct in the wild that still survive in captivity (EW). The Red List also provides detailed information of the incidence of drivers leading to species declines, and ultimately extinction, which we summarized

Table 1

Drivers of extinction affecting threatened bird species considered in this study. IUCN codes derived from the major threats classification version 2.1 (<http://intranet.iucn.org/webfiles/doc/SSC/RedList/AuthorityF/threats.rtf> address two issues.) are also shown.

Threat cause	IUCN codes major threats ver. 2.1	Code
Habitat destruction agriculture	1.1 (except 1.1.4)	HD1
Habitat destruction livestock	1.1.4	HD2
Habitat destruction Other/unspecified	1.2–1.9 (except 1.5), or simply 1	HD3
Invasive species competition	2.1	IS1
Invasive species predation	2.2	IS2
Invasive species pathogens	2.4	IS3
Invasive species habitat destruction	1.5	IS4
Harvesting/persecution	3 and 5	HAR
Pollution	6	POL
Others	Other threat codes	OTH

in 10 main categories (Table 1). These categories were based in the classification of major threats version 2.1 (<http://intranet.iucn.org/webfiles/doc/SSC/RedList/AuthorityF/threats.rtf>, accessed March 2009), which has been recently updated by the threats classification scheme version 3.0 (http://www.iucnredlist.org/static/major_threats). The listing of the 10 driver categories in each bird species fact sheet was translated to a presence–absence matrix in which bird species were rows and extinction drivers were columns (see Supplementary material). In this matrix, every bird species could be affected by more than one extinction driver, with mean number of driver categories cited per bird species being 2.9 (± 1.3 S.D.). Although the Red List has been criticized in its details, it remains the most complete, updated and comprehensive source for information on endangered and extinct birds (Butchart et al., 2004; Rodrigues et al., 2006; Mace et al., 2008).

Information on breeding ranges (in km²) was available for 1119 threatened extant species from the BirdLife International database (www.birlife.org). Breeding range is one of the criteria used when assigning species to threat categories (IUCN, 2001). However, this fact should not influence our results, as we only analyzed the relationships between range size and the impacts of extinction-promoting drivers. Extinct species were not included in any analyses involving breeding area.

We classified species into biogeographical realms (BR) to deal with the possibility that the relative impacts of extinction drivers varied across regions. Breeding bird ranges were used to classify species as belonging to one of the following realms: Afrotropic, Australasia, Indo-Malay, Nearctic, Neotropic, Oceania and Palearctic (Olson et al., 2001). Whenever a species’ breeding range extended across two or more realms (eight cases), it was excluded from any analysis involving BR as a factor. Birds were classified as island species when their whole breeding ranges were exclusively located on islands and as “mainland” otherwise (Manne et al., 1999). Australia was considered a mainland in the Australasian realm.

2.2. Defining and estimating extinction risk

We defined the extinction risk of a given family as the likelihood that the species it contains are going extinct or have already gone extinct. To estimate extinction risk per family, we recorded the number of EX, CR, EN and VU species included in each bird family that contained threatened species, and calculated the weighted proportion of threatened or extinct species following this formula:

$$\text{Extinction risk family } i = \frac{\text{EX}_i + 0.75 \times \text{CR}_i + 0.2 \times \text{EN}_i + 0.02 \times \text{VU}_i}{N_i}$$

where EX_{*i*}, CR_{*i*}, EN_{*i*} and VU_{*i*} are, respectively, the number of species classified as extinct, critically endangered, endangered or vulnerable within family *i*, and N_{*i*} is the total number of species in the family, whether threatened or not (from Sibley and Monroe, 1990). These total numbers of species (N_{*i*}) were corrected by adding to the list by Sibley and Monroe (1990) the number of newly described species that are considered threatened in the Red List. The extinction risk index varies between 0 and 1, reaching its maximum value when all species within a family have already gone extinct. Zero-values (i.e. no threatened species) were not possible in our data set, since it dealt only with threatened bird species and therefore families included in it were those containing at least one threatened species. Extinction risk values were square root-transformed prior to statistical analyses to improve normality (Owens and Bennett, 2000).

The weights given to CR, EN and VU were based on Red List criterion E that deals with the quantitative assessment of species’ extinction risk within a given time frame (IUCN, 2001; Mace

et al., 2008). This time frame can be measured in years or generations, but following Brooke et al. (2008) we used only year values. Criterion E establishes extinction probability thresholds to assign species to threat categories, which for CR species is a 50% probability of extinction in 10 years, for EN a 20% in 20 years, and for VU a 10% in 100 years. The thresholds associated with CR and VU categories were recalculated for a period of 20 years, in order to obtain probability values that could be compared across categories. These corrections necessarily assume that extinction risk was homogeneously distributed through the time span considered (i.e. a VU species with an extinction probability of 10% in 100 years would have a 2% probability of extinction in 20 years). Although the IUCN advises that extinction probabilities derived from criterion E should not be used to infer extinction risk of species assessed under other criteria (IUCN, 2001), these thresholds are objective touchstones relating threat categories and extinction risk in a specific period of time.

The weights given to the different threat categories can have important influences in the final estimation of extinction risk values (Butchart et al., 2004), something that could potentially modify the results of analyses involving extinction risk. In order to ensure that our results were not dependent on the employment of specific weight values we calculated three additional estimators of extinction risk, differing in the weights given to each threat category. The first alternative approach used the proportion of threatened and extinct species within each family (i.e. weighting equally the different threat categories). The second estimator employed equal-step weights for the different threat categories, being 1, 2, 3 and 4 for VU, EN, CR and EX – EW species, respectively. The third alternative index used the geometric mean weights calculated by Butchart et al. (2004) based on the relative extinction risk derived from the different IUCN criteria. The complete formulas used to calculate these indexes are given in [Appendix A](#).

2.3. Estimating gradients in drivers of extinction

We used a principal components analysis (PCA) to summarize the information on extinction drivers affecting the 1306 threatened or extinct bird species for which at least one driver was cited in the Red List (i.e. there was no information on drivers of declines for 35 bird species, see [Supplementary material](#)). PCA is an indirect ordination analysis that recombines the major linear patterns of covariation within a multivariate dataset (in this case, drivers of extinction) into a few axes, providing a dimensionally reduced summary of the original data ([McGarigal et al., 2000](#)). The matrix submitted to the PCA, with 1306 rows (i.e. bird species) and 10 columns (i.e. extinction drivers summarized in [Table 1](#)), contains the occurrences of extinction drivers per species. The axes produced by the PCA are continuous variables (PCA species' scores) that can be interpreted as gradients of variation in the original data set and used in further analyses, either as dependent or independent variables. We favored the use of PCA over other ordination techniques (e.g. correspondence analysis) because it assumes linear relationships, which are more directly interpretable, between the original variables and the gradients of variation obtained. Moreover, recent work ([Hirst and Jackson, 2007](#)) has shown that PCA successfully deals with presence–absence data.

Since habitat destruction and the impacts of invasive species are the considered the two main causes of biodiversity loss (e.g. [Didham et al., 2007](#)), our splitting of the IUCN hierarchy of threats favoured the creation of a habitat destruction – invasive species gradient as a result of PCA. With this aim, these two main threat types group together 7 out of the 10 extinction drivers considered in this work (see [Table 1](#)).

We calculated the relative position of each bird family in the space defined by PC1 and PC2 from the mean scores of species

belonging to that family. [Blackburn et al. \(2004\)](#) suggested that drivers of extinction could have historically changed, with a decreasing influence of the impacts of invasive species. To deal with this possible bias in our dataset we calculated the position of each bird family along PC1 and PC2 in two different ways: (i) using data from all species included in the Red List; and (ii) excluding extinct species.

2.4. Drivers leading to extinction and extinction risk

We analyzed the possible associations between extinction risk and threat gradients at the family level, both for the complete and the extant-only data, with a phylogenetic generalized least squares (PGLS) approach ([Freckleton et al., 2002](#); [Phillimore et al., 2006](#); [Sol and Price, 2008](#)). This method is based on the estimation of a parameter λ , which ranges between 0 and 1 and measures the degree to which the variance/covariance matrix follows a Brownian model of evolution (i.e. constant–variance random process) ([Freckleton et al., 2002](#)). When $\lambda = 0$ trait evolution is independent of phylogeny, while a value of $\lambda = 1$ indicates that traits covary in direct proportion to species' shared evolutionary history. We simultaneously estimated λ and fitted GLS models to test for the effect of the identified threat gradients on the variation of extinction risk across bird families. The total number of species in each family (both threatened and unthreatened, \log_{10} -transformed) was also included in the models to deal with the fact that species-poor taxa tend to have higher extinction risk values. This correction is especially important in our data set, which includes only bird families with at least one threatened species and therefore tends to ignore species-poor families with low extinction risk. Our phylogenetic hypothesis followed that of [Sibley and Ahlquist \(1990\)](#) with branch lengths estimated using genetic distances. This phylogeny has been criticized in its details, but it remains the only complete bird phylogeny for which branch-lengths are available, and gives results broadly consistent with analyses based on smaller portions of the phylogenetic tree ([Phillimore et al., 2006](#)).

We also performed PGLS analyses using the three alternative extinction risk indices as dependent variables, using both the complete and the extant-only data. Results regarding the relationships between extinction risk and the gradients in threat drivers were qualitatively equal ([Appendix A](#)), independently of the index of extinction risk employed.

2.5. Drivers leading to taxonomic homogenization

We tested whether human-related causes of species decline equally contribute to the process of taxonomic homogenization with an analysis at the species level, since species contain more variability for range size and island distributions than higher taxonomic levels. Phylogenetic information was unavailable for many of the studied species, including those that are currently extinct, and hence we could not use phylogenetic-based methods in this part of the analyses. In addition, the incidence of extinction drivers can vary across biogeographical realms, increasing the problems of pseudoreplication. Generalized Linear Mixed Models (GLMM) provide a framework to simultaneously deal with the problem of taxonomic and regional autocorrelations ([Blackburn and Duncan, 2001](#)).

By including taxonomy and regions as random factors, GLMM take the clustered structure of data into account when carrying out statistical analyses to provide estimates of SE corrected for the resulting non-independence. We tested how range size and island distribution affect the principal gradients in threat drivers with separate models for PC1 and PC2, where island distribution and breeding range (log-transformed) were treated as fixed factor and the taxonomy (orders and families nested within orders) and

biogeographic realms as random factors. We compared full models (including both fixed factors and their interaction and random factors) and null models (including only random factors) through the changes in the Akaike information criteria (AIC). For GLMM fitting we assumed normal error distribution and used restricted maximum likelihood to estimate random effect parameters.

3. Results

The PCA defined two main gradients of variation in the incidence of extinction-promoting drivers (Table 1), which altogether accounted for 37.2% of the total variation (Fig. 1). The first component (PC1) was positively associated with all drivers related to habitat destruction and negatively associated with all drivers related to invasive species. Thus, PC1 defined a continuous gradient from risks primarily caused by invasive species (negative extreme) to

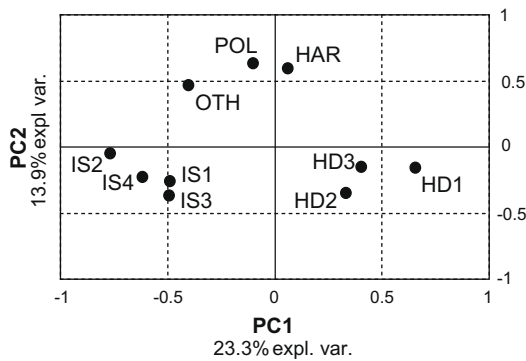


Fig. 1. Identification of the main gradients in drivers of avian extinction. Projections of each original variable's loadings on the space defined by PC1 and PC2 resulting from a principal component analysis (PCA) on drivers of extinction affecting threatened bird species (codes as in Table 1, original data given as Supplementary material).

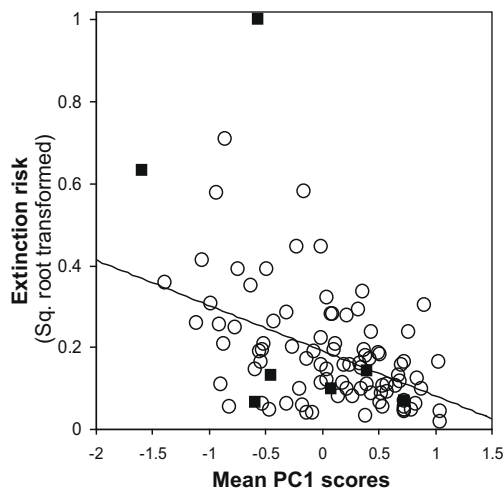


Fig. 2. Relationship between the invasive species – habitat destruction gradient (PC1) and the extinction risk for bird families. Empty circles represent the 90 families included in the PGLS analysis (see Table 2), while filled squares represent six families that could not be used in this analysis: New Zealand wattlebirds (Callaeatidae), mesites (Mesitornithidae), asities (Philepittidae), rockfowl (Picathartidae), Australasian robins (Petroicidae), tree kingfishers (Halcyonidae), and dodos and solitaires (Raphidae). The negative relationship means that highly threatened bird families tend to be those more intensively affected by invasive species. The regression line was calculated exclusively from those families included in the PGLS.

those mainly associated with habitat destruction (positive extreme). PC2 was positively associated with two drivers, pollution and harvesting, describing a gradient in which bird species scoring towards the positive extreme were primarily affected by pollution and harvesting and those scoring towards the negative extreme mainly affected by habitat destruction and/or invasive species (Fig. 1).

Extinction risk of bird families markedly varied across avian taxa, being negatively associated with mean PC1 scores (Fig. 2), indicating that avian families threatened mainly by invasive species tended to be at higher risk (Table 2). In contrast, families containing species primarily threatened by habitat destruction presented lower extinction risk. Neither the impacts of hunting and pollution (PC2) nor the number of species were associated with the number of threatened species per bird family, as suggested by the non-significant effects on extinction risk (Table 2). Extinction risk of bird families was also negatively associated with mean PC1 scores when extinct species were excluded from the estimation of drivers of decline affecting bird families (Table 2). Thus, the observed pattern is likely to reflect an ongoing process.

Both island distribution and breeding range size had significant effects on the gradient of drivers of extinction defined by PC1

Table 2

Results from the phylogenetic generalized least squares models (PGLS) testing the effects of the gradients in drivers of extinction (PC1 and PC2) and species richness on the risk of extinction of avian families. Mean values of PC1 and PC2 for bird families were calculated in two different ways, producing two PGLS models: (i) using data from all species ($N = 90$ families; $R^2 = 0.21$); and (ii) excluding data from extinct species ($N = 89$ families; $R^2 = 0.20$). The maximum likelihood estimate of λ was 0.62 in the analysis involving all species and 0.724 in the analysis using only extant species, indicating a moderate level of phylogenetic inertia in our extinction risk data.

	<i>b</i>	SE	<i>t</i> -Value	<i>P</i>
<i>All species</i>				
PC1	-0.104	0.022	-4.72	<0.001
PC2	-0.029	0.019	-1.51	0.14
<i>N</i> species	-0.009	0.0189	-0.50	0.62
<i>Extant species only</i>				
PC1	-0.094	0.021	-4.43	<0.001
PC2	-0.038	0.019	-2.03	0.045
<i>N</i> species	0.002	0.018	0.14	0.89

Table 3

Fixed and random effects in generalized linear mixed models (GLMMs) on gradients of extinction drivers. In the comparisons between islands and mainlands, islands are recorded as 'zero'. The change in Akaike information criteria between final and null models (including only random factors) is also shown.

Fixed	Estimate	SE	<i>t</i> -Value	<i>P</i>
<i>PC1</i>				
Island	1.776	0.126	14.14	<0.001
Breeding area	0.312	0.022	14.10	<0.001
Island × Br. area	-0.341	0.031	-10.97	<0.001
<i>Random</i>				
Realm	0.190	0.113	1.50	0.134
Orders	0.030	0.020	1.68	0.093
Families within orders	0.036	0.014	2.56	0.010
ΔAIC with null model	-317.7			
<i>PC2</i>				
Island	-0.402	0.155	-2.59	0.010
Br. area	0.027	0.027	1.00	0.316
Island × Br. area	0.082	0.038	2.14	0.033
<i>Random</i>				
Realm	0.136	0.086	1.57	0.115
Orders	0.078	0.030	2.58	0.010
Families within orders	0.182	0.078	2.33	0.020
ΔAIC with null model	-0.3			

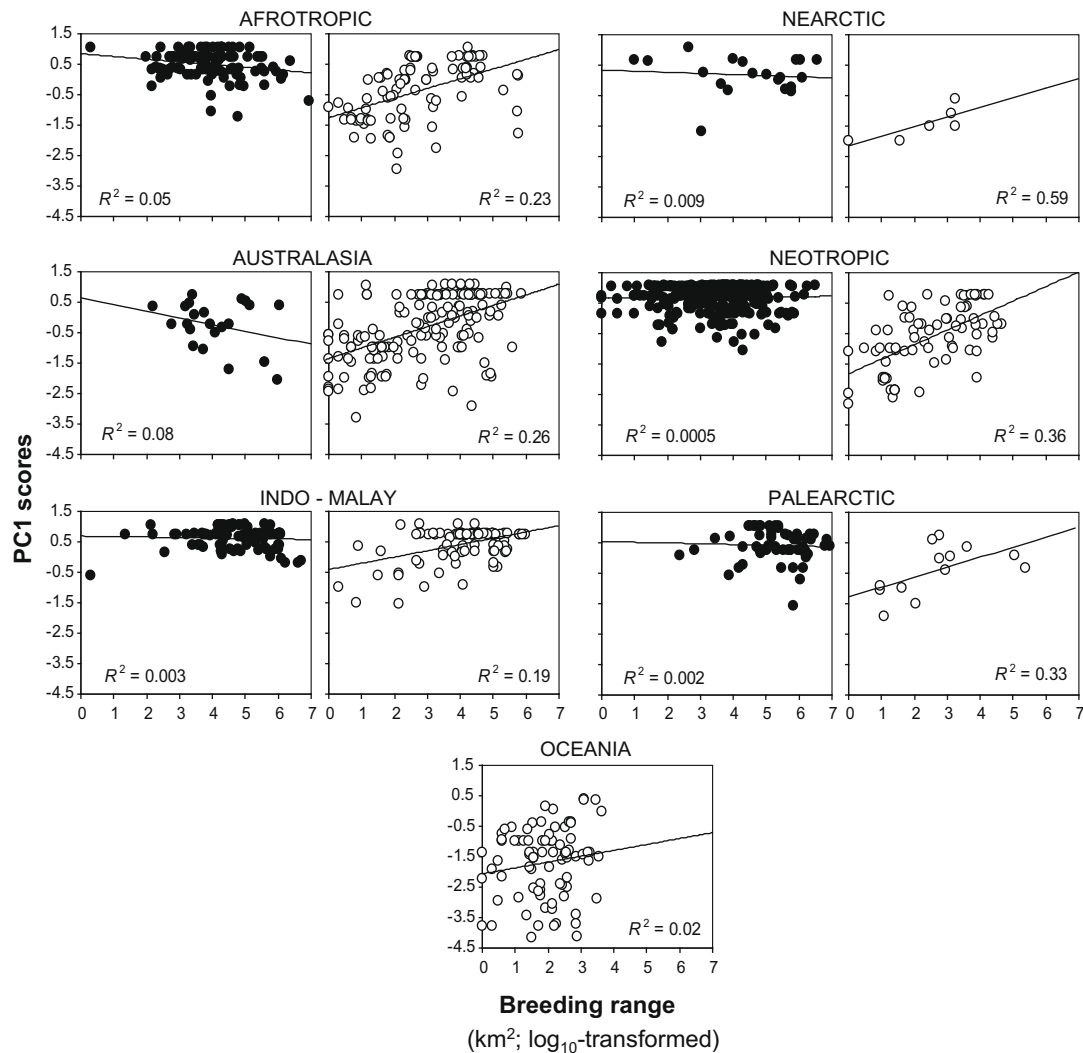


Fig. 3. Relationships between the size of the breeding range and the scores on PC1 for threatened bird species presented separately for those with island (empty circles) or continental (filled circles) distributions and for the seven biogeographic realms considered in this study. Small-range island species tend to be threatened mainly by invasive species (as indicated by a low score on PCA axis 1). Regression lines and coefficients of determination (R^2) are shown for each individual relationship.

(Table 3). Bird species threatened mainly by invasive species tended to be insular and be restricted to small distribution ranges. However, the relationship between PC1 and the breeding area was clearly different for island and mainland species, as shown by the existence of a significant interaction between island and breeding area (Table 3). Island birds with small breeding ranges were strongly affected by invasive species, a relationship that was clear throughout all the analyzed biogeographic realms, with the sole exception of Oceania (Fig. 3). Thus, threats posed by invasive species appeared as a key mechanism driving taxonomic homogenization on islands, but not on mainlands. In contrast, the gradient of pollution and harvesting impact (PC2) was not significantly associated with breeding area (Table 3), suggesting a minor role of this factor as driver of taxonomic homogenization.

4. Discussion

Current rates of biodiversity loss are caused by a wide range of mechanisms but, as shown in the present study, some extrinsic drivers may have a disproportionate impact by inducing taxonomical asymmetries in extinction risk and increasing taxonomic homogenization. Specifically, our analyses suggest that invasive

species are having a more important impact on biodiversity patterns than it would be predicted from the number of species affected.

In birds, a large proportion of historic extinctions have involved predation by invasive mammals (e.g. Blackburn et al., 2004; Duncan and Blackburn, 2007), which along with direct human harvesting, had a huge impact upon less diversified, mostly island lineages (Johnson and Stattersfield, 1990; Biber, 2002). This disproportionate concentration of extinction events upon certain taxa resulted in rapid loss of evolutionary history, thus magnifying the biodiversity loss derived from extinctions (von Euler, 2001). However, present causes of species declines are dominated by habitat destruction (Brooks et al., 2002). This factor is so widespread that it might have diluted the historical extinction risk selectivity reported in previous works (e.g. von Euler, 2001), producing a random extinction scenario [a “field of bullets” (*sensu* Raup, 1991)]. Notwithstanding, our analyses show that disproportionate losses of supra-specific taxa can still result from impacts of invasive species, a pattern that would be superimposed to that of no-selectivity produced by habitat destruction.

Bird species highly threatened by invasive species tend to have small ranges restricted to islands. Since the level of island ende-

mism is not randomly distributed across bird taxonomy (McCall et al., 1996), bird families having the highest proportion of island endemics should be more sensitive to invasive species and show the highest overall extinction risk. Indeed, the three bird families with the highest extinction risk values [dodos and solitaires (Raphidae), New Zealand wrens (Acanthisittidae) and New Zealand wattlebirds (Callaeatidae)] are island endemics. These are species-poor families, but the pattern is also found in richer families. Some species-rich families that show both a high threat by invasive species and high extinction risk, such as rails (Rallidae), petrels and shearwaters (Procellariidae) parrots (Psittacidae) or pigeons and doves (Columbidae), also have a high proportion of island endemics (McCall et al., 1996; Lockwood et al., 2000). Lockwood et al. (2000) classified some of these families (Rallidae, Procellariidae) among the 'losers' of the global process of avian taxonomic homogenization, since they concentrated a disproportionate amount of endangered and extinct species while not being favored by introductions in new areas. Both the 'winners' (e.g. Old World sparrows [Passeridae]) and 'survivors' (e.g. tyrant flycatchers [Tyrannidae]) of this homogenization process had small proportions of island endemics. The level of island endemism, which is also a surrogate of the smallness of distribution ranges, has thus been identified as one of the factors influencing avian homogenization patterns at the family level (Lockwood et al., 2000). Our results show that the relationship between the level of endemism and the concentration of both extinct and threatened species in bird families can be driven by the impacts of invasive species, thus proposing a mechanism to explain the homogenization patterns identified by Lockwood et al. (2000).

At the species level, the disproportionate incidence of threats posed by invasive species on highly endemic island birds should accelerate taxonomic homogenization worldwide, both across islands and between islands and continents. The mechanisms classically suggested by which invasive species promote biotic homogenization include the expansion of already widespread species and their negative impact on endemic species (Duncan et al., 2003; Olden and Poff, 2003; Cassey et al., 2007). Our results nonetheless suggest that species introduced to islands may increase biotic homogenization not only directly, through the establishment of non-indigenous species themselves, but also indirectly through their disproportionate impact on island endemic biodiversity loss. On continents, where the impacts of invasive species on natives are often lower, we did not find clear associations between breeding range and any specific driver. Taxonomic homogenization of continental avifaunas should nevertheless be promoted by the extinction proneness of range-restricted species (Manne et al., 1999).

The importance of invasive species in ecological change and biodiversity loss has been recently questioned by some (Gurevich and Padilla, 2004; MacDougall and Turkington, 2005) on the grounds that the frequent positive correlation between habitat degradation and the number of invasive species makes it difficult to tease their independent effects apart (Didham et al., 2005). However, evidence is accumulating that invasive species are causal drivers, and not merely passengers (co-occurring or synergistic), of biodiversity loss; at least for animal groups including birds (Light and Marchetti, 2007; Butchart, 2008), and particularly for birds on islands (Savidge, 1987; Blackburn et al., 2004). Habitat destruction is probably the most common threatening agent for birds, and in our dataset it affected over 85% of the species. Nevertheless, our results show clear associations between the intensity of threats posed by invasive species (as defined by PC1) and higher extinction risk and enhanced biotic homogenization. Even assuming a constant relative influence of habitat destruction along the gradient defined by PC1 (a rather improbable event, see Fig. 1), these associations would still be linked to

the impacts of invasive species. However, it is worth noting that drivers of decline are not necessarily independent, and that different drivers can act simultaneously, even producing synergistic effects. In fact, the negative impacts of invasive species on native ones can increase following habitat degradation or loss, which can affect the functional relationships between native and invasive biotas (e.g. increasing the strength of the *per capita* interaction) (Didham et al., 2007).

Our results show differences on the relationships between drivers of species decline and global avian biodiversity loss. Even though habitat destruction is presently the main large scale factor causing bird species to decline and eventually leading to their extinction (Brooks et al., 2002), invasive species seem to be having a disproportionate impact in the loss of evolutionary history and in the taxonomic homogenization of avifaunas. In this context, we suggest that future conservation efforts should take explicitly into account differences in the relative impact of extinction drivers on global biodiversity loss. Increased attention should indeed be placed on the threats posed by invasive species (Didham et al., 2007), especially so in areas where these interact with impacts produced by habitat destruction.

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Appendix A

Results from the phylogenetic generalized least squares models (PGLS) testing the effects of the gradients in drivers of extinction (PC1 and PC2) derived from a principal components analysis (see Fig. 1 for gradients' interpretation) and species richness (\log_{10} -transformed) on three different estimators of extinction risk of avian families. Since drivers of extinction could have historically changed (Blackburn et al., 2004), mean values of PC1 and PC2 for bird families were calculated in two different ways: (i) using data from all species ($N = 90$ families); and (ii) excluding data from extinct species ($N = 89$ families).

Estimators of extinction risk of avian families:

Proportion of threatened species in family i

$$\frac{EX_i + CR_i + EN_i + VU_i}{N_i} \quad (A.1)$$

Equal-step weights for threat categories in family i

$$\frac{4 \times EX_i + 3 \times CR_i + 2 \times EN_i + VU_i}{4 \times N_i} \quad (A.2)$$

Geometric mean weights for threat categories in family i

$$\frac{EX_i + 0.5 \times CR_i + 0.05 \times EN_i + 0.005 \times VU_i}{N_i} \quad (A.3)$$

where EX_i , CR_i , EN_i and VU_i are, respectively, the number of species classified as extinct (including extinct in the wild), critically endangered, endangered or vulnerable within family i , and N_i is the total number of species in the family, whether threatened or not (from

Sibley and Monroe, 1990). Geometric mean weights given in Eq. (A.3) are those reported by Butchart et al. (2004).

	Prop. threatened		Equal-step weights		Geometric mean weights	
	<i>b</i>	<i>P</i>	<i>b</i>	<i>P</i>	<i>b</i>	<i>P</i>
<i>All species</i>	$\lambda = 0.944$ $R^2 = 0.29$		$\lambda = 0.999$ $R^2 = 0.26$		$\lambda = 0.178$ $R^2 = 0.20$	
PC1	-0.091	0.001	-0.090	<0.001	-0.110	<0.001
PC2	-0.016	0.51	-0.029	0.12	-0.009	0.64
<i>N species</i>	-0.105	<0.001	-0.051	0.003	-0.002	0.92
<i>Extant species only</i>	$\lambda = 0.943$ $R^2 = 0.28$		$\lambda = 0.999$ $R^2 = 0.24$		$\lambda = 0.33$ $R^2 = 0.17$	
PC1	-0.094	0.001	-0.086	<0.001	-0.094	<0.001
PC2	-0.017	0.49	-0.033	0.07	-0.018	0.32
<i>N species</i>	-0.101	<0.001	-0.044	0.01	-0.016	0.42

Appendix B. Supplementary data

Drivers of extinction affecting threatened and extinct bird species. Complete dataset. Data extracted from the IUCN 2006 Red List of Threatened Species (www.iucnredlist.org) and the Birdlife International database (www.birdlife.org). Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.biocon.2009.03.034.

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