

# ECOGRAPHY

## Research article

### Testing the links between bird diversity, alien species and disturbance within a human-modified landscape

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Introduced alien species are associated with lower taxonomic, functional and phylogenetic diversity of native communities and negative impacts on ecosystem functioning. This is particularly evident in habitats where human disturbance may favour alien species, posing an additional stressor on native communities. Following the community resistance hypothesis (higher diversity promotes higher resistance to invasion), we predicted: 1) higher taxonomic, functional and phylogenetic diversity (TD, FD and PD respectively) in non-invaded bird communities (i.e. no alien bird species); and 2) higher diversity and resistance to invasion in less human-disturbed areas. We surveyed bird communities in a modified Mediterranean landscape subject to varying levels of human disturbance. We tested whether TD, FD and PD were significantly different between non-invaded and invaded bird communities, and assessed the effect of land classes (forest, agriculture, urban), landscape composition and heterogeneity on these metrics. We found that non-invaded communities retained higher TD and FD, but not PD, than invaded communities. Alien birds occupied marginal niches in invaded communities, and did not fully compensate for the taxonomic and functional diversity loss caused by the absence of native species. These results were consistent across different land classes, suggesting weak environmental filtering of communities. Generally, less human-modified and more heterogeneous areas supported higher TD regardless of the presence of alien species. FD and PD of invaded communities decreased with increases in human-modified areas, whereas non-invaded communities were not affected. Our results suggest that even within a human-modified landscape, invaded community diversity is more affected by, and thus has a lower resilience to, disturbance. Restoring and protecting natural habitats within human-modified landscapes is likely to increase the resilience of native species.

Keywords: biological invasion, bird assemblage, community resistance, diversity metrics, human-altered landscape, non-native species



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## Introduction

Biological invasions are well-established as one of the greatest threats to ecosystems worldwide due to their negative impacts on native species, communities and ecosystem functioning (Vilà and Hulme 2017, Pyšek et al. 2020). The introduction of alien species has direct and indirect effects on native biodiversity, potentially disrupting the recipient community structure (White et al. 2006) through alterations of functional and phylogenetic diversity (FD and PD, respectively; Ricciardi et al. 2013). This can occur through expansion or contraction of native functional and phylogenetic space, affecting ecosystem functioning and biodiversity maintenance (Gerhold et al. 2011, Finerty et al. 2016). Studying FD and PD in synergy could lead to a more comprehensive approach to understanding impacts of alien species on communities (Cadotte 2013, Galland et al. 2019), since FD is associated with ecosystem functioning (Saavedra et al. 2014, Matuoka et al. 2020), and PD can express differences between species that are not captured by FD (Whitfeld et al. 2014).

Community resistance (i.e. the capacity of a community to withstand disturbance; Lake 2013) to invasion has been hypothesised to be affected in two distinct and opposite ways. Taxonomically, functionally and phylogenetically diverse communities may be more resistant to alien establishment due to higher competition and greater effectiveness in using the resources available (the biotic resistance hypothesis; Elton 1958, Hejda and de Bello 2013, Lososová et al. 2015). Conversely, more diverse communities may have high resource availability that could also be exploited by alien species, inferring a lower resistance to invasion (the biotic acceptance hypothesis; Stohlgren et al. 2006, Andrikou-Charitidou and Kallimanis 2021).

Another important ecological property of a community lies in the concept of ecological resilience, which measures the ability of a given system to absorb changes in order to maintain the same identity (Folke et al. 2010). Since resistance is inversely correlated with the degree of change following a disturbance event (Justus 2007), a resilient ecological system should better resist disturbance events such as invasions, and climate or land use changes (Haegeman et al. 2016). Functional evenness (FEve, a component of FD) has been used as a proxy for the resilience of communities (Lee and Martin 2017, Kosman et al. 2019, Morelli et al. 2020a,b). A high level of evenness can be linked to high functional redundancy which likely can guarantee elasticity in the community (Morelli et al. 2020b) and a higher level of competitive exclusion (i.e. thus lowering the probability of invasion; Rodríguez et al. 2015). Moreover, resilience can be a useful measure to assess resource use in a given space (Mouchet et al. 2010), with high functional evenness representing efficient use of resources by species in the community (Prescott et al. 2016, Lee and Martin 2017), and low functional evenness implying under-exploitation of available resources, leading to higher susceptibility of communities to disturbance (e.g. biological invasions; Shea and Chesson 2002). Based on the latter, under-exploitation could imply

the presence of vacant niches in the community, which could be occupied, particularly in human-modified areas, by alien species (Sol et al. 2012). For example, the common waxbill *Estrilda astrid* has been found not to overlap appreciably with the ecological niches of native bird species in Portugal, suggesting establishment in unsaturated communities (Batalha et al. 2013) and leading to a high level of niche differentiation within a community. Niche diversity can be measured through the Functional divergence of a community (FDiv), with high values representing high levels of niche differentiation (e.g. that could be promoted by community invasion; Mathers et al. 2020) leading to potentially lower competition for resources (Prescott et al. 2016).

Disturbed areas (e.g. urban and agricultural habitat in human-modified landscapes) typically have lower native diversity, but are well known to favour alien species establishment in several taxa (Hulme 2009, Pyšek et al. 2010, Cardador and Blackburn 2020). Alien birds, for example, can be better than native bird species at exploiting the ecological opportunities that arise in human-modified landscapes (the opportunism hypothesis; Sol et al. 2012). Anthropized areas are thus highly diversified repositories of alien bird species (Chiron et al. 2009, Bonter et al. 2010) and land use changes caused by the expansion of human-managed areas worldwide will likely increase the spread of generalist, opportunistic non-native species at the expense of native species (McKinney 2006). Moreover, bird communities in disturbed areas are at risk of biotic homogenization processes acting on the three diversity dimensions (taxonomical, functional and phylogenetic; Liang et al. 2019), leading to a generalized decrease in diversity. Since, at a local scale, several studies have reported how high levels of FD and PD lead to higher resistance to invasion (Gerhold et al. 2011, Lososová et al. 2015), the decrease in these diversity dimensions in communities inhabiting disturbed areas could hamper their resistance, making them more susceptible to invasion.

A further factor that may influence the resistance of communities to invasion is habitat heterogeneity. Human-modified landscapes may increase habitat heterogeneity through habitat modification (i.e. fragmentation; Fahrig 2003) which could lead to a higher diversity of both native and alien species as a consequence of a higher availability of habitats and resources (Andrikou-Charitidou and Kallimanis 2021). Alternatively, in landscapes dominated by agro- and urban ecosystems, higher levels of diversity could be expected in more heterogeneous areas that contain remnant (semi-) natural features (e.g. shrublands, native forest; Fahrig et al. 2015, Chiatante et al. 2021) that could favour native species.

Recent studies on the above three diversity dimensions (TD, FD and PD) in bird communities have focused on the association between native bird diversity and alien bird species richness at a regional scale, finding a positive association between the two (McKinney and Kark 2017, Andrikou-Charitidou and Kallimanis 2021). Nonetheless, it is at the local community scale that impacts on biodiversity and ecosystem functioning take place (Loiola et al. 2018). At this scale, the impact could be predicted by two contrasting scenarios (Loiola et al. 2018):

alien species establish in a portion of functional and phylogenetic space formerly occupied by native species (increasing the similarity between species in invaded communities); or, alien species fill the niche-gap in a community (limiting similarity), thus expanding the functional and phylogenetic space of invaded communities, leading to higher FD and PD compared to non-invaded communities.

To assess which of these two mechanisms could impact native communities, a set of tests comparing the three diversity dimensions between non-invaded and invaded communities is needed (Thuiller et al. 2010, Loiola et al. 2018): 1) *non-invaded* versus *invaded* communities (i.e. assessing the overall effect of invasion); 2) *non-invaded* versus *invaded* communities excluding alien species (assessing if *invaded* communities are more prone to invasion than *non-invaded* communities or if alien species replace native species' functional and phylogenetic space in *invaded* communities); 3) *invaded* versus *invaded* communities excluding alien species (i.e. assessing the difference in the functional and phylogenetic space between alien and native species of the same community). Here, we applied this approach to assess the impact of alien birds on bird community diversity by estimating TD, FD and PD in a highly human-modified landscape in southern Portugal with several alien birds that are currently establishing new populations or expanding existing ones. It is hypothesised that higher resilience and lower alien species impact (higher TD, FD and PD) are more prevalent in non-invaded bird communities inhabiting areas with lower levels of human-disturbance (e.g. shrublands, native forest) and with higher heterogeneity (i.e. those containing remnant semi-natural habitats). The novelty of our study lies in the understanding of the degree of impact of alien bird species on the diversity of bird communities, and how this interacts with human modification of the landscape, in order to better assess the vulnerability of native communities to alien bird species invasion.

## Material and methods

### Study area

We conducted the study in the Tagus estuary area, Portugal (Fig. 1). The landscape is characterised by agriculture (e.g. annual crops, rice fields, olive groves, pastures; 34.1%), forest (27.6%), including both forest plantation and native forest (montado, a traditional agro-forest ecosystem of scattered cork oak *Quercus suber* in the area sometimes mixed with umbrella pines *Pinus pinea*; Correia 1993), shrubland (3.5%), urban and anthropized areas (e.g. city of Lisbon, road and railways; 20.1%), and wetland areas (e.g. salines, marshes; 14.7%). The entire study region can be defined as Mediterranean from a climatic point of view, with four to five months of aridity during the summer (Espírito-Santo et al. 2021).

### Study design

We selected 189 points using a random sampling method that avoided close proximity among points (mean nearest

neighbour distance between points was 1349.792 m, with minimum and maximum distance = 473.1 and 46521.4 m respectively; Fig. 1, Supporting information), stratified according to the three main land classes: agricultural,  $n=86$ ; forest,  $n=50$ ; and urban = 53. Due to restrictions on access (military areas and private property), we were able to visit only 50 points in the forest land class. To characterise the habitat around each point, we considered composition and heterogeneity variables within a buffer of 500 m radius (Graham and Blake 2001, Marcolin et al. 2021). Composition was expressed as the percentage cover of seven land use categories (Carta de Ocupação do Solo maps available for Portugal; IGP 2020) that were a priori considered as potentially relevant to bird distributions within different (decreasing) levels of human disturbance: 1) urban and industrial, 2) intensive agriculture, 3) rice-fields, 4) extensive agriculture, 5) forest plantation, 6) shrubland and 7) native forest. Landscape heterogeneity was calculated using the Shannon–Weiner diversity index of the seven land use categories (SHDI). In addition to providing a measure of heterogeneity, SHDI was also correlated with configuration metrics such as edge length and edge density (both Spearman's  $Rho=0.87$ ), and hence it represented the degree of habitat fragmentation in the landscape. Landscape composition and heterogeneity variables were calculated using QGIS ver. 3.26.3 and 'landscapemetrics' R package through *sample\_lsm* function (www.r-project.org, Hesselbarth et al. 2019). We scaled all landscape variables to better evaluate collinearity (Cade 2015), testing for multicollinearity through the Spearman correlation coefficient. We retained all variables since Spearman's  $Rho$  was  $< 0.70$  in all cases (Dormann et al. 2013, Harrison et al. 2018). For a more detailed description, see Supporting information.

### Bird survey and bird traits

Bird surveys were conducted by a single observer (anon.) using 10 min point counts (Bibby et al. 2000). Points were visited twice per year (late March–early April and late April–late May) in two consecutive years (2021–2022) during the early morning under calm and dry weather conditions. To avoid possible bias due to variation in diurnal activity of birds, points were visited in a different order during the second survey period, leaving at least three weeks between consecutive visits to the same point. All birds contacted, visually and acoustically, were recorded within a maximum radius of 200 m from the centre of the point. We later excluded birds flying over (e.g. swallows, swifts *Apus* sp.), aquatic birds (i.e. Ardeidae species), raptors and migrating species from the analysis that were inadequately sampled by our approach (Supporting information) (Marcolin et al. 2021).

Species were classified as native or alien, the latter being species whose native range is outside Europe and for whom their provenance in Europe is known, or very strongly suspected, to be through deliberate or accidental introduction by humans (five species, Supporting information). The exception was feral pigeon *Columbia livia* var. *domestica*



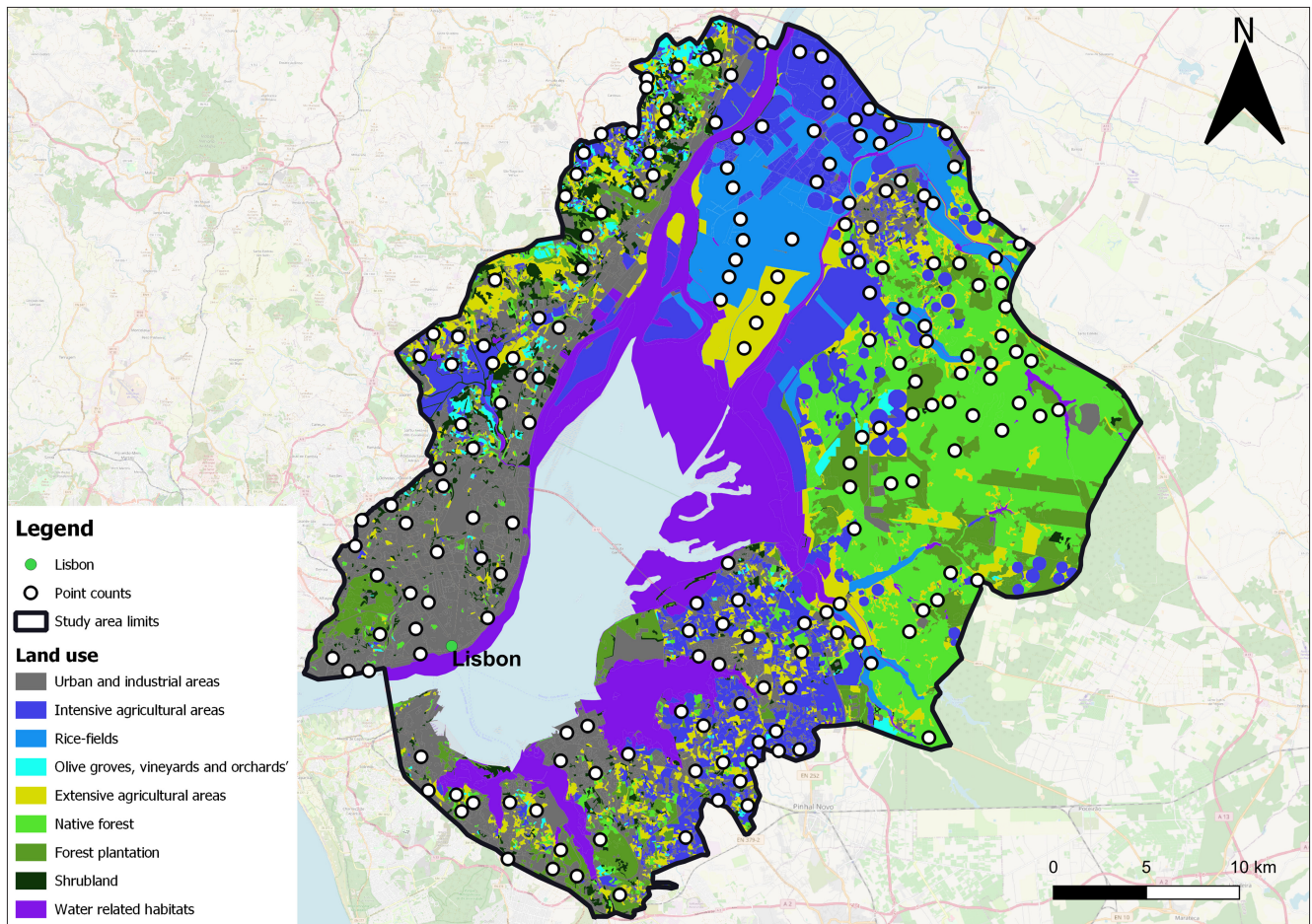


Figure 1. Study area around the Tagus Estuary, Portugal. White dots represent the random points where bird point counts were performed. Background map colours – dark green: forest; light yellow: farmland; light green: meadow; grey: urban area; light blue: water surface. Two land use cover (Olive groves, vineyards and orchards and Water related habitats) were not considered for analyses as they covered a very small area inside the buffers (Supporting information). Map source: ©Open Street Map 2022.

whose status is unclear. Although this species derives from the wild rock dove, a declining species which still has native populations in Europe, the long history of domestication of this species has led some to classify it as alien (Boano et al. 2019, Lowther and Johnston 2020). Given this and the often very significant numbers of feral pigeon, we carried out the main analyses considering it both as a native and as an alien species.

We classified the surveyed bird species using a set of 10 functional traits that reflected resource-use of individuals (Flynn et al. 2009) and resource overlap between species (Andrikou-Charitidou et al. 2020), and that influence a species' ability to respond to habitat changes (Anderle et al. 2022): 1) clutch size; 2) number of broods per year; 3) body mass; 4) migratory status; 5) territoriality; 6) breeding season habitat use; 7) breeding season diet; 8) foraging stratum; 9) foraging technique; and 10) nesting habit (Supporting information for a detailed description and data sources). Apart from clutch size, number of broods per year and body mass, the categories from the other traits were translated into binary variables (i.e. each trait

was either present or absent for a given species; Supporting information). To account for the different scales of continuous traits, clutch size, broods per year and body mass (previously log-transformed) were scaled to values between 0 and 1. There was no marked intercorrelation between trait variables (all Pearson's  $r \leq 0.70$ ; Dormann et al. 2013, Harrison et al. 2018).

To test the effect of alien bird species presence on the diversity metrics of bird communities, we followed the classifications of Loiola et al. (2018): community type was defined for each point as *invaded* when at least one alien species was found in at least one visit (*non-invaded* versus *invaded* communities). Moreover, to study the contribution of alien species to the diversity metrics of the native component of a community, we considered a third community type, that of the native species in *invaded* communities, i.e. excluding alien species from the *invaded* communities (*invaded no alien*; Supporting information). This classification represented a low threshold in that it required the presence of a single alien species on a single visit to result in a definition of *invaded*. We thus also explored an alternative,

more conservative, classification, defining a community as *invaded* when at least one alien species was found in at least two visits (two out of four, 50% of the visits). This approach resulted in fewer communities classed as invaded, hence there were fewer significant effects. However, the overall patterns were very similar between the two analyses (Supporting information), and in particular there was a high degree of concordance in terms of the effects of key significant land cover variables. We thus maintain the first classification in the main results of the paper.

### Taxonomic, functional and phylogenetic diversity metrics

For abundance estimates of each bird species, we pooled the data using the maximum abundance recorded between the two survey periods, per point, per year. We calculated several diversity metrics to characterize each community and community type, based on taxonomic diversity (TD), functional diversity (FD) and phylogenetic diversity (PD; Table 1). As a measure of TD, we used the species richness observed. To have a comprehensive understanding of the functionality of bird communities, we computed two metrics of FD based on the 10 functional traits: functional divergence (FDiv), and functional evenness (FEve). Moreover, we used all the traits to visually represent the position of bird species in the functional space (i.e. ecological niche) of bird communities, performing a principal coordinates analysis (PCoA) based on a dissimilarity matrix calculated through the Gower distance (due to the presence of both categorical and continuous traits; Pavoine et al. 2009). We assessed the amount of phylogenetic variation of each community through one PD metric, the mean pairwise distance (MPD). To calculate phylogenetic diversity, 1000 phylogenetic trees based on the Hackett backbone (Hackett et al. 2008) were downloaded from <http://birdtree.org/> (Jetz et al. 2012) and the observed MPD was calculated as a mean from all 1000 trees for each point (Cosset and Edwards 2017). As there was no strong correlation between diversity variables (Spearman's  $\rho \leq 0.40$ ), observed values were used for all analyses (i.e. it was not necessary to measure the standardized effect size of metrics, following Loiola et al. 2018). We calculated all metrics using the packages 'FD' through *dbFD* function (Laliberte and Legendre 2010), 'adiv' through *gowdis* function (Pavoine 2020) and 'picante' through *mpd* function (Kembel et al. 2010) in R ver. 4.1.1 ([www.r-project.org](http://www.r-project.org)).

## Data analysis

### Comparison of diversity metrics between community types

We compared TD, FD (i.e. FDiv and FEve) and PD (i.e. MPD) between community types, following the three tests used in Loiola et al. 2018: test 1, comparing non-invaded and invaded communities (*non-invaded* versus *invaded*; test 1); test 2, comparing native species of non-invaded communities and native species of invaded communities (*non-invaded* versus *invaded no alien*); and, test 3, within invaded plots including and excluding alien species (*invaded* versus *invaded no alien*). We performed the above tests *across* (i.e. considering all the communities together) and *within* the main three land classes (i.e. performing the test only between communities belonging to the same main land class used for the stratified random sampling), to assess the effect of environmental filtering on the specific species pool within a given land-use (Loiola et al. 2018). Both for *across* and *within* land classes analyses, to evaluate whether differences of the various metrics between community types were significant, we built linear mixed-effect models (LMM) with normal errors using the maximum log-likelihood method. For test 1 and test 2 we considered community type as a two-level categorical variables (i.e. *non-invaded* or *invaded* and *non-invaded* or *invaded no alien* respectively) as fixed effects while, for test 3, we used an intercept only model with the difference between the two community metrics (e.g. species richness of *invaded* – species richness of *invaded no alien*) as the response variable to test whether it was significantly different from zero. To account for the dependence of observations from the same location in different years, we used point ID as a random effect (i.e. 189 levels) in each model. Due to the non-normality of the observed functional divergence (FDiv) and functional evenness (FEve) metrics, we applied a power and logit transformation, respectively, before performing the LMM analysis. Afterwards, we verified the normality of residuals for each model by inspecting the normal quantiles vs residuals plot through the *qqPlot* function in R.

### Effect of landscape composition and heterogeneity on diversity metrics

To assess the effect of landscape variables on diversity metrics, we built linear mixed-effect models (LMM) with

Table 1. Diversity metrics used for the analysis: taxonomic diversity, functional diversity and phylogenetic diversity

Diversity type	Diversity index	Description
TD	Species richness	Number of species per community
FD	FDiv (Functional divergence)	Degree of functional dissimilarity within the community weighted by abundance (Villéger et al. 2008).
	FEve (Functional evenness)	Regularity of distribution of species abundances in functional space as a measure of resource utilization (Villéger et al. 2008).
PD	MPD (Mean pairwise distance)	Average nodal distance on a phylogenetic tree between species of a community (Webb 2000). High values indicate species in the community are distributed across a wide range of clades, while low values mean the species in the community are clustered.



normal errors using the maximum log-likelihood method, considering all landscape composition variables and SHDI as fixed effects. As above, to account for the dependence of observations from the same location in different years, we used point ID as a random effect (i.e. 189 levels). Models were run separately for each of the three community types. We calculated Akaike's information criterion (AIC) to rank each candidate model. Then, we carried out model averaging (Richards 2008) on all models with  $< 2 \Delta AIC_c$  using the R package 'MuMIn' through the *model.avg* function (Bartoń 2022). We verified the normality of residuals for each model by inspecting the normal quantiles versus residuals plot through the *qqPlot* function in R. Moreover, we tested for spatial autocorrelation by using spline correlograms (Bjørnstad and Falck 2001) with 1000 bootstrap resamples (Santana et al. 2017). We inspected the resulting correlogram plots of the full model residuals (Zuur et al. 2009), and assumed absence of spatial autocorrelation when 95% confidence intervals included zero, finding no evidence of any spatial autocorrelation, concluding that our points were spatially independent (Supporting information).

## Results

We recorded a total of 9476 birds belonging to 69 species (Supporting information). The most abundant species were house sparrow *Passer domesticus*, spotless starling *Sturnus unicolor* and feral pigeon (36% of all observed birds; Supporting information). Out of the 189 points, 100 points were found to be inhabited by *non-invaded* communities and 89 by *invaded* communities (Supporting information). The average number of alien species in *invaded* communities was  $1.22 \pm 0.42$ . Both *non-invaded* and *invaded* community types were found in the three main land classes (urban, agricultural and forest). Considering the feral pigeon as an alien species led to an increase of *invaded* communities from 89 to 116 communities.

Regarding the functional space, the first two axes of the PCoA, accounted for 38% of the total functional variance (Supporting information). Two out of five alien species (*Thectocercus acuticaudatus* and *Psittacula krameri*) were found to occupy a marginal position in the trait space. *E. astrid* and *Euplectes afer* seemingly were closer to other native species *Emberiza calandra* while, *Acridotheres cristatellus* was the only alien species that showed a closer similarity to native species *P. domesticus* than the other four.

### Comparison of diversity metrics between community types

The LMM results comparing *non-invaded* and *invaded* communities (test 1) revealed significantly higher TD (species richness; p-value  $< 0.001$ ), FD (FDiv and FEve; p-value  $< 0.001$  and p-value  $< 0.01$  respectively), but not MPD (p-value = 0.101), in the *non-invaded* communities (Fig. 2,

Supporting information). We found similar results between *non-invaded* and *invaded no alien* communities, when MPD was also significantly higher in the *non-invaded* communities (test 2, all p-values  $< 0.037$ ; Fig. 2, Supporting information). When we compared *invaded* versus *invaded no alien* communities (test 3), TD, FDiv and MPD were significantly higher in *invaded* communities, while FEve was higher for *invaded no alien* communities (all p-values  $< 0.031$ ; Fig. 2, Supporting information).

Trends for TD (species richness), FD (FDiv and FEve) and PD (MPD for test 2 and test 3) were similar, but clearer, in communities considering feral pigeon as alien compared to communities considering feral pigeon as native (all p-values  $< 0.001$ ). The results for MPD remained unaltered considering feral pigeon as alien for test 1, with no significant difference in MPD between *non-invaded* and *invaded* communities (test 1; p-value = 0.407; Supporting information).

Finally, the three tests performed within land classes (i.e. performing the test only between communities belonging to the same main land class) showed similar patterns as the tests *across* land classes (i.e. considering all the communities together), except that MPD was higher in *invaded* than *non-invaded* and *invaded no alien* communities in urban areas (*within* land class comparison, p-value  $< 0.035$  and p-value  $< 0.001$  respectively), and FEve was similar between communities in both urban and forest classes (Supporting information).

### Effect of landscape composition and heterogeneity on diversity metrics

According to the LMMs, TD was positively associated with agricultural and forest areas (both plantation and native), and landscape heterogeneity (SHDI), in *non-invaded* communities (Fig. 3, Supporting information). Native forest and SHDI were positively related to TD both in *invaded* and *invaded no alien* communities, whereas rice field areas were negatively related to TD in both communities (Fig. 3, Supporting information). In *non-invaded* communities, agricultural areas negatively affected this metric (Fig. 3, Supporting information). In *invaded* communities, forest plantation and shrubland were positively associated with FDiv, while they were negatively associated with SHDI in *invaded no alien* communities (Fig. 3, Supporting information). The FEve was negatively associated with urban (all communities) and intensive agricultural areas (*non-invaded* communities), and was positively associated with forest plantation in both *invaded* and *invaded no alien* communities (Fig. 3, Supporting information). Rice field areas were negatively associated with MPD in the three communities (Fig. 3, Supporting information). MPD was also negatively associated with intensive agricultural areas and SHDI in *invaded* communities, while it was negatively associated with urban areas in *invaded no alien* communities (Fig. 3, Supporting information).

LMM models showed similar results to the above when considering feral pigeon as an alien species (Supporting

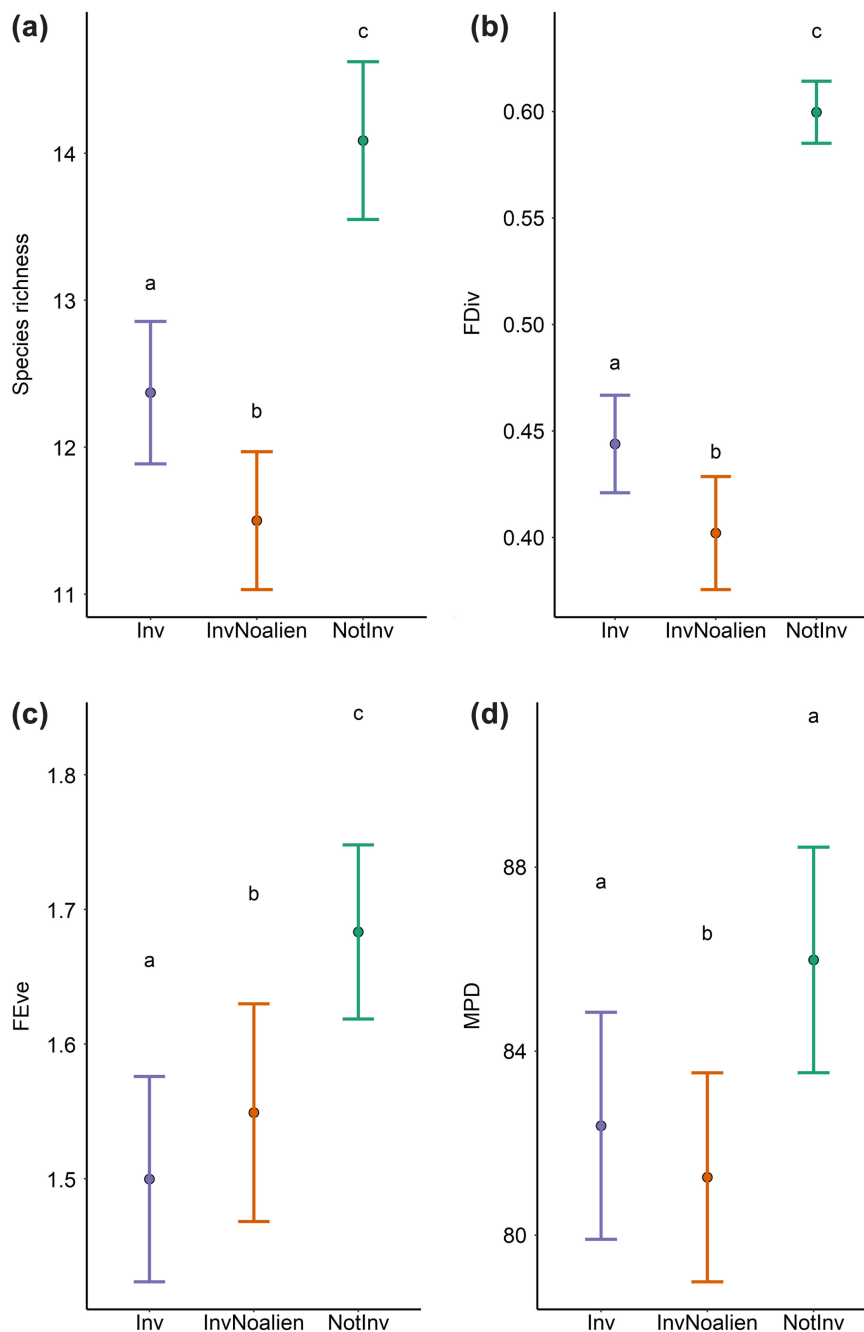


Figure 2. Taxonomic diversity (species richness); (a) functional diversity (functional divergence, functional evenness; (b)–(c) and phylogenetic diversity (MPD) (d) of communities considering feral pigeon as native species, *across* land classes. Inv = bird communities invaded by alien species (purple). InvNoalien = bird communities invaded by alien species accounting only for native species (orange). NotInv = *non-invaded* bird communities (green). Shared letters indicate no significant difference; different letters indicate significant difference (based on LMMs results). Points represent the average raw values, lines are the range of the 95% CI. FDiv was power transformed and FEve was logit transformed. For metric descriptions, see Table 1.

information) in that associations with agricultural and urban areas and SHDI were generally consistent. The major differences between the two analyses were found for FDiv of *non-invaded* and *invaded no alien* and FEve of *invaded no alien* communities, and MPD of *non-invaded* and *invaded no alien* communities (Supporting information).

## Discussion

Our study showed how *non-invaded* bird communities retained higher taxonomic and functional, but not phylogenetic, diversity (TD, FD and PD respectively) than *invaded* communities in a highly human-modified landscape, thus

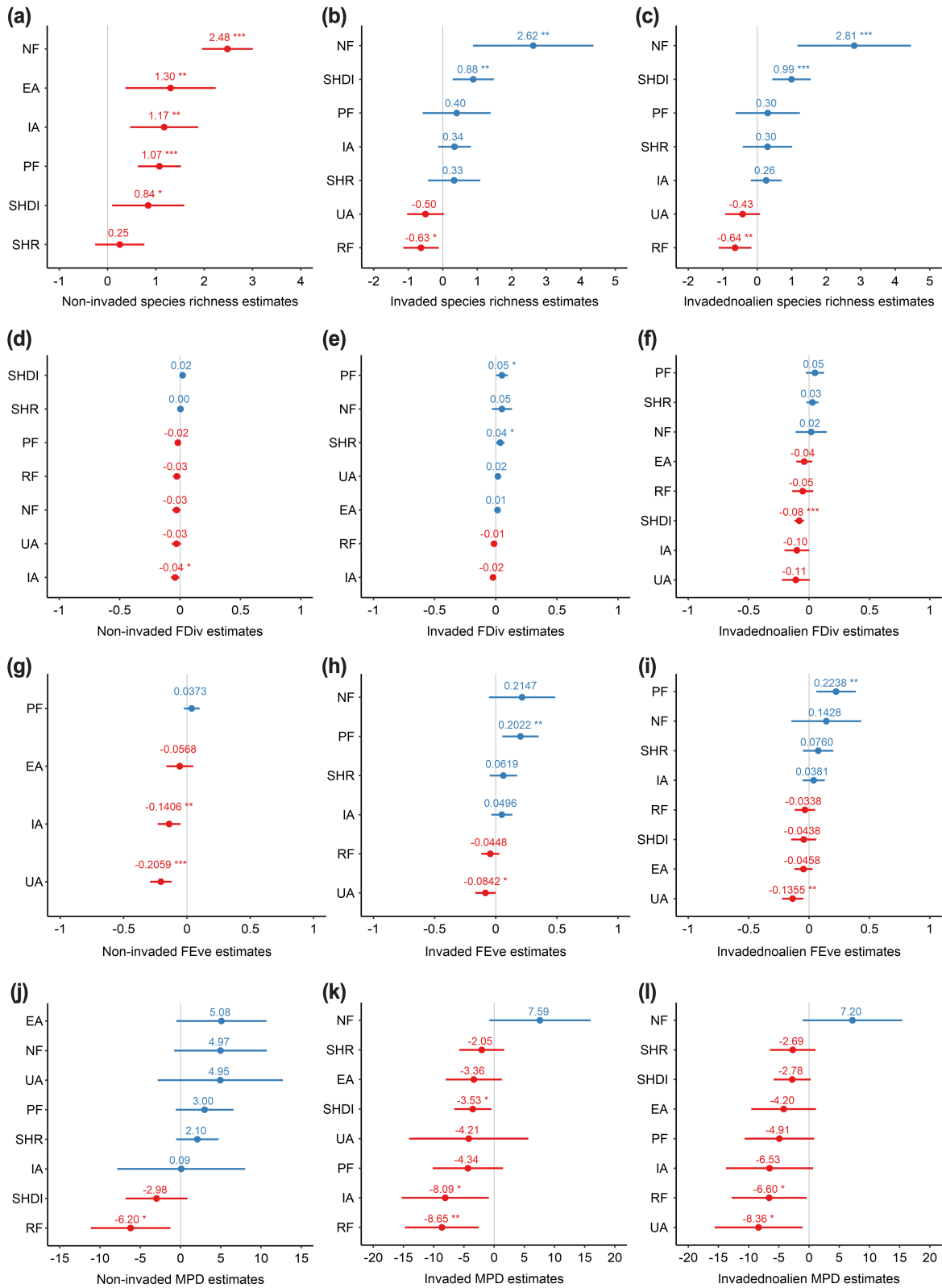


Figure 3. Estimates from the model averaging of land use cover variables on diversity metrics of communities. Taxonomic diversity: species richness, (a)–(c) functional diversity: FDiv (power transformed) – functional divergence (d)–(f); FEve (logit transformed) – functional evenness, (g)–(i). Phylogenetic diversity: MPD – mean pairwise distance, (j)–(l). Non-invaded = non-invaded bird communities. Invaded = bird communities invaded by alien species. InvadedNoalien = bird communities invaded by alien species accounting only for native species.



Figure 3. Continued.

\*  $p < 0.05$ ; \*\*  $p < 0.01$ ; \*\*\*  $p < 0.001$ . Red lines: negative estimates (except in 'a'); Blue lines: positive estimates. Points represent the average estimate values, lines are the range of the 95% CI. The grey vertical indicates an estimate of 0 (95% CI intersecting with 0 are not significant). UA=urban and industrial; IA=intensive agricultural; RF=rice field; EA=extensive agricultural; PF=forest plantation; SHR=shrubland; NF=native forest; SHDI=Shannon–Weiner diversity index of the seven land use categories. Note that the results are based on averaged models from the best model set which varies in terms of the independent variables included for each separate model.

supporting the idea that higher species diversity shapes community resistance to invasions (the biotic resistance hypothesis; Elton 1958, Gerhold et al. 2011, Lososová et al. 2015). Moreover, we infer that it is more likely that alien birds occupy marginal niches in bird communities characterised by low TD, FD and PD (*invaded* versus *invaded no alien*), thus they do not fully compensate for the taxonomic and functional diversity loss caused by the absence of native species in *invaded* sites. TD was enhanced in less disturbed areas in all bird communities, whereas decreases in FD and PD with an increase in disturbed areas were found almost exclusively in *invaded* communities. TD was positively associated with landscape heterogeneity (SHDI) in all communities, while FD and PD showed negative associations with SHDI only for *invaded* communities. Finally, these results were similar (but stronger) when we considered those communities where the feral pigeon was present as *invaded* (i.e. when it was treated as an alien species), suggesting that this ubiquitous bird has more characteristics of an alien than native species in terms of its effects on the diversity metrics considered here.

### Diversity metrics and community types

The higher TD and FD found in *non-invaded* compared to *invaded* bird communities (test 1) across land classes (i.e. considering all the communities together) likely suggests a general negative impact of alien species on native bird communities inhabiting the area. TD, FD and PD were higher in *non-invaded* than *invaded no alien* communities (i.e. *invaded* communities considering only native species; test 2). These findings could represent a loss of ecosystem functioning in the *invaded* bird communities (e.g. through loss of functional groups; Flynn et al. 2009, Cadotte et al. 2011). For example, high functional divergence (FDiv) implies a high niche differentiation in the community (Cosset and Edwards 2017), suggesting that the *non-invaded* communities provide a more diverse pool of functional processes than *invaded* communities (Edwards et al. 2013). Similar reasoning could be applied when accounting for functional evenness (FEve), since high values of FEve reflect efficient use of resources by species in the community (Lee and Martin 2017). Therefore, *non-invaded* showed higher resilience (i.e. FEve) than *invaded* communities (test 1), and lower susceptibility to disturbance than *invaded no alien* communities (test 2). This supports the biotic resistance hypothesis, i.e. higher diversity promotes resistance to invasion (Ordonez 2010).

Following test 3 (*invaded* versus *invaded no alien*), our results showed that alien species were functionally different from the native species of the resident *invaded* community assemblages. FDiv was higher in *invaded* than *invaded no alien* communities, suggesting that alien species provide a set

of functional traits that differ from those of the native species (Cardoso et al. 2018). These results were seemingly confirmed by the PCoA, particularly for the blue-crowned parakeet *T. acuticaudatus* and rose-ringed parakeet *P. krameri* that were quite dissimilar (in terms of functional space) from the native birds of our study area (e.g. they typically feed on fruit not used by native bird species; pers. obs.). Therefore, alien species may show different adaptations to native species, leading to higher niche differentiation of *invaded* communities, and suggesting that alien species usually occupy a marginal ecological niche in those communities (Batalha et al. 2013). Nonetheless, the FEve was significantly lower in *invaded* than *invaded no alien* communities. Thus, despite that alien species have a higher niche differentiation in *invaded* communities, they do not provide a more efficient use of resources than the remaining native species in the community.

In terms of PD, *non-invaded* communities had higher mean pairwise distance (MPD) only than *invaded no alien* communities (test 2), and species in *invaded no alien* communities were more clustered (lower MPD) than species in *invaded* communities (test 3). The results of test 2, along with the TD and FD results, support the resistance hypothesis. Higher PD could imply a community characterized by the accumulation of several adaptations (i.e. reflecting differences between functionally similar species not accounted by FD; Whitfeld et al. 2014), leading to increased competition and hampering alien species spread (Ketola et al. 2017). Finally, since alien species in *invaded* communities expand the phylogenetic space compared to *invaded no alien* communities (test 3), it is more likely that alien species are favoured in more clustered communities (Lososová et al. 2015), occupying novel phylogenetic space in the *invaded* community.

These patterns were similar when we compared the diversity metrics within land classes (i.e. performing the tests only between communities belonging to the same land class) to exclude the effect of environmental filtering on bird community assemblages (Loiola et al. 2018). Nonetheless, MPD was higher for *invaded* than *non-invaded* and *invaded no alien* bird communities within urban areas, suggesting a higher vulnerability to alien species invasion (i.e. a phylogenetic gap). Moreover, no differences were found between community types within forest, either due to the low proportion of *invaded* communities (e.g. montado areas were more resistant to invasion than forest plantation), or because alien bird species were less influenced by environmental filtering compared to native bird communities (Lazarina et al. 2022).

### Landscape effects on diversity metrics

Diversity metrics were affected differently by landscape composition and heterogeneity in the study area. Different

responses among the diversity metrics considered have been found in various other taxa (Sayer et al. 2017, Wong et al. 2020), showing that TD, FD and PD might not respond consistently along landscape or invasion gradients. Native forest cover had a positive effect on TD across each community type, as did landscape heterogeneity. Nonetheless, agricultural areas (both intensive and extensive) were also positively associated with TD in *non-invaded* communities, while rice field areas were negatively associated with TD both in *invaded* and *invaded no alien* communities. Indeed, more disturbed areas (extensive and intensive agricultural, urban and rice field areas) were negatively associated with both FD and PD. This decrease in FD and PD is usually followed by biotic homogenization of bird communities inhabiting disturbed areas (Morelli et al. 2016, Liang et al. 2019). Therefore, bird communities inhabiting those areas could be more susceptible to future alien species establishment (both for *non-invaded* and *invaded* communities) as they are likely better at exploiting novel opportunities in disturbed areas compared to native species (the opportunism hypothesis; Sol et al. 2012). FD and PD were positively associated with forest plantation (*invaded* communities), while, apart from shrubland (*invaded* communities), FD and PD were not enhanced in less disturbed areas. In the first case, a similar pattern was found in New Zealand where alien forest bird species were associated more with ‘exotic forest’ (Barnagaud et al. 2022). In the latter, this could be expected in more heterogeneous areas that contain residual semi-natural features (less disturbed areas in this study) such as shrublands (as discussed in Fahrig et al. 2015, Chiatante et al. 2021), enhancing native (Carpio et al. 2017), but not alien, bird species (as in our study).

Conversely, disturbance (e.g. human modification) may actually increase landscape heterogeneity (i.e. fragmentation; Fahrig 2003). At a large scale, heterogeneity may be associated with an increase in alien bird species richness since it might offer them novel niche opportunities (Andrikou-Charitidou and Kallimanis 2021). This seems to be partially confirmed at the relatively fine scale in this study since landscape heterogeneity (SHDI) was positively associated with the TD of *invaded* communities, and negatively associated with the FD and PD of native bird species in *invaded* communities (i.e. *invaded no alien*), probably because of the higher flexibility of alien species in exploiting those ecological opportunities arising from a fragmented/disturbed landscape (as per the ‘opportunism hypothesis’; Sol et al. 2012). However, there were also positive associations between TD and SHDI in *non-invaded* communities, suggesting a general positive effect of heterogeneity (as per Andrikou-Charitidou and Kallimanis 2021), which supports the biotic acceptance hypothesis (Stohlgren et al. 2006). In summary, the effects of landscape heterogeneity on *invaded* and *non-invaded* bird community diversity are complex and seem to depend on the precise measure of diversity under consideration.

### Broader implications

Our study suggests that the presence of alien species is associated with negative impacts on native bird communities, and

that the functional and taxonomic diversity that alien species contribute does not compensate for the loss of native species. We should stress, however, that our approach is correlational and thus we are unable to fully assess the precise mechanisms that might underpin the observed associations. In terms of the generally lower diversity of native species in invaded communities, there are three possible effects: 1) alien species directly affect native species (e.g. through competition); 2) naturally lower (native) diversity areas are more likely to host alien species; and, 3) lower native diversity due to human disturbance facilitates alien species establishment. It is difficult to tease these effects apart with the data available, but all three provide plausible explanations, and they are not mutually exclusive. However, we believe that our results more clearly support the third option. This is because, in the least disturbed land class (forest), there was no difference in any diversity metric between *non-invaded* and *invaded* communities (*within* land class analysis). However, native diversity was generally lower in the more disturbed land classes (urban and agriculture), suggesting that disturbance facilitates alien species establishment. If direct effects of alien species were affecting native species independently of disturbance, then differences would be expected also in more natural habitats. Detailed ecological studies on interactions between native and alien species are needed to explore these ideas further.

Urban and agricultural areas showed negative associations with diversity in all community types. Although such disturbed areas are not natural, they are still vital for biodiversity conservation (Batáry et al. 2020), especially in the highly modified landscapes of most of Europe. Future management strategies should therefore prioritize habitat restoration in these areas (e.g. increasing urban green spaces, improving heterogeneity features in agricultural landscapes) to minimise the chances of establishment of alien species, and to increase the resistance of *invaded* communities. In our study region at least, this should include the classification of the near-ubiquitous feral pigeon as an alien species. Moreover, our results suggest that native forest was more resistant to alien bird species, thus highlighting how this habitat should be protected and restored in human-modified landscapes. Restoration strategies are well supported by the EU ‘Nature Restoration Law’ (i.e. European Green Deal) and should be implemented along with the impact assessment of alien birds on native bird communities through functional and phylogenetic perspectives, instead of focusing on a single alien species or diversity metrics.

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**Fabio Marcolin:** Conceptualization (equal); Data curation (lead); Formal analysis (lead); Investigation (lead); Methodology (equal); Visualization (lead); Writing – original draft (lead); Writing – review and editing (lead). **Pedro Segurado:** Conceptualization (equal); Data curation (supporting); Formal analysis (supporting); Investigation (supporting); Methodology (equal); Visualization (supporting); Writing – original draft (supporting); Writing – review and editing (supporting). **Dan Chamberlain:** Conceptualization (equal); Data curation (supporting); Formal analysis (supporting); Investigation (supporting); Methodology (equal); Visualization (supporting); Writing – original draft (supporting); Writing – review and editing (supporting). **Luís Reino:** Conceptualization (equal); Data curation (supporting); Formal analysis (supporting); Investigation (supporting); Methodology (equal); Visualization (supporting); Writing – original draft (supporting); Writing – review and editing (supporting).

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### Data availability statement

Data are available from the Dryad Digital Repository: <https://doi.org/10.5061/dryad.66t1g1k6v> (Marcolin et al. 2023).

### Supporting information

The Supporting information associated with this article is available with the online version.

### References

- Anderle, M., Paniccia, C., Brambilla, M., Hilpold, A., Volani, S., Tasser, E., Seeber, J. and Tappeiner, U. 2022. The contribution of landscape features, climate and topography in shaping taxonomical and functional diversity of avian communities in a heterogeneous Alpine region. – *Oecologia* 199: 499–512.
- Andrikou-Charitidou, A., Boutsis, G., Karadimou, E. and Kallimanis, A. S. 2020. Untangling the positive association of phylogenetic, functional, and taxonomic diversity with alien bird species richness. – *Ecosphere* 11: e03007.
- Andrikou-Charitidou, A. and Kallimanis, A. 2021. The different facets of native bird diversity (taxonomic, functional and phylogenetic) as predictors of alien birds increasing richness and expanding range in Great Britain. – *Acta Oecol.* 112: 103750.
- Barnagaud, J. Y., Brockerhoff, E. G., Mossion, R., Dufour, P., Pavoine, S., Deconchat, M. and Barbaro, L. 2022. Trait-habitat associations explain novel bird assemblages mixing native and alien species across New Zealand landscapes. – *Divers. Distrib.* 28: 38–52.
- Bartoń, K. 2022. MuMIn: multi-model inference. – R package ver. 1.46, <https://CRAN.R-project.org/package=MuMIn>.
- Batalha, H. R., Ramos, J. A. and Cardoso, G. C. 2013. A successful avian invasion occupies a marginal ecological niche. – *Acta Oecol.* 49: 92–98.
- Bibby, C. J., Burgess, N. D., Hillis, D. M., Hill, D. A. and Mustoe, S. 2000. Bird census techniques. – Elsevier.
- Bjørnstad, O. N. and Falck, W. 2001. Nonparametric spatial covariance functions: estimation and testing. – *Environ. Ecol. Stat.* 8: 53–70.
- Boano, G., Perco, F., Pavia, M. and Baldaccini, N. E. 2019. *Columba livia* domestic breed, invasive entity also alien for Italy. – *RIO* 88: 3–10. In Italian.
- Bonter, D. N., Zuckerberg, B. and Dickinson, J. L. 2010. Invasive birds in a novel landscape: habitat associations and effects on established species. – *Ecography* 33: 494–502.
- Cade, B. S. 2015. Model averaging and muddled multimodel inferences. – *Ecology* 96: 2370–2382.
- Cadotte, M. W., Carscadden, K. and Mirotchnick, N. 2011. Beyond species: functional diversity and the maintenance of ecological processes and services. – *J. Appl. Ecol.* 48: 1079–1087.
- Cadotte, M. W. 2013. Experimental evidence that evolutionarily diverse assemblages result in higher productivity. – *Proc. Natl Acad. Sci. USA* 110: 8996–9000.
- Cardador, L. and Blackburn, T. M. 2020. A global assessment of human influence on niche shifts and risk predictions of bird invasions. – *Global Ecol. Biogeogr.* 29: 1956–1966.
- Cardoso, G. C., Rodrigues, G. C., Alves, P., Vicente, J. R. and Honrado, J. P. 2018. Naturalized plants decrease diet similarity between an invasive bird and its most similar native species. – *J. Avian Biol.* 49: e01814.
- Carpio, A. J., Barasona, J. A., Guerrero-Casado, J., Oteros, J., Tortosa, F. S. and Acevedo, P. 2017. An assessment of conflict areas between alien and native species richness of terrestrial vertebrates on a macro-ecological scale in a Mediterranean hotspot. – *Anim. Conserv.* 20: 433–443.
- Chiatante, G., Pellitteri-Rosa, D., Torretta, E., Marzano, F. N. and Meriggi, A. 2021. Indicators of biodiversity in an intensively cultivated and heavily human modified landscape. – *Ecol. Indic.* 130: 108060.
- Chiron, F., Shirley, S. and Kark, S. 2009. Human-related processes drive the richness of exotic birds in Europe. – *Proc. R. Soc. B* 276: 47–53.
- Correia, T. P. 1993. Threatened landscape in Alentejo, Portugal: the 'montado' and other 'agro-silvo-pastoral' systems. – *Landscape Urban Plan* 24: 43–48.
- Cosset, C. C. P. and Edwards, D. P. 2017. The effects of restoring logged tropical forests on avian phylogenetic and functional diversity. – *Ecol. Appl.* 27: 1932–1945.
- Dormann, C. F., Elith, J., Bacher, S., Buchmann, C., Carl, G., Carré, G., Marquéz, J. R. G., Gruber, B., Lafourcade, B., Leitão, P. J., Münkemüller, T., McClean, C., Osborne, P. E., Reineking, B., Schröder, B., Skidmore, A. K., Zurell, D. and Lautenbach, S. 2013. Collinearity: a review of methods to deal with it and a simulation study evaluating their performance. – *Ecography* 36: 27–46.
- Edwards, F. A., Edwards, D. P., Hamer, K. C. and Davies, R. G. 2013. Impacts of logging and conversion of rainforest to oil palm on the functional diversity of birds in Sundaland. – *Ibis* 155: 313–326.



- Elton, C. S. 1958. The ecology of invasions by plants and animals. – Methuen.
- Espírito-Santo, D., Costa, J. C., Arsénio, P., Mesquita, S., Ribeiro, S., Capelo, J. and Aguiar, C. 2021. A vegetação de Portugal. – Imprensa Nacional Lisbon. In Portuguese.
- Finerty, G. E., de Bello, F., Bílá, K., Berg, M. P., Dias, A. T. C., Pezzatti, G. B. and Moretti, M. 2016. Exotic or not, leaf trait dissimilarity modulates the effect of dominant species on mixed litter decomposition. – *J. Ecol.* 104: 1400–1409.
- Fahrig, L. 2003. Effects of habitat fragmentation on biodiversity. – *Annu. Rev. Ecol. Evol. Syst.* 34: 487–515.
- Fahrig, L., Girard, J., Duro, D., Pasher, J., Smith, A., Javorek, S., King, D., Lindsay, K. F., Mitchell, S. and Tischendorf, L. 2015. Farmlands with smaller crop fields have higher within-field biodiversity. – *Agric. Ecosyst. Environ.* 200: 219–234.
- Flynn, D. F. B., Gogol-Prokurat, M., Nogeire, T., Molinari, N., Richers, B. T., Lin, B. B., Simpson, N., Mayfield, M. M. and DeClerck, F. 2009. Loss of functional diversity under land use intensification across multiple taxa. – *Ecol. Lett.* 12: 22–33.
- Folke, C., Carpenter, S. R., Walker, B., Scheffer, M., Chapin, T. and Rockström, J. 2010. Resilience thinking: integrating resilience, adaptability and transformability. – *Ecol. Soc.* 15: 20–28.
- Galland, T., Guillaume, A., Dvořáková, H., E-Vojtkó, A., Orbán, I., Lussu, M. Puy, J., Blažek, P., Lanta, V., Lepš, J., de Bello, F., Pérez Carmona, C., Valecia, E. and Götzenberger, L. 2019. Colonization resistance and establishment success along gradients of functional and phylogenetic diversity in experimental plant communities. – *J. Ecol.* 107: 2090–2104.
- Gerhold, P., Pärtel, M., Tackenberg, O., Hennekens, S. M., Bartish, I., Schaminée, J. H. J., Fergus, A. J. F., Ozinga, W. A. and Prinzing, A. 2011. Phylogenetically poor plant communities receive more alien species, which more easily coexist with natives. – *Am. Nat.* 177: 668–680.
- Graham, C. H. and Blake, J. G. 2001. Influence of patch-and landscape-level factors on bird assemblages in a fragmented tropical landscape. – *Ecol. Appl.* 11: 1709–1721.
- IGP 2020. IGP Carta de ocupação do solo [Land cover maps]. – Instituto Geográfico Português (2018). In Portuguese. <https://www.dgterritorio.gov.pt/Carta-de-Uso-e-Ocupacao-do-Solo-para-2018>.
- Hackett, S. J., Kimball, R. T., Reddy, S., Bowie, R. C. K., Braun, E. L., Braun, M. J., Chojnowski, J. L., Cox, W. A., Han, K. L., Harshman, J., Huddleston, C. J., Marks, B. D., Miglia, K. J., Moore, W. S., Sheldon, F. H., Steadman, D. W., Witt, C. C. and Yuri, T. 2008. A phylogenomic study of birds reveals their evolutionary history. – *Science* 320: 1763–1768.
- Haegeman, B., Arnoldi, J.-F., Wang, S., De Mazancourt, C., Montoya, J. M. and Loreau, M. 2016. Resilience, invariability, and ecological stability across levels of organization. – *bioRxiv*, <https://doi.org/10.1101/085852>.
- Harrison, X. A., Donaldson, L., Correa-Cano, M. E., Evans, J., Fisher, D. N., Goodwin, C. E. D., Robinson, B. S., Hodgson, D. J. and Inger, R. 2018. A brief introduction to mixed effects modelling and multi-model inference in ecology. – *PeerJ* 6: e4794.
- Hejda, M. and de Bello, F. 2013. Impact of plant invasions on functional diversity in the vegetation of central Europe. – *J. Veg. Sci.* 24: 890–897.
- Hesselbarth, M. H. K., Sciaini, M., With, K. A., Wiegand, K. and Nowosad, J. 2019. landscapemetrics: an open-source R tool to calculate landscape metrics. – *Ecography* 42: 1648–1657.
- Hulme, P. E. 2009. Trade, transport and trouble: managing invasive species pathways in an era of globalization. – *Int. J. Appl. Ecol.* 46: 10–18.
- Jetz, W., Thomas, G. H., Joy, J. B., Hartmann, K. and Mooers, A. O. 2012. The global diversity of birds in space and time. – *Nature* 491: 444–448.
- Justus, J. 2007. Complexity, diversity, and stability. – In: Sahotra, S. and Plutynski, A. (eds), *A companion to the philosophy of biology*. Blackwell, pp. 321–350.
- Kembel, S. W., Cowan, P. D., Helmus, M. R., Cornwell, W. K., Morlon, H., Ackerly, D. D., Blomberg, S. P. and Webb, C. O. 2010. Picante: R tools for integrating phylogenies and ecology. – *Bioinformatics* 26: 1463–1464.
- Ketola, T., Saarinen, K. and Lindström, L. 2017. Propagule pressure increase and phylogenetic diversity decrease community's susceptibility to invasion. – *BMC Ecol.* 17: 1–6.
- Kosman, E., Burgio, K. R., Presley, S. J., Willig, M. R. and Scheiner, S. M. 2019. Conservation prioritization based on trait-based metrics illustrated with global parrot distributions. – *Divers. Distrib.* 25: 1156–1165.
- Lake, P. S. 2013. Resistance, resilience and restoration. – *Ecol. Manage. Restor.* 14: 20–24.
- Laliberte, E. and Legendre, P. 2010. A distance-based framework for measuring functional diversity from multiple traits. – *Ecology* 91: 299–305.
- Lazarina, M., Sgardelis, S. P., Michailidou, D. E., Tsianou, M., Andrikou-Charitidou, A., Touloumis, K. and Kallimanis, A. S. 2022. Replacement drives native  $\beta$ -diversity of British avifauna, while richness differences shape alien  $\beta$ -diversity. – *Divers. Distrib.* 29: 299–305.
- Lee, M. B. and Martin, J. A. 2017. Avian species and functional diversity in agricultural landscapes: does landscape heterogeneity matter? – *PLoS One* 12: e0170540.
- Liang, C., Yang, G., Wang, N., Feng, G., Yang, F., Svenning, J. C. and Yang, J. 2019. Taxonomic, phylogenetic and functional homogenization of bird communities due to land use change. – *Biol. Conserv.* 236: 37–43.
- Loiola, P. P., de Bello, F., Chytrý, M., Götzenberger, L., Carmona, C. P., Pyšek, P. and Lososová, Z. 2018. Invaders among locals: alien species decrease phylogenetic and functional diversity while increasing dissimilarity among native community members. – *J. Ecol.* 106: 2230–2241.
- Lososová, Z., de Bello, F., Chytrý, M., Kühn, I., Pyšek, P., Sádlo, J., Winter, M. and Zelený, D. 2015. Alien plants invade more phylogenetically clustered community types and cause even stronger clustering. – *Global Ecol. Biogeogr.* 24: 786–794.
- Lowther, P. E. and Johnston, R. F. 2020. Rock pigeon (*Columba livia*), ver. 1.0. – In: Billerman, S. M. (ed.), *Birds of the world*. Cornell Lab of Ornithology.
- Marcolin, F., Lakatos, T., Gallé, R. and Batáry, P. 2021. Fragment connectivity shapes bird communities through functional trait filtering in two types of grasslands. – *GECCO* 28: e01687.
- Marcolin, F., Segurado, P., Chamberlain, D. and Reino, L. 2023. Data from: Testing the links between bird diversity, alien species and disturbance within a human-modified landscape. – Dryad Digital Repository, <https://doi.org/10.5061/dryad.66t1g1k6v>.
- Mathers, K. L., White, J. C., Guareschi, S., Hill, M. J., Heino, J. and Chadd, R. 2020. Invasive crayfish alter the long-term functional biodiversity of lotic macroinvertebrate communities. – *Funct. Ecol.* 34: 2350–2361.
- Matuoka, M. A., Benchimol, M., Almeida-Rocha, J. M. de and Morante-Filho, J. C. 2020. Effects of anthropogenic distur-



- bances on bird functional diversity: a global meta-analysis. – *Ecol. Indic.* 116: e106471.
- McKinney, M. L. 2006. Urbanization as a major cause of biotic homogenization. – *Biol. Conserv.* 127: 247–260.
- McKinney, M. and Kark, S. 2017. Factors shaping avian alien species richness in Australia vs Europe. – *Divers. Distrib.* 23: 1334–1342.
- Morelli, F., Benedetti, Y., Ibáñez-Álamo, J. D., Jokimäki, J., Mänd, R., Tryjanowski, P. and Möller, A. P. 2016. Evidence of evolutionary homogenization of bird communities in urban environments across Europe. – *Global Ecol. Biogeogr.* 25: 1284–1293.
- Morelli, F., Benedetti, Y., Ibáñez-Álamo, J. D., Tryjanowski, P., Jokimäki, J., Kaisanlahti-Jokimäki, M. L., Pérez-Contreras, T., Sprau, P., Suhonen, J., Yosef, R., Díaz, M. and Möller, A. P. 2020a. Insurance for the future? Potential avian community resilience in cities across Europe. – *Clim. Change* 159: 195–214.
- Morelli, F., Benedetti, Y., Jerzak, L., Kubecka, J. and Delgado, J. D. 2020b. Combining the potential resilience of avian communities with climate change scenarios to identify areas of conservation concern. – *Ecol. Indic.* 116: 106509.
- Mouchet, M. A., Villéger, S., Mason, N. W. and Moullot, D. 2010. Functional diversity measures: an overview of their redundancy and their ability to discriminate community assembly rules. – *Funct. Ecol.* 24: 867–876.
- Ordóñez, A., Wright, I. J. and Olff, H. 2010. Functional differences between native and alien species: a global-scale comparison. – *Funct. Ecol.* 24: 1353–1361.
- Pavoine, S., Vallet, J., Dufour, A. B., Gachet, S. and Daniel, H. 2009. On the challenge of treating various types of variables: application for improving the measurement of functional diversity. – *Oikos* 118: 391–402.
- Pavoine, S. 2020. *adiv*: an R package to analyse biodiversity in ecology. – *Methods Ecol. Evol.* 11: 1106–1112.
- Prescott, G. W., Gilroy, J. J., Haugaasen, T., Uribe, C. A. M., Foster, W. A. and Edwards, D. P. 2016. Reducing the impacts of Neotropical oil palm development on functional diversity. – *Biol. Conserv.* 197: 139–145.
- Pyšek, P., Bacher, S., Chytrý, M., Jarošík, V., Wild, J., Celestigrapow, L., Gassó, N., Kenis, M., Lambdon, P. W., Nentwig, W., Pergl, J., Roques, A., Sádlo, J., Solarz, W., Vilà, M. and Hulme, P. E. 2010. Contrasting patterns in the invasions of European terrestrial and freshwater habitats by alien plants, insects and vertebrates. – *Global Ecol. Biogeogr.* 19: 317–331.
- Pyšek, P. et al. 2020. Scientists' warning on invasive alien species. – *Biol. Rev.* 95: 1511–1534.
- Ricciardi, A., Hoopes, M. F., Marchetti, M. P. and Lockwood, J. L. 2013. Progress toward understanding the ecological impacts of nonnative species. – *Ecol. Monogr.* 83: 263–282.
- Richards, S. A. 2008. Dealing with overdispersed count data in applied ecology. – *J. Appl. Ecol.* 45: 218–227.
- Rodríguez, R. A., Herrera, A. M., Santander, J., Miranda, J. V., Fernández-Rodríguez, M. J., Quirós, Á., Riera, R., Fernández-Palacios, J. M., Otto, R., Escudero, C., Jiménez-Rodríguez, A., Navarro-Cerrillo, R., Perdomo, M. and Delgado, J. D., 2015. Uncertainty principle in niche assessment: a solution to the dilemma redundancy vs. competitive exclusion, and some analytical consequences. – *Ecol. Modell.* 316: 87–110
- Saavedra, F., Hensen, I., Beck, S. G., Böhning-Gaese, K., Lippok, D., Töpfer, T. and Schleuning, M. 2014. Functional importance of avian seed dispersers changes in response to human-induced forest edges in tropical seed-dispersal networks. – *Oecologia* 176: 837–848.
- Santana, J., Reino, L., Stoate, C., Moreira, F., Ribeiro, P. F., Santos, J. L., Rotenberry, J. T. and Beja, P. 2017. Combined effects of landscape composition and heterogeneity on farmland avian diversity. – *Ecol. Evol.* 7: 1212–1223.
- Sayer, C. A., Bullock, J. M. and Martin, P. A. 2017. Dynamics of avian species and functional diversity in secondary tropical forests. – *Biol. Conserv.* 211: 1–9.
- Shea, K. and Chesson, P. 2002. Community ecology theory as a framework for biological invasions. – *Trends Ecol. Evol.* 17: 170–176.
- Sol, D., Bartomeus, I. and Griffin, A. S. 2012. The paradox of invasion in birds: competitive superiority or ecological opportunism? – *Oecologia* 169: 553–564.
- Stohlgren, T. J., Barnett, D., Flather, C., Fuller, P., Peterjohn, B., Kartesz, J. and Master, L. L. 2006. Species richness and patterns of invasion in plants, birds, and fishes in the United States. – *Biol. Invas.* 8: 427–447.
- Thuiller, W., Gallien, L., Boulangeat, I., De Bello, F., Münkemüller, T., Roquet, C. and Lavergne, S. 2010. Resolving Darwin's naturalization conundrum: a quest for evidence. – *Divers. Distrib.* 16: 461–475.
- Vilà, M. and Hulme, P. E. (eds.). 2017. *Impact of Biology. Invasions on ecosystem services*, vol. 12. – Springer.
- Villéger, S., Mason, N. W. H. and Moullot, D. 2008. New multidimensional functional diversity indices for a multifaceted framework in functional ecology. – *Ecology* 89: 2290–2301.
- Webb, C. O. 2000. Exploring the phylogenetic structure of ecological communities: an example for rain forest trees. – *Am. Nat.* 156: 145–155.
- White, E. M., Wilson, J. C. and Clarke, A. R. 2006. Biotic indirect effects: A neglected concept in invasion biology. – *Divers. Distrib.* 12: 443–455.
- Whitfeld, T. J. S., Lodge, A. G., Roth, A. M. and Reich, P. B. 2014. Community phylogenetic diversity and abiotic site characteristics influence abundance of the invasive plant *Rhamnus cathartica* L. – *J. Plant Ecol.* 7: 202–209.
- Wong, M. K., Guénard, B. and Lewis, O. T. 2020. The cryptic impacts of invasion: functional homogenization of tropical ant communities by invasive fire ants. – *Oikos* 129: 585–597.
- Zuur, A. F., Ieno, E. N., Walker, N. J., Saveliev, A. A. and Smith, G. M. 2009. *Mixed effects models and extensions in ecology with R*, Vol. 571. Springer.