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Non-native parrot species expand the trait space of avian communities by filling empty niches in urban areas

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Non-native species are one of the greatest threats to biodiversity worldwide due to their direct and indirect effects on native communities. There are two opposing hypotheses to explain how non-native species successfully establish outside their native range. The first posits that non-native species are closely related to local native species through environmental filtering, which selects species with similar traits; the second posits that non-native species are distantly related to native species in the area in which they establish due to limiting similarity, which minimizes competition. We assessed support for these two hypotheses by characterizing the functional trait space of terrestrial bird communities in Italian cities. We surveyed 220 points in breeding and winter periods along an urbanization gradient in six cities. We assessed whether two non-native bird species, Rose-ringed Parakeet *Psittacula krameri* and Monk Parakeet *Myiopsitta monachus*, conformed to either of the two opposing hypotheses by calculating functional diversity metrics (Functional Dispersion, i.e. quantification of the distribution of functional elements in the niche space, and Contribution, i.e. contribution of each species to the niche space) for each community. We then modelled these metrics in relation to the presence or absence of the two non-native parakeet species along the urbanization gradient. We found that non-native parakeet species probably established in the vacant functional niche space of urban bird communities. Our results support the hypothesis that limiting similarity allows the establishment of non-native parakeets at the local scale by reducing competition with native species due to trait dissimilarity. Urban environments offer novel opportunities for the parakeets that are not exploited by the native species present. This insight into niche space processes in urban areas, which can act as centres for expansion of non-native birds into other environments, can be used when implementing

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management strategies to enhance environmental filtering in these areas, thus reducing the chances of further establishment of non-native species.

Keywords: assembly rules, biological invasions, bird assemblage, functional diversity, urban areas.

Invasive non-native species are one of the five major threats to native biota worldwide, with impacts ranging from local to global scales (IPBES 2019, Jaureguiberry *et al.* 2022). The establishment of these species can directly or indirectly disrupt the recipient community structure, altering its functional and phylogenetic diversity (White *et al.* 2006, Ricciardi *et al.* 2013).

Ecological communities follow hierarchical and dynamic assembly processes, and are typically shaped by three major filters acting sequentially: dispersal (can a species arrive?), environmental (can it tolerate local abiotic conditions?) and biotic interactions (can it persist alongside or displace resident species?) (Weiher *et al.* 2011, Kraft *et al.* 2015, Pinto-Ledezma *et al.* 2020, Mammola *et al.* 2024). Human activities have profoundly altered each of these filters by facilitating dispersal through intentional or accidental introductions, modifying environments through land-use change and reshaping biotic interactions by removing or adding competitors and predators. Ultimately, this results in the reshuffling of local community composition that can impair biodiversity and ecosystem functioning, with cascading effects on human welfare (Capinha *et al.* 2015, Vilà & Hulme 2017, Pinto-Ledezma *et al.* 2020).

Non-native species are those that could not have reached the areas in which they occur without human intervention (Russell & Blackburn 2017), yet not all non-native species are able to become established at a local scale (Richardson & Pyšek 2012). There are two opposing mechanisms that have been proposed to explain how some non-native species are able to establish in the non-native range. Environmental filtering occurs when only species with traits enabling adaptation to local abiotic conditions persist. This results in communities of functionally similar species due to strong habitat filtering (de Bello *et al.* 2021), leading to trait underdispersion. Conversely, limiting similarity occurs when non-native species establish because they possess traits that reduce niche overlap with residents, allowing them to exploit novel or underused resources, and so they avoid strong competition (Cadotte *et al.* 2017, Hess *et al.* 2020). This is consistent with the Opportunism Hypothesis (for non-native birds; Sol *et al.* 2012) and leads to trait overdispersion, reflecting a broader diversity of strategies among coexisting native and non-native species (de Bello *et al.* 2021).

Most studies that have tried to address which of these two hypotheses lead to non-native species establishment have focused on phylogenetic relatedness between non-native and native species of plants, reporting contradictory findings (Cardoso *et al.* 2015, Cadotte *et al.* 2018), with closely and distantly related non-native species established at both regional and local scales (Bennett 2019). Moreover, recent tests on non-native birds strongly support environmental filtering, highlighting that non-native species have a greater chance of establishment in communities inhabiting highly human-disturbed areas where closely related relatives are present, irrespective of the spatial scale (Sol *et al.* 2022). Similar results have also been found at regional (based on phylogenetic diversity metrics; Maitner *et al.* 2012) and global (also accounting for functional traits; Redding *et al.* 2019) spatial scales. Nonetheless, these previous studies have only considered a fraction of the annual cycle (generally the breeding period), disregarding interactions occurring in other phases of the non-breeding period that can nevertheless be important in understanding community dynamics, thus limiting the generality of such conclusions (Ibáñez-Álamo *et al.* 2024).

To assess which of the two hypotheses (environmental filtering or limiting similarity) explains the establishment of non-native parakeets within native terrestrial communities, we applied a functional diversity approach to bird communities (both in the breeding season and winter periods) inhabiting six Italian cities. In these cities, the dominant terrestrial non-native bird species are the Ring-necked Parakeet *Psittacula krameri* and the Monk Parakeet *Myiopsitta monachus*, which have established large populations over recent decades (e.g. since the late 1980s in Rome; Mori 2022). Both species are phylogenetically distinct from any other European native bird species inhabiting urban areas. Moreover, both Ring-necked

Parakeets and Monk Parakeets are among the most successful non-native bird species globally, being established in over 46 and 26 countries across five continents, respectively (Royle & Donner 2021).

Recently, Marcolin *et al.* (2023) found evidence that limiting similarity rather than environmental filtering was more important in explaining the distribution of non-native species along a highly modified urban–rural gradient. However, it remains unclear how the functional diversity of invaded versus non-invaded communities is affected. If limiting similarity is the dominant mechanism, we would expect that non-native species occupy vacant functional niche space in urban areas, leading to overdispersion of the trait space. In this case, both native and non-native species will show high trait diversity, with higher overdispersion (i.e. increasing trait diversity) from rural to more urban areas. Conversely, we could expect environmental filtering to act on similar traits in both native and non-native species. If this is the main driving mechanism, functional diversity will be limited by the filter imposed by the environment, leading to underdispersion of the trait space. We tested these two alternative predictions in urban habitats, focusing on two of the most successful terrestrial non-native birds worldwide, while also assessing if there was a different response of community functional diversity between breeding and winter periods (e.g. Ibáñez-Álamo *et al.* 2024).

METHODS

Study areas and sampling design

We conducted the study on the Italian peninsula in six cities that covered a latitudinal gradient of c. 550 km (Fig. 1). Survey sites were selected using a standardized sampling design developed for a broader urban biodiversity study (Assandri *et al.* 2025, Biella *et al.* 2025), which stratified the urban landscape according to greenspace cover and greenspace fragmentation, each divided into four strata. This created 16 possible strata (a 4 × 4 design), from which up to 16 1-km squares were chosen per city. Within each 1-km square, three survey locations were selected that maximized bird detectability and which represented three different habitat types: urban green space, the urban matrix (i.e. built-up areas dominated by impervious surfaces) and the transition zone (or edge) between these two habitats. A random selection of points was not feasible because of limited access, especially to private areas, within the urban landscape. For each city, the ideal maximum number of point counts was therefore 48, although in many cases, not every combination of the stratified design was available, and there were also some problems (e.g. from disturbance) that led to a lower number of point counts. The final sample of point count sites surveyed in each city was: 47 in Turin, 45 in Milan, 34 in Florence, 35 in Rome, 32 in Naples and 27 in Campobasso, for a total of 220 sites sampled.

Within a 100-m radius around each point, we generated a small-scale land-cover map by using orthophotos and field validation. From this, we extracted a measure of the percentage cover of impervious surfaces (imperviousness) as a measure of the degree of urbanization by aggregating urban cover categories (e.g. residential areas, roads, industrial areas) to create an urban gradient that ranged from less urbanized areas (e.g. urban parks with high green space cover) to more urbanized areas (e.g. historical city centres, densely populated areas).

Bird surveys

We surveyed terrestrial bird communities using 10-min point counts (Bibby *et al.* 2000) within a 100-m fixed radius (the same scale as the land-cover variables; see above), recording all birds contacted visually and acoustically. We visited points twice during the breeding season in April–June 2023 and once during the following winter in December 2023–January 2024, in the early morning under calm and dry weather conditions. During the breeding season, to avoid possible biases due to variation in the diurnal activity of birds, for a given day we visited points in a different order during the second survey period, leaving at least 3 weeks between consecutive visits to the same point. Additionally, in winter, we carried out an extra 5-min survey period after the standard 10-min point count when the observer actively searched for birds within the fixed radius. This was done to increase species detection due to lower singing activity outside the breeding season. Species and individuals detected in this additional period were added to the point count. Following Marcolin *et al.* (2021), we excluded from the analyses the following species that were not adequately sampled by our approach: (1) birds flying over (e.g. swifts *Apus* sp.); (2) native and non-native aquatic birds (i.e. non-native Mandarin

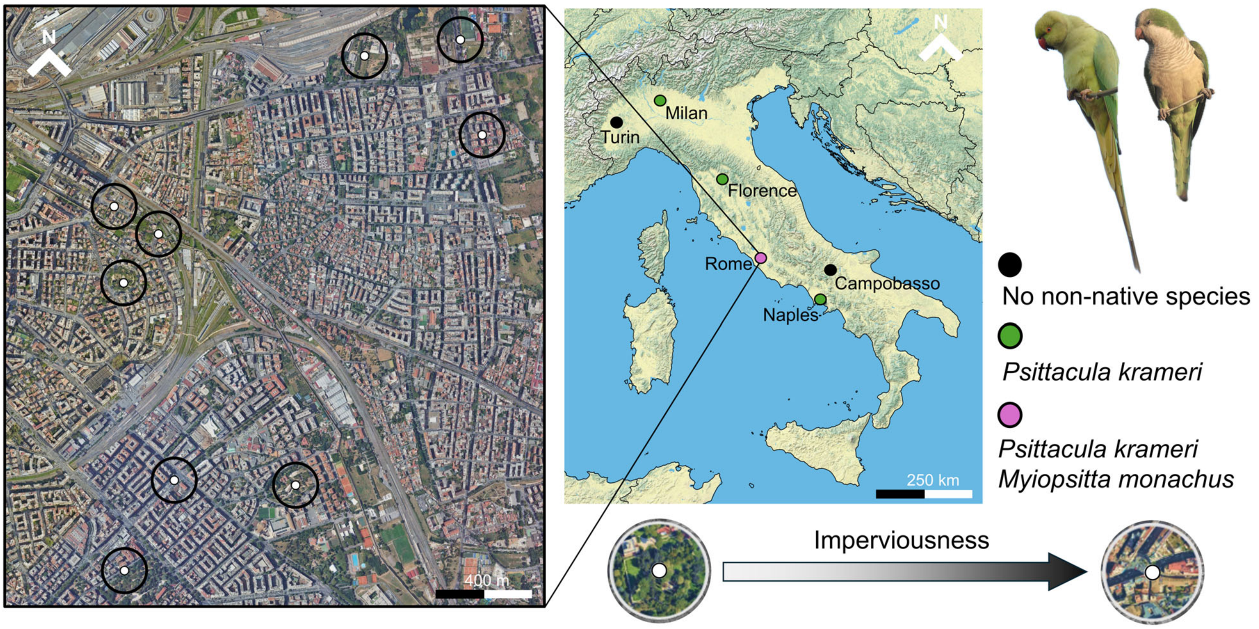

Figure 1. Location of the six cities surveyed along the Italian peninsula (right) represented by different colours depending on the presence (green and purple dot) or absence (black dot) of non-native parakeet species.An example of the study design (left) with point counts (white dots) and the 100-m buffer (dark circle) across different urbanization levels (imperviousness) is shown for the city of Rome. Satellite imagery © Google Maps (2025).

Duck *Aix galericulata* and native Rallidae and Ardeidae); (3) migrating birds that were not interacting with the habitat at a given point; and (4) raptors (both diurnal and nocturnal). For abundance estimates of each bird species recorded during the breeding period, we used the maximum count recorded over the two visits for each point, excluding any juvenile individuals counted. For the winter period, this was not necessary as there was only a single visit to each point.

We followed an existing classification (Loiola *et al.* 2018) to define each community: as invaded when at least one of the non-native species considered (Monk Parakeet or Ring-necked Parakeet) was found in at least one visit during the breeding period, or was found in the only visit during the winter period; and, as non-invaded otherwise. Moreover, the native component of invaded communities was examined by excluding non-native species from the invaded communities (invaded no alien, where 'alien' means non-native).

Trait data

We classified the surveyed bird species using a set of 29 functional traits (belonging to 10 functional trait groups) retrieved from the literature (Pearman *et al.* 2014, Wilman *et al.* 2014, Storchová & Hořák 2018, Tobias *et al.* 2022). These traits all have a hypothesized functional link between the species and their habitat (e.g. food or habitat type used to search for food or nesting; Barnagaud *et al.* 2017, 2022), hence defining their functional niche space along multiple independent axes (Hutchinson 1957; see Table 1 for details). Categorical variables were converted into binary variables (i.e. each trait was either present or absent for a given species). Clutch size, the number of broods per year, fledging period and body mass were maintained as continuous variables. We used the nesting habit trait only for communities in the breeding season. As recommended (Palacio *et al.* 2022), we scaled continuous trait variables to values between 0 and 1, i.e. clutch size, number of broods per year, fledging period and body mass (the latter two previously log-transformed to avoid extreme values; LaBarbera 1989). We subsequently excluded the 'pounce' foraging technique trait variable because of its high correlation with the vertebrate diet trait variable (Pearson's $r = 0.78$ df = 60, and $r = 0.92$ df = 58, in the breeding and winter periods, respectively, all other Pearson's $r \leq \pm 0.70$; Dormann *et al.* 2013, Harrison *et al.* 2018; see Tables S1–S3).

Functional space estimation and functional diversity metrics

We defined the trait space of each community (i.e. non-invaded, invaded and invaded no alien) using probabilistic hypervolumes (Blonder *et al.* 2014, 2018), accounting for species abundances, through the kernel.build function from the R package 'BAT' version 2.9.6 (Cardoso *et al.* 2015, 2024). We chose this approach because it offers a probabilistic description of a trait space of a given community and a clear link with the Hutchinsonian niche (Mammola & Cardoso 2020, Mammola *et al.* 2021). Before the analyses, as standard, we excluded communities with a species richness less than 3 to avoid calculation of uninformative trait space (Mammola *et al.* 2024), resulting in 217 and 214 communities for the breeding and winter periods, respectively. Because our trait matrix included both continuous and binary traits, we used Gower's distance (using the gawdis function from the 'gawdis' R package; de Bello *et al.* 2021) to estimate trait dissimilarity among species (Gower 1971). As different traits were composed of several binary variables (e.g. 'diet' was composed of four categories each treated as an absence/presence variable; see Table 1), we grouped each variable that reflected the same trait information (e.g. the four variables of 'diet' were treated as part of the same trait), giving an equal weight to the 10 trait groups (i.e. treating these traits as fuzzy variables as suggested in de Bello *et al.* 2021). We then performed a principal coordinate analysis (PCoA, R package 'ape' version

Table 1. Table of bird traits with details about the variable, justification for its inclusion in the analyses and source. Diet during breeding and winter periods, Foraging stratum, Foraging technique and Nesting habit trait categories were transformed into binary variables: 0, absence of the category, 1, presence of the category of that trait; categories are not mutually exclusive within a given trait group (i.e. multiple traits can be present).

Trait group	Variable description	Justification	Source
Clutch size	Continuous (number of eggs) – scaled	Clutch size evolved in response to environment and resource constraints and stability	Storchová & Hořák (2018)
Broods per year	Continuous (number of broods) – scaled	Number of broods per year is affected by phenology and resource seasonality and can be associated with urbanization tolerance	Storchová & Hořák (2018)
Fledging period	Continuous (days) – scaled	Age at fledging reflects resource stability and colonization ability in an urban context	Storchová & Hořák (2018)
Body mass	Continuous (grams) – scaled	Proxy of ecophysiological conditions, resource exploitation, life history and tolerance to disturbance and dispersal ability	Tobias *et al.* (2022)
Migratory status	Categorical (three classes: sedentary, partially migratory, fully migratory)	Migrants are associated with seasonal use of resources and higher specialization, which might be detrimental in an urban context	Tobias *et al.* (2022)
Territoriality	Binary (0/1)	Defence of a territory might influence inter-specific dynamics and predation, as well as resource exploitation	Storchová & Hořák (2018)
Diet during breeding and winter period	Binary (0/1 invertivore, vertivore, frugivore, granivore)	Diet affects competition dynamics within an urban bird assemblage and is related to the habitat	Pearman *et al.* (2014)
Foraging stratum	Binary (0/1 around water surface, ground, understorey, mid-high, canopy, aerial)	Three-dimensional use of the urban environment gives insights about the ability of a given species to use resources and exploit habitat structures	Pearman *et al.* (2014)
Foraging technique	Binary (0/1 air-aquatic pursuit, sally, foliage glean, pounce, peck, dig, overturn, probe)	Foraging technique gives insights about the ability and plasticity of a given species in resource exploitation in the urban environment	Pearman *et al.* (2014)
Nesting habit	Binary (0/1 ground, cavity, open arboreal, close to ground, closed-arboreal)	Nest-site availability differs among urban habitats and affects predation exposure and inter-specific competition	Storchová & Hořák (2018)

5.6.2; Paradis & Schliep 2019) on the resulting distance matrix, extracting the first three orthogonal axes, which we later used to delineate the probabilistic hypervolumes for each community. These three axes captured over 50% of the variation in the trait matrix (56% for the breeding and 62% for the winter period, respectively), while ensuring a manageable computation time (Mammola *et al.* 2024). As we were interested in understanding how the presence of non-native parakeets affected the overall spread and density of traits, we assessed whether *invaded* communities had a higher diversity of traits than *non-invaded* communities (Mammola & Cardoso 2020). In this way, we estimated the functional dispersion of each community hypervolume (i.e. quantification of the distribution of diverse functional elements in the trait space) through the BAT kernel.dispersion function (Cardoso *et al.* 2024).

We subsequently used the BAT kernel.contribution function to understand the relative functional contribution of each species to the overall trait space volume of each community, allowing an understanding of the extent to which each species was contributing to underdispersion (i.e. environmental filtering) or overdispersion (i.e. limiting similarity) of the community. Because nesting is a limiting factor, particularly in urban areas (Lakatos *et al.* 2022), and because we aimed to compare species' contributions to functional space between seasons, we repeated the whole analytical pipeline constructing hypervolumes for the breeding season excluding the nesting trait (breeding without nesting habit; 59% of variance explained by the PCoA).

Null modelling

Functional diversity metrics are dependent on the species richness of the studied communities. Statistically accounting for this dependence using a null modelling approach can reveal patterns of trait divergence or convergence that are associated with the rules of community assembly (Mammola & Cardoso 2020, de Bello *et al.* 2021). To this end, we generated 999 null distributions randomizing the association between species and their trait values by permuting the rows of the first three PCoA trait axes (Mammola *et al.* 2024), while preserving the observed community composition and species abundances, followed by the estimation of hypervolume-based trait space. This approach maintains the overall trait structure, but removes any link between traits and species identity, providing a null expectation for functional dispersion under random trait assembly (Mammola & Cardoso 2020, de Bello *et al.* 2021). For each of the 999 random iterations, we calculated both functional dispersion and contribution metrics to derive expected values. Subsequently, we expressed the deviation of the observed values of the functional dispersion and contribution metrics (calculated without randomizations) from the values expected from the random iterations (i.e. the null models). This deviation was calculated by means of standardized effect sizes (SES) using the formula: (observed values − mean of expected values)/standard deviation of expected values.

Positive SES values reflect an overdispersed community (i.e. influenced by limiting similarity) and negative SES values reflect an underdispersed community (i.e. influenced by environmental filtering). We calculated parametric (for functional dispersion) and non-parametric (for functional contribution) SES values using a probit distribution (Mammola *et al.* 2024). In the latter case, a non-parametric SES was necessary because null values showed an asymmetric, left-skewed distribution that arises because functional contribution values are bounded at 0 (Mammola *et al.* 2024).

Statistical analyses

Through regression analyses, we assessed whether non-native parakeets occupied a vacant niche in the functional space of urban bird communities. Specifically, we used linear mixed effects models (R package nlme version 3.1-163; Pinheiro *et al.* 2023) to model the relationship between SES values for functional dispersion with season (breeding versus winter) and the presence of non-native species and imperviousness (i.e. the urbanization gradient) as predictor variables. Moreover, we included the interactions between season and the presence of non-native species, and season and imperviousness, to test for seasonal effects on community dynamics (Alba *et al.* 2025). Furthermore, to test the functional dispersion of invaded communities accounting only for the native species component (i.e. invaded no alien), we tested whether there was a significant difference in functional dispersion as measured by SES values of invaded and invaded no alien communities within each season (i.e. one model each). This was undertaken using an intercept-only model, testing whether the difference between the two community types (i.e. SES functional dispersion of invaded – SES functional dispersion of invaded no alien) was significantly different from zero. All models included a nested random intercept structure represented by point count identity (217 levels in the breeding period and 214 levels in the winter, respectively) within each city (six levels; i.e. random = ~1|city/point count identity), accounting for the non-independence of the data because we sampled the same points repeatedly within cities. We checked model fit with the R package 'performance' version 0.10.9 (Lüdecke *et al.* 2021) by visually inspecting the normality of residuals, heteroskedasticity and degree of collinearity, finding acceptable model fit in each case. Furthermore, we found no evidence of spatial autocorrelation in model residuals using the function check.autocorrelation from the performance package. We ran all our analysis in R version 4.3.2 (R Core Team 2023).

RESULTS

We recorded a total of 18 594 individuals belonging to 119 species, with 93 species contacted during the breeding surveys and 79 during the winter period. We retained 62 (breeding) and 60 (winter) species for analyses after excluding inadequately sampled species, totalling 12 481 individuals. The six most abundant species (55% of all recorded birds in both periods) were Feral Pigeon *Columba livia domestica*, Italian Sparrow *Passer italiae*, Common Starling *Sturnus vulgaris*, Common Blackbird *Turdus merula*, Common Wood Pigeon *Columba palumbus* and European Robin *Erithacus rubecula*.

Excluding Turin and Campobasso (in which there were no parakeets established), 68 out of the 146 points were found to be inhabited by non-native parakeets. The Rose-ringed Parakeet was found in all four invaded cities (i.e. Florence, Milan, Naples and Rome in 67 points, 46% of points within invaded cities, with 388 individuals). The Monk Parakeet was found only in Rome (21 points with 129 individuals, resulting in 14% of points in invaded cities), where the Rose-ringed Parakeet was also present on all except one of those points. Both species were recorded in both periods. No other terrestrial non-native bird species was recorded in any survey, so these two species fully represent the non-native terrestrial bird community in our sample.

Distributions of SES values for the functional dispersion of each community and each period were right-skewed, with 58% of urban bird communities mainly functionally overdispersed and 42% underdispersed (Fig. 2), meaning that the composition of most communities was influenced more by limiting similarity than environmental filtering. Four communities were significantly overdispersed (one in the breeding period and three in the winter period; $P < 0.05$) and four were underdispersed (all in the winter period; $P < 0.05$); the remaining communities, despite not deviating significantly from the null model, showed varied over−/underdispersion across cities and seasons.

There was no obvious latitudinal trend of over- or underdispersed communities, with more underdispersed communities (i.e. environmental filtering) in Turin and Campobasso in the winter period (both cities were without established parakeet species, i.e. they were non-invaded communities; Fig. 2). Moreover, most invaded communities (i.e. parakeet species present) showed a marked overdispersion (i.e. limiting similarity) in all cities in both surveyed periods (Fig. 2 & Fig. S1).

The functional contribution of non-native parakeets was always overdispersed, with the Monk Parakeet located in the right-end of the distribution for the city of Rome (Fig. 3), illustrating the contribution of these species to the diversification of traits (and hence trait space and function) in the community in which they occur. Moreover, the overdispersion for the functional contribution of non-native parakeets was more pronounced when excluding the nesting trait in all invaded cities (Fig. 3), suggesting that this trait could be a source of competition (more diverse traits imply less competition, i.e. overdispersion) between native species and non-native parakeets.

Results from the linear mixed effects models on SES values of functional dispersion (see Table S4 for full model results) showed a significant effect of season (df = 1/208, $F = 5.380$, $P = 0.021$), with higher SES values in the breeding than in the winter period (i.e. higher overdispersion both for non-invaded and invaded communities, therefore increasing limiting similarity; Fig. 4). SES increased significantly with both the urbanization gradient (df = 1/210, $F = 16.381$, $P < 0.001$) and the presence of non-native parakeets (df = 1/208, $F = 87.050$, $P < 0.001$). Furthermore, the

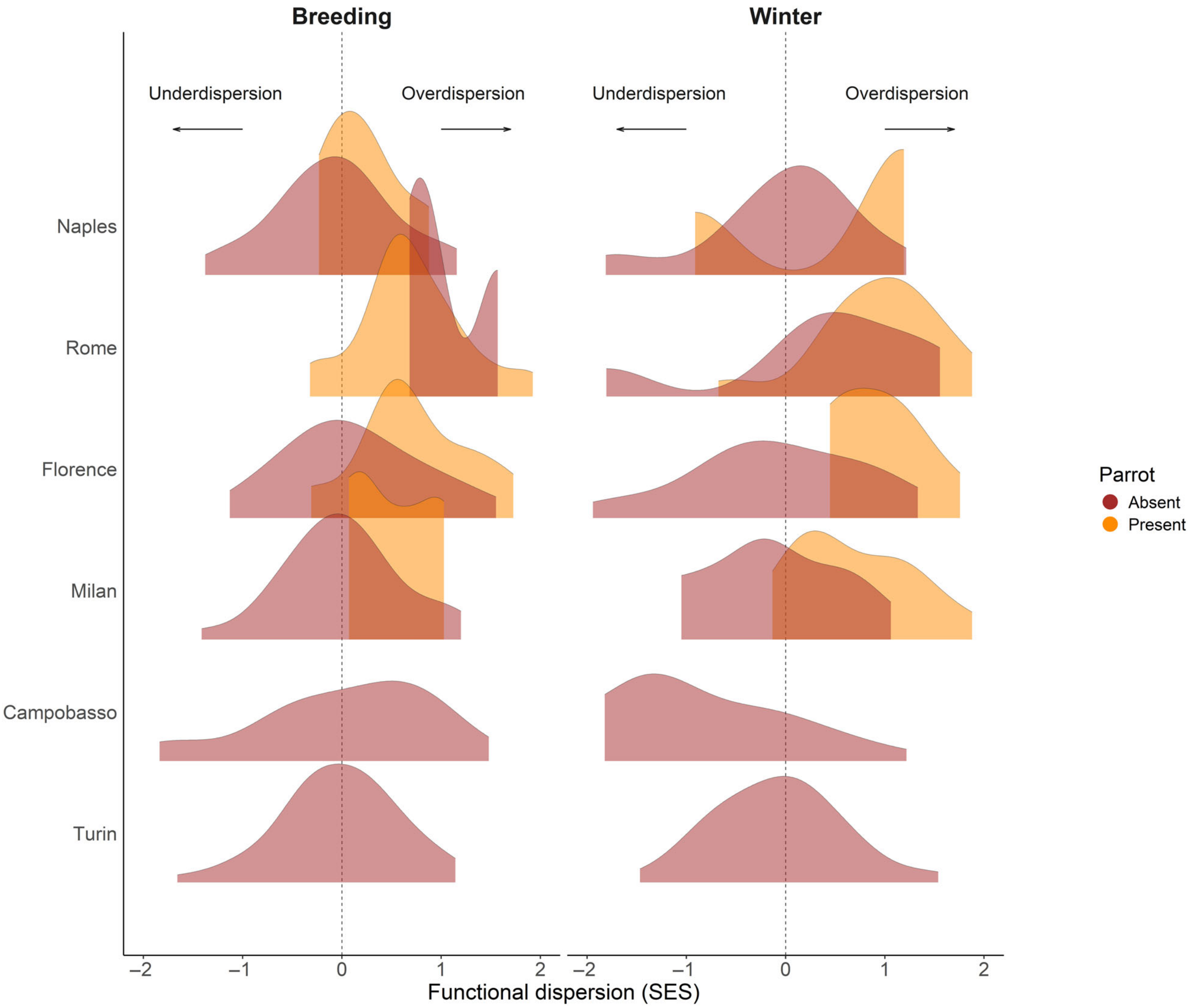

Figure 2. Kernel distribution of standardized effect size (SES) values for functional dispersion (i.e. quantification of the distribution of diversity of functions in the trait space) in breeding and winter periods for the overall communities (top row) and for communities within each city. Brown represents the non-invaded communities (i.e. no non-native species were found in all visits) and orange represents the invaded communities (i.e. at least one non-native species was found in at least one visit). Underdispersed communities are represented by negative SES values (i.e. communities influenced by environmental filtering). Overdispersed communities are represented by positive SES values (i.e. communities influenced by limiting similarity).

interaction between season and the presence of non-native parakeets was significant (df = 1/208, $F = 11.293$, $P < 0.001$), where the response to the urbanization gradient was stronger in non-invaded communities in the winter period. There was higher overdispersion (positive SES values) in invaded compared with non-invaded communities in both periods (i.e. no overlap in the confidence intervals; Fig. 4). Moreover, underdispersion was more pronounced in non-invaded communities in the winter than in the breeding period (i.e. SES <0 in most cases in winter; Fig. 4), showing a more marked effect of environmental filtering during this season. There was no significant interaction between season and the urbanization gradient (df = 1/208, $F = 1.551$, $P = 0.214$; Fig. 4).

Finally, there was no significant difference between SES values of *invaded* and *invaded no alien* communities either in the breeding (df = 1/60, $F = 0.006$, $P = 0.940$) or winter period (df = 1/53, $F = 2.243$, $P = 0.140$; see Table S4 & Fig. S2).

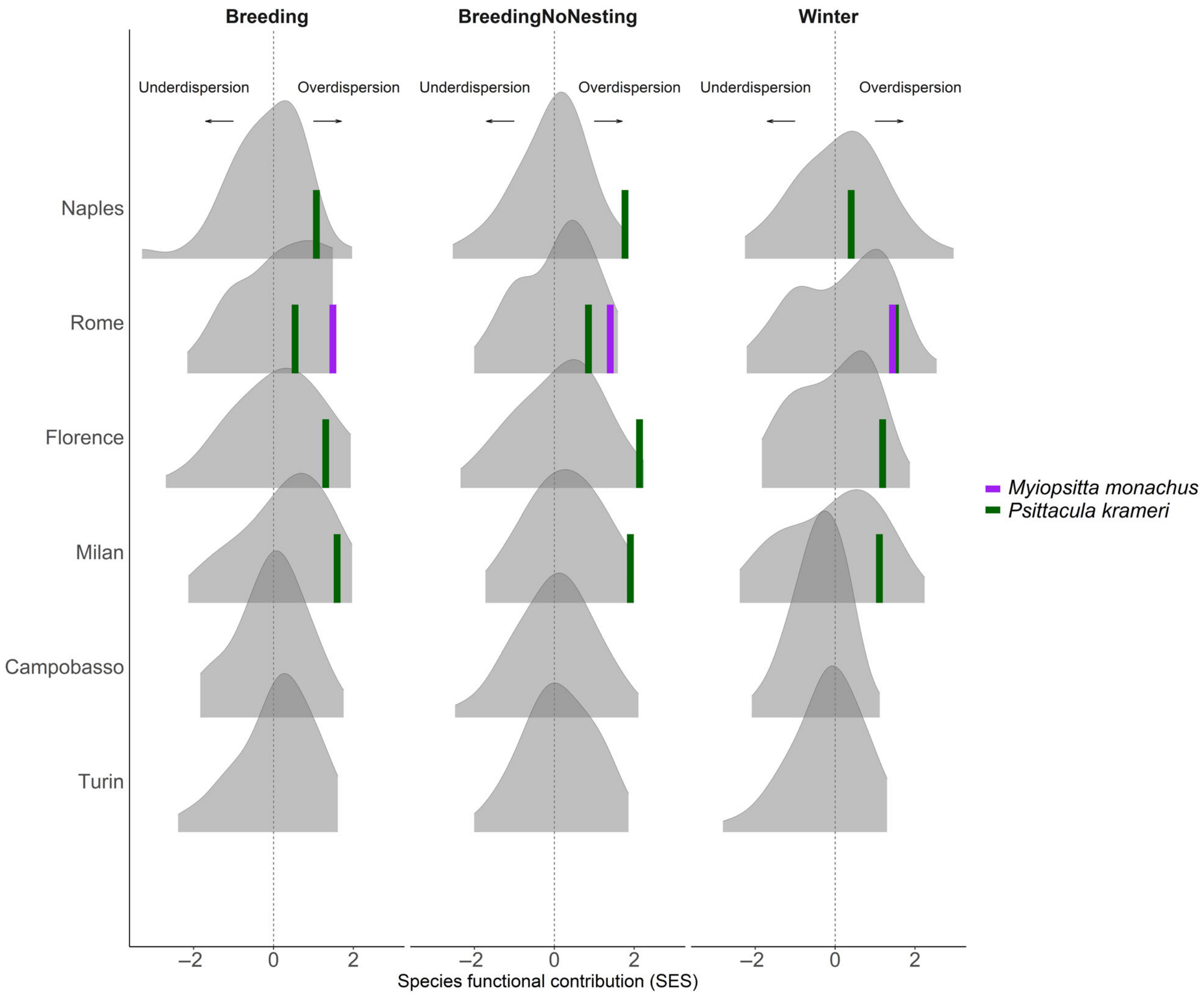

Figure 3. Kernel distribution of standardized effect size (SES) values for Functional Contribution (i.e. relative contribution of each species to the overall trait space volume) in breeding and winter periods for each city, including the comparison in which the breeding period was analysed without the nesting traits (BreedingNoNesting). Purple (*Myiopsitta monachus*) and green (*Psittacula krameri*) vertical lines represent the functional contribution of the non-native parakeets to the overall bird communities, respectively. Underdispersed species contributions are represented by negative SES values (i.e. communities influenced by environmental filtering). Overdispersed species contributions are represented by positive SES values (i.e. communities influenced by limiting similarity).

DISCUSSION

Our study tested two contrasting hypotheses about the establishment of two species of parakeet, a widespread invasive species group in many parts of the world, in urban bird communities. We found stronger support for a scenario where limiting similarity is the key driving force affecting parakeet species establishment in urban bird communities. Specifically, parakeets are less likely to occupy similar niche space to native species, thus reducing competition. This suggests that these non-native species occupy vacant niche space in the invaded communities. This was the case in both breeding and winter periods, and limiting similarity increased along the urbanization gradient. Non-invaded communities (i.e. without established parakeets) showed an opposite response to urbanization, whereby the assembly of communities in less urbanized areas was predominantly driven by environmental filtering (i.e. underdispersion of the trait space). These findings corroborate previous

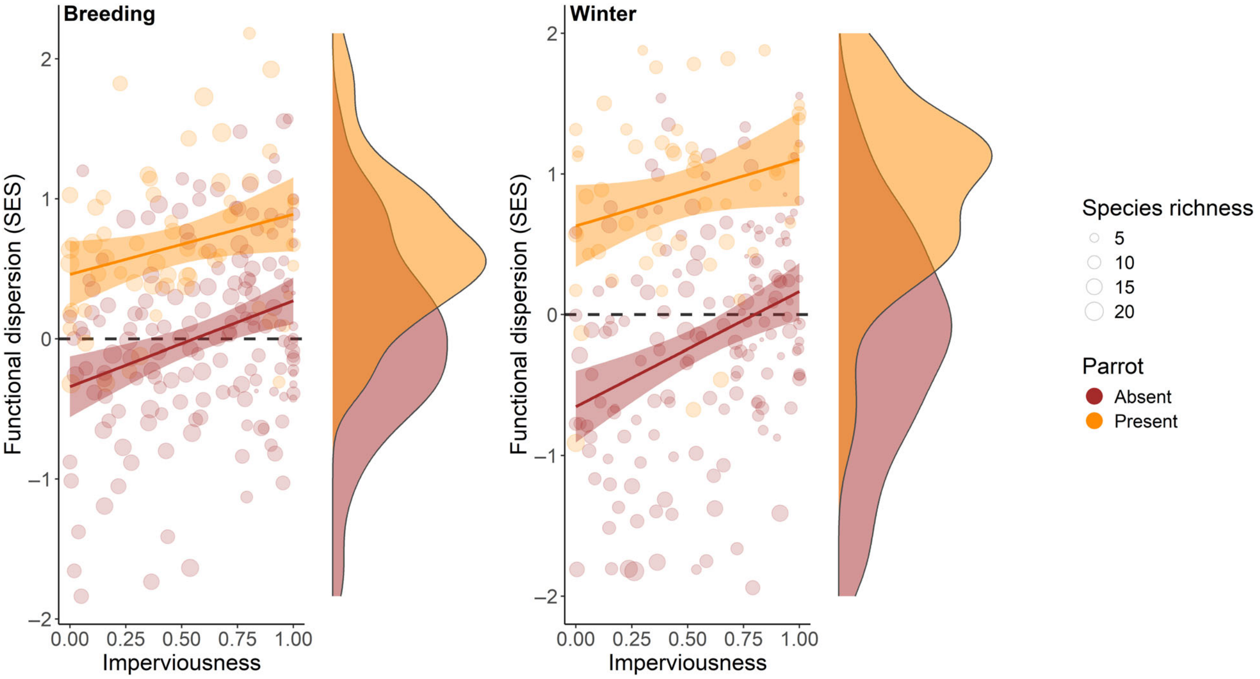

Figure 4. Response of standardized effect size (SES) values for functional dispersion (i.e. quantification of the distribution of diversity of functions in the trait space) to the urbanization gradient (i.e. Imperviousness) in the breeding and winter periods. Dot size is proportional to community species richness. The density curves represent the distribution of SES values. Brown represents the non-invaded communities (i.e. no non-native species were found in all visits) and orange represents the invaded communities (i.e. at least one non-native species was found in at least one visit). Underdispersed communities are represented by negative SES values (i.e. communities influenced by environmental filtering). Overdispersed communities are represented by positive SES values (i.e. communities influenced by limiting similarity). Shaded colours around the regression lines represent the 95% confidence intervals.

suggestions that non-native bird species, including the Rose-ringed Parakeet, could exploit and fill vacant niche space in urban areas (South Africa; Ivanova & Symes 2019). They also accord with findings from invaded bird communities (i.e. non-native species occupying vacant niche space in Portugal; Marcolin *et al.* 2023) and both the non-native Common Waxbill *Estrilda astrild* and Red-billed Leiothrix *Leiothrix lutea* occupying vacant niche space due to a different set of functional traits compared with native species (Vall-llosera *et al.* 2016, Cardoso *et al.* 2018). These results are also supported by observations of non-native parakeets feeding commonly on fruits that are not used by native bird species (F.M. pers. obs.). Furthermore, the functional contribution of non-native parakeets in our study was always located at the right end of the distribution for all invaded cities, highlighting the strong contribution of these species to the functional diversity of the community (i.e. increasing it through provision of diverse traits). The general overdispersion of the invaded communities in the four cities in which parakeets were established (Milan, Florence, Rome and Naples) supports the contention that non-native species increase the diversity of functions provided relative to the non-invaded communities in Turin and Campobasso that were generally more underdispersed (i.e. environmental filtering; see Fig. 2).

Dispersion increased in relation to the urbanization gradient (i.e. as measured by imperviousness) in both invaded and non-invaded communities, although in the former there was always overdispersion, whereas in the latter, communities were mostly underdispersed along the gradient. These findings indicate that both processes probably operate simultaneously, but their relative strengths shift along the urbanization gradient, with limiting similarity prevailing where disturbance is greatest. This increasing importance of limiting similarity in more urbanized areas could be explained by the change in bird species composition, supporting the Opportunism Hypothesis (Sol *et al.* 2012), which proposes that more urbanized and disturbed areas provide niche space that is better exploited both by native generalist species and non-native bird species than by specialized native bird species (as could be found in less urbanized areas). Therefore, the change in bird species composition favouring generalists (e.g. Hooded Crow *Corvus cornix*) along with non-native species (Sol *et al.* 2012, Møller *et al.* 2015) leads to a differentiation in traits that are more suitable for exploiting the scarce resources available in more urbanized areas (i.e. limiting similarity). This is supported by the fact that invaded no alien communities (i.e. the native species in invaded bird communities) did not differ substantially from invaded communities in their response to urbanization. This suggests that parakeets, as generalist non-native species, tend to establish in communities that are already strongly shaped by limiting similarity (Vall-llosera *et al.* 2016), probably because of the generally negative effects of urbanization on bird community composition and functional diversity (Sol *et al.* 2017, La Sorte *et al.* 2018).

The distinction between overdispersed invaded communities and underdispersed non-invaded communities was more evident during the winter, when the community composition changes as a result of migration or dispersal (i.e. some species migrate to their wintering grounds, while others move into the city in the non-breeding period). Most incoming wintering birds are granivorous species that may struggle to find appropriate resources in urban environments (Lakatos *et al.* 2022), especially in southern Europe where garden bird feeding is uncommon (Reynolds *et al.* 2017), so granivores must exploit the resources naturally present (Lakatos *et al.* 2022). Furthermore, because resources are more limited in the winter, competition in more urbanized areas is likely to be higher, leading to an increase in the overdispersion of the niche space of invaded bird communities. Therefore, birds need dissimilar traits to exploit scarce resources to avoid competition with the other species present in the community (e.g. diverse feeding strategies).

Our findings are somewhat at odds with recent assessments of these hypotheses for bird communities. Several studies have found evidence of environmental filtering (Maitner *et al.* 2012, Redding *et al.* 2019), also independently of spatial scale (Sol *et al.* 2022). These studies focused on phylogenetic relatedness between species, using phylogenetic diversity metrics, with one study also considering functional diversity metrics (Sol *et al.* 2022). These previous findings lend support to the Pre-Adaptation Hypothesis of Darwin's Naturalization Conundrum (Diez *et al.* 2008). This hypothesis states that non-native species that are closely related to resident native species are more likely to establish in native assemblages because they share similar traits, allowing them to colonize and persist under local abiotic conditions because they are subject to the same environmental filtering (Bennett 2019). However, our results were more consistent with the opposite hypothesis of the Darwin's Naturalization Conundrum: Darwin's Naturalization Hypothesis (Daehler 2001). This hypothesis states that non-native species should be distantly related to native species to avoid interspecific competition and thus competitive exclusion due to limiting similarity. Therefore, they should show dissimilar traits compared with resident species, assuming stronger competition among similar species (Bennett 2019), as is the case with parakeets.

Our study included only two non-native bird species, whereas other studies have included several non-native species. Moreover, we analysed bird communities that have been invaded for some years (Mori 2022), so we missed the early invasion stages. Early in the invasion process, non-native species may establish in communities where closely related species occur (Cadotte *et al.* 2018), but this may be followed by later stages where niche overlap could lead to the extinction of native species, thus opening the phylogenetic gap (Cadotte *et al.* 2018). In other words, a process of environmental filtering could have happened before our surveys. However, we consider this unlikely as native species in Italian urban areas, and more generally in European urban areas, have no phylogenetically closely related species to parakeets (i.e. there are no native Psittaciformes occurring in Europe). Therefore, we are confident that phylogenetic similarity had not caused enhanced competition with native species with the latter becoming locally extinct in invaded communities. Furthermore, most non-native terrestrial species established in Italian cities are Psittaciformes, with only a few isolated cases for passerine species that have yet to spread beyond their original area of establishment (e.g. Common Myna *Acridotheres tristis* near Salerno and Caserta, southern Italy; Mori *et al.* 2020). Therefore, we sampled the main non-native terrestrial bird species of Italian cities. Nonetheless, our point count method considered only 1 year of sampling, which may not be sufficient to capture interannual variation in community structure (both in the breeding and winter periods) or to detect winter bird species. However, a recent study did not find any interannual variation (over 2 years) for bird communities sampled with point counts in similar habitats (Marcolin *et al.* 2023).

CONCLUSIONS

Our findings support the limiting similarity hypothesis, with parakeet species probably occupying vacant niches in invaded bird communities and, based on our functional approach, seemingly with possible limited negative effects through competition with native bird species. Parakeets are well established in many European, and indeed global, cities (Pârâu *et al.* 2016) where they probably survive due to limited competition with the depauperate native avifauna, with little effect on existing native species. Nevertheless, we should not conclude that non-native parakeets do not have impacts on native fauna, especially outside urban areas. There is evidence that both Rose-ringed Parakeet and Monk Parakeet can be a crop pest in their native and introduced ranges (Menchetti & Mori 2014, Castro *et al.* 2022), and there is also some evidence of negative effects of Rose-ringed Parakeets on cavity-nesting birds (e.g. Eurasian Nuthatch *Sitta europaea*; Strubbe & Matthysen 2009 and Lesser Kestrel *Falco naumanni*; Hernández-Brito *et al.* 2014) and urban bats (Hernández-Brito *et al.* 2018) in their introduced range in Europe (but see Menchetti & Mori 2014 for a full review on the impacts of non-native parrots). The Rose-ringed Parakeet is also a common non-native species globally (Royle & Donner 2021), and there are invaded regions of the world where its impacts could go unnoticed (Evans *et al.* 2021). More generally, urban areas enhance the probability of non-native species establishment and so may act as centres for expansion of non-native birds into other environments (Cardador & Blackburn 2019, Cardador *et al.* 2022). In a broader habitat context, non-native species seem to be more affected by environmental filtering than native species, preventing their establishment in more natural areas that are generally less favourable to non-native bird species (Marcolin *et al.* 2023), probably because of the greater resistance to invasion of more diverse ecological communities (the biotic resistance hypothesis; Elton 1958, Lososová *et al.* 2015). Given that relatively more intact, biodiverse habitats tend to reduce the probability of establishment of non-native species (Marcolin *et al.* 2023), implementing management strategies to enhance environmental filtering in urban areas may reduce the chances of further establishment of non-native species by favouring native species better adapted to the existing environmental conditions.

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AUTHOR CONTRIBUTIONS

Fabio Marcolin: Conceptualization; investigation; writing – original draft; methodology; validation; visualization; writing – review and editing; formal analysis; data curation. **Riccardo Alba:** Conceptualization; investigation; writing – original draft; methodology; validation; visualization; writing – review and editing; formal analysis; data curation. **Stefano Mammola:** Methodology; writing – review and editing; formal analysis; validation; visualization; data curation; writing – original draft. **Giacomo Assandri:** Conceptualization; investigation; writing – review and editing; methodology; data curation. **Luca Ilahiane:** Conceptualization; investigation; methodology; writing – review and editing; data curation. **Diego Rubolini:** Conceptualization; methodology; writing – review and editing; supervision. **Luís Reino:** Writing – review and editing; supervision. **Dan Chamberlain:** Funding acquisition; conceptualization; writing – original draft; writing – review and editing; validation; supervision.

ETHICAL NOTE

None.

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CONFLICT OF INTEREST

The authors declare that they have no known competing interests.

Data Availability Statement

The data that support the findings of this study are openly available on the Zenodo repository, DOI 10.5281/zenodo.18172553.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Figure S1. Kernel distribution of standardized effect size (SES) values for functional dispersion (i.e. quantification of the distribution of diversity of functions in the trait space) in the breeding and winter periods for the overall communities and for communities within each city.

Figure S2. Response of standardized effect size (SES) values of functional dispersion (i.e. quantification of the distribution of diversity of functions in the trait space) to the gradient of urbanization (i.e. Imperviousness) in the breeding and winter periods, including and excluding non-native parakeets. Dot size is proportional to community species richness.

Table S1. Pearson's correlation coefficients between species traits used for the Breeding period.

Table S2. Pearson's correlation coefficients between species traits used for the Breeding period excluding the Nest habit traits to compare with the Winter period.

Table S3. Pearson's correlation coefficients between species traits used for the Winter period.

Table S4. Linear mixed effects model outputs for effects on standardized effect size (SES) values for functional dispersion.