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Alien species richness is currently unbounded in all but the most urbanized bird communities

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Abstract:	Urban areas suffer high pressure of introductions of alien species compared to other habitats due to intensive human activities. As trading globally continues to rise, more species will likely be introduced into urban areas. To determine whether this increase in introduction pressure will lead to increased alien species richness in urban areas, or whether other processes would act to impose an upper limit on species richness, we examined how the shape of the relationship between alien species richness and the number of introduced species over time (i.e. introduction pressure) varies along gradients of urbanization. We collected species composition data from urban bird surveys worldwide and used a global database of alien bird introductions to quantify how many species have been introduced over time at different sites. We found that urbanization gradually modified the shape of the studied relationship from linear to asymptotic. Only communities in extremely urbanized environments were associated with an asymptotic relationship, suggesting that alien bird richness has likely not reached its ecological limit in most urban areas. Our results show that urbanization can reduce the importance of introduction pressure in determining alien species richness. Additionally, the results predict that alien species richness will increase at finer spatial scales, especially if the introduced species can survive in urban areas outside of their native range.

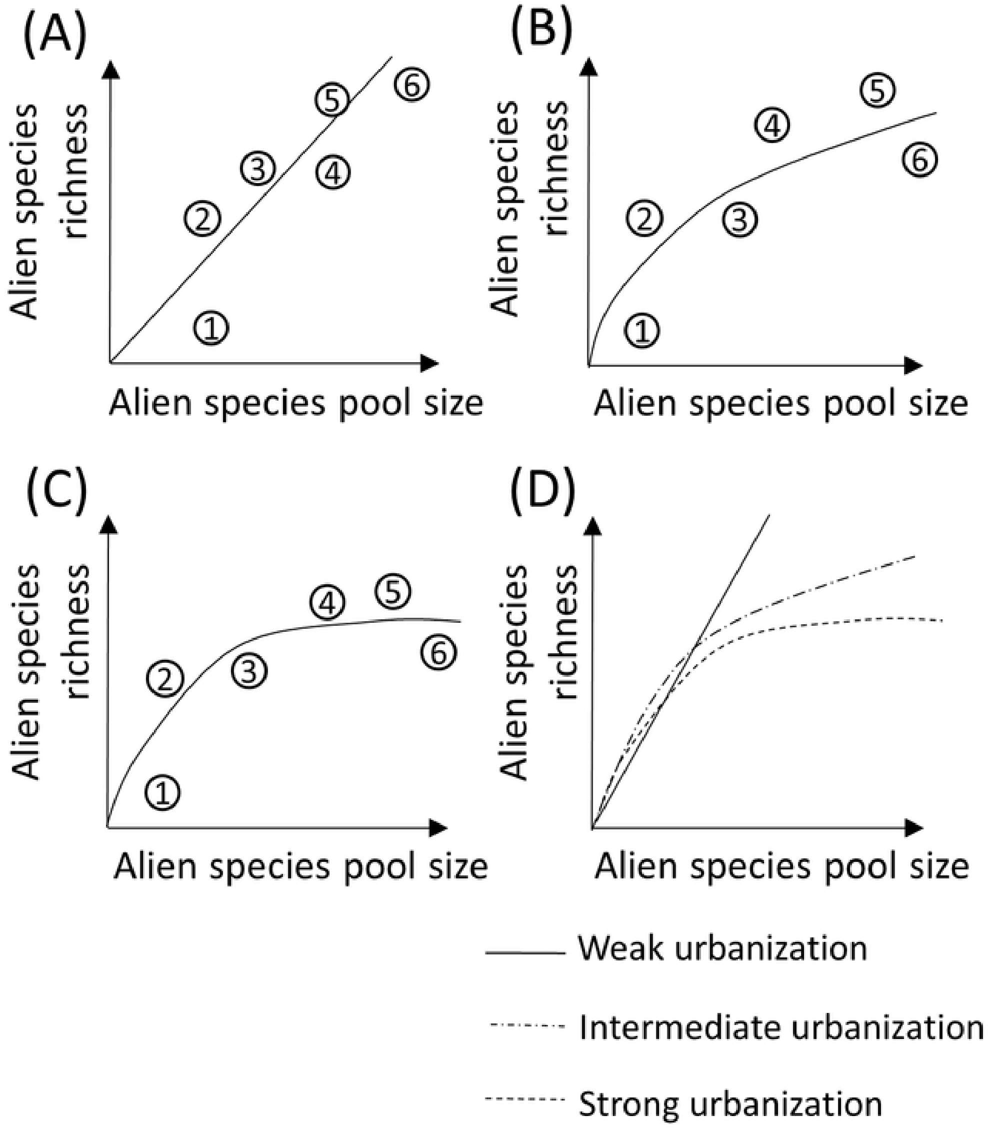

Figure 1. Illustrating (A) linear, (B) decelerating and (C) asymptotic forms of the alien species richness – alien species pool relationship, and (D) how they are expected to change as urbanization increases. Numbered data points represent sites with hypothetical alien species richness and alien species pool size. The slope of the relationship indicates average probability of establishment and a linear relationship has a constant slope, therefore species introduced into sites with varying alien species pool size should have the same probability of establishment. The slope of a decelerating or asymptotic relationship decreases gradually to zero as alien species pool size increases, indicating that introductions occurring in sites at the linear phase (e.g. site 1) would have a higher probability resulting in successful establishment compared to those occurring at the asymptotic phase (e.g. site 6).

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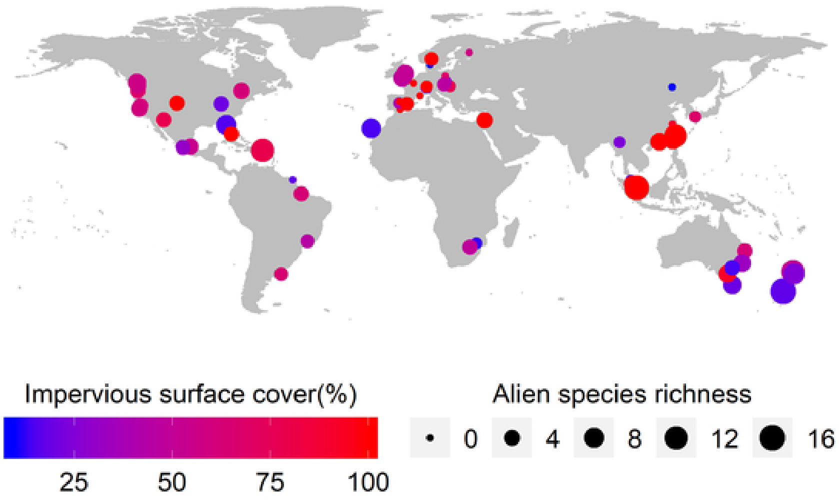

Figure 2. The distribution of study sites (n=61), as well as their observed alien species richness and impervious surface cover.

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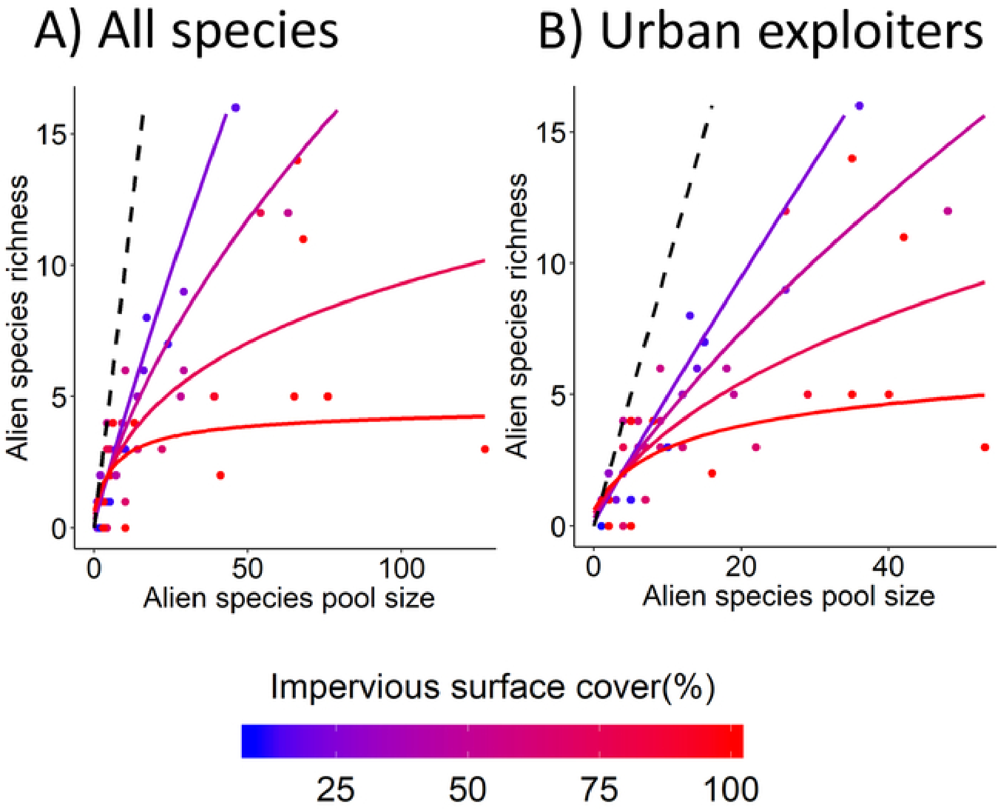

Figure 3. The predicted alien species richness - alien species pool relationship at different impervious surface cover values (25%, 50%, 75% and 100%) based on fixed-effects only. The size of the alien species pool was quantified as (A) the number of introduced species and (B) introduced urban exploiters only. The dashed line is the expected relationship when all species in the species pool can establish (i.e. alien species richness = alien species pool size). The color of lines and points follows the impervious surface cover gradient as indicated in the legend. Here, the predictions are based on the results of linear mixed models with log-ratio transformed alien species richness as the response variable. Analyses were done with log-transformed, centered and scaled predictors, but were back-transformed for ease of interpretation here.

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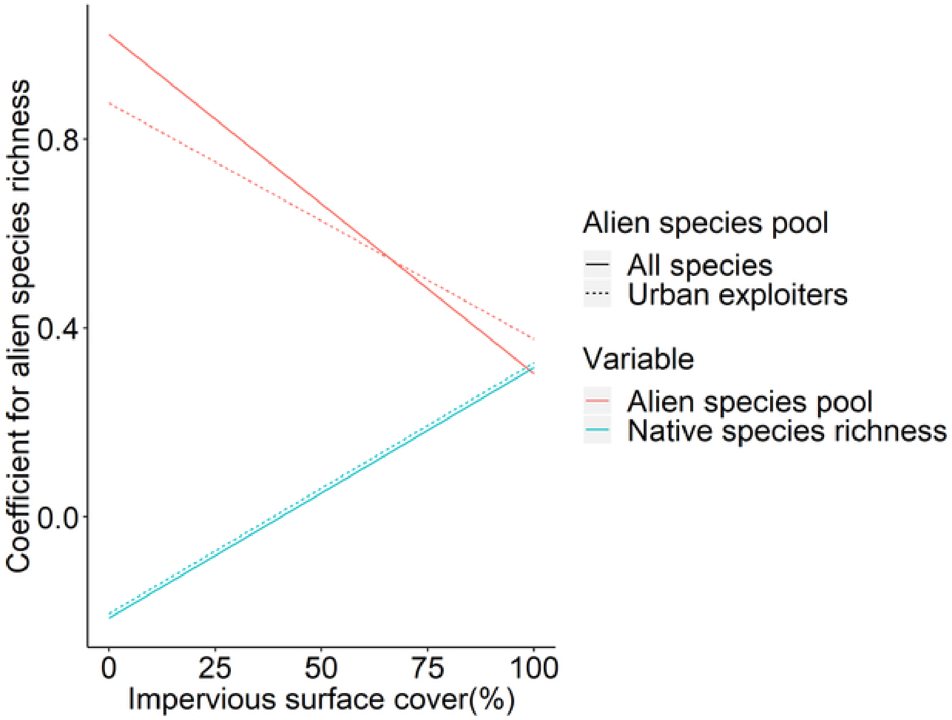

Figure 4. The coefficient of native species richness and log-transformed alien species pool size at different impervious surface cover values. Coefficient estimates were based on the model with the smallest AICc. Linear mixed modeling was conducted with centered and scaled predictors, but the impervious surface cover values here were back-transformed for ease of interpretation.

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Alien species richness is currently unbounded in all but the most urbanized bird communities

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Abstract

Keywords: alien species richness, community saturation, habitat filtering, invasion ecology, species pool, urban ecology

(Abstract)

Urban areas suffer high pressure of introductions of alien species compared to other habitats due to intensive human activities. As trading globally continues to rise, more species will likely be introduced into urban areas. To determine whether this increase in introduction pressure will lead to increased alien species richness in urban areas, or whether other processes would act to impose an upper limit on species richness, we examined how the shape of the relationship between alien species richness and the number of introduced species over time (i.e. introduction pressure) varies along gradients of urbanization. We collected species composition data from urban bird surveys worldwide and used a global database of alien bird introductions to quantify how many species have been introduced over time at different sites. We found that urbanization gradually modified the shape of the studied relationship from linear to asymptotic. Only communities in extremely urbanized environments were associated with an asymptotic relationship, suggesting that alien bird richness has likely not reached its ecological limit in most urban areas. Our results show that urbanization can reduce the importance of introduction pressure in determining alien species richness. Additionally, the results predict that alien species richness will increase at finer spatial scales, especially if the introduced species can survive in urban areas outside of their native range.

Introduction

Due to increasing imports of commodities from both historical and new regions, more alien species are predicted to emerge at the global scale, resulting in larger potential source pools of alien species (Seebens et al. 2018). Whether this will increase alien species richness at smaller spatial scales is unclear, since local processes (e.g. competition, habitat filtering) can reduce the effect of species pool size (defined as the number of species available to colonize a community) by limiting species richness inside communities (Cornell and Harrison 2014). To assess the importance of species pool size in structuring communities and whether local richness is unbounded, one typical approach is to assess whether an asymptotic response occurs when local species richness is correlated with species pool size (Olivares et al. 2018). Studies often define species pool sizes at larger spatial scales (e.g. regional species richness) (Cornell and Harrison 2014), yet this approach does not work well for alien species because they can overcome long-distance geographical barriers through human transportation. A better approach would be to use historical introduction records and quantify alien species pool size as the number of introduced species over time at each site. This includes all introduced species irrespective of successful or failed establishments, and all introduction pathways (e.g. spread, escaped, released), since alien species richness is the product of a multi-stage process involving transportation, introduction, establishment and spread (Blackburn et al. 2011)

Like local–regional species richness relationships (Cornell and Harrison 2014), various processes can differentially shape the relationship between alien species richness and alien species pool size, thus assessing its final form can be an indirect, pattern-based approach to understand whether alien species richness is bounded by local processes in communities (Figure 1). A decelerating or asymptotic relationship is characterized by an increasing proportion of species unable to colonize the community as species pool size increases, which can be explained by ecological processes such as harsh biotic or abiotic conditions (habitat filtering) or reduced niche availability (niche limitation) (Srivastava 1999). If these processes do not limit species richness inside communities, species pool size should exhibit the highest importance in determining local species richness and therefore the relationship should be linear. As the slope of any given alien species richness–alien species pool size relationship indicates the average probability of establishment per introduced species (Lonsdale 1999), the form of the relationship can be used to assess whether alien species richness in communities will increase in the future. For example, an asymptotic relationship indicates that sites located at the linear phase have an “unbounded” alien species richness, while those at the asymptotic phase have an alien species richness “capped” by other processes (Figure 1) (Olivares et al. 2018).

Studies analyzing local–regional species richness relationships have revealed that linear, asymptotic and decelerating functions are equally abundant, indicating that both regional and local processes are important in determining local species richness (Szava-Kovats et al. 2013). However, when analyzing native and alien species separately, alien species tend to exhibit a stronger decelerating trend in local–regional species richness relationships compared to native species, suggesting they are more strongly governed by species pool size (Angermeier and Winston 1998). Also, the relative importance of species pool size and local processes can vary between habitats given different abiotic and biotic stresses. For example, Huston (1999) showed that species pool effects exert the strongest control on local plant species richness at sites with intermediate productivity, while at sites with low and high productivity local processes are more important due to enhanced habitat filtering and niche limitation respectively.

Understanding what determines alien species richness in urban communities is crucial, since urban areas can act as propagule sources for alien species to invade adjacent natural habitats (McLean et al. 2017). Once established, alien species that are active dispersers can spread to nearby natural habitats if they find the environment preferable (Abellán et al. 2017), while the spread of passive dispersers can be facilitated by human transportation (Von der Lipper and Kowarik 2008) or dispersal corridors such as rivers (Sämuel and Kowarik 2010). Urban areas are expected to increase by 1.2 million km^2 by 2030 (tripling the urban area present in 2000), with most increases projected to take place in biodiversity hotspots (Seto et al. 2012). Typically, urban areas have higher alien species richness compared to other habitats due to a combination of highly-altered abiotic environments (e.g. nutrient dynamics), biotic conditions (e.g. lack of natural enemies) and increased introduction effort (Cadotte et al. 2017). Urbanization has been shown to act as a strong ecological filter for organisms (Sol et al. 2014), thus the relative importance of local processes in determining species richness should increase, causing an increasingly decelerated/asymptotic alien species richness–alien species pool size relationship along urbanization gradients, although local processes are not necessarily strong in structuring communities even in extremely urbanized sites (e.g. in Hong Kong, Tsang and Bonebrake 2017).

Birds represent an excellent opportunity to study the alien species richness–alien species pool size relationship between habitats because historical introduction records are of high quality (Dyer et al. 2017b) and thus alien species pool size at different sites can be quantified reliably (Blackburn et al. 2008). At the global level, the main driver of bird introductions has gradually changed from purposeful introductions by Acclimatization Societies to unplanned introductions (or releases) as a result of the cage bird trade, and the number of introductions tripled in the late 20th century compared to the mid and late 19th century (Dyer et al. 2017a). Compared to other variables (e.g. native species richness, mean annual temperature), colonization pressure (the number of released and escaped species, *sensu* Lockwood et al. 2009) has been shown to exert one of the strongest impacts in governing alien bird richness of communities across Europe (Chiron et al. 2009) and globally (Dyer et al. 2017a). However, the same pattern has not been found in Australia, where bird introductions have primarily occurred in highly-urbanized sites (McKinney and Kark 2017). Despite large alien species pool sizes, the strong filtering effect mediated by urbanization on birds (Sol et al. 2014) might limit alien species richness in urban bird communities, since the lack of suitable environmental conditions can decrease establishment success of introduced species (Duncan et al. 2003).

Our study aims to assess whether urbanization promotes habitat filtering in bounding alien species richness. We collected data from urban bird surveys worldwide and gathered information about the introduction history at different sites using a global database of alien bird introductions. Due to enhanced habitat filtering, we predict that the alien species richness–alien species pool size relationship will become increasingly decelerated or even asymptotic as urbanization intensifies. Additionally, once species that do not have the ability to survive in urban areas are excluded from alien species pool, we expect that more communities will exhibit a linear alien species richness–alien species pool size relationship. As the form of the relationship between species richness and species pool size may fail to reflect the relative importance of local and regional processes (e.g. Hilderbrand 2005), we also quantify the relative importance of alien species pool size and other environmental variables (Table 1) in determining alien species richness.

Methods

Bird survey data

To maximize the number of studies included, we adopted a structured (but not systematic) approach in finding relevant urban bird studies. We used a variety of search terms such as ‘urban’, ‘birds’, ‘urbanization’, ‘urban-rural’, ‘urban parks’ and ‘gardens’ in searching for relevant bird studies on Google Scholar. The Chinese equivalent of ‘birds’ and ‘urban’ were also used as search terms on CNKI (www.cnki.net, a chinese literature database). We also examined references in previous studies (e.g. Aronson et al. 2014) to include as many studies as possible. As the initial search returned studies mostly from Europe and North America, we further included country or region names (e.g. Australia, Puerto Rico) to conduct additional searches to fill data gaps. Papers or theses were included only if the number of individuals of each species were reported. If density data were reported, we only included studies that gave sufficient details on the methodology to allow calculation of observed abundance (which is necessary for constructing rarefaction curves, see the “preliminary analyses” section). Studies reporting abundance in other forms, such as frequency of occurrence, were excluded. Furthermore, we only included studies that did not subset to a particular type of bird (e.g. Passeriformes / forest specialists / native birds). The literature search yielded 63 communities from 49 studies. These studies had different sampling designs (e.g. season, sample size, sampling grain), thus introducing additional variance and consequently inflating the probability of type-II errors. If studies reported species composition at multiple sites, we always used data from the most-urbanized sites. For example, if studies reported compositional data along an urbanization gradient (e.g. ‘urban’, ‘suburban’, ‘rural’), we always used the data from ‘urban’. If a categorical urbanization level was not assigned, we identified the most urbanized sites based on site descriptions (e.g. area of the park, whether the habitat is located in the city center). To avoid the ‘double zero problem’ (Legendre and Legendre 2012), two communities were excluded due to zero introduction records; thus we used 61 urban communities from 48 studies in total, covering all continents except Antarctica (Figure 2, Supplementary material Appendix 1).

Alien species richness

To quantify alien species richness, we used the Global Avian Invasions Atlas (GAVIA), which contained 27,723 records of alien birds in 230 countries or administrative areas at the time of accession (July, 2018) (Dyer et al. 2017b). The database is based on published studies (~700), as well as consultations with regional experts and organizations. Records in GAVIA describe the species and location of each introduction event, as well as the outcome and pathway of introduction. We used range maps of 719 alien bird species, which were generated based on records with sufficient detail (e.g. with specific location, such as sub-states, of introduction events) (Dyer et al. 2017a). We then overlaid these range maps with city coordinates (obtained via GoogleEarth) to obtain a list of introduced species for each site. These lists were subsequently compared to the species lists provided by each study, which in total contained 915 bird species, and allowed classification of alien birds in each site. We also checked for synonyms of each species using HBW and BirdLife Taxonomic Checklist v2 (BirdLife International 2017) to ensure that all alien birds were correctly identified.

Size of alien species pools

We obtained the alien species pool size of each city by overlaying each GAVIA range map with city coordinates. All introduction records were included irrespective of pathways and outcomes of introduction. We used two measures for subsequent analyses separately to investigate whether habitat filtering limits alien species richness. One measure included all introduction records regardless of the environmental tolerance of the species, while the other measure only included introduced species that are known to establish in urban areas (i.e. urban exploiters). Species persistence in urban areas was determined by whether they were listed as using the habitat coded as ‘Artificial/Terrestrial - Urban Areas’ in the IUCN database (IUCN 2018), or whether they were recorded in studies included in our database.

Abiotic and biotic variables

The definition of ‘urban’ varied across studies, thus we quantified urbanization extent at each site using ‘Global Impervious Surface Area’ (Elvidge et al. 2007). The database has been demonstrated to have high accuracy and spatial resolution (1 km^2 grids), and provides a continuous measure of the extent of urbanization (rather than binary classifying grids as urban or non-urban areas) (Potere et al. 2009). As the exact location of bird surveys were generally not noted, we drew a 15 km radius circle at each site. The circle was large enough to include each city, although it could also include suburban, rural or natural habitats as well, resulting in underestimations of the urbanization extent when averaging impervious surface cover across 1 km^2 grids. Given that we always used the compositional data at the most urbanized sites for each study, we averaged the top-25 grids with the highest impervious surface cover rather than averaging across all grids in each city.

For other abiotic variables, we identified geographic coordinates of the 25 grids with the highest impervious surface cover in each city and obtained their mean annual temperature and annual precipitation from the BIOCLIM v2.0 database, available from WorldClim (<www.worldclim.org>) at a spatial resolution of 30 arc-seconds (~1 km^2) (Fick and Hijmans 2017). These values, as well as the impervious surface cover, were then averaged across grids at each city for subsequent analysis. We also quantified native species richness as the number of native species observed during the survey. Data on abiotic variables, as well as alien species pool size, were collected using the R- package *raster* (Hijmans et al. 2017).

Preliminary analyses

Rarefaction analyses showed that the sample coverage (the completeness of sampling, *sensu* Chao and Jost 2012) of species richness at all sites ranged between 0.97-1.00 (Supplementary material Appendix 2), indicating that all communities were well-sampled and justified the use of observed alien and native species richness in subsequent analyses. To minimize the effect of arbitrarily defining the number of grids, we quantified the average impervious surface cover from the top-50 and top-100 grids, and the associated average of annual precipitation and mean annual temperature. We detected high correlations between averages quantified based on different numbers of grids (Pearson correlation, $R \geq 0.97$), thus we only used the values obtained from averaging across the top-25 grids in subsequent analyses. We also checked for collinearity between independent variables (see below) via Pearson correlations. All independent variables showed low collinearity between one another (max $R = 0.44$), hence all variables were retained in subsequent analyses. Rarefaction analyses were conducted using R- package *iNEXT* (Hsieh et al. 2016)

Form of the alien species richness–alien species pool size relationship

We analyzed how urbanization modified the relationship following Szava-Kovats et al. (2012), which has improved performance in detecting decelerating or asymptotic functions. We applied an additive log ratio transformation to alien species richness:

$$\ln \frac{Alien\ species\ richness_A + 1}{Alien\ species\ pool\ size_A - Alien\ species\ richness_A + 1}$$

where subscript *A* denotes the value of the variable at site A. The numerator and denominator are increased by one to allow zero alien species richness in communities (Helm et al. 2015). The log-ratio transformation is effective in removing the mathematic constraints that alien species richness must be smaller or equal to alien species pool size and both must be positive, which makes regression analyses operate in a wedge-shaped space, in which any pair of random variables would result in positive correlations (Szava-Kovats et al. 2012). As predictors, we included log-transformed alien species pool size [ln(alien species pool size +1)], impervious surface cover and the second-order interaction term between them. Linear predictors were centered and rescaled to minimize collinearity between linear predictors and their associated interaction, as well as allowing comparisons of the relative importance between predictors based on magnitude of coefficients (Schielzeth 2010). We conducted linear mixed modeling, with biogeographical realm (Olson et al. 2001) added as a random intercept to account for spatial autocorrelation between observations that share similar histories of introduction or other human activities, or current environmental conditions, which can all affect current alien species richness (Dyer et al. 2017a). Some studies provided data for multiple sites, and in one case in different biogeographical realms, thus we included the identity of study as another random intercept without nesting within biogeographical realms to control for unknown methodological effects. We fit linear mixed models with restricted maximum likelihood to produce less biased estimates of standard deviations compared to maximum likelihood (Bolker et al. 2009). Model performance was evaluated with both AICc and R^2 as defined in Nakagawa and Schielzeth (2013). To ensure spatial autocorrelation did not affect the results, we computed Moran's I for the residuals of the model with smallest AICc at 12 distance classes (as determined by Sturges rule) and computed Holm's corrected p-values (Legendre and Legendre 2012). Additionally, we performed the Johnson-Neyman procedure, which calculated the slope of log-transformed alien species pool size and its 95% confidence interval (95% CI) under different impervious surface cover. We also controlled for the false discovery rate using procedures described in Esarey and Sumner (2015). We used the slope of log-transformed alien species pool size to identify the conditions under which the alien species richness–alien species pool size relationship exhibited an asymptotic response. Following Szava-Kovats et al. (2013), an asymptotic relationship was declared if the slope of log-transformed alien species pool size overlapped with -1 but not 0, while those overlapping with 0 but not -1 were classified as linear relationships. If the 95% CI lay entirely within 0 and -1, the relationship was classified as decelerating but not asymptotic.

Relative importance of determinants of alien species richness

To examine how urbanization affects the relative importance of alien species pool size and other environmental variables (Table 1) in shaping alien species richness, we included them and their second order interactions with impervious surface cover as predictors. As the previous analysis revealed that alien species richness–alien species pool size relationships changed from linear to asymptotic as urbanization increases, we log-transformed alien species richness and alien species pool size (Szava-Kovats et al. 2013). The second order interaction term between log-transformed alien species pool size and impervious surface cover allowed the shape of the alien species richness–alien species pool size relationship to vary according to impervious surface cover when analyzed using linear models. We additionally log-transformed annual precipitation to reduce its right-skewness, while other variables were untransformed. As with the above analysis, we rescaled and centered all predictors such that their relative importance could be compared (Schielzeth 2010), and used biogeographical realm and identity of study as random intercepts. Linear mixed models were fitted by maximum likelihood instead of restricted maximum likelihood to allow model comparison (Bolker et al. 2009). We first fit a full model to assess the significance of each linear and interaction term. When examining the subset of best models (ΔAICc ≤ 2), only one model remained after removing models containing uninformative parameters (Arnold 2010). Thus, no model averaging was performed, and we simply constructed additional linear mixed models to evaluate model performance and significance of the retained predictors. Using the model with the smallest AICc and Chi-squared tests, we assessed whether model performance significantly improved after inclusion of interaction terms. We also checked spatial autocorrelations using Moran's I and Holm's corrected p-value.

Linear mixed modelling was conducted with the R- package 'lme4' (Bates et al. 2017), while model selection and spatial autocorrelation checking was conducted using packages 'MuMIn' (Bartoń 2015) and 'pgrimess' (Giraudoux 2017). The Johnson-Neyman procedure was conducted using the package 'jtools' (Long 2018).

Data deposition

Data and R scripts are available from the Dryad Digital Repository: <https://doi.org/10.5061/dryad.XXXXX> (Tsang et al. 2019).

Results

In total, we recorded 915 bird species, of which 76 have been recorded as "alien" in at least one site, and 342 species have been introduced into at least one site. The most widespread birds were *Columba livia* and *Passer domesticus*, which occurred as native or alien species in more than 75% of the sites. These species were also introduced into more than half of the sites, and $\geq$ 77% of their introductions led to successful establishment in urban areas. The number of introduced bird species, regardless of whether they can persist in urban environments, ranged from 1 (6 sites) to 127 (Miami, FL, USA) and had a median of 7 species, yet alien species richness only ranged from 0 (12 sites) to 16 (Dunedin, New Zealand) and had a median of 3 species. Urban exploiters made up 39.02% (Valencia, Spain) – 100% (24 sites) and on average 80.84 ± 19.21% (mean ± SD) of all introduced bird species at each site. The urbanization extent varied between sites, with impervious surface cover averaging 57.37 ± 32.01% (mean ± SD) and ranging from 9.42 (Brønderslev, Denmark) – 100%. Impervious surface cover at 10 sites, such as Hong Kong, Paris (France) and Miami (FL, USA), reached 100%, while 25 sites (e.g. Hamilton (New Zealand), Tenerife (Spain)) had < 50% impervious surface cover.

Regardless of the definitions of alien species pool size, all analyses showed an increasingly decelerated relationship between alien species richness and alien species pool size as impervious surface cover increases (Figure 3). The main effect of log-transformed alien species pool size and its interaction with impervious surface cover were always negative and significant ($p < 0.001$, see Supplementary material Appendix 3 for full results). No significant spatial autocorrelation was detected (Max. Moran's I = 0.13). The Johnson-Neyman procedure revealed the alien species richness–alien species pool size relationships ranged from linear to asymptotic. When all species were included, the alien species richness–

alien species pool size relationship changed from linear to decelerating when impervious surface cover reached 29% and started reaching an asymptote when impervious surface cover equaled 75%. Excluding introduction records with species that do not typically establish in urban areas led to more urban communities exhibiting a linear response (Impervious surface cover $\leq$ 41%), but fewer showing an asymptotic response (Impervious surface cover $\geq$ 87%).

For the analysis on log-transformed alien species richness, we detected positive main effects of native species richness and log-transformed alien species pool size in all models (Table 2). Both full models revealed a significant negative interaction between log-transformed alien species pool size and impervious surface cover, as well as a significant positive interaction between impervious surface cover and native species richness. The coefficient of log-transformation alien species pool size was always larger than native species richness along the urbanization gradient, but this difference declined as impervious surface cover increased (Table 2, Figure 4). The best models were formed by these significant interaction predictors and their associated linear predictors only. Chi-squared tests revealed that including interaction terms between all linear predictors significantly improved model performance ($p < 0.001$), with AICc dropping by 13.13 – 23.56 and R^2 increasing by 8 – 15% (Supplementary material Appendix 4). No significant spatial autocorrelation was detected (Max. Moran's $I = 0.07$).

Discussion

Consistent with our predictions, we found an increasingly decelerated alien species richness–alien species pool size relationship for birds as urbanization intensifies (Figure 3A), highlighting that alien species richness has yet to reach a limit in less-urbanized sites. The relationship was asymptotic for highly-urbanized sites, and the mechanism limiting alien species richness is likely to be habitat filtering, since the relationship became more linear (i.e. increased probability of establishment) when alien species pool only included urban exploiters (Figure 3B). The importance of habitat filtering in limiting alien species richness is further supported by analyses showing an increasingly positive correlation between native and alien species richness as impervious surface cover increased (Table 2, Figure 4), which supports the biotic acceptance hypothesis and implies that favorable habitat conditions increase both alien and native species richness (Stohlgren et al. 2006). Overall, our results indicate that few urban areas (if any) are invulnerable to further bird introductions, especially when species that can bypass habitat filters are introduced.

Habitat suitability is the primary determinant of establishment success for introduced birds once the founding population size exceeds 50 – 100 individuals (Duncan et al. 2014). Urban areas have many unique characteristics, such as the presence of novel resources (e.g. anthropogenic foods) and predators (e.g. domestic cats), and species must overcome these challenges to persist in such environments (Shochat et al. 2006). In particular, urban exploiters are often generalist species (e.g. Kark et al. 2007, Evans et al. 2011, Sol et al. 2014), which are better at exploiting novel foods (Overington et al. 2011, Ducatez et al. 2015). Regardless of the mechanisms, urban exploiters, on average, constitute 80% of alien species pool size at each site, indicating that the filtering effect caused by urbanization is weak for introduced birds. This also explains why model performance only increased by 8 – 15% when interactions between impervious surface cover and other predictors were included. As bird introductions are biased by urban exploiters, other gradients, such as elevation and productivity, may have more pronounced impacts in modifying the importance of the filtering effect compared to the urbanization gradient.

An increasingly decelerated relationship between alien species richness and alien species pool size along the urbanization gradient persisted after removing species unable to survive in urban areas (Figure 3B). This is unlikely to be explained by niche limitation (Cornell and Harrison 2014), as we detected an increasingly positive correlation between native and alien species richness (Table 2, Figure 4). If niche limitation is the primary explanation, native and alien species richness should be negatively correlated, since increased natives should further limit niche space available to introduced species, leading to lower establishment success via enhanced competition (Elton 1958, Case 1990, Shea and Chesson 2002). The lack of support for niche limitation can be explained by the large spatial scales (Byers and Noonburg 2003) and a lack of communities from natural habitats (Bertness and Callaway 1994) in this study. We suggest that the increasingly decelerated relationship could still be caused by habitat filtering. We classified species that can persist in any urban habitat as “urban exploiters”, yet our study covers a large urbanization gradient (impervious surface cover ranged from 9.42 – 100%) and increasing urbanization is known to reduce urban bird diversity (Aronson et al. 2014). Therefore, a greater proportion of “urban exploiters” might be filtered from highly-urbanized sites, which promotes an increasingly decelerated relationship along urbanization gradients (Srivastava 1999).

Alien species richness–alien species pool size relationships are broadly and likely to be affected by propagule pressure (a composite measure of the number of individuals introduced), which is known to be an important predictor of establishment success (Cassey et al. 2018). When introductions occur repeatedly, propagule pressure accumulates over time and establishment success increases, therefore the current alien species richness–alien species pool size relationship might be more linear than relationships from the past. Indeed, Abellán et al. (2017) found that the time since the first introduction event increased establishment success of introduced birds, possibly explained by higher cumulative numbers of propagules. By this logic, sites with a longer introduction history may have accumulated more propagules, and hence exhibit a more linear alien species richness–alien species pool size relationship. However, variation in propagule pressure between sites are unlikely to explain our results, since highly-urbanized sites should have a longer introduction history, and hence higher propagule pressure compared to less-urbanized sites (Cadotte et al. 2017, McKinney and Kark 2017). Yet, we still detected an increasingly decelerating alien species richness–alien species pool size relationship with increasing urbanization.

The form of the alien species richness–alien species pool size relationship is based on historical introductions, and future introductions may enhance its linearity. First, as economic activities continue, propagule pressure will continue to accumulate and some species may eventually establish (Abellán et al. 2017), thus promoting a more linear alien species richness–alien species pool size relationship. Additionally, the sources of introduced birds have gradually changed from European colonies to the Indian subcontinent, Indochina and sub-Saharan Africa (Dyer et al. 2017a), which expand alien species pools and might prevent alien species richness from reaching an asymptote (Leibhold et al. 2017). Finally, regardless of the current shape, the slope of the alien species richness–alien species pool size relationship may become more positive should new invading species contain traits promoting coexistence (e.g. better dispersal ability, low niche overlap with residential species) (Cornell and Lawton 1992).

To limit the increase of alien species richness in urban bird communities, our results suggest that less-urbanized sites should be prioritized for monitoring, as they have yet to reach a limit in alien species richness. This includes areas at the periphery of cities, as well as less-urbanized habitats in city cores (e.g. remnants of natural habitats), since urban areas can be extremely heterogenous in terms of urbanization extent (Ramalho and Hobbs 2012) and these habitats might be refuges for alien birds that cannot tolerate highly-urbanized environments (McKinney and Kark 2017). Habitat filtering is strongest in highly-urbanized sites and limits their alien species richness, yet urban exploiters are likely to bypass the filter and successfully establish should future introductions occur. Some urban exploiters (e.g. Estrildidae & Columbidae species, Sol et al. 2017) have been involved in the cage bird trade (Su et al. 2014), which is the primary driver of modern bird introductions (Dyer et al. 2017a), and show high extent of spread after establishment (Dyer et al. 2016, Abellán et al. 2017). Therefore, the trade of urban exploiters should be prioritized for bans or regulations to prevent them establishing in urban areas, which may facilitate them invading adjacent less-urbanized habitats (McLean et al. 2017).

Whether species richness is limited or unlimited in communities remains an open question in ecology (Cornell and Harrison 2014). Here, we showed that habitat filtering is an important mechanism bounding alien species richness in highly-urbanized habitats. Once species that cannot exploit urban areas were excluded, more communities were associated with a non-asymptotic alien species richness–alien species pool size relationship, showing no sign of reaching an upper limit in alien species richness. This indicates that most urban bird communities are still far from reaching the upper limit (if any) of alien species richness, and they are especially susceptible to the introductions of urban exploiters. Similar to predictions at the global scale (Seebens et al. 2017), we predict that alien bird species richness in urban areas will continue to increase at smaller spatial scales due to increasing globalization and expanded alien species pool (Seebens et al. 2018).

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Supplementary material (Appendix ECOG-04412 at <www.ecography.org/appendix/ecog-04412>). Appendix 1–4.

Questions to authors:

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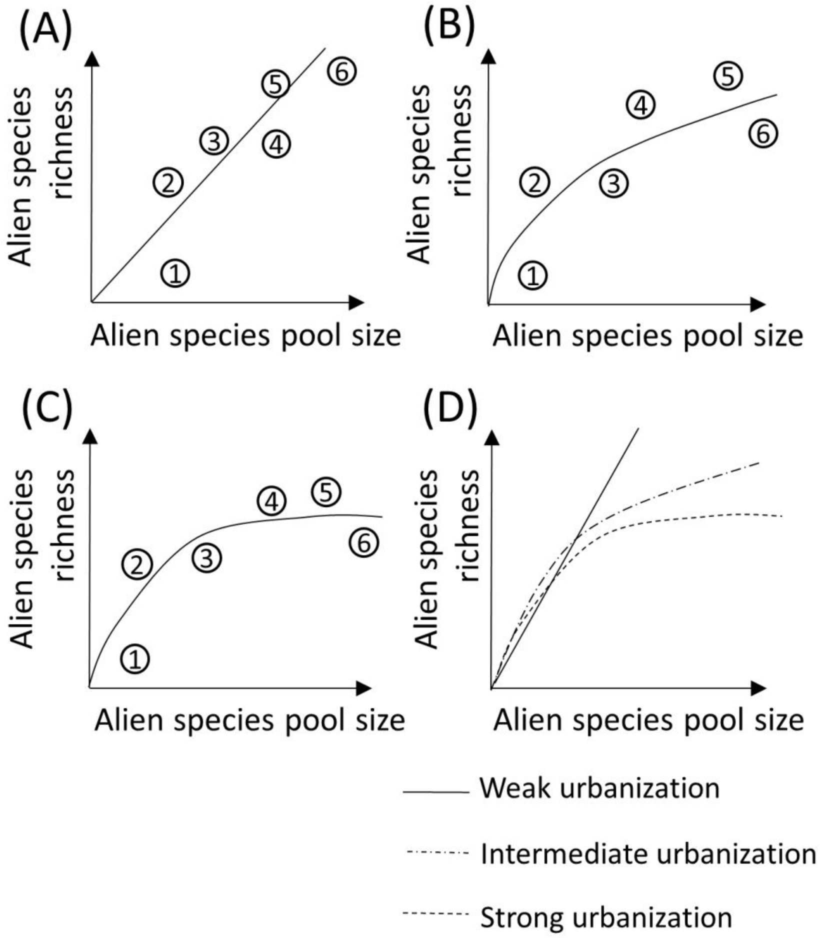

Figure 1. Illustrating (A) linear, (B) decelerating and (C) asymptotic forms of the alien species richness – alien species pool relationship, and (D) how they are expected to change as urbanization increases. Numbered data points represent sites with hypothetical alien species richness and alien species pool size. The slope of the relationship indicates average probability of establishment and a linear relationship has a constant slope, therefore species introduced into sites with varying alien species pool size should have the same probability of establishment. The slope of a decelerating or asymptotic relationship decreases gradually to zero as alien species pool size increases, indicating that introductions occurring in sites at the

linear phase (e.g. site 1) would have a higher probability resulting in successful establishment compared to those occurring at the asymptotic phase (e.g. site 6).

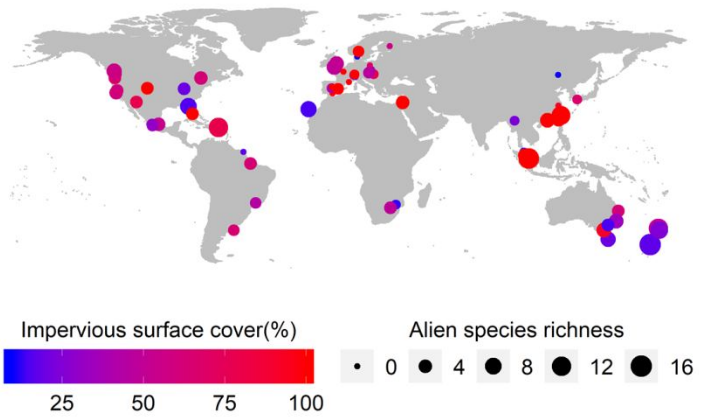

Figure 2. The distribution of study sites (n = 61), as well as their observed alien species richness and impervious surface cover.

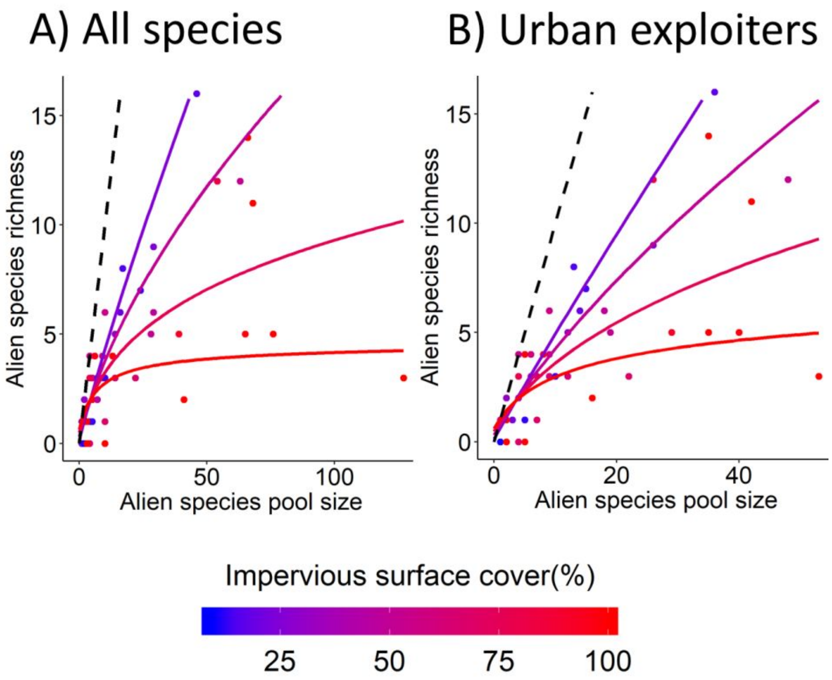

Figure 3. The predicted alien species richness - alien species pool relationship at different impervious surface cover values (25%, 50%, 75% and 100%) based on fixed-effects only. The size of the alien species pool was quantified as (A) the number of introduced species and (B) introduced urban exploiters only. The dashed line is the expected relationship when all species in the species pool can establish (i.e. alien species richness = alien species pool size). The color of lines and points follows the impervious surface cover gradient as indicated in the legend. Here, the predictions are based on the results of linear mixed models with log-ratio transformed alien species richness as the response variable. Analyses were done with log-transformed, centered and scaled predictors, but were back-transformed for ease of interpretation here.

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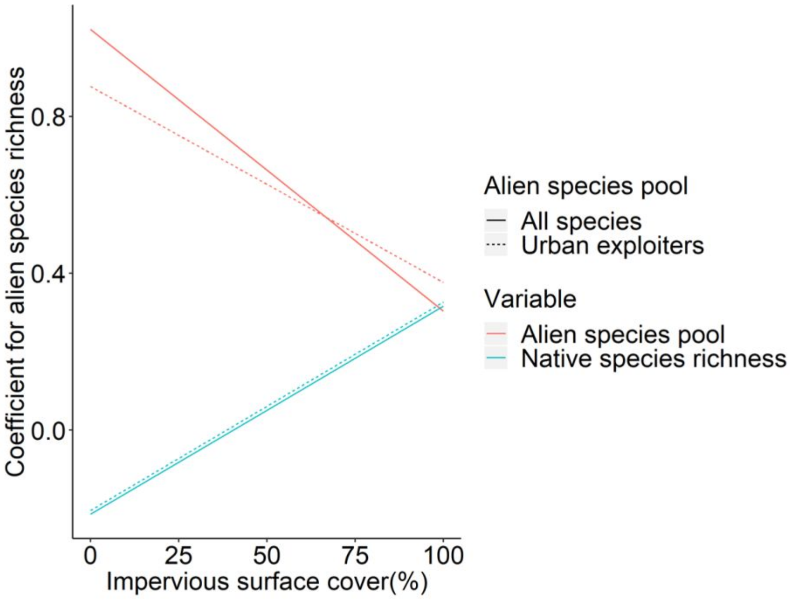
639 

640 Figure 4. The coefficient of native species richness and log-transformed alien species pool 641 size at different impervious surface cover values. Coefficient estimates were based on the 642 model with the smallest AICc. Linear mixed modeling was conducted with centered and 643 scaled predictors, but the impervious surface cover values here were back-transformed for 644 ease of interpretation.

645

Tables 1. Predicted effects of different variables on alien species richness. The magnitude of the effect is predicted to increase as impervious surface cover increases. '+' signs predict a positive effect by the variable on alien species richness, while '–' signs predict a negative effect.

Variables	Predicted effect	Rationale
Impervious surface cover	–	Few species contain adaptations for urban life (Sol et al. 2014).
Mean annual temperature	+	Increased temperature leads to increased alien bird species richness in Australia, possibly indicating more favorable conditions (McKinney and Kark 2017).
Annual precipitation	–	Increased precipitation leads to reduced alien bird species richness on oceanic islands, possibly indicating unfavorable conditions (Blackburn et al. 2016).
Native species richness	–	Increased species richness in a community enhances niche limitation (Elton 1958).
	+	Increased species richness indicates favorable environmental conditions for alien species (Stohlgren et al. 2006).

Table 2. Results of linear mixed models analyzing the determinants of log-transformed alien species richness, based on different definitions of alien species pool. The best model has the smallest AICc. R^2m and R^2c represents marginal and conditional R^2 respectively. Bold values indicate statistical significance ($p < 0.05$), while '–' indicates that the variable was not retained in the best model. All variables were centered and scaled. Variable names are abbreviated: alien species pool (ASP); impervious surface cover (ISC); mean annual temperature (MAT); annual precipitation (AP); native species richness (NSR).

	All species				Urban exploiters			
	Full model		Best model		Full model		Best model	
	Slope	p	Slope	p	Slope	p	Slope	p
Intercept	**1.34**	**< 0.001**	**1.36**	**< 0.001**	**1.28**	**< 0.001**	**1.31**	**< 0.001**
ln(ASP + 1)	**0.58**	**< 0.001**	**0.61**	**< 0.001**	**0.56**	**< 0.001**	**0.59**	**< 0.001**
ISC	**-0.12**	**0.01**	**-0.13**	**0.006**	-0.10	0.05	**-0.10**	**0.04**
MAT	0.03	0.66	–	–	0.07	0.23	–	–
ln(AP)	0.02	0.70	–	–	0.03	0.66	–	–
NSR	0.09	0.06	**0.09**	**0.04**	0.09	0.06	**0.10**	**0.03**
ln(ASP + 1) × ISC	**-0.23**	**< 0.001**	**-0.23**	**< 0.001**	**-0.16**	**0.003**	**-0.16**	**0.001**
MAT × ISC	0.001	0.98	–	–	-0.01	0.87	–	–
In(AP) × ISC	0.04	0.39	–	–	0.06	0.27	–	–

NSR × ISC	**0.17**	**0.002**	**0.17**	**0.001**	**0.18**	**0.002**	**0.17**	**0.002**
	R^2m	R^2c	R^2m	R^2c	R^2m	R^2c	R^2m	R^2c
	0.72	0.83	0.70	0.83	0.74	0.80	0.71	0.80

ECOGRAPHY

Research

Alien species richness is currently unbounded in all but the most urbanized bird communities

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Urban areas suffer high pressure of introductions of alien species compared to other habitats due to intensive human activities. As trading globally continues to rise, more species will likely be introduced into urban areas. To determine whether this increase in introduction pressure will lead to increased alien species richness in urban areas, or whether other processes would act to impose an upper limit on species richness, we examined how the shape of the relationship between alien species richness and the number of introduced species over time (i.e. introduction pressure) varies along gradients of urbanization. We collected species composition data from urban bird surveys worldwide and used a global database of alien bird introductions to quantify how many species have been introduced over time at different sites. We found that urbanization gradually modified the shape of the studied relationship from linear to asymptotic. Only communities in extremely urbanized environments were associated with an asymptotic relationship, suggesting that alien bird richness has likely not reached its ecological limit in most urban areas. Our results show that urbanization can reduce the importance of introduction pressure in determining alien species richness. Additionally, the results predict that alien species richness will increase at finer spatial scales, especially if the introduced species can survive in urban areas outside of their native range.

Keywords: alien species richness, community saturation, habitat filtering, invasion ecology, species pool, urban ecology

Introduction

Due to increasing imports of commodities from both historical and new regions, more alien species are predicted to emerge at the global scale, resulting in larger potential source pools of alien species (Seebens et al. 2018). Whether this will increase alien species richness at smaller spatial scales is unclear, since local processes (e.g. competition, habitat filtering) can reduce the effect of species pool size (defined as the number of species available to colonize a community) by limiting species richness inside communities (Cornell and Harrison 2014). To assess the importance of species pool size in structuring communities and whether local richness is unbounded, one typical

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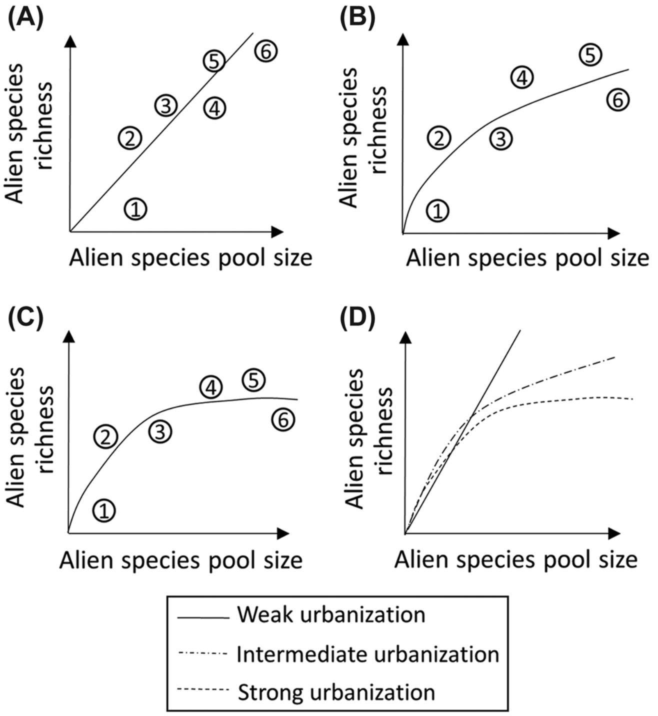
approach is to assess whether an asymptotic response occurs when local species richness is correlated with species pool size (Olivares et al. 2018). Studies often define species pool sizes at larger spatial scales (e.g. regional species richness) (Cornell and Harrison 2014), yet this approach does not work well for alien species because they can overcome long-distance geographical barriers through human transportation. A better approach would be to use historical introduction records and quantify alien species pool size as the number of introduced species over time at each site. This includes all introduced species irrespective of successful or failed establishments, and all introduction pathways (e.g. spread, escaped, released), since alien species richness is the product of a multi-stage process involving transportation, introduction, establishment and spread (Blackburn et al. 2011).

Like local–regional species richness relationships (Cornell and Harrison 2014), various processes can differentially shape the relationship between alien species richness and alien species pool size, thus assessing its final form can be an indirect, pattern-based approach to understand whether alien species richness is bounded by local processes in communities (Fig. 1). A decelerating or asymptotic relationship is characterized by an increasing proportion of species unable to colonize the community as species pool size increases, which can be explained by ecological processes such as harsh biotic or abiotic conditions (habitat filtering) or reduced niche availability (niche limitation) (Srivastava 1999). If these processes do not limit species richness inside communities, species pool size should exhibit the highest importance in determining local species richness and therefore the relationship should be linear. As the slope of any given alien species richness–alien species pool size relationship indicates the average probability of establishment per introduced species (Lonsdale 1999), the form of the relationship can be used to assess whether alien species richness in communities will increase in the future. For example, an asymptotic relationship indicates that sites located at the linear phase have an 'unbounded' alien species richness, while those at the asymptotic phase have an alien species richness 'capped' by other processes (Fig. 1) (Olivares et al. 2018).

Studies analyzing local–regional species richness relationships have revealed that linear, asymptotic and decelerating functions are equally abundant, indicating that both regional and local processes are important in determining local species richness (Szava-Kovats et al. 2013). However, when analyzing native and alien species separately, alien species tend to exhibit a stronger decelerating trend in local–regional species richness relationships compared to native species, suggesting they are more strongly governed by species pool size (Angermeier and Winston 1998). Also, the relative importance of species pool size and local processes can vary between habitats given different abiotic and biotic stresses. For example, Huston (1999) showed that species pool effects exert the strongest control on local plant species richness at sites with intermediate productivity, while at sites with low and high productivity local processes are more important due to enhanced habitat filtering and niche limitation respectively.



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Understanding what determines alien species richness in urban communities is crucial, since urban areas can act as propagule sources for alien species to invade adjacent natural habitats (McLean et al. 2017). Once established, alien species that are active dispersers can spread to nearby natural habitats if they find the environment preferable (Abellán et al. 2017), while the spread of passive dispersers can be facilitated by human transportation (Von der Lippe and Kowarik 2008) or dispersal corridors such as rivers (Säumel and Kowarik 2010). Urban areas are expected to increase by 1.2 million km^2 by 2030 (tripling the urban area present in 2000), with most increases projected to take place in biodiversity hotspots (Seto et al. 2012). Typically, urban areas have higher alien species richness compared to other habitats due to a combination of highly-altered abiotic environments (e.g. nutrient dynamics), biotic conditions (e.g. lack of natural enemies) and increased introduction effort (Cadotte et al.

2017). Urbanization has been shown to act as a strong ecological filter for organisms (Sol et al. 2014), thus the relative importance of local processes in determining species richness should increase, causing an increasingly decelerated/asymptotic alien species richness–alien species pool size relationship along urbanization gradients, although local processes are not necessarily strong in structuring communities even in extremely urbanized sites (e.g. in Hong Kong, Tsang and Bonebrake 2017).

Birds represent an excellent opportunity to study the alien species richness–alien species pool size relationship between habitats because historical introduction records are of high quality (Dyer et al. 2017b) and thus alien species pool size at different sites can be quantified reliably (Blackburn et al. 2008). At the global level, the main driver of bird introductions has gradually changed from purposeful introductions by Acclimatization Societies to unplanned introductions (or releases) as a result of the cage bird trade, and the number of introductions tripled in the late 20th century compared to the mid and late 19th century (Dyer et al. 2017a). Compared to other variables (e.g. native species richness, mean annual temperature), colonization pressure (the number of released and escaped species, sensu Lockwood et al. 2009) has been shown to exert one of the strongest impacts in governing alien bird richness of communities across Europe (Chiron et al. 2009) and globally (Dyer et al. 2017a). However, the same pattern has not been found in Australia, where bird introductions have primarily occurred in highly-urbanized sites (McKinney and Kark 2017). Despite large alien species pool sizes, the strong filtering effect mediated by urbanization on birds (Sol et al. 2014) might limit alien species richness in urban bird communities, since the lack of suitable environmental conditions can decrease establishment success of introduced species (Duncan et al. 2003).

Our study aims to assess whether urbanization promotes habitat filtering in bounding alien species richness. We collected data from urban bird surveys worldwide and gathered information about the introduction history at different sites using a global database of alien bird introductions. Due to enhanced habitat filtering, we predict that the alien species richness–alien species pool size relationship will become increasingly decelerated or even asymptotic as urbanization intensifies. Additionally, once species that do not have the ability to survive in urban areas are excluded from alien species pool, we expect that more communities will exhibit a linear alien species richness–alien species pool size relationship. As the form of the relationship between species richness and species pool size may fail to reflect the relative importance of local and regional processes (Hillebrand 2005), we also quantify the relative importance of alien species pool size and other environmental variables (Table 1) in determining alien species richness.

Methods

Bird survey data

To maximize the number of studies included, we adopted a structured (but not systematic) approach in finding relevant urban bird studies. We used a variety of search terms such as ‘urban’, ‘birds’, ‘urbanization’, ‘urban-rural’, ‘urban parks’ and ‘gardens’ in searching for relevant bird studies on Google Scholar. The Chinese equivalent of ‘birds’ and ‘urban’ were also used as search terms on CNKI (<www.cnki.net>, a chinese literature database). We also examined references in previous studies (Aronson et al. 2014) to include as many studies as possible. As the initial search returned studies mostly from Europe and North America, we further included country or region names (e.g. Australia, Puerto Rico) to conduct additional searches to fill data gaps. Papers or theses were included only if the number of individuals of each species were reported. If density data were reported, we only included studies that gave sufficient details on the methodology to allow calculation of observed abundance (which is necessary for constructing rarefaction curves, see the ‘preliminary analyses’ section). Studies reporting abundance in other forms, such as frequency of occurrence, were excluded. Furthermore, we only included studies that did not subset to a particular type of bird (e.g. passeriformes/forest specialists/native birds). The literature search yielded 63 communities from 49 studies. These studies had different sampling designs (e.g. season, sample size, sampling grain), thus introducing additional variance and consequently inflating the probability of type-II errors. If studies reported species composition at multiple sites, we always used data from the most-urbanized sites. For example, if studies reported compositional data along an urbanization gradient (e.g. ‘urban’, ‘suburban’, ‘rural’), we always used the data from ‘urban’. If a

Table 1. Predicted effects of different variables on alien species richness. The magnitude of the effect is predicted to increase as impervious surface cover increases. ‘+’ signs predict a positive effect by the variable on alien species richness, while ‘–’ signs predict a negative effect.

Variables	Predicted effect	Rationale
Impervious surface cover	–	Few species contain adaptations for urban life (Sol et al. 2014)
Mean annual temperature	+	Increased temperature leads to increased alien bird species richness in Australia, possibly indicating more favorable conditions (McKinney and Kark 2017)
Annual precipitation	–	Increased precipitation leads to reduced alien bird species richness on oceanic islands, possibly indicating unfavorable conditions (Blackburn et al. 2016)
Native species richness	–	Increased species richness in a community enhances niche limitation (Elton 1958)
	+	Increased species richness indicates favorable environmental conditions for alien species (Stohlgren et al. 2006)

categorical urbanization level was not assigned, we identified the most urbanized sites based on site descriptions (e.g. area of the park, whether the habitat is located in the city center). To avoid the 'double zero problem' (Legendre and Legendre 2012), two communities were excluded due to zero introduction records; thus we used 61 urban communities from 48 studies in total, covering all continents except Antarctica (Fig. 2, Supplementary material Appendix 1).

Alien species richness

To quantify alien species richness, we used the Global Avian Invasions Atlas (GAVIA), which contained 27 723 records of alien birds in 230 countries or administrative areas at the time of accession (July, 2018) (Dyer et al. 2017b). The database is based on published studies (~700), as well as consultations with regional experts and organizations. Records in GAVIA describe the species and location of each introduction event, as well as the outcome and pathway of introduction. We used range maps of 719 alien bird species, which were generated based on records with sufficient detail (e.g. with specific location, such as sub-states, of introduction events) (Dyer et al. 2017a). We then overlaid these range maps with city coordinates (obtained via GoogleEarth) to obtain a list of introduced species for each site. These lists were subsequently compared to the species lists provided by each study, which in total contained 915 bird species, and allowed classification of alien birds in each site. We also checked for synonyms of each species using HBW and BirdLife Taxonomic Checklist v2 (BirdLife International 2017) to ensure that all alien birds were correctly identified.

Size of alien species pools

We obtained the alien species pool size of each city by overlaying each GAVIA range map with city coordinates. All introduction records were included irrespective of pathways and outcomes of introduction. We used two measures for subsequent analyses separately to investigate whether habitat filtering limits alien species richness. One measure included all introduction records regardless of the environmental tolerance of the species, while the other measure only included introduced species that are known to establish in urban areas (i.e. urban exploiters). Species persistence in urban areas was determined by whether they were listed as using the habitat coded as 'artificial/terrestrial – urban areas' in the IUCN database (IUCN 2018), or whether they were recorded in studies included in our database.

Abiotic and biotic variables

The definition of 'urban' varied across studies, thus we quantified urbanization extent at each site using 'Global Impervious Surface Area' (Elvidge et al. 2007). The database has been demonstrated to have high accuracy and spatial resolution (1 km^2 grids), and provides a continuous measure of the extent of urbanization (rather than binary classifying grids as urban or non-urban areas) (Potere et al. 2009). As the exact location of bird surveys were generally not noted, we drew a 15 km radius circle at each site. The circle was large enough to include each city, although it could also include suburban, rural or natural habitats as well, resulting in underestimations of the urbanization extent when averaging impervious surface cover across 1 km^2 grids. Given that we always used the compositional data at the most urbanized sites for each study, we averaged the top-25 grids with the highest impervious surface cover rather than averaging across all grids in each city.

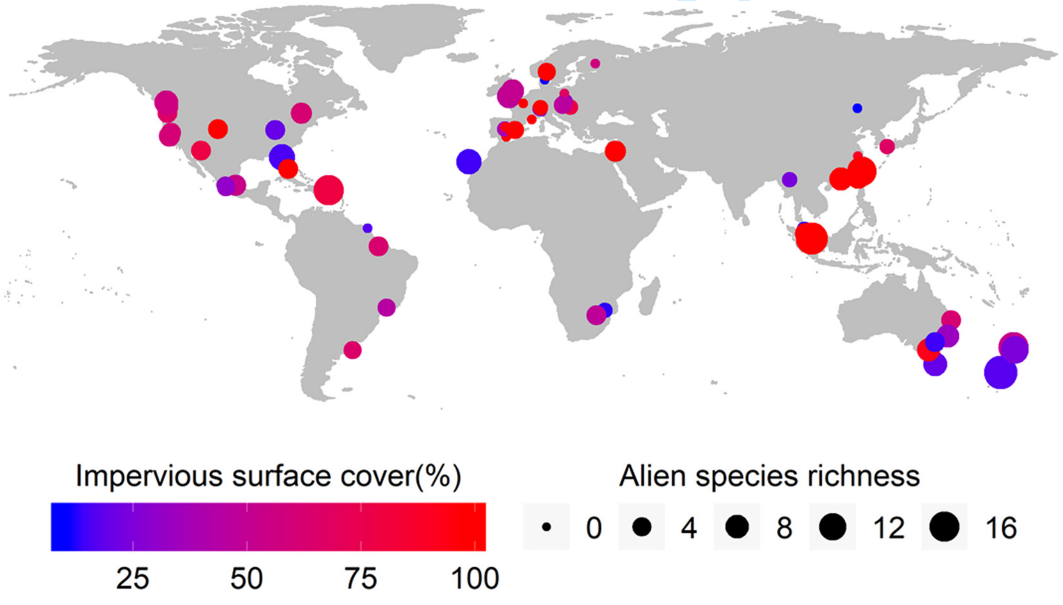

Figure 2. The distribution of study sites (n = 61), as well as their observed alien species richness and impervious surface cover.

For other abiotic variables, we identified geographic coordinates of the 25 grids with the highest impervious surface cover in each city and obtained their mean annual temperature and annual precipitation from the BIOCLIM v2.0 database, available from WorldClim (<www.worldclim.org>) at a spatial resolution of 30 arc-seconds (~1 km^2) (Fick and Hijmans 2017). These values, as well as the impervious surface cover, were then averaged across grids at each city for subsequent analysis. We also quantified native species richness as the number of native species observed during the survey. Data on abiotic variables, as well as alien species pool size, were collected using the R-package raster (Hijmans et al. 2017).

Preliminary analyses

Rarefaction analyses showed that the sample coverage (the completeness of sampling, sensu Chao and Jost 2012) of species richness at all sites ranged between 0.97 and 1.00 (Supplementary material Appendix 2), indicating that all communities were well-sampled and justified the use of observed alien and native species richness in subsequent analyses. To minimize the effect of arbitrarily defining the number of grids, we quantified the average impervious surface cover from the top-50 and top-100 grids, and the associated average of annual precipitation and mean annual temperature. We detected high correlations between averages quantified based on different numbers of grids (Pearson correlation, $R \geq 0.97$), thus we only used the values obtained from averaging across the top-25 grids in subsequent analyses. We also checked for collinearity between independent variables (see below) via Pearson correlations. All independent variables showed low collinearity between one another (max $R = 0.44$), hence all variables were retained in subsequent analyses. Rarefaction analyses were conducted using R-package iNEXT (Hsieh et al. 2016).

Form of the alien species richness–alien species pool size relationship

We analyzed how urbanization modified the relationship following Szava-Kovats et al. (2012), which has improved performance in detecting decelerating or asymptotic functions. We applied an additive log ratio transformation to alien species richness:

$$\ln \frac{\text{Alien species richness}_A + 1}{\text{Alien species pool size}_A - \text{Alien species richness}_A + 1}$$

where subscript A denotes the value of the variable at site A. The numerator and denominator are increased by one to allow zero alien species richness in communities (Helm et al. 2015). The log-ratio transformation is effective in removing the mathematic constraints that alien species richness must be smaller or equal to alien species pool size and both must be positive, which makes regression analyses operate in a wedge-shaped space, in which any pair of random variables would result in positive correlations (Szava-Kovats et al. 2012). As predictors, we included log-transformed alien species pool size [ln(alien species pool size +1)], impervious surface cover and the second-order interaction term between them. Linear predictors were centered and rescaled to minimize collinearity between linear predictors and their associated interaction, as well as allowing comparisons of the relative importance between predictors based on magnitude of coefficients (Schielzeth 2010). We conducted linear mixed modeling, with biogeographical realm (Olson et al. 2001) added as a random intercept to account for spatial autocorrelation between observations that share similar histories of introduction or other human activities, or current environmental conditions, which can all affect current alien species richness (Dyer et al. 2017a). Some studies provided data for multiple sites, and in one case in different biogeographical realms, thus we included the identity of study as another random intercept without nesting within biogeographical realms to control for unknown methodological effects. We fit linear mixed models with restricted maximum likelihood to produce less biased estimates of standard deviations compared to maximum likelihood (Bolker et al. 2009). Model performance was evaluated with both AICc and R^2 as defined in Nakagawa and Schielzeth (2013). To ensure spatial autocorrelation did not affect the results, we computed Moran's I for the residuals of the model with smallest AICc at 12 distance classes (as determined by Sturges rule) and computed Holm's corrected p-values (Legendre and Legendre 2012). Additionally, we performed the Johnson–Neyman procedure, which calculated the slope of log-transformed alien species pool size and its 95% confidence interval (95% CI) under different impervious surface cover. We also controlled for the false discovery rate using procedures described in Esarey and Sumner (2015). We used the slope of log-transformed alien species pool size to identify the conditions under which the alien species richness–alien species pool size relationship exhibited an asymptotic response. Following Szava-Kovats et al. (2013), an asymptotic relationship was declared if the slope of log-transformed alien species pool size overlapped with −1 but not 0, while those overlapping with 0 but not −1 were classified as linear relationships. If the 95% CI lay entirely within 0 and −1, the relationship was classified as decelerating but not asymptotic.

Relative importance of determinants of alien species richness

To examine how urbanization affects the relative importance of alien species pool size and other environmental variables (Table 1) in shaping alien species richness, we included them and their second order interactions with impervious surface cover as predictors. As the previous analysis revealed that alien species richness–alien species pool size relationships changed from linear to asymptotic as urbanization increases, we log-transformed alien species richness and alien species pool size (Szava-Kovats et al. 2013). The second order interaction term between log-transformed alien species pool size and impervious surface cover allowed the shape of the alien species richness–alien species pool size relationship to vary according to impervious surface cover when analyzed using linear models. We additionally log-transformed annual precipitation to reduce its right-skewness, while other variables were untransformed. As with the above analysis, we rescaled and centered all predictors such that their relative importance could be compared (Schielzeth 2010), and used biogeographical realm and identity of study as random intercepts. Linear mixed models were fitted by maximum likelihood instead of restricted maximum likelihood to allow model comparison (Bolker et al. 2009). We first fit a full model to assess the significance of each linear and interaction term. When examining the subset of best models ($\Delta AICc \leq 2$), only one model remained after removing models containing uninformative parameters (Arnold 2010). Thus, no model averaging was performed, and we simply constructed additional linear mixed models to evaluate model performance and significance of the retained predictors. Using the model with the smallest AICc and Chi-squared tests, we assessed whether model performance significantly improved after inclusion of interaction terms. We also checked spatial autocorrelations using Moran's I and Holm's corrected p-value.

Linear mixed modelling was conducted with the R-package 'lme4' (Bates et al. 2017), while model selection and spatial autocorrelation checking was conducted using packages 'MuMIn' (Bartoń 2015) and 'pgirmess' (Giraudoux 2017). The Johnson–Neyman procedure was conducted using the package 'jtools' (Long 2018).

Data deposition

Data and R scripts are available from the Dryad Digital Repository: <https://doi.org/10.5061/dryad.XXXXX> (Tsang et al. 2019).

Results

In total, we recorded 915 bird species, of which 76 have been recorded as 'alien' in at least one site, and 342 species have been introduced into at least one site. The most widespread birds were *Columba livia* and *Passer domesticus*, which occurred as native or alien species in more than 75% of the sites. These species were also introduced into more than half of the sites, and ≥77% of their introductions led to successful establishment in urban areas. The number of introduced bird species, regardless of whether they can persist in urban environments, ranged from 1 (6 sites) to 127 (Miami, FL, USA) and had a median of 7 species, yet alien species richness only ranged from 0 (12 sites) to 16 (Dunedin, New Zealand) and had a median of 3 species. Urban exploiters made up 39.02% (Valencia, Spain) – 100% (24 sites) and on average 80.84 ± 19.21% (mean ± SD) of all introduced bird species at each site. The urbanization extent varied between sites, with impervious surface cover averaging 57.37 ± 32.01% (mean ± SD) and ranging from 9.42 (Brønderslev, Denmark) – 100%. Impervious surface cover at 10 sites, such as Hong Kong, Paris (France) and Miami (FL, USA), reached 100%, while 25 sites (e.g. Hamilton (New Zealand), Tenerife (Spain)) had <50% impervious surface cover.

Regardless of the definitions of alien species pool size, all analyses showed an increasingly decelerated relationship between alien species richness and alien species pool size as impervious surface cover increases (Fig. 3). The main effect of log-transformed alien species pool size and its interaction with impervious surface cover were always negative and significant ($p < 0.001$, see Supplementary material Appendix 3 for full results). No significant spatial autocorrelation was detected (Max. Moran's $I = 0.13$). The Johnson–Neyman procedure revealed the alien species richness–alien species pool size relationships ranged from linear to asymptotic. When all species were included, the alien species richness–alien species pool size relationship changed from linear to decelerating when impervious surface cover reached 29% and started reaching an asymptote when impervious surface cover equaled 75%. Excluding introduction records with species that do not typically establish in urban areas led to more urban communities exhibiting a linear response (Impervious surface cover ≤41%), but fewer showing an asymptotic response (Impervious surface cover ≥ 87%).

For the analysis on log-transformed alien species richness, we detected positive main effects of native species richness

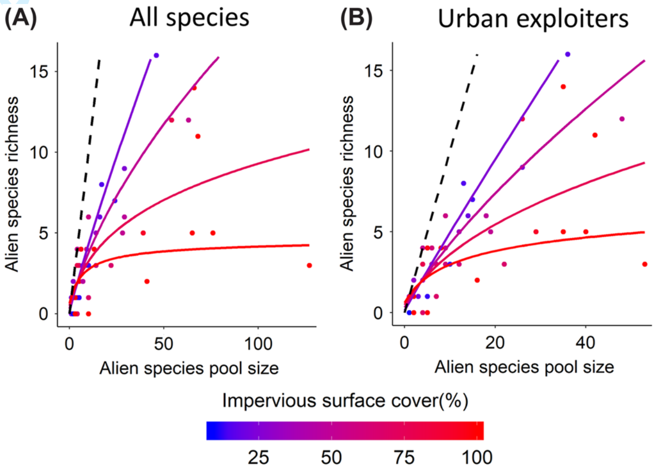

Figure 3. The predicted alien species richness–alien species pool relationship at different impervious surface cover values (25, 50, 75 and 100%) based on fixed-effects only. The size of the alien species pool was quantified as (A) the number of introduced species and (B) introduced urban exploiters only. The dashed line is the expected relationship when all species in the species pool can establish (i.e. alien species richness = alien species pool size). The color of lines and points follows the impervious surface cover gradient as indicated in the legend. Here, the predictions are based on the results of linear mixed models with log-ratio transformed alien species richness as the response variable. Analyses were done with log-transformed, centered and scaled predictors, but were back-transformed for ease of interpretation here.

Table 2. Results of linear mixed models analyzing the determinants of log-transformed alien species richness, based on different definitions of alien species pool. The best model has the smallest AICc. R^2m and R^2c represents marginal and conditional R^2 respectively. Bold values indicate statistical significance ($p < 0.05$), while '–' indicates that the variable was not retained in the best model. All variables were centered and scaled. Variable names are abbreviated: alien species pool (ASP); impervious surface cover (ISC); mean annual temperature (MAT); annual precipitation (AP); native species richness (NSR).

	All species				Urban exploiters			
	Full model		Best model		Full model		Best model	
	Slope	p	Slope	p	Slope	p	Slope	p
Intercept	**1.34**	**< 0.001**	**1.36**	**< 0.001**	**1.28**	**< 0.001**	**1.31**	**< 0.001**
ln(ASP + 1)	**0.58**	**< 0.001**	**0.61**	**< 0.001**	**0.56**	**< 0.001**	**0.59**	**< 0.001**
ISC	**−0.12**	**0.01**	**−0.13**	**0.006**	−0.10	0.05	**−0.10**	**0.04**
MAT	0.03	0.66	–	–	0.07	0.23	–	–
ln(AP)	0.02	0.70	–	–	0.03	0.66	–	–
NSR	0.09	0.06	**0.09**	**0.04**	0.09	0.06	**0.10**	**0.03**
ln(ASP + 1) × ISC	**−0.23**	**< 0.001**	**−0.23**	**< 0.001**	**−0.16**	**0.003**	**−0.16**	**0.001**
MAT × ISC	0.001	0.98	–	–	−0.01	0.87	–	–
ln(AP) × ISC	0.04	0.39	–	–	0.06	0.27	–	–
NSR × ISC	**0.17**	**0.002**	**0.17**	**0.001**	**0.18**	**0.002**	**0.17**	**0.002**
	R^2m	R^2c	R^2m	R^2c	R^2m	R^2c	R^2m	R^2c
	0.72	0.83	0.70	0.83	0.74	0.80	0.71	0.80

and log-transformed alien species pool size in all models (Table 2). Both full models revealed a significant negative interaction between log-transformed alien species pool size and impervious surface cover, as well as a significant positive interaction between impervious surface cover and native species richness. The coefficient of log-transformation alien species pool size was always larger than native species richness along the urbanization gradient, but this difference declined as impervious surface cover increased (Table 2, Fig. 4). The best models were formed by these significant interaction predictors and their associated linear predictors only. Chi-squared tests revealed that including interaction terms between all linear predictors significantly improved model performance ($p < 0.001$), with AICc dropping by 13.13–23.56 and R^2 increasing by 8–15% (Supplementary material Appendix 4). No significant spatial autocorrelation was detected (Max. Moran's I = 0.07).

Discussion

Consistent with our predictions, we found an increasingly decelerated alien species richness–alien species pool size relationship for birds as urbanization intensifies (Fig. 3A), highlighting that alien species richness has yet to reach a limit in less-urbanized sites. The relationship was asymptotic for highly-urbanized sites, and the mechanism limiting alien species richness is likely to be habitat filtering, since the relationship became more linear (i.e. increased probability of establishment) when alien species pool only included urban exploiters (Fig. 3B). The importance of habitat filtering in limiting alien species richness is further supported by analyses showing an increasingly positive correlation between native and alien species richness as impervious surface cover increased (Table 2, Fig. 4), which supports the biotic acceptance hypothesis and implies that favorable habitat conditions increase both alien and native species richness (Stohlgren et al. 2006). Overall, our results indicate that few urban areas (if any) are invulnerable to further bird introductions, especially when species that can bypass habitat filters are introduced.

Habitat suitability is the primary determinant of establishment success for introduced birds once the founding population size exceeds 50–100 individuals (Duncan et al. 2014). Urban areas have many unique characteristics, such as the presence of novel resources (e.g. anthropogenic foods) and predators (e.g. domestic cats), and species must overcome these challenges to persist in such environments

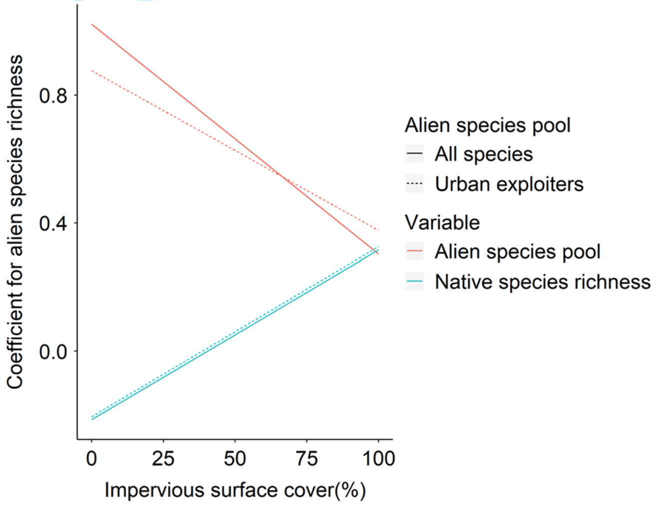

Figure 4. The coefficient of native species richness and log-transformed alien species pool size at different impervious surface cover values. Coefficient estimates were based on the model with the smallest AICc. Linear mixed modeling was conducted with centered and scaled predictors, but the impervious surface cover values here were back-transformed for ease of interpretation.

(Shochat et al. 2006). In particular, urban exploiters are often generalist species (Kark et al. 2007, Evans et al. 2011, Sol et al. 2014), which are better at exploiting novel foods (Overington et al. 2011, Ducatez et al. 2015). Regardless of the mechanisms, urban exploiters, on average, constitute 80% of alien species pool size at each site, indicating that the filtering effect caused by urbanization is weak for introduced birds. This also explains why model performance only increased by 8–15% when interactions between impervious surface cover and other predictors were included. As bird introductions are biased by urban exploiters, other gradients, such as elevation and productivity, may have more pronounced impacts in modifying the importance of the filtering effect compared to the urbanization gradient.

An increasingly decelerated relationship between alien species richness and alien species pool size along the urbanization gradient persisted after removing species unable to survive in urban areas (Fig. 3B). This is unlikely to be explained by niche limitation (Cornell and Harrison 2014), as we detected an increasingly positive correlation between native and alien species richness (Table 2, Fig. 4). If niche limitation is the primary explanation, native and alien species richness should be negatively correlated, since increased natives should further limit niche space available to introduced species, leading to lower establishment success via enhanced competition (Elton 1958, Case 1990, Shea and Chesson 2002). The lack of support for niche limitation can be explained by the large spatial scales (Byers and Noonburg 2003) and a lack of communities from natural habitats (Bertness and Callaway 1994) in this study. We suggest that the increasingly decelerated relationship could still be caused by habitat filtering. We classified species that can persist in any urban habitat as 'urban exploiters', yet our study covers a large urbanization gradient (impervious surface cover ranged from 9.42 to 100%) and increasing urbanization is known to reduce urban bird diversity (Aronson et al. 2014). Therefore, a greater proportion of 'urban exploiters' might be filtered from highly-urbanized sites, which promotes an increasingly decelerated relationship along urbanization gradients (Srivastava 1999).

Alien species richness–alien species pool size relationships are broadly and likely to be affected by propagule pressure (a composite measure of the number of individuals introduced), which is known to be an important predictor of establishment success (Cassey et al. 2018). When introductions occur repeatedly, propagule pressure accumulates over time and establishment success increases, therefore the current alien species richness–alien species pool size relationship might be more linear than relationships from the past. Indeed, Abellán et al. (2017) found that the time since the first introduction event increased establishment success of introduced birds, possibly explained by higher cumulative numbers of propagules. By this logic, sites with a longer introduction history may have accumulated more propagules, and hence exhibit a more linear alien species richness–alien species pool size relationship. However, variation in propagule pressure between sites are unlikely to explain our results, since highly-urbanized sites should have a longer introduction history, and hence higher propagule pressure compared to less-urbanized sites (Cadotte et al. 2017, McKinney and Kark 2017). Yet, we still detected an increasingly decelerating alien species richness–alien species pool size relationship with increasing urbanization.

The form of the alien species richness–alien species pool size relationship is based on historical introductions, and future introductions may enhance its linearity. First, as economic activities continue, propagule pressure will continue to accumulate and some species may eventually establish (Abellán et al. 2017), thus promoting a more linear alien species richness–alien species pool size relationship. Additionally, the sources of introduced birds have gradually changed from European colonies to the Indian subcontinent, Indochina and sub-Saharan Africa (Dyer et al. 2017a), which expand alien species pools and might prevent alien species richness from reaching an asymptote (Liebhold et al. 2017). Finally, regardless of the current shape, the slope of the alien species richness–alien species pool size relationship may become more positive should new invading species contain traits promoting coexistence (e.g. better dispersal ability, low niche overlap with residential species) (Cornell and Lawton 1992).

To limit the increase of alien species richness in urban bird communities, our results suggest that less-urbanized sites should be prioritized for monitoring, as they have yet to reach a limit in alien species richness. This includes areas at the periphery of cities, as well as less-urbanized habitats in city cores (e.g. remnants of natural habitats), since urban areas can be extremely heterogenous in terms of urbanization extent (Ramalho and Hobbs 2012) and these habitats might be refuges for alien birds that cannot tolerate highly-urbanized environments (McKinney and Kark 2017). Habitat filtering is strongest in highly-urbanized sites and limits their alien species richness, yet urban exploiters are likely to bypass the filter and successfully establish should future introductions occur. Some urban exploiters (e.g. Estrildidae and Columbidae species, Sol et al. 2017) have been involved in the cage bird trade (Su et al. 2014), which is the primary driver of modern bird introductions (Dyer et al. 2017a), and show high extent of spread after establishment (Dyer et al. 2016, Abellán et al. 2017). Therefore, the trade of urban exploiters should be prioritized for bans or regulations to prevent them establishing in urban areas, which may facilitate them invading adjacent less-urbanized habitats (McLean et al. 2017).

Whether species richness is limited or unlimited in communities remains an open question in ecology (Cornell and Harrison 2014). Here, we showed that habitat filtering is an important mechanism bounding alien species richness in highly-urbanized habitats. Once species that cannot exploit urban areas were excluded, more communities were associated with a non-asymptotic alien species richness–alien species pool size relationship, showing no sign of reaching an upper limit in alien species richness. This indicates that most urban bird communities are still far from reaching the upper limit (if any) of alien species richness, and they are especially susceptible to the introductions of urban exploiters. Similar to predictions at the global scale (Seebens et al. 2017), we predict that alien bird species richness in urban areas will continue to increase at smaller spatial scales due to increasing globalization and expanded alien species pool (Seebens et al. 2018).

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Supplementary material (available online as Appendix ecog-04412 at <www.ecography.org/appendix/ecog-04412>). Appendix 1–4.

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Q1 Lockwood et al. 2009 cited in the text but not provided in the list.
Q2, Q4 Please insert doi-number for Dryad Digital Repository: <https://doi.org/10.5061/dryad.XXXXX>.
Q3 Shochat et al. 2006 cited in the text but not provided in the list.