

Factors shaping avian alien species richness in Australia vs Europe

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Abstract

Aim: We aim to examine the relative importance of human activity-related and natural variables in shaping spatial patterns of alien bird species richness at the continental scale for Australia. We examine the drivers shaping establishment of alien birds in Australia in the framework of the human activity hypothesis and the biotic acceptance hypothesis (the “rich get richer” model of biotic invasion), and directly compare our results to Europe.

Location: Continental Australia, Tasmania, Continental Europe, United Kingdom.

Methods: We use compiled atlas data on alien bird richness in continental Australia and Tasmania together and separately, records of known alien bird introduction events compiled from various sources and a suite of biogeographic variables to evaluate drivers of alien bird richness at a 50-km resolution in Australia. We use hierarchical partitioning and spatial generalized linear models to quantify the relative contribution of each environmental variable to alien bird richness. We then compare our results directly to those from a previous continental-scale study in Europe and in the UK.

Results: We identify 24 established alien bird species across Australia (including nearshore islands and Tasmania) and present a detailed map of alien bird richness in Australia. We discover that in Australia, native bird species richness and land cover heterogeneity are the strongest predictors of alien bird richness at a 50-km resolution, supporting the “rich get richer” model of species invasion.

Main conclusions: Our results are contrary to Europe, where the human activity hypothesis was best supported. By performing a cross-continental comparison of drivers of alien bird richness, we show that processes shaping alien establishment and spread can vary across continents with variable human impact history and should be examined on a case-by-case basis before endorsing general hypotheses.

KEYWORDS

Alien species, Australia, biotic invasions, birds, Europe, human activity

1 | INTRODUCTION

Invasive alien species impact native biodiversity, ecosystem processes and humans (Hulme, 2009; Hulme, Pyšek, Nentwig, & Vilà, 2009; McGeoch et al., 2010; Pimentel, Zuniga, & Morrison, 2005; Sala et al., 2000). In invasion ecology, it is useful to separate the invasion process

into “stages,” where processes affecting transport, establishment and spread can be assessed together or separately (Duncan, Blackburn, & Sol, 2003; Leprieur, Beauchard, Blanchet, Oberdorff, & Brosse, 2008). Hypotheses explaining alien species establishment and spread can be either niche-based or neutral (Fridley, Brown, & Bruno, 2004; Fridley et al., 2007). For example, the biotic resistance hypothesis predicts

alien species are less likely to invade areas with higher native species richness because of competition with natives for limited niche space (Elton, 2000; Levine, Adler, & Yelenik, 2004; Maron & Vilà, 2001). The contrary biotic acceptance hypothesis, sometimes termed the “rich get richer” model, suggests that mean resource availability and favourable environmental conditions enhance both native and exotic species richness, and represents a neutral invasion hypothesis (Tilman, 1999). Recently, another neutral “human activity” invasion hypothesis has emerged, positing that disturbance, importation and human-driven dispersal increase propagule pressure and hence are the main drivers of alien species establishment and spread (Blackburn, Cassey, & Lockwood, 2008; Leprieur et al., 2008; Taylor & Irwin, 2004). Propagule pressure, as a primary neutral process in initial alien establishment success, is supported widely in biotic invasion literature (Blackburn, Prowse, Lockwood, & Cassey, 2011, 2013; Colautti, Grigorovich, & MacIsaac, 2006; Holle & Simberloff, 2005; Lockwood, Cassey, & Blackburn, 2005, 2009; Lockwood, Hoopes, & Marchetti, 2013; Simberloff, 2009). However, subsequent spread throughout the invaded range is more difficult to attribute to propagule pressure alone.

The “rich get richer” and “human activity” hypotheses both elegantly explain alien species establishment and spread. However, comparing support for these two hypotheses has pitfalls. Cities and urban centres are often located in areas that already have high biodiversity and resource availability (Luck, 2007), and disentangling the relationship between native species richness, alien species richness and human activity can be difficult. Furthermore, Blanchet et al. (2009) suggested that the emergence of the human activity hypothesis has largely been the result of study bias towards highly human-impacted regions and should not be extrapolated across biogeographic realms. Regardless, neutral invasion hypotheses such as the human activity hypothesis, “rich get richer” model, and the propagule pressure hypothesis have come to dominate invasion literature over niche-based hypotheses such as biotic resistance (Blanchet et al., 2009; Lockwood et al., 2009; Nuñez, Moretti, & Simberloff, 2011). However, in a direct test of the propagule pressure hypothesis, Nuñez et al. (2011) showed that propagule pressure could not explain alien woody species richness patterns on an island in Argentina. Other studies suggest the dichotomy between neutral processes like propagule pressure and niche-based processes like biotic resistance is not clear-cut (Holle & Simberloff, 2005; Hollebone & Hay, 2007).

It therefore remains unclear what role the various neutral processes have in shaping alien species establishment and spread, and whether support for either the human activity hypothesis or the “rich get richer” model is context-dependent (Blanchet et al., 2009). Clearly, human impact varies in intensity and history around the world. Introduced species propagule pressure varies with human impact as well as politics and socio-economy (e.g., cultural and economic importance of non-native species, recent advances in customs and quarantine practices; Chiron, Shirley, & Kark, 2010).

In this study, we aim to examine the relative importance of the human activity, propagule pressure and “rich get richer” hypotheses in the context of varying human impacts and histories. Our objective is to

simultaneously evaluate the predictive importance of human-related and natural variables to bird invasion in Australia, a continent with a moderate history of human impact post-European settlement, and compare the results with an earlier study of introduced birds in Europe by Chiron, Shirley, & Kark, (2009), who found that at the whole-Europe extent, the major factors shaping establishment patterns of alien birds in Europe were the number of species introduced, also termed community-level propagule pressure (Chiron et al., 2009) or colonization pressure (Lockwood et al., 2009), followed by human footprint (Sanderson et al., 2002). Native species richness, mean resource availability (i.e., NDVI as a measure of net primary productivity) and abiotic conditions (i.e., minimum temperature) played a minor role explaining the number of alien species established across Europe. Australia and Europe make an interesting comparison given their different histories of human impact. Much of Europe has a relatively high human population density, abundant urban and agricultural settlements, and has been under substantial human impact for many thousands of years. Some of its alien species were introduced over a thousand years ago (e.g., the ring-necked pheasant (*Phasianus colchicus*), which was introduced into Europe by the Romans (Lowe, 1933)). In Australia, as a counterexample, Europeans colonized the continent only two centuries ago, and today, the overall human population density remains substantially lower than that of Europe, with comparable land area (Appendix S1). Australia is the most recent continent to be populated by Europeans, and 90% of the human population is concentrated in coastal regions, with 89% living in urban centres (Australian Bureau of Statistics, 2012). Europe's population is more diffuse, with 42.2% in cities, 30.2% in towns and suburbs and 27.6% in rural areas (Eurostat, 2015).

We hypothesize that in Australia, where history of human activity post-European settlement is relatively recent, less intense and spatially concentrated compared with Europe, biological invasions are shaped primarily by natural factors—biotic and abiotic—rather than human activity. We predict that coarse-scale patterns of alien bird species richness in Australia will be best explained by native species richness, resource availability and resource heterogeneity (positive relationship), supporting the “rich get richer” model of species invasion.

2 | METHODS

2.1 | Data

We generated a spatially explicit data set of avian introduction events in Australia between the years 1788 A.D. and 2000 A.D. using information collated from books, journal articles, reports, published and unpublished atlas projects, grey literature, bird guides and bird checklists. We did not include in the analysis species native to Australia but present outside their native ranges in other parts of Australia. We did not include any introduction events without valid spatial data. We included all of mainland Australia and Tasmania, as well as any continental Australian islands. We did not include oceanic islands or territories and holdings away from mainland Australia (e.g., Christmas Island, Lord Howe Island, Norfolk Island).

We compiled survey location data for exotic birds established in Australia using data provided by Birdlife Australia and by the Atlas of Living Australia (<http://www.ala.org.au>, accessed 12/31 2014; Barrett, Silcocks, Barry, Cunningham, & Poulter, 2003). Using the data from these sources collected since the start of the year 2000, we generated a layer of alien bird species richness in Australia and its continental islands. We used this time period to reflect the recent/current richness of established alien species. We used ArcGIS 10.2 (ESRI, Redlands, CA, USA) to assign all data to 0.50×0.50 decimal degree ($\sim 50 \times \sim 50$ km) grid cells. This scale was used by Chiron et al., (2009) for their analysis of bird introductions in Europe and allows comparison between their study and ours.

Using alien species richness as the response variable, we examined a set of human-related and natural (biotic and abiotic) variables proposed by Chiron et al. (2009). Human-related variables were (i) the number of alien species introduced, sensu Chiron et al. (2009), and (ii) human footprint, which is an index that includes human population density, land use and infrastructure, and human access (e.g., roads). "Natural" variables were (i) native bird species richness, (ii) mean normalized difference vegetation index (NDVI), a measure of plant productivity and surrogate for mean resource availability (Kerr & Ostrovsky, 2003), (iii) mean daily minimum temperature, a measure of abiotic condition favourability and (iv) land cover diversity, a surrogate of resource heterogeneity. We derived number of alien species introduced from the introduction events database we compiled. We derived native bird species richness using data collated by Birdlife Australia (Barrett et al., 2003). We derived mean NDVI using 5 km monthly composite imagery available from the Australian Bureau of Meteorology (TERN/AusCover, 1992–2013), computing the average across monthly values for all months beginning in 1992 and running through February 2014 and resampling to 50-km resolution. We acquired temperature data from the Australia Bureau of Meteorology Base Climatological Data Sets (Australian Government Bureau of Meteorology, 2009). We calculated land cover diversity by extracting the number of unique land cover types within each $\sim 50 \times 50$ km grid cell, using the Land Cover Type Yearly L3 Global 500 m SIN Grid, mosaicked and remapped for Australia (original data were supplied by the Land Processes Distributed Active Archive Center (LPDAAC), located at the U.S. Geological Survey (USGS) Earth Resources Observation and Science Center (EROS) <http://lpdaac.usgs.gov>) (Paget & King, 2008). We also included categorical variables of (i) political state and (ii) whether the data were located on an island or mainland. In our study, the variable "State" represented a spatially and socio-economically unstructured variable.

2.2 | Statistical analyses

Following Chiron et al., (2009), we used hierarchical partitioning to calculate independent explanatory power (R -value, corrected for joint contributions of other variables and expressed as the percentage of total independent deviance explained) for each explanatory variable (Chevan & Sutherland, 1991; Leprieur et al., 2008; Mac Nally, 2002), according to the following model:

$$bRich_{alien} \sim bRich_{native} + NDVI + TEMP + HabDIV + PRESSURE + HFP + State + Island$$

where $bRich_x$ is alien or native bird richness, NDVI is mean annual NDVI, an index of primary productivity, TEMP is mean minimum annual temperature, HabDIV is the number of discreet land cover types contained within each pixel, PRESSURE is the number of alien species known to have been introduced in each pixel and HFP is the human footprint index, a measure of human activity. State and Island are categorical variables representing the Australian political state within which the cell falls and whether or not the cell is on an island, respectively. We specified a Poisson error for the response variable. While hierarchical partitioning can be invalid for models using nine or more independent variables (Olea, Mateo-Tomás, & de Frutos, 2010), our model falls below that threshold. Hierarchical partitioning alleviates multicollinearity in explanatory variables (Chevan & Sutherland, 1991). This is important because, for example, human activity might be greatest in areas with the greatest intrinsic productivity, which would also mean higher NDVI values and likely higher native species richness (Luck, 2007). Additionally, community-level propagule pressure is likely greatest in areas where human activity is highest, which is why human activity has often been used as a surrogate for propagule pressure. By explicitly incorporating community-level propagule pressure as well as a surrogate for propagule pressure, human footprint, Chiron et al., (2009) showed that surrogates might not effectively capture the importance of community-level propagule pressure. We assessed statistical significance by calculating pseudo- Z scores for each explanatory variable using 1,000 randomizations (Chiron et al., 2009; Leprieur et al., 2008). We used log-likelihood as our measure of goodness of fit.

While hierarchical partitioning is useful compared to traditional linear modelling when variables are multicollinear, it does not assess the form of the relationships between variables (i.e., positive or negative). To assess the form of the relationship between the response and the explanatory variables, and to overcome the confounding effect of spatial autocorrelation, we used a generalized least-squares model (GLS) incorporating a distance-based spatial correlation structure (Chiron et al., 2009; Leprieur et al., 2008; Pinheiro & Bates, 2000; Sol, Vila, & Kühn, 2008). We performed a Spearman correlation test on each explanatory variable and the residuals from a respective GLS model excluding that explanatory variable (Chiron et al., 2009; Leprieur et al., 2008). To determine the proper spatial correlation structure, we used GLS regressions of alien species richness on the full set of independent variables, incorporating linear, exponential, Gaussian and spherical spatial correlation structures in separate models. We compared these models and a model without spatial correlation structure using AIC to select the most appropriate model structure. By incorporating both the hierarchical partitioning and Spearman correlation tests, we were able to evaluate important relationships between alien species richness and environmental predictors (e.g., the native–exotic richness relationship), and also assess the relative importance of such relationships in the context of the human activity hypothesis.

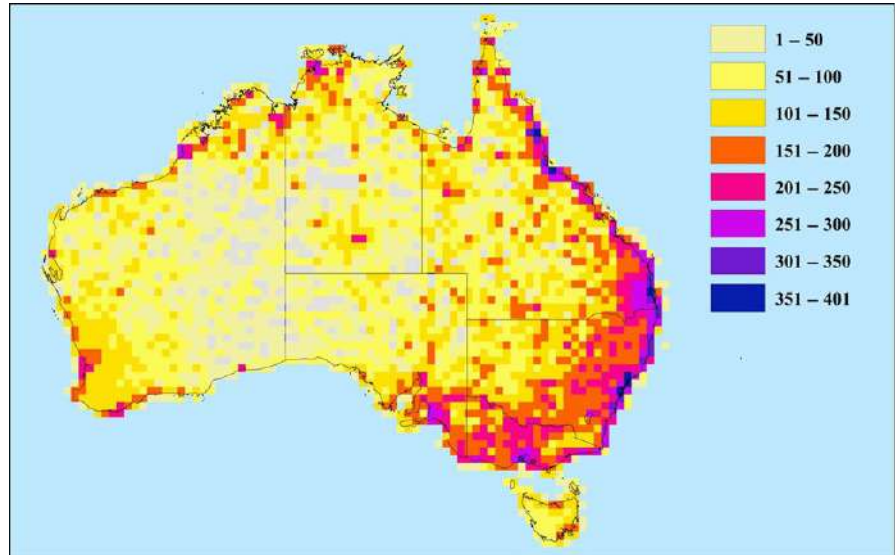


FIGURE 1 Native bird species richness in continental Australia at $\sim 50 \text{ km} \times 50 \text{ km}$ resolution. [Colour figure can be viewed at wileyonlinelibrary.com]

For a more direct comparison with the study by Chiron et al. (2009), who isolated the UK in their analysis because of its insularity and greater densities in reported introduction events (Figure 2), we repeated the analysis for Tasmania alone, assigning the large island of Tasmania as “mainland” and smaller islands comprising the state as “island.” This allowed us to assess the explanatory power of the methods in Australia in a scenario where introduction events data are more evenly distributed (fewer cells with no events). Also, while Tasmania and the UK are quite different, their relationships to their respective mainlands can be quite similar. The UK is more densely populated than Tasmania, especially London and the southern reaches of the island. However, both the UK and Tasmania are markedly colder and wetter than their respective nearby mainland. Furthermore, Tasmania is interesting as one of the earliest places settled by Europeans, with almost immediate efforts by acclimatizers to introduce European birds like the European Starling (*Sturnus vulgaris*) around the year 1800 (Littler, 1902; Tardif, 2003). The discrete variable “Australian State” was removed from the Tasmania-only analysis. To perform the hierarchical partitioning analysis, we used the package *hier.part* in the R statistical software version 3.0.1 (R Development Core Team, 2008; Walsh, Mac Nally, & Walsh, 2013). To perform the GLS, we used the R package *nlme* (Pinheiro, Bates, DebRoy, & Sarkar, 2013). To perform the Spearman rank correlation test, we used the R package *Hmisc* (Harrell, 2008). We did not centre, standardize or otherwise transform any of our data prior to analysis, as we were not concerned with effect sizes based on regression coefficients, but rather primarily proportions of variance explained (Baguley, 2009). Data used in our analyses, as well as R scripts, can be found in Data S3, S4, & S5.

3 | RESULTS

Overall, we recorded introductions of 60 alien bird species in Australia in 613 spatially referenced species introduction events between the years 1788 and 2000 A.D. (A list of events, outcomes and further

information can be found in Data S4.). Twenty-four of these species (40%) had established breeding populations in Australia by 2014 (Appendix S2), compared to 75 (43%) alien bird species established in Europe by the year 2000 (Chiron et al., 2009). Five of the established bird species are also established aliens (non-native) in Europe (Appendix S2; Olenin & Didžiulis, 2009; Kumschick & Nentwig, 2010). For all analyses, we examined only data from grid cells that contained at least one Birdlife Australia survey record ($n = 2,815$; $\sim 92\%$ the entire continent). Of the cells we examined, 194 had at least one known alien bird introduction event. The number of species introduced per grid cell ranged from 0 to 24. Numbers of that subset considered “successful” ranged from 0 to 14 per grid cell. Alien bird species richness per grid cell ranged from 0 to 18 (some species now appear in more cells than those in which they were introduced; Figure 2c,d). Native species richness per grid cell ranged from 1 to 401 (Figure 1).

Alien bird introductions in Australia were generally concentrated around large cities and urban centres. Of all introduction events, 374 (61%) were within 100 km of a State capital city or other similarly highly populated urban centre (Figure 2c,d). These introduction events represented 48 (80%) of all the non-Australian avian species introduced into Australia, and 24 (100%) of all the alien bird species currently established in Australia. In other words, all the currently established alien birds in Australia were at some point introduced near a city. Also, the greatest numbers of established alien species were around large cities, along the eastern coast of Australia, and in Tasmania (Figure 2c,d). Most areas in Australia had relatively low numbers of established alien bird species or none at all.

The sum of all the independently explained variance represented 32.4% of total explained variance. We found that in Australia, native bird species richness explained the greatest proportion (28.13%) of independently explained deviance in the data in the hierarchical partitioning (Table 1a). Apart from the variable of State (which accounted for 24.17% of the total independently explained deviance), other natural environmental variables each explained more deviance than either of the human-related variables, human footprint and number of alien

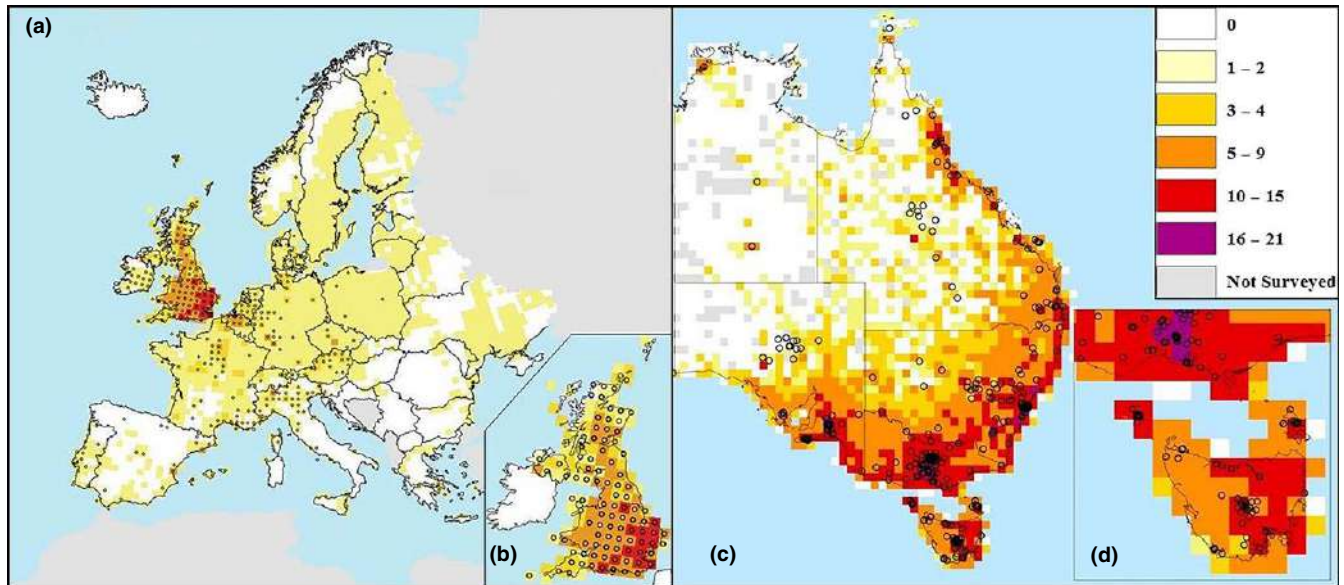


FIGURE 2 Alien bird species richness in (a) western Europe, (b) Great Britain, (c) eastern Australia and (d) Tasmania at $\sim 50 \times 50$ km resolution. Open black circles represent known introduction events of alien birds; concentrations of open black circles appear as dense black regions. Parts (a) and (b) are used with permission from Chiron et al. (2009) and with permission from The Royal Society. [Colour figure can be viewed at wileyonlinelibrary.com]

TABLE 1 Percentage deviance in alien bird species richness (~ 50 km \times 50 km resolution) explained independently by each variable, from the results of hierarchical partitioning analysis

Variable	(a)				(b)			
	Percentage Deviance Explained		Direction and Correlation p -value		Percentage Explained		Direction and Correlation p -value	
	Australia	Europe	Australia	Eur	Tasmania	UK	Tasmania	UK
Native bird richness	28.13*	1.1*	+(<.0001)	+(.246)	39.56*	22.2*	+(<.0009)	+(<.001)
Mean NDVI	12.19*	2.4*	+(<.0001)	+(.016)	4.41	1.52	+(.1988)	-(.090)
Minimum Temperature	9.29*	0.5*	-(<.0001)	+(.034)	1.82	8.8*	-(.3512)	-(.784)
Human Footprint	8.29*	7.8*	+(<.0001)	+(<.001)	5.03	19.8*	+(.1008)	+(.04)
Number of Alien Spp. Introduced	1.56*	28.8*	+(<.0001)	+(<.001)	7.4	45.4*	+(.0232)	+(.048)
Habitat/Land cover Diversity	15.75*	0.2	+(<.0001)	-(.624)	40.2*	2.2	+(.0017)	-(.005)
Country/State	24.17*	44.4*	—	—	—	—	—	—
Mainland vs Island	0.62*	14.7*	—	—	1.58	—	—	—
Total deviance	100%	100%	—	—	100%	100%	—	—

Significance is based on the results of a randomization test and is marked with an asterisk. The independent direction of the relationship and correlation strength (p -value) are the results from Spearman rank correlation tests. Europe and UK values are used with permission from Chiron et al., 2009.

species introduced. The GLS specifying exponential spatial covariance structure performed the best (had the lowest AIC). Therefore, we employed an exponential spatial covariance structure in our subsequent GLS analyses to test correlations of individual continuous variables with the models' residuals. From the Spearman rank correlation tests within Australia, all the continuous variables except for minimum temperature showed a positive relationship with alien bird richness. All continuous variable correlations from the Spearman correlation tests had p -values $<.0001$ (Table 1).

Within Tasmania only, we examined 54 grid cells representing approximately 90% of the entire island area. There were 15 known alien bird species introduced. Of the surveyed cells, 20 had at least one known alien species introduction event. Numbers of species introduced per grid cell ranged from zero to eight. Numbers of that subset considered "successful" ranged from zero to six per grid cell. Alien bird species richness per grid cell ranged from 1 to 13. The number of established exotic bird species in Tasmania was 14. Hierarchical partitioning showed a considerable difference from the Australia-wide

analysis to Tasmania (28.13%–39.56%, respectively) in the proportion of variation explained by native species richness and by number of species introduced (Table 1b). Additionally, land cover diversity increased in importance, accounting for 40.2% of deviance explained, while all other variables remained relatively low in importance, despite the removal of the variable “State” (Table 1b). While all variables were found to be significant by the randomization process in the analysis of the entire continent, only native species richness and land cover diversity were significant in the Tasmania-only analysis. The GLS with exponential spatial correlation structure had the lowest AIC and was used to find the independent variable correlations and correlation significance. The directions of the correlations in Tasmania agreed with the Australia-wide results, with only minimum temperature showing a negative relationship to alien bird species richness.

4 | DISCUSSION

Comparing two continents, Europe and Australia, our results highlight the importance of context in evaluating drivers of alien species invasion. In Europe, the human activity hypothesis is most strongly supported (Chiron et al., 2009). We find that for Australia, the “rich get richer” model of invasion has the greatest support. In Australia, alien bird richness is positively related to variables representing productivity and resource availability (mean NDVI), resource heterogeneity (land cover diversity) and native bird richness. We also found that alien bird richness is negatively related to minimum temperature. Australia, on average, is the hottest continent on Earth (Nie & Norton, 2009), so in the case of Australia, hot weather may represent unfavourable abiotic conditions for alien bird establishment. These results support the “rich get richer” model, which posits that, at a coarse resolution, areas with greater resource availability, resource heterogeneity and favourable abiotic conditions will harbour greater number of both native and alien species. The different results for Europe and Australia can be attributed to differences in human impact. The Australian landscape of urban, suburban, remnant forest and agriculture is likely more diffuse and less discrete than in Europe. Research suggests that peri-urban Australia is diffuse, with substantial penetration by agriculture (up to 25% of agricultural production is in the peri-urban environment), remnant vegetation and substantial inclusion of green spaces and private gardens (Houston, 2005; Shanahan, Lin, Gaston, Bush, & Fuller, 2014). So even in its more human-impacted areas, parts of Australia are likely more intrinsically welcoming to invading birds.

The results from our Tasmania-only analysis are particularly interesting compared to Chiron et al. (2009) and their analysis of the UK. The results in the UK, relative to mainland Europe, showed mixed results in support for the human activity, propagule pressure or “rich get richer” hypotheses (once the deviance attributable to “political state” was re-distributed); human footprint, propagule pressure and native bird species richness each increased notably in importance (Table 1). However, in Tasmania, only the “richer get richer” model had greater support relative to mainland Australia; land cover diversity and native bird species richness were by far the most important predictors

of alien bird species richness (Table 1). These results further highlight the importance of context when evaluating invasion hypotheses. Tasmania, even though more similar to the UK climatically than mainland Australia and with a strong history of acclimatization pressure, is less impacted by humans than Europe.

As noted earlier, niche-based models (e.g., biotic resistance) and neutral models like the “rich get richer” model are not necessarily mutually exclusive. Biotic resistance is best examined at a spatial scale where individuals have a high probability of competing for resources, where a negative native–exotic species relationship would indicate biotic resistance (Byers & Noonburg, 2003; Davies et al., 2005). The native–exotic richness relationship (NERR) is almost always positive at coarse spatial resolutions (the case in our results), but unpredictable at finer scales (Byers & Noonburg, 2003; Davies et al., 2005; Fridley et al., 2004, 2007; Herben, Mandak, Bimova, & Munzbergova, 2004). Subsequent hypotheses have seemingly reconciled the discrepancy between fine and coarse-scale NERRs by attributing positive NERRs at coarse resolutions to increased spatial heterogeneity at coarse resolutions (Byers & Noonburg, 2003; Davies et al., 2005; Fridley et al., 2007; Shea & Chesson, 2002). Simply, the biotic resistance hypothesis is not testable or applicable at the resolution of our study. Our results would not support the biotic resistance hypothesis *per se*; they show a positive relationship between native and alien species richness. However, we cannot refute that biotic resistance is not taking place at some finer scale in Australia.

Studies show that coarse-resolution NERRs are dampened by controlling for human-related variables and spatially structured variables, questioning any causal relationship between native and alien species richness (Rejmánek, 2003; Taylor & Irwin, 2004). This seems to favour human activity-based neutral models of invasion. However, Blanchet et al. (2009) showed that biotic resistance/acceptance can be valid when accounting for contextual variables such as development intensity and history. The results from that study predict that invasive species richness in areas with long histories of intense development (e.g., Europe) would best be predicted by human activity-related hypotheses, while areas with lesser historic human activity (e.g., Australia) would favour biological hypotheses. Our findings support this suggestion. Indeed, Australia does not have a long history of European human impact, but that history has been intense in places, particularly in and around major river systems (Blanchet et al., 2009). Moreover, Chiron et al. (2009) did not refute the “rich get richer” model; they demonstrated a positive NERR in birds, as well as a positive relationship between primary productivity and alien bird richness. However, human activities were shown to outweigh natural variables when explaining alien bird richness.

Invasion hypotheses are often treated as mutually exclusive, particularly along the division between human activity- and environmental-oriented hypotheses (Chiron et al., 2009; Jeschke et al., 2012). Our results best support the “rich get richer” model of species invasion. However, they do not refute the human activity hypothesis. Our results show a positive relationship between alien bird species and human footprint and our measure of community-level propagule pressure. Also, the proximity to cities of potentially

influential introduction events and the high numbers of established alien birds makes it clear that urban centres are important foci for alien species introductions. Therefore, our results also support, albeit to a lesser degree, the human activity hypothesis. While generality is ideal, universal rules for predicting invasions have been difficult to produce (Jeschke et al., 2012). We hypothesize that for birds in the early stages of invasion—introduction and establishment of breeding populations—human activity does indeed play an important role in fostering alien invasions. However, subsequent spread and establishment outside of the initial introduction “ground zero” will depend on context. If the landscape has been highly impacted by humans (as in Europe) and is therefore less inherently hospitable, human activity will necessarily continue to be the fostering agent in species invasion. However, if the subsequent invaded area is more “natural,” its invasibility can be reflected in the number of native species it supports. Indeed, Dyer et al. (2017) showed that when examined at the global resolution, introduction effort was the primary predictor of alien bird richness, but could not discount the importance of native bird richness as a measure of the invasibility of an area. It is increasingly clear that introduction effort is most important for establishment of alien birds, but given a species is established, other invasion processes determine spread.

4.1 | Conservation implications and future directions

The human activity hypothesis and “rich get richer” model have various conservation implications. Chiron et al.’s (2009) findings, which strongly supported the human activity hypothesis, are important for invasive species management in Europe because they imply that any additional alien species introductions potentially could result in establishment of the non-native populations under a wide range of prevailing environmental conditions. Conversely, it could also mean that interventions into human-related drivers will be more effective than actions to mitigate other environmental factors, which can be a lost cause (Chiron et al., 2010). Chiron et al. (2009) did not emphasize the negative correlation between alien bird richness and both resource availability (i.e., mean NDVI) and resource heterogeneity (i.e., habitat diversity) in their analysis of the UK, perhaps because findings were insignificant and accounted for small proportions of deviance explained. However, in the context of the UK, which is historically highly impacted by humans, this could indicate a case of a limited “niche opportunity” (Davies et al., 2005; Fridley et al., 2007) in the UK, where further avian invasions are less likely without great human facilitation. If this is the case, the argument for interventions in human-related drivers is strengthened.

Our results might mean that future bird invasions are in Australia are still likely, based solely on the apparent hospitality of the Australian landscape. As such some of Australia’s most notable avian invaders (e.g., the Indian myna, *Acridotheres tristis*) have had little to moderate ecological impact in Australia (Grarock, Tidemann, Wood, & Lindenmayer, 2012, 2014). This is perhaps because impact of alien species on ecosystem function is related to dissimilarity of traits

between invaders and members of the recipient community (Chapin et al., 2000; Crawley, Brown, Heard, & Edwards, 1999; Dukes & Mooney, 2004; Strauss, Webb, & Salamin, 2006). As functional diversity is highly correlated with species richness, areas with higher native species richness may be less likely to be impacted when invaded (Díaz & Cabido, 2001; Hooper et al., 2002; Valéry, Fritz, Lefeuvre, & Simberloff, 2008; Walsh et al., 2012). In this way, Australia may have been living on borrowed time. If native diversity is lost in the future, the ecological impacts of alien bird species may increase. Therefore, there are incentives both to prevent further invasions although regulatory and cultural means, but also to limit potential impacts by maintaining native biodiversity.

We acknowledge that while our database of introduction records is useful, it is by no means complete. A complete database of all introduction events, even in discrete time, is likely impossible to generate because introduction methods such as pet escapes are too numerous and undocumented, while still being tremendously important (Hulme, 2015). However, we still included an often-used proxy in human footprint, which combined with our explicit measure of community-level propagule pressure, should be sufficient to conclude that native species richness was indeed the strongest predictor of alien species richness. Additionally, previous similar studies have suggested that a sampling bias, autocorrelation between explanatory variables or the variation in human-related variables could artificially inflate the importance of human-related or environmental drivers of alien species establishment (Blanchet et al., 2009; Leprieur et al., 2008).

In summary, in this study, we were able to examine different classes (human-oriented vs biotic community-oriented) of invasion hypotheses. Specifically, by way of comparing Australia and Europe, we showed that extent and intensity of human activity, an important contextual consideration, can influence how we evaluate drivers of species invasion and therefore various invasion hypotheses. By simultaneously analysing the importance of human-related and natural variables in explaining alien bird richness, we showed that in the context of Australia—a relatively recently and lesser human-impacted country—the “rich get richer” model of species invasion is valid at a coarse spatial resolution. We have shown that both human activity, whether in the form of introduction effort or modifying habitat, and biotic acceptance (the “rich get richer”) could play a complementary role in shaping patterns of species invasion. While human activity can seem less important ecologically, its importance is only highlighted from a management perspective. Once an alien species is established, the surrounding native community can facilitate invasion. Given that wholesale modification of the landscape in order to stop invasion spread is not likely feasible—not to mention the potential negative impacts on the native community—targeting human facilitators of invasion is still the best option for preventing future invasions. However, by comparing two continents with varying human impact histories, we show that merely considering human-related variables is not sufficient for evaluating regional susceptibility to invasion, particularly in lesser impacted areas.

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REFERENCES

- Australian Bureau of Statistics. (2012) *Year book Australia*, 2012. Canberra: ABS.
- Australian Government Bureau of Meteorology. (2009) Mean monthly and mean annual maximum, minimum and mean temperature data (base climatological data sets).
- Baguley, T. (2009). Standardized or simple effect size: What should be reported? *British Journal of Psychology*, *100*, 603–617.
- Barrett, G., Silcocks, A., Barry, S., Cunningham, R., & Poulter, R. (2003). *The New Atlas of Australian Birds*. (Birds Australia: Melbourne).
- Blackburn, T. M., Cassey, P., & Lockwood, J. L. (2008). The island biogeography of exotic bird species. *Global Ecology and Biogeography*, *17*, 246–251.
- Blackburn, T. M., Prowse, T. A., Lockwood, J. L., & Cassey, P. (2011). Passerine introductions to New Zealand support a positive effect of propagule pressure on establishment success. *Biodiversity and Conservation*, *20*, 2189–2199.
- Blackburn, T. M., Prowse, T. A., Lockwood, J. L., & Cassey, P. (2013). Propagule pressure as a driver of establishment success in deliberately introduced exotic species: Fact or artefact? *Biological Invasions*, *15*, 1459–1469.
- Blanchet, S., Leprieur, F., Beauchard, O., Staes, J., Oberdorff, T., & Brosse, S. (2009). Broad-scale determinants of non-native fish species richness are context-dependent. *Proceedings of the Royal Society of London B: Biological Sciences*, *276*, 2385–2394.
- Byers, J. E., & Noonburg, E. G. (2003). Scale dependent effects of biotic resistance to biological invasion. *Ecology*, *84*, 1428–1433.
- Chapin, F. S. III, Zavaleta, E. S., Eviner, V. T., Naylor, R. L., Vitousek, P. M., Reynolds, H. L., ... Diaz, S. (2000). Consequences of changing biodiversity. *Nature*, *405*, 234–242.
- Chevan, A., & Sutherland, M. (1991). Hierarchical partitioning. *The American Statistician*, *45*, 90–96.
- Chiron, F., Shirley, S., & Kark, S. (2009). Human-related processes drive the richness of exotic birds in Europe. *Proceedings of the Royal Society B: Biological Sciences*, *276*, 47–53.
- Chiron, F., Shirley, S. M., & Kark, S. (2010). Behind the iron curtain: Socio-economic and political factors shaped exotic bird introductions into Europe. *Biological conservation*, *143*, 351–356.
- Colautti, R. I., Grigorovich, I. A., & MacIsaac, H. J. (2006). Propagule pressure: A null model for biological invasions. *Biological Invasions*, *8*, 1023–1037.
- Crawley, M. J., Brown, S. L., Heard, M. S., & Edwards, G. R. (1999). Invasion-resistance in experimental grassland communities: Species richness or species identity? *Ecology Letters*, *2*, 140–148.
- Davies, K. F., Chesson, P., Harrison, S., Inouye, B. D., Melbourne, B. A., & Rice, K. J. (2005). Spatial heterogeneity explains the scale dependence of the native-exotic diversity relationship. *Ecology*, *86*, 1602–1610.
- Díaz, S., & Cabido, M. (2001). Vive la difference: Plant functional diversity matters to ecosystem processes. *Trends in Ecology & Evolution*, *16*, 646–655.
- Dukes, J. S., & Mooney, H. A. (2004). Disruption of ecosystem processes in western North America by invasive species. *Revista chilena de historia natural*, *77*, 411–437.
- Duncan, R. P., Blackburn, T. M., & Sol, D. (2003). The Ecology of Bird Introductions. *Annual Review of Ecology, Evolution, and Systematics*, *34*, 71–98.
- Dyer, E. E., Cassey, P., Redding, D. W., Collen, B., Franks, V., Gaston, K. J., ... Blackburn, T. M. (2017). The Global Distribution and Drivers of Alien Bird Species Richness. *PLOS Biology*, *15*, e2000942.
- Elton, C. S. (2000). *The ecology of invasions by animals and plants*. Chicago, Illinois, USA: University of Chicago Press.
- Eurostat. (2015). *Eurostat regional yearbook*. Luxembourg: Publications Office of the European Union.
- Fridley, J. D., Brown, R. L., & Bruno, J. F. (2004). Null models of exotic invasion and scale-dependent patterns of native and exotic species richness. *Ecology*, *85*, 3215–3222.
- Fridley, J. D., Stachowicz, J. J., Naeem, S., Sax, D. F., Seabloom, E. W., Smith, M. D., ... Holle, B. V. (2007). The Invasion Paradox: Reconciling pattern and process in species invasions. *Ecology*, *88*, 3–17.
- Grarock, K., Tidemann, C. R., Wood, J., & Lindenmayer, D. B. (2012). Is it benign or is it a pariah? Empirical evidence for the impact of the common myna (*Acridotheres tristis*) on Australian birds. *PLoS ONE*, *7*, e40622.
- Grarock, K., Tidemann, C. R., Wood, J. T., & Lindenmayer, D. B. (2014). Are invasive species drivers of native species decline or passengers of habitat modification? A case study of the impact of the common myna (*Acridotheres tristis*) on Australian bird species. *Austral Ecology*, *39*, 106–114.
- Harrell, F. E. Jr. (2008). Hmisc: harrell miscellaneous. R package version, 3.5-2.
- Herben, T., Mandak, B., Bimova, K., & Munzbergova, Z. (2004). Invasibility and species richness of a community: A neutral model and a survey of published data. *Ecology*, *85*, 3223–3233.
- Holle, B. V., & Simberloff, D. (2005). Ecological resistance to biological invasion overwhelmed by propagule pressure. *Ecology*, *86*, 3212–3218.
- Hollebone, A. L., & Hay, M. E. (2007). Propagule pressure of an invasive crab overwhelms native biotic resistance. *Marine Ecology Progress Series*, *342*, 191–196.
- Hooper, D., Solan, M., Symstad, A., Diaz, S., Gessner, M., Buchmann, N., ... Mermillod-Blondin, F. (2002). Species diversity, functional diversity and ecosystem functioning. *Biodiversity and Ecosystem Functioning: Syntheses and Perspectives*, *17*, 195–208.
- Houston, P. (2005). Re-valuing the fringe: Some findings on the value of agricultural production in Australia's peri-urban regions. *Geographical Research*, *43*, 209–223.
- Hulme, P. E. (2009). Trade, transport and trouble: Managing invasive species pathways in an era of globalization. *Journal of Applied Ecology*, *46*, 10–18.
- Hulme, P. E. (2015). Invasion pathways at a crossroad: Policy and research challenges for managing alien species introductions. *Journal of Applied Ecology*, *52*, 1418–1424.
- Hulme, P. E., Pyšek, P., Nentwig, W., & Vilà, M. (2009). Will threat of biological invasions unite the European Union? *Science*, *324*, 40–41.
- Jeschke, J., Aparicio, L. G., Haider, S., Heger, T., Lortie, C., Pyšek, P., & Strayer, D. (2012). Support for major hypotheses in invasion biology is uneven and declining. *NeoBiota*, *14*, 1.
- Kerr, J. T., & Ostrovsky, M. (2003). From space to species: Ecological applications for remote sensing. *Trends in Ecology & Evolution*, *18*, 299–305.
- Kumschick, S., & Nentwig, W. (2010). Some alien birds have as severe an impact as the most effectual alien mammals in Europe. *Biological conservation*, *143*, 2757–2762.
- Leprieur, F., Beauchard, O., Blanchet, S., Oberdorff, T., & Brosse, S. (2008). Fish invasions in the world's river systems: When natural processes are blurred by human activities. *PLoS biology*, *6*, e28.
- Levine, J. M., Adler, P. B., & Yelenik, S. G. (2004). A meta-analysis of biotic resistance to exotic plant invasions. *Ecology Letters*, *7*, 975–989.
- Littler, F. M. (1902). European birds in Tasmania. *Emu*, *1*, 121–124.
- Lockwood, J. L., Cassey, P., & Blackburn, T. M. (2005). The role of propagule pressure in explaining species invasions. *Trends in Ecology & Evolution*, *20*, 223–228.
- Lockwood, J. L., Cassey, P., & Blackburn, T. M. (2009). The more you introduce the more you get: The role of colonization pressure and propagule pressure in invasion ecology. *Diversity and Distributions*, *15*, 904–910.

- Lockwood, J. L., Hoopes, M. F., & Marchetti, M. P. (2013). *Invasion ecology*. Chichester, West Sussex, UK: John Wiley & Sons.
- Lowe, P. R. (1933). The differential characters in the tarso-metatarsi of Gallus and Phasianus as they bear on the problem of the introduction of the pheasant into Europe and the British Isles. *Ibis*, *75*, 332–343.
- Luck, G. W. (2007). A review of the relationships between human population density and biodiversity. *Biological Reviews*, *82*, 607–645.
- Mac Nally, R. (2002). Multiple regression and inference in ecology and conservation biology: Further comments on identifying important predictor variables. *Biodiversity & Conservation*, *11*, 1397–1401.
- Maron, J. L., & Vilà, M. (2001). When do herbivores affect plant invasion? Evidence for the natural enemies and biotic resistance hypotheses. *Oikos*, *95*, 361–373.
- McGeoch, M. A., Butchart, S. H. M., Spear, D., Marais, E., Kleynhans, E. J., Symes, A., ... Hoffmann, M. (2010). Global indicators of biological invasion: Species numbers, biodiversity impact and policy responses. *Diversity and Distributions*, *16*, 95–108.
- Nie, Z., & Norton, M. R. (2009). Stress Tolerance and Persistence of Perennial Grasses: The Role of the Summer Dormancy Trait in Temperate Australia. *Crop Science*, *49*, 2405–2411.
- Núñez, M. A., Moretti, A., & Simberloff, D. (2011). Propagule pressure hypothesis not supported by an 80-year experiment on woody species invasion. *Oikos*, *120*, 1311–1316.
- Olea, P. P., Mateo-Tomás, P., & de Frutos, Á. (2010). Estimating and Modelling Bias of the Hierarchical Partitioning Public-Domain Software: Implications in Environmental Management and Conservation. *PLoS ONE*, *5*, e11698.
- Olenin, S., & Didžiulis, V. (2009). Introduction to the list of alien taxa. *Handbook of alien species in Europe* (pp. 129–132). Dordrecht, Netherlands: Springer.
- Paget, M. J., & King, E. A. (2008). MODIS Land data sets for the Australian region.
- Pimentel, D., Zuniga, R., & Morrison, D. (2005). Update on the environmental and economic costs associated with alien-invasive species in the United States. *Ecological economics*, *52*, 273–288.
- Pinheiro, J. C., & Bates, D. M. (2000). *Mixed effects models in S and S-PLUS*. New York, USA: Springer.
- Pinheiro, J., Bates, D., DebRoy, S., & Sarkar, D. (2013). the R Core team (2011) nlme: linear and nonlinear mixed effects models. R package version 3.1-102.
- R Development Core Team. (2008). *R: A language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing.
- Rejmánek, M. (2003). The rich get richer – responses. *Frontiers in Ecology and the Environment*, *1*, 122–123.
- Sala, O. E., Chapin, F. S., Armesto, J. J., Berlow, E., Bloomfield, J., Dirzo, R., ... Kinzig, A. (2000). Global biodiversity scenarios for the year 2100. *Science*, *287*, 1770–1774.
- Sanderson, E. W., Jaiteh, M., Levy, M. A., Redford, K. H., Wannebo, A. V., & Woolmer, G. (2002). The Human Footprint and the Last of the Wild: The human footprint is a global map of human influence on the land surface, which suggests that human beings are stewards of nature, whether we like it or not. *BioScience*, *52*, 891–904.
- Shanahan, D. F., Lin, B. B., Gaston, K. J., Bush, R., & Fuller, R. A. (2014). Socio-economic inequalities in access to nature on public and private lands: A case study from Brisbane, Australia. *Landscape and Urban Planning*, *130*, 14–23.
- Shea, K., & Chesson, P. (2002). Community ecology theory as a framework for biological invasions. *Trends in Ecology & Evolution*, *17*, 170–176.
- Simberloff, D. (2009). The role of propagule pressure in biological invasions. *Annual Review of Ecology, Evolution, and Systematics*, *40*, 81–102.
- Sol, D., Vila, M., & Kühn, I. (2008). The comparative analysis of historical alien introductions. *Biological Invasions*, *10*, 1119–1129.
- Strauss, S. Y., Webb, C. O., & Salamin, N. (2006). Exotic taxa less related to native species are more invasive. *Proceedings of the National Academy of Sciences*, *103*, 5841–5845.
- Tardif, P. (2003). *John Bowen's Hobart: The beginning of European settlement in Tasmania*. Tasmanian Historical Research Association, Sandy Bay, Tasmania, Australia.
- Taylor, B. W., & Irwin, R. E. (2004). Linking economic activities to the distribution of exotic plants. *Proceedings of the National Academy of Sciences of the United States of America*, *101*, 17725–17730.
- TERN/AusCover. (1992-2013) AVHRR-NDVI 5 km Monthly Composite. Made available by the AusCover facility (<http://www.auscover.org.au>) of the Terrestrial Ecosystem Research Network (TERN, <http://www.tern.org.au>).
- Tilman, D. (1999). The ecological consequences of changes in biodiversity: A search for general principles 101. *Ecology*, *80*, 1455–1474.
- Valéry, L., Fritz, H., Lefeuvre, J.-C., & Simberloff, D. (2008). In search of a real definition of the biological invasion phenomenon itself. *Biological Invasions*, *10*, 1345–1351.
- Walsh, C., Mac Nally, R., & Walsh, C. (2013). The hier.part package: hierarchical partitioning. R package version 1.0-4. (<http://cran.r-project.org/>).
- Walsh, J. C., Venter, O., Watson, J. E., Fuller, R. A., Blackburn, T. M., & Possingham, H. P. (2012). Exotic species richness and native species endemism increase the impact of exotic species on islands. *Global Ecology and Biogeography*, *21*, 841–850.

SUPPORTING INFORMATION

BIOSKETCH

The Biodiversity Research Group (KarkGroup.org) is a team of academics, postdoctoral fellows and students who are interested in spatial patterns and processes shaping biodiversity, with emphasis on conservation science and ecology. The Group works on a wide range of conservation, environmental and ecological aspects and collaborates with multiple groups worldwide in both terrestrial and marine ecosystems and across spatial scales, ranging from regional to global to help solve key environmental questions and challenges, with focus on invasive and native species in a changing world. SK and MM contributed to study conception and design, as well as critical revision. MM collated, analysed, and interpreted data, and drafted the manuscript. SK provided financial support for the study.

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