Taxonomic homogenization in ungulates: patterns and mechanisms at local and global scales

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ABSTRACT

Aim The aim of this paper is to examine taxonomic homogenization in ungulates globally and at the local scale in South Africa. Specifically, we aim to examine the roles of distance, scale, time, extinctions vs. introductions, and extralimital vs. extraregional introductions in the homogenization of ungulate biotas, and to determine pathways of introduction of ungulate species globally and the proximate explanatory variables of ungulate introductions in South Africa.

Location Forty-one countries globally and three spatial resolutions in South Africa.

Methods Indigenous, extirpated and established introduced ungulate species data were obtained for countries globally, and at a quarter-degree grid-cell resolution in South Africa. Homogenization was calculated using Jaccard's index of similarity (JI) for countries globally and for three spatial resolutions in South Africa. Zoo holdings and transfer data from the International Species Information System database were used to investigate the relationship between non-indigenous ungulate species introductions and the number of non-indigenous ungulate species in zoos. Relationships between JI and species richness, and between numbers of introductions and several environmental and social factors were examined using generalized linear models.

Results Homogenization in ungulates was 2% for countries globally and 8% at the coarsest resolution in South Africa. Homogenization increased with increasing resolution and with time, but it decreased with increasing percentage change in species richness. Globally, introductions contributed more to homogenization than did extinctions. Within South Africa, extralimital introductions contributed more to the homogenization of ungulate assemblages than did extraregional ones, and ungulates were typically introduced to high-income areas with high human population and livestock densities. The same was not true in the past, when ungulates were introduced to ungulate species-poor areas. The number of non-indigenous ungulate species established in a country is significantly related to the number of non-indigenous ungulate species in zoos in the country, possibly owing to sales of surplus animals from zoos.

Main conclusions Ungulate faunas are homogenized at both the global scale and in South Africa, with extralimital introductions being of considerable significance regionally. In consequence, increasing attention will have to be given to the conservation consequences of ungulate translocations, both within particular geopolitical regions and across the globe.

Keywords

Biological invasions, conservation biogeography, *ex situ* conservation, extinctions, homogenization, mammals, scale, South Africa, temporal variation.

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INTRODUCTION

Anthropogenic, biotic homogenization is now recognized as an important problem in conservation. Regionally distinct, indigenous assemblages are being replaced with more cosmopolitan, non-indigenous ones, as a consequence of extinctions, the introduction of non-indigenous species, or some combination of the two (McKinney & Lockwood, 1999; Olden & Poff, 2004; Olden, 2006). Although biotic differentiation can result from these processes (Olden & Poff, 2003), most studies have demonstrated the converse (Olden, 2006). Homogenization has impacts distinct from invasion by single species, including reduction of resistance to environmental change, foodweb simplification, and increased susceptibility to further invasions (Olden *et al.*, 2004).

Despite its growing significance, many aspects of biotic homogenization remain poorly investigated. The range of taxa for which and the number of regions in which biotic homogenization has been explored are relatively small. Most work has focused on taxonomic homogenization in plants or fish, predominantly in continental North America (e.g. Rahel, 2000; Rejmánek, 2000; McKinney, 2004a, 2005; Taylor, 2004), with investigations of homogenization at other levels and for other groups being less common (Lockwood *et al.*, 2000; Olden, 2006; Smith, 2006). The effects of spatial scale and autocorrelation on the extent of homogenization or differentiation are also poorly documented (Taylor, 2004; Marchetti *et al.*, 2006; see also Nekola & White, 1999).

Similarly, the underlying proximate causes of homogenization are incompletely known, although they are clearly intimately related to the causes of extinction and the mechanisms that result in the successful introduction and establishment of non-indigenous species (see e.g. Lawton & May, 1995; Blackburn *et al.*, 2004; Lockwood *et al.*, 2005; Light & Marchetti, 2007). These might include urbanization, landscape alteration by humans, climate change favouring introduced over indigenous species, interactions between indigenous and invasive species, and synergies between introduced species (Richardson *et al.*, 2000; Prinzing *et al.*, 2002; Stachowicz *et al.*, 2002; Goulson, 2003; McKinney, 2006a; Richardson & Pyšek, 2006; Chown *et al.*, 2007).

Likewise, the relationships between rates of introduction and extinction, changes in species richness, and changes in community similarity at the taxonomic level are not well understood, although a wide variety of predictions have been made (Olden & Poff, 2003). In this context, the contribution of introductions of species outside their natural geographic ranges within a given geopolitical (or biogeographical) area (i.e. extralimital introductions) relative to introductions from wholly outside the geopolitical area (extraregional introductions) is poorly known. McKinney (2005) found that extralimital introductions led to greater homogenization than did extraregional introductions for fish and plants in the continental United States. Such extralimital introductions are surprisingly common, given the legislative frameworks within which introductions of non-indigenous species are regulated

(United Nations, 1993; DEST, 1996; Clinton, 1999; Anonymous, 2004; Environment Canada, 2004). They also have considerable implications for genetic homogenization (see Olden *et al.*, 2004), especially in those regions with substantial spatially structured genetic variation.

These gaps in current knowledge have been identified as 'pressing research needs' by Olden (2006), who called for further research efforts in this area. Recognizing that modern introductions of non-indigenous species constitute an unprecedented kind of environmental change (Cassey *et al.*, 2005; Ricciardi, 2007), we answer this call by investigating biotic homogenization in ungulates at the global level, and at the local level within South Africa. Ungulates were chosen for several reasons. They have a substantial history of translocation for economic (including recreational) purposes and remain of considerable interest in this regard (Hofer, 2002; Long, 2003; Dryden & Craig-Smith, 2004; Lindsey *et al.*, 2007). They have also become the subject of contentious translocation proposals for 're-wilding' (Donlan, 2005; Zimov, 2006), and, furthermore, the genetic consequences of translocations are of serious concern (Allendorf *et al.*, 2001; Hartl *et al.*, 2003; Randi, 2005). Examination of homogenization at the global level, and at the country level in South Africa, also provides substantial scope for understanding the contribution of scale to patterns of homogenization, and for understanding the proximate reasons for extralimital introductions (or translocations).

Specifically, in this study, we determine: (1) the patterns of taxonomic homogenization in ungulates for countries globally and in South Africa at three spatial resolutions; (2) how homogenization has changed over time in South Africa; (3) how homogenization differs with changes in species richness; (4) whether ungulate assemblages within a region are more likely to be homogenized by extralimital introductions than by extraregional introductions; and (5) whether extirpations within countries have contributed to homogenization and how this is likely to change if species that are currently considered to be endangered or in a higher IUCN threat category (IUCN, 2006) are considered extinct. Given that many ungulate introductions are intentional (Long, 2003; but see Brooke *et al.*, 1986; Baker, 1990 for exceptions), we also examine briefly: (6) the pathways of introduction at the global scale; and (7) proximate explanatory variables for ungulate introductions at the local scale within South Africa.

METHODS

Taxa, regions and data sources

By convention we take the ungulates to include the orders Artiodactyla and Perissodactyla (following Wilson & Reeder, 2005), acknowledging that such a grouping is polyphyletic (e.g. Bininda-Emonds *et al.*, 2007).

At the global level, the study was conducted on a geopolitical basis [i.e. by country – for similar geopolitical approaches see Qian & Ricklefs (2006) and Olden (2006)], largely because data on introduced species are typically recorded in this way (Lever,

1985; Long, 2003). Species data for each country were obtained for indigenous species from Wilson & Reeder (2005), and for established non-indigenous ungulates (EST) from Lever (1985) and Long (2003). Those indigenous species that have been extirpated (EXT) were also noted, and data for endangered ungulates were obtained from the IUCN's (2006) *Red List of Threatened Species* in order to represent those species that are likely to become extinct in the near future. In this variable, END, those species already extinct were also included.

At the local scale, the study focused on South Africa (1,219,912 km²), a country rich in both indigenous (Wilson & Reeder, 2005) and non-indigenous (Brooke *et al.*, 1986; Castley *et al.*, 2001) ungulate species. Here, a quarter-degree grid-cell (*c.* 25 km × *c.* 27 km = *c.* 675 km²) resolution was used. These data were also concatenated to one-degree grid-cells (ODGC) (*c.* 100 km × *c.* 108 km = *c.* 10,800 km²) and two-degree grid-cells (TDGCs) (*c.* 200 km × *c.* 216 km = *c.* 43,200 km²). Indigenous ungulate data were assigned to quarter-degree grid-cells (QDGCs) for a species if more than half of the grid-cell fell within the species extent of occurrence provided by Keith (2004). For ungulate introductions, the hunt and game sale advertisements in the classified section of the Afrikaans *Landbou Weekblad* (Farmer's Weekly) magazine were searched for all issues between 1965 and 2005. Hunt and sale advertisements were assumed to indicate the presence of an established population of the species in the specified area. That is, farmers were assumed to be advertising excess stock from an established population on their land. However, the absence of an advertisement does not indicate the absence of an established population, and only QDGCs with advertisement data were included in analyses. This potential bias should be kept in mind throughout. Data from large auctions were specifically excluded because the provenance of the species sold at auctions is less certain. Data collected included year, place and species. In the absence of place names, the dialling code provided was recorded. Dialling codes were assigned to QDGCs using telephone directories dating back to the relevant time period. Less than 30% of the data was compiled using dialling codes. Dialling codes covered areas of *c.* 1500 km² (just over two QDGCs) for most of the study period, but by 2005 dialling codes covered areas of up to 30,000 km². In instances where the area covered by a dialling code included several places, data were assigned to a central QDGC. Advertisements listing mobile phone numbers were not used. The coordinates of places were obtained using a hierarchy of coordinate search websites: <http://www.routes.co.za>, <http://www.fallingrain.com/world/SF> and <http://www.earth-search.net>. Data were divided into species introduced from other regions in South Africa (extralimital) and species introductions from outside the country (extraregional). For validation, the *Landbou Weekblad* data were compared with introduction data obtained from other, independent studies (see Table S1 in the Supporting Information). Typically, the congruence in species presence between the data sets was high.

To investigate the proximate explanatory variables for non-indigenous ungulate introductions at the local scale in South Africa, four predictors of the number of established introduc-

tions were examined at the QDGC scale: indigenous ungulate species richness; agricultural marginality; average annual income; and human population density (Statistics South Africa, 1996). It was assumed that introductions to farms may be made to enhance the economic viability of the farm (more pronounced in agriculturally marginal areas, in areas with low average income, and possibly in areas of low population density). Livestock data for 2005, specifically the total number of goats, cattle, sheep and pigs (Department of Agriculture, 2005), were used as a measure of marginality, as was average annual income (Statistics South Africa, 2001). The agricultural production and human population density data are likely to have changed over the 40 years of analysis. However, good spatial data on both, stretching back to 1965, are not readily available (see Evans *et al.*, 2006, for data on human population density change for South Africa between 1996 and 2001).

Analyses

Homogenization was represented by the change in similarity between sites (countries or degree grid cells) as a result of introductions, and for a second analysis as a result of both introductions and extinctions. Values of similarity were calculated using Jaccard's index of similarity (JI); that is, the number of shared species divided by the total number of species between a pairwise comparison (Jaccard, 1912). Although other estimates of turnover could potentially be used (see Koleff *et al.*, 2003), JI is appropriate for examining changes in similarities that result from alterations in the matching component of species in paired sites, and should be much less sensitive to changes in the non-shared components (see Fig. S1). EstimateS Win 7.51 (Colwell, 2005) was used to obtain the total number of species, number of shared species and JI for each pairwise comparison. Because the pairwise values are not independent of each other owing to the fact that the same place is used in multiple comparisons, sensitivity analyses were used to determine the minimum number of data points that result in statistical significance for each analysis.

Distance, spatial scale and species richness

A species-by-country matrix of indigenous ungulates was compiled to represent the state of the ungulate biota in countries globally before introductions and extirpations. Further matrices were compiled to represent the state of ungulate biotas after the introduction of non-indigenous species (recalling that only established introductions were considered), after extirpations (with and without the inclusion of IUCN red-listed species as extirpated), and as a result of both of these processes. Fifty-one ungulates were recorded as endangered (or of higher threat category) by the IUCN (2006), and of these species 32 occur in, and would be lost from, the 41 countries analysed. Only countries with both indigenous ungulates and established non-indigenous ungulates were included in the analyses. The mean country size for the 41 countries used in the analyses was

670,205 km² (data from ArcGIS 3.3, ESRI, 2002). The distance between the centroids of countries was calculated using Shirokov's spherical law of cosines (Dale, 2005).

At each spatial scale in South Africa, species matrices were also constructed for indigenous ungulates and established introductions. At the QDGC scale, matrices were compiled for extralimital and extraregional introductions. Only QDGCs with introduction data were included in analyses. The distance between degree grid-cells was calculated as above.

The importance of scale for analyses of homogenization was investigated in two ways. First, predicted mean homogenization was calculated using generalized linear models (GLMs) (normal distribution, identity-link function) and compared for countries globally and at the QDGC, ODGC and TDGC scales in South Africa using the Wald chi-square test. Second, the relationship between homogenization and log₁₀ distance was assessed at each scale using a GLM (normal distribution, identity-link function). Although the comparisons within South Africa concern a change in resolution whilst holding extent constant, the global-scale analysis includes a change not only in extent but also in resolution. The extent of the non-independence effect of the paired sites was examined by calculating the minimum number of data points that result in statistical significance. The estimates for the homogenization-distance relationships obtained from the models were then compared using the GT2 method (Sokal & Rohlf, 1997). Because Koleff *et al.* (2003) suggested that increasing scale leads to an increase in the number of shared species, and Olden (2006) proposed that homogenization increases with increasing scale and increased change in species richness, the relationships between homogenization and percentage change in species richness and between mean homogenization and the number of shared species were explored across spatial scales. Predicted mean homogenization, mean percentage change in species richness, and the mean number of shared species were obtained from GLMs (normal distribution, identity-link function), at the four scales. Pearson's product moment correlations were then used to establish the relationships between mean homogenization and mean percentage change in species richness and between mean homogenization and the mean number of shared species at the three scales in South Africa.

To assess the contribution of species-richness change to homogenization at the within-scale level, the percentage change in species richness was calculated for each pairwise country comparison and for QDGCs in South Africa as the total number of established non-indigenous ungulates at both sites divided by the total number of indigenous ungulates at both sites. The importance of species-richness change for homogenization was then assessed in two ways. First, the relationship between homogenization and log₁₀ of the total number of non-indigenous ungulates was determined using GLMs (normal distribution, identity-link function) for countries globally and for QDGCs in South Africa. Second, to establish the relationship between homogenization and log₁₀ percentage change in species richness, as is more

typically done (Olden, 2006), GLMs (normal distribution, identity-link function) were used for countries globally and for QDGCs in South Africa. A log transformation was chosen over an arcsin transformation as it was more appropriate for the data. Again, the extent of the non-independence effect was examined by calculating the minimum number of data points that result in statistical significance.

Extinctions, extraregional introductions, extralimital introductions and time

Two types of extirpations were considered on a country-by-country basis: those species that have been extirpated from countries globally (EXT); and endangered species that are likely to go extinct in the future (inclusive of those species already extirpated) (END). The importance of introductions vs. extinctions in homogenization was established by comparing the outcomes of homogenization resulting from five distinct scenarios: established non-indigenous species only (EST); extirpations only (both EXT and END); and a combination of established non-indigenous species and extirpations (both EST+EXT and EST+END). First, predicted mean homogenization as a consequence of EST, EXT, END, EST+EXT and EST+END was calculated using GLMs (normal distribution, identity-link function) and compared using the Wald chi-square test. Second, the relationships between homogenization as a result of EST, EXT, END, EST+EXT and EST+END and log₁₀ distance were assessed using GLMs (normal distribution, identity-link function). The extent of the non-independence effect was examined as above. The estimates for the homogenization-distance relationships for EST, EXT, END, EST+EXT and EST+END were then compared using the GT2 method (Sokal & Rohlf, 1997).

The relative contribution of extralimital vs. extraregional introductions to homogenization at the QDGC scale in South Africa was determined in two ways. First, predicted mean homogenization as a result of extralimital introductions, extraregional introductions and all introductions was calculated using GLMs (normal distribution, identity-link function) and compared using Wald chi-square tests. Second, the relationships between homogenization as a result of extralimital introductions, extraregional introductions and all introductions and log₁₀ distance were assessed using GLMs (normal distribution, identity-link function). The extent of the non-independence effect was examined as above. The estimates for the homogenization-distance relationships were then compared using the GT2 method (Sokal & Rohlf, 1997).

Temporal trends in homogenization were investigated in South Africa at the QDGC scale for extraregional and extralimital introductions separately. Introduction data for more than 30 QDGCs were obtained between 1965 and 1971. For each year, from 1971 to 2005, the mean homogenization resulting from extraregional introductions only and the mean homogenization resulting from extralimital introductions only

were calculated. For homogenization resulting from extraregional introductions, only QDGCs with extraregional advertisements were used in analyses. The same was done for extralimital advertisements. This approach results in a different calculation of homogenization from that above, in which the contribution of homogenization resulting from extraregional and extralimital introductions was assessed for QDGCs with any introductions (extraregional or extralimital). The relationship between mean homogenization for each year and time was determined for extralimital and extraregional introductions using GLMs (normal distribution, identity-link function). Best subset models were built using time as both a linear and a quadratic term, to determine whether a linear or quadratic function best fits the data. The Akaike information criterion was used to select the best model, with Akaike weight used to indicate the likelihood of a model being the best of the full set of models (Johnson & Omland, 2004).

Pathways and correlates of ungulate introductions

Initial assessments of data from Long (2003) and Lever (1985) suggested that ungulate introductions might be a consequence of the release of non-indigenous species from zoos. To determine whether zoos could be contributing to ungulate introductions globally, established non-indigenous ungulate data from Long (2003) and Lever (1985), and zoo holdings and transfer data from the International Species Information System (ISIS) database (ISIS, 2007) were used. Spatial autocorrelation in the data was investigated using correlograms constructed in *sam* (Rangel *et al.*, 2006). Correlograms were constructed for each variable used in this analysis, and the significance of each correlogram was determined by Oden's (1984) method. No significant spatial autocorrelation at $P < 0.05$ was found for any of the variables used in this analysis. Nonetheless, latitude and longitude were included in analyses. The relationships between the number of established non-indigenous ungulates and indigenous ungulate species richness, human population size, area of country, number of zoos in the country, number of indigenous ungulate species in zoos, non-indigenous ungulate species richness in zoos and the number of non-indigenous ungulate species sold from zoos to the public were assessed using GLMs (Poisson distribution, log-link function, corrected for overdispersion). Many of the predictor variables are highly correlated with each other (see Table S2). Before best subset models were built, collinearity was examined and removed by selecting a subset of variables that had high tolerances (see Quinn & Keough, 2003, p. 128). The variables used for the final model building were the number of ungulate species in zoos, the indigenous ungulate species richness of the country in question, its area, and the latitude and longitude of its central point. The Akaike information criterion was used to select the best model as above.

The relationships between the number of extralimital and extraregional introductions at the QDGC scale and indigenous ungulate species richness, livestock numbers, average annual

income and human population density were assessed using GLMs (Poisson distribution, log-link function, corrected for overdispersion where necessary). To investigate whether spatial autocorrelation was present in the introduction data or any of the predictor variables, correlograms were constructed using *sam* as described above. The only variable that showed significant, but typically low, values of spatial autocorrelation at $P < 0.05$ was indigenous ungulate species richness. Autocorrelation was therefore not given further consideration. In these analyses, tolerance was typically high for the independent predictors in the models and none were excluded. The Akaike information criterion was used to select the best model as above. Predictor variables were $\log_{10}$ -transformed before analyses.

RESULTS

Distance, spatial scale, and species richness

Ungulate faunas showed substantial homogenization at the local scale in South Africa (across 297 QDGCs, 91 ODGCs and 28 TDGCs), and globally for the 41 countries analysed (Figs 1 & 2). Many ungulate assemblages in close proximity to each other have become differentiated through introductions as they share more indigenous than introduced species. Over longer distances, more introduced species than indigenous species are shared (Fig. 1, Table 1a). Within South Africa, mean homogenization increased significantly from the QDGC to the TDGC scale (Fig. 2), with mean homogenization being significantly different at each scale ($\chi^2 = 238$, $P < 0.001$). However, the relationship between homogenization and distance did not differ between the ODGC and TDGC scales (Table 1a). Significant relationships were found between mean homogenization and mean species richness ($r = 0.99$,

Figure 1 The relationship between homogenization and distance for (a) countries globally ($n = 820$ pairwise comparisons), and (b) quarter-degree grid-cells in South Africa ($n = 73920$ pairwise comparisons).

Figure 2 Predicted (a) mean homogenization, (b) mean change in species richness, (c) mean percentage change in species richness and (d) mean number of shared non-indigenous (NI) species with 95% confidence limits calculated using generalized linear models (GLMs; normal distribution, identity-link function) for countries globally ($n = 820$ pairwise comparisons) and at the quarter-degree grid-cell (QDGC) ($n = 73920$ pairwise comparisons), one-degree grid-cell (ODGC) ($n = 6786$ pairwise comparisons) and two-degree grid-cell (TDGC) ($n = 378$ pairwise comparisons) resolution in South Africa.

$P < 0.001$) and mean homogenization and mean number of shared species ($r = 0.99$, $P = 0.01$) at the three local resolutions, but not between mean homogenization and mean percentage change in species richness ($r = 0.96$, $P = 0.184$).

At the QDGC scale within South Africa, increasing numbers of introductions typically resulted in differentiation of the ungulate fauna, and this was true also of an increase in the percentage change in species richness (Table 2, Fig. 3). By contrast, at the global scale, homogenization increased with the number of established introductions, but no significant relationship was found between homogenization and percentage change in species richness (Table 2, Fig. 3). The primary reason for these differences between scales appears to be a stronger relationship between the number of introductions and percentage species richness change at the QDGC scale in South Africa ($r = 0.91$, $P < 0.001$) than between countries globally ($r = 0.53$, $P < 0.001$).

Extinctions, extraregional introductions, extralimital introductions and time

At the global scale, introductions have resulted in significantly larger values of homogenization [mean homogenization ($H = 2.07 \pm 0.22\%$)] than have realized extinctions ($H = 0.44 \pm 0.20\%$; $\chi^2 = 34.20$, $P < 0.001$), and the extinctions that have taken place do not significantly increase the level of homogenization above that resulting from introductions only (EXT+EST $H = 2.32 \pm 0.27\%$; $\chi^2 = 0.49$, $P = 0.50$). When endangered taxa are presumed to become extinct, and when this value is added to known extinctions (END

$H = 1.34 \pm 0.22\%$), homogenization is significantly higher than it is from realized extinctions ($\chi^2 = 21.32$, $P < 0.001$) but still lower than homogenization resulting from introductions ($\chi^2 = 5.5913$, $P = 0.018$). However, homogenization as a result of introductions and additional extinctions (END+EST $H = 2.83 \pm 0.27\%$) is significantly higher than homogenization resulting from current introductions by themselves ($\chi^2 = 4.00$, $P = 0.046$). By contrast, extinctions tend to reduce the slope of the positive relationship between distance and homogenization, because extinctions tend to differentiate more distant sites and homogenize sites in close proximity (Table 1b).

Extraregional and extralimital introductions make quite different contributions to homogenization in South Africa at the QDGC scale. Homogenization was most profoundly influenced by introductions of extralimital species ($H = 4.61 \pm 0.07\%$), and extraregional ungulates tended to differentiate ungulate assemblages ($H = -3.83 \pm 0.07\%$). The absolute extent of homogenization resulting from extralimital species was significantly higher than that resulting from extraregional introductions ($\chi^2 = 119.11$, $P < 0.001$), and extraregional introductions greatly reduced the total homogenization when homogenization resulting from extralimital introductions was compared with homogenization resulting from all introductions ($H = 1.34 \pm 0.07\%$; $\chi^2 = 1178.1$, $P < 0.001$). Likewise, a weaker relationship between distance and homogenization was found for extraregional than for extralimital introductions (Table 1c).

From 1965 to 2005, 18 species from outside South Africa were advertised in the *Landbou Weekblad* magazine. Homogenization by extralimital introductions increased rapidly with

Table 1 The contribution of (a) scale [quarter-degree grid-cell (QDGC), one-degree grid-cell (ODGC), and two-degree grid-cell (TDGC)], (b) introductions (EST) and extinctions (EXT and END) for 41 countries, and (c) extralimital (EXTRALIM), extra-regional (EXTRAREG) and all (NI) introductions in South Africa at the QDGC resolution, to the relationship between homogenization and $\log_{10}$ distance calculated using generalized linear models (GLMs) (normal distribution, identity-link function).

	Estimate $\pm$ SE	Wald statistic	Min % data for $P < 0.05$	n
(a)				
QDGC	21.4 $\pm$ 0.2 ^A	11158	23	73,920
ODGC	26.8 $\pm$ 0.7 ^B	1470	33	6786
TDGC	29.4 $\pm$ 2.5 ^B	134	37	378
Country	5.77 $\pm$ 0.7 ^C	80	12	820
(b)				
EST	5.77 $\pm$ 0.7 ^A	80	12	820
EXT	-1.22 $\pm$ 0.3 ^B	22	4	820
END	-4.99 $\pm$ 0.4 ^C	157	21	820
EXT+EST	5.24 $\pm$ 0.7 ^{AD}	59	9	820
END+EST	3.95 $\pm$ 0.7 ^D	30	5	820
(c)				
NI	21.4 $\pm$ 0.20 ^A	11158	23	73,920
EXTRAREG	6.74 $\pm$ 0.08 ^B	8172	18	73,920
EXTRALIM	18.2 $\pm$ 0.20 ^C	7930	17	73,920

Estimate $\pm$ SE, estimate $\pm$ standard error of the GLM relationship between homogenization and $\log_{10}$ distance. Different superscript letters indicate significant differences between estimates from the GLMs based on the GT2 method. All Wald statistics are significant at $P < 0.001$. Min % data for $P < 0.05$, to account for non-independence in the data, the minimum percentage of data that results in statistical significance at $P < 0.05$ is reported. n is the number of pairwise comparisons.

time after initially having a smaller homogenizing effect than the differentiating effect of extraregional introductions (Fig. 4).

Pathways and correlates of ungulate introductions

Of the 47 countries for which data were obtained from the ISIS data base, 32 countries had zoos that sold non-indigenous

Table 2 The relationships between homogenization and non-indigenous (NI) species and homogenization and percentage change in species richness for 41 countries globally and at the quarter-degree grid-cell resolution (QDGC) in South Africa (SA) calculated using generalized linear models (GLMs) (normal distribution, identity-link function).

	Estimate $\pm$ SE	Wald statistic	Min % data for $P < 0.05$	n
$\log_{10}$ number of established NI species (Country)	6.24 $\pm$ 1.04	36	6	820
$\log_{10}$ number of established NI species (QDGC, SA)	-17.4 $\pm$ 0.24	5433	12	73,920
$\log_{10}$ % change in species richness (Country)	-2.04 $\pm$ 1.04	4	n.s.	820
$\log_{10}$ % change in species richness (QDGC, SA)	-15.9 $\pm$ 0.15	11165	23	73,920

Estimate $\pm$ SE, estimate $\pm$ standard error of the GLM relationship between homogenization and each parameter. All Wald statistics are significant at $P < 0.001$. Min % data for $P < 0.05$, to account for non-independence in the data the minimum percentage of data that results in statistical significance at $P < 0.05$ is reported. n is the number of pairwise comparisons; n.s. indicates that the relationship is not significant.

Figure 3 The relationship between homogenization and percentage change in species richness for (a) countries globally ($n = 820$ pairwise comparisons) and (b) quarter-degree grid-cells in South Africa ($n = 73920$ pairwise comparisons).

ungulates to private individuals during the period 1970–2005. One hundred and twelve ungulate species were sold from zoos in countries to which they are not indigenous. Zoos in the United States sold 92 non-indigenous ungulate species, zoos in Germany sold 57, and zoos in South Africa sold 32 non-indigenous ungulate species. Based on this information it seems likely that zoos have provided a pathway of introduction for ungulate species in the past. The best-fitting model for established, non-indigenous ungulate species in a country included the number of non-indigenous ungulate species in zoos in the country (strongly collinear with the number of non-indigenous ungulate species sold from zoos; see Table S2), the indigenous ungulate species richness of the country, and the country area and longitude (Table 3a, Akaike weight $w_i = 0.60$). Established, non-indigenous ungulate species richness is high where indigenous ungulate species richness is low and many non-indigenous ungulate species are present in zoos.

Within South Africa, the best-fitting model ($w_i = 0.70$) for numbers of extralimital introductions included all of the variables with the exception of income (Table 3b). The

Figure 4 Temporal trends in homogenization as a result of extraregional [from 1971 ($n = 190$ pairwise comparisons) to 2005 ($n = 12246$)] and extralimital [from 1971 ($n = 1035$) to 2005 ($n = 40186$)] introductions in South Africa, at the quarter-degree grid-cell resolution, between 1971 and 2005. For extralimital introductions the equation for the relationship between homogenization and time is $y = 0.0019x^2 + 0.11x + 0.39$ ($\chi^2 = 101$, $P < 0.001$), and for extralimital introductions the equation is $y = -0.0035x^2 + 0.13x - 5.42$ ($\chi^2 = 36$, $P < 0.001$), where time = year – 1970. Both models had the highest Akaike weights ($w_i > 0.95$) relative to the other models examined.

model indicates that numbers of extralimital introduced species tend to be greatest in areas of low indigenous species richness, high human population density, and high livestock numbers. For extraregional introductions, the best-fitting model ($w_i = 0.45$) suggested that the numbers of extraregional introduced species tended to be largest in

areas with greatest population density, largest numbers of livestock, and where income was highest (Table 3c).

DISCUSSION

Distance and spatial scale

In keeping with Olden & Poff's (2003) predictions and other empirical work (Qian & Ricklefs, 2006; but see also McKinney, 2004a,b, for contrasting findings), introduced species increased differentiation at small distances, but reduced it over large ones. This outcome was largely a result of positive autocorrelation of indigenous assemblages over shorter distances (Thomson *et al.*, 1996; Legendre & Legendre, 1998; van Rensburg *et al.*, 2002), which increases the likelihood that introduced species will differentiate assemblages in close proximity to each other. By contrast, more distant sites will be more different than expected by chance, and the addition of introduced species therefore has a greater likelihood of increasing their similarity. At the largest distances ($c. > 10,000$ km), globally, countries share no indigenous species. In consequence, differentiation cannot proceed further, resulting in a hard boundary at 0% change (Fig. 1). Above these distances, the only possibility of multiple introductions is either no change in homogenization, or an increase thereof. As distance between sites declines below this threshold, which is likely to be taxon-specific, given differences among groups in average range sizes and dispersal abilities (Brown *et al.*, 1996; Gaston, 2003; Lester *et al.*, 2007), an increasing number of species will be shared, enabling the differentiation of sites with the addition of new species.

Changes in the resolution and extent of studies are expected to influence values of homogenization (see Olden & Poff, 2003

Table 3 The top three generalized linear models (Poisson distribution, log-link function, corrected for overdispersion) for (a) the number of established non-indigenous ungulates in each country, (b) the number of extralimital ungulates per quarter-degree grid-cell (QDGC) in South Africa and (c) the number of extraregional ungulates per quarter-degree grid-cell (QDGC) in South Africa.

	AIC	w_i	χ^2	n
(a) Number of established non-indigenous ungulates in each country				
NISPPZOO ⁺ + INDIG ⁺ + AREA ⁺ + LAT [–]	123	0.60	61	41
NISPPZOO ⁺ + INDIG ⁺ + AREA ⁺ + LAT [–] + LONG ⁺	125	0.22	61	41
NISPPZOO ⁺ + INDIG ⁺ + LAT [–]	126	0.13	53	41
(b) Number of extralimital ungulates per QDGC in South Africa				
INDIG [–] + POP ⁺ + LIVESTOCK ⁺	753	0.70	77	284
INDIG [–] + POP ⁺ + LIVESTOCK ⁺ + INCOME ^{–NS}	754	0.30	77	284
POP ⁺ + LIVESTOCK ⁺	776	0.00	51	284
(c) Number of extraregional ungulates per QDGC in South Africa				
POP ⁺ + INCOME ⁺ + LIVESTOCK ⁺	483	0.45	20	157
POP ⁺ + INCOME ⁺ + LIVESTOCK ⁺ + INDIG ^{–NS}	485	0.16	20	157
POP ⁺ + LIVESTOCK ⁺	486	0.14	15	157

Best subset models were selected using the Akaike information criterion (AIC) and Akaike weights (w_i). The direction of relationship is in superscript for each predictor variable. NS indicates that the relationship is not significant. All maximum log-likelihood ratio chi-square (χ^2) results were significant at $P < 0.001$. n is the number of pairwise comparisons.

NISPPZOO, number of non-indigenous ungulate species in zoos; INDIG, indigenous ungulate species richness; AREA, area of country; LAT, latitude of country; LONG, longitude of country; POP, human population density; LIVESTOCK, total livestock numbers; INCOME, mean annual income.

and below). Nonetheless, with adequate recognition of the influence of scale on homogenization, the present results can be compared with those of previous studies conducted using JI (see Table S3). The largest extent analysed to date using species identities and JI has been plants in North America at the province and state resolution (Rejmánek, 2000; Qian & Ricklefs, 2006). The largest resolution examined has been territories and provinces in Canada (Taylor, 2004). Although narrower in extent than the present work, it is nonetheless clear that homogenization values found here at the global scale (2%) are larger than those found for plants in North America (Rejmánek, 2000; Qian & Ricklefs, 2006) and fish in Canada (Taylor, 2004), but lower than those found for fish in the United States (Rahel, 2000). Like the QDGC-scale data used in this study, the finest-resolution studies that have been conducted are not contiguous (Radomski & Goeman, 1995; McKinney, 2004b; Castro *et al.*, 2007). The homogenization results for plants (McKinney, 2004a; Castro *et al.*, 2007) compare well with homogenization seen at the QDGC scale here (1%). The TDGC resolution (8% homogenization) can be compared with studies on fish at a zoogeographic province resolution in California (Marchetti *et al.*, 2001) and at a basin resolution in the Iberian Peninsula (Clavero & García-Berthou, 2006), which in both cases show much higher homogenization than was documented here.

In keeping with Olden's (2006) prediction, homogenization increased with a decline in spatial resolution. Differential detectability or observation of introductions and extinctions (Olden & Poff, 2003; Olden, 2006) cannot account for this result, given the way in which this study was done. Rather, the change in homogenization is probably a consequence solely of the way that grain influences patterns of spatial autocorrelation among indigenous species and among introductions. Generally, it is expected that the matching (or shared species) component (see Fig. S1) of JI will increase with coarser grain owing to growing positive autocorrelation, and therefore growing continuity among pairwise site comparisons (Lennon *et al.*, 2001). In consequence, the increase in homogenization with coarser grain size found here means that the numbers of introduced species common to assemblages in paired sites must increase more rapidly than the number of indigenous species common to both assemblages. Clearly, at some point this differential will not be sustainable, and therefore one might expect a decline as resolution becomes even coarser. This effect probably explains the similarity between the homogenization values at the global and QDGC scales found in the present study.

Although JI is sensitive to total species richness and to richness differences between sites (Lennon *et al.*, 2001; Koleff *et al.*, 2003), its behaviour provides a measure of homogenization, owing to the introduction of non-indigenous species, that accords with expectation. In other words, homogenization is recorded as greater when a fixed number of new shared species is added to species-poor assemblages than it is when the same number of shared new species is added to species-rich assemblages. Likewise, if species richness differs between

assemblages, the symmetry of the index means that it is relatively insensitive to these differences as long as they are largely restricted to the non-shared component (see Fig. S1) of the assemblages (see Koleff *et al.*, 2003). By contrast, differences in the matched component of assemblages mean substantial changes in JI, which is precisely what is meant by homogenization via the introduction of new, shared species. Olden & Poff (2003) criticized change in JI as a measure of homogenization when they noted that this measure results in an 'inflation' of homogenization in species-poor assemblages by comparison with species-rich assemblages. At least on a species-richness basis (i.e. ignoring the fact that single species can have substantial impacts on whole systems – see, for example, Courchamp *et al.*, 2003; O'Dowd *et al.*, 2003), it is our view that this 'inflation' is precisely what should be recorded as homogenization. Two assemblages that previously had a total of 10 species, of which five were shared, and which following introductions have an additional five shared species are clearly more homogenized than two assemblages that have a total of 200 species, with 100 shared initially, and 105 shared following invasion. Although many other indices of turnover exist, they often show complex patterns of response of each of the components to changing richness. Moreover, in several cases they are more sensitive to species gains and losses than to continuity (reviewed in Koleff *et al.*, 2003). If the aim of a study is to document homogenization as a consequence of species extinctions (a significant component of the homogenization process – see McKinney & Lockwood, 1999), then some of these other indices may be more useful than JI, especially because JI is much less sensitive to losses of non-shared species than it is to gains of shared species. However, when homogenization as a consequence of introductions is the major focus of an investigation, then JI is appropriate.

Species richness and homogenization

The influence of a change in species richness on homogenization differed between South Africa (at the QDGC scale) and the global investigation. In the former case, both an increase in numbers of introduced ungulate species and an increase in the percentage species richness of a pair of sites resulted in differentiation of the assemblages. The similarity of these results is a consequence of the strong relationship between the number of introduced species and the change in percentage species richness. Sites with the greatest change in percentage species richness (and highest number of introductions) tend to have been species-poor sites where different new ungulate species were added. However, this tendency shows considerable variation, and it is clear from Fig. 3 that a site showing 100% increase in richness could either show homogenization or differentiation. Moreover, a lower bound to differentiation also exists as a consequence of different introductions to initially identical assemblages (Fig. 3). For example, if two assemblages with a Jaccard similarity of 1, i.e. $b = c = 0$ (see Fig. S1), face an increase in species richness of 50%, where none of the introduced species are shared,

differentiation = $1 - (a/(0.5a + a)) = 0.3333$, where a equals the number of shared species initially, and, in this case, a also equals the total number of species initially. The maximal change in similarity is likely to be reached in instances where two assemblages originally have no species in common, and the introduced species are those already indigenous to one of the assemblages (although they may come from elsewhere in their range). Olden (2006) showed a strong positive logarithmic relationship between homogenization and percentage change in species richness for fish and plants using previously published data sets. Marchetti *et al.* (2001) and Rooney *et al.* (2004) showed positive linear relationships, in fish and plants, respectively. However, homogenization in South African ungulates shows a negative relationship with percentage change in species richness as a result of large numbers of different ungulate species introductions to species-poor assemblages.

At the global scale, the relationship between the number of introduced species and the percentage change in species richness is weak ($r = 0.53$, $P < 0.001$), so accounting for the significant relationship between homogenization and number of ungulate introductions, but the absence of such a relationship with percentage change in species richness. In other words, large numbers of additions do not typically lead to large changes in percentage species richness, and *vice versa*. Overall, at the global scale the effect of changing species richness on homogenization was generally weak, and, although it was positive, the data showed much variation.

Homogenization, extinctions, and the provenance of introductions

At the global scale, extinctions contributed only marginally to changes in homogenization (typically $< 0.5\%$). However, when extinctions predicted on the basis of IUCN endangerment criteria (a pessimistic, but perhaps not entirely unrealistic outlook – Lawton & May, 1995; Ceballos & Ehrlich, 2002; Thomas *et al.*, 2004) were incorporated into the analyses, the resultant changes in homogenization significantly increased homogenization by introductions only. Indeed, homogenization by extinction may be an underestimate, given that JI is typically less sensitive to changes in species gains and losses than to changes in species continuity (Koleff *et al.*, 2003). However, using indices that are more sensitive to gains and losses invariably means underestimating changes in continuity, and therefore no additional analyses were undertaken here. Nonetheless, these results show that, whereas introductions may presently be the major cause of homogenization owing to larger numbers of introductions than extinctions (see also Gaston *et al.*, 2003), this situation could change as extinction proceeds and larger numbers of species go extinct (McKinney & Lockwood, 1999). Moreover, the spatial pattern of this homogenization is likely to be complex, given that extinctions (both realized and predicted) are likely to produce increasing differentiation with increasing distance between sites, whereas introductions often have the opposite effect.

Despite the recognition that the introduction of species to areas outside their typical range in a given country constitutes an introduction (McKinney, 2001, 2005; Copp *et al.*, 2005), such extralimital introductions are only beginning to be investigated from the perspective of taxonomic homogenization (McKinney, 2005). However, translocations of this nature have long been of conservation concern because of the likelihood of interspecific hybridization (Fabricius *et al.*, 1988), and because such introductions may have a substantial influence on local ecosystems from which they were previously absent (e.g. Bond & Loffell, 2001). Our results demonstrate not only that extralimital introductions are the major source of homogenization of ungulate assemblages in South Africa, and that they tend to increase the similarity of distant sites more substantially than extraregional introductions, but also that over time the increase in homogenization owes more to translocations within the country than to the introduction of species from outside the country. Although extraregional introductions can clearly lead to substantial impacts on systems (and the invasions literature is concerned largely with such impacts – Vitousek *et al.*, 1996; Clavero & García-Berthou, 2005), the potential for changes in patterns of diversity and system functioning as a consequence of translocations should not be underestimated.

Pathways and correlates of introductions

At present, the predictors of numbers of extralimital and extraregional introductions are similar. More species are introduced to areas with higher incomes and greater livestock density than to areas with lower incomes and lower livestock density, probably reflecting the tendency of game farms and similar operations to introduce species from elsewhere (Appendix S1 and Table S4). One exception was the tendency for extralimital introductions to take place into areas with low indigenous species richness. The large available pool of extralimital species for introduction to species-poor areas can account for the relationship, which also bears out the suggestion that introductions are made to increase diversity in areas that are 'devoid' of ungulate species to attract hunting or ecotourism clients (Castley *et al.*, 2001). The closest analogy is the introduction of game fish to areas with low indigenous fish diversity (McKinney, 2001). To determine whether there is a stronger relationship than would be expected between extralimital introductions to QDGCs and indigenous ungulate species richness a null model was run (see Appendix S1). On comparison with the null model, relatively more extralimital species are being introduced to species-rich areas (see Appendix S1).

In the past, introductions may have taken place for different reasons. When relationships between the numbers of extraregional introductions and each of the independent variables were examined year-by-year, initially the trends were quite different from those found for the present (Appendix S1 and Fig. S2). That is, new extraregional ungulate species tended to be introduced into areas that were species-poor for indigenous

ungulate species and less productive for livestock (Fig. S2). However, the trend gradually vanished, with income and population density remaining as the major predictors (Fig. S2). In other words, through time, more introductions have been made to higher-income, more densely populated areas than to others. The influence of large urban areas placing larger numbers of game advertisements cannot account for the trend because it remains when data from these areas are excluded from the analysis (results not shown).

In many ways, the present (rather than the presumed historical) correlates accord with what has been found in other studies. For example, McKinney (2001) found significant positive relationships between non-indigenous plant species richness and human population density in the United States, as did Smith (2006) for herptiles in Florida, and McKinney (2006a) for mammals, herptiles and plants at a global scale. These relationships between non-indigenous species and human population numbers are probably related to propagule pressure (Williamson, 1996; Colautti *et al.*, 2006), and to the circumstances that promote higher species richness generally. In the latter case, indigenous and introduced species richness are strongly related at large spatial scales both in South Africa (Richardson *et al.*, 2005) and elsewhere (e.g. Chown *et al.*, 2005; Fridley *et al.*, 2007), as are indigenous species richness and human population density (Chown *et al.*, 2003; Gaston, 2004). Nonetheless, in other taxa, such as non-indigenous fish in the United States (McKinney, 2001) and birds globally (McKinney, 2006b), introduced species richness is not significantly related to human population density.

At the global scale, our analyses suggest that introductions tend to take place to species-poor countries, and, curiously, that introductions are positively related to the numbers of non-indigenous ungulate species in zoos in that country. Although the latter relationship does not necessarily imply cause and effect, it is clear from the ISIS database that zoos sell off their surplus animals to non-zoo buyers. The number of non-indigenous ungulate species sold from zoos in a country is also strongly correlated with the number of ungulate species in zoos in that country (Table S2). Sales from zoos are often the subject of a formal permitting process (at least in some provinces of South Africa), and will not necessarily lead to the kinds of consequences that invasive, as opposed to introduced, naturalized species (see Pyšek *et al.*, 2004, for definitions) will have for conservation. Nonetheless, that any relationship at all between numbers of established introductions and numbers of zoo holdings should exist is cause for at least some concern. Although the relationship may well result from an unrelated, underlying variable, it does suggest that the manner in which zoos deal with surplus animals needs to be given some thought. Of course, not all *ex situ* conservation results in the supplementation of indigenous populations by surplus stock.

In conclusion, this study of homogenization in ungulates in many ways bears out theoretical expectations and empirical findings from other groups. It indicates that homogenization in ungulates has taken place, and that extralimital introductions may be of considerable significance in the process

regionally. Our results indicate that increasing attention will have to be given to the conservation consequences of ungulate translocations, both within particular geopolitical regions and across the globe.

ACKNOWLEDGEMENTS

We thank the National Zoological Gardens of South Africa for access to the ISIS, *Landbou Weekblad* for access to back issues, John Wilson for help with the null model, and John Wilson, Nicola van Wilgen and two anonymous referees for commenting on an earlier version of the manuscript.

REFERENCES

- Allendorf, F.W., Leary, R.F., Spruell, P. & Wenburg, J.K. (2001) The problems with hybrids: setting conservation guidelines. *Trends in Ecology and Evolution*, **16**, 613–622.
- Anonymous (2004) National Environmental Management: Biodiversity Act. *Government Gazette*, vol. 467, no. 26436, pp. 1–84. Cape Town.
- Baker, S.J. (1990) Escaped exotic mammals in Britain. *Mammal Review*, **20**, 75–96.
- Bininda-Emonds, O.R.P., Cardillo, M., Jones, K.E., MacPhee, R.D.E., Beck, R.M.D., Grenyer, R., Price, S.A., Vos, R.A., Gittleman, J.L. & Purvis, A. (2007) The delayed rise of present-day mammals. *Nature*, **446**, 507–512.
- Blackburn, T.M., Cassey, P., Duncan, R.P., Evans, K.L. & Gaston, K.J. (2004) Avian extinction and mammalian introductions on oceanic islands. *Science*, **305**, 1955–1958.
- Bond, W.J. & Loffell, D. (2001) Introduction of giraffe changes *Acacia* distribution in a South African savanna. *African Journal of Ecology*, **39**, 286–294.
- Brooke, R.K., Lloyd, P.H. & de Villiers, A.L. (1986) Alien and translocated terrestrial vertebrates in South Africa. *The ecology and management of biological invasions in southern Africa* (ed. by I.A.W. Macdonald, F.J. Kruger and A.A. Ferrar), pp. 63–74. Oxford University Press, Cape Town.
- Brown, J.H., Stevens, G.C. & Kaufman, D.M. (1996) The geographic range: size, shape, boundaries, and internal structure. *Annual Review of Ecology and Systematics*, **27**, 597–623.
- Cassey, P., Blackburn, T.M., Duncan, R.P. & Chown, S.L. (2005) Concerning invasive species: reply to Brown and Sax. *Austral Ecology*, **30**, 475–480.
- Castley, J.G., Boshoff, A.F. & Kerley, G.I.H. (2001) Compromising South Africa's natural biodiversity – inappropriate herbivore introductions. *South African Journal of Science*, **97**, 344–348.
- Castro, S.A., Munoz, M. & Jaksic, F.M. (2007) Transit towards floristic homogenization on oceanic islands in the south-eastern Pacific: comparing pre-European and current floras. *Journal of Biogeography*, **34**, 213–222.
- Ceballos, G. & Ehrlich, P.R. (2002) Mammal population losses and the extinction crisis. *Science*, **296**, 904–907.
- Chown, S.L., van Rensburg, B.J., Gaston, K.J., Rodrigues, A.S.L. & van Jaarsveld, A.S. (2003) Energy, species richness,

- and human population size: conservation implications at a national scale. *Ecological Applications*, **13**, 1233–1241.
- Chown, S.L., Hull, B. & Gaston, K.J. (2005) Human impacts, energy availability and invasion across Southern Ocean Islands. *Global Ecology and Biogeography*, **14**, 521–528.
- Chown, S.L., Slabber, S., McGeoch, M.A., Janion, C. & Leinaas, H.P. (2007) Phenotypic plasticity mediates climate change responses among invasive and indigenous arthropods. *Proceedings of the Royal Society B: Biological Sciences*, **274**, 2531–2537.
- Clavero, M. & García-Berthou, E. (2005) Invasive species are a leading cause of animal extinctions. *Trends in Ecology and Evolution*, **20**, 110.
- Clavero, M. & García-Berthou, E. (2006) Homogenization dynamics and introduction routes of invasive freshwater fish in the Iberian peninsular. *Ecological Applications*, **16**, 2313–2324.
- Clinton, W.J. (1999) *Invasive species*. Executive order 13112, The White House, Washington.
- Colautti, R.I., Grigorovich, I.A. & MacIsaac, H.J. (2006) Propagule pressure: a null model for biological invasions. *Biological Invasions*, **8**, 1023–1037.
- Colwell, R.K. (2005) *EstimateS: statistical estimation of species richness and shared species from samples*, Version 7.5. <http://purl.oclc.org/estimateS>.
- Copp, G.H., Bianco, P.G., Bogutskaya, N.G., Eros, T., Falka, I., Ferreira, M.T., Fox, M.G., Freyhof, J., Gozlan, R.E., Grabowska, J., Kovac, V., Moreno-Amich, R., Naseka, A.M., Penaz, M., Povz, M., Przybylski, M., Robillard, M., Russell, I.C., Stakenas, S., Sumer, S., Vila-Gispert, A. & Wiesner, C. (2005) To be or not to be, a nonnative freshwater fish? *Journal of Applied Ichthyology*, **21**, 242–262.
- Courchamp, F., Chapuis, J.-L. & Pascal, M. (2003) Mammal invaders on islands: impact, control and control impact. *Biological Reviews*, **78**, 347–383.
- Dale, P. (2005) *Introduction to mathematical techniques used in GIS*. CRC Press, Boca Raton, FL.
- Department of Agriculture (2005) *Estimated livestock numbers*. Agricultural Statistics Division, Department of Agriculture, Pretoria, South Africa.
- DEST (1996) *National strategy for the conservation of Australia's biological diversity*. Department of the Environment, Sport and Territories, Canberra, Australia.
- Donlan, J. (2005) Re-wilding North America. *Nature*, **436**, 913–914.
- Dryden, G.M. & Craig-Smith, S.J. (2004) *Safari hunting of Australian exotic wild game*. Rural Industries Research and Development Corporation, Barton.
- Environment Canada (2004) *An invasive alien species strategy for Canada*. Government of Canada, Ottawa.
- ESRI (2002) *ArcView 3.3*. Environmental Systems Research Institute Inc., Redlands.
- Evans, K.L., van Rensburg, B.J., Gaston, K.J. & Chown, S.L. (2006) People, species richness and human population growth. *Global Ecology and Biogeography*, **15**, 625–636.
- Fabricsius, C., Lowry, D. & van den Berg, P. (1988) Fecund black wildebeest x blue wildebeest hybrids. *South African Journal of Wildlife Research*, **18**, 35–37.
- Fridley, J.D., Stachowicz, J.J., Naeem, S., Sax, D.F., Seabloom, E.W., Smith, M.D., Stohlgren, T.J., Tilman, D. & Von Hollei, B. (2007) The invasion paradox: reconciling pattern and process in species invasions. *Ecology*, **88**, 3–17.
- Gaston, K.J. (2003) *The structure and dynamics of geographic ranges*. Oxford University Press, Oxford.
- Gaston, K.J. (2004) Macroecology and people. *Basic and Applied Ecology*, **5**, 303–307.
- Gaston, K.J., Jones, A.G., Hänel, C. & Chown, S.L. (2003) Rates of species introduction to a remote oceanic island. *Proceedings of the Royal Society B: Biological Sciences*, **270**, 1091–1098.
- Goulson, D. (2003) Effects of introduced bees on native ecosystems. *Annual Review of Ecology, Evolution and Systematics*, **34**, 1–26.
- Hartl, G.B., Zachos, F. & Nadlinger, K. (2003) Genetic diversity in European red deer (*Cervus elaphus* L.): anthropogenic influences on natural populations. *Comptes Rendus Biologies*, **326**, S37–S42.
- Hofer, D. (2002) *The lion's share of the hunt: trophy hunting and conservation: a review of the legal Eurasian tourist hunting market and trophy trade under CITES*. TRAFFIC Europe, Brussels.
- ISIS (2007) *International species information system*. <http://www.isis.org>.
- IUCN (2006) *IUCN red list of threatened species*. <http://www.iucnredlist.org>.
- Jaccard, P. (1912) The distribution of the flora in the alpine zone. *New Phytologist*, **11**, 37–50.
- Johnson, J.B. & Omland, K.S. (2004) Model selection in ecology and evolution. *Trends in Ecology and Evolution*, **19**, 101–108.
- Keith, M. (Technical ed.) (2004) *Geographic information system (GIS) data of South African mammal taxa*. Department of Zoology and Entomology, University of Pretoria, Pretoria. <http://zoology.up.ac.za/samammals/>.
- Koleff, P., Gaston, K.J. & Lennon, J.L. (2003) Measuring beta diversity for presence-absence data. *Journal of Animal Ecology*, **72**, 367–382.
- Lawton, J.H. & May, R.M. (1995) *Extinction rates*. Oxford University Press, New York.
- Legendre, P. & Legendre, L. (1998) *Numerical ecology*. Elsevier, Amsterdam.
- Lennon, J.J., Koleff, P., Greenwood, J.J.D. & Gaston, K.J. (2001) The geographical structure of British bird distributions: diversity, spatial turnover and scale. *Journal of Animal Ecology*, **70**, 966–979.
- Lester, S.E., Ruttenberg, B.I., Gaines, S.D. & Kinlan, B.P. (2007) The relationship between dispersal ability and geographic range size. *Ecology Letters*, **10**, 745–758.
- Lever, C. (1985) *Naturalized mammals of the world*. Longman Inc., New York.
- Light, T. & Marchetti, M.P. (2007) Distinguishing between invasions and habitat changes as drivers of diversity loss

- among California's freshwater fishes. *Conservation Biology*, **21**, 434–446.
- Lindsey, P.A., Roulet, P.A. & Romanach, S.S. (2007) Economic and conservation significance of the trophy hunting industry in sub-Saharan Africa. *Biological Conservation*, **134**, 455–469.
- Lockwood, J.L., Brookes, T.M. & McKinney, M.L. (2000) Taxonomic homogenization of the global avifauna. *Animal Conservation*, **3**, 27–35.
- Lockwood, J.L., Cassey, P. & Blackburn, T. (2005) The role of propagule pressure in explaining species invasions. *Trends in Ecology and Evolution*, **20**, 223–228.
- Long, J.L. (2003) *Introduced mammals of the world: their history, distribution, and influence*. CSIRO publishing, Collingwood.
- Marchetti, M., Light, T., Feliciano, J., Armstrong, T., Hogan, Z., Viers, J. & Moyle, P.B. (2001) Homogenization of California's fish fauna through abiotic change. *Biotic homogenization* (ed. by J.L. Lockwood and M.L. McKinney), pp. 259–278. Kluwer Academic/Plenum Publishers, New York.
- Marchetti, M.P., Lockwood, J.L. & Light, T. (2006) Effects of urbanization on California's fish diversity: differentiation, homogenization and the influence of spatial scale. *Biological Conservation*, **127**, 310–318.
- McKinney, M.L. (2001) Effects of human population, area, and time on non-native plant and fish diversity in the United States. *Biological Conservation*, **100**, 243–252.
- McKinney, M.L. (2004a) Do exotics homogenize or differentiate communities? Roles of sampling and exotic species richness. *Biological Invasions*, **6**, 495–504.
- McKinney, M.L. (2004b) Measuring floristic homogenization by non-native plants in North America. *Global Ecology and Biogeography*, **13**, 47–53.
- McKinney, M.L. (2005) Species introduced from nearby sources have a more homogenizing effect than species from distant sources: evidence from plants and fishes in the USA. *Diversity and Distributions*, **11**, 367–374.
- McKinney, M.L. (2006a) Correlated non-native species richness of birds, mammals, herptiles and plants: scale effects of area, human population and native plants. *Biological Invasions*, **8**, 415–425.
- McKinney, M.L. (2006b) Urbanization as a major cause of biotic homogenization. *Biological Conservation*, **127**, 247–260.
- McKinney, M.L. & Lockwood, J.L. (1999) Biotic homogenization: a few winners replacing many losers in the next mass extinction. *Trends in Ecology and Evolution*, **14**, 450–453.
- Nekola, J.C. & White, P.S. (1999) The distance decay of similarity in biogeography and ecology. *Journal of Biogeography*, **26**, 867–878.
- O'Dowd, D.J., Green, P.T. & Lake, P.S. (2003) Invasional 'meltdown' on an oceanic island. *Ecology Letters*, **6**, 812–817.
- Oden, N.L. (1984) Assessing the significance of a spatial correlogram. *Geographical Analysis*, **16**, 1–16.
- Olden, J.D. (2006) Biotic homogenization: a new research agenda for conservation biogeography. *Journal of Biogeography*, **33**, 2027–2039.
- Olden, J.D. & Poff, N.L. (2003) Toward a mechanistic understanding and prediction of biotic homogenization. *The American Naturalist*, **162**, 442–460.
- Olden, J.D. & Poff, N.L. (2004) Ecological processes driving biotic homogenization: testing a mechanistic model using fish faunas. *Ecology*, **85**, 1867–1875.
- Olden, J.D., Poff, N.L., Douglas, M.R., Douglas, M.E. & Fausch, K.D. (2004) Ecological and evolutionary consequences of biotic homogenization. *Trends in Ecology and Evolution*, **19**, 18–24.
- Prinzing, A., Durka, W., Klotz, S. & Brandl, R. (2002) Which species become aliens? *Evolutionary Ecology Research*, **4**, 385–405.
- Pyšek, P., Richardson, D.M., Rejmánek, M., Webster, G.L. & Williamson, M. (2004) Alien plants in checklists and floras: towards better communication between taxonomists and ecologists. *Taxon*, **53**, 131–143.
- Qian, H. & Ricklefs, R.E. (2006) The role of exotic species in homogenizing flora. *Ecology Letters*, **9**, 1293–1298.
- Quinn, G.P. & Keough, M.J. (2003) *Experimental design and data analysis for biologists*. Cambridge University Press, Cambridge.
- Radomski, P.J. & Goeman, T.J. (1995) The homogenizing of Minnesota lake fish assemblages. *Fisheries*, **20**, 20–23.
- Rahel, F.J. (2000) Homogenization of fish faunas across the United States. *Science*, **288**, 854–856.
- Randi, E. (2005) Management of wild ungulate populations in Italy: captive-breeding, hybridisation and genetic consequences of translocations. *Veterinary Research Communications*, **29**, 71–75.
- Rangel, T.F.L.V.B., Diniz-Filho, J.A.F. & Bini, L.M. (2006) Towards an integrated computational tool for spatial analysis in macroecology and biogeography. *Global Ecology and Biogeography*, **15**, 321–327.
- Rejmánek, M. (2000) A must look for North American biogeographers. *Diversity and Distributions*, **6**, 208–211.
- van Rensburg, B.J., Chown, S.L. & Gaston, K.J. (2002) Species richness, environmental correlates, and spatial scale: a test using South African birds. *The American Naturalist*, **159**, 566–577.
- Ricciardi, A. (2007) Are modern biological invasions an unprecedented form of global change? *Conservation Biology*, **21**, 329–336.
- Richardson, D.M. & Pyšek, P. (2006) Plant invasions: merging the concepts of species invasiveness and community invasibility. *Progress in Physical Geography*, **30**, 409–431.
- Richardson, D.M., Pyšek, P., Rejmánek, M., Barbour, M.G., Panetta, F.D. & West, C.J. (2000) Naturalization and invasion of alien plants: concepts and definitions. *Diversity and Distributions*, **6**, 93–107.
- Richardson, D.M., Rouget, M., Ralston, S.J., Cowling, R.M., van Rensburg, B.J. & Thuiller, W. (2005) Species richness of alien plants in South Africa: environmental correlates and

- the relationship with indigenous plant species richness. *Écoscience*, **12**, 391–402.
- Rooney, T.P., Wiegmann, S.M., Rogers, D.A. & Waller, D.M. (2004) Biotic impoverishment and homogenization in unfragmented forest understory communities. *Conservation Biology*, **18**, 787–798.
- Smith, K.G. (2006) Patterns of nonindigenous herpetofaunal richness and biotic homogenization among Florida counties. *Biological Conservation*, **127**, 327–335.
- Sokal, R.R. & Rohlf, F.J. (1997) *Biometry: the principles and practice of statistics in biological research*, 3rd edn. W.H. Freeman & co., New York.
- Stachowicz, J.J., Fried, H., Osman, R.W. & Whitlatch, R.B. (2002) Biodiversity, invasion resistance, and marine ecosystem function: reconciling pattern and process. *Ecology*, **83**, 2575–2590.
- Statistics South Africa (1996) *Population census, 1996*. <http://www.statssa.gov.za>
- Statistics South Africa (2001) *Personal income data, 2001*. <http://www.statssa.gov.za>
- Taylor, E.B. (2004) An analysis of homogenization and differentiation of Canadian freshwater fish faunas with an emphasis on British Columbia. *Canadian Journal of Fisheries and Aquatic Sciences*, **61**, 68–79.
- Thomas, C.D., Cameron, A., Green, R.E., Bakkenes, M., Beaumont, L.J., Collingham, Y.C., Erasmus, B.F.N., de Siqueira, M.F., Grainger, A., Hannah, L., Hughes, L., Huntley, B., van Jaarsveld, A.S., Midgley, G.F., Miles, L., Ortega-Huerta, M.A., Peterson, A.T., Phillips, O.L. & Williams, S.E. (2004) Extinction risk from climate change. *Nature*, **427**, 145–148.
- Thomson, J.D., Weiblen, G., Thomson, B.A., Alfaro, S. & Legendre, P. (1996) Untangling multiple factors in spatial distributions: lilies, gophers, and rocks. *Ecology*, **77**, 1698–1715.
- United Nations (1993) *Convention on biological diversity*. UN Treaty Series. No. 30619. Vol. 1760, New York.
- Vitousek, P.M., Dantonio, C.M., Loope, L.L. & Westbrooks, R. (1996) Biological invasions as global environmental change. *American Scientist*, **84**, 468–478.
- Williamson, M. (1996) *Biological invasions*. Chapman & Hall, London.
- Wilson, D.E. & Reeder, D.M. (2005) *Mammal species of the world*, 3rd edn. John Hopkins University Press, Baltimore.
- Zimov, S.A. (2006) Pleistocene Park: return of the mammoth's ecosystem. *Science*, **308**, 796–798.

SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Appendix S1 Supplementary methods and supplementary results.

Figure S1 Schematic of parameters used to calculate JI.

Figure S2 Temporal trends in correlates of extraregional introductions.

Table S1 Extraregional ungulate introduction data, for South Africa, from the literature.

Table S2 Correlation matrix of predictors of ungulate introductions to countries.

Table S3 Extent and resolution of homogenization studies using JI.

Table S4 Provincial correlates of ungulate introductions.

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Editor: Lisa Manne