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

Dian Spear* and Steven L. Chown

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.
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,
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 (extraliminal) 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 introductions 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 (recollecting 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 1964 km².
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 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 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 \( \log_{10} \) 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 \( \log_{10} \) 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 \( \log_{10} \) 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 \( \log_{10} \) 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. Auto-correlation 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 ($r = 0.99$, $P < 0.001$).

![Figure 1](image.png)

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).
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, extraliminal introductions and time

At the global scale, introductions have resulted in significantly larger values of homogenization \( \text{mean homogenization} (H) = 2.07 \pm 0.22\% \) 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 \( (\text{EXT+EST} \ H = 2.32 \pm 0.27\%; \chi^2 = 0.49, \ P = 0.50) \). When endangered taxa are presumed to become extinct, and when this value is added to known extinctions \( (\text{END} \ H = 1.34 \pm 0.22\%) \), 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 \( (\text{END+EST} \ H = 1.34 \pm 0.07\%) \) 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 extraliminal introductions make quite different contributions to homogenization in South Africa at the QDGC scale. Homogenization was most profoundly influenced by introductions of extraliminal 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 extraliminal 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 extraliminal 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 extraliminal introductions (Table 1c).

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

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).

<table>
<thead>
<tr>
<th>Estimate ± SE</th>
<th>Wald statistic</th>
<th>Min % data for (P &lt; 0.05)</th>
<th>(n)</th>
</tr>
</thead>
<tbody>
<tr>
<td>log(_{10}) number of established NI species (Country)</td>
<td>6.24 ± 1.04</td>
<td>36</td>
<td>6</td>
</tr>
<tr>
<td>log(_{10}) number of established NI species (QDGC, SA)</td>
<td>−17.4 ± 0.24</td>
<td>5433</td>
<td>12</td>
</tr>
<tr>
<td>log(_{10}) % change in species richness (Country)</td>
<td>−2.04 ± 1.04</td>
<td>4</td>
<td>n.s.</td>
</tr>
<tr>
<td>log(_{10}) % change in species richness (QDGC, SA)</td>
<td>−15.9 ± 0.15</td>
<td>11165</td>
<td>23</td>
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</table>

Estimate ± SE, estimate ± 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-indepen-
dence 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.

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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 \((n = 73920 pairwise comparisons)\).

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 (EST 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 homogeni-
zation and log\(_{10}\) distance calculated using generalized linear
models (GLMs) (normal distribution, identity-link function).

<table>
<thead>
<tr>
<th>Estimate ± SE</th>
<th>Wald statistic</th>
<th>Min % data for (P &lt; 0.05)</th>
<th>(n)</th>
</tr>
</thead>
<tbody>
<tr>
<td>(a) QDGC</td>
<td>21.4 ± 0.2(^A)</td>
<td>11158</td>
<td>23</td>
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<tr>
<td>ODGC</td>
<td>26.8 ± 0.7(^B)</td>
<td>1470</td>
<td>33</td>
</tr>
<tr>
<td>TDGC</td>
<td>29.4 ± 2.5(^B)</td>
<td>134</td>
<td>37</td>
</tr>
<tr>
<td>Country</td>
<td>5.77 ± 0.7(^IC)</td>
<td>80</td>
<td>12</td>
</tr>
<tr>
<td>(b) EST</td>
<td>5.77 ± 0.7(^A)</td>
<td>80</td>
<td>12</td>
</tr>
<tr>
<td>EXT</td>
<td>−1.22 ± 0.3(^B)</td>
<td>22</td>
<td>4</td>
</tr>
<tr>
<td>END</td>
<td>−4.99 ± 0.4(^C)</td>
<td>157</td>
<td>21</td>
</tr>
<tr>
<td>EXT+EST</td>
<td>5.24 ± 0.7(^{AD})</td>
<td>59</td>
<td>9</td>
</tr>
<tr>
<td>END+EST</td>
<td>3.95 ± 0.7(^{D})</td>
<td>30</td>
<td>5</td>
</tr>
<tr>
<td>(c) NI</td>
<td>21.4 ± 0.20(^A)</td>
<td>11158</td>
<td>23</td>
</tr>
<tr>
<td>EXTRAREG</td>
<td>6.74 ± 0.08(^B)</td>
<td>8172</td>
<td>18</td>
</tr>
<tr>
<td>EXTRALIM</td>
<td>18.2 ± 0.20(^C)</td>
<td>7930</td>
<td>17</td>
</tr>
</tbody>
</table>

Estimate ± SE, estimate ± 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-indepen-
dence 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.
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.

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

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 ($\chi^2$) 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,
Homogenization in ungulates

differentiation \( = 1 - \frac{a(0.5a + a)}{a} \) = 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 substantively 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.

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REFERENCES


DEST (1996) *National strategy for the conservation of Australia’s biological diversity*. Department of the Environment, Sport and Territories, Canberra, Australia.


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.


**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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