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# Forecasting faunal and floral homogenization associated with human population geography in North America

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## ABSTRACT

Human population and urbanization is unprecedented in its rate of growth and geographic scope. With the help of humans, exotic species have piggybacked their way to distant lands, which in combination with the loss of endemic native species, has led to the convergence of biological communities toward common and ubiquitous forms. However, the extent to which this “biotic homogenization” varies along gradients of human population size and urbanization remains mostly unexplored, especially at broad spatial scales. The present paper combines a recent conceptual model of homogenization with estimates of species invasions and extinctions to provide the first estimates of homogenization for five major taxonomic groups – land birds, freshwater fish, terrestrial mammals, plants, and freshwater reptiles and amphibians – at the continental-scale of North America (exclusive of Mexico). On average, the greatest levels of biotic homogenization were predicted for plants (22%) and fishes (14%), followed by reptiles/amphibians (12%), mammals (9%) and birds (8%). Substantial spatial variation in predictions of community similarity exists and emphasize that the outcome of species invasions and extinctions may not only increase community similarity, but may also decrease it (i.e., differentiation). Homogenization is predicted to be greatest for fish in southwestern and northeastern US, highest in eastern North America for plants, greatest for birds and mammals along the west coast of North America, and peak in southern US for reptiles and amphibians. We show that predicted change in community similarity for all taxonomic groups is positively related to human population size and urbanization, thus providing the first quantitative linkage between human population geography and homogenization for a number of major taxonomic groups at the continental-scale of North America. Our study helps identify regional hotspots of biotic homogenization across North America, thus setting the stage for future studies where more directed investigations of biotic homogenization along urban gradients can be conducted.

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## 1. Introduction

The 20th century has witnessed the radical alteration of the world’s population geography. Human population size and urbanization continue to increase at unprecedented rates,

and have exacted substantial ecological costs on the outlying rural environment (Wakermagel et al., 2002). As noted by the urban historian, Lewis Mumford (1961), the ecological impacts of urbanization are experienced far beyond the urban fringe, where “the inadequate and impaired carry capacity

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of the urbanized region is offset by the plundering of non-urban hinterlands". Indeed, human activities are taxing the environment in a great number of ways, not in the least through the overexploitation of our natural resources (e.g., Fitzhugh and Richter, 2004).

Humanity's migrations across, and subsequent urbanization of, the landscape have had innumerable effects on the many organisms in which we share this world (McKinney, 2002). Implications of human population geography (used here to refer to the size and distribution of human populations) include environmental degradation and the transport and introduction of foreign species, both of which are considered primary threats to native species persistence (Vitousek et al., 1997; Wilcove et al., 1998). In the face of increased human dominance of the biosphere, recent decades have seen significant changes in biodiversity. Global species diversity has decreased over time as a result of native species extinctions, but at regional and local scales species diversity has typically increased because the introduction of exotic species have outpaced the loss of native species (Sax and Gaines, 2003). However, increases in local or alpha-diversity is commonly at the expense of decreased beta-diversity or increased community similarity among regions. The process by which regionally distinct, native communities are gradually replaced by locally expanding, cosmopolitan, non-native communities is called biotic homogenization (McKinney and Lockwood, 1999). Biotic homogenization is considered among the greatest threats to biological life, and is now recognized as a distinct facet of the broader biodiversity crisis having significant ecological and evolutionary consequences (Olden et al., 2004). Evidence for homogenization is widespread and encompasses a number of faunal and floral groups (e.g., Rahel, 2000; Rejmánek, 2000; Blair, 2001; Duncan and Lockwood, 2001; Marchetti et al., 2001; Jokimäki and Kuisanlahti-Jokimäki, 2003; Crooks et al., 2004; McKinney, 2004a; Rooney et al., 2004).

The role of human population geography in homogenizing faunas and floras of North America is the subject of this paper. Anthropogenic change to natural environments associated with humans is considered one of the primary threats to biodiversity (Sala et al., 2000), but what remains unclear is the manner such impacts influence rates and specific outcomes of species invasions and extirpations and therefore shape patterns of biotic homogenization. Current ecological knowledge support the potential linkage between human population geography and homogenization. First, a wealth of empirical evidence supports strong associations between human population size and the number of threatened/extinct and introduced species (e.g., Kerr and Currie, 1995; Kirkland and Ostfeld, 1999; McKinney, 2001a; McKee et al., 2003). Second, evidence also points strongly to the more obvious importance of species invasions and extinctions in driving the homogenization of biotas (McKinney and Lockwood, 1999; Rahel, 2002; Olden et al., 2004).

By virtue of these empirical relationships, one would expect that biotic homogenization should vary directly as a function of human population size and urbanization. Indeed, quantitative evidence for this association exists at small spatial scales for birds (Blair, 2001, 2004; Jokimäki and Kuisanlahti-Jokimäki, 2003; Crooks et al., 2004) and fishes

(Walters et al., 2003), although much progress is still needed on this topic (see subsequent papers in this special issue). Because only a limited number of studies have formally quantified homogenization, there is a need to establish statistical associations between characteristics of human populations and homogenization so that we can forecast spatial and temporal patterns of biotic homogenization. This is particularly important given that studies of homogenization at broad spatial scales have focused almost exclusively on freshwater fishes (e.g., Rahel, 2000; Taylor, 2004), and we therefore know very little about levels of homogenization for most other taxonomic groups.

The objective of this study is to explore interrelationships between gradients of human population geography and patterns of biotic homogenization across North America. We use estimates of species invasions and extinctions for political divisions of North America and the predictive model of Olden and Poff (2003) to predict patterns biotic homogenization/differentiation for 5 major taxonomic groups – land birds, freshwater fish, terrestrial mammals, plants, and reptiles and amphibians. Estimates of faunal and floral homogenization are then associated with human population size and urbanization across these regions with the goal of better understanding the correlative nature of this relationship at broad spatial scales for multiple taxonomic groups.

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## 2. Methods

Our analysis was fourfold. First, we calculated measures of human population geography for the 63 political divisions (10 provinces and 3 territories of Canada and 50 states of the United States) of North America (excluding Mexico). Second, using electronic databases and published sources we quantified the number of threatened/endangered/extinct (hereafter called TEE species) and non-native species for each division for each of 5 major taxonomic groups – land birds, freshwater fish, terrestrial mammals, terrestrial plants, and reptiles and amphibians. Third, we used species richness data and the model of Olden and Poff (2003) to predict expected levels of change in community similarity (i.e., homogenization or differentiation) according to 14 different invasion-extinction scenarios. We then examined spatial patterns of model predictions for each taxonomic group according to those invasion-extinction scenarios believed to be playing the most dominant role in nature according to the literature. Next, we validated the model using empirical estimates of homogenization for the only faunal group in North America having quantitative data at a broad spatial scale – fish. Fourth, we examine the relationship between human population and model estimates of community similarity change for each taxonomic group.

### 2.1. Quantifying human population geography

We calculated two descriptors of human population geography that have been used extensively in literature and have repeatedly shown negative associations with species diversity: (1) total population size expressed on a log<sub>10</sub>-scale, and (2) urban population size expressed as the percentage of the total population residing in urban areas. We also included to-

tal surface area (km<sup>2</sup>) to account for the potential effects of political division size in the analysis. All data were obtained from Statistics Canada Census (<http://www.statcan.ca/>) and US Census Bureau (<http://www.census.gov/>) for the year 2000.

## 2.2. Estimating TEE and non-native species richness

The number of TEE and non-native species was calculated for each of 63 political divisions for each of 5 major taxonomic groups in North America. The number of TEE species for all taxonomic groups in Canada was obtained from two recent publications: *Wild Species* report by the Canadian Endangered Species Conservation Council (CESCC, 2001) and *Canadian Species at Risk* report by the Committee on the Status of Endangered Wildlife in Canada (COSEWIC, 2004). We included those species classified as either extirpated/extinct or at risk from CESCC (2001) or as extinct, extirpated, endangered or threatened from COSEWIC (2004). For the United States, TEE species richness was derived from the following sources: bird species from *AviBase*, 2003; fish and plant species from the *Precious Heritage* report produced by the Natural Heritage Program (Stein et al., 2000) that included only those species classified as presumed extinct, possibly extinct, critically imperiled, imperiled or vulnerable (see McKinney, 2001a for details); and mammal and reptile/amphibian species from US Natural Heritage Programs and Conservation Data Centers, and publications by the US Fish and Wildlife Service and State Departments of Natural Resources and Game and Fish. For bird, mammal and reptile/amphibian species we included those species presumed extinct or listed as threatened or endangered under federal or state laws as of December 2004.

The number of non-native species for all taxonomic groups in Canada was obtained from CESCC (2001) and COSEWIC (2004), except for plant species data, which were collected from the *Invasive Species of Canada Survey* by Haber (2002). For the United States, the number of non-native species was derived from the following sources: bird species from *AviBase*, 2003; fish from Fuller et al. (1999), mammal and reptile/amphibian species from publications by the US Fish and Wildlife Service and State Departments of Natural Resources and Game and Fish; and plant species from a recent overview of the United States' biological resources (Mac et al., 1998). For all taxonomic groups we tallied the total number of non-native species introduced from either outside the focal state or from outside of North America (i.e., exotic) that now have confirmed self-reproducing populations. The only exception was for plant species where data availability required us to include only those species originating from outside of North America.

Although we believe the aforementioned datasets are of high quality, we note that by using them together a number of biases are likely to arise. For example, the definitions of "threatened" and "endangered" differ among data sources and, consequently, differ among taxonomic groups. Specifically, the criteria for classifying a threatened or endangered species for Canada differs from that used by the Natural Heritage Program or those defined under US federal or state law. While we recognize this and other limitation(s), these are the

best available data and we believe them appropriate for an analysis conducted at the given spatial scale.

## 2.3. Predicting faunal and floral homogenization/differentiation

Biotic homogenization is driven by the combined effects of native species extinctions and invasions of non-native species (McKinney and Lockwood, 1999). Taxonomic homogenization (used synonymously with biotic homogenization in the literature) refers to an increase in the species compositional similarity among a set of communities, and it is quantified simply as the change in the pair-wise community similarity (based on species presence/absence) over a specified time interval. Olden and Poff (2003) recently developed a conceptual model detailing how the number and manner in which species invasions and extinctions occur (called invasion–extinction scenarios) may lead to different levels of either biotic homogenization or differentiation. This model describes 14 different invasion–extinction scenarios in which interactions between native species, non-native species, and the environment can lead change in community similarity (see Fig. 1 of Olden and Poff, 2003). The scenarios are divided into three main categories: scenarios where species invasions occur without any extinction (I1–I2), scenarios where species extinctions occur with no invasions (E1–E4), and scenarios where both species invasions and extinctions occur in the recipient communities (IE1–IE8) (see Appendix A). For each invasion–extinction scenario the model uses a Monte Carlo procedure to systematically vary the following parameters across a range of values: (1) the number of introduced and extinct species; (2) the initial similarity among the communities; and (3) the initial species richness of the communities (Olden and Poff, 2003). The model output is predicted change in community similarity based on Jaccard's coefficient of similarity, the most commonly used metric to quantify homogenization. Predictions from this model were recently validated using empirical estimates of fish fauna homogenization at three spatial scales in the US (the entire continent, zoogeographic provinces in California, and watersheds within these provinces), and the results showed very strong support for the model (Olden and Poff, 2004). In summary, the conceptual model of Olden and Poff (2003) formalizes our current understanding of mechanisms driving biotic homogenization and given the universality of the invasion–extinction scenarios and its robust performance for fish communities, we argue it offers a predictive framework for forecasting future patterns of homogenization for a variety of taxonomic groups.

We applied the previously-described model to generate predictions of change in community similarity (i.e., predicted levels of homogenization or differentiation) for the political divisions of Canada and US for each of taxonomic groups. Model input parameters include the number of introduced and extinct species for each political division, the initial similarity among the divisions, and the initial species richness of the divisions. First, we used estimates of non-native and TEE species richness for each of the taxonomic groups, where TEE species richness was used to indicate the number of species that have, or are likely to, go extinct in each political division (following Duncan and Lockwood, 2001). Second, given the

wide range of initial similarities that are likely to occur in nature across the taxonomic groups, we generated model predictions for an initial community similarity of Jaccard's coefficient = 0.25 (i.e., 25% similarity in community composition). We consider this value to be both conservative and representative for the different groups, including North American fishes (mean Jaccard's coefficient = 0.21: Rahel, 2000; Taylor, 2004) and floras (mean Jaccard's coefficient = 0.43: Rejmánek, 2000). Third, because model predictions have been shown to be independent of species richness exceeding 20 (Olden and Poff, 2003), we set initial species richness to values considered reasonable for each taxonomic group, i.e.,  $n = 25$  for mammals and reptiles/amphibians,  $n = 100$  for birds and fishes, and  $n = 1000$  for plants. All simulations were conducted following the protocols of Olden and Poff (2003) and using computer macros in MatLab (The MathWorks, Natick, Massachusetts, USA).

We present model predictions for all scenarios except E1–E4 because empirical data show that the invasion of North America by non-natives is extensive. Next, we consulted the ecological literature to select the most likely invasion–extinction scenario responsible for causing changes in community similarity for each taxonomic group. We used three lines of reasoning. First, there is abundant empirical data showing that species invasions and extinction are not random, but are related in large part to intrinsic life-history characteristics of species (e.g., reviewed by McKinney, 1997; Kolar and Lodge, 2001). This rich collection of empirical evidence enabled us to reduce the possible set of scenarios to those involving the invasion of the same species and extinction of the same species (i.e., IE1–IE4). Second, non-random patterns of habitat degradation lead to non-random and patchily-distributed patterns of extinctions (e.g., Seabloom et al., 2002), thus enabling us reasonably to eliminate scenarios IE1 and IE2. Third, to distinguish whether those species driven to extinction are likely to be shared or not shared among political divisions, and thus differentiate between scenarios IE3 and IE4, we con-

sidered the size of the sampling grain (i.e., political divisions), the general zoogeography of the different taxonomic groups and the published literature. For fishes we selected scenario IE3 (see Olden and Poff, 2004), for birds and reptiles/amphibians we selected IE4 (see Blair, 2004 for birds) and for plants and mammals we averaged the predictions from scenarios IE3 and IE4 given our uncertainty in the relative roles of these two mechanisms for biotic homogenization (see Rooney et al., 2004 for plants). In short, the selected scenarios are in agreement with current empirical evidence that points to the occurrence of widespread introductions of cosmopolitan, non-native species and the non-random extirpation of native species at broad spatial scales, and therefore are likely to represent the dominant mechanisms driving the homogenization of these groups.

Model predictions for fish homogenization were validated against empirical estimates reported for Canada (Taylor, 2004) and the US (Rahel, 2000). Next, predictions of community similarity change for each taxonomic group were projected across North America and tested for their association with human population size, percent population urbanization and total surface area using multiple regression analysis.

### 3. Results

#### 3.1. Predictions of faunal and floral homogenization

Predictions of homogenization/differentiation for North America varied greatly among the taxonomic groups and within taxonomic groups depending on the invasion–extinction scenario (Table 1). Here, we limit our interpretations to those invasion–extinction scenarios that are supported by the literature to be operating at a broad spatial scale, but for completeness present the results for all scenarios. Model predictions according to scenario I1 – describing invasions by cosmopolitan species (i.e., species of the same identity) and

**Table 1 – Model predictions of faunal and floral homogenization in North America**

| Invasion–extinction scenario    | Major taxonomic group |                    |                    |                    |                         |
|---------------------------------|-----------------------|--------------------|--------------------|--------------------|-------------------------|
|                                 | Birds                 | Fishes             | Mammals            | Plants             | Reptiles and amphibians |
| <i>Invasion-only</i>            |                       |                    |                    |                    |                         |
| I1                              | 4.7 (2.2)             | 21.7 (10.8)        | 14.6 (7.2)         | 24.9 (7.7)         | 5.9 (7.2)               |
| I2                              | –2.9 (1.2)            | –10.7 (4.8)        | –7.9 (3.2)         | –12.2 (3.1)        | –3.3 (3.6)              |
| <i>Invasion and extinctions</i> |                       |                    |                    |                    |                         |
| IE1                             | –4.2 (10.9)           | 16.6 (12.1)        | 0.2 (13.2)         | 19.6 (10.4)        | –16.3 (21.1)            |
| IE2                             | 12.2 (8.4)            | 31.3 (16.4)        | 32.1 (11.9)        | 33.3 (13.0)        | 19.8 (15.1)             |
| IE3                             | –5.4 (8.7)            | <b>13.6 (12.6)</b> | <b>–3.4 (12.0)</b> | <b>16.4 (11.5)</b> | –15.2 (16.4)            |
| IE4                             | <b>7.8 (4.1)</b>      | 25.8 (12.8)        | <b>21.5 (8.4)</b>  | <b>28.5 (9.3)</b>  | <b>12.0 (8.8)</b>       |
| IE5                             | –12.1 (11.9)          | –16.8 (9.0)        | –23.8 (11.3)       | –18.7 (9.4)        | –26.3 (20.7)            |
| IE6                             | 1.9 (4.2)             | –8.8 (5.2)         | –1.8 (6.1)         | –10.8 (3.5)        | 4.0 (7.5)               |
| IE7                             | –12.4 (9.1)           | –16.8 (8.4)        | –23.0 (9.2)        | –18.5 (8.4)        | –23.0 (15.6)            |
| IE8                             | –0.9 (1.8)            | –9.8 (5.0)         | –5.4 (4.1)         | –11.6 (3.1)        | –0.2 (4.4)              |

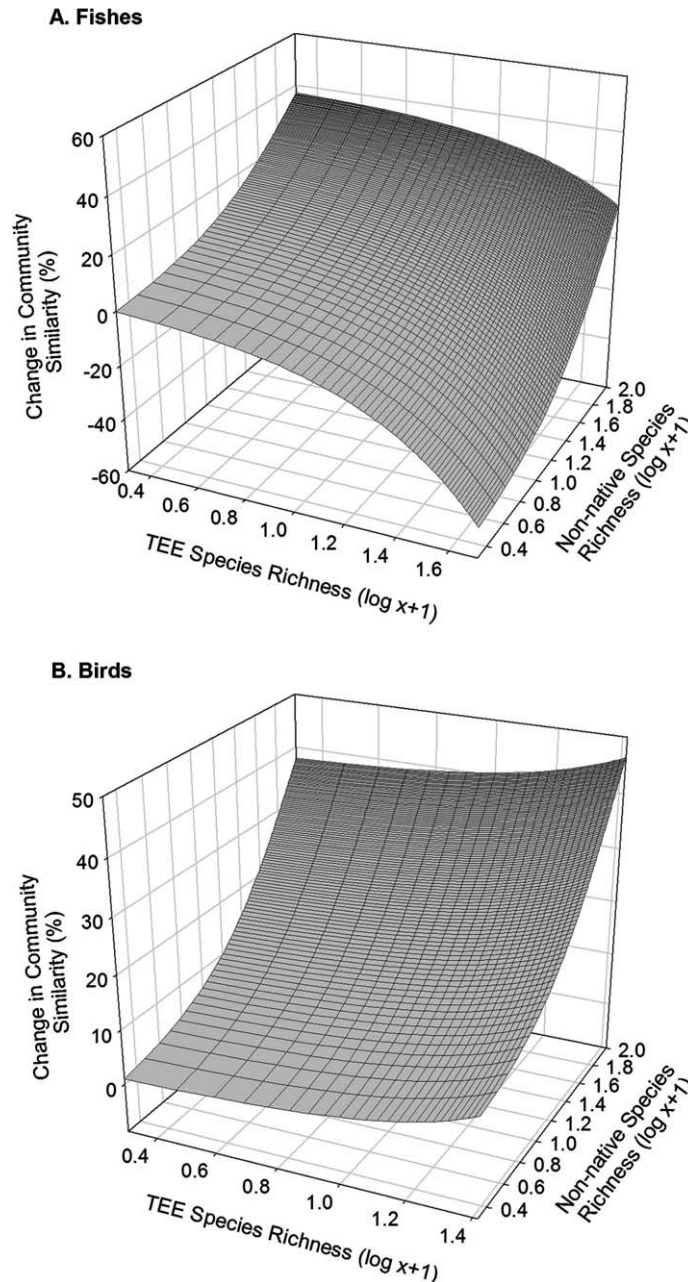
Reported values are mean and standard deviation (in parentheses) of change in community similarity, where positive values indicate homogenization and negative values indicate differentiation. Values are averaged across political divisions of Canada and the US. Underlined-bold values indicate the invasion–extinction scenario that current ecological knowledge suggests may be the most dominant driver of homogenization for the particular taxonomic group (see text). Scenario descriptions are in Appendix A.



no species extinctions – indicated the greatest levels of homogenization for plants (25%) and fishes (22%), followed by mammals (15%), reptiles/amphibians (6%) and birds (5%). These values reflect estimates of present-day homogenization given the small number of species extinctions that have occurred.

Given the potential extinction risk to threatened and endangered species, it is more likely that changes in community similarity will be better reflected by mechanisms depicted in scenarios IE3 or IE4 (i.e., species invasions following I1 coupled with the non-random extinction of similar spe-

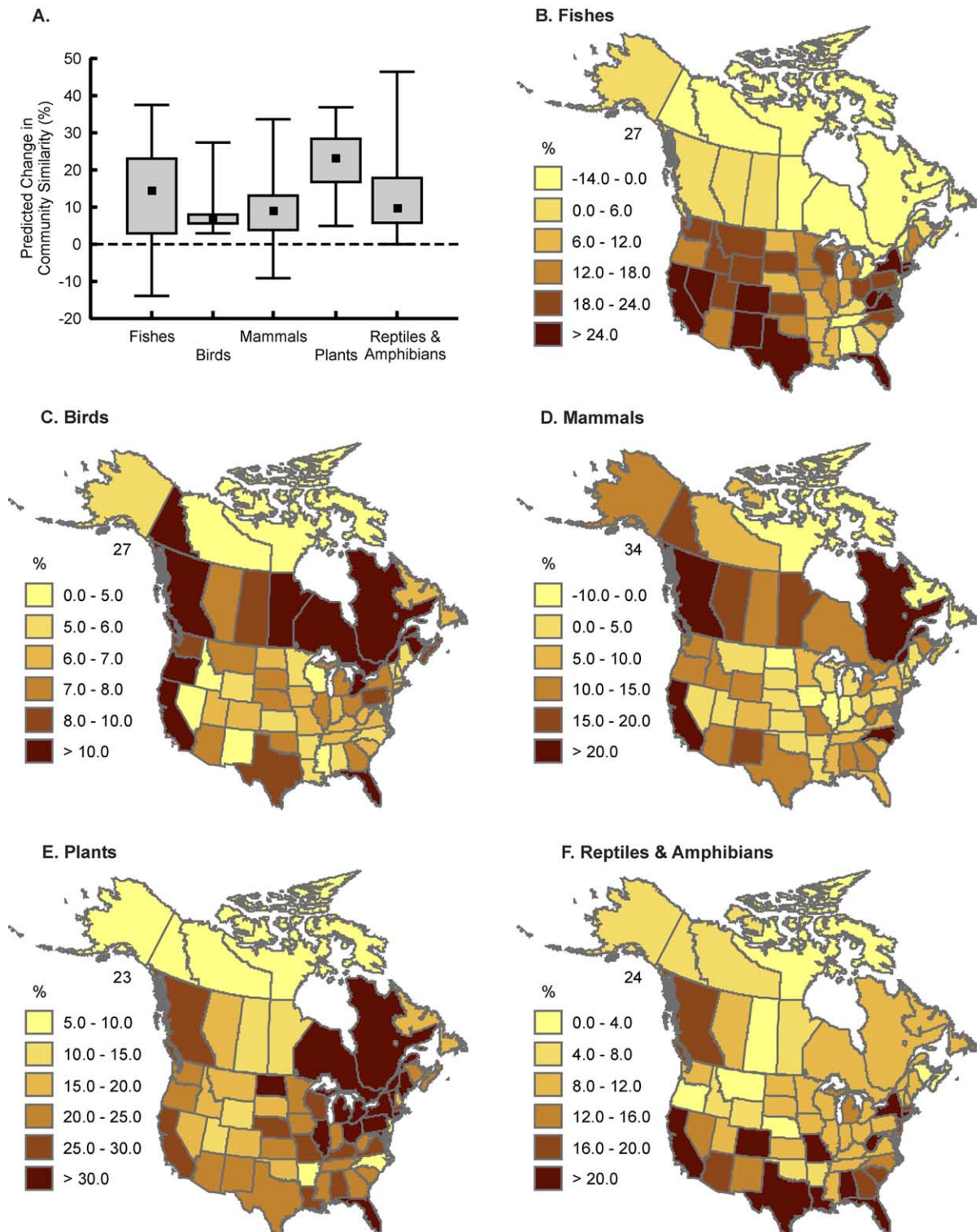
cies). According to scenario IE3, fish and plant communities of North America are, on average, predicted to exhibit homogenization whereas bird, mammal and reptile/amphibian communities are predicted to exhibit differentiation. Under this scenario, the homogenizing force of similar invasive species is countered by the differentiating force of previously shared species going extinct (i.e., communities are sharing fewer native species). This is illustrated for fishes in Fig. 1A. In contrast, under scenario IE4 the extinction of previously unshared species leads to greater similarity in community composition and resulted in predicted homogenization for



**Fig. 1 – Model predictions of change in community similarity as a function of the number of non-native and TEE species according to scenario IE3 for fishes (A) and scenario IE4 for birds (B). Positive changes indicate homogenization and negative changes indicate differentiation. Scenario descriptions are in Appendix A.**

all taxonomic groups. This is illustrated for birds in Fig. 1B. For birds, mammals and reptiles/amphibians, whether or not species driven to extinction were originally shared or

not shared, that is, whether scenario IE3 or IE4 is playing the most dominant role, dictates whether we expect mean levels of homogenization or differentiation for these groups

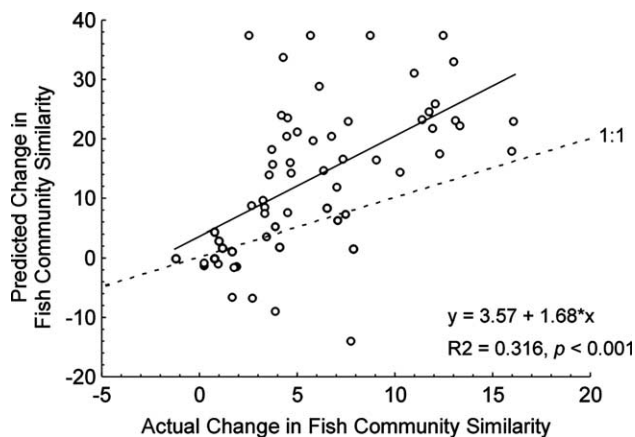


**Fig. 2** – Model predictions of change in community similarity for fishes (B), birds (C) mammals (D), plants (E) and reptiles/amphibians (F) across North America based on *a priori* invasion–extinction scenarios – see text. Predictions for Hawaii are presented numerically below Alaska. Panel A summarizes the predictions for all provinces/states, where the middle line of the box is the median, upper and lower lines are the 75th and 25th percentiles and the whiskers represent the 95% confidence interval.

in North America. Importantly, these predictions assume that TEE species are lost and no further non-native species are gained.

A number of interesting spatial patterns emerged when we mapped predictions of homogenization/differentiation for each taxonomic group according to the invasion–extinction scenario best supported by the published literature (Fig. 2, see Table 1). Homogenization of fish communities is predicted to be greatest in southwestern and northeastern US and lowest (and slight differentiation) in Canada and the southern US. Bird communities, in contrast, exhibit relatively lower levels of predicted homogenization, showing maximum levels along the western coast of North America, eastern Canada and in Florida and Hawaii. Mammals showed similar spatial patterns of predicted homogenization, with the greatest levels in western US and Hawaii and slight differentiation in central US. Predicted hotspots of plant homogenization were concentrated in northeastern North America and mid-western US, whereas the homogenization of reptile and amphibian communities was more spatially-variable, but occurred mainly in southern and southwestern US.

Next, we validated the model predictions against empirical estimates of fish community homogenization across North America, as reported by Rahel (2000) for the US and Taylor (2004) for Canada (Fig. 3). Both studies compared present day to pre-European settlement fish faunas for the 13 provinces/territories of Canada (Taylor, 2004) and the 48 conterminous states of the US (Rahel, 2000). On average, comparisons of fish faunal composition between pairs of provinces/territories and pairs of states revealed a 1.3% and 7.2% increase in similarity, respectively (mean 6.8%,  $n = 61$ ). We found a positive and statistical significant relationship between predicted and actual estimates of average pair-wise changes in community similarity among the political divisions. Importantly, however, the model consistently over-estimated fish homogenization, and the degree of this bias increased with greater observed increases in actual community similarity. These results indicate that our estimates of fish homogenization and likely the other taxonomic groups are inflated.



**Fig. 3 – Actual versus predicted change in fish community similarity for the political divisions of North America. Actual data is from Rahel (2000) for US ( $n = 50$ ) and Taylor (2004) for Canada ( $n = 13$ ).**

**3.2. Associations between human population geography and biotic homogenization**

Biotic homogenization showed a statistically significant relationship with human population geography for all major taxonomic groups (Table 2). The strength of the regression model was greatest for reptile/amphibian and plant homogenization, and weakness for mammal and bird homogenization, and on average the regression models explained only a quarter of the variation in biotic homogenization. Percent urbanization was the most effective predictor of bird, fish and mammal

**Table 2 – Results of multiple regression analysis on predicted homogenization as a function of human population size (log<sub>10</sub>-scale), percent urbanization and total area (km<sup>2</sup>)**

|                                | Coefficient  | Partial $r^2$ | P      |
|--------------------------------|--|---------------|--------|
| <i>Birds</i>                   |  |               |        |
| Population size                | -0.018   | 0.01          | 0.918  |
| % urban population             | 0.422  | 0.14          | 0.010  |
| Total area                     | 0.086  | 0.03          | 0.512  |
| Model                          | $F_{3,59} = 4.26,$<br>$R^2 = 0.180,$<br>$P = 0.009$  |               |        |
| <i>Fishes</i>                  |  |               |        |
| Population size                | 0.159  | 0.05          | 0.281  |
| % urban population             | 0.320  | 0.11          | 0.025  |
| Total area                     | -0.232   | 0.10          | 0.069  |
| Model                          | $F_{3,59} = 7.00,$<br>$R^2 = 0.263,$<br>$P < 0.001$  |               |        |
| <i>Fishes – actual</i>         |  |               |        |
| Population size                | -0.150   | 0.04          | 0.333  |
| % urban population             | 0.441  | 0.12          | <0.001 |
| Total area                     | -0.410   | 0.11          | <0.001 |
| Model                          | $F_{3,59} = 6.93,$<br>$R^2 = 0.267,$<br>$P < 0.001$  |               |        |
| <i>Mammals</i>                 |  |               |        |
| Population size                | -0.022   | 0.01          | 0.891  |
| % urban population             | 0.343  | 0.09          | 0.022  |
| Total area                     | 0.203  | 0.05          | 0.125  |
| Model                          | $F_{3,59} = 3.57,$<br>$R^2 = 0.154,$<br>$P = 0.019$  |               |        |
| <i>Plants</i>                  |  |               |        |
| Population size                | 0.549  | 0.21          | <0.001 |
| % urban population             | -0.099   | 0.04          | 0.454  |
| Total area                     | -0.139   | 0.07          | 0.242  |
| Model                          | $F_{3,59} = 9.34,$<br>$R^2 = 0.322,$<br>$P < 0.001$  |               |        |
| <i>Reptiles and amphibians</i> |  |               |        |
| Population size                | 0.432  | 0.20          | <0.001 |
| % urban population             | 0.195  | 0.10          | 0.141  |
| Total area                     | -0.065   | 0.04          | 0.577  |
| Model                          | $F_{3,59} = 10.11,$<br>$R^2 = 0.340,$<br>$P < 0.001$ |               |        |

'Actual' refers to empirical values of fish fauna homogenization based on data from Rahel (2000) and Taylor (2004).



homogenization, whereas human population size was the only significant correlate of plant and herpetofaunal homogenization. All relationships were positive, thus suggesting that human activities are related to increasing levels of biotic homogenization in North America. Model results show that bird communities illustrate the fastest rate of homogenization in response to urbanization, whereas plant homogenization was the most responsive to increases in human population size. In general, the strength of the homogenization-human population relationships were low (15–34% variance explained), however, the amount of explained variation in actual fish homogenization was remarkably similar to the amount of variation explained in predicted fish homogenization (Table 2).

#### 4. Discussion

Biotic homogenization is considered one of the most important forms of biotic impoverishment worldwide (McKinney and Lockwood, 1999) and is recognized as an important component of the modern biodiversity crisis (Olden et al., 2004). The phrase *biotic homogenization* is increasingly used in the literature, although limited empirical quantification continues to impede our ability to make robust statements regarding its magnitude and spatial extent for different taxonomic groups. In the present study we combined the predictive model of Olden and Poff (2003) with empirical data on species invasions and extinctions to provide the first quantitative estimates of homogenization for a number of major taxonomic groups at the continental-scale of North America. Using most likely ecological scenarios for each group, we predict that both faunas and floras have been homogenized across North America. This finding is supported at smaller spatial scales for birds (Blair, 2001, 2004), fishes (Radomski and Goeman, 1995; Marchetti et al., 2001), plants (McKinney, 2004a; Rooney et al., 2004) and amphibians (Duncan and Lockwood, 2001). However, substantial spatial variation in predictions of community similarity exists and emphasize that the outcome of species invasions and extinctions may not only increase community similarity, but may also decrease. In fact, in many areas of North America, we predict communities have become differentiated; a finding also supported in the literature for a number of groups: e.g., Jokimäki and Kainanlahti-Jokimäki (2003) for birds, Taylor (2004) for fishes, McKinney (2004b) for plants, Smith (this issue) for amphibians and reptiles.

Our study identifies potential hotspots of biotic homogenization across North America, thus setting the stage for future studies where more detailed and directed investigations can be conducted to quantify homogenization using empirical data, and identify the specific environmental drivers responsible for these changes. In concordance with the findings of Rahel (2000) and Taylor (2004), our results suggest that fish homogenization is greatest in southwestern and northeastern US and lowest in Canada, where slight differentiation has occurred. These patterns correspond, in large part, with areas containing the highest numbers of non-native species (Fuller et al., 1999). Plant communities are predicted to exhibit the greatest degree of biotic homogenization in eastern North America, again in areas exhibiting the highest numbers of plant invasions (McKinney, 2001a; Reichard and White,

2001). These findings support the hypothesis forwarded by Rahel (2000) and Marchetti et al. (2001) for fishes and McKinney (2004a) and Rooney et al. (2004) for plants that non-native species invasions may be more important than species extinctions in driving biotic homogenization (but see Duncan and Lockwood, 2001 for the opposing argument for highly endemic fish faunas). Our model predicts bird and mammal community homogenization to be greatest along the west coast of North America and in most of Canada, whereas community similarity for reptiles and amphibians are expected to peak in southern US. These results are in agreement with recent state-level studies for birds (Blair, 2004) and amphibians (Duncan and Lockwood, 2001), but see Smith (this issue). In addition to predictions of biotic homogenization, results from our study can be compared to empirical estimates of community similarity change (once they are available) to better understand the specific invasion and extinction processes that are likely responsible. For example, Olden and Poff (2004) found that mechanisms depicting widespread introductions of cosmopolitan fish species and either no or differential spatial patterns of native species extirpations explained fish fauna homogenization across multiple spatial scales in the US (in support of scenario I1 and IE3).

Estimates of biotic homogenization presented in this study should be interpreted with caution because they were not generated from data on species identities but from data on species richness and the perceived importance of particular mechanisms driving community change. Therefore, our predictions are, in some part, influenced by the magnitude of non-native species richness. However, given the paucity of quantitative estimates of biotic homogenization, especially at broad spatial scales, our study provides a good first-cut comparison of homogenization among different taxonomic groups. Given differences in regional rates of species invasions and extinctions (as in island vs. continental bird and plant communities: Case, 1996; Lonsdale, 1999; or between island biota: Chown et al., 1998), we would expect different degrees of biotic homogenization in different systems, as well as different mechanisms to drive these patterns. If marine species are less prone to extinction than terrestrial species (Carlton and Geller, 1993) and rates of spread of invasive species are generally lower in marine systems compared to terrestrial systems (Groscholz, 1996), we might expect greater rates of homogenization in terrestrial ecosystems. However, such predictions are independent of taxonomic patterns in species invasions, and therefore, given the relatively higher numbers of cosmopolitan species in marine ecosystems, one can predict that marine systems have exhibited greater homogenization (Rapoport, 1994). Once data are collected and synthesized in an appropriate manner, it will be possible to test such hypotheses and the model of Olden and Poff (2003) can help differentiate among candidate ecological mechanisms that best describe observed patterns of homogenization.

Our results suggest that human population growth and urbanization has paved, figuratively, the way to a period characterized by increasing levels of biotic homogenization. The present study is the first to establish a positive link between homogenization and human population geography at a broad spatial scale, and it does so for five major taxonomic groups.



Urbanization does not, by itself, identify the proximate causal mechanisms threatening the homogenization of biological communities. Recent studies, however, allude to these mechanisms for fishes and birds. In aquatic ecosystems, urbanization causes major changes in hydrology, geomorphology, and water quality that have associated impacts on fish diversity, density and biotic integrity (Allan, 2004) and fish community homogenization in the American southeast (Scott and Helfman, 2001; Walters et al., 2003). Although these latter two studies did not quantify homogenization *per se*, they did find that cosmopolitan species richness increased and endemic species richness decreased along a human impact gradient. These studies provide complementary insight into the possible mechanisms responsible for this relationship. Scott and Helfman (2001) used a watershed-scale measure of land use intensity (describing % of basin deforested, and density of buildings and roads), and suggested that land-use change associated with urbanization has essentially led to abiotic homogenization of streambed substrate conditions (in addition to water temperature). The results of Walters et al. (2003) support this idea by establishing that local-scale siltation reduces habitat complexity and favours introduced species that are silt-tolerant, while at the same time is negatively affecting endemic species. In another study, Marchetti et al. (2001) observed that measures of human occupancy and aquatic habitat alteration, including the number of dams and aqueduct density, were associated with increased fish community similarity in California. All these studies highlight that the effects of urbanization on biotic homogenization are likely to be manifested through a number of ecological mechanisms.

Urbanization has similar negative impacts on birds (Marzluff, 2001), and urban–rural gradient studies have provided important insight into associations between urbanization and avifauna homogenization. Blair (2004) found that similarity of bird communities was positively correlated along urban gradients in oak-woodlands in northern California and eastern broadleaf forests in Ohio. The overlap in the bird communities increased from approximately 5% in the least developed sites to approximately 20% in the most urbanized sites, a result of the replacement of local endemic species (often urban-sensitive species) by ubiquitous non-native species (urban-adapted species). Crooks et al. (2004) extended this comparison and found that avian assemblages in southern California were progressively more similar to those in northern California and Ohio as sites become more urban. In contrast, Jokimäki and Kaisanlahti-Jokimäki (2003) found that avifauna similarity of town centres in Europe was actually lower than in less urbanized habitats, and cautioned that urbanization should not be viewed as a process that monotonically increases the similarity of bird communities.

Although we found a significant relationship between human population size and urbanization and estimates of faunal and floral homogenization, somewhere between two-thirds and three-quarters of the variation could not be explained by our statistical models. Clearly, future research is needed to account for this residual variation, although it is interesting that similar explanatory power has been reported for threaten species richness. McKinney (2001b)

found that population density accounted for only 16–33% of the variation in nation-by-nation levels of threat to continental mammal and bird species. Similarly, Kirkland and Ostfeld (1999) could explain only 16% of the variation in the number of federally-listed mammals in the US using total population size, and Thompson and Jones (1999) only accounted for about 35% of the variation in the number of threatened plants in Britain. Although one could argue that additional variables would likely improve our predictions of biotic homogenization (i.e., variables specific to the different taxonomic groups), we believe that efforts should instead focus on developing more innovative descriptors of human population geography. For example, because the process of biotic homogenization encompass both spatial and temporal components, variables describing changes in human population geography over time and space are likely to be more predictive compared to static variables.

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## 5. Conclusion

The future is certain to bring considerable ecological shuffling as people influence ecosystems in various ways, not the least through both purposeful and accidental introduction of species. Humans are the primary agents of homogenization, yet we have many interests in slowing its progress. Urban areas provide perhaps the best example of biotic homogenization and at the same time may also provide the best opportunity for mitigation. The majority of the American public lives in or near urban areas; therefore, there may be greater opportunities for creating an informed public that can strengthen political pressure to promote conservation policies (McKinney, 2002). Indeed, residents of urban areas tend to place a much higher value on species conservation than those living in rural areas, likely because these areas are the most biological impoverished (Turner et al., 2004). Enhancing our understanding and prediction of biotic homogenization will require greater efforts in quantifying patterns of homogenization for different taxonomic groups and elucidating the major factors responsible for driving this process.

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## Appendix A

Description of the invasion–extinction scenarios in the model of Olden and Poff (2003).

### Invasion–Extinction Scenarios

#### Invasion-only

I1 – Same species invade, no extinction of resident species  
I2 – Different species invade, no extinction of resident species

#### Extinction-only

E1 – No species invasion, extinction of same species in both communities  
E2 – No species invasion, extinction of different species in both communities  
E3 – No species invasion, extinction in one community of a species that was originally shared by both communities  
E4 – No species invasion, extinction in one community of a species that was originally not shared by both communities

#### Invasion and Extinction

IE1 – Same species invade, extinction of same species in both communities  
IE2 – Same species invade, extinction of different species in both communities  
IE3 – Same species invade, extinction in one community of a species that was originally shared by both communities  
IE4 – Same species invade, extinction in one community of a species that was originally not shared by both communities  
IE5 – Different species invade, extinction of same species in both communities  
IE6 – Different species invade, extinction of different species in both communities  
IE7 – Different species invade, extinction in one community of a species that was originally shared by both communities  
IE8 – Different species invade, extinction in one community of a species that was originally not shared by both communities

## REFERENCES

- Allan, J.D., 2004. Landscapes and riverscapes: the influence of land use on stream ecosystems. *Annual Review of Ecology and Systematics* 35, 257–284.
- AviBase (2003). Available from: <http://www.bsc-eoc.org/avibase/avibase.jsp>.
- Blair, R.B., 2001. Birds and butterflies along urban gradients in two ecoregions of the United States: is urbanization creating a homogeneous fauna. In: Lockwood, J.L., McKinney, M.L. (Eds.), *Biotic Homogenization*. Kluwer Academic/Plenum Publishers, New York, pp. 33–56.
- Blair, R.B., 2004. The effects of urban sprawl on birds at multiple levels of biological organization. *Ecology and Society* 9. Available on-line from: <http://www.ecologyandsociety.org/vol9/iss5/art2/>.
- Carlton, J.T., Geller, J., 1993. Ecological roulette: the global transport and invasion of nonindigenous marine organisms. *Science* 261, 78–82.
- Case, T.J., 1996. Global patterns in the establishment and distribution of exotic birds. *Biological Conservation* 78, 97–106.
- [CESCC] Canadian Endangered Species Conservation Council. 2001. *Wild Species 2000: The General Status of Species in Canada*. Ottawa: Minister of Public Works and Government Services Canada.
- Chown, S.L., Gremman, N.J.M., Gaston, K.J., 1998. Ecological biogeography of southern ocean islands: species-area relationships, human impacts, and conservation. *American Naturalist* 152, 562–575.
- [COSEWIC] Committee on the Status of Endangered Wildlife in Canada, 2004. *Canadian Species at Risk*, May 2004.
- Crooks, K.R., Suarez, A.V., Bolger, D.T., 2004. Avian assemblages along a gradient of urbanization in a highly fragmented landscape. *Biological Conservation* 115, 451–462.
- Duncan, J.R., Lockwood, J.L., 2001. Spatial homogenization of aquatic fauna of Tennessee: extinction and invasion following land use change and habitat alteration. In: Lockwood, J.L., McKinney, M.L. (Eds.), *Biotic Homogenization*. Kluwer Academic/Plenum Publishers, New York, pp. 245–258.
- Fitzhugh, T.W., Richter, B.D., 2004. Quenching urban thirst: growing cities and their impacts on freshwater ecosystems. *BioScience* 54, 741–754.
- Fuller, P.L., Nico, G., Williams, J.D., 1999. Nonindigenous fishes introduced into inland waters of the United States. Bethesda, Maryland.
- Grosholz, E.D., 1996. Contrasting rates of spread for introduced species in terrestrial and marine systems. *Ecology* 77, 1680–1686.
- Haber, E., 2002. *Invasive Species of Canada Survey 2002*. Canadian Wildlife Service, Environment Canada.
- Jokimäki, J., Kaisanlahti-Jokimäki, M.-L., 2003. Spatial similarity of urban bird communities: a multiscale approach. *Journal of Biogeography* 30, 1183–1193.
- Kerr, J.T., Currie, D.J., 1995. Effects of human activity on global extinction risk. *Conservation Biology* 9, 1528–1539.
- Kirkland, G.L., Ostfeld, R.S., 1999. Factors influencing variation among states in the number of federally listed mammals in the United States. *Journal of Mammalogy* 80, 711–719.
- Kolar, C.S., Lodge, D.M., 2001. Progress in invasion biology: predicting invaders. *Trends in Ecology and Evolution* 16, 199–204.
- Lonsdale, W.M., 1999. Global patterns of plant invasions and the concept of invasibility. *Ecology* 80, 1522–1536.
- Mac, M.J., Opler, P.A., Haecker, C.E., Doran, P.D., 1998. *Status and Trends of the Nation's Biological Resources*, 1. US Geological Survey, Reston, Virginia.
- Marchetti, M.P., Light, T., Feliciano, J., Armstrong, T., Hogan, Z., Viers, J., Moyle, P.B., 2001. Homogenization of California's fish fauna through abiotic change. In: Lockwood, J.L., McKinney, M.L. (Eds.), *Biotic Homogenization*. Kluwer Academic/Plenum Publishers, New York, pp. 259–278.
- Marzluff, J.M., 2001. Worldwide urbanization and its effects on birds. In: Marzluff, J.M., Bowman, R., Donnelly, R. (Eds.), *Avian ecology in an urbanizing world*. Kluwer Academic, Massachusetts, USA, pp. 19–47.
- McKee, J.K., Sciulli, P.W., Foose, C.D., Waite, T.A., 2003. Forecasting global biodiversity threats associated with human population growth. *Biological Conservation* 115, 161–164.
- McKinney, M.L., 1997. Extinction vulnerability and selectivity: combining ecological and paleontological views. *Annual Review in Ecological and Systematics* 28, 495–516.

- McKinney, M.L., 2001a. 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., 2001b. Role of human population size in raising bird and mammal threat among nations. *Animal Conservation* 4, 45–57.
- McKinney, M.L., 2002. Urbanization, biodiversity, and conservation. *BioScience* 52, 883–890.
- McKinney, M.L., 2004a. Measuring floristic homogenization by non-native plants in North America. *Global Ecology and Biogeography* 13, 47–53.
- McKinney, M.L., 2004b. Do exotics homogenize or differentiate communities? Roles of sampling and exotic species richness. *Biological Invasions* 6, 495–504.
- 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.
- Mumford, L., 1961. *The City in History: Its Origins, its Transformations, and its Prospects*. Harcourt, Brace and World, Inc., New York, NY.
- Olden, J.D., Poff, N.L., 2003. Toward a mechanistic understanding and prediction of biotic homogenization. *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.
- 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.
- Rahel, F.J., 2002. Homogenization of freshwater faunas. *Annual Review of Ecology and Systematics* 33, 291–315.
- Rapoport, E.H., 1994. Remarks on marine and continental biogeography: an areographical viewpoint. *Philosophical Transactions of the Royal Society of London* 343, 71–78.
- Reichard, S.H., White, P., 2001. Horticulture as a pathway of invasive plant introductions in the United States. *BioScience* 51, 103–113.
- Rejmánek, M., 2000. A must look for North American biogeographers. *Diversity and Distributions* 6, 208–211.
- 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.
- Sala, O.E. et al., 2000. Biodiversity – global biodiversity scenarios for the year. *Science* 287, 1770–1774.
- Sax, D.F., Gaines, S.D., 2003. Species diversity: from global decreases to local increases. *Trends in Ecology and Evolution* 18, 561–566.
- Scott, M.C., Helfman, G.S., 2001. Native invasions, homogenization, and the mismeasure of integrity of fish assemblages. *Fisheries* 26, 6–15.
- Seabloom, E.W., Dobson, A.P., Stoms, D.M., 2002. Extinction rates under nonrandom patterns of habitat loss. *Proceedings of the National Academy of Science USA* 99, 11229–11234.
- Stein, B.A., Kutner, L., Adams, J., 2000. *Precious Heritage*. Oxford University Press, Oxford, UK.
- 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.
- Thompson, K., Jones, A., 1999. Human population density and prediction of local plant extinctions in Britain. *Conservation Biology* 13, 185–190.
- Turner, W.R., Nakamura, T., Dinetti, M., 2004. Global urbanization and the separation of humans from nature. *BioScience* 54, 585–590.
- Vitousek, P.M., Mooney, H.A., Lubchenco, J., Melillo, J.M., 1997. Human domination of Earth's ecosystems. *Science* 277, 494–499.
- Wakermagel, M., Schulz, N.B., Dumling, D., Linares, A.C., Jenkins, M., Kapos, V., Monfreda, C., Loh, J., Myers, N., Norgaard, R., Randers, J., 2002. Tracing the ecological overshoot of the human economy. *Proceedings of the National Academy of Science, USA* 99, 9266–9271.
- Walters, D.M., Leigh, D.S., Bearden, A.B., 2003. Urbanization, sedimentation, and the homogenization of fish assemblages in the Etowah River Basin, USA. *Hydrobiologia* 494, 5–10.
- Wilcove, D.S., Rothstein, D., Dubow, J., Phillips, A., Losos, E., 1998. Quantifying threats to imperiled species in the United States. *BioScience* 48, 607–615.