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Species compositional similarity and ecoregions: Do ecoregion boundaries represent zones of high species turnover?

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Abstract

The concept of an ecoregion, a discrete spatial area where species composition is presumed to be relatively homogeneous compared to that between areas, has become an increasingly common conservation tool. We test the effectiveness of one ecoregion delineation (World Wildlife Fund) in capturing patterns of change in species composition of birds, mammals, and trees across the United States (excluding Hawaii) and Canada, and describe the extent to which each ecoregion boundary is concurrent with relatively large changes in species composition. Digitized range maps were used to record presence/absence in 50 × 50 km equal-area grid cells covering the study area. Jaccard's index of similarity was calculated for all pairs of cells in the same or adjacent ecoregions. The average rate at which similarity declined with geographic distance was calculated using pairs of cells within the same ecoregion (intra-ecoregion turnover) or using pairs of cells in adjacent ecoregions (inter-ecoregion turnover). The intra-ecoregion rate varies widely among ecoregions and between taxa, with trees having a faster rate of similarity decline than mammals or birds. For all three species groups, most ecoregion boundaries have similar rates across them (inter-ecoregion) than that within each adjacent ecoregion (intra-ecoregion), with the exception of zones of transition between biomes and major geographical features. Although the ecoregion concept is useful for many other conservation applications, the lack of systematic, high turnover rates along ecoregion boundaries suggests that ecoregions should not be used as a quantitative basis for delineating geographic areas of a particular taxonomic group.

Keywords: Biodiversity; Species turnover; Distance decay; Jaccard's similarity index; Ranges

1. Introduction

Understanding the spatial variation in species composition is one of the fundamental goals of conservation biology (Margules and Pressey, 2000). There is a long and rich history of attempts to divide the world into discrete regions that describe biologically meaningful spatial patterns. Early efforts to delineate such regions defined zones of relatively broad spatial extent, based on climatic regimes (lifezones, Merriam, 1895; Holdridge, 1947), dominant plant physiognomy (biomes, Carpenter, 1939), or biogeographic history (realms, provinces, Agassiz, 1850; Wallace, 1894). More recently, with the concept of the ecoregion, the delineation of spatial regions has become increasingly detailed (Krupnick and Kress, 2003). Ecoregions are generally defined as finite spatial areas, smaller than a biome, where environmental conditions or species assemblages are presumed to be relatively homogeneous compared with

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the heterogeneity that occurs over a broader spatial area (cf., Ray, 1987; Olson et al., 2001). Though specific criteria used to define a set of ecoregions vary, most include information on patterns in climate, potential natural vegetation, soil type, and land surface form (Omernik, 1987; Omernik and Griffith, 1991; Bailey, 1996, 1998; Olson et al., 2001). Some ecoregion delineations additionally attempt to incorporate the biogeographic history that influences distinct biotas (Olson et al., 2001).

Designed to represent a more ecologically relevant planning unit than political boundaries, ecoregions are fast becoming a standard tool for conservation planning (Wikramanayake et al., 2002; Magnusson, 2004). In recent years, several environmental organizations including The Nature Conservancy, World Wildlife Fund, and the United States Environmental Protection Agency have used ecoregions to facilitate planning and resource allocation from local to continental scales (Ricketts et al., 1999; Olson and Dinerstein, 2002; Wikramanayake et al., 2002; Fa et al., 2004). Conceptually ecoregions are discrete units in space with distinct boundaries (cf., Olson et al., 2001), but environmental conditions and species assemblages often change in a continuous, gradual fashion. This disparity may lead to difficulties in delineating ecoregions that maximize heterogeneity (e.g., in species composition) between ecoregions, rendering distinct boundaries inappropriate where there is a continuum in environmental conditions or species assemblages. Furthermore, ecoregions are frequently delineated for the biota as a whole and may vary in their ability to represent patterns of specific groups of taxa (Mac Nally et al., 2002). The increasing use of ecoregions as units for conservation planning (Fa et al., 2004) makes testing their efficacy in describing spatially distinct environmental areas imperative (Magnusson, 2004).

Recent studies have examined patterns of species composition among ecoregions for single taxonomic groups such as plants (Wright et al., 1998), littoral macroinvertebrates (Johnson, 2000; Marchant et al., 2000), and boreal headwater streams (Heino et al., 2002), with species composition generally showing weak to moderate correspondence with ecoregion boundaries. To date, however, few studies have systematically examined the effectiveness of ecoregions at capturing spatially distinct areas for multiple taxonomic groups over a broad spatial extent.

Here, we use the best available range data (i.e., presence/absence) for birds, mammals, and trees to test the effectiveness of an ecoregion framework in capturing patterns of change in species composition across the United States and Canada. We focus on the ecoregions as defined by the World Wildlife Fund Terrestrial Ecoregions of the World (Olson et al., 2001), and consider each taxonomic group separately, to draw out ecological differences in these groups. Specifically, we ask the following questions about species turnover between two points in space, where species turnover is defined as the proportional change in species composition at a given geographic distance (i.e., Jaccard's similarity):

1. Is species turnover greater between ecoregions (i.e., across ecoregional boundaries) than within ecoregions?
2. Where do ecoregion boundaries correspond with areas of relatively high or relatively low turnover?
3. To what extent do trends vary among the three taxonomic groups?

2. Methods

2.1. Range data

We used digitized range maps for three well-studied groups (trees, mammals, and birds) for the United States and Canada to record presence/absence in 50×50 km equal-area grid cells covering the United States (excluding Hawaii) and Canada. Presence/absence data contain less information than data on absolute or relative abundance, and the patterns of turnover calculated would thus be slightly different. This is problematic because presence/absence data contain no information on transitions between two areas with identical species pools but different dominant species, even though such transitions are incorporated into ecoregion planning (Olson et al., 2001). However, there is simply no consistent source of relative abundance data on a continental scale for our three taxonomic groups, and so we proceeded with the best available data. We believe that our results are a useful first step toward analyzing continental-wide patterns of species turnover. Moreover, both presence/absence range data and ecoregion sets are being used to make conservation decisions, and analyzing their concordance is thus important in and of itself.

We based our analyses on range data rather than occurrence data (i.e., species lists for geographical units such as counties) because preliminary analyses suggested that the available occurrence data are often of poor quality, with many false absences. For example, preliminary analysis of data from the United States Division of Agriculture Plants database and from the Nature Conservancy and Natural Heritage datasets suggested that false absences posed serious problems for the analysis, although the authors concede that future analyses in other manuscripts may find ways around these problems. Range maps generally have fewer false absences than occurrence data, but instead may contain false presences which could result in an underestimation of species turnover (McCune and Grace, 2002). However, this should not bias the general conclusions of our analyses as long as the amount of false presences is not strongly geographically biased (i.e., one region has data of poorer quality for many species), which does not appear to be the case for the US and Canada. Another advantage of range maps is that they are often based on both current and short-term historical occurrence data (see primary citations below), and the process of interpolation between these data points thus smoothes over some of the most dramatic changes in species distribution caused by anthropogenic global change.

Analyses based on comparisons between range data and ecoregions are potentially confounded by inter-dependencies among data sources. Most directly, the range limits of some species, either current or (more commonly) historical, may have been used to delineate ecoregions (e.g., dominant tree species). More indirectly, species range maps are often interpolated from occurrence data using expert knowledge of the same abiotic factors (e.g., temperature, precipitation, edaphic conditions) that are often used to design a set of ecoregions. We expect that the World Wildlife Fund ecoregions avoid direct inter-dependency, as the complex, iterative process used to create this set of ecoregions did not employ single species range maps (Olson et al., 2001). Further, as we are examining rates of turnover (similarity decline per km) among numerous species, indirect data dependencies should be minimized, as range maps are developed with reference to the particular ecological factors important to each species individually. Moreover, occurrences of birds, mammals, and trees in the US and Canada are well-documented, which reduces the amount of interpolation used in preparing range maps.

Digital range datasets for birds and mammals of the Western Hemisphere have recently been compiled and are freely available on the World Wide Web with the intention that they be used for conservation activities (Patterson et al., 2003; Ridgely et al., 2003; http://natureserve.org/getDataanimalData.jsp). From these data sets, we selected all native species of birds ($n = 645$) and mammals ($n = 355$) occurring in the study area as permanent, breeding, or non-breeding residents. Species that occur only as passage migrants were omitted from the analyses, as were the portions of individual species' ranges used by the species as migration passage. Minimum mapping units are based on the resolution of the original range maps, which vary widely. Note that because the ranges of birds and mammals are fairly large compared with other taxonomic groups, our results may not speak to patterns of turnover of taxonomic groups with much smaller ranges. Moreover, as patterns of total species richness will likely be driven by other, more speciose taxonomic groups, our results may not speak to overall patterns of turnover of all North American species taken together.

Range data for 272 common tree species have been digitized from Little (1971, 1977), and are also available on the internet (http://esp.cr.usgs.gov/data/atlas/little/). We used all available, digitized range data from Little's range maps, which represent the best consistently produced data on tree species ranges for North America. Unfortunately, digitized versions of Little's maps of trees limited to Florida were not available, and so the patterns of turnover for trees in the southern portion of the state, where tree diversity increases substantially, are underestimated and potentially biased. Moreover, the fact that Little did not include all rare species in his atlas may bias observed patterns of turnover as levels of endemism are likely to vary geographically, although the pattern of turnover of common tree species should at least be correlated with the pattern of turnover of all tree species (cf., Lennon et al., 2004). Minimum mapping units for Little's range maps are undefined, but appear to be smaller (i.e., more fine-grained) than the minimum mapping units for birds or mammals. All range data were projected to Lambert equal-area projection (−100°, 45°), to minimize distortion.

A grid of 8580, 50×50 km cells was overlaid on the study region, and the presence or absence of every species in each grid cell recorded. A graphical examination of the range data suggests that 50 km cells are small enough to capture patterns of turnover within ecoregions (i.e., there are at least 10 cells in most ecoregions) but larger than the apparent minimum mapping unit of the underlying range maps (i.e., most features of the range maps are more finely detailed than 50 km blocks). We acknowledge that our use of 50 km cells prohibits us from speaking of species turnover at spatial scales smaller than 50 km, and that variation in species turnover at small scales may be governed by decidedly different ecological processes than those that affect our analysis (cf., Levin, 1992).

Three methods were tested for assigning species presence to each grid cell. The first method considered a species present if any part of a species' range touched a cell, the second method considered a species present if a majority of the cell was within a species' range, and the third method considered a species present if the entire cell was within a species' range. Preliminary analyses demonstrated similar results (i.e., Fig. 4 would look essentially identical) from all three methods and therefore only results obtained using the first methodology (i.e. any presence in a cell is enough to count) are discussed here.

2.2. Ecoregions

We used World Wildlife Fund's Terrestrial Ecoregions of the United States and Canada as our ecoregion layer. Unlike many other ecoregion classifications, which are based primarily on biophysical features such as climate and topography, World Wildlife Fund's ecoregions include biogeographic knowledge and therefore reflect the historic events and processes that have shaped biodiversity distribution. Furthermore, these ecoregions were developed primarily as units for conservation action for the entire suite of species, rather than for a single taxon (Ricketts et al., 1999; Olson et al., 2001). The 109 terrestrial ecoregions delineated for the continental United States, Canada, and Alaska were based on Omernik (1995), the Ecological Stratification Working Group (1995) and Gallant et al. (1995), respectively. These regions were then modified in several ways: merged when two neighboring ecoregions did not represent shifts in biogeographic and biodiversity patterns, or split when one ecoregion contained exceptionally distinct assemblages of species or unique habitats. The map was further modified when local experts critiqued the draft and as new data were gathered (Ricketts et al., 1999).

We included 107 ecoregions out of the 110 World Wildlife Fund ecoregions (Table 1) covering the United States (excluding Hawaii) and Canada. Two World Wildlife Fund ecoregions was excluded because they were too small for our analyses (e.g., Great Basin montane forests). One ecoregion, the Rock and Ice ecoregion, was excluded as it was a catchall category for desolate areas with little biota. Each of the grid cells used to record species distributions was assigned to the ecoregion that occupied the majority of that cell's area. Preliminary analyses using other assignment rules suggest our results are robust for a number of methods of assigning cells to ecoregions.

2.3. Statistical analyses

To test the efficacy of ecoregions in capturing homogenous species assemblages, we compared the rate of similarity decline (i.e., distance decay) of pairs of cells in the same ecoregion to that of pairs of cells in neighboring ecoregions. It is important to account for how similarity declines for distance because areas close to one another tend to be more similar than areas farther apart, whether they are in the same ecoregion or not (see discussion below). Distance decay (sensu Nekola and White, 1999) is calculated by regressing the similarity between pairs of cells against the distance between them. If ecoregion boundaries coincide with heterogeneity in species assemblages, the rate of loss of similarity in species composition (i.e., the slope coefficient from the regression, negative in all cases) should be greater (i.e., more negative) between the pair of ecoregions on either side of the boundary than within either of the ecoregions.

Inter-ecoregion pairs of cells can be geographically further apart than intra-ecoregion pairs of cells (for obvious geometric reasons), and this difference may bias the comparative rates of species turnover estimated. Accordingly, we limited our analyses only to pairs of cells, both inter- and intra-ecoregion, within 250 km of each other. This approach avoided comparing regions that are very far away from one another. In addition, we removed from the analysis inter-ecoregion pairs of cells that were outside the range of distances found in the corresponding set of intra-ecoregion pairs of cells. Due to the 250 km limit, this second filter only affected the analysis of a few small ecoregions (e.g., Arizona Mountain Forests). Graphical comparisons of the distribution of cell-to-cell distances within and across ecoregions suggest that these filters removed much of the difference in mean cell-to-cell distances.

Similarity was calculated using Jaccard's index (Jaccard, 1901) as it has performed well in both theoretical and empirical studies (Faith et al., 1987; Boyce and Ellison, 2001) that compare the various species compositional metrics, and is easily interpretable as the proportion of species shared between two sites. Note that some concerns have been raised about the appropriateness of Jaccard's and other similar indices in situations where species richness is radically different between sites (Koleff et al., 2003), but we believe that by comparing species composition in cells geographically close to one another we have avoided the crux of this problem. We repeated the analyses described below with other distance metrics (e.g., Sørenson's index), and obtained similar results.

Distance decay regressions were fit in log-linear space (i.e., log(similarity) $\sim$ distance) to linearize the relationship between similarity and distance, thus allowing direct estimation of the rate of change in composition over space. We defined the similarity at 0 km distance as 1 (i.e., perfect similarity), which is trivially true for range data, by only fitting a slope term and not an intercept term in log-linear space. This restriction in the form of the equation did not appear to substantially reduce the R^2 of the regressions. We analyzed each taxonomic group separately, as they show different patterns of turnover that we wanted to highlight. Note however that the exclusion of rare species for trees limits their comparability to mammals and birds to some extent.

In order to interpret differences between our estimates of intra- and inter-ecoregion turnover rates, it was necessary to construct confidence intervals around these rate estimates. Ordinary least-squares methods of putting confidence intervals on parameters are inappropriate here, as each point represents a similarity between a pair of cells, and thus points are not independent of one another. The label permutation done in Mantel tests (Mantel, 1967; McCune and Grace, 2002) is appealing, since it takes this dependency into account, but was unsuitable for two reasons: first, the randomization requires calculating (and then permuting) a full matrix of similarity values, which would be computationally prohibitive with thousands of cells; second, the label

Table 1
Intra-ecoregion turnover rates for the 107 World Wildlife Fund ecoregions

Ecoregion name	Tree	Birds	Mammals
Wilamette Valley forests	0.732–0.800	0.885–0.904	0.874–0.885
Western Great Lakes forests	0.885–0.896	0.930–0.934	0.924–0.927
Eastern forest/boreal transition	0.866–0.876	0.924–0.927	0.946–0.950
Upper midwest forests	0.846–0.855	0.906–0.912	0.912–0.918
Southern Great Lakes forests	0.854–0.867	0.929–0.931	0.931–0.937
Eastern Great Lakes lowland forests	0.873–0.898	0.931–0.934	0.779–0.883
New England/Acadian forests	0.917–0.925	0.924–0.929	0.898–0.928
Gulf of St. Lawrence lowland forests	0.945–0.953	0.925–0.934	0.460–0.650
Northeastern coastal forests	0.830–0.848	0.889–0.904	0.912–0.923
Allegheny Highlands forests	0.812–0.826	0.939–0.943	0.928–0.933
Appalachians/Blue Ridge forests	0.838–0.850	0.939–0.944	0.920–0.930
Appalachian mixed mesophytic forests	0.839–0.846	0.916–0.919	0.899–0.908
Central US hardwood forests	0.857–0.861	0.945–0.947	0.906–0.911
Ozark Mountain forests	0.818–0.841	0.958–0.958	0.914–0.914
Mississippi lowland forests	0.782–0.807	0.938–0.948	0.933–0.944
East Central Texas forests	0.686–0.733	0.880–0.880	0.879–0.879
Southeastern mixed forests	0.849–0.859	0.911–0.921	0.867–0.878
Northern Pacific coastal forests	0.810–0.831	0.883–0.895	0.367–0.405
Queen Charlotte Islands	0.783–0.836	0.970–0.976	0.680–0.790
Central British Columbia Mountain forests	0.748–0.805	0.929–0.933	0.911–0.917
Alberta Mountain forests	0.804–0.838	0.914–0.926	0.936–0.944
Fraser Plateau and Basin complex	0.862–0.879	0.913–0.918	0.918–0.924
Northern transitional alpine forests	0.682–0.755	0.934–0.944	0.937–0.949
Alberta/British Columbia foothills forests	0.886–0.902	0.902–0.909	0.905–0.913
North Central Rockies forests	0.820–0.834	0.915–0.919	0.899–0.904
Okanogan dry forests	0.816–0.838	0.934–0.940	0.870–0.877
Cascade Mountains leeward forests	0.749–0.773	0.894–0.904	0.859–0.876
British Columbia mainland coastal forests	0.828–0.853	0.862–0.873	0.620–0.734
Central Pacific coastal forests	0.824–0.836	0.888–0.903	0.639–0.739
Puget lowland forests	0.827–0.841	0.865–0.881	0.550–0.794
Central and Southern Cascades forests	0.753–0.790	0.883–0.895	0.847–0.871
Eastern Cascades forests	0.520–0.581	0.898–0.905	0.813–0.831
Blue Mountain forests	0.644–0.668	0.899–0.910	0.870–0.887
Klamath–Siskiyou forests	0.710–0.730	0.836–0.858	0.859–0.874
Northern California coastal forests	0.691–0.745	0.933–0.943	0.869–0.888
Sierra Nevada forests	0.686–0.728	0.865–0.876	0.829–0.844
South Central Rockies forests	0.810–0.825	0.908–0.912	0.878–0.884
Wasatch and Uinta montane forests	0.794–0.831	0.912–0.917	0.871–0.881
Colorado Rockies forests	0.763–0.782	0.898–0.902	0.845–0.850
Arizona Mountains forests	0.620–0.656	0.860–0.889	0.784–0.818
Sierra Madre Occidental pine-oak forests	0.410–0.715	0.890–0.890	0.874–0.874
Piney Woods forests	0.861–0.869	0.938–0.938	0.914–0.914
Atlantic coastal pine barrens	0.775–0.836	0.925–0.945	0.918–0.949
Middle Atlantic coastal forests	0.836–0.848	0.907–0.919	0.908–0.917
Southeastern conifer forests	0.802–0.812	0.917–0.917	0.948–0.948
Florida sand pine scrub	0.604–0.733	0.901–0.901	0.954–0.954
Palouse grasslands	0.528–0.591	0.897–0.910	0.832–0.847
California Central Valley grasslands	0.475–0.530	0.880–0.888	0.821–0.832
Canadian Aspen forests and parklands	0.868–0.876	0.919–0.922	0.896–0.902
Northern mix grasslands	0.794–0.817	0.912–0.918	0.889–0.898
Montana Valley and Foothill grasslands	0.688–0.734	0.900–0.908	0.852–0.861
Northern short grasslands	0.776–0.786	0.912–0.914	0.876–0.879
Northern tall grasslands	0.770–0.799	0.897–0.909	0.905–0.913
Central tall grasslands	0.774–0.786	0.918–0.921	0.924–0.929
Flint Hills tall grasslands	0.669–0.728	0.886–0.890	0.913–0.928
Nebraska Sand Hills mixed grasslands	0.769–0.803	0.907–0.914	0.907–0.918
Western short grasslands	0.554–0.574	0.853–0.857	0.837–0.845
Central and Southern mixed grasslands	0.732–0.754	0.880–0.885	0.873–0.877
Central forest/grassland transition zone	0.831–0.844	0.942–0.945	0.925–0.929
Edwards Plateau savanna	0.569–0.616	0.877–0.877	0.832–0.832
Texas blackland prairie	0.768–0.791	0.897–0.897	0.893–0.893
Western gulf coastal grasslands	0.306–0.354	0.926–0.926	0.834–0.834
Everglades	0.563–0.637	0.904–0.904	0.905–0.905

Table 1 (*continued*)

Ecoregion name	Tree	Birds	Mammals
California interior chaparral and woodlands	0.556–0.604	0.839–0.853	0.798–0.820
California montane chaparral and woodlands	0.679–0.734	0.890–0.911	0.829–0.877
California coastal sage and chaparral	0.514–0.583	0.852–0.852	0.450–0.450
Snake/Columbia shrub steppe	0.424–0.440	0.896–0.899	0.868–0.877
Great Basin shrub steppe	0.543–0.555	0.905–0.910	0.862–0.867
Wyoming Basin shrub steppe	0.516–0.534	0.914–0.917	0.873–0.881
Colorado Plateau shrublands	0.545–0.564	0.907–0.910	0.843–0.853
Mojave desert	0.488–0.510	0.800–0.808	0.768–0.777
Sonoran desert	0.589–0.628	0.832–0.832	0.831–0.831
Chihuahuan desert	0.461–0.478	0.883–0.883	0.872–0.872
Tamaulipan mezquital	0.695–0.770	0.870–0.870	0.861–0.861
Interior Alaska/Yukon lowland taiga	0.782–0.801	0.908–0.917	0.932–0.937
Alaska Peninsula montane taiga	0.353–0.434	0.835–0.873	0.380–0.478
Cook Inlet taiga	0.691–0.764	0.865–0.888	0.914–0.930
Copper Plateau taiga	0.888–0.937	0.892–0.914	0.895–0.922
Northwest Territories taiga	0.785–0.806	0.880–0.887	0.900–0.904
Yukon Interior dry forests	0.909–0.923	0.931–0.937	0.935–0.944
Northern Cordillera forests	0.815–0.834	0.940–0.942	0.926–0.929
Muskwa/Slave Lake forests	0.929–0.941	0.927–0.929	0.927–0.933
Northern Canadian Shield taiga	0.743–0.770	0.829–0.836	0.872–0.878
Mid-Continental Canadian forests	0.944–0.949	0.943–0.947	0.938–0.944
Midwestern Canadian Shield forests	0.912–0.920	0.923–0.927	0.953–0.956
Central Canadian Shield forests	0.922–0.927	0.922–0.928	0.948–0.953
Southern Hudson Bay taiga	0.809–0.838	0.868–0.876	0.945–0.950
Eastern Canadian Shield taiga	0.821–0.848	0.879–0.887	0.944–0.949
Eastern Canadian forests	0.897–0.907	0.874–0.880	0.812–0.839
Newfoundland Highland forests	0.869–0.947	0.896–0.934	0.917–0.953
South Avalon–Burin oceanic barrens	0.936–0.957	0.932–0.959	0.949–0.994
Aleutian Islands tundra	No data	0.878–0.940	0.939–0.999
Beringia lowland tundra	0.131–0.168	0.764–0.811	0.703–0.811
Beringia upland tundra	0.135–0.182	0.761–0.804	0.868–0.924
Alaska/St. Elias Range tundra	0.687–0.734	0.914–0.920	0.950–0.955
Pacific Coastal mountain icefields and tundra	0.579–0.649	0.876–0.884	0.800–0.875
Interior Yukon/Alaska alpine tundra	0.868–0.880	0.934–0.938	0.942–0.946
Ogilvie/MacKenzie alpine tundra	0.594–0.623	0.926–0.930	0.945–0.949
Brooks/British Range tundra	0.154–0.192	0.791–0.807	0.896–0.907
Arctic foothills tundra	0.112–0.141	0.779–0.790	0.909–0.918
Arctic coastal tundra	0.153–0.222	0.867–0.888	0.898–0.913
Low Arctic tundra	0.200–0.230	0.875–0.880	0.896–0.914
Middle Arctic tundra	0.075–0.138	0.905–0.910	0.862–0.882
High Arctic tundra	No data	0.864–0.874	0.660–0.699
Davis Highlands tundra	No data	0.913–0.929	0.916–0.969
Baffin coastal tundra	No data	0.974–0.990	1.006–1.008
Torngat Mountain tundra	0.084–0.119	0.884–0.912	0.919–0.930

A few ecoregions in the Arctic have no tree species, and are marked "no data". The range shown is the range of rate parameter calculated from regressions of similarity as a function of log(distance), using the statistical resampling technique described in the text. The rate parameter is expressed here as the proportion of similarity remaining at 100 km distance. Note that the range of values shown is an estimate of the precision with which the value of the parameter is estimated. The range should not be interpreted as an estimate of the range of similarity values that occur between cells at 100 km in a given ecoregion, which is generally broader.

permutation poses a hypothesis that is uninteresting ecologically, since randomly permuting the ecoregion labels of cells would create a salt-and-pepper type graph where cells of the same ecoregion would be far apart geographically.

To address these concerns, we constructed 999 random subsamples of the original cell data, each time randomly removing 1/3 of the cells (different proportions were experimented with, and did not significantly influence the results). For each subsample, Jaccard similarities were calculated, and turnover rates were estimated using the regression method described above. The result was a distribution of turnover rates for each inter- or intra-ecoregion rate calculated. Approximate 90% confidence 'intervals' were found by taking the 5th and 95th quantiles of the subsampled data (the 50th and 950th greatest values from the subsampled and original data), and two turnover rates were considered different if their intervals did not overlap. This procedure effectively answers the question: are there one or a few cells in an ecoregion(s) that are influencing the estimated turnover rate strongly?

3. Results

The negative slope of the regression line for the typical distance–decay curve (Fig. 1) indicates that sites further apart are generally less similar in species composition. For our data, all but one of the intra-ecoregion turnover rates had the expected sign (i.e., similarity declines with distance). Similarly, the vast majority of the inter-ecoregion turnover rates had the expected sign. The few cases in which similarity increased with distance occurred as statistical artifacts, in areas of low species richness, where the loss of even a single species between grid cells produced a large change in Jaccard's index of similarity. In these cases, the regression-based approach, which assumes continuity in the measure of similarity, is inappropriate. Such curves were excluded from further analyses. The considerable scatter around the best-fit regression line (Fig. 1) reflects the obvious point that factors other than distance produce variability in species composition.

Most of the patterns revealed by comparisons of intra-ecoregion and inter-ecoregion distance–decay curves were described by two cases. In one case, higher rates of turnover corresponded with ecoregion boundaries such that turnover between ecoregions was higher than turnover within. An example of this case occurred at the boundary between the Appalachian Forest ecoregion and the Northeastern Coastal Forest ecoregion (Fig. 2(a)). At any given distance, pairs of cells within one of these ecoregions were more similar than pairs of cells across their shared boundary. Graphically, this case was indicated when the inter-ecoregion distance–decay curve fell below the two intra-ecoregion curves (Fig. 2(a)). In contrast, some ecoregion boundaries exhibited weaker correspondence with high turnover. For example, turnover across the boundary between the Nebraska Sand Hills and Western Short Grassland ecoregions was greater, at any given distance, than turnover within one of the ecoregions sharing the boundary (Western Short Grassland), and less than turnover within the other (Fig. 2(b)). Graphically, this case was indicated when the inter-ecoregion distance–decay curve fell between the two intra-ecoregion curves. The third possibility, where the inter-ecoregion curve for a particular boundary lay above the two intra-ecoregion curves, was rare.

Turnover rates from all intra-ecoregion regressions are displayed in Table 1. Also included are the R^2 of the regression, to help readers evaluate the fit of each regression. Note that these are only advisory, because the non-independence between pairs of points violates one of the assumptions of least-squares regression. For ease of interpretation, we also supply the similarity remaining between pairs of cells 100 km apart, which is a simple transformation of the calculated slope. Similarly, tabular values of inter-ecoregion turnover rates for all adjacent ecoregions are presented in Table 2.

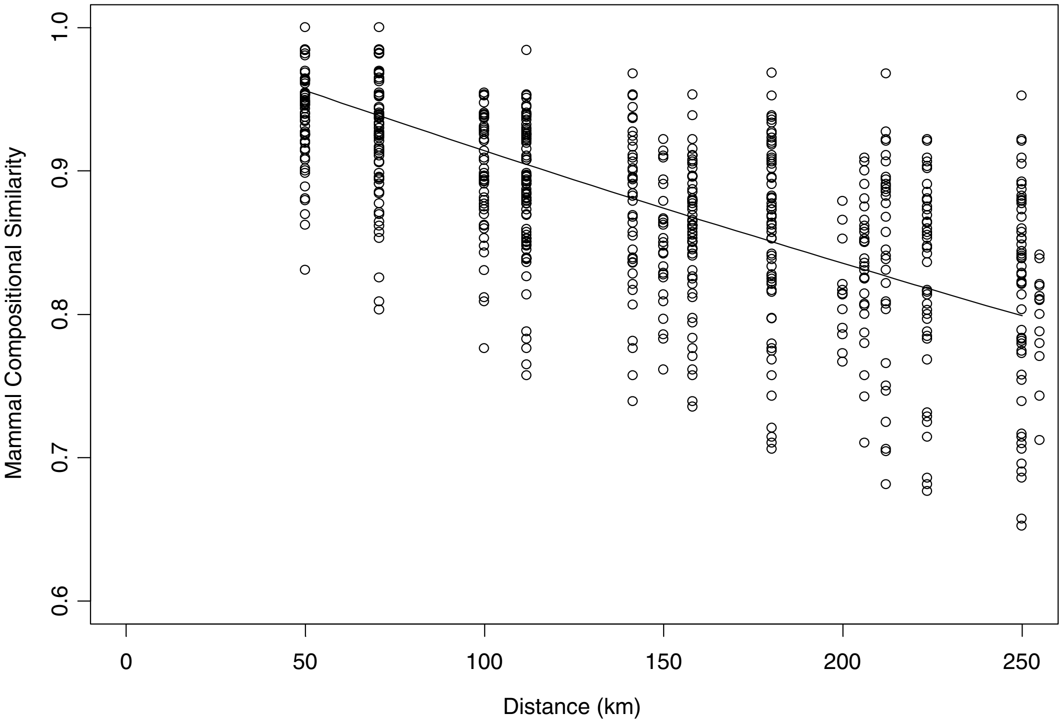

Fig. 1. Example scatterplot of distance versus similarity for one ecoregion, with regression line overlaid. Note that the regression was fit on the log(similarity), but is here transformed to the original space for display purposes.

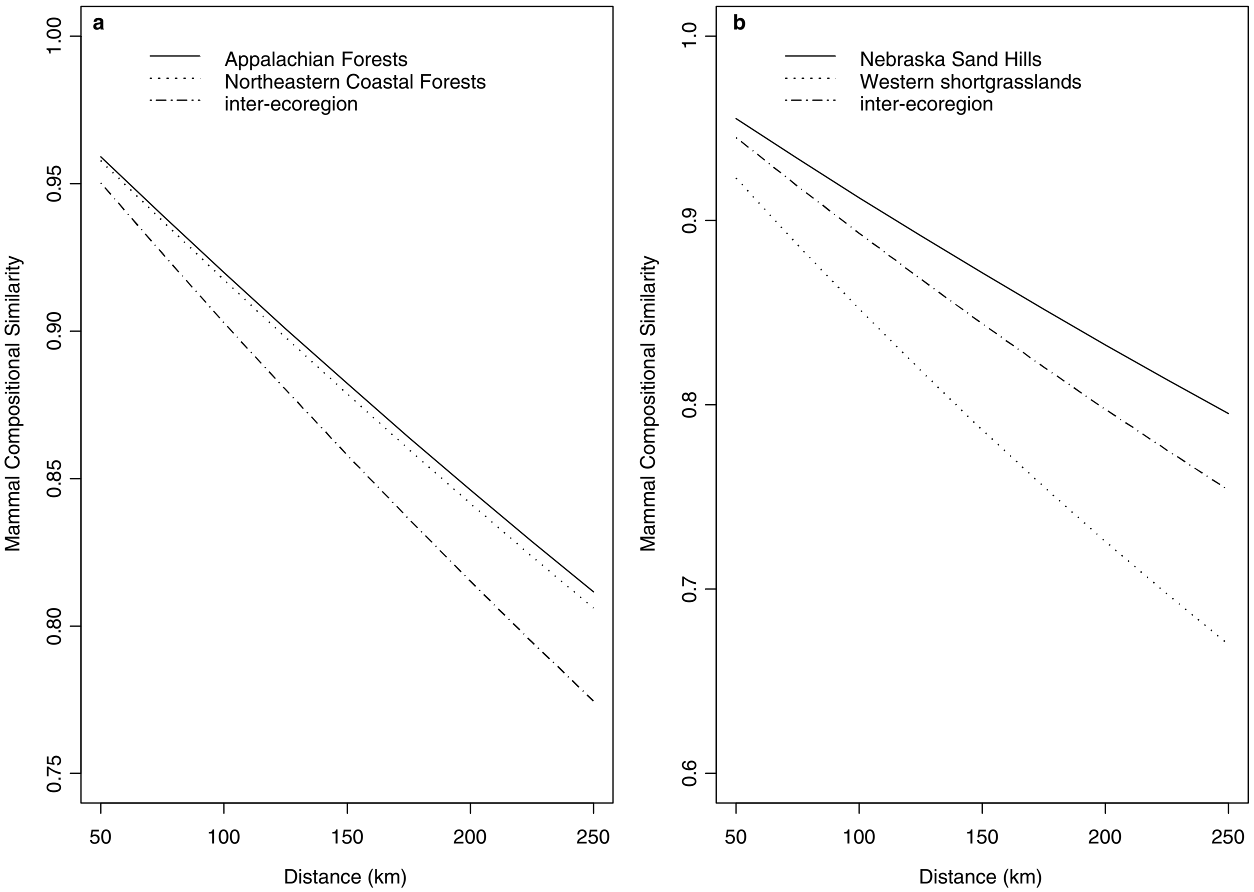

Fig. 2. Two-panel graph (distance versus log(similarity), with regression line only) showing the two most common cases that occur when comparing different ecoregions. Note the discontinuous scale on the *x*-axis. (a) At any given distance, pairs of cells within the same ecoregion are more similar than pairs of cells in different ecoregions. (b) At any given distance, pairs of cells in different ecoregions are intermediate in similarity as compared with pairs of cells that are within ecoregions (i.e., the inter-ecoregion curve is between the two intra-ecoregion curves).

The geographic distribution of intra-ecoregion turnover revealed several commonalities among mammals, birds, and trees (Fig. 3). Most notably, all three groups exhibited relatively high rates of decline in similarity in the southwest United States. Similarly, all three groups had relatively low turnover in the southern portions of the Canadian Shield. The high turnover rates in the Arctic occurred as an artifact of low species richness (Koleff et al., 2003). The most obvious difference between species groups appeared in Nova Scotia, where there were relatively high rates of decline in similarity for mammals and birds, and relatively low rates for trees (Fig. 3).

The degree to which various ecoregion boundaries are consistent with patterns of turnover is shown in Fig. 4, which summarizes the qualitative patterns shown in Fig. 2 for all ecoregion boundaries in the US and Canada. For 40.4% of ecoregion boundaries, turnover of bird species was greater across the boundary than within either of the two adjoining ecoregions. This rate of correspondence between ecoregion boundaries and high turnover was much greater than that observed for mammals (25.4%) or trees (15.1%), although in the latter case the comparison is difficult to analyze due to the missing rare tree species. For all three species groups, ecoregion boundaries that coincide with major biome boundaries (e.g., the transition from eastern deciduous forest to grassland) generally corresponded with high rates of turnover (Fig. 4).

4. Discussion

For all three groups of species studied (trees, birds, and mammals), most pairs of adjacent ecoregions have a rate of species turnover that is no higher across the shared ecoregion boundary than within each ecoregion. This suggests that, for the World Wildlife Fund ecoregions, most ecoregion boundaries are not representative of unusually high rates of change in community composition, as change in species composition across this line in the landscape is not significantly greater than other nearby areas. It should be noted, however, that results based on other taxonomic groups may differ, especially those with smaller average range size. Similarly, if abundance

Table 2
Inter-ecoregion turnover rates for pairs of adjacent ecoregions

Ecoregion 1	Ecoregion 2	Trees	Birds	Mammals
Williamette Valley forests	Central Pacific coastal forests	0.749–0.771	0.850–0.879	0.820–0.844
Williamette Valley forests	Puget lowland forests	0.828–0.861	0.875–0.896	0.838–0.851
Williamette Valley forests	Central and Southern Cascades forests	0.655–0.690	0.832–0.860	0.831–0.841
Williamette Valley forests	Klamath–Siskiyou forests	0.721–0.770	0.883–0.907	0.866–0.895
Western Great Lakes forests	Upper midwest forests	0.854–0.862	0.890–0.896	0.906–0.911
Western Great Lakes forests	Southern Great Lakes forests	0.808–0.829	0.905–0.912	0.909–0.919
Western Great Lakes forests	Canadian Aspen forests and parklands	0.814–0.834	0.906–0.912	0.884–0.897
Western Great Lakes forests	Northern tall grasslands	0.722–0.742	0.871–0.877	0.882–0.890
Western Great Lakes forests	Midwestern Canadian Shield forests	0.824–0.843	0.902–0.911	0.912–0.922
Western Great Lakes forests	Central Canadian Shield forests	0.829–0.846	0.918–0.923	0.928–0.940
Eastern forest/boreal transition	Eastern Great Lakes lowland forests	0.849–0.860	0.903–0.908	0.803–0.839
Eastern forest/boreal transition	Central Canadian Shield forests	0.872–0.885	0.921–0.925	0.949–0.953
Eastern forest/boreal transition	Eastern Canadian forests	0.842–0.859	0.911–0.916	0.933–0.942
Upper midwest forests	Southern Great Lakes forests	0.803–0.817	0.920–0.925	0.896–0.910
Upper midwest forests	Northern tall grasslands	0.686–0.716	0.899–0.906	0.915–0.926
Upper midwest forests	Central tall grasslands	0.742–0.764	0.902–0.910	0.915–0.921
Upper midwest forests	Central forest/grassland transition zone	0.832–0.841	0.924–0.931	0.896–0.905
Southern Great Lakes forests	Eastern Great Lakes lowland forests	0.838–0.845	0.917–0.922	0.796–0.857
Southern Great Lakes forests	Allegheny Highlands forests	0.839–0.848	0.924–0.929	0.922–0.928
Southern Great Lakes forests	Appalachian mixed mesophytic forests	0.852–0.861	0.915–0.922	0.908–0.914
Southern Great Lakes forests	Central US hardwood forests	0.829–0.838	0.933–0.939	0.906–0.911
Southern Great Lakes forests	Central forest/grassland transition zone	0.834–0.856	0.941–0.945	0.929–0.934
Eastern Great Lakes lowland forests	New England/Acadian forests	0.888–0.900	0.912–0.916	0.947–0.954
New England/Acadian forests	Gulf of St. Lawrence lowland forests	0.945–0.951	0.936–0.939	0.723–0.784
New England/Acadian forests	Northeastern coastal forests	0.877–0.885	0.873–0.880	0.927–0.930
New England/Acadian forests	Appalachians/Blue Ridge forests	0.914–0.929	0.917–0.928	0.962–0.974
New England/Acadian forests	Eastern Canadian forests	0.856–0.872	0.927–0.932	0.862–0.894
Northeastern coastal forests	Allegheny Highlands forests	0.801–0.821	0.863–0.883	0.903–0.917
Northeastern coastal forests	Appalachians/Blue Ridge forests	0.813–0.845	0.860–0.881	0.897–0.910
Northeastern coastal forests	Southeastern mixed forests	0.772–0.794	0.893–0.907	0.889–0.900
Northeastern coastal forests	Atlantic coastal pine barrens	0.763–0.782	0.891–0.905	0.888–0.897
Northeastern coastal forests	Middle Atlantic coastal forests	0.700–0.719	0.877–0.903	0.880–0.900
Allegheny Highlands forests	Appalachians/Blue Ridge forests	0.819–0.835	0.922–0.925	0.915–0.922
Allegheny Highlands forests	Appalachian mixed mesophytic forests	0.813–0.833	0.927–0.938	0.926–0.931
Appalachians/Blue Ridge forests	Appalachian mixed mesophytic forests	0.837–0.843	0.918–0.923	0.909–0.915
Appalachians/Blue Ridge forests	Southeastern mixed forests	0.762–0.783	0.868–0.876	0.848–0.854
Appalachian mixed mesophytic forests	Central US hardwood forests	0.848–0.855	0.928–0.936	0.908–0.916
Appalachian mixed mesophytic forests	Southeastern mixed forests	0.830–0.853	0.887–0.898	0.877–0.888
Central US hardwood forests	Ozark Mountain forests	0.835–0.845	0.954–0.956	0.890–0.896
Central US hardwood forests	Mississipi lowland forests	0.826–0.837	0.933–0.937	0.912–0.921
Central US hardwood forests	Southeastern mixed forests	0.862–0.870	0.947–0.954	0.928–0.942
Central US hardwood forests	Central forest/grassland transition zone	0.853–0.865	0.932–0.934	0.896–0.901
Ozark Mountain forests	Mississipi lowland forests	0.801–0.822	0.941–0.941	0.915–0.915
Ozark Mountain forests	Piney Woods forests	0.796–0.810	0.941–0.941	0.903–0.903
Ozark Mountain forests	Central forest/grassland transition zone	0.766–0.784	0.925–0.925	0.867–0.867
Mississipi lowland forests	Southeastern mixed forests	0.769–0.811	0.928–0.941	0.930–0.948
Mississipi lowland forests	Piney Woods forests	0.794–0.826	0.947–0.947	0.933–0.933
Mississipi lowland forests	Southeastern conifer forests	0.735–0.786	0.923–0.923	0.956–0.956
Mississipi lowland forests	Western guld coastal grasslands	0.354–0.438	0.896–0.896	0.854–0.854
East Central Texas forests	Piney Woods forests	0.743–0.781	0.913–0.913	0.887–0.887
East Central Texas forests	Central forest/grassland transition zone	0.716–0.738	0.897–0.897	0.861–0.861
East Central Texas forests	Texas blackland prairie	0.701–0.735	0.889–0.889	0.888–0.888
East Central Texas forests	Western guld coastal grasslands	0.559–0.616	0.832–0.832	0.857–0.857
East Central Texas forests	Tamaulipan mezquital	0.497–0.569	0.856–0.856	0.831–0.831
Southeastern mixed forests	Middle Atlantic coastal forests	0.780–0.789	0.858–0.865	0.861–0.873
Southeastern mixed forests	Southeastern conifer forests	0.822–0.829	0.900–0.900	0.922–0.922
Northern Pacific coastal forests	Alaska Peninsula montane taiga	0.551–0.580	0.799–0.860	0.348–0.408
Northern Pacific coastal forests	Cook Inlet taiga	0.565–0.600	0.808–0.868	0.351–0.765
Northern Pacific coastal forests	Pacific Coastal mountain icefields and tundra	0.721–0.761	0.829–0.843	0.411–0.511
Central British Columbia Mountain forests	Alberta Mountain forests	0.814–0.853	0.929–0.932	0.911–0.926
Central British Columbia Mountain forests	Fraser Plateau and Basin complex	0.784–0.810	0.926–0.931	0.910–0.920
Central British Columbia Mountain forests	Northern transitional alpine forests	0.762–0.781	0.918–0.924	0.921–0.930
Central British Columbia Mountain forests	Alberta/British Columbia foothills forests	0.788–0.839	0.897–0.901	0.896–0.902

Table 2 (*continued*)

Ecoregion 1	Ecoregion 2	Trees	Birds	Mammals
Central British Columbia Mountain forests	North Central Rockies forests	0.821–0.867	0.915–0.924	0.911–0.923
Central British Columbia Mountain forests	Canadian Aspen forests and parklands	0.774–0.815	0.884–0.889	0.883–0.895
Central British Columbia Mountain forests	Northern Cordillera forests	0.720–0.743	0.934–0.938	0.921–0.927
Alberta Mountain forests	Alberta/British Columbia foothills forests	0.801–0.850	0.846–0.861	0.872–0.880
Alberta Mountain forests	North Central Rockies forests	0.720–0.745	0.886–0.895	0.874–0.880
Fraser Plateau and Basin complex	Northern transitional alpine forests	0.810–0.828	0.929–0.934	0.940–0.946
Fraser Plateau and Basin complex	North Central Rockies forests	0.870–0.879	0.923–0.927	0.901–0.909
Fraser Plateau and Basin complex	Okanogan dry forests	0.880–0.891	0.913–0.918	0.894–0.906
Fraser Plateau and Basin complex	Cascade Mountains leeward forests	0.785–0.799	0.897–0.901	0.852–0.862
Fraser Plateau and Basin complex	British Columbia mainland coastal forests	0.611–0.630	0.830–0.836	0.806–0.841
Northern transitional alpine forests	British Columbia mainland coastal forests	0.620–0.648	0.820–0.846	0.788–0.909
Northern transitional alpine forests	Northern Cordillera forests	0.700–0.748	0.934–0.941	0.919–0.926
Northern transitional alpine forests	Pacific Coastal mountain icefields and tundra	0.560–0.619	0.858–0.865	0.864–0.908
Alberta/British Columbia foothills forests	North Central Rockies forests	0.698–0.711	0.837–0.851	0.853–0.866
Alberta/British Columbia foothills forests	Canadian Aspen forests and parklands	0.871–0.886	0.914–0.924	0.896–0.907
Alberta/British Columbia foothills forests	Northern Cordillera forests	0.726–0.787	0.893–0.904	0.911–0.924
Alberta/British Columbia foothills forests	Muska/Slave Lake forests	0.926–0.939	0.926–0.930	0.938–0.944
Alberta/British Columbia foothills forests	Mid-Continental Canadian forests	0.899–0.909	0.939–0.947	0.915–0.929
North Central Rockies forests	Okanogan dry forests	0.844–0.849	0.921–0.927	0.871–0.876
North Central Rockies forests	South Central Rockies forests	0.790–0.804	0.919–0.925	0.892–0.901
North Central Rockies forests	Palouse grasslands	0.664–0.688	0.897–0.901	0.827–0.837
North Central Rockies forests	Canadian Aspen forests and parklands	0.657–0.680	0.815–0.830	0.820–0.831
North Central Rockies forests	Montana Valley and Foothill grasslands	0.627–0.656	0.873–0.887	0.853–0.863
Okanogan dry forests	Cascade Mountains leeward forests	0.785–0.805	0.906–0.912	0.834–0.844
Okanogan dry forests	Palouse grasslands	0.635–0.694	0.896–0.908	0.837–0.847
Cascade Mountains leeward forests	British Columbia mainland coastal forests	0.681–0.715	0.849–0.856	0.846–0.856
Cascade Mountains leeward forests	Eastern Cascades forests	0.770–0.809	0.912–0.924	0.851–0.874
Cascade Mountains leeward forests	Palouse grasslands	0.568–0.617	0.890–0.903	0.781–0.802
Cascade Mountains leeward forests	Snake/Columbia shrub steppe	0.390–0.473	0.868–0.878	0.757–0.787
British Columbia mainland coastal forests	Central Pacific coastal forests	0.833–0.849	0.843–0.852	0.488–0.533
British Columbia mainland coastal forests	Puget lowland forests	0.786–0.805	0.844–0.856	0.693–0.715
British Columbia mainland coastal forests	Central and Southern Cascades forests	0.832–0.860	0.880–0.908	0.869–0.890
British Columbia mainland coastal forests	Pacific Coastal mountain icefields and tundra	0.767–0.819	0.873–0.889	0.805–0.910
Central Pacific coastal forests	Puget lowland forests	0.825–0.834	0.865–0.873	0.556–0.654
Central Pacific coastal forests	Klamath–Siskiyou forests	0.644–0.688	0.829–0.851	0.834–0.850
Central Pacific coastal forests	Northern California coastal forests	0.807–0.828	0.908–0.937	0.880–0.892
Puget lowland forests	Central and Southern Cascades forests	0.779–0.813	0.838–0.859	0.779–0.867
Central and Southern Cascades forests	Eastern Cascades forests	0.578–0.618	0.870–0.882	0.796–0.809
Central and Southern Cascades forests	Klamath–Siskiyou forests	0.701–0.760	0.853–0.870	0.873–0.883
Eastern Cascades forests	Blue Mountain forests	0.642–0.689	0.882–0.890	0.799–0.824
Eastern Cascades forests	Klamath–Siskiyou forests	0.515–0.562	0.844–0.853	0.787–0.806
Eastern Cascades forests	Sierra Nevada forests	0.588–0.642	0.877–0.891	0.829–0.855
Eastern Cascades forests	Snake/Columbia shrub steppe	0.439–0.469	0.877–0.884	0.789–0.808
Blue Mountain forests	South Central Rockies forests	0.702–0.774	0.916–0.921	0.867–0.878
Blue Mountain forests	Palouse grasslands	0.620–0.649	0.904–0.910	0.865–0.874
Blue Mountain forests	Snake/Columbia shrub steppe	0.467–0.482	0.875–0.879	0.844–0.850
Klamath–Siskiyou forests	Northern California coastal forests	0.597–0.636	0.817–0.835	0.841–0.853
Klamath–Siskiyou forests	Sierra Nevada forests	0.689–0.703	0.854–0.867	0.794–0.805
Klamath–Siskiyou forests	California interior chaparral and woodlands	0.662–0.702	0.848–0.863	0.843–0.853
Northern California coastal forests	California interior chaparral and woodlands	0.561–0.636	0.832–0.849	0.811–0.826
Sierra Nevada forests	California interior chaparral and woodlands	0.551–0.595	0.821–0.828	0.744–0.758
Sierra Nevada forests	California montane chaparral and woodlands	0.595–0.630	0.813–0.838	0.746–0.765
Sierra Nevada forests	Snake/Columbia shrub steppe	0.440–0.475	0.851–0.869	0.791–0.813
Sierra Nevada forests	Great Basin shrub steppe	0.301–0.336	0.822–0.834	0.735–0.753
Sierra Nevada forests	Mojave desert	0.261–0.307	0.793–0.811	0.708–0.723
South Central Rockies forests	Palouse grasslands	0.691–0.727	0.922–0.927	0.889–0.902
South Central Rockies forests	Montana Valley and Foothill grasslands	0.785–0.801	0.908–0.911	0.867–0.873
South Central Rockies forests	Northern short grasslands	0.584–0.606	0.894–0.900	0.845–0.859
South Central Rockies forests	Snake/Columbia shrub steppe	0.525–0.569	0.882–0.889	0.849–0.858
South Central Rockies forests	Great Basin shrub steppe	0.713–0.767	0.895–0.899	0.865–0.877
South Central Rockies forests	Wyoming Basin shrub steppe	0.575–0.594	0.912–0.915	0.870–0.878
Wasatch and Uinta montane forests	Great Basin shrub steppe	0.554–0.572	0.907–0.911	0.842–0.848
Wasatch and Uinta montane forests	Wyoming Basin shrub steppe	0.553–0.596	0.912–0.917	0.852–0.863

(*continued on next page*)

Table 2 (*continued*)

Ecoregion 1	Ecoregion 2	Trees	Birds	Mammals
Wasatch and Uinta montane forests	Colorado shrub steppe	0.609–0.634	0.908–0.911	0.840–0.853
Colorado Rockies forests	Northern short grasslands	0.573–0.619	0.876–0.879	0.862–0.871
Colorado Rockies forests	Western short grasslands	0.420–0.444	0.826–0.833	0.790–0.798
Colorado Rockies forests	Wyoming Basin shrub steppe	0.562–0.587	0.902–0.907	0.848–0.858
Colorado Rockies forests	Colorado shrub steppe	0.616–0.639	0.899–0.902	0.855–0.862
Arizona Mountains forests	Sierra Madre Occidental pine–oak forests	0.666–0.700	0.870–0.870	0.816–0.816
Arizona Mountains forests	Colorado shrub steppe	0.489–0.505	0.908–0.910	0.796–0.807
Arizona Mountains forests	Sonoran desert	0.372–0.406	0.793–0.822	0.783–0.783
Sierra Madre Occidental pine-oak forests	Sonoran desert	0.362–0.441	0.818–0.818	0.849–0.849
Sierra Madre Occidental pine-oak forests	Chihuahuan desert	0.552–0.587	0.875–0.875	0.854–0.854
Piney Woods forests	Central forest/grassland transition zone	0.743–0.761	0.918–0.918	0.877–0.877
Piney Woods forests	Texas blackland prairie	0.683–0.696	0.902–0.902	0.875–0.875
Piney Woods forests	Western guld coastal grasslands	0.511–0.552	0.856–0.856	0.867–0.867
Middle Atlantic coastal forests	Southeastern conifer forests	0.843–0.855	0.918–0.918	0.953–0.953
Southeastern conifer forests	Florida sand pine scrub	0.713–0.742	0.919–0.919	0.945–0.945
Southeastern conifer forests	Western guld coastal grasslands	0.358–0.418	0.913–0.913	0.830–0.830
Southeastern conifer forests	Everglades	0.621–0.648	0.908–0.908	0.884–0.884
Florida sand pine scrub	Everglades	0.575–0.771	0.893–0.893	0.885–0.885
Palouse grasslands	Snake/Columbia shrub steppe	0.471–0.500	0.883–0.887	0.815–0.825
California Central Valley grasslands	California interior chaparral and woodlands	0.400–0.479	0.836–0.844	0.791–0.800
Canadian Aspen forests and parklands	Northern mix grasslands	0.742–0.760	0.890–0.895	0.876–0.882
Canadian Aspen forests and parklands	Montana Valley and Foothill grasslands	0.606–0.654	0.868–0.877	0.854–0.862
Canadian Aspen forests and parklands	Northern tall grasslands	0.824–0.842	0.901–0.909	0.892–0.899
Canadian Aspen forests and parklands	Muska/Slave Lake forests	0.923–0.939	0.931–0.935	0.959–0.966
Canadian Aspen forests and parklands	Mid-Continental Canadian forests	0.909–0.918	0.923–0.927	0.900–0.907
Northern mix grasslands	Montana Valley and Foothill grasslands	0.623–0.677	0.866–0.881	0.827–0.841
Northern mix grasslands	Northern short grasslands	0.781–0.808	0.901–0.906	0.854–0.861
Northern mix grasslands	Northern tall grasslands	0.774–0.798	0.893–0.896	0.890–0.895
Northern mix grasslands	Central tall grasslands	0.789–0.811	0.890–0.895	0.875–0.885
Northern mix grasslands	Nebraska Sand Hills mixed grasslands	0.830–0.862	0.897–0.909	0.877–0.900
Northern mix grasslands	Central and Southern mixed grasslands	0.838–0.877	0.895–0.903	0.901–0.909
Montana Valley and Foothill grasslands	Northern short grasslands	0.613–0.654	0.892–0.904	0.824–0.854
Montana Valley and Foothill grasslands	Snake/Columbia shrub steppe	0.655–0.718	0.886–0.903	0.881–0.890
Northern short grasslands	Nebraska Sand Hills mixed grasslands	0.773–0.799	0.905–0.912	0.864–0.875
Northern short grasslands	Western short grasslands	0.688–0.732	0.885–0.890	0.868–0.876
Northern short grasslands	Wyoming Basin shrub steppe	0.530–0.551	0.891–0.895	0.878–0.885
Northern tall grasslands	Central tall grasslands	0.795–0.839	0.903–0.909	0.924–0.934
Northern tall grasslands	Mid-Continental Canadian forests	0.888–0.925	0.927–0.931	0.886–0.907
Central tall grasslands	Flint Hills tall grasslands	0.787–0.815	0.875–0.881	0.904–0.913
Central tall grasslands	Central and Southern mixed grasslands	0.742–0.768	0.872–0.878	0.887–0.891
Central tall grasslands	Central forest/grassland transition zone	0.834–0.847	0.937–0.943	0.932–0.936
Flint Hills tall grasslands	Central and Southern mixed grasslands	0.698–0.743	0.870–0.872	0.854–0.874
Flint Hills tall grasslands	Central forest/grassland transition zone	0.741–0.796	0.895–0.903	0.907–0.913
Nebraska Sand Hills mixed grasslands	Western short grasslands	0.676–0.696	0.890–0.897	0.888–0.899
Nebraska Sand Hills mixed grasslands	Central and Southern mixed grasslands	0.829–0.844	0.907–0.910	0.908–0.916
Western short grasslands	Central and Southern mixed grasslands	0.618–0.640	0.885–0.892	0.876–0.881
Western short grasslands	Colorado shrub steppe	0.406–0.453	0.837–0.850	0.808–0.824
Central and Southern mixed grasslands	Central forest/grassland transition zone	0.685–0.707	0.879–0.886	0.868–0.882
Central and Southern mixed grasslands	Edwards Plateau savanna	0.600–0.634	0.886–0.886	0.855–0.855
Central forest/grassland transition zone	Edwards Plateau savanna	0.710–0.742	0.890–0.890	0.862–0.862
Central forest/grassland transition zone	Texas blackland prairie	0.753–0.769	0.896–0.896	0.859–0.859
Edwards Plateau savanna	Texas blackland prairie	0.707–0.736	0.885–0.885	0.825–0.825
Edwards Plateau savanna	Tamaulipan mezquital	0.401–0.443	0.866–0.866	0.833–0.833
Texas blackland prairie	Tamaulipan mezquital	0.399–0.493	0.864–0.864	0.825–0.825
Western guld coastal grasslands	Tamaulipan mezquital	0.641–0.720	0.833–0.833	0.850–0.850
California interior chaparral and woodlands	California montane chaparral and woodlands	0.591–0.647	0.862–0.886	0.824–0.851
California montane chaparral and woodlands	California coastal sage and chaparral	0.496–0.553	0.732–0.839	0.112–0.424
California montane chaparral and woodlands	Mojave desert	0.399–0.420	0.782–0.803	0.719–0.747
California montane chaparral and woodlands	Sonoran desert	0.369–0.685	0.822–0.822	0.789–0.789
California coastal sage and chaparral	Sonoran desert	0.303–0.361	0.794–0.794	0.775–0.775
Snake/Columbia shrub steppe	Great Basin shrub steppe	0.465–0.493	0.908–0.912	0.882–0.891
Great Basin shrub steppe	Wyoming Basin shrub steppe	0.559–0.615	0.909–0.915	0.837–0.849
Great Basin shrub steppe	Colorado shrub steppe	0.548–0.581	0.895–0.902	0.826–0.837

Table 2 (*continued*)

Ecoregion 1	Ecoregion 2	Trees	Birds	Mammals
Great Basin shrub steppe	Mojave desert	0.492–0.514	0.842–0.849	0.795–0.805
Wyoming Basin shrub steppe	Colorado shrub steppe	0.568–0.598	0.916–0.920	0.850–0.857
Colorado shrub steppe	Mojave desert	0.510–0.535	0.828–0.838	0.779–0.791
Colorado shrub steppe	Sonoran desert	0.408–0.456	0.803–0.821	0.795–0.814
Mojave desert	Sonoran desert	0.576–0.611	0.818–0.838	0.813–0.827
Interior Alaska/Yukon lowland taiga	Beringia lowland tundra	0.287–0.355	0.798–0.814	0.911–0.920
Interior Alaska/Yukon lowland taiga	Beringiaupland tundra	0.563–0.624	0.843–0.855	0.912–0.919
Interior Alaska/Yukon lowland taiga	Alaska/St. Elias Range tundra	0.742–0.773	0.908–0.913	0.963–0.967
Interior Alaska/Yukon lowland taiga	Interior Yukon/Alaska alpine tundra	0.822–0.837	0.916–0.921	0.939–0.942
Interior Alaska/Yukon lowland taiga	Ogilvie/MacKenzie alpine tundra	0.692–0.761	0.908–0.917	0.929–0.936
Interior Alaska/Yukon lowland taiga	Brooks/British Range tundra	0.372–0.408	0.811–0.822	0.875–0.880
Interior Alaska/Yukon lowland taiga	Arctic foothills tundra	0.242–0.329	0.740–0.761	0.844–0.855
Alaska Peninsula montane taiga	Beringia lowland tundra	0.315–0.383	0.829–0.849	0.553–0.699
Alaska Peninsula montane taiga	Alaska/St. Elias Range tundra	0.431–0.502	0.817–0.850	0.538–0.776
Cook Inlet taiga	Alaska/St. Elias Range tundra	0.650–0.700	0.876–0.892	0.926–0.941
Cook Inlet taiga	Pacific Coastal mountain icefields and tundra	0.585–0.657	0.866–0.874	0.911–0.927
Copper Plateau taiga	Alaska/St. Elias Range tundra	0.843–0.865	0.920–0.938	0.936–0.952
Copper Plateau taiga	Pacific Coastal mountain icefields and tundra	0.476–0.605	0.828–0.843	0.911–0.928
Northwest Territories taiga	Northern Cordillera forests	0.753–0.798	0.915–0.922	0.901–0.908
Northwest Territories taiga	Muska/Slave Lake forests	0.787–0.809	0.901–0.908	0.897–0.902
Northwest Territories taiga	Northern Canadian Shield taiga	0.889–0.906	0.865–0.872	0.907–0.914
Northwest Territories taiga	Ogilvie/MacKenzie alpine tundra	0.611–0.630	0.905–0.910	0.906–0.914
Northwest Territories taiga	Brooks/British Range tundra	0.469–0.510	0.854–0.865	0.884–0.896
Northwest Territories taiga	Arctic coastal tundra	0.387–0.467	0.768–0.778	0.847–0.860
Northwest Territories taiga	Low Arctic tundra	0.609–0.672	0.789–0.802	0.861–0.869
Yukon Interior dry forests	Northern Cordillera forests	0.851–0.862	0.930–0.935	0.936–0.938
Yukon Interior dry forests	Interior Yukon/Alaska alpine tundra	0.888–0.898	0.932–0.935	0.932–0.937
Northern Cordillera forests	Muska/Slave Lake forests	0.808–0.866	0.913–0.915	0.912–0.916
Northern Cordillera forests	Alaska/St. Elias Range tundra	0.346–0.432	0.877–0.885	0.885–0.907
Northern Cordillera forests	Pacific Coastal mountain icefields and tundra	0.513–0.560	0.861–0.869	0.825–0.855
Northern Cordillera forests	Interior Yukon/Alaska alpine tundra	0.848–0.890	0.929–0.937	0.938–0.943
Northern Cordillera forests	Ogilvie/MacKenzie alpine tundra	0.725–0.764	0.926–0.928	0.930–0.937
Muska/Slave Lake forests	Mid-Continental Canadian forests	0.945–0.958	0.942–0.946	0.948–0.954
Northern Canadian Shield taiga	Mid-Continental Canadian forests	0.836–0.864	0.879–0.895	0.904–0.918
Northern Canadian Shield taiga	Midwestern Canadian Shield forests	0.845–0.855	0.880–0.890	0.928–0.935
Northern Canadian Shield taiga	Southern Hudson Bay taiga	0.747–0.767	0.848–0.862	0.876–0.896
Northern Canadian Shield taiga	Low Arctic tundra	0.351–0.393	0.785–0.803	0.836–0.850
Mid-Continental Canadian forests	Midwestern Canadian Shield forests	0.908–0.918	0.912–0.917	0.927–0.931
Midwestern Canadian Shield forests	Central Canadian Shield forests	0.952–0.957	0.928–0.932	0.959–0.963
Midwestern Canadian Shield forests	Southern Hudson Bay taiga	0.852–0.871	0.844–0.851	0.950–0.953
Central Canadian Shield forests	Southern Hudson Bay taiga	0.902–0.910	0.886–0.893	0.929–0.933
Central Canadian Shield forests	Eastern Canadian Shield taiga	0.875–0.885	0.876–0.888	0.920–0.936
Central Canadian Shield forests	Eastern Canadian forests	0.949–0.961	0.888–0.900	0.926–0.938
Southern Hudson Bay taiga	Eastern Canadian Shield taiga	0.815–0.846	0.839–0.861	0.915–0.929
Southern Hudson Bay taiga	Low Arctic tundra	0.167–0.269	0.746–0.786	0.734–0.767
Eastern Canadian Shield taiga	Eastern Canadian forests	0.886–0.900	0.883–0.887	0.928–0.936
Eastern Canadian Shield taiga	Low Arctic tundra	0.175–0.199	0.800–0.810	0.864–0.872
Eastern Canadian Shield taiga	Torngat Mountain tundra	0.322–0.408	0.804–0.821	0.849–0.866
Eastern Canadian forests	Newfoundland Highland forests	0.907–0.922	0.884–0.895	0.732–0.791
Eastern Canadian forests	South Avalon–Burin oceanic barrens	0.922–0.935	0.946–0.952	0.887–0.905
Beringia lowland tundra	Beringiaupland tundra	0.203–0.245	0.795–0.811	0.851–0.900
Beringia lowland tundra	Alaska/St. Elias Range tundra	0.524–0.581	0.873–0.881	0.951–0.961
Beringia lowland tundra	Interior Yukon/Alaska alpine tundra	0.185–0.317	0.818–0.846	0.920–0.932
Alaska/St. Elias Range tundra	Pacific Coastal mountain icefields and tundra	0.401–0.469	0.848–0.855	0.909–0.915
Alaska/St. Elias Range tundra	Interior Yukon/Alaska alpine tundra	0.777–0.834	0.913–0.921	0.937–0.944
Interior Yukon/Alaska alpine tundra	Ogilvie/MacKenzie alpine tundra	0.696–0.719	0.930–0.933	0.949–0.953
Interior Yukon/Alaska alpine tundra	Brooks/British Range tundra	0.357–0.426	0.784–0.810	0.875–0.885
Brooks/British Range tundra	Arctic foothills tundra	0.161–0.198	0.721–0.734	0.875–0.883
Brooks/British Range tundra	Arctic coastal tundra	0.143–0.171	0.712–0.736	0.832–0.844
Arctic foothills tundra	Arctic coastal tundra	0.094–0.108	0.746–0.773	0.887–0.895
Arctic coastal tundra	Low Arctic tundra	0.263–0.453	0.847–0.855	0.893–0.903
Arctic coastal tundra	Middle Arctic tundra	0.130–0.177	0.903–0.925	0.889–0.938

(*continued on next page*)

Table 2 (*continued*)

Ecoregion 1	Ecoregion 2	Trees	Birds	Mammals
Low Arctic tundra	Middle Arctic tundra	0.133–0.145	0.864–0.871	0.713–0.738
Middle Arctic tundra	High Arctic tundra	No data	0.839–0.848	0.739–0.789
Middle Arctic tundra	Davis Highlands tundra	No data	0.823–0.842	0.986–0.998
High Arctic tundra	Davis Highlands tundra	No data	0.829–0.844	0.861–0.902
Davis Highlands tundra	Baffin coastal tundra	No data	0.918–0.933	0.993–1.006

A few ecoregions in the Arctic have no tree species, and are marked "no data". Two ecoregions also have no adjacent ecoregions (Queen Charlotte Islands and Aleutian Islands Tundra), and are excluded from our analysis. The range shown is the range of rate parameter calculated from regressions of similarity as a function of log(distance), using the statistical resampling technique described in the text. The rate parameter is expressed here as the proportion of similarity remaining at 100 km distance. Note that the range of values shown is an estimate of the precision with which the value of the parameter is estimated. The range should not be interpreted as an estimate of the range of similarity values that occur between cells at 100 km in adjacent ecoregions, which is generally broader.

data were available and our results repeated using an appropriate similarity metric, our results may differ. Our results should be seen as a first step, using a unique methodology, toward the systematic testing of ecoregions using species composition data. More importantly, our results should not be interpreted normatively. Ecoregions are undoubtedly a useful tool for conservation planning in many situations, and our results only address one particular application of ecoregions (cf., Magnusson, 2004).

Some ecoregion boundaries were supported by our analyses for all three species groups. Often this occurs when the ecoregion boundary is roughly concurrent with an ecotone between two biome types, as in the transition between the Northern Mixed Grasslands ecoregion and the Canadian Aspen Forests ecoregion. Ecoregion boundaries that track major mountain ranges also correspond with high turnover, such as the transition between the Northern California Coastal Forest ecoregion and the Klamath–Siskiyou ecoregion. However, there exist several areas of substantial environmental change where we would expect to see high rates of turnover and do not detect it. Thus, much further testing is needed to confirm the apparent trend of high turnover across boundaries at major biome transitions or major topographic features.

Differences among the three species groups in the spatial pattern of correspondence between ecoregion boundaries and high turnover are illuminating. For example, the boundary between the Eastern Great Lakes Lowland Forest ecoregion and the New England/Acadian Forest ecoregion has a higher rate of species turnover for birds than for mammals and trees, presumably because many coastal bird species have ranges that overlap with the New England/Acadian Forest ecoregion but not with the more continental Eastern Great Lakes Lowland Forest ecoregion. A more widespread difference between species groups is the tendency for turnover rates (intra- or inter-ecoregions) to be higher for trees than for mammals and birds. This may be simply because of the limited dataset available for trees, with just a subset of dominant tree species available. However, turnover patterns for the common tree species described by Little (1977) may be reasonably correlated with overall turnover patterns for all tree species (Lennon et al., 2004). That our tree group does not represent a monophyletic group may also increase rates of species turnover, since different families of vascular plants may respond very differently to environmental heterogeneity. Finally, turnover rates may be higher for trees because trees arguably have a lower capacity for dispersal than birds or mammals, which may affect speciation and certainly has affected recolonization since the last ice age.

Throughout the history of community ecology, there has been a debate, now nearly a century old, over the nature of ecological communities. One viewpoint considers ecological communities as relatively discrete entities, with limited areas of high species turnover (or ecotones) between communities (Clements, 1916). Another viewpoint considers variation in species composition to be relatively continuous, with the response of species to environmental variation being highly individualistic (Gleason, 1917). Our results, at a much larger scale, suggest that species composition over continental scales rarely shows distinct ecotones, and in general there is continuous change in species composition over space, consistent with this latter viewpoint of gradient change. These results are not surprising. Those who define ecoregion boundaries are well aware that the ecoregion boundaries do not always (or even often) represent abrupt transitions in species composition, and that a boundary that is an ecotone for one taxonomic group may not be an ecotone for other taxonomic groups (Olson et al., 2001). However, places with drastic changes in abiotic conditions, like mountain ranges, or biotic conditions, like transition zones between biomes, often have more abrupt changes in species composition in our results, and here the ecoregion boundaries may be more coincident with areas of high species turnover (cf., Whittaker, 1967).

Our results have implications for the development and use of ecoregions. First, when a set of ecoregions is employed, it should be remembered that the ecoregion

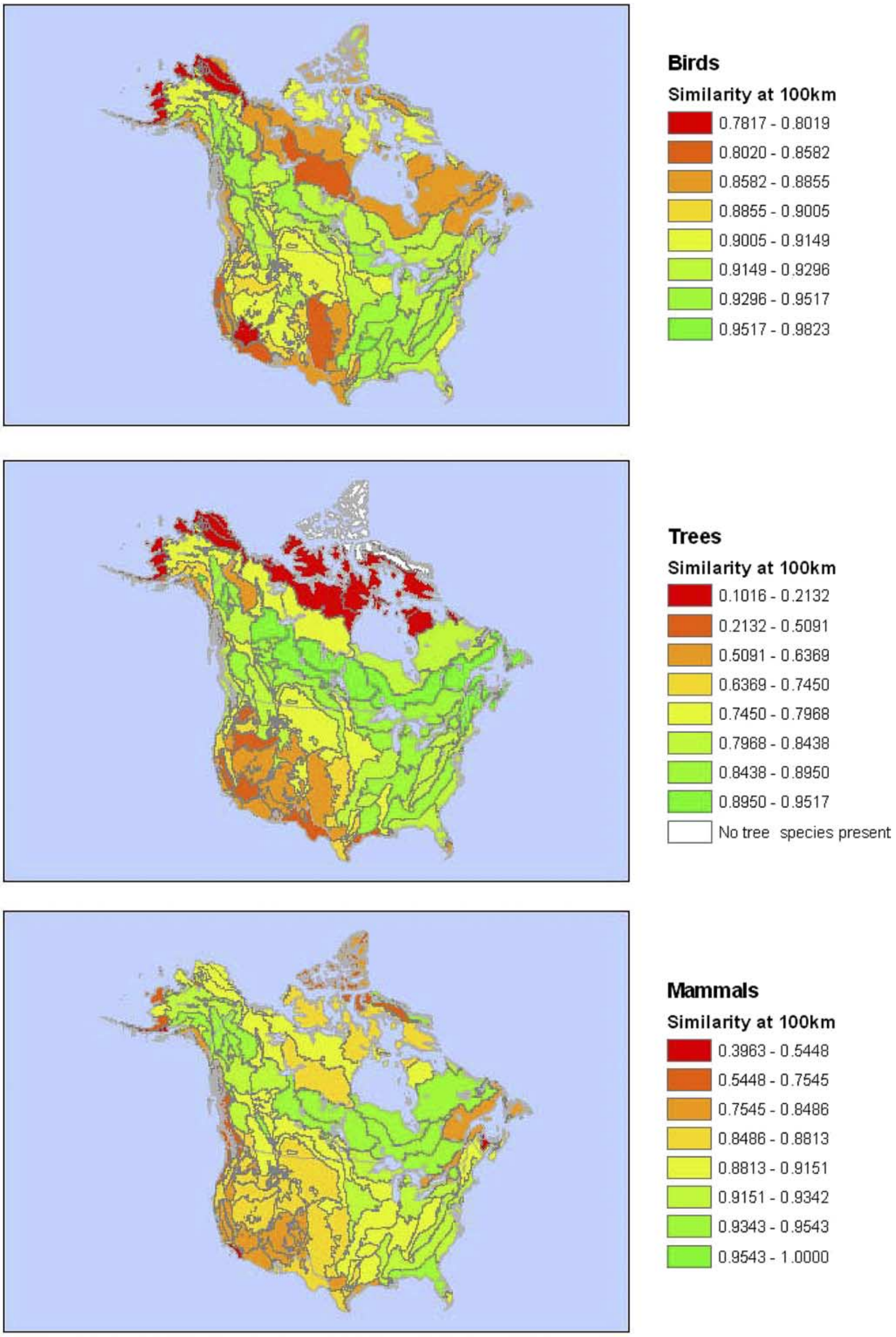

Fig. 3. A three-panel color map, showing the intra-ecoregion turnover rate for the US and Canada. Each panel corresponds to data from one of our species groups (i.e., mammals, trees, or birds), and each ecoregion polygon is colored according to how fast the rate of species turnover per kilometer is, expressed here as the similarity that remains at a pair of cells 100 km apart. As the three groups show different ranges of turnover rates, the color scales are relative between groups, with red shades representing fast rates of turnover and green shades slow rates. Country borders and the edges of major water-bodies are shown in grey, for illustrative purposes. See text for details.

boundaries that represent a zone of high species turnover for a particular species group do not necessarily represent a zone of high species turnover for other species groups. This implies that a discrete set of ecoregions developed for one purpose by an organization such as World Wildlife Fund is potentially not appropriate for some other uses. For example, if researchers wish to stratify sampling over ecoregions, they should ensure

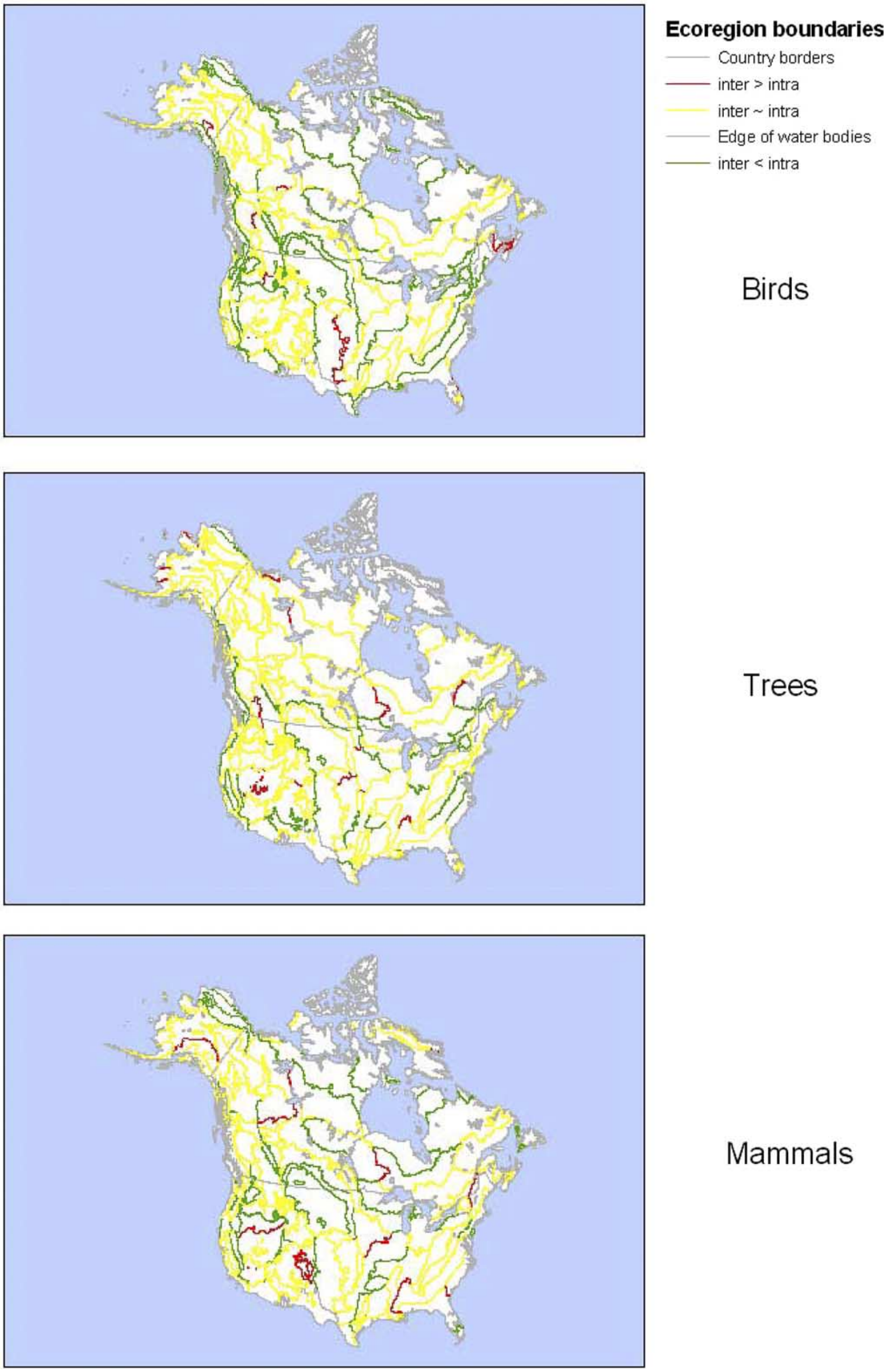

Fig. 4. A three-panel color map, showing the edges between ecoregions color-coded so that they are: green if the inter-ecoregion turnover is significantly greater than both intra-ecoregion turnovers; yellow if the inter-ecoregion turnover is between the two intra-ecoregion turnovers; red if the inter-ecoregion turnover is significantly less than both intra-ecoregion turnovers. Country borders and the edges of major water-bodies are shown in grey, for illustrative purposes. See text for details.

that the set of ecoregions they use has relevance for the taxonomic group or ecological process they are studying. Similarly, if conservation planners wish to use ecoregions as planning units for the protection of a particular taxonomic group (e.g., aiming to protect a proportion of each ecoregion), they should ensure that the set of ecoregions used adequately captures patterns of turnover for that group.

These considerations suggest one possible approach in the future when discrete planning units are wanted that are relevant to particular taxa or processes (only one of the possible uses of ecoregions), with different sets of ‘ecoregions’ being designed for major taxonomic groups or ecological processes. Each set of ‘ecoregions’ would then be used in the planning process when considering a particular major taxonomic group. It is possible that at higher levels of spatial organization (i.e., biomes and major physiographic regions) these different sets of ‘ecoregions’ boundaries would largely coincide, allowing for a nested structure: higher-level units (i.e., biomes) would be spatially consistent across taxa, while within these units lower-level ‘ecoregion’ boundaries would need to be taxon-specific.

5. Conclusions

Conservation planners inevitably must define the extent of the region they are planning for and develop methods of ensuring adequate representation of species assemblages. Ecoregions delineated for multiple taxa provide a biogeographic framework for conservation at broad scales that is undoubtedly preferable to political boundaries (Pimm, 1999). However, our results suggest that ecoregions drawn to capture patterns of the entire biota may not capture the pattern of any single taxonomic group adequately, and therefore interpretation using ecoregions for any single taxonomic group should be done with care.

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