
Temperate Terrestrial Vertebrate Faunas in North and South America: Interplay of Ecology, Evolution, and Geography with Biodiversity

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Abstract: *To help identify the factors that govern species richness in biological preserves, we performed a comparative study of terrestrial vertebrate species richness for two analogous montane areas critical for biodiversity conservation: the Greater Yellowstone region of the Rocky Mountains, United States, and the Nahuel Huapi region, Patagonia, around Bariloche, Argentina. We explored the ecological interactions of such factors as latitude, habitat heterogeneity, inferred productivity, geographic context, history of lineage, and history of environment in generating and maintaining species richness. Overall species richness of terrestrial vertebrates was higher in the Yellowstone area, but patterns were not uniform across vertebrate classes. Ectotherms (reptiles and amphibians) were more diverse in the Patagonian site, whereas endotherms (birds and mammals) were more diverse in the Yellowstone site. The higher diversity of Patagonian ectotherms is a result of abnormally high numbers of species within two specialized taxa: frogs and the lizard genus *Liolaemus*. There were high percentages of endemic species (68% of amphibians, 35% of reptiles, 15% of mammals) and feral, non-native mammals (19%) in Patagonia. These results imply that (1) biodiversity is generated and maintained by a combination of local phenomena and by continental area and related historical constraints; (2) the relative weight of the various influences may differ for ectotherms (fit latitudinal and related models) and endotherms (fit history-based models); and (3) because larger-scale processes are so important for the maintenance of natural biological diversity, it is crucial that biological reserves be selected and managed with an understanding of the geographical and geological context of the continents on which they are located. Reserves located on large continents with connections to other continents preserve large numbers of species per given unit of geographic area and protect critical habitat for species such as migrants that require large areas for maintenance of persistent populations. In contrast, reserves located on relatively isolated continents protect a high number of evolutionarily unique species per given unit of geographic area and have a high potential for colonization by exotic species.*

Fauna de Vertebrados Terrestres Templados en Norte y Suramérica: Interacción Entre la Ecología, la Evolución y la Geografía con la Biodiversidad

Resumen: *Para ayudar a identificar los factores que gobiernan la riqueza de especies en las reservas biológicas, llevamos a cabo un estudio comparativo de la riqueza de especies de vertebrados terrestres para dos áreas montañosas críticas para la conservación de la biodiversidad: la gran región del Yellowstone en las Montañas Rocallosas, Estados Unidos y la región del Nahuel Huapi, Patagonia, alrededor de Bariloche, Argentina. Exploramos las interacciones ecológicas de factores tales como la latitud, la heterogeneidad del hábitat, la productividad inferida, el contexto geográfico, la historia del linaje y la historia del ambiente en la generación y man-*

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tenimiento de la riqueza de especies. En general, la riqueza de especies de vertebrados terrestres fue mayor en el área de Yellowstone, pero los patrones no fueron uniformes en las diferentes clases de vertebrados. Los ectotermos (reptiles y anfibios) fueron más diversos en el sitio de la Patagonia, mientras que los endotermos (aves y mamíferos) fueron más diversos en el sitio de Yellowstone. La mayor diversidad de ectotermos en la Patagonia se debe a números anormalmente altos de especies dentro de dos taxones especializados: ranas y lagartijas del género Liolaemus. Hubo porcentajes altos de especies endémicas (68% de anfibios, 35% de reptiles, 15% de mamíferos) y de mamíferos silvestres no nativos (19%) en la Patagonia. Estos resultados implican que (1) la biodiversidad es generada y mantenida por una combinación de fenómenos locales y por restricciones de áreas continentales históricamente relacionados; (2) el peso relativo de las diferentes influencias puede diferir para los ectotermos (adaptación latitudinal y modelos relacionados) y endotermos (modelos basados en adaptación histórica) y (3) debido a que los procesos a gran escala son tan importantes para el mantenimiento de la diversidad natural biológica, es crucial que las reservas sean seleccionadas y manejadas con un entendimiento del contexto geográfico y geológico de los continentes en los cuales se localizan. Las reservas localizadas en continentes grandes con conexiones a otros continentes preservan un gran número de especies por unidad de área geográfica dada y protegen hábitat crítico para especies tales como las migradoras que requieren de áreas grandes para el mantenimiento de poblaciones persistentes. En contraste, las reservas ubicadas en continentes relativamente aislados protegen un número alto de especies evolutivamente únicas por unidad de área geográfica dada y tienen un alto potencial para la colonización por especies exóticas.

Introduction

The concept of biodiversity figures prominently in conservation efforts because it has become a global currency for discussing a variety of phenomena such as ecosystem resilience and stability (McNaughton 1977; Naeem et al. 1994; Tilman & Downing 1994); ecosystem evolution (Sepkoski 1978; Maurer 1989; Stucky 1990); human effects on ecosystems (Bazzaz 1983; Vitousek 1990); and economic valuation (Ehrlich & Wilson 1991; Randall 1991; Pearce & Moran 1994; Costanza et al. 1997). Yet we know little about what creates and maintains biodiversity patterns in specific landscapes (Hawksworth & Kalin-Arroyo 1995), which limits our ability to devise practical strategies for conserving biodiversity.

To help specify the key aspects of biodiversity conservation strategies, we examined the question of what generates and maintains biodiversity in a pair of similar mountainous environments in temperate latitudes: the Greater Yellowstone Region, which centers on Yellowstone and Grand Teton national parks, United States, and northern Patagonia, which incorporates Nahuel Huapi and Lanin National Parks, Argentina. Each region encompasses multiple environmental gradients and some of the most ecologically intact areas left on Earth. Hence, biodiversity in both regions is likely to approximate historic species richness. The Yellowstone site has at its core the world's first national park (established in 1872) and is arguably the largest relatively intact temperate ecosystem in the world (Reese 1984). The Patagonian site is centered on the world's third oldest national park, Nahuel Huapi (established 1903). Based on comparisons of these two areas, we identify how aspects of ecological history—history of lineage, environment, and geographical context—interact with existing resources to

generate and maintain biodiversity within regions. Defining this complex set of interacting factors is a prerequisite for identifying specific regions and specific reasons why biodiversity conservation efforts are necessary.

Biodiversity Regulation in Temperate North and South America

Factors that influence biodiversity include (1) latitude (Darwin 1859; Fischer 1960; MacArthur 1972; Stevens 1989); (2) elevation (Gentry & Dodson 1987; Stevens 1992); (3) habitat diversity (MacArthur & MacArthur 1961; Huston 1994); (4) productivity (Rosenzweig 1995); (5) size of the continent on which the biota are located (MacArthur & Wilson 1967; Brown 1995; Rosenzweig 1995); (6) niche requirements of the species involved (Huston 1994; Pianka 1994); and (7) historical constraints such as phylogeny (Brooks & McLennan 1993), environmental change and other disturbances (Vuilleumier & Simberloff 1980; Barnosky 1994; Bennett 1997), and isolation (Mayr 1965; MacArthur & Wilson 1967; Webb 1991). Factors 1–4 influence ecological processes related to resource availability, whereas factors 5–7 ultimately relate to longer-term evolutionary processes, but the ecological and evolutionary processes are mutually interactive and interconnected (Vuilleumier & Simberloff 1980). The challenge is to tease apart the interconnections to clarify which pathway of ecological history is expressed by a given biodiversity pattern.

Ecological Processes Influencing Species Diversity

Nearly all major plant and animal groups show decreasing species richness with increasing latitude (MacArthur

1972; J. M. Savage 1973; Schall & Pianka 1978; Stevens 1989; Gaston et al. 1995; Brown & Lomolino 1998). Understanding this latitudinal gradient is not straightforward because many factors also are correlated with the gradient, such as primary productivity, temperature gradients, and moisture variability (Rosenzweig & Abramsky 1993; Huston 1994; Pianka 1994). Climate has also been implicated in producing the diversity gradient (May 1973; Turner et al. 1987; Tilman & Pacala 1993), again because milder and more equable climates generally correlate with increased productivity. Similar ideas have been applied to explain observed patterns of decreasing diversity with elevation within any given latitude.

Most studies attribute causality to the increased availability of resources toward the tropics or with lower elevations (Pianka 1994; Brown & Lomolino 1998). Examples of relevant ecological processes include competition, predation, and disturbance operating within communities (Huston 1994) or the availability and spatial distribution of microhabitats (MacArthur 1972; Cody 1974; Diamond 1975). These processes must operate mainly at the local scale. As a result, many explanations for the number of species found within a geographic region are based on examinations of ecological processes that operate on scales equal to or smaller than the study site (e.g., Wiens 1989a, 1989b; Huston 1994; Tilman et al. 1996). Considering only the latitudinal position and availability of resources in each of our study regions, greater species richness would be expected in Patagonia than in Yellowstone (Appendix).

Geographic Context and Continental Area

Species richness also is profoundly affected by processes operating above the scale of the typical study site (Noss 1983, 1990; Ricklefs 1987; Root 1988; Brown & Maurer 1989; Holt 1993; Ricklefs & Schluter 1993; Rosenzweig 1995; Maurer 1999; Tilman 1999). Terborgh (1977) and Rosenzweig (1995) note that global species diversity may be higher in the tropics than in the temperate zone, not simply because of resources but because the geographic area in the tropics is considerably greater than in the temperate zone. Rosenzweig hypothesizes that speciation rates are higher in larger provincial areas in part because of larger ranges of individual taxa, regardless of latitude.

The North American temperate zone should therefore have larger geographic ranges and higher speciation rates than the South American zone (Appendix). In addition, Rapoport (1982) and Stevens (1989) suggest that species from lower latitudes have smaller latitudinal ranges, possibly correlated with geographic range size. Later workers (Gaston et al. 1998) point out that the correlation between latitudinal range and latitude is less universal than Stevens thought. If links exist between latitude, geographic area, species range size, and speciation rate, then smaller geographic ranges in Patagonian taxa than in Yel-

lowstone taxa would act to depress standing diversity, counterbalancing the diversity-increasing effects of lower latitude and more diverse habitats (Appendix).

Speciation and Extinction

Most discussions of the effect of evolutionary processes on species richness implicitly assume that background extinction events are constant through geological time (except for mass extinction events) and that therefore processes governing the number of speciation events provide the strongest influence on the standing diversity of a site over the long term (e.g., Huston 1994; Rosenzweig 1995). This assumption can functionally link a history-based explanation (e.g., faunal turnover) to a resource-based one if the distribution of resources over long time periods ultimately controls speciation rates. For example, resource partitioning assumes that species originate or evolve new adaptations to prevent them from experiencing too much niche overlap (Schoener 1974). From such considerations one would predict that, because of higher resource availability in the Patagonian site (Appendix), origination rates would be higher there, which would lead to higher species richness.

Assuming that speciation is controlled ultimately by resources ignores macroevolutionary phenomena that may produce emergent properties influencing speciation and extinction dynamics but that are not rooted to resource distributions. Among such emergent properties are generation times, dispersal abilities, mate-recognition systems, and communication mechanisms. Speciation per se (especially by models that mainly consider links to resources) may not be the sole determinant of species richness in a given region. Differences in species richness between two areas could also arise if speciation rates were constant but extinction rates differed (Maurer & Nott 1998). The processes that produce high extinction rates may be fundamentally different from those that produce high speciation rates. For example, rapid environmental change might elevate extinction rates, whereas short generation time might accelerate speciation rate.

Separating the relative effects of speciation and extinction on species richness is difficult. The rate of diversification of a group of species varies with the number of species in it (Rosenzweig 1975; Sepkoski 1978; Alroy 1998). When there are few species, rates of diversification are positive and rapid; when there are many, rates of diversification tend to be negative. The average number of species found in a given area depends on how rapidly the rate of diversification declines with increasing species richness (Maurer & Nott 1998; Maurer 1999). For a given number of species, the diversification rate is determined by the rate of speciation minus the rate of extinction. Thus, it is necessary to know how the per-species rates of speciation and extinction change with species number to understand what determines the av-

erage number of species in a given region. Speciation and extinction rates cannot be measured directly for our study areas. We used numbers of species per genus as an index of differences between speciation and extinction rates, because genera are longer-lived in the fossil record than species (2–6 million years for mammalian genera, with a median of 3 million years, vs. 0.2–3 million years, with a median of 1.5 million years, for mammalian species [D. E. Savage 1977; Stanley 1978; Alroy 1996]). Therefore, if the difference between extinction and speciation rates is driving differences in species richness between our two study areas, we should see differences in ratios of species per genus within major taxonomic groups. If the ratios of species to genera are lower in Patagonia, a factor in addition to present resource distribution (i.e., one related to long-term processes driving extinction and speciation rates) must be influencing the patterns, because resources and habitat heterogeneity are greater at the Patagonia site (Appendix).

Effects of Isolation

The percentage of endemic species increases with degree of isolation and island size (Mayr 1965; MacArthur & Wilson 1967). Our Patagonian study site is effectively located on a large island because it is in a temperate area isolated from other temperate regions. Its last direct connection with Africa was about 100 million years ago, and complete separation from Antarctica occurred about 30 million years ago (Pitman et al. 1993). Since then, immigration of temperate taxa has been from North America, which means dispersal filtered through a subtropical-tropical barrier. Thus, native temperate Patagonian species either have evolved in situ from tropical-subtropical relatives (e.g., hystricognath rodents and didelphimorph marsupials), represent relicts of temperate taxa from more ancient dispersal events (e.g., rheas, microbiothere marsupials), or have dispersed through a subtropical-tropical filter (e.g., thrushes and cricetid rodents). Thus, endemism should be higher in the Patagonian site.

Of particular importance to conservation efforts is the invasibility of a native biota. Areas that are isolated, such as islands, are more susceptible to successful invasion because on average there have not been enough immigrants to saturate available habitats (MacArthur & Wilson 1967; Rosenzweig 1995). Because of the isolation and putative endemism of the Patagonian fauna, exotics would be expected to establish themselves relatively easily there.

Methods

Study Areas

The Yellowstone study grid ranges from lat 46°03'N to 43°00'N (just north of Bozeman, Montana, to the middle

of Wyoming) and from long. 111°30'W to 109°58'W (near Island Park, Idaho, to the eastern border of Yellowstone Park). In northern Patagonia, the study grid ranges from lat. 42°00'S to 38°54'S (approximately Alumine to El Bolsón) and from long. 71°52'W to 70°29'W (approximately the Argentine–Chilean border to the confluence of the Rio Collón Curá and Río Limay) (Fig. 1). The equally sized study grids (40,800 km²) each include approximately 25% national parkland. The Patagonian site includes the 11,370 km² of Nahuel Huapi and Lanin National Parks, and the Yellowstone area includes the 9130 km² of Yellowstone and Grand Teton national parks. Both are temperate latitude sites that straddle the continental divide. (See Appendix for other relevant details.)

Measures of Diversity and Taxonomy

Although biodiversity can be measured on biological levels that range from higher taxa to genes, concentration on generic and species richness was mandated by the nature of our data and the questions we were addressing. Species richness, our primary biodiversity index, has been cited as a “suitable measure for most broad-scale comparisons of diversity” (Schluter & Ricklefs 1993).

We used the taxonomy as it is recognized currently for mammals (Wilson & Reeder 1993), birds (Sibley & Monroe [1990] and American Ornithologists' Union [1998], with priority given to American Ornithologists' Union in cases of conflict), reptiles (Frost & Etheridge 1989), and amphibians (Frost 1985; Stebbins 1985). We defined endemics as those species found only in the vicinity of our study areas (i.e., those restricted to the Patagonian Andes between latitudes 36°S and 44°S and those restricted to the northern Rocky Mountains between latitudes 40°N and 48°N).

Databases

We divided both study areas into 10 × 10 km cells (408 cells per study site). For each cell we compiled the list of species of mammals, birds, reptiles, and amphibians that live there. We used a geographic information system (ARC/INFO) to compile species richness in each cell (Fig. 1); then data from all cells were aggregated to provide an estimate of species richness for each study area. The cell-by-cell data were used to assess the adequacy of the overall species richness counts for each study area. We do not discuss patterns among cells within each study area (beta diversity), which goes beyond our objectives and requires further treatment and standardization of the datasets. We were concerned particularly with assessing the adequacy of our aggregate data for comparisons, because the species data for the two areas were compiled in different ways.

The Patagonian data were compiled from 1981–1999 by Michael Christie and colleagues, first as part of a

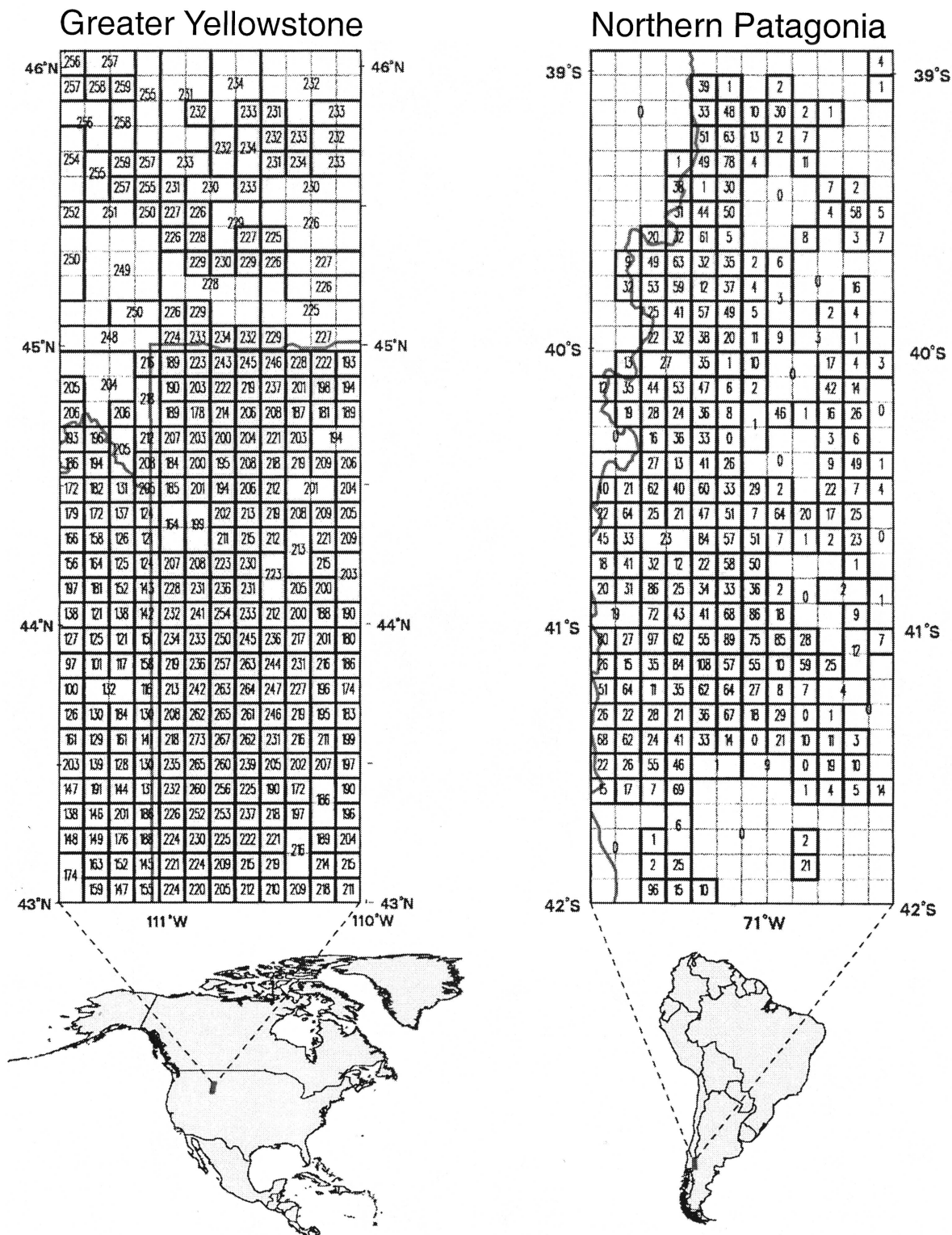


Figure 1. Yellowstone and Northern Patagonia study sites and total species richness in each cell (amphibians, reptiles, birds, mammals). Gray lines indicate state boundaries (Montana to the north, Wyoming to the east, Idaho to the west) in North America and the border between Chile (west) and Argentina (east) in South America. Continents depicted as Robinson projection with long. -75°W as central meridian. Data are available for all 408 cells in Yellowstone and for 258 cells in Patagonia.

Parques Nacional project to catalog terrestrial vertebrate biodiversity in and around Nahuel Huapi and Lanin National Parks and later as an attempt to continue building the dataset for the entire northwestern Patagonian region (Christie et al. 1984a, 1984b, 2001; Pearson 1995). Crews were sent to each 100-km² cell to systematically observe and record the species that lived there. Bibliographic or museum data were used only when records could be placed within a given cell. About 50 transient bird species (defined as less than three records, mainly oceanic birds) were not included in the analysis. Therefore, the Patagonian database is primarily a "ground-truth" database. The most likely error is that too few species were recorded because investigators may not have seen every species that occurs in the cell. Compounding this potential problem is that some cells in Patagonia have no data (Fig. 1). Finally, cells where people live may have higher counts of species because more people have reported data.

In contrast, we placed species in the Yellowstone cells by utilizing published range maps of vertebrate species (Stebbins 1954, 1985; Rossman et al. 1966; Hoffman & Pattie 1968; Burt & Grossenheider 1976; Hall 1981; Thompson 1982; Johnsgard 1986; Clark & Stromberg 1987; Clark et al. 1989; Dobkin 1994; Koch & Peterson 1995; Reichel & Flath 1995; Hadly 1996; McEneaney 1996; Reeder & Weins 1996; Schaffer & McKnight 1996; Skaar 1996; Green et al. 1997; Oakleaf et al. 1997). We then augmented and refined the range-map data with the published results of the Idaho (Groves et al. 1997) and Wyoming (Merrill et al. 1996) gap analysis projects and our personal knowledge of habitats in the Greater Yellowstone Area. Therefore, the data for the Yellowstone site may include too many species in a cell, just the opposite of the error direction for the Patagonian data.

Domestic species confined around human occupations (dogs, cats, chickens, goats, sheep, etc.) were not included in the list from either study site. Cows (*Bos taurus*) were included in the Patagonian species counts

because of their ecological integration into the national parks. Cows were not included in the Yellowstone counts because they were absent in the parks. Introduced game species (for example, *Cervus elaphus*) were counted in the Patagonian data set only if they had prospered to the extent that there were naturally reproducing populations spreading significantly from the original site of introduction.

Statistical Methods

We constructed sampling curves to determine whether species counts in each area were likely to increase if additional cells (e.g., a slightly larger area) were added and to assess whether the cells without survey data were depressing apparent species richness in the Patagonian site (Fig. 2). For a single sampling bout, cells were drawn randomly without replacement, and the number of new species in each cell accumulated until all cells were sampled. Cells with a species richness of zero (i.e., those that had not been surveyed) were excluded. This procedure was repeated 100 times for each taxon in each of the two study regions. The average and two standard deviations around the average were calculated for each study area.

Results

Overall Patterns

The sampling curves for Patagonian and Yellowstone birds and mammals reached asymptotes, with slopes rising minusculely by the end of the sampling bouts (Fig. 2). Therefore, it is unlikely that sampling a slightly larger area or adding data from unsurveyed cells in Patagonia would add significant numbers of species. The curves demonstrate that we adequately represented the total richness of terrestrial vertebrate species in the two study regions.

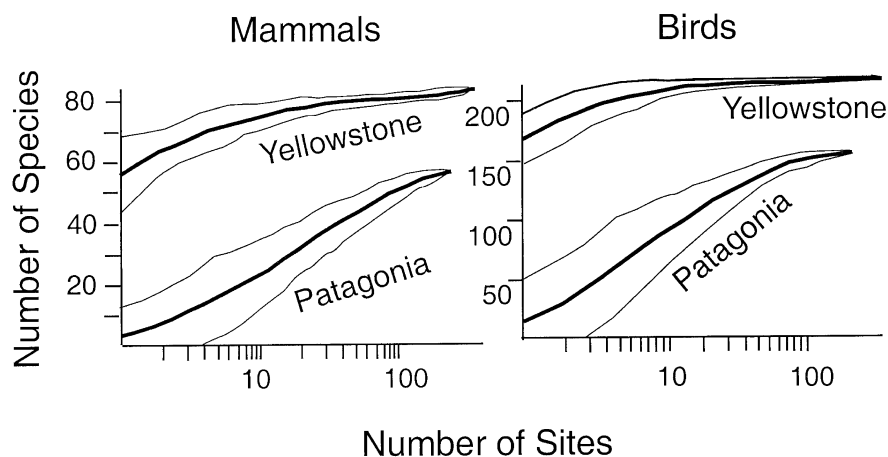


Figure 2. Randomized species-accumulation curves for birds and mammals in the Yellowstone and Patagonian study areas. Curves represent means and ± 2 SD from 100 randomizations. Curves approach asymptotes, implying relatively complete sampling.

We calculated species richness, generic richness, and the ratio of species to genera for amphibians, reptiles, birds, and mammals (Table 1). These combined groups included 254 species for the Patagonian study site and 312 species for the Yellowstone site (species lists are available upon request from the authors). Even for the Patagonian site, these numbers match well with the counts derived from published geographic ranges of species (Olrog 1979; Cei 1980, 1986; Christie et al. 1984a, 1984b, 2001; Narosky & Yzurieta 1989; Ridgely & Tudor 1989, 1994; Redford & Eisenberg 1992; Gallari et al. 1996; Laelau 1997); therefore, the overall lower species richness in Patagonia is not caused by different methods of compiling the data, which is concordant with the evidence from our sampling curves.

Neither are the differences in richness explained primarily by less knowledge of the taxonomy and phylogeny of the Patagonian fauna. M. Christie (unpublished data) compiled species detection curves for Argentina and Chile indicating that more work will not significantly increase species counts for birds or large mammals. Although small-mammal species might increase by at most 10%, this would not affect the overall patterns, which show a 23% increase in South American mammals is necessary to equal the North American mammalian richness (Table 1).

Although the overall species richness of terrestrial vertebrates in the Patagonian site was lower than that in the Yellowstone site, ectotherms (amphibians and reptiles) and endotherms (birds and mammals) exhibited different patterns: ectotherms exhibited higher species

richness in Patagonia, whereas endotherms exhibited higher species richness in Yellowstone (Table 1). Future work on the systematics of reptiles and amphibians will probably increase species richness for those groups in Patagonia, making the differences in richness between Yellowstone and Patagonia even more pronounced.

Richness of Reptiles and Amphibians

The higher richness of reptiles and amphibians in Patagonia was found primarily at the species level. Generic richness for reptiles in the two regions was identical (8 genera). In Yellowstone, however, there were 11 fewer species and a lower average number of species per genera (mean of 2.5 species/genus in Patagonia vs. 1.13 in Yellowstone). This discrepancy is accounted for by a single genus from Patagonia, *Liolaemus*, which contains 13 of the 20 total species of reptiles in the Patagonian study site. No other reptile genus in Patagonia had more than 1 species per genus represented (Table 2). Lizards were the most speciose reptiles in Patagonia, whereas snakes (6 species) were the most speciose reptiles in greater Yellowstone.

For amphibians there were 10 fewer species and, on average, fewer species per genus in Yellowstone than in Patagonia (mean of 2.38 species/genus in Patagonia vs. 1.80 in Yellowstone). This pattern resembled the pattern for reptiles, although it was less extreme and the distribution of richness across genera was more even in the Patagonian amphibians than in the reptiles. Each

Table 1. Comparison of species and generic richness in the Patagonian and Yellowstone study areas.^a

<i>Taxon</i>	<i>Species</i>	<i>Genera</i>	<i>Species/genus</i>	<i>Endemic species^b</i>	<i>Exotic species^b</i>
Amphibians					
Patagonia	19	8	2.38	13 (68.4)	0 (0)
Yellowstone	9	5	1.80	0 (0)	1 (1.11)
Reptiles					
Patagonia	20	8	2.50	7 (35.00)	0 (0)
Yellowstone	9	8	1.13	0 (0)	0 (0)
Birds (with exotics)					
Patagonia	156	110	1.42	0 (0)	4 (2.56)
Yellowstone	210	149	1.41	0 (0)	7 (3.33)
Birds (without exotics)					
Patagonia	152	107	1.42	0 (0)	—
Yellowstone	203	142	1.43	0 (0)	—
Mammals (with exotics)					
Patagonia	59	48	1.23	9 (15.25)	11 (18.97)
Yellowstone	84	51	1.65	2 (2.38)	1 (1.19)
Mammals (without exotics)					
Patagonia	48	38	1.26	9 (19.15)	—
Yellowstone	83	50	1.66	2 (2.41)	—
Totals					
Patagonia	254	174	1.46	29 (11.42)	15 (5.91)
Yellowstone	312	213	1.46	2 (0.06)	8 (2.56)

^aSpecies lists available from authors upon request.

^bPercentage of species in parentheses.

Table 2. Comparison of species per genera by family for Greater Yellowstone and Patagonian study areas.

Family	Yellowstone			Patagonia		
	no. of species	no. of genera	species/genera	no. of species	no. of genera	species/genera
Amphibians						
Ambystomidae	1	1	1.00			
Bufo	2	1	2.00	4	1	4.00
Pelobatidae	2	1	2.00			
Hylidae	1	1	1.00			
Ranidae	3	1	3.00			
Rhinodermatidae				1	1	1.00
Leptocactylidae				14	6	2.33
Reptiles						
Boidae	1	1	1.00			
Colubridae	4	3	1.33	2	2	1.00
Viperidae	1	1	1.00			
Emydidae	1	1	1.00			
Phrynosomatidae	2	2	1.00			
Amphisbaenidae				1	1	1.00
Geckonidae				1	1	1.00
Tropiduridae				15	3	5.00
Polychrotidae				1	1	1.00
Birds						
Rheidae				1	1	1.00
Tinamidae				1	1	1.00
Gaviidae	1	1	1.00			
Podicipedidae	4	3	1.33	4	2	2.00
Pelicanidae	1	1	1.00			
Phalacrocoracidae	1	1	1.00	2	1	2.00
Ardeidae	3	3	1.00	4	4	1.00
Threskiornithidae	1	1	1.00	1	1	1.00
Phoenicopteridae				1	1	1.00
Anatidae	22	10	2.20	16	8	2.00
Cathartidae	1	1	1.00	3	3	1.00
Accipitridae	10	6	1.67	9	6	1.50
Falconidae	4	1	4.00	6	3	2.00
Odontophoridae				1	1	1.00
Phasianidae	8	8	1.00	1	1	1.00
Rallidae	3	3	1.00	6	3	2.00
Gruidae	1	1	1.00			
Charadriidae	1	1	1.00	3	3	1.00
Recurvirostridae	2	2	1.00			
Scolopacidae	7	7	1.00	4	3	1.33
Thinocoridae				3	2	1.50
Laridae	6	3	2.00	3	1	3.00
Columbidae	2	2	1.00	4	3	1.33
Cucullidae	2	1	2.00			
Psittacidae				2	2	1.00
Tytonidae				1	1	1.00
Strigidae	10	7	1.43	4	4	1.00
Caprimulgidae	2	2	1.00	1	1	1.00
Apodidae	2	2	1.00			
Trochilidae	4	3	1.33	2	2	1.00
Alcedinidae	1	1	1.00	1	1	1.00
Picidae	8	4	2.00	3	3	1.00
Furnariidae				16	11	1.45
Rhinocryptidae				4	4	1.00
Tyrannidae	11	4	2.75	21	13	1.62
Phytotomidae				1	1	1.00
Laniidae	1	1	1.00			
Vireonidae	3	1	3.00			

continued

Table 2. (continued)

Family	Yellowstone			Patagonia		
	no. of species	no. of genera	species/genera	no. of species	no. of genera	species/genera
Corvidae	7	6	1.17			
Alaudidae	1	1	1.00			
Hirundinidae	6	4	1.50	3	3	1.00
Sittidae	3	1	3.00			
Paridae	2	1	2.00			
Certhiidae	1	1	1.00			
Troglodytidae	4	4	1.00	2	2	1.00
Cinclidae	1	1	2.00			
Regulidae	2	1	2.00			
Turdidae	6	4	1.50	1	1	1.00
Mimidae	2	2	1.00	2	1	2.00
Sturnidae	1	1	1.00			
Motacillidae	2	1	2.00	2	1	2.00
Bombycillidae	1	1	1.00			
Parulidae	10	8	1.25			
Thraupidae	1	1	1.00			
Emberizidae	18	13	1.38	4	1	4.00
Cardinalidae	2	2	1.00			
Fringillidae	9	6	1.50	2	1	2.00
Icteridae	8	8	1.00	10	8	1.25
Passeridae	1	1	1.00	1	1	1.00
Mammals						
Didelphidae				2	2	1.00
Caenolestidae				1	1	1.00
Microbiotheriidae				1	1	1.00
Dasypodidae				2	2	1.00
Soricidae	7	1	7.00			
Vespertilionidae	12	6	2.00	4	3	1.33
Molassidae				1	1	1.00
Canidae	3	2	1.50	2	1	2.00
Felidae	3	2	1.50	4	2	2.00
Mustelidae	10	7	1.43	5	5	1.00
Procyonidae	1	1	1.00			
Ursidae	2	1	2.00			
Cervidae	4	3	1.33	5	5	1.00
Antilocapridae	1	1	1.00			
Suidae				1	1	1.00
Camelidae				1	1	1.00
Bovidae	3	3	1.00	1	1	1.00
Muridae	14	10	1.40	18	14	1.27
Sciuridae	12	6	2.00			
Castoridae	1	1	1.00			
Geomyidae	2	1	2.00			
Heteromyidae	1	1	1.00			
Dipodidae	1	1	1.00			
Erithizontidae	1	1	1.00			
Chincillidae				1	1	1.00
Caviidae				1	1	1.00
Ctenomyidae				3	1	3.00
Octodontidae				3	2	1.50
Myocastoridae				1	1	1.00
Ochotonidae	1	1	1.00			
Leporidae	5	2	2.50	2	2	1.00

of the Patagonian amphibian genera contained between 1 and 4 species, and the Yellowstone amphibian genera each had 1–3 species (Tables 1 & 2). The discrepancy in diversity patterns was manifested primarily in the frogs: Patagonia had 15 species distributed in 7 genera,

whereas Yellowstone had only 4 species and 2 genera. Both areas had 4 species of toads (1 genus in Patagonia and 2 in Yellowstone). The Patagonian site lacked salamanders, of which the Yellowstone site had only 1 species.

Richness of Mammals and Birds

Mammals were notably more species rich in Yellowstone (Table 1). When only native species of mammals were considered, higher richness in Yellowstone was evident at the generic level (50 genera in Yellowstone vs. 38 in Patagonia), but richness differences were driven mostly at the specific level (83 species in Yellowstone vs. 48 in Patagonia). When exotic and native species were considered, the higher richness in Yellowstone was almost entirely at the specific level (48 vs. 51 genera and 59 vs. 84 species for Patagonia vs. Yellowstone, respectively). The added Yellowstone species were primarily squirrels, shrews, and vespertilionid bats (Table 2).

Birds also were more species rich in the Yellowstone site. Unlike the other vertebrate classes, higher generic richness in Yellowstone accounted for much of the higher species richness. Although both Patagonia and Yellowstone shared similar numbers of species per genus (Table 1), considerably more genera in Yellowstone resulted in considerably more species. This held true for counts derived only of native species and for counts that combined native and exotic species (Table 1). The increase in species richness in Yellowstone was due mainly to more anatids, strigids, corvids, emberizids, parulids, and fringillids (Table 2).

Endemics and Exotics

The Patagonian site had substantially more endemic species of reptiles, amphibians, and mammals and more feral exotic mammals (Veblen et al. 1992) than Yellowstone (Table 1). Vuilleumier (1968) and Pearson and Pearson (1982) attributed high endemism to association with the geographically isolated *Nothofagus* forests in Patagonia.

Discussion

Driving Force of Biodiversity

Reptiles and amphibians conform to the prediction that latitudinal position and attendant higher mean annual temperature, precipitation, and probably primary productivity correlate with increased species richness. This result can be added to numerous other examples demonstrating that resources on the landscape influence diversity. The patterns in reptile and amphibian diversity also demonstrate the importance of lineage in influencing biodiversity. Were it not for the remarkable radiation of species within the genus *Liolaemus* and the more diverse frog fauna in Patagonia, little difference in herptile biodiversity would exist between the two study regions.

The species richness patterns in endotherms in the two study sites was fundamentally different than that in

ectotherms, especially in direction (higher species richness in Yellowstone) and to a lesser extent in taxonomic evenness (a few highly speciose ectotherm genera in Patagonia vs. more equal distribution of endotherm species per genus in both regions) (Table 2). The pattern observed in the endotherms conforms closely to that predicted if continental-area effects are important in controlling overall richness. The Yellowstone area is set in a geographic context that "samples" the overlapping edges of wide geographic ranges of mammal and bird species whose ranges are actually centered in the Great Plains to the east, the Great Basin and Columbia Basin to the west and southwest, the central Rockies to the south, and the boreal region to the north. In Patagonia the geographic ranges of taxa are more restricted, in part because of the narrow strip of temperate land on which the study site is located.

If continental-area effects so strongly influence biodiversity patterns in endotherms, what are the underlying processes? Ultimately, species richness in a given area reflects a complicated, nonlinear interaction between species richness and rates of origination (speciation events), immigration, extinction, and extirpation (loss of species due to range shifts). When the rate of diversification depends on species richness, taxa with the highest maximum rate of diversification and lowest declines in diversification rate with increasing richness will maintain the highest average species richness (Alroy 1998; Maurer & Nott 1998; Maurer 1999). The probability of speciation events increases with increasing geographic range size (Rosenzweig 1995); likewise, the probability of a species invading a new area increases with increasing range size, because the larger the range, the larger the source area from which immigrants can propagate. Also with increasing range size, the probability of both extinction and extirpation decreases, because larger range sizes generally indicate larger population size and a less fragmented range (Maurer & Nott 1998; Maurer 1999).

A cursory examination of geographic range sizes for mammals and birds (Hall 1981; Christie et al. 1984a, 2001; Narosky & Yzurieta 1989; Ridgely & Tudor 1989, 1994; Sibley & Monroe 1990; Redford & Eisenberg 1992; Merrill et al. 1996) suggests that geographic ranges are generally smaller for the Patagonian species than for the Yellowstone species. Concordantly, in Patagonia, litter size and home-range size of small mammals generally are smaller than in forest species of comparable size in the northern hemisphere (Pearson 1983). Hence, in Patagonia, maximum rates of origination and immigration are expected to be lower and maximum rates of extinction and extirpation are expected to be higher (Terborgh & Winter 1982). Furthermore, we expect that rates of diversification will be more sensitive to increases in species richness for taxa in Patagonia than in Yellowstone. That is, in Patagonia, the likelihood of extinction of a

species will increase faster and the likelihood of speciation will decline faster with increasing diversity than for a comparable species in Yellowstone. The combination of lower rates of maximum diversification and increased sensitivity of diversification rates to changes in species richness could explain the lower species richness we observed in Patagonia.

The expectation that maximum rates of species loss have been higher in Patagonia is consistent with the fact that Patagonia is more isolated than Yellowstone. For example, during Pleistocene climatic changes, mammalian ranges in the Yellowstone area contracted into refugia in all directions, and immigrant taxa were provided from an extensive boreal and temperate area to the north (including Eurasia), west, and east during interglacial periods. In contrast, during the same time in Patagonia, refugia and immigration were limited because of the narrow strip of land the Andes occupy, tropical and subtropical filters to the north, and lack of connections to an extensive boreal area or other continents to the south (Webb 1984, 1991). Similar constraints would have operated in the Patagonian site throughout most of the Cenozoic.

If the loss rate of species has been higher in Patagonia over evolutionary time, we would expect to see fewer species per genus there, because extinction or extirpation would tend (on average) to cull a higher percentage of species that arose within any single genus. This generally is the observed pattern for mammals represented by the same families in the two areas, and for mammals in general (Tables 1 & 2).

Higher average rates of species loss in Patagonia, coupled with its greater degree of isolation from other temperate continents, might also lead to a higher percentage of endemic taxa, which our data indicate is the case for classes other than birds. This high endemism may also relate to the apparently more patchy habitats that we suspect characterize the Patagonian site. Analyses to quantify habitat heterogeneity are beyond the scope of this paper.

A combination of a high rate of species loss and more patchy habitats implies that abundant "niche space" should be available for colonization in Patagonia. If this is the case, introduced (exotic) species should be able to establish themselves relatively easily in Patagonia. Our data indicate that this may be the case for mammals. Exotic mammal species in Patagonia include large herbivores (three cervids, feral cows, wild boar), carnivores (mink), rodents, and hares. Interestingly, birds exhibited similarly small percentages of exotic species in Patagonia and Yellowstone (Table 2). The difference between birds and mammals may reflect the fact that volant birds can quickly disperse over great distances, which allows them to locate, occupy, and rapidly saturate available niches, an idea that is consistent with the observation that vegetation and climatic conditions determine major patterns of bird species richness (Cueto & Lopez de

Casenave 1999). This implies that good dispersers are less limited by historical constraints than by available resources. Alternatively, the data may simply reflect that people have not attempted to introduce exotic game species of mammals into greater Yellowstone, whereas such was common practice in the early twentieth century in Patagonia (Veblen et al. 1992).

Conclusions

Our analysis indicates that (1) overall species richness of terrestrial vertebrates is higher in the Yellowstone area; (2) species richness of ectotherms is higher in Patagonia; (3) richness of endotherms is higher in Yellowstone; (4) exotic mammals and (5) endemic reptiles, amphibians, and mammals are more frequent in Patagonia. From these conclusions we infer that biodiversity is generated and controlled by complex interactions among ecological processes manifested on temporally short scales (years to perhaps centuries) and ecological history manifested over temporally long scales (millennia to millions of years). Important short-term and local ecological processes include availability of resources and competition. Important aspects of ecological history include history of lineage, history of environment, and geographical context. Ectotherms (reptiles and amphibians) in the Yellowstone-Patagonia comparison exhibit a species-richness pattern consistent with resource-based constraints and history of lineage being the most heavily weighted terms in the diversity equation. Endotherms (mammals and birds) exhibit diversity patterns that seem heavily influenced by the history of environment and geographical context of the ecosystem under consideration.

These results lead to insights about what biodiversity conservation actually conserves in the two study areas. Clearly, terrestrial vertebrate diversity in both areas depends on and to some extent is controlled by the resources that exist there today. But the ecological dramas that led to the respective modern patterns were different. Conservation efforts in Yellowstone are important to preserve not only the last remnants of a geographically large temperate latitude ecosystem, but also the results of a long (millions of years) ecological experiment that featured interchange of species between Eurasia and North America and the march of species in and out of refugia during environmental changes. It therefore is an example of a system that had the possibility of replenishment by pre-existing and new species after each environmental perturbation. The expectation, borne out by the data, is of relatively high species richness, probably with assemblages of species that have been associated for ecologically long periods of time (thousands to tens of thousands of years). In such areas, biodiversity conservation has the effect of preserving maximum num-

bers of species per given unit of geographic area and of providing an ecological snapshot of how continental-level faunal interchange coupled with in situ evolution (minus extinction and extirpation) accumulates over geologically long time periods. Moreover, such areas are particularly critical as habitats for species, such as migratory birds, that utilize continental-scale resources.

Biodiversity conservation in Patagonia is important for a different reason. The geographical context is one of largely limited faunal interchange. Thus, dispersal and expansion and contraction of geographic ranges has contributed to building biodiversity less in Patagonia than in Yellowstone. The histories of lineages—which species got there and the evolutionary accidents that allowed them to radiate or avoid relatively high rates of extinction, given the resources available at the time—more heavily influenced the existing richness of the Patagonian fauna. Therefore Patagonia offers a snapshot of an inherently shorter-lived ecological assemblage. The expectation, again borne out by the data, is of relatively low species richness, high numbers of endemics, considerable potential for open ecological niches, and considerable potential for extinction. Such areas may be particularly prone to elevated extinction of endemics and/or colonization by exotics in the face of global change. In these kinds of areas, biodiversity conservation has the effect of preserving per unit of geographic area a proportionately higher number of evolutionarily unique species, such as species within *Liolaemus*. Because the opportunities for recolonization are so limited and the geographic ranges of species are small, localized conservation efforts are especially crucial. In addition, although overall species richness is greater in Yellowstone, the number of endemic species is greater in Patagonia, suggesting that the “uniqueness” of a fauna is not necessarily tied to species richness.

We expect that other biological reserves located within large continents with connections to other continents will parallel the biodiversity patterns and processes of the Yellowstone area. Areas with a geographical context of isolation within continents, or on islands, should parallel the Patagonian example. These expectations merit refinement by (1) further standardization of the data sets from Patagonia and Yellowstone, such that beta diversity patterns can be analyzed; (2) detailed analysis of diversity patterns and their relationships to specific biophysical parameters within each study site; (3) rigorous phylogenetic and natural-history studies on key taxa; and (4) application of parallel comparative techniques to other landscapes. Our analysis strongly suggests that efforts to manage biodiversity will benefit from taking into account not only the resources that are restricted to the landscape of interest but also the larger-scale ecological processes tied to history of lineage, history of environment, and geographical context. Our data suggest that these larger-scale processes strongly inter-

act with the local ones in generating and maintaining biodiversity, and that they do so in different ways for different taxa. For example, different weighting of the factors related to ecological history and modern resources seems to control biodiversity in ectotherms and endotherms. These points emphasize that biodiversity management plans for a region need to be based on analysis of a variety of taxa and a firm understanding of the ecological history of those taxa.

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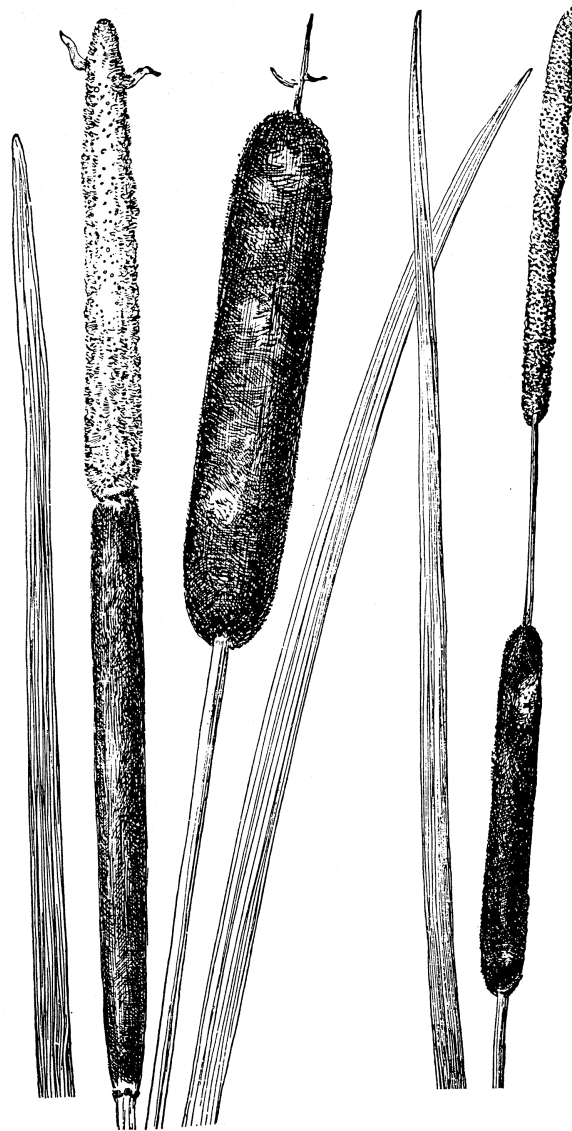
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Appendix

Characteristics of the Patagonia and Yellowstone study sites and implications for predicting species richness of terrestrial vertebrates.

<i>Attribute</i>	<i>Yellowstone</i>	<i>Patagonia</i>	<i>Comments</i>	<i>Prediction for comparative species richness</i>
Study-area size (km ²)	40,800	40,800		no difference
Latitude	46° 03' -43° 00' N	42° 00' -38° 54' S	Patagonia 4° closer to equator	higher in Patagonia
Topography	northwest-southeast trending mountains	north-south trending mountains		no difference
Elevation (m)	1372 to 4177	200 to 3554	more elevational difference in Patagonia, 850 m lower on average	higher in Patagonia
Mean annual precipitation (mm)	200–1700 from lowest to highest areas (drier than Patagonia)	300–4000 from lowest to highest areas (wetter than Yellowstone)	Hoffmann 1975; Steinhauser 1979; Despain 1990	higher in Patagonia
Mean annual temperature (°C)	2.5–7.5	5.0–7.5	Hoffmann 1975; Steinhauser 1979	higher in Patagonia
Direction of climatic gradient	northwest to southeast	west to east	climatic gradient is more pronounced in Patagonia	higher in Patagonia
Inferred net primary productivity	higher elevations dominated by conifers (<i>Pinus</i> spp., <i>Abies lasiocarpa</i> , <i>Picea engelmannii</i>), with open understory; middle and lower elevations by <i>Pseudotsuga menziesii</i> , <i>Populus tremuloides</i> , <i>Pinus flexilis</i> , <i>Artemisia</i> spp., Graminiae (Despain 1990)	higher elevations feature deciduous lenga forests (<i>Nothofagus pumilio</i>) with thick bamboo (<i>Chusquea culeou</i>) understory in wetter areas; lower elevations include steppe, grasses (<i>Stipa</i> spp.), and bushes such as neneo (<i>Mulinum spinosum</i>); ecotonal habitats characterized by small trees such as maiten (<i>Maitenus boaria</i>), radial (<i>Lomatia birsuta</i>), and nire (<i>Nothofagus antarctica</i>), bushes such as espina negra (<i>Colletia spinosissima</i>), retamo (<i>Dioslea juncea</i>), <i>Adesmia</i> , and <i>Berberis</i> ; to the west, evergreen coihue forest (<i>Nothofagus dombeyi</i>) covers the lower elevations, mixed with several other <i>Nothofagus</i> species and a few conifers, such as the araucaria (<i>Araucaria araucana</i>) and the austral cypress (<i>Austrocedrus chilensis</i>) (Martin 1997)	higher in Patagonia because of warmer average temperatures, more precipitation, lower latitude	probably higher in Patagonia
Vegetation			study areas share no plant species except those introduced by humans	higher in Patagonia

continued

Appendix (continued)

Attribute	Yellowstone	Patagonia	Comments	Prediction for comparative species richness
Habitat diversity (no. of habitats)				
History of land use	~25% of study area is national park; Yellowstone established 1872, Grand Teton Park 1929; surrounding park lands historically used primarily as cattle and sheep ranches, with national forest or other public multiuse lands abundant; no grazing in parks; ecotourism and rapid population growth characterize last decade ^a ; population density 2.0 people/km ²	~25% of study area is national park; Nahuel Huapi Park established 1903 (Lanin 1937); surrounding park lands historically used primarily as cattle and sheep ranches; much of surrounding land now part of biotic reserve system; limited grazing allowed in parks; ecotourism and rapid population growth have characterized the last decade ^b ; overall population density 1.9 people/km ²	range of precipitation, temperature, and vegetation suggest more diversity in Patagonia	no reason to expect appreciable differences
Geological history	early Cenozoic, basaltic volcanism; middle Cenozoic, extensional tectonics and bimodal volcanism; Pleistocene, glaciation (25–30% of landscape covered by glacial ice), abundant volcanism	early Cenozoic, basaltic volcanism; middle Cenozoic, extensional tectonics and bimodal volcanism; Pleistocene, glaciation (20–25% of landscape covered by glacial ice), volcanism pronounced	similar geological processes have resulted in remarkably analogous landscapes, including large glacial lakes, glacial landforms, and volcanic soils	no reason to expect appreciable differences
Disturbance	natural wildfires, extremely cold winter temperatures frequent	natural wildfires less frequent but perhaps compensated by prehistoric burning; high winds more frequent	large-scale disturbances probably similar in the two areas due to similar geological histories and processes	no reason to expect appreciable differences
Isolation of biota	connections to Canada, Eurasia provide abundant immigration and refugia throughout the Cenozoic Era	isolated from other temperate and boreal areas for most of the Cenozoic Era	some faunal interchange between North and South America in the early and middle Tertiary; Pleistocene interchange beginning about 2 million years ago, coincident with increased faunal turnover on both continents	higher in Yellowstone
Size of temperate landmass of study site	14,256,105 km ² ; lat. 30°–60° N	2,625,755 km ² ; lat. 30°–60° S	larger land areas may lead to larger geographic ranges, which in turn lead to lower ratios of extinction to origination (Rosenzweig 1995)	higher in Yellowstone

^a Gallatin County, Montana, 49,000 people in late 1980s to 68,000 in 1997.^b Bariloche, Argentina, 40,000 people in late 1980s to 78,000 in 1997.