RESEARCH PAPER

Non-random patterns in the Yellowstone ecosystem: inferences from mammalian body size, order and biogeographical affinity

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ABSTRACT

Aim Our aim was to investigate how the environment, species characteristics and historical factors at the subcontinental scale affect patterns of diversity. We used the assembly of the Yellowstone biota over the past 10,000 years as a natural experiment for investigating the processes that generate a modern non-volant mammal species pool.

Location The data represent species from throughout North America with special attention to the non-volant mammals of Yellowstone National Park, USA.

Methods We used digitized range maps to determine biogeographical affinity for all non-volant mammals in the Rocky Mountains, Deserts and Great Plains biogeographical regions of North America. This biogeographical affinity, along with taxonomic order and body size class, was used to test whether non-random patterns exist in the assemblage of Yellowstone non-volant mammals. These characteristics were also used to investigate the strength of non-random processes, such as habitat or taxon filtering, on particular groups of species or individual species.

Results Our results indicated that the Yellowstone fauna is composed of a non-random subset of mammals from specific body size classes and with particular biogeographical affinities. Analyses by taxonomic order found significantly more Carnivora from the Rocky Mountains region and significantly fewer Rodentia from the Deserts region than expected from random assembly. Analyses using body size classes revealed deviations from expectations, including several significant differences between the frequency distribution of regional body sizes and the distribution of those species found within Yellowstone.

Main conclusions Our novel approach explores processes affecting species pool assembly in the Yellowstone region and elsewhere, and particularly identifies unique properties of species that may contribute to non-random assembly. Focusing on the mechanisms generating diversity, not just current diversity patterns, will assist the design of conservation strategies given future environmental change scenarios.

Keywords

Biodiversity, biogeography, community assembly, macroecology, mammals, National Parks, North America, spatial patterns, USA.

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INTRODUCTION

For centuries scientists have been intrigued by the distribution of species across the globe and the processes that give rise to the observed patterns. Early biogeographers focused on historical context, vicariance and dispersal to make sense of the global species patterns (Wallace, 1881; MacArthur & Wilson, 1963). With improved remote sensing and computing technology, there has been renewed attention to the role of the modern abiotic environment in shaping global or continental patterns of biodiversity. This is most apparent in the large number of recent studies on the latitudinal gradient in species richness (Currie, 1991; Kerr & Packer, 1997; Hawkins *et al.*, 2003; Willig *et al.*, 2003), the distribution of body sizes (Brown & Nicoletto, 1991; Arita & Figueroa, 1999; Maurer *et al.*, 2004; Smith *et al.*, 2004) and other macroecological patterns. A variety of properties of the

physical environment have been shown to correlate with species diversity (Fraser, 1998; Rahbek & Graves, 2001; Hawkins *et al.*, 2003; Willig *et al.*, 2003), but these techniques have been limited both because correlations do not necessarily reveal the mechanisms and because measures of richness generally ignore species identity. In contrast, community ecologists have produced an extensive body of literature regarding the drivers of local species richness and diversity. Often local interactions, such as direct competition and habitat partitioning, are shown to underlie diversity at a local scale (e.g. MacArthur & Levins, 1964; Brown, 1989; Kelt *et al.*, 1995).

Recently, there has been interest in bridging the local studies with those of continental extent, by studying 'regional' level, or mesoscale, processes. Many authors recognize that while local interactions are important in shaping diversity, the local processes are strongly influenced by processes working over a greater spatial extent and time (Ricklefs & Schluter, 1993; Whittaker *et al.*, 2001; Ricklefs, 2004; Graves & Rahbek, 2005; Rahbek, 2005). Local processes reduce diversity through competitive exclusion, extinction and stochastic variation, while regional processes can increase diversity through dispersal (both long-distance and local) and speciation within regions (Ricklefs & Schluter, 1993; Cracraft, 1994). The relative importance of these processes to a species pool is likely to vary among taxonomic groups and regions, and understanding the mechanisms driving this variability is critical to understanding patterns of spatial diversity (Ricklefs & Schluter, 1993).

While interest in the role of regional and historical processes in determining local patterns of species richness has been growing (Cornell & Lawton, 1992; Kelt, 1999; Qian & Ricklefs, 2000), we still have a relatively poor understanding of the direct effects of these processes (Stone *et al.*, 1996; Wiens & Donoghue, 2004). Processes affecting regional diversity have proven difficult to study because of the need to combine a broad geographical extent with fine spatial resolution. In addition, few studies have focused on a time-scale between evolutionary time (centuries to millions of years) and local interaction (seconds to decades). Here we use advances in GIS technology and recently digitized data to investigate the role of regional processes in shaping a species pool. Our study is directly relevant to conservation and policy management decision-making, because we specifically target temporal and spatial scales useful in planning for future responses and changes in diversity.

In this study, we focus on the non-volant mammals of Yellowstone National Park (YNP) to investigate how the environment, species characteristics and historical factors at a subcontinental extent affect patterns of diversity. At 8987 km^2, YNP is far larger than the typical 'local' plot and its extent is less than an entire 'region', yet we feel it is an excellent unit for this type of study for several reasons. The Yellowstone landscape is relatively young, having been covered by the Yellowstone icecap during the last glacial maximum 18,000 years ago (Pierce, 1979). The YNP habitat became available to new colonizers at least several thousand years subsequent to the retreat of the glacial ice and the megafaunal extinctions that occurred in North America (Barnosky *et al.*, 2004; Lyons *et al.*, 2004). Several lines of evidence

have demonstrated relative stability in the species composition of YNP over the last several thousand years, including palynological records and fossil collections (Whitlock & Bartlein 1993; Hadly 1996; Barnosky *et al.*, 2001; Lyons, 2003). Additionally, YNP contains a variety of local habitats and is located near the intersection of three distinct biogeographical regions that could have served as potential species source pools as new habitat became available. We consider history to be an important factor underlying diversification processes; however, we assume there has been no evolution of new species *in situ* during the last 18,000 years since glacial retreat, which leaves colonization, evolutionary history, local extinction, local interactions and stochastic processes as the factors producing the present Yellowstone diversity. Finally, because the YNP boundary is determined politically, rather than biologically, our results can be applied to understanding the limitations of such a boundary and improve the ways we manage the world's oldest national park.

We use the non-volant mammalian species assemblage of YNP to test whether stochastic processes or other, non-random mechanisms affected assembly. Our null hypothesis is that stochastic processes generated the YNP mammal species assemblage. We test this hypothesis from three perspectives: biogeographical affinity, body size frequency distribution, and distribution across mammalian orders. If stochastic processes have dominated assembly, we expect a biota that contains an equal percentage of species with affinity for each of the surrounding biogeographical regions and a random distribution of body size classes and mammalian orders with respect to the available species pool in each biogeographical region. Alternatively, non-stochastic processes could have generated the modern biota. We utilize biogeographical affinity, with body size and mammalian order as proxies for a suite of natural history characteristics (Brown & Nicoletto, 1991; Brown, 1995), to investigate non-random patterns in the assemblage.

We employ present species geographical ranges as one instrument to study the processes responsible for creating species-richness patterns across a fairly large geographical region. A species' geographical range has been called the basic unit of biogeography (Brown *et al.*, 1996), and thus the factors that generate and maintain the geographical range have been the object of much study (e.g. Root, 1988; Brown *et al.*, 1996; Gaston, 1998; Colwell & Lees, 2000). A geographical range contains information about a species' evolutionary history, physiology and dispersal ability (Brown *et al.*, 1996), as well as certain local interactions (Stone *et al.*, 1996; Holt, 2003). The lack of concordance between historical and present ranges is an important tool for assessing recent fragmentation and population decline; however, historical (pre-European) ranges are the most illustrative for our purpose. We do not presume the boundaries of the geographical ranges to be exact, and the coarse spatial grain of our analyses allows for a small degree of spatial variation in the range edge without affecting our conclusions. While we acknowledge limitations in relying upon range maps, especially that of overrepresentation, a paucity of information on abundance and incomplete sampling, we are confident that the geographical range is a critical tool for our initial analyses.

Our study makes an additional advance not only by looking at patterns of richness, but also by investigating the identity of the species creating the patterns. We computed the amount of overlap between a species' geographical range and the extent of a given biogeographical region to show biogeographical affinity. This biogeographical affinity is interpreted as a characteristic preference of the organism that captures the factors that have created the range, especially the effects of history, competition and environmental barriers, in a way that can provide greater insight into regional patterns of diversity than the raw geographical range alone. We use species identities, and therefore their biological characteristics, to elucidate the mechanisms that have shaped diversity patterns.

MATERIALS AND METHODS

We first determined the geographical extent of the mammal species of YNP. To accomplish this we overlapped range maps for all species on the YNP mammal checklist. Range maps for all non-volant mammals of the Western Hemisphere are available as GIS vector format from natureserve.org. Data were provided by NatureServe in collaboration with Bruce Patterson, Wes Sechrest, Marcelo Tognelli, Gerardo Ceballos, The Nature Conservancy — Migratory Bird Program, Conservation International — CABS, World Wildlife Fund — US, and Environment Canada — WILDSPACE. Range maps for species of mammals found on the official checklist of YNP (http://www.nps.gov/yell/nature/ animals/mammalscheck.htm) were downloaded and projected to NAD 1983 Albers equal-area maps. These range maps are the most up to date, digitized and publicly available, and in most cases incorporate historical field collections and expert opinion. These range maps reflect historical distributions, which are potentially different from Holocene distributions. We qualitatively assessed these differences using the FAUNMAP database (data not available for all species; FAUNMAP Working Group, 1994); while many ranges show differences through time, the data do not indicate shifts in ranges for the mammal species of interest through the last several thousand years that affect our conclusions.

The ranges were intersected with the map of North American major habitat types, a rough equivalent to biomes (available at http://www.worldwildlife.org/science/data/terreco.cfm), which refer to broad vegetative structures and general dynamics of the ecological system of a region (Ricketts et al., 1999). Yellowstone National Park sits at the junction of three distinct regions (Fig. 1a): to the west and south, the Deserts (DS), which includes the Great Basin, Sonoran, Chihuahuan and Mojave Deserts; to the north and south, the Rocky Mountains (RM); and to the east, the Great Plains (GP). We chose these boundaries for our analyses because they represent distinct biogeographical areas, have similar area size and experience unique climatic histories (Wright, 1984). By using a widely accepted, existing framework our results will contribute to ongoing efforts by others. Here we refer to each region as a biogeographical region for clarity in our emphasis on the history and distribution of mammal species. Biogeographical affinity was determined for each species based upon a threshold of overlap. We used 50% overlap as the lowest threshold. A species

is said to demonstrate biogeographical affinity when at least a simple majority of its range is within one of the biogeographical regions. If a species' range did not overlap any of the three biogeographical regions at the specified threshold it was termed widespread. The sensitivity of biogeographical affinity to the overlap threshold was investigated at 75% and 90%.

To determine whether the number of species in YNP from a biogeographical region was biased due to a difference in the size of the potential species pool in that biogeographical region, we calculated a total biogeographical region species pool (TSP). Affinity was determined for all species whose ranges overlapped with any of the three biogeographical regions (50% threshold). The group of species with affinity was then used as the TSP. The number of species in YNP with affinity to each region was then divided by this TSP for that region to give a percentage contribution, which takes into account the differences in source pool number. Much debate has surrounded appropriate determination of source pools (e.g. Stone et al., 1996; Graves & Rahbek, 2005). Here we use the modern geographical extent of YNP species to gain insight into the potential source pool geometry of YNP. The extent of this geometry across much of western North America informed our decision to use the three regions to try and understand the historical source pool.

We use average species body size as a proxy for mechanisms that have contributed to the present diversity patterns. The body size data used in all analyses came from a recent compilation of mammalian body size data (Smith et al., 2003), and was supplemented with additional sources when necessary (Silva & Downing, 1995; Wilson & Ruff, 1999). We also used mammalian order as a proxy for ecological and evolutionary characteristics, such as feeding guild and locomotion. Taxonomy follows that of Wilson & Reeder (1993).

RESULTS

Of the 300 mammals included in this study, 272 demonstrated biogeographical affinity for one of the regions, while 28 did not. The total species pool at a 50% threshold was greatest in the DS. Biogeographical affinity for mammals in YNP was highly sensitive to the threshold at which affinity was defined (Table 1). At the 50% threshold, 34 of the 54 YNP species demonstrated

Table 1 Biogeographical affinity of Yellowstone National Park (YNP) mammal species at different thresholds. Total species pool is the number of species with affinity at 50% threshold, regardless of whether their range overlaps YNP. Percentage of total species pool for 50% threshold is in parentheses

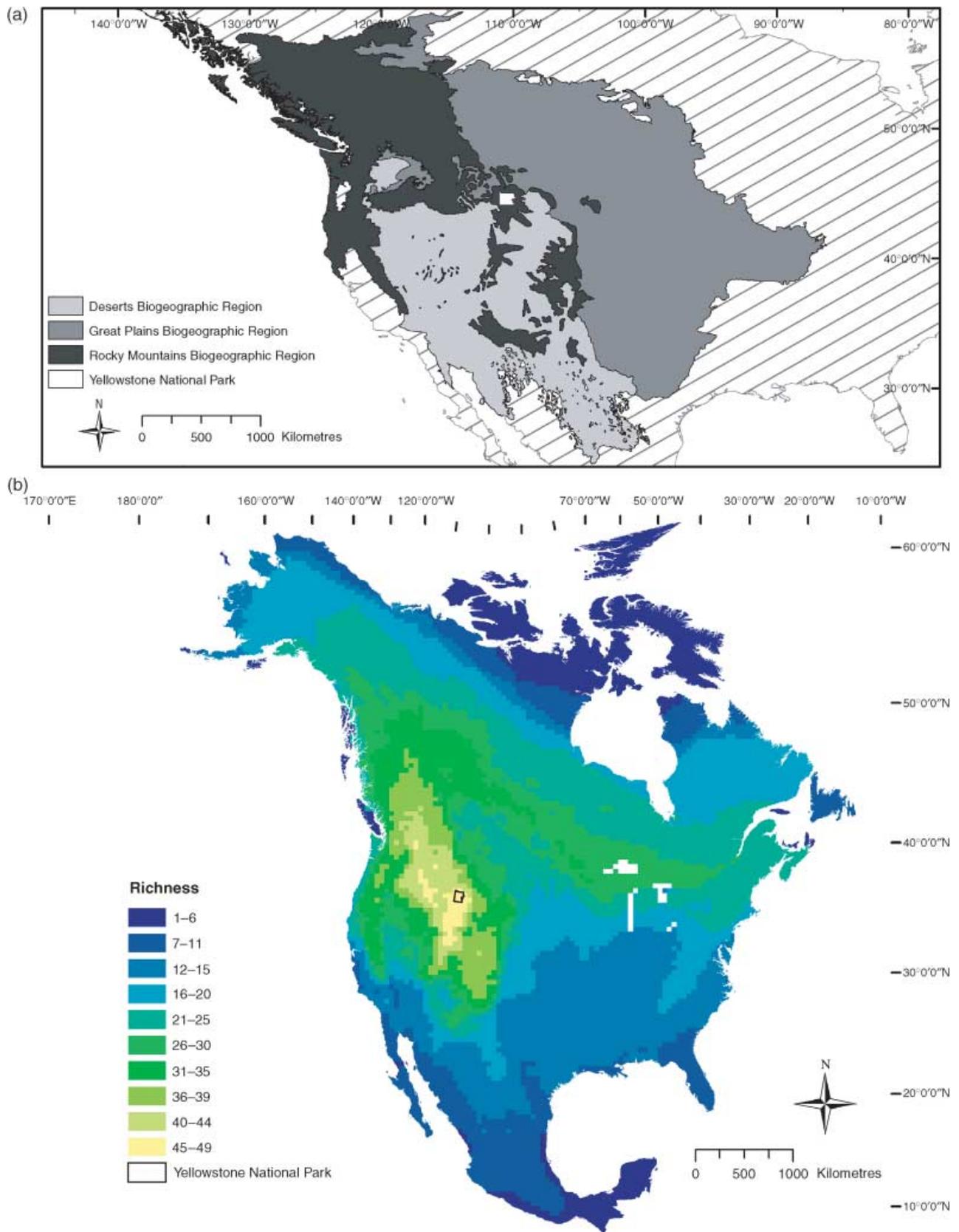|	50% threshold	75% threshold	90% threshold	Total species pool at 50% threshold
Rocky Mountains	18 (20%)	4	0	89
Deserts	4 (3%)	0	0	118
Great Plains	12 (18%)	0	0	65
Widespread	20 (71%)	50	54	28

Figure 1 Biogeographical boundaries and geographical extent of Yellowstone National Park (YNP) mammals. (a) The geographical boundary of the Desert, Great Plains and Rocky Mountains biogeographical regions, and the situation of YNP. (b) Overlay of geographic ranges for all YNP species, where richness indicates the number of ranges that overlap at a given location in North America. Both maps are shown in NAD 1983 Albers Equal Area Projection.

Table 2 Numbers of mammalian species by order and biogeographical affinity

Order	Great plains	Rocky mountains	Deserts	Widespread	Order total
Artiodactyla	3/4	1/4	0/0	3/3	7/11
Carnivora†	4/7	8/10**	0/10	5/6**	17/33
Insectivora§††	0/8	2/16	0/7	3/3	5/34
Lagomorpha	1/3	2/4	1/4	1/2	5/13
Rodentia§§†††	4/43	5/55	3/97**	8/14*	20/209
Total	12/65	18/89	4/118**	20/28**	54/300

For each of the ratios displayed in the table, the denominator is the number of species from the total species pool ($n = 300$; see text) found in the given biogeographical region and order; the numerator is the number of those species found in Yellowstone National Park ($n = 54$; binomial test; Bonferroni corrected significance, $*P < 0.0025$, $**P < 0.001$). The number of species, within an order, from the total species pool is not distributed evenly across biogeographical regions (chi-square test: Insectivora, $§P < 0.02$; Rodentia, $§§P \ll 0.001$). Significance was also tested with expected frequencies of species in Yellowstone by order weighted according to actual distribution of orders from the total species pool (chi-square test: Carnivora, $†P < 0.05$; Insectivora, $††P < 0.001$; Rodentia, $†††P \ll 0.001$).

biogeographical affinity to one of the three surrounding biogeographical regions, whereas at the 90% threshold none of the 54 species had affinity.

Figure 1(a) shows the boundary for the DS, GP and RM biogeographical regions, and the location of YNP. Figure 1(b) displays the compilation of the range maps for the YNP mammal species pool. This map reveals the geographical extent across North America of species resident to YNP. It shows the highest species richness in the direction of the northern Rocky Mountains, as well as the southern Rocky Mountains, the Sierra Nevada and higher latitudes in Canada. There is a precipitous decline in richness to the east, beyond approximately 102° W longitude.

We first analysed the TSP for biases in distribution of orders across the three biogeographical regions (table 2). The Rodentia are not evenly distributed across the biogeographical regions ($P \ll 0.001$, chi-square test), with fewer than expected widespread Rodentia and more DS Rodentia than expected. The Insectivora were not evenly distributed ($P < 0.02$, chi-square test).

When separated by order and biogeographical affinity, the YNP species pool is significantly different to the total species pool ($P < 0.001$; Mantel–Haenszel test). Analysis of the species pool for each region by order (Table 2) shows a significantly higher number of Carnivora with affinity for the RM biogeographical region ($P < 0.001$; binomial test), a higher number of widespread Rodentia ($P < 0.002$; binomial test) and a lower number of Rodentia with affinity for the DS region ($P < 0.0001$; binomial test) than expected by chance. Additionally, we found higher numbers of widespread Carnivora in the Yellowstone species pool ($P < 0.001$; binomial test), a higher total number of widespread species ($P \ll 0.001$; binomial test) and fewer total DS species ($P < 0.001$; binomial test, Bonferroni corrected significance for all binomial tests $P = 0.0025$). These results were significant for Carnivora, Rodentia and Insectivora when expected frequencies of species
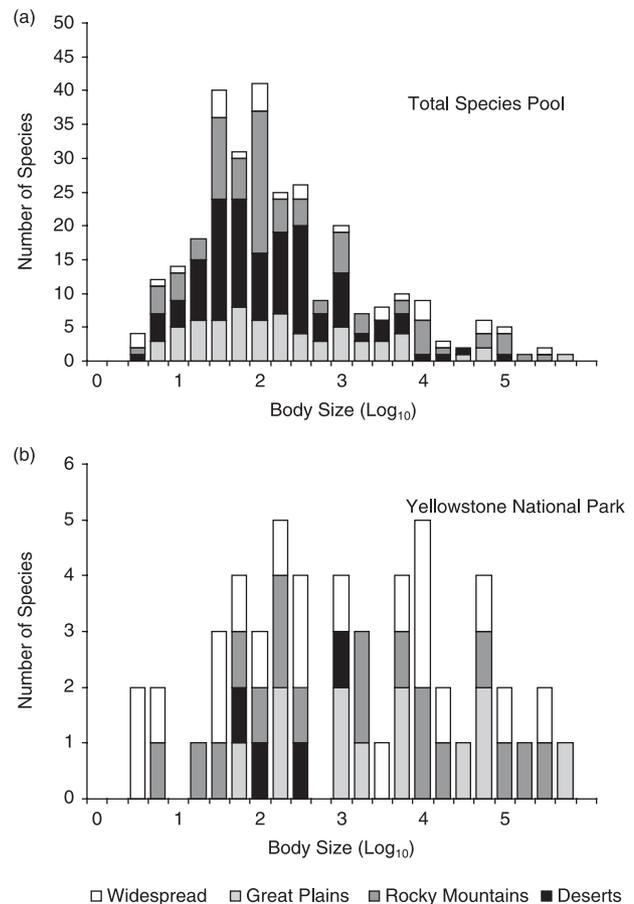

(a)

(b)

□ Widespread ▨ Great Plains ▨ Rocky Mountains ■ Deserts

Figure 2 Mammal body size frequency distributions. (a) Body size frequency distribution for total species pool broken down by biogeographical affinity. (b) Body size frequency distribution for all Yellowstone National Park (YNP) species by biogeographical affinity (Widespread: open bars; Rocky Mountains: dark grey bars; Deserts: black bars; Great Plains: light grey bars). The body size distribution for YNP mammals was statistically different from the distribution for the pool of all species (Kolmogorov–Smirnov test, $P \ll 0.001$). Species were assigned biogeographic affinity if at least 50% of the species' geographic range overlaps with a particular biogeographic region.

from orders within Yellowstone were weighted according to actual distribution of orders from the TSP (chi-square test: Carnivora, $P < 0.05$; Rodentia, $P \ll 0.001$; Insectivora, $P < 0.001$).

The body size frequency distribution for all mammals whose ranges overlap at least one of the three biogeographical regions is unimodal and right-skewed (mode = 2.0, mean = 2.16, skewness = 1.00, kurtosis = 0.77; Fig. 2a). The body size frequency distribution for mammals found in YNP is not skewed and is weakly bimodal (mode = 2.25, 4.0, mean = 3.00, skewness = 0.08, kurtosis = −0.89; Fig. 2b). We used a Kolmogorov–Smirnov test to determine whether the body size distribution for YNP mammals was statistically different from the distribution for the complete pool of species. The YNP body size distribution was significantly different from the distribution of body sizes of the three biogeographical regions combined ($P \ll 0.001$).
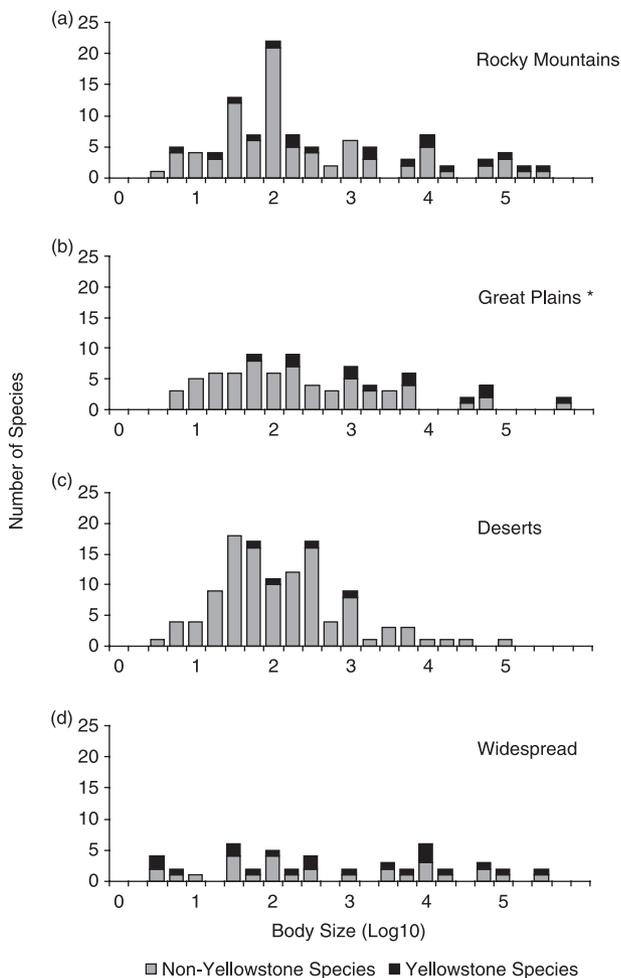
kurtosis = 0.51), while the distributions of GP, DS and widespread species were weakly modal or bimodal (GP: mode = 1.75, 2.25, mean = 2.18, skewness = 0.92, kurtosis = 0.85; DS: mode = 1.50, mean = 1.98, skewness = 0.876, kurtosis = 1.10; Widespread, mode = 1.5, 4.0, mean = 2.60, skewness = 0.34, kurtosis = −0.97; Fig. 3a–d). We tested to determine whether there was a difference between the distribution of YNP species and non-YNP species within each biogeographical region. We found that the GP distributions were significantly different than expected by chance ($P < 0.01$; Kolmogorov–Smirnov test), the RM distributions were different, although not at $P < 0.05$ ($P = 0.067$; Kolmogorov–Smirnov test). The DS and widespread body size distributions of YNP species were not significantly different from the distribution of DS and widespread non-YNP species ($P = 0.34$ and $P = 0.64$, respectively; Kolmogorov–Smirnov test).

DISCUSSION

Our analyses indicate that non-random processes have affected the assembly of the Yellowstone biota. While many YNP mammals have large geographical ranges and representatives of the YNP assemblage can be found throughout North America, our results demonstrate that biases in body size distribution and mammalian order reject our null hypothesis of stochastic assembly. The burden then falls on understanding these non-random patterns and the underlying mechanisms.

From our results, we posit two non-stochastic processes that may have dominated the assembly: habitat filtering and taxon filtering. Although YNP is located at the boundary of three distinct biogeographical regions, it is not trisected by these regions, but instead sits completely within the Rocky Mountains biogeographical region. A habitat filtering hypothesis explains the species assemblage bias for those species with strong affinity to the RM biogeographical region, because, as a community, these species occupy identical habitats in the region, and would preferentially colonize and persist in YNP. While many species show biogeographical affinity for a particular biogeographical region at the 50% threshold, few have affinity at 75% threshold and no species have affinity at 90% threshold. The highest percentage of a regional species pool and absolute number of species are those that have affinity for the RM biogeographical region, which supports habitat filtering. If habitat filtering were the only process affecting assembly we expect the YNP body size distribution to reflect the body size distribution for the RM species pool more than the distribution for the entire species pool. Our results do not support this extension of the hypothesis. While the distributions do not appear similar overall, the YNP RM species are a uniform sample of the larger RM pool, whereas the YNP GP and DS species are not a uniform sample of the larger GP and DS pools, respectively. With habitat filtering we would also expect fewer species from the DS and GP biogeographical regions; the lower number of total DS species supports this idea. The lack of affinity at higher thresholds suggests that mechanisms beyond the changing abiotic characteristics of one biome to the next have also played a role in shaping mammalian distributions, and in turn, membership in the YNP biota. Species characteristics, such as body size or

Figure 3 Mammal body size frequency distributions according to biogeographical affinity. Body size frequency distributions of Yellowstone National Park (YNP) mammals separated according to biogeographical affinity at a 50% threshold of overlap, for species found in YNP (black) and those with affinity but not found within the park (grey). Mode, skewness and kurtosis are given for distribution including YNP and non-YNP mammals for each region: (a) Rocky Mountains, mode = 2.0, mean = 2.24, skewness = 1.05, kurtosis = 0.51; (b) Great Plains, mode = 1.75, 2.25, mean = 2.18, skewness = 0.92, kurtosis = 0.85; (c) Deserts, mode = 1.50, mean = 1.98, skewness = 0.87, kurtosis = 1.10; (d) Widespread, mode = 1.5, 4.0, mean = 2.60, skewness = 0.34, kurtosis = −0.97. The Kolmogorov-Smirnov test was used to compare distributions of YNP species with distribution of non-YNP species. The Great Plains distribution is significantly different than expected by chance (*$P < 0.01$) The Rocky Mountains distribution was different, although not at $P < 0.05$ ($P = 0.067$). The Deserts and Widespread body size distributions were not significantly different from those expected by chance ($P = 0.34$ and $P = 0.64$, respectively).

We also plotted the body size frequency distribution of species showing biogeographical affinity at a 50% threshold of overlap, for species found in YNP and those with affinity but not found within the park (Fig. 3). The RM distribution was modal and right-skewed (mode = 1.875, mean = 2.24 skewness = 1.05,

feeding guild, may have controlled the community assembly and thus colonization and persistence of species in YNP, resulting in a non-random composition. We explored this idea further in our analyses of order and body size.

In the YNP species pool there are several biases present in the affinity of mammalian orders represented which reject the stochastic null hypotheses, and instead suggest an important role for taxon-specific characteristics (i.e. body size, feeding guild, dispersal ability and evolutionary history) in assembly. An assembly mechanism that acts on a specific taxon or group of taxa would be detected by a species pool with equal representation from each biogeographical region, but a bias in the distribution of mammalian order and body size class. Although the total number of RM and WSP species is not different from that expected at random, there is a significantly greater number of Carnivora with affinity for the RM biogeographical region and WSP Carnivora. This indicates a relative advantage of RM carnivores over carnivores from other biogeographical regions in colonizing and persisting in YNP [the reintroduction of the grey wolf (*Canis lupus*) does not influence this result because it was found naturally in YNP prior to extirpation by hunting in the 1930s]; the significantly greater number of widespread Carnivora further supports the idea that carnivores have preferentially colonized and persisted in YNP. Because we have already established an effect of the affinity for the RM biogeographical region based upon greater suitability to the habitat and there also are significantly higher numbers of total widespread species, it is difficult to know definitively the role of the carnivorous diet, or associated characteristics, on membership of the species assemblage.

Unlike the Carnivora, the Rodentia do not show a bias towards the RM biogeographical region, and instead show several biases that suggest an important role for a taxon-specific process in assembly. The number of Rodentia showing affinity for the RM biogeographical region is no different from expected by chance. When considering the distribution of the Rodentia order across the biogeographical regions, our results indicate fewer widespread Rodentia and more DS Rodentia than expected. However, when we consider only those Rodentia found within YNP we find significantly more widespread (no affinity) Rodentia and fewer DS Rodentia than expected. These results are supported even at the most conservative threshold for affinity and when the expected frequencies for Rodentia in YNP were weighted by the actual distribution of the Rodentia order across biogeographical regions. These results strongly support the taxon filtering hypothesis, which states that there are particular characteristics about a taxon that have enabled it to colonize and persist in YNP, or conversely, that have prevented a taxon from establishing in YNP.

To explain such a bias we propose that the widespread species are generalist species capable of persisting in a much wider range of habitats compared with Rodentia that show affinity to the DS, that the widespread species utilize a habitat type that is found throughout more than one biogeographical region, or that there are significant differences in dispersal ability. Our methods allow for inspection of the identity of those species driving these results. In fact, the literature indicates that the widespread species (*Clethrionomys gapperi*, *Marmota flaviventris*, *Erethizon dorsatum*,

Microtus longicaudus, *Neotoma cinerea*, *Peromyscus maniculatus*, *Tamiasciurus hudsonicus*, *Tamias minimus*) are mostly forest-dwelling species. This forest habitat is found throughout the RM region as well as in higher elevations throughout the DS. In contrast, the species with affinity to the DS (*Sylvilagus audubonii*, *Microtus montanus*, *Spermophilus armatus* and *Tamias umbrinus*) are found in a range of habitats, including deserts, arid grasslands and closed spruce–fir forests (Nowak, 1999). The relative dispersal ability of these species also varies from high to low. These natural history facts suggest that competitive ability of species for available resources is a possible mechanism affecting the ability of species with affinity to the DS region to colonize and persist in Yellowstone, a mechanism that falls under our taxon filtering hypothesis. The use of species identity to understand the observed patterns enables us to detect the influence of a taxon filter on assembling the YNP species pool. We explored this hypothesis further in our body size analyses.

Mammal body size distributions have been found to scale according to spatial extent (Brown & Nicoletto, 1991; Brown, 1995; Marquet & Cofré, 1999). For North American mammals, the body size distribution for the continental extent is highly modal (centred on 100–200 g) and right skewed, while the frequency distribution for a small, relatively homogeneous extent is essentially uniform, with frequency distributions for North American biomes intermediate between these two (Brown & Nicoletto, 1991; Kozlowski & Gawelczyk, 2002). Therefore, we expected that the frequency distribution of YNP mammal body size would not be a random subset of the larger species pool (the total species pool contained in the surrounding three biogeographical regions). In fact, our body size results reject the stochastic assembly hypothesis. Additionally, because YNP is substantially smaller in area than the total area of any one biogeographical region but contains multiple habitat types, we also expected the YNP distribution to be intermediate between a uniform distribution and the right skewed distribution of the larger source pool. Our results do not support this prediction; instead, the frequency distribution of YNP mammals is actually less uniform than that of the source distribution. The two modes in the Yellowstone body size distribution correspond to 175 g and 10,000 g. The mode at 10,000 g is driven by the large number of RM Carnivora, while the smaller modal size contains a variety of different orders. This distribution is perhaps more consistent with the North American mammal body size distribution during the Pleistocene (Lyons *et al.*, 2004). This result has important conservation implications for Yellowstone, as it reinforces the idea of Yellowstone as an intact ecosystem and representing one of the last natural megafaunal assemblages.

The body size frequency distribution of YNP mammals compared with that of the species pool of a particular biogeographical region also shows interesting biases. Specifically, mammalian body sizes are evenly distributed from both the RM region and widespread species. In part, the evenness of body sizes in YNP is explained by the bias against small mammals from the DS and GP biogeographical regions, both of which are diverse with respect to Rodentia.

There are several possible explanations for the observed differences in body size distributions. Both the taxon and habitat filtering

hypotheses can explain the distribution, as either one could affect body size classes in a biased way — small-bodied species are filtered out from the larger pool while the large- and medium-bodied species are less affected by that particular filter. Small-bodied species generally have less dispersal ability than large mammals, and this may be an important factor contributing to the observed pattern. This would support the taxon filtering hypothesis, as it is the species dispersal characteristics that limit membership, rather than a property of the habitat. However, much of formerly glaciated Canada is populated by small mammals that have dispersed from south of the maximal glacial margin, a distance far greater than necessary to colonize YNP from any of the surrounding biogeographical regions we studied. Another hypothesis is that in YNP the body size distribution for mammals is affected by the presence of other classes of organisms, especially small birds and herptiles. If this is the case, competition and energetic constraints may be driving the distribution of mammal body sizes. Testing these hypotheses is beyond the scope of this study but should be explored in the future.

In this study we reject the hypothesis that the biota found in Yellowstone National Park is the product of stochastic processes. We conclude that habitat has played a role in determining which mammalian orders are present, and that habitat and taxon effects have influenced the distribution of mammalian body sizes found in the Yellowstone region. These results are relevant to conservation efforts because they augment our understanding of not just the patterns, but also the ecological and historical mechanisms that have created those patterns. Our spatially explicit knowledge of species distributions will be important for understanding which environmental factors might be acting as barriers to species and how certain species might respond to changing environmental conditions, as well as predicting key movement corridors to consider. It is possible to move beyond simply identifying obvious corridors for large animals to designing corridors with consideration of the mechanisms affecting individual species' (large and small) perceptions of the environment, and their abilities to move across it. Our methodology also provides insight into the individualistic nature of members of the mammalian species pool. Because community disassembly, or reorganization, is a likely consequence during rapid climatic changes (Graham *et al.*, 1996; Barnosky *et al.*, 2003), it will be critical to improve our ability to predict what that reorganization might look like under different scenarios of future change.

There are several limitations of this study and opportunities for further development of these methods. Specifically, the mammalian community is only a part of the entire biotic community of YNP. Future studies will explore the mechanisms affecting the assembly of other members of the vertebrate community and the influence of vertebrate groups on each other. In this study, we are able to exclude the role of speciation because of the particular geological history of Yellowstone; this will not be the case in all systems (e.g. Barnosky *et al.*, 2001). To make our results relevant to other vertebrate assemblages, we will need to test explicitly the influence of *in situ* speciation. We acknowledge the differences between global, regional and local extent in affecting diversity, but we do not explore the role of changing scale any further. We

view this as a critical direction for future work because the influence of range size distribution on species-richness patterns is related to the spatial scale at which different taxa perceive the environment, according to dispersal capabilities or their body size (Rahbek, 2005). Finally, while our study is limited to the species level, it will be important to understand the kinds of genetic or population level changes occurring which allow for persistence and range adjustment in YNP. This type of analysis is in its infancy (Hadly *et al.*, 1998, 2004) and will provide results for a unified framework of processes generating and maintaining vertebrate diversity.

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