



Can protected areas really maintain mammalian diversity? Insights from a nestedness analysis of the Colorado Plateau



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ARTICLE INFO

Keywords:

Species nested assemblages
Mammals
Protected areas
Historic range maps
Land management
Colorado Plateau

ABSTRACT

Protected areas are considered a primary place for biodiversity conservation; however, under current rates of global change, it is increasingly important to understand how effective existing reserves are in protecting biodiversity. We examine how U.S. National Park Service lands on the Colorado Plateau (USA) contribute to biodiversity conservation and whether local extirpations have led to an erosion of regional biodiversity. Species range adjustments are among the first signs of biome change, so tracing regional biodiversity change is an efficient way to identify the early phases of major biome shifts. We use analysis of nested mammalian species assemblages to 1) determine if Colorado Plateau mammal assemblages are significantly nested and, 2) clarify which properties of protected lands correlate with nestedness and species richness. We compare species lists from surveys of contemporary resident species to lists from historical range maps that record species ranges from the ~100 years ago, and find that reserves retain essentially the same mammalian diversity and biogeographic patterns that were present in the early 1900s. This suggests that “faunal relaxation” has not occurred in this landscape, and that mammal diversity conservation in these lands has been largely effective for most species thus far. However, anthropogenic climate change is affecting the environmental conditions that influence species distributions, lands surrounding parks are under pressure for human uses, and increasing numbers of visitors are using parks while financial resources are ever more uncertain. Therefore, understanding how nestedness patterns are governed by human-dominated landscapes will be an important conservation tool for quickly assessing diversity change in the future.

1. Introduction

The efficacy of biodiversity reserves in protecting species is a crucial question in conservation biology. Evaluation of reserve success, and identification of causal mechanisms for that success, are increasingly important in light of rapid, high-magnitude global changes now underway (Coad et al. 2013; Geldmann et al. 2013), including climate change, altered fire regimes, and encroaching agricultural, urban, and other development (Barnosky et al. 2014). In this regard, reserves would ideally be located in areas where they capture high levels of biodiversity and where they are likely to be able to protect that diversity in the long term (Margules & Pressey 2000). One potential obstacle to conservation efforts, however, is the fact that many reserves were originally created for reasons other than protection of biodiversity. For example, in the American West some reserves were designated in areas that have relatively little commercial value, where land was

readily available, or where scenic beauty or recreation value was (and remains) high (Pressey 1994; Meir et al. 2004; Geldmann et al. 2013). Thus some species and ecosystems are unprotected, which has potentially reduced the conservation effectiveness of some reserves and is purported to have raised the cost of conservation due to limited management capacity and lack of an overarching plan for reserve creation (Pressey 1994; Le Saout et al. 2013; Geldmann et al. 2013). Limited funding is yet another potential barrier to biodiversity conservation, so the relationship between budget and conservation success is of primary importance. Finally, even those reserves set aside particularly to conserve biodiversity may not be effective at doing so. They could be too small, ill-suited for long-term maintenance of species that were documented there, poorly placed with respect to other regional reserves, or ineffective at conservation of the larger species pool. Such historical legacies give rise to two key questions: how does the extensive network of existing reserves contribute to conserving

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regional biodiversity; and are local extirpations a sign of a major disruption to regional biodiversity?

Analysis of nested species assemblages is one way to answer these questions. For a collection of sites in the same biogeographic region, a system is nested when the lists of species at species-poor sites are predictable subsets of the species lists at high-diversity sites. Nestedness is valuable as a conservation tool because, by comparing beta diversity across a group of sites, it illustrates how local diversity contributes to the overall regional diversity. Nestedness simultaneously identifies sites that have low diversity or unexpected diversity patterns (e.g., a site with many unusual species but few common species), as well as species that are narrowly distributed and therefore at risk of regional extirpation. Yet another advantage to conservation, nestedness uses presence/absence data which are relatively easy to collect (as compared to population size or demographic information, for example) and so can be monitored through time with limited resources (Frick et al. 2009). Causes of nested assemblages have typically been framed as a dichotomy between differential colonization driven by variations in the degree of site isolation, and selective extinction due to differences in geographic area (MacArthur & Wilson 1963). These processes are underlain by a log-series distribution of species abundances, where some species are common but most species are rare (Preston 1948). Species life histories have also been invoked as non-random drivers of species abundances, governing nested subset patterns (Hadly & Maurer 2001).

We use analysis of nestedness to investigate change in regional biogeographic patterns of the mammalian communities of Colorado Plateau (USA) National Park Service (NPS) lands. The Colorado Plateau (CP) is a promising region for targeted conservation and management planning for several reasons. Approximately 49% of the CP is public land or privately owned conservation land (e.g., The Nature Conservancy), so management can be coordinated across large spatial scales. The CP is also one of the most biologically diverse ecoregions in North America, with high endemism (Nabhan et al. 2005), yet it faces a variety of land use pressures, including tourism and recreation, livestock grazing, renewable energy and fossil fuel development, and mining (Schwinning et al. 2008). The region is already experiencing impacts from anthropogenic climate change (Garfin et al. 2014) and expansion of non-native, disruptive species such as cheatgrass (*Bromus tectorum*) (Knapp 1996, Kokaly 2011). These anthropogenic pressures are globally pervasive, so what we learn from the CP is relevant to conservation elsewhere. Finally, extirpations have already taken place on the CP in the last 100 years, including jaguar (*Panthera onca*), grizzly bear (*Ursus arctos*), black-footed ferret (*Mustela nigripes*, now reintroduced in small populations (Belant et al. 2015)), gray wolf (*Canis lupus*), and wolverine (*Gulo gulo*) (Zimmerman & Carr 2004).

In this study, we evaluate 1) if mammal assemblages are more nested across the CP than expected from null models; and, 2) which properties of protected lands correlate with nestedness and species richness. Based on species-area relationships, we expect that larger protected areas will support more species; however, other properties, like latitude and habitat diversity, can also influence species nestedness patterns (MacArthur & Wilson 1963; Hadly & Maurer 2001).

We also compare current to historic biogeographic patterns by assessing nestedness for survey-based lists of contemporary resident species to species lists generated from historical range maps (from data collected in the late 1800s through mid 1900s). Range map data represent a prediction of what historical mammal diversity would be if there have been no major changes in residency over the last century. Although wholesale conversion of land for urbanization or agriculture is still limited on the CP (only 5.3% and 0.8% of CP shrub lands have been urbanized or converted to agriculture, respectively; Ricketts & Imhoff 2003), it is unclear to what extent land uses like livestock grazing present barriers to native species and thereby fragment suitable habitat. If a century of human land use on the CP has isolated the protected areas, then we would expect to find significantly

more nestedness in these areas today compared to our historic dataset. Conversely, if the biogeographic pattern present today is unchanged from the historic dataset, then we would infer that anthropogenic impacts have not changed the underlying biogeographic processes structuring the CP ecoregion. In the case that we observe a change in the nested pattern, selective extinction, or “faunal relaxation,” rather than dispersal dynamics, is a more likely cause—though reduced dispersal ability may also play a role—because species were presumably once spread across the whole region but are now only protected in a subset of that area (Brown 1971).

By evaluating macroscopic patterns such as nestedness, instead of the specifics of changing species identities, we are evaluating the conservation of community-wide biogeographic processes, such as immigration and extinction, across the region. If the macroscopic patterns (i.e. total richness and nestedness) remain the same through time, we conclude the underlying processes have been preserved. If presence-absence matrices from surveys and range map data are nested to a similar degree and exhibit similar levels of species richness, then these protected lands are maintaining historic levels and biogeographic patterns of mammalian diversity. Some habitats have naturally lower species richness, so measuring broad-scale patterns of diversity like nestedness, rather than magnitude of richness, is potentially a better way of quantifying meaningful changes in that diversity.

2. Methods

2.1. Data sources

Surveyed mammal species lists for 25 CP National Parks, Monuments, and Historical Sites (hereafter referred to simply as “parks”; Fig. 1) were downloaded from the NPSpecies database (available at: <https://irma.nps.gov/NPSpecies/>). The surveys include 120 mammal species native to North America (A1). Introduced species, specifically goats (*Capra hircus*) and house mice (*Mus musculus*), were excluded. For some parks, the species lists in NPSpecies were compiled from field inventories conducted with the purpose of producing species lists for the park; in other cases, the species lists were compiled from publications that document field surveys for particular species or group (Loar 2011). This potential source of bias has not been quantified. However, each list was vetted by a taxonomic expert and reviewed for completeness and accuracy at the time of certification. All park species lists in our study were certified between 2005 and 2007 (Loar 2013). Species that were once documented in the park based on firm evidence (e.g. voucher specimens) but which no longer occur there are listed in NPSpecies as “historic” regardless of when the extirpation took place (Loar 2011). Species occurrences in NPSpecies are categorized by degree of confidence: we included species “present in park” and “probably present” because both indicate high confidence that the species occurs in the park as of certification (Loar 2013). Additionally, excluding species categorized as “probably present” had no statistical and minimal qualitative impacts on the results.

Historic range map data are from *The Mammals of North America* (Hall & Kelson 1959). These maps are based on recorded specimens and sightings of species from the late 1800s and early 1900s. As such, the maps represent a post-European, pre-industrial baseline of diversity prior to extensive land conversion for human use (Laliberte & Ripple 2004). Overlap between park boundaries and species ranges were determined by georeferencing the historic observations and range boundaries using GoogleEarth (Google Inc. 2015). 125 species had range maps that overlap with CP parks (A2). We made minimal changes to the taxonomy of surveyed and historic distribution data in order to update taxonomy to reflect current knowledge and to minimize potential errors due to taxonomic revisions made since the surveys and range maps were compiled (A3).

Many mammals, particularly small mammals, have specific habitats that may not occur in all parks. The continental-scale range map data

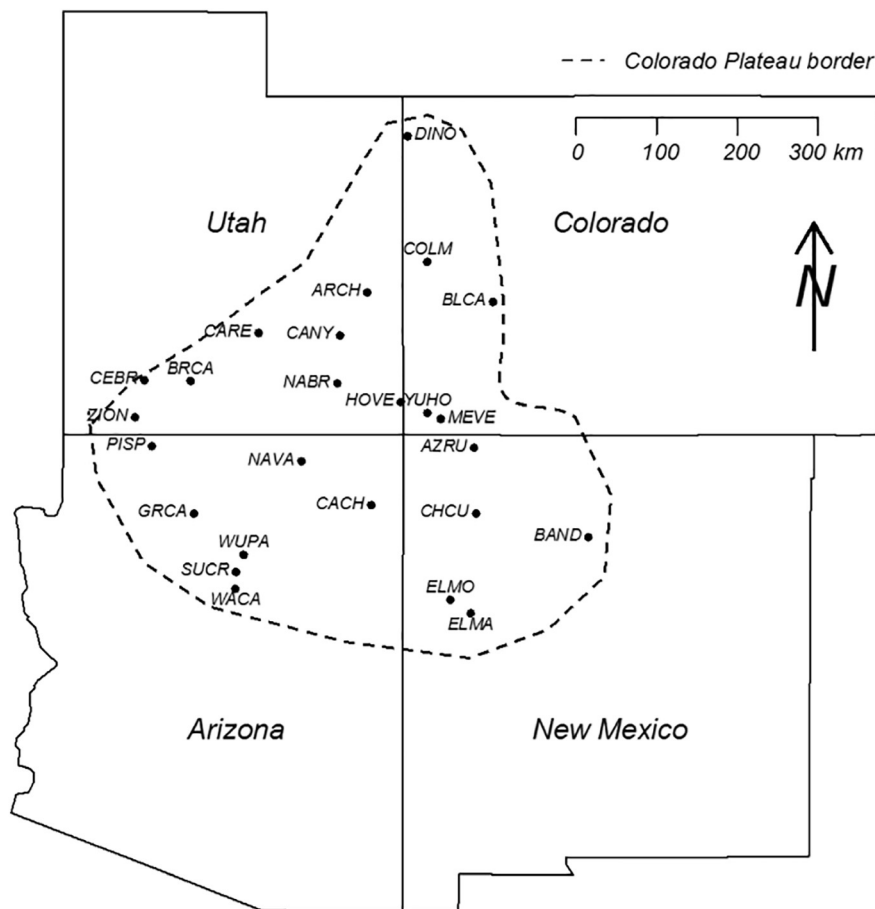


Fig. 1. [single or 1.5 column fitting] Regional map. Illustrates location of NPS sites evaluated in this study. Dashed line illustrates the approximate boundary of the Colorado Plateau. ARCH: Arches National Park (NP); AZRU: Aztec Ruins National Monument (NM); BAND: Bandelier NM; BLCA: Black Canyon of the Gunnison NP; CACH: Canyon de Chelly NM; CANY: Canyonlands NP; CARE: Capitol Reef NP; CEBR: Cedar Breaks NM; CHCU: Chaco Culture National Historical Park (NHP); COLM: Colorado NM; DINO: Dinosaur NM; ELMA: El Malpais NM; ELMO: El Morro NM; GRCA: Grand Canyon NP; HOVE: Hovenweep NM; MEVE: Mesa Verde NP; NABR: Natural Bridges NM; NAVA: Navajo NM; PISP: Pipe Spring NP; SUCR: Sunset Crater NM; WACA: Walnut Canyon NM; WUPA: Wupatki NM; YUHO: Yucca House; ZION: Zion NP.

used here may over-predict species presence, particularly in smaller parks which are likely to sample fewer microhabitats. To test for this bias, we calculated the proportion of species that were predicted to occur in each park, but which were not present in the survey data. We then tested for a relationship between park geographic area and the proportion of species not surveyed using a Spearman's correlation. We used jackknife "leave one out" to evaluate whether observed correlations were primarily driven by specific parks.

2.2. Nestedness

2.2.1. Nested metrics and null models

We used the *Nestedness based on Overlap and Decreasing Fill* (NODF) metric developed by Almeida-Neto et al. (2008) to test for a nested subset pattern across the 25 parks, and used two null models to compare the observed data to 500 simulated random matrices. Unlike other metrics, NODF directly quantifies decreasing row and column sums, and overlap of presences from more nested to less nested columns/rows (Almeida-Neto et al. 2008). Furthermore, although NODF is affected by matrix fill (as are most nested metrics), it is not affected by matrix size, shape, or orientation (Almeida-Neto et al. 2008) and is more conservative and less prone to Type-I error than other metrics (Almeida-Neto et al. 2008). NODF calculates a nested score not just for the entire matrix, but for rows and columns separately, so we can evaluate whether the whole matrix score is most influenced by species or by site differences.

We employ two null models—c0 (Jonsson 2001), and quasiswap

(Miklos & Podani, 2004)—in order to standardize our findings across sites which may experience differences in sampling effort and across taxa which may have genuine differences in overall prevalence and abundance. The degree to which our observed nestedness values deviate from these null predictions provides a useful summary of the pattern while accounting for potential biases and ecological differences between taxa. Controversy as to which statistical and analytical methods are best for evaluating nestedness has yielded many studies on the performance of different null models with different metrics (e.g., Gotelli & Entsminger 2001, Miklos & Podani, 2004, Moore & Swihart 2007, Ulrich & Gotelli 2007a). The null model quasiswap randomly reorganizes the data from the observed matrix, but retains the observed row and column sums, so it is referred to as a "fixed-fixed" (FF) null model (Almeida-Neto et al. 2008)—meaning that neither site richness nor the number of sites in which a species occurs can vary. At the opposite end of the spectrum, equiprobable-equiprobable (EE) null models allow both row and column sums to vary. The c0 null model falls between FF and EE models: c0 maintains the observed species frequencies but allows site richness to vary (Jonsson 2001). In simulations, when paired with the NODF metric FF null models were able to correctly detect random (non-nested) datasets 96% of the time, versus 93% of the time for EE models (Almeida-Neto et al. 2008). EE models are much more prone to Type I error compared to FF models when paired with other nested metrics like Nested Temperature (Ulrich and Gotelli 2007a), and so there is a strong preference in the recent nestedness literature toward the use of FF nulls. However, FF nulls in turn are more prone to Type II error (Ulrich and Gotelli 2007b).

Furthermore, FF models assume that site richness and species commonness are intrinsic to the system. Unlike true islands, the parks in our study are not strictly isolated from one another and so site richness is not necessarily an inherent property of sites. Therefore, a null model that allows site richness to vary, as c0 does, is a better reflection of reality in spite of the statistical advantages of an FF null. We compare results from the equiprobable-fixed null model, c0, and the fixed-fixed model, quasiswap.

All statistical analyses were performed in R (R Core Team 2015); analyses of nestedness were performed using the vegan package (Oksanen et al., 2015) in R.

2.2.2. Nested analyses

We compared nestedness for survey and historic range map data in three ways. First, we determined if both datasets were significantly nested as compared to the c0 and quasiswap null models. Second, we used a Spearman's test to determine if the nested rank of sites was significantly different between the datasets. Third, we used Spearman's test to compare species rank between datasets. To do this we first removed any species that were not present in both datasets—17 species were removed from the range maps data because they were not surveyed, while 12 species were removed from the survey data because they were not recorded in the range maps. This left a total of 108 shared species.

2.3. Park attributes

Data about the parks—minimum and maximum elevation, elevation range, year of designation, visitation, budget, area, latitude, and longitude—were gathered from National Park Service documentation (NPS 2005; NPS 2016a, NPS 2016b) and GoogleEarth (Google Inc. 2015) (A4). We summed park budgets from 2000 through 2015 and used the United States Bureau of Labor Statistics Consumer Price Index inflation calculator (available at data.bls.gov/cgi-bin/cpiccalc.pl) to adjust for inflation to 2015 levels. We also summed visitation from 2000 through 2015.

Correlations between mammal diversity and park attributes were analyzed in two ways: first, we used Spearman's tests (with and without a Holm p -value adjustment for multiple tests) to quantify the relationship between park nested rank (from the survey dataset) and the nine park attributes. Second, to test the ability of park attributes to explain site richness and nested rank, we used stepwise Bayesian Information Criterion (BIC) model selection to select the best multiple linear regression (mlr) model. Specifically, we used the stepAIC function in the MASS package in R (Venables & Ripley 2002) to search among all possible linear models between the null model (richness \sim 1) and the full set of variables (richness \sim Elevation Range + Budget + Area + Longitude + Minimum Elevation + Maximum Elevation + Year Created + Visitation + Latitude) (A5). All of the final variables were significant at the $\alpha = 0.05$ level (with Holm p value adjustment) when correlated individually with richness. The proportion of the variation in species richness explained by each of the park attributes was quantified by variance partitioning, using the hier.part package in R (Walsh & MacNally 2013).

Finally, we tested for a difference between parks that were more nested in modern surveys than they were historically (below the 1:1 line in Fig. 2) and parks that were less nested today than they were in the past (above the 1:1 line in Fig. 2). We compared park attributes for these two groups using Wilcoxon rank sum tests (with and without a Holm p value adjustment for multiple tests).

3. Results

3.1. Nested analyses

Survey and range map data were significantly more nested than

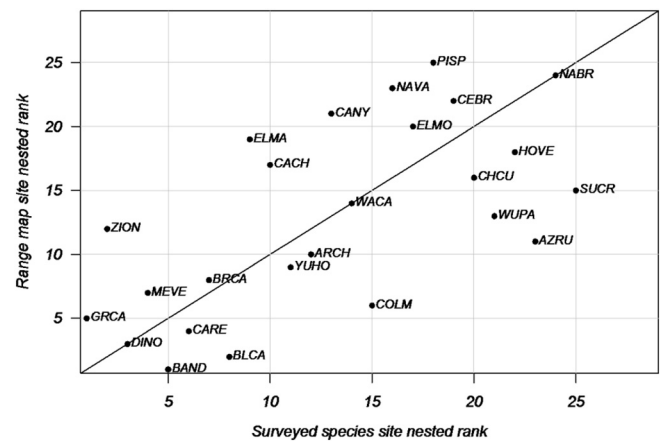


Fig. 2. [single or 1.5 column fitting] Survey versus range map site nested rank. See Fig. 1 for site abbreviations.

random when compared to the c0 null, though neither were significant when compared to quasiswap. Richness is higher in the range maps than in surveys (except for Grand Canyon and Zion National Parks), but surveyed and range map presence absence matrices produced the same overall NODF results (Table 1; A5) and site ranks (Fig. 2; Spearman's $\rho = 0.638$, p value $< 7 \times 10^{-4}$). Species ranks were strongly correlated (Fig. 3; Spearman's $\rho = 0.886$, p value $< 2 \times 10^{-16}$) between datasets. Fill was higher in the range map matrix, which likely accounts for the slightly higher NODF scores. We found a significant, but weak, inverse relationship between park area and the proportion of species in the range map data that were not actually surveyed (Spearman's $\rho = -0.472$, p value = 0.017). The jackknife sensitivity analysis indicated that this result is consistent and that no single park drives the correlation (mean Spearman's ρ : -0.471 ; range: -0.609 to -0.401). We therefore conclude that over-prediction in the range map is possible, but relatively small.

3.2. Park attributes

Both park nested rank and park species richness positively correlated with area, budget, visitation, maximum elevation, and elevation range (Table 2). These predictor variables were also correlated with one another (A6). Stepwise BIC model selection produced a model that includes elevation range, budget, and area as explanatory of park richness and nested rank (Table 3). Variance partitioning analysis reveals that these three variables, though correlated with one another, individually explain 24.17%, 22.32%, and 14.57% (respectively) of the variation in species richness (A6). There was no significant difference in the park attributes for sites that were more nested versus less nested than expected.

4. Discussion

Protected areas like National Parks are considered primary places for biodiversity conservation. Given current rates of global change, it is

Table 1

Nestedness based on Overlap and Decreasing Fill (NODF) scores for surveyed and range map presence/absence data for Colorado Plateau NPS sites.

Dataset	NODF (species)	NODF (sites)	NODF (whole matrix)	Matrix fill
Surveyed species	66.37*	78.27*	66.82*	0.451
Range map species	70.82*	77.04	70.58*	0.555

* significant ($p < 0.01$) when compared to the c0 null model; there was no significance when compared to the quasiswap null model.

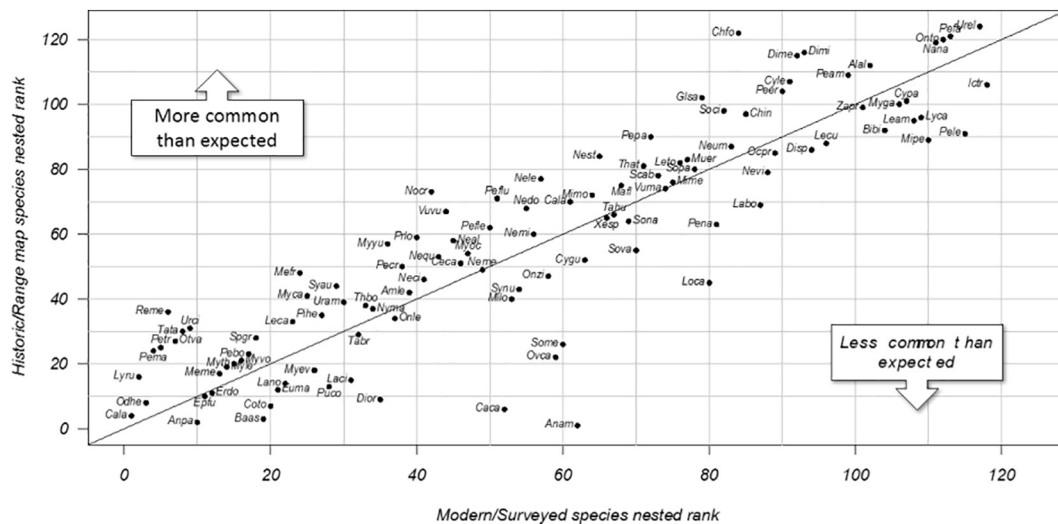


Fig. 3. [2 column-fitting] Survey versus range map species nested rank. Alal = *Alces alces*; Amle = *Ammospermophilus leucurus*; Anam = *Antilocapra americana*; Anpa = *Antrozous pallidus*; Baas = *Bassariscus astutus*; Bibi = *Bison bison*; Cala = *Callospermophilus lateralis*; Cala = *Canis latrans*; Caca = *Castor canadensis*; Ceca = *Cervus canadensis*; Chfo = *Chaetodipus formosus*; Chin = *Chaetodipus intermedius*; Coto = *Corynorhinus townsendii*; Cygu = *Cynomys gunnisoni*; Cyle = *Cynomys leucurus*; Cypa = *Cynomys parvidens*; Dime = *Dipodomys merriami*; Dimi = *Dipodomys microps*; Dior = *Dipodomys ordii*; Disp = *Dipodomys spectabilis*; Epfu = *Eptesicus fuscus*; Erdo = *Erethizon dorsatum*; Euma = *Euderma maculatum*; Glsa = *Glaucomys sabrinus*; Ictr = *Ictidomys tridecemlineatus*; Lano = *Lasionycteris noctivagans*; Labo = *Lastiurus borealis/blossevillii*; Laci = *Lasiurus cinereus*; Lecu = *Lemmiscus curtatus*; Leam = *Lepus americanus*; Leca = *Lepus californicus*; Leto = *Lepus townsendii*; Loca = *Lontra canadensis*; Lyca = *Lynx canadensis*; Lyru = *Lynx rufus*; Mafl = *Marmota flaviventris*; Meme = *Mephitis mephitis*; Milo = *Microtus longicaudus*; Mime = *Microtus mexicanus*; Mimo = *Microtus montanus*; Mipe = *Microtus pennsylvanicus*; Muer = *Mustela erminea*; Mefr = *Mustela frenata*; Myga = *Myodes gapperi*; Myca = *Myotis californicus*; Myev = *Myotis evotis*; Myle = *Myotis leibii/ciliolabrum/subulatus*; Myoc = *Myotis occultus/lucifugus*; Myth = *Myotis thysanodes*; Myvo = *Myotis volans*; Myyu = *Myotis yumanensis*; Nana = *Nasua narica*; Nedo = *Neotamias dorsalis*; Nemi = *Neotamias minimus*; Nequ = *Neotamias quadivittatus/rufus*; Neum = *Neotamias umbrinus*; Neal = *Neotoma albigula*; Neci = *Neotoma cinerea*; Nele = *Neotoma lepida/devia*; Neme = *Neotoma mexicana*; Nest = *Neotoma stephensi*; Nevi = *Neovison vison*; Nocr = *Notiosorex crawfordi*; Nyma = *Nyctinomops macrotis*; Ocpr = *Ochotona princeps*; Odhe = *Odocoileus hemionus*; Onzi = *Ondatra zibethicus*; Onle = *Onychomys leucogaster*; Onto = *Onychomys torridus*; Otva = *Otospermophilus variegatus*; Ovca = *Ovis canadensis*; Peam = *Perognathus amplus*; Pefa = *Perognathus fasciatus*; Pefle = *Perognathus flavescens*; Peflu = *Perognathus flavus*; Pepa = *Perognathus parvus*; Pebo = *Peromyscus boylii*; Pecr = *Peromyscus crinitus*; Peer = *Peromyscus eremicus*; Pele = *Peromyscus leucopus*; Pema = *Peromyscus maniculatus*; Pena = *Peromyscus nasutus*; Petr = *Peromyscus truei*; Pihe = *Pipistrellus hesperus*; Prlo = *Procyon lotor*; Puco = *Puma concolor*; Reme = *Reithrodontomys megalotis*; Scab = *Sciurus aberti*; Soci = *Sorex cinereus*; Some = *Sorex merriami*; Sona = *Sorex nanus*; Sopa = *Sorex palustris*; Sovo = *Sorex vagrans/monticolus*; Spgr = *Spilogale gracilis*; Syau = *Sylvilagus audubonii*; Synu = *Sylvilagus nuttallii*; Tabr = *Tadarida brasiliensis*; Tahu = *Tamiasciurus hudsonicus*; Tata = *Taxidea taxus*; Thbo = *Thomomys bottae/umbrinus*; That = *Thomomys talpoides*; Urel = *Urocyon elegans*; Urci = *Urocyon cinereoargenteus*; Uram = *Ursus americanus*; Vuma = *Vulpes macrotis*; Vuvu = *Vulpes vulpes*; Xesp = *Xerospermophilus spilosoma*; Zapr = *Zapus princeps*.

Table 2
Results of Spearman's tests of park attributes versus park nested rank, and linear regressions of park attributes versus park species richness.

Park attribute	Spearman's rho	Linear regression adjusted R-squared
Year created	-0.059	-0.034
Budget	0.731***	0.526***
Latitude	0.203	0.00007
Longitude	0.015	-0.043
Minimum elevation	-0.082	-0.038
Maximum elevation	0.627**	0.280*
Elevation range	0.678**	0.600***
visitation	0.611**	0.470***
Area	0.665**	0.405**

With Holm p adjustment: * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$.

Table 3
Results of Bayesian Information Criterion (BIC) stepwise model selection, showing BIC values for the final model versus models with additional, or fewer, variables. RSS: residual sum of squares; Final model: Richness ~ Elevation Range + Budget + Area.

Model	Sum of squares	RSS	BIC
Final model	112.32	507.14	85.93
+ Longitude	39.54	467.60	87.16
-Area	112.32	619.46	87.55
+ Minimum elevation	8.98	498.15	88.68
+ Maximum elevation	8.98	498.15	88.68
+ Year created	3.53	503.61	88.94
+ Visitation	2.76	504.37	88.98
+ Latitude	2.62	504.51	88.98
-Budget	224.74	731.87	91.56
-Elevation range	427.68	934.82	97.43

increasingly important to understand how effective existing protected areas are in conserving biodiversity. In this study, we examined how U.S. National Parks on the CP contribute to mammalian biodiversity conservation, and whether local extirpations have led to an erosion of regional biodiversity. Rather than evaluating loss and gain of individual species, we evaluated the macroscopic biogeographic pattern of species nestedness. Nestedness records community-wide biogeographic processes across the region and so if patterns of nestedness remain the same through time, we conclude that underlying processes have been preserved.

4.1. Nestedness, diversity, and park attributes

Nested patterns are common in nature (Ulrich & Gotelli 2007b; Moore & Swihart 2007). However, there are no hard boundaries between parks and the areas that comprise the land matrix in our study, so we might not expect a nested pattern (but see Hadly & Maurer 2001, McGill et al. 2005). Nevertheless, mammals in CP parks (in both modern survey and historic range maps datasets) were significantly more nested than random when compared to a semi-conservative (c0) null model meant to reflect the permeable boundaries of these sites. Though not significant when compared to the highly-conservative quasiswap null model, high NODF scores nevertheless suggest a strong pattern of nestedness. Comparisons between historic range map and modern survey data reveals if biogeographic patterns across the CP have changed over the last century because the range map data used here include portions of the historic ranges of species where they have been extirpated within the last hundred years or so. We found negligible differences between nested scores for modern survey and historic range map presence/absence matrices (Table 1)—this, in spite

of the fact that historic range maps may slightly over predict richness. This demonstrates that active and/or passive conservation efforts at these parks have been successful up to the point that survey data were compiled (depending on the park, 2005 or later).

We have found significant positive correlations between mammal diversity and area, elevation range, budget, and visitation. Only area, elevation range, and budget were included in the final mlr model with the lowest BIC values. There are also correlations among these park attributes and it is unclear if they are causally related to one another (A6). Disentangling these correlations will require additional, fine-scale data on aspects of area and elevation that contribute to diversity, such as number of habitat types, which is only crudely approximated by elevation range. There are several possible explanations for the correlation between budget and diversity. Based on species-area relationships, larger parks are expected to have more species, and larger parks receive higher budgets. Additionally, it is possible that more funding does indeed lead to higher conservation effort and therefore more successful species protection. Larger budgets might also allow for better surveying, which is important because biodiversity management plans cannot proceed without adequate knowledge of what species are present. This issue is addressed in the NPSpecies documentation: some parks did not receive “enough funding to produce the same level of data quality” and so gaps in data at certain parks would make diversity appear lower (Loar 2011). However, the relationship between budget and species diversity is likely to be indirect and potentially quite complicated, requiring data about how funding is allocated within each site. Indeed, funding priorities of a park may be more important than overall budget (P. Henderson, personal communication). Further, range map and survey data produce similar results, which suggests that aspects of parks that are not related to management—like fundamental species-area relationships—drive the observed biogeographic patterns. Thus, conservation strategies should prioritize protecting the largest continuous regions so as to secure the subset of species that are only found in the largest parks.

Ultimately, it will be necessary to obtain data from multiuse lands under different management regimes in order to put into perspective the status of reserves with a strict mandate for biodiversity protection, like the NPS sites assessed here. Potentially destructive uses like mining and grazing are currently permissible on all but a third of U.S. public lands (Klinkenborg, 2013). Yet multiuse lands form important geographic connections between islands of more strictly protected land, and they likely provide habitat and migration corridors across the landscape. Key questions are: how diversity of strictly protected areas compares to surrounding, multiuse lands; whether protected areas are suffering from detrimental impacts in this multiuse matrix; and if, in turn, strictly protected lands can “rescue” biodiversity in multiuse lands by serving as population sources.

4.2. Species present in historic range maps but not in modern surveys

Among the species that were historically recorded in parks but which were not surveyed recently, two broad categories emerge: species that are genuinely in decline or have been extirpated within the last century, and species generally found in regions adjacent to the CP (e.g. Rockies or Great Basin). In particular, *Panthera onca* (jaguar), *Mustela nigripes* (black-footed ferret), *Bison bison* (American bison), *Canis lupus* (gray wolf), *Ursus arctos* (brown or grizzly bear), and *Castor canadensis* (American beaver) are known to have declined or been extirpated since Europeans arrived in North America as the result of human hunting or eradication efforts (Mech 1970; Outwater 1996, Belant et al. 2015; National Park Service 2015; Povilitis 2015; McLellan et al. 2016). Of these, *P. onca*, *M. nigripes*, *U. arctos*, and *C. lupus* are not reported in any of the park surveys.

Other species recorded in historic range maps but not in modern surveyed include the following species, which generally occur in regions neighboring the CP: *Brachylagus idahoensis* (pygmy rabbit),

Chaetodipus penicillatus (desert pocket mouse), *Reithrodontomys montanus* (Plains harvest mouse), *Neotoma micropus* (Southern plains woodrat), *Cynomys ludovicianus* (black-tailed prairie dog), *Phenacomys intermedius* (Western heather vole), *Microtus richardsoni* (water vole), *Gulo gulo* (wolverine), *Martes americana* (American marten), *Martes pennanti* (fisher), *Vulpes velox* (swift fox), *Odocoileus virginianus* (white-tailed deer), and *Myotis velifer* (cave myotis). Notably, all of these species are generally found northward (e.g., northern Rocky Mountains) or eastward (e.g., Great Plains) except for *C. penicillatus* (Sonoran Desert), *M. velifer* (southern New Mexico and Arizona, and Central America), and *B. idahoensis* (Great Basin). Finally, *Antilocapra americana* (pronghorn), *Ovis canadensis* (bighorn sheep), *Lontra canadensis* (North American river otter), and *Sorex merriami* (Merriam's shrew) were all surveyed in far fewer parks than expected from historic range maps. The reason for this is unclear, as all four species are thought to be widespread with stable populations (except *S. merriami* for which the population trend is unknown) (Festa-Bianchet 2008; Serfass et al. 2015; Cassola 2016; IUCN SSC Antelope Specialist Group, 2016).

Discrepancies between historic range maps and modern surveys could be due to range contractions/shifts, or to inaccuracies in the original range maps. However, in spite of these site-by-site discrepancies, both the nested rank of sites and the rank of species are significantly correlated between the survey and range map datasets. This means that species and sites are arranged in essentially the same order in the nested matrices (Figs. 2 and 3). Sites that fall far from the 1:1 line in Fig. 2 have surveyed diversity that deviates from the expectation of range maps. For example, Colorado NM had lower diversity while Canyonlands NP had higher surveyed diversity than in surveys than in historic range maps. Sites with higher modern surveyed diversity than historic range map diversity were not unified by any set of park attributes tested here. Fig. 3 illustrates the same principle for species nested rank: species that fall far below the 1:1 line were less common in the modern than they were historically and therefore should be of conservation concern.

4.3. Species surveyed in the modern but not historically present

Twelve species reported in the survey data for CP parks were not in historic range maps: *Myotis auriculus* (southwestern Myotis), *Idionycteris phyllotis* (Allen's big-eared bat), *Choeronycteris mexicana* (Mexican long-tongued bat), *Eumops perotis* (Western mastiff bat), *Ammospermophilus harrisi* (Harris's antelope squirrel), *Neotamias cinereicollis* (gray-collared chipmunk), *Perognathus longimembris* (little pocket mouse), *Sigmodon fulviventris* (Tawny-bellied cotton mouse), *Zapus hudsonius* (meadow jumping mouse), *Sorex preblei* (Preble's shrew), *Pecari tajacu* (collared peccary), and *Conepatus leuconotus* (American hog-nosed skunk). Most have range map boundaries that fall extraordinarily close to the parks in which they were surveyed. In each case, the species could be expanding into new regions, or the original range maps may be inaccurate. It is interesting to note that all of these species are generally found south of the Colorado Plateau, so northward range expansion would be predicted if these species are migrating in response to climate change. This, in contrast to the species that were missing from surveys, which were predominantly species found at higher latitudes or elevations.

Mismatches between range map predictions and surveyed species may indicate local extirpations or range expansions—for example, the loss of populations of *Castor canadensis* (Outwater 1996)—but may also highlight inexact depictions of species occurrences in the original range maps. The range maps used here from The Mammals of North America (Hall & Kelson 1959) are based on historic specimen records, expertise, and then-current knowledge of species habits and preferences. Despite our taxonomic updates and modifications to reduce error, historical inaccuracies resulting from taxonomic issues or incomplete knowledge of the biology of particular species, in some cases may have persisted.

This is a crucial concern for species distribution modeling and other analytical and predictive methods that rely on historical range maps: range maps must be ground-truthed by comparison to historical collections and reports, up-to-date taxonomic information, and the knowledge of experts who have field experience in the region of interest.

4.4. Data limitations

Differences in how data were collected for NPSpecies certainly introduce error, and this is a limitation of our study. However, those differences would not a priori bias our results in any particular direction. Yet another limitation is that many small mammals have very specific habitat requirements, and range maps drawn on a continental scale over-predict where those species occur locally. Historic survey data are not available for all of the sites studied here, and historic specimen collection is also biased by differences in collection effort and method. We tested for a bias in the range map species lists and found a significant, weakly positive relationship between park area and the number of species expected to occur in a site that were not actually surveyed. Thus, the data used here should be considered a coarse estimate of both historic and modern mammal diversity.

Patterns of nestedness result from several biological processes, and so our findings could be due to selective extinction, differential colonization, or changes in underlying species abundances. For example, if species have different colonization rates, then most parks would have strong colonizers but only very diverse parks would have weak colonizers as well. By and large, land use on the CP is patchy, both spatially and through time, so the parks are not truly isolated. Even widespread human impacts like livestock grazing do not necessarily cause wholesale habitat destruction that would preclude coexistence with many native species. An important question is whether the mammal diversity retention we have documented here is the result of effective management within the parks, or due to the fact that human impacts on the CP more broadly remain relatively light. It will be important to gather and incorporate data from multiuse lands surrounding the parks, in order to assess the ability of species to persist in less-strictly protected lands and to disperse from one protected area to the next. Without information about the status of mammal diversity outside the parks, we cannot claim that the observed diversity retention at these sites is due to differences in management or quality between parks and surrounding multiuse lands.

Finally, nestedness analyses provide a broad-brush assessment of regional diversity patterns, but this is only one aspect of diversity. As with any method that relies on presence/absence data, population-scale information—like abundance, age structure, variance, etc.—are obscured and the underlying drivers of abundance patterns may not be properly understood. However, used in concert with other methods, nestedness can help to prioritize conservation issues because it is reasonably quick, inexpensive, and useful in ascertainment of local and regional species diversity.

5. Conclusions

Protected areas such as NPS lands are considered a primary place for biodiversity conservation today and as climate change and other anthropogenic impacts intensify (Le Saout et al. 2013). In anticipation of major biome shifts expected to result from future climate change, the NPS is developing critical climate change adaptation strategies (Gonzalez 2011). Species range adjustments and the resulting local extirpations and novel occurrences of extralimital species (species that are not found in the region) are the first steps leading to biome change. Therefore, tracing regional diversity change with a metric like nestedness is an efficient way to identify the early phases of major biome shifts.

The results we report here are encouraging with regard to mammalian diversity retention in spite of historical and modern pressures. According to our analyses, CP parks retain essentially the same biogeographic patterns and levels of mammalian diversity that were present when the parks were established. This suggests that “faunal relaxation” has not yet occurred in these NPS sites, and that mammalian diversity conservation in these parks is effective for most species, despite the extirpation or decline of several. Even with those few extirpations, the system appears not yet demonstrably outside the historical baseline in terms of overall numbers and distribution of species. While we focus on mammals here, the same principles and analytic techniques can be applied to other taxonomic groups. Our analysis suggests that mammals in the CP have not changed significantly in their relative abundances over a century. An important caveat, however, is that all comparisons were made from inferences based on presence-absence data. Thus, relative abundances could remain constant while overall abundance could decline or increase dramatically without detection. Further, certain species have a larger impact on ecosystem function and on the landscape more broadly; for example, ecosystem engineers like beaver, or apex predators like jaguar. Notably, most of the species that have been extirpated or dramatically declined on CP in last century are considered to play these kinds of disproportionately-large roles in the ecosystem.

Ongoing anthropogenic impacts may well challenge historical baselines in the future. Rapid climate change is affecting the environmental variables that influence and in some cases control species distributions. Invasive species are increasing in abundance and diversity. Lands surrounding parks are also under pressure for energy development, recreation, and agriculture. Finally, increasing numbers of visitors are using parks while financial resources are ever more uncertain. In the face of these growing pressures, managing biodiversity into the future will require repeated evaluation of metrics like those used here, as well as others that take into account regional and temporal patterns. Nestedness is a useful tool for land managers to quickly identify species that are either at risk, or that are poorly targeted for sampling. This is because species that become more nested over time are probably experiencing unusual declines across the region and their conservation status should be carefully evaluated (McDonald and Brown 1992). Metrics can be improved with information from the fossil record, which can reveal the effects of past climate change and establish long-term faunal and floral baselines, and by incorporating abundance data to assess population viability.

Acknowledgements

Thanks to the Barnosky Lab, the Hadly lab, P. Busby, and S. Macway, for helpful discussion. This project relies on a public database, NPSpecies—The National Park Service Biodiversity Database, hosted by Integrated Resource Management Applications. M.A.S. was supported by NSF grant DGE 1106400 and a University of California Museum of Paleontology fellowship. D.S.K. was supported by a Killam Postdoctoral Fellowship. A.J.R. was supported by the Berkeley Initiative in Global Change Biology and the Moore Foundation.

Appendix A. Supplementary data

Survey and range map presence/absence matrices (A1 and A2, respectively); a list of taxonomic updates applied to NPSpecies and Hall and Kelson (1959) data (A3); park attribute data (A4); a table that summarizes nested rank of species in survey and historic range maps data sets (A5); and a statistical exploration of correlation among park attributes (A6) are available online.

Supplementary data to this article can be found online at <http://dx.doi.org/10.1016/j.biocon.2017.03.021>.

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