Biological Conservation 209 (2017) 546–553

Contents lists available at ScienceDirect

Biological Conservation

journal homepage: www.elsevier.com/locate/biocon

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

M. Allison Stegner[a,*], Daniel S. Karp[b], Andrew J. Rominger[c], Elizabeth A. Hadly[d]

[a] *Department of Zoology, University of Wisconsin, Madison, 430 Lincoln Drive, Madison, WI 53703, USA*
[b] *Department of Wildlife, Fish, and Conservation Biology, University of California, Davis, 1088 Academic Surge, One Shields Avenue, Davis, CA 95616, USA*
[c] *Department of Environmental Science, Policy and Management, Mulford Hall, 130 Hilgard Way, University of California, Berkeley, CA 94720, USA*
[d] *Department of Biology, 371 Serra Mall, Stanford University, Stanford, CA 94305-5020, USA*

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

---

[*] Corresponding author.
E-mail address: mstegner@wisc.edu (M.A. Stegner).

http://dx.doi.org/10.1016/j.biocon.2017.03.021
Received 6 December 2016; Received in revised form 24 March 2017; Accepted 27 March 2017

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 endemicity (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