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SPECIAL FEATURE: SCIENCE FOR OUR NATIONAL PARKS' SECOND CENTURY

A macroecological perspective on strategic bat conservation in the U.S. National Park Service

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Abstract. North American bat populations face unprecedented threats from disease and rapid environmental change, requiring a commensurate strategic conservation response. Protected-area networks have tremendous potential to support coordinated resource protection, disease surveillance, and population monitoring that could become a cornerstone of 21st-century bat conservation. To motivate this idea, we develop a macroecological perspective about bat diversity and associated conservation challenges and opportunities on U.S. National Park Service (NPS) lands. We compared occurrence records from parks against published range maps. Only 55 (19%) of parks reported as present ≥90% of the bat species expected based on range maps, highlighting the information-gap challenge. Discrepancies suggest substantial under-reporting and under-sampling of bats on NPS lands; inadequate range maps and habitat specificity are implicated for some species. Despite these discrepancies, 50 species, including several range-restricted and endangered taxa, were reported in at least one park unit, including those in the Caribbean and tropical Pacific. Species richness increased with park area at a rate (z) of ~0.1, a pattern confounded by covariation with latitude, elevation, and habitat. When accounting for these factors, richness decreased predictably at higher latitudes and increased at mid-elevations and with greater numbers of keystone underground habitat structures (caves and mines), reflecting a strong species–energy relationship. The inclusion of covariates that represented percentage of natural vs. human-modified (converted) landscapes and elevation range—a proxy for environmental heterogeneity—was uninformative. White-nose syndrome (WNS) presents a tremendous challenge to the NPS: All 12 species currently known to be affected by the disease or to host the causal fungus are represented in the NPS system. One hundred and twenty-seven NPS parks are in counties currently or likely to become WNS-positive by 2026. All parks are expected to experience increasing temperatures in coming decades; forecasted climate change velocity is particularly high (>1 SD) for 50 parks. Seventeen parks are in the vicinity of high (>1 SD) wind turbine density. Based on these biogeographic patterns, we suggest ways to prioritize NPS parks for additional inventories, monitoring, and resource protection. Our results demonstrate how macroecology and bioinformatics together can guide strategic conservation capacity-building among protected areas.

Key words: Chiroptera; climate change; conservation; land use change; national parks; prioritization; protected areas; Special Feature: Science for Our National Parks' Second Century; species–area relationship; species–energy relationship; white-nose syndrome; wind energy.

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Introduction

North American bat populations face novel and growing threats (see O'Shea et al. 2016 for a review) from white-nose syndrome (WNS; Blehert et al. 2009, Maher et al. 2012, Warnecke et al. 2012, O'Regan et al. 2015), accelerated rates of wind energy development (Arnett et al. 2008, Arnett and Baerwald 2013), land use change (Russo and Ancillotto 2015, Jung and Threlfall 2016), and accelerated climate change (Humphries et al. 2002, Jones et al. 2009, Adams 2010, Sherwin et al. 2013). Despite advances in acoustic detection methods and other technologies, understanding the impacts of these threats on populations and across entire species' ranges continues to be limited by the challenges associated with studying the cryptic and overdispersed habits of bats (O'Shea et al. 2003, Hayes et al. 2009, Weller et al. 2009, Meyer 2015). This information gap hampers effective conservation, and bat conservation efforts generally lag behind those being made for other at-risk taxa, including birds, amphibians, and some of the larger marine and terrestrial mammals. However, WNS has been a catalyst for bat conservation in the United States and Canada (COSEWIC 2013, Federal Register 2015) because formerly common bat species are now faced with regional extirpation (Frick et al. 2010*a*, 2015, Russell et al. 2015) and land management organizations have recognized the need to increase attention on bat conservation (USFWS 2011, Loeb et al. 2015, Kingston et al. 2016). The continental network of national parks and refuges in particular has tremendous potential to support coordinated resource protection, disease surveillance, and population monitoring that could become a cornerstone of 21st-century bat conservation in North America, but no systematic assessment of this potential has been made.

Macroecology, the study of broad regional- and continental-scale biogeographic patterns and their underlying mechanisms (Brown 1995), provides a system-wide perspective on bats in parks and protected areas that can be useful for guiding strategic conservation decisions. Macroecological insights from broadscale species distribution and abundance data are playing an increasingly important role in conservation (Johnson 1998, Kerr et al. 2007), particularly for understanding impacts of global change on biological diversity, identifying gaps in protected-area networks, and for planning and reserve design (Myers et al. 2000, Andelman and Willig 2003, Diniz-Filho et al. 2008). Macroecological analyses of bats in North America and on other continents have demonstrated strong and predictable latitudinal and elevational gradients in species richness (Kaufman and Willig 1998, Stevens and Willig 2002, Rodriguez and Arita 2004, McCain 2007), suggesting a strong species–energy relationship (SER; Wright 1983, Hawkins et al. 2003).

Bats have "slow" life history strategies relative to other mammals of their size (Barclay and Harder 2003) and are constrained by tight energy budgets. The ability to procure and conserve energy is a fundamental driver of bat distribution and abundance patterns (Humphrey 1975, Humphries et al. 2002). Energetics has emerged as a more proximal driver of contemporary extinction risk among North American bats than historic factors such as range size, foraging specialization, and wing morphology (Jones et al. 2003, Safi and Kerth 2004, Schipper et al. 2008, Sherwin et al. 2013, Frick et al. 2015). Notably, some of the most wide-ranging species are now on an accelerated trajectory toward extinction as a result of disease and wind energy production (Kunz et al. 2007, Frick et al. 2010*a*, 2015, Russell et al. 2015, O'Shea et al. 2016). These two sources of unprecedented mass adult mortalities in bats (O'Shea et al. 2016) are particularly conspicuous because of their interferences to key evolutionarily successful energy conservation strategies: hibernation and migration. Climate change is also likely to impact many bat species by way of energy budgets, including species with broad ranges and no previously identified vulnerability (Humphries et al. 2002, Adams 2010, Sherwin et al. 2013, O'Shea et al. 2016). Urbanization and other kinds of habitat-fragmenting land use changes are also thought to be altering species distribution patterns and community compositions in part because of energetics-related impacts on fitness (e.g., loss of secure roosts, soundscape "jamming," and interferences to efficient foraging; Russo and Ancillotto 2015). Energetics, when viewed through the lens of macroecology, therefore emerges as a useful conceptual framework for NPS and other protected-area networks to approach strategic bat conservation planning. In particular, energetics provides the mechanistic

understanding for macroecological patterns of bat diversity and conservation risk, and the theoretical and practical foundation for targeting locations (e.g., high-diversity parks) and habitat resources (e.g., high-value roosting features) for conservation actions.

Here, we develop a macroecological perspective on bats across the system of parks and protected areas of the U.S. National Park Service (NPS) and use it to motivate strategic conservation planning within the NPS and across the broader network of American protected areas more generally (e.g., Mexican, Canadian, and U.S. parks and refuges). In an analysis of IUCN category I and II protected areas throughout the western hemisphere, Andelman and Willig (2003) found that 82% of threatened and range-restricted bat species were poorly represented among the protected-area network. However, this gap will differ considerably when focused on North America because the size and number of protected areas are biased toward North America (e.g., 35% of total reserve area is in Alaska; Andelman and Willig 2003) but North American bat species richness is considerably less and the ranges of those species considerably greater than in tropical America (i.e., Rapoport's rule; Pagel et al. 1991, Rohde 1999, Stevens and Willig 2002, Andelman and Willig 2003, Rodriguez and Arita 2004). Furthermore, many NPS park units were left off the list used by Andelman and Willig (2003) because they are ranked as IUCN category III or greater, yet still offer a high degree of resource protection. Newmark (1995) assessed extinction risk of mammals in a subset of western NPS park units but excluded bats, and no other systematic analysis of the overlap between bat ranges and protected areas has been performed elsewhere in the world.

We focus on the U.S. National Park System in part because of the recently available records of bat occurrence data for parks assembled as part of the agency's inventory and monitoring (I&M) program (Fancy et al. 2009), but also because of the long-term commitment by NPS to manage parks for resource protection. The parks in the NPS provide a particularly high degree of protection from development (Fancy et al. 2009), offering baselines for comparison with other lands, and that can serve as nodes on monitoring and conservation networks (Loeb et al. 2015). Therefore, the insights generated about bat species diversity and energy relationships by evaluating macroecological patterns of bats on NPS lands have broader implications for other components in the American protected-area network. As with other federal protected-area systems such as Parks Canada and the U.S. national wildlife refuge system, the NPS system does not provide a random and representative collection of ecosystems, but it does contain numerous widely distributed park units throughout the continent, and on outlying archipelagos, across a very large number of different types of ecosystems.

We harvested the records of bat presences contained within the agency's NPSpecies database and compared these records with published range maps, WNS spread models, park land use change metrics, climate change velocities, park-vicinity wind turbine densities, and summaries of cave/karst and abandoned mine features in parks. We used models to describe basic patterns of park species–area and species-energy relationships. Our objective was to understand the potential of the NPS system to contribute to North American bat conservation by describing the bat diversity contained within the NPS footprint and the bat conservation challenges and opportunities facing the agency in the coming decades. We begin by evaluating the completeness of park bat species lists by comparing the apparent discrepancies between records of presence in parks and the lists of species expected to occur in parks based on range map overlap. Closing these gaps with improved reporting and additional inventories becomes the first tangible recommendation for strategic NPS bat conservation that we identify. After acknowledging these gaps, we then address the following questions. (1) What is the distribution of species among NPS park units? (2) Do macroecological patterns of bat species richness reflect hypothesized species–area and species-energy relationships? (3) Which parks have substantial numbers of bat species, or rare or threatened species, and therefore might be prioritized for NPS bat conservation? (4) Which parks with important bat resources (e.g., high richness and rarity) are at high risk of WNS, wind power development, climate change, and urbanization and other land use changes? We provide an attributed list of parks as a reference that helps answer these questions and that can be used to

prioritize strategic investments in bat conservation activities across the NPS.

Materials and Methods

Bat occurrence and distribution data

The NPSpecies database (https://irma.nps.gov/NPSpecies/) was developed as part of the NPS investment in a natural resources I&M program (Fancy et al. 2009) through a funding initiative called the Natural Resources Challenge (Fancy et al. 2009). Vertebrates, including bats, were inventoried in many parks during the first phase of the I&M program approximately between the years 2000 and 2005, with some additions to the database occurring sporadically in subsequent years. The period 2000–2005 pre-dates the increasingly widespread use of automated bat activity detectors, and observed presence records were obtained primarily through direct capture of individual bats. However, it was not possible for us to ascertain the details about methods used in each park, accepting that the assemblage of records was compiled from multiple methods.

The Natural Resources Challenge initially identified 270 park units with substantial natural resources that were included in the I&M program (Fancy et al. 2009). These parks and others added subsequently were targeted for thorough vertebrate inventories with an agency-wide goal of documenting ≥90% of the species expected to occur in each of these parks (Fancy et al. 2009). From these we compiled a final list of 287 park units for analysis that are now included in the I&M program and that are likely to have been surveyed for bats as part of the inventory process. It was clear to us at the outset of the analysis, however, that not all parks eligible for thorough inventories had received them and that under-reporting and under-sampling of bats had occurred in some parks. Factors including staff turnover, incomplete documentation, and inefficiencies in agency-wide information retrieval precluded our ability to comprehensively determine which of the 287 parks had actually been surveyed recently for bats, and which had not. Rather, this question became part of our study and we report on the apparent discrepancies between documented presence records and expectations based on range maps in *Results*.

We queried NPSpecies in October 2015 for the most-recent snapshot of records of bats listed as present in parks (i.e., observed), excluding other records designating species thought to be probably present and unconfirmed. Although these other designations could have been used to develop lists of expected species, we found usage of these designations to be inconsistent and incomplete for many parks. Similarly, although other sources of bat occurrence data exist (e.g., Biodiversity Information Serving Our Nation), these sources do not represent systematic inventories and further exhibit sampling biases that are not consistently documented.

For comparison against the observed NPSpecies records, and to develop a consistent and authoritative perspective on species expected to occur in parks, we overlaid range maps provided by NatureServe (Patterson et al. 2007), IUCN (http://www.iucnredlist.org/technical-documents/spatial-data), and the National Atlas (https://catalog.data.gov/dataset/north-american-bat-ranges-direct-download) with park boundaries. These maps were consistent with one another for most species, but differences were apparent for some species (illustrated with non-overlapping colored polygons in Appendix S1). These three sources provided the best available peer-reviewed GIS data sets that extended consistently across the NPS footprint. Although some parks encompassed by these highly generalized range maps do not contain suitable habitats for some species, the volancy and scale of nightly movements of bats for commuting, water-drinking, and foraging create opportunities for survey encounters even in small parks and in parks where specific roost features such as cliffs and snags are not available.

Taxonomy

We prepared a list of 61 species and three additional subspecies of bats for analysis, based on range map overlap with and proximity to NPS park units, including parks in the Caribbean and tropical Pacific (Table 1). We included the three additional subspecies because they are listed as threatened or endangered by the U.S. Fish and Wildlife Service (USFWS). We used the integrated taxonomic information system (ITIS) and references therein (Simmons 2005) as our primary reference for currently accepted taxonomy

Table 1. List of 64 bat species and subspecies included in the study and the park counts of observed (present records from the NPSpecies database) and expected species (based on range map overlap), with comments provided for nomenclature decisions.

Scientific name	Common name	Observed	Expected	Comments
Eptesicus fuscus†	Big brown bat	178	252	
Lasiurus cinereus‡	Hoary bat	127	249	
Myotis lucifugus†	Little brown myotis	123	200	
Lasionycteris noctivagans‡,§	Silver-haired bat	108	229	
Lasiurus borealis‡,§	Eastern red bat	90	137	
Tadarida brasiliensis	Mexican free-tailed bat	75	126	
Myotis californicus	California myotis	74	91	
Corynorhinus townsendii	Townsend's big-eared bat	73	123	
Myotis volans	Long-legged myotis	69	109	
Perimyotis subflavus†	Tricolored bat	69	129	
Myotis ciliolabrum	Western small-footed myotis	67	105	Includes *Myotis melanorhinus* and all western *Myotis leibii*
Myotis yumanensis	Yuma myotis	66	99	
Myotis thysanodes	Fringed myotis	65	96	
Antrozous pallidus	Pallid Bat	61	102	
Myotis evotis	Western long-eared myotis	56	86	
Myotis septentrionalis†,¶	Northern long-eared myotis	56	97	
Parastrellus hesperus	Canyon bat	53	67	
Nycticeius humeralis	Evening bat	37	102	
Nyctinomops macrotis	Big free-tailed bat	31	61	
Euderma maculatum	Spotted bat	30	70	
Lasiurus blossevillii	Western red bat	21	106	Includes *L. borealis* records from parks in California, Arizona, New Mexico
Myotis leibii†	Eastern small-footed myotis	16	77	
Eumops perotis	Western mastiff bat	14	26	
Idionycteris phyllotis	Allen's big-eared bat	13	28	
Myotis grisescens†,¶	Gray myotis	13	26	
Myotis velifer	Cave myotis	12	24	
Lasiurus seminolus	Seminole bat	11	46	
Myotis sodalis†,¶	Indiana myotis	11	69	
Corynorhinus rafinesquii§	Rafinesque's big-eared bat	10	49	
Myotis auriculus	Southwestern myotis	9	7	
Nyctinomops femorosaccus	Pocketed free-tailed bat	8	15	
Choeronycteris mexicana	Mexican long-tongued bat	6	8	
L. cinereus semotus¶	Hawaiian hoary bat	6	7	
Lasiurus intermedius	Northern yellow bat	6	30	
Myotis austroriparius§	Southeastern myotis	6	27	
Lasiurus xanthinus	Western yellow bat	5	16	Includes all *Lasiurus ega* reported from New Mexico, Arizona
Macrotus californicus	California leaf-nosed bat	5	15	
Leptonycteris yerbabuenae¶	Lesser long-nosed bat	4	7	Includes all *Leptonycteris curasoae* reports
Mormoops megalophylla	Ghost-faced bat	2	13	
Artibeus jamaicensis	Jamaican fruit-eating bat	1	4	
Brachyphylla cavernarum	Antillean fruit-eating bat	1	2	
Corynorhinus townsendii ingens¶	Ozark big-eared bat	1	2	
Corynorhinus townsendii virginianus§,¶	Virginia big-eared bat	1	5	
Diphylla ecaudata	Hairy-legged vampire bat	1	2	
Eumops floridanus¶	Florida bonneted bat	1	2	*E. glaucinus floridanus*; not reported present in NPSpecies for Everglades NP but known to occur there

Table 1. Continued.

Scientific name	Common name	Observed	Expected	Comments
Eumops underwoodi	Underwood's mastiff bat	1	2	
Molossus molossus	Pallas's mastiff bat	1	2	
Myotis occultus	Arizona myotis	1	35	
Noctilio leporinus	Greater bulldog bat	1	1	
Stenoderma rufum	Red fig-eating bat	1	1	
Leptonycteris nivalis¶	Mexican long-nosed bat	1	1	Retained only for Big Bend NP, all others *L. yerbabuenae*
Pteropus samoensis	Samoan flying fox	1	1	
Pteropus tonganus	Pacific flying fox	1	1	
Myotis keenii	Keen's myotis	0	1	Retained only for Olympic NP, not yet reported present in NPSpecies but likely
Pteropus tokudae¶	Guam flying fox	0	1	Historic (extirpated?)
Pteropus mariannus¶	Marianas flying fox	0	1	Historic (extirpated?)
Emballonura semicaudata	Polynesian sheath-tailed bat	0	1	Historic (extirpated?)
Mormoops blainvillii	Antillean ghost-faced bat	0	0	Puerto Rico: plausible for VIIS
Pteronotus parnellii	Common mustached bat	0	0	Puerto Rico: plausible for VIIS
Pteronotus quadridens	Sooty mustached bat	0	0	Puerto Rico: plausible for VIIS
Erophylla bombifrons	Brown flower bat	0	0	Puerto Rico: plausible for VIIS
Natalus mexicanus	Mexican greater funnel-eared bat	0	7	Mexico–U.S. borderland
Lasiurus ega	Southern yellow bat	0	2	Mexico–U.S. borderland
Lasiurus minor	Little red bat	0	0	Puerto Rico: plausible for VIIS

† Known to be susceptible to white-nose syndrome.
‡ Killed in large numbers at some wind farms.
§ Individuals have been found positive to *Pseudogymnoascus destructans.*
¶ Federally listed as threatened or endangered.

and nomenclature. However, in some cases we retained older or more established taxonomic designations, for example, subsuming *Myotis melanorhinus* under *Myotis ciliolabrum*, the western small-footed myotis (Holloway and Barclay 2001), and accepting the synonym *Eumops floridanus* for the Florida bonneted bat, used by the USFWS in its recent endangered species listing decision (Federal Register 2013). Table 1 lists the taxonomic decisions made for the purposes of this study that deviate from ITIS.

Species–area and species–energy models

We constructed two types of models to explore the relationship between bat species richness and park area, mean and range of elevation, latitude (park boundary centroid), anthropogenic land use change, and count of the number of underground habitat features associated with each park. We did not include in these models other biogeographic factors that are either too recent (e.g., WNS, wind turbine density) to have had a significant effect on richness, or are based on future projections (climate change). First, we constructed a classical non-linear species–area curve (SAR), $S = cAz$ + error, with additive error (Rosenzweig 1995, Xiao et al. 2011). We also fit a log-linear model with multiplicative error and used Xiao et al.'s (2011) method to assess goodness-of-fit. Although the SAR model provided a better fit (ΔAICc $\gg$ 2), we used a log-linear model with negative binomial error for overdispersed species counts (Hilbe 2011) to explore the bat SER with covariates included for latitude, quadratic elevation, range of elevation, percentage of natural (vs. non-anthropogenic or non-built converted) land cover, and count of underground habitat features (caves and mines). Note that although estimates of z from SARs are typically compared between mainland and island data sets, for this study, given high levels of under-reporting and under-sampling and the relatively small numbers (sample size) of land bridge and especially oceanic islands, we pooled all park units for models. We leave a more thorough SAR examination for future analysis, preferably after reporting and sampling gaps have been closed. We fit models in R (R Core Team

2015) and used the MASS package (Venables and Ripley 2002) for fitting negative binomial models.

Keystone roost structures and bat conservation risk factors in parks

To elaborate on the challenges and opportunities for strategic bat conservation in parks, we assembled information about the reported numbers of abandoned mines and cave and karst features in parks provided to us by the NPS Biological Resources Division and Geological Resources Division. These underground habitats serve as keystone structures (Tews et al. 2004) for summer pup-rearing and winter hibernation of many species of bats (Humphrey 1975, Pierson 1998). We considered that these resources are likely to elevate bat diversity within parks and create opportunities for doing conservation activities, but also expose parks to becoming hosts to WNS. Already, parks with caves and mines have had to react quickly to the spread of WNS, putting in place visitor screening, gates, and other protective measures to try and slow the inadvertent human spread of the disease. We considered also including information about the numbers of old buildings, tree snags, and cliff and canyon features in parks, which are also critical keystone structures for maternity colonies and hibernation, but we were unable to find suitable comprehensive coverage of such data within the NPS footprint.

We used a GIS overlay to identify parks with other bat conservation challenges, focusing on the presence of WNS, wind power development, land use change, and anticipated climate changes. We overlaid park boundaries with counties recorded to be infected with or suspected to be infected with WNS, as reported in October 2015. We identified parks within the WNS buffer zone, current as of October 2015, published by USFWS as part of the listing of the northern long-eared bat for federal endangered species protection (*Myotis septentrionalis*; Federal Register 2015; available at http://www.fws.gov/midwest/endangered/mammals/nleb/). We also overlaid park boundaries with counties forecasted to be infected with WNS within a decade (by 2026) according to disease spread models developed and shared with us by Maher et al. (2012). The models of Maher et al. (2012) are in close agreement with findings of O'Regan et al. (2015), who predict that >80% of U.S. counties will be infected with WNS before the disease spread is curtailed by local extirpation of colonies. Note that after our analysis in March 2016, WNS was confirmed in King County, Washington, D.C. (Lorch et al. 2016). Although the county was predicted by Maher et al. (2012) to become infected within 10 yr, the rate of spread across western North America outpaced predictions and underscores the urgency of our analysis and a corresponding NPS response.

To address urbanization and other anthropogenic land cover type conversions in and near NPS units, we used the percentage of natural vs. converted land cover metric (hereafter referred to as percentage of natural) calculated by the agency's NPScape program (Monahan et al. 2012, NPS 2014), which aggregates developed and agricultural USGS Anderson Level 1 land cover types from the 2011 Natural Land Cover Dataset (Homer et al. 2015) to represent converted lands. The proportional change from natural to converted land cover is an intuitive, widely used, and parsimonious measure of net human land use pressure on protected areas (O'Neill et al. 1997) that is likely to also represent habitat changes that adversely impact bat biodiversity (Russo and Ancillotto 2015).

We assembled information about predicted climate change velocity of parks and the densities of wind turbines within 30 km of park boundaries. Climate change velocity was calculated as the mean rate of change in temperature over time (future − current; °C/yr) divided by the maximum rate of temperature change over space (°C/km), following methods outlined by Loarie et al. (2009). We obtained current and future gridded estimates of annual mean temperature from WorldClim (Hijmans et al. 2005). Data were obtained at 30 arc second spatial resolution and re-projected using an equal-area projection to 800 m. Estimates of future temperature were based on the ensemble average of 17 individual climate models available through the Coupled Model Intercomparison Project Phase 5 (CMIP5): ACCESS1-0, BCC-CSM1-1, CCSM4, CNRM-CM5, GFDL-CM3, GISS-E2-R, HadGEM2-AO, HadGEM2-CC, HadGEM2-ES, INMCM4, IPSL-CM5A-LR, MIROC-ESM-CHEM, MIROC-ESM, MIROC5, MPI-ESM-LR,

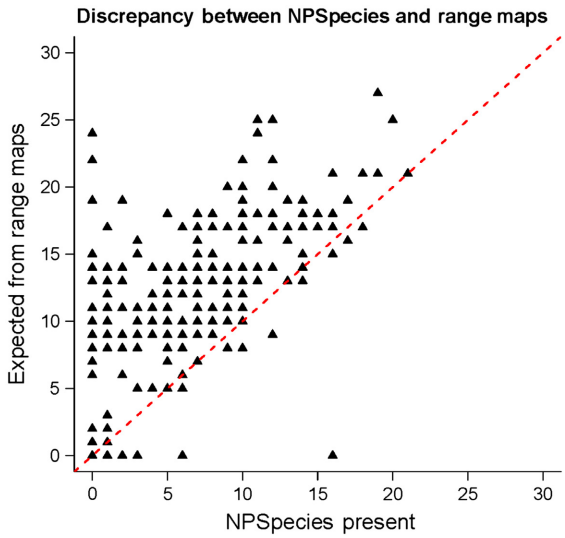

Fig. 1. A scatterplot showing the discrepancy between expected and reported (in NPSpecies) species richness in NPS park units. Symbols above the diagonal red line indicate parks with fewer species recorded present than are expected. Very few park units meet or exceed expected counts (below the line). Parks below the line suggest extralimital occurrences and, in several extreme cases with zero species expected but many species reported, mapping errors. NPS, National Park Service.

MRI-CGCM3, and NorESM1-M. The individual CMIP5 models were downscaled and calibrated (bias corrected) using WorldClim as the current (1950–2000) baseline. We considered a 2061–2080 future (referenced as 2070) and a "business as usual" representative concentration pathway (RCP) of 8.5 W/m^2 (RCP 8.5).

We computed wind turbine density (turbines/km^2) with data obtained from the U.S. Federal Aviation Administration's (FAA's) Obstruction Analysis/Airport Airspace Analysis (OE/AAA), compiled by the USFWS (https://www.fws.gov/southwest/es/Energy_Wind_FAA.html). We evaluated three USFWS turbine determination classes: determined non-hazard with built date, determined non-hazard without built date, and not yet determined (i.e., whether proposed turbine poses a hazard to aviation has not been determined). Combined, these three determination classes represent our best current estimate of existing and potential wind turbines within the vicinity of NPS park units.

Results

Discrepancies between observed and expected species

Based on range maps, we determined that 64 unique taxa, including three recognized subspecies, had range maps that overlapped or were within very close proximity of NPS park units (Table 1). There was considerable discrepancy between the counts of observed species and species expected based on range maps (Fig. 1). Of the 287 park units evaluated, only 55 (19%) reported as present ≥90% of the taxa expected based on range maps (Data S1). Nineteen parks with ≥10 expected species reported zero species present. Forty-eight parks met or exceeded the number of bat taxa expected; of those that did, seven were island parks (e.g., Isle Royale National Park) where range map coverage was incomplete but bats are reported. A careful examination of maps in Appendix S1 reveals that, even for well-studied species such as the little brown myotis, geographically clustered extralimital park reports (in the U.S. southwest) suggest legitimate distribution knowledge gaps as an additional explanation for positive discrepancies between parks and range maps. Data S2 provides the detailed lists of bat species recorded as present in NPSpecies and expected based on range map overlap with park boundaries.

Bat diversity in parks

Fifty of the 61 possible bat species and the three additional subspecies were reported present in at least one park unit (Table 1). Species richness reported in parks ranged from 0 for some parks in northern Alaska to 21 in Big Bend National Park (Fig. 2 and Data S1). There were 50 parks with notably high bat species diversity, reporting as present >10 species (Fig. 2 and Data S1). The majority of the 11 species not reported present in any park but considered to be possible based on range were in the Caribbean island of Puerto Rico and nearby Antillean Islands, where they could plausibly occur in Virgin Islands National Park (Table 1). Three species of Old World flying foxes (Table 1) still extant in some portions of their range are reported as being extirpated from the islands of Guam and Saipan, Northern Mariana Island, where they are believed to have occurred historically in or near American

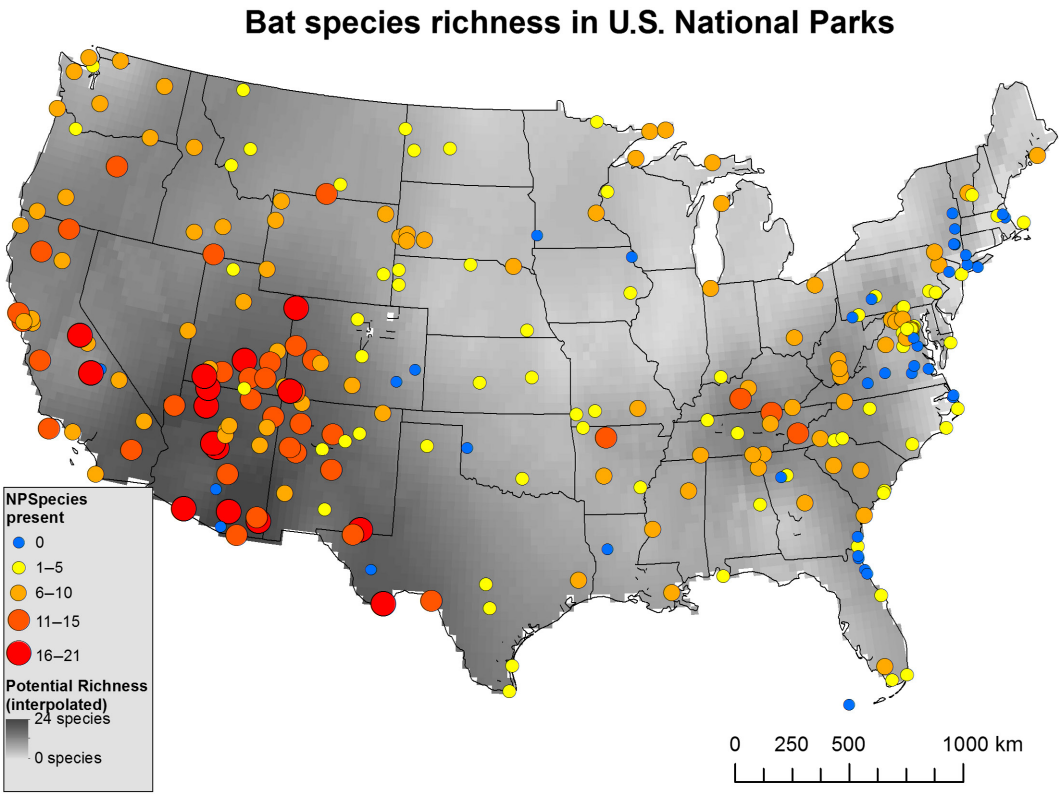

Fig. 2. Bat species richness in parks (point symbols) from NPSpecies presence records, overlayed on potential bat species richness in the continental United States, interpolated from an overlay of range maps and park boundaries. NPS, National Park Service.

Memorial Park and War in the Pacific National Historical Park. In Appendix S1, we provide maps of published ranges (for the continental United States, Hawaii, and Caribbean only; parks in the western Pacific were not mapped) and occurrence records evaluated for the study.

Species–area and species–energy patterns

In spite of the apparent discrepancies between observed and expected species, park species richness was strongly correlated with park area, latitude (Fig. 2), elevation, and underground habitat, as expected from theory (Figs. 3, 4). We found no evidence that species richness was influenced by the percentage of natural gradient represented by the 287 parks included in the study or by the elevation ranges in parks ($P \approx 0.5$ for both covariate parameter estimates). Notably, percentage of natural values for parks is relatively high (e.g., >50%), even in the eastern United States (Fig. 5). In portions of the eastern United States (Appalachian Highlands) where percentage of natural approaches or drops below 50% (Fig. 5), bat species richness is also relatively high (Fig. 2).

We estimated that species richness increased at an approximate rate (z) of 0.11 with the classical SAR model (Fig. 3), higher for the naïve multiplicative error model (z = 0.23), adjusted downward ($z = 0.16$) after accounting for latitude, quadratic elevation, and underground habitat availability. Area remained a significant ($P < 0.05$) positive correlate with bat species richness even after accounting for these other factors (i.e., by $e^{0.16}$ ~ 1.17 times for each SD increase in area [km]; Fig. 4). Bat species richness also decreased significantly ($P < 0.05$) with increasing latitude, increased significantly with elevation but then decreased with elevation^2 (i.e., peaked at mid-elevation), and increased significantly as the count of underground habitat features increased (Fig. 4).

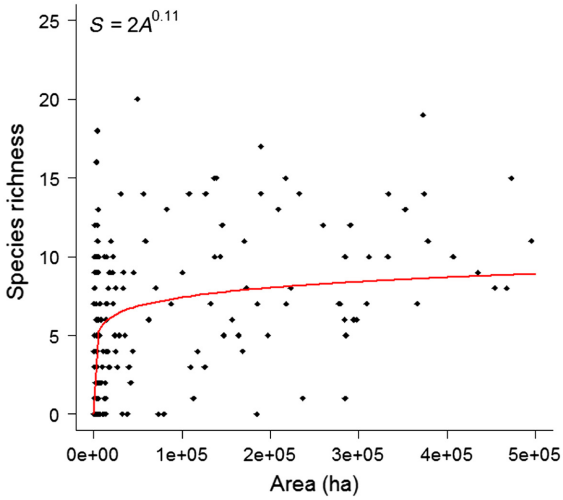

Fig. 3. A species–area curve for bat species richness reported from NPSpecies vs. area of individual NPS park units (symbols). The slope, *z*, was estimated to be 0.11. NPS, National Park Service.

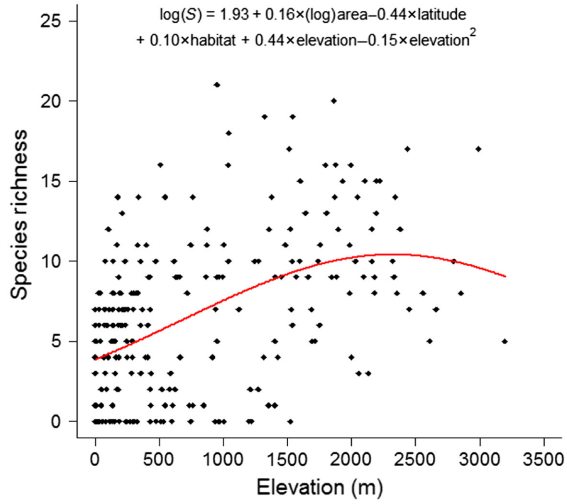

Fig. 4. A species–energy curve for bat species richness along the elevational gradient of NPS park units. Covariates were standardized and coefficients are interpreted, when exponentiated, as the estimated multiplicative effect on richness for each 1-SD increase in covariate. We used a reduced model without elevation range and percentage of natural for analysis; these two variables were uninformative when included in a full model ($P \approx 0.05$). All other variables retained in the model were statistically significant ($P < 0.05$). NPS, National Park Service.

Distribution of at-risk bat species

Included among the list of 53 unique taxa reported as present in at least one park unit are all 12 species currently understood to be susceptible to WNS or to have been found carrying the disease-causing fungus *Pseudogymnoascus destructans* (https://www.whitenosesyndrome.org/ [accessed October 2015]; Table 1). This includes continentally distributed and abundant species such as the big brown bat (*Eptesicus fuscus*), silver-haired bat (*Lasionycteris noctivagans*), and little brown bat (*Myotis lucifugus*), each of which have been documented in over 100 park units and likely occur in >200 parks (Table 1). The tree-roosting migratory bats most vulnerable to fatality at wind power generating facilities (hoary bat [*Lasiurus cinereus*], eastern red bat [*Lasiurus borealis*], and silver-haired bat) are also well represented across the NPS system, reported present in >100 parks (Table 1). Nine species protected under the U.S. Endangered Species Act as threatened or endangered were reported present in parks, including the recently listed northern long-eared myotis (*Myotis septentrionalis*) which occurs in >50 parks and likely in ~100 parks within its range (Table 1). Also included are rare species with very narrow distributions (Table 1 and Appendix S1) that occur (or likely do and are not reported) in only one or few parks, such as the Florida bonneted bat (*Eumops floridanus*; Appendix S1: Fig. S14), Keen's myotis (*Myotis keenii*; Appendix S1: Fig. S41), Hawaiian hoary bat (*L. cinereus semotus*; Appendix S1: Fig. S22), and the big-eared bat *Corynorhinus* subspecies (Table 1; Appendix S1: Fig. S6). It is also noteworthy that multiple tropical species found in 1 or few parks reach their (current) northern range extent along the southern edge of the NPS footprint in the Caribbean and southern portion of the continental United States (Table 1 and Appendix S1). Data S1 provides the list of parks with these aforementioned species attributes.

Current and predicted distribution of WNS in parks

As of October 2015 there were 43 park units in counties confirmed or suspected to be WNS-positive (Fig. 6 and Data S1). This included 11 parks with WNS-positive bats actually having been found within or immediately adjacent to park boundaries. An additional 84 units are in counties that are likely to be WNS-positive within

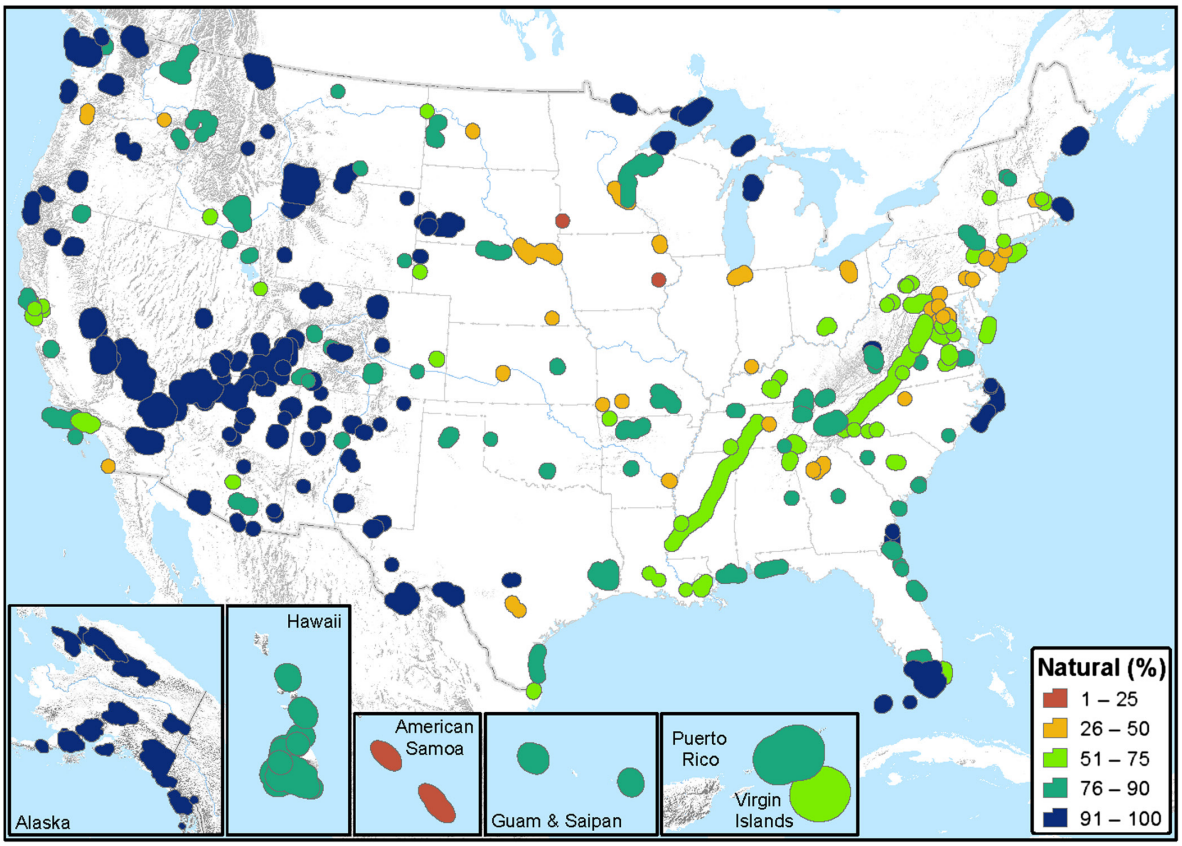

Fig. 5. Percentage of natural vs. converted land cover (referred to as percentage of natural in the text) in parks and 30-km buffer areas of analysis. This metric was calculated from 2011 National Land Cover Dataset (Homer et al. 2015) by the National Park Service NPScape program (Monahan et al. 2012).

a decade (by 2026), as determined by overlaying park boundaries with forecasts made by Maher et al. (2012); Fig. 6 and Data S1). One hundred and three parks occur within the WNS buffer zone (Fig. 6). In March 2016, after our analysis was complete, WNS was confirmed in King County, Washington (Fig. 6), ~2000 miles west of the previously most-westward infected county in Minnesota. Although no NPS units are in King County, the site of infection is only ~30 miles north of Mt. Rainier National Park.

Patterns of wind energy development and climate change in parks

Wind turbine densities within 30-km areas of interest around NPS park units were relatively low in most areas of the continental United States but with conspicuously high patterns along the Appalachian highlands, Texas gulf coast, central plains, and in California (Fig. 7). Seventeen parks were in the vicinity of high (>1 SD) wind turbine density. Comparison of Figs. 2, 7, and with range maps for the continentally distributed hoary bat, silver-haired bat, and eastern red bat (Appendix S1), reveal considerable overlap with turbine density in these regions. Climate change velocities estimated for parks were invariably positive for all parks, and particularly strong along the Atlantic and Gulf coasts, and in the Great Lakes region (Fig. 8). Velocity was particularly high (>1 SD) for 50 parks.

Discussion

We provide the first comprehensive review of the bat species occurring within the NPS system, and the associated potential of NPS to contribute to North American bat conservation. No other examination of bats has been made for other protected-area networks except for the gap

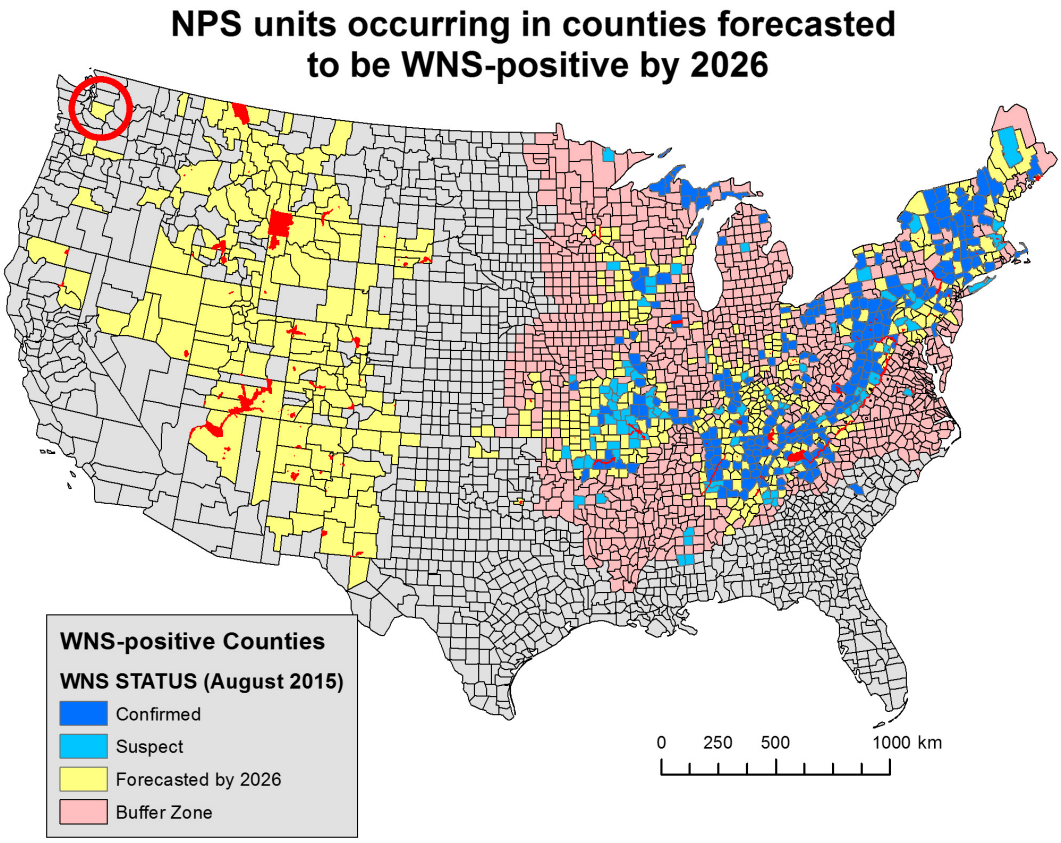

Fig. 6. Continental U.S. counties with National Park Service (NPS) units (in red) that are confirmed, suspected, or forecasted to have white-nose syndrome (WNS) infecting bats within the next decade. Forecasts are based upon models of Maher et al. (2012). The WNS buffer zone shown here was developed and maintained by the U.S. Fish and Wildlife Service (http://www.fws.gov/midwest/endangered/mammals/nleb/ [accessed October 2015]). Note that King County, Washington (circled in red) became WNS-positive in March 2016, outpacing predictions from Maher et al. (2012).

analysis performed by Andelman and Willig (2003) for bat range overlap with IUCN category I and II protected areas in the western hemisphere. Clearly, this is in large part a result of the historic paucity of bat occurrence data; our analysis shows this information-gap challenge remains a limitation, even for the NPS, in spite of the focused inventory efforts recently undertaken by the agency (Fancy et al. 2009). More than half of the 287 parks evaluated appear to be under-sampled and/or under-reported for bats. However, as conservation concerns about bats motivates new broadscale survey efforts (Barlow et al. 2015, Loeb et al. 2015, Meyer 2015, Kingston et al. 2016) and new data become available for other protected-area networks, analyses similar to ours can also be used to inform strategic bat conservation. Closing the gap between observed and expected species will be an intuitive and concrete conservation measure needing to be taken by NPS and other protected-area networks.

Historically, bat conservation in the NPS has been performed on a park-by-park basis. Our synthesis of range-wide information provides a novel macroecological perspective and establishes a foundation for guiding a more strategic agency-wide approach. Some of our findings have already been used in decisions about allocating funding to parks for addressing WNS (M. Wild, *personal communication*). We found that the NPS footprint overlaps considerably with ranges of most of the bats of North America, underscoring the tremendous potential role that

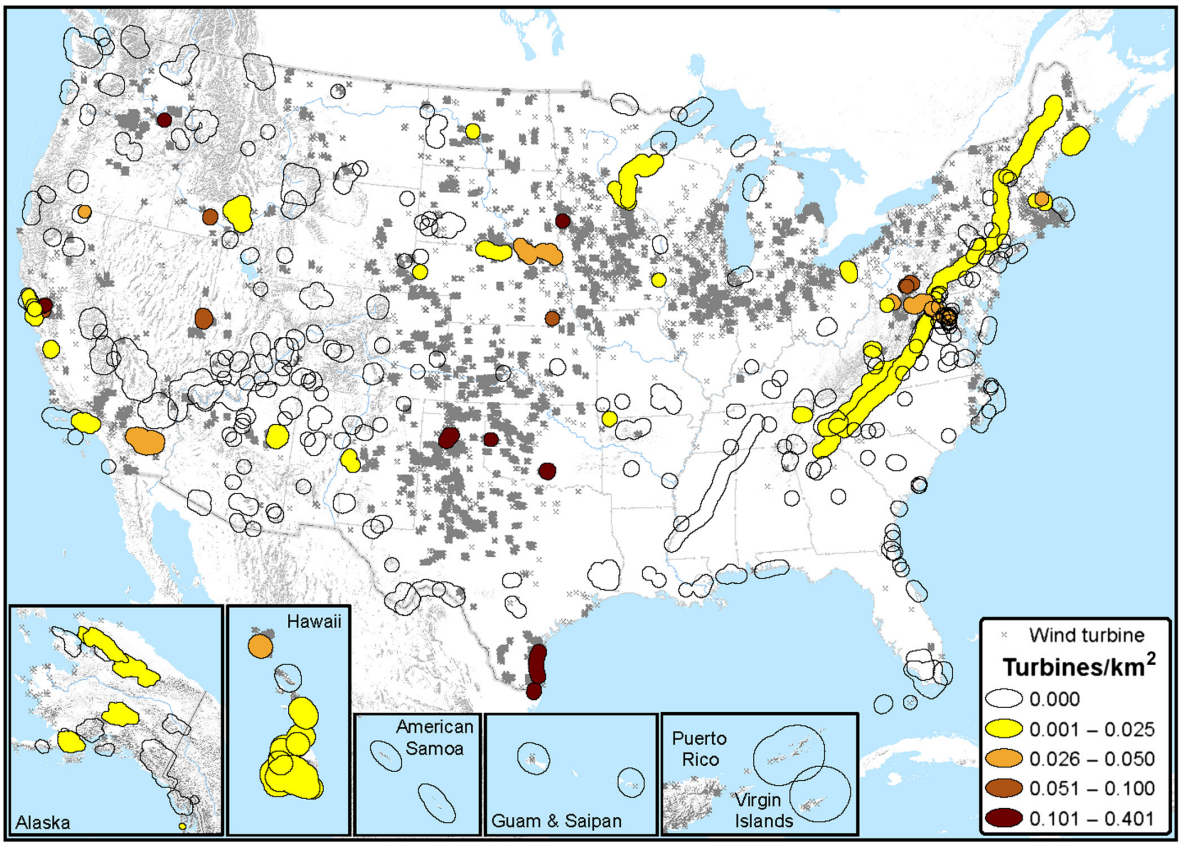

Fig. 7. Wind power generation turbine density (gray symbols) and 30-km areas of interest around NPS parks colored by turbine density. NPS, National Park Service.

the NPS system can play in strategic bat conservation in the coming decades. As expected, we found a much smaller protected-area gap than that described by Andelman and Willig (2003), with every species on the continental United States and in Canada and Alaska occurring in at least one NPS unit. Fifty parks can be considered highly diverse for bats, each with >10 species documented in NPSpecies, and this number will increase when park reporting and sampling gaps are closed. Importantly, several NPS park units harbor rare and range-restricted species, and may provide the only protected-area habitat (e.g., for the Florida bonneted bat). Notably, with few parks in the western Pacific and Caribbean, the agency's contribution to conservation of tropical bats is limited, but potentially critical for the conservation of the Hawaiian hoary bat which is endemic to Hawaii and where the NPS has a very substantial footprint (Data S1 and Appendix S1). The small size of many NPS park units (e.g., historic sites) limits opportunities for bat conservation in some cases, although small parks may harbor highly protected keystone roost features such as cliffs, caves, old trees, and buildings, making some small parks disproportionately important for bat conservation.

Species–energy patterns

We found a clear pattern of species richness along environmental gradients consistent with species–energy theory. Bat species richness increased with park area at a rate of ~0.1. Although low, this is a similar rate reported for many mainland SARs, especially when generated from nonnested accumulations for highly vagile species (Connor and McCoy 1979, Rosenzweig 1995). Species–area curves generated for bats are few, but generally show similarly low z values (Koopman 1958, Rodriguez and Arita 2004, Pederson et al. 2009). Specifically, our estimate of z is highly congruent with those estimated by

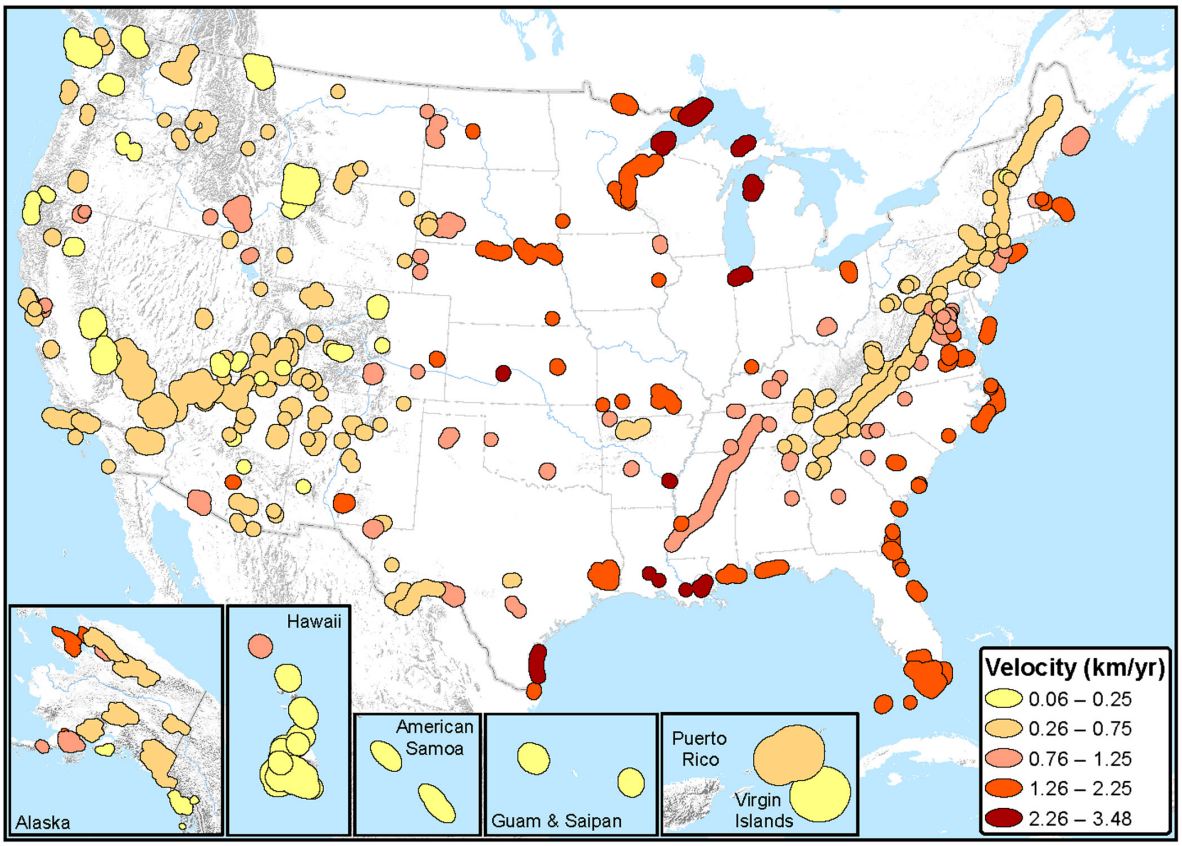

Fig. 8. Forecasted climate (temperature) change velocities of NPS park units. NPS, National Park Service.

Rodriguez and Arita (2004) for North America. The species–area slope for NPS park units is necessarily shallow because parks do not function as true islands and bats are volant and wide-ranging, with low beta diversity (i.e., species turnover; Rodriguez and Arita 2004). Nonetheless, the same curve fitted to potential counts from range map overlap yielded a flat line (result not shown), indicating that in spite of under-reporting and under-sampling, the available counts from NPSpecies do reflect local environmental filtering of the available species pool.

In addition to the importance of park area to bat species richness, we also found clear evidence of increasing richness at lower latitudes, at mid-elevations, and in parks with higher numbers of underground habitat features. While these patterns were expected based on theory (Brown and Maurer 1989, Pagel et al. 1991, Kaufman and Willig 1998, Rohde 1999, Rodriguez and Arita 2004), we nonetheless found the strength of these patterns striking given the scale of analysis and the noise introduced from under-reporting and under-sampling and from the unknown accuracies of the counts of underground roost habitat features. We suspect that these patterns will become even clearer as data gaps are closed. In a meta-analysis of bat faunas from around the world, McCain (2007) reported a recurring pattern of mid-elevation bat richness peaks in temperate regions, most pronounced in arid mountain ranges. Moreover, she also found consistency in the richness–abundance relationship. Both of these patterns underscore the importance of environmental productivity (energy, more generally) for bats (McCain 2007). Focused analyses of individual regional bat faunas have also revealed similar kinds of species–energy patterns (Rodhouse et al. 2012, 2015). Within this context, the species–energy patterns evident for bats among parks provides the biogeographic basis for developing the energetics conceptual

framework for bat conservation in the NPS system and across North America, more generally.

Interestingly, the inclusion of elevation range and percentage of natural (proportion of natural vs. converted land cover) in our species–energy model was equivocal, apparently providing no additional information about variation in bat species richness among parks at the scale of our analysis. Elevation range has been a widely used proxy for topographic roughness and environmental or habitat heterogeneity, with a typically positive relationship to species richness (Stein and Kreft 2015). Few studies about bat diversity have addressed this question, but ours and one other conducted about bats across a large geographic region in North America (Rodhouse et al. 2015) were equivocal about the relationship. Scale and metrics used could be obscuring the signal, but heterogeneity itself does not appear to be as strong a driver of bat diversity as environmental energy (latitude, temperature, productivity) has been shown to be (Willig et al. 2003, McCain 2007, Rodhouse et al. 2012, 2015), especially for temperate faunas with many generalist insectivores. This may also explain why our study and many other investigations into urbanization and anthropogenic land cover change have also shown equivocal or otherwise subtle impacts on bat diversity (e.g., on individual fitness; Russo and Ancillotto 2015, Jung and Threlfall 2016). Losses of specific structurally complex land cover types, especially forests, may be more detrimental to bats in parks than urbanization per se (Johnson et al. 2008). Urban areas with forested parks may actually support higher bat diversity than surrounding rural areas dominated by structurally simple agricultural cover types (Ghert and Chelsvig 2004). Furthermore, the presence or absence of keystone structures—the snags, cliffs, underground habitats, and old buildings which are used for pup-rearing and hibernation—is such a dominant factor in explaining patterns of bat diversity (Humphrey 1975, Pierson 1998, Kalcounis-Ruppell et al. 2005, Rodhouse et al. 2015) that any importance of net land cover change will be obscured.

Bats and parks at risk

Our study highlights both the bat diversity harbored among the collective network of NPS protected areas and the corresponding bat conservation challenges facing the agency. Foremost among these is WNS, which appears likely to affect hundreds of park units within the decade either because of infected hibernacula in or near the park or because they harbor summertime populations of WNS-vulnerable species that will experience net population declines from winter mortality. Continued population declines are likely in spite of the growing evidence that some amelioration of WNS morbidity may be occurring in previously affected areas (Langwig et al. 2012, 2015, Frick et al. 2015, Maslo et al. 2015). It is likely that WNS-induced population declines will affect, and can be monitored and researched in, many more than those 165 parks specifically identified at risk of WNS in Data S1 (those that are infected, likely to be infected, or in the buffer zone), especially now that the disease is established in the western United States (Fig. 6).

As with WNS, wind energy development and climate change present similar, albeit somewhat more diffuse and less proximal service-wide challenges for the NPS. Bat-turbine collisions and barotrauma have resulted in thousands of bat deaths in North America in recent years (O'Shea et al. 2016), impacting a different suite of species than those affected by WNS but ones that are also very broadly distributed (Appendix S1). Fig. 7 illustrates the extent of the problem with high densities of turbines near parks in several regions of the country. Likewise, climatic changes resulting in increasing temperatures are expected to occur within the coming decades in every NPS unit (Fig. 8; Monahan and Fisichelli 2014). Although the potential impacts of climate change on bats are not yet well understood (Sherwin et al. 2013) and some species (e.g., wide-ranging tropical species such as the Mexican free-tailed bat) may actually benefit from elevated temperatures and advancing phenology in parks (Monahan et al. 2016), the tight energy budgets associated with the unique physiology and morphology of the order have clear implications. For example, through bioenergetic models, Humphries et al. (2002) demonstrated that temperature changes are likely to substantially alter wintering bat distributions and Adams (2010) demonstrated that elevated rates of evapotranspiration and reductions in surface water availability in the western United States are likely to substantially depress

reproductive rates of widespread and abundant species such as the western long-eared myotis (*Myotis evotis*). The parks identified in Data S1 with high climate change velocities may be good candidates for targeted bat monitoring to assess these kinds of hypothesized effects of climate change.

Finally, urbanization and anthropogenic land cover change also must be considered as an additional risk for bats in parks, especially when keystone roosting structures are also lost. Despite the equivocal or subtle impacts of urbanization on contemporary bat faunas in parks apparent from our study and others (Johnson et al. 2008, Loeb et al. 2009) discussed in the previous section, many NPS units are likely to experience substantial land cover changes relative to current conditions (Fig. 5) in the coming decades as human populations in many park neighborhoods continues to grow (Svancara et al. 2009, Davis and Hansen 2011, Hansen et al. 2014). However, because there is some evidence that bats will persist in urban parks with structurally complex vegetation, especially forested parks, NPS units should be considered as potential refugia for bats in regions of the country where human land use pressure is high.

Conclusion: an energetics framework for strategic bat conservation in the NPS

There is strong theoretical and empirical support for the importance of the SER for bats (Wright 1983, Hawkins et al. 2003, Rodriguez and Arita 2004, McCain 2007), and growing evidence that energetics is a key contemporary factor for extinction risks among North American bats (Frick et al. 2015). Therefore, energetics emerges as a unifying conceptual framework for strategic bat conservation. The tight energy budgets of bats, especially in temperate regions, mean that they must procure large amounts of energy (e.g., insect consumption; Frick et al. 2010*b*) efficiently and conserve that energy in secure roosts (even in summer for the continental winter migrators). The availability of roosts has long been understood to be a primary driver of temperate-zone bat distributions (Humphrey 1975, Pierson 1998, Humphries et al. 2002, Kalcounis-Ruppell et al. 2005), and the conservation implications of this are evident. Furthermore, the high trophic position of bats, particularly temperate-zone insectivores, has been given as one of several reasons that bats are good bioindicators (Jones et al. 2009, Russo and Jones 2015).

Within this energetics context, our analysis, consolidated as a list of parks with bat resource attributes in Data S1, leads to a series of three tangible, intuitive steps that can be taken across the NPS and in other protected-area networks. First, it is clear that additional inventories of bats are needed in areas with high potential bat species richness and even in less speciose regions with rare and threatened taxa (e.g., within the range of the northern long-eared bat). Within the NPS, we identified 19 parks that showed (as of October 2015) zero bats present in NPSpecies but ≥10 species possible based on range maps. These discrepancies and others such as them offer a parsimonious and transparent way to allocate limited resources for surveys among parks. Importantly, many discrepancies can be resolved quickly by updating databases (e.g., NPSpecies) with records provided by recently completed surveys.

Second, the system of NPS parks and protected areas can serve as nodes for long-term status and trends monitoring programs, such as has been outlined by Loeb et al. (2015) and advocated for by others (Meyer 2015). Note that because the scale of nightly and seasonal movements of bats is so large, the information gained from monitoring within individual parks is much more limited than when many parks are assembled into a broader monitoring network using shared protocols, such as was envisioned by Loeb et al. (2015) and broadly reviewed by Kingston et al. 2016. The existing capacity of the NPS I&M Program (Fancy et al. 2009) is indicative of the important role for NPS in coordinated bat monitoring across the agency and with partner organizations. We suggest two possible approaches for developing coordinated monitoring among NPS park units and with partners outside the agency: (1) surveillance monitoring for net trends in regional populations as a contributing partner to the North American Bat Monitoring Program (NABat; Loeb et al. 2015) or similar program, and (2) targeted hypothesis-driven monitoring in smaller subsets of parks to address specific questions. Our study points to several potentially fruitful avenues of focused inquiry, and our maps of risk to land use conversion (Fig. 5), WNS (Fig. 6), wind turbine collision (Fig. 7), and climate change

(Fig. 8) provide testable hypotheses. For example, WNS-effects monitoring could be developed in parks identified as being at risk of the disease within 10 yr and also in parks outside that zone as controls. It is also possible that the two monitoring approaches, surveillance and hypothesis-driven, could be integrated into a service-wide bat monitoring strategy (Nichols and Williams 2006). In general, because of the diffuse impacts of specific stressors (e.g., migrating bats killed at wind farms come from very large "catchment areas"; Baerwald et al. 2014), the net effects on bat populations will likely be best quantified via these kinds of proposed large-scale monitoring strategies.

Third, conservation and resource protection measures can be prioritized so that limited resources can be directed to parks with the most important bat resources. Within the energetics framework, NPS can use the attributed list of parks in Data S1 to begin this prioritization. Parks with high species richness, rare or under-represented species, and underground habitat features are likely candidates for focus, although we hasten to add that there are other potential considerations, such as low-diversity parks that provide critical habitat for rare species or unique populations (e.g., range margins), or other cases where multiple parks in the network effectively scale up bat conservation by coordinating their management and protection for one or more shared species. Other important information about roost availability, including inventories of old buildings and tree snags (standing dead and decaying trees), would enhance the effort, as many bat species are also dependent on these features for energy conservation during roosting and hibernation (Pierson 1998). In general, it is evident that a service-wide conservation strategy to protect important roost structures, so-called keystone structures (sensu Tews et al. 2004, Rodhouse et al. 2015), across parks with high value to bat conservation is warranted. Such a strategy is consistent with the "preserve and protect" NPS mission (Fancy et al. 2009) and can be seen as mitigation or resiliency-building against outside-in environmental changes that the NPS will not be able to prevent from occurring within its park boundaries. But our analysis has shown that many NPS parks share not only the same acute and growing bat conservation challenges, but also many emergent opportunities for leveraging resources and expertise around these shared challenges. Given the importance of bat welfare to society (Boyles et al. 2011, Kunz et al. 2011), NPS, as a public steward, has a growing role to play in American bat conservation in the coming decades.

Acknowledgments

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