



Establishing conservation baselines with dynamic distribution models for bat populations facing imminent decline

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ABSTRACT

Aim Bat mortality rates from white-nose syndrome and wind power development are unprecedented. Cryptic and wide-ranging behaviours of bats make them difficult to survey, and population estimation is often intractable. We advance a model-based framework for making spatially explicit predictions about summertime distributions of bats from capture and acoustic surveys. Motivated by species-energy and life-history theory, our models describe hypotheses about spatio-temporal variation in bat distributions along environmental gradients and life-history attributes, providing a statistical basis for conservation decision-making.

Location Oregon and Washington, USA.

Methods We developed Bayesian hierarchical models for 14 bat species from an 8-year monitoring dataset across a ~430,000 km² study area. Models accounted for imperfect detection and were temporally dynamic. We mapped predicted occurrence probabilities and prediction uncertainties as baselines for assessing future declines.

Results Forest cover, snag abundance and cliffs were important predictors for most species. Species occurrence patterns varied along elevation and precipitation gradients, suggesting a potential hump-shaped diversity–productivity relationship. Annual turnover in occurrence was generally low, and occurrence probabilities were stable among most species. We found modest evidence that turnover covaried with the relative riskiness of bat roosting and migration. The fringed myotis (*Myotis thysanodes*), canyon bat (*Parastrellus hesperus*) and pallid bat (*Antrozous pallidus*) were rare; fringed myotis occurrence probabilities declined over the study period. We simulated anticipated declines to demonstrate that mapped occurrence probabilities, updated over time, provide an intuitive way to assess bat conservation status for a broad audience.

Main conclusions Landscape keystone structures associated with roosting habitat emerged as regionally important predictors of bat distributions. The challenges of bat monitoring have constrained previous species distribution modelling efforts to temporally static presence-only approaches. Our approach extends to broader spatial and temporal scales than has been possible in the past for bats, making a substantial increase in capacity for bat conservation.

Keywords

Bayesian hierarchical model, Chiroptera, keystone structures, life history, spatio-temporal variation, species distribution modelling, species-energy theory, trend, turnover.

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INTRODUCTION

Bats face acute threats throughout the world and many species face elevated extinction risk (Jones *et al.*, 2003; Safi & Kerth, 2004). In North America, disease and energy development are impacting numerous bat species. Several million bats are estimated to have died from white-nose syndrome (WNS) since 2006 (COSEWIC, 2013; USFWS, 2013), triggering rapid changes in bat conservation priorities in the USA and Canada. Species thought to be widespread and at low risk to decline prior to the incursion of WNS now face non-trivial extinction probabilities (Frick *et al.*, 2010), are listed as endangered in Canada and have been considered for protection under the US Endangered Species Act (COSEWIC, 2013; USFWS, 2013). The spread of WNS throughout eastern North America and Canada is expected to continue across much of the continent (Maher *et al.*, 2012). Annual bat mortalities associated with wind turbines number in the thousands (Arnett *et al.*, 2008; Arnett & Baerwald, 2013). Hayes (2013) estimated 600,000 turbine-related bat deaths occurred in the United States in 2012 (but see Huso & Dalthorp, 2014). Cumulative impacts of WNS and habitat loss are apparent for some species (Thogmartin *et al.*, 2012). Accelerated climate change is expected to exacerbate these impacts (e.g. Adams, 2010).

These novel stressors are outpacing the slow life-history traits of bats, characterized by low adult mortality, remarkable longevity (e.g. > 30 years, Fenton & Barclay, 1980) and low fecundity (Barclay & Harder, 2003). These traits are associated with the evolutionarily successful strategies of flight and hibernation, yet now make them vulnerable to wind power turbines and WNS. Species formerly thought to be widespread and at low risk to decline such as the hoary bat (*Lasiurus cinereus*) and little brown myotis (*Myotis lucifugus*) are particularly vulnerable (Arnett *et al.*, 2008; Frick *et al.*, 2010), accelerating the need for improved ways to assess the status of bat populations at appropriately broad regional and range-wide scales (Jones *et al.*, 2009; Meyer, 2015). The cryptic and wide-ranging nature of bats makes them difficult to survey, and population abundance estimation remains intractable for most species (Hayes *et al.*, 2009). However, summertime distributions of bats based on occupancy metrics can be described from regional capture and acoustic surveys that, when repeated over time, provide trend information fundamental to conservation assessments and for modelling spatio-temporal variation in bat distributions.

Bat species distribution modelling has primarily described habitat associations with temporally static presence-only datasets (Jaberg & Guisan, 2001; Milne *et al.*, 2006; Bellamy *et al.*, 2013). While such models have identified associations of bats with landscape features such as forest cover, they lack the ability to investigate temporal dynamics (e.g. trend) and other important sources of variation, including detectability (Yackulic *et al.*, 2013). Recent development of monitoring

programmes in North America, Europe and elsewhere that repeatedly deploy acoustic detectors and mist netting to survey sites dispersed across large geographic regions (e.g. Ormsbee *et al.*, 2006; Barlow *et al.*, 2015; Loeb *et al.*, 2015) creates opportunities to employ more sophisticated dynamic perspectives on bat distributions using occupancy models (Rodhouse *et al.*, 2012). These programmes are being designed with increased statistical sophistication to improve the scope of inference (Rodhouse *et al.*, 2011; Loeb *et al.*, 2015) and to account for challenges such as imperfect detection (Rodhouse *et al.*, 2012; Clement *et al.*, 2014). This enhances our capacity to address conservation questions about range shifts, latent population declines and their biogeographic covariates.

We used an 8-year monitoring dataset generated from capture and acoustic surveys across Oregon and Washington, USA, to develop temporally dynamic Bayesian hierarchical distribution models for 14 species of bats. Our fundamental objective was to establish species-specific baselines of predicted occurrence probabilities, accounting for imperfect detection and annual turnover, against which future declines can be evaluated and communicated with maps. We motivated our modelling from two bodies of theory particularly relevant to bats: species-energy theory and life-history theory. From species-energy theory, the 'more individuals hypothesis' holds that occurrence probabilities of a species will be higher in areas where 'energy', in the form of resources (e.g. primary production) important for individual survival and reproduction, is more abundant (Wright, 1983; Evans *et al.*, 2005). Temperate-region Vespertilionidae are constrained by tight energy budgets (McNab, 1980; Humphries *et al.*, 2002; Barclay & Harder, 2003), and summertime distribution and abundance depend on the ability of individual bats to efficiently procure large amounts of high-energy invertebrate prey and to conserve that energy in thermally stable (e.g. cliffs vs. foliage) roosts (Humphrey, 1975; Humphries *et al.*, 2002). We modelled occurrence patterns along gradients of landscape features associated with 'keystone structures' (*sensu* Tews *et al.*, 2004) used for roosting (large diameter snags and cliffs) and that represent habitat heterogeneity (landscape rugosity) and available environmental energy (elevation and precipitation).

Motivating our choice of dynamic model, we hypothesized that annual turnover in occurrence will generally be low because of the invariably slow life-history strategies of the studied species and because of fidelity to foraging and roosting areas reported for several of the studied species (Lewis, 1995; Barclay & Brigham, 2001; Rodhouse & Hyde, 2014). We also tested the hypothesis that turnover would covary with the relative riskiness of the species' roosting and wintering strategies. We were particularly interested in the potential for higher rates of turnover for tree-roosting and migratory species compared to locally hibernating species and those that use more secure roosts such as rock features. We used the estimated dynamic model parameters to simulate a

hypothetical decline for the little brown myotis using a conservative rate of potential decline relative to recent reports (Frick *et al.*, 2010). We simulated this decline while incorporating estimated baseline interannual variation (turnover) and parameter uncertainty to demonstrate the utility of the modelling framework for evaluating anticipated declines to bats in the region.

METHODS

Bat survey data

We utilized mist-net and acoustic records for 14 (Table 1) of the 16 species of bats found in Oregon and Washington, USA, obtained during 2003–2010 from the ‘Bat Grid’ interagency bat monitoring program (Ormsbee *et al.*, 2006; Hayes *et al.*, 2009), following a standard protocol and described in detail by Rodhouse *et al.* (2012) and in Appendix S1 in Supporting Information. Detection histories were developed from field survey data collected within 241 of the 4500 total 10×10 km sample units (Fig. 1). Data were collected between 1 June and 15 September on nights where capture and recording efforts lasted ≥ 2 h. Surveyed sample units were typically visited 1–3 times per season (12 visits maximum). We excluded the Mexican free-tailed bat (*Tadarida brasiliensis*) and Keen’s myotis (*Myotis keenii*) because of their restricted ranges in the study region (Verts & Carraway, 1998; Hayes & Wiles, 2013).

Distribution models

We used the hierarchical occupancy modelling approach developed by Royle & Dorazio (2008), previously applied to a subset of the Bat Grid dataset (Rodhouse *et al.*, 2012), to

develop dynamic distribution models for 14 studied species. This approach uses a temporally autoregressive model structure that is convenient for making probabilistic inferences about species occurrence patterns over time. We include spatially explicit environmental predictors, enabling inferences about occurrence probabilities to be mapped across the entire region. The hierarchical approach also explicitly incorporates the detection process. We modelled the probability of occurrence as $\text{logit}(\psi_t) = a_t + b_t * z(i, t-1) + \beta_1 * X_1 + \dots + \beta_k * X_k$, in which ψ_t represents the occurrence probability in year t , $a_t + b_t * z(i, t-1)$ represents the autoregressive parameterization for colonization and survival probabilities of each sample unit $i = 1$ to n , and $\beta_1 * X_1 + \dots + \beta_k * X_k$ represent the additive effects of environmental predictors 1 to k associated with each sample unit on probability of occurrence. We modelled detectability as $\text{logit}(p_{ijt}) = \alpha_0 + \alpha_1 * \text{date}_{ijt} + \alpha_2 * \text{duration}_{ijt} + \alpha_3 * I(\text{acoustic}_{ijt})$, where p_{ijt} represents the probability of detection in sample unit i during survey j and year t , as a function of survey date, duration and method (i.e. an indicator variable for surveys when acoustic detectors were used). We expected that detectability would increase with the progression of summer, particularly as juveniles became volant, and would be higher during long survey duration and when acoustic detectors were employed.

We focused on ψ_{2010} , the probability of occurrence in 2010, for mapping baseline distributions. This was the final year represented in our analysis, and ψ_{2010} provided a dynamic view on the contemporary status of each species, conditioned on occurrence states of the previous 7 years. We estimated turnover as the probability of a previously unoccupied sampling unit becoming occupied (Royle & Dorazio, 2008). We estimated each of the seven annual step changes in occupancy with the growth rate, $\lambda_t = \psi_t / \psi_{t-1}$ (MacKenzie

Table 1 List of study species, species names and codes used in figures and appendices, and predictions from hypotheses about relative variation in turnover. Posterior mean of AUC (area under the curve of the receiver operating characteristic) model predictive performance measure is reported for 11 species (see Appendix S3 for full posterior distributions). The column for cliffs and canyons indicate published habitat association used to guide inclusion of this predictor in models for five species.

Species name	Species code	Common name	Turnover prediction	AUC	Cliffs canyons
<i>Myotis evotis</i>	MYEV	Western long-eared myotis	Low	0.76	Low
<i>Myotis thysanodes</i>	MYTH	Fringed myotis	High	0.76	Moderate
<i>Myotis lucifugus</i>	MYLU	Little brown myotis	Low	0.78	Low
<i>Myotis volans</i>	MYVO	Long-legged myotis	High	0.69	Low
<i>Myotis ciliolabrum</i>	MYCI	Western small-footed myotis	Low	0.67	High
<i>Myotis californicus</i>	MYCA	California myotis	High	0.74	Low
<i>Myotis yumanensis</i>	MYYU	Yuma myotis	Low	0.90	Low
<i>Lasiomyotis noctivagans</i>	LANO	Silver-haired bat	High	0.72	Low
<i>Lasiurus cinereus</i>	LACI	Hoary bat	High	0.75	Low
<i>Antrozous pallidus</i>	ANPA	Pallid bat	Low	NA	High
<i>Eptesicus fuscus</i>	EPFU	Big brown bat	Low	0.65	Low
<i>Parastrellus hesperus</i>	PAHE	Canyon bat	Low	0.95	High
<i>Corynorhinus townsendii</i>	COTO	Townsend’s big-eared bat	Low	NA	Low
<i>Euderma maculatum</i>	EUMA	Spotted bat	Low	NA	High

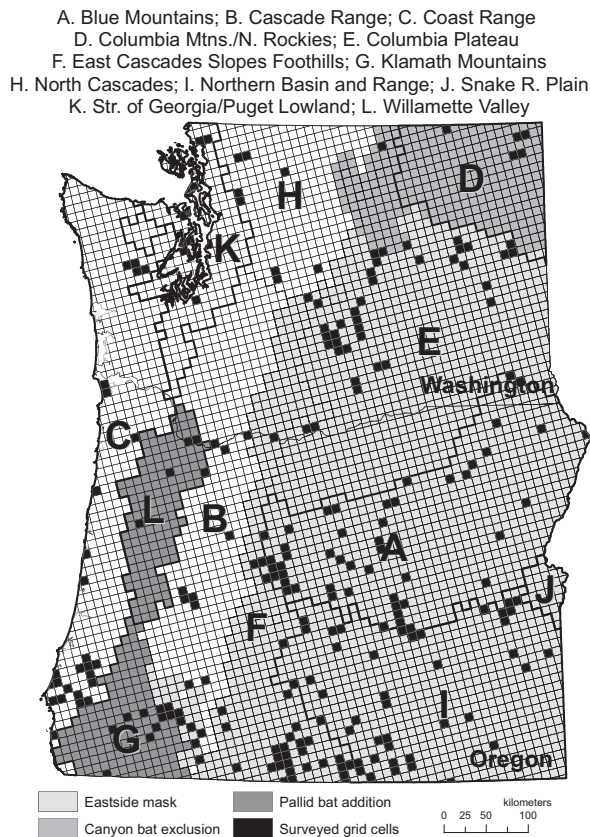


Figure 1 Study area and 241 surveyed sample units, with ecoregions and masks used for four range-restricted desert species.

et al., 2006) and overall trend as the total proportional (net) change in the probability of occurrence over the study period, ψ_{2010}/ψ_{2003} ($\lambda_{2010/2003}$). To evaluate the predictive performance of models, we used leave-one-out cross-validation and estimated the area under the curve (AUC) of the receiver operating characteristic (Fielding & Bell, 1997; Ntzoufras, 2009). Additional details, including an exploration of spatial autocorrelation, model fitting and evaluation of model predictive performance, are provided in Appendix S1.

Environmental predictors

We developed direct or proxy measures of roosting habitat availability and habitat heterogeneity and available environmental energy to include as prediction covariates using a geographic information system (GIS; Appendix S2). Previous studies have consistently found landscape-scale environmental attributes aggregated to coarse-scale units of analysis (e.g. using a GIS) to be meaningful predictors of bat distributions (Jaberg & Guisan, 2001; Milne *et al.*, 2006; Sattler *et al.*, 2007; Rodhouse *et al.*, 2012). We assembled datasets representing elevation, topographic rugosity ('roughness'), precipitation, forest and cliff land cover, and large diameter snag abundance; the latter two being particularly important keystone structures used for roosting and pup-rearing by many

bats in the region (Verts & Carraway, 1998; Hayes, 2003). We used roughness to represent habitat heterogeneity, and elevation and precipitation as measures of productivity. In our region, precipitation and forest cover are highly correlated with net primary productivity ($\rho = 0.7$; Rodhouse *et al.*, 2012) although only moderately correlated with each other ($\rho = 0.5$). Elevation is negatively correlated with productivity ($\rho = -0.5$). We included the cliffs and canyons predictor for five species, drawing on published habitat associations (Table 1; Verts & Carraway, 1998). Because forest cover and snag abundance datasets were correlated, we included these covariates in separate models, fitting snag models only for those species in which forest cover was first estimated to be an influential covariate. Caves and mines are also important keystone structures; in our study, only one species (Townsend's big-eared bat [*Corynorhinus townsendii*]) is an obligate of these features (Verts & Carraway, 1998). We attempted to compile a GIS dataset but found that these features have not been reliably mapped in our region.

We used land cover data from the Northwest Gap Analysis Program (GAP) 30-m resolution land cover map to develop per cent cover of forests and cliffs and canyons for each sample unit (GAP, 2008). For forest cover, we aggregated areas mapped by GAP as 'forest and woodland systems' and summarized each sample unit by per cent forest and woodland cover. For cliffs and canyons cover, we aggregated areas mapped in GAP, level 2 as 'sparse and barren systems' that also were mapped as 'cliff, canyon and talus' and summarized each sample unit by per cent cliffs and canyon cover. We developed our snag abundance predictor from a 30-m resolution forest structure dataset created for the study region (LEMMA, 2014; Ohmann & Gregory, 2002). From this dataset, we calculated mean density of snags ≥ 25 cm diameter per hectare for each sample unit. We used a US Geological Survey 10-m digital elevation model to calculate sample unit mean elevation and standard deviation of elevation for topographic roughness. We calculated mean annual precipitation for each sample unit from the grand mean of 800-m resolution annual precipitation totals over the 8-year study period (PRISM, 2015; Daly *et al.*, 2008).

Four arid-land species (canyon bat [*Parastrellus hesperus*], pallid bat [*Antrozous pallidus*], spotted bat [*Euderm maculatum*] and small-footed myotis [*Myotis ciliolabrum*]) have ranges restricted or primarily restricted to east of the Cascade Range where such habitat predominates (Verts & Carraway, 1998). We created a mask from the GAP level 1 ecoregions to constrain our analyses to better match the established ranges of these species (Fig. 1). We included a portion of the southern Cascades ecoregion where these species are known to occur (Verts & Carraway, 1998). We also included the Klamath Mountains and Willamette Valley ecoregions west of the Cascade Range for the pallid bat (Verts & Carraway, 1998). The range of the canyon bat was reduced in NE Washington where the species does not occur, following county boundaries described by Hayes & Wiles (2013).

Decline simulations

Because the little brown myotis has experienced a dramatic increase in extinction risk in eastern North America as a result of WNS (Frick *et al.*, 2010; COSEWIC, 2013) and is the only species in our study currently affected by the disease, we used our model of the little brown myotis to simulate a 10% annual rate of decline. This is a relatively conservative scenario for the potential WNS effect on this species (Frick *et al.*, 2010). We simulated 100 10-year detection history matrices with sample size $n = 241$ and 4 within-season revisits, using 100 draws from parameter posterior distributions obtained from the initial fitted model. We imposed a deterministic decline by multiplying the estimated recolonization and survival rate parameters, a_t and b_t , by 0.9 for each of the 10 simulated years. Figure 2 shows how parameter uncertainty and the background 'noise' of annual turnover rates contributed from a_t and b_t were manifest in simulations. We then fit the dynamic hierarchical occupancy model to each of the 100 simulated detection history matrices to estimate trend and map predictions for comparison with the current baseline distribution map.

RESULTS

Rarity and commonness

Raw encounter patterns varied widely among species, reflecting the relative rarity and commonness of species, success of

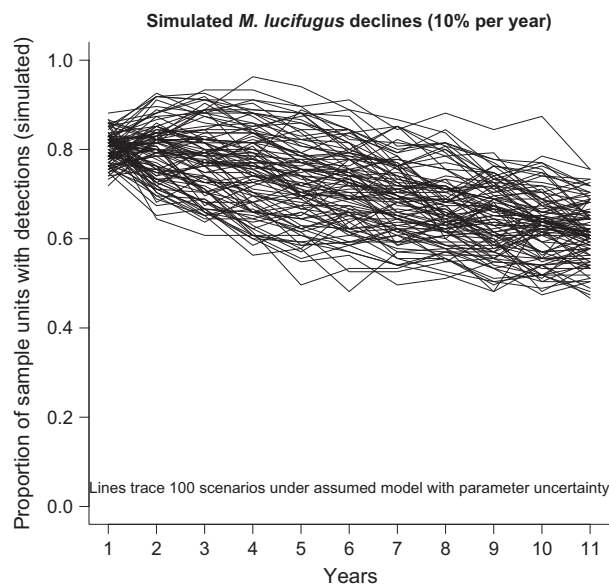


Figure 2 Simulated declines in little brown myotis occurrence probabilities over 10 years. The Bayesian approach provided a natural way to incorporate parameter uncertainty by drawing from parameter posterior distributions for each of the iterations. The autoregressive model structure provided background 'noise' reflecting annual turnover estimates.

survey methods and model performances. The spotted bat, Townsend's big-eared bat and pallid bat were so infrequently encountered that we did not generate predictive maps for them. Predictive performances of models for the remaining 11 species, as measured by the posterior mean estimates of AUC, ranged from 0.65 to 0.95, lowest for the big brown bat (*Eptesicus fuscus*) and highest for the Yuma myotis (*Myotis yumanensis*) and canyon bat (Table 1 and Appendix S3). Among species, the probability of detection within a nightly survey > 2 h in duration was invariably low (< 0.50), but relatively precisely estimated (e.g. $SD < 0.10$; Fig. 3a). Detectability was lowest for the pallid bat (Fig. 3a). The mean estimated effect sizes for survey date on detectability were near 0 for all species (Appendix S4). Similar patterns were found in the estimates for the influence of survey duration as well (Appendix S4). Predictably (having been investigated by Rodhouse *et al.*, 2012), the influence of acoustic survey method was clearly positive for all species except for 5, including the 'whispering' Townsend's big-eared bat, for which acoustic methods did not appreciably contribute to detectability (Fig. 3b).

Our predictive distribution maps indicated that most of the 11 mapped species were widespread (Appendix S5). Prediction errors were generally inversely correlated with occurrence probabilities (Appendix S5). Intuitively, model prediction uncertainty was highest where species occurrences

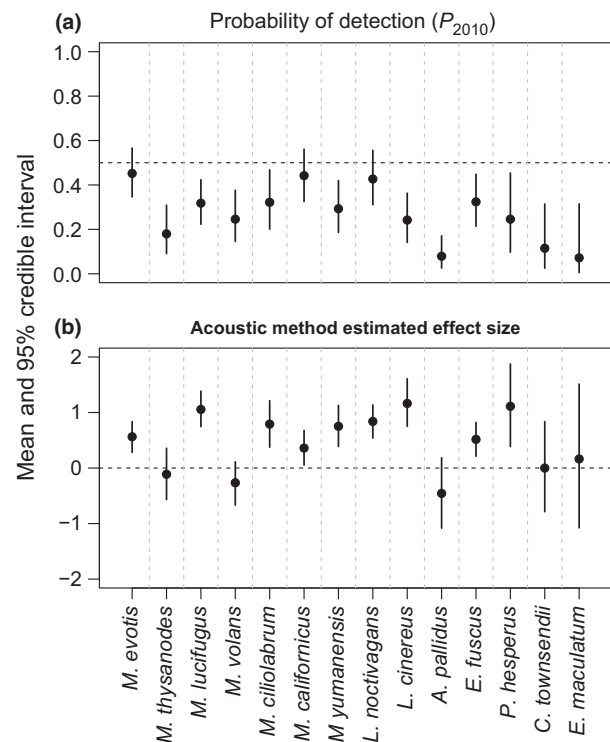


Figure 3 Estimated posterior means and 95% CIs for (a) probability of detection in 2010 and (b) the estimated effect size of acoustic survey method on detectability (see Appendix S4 for additional predictors).

were lowest and least predictable. Region-wide rarity is evident for two mapped species, canyon bat and fringed myotis, in which detection probabilities and model performances were acceptable (Fig. 3a and Table 1) but probability of occurrence was low and patchily distributed (Fig. 4).

Biogeographic insights

Keystone roosting structures

Our models underscored the biogeographic importance of landscape keystone structures to bats in the region and revealed patterns of regional faunal assembly (Fig. 5 and Appendix S5). Forest cover was a positive predictor of occurrence for 12 species and strongly influential in models for six species (Fig. 5a). Of those, results for the silver-haired bat (*Lasionycteris noctivagans*), long-legged myotis (*Myotis volans*) and California myotis (*Myotis californicus*) also showed very strong evidence for an association with snag abundance (Table 2). Probabilities of occurrence for these species increased > 7 times ($\exp^{2.0}$) for each SD increase in

snag abundance. All seven species that were modelled along the snag abundance gradient showed at least a modestly positive association (Table 2), providing compelling evidence of the importance of snags, and forest cover more generally, to the biogeography of bats in the region. The abundance of canyons and cliffs was positively associated with occurrence probabilities for the cliff-obligate arid-land species, as expected, but not for fringed myotis (Fig. 5b).

Habitat heterogeneity and environmental energy

The inclusion of elevation and precipitation in models were also revealing. Occurrence probabilities of the long-eared myotis, long-legged myotis and small-footed myotis were positively influenced by elevation, whereas most other species were negatively associated with elevation (Appendix S4). Precipitation was a modest negative influence for most species, with notable positive exceptions for long-eared myotis, little brown myotis and California myotis. Roughness was generally not influential in models, although occurrence of Townsend's big-eared bat was strongly positively influenced by

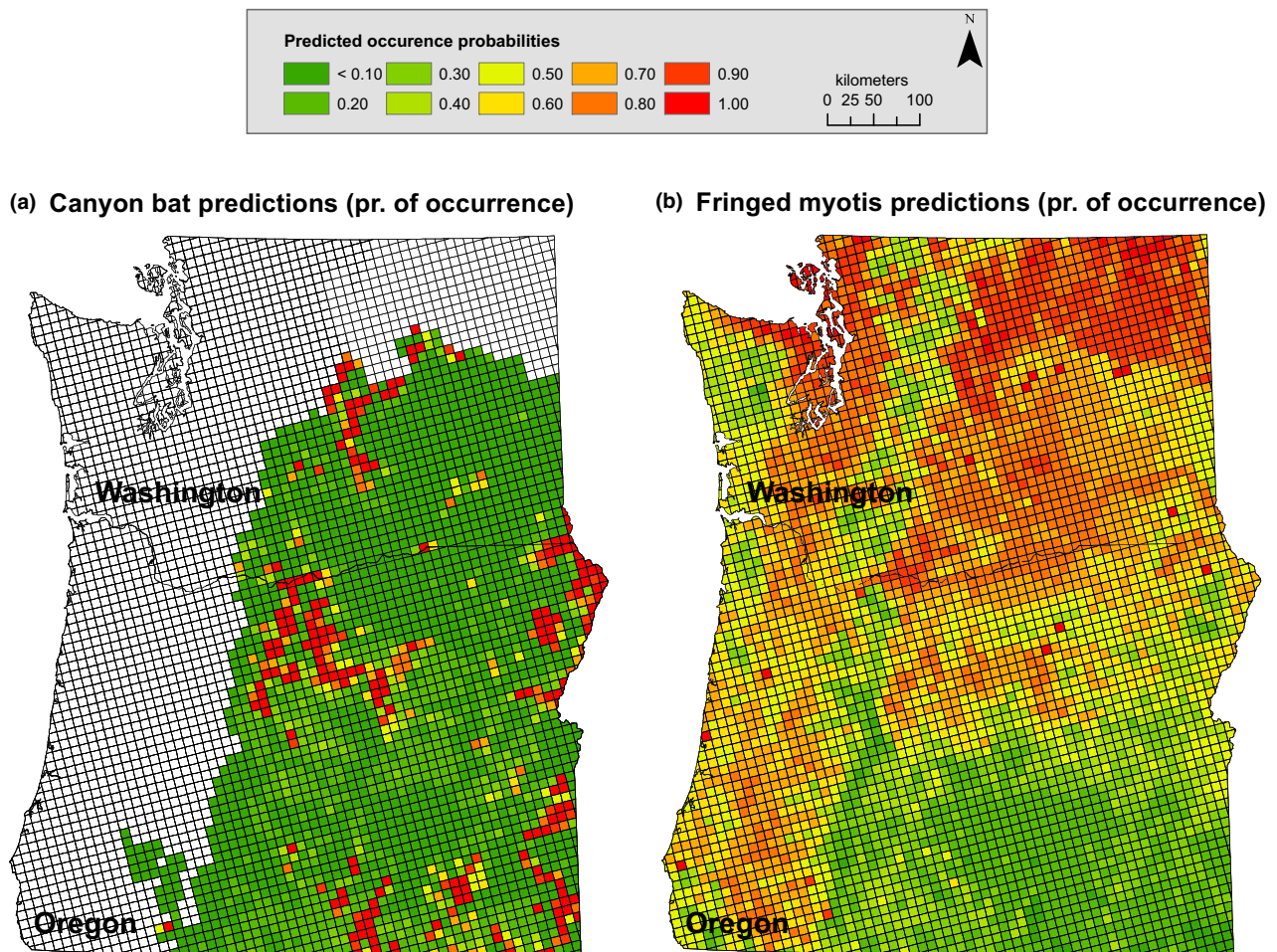


Figure 4 (a) Canyon bat predicted distribution map. Sample units outside the current geographic range of this species (eastside mask and canyon bat exclusion in Fig. 1) were removed from the dataset for this species. (b) Fringed myotis predicted distribution map.

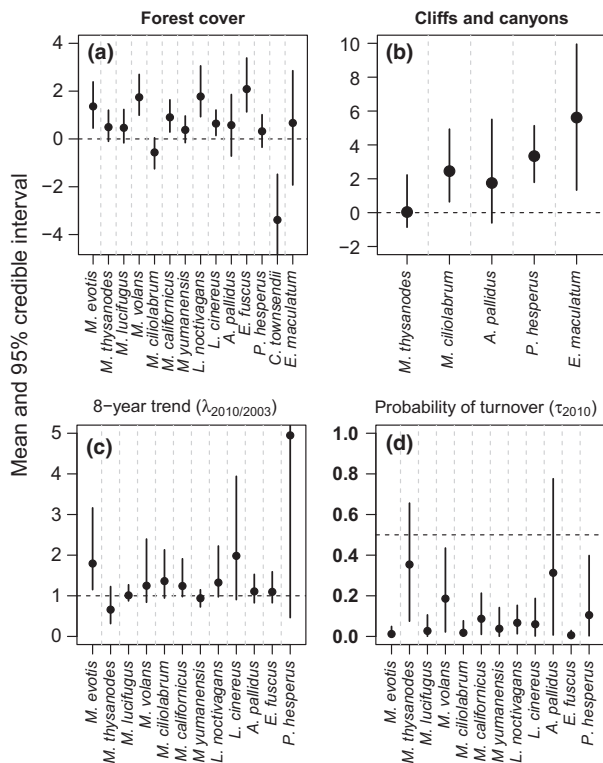


Figure 5 Estimated posterior means and 95% CIs for effect sizes of (a) forest and (b) canyons and cliffs cover on occurrence, (c) trend ($\lambda_{2010/2003}$) and (d) 2010 turnover probability (see Appendix S4 for additional predictors).

elevated roughness, possibly reflecting the species affinity with caves and mines.

Trends and turnover

Our measure of net trend over the study period (Fig. 5c) revealed flat or slightly positive trends among most species; yearly step trends (λ_t ; results not shown) provided similar evidence, with most estimates ~ 1 or > 1 but with low precision. Exceptions included the high but imprecise positive trend for the canyon bat and positive trends for the long-eared myotis and hoary bat (Fig. 5c). The fringed myotis is the only species that showed a decline in occurrence (Fig. 5c). Turnover was also low among many species but variable (Fig. 5d). The lowest and most precise estimates were for the long-eared myotis, little brown myotis, small-footed myotis, Yuma myotis and big brown bat. We did not achieve adequate model performance to generate meaningful estimates of turnover and trend for the spotted bat and Townsend's big-eared bat, excluded from Fig. 5(c,d).

Decline simulations

Simulation of a steady deterministic (e.g. from extrinsic forces such as WNS) 10% annual rate of decline for the little brown myotis over 10 years resulted in clearly evident

reduced occurrence probabilities against the backdrop of estimated baseline annual turnover and parameter uncertainty (Fig. 6). Ninety-two per cent of simulation iterations drawn from parameter posterior distributions (Fig. 2) resulted in an upper 95% credible interval for trend < 1.0 .

DISCUSSION

We developed geographically extensive dynamic summertime distribution models for 14 species of bats using a Bayesian hierarchical approach that accounted for imperfect detection and temporal non-stationarity (Royle & Dorazio, 2008). We used these models to predict and map occurrence probabilities and prediction uncertainties for 11 of these species along environmental gradients representing keystone roost structure and resource availability. The challenges of bat monitoring have constrained previous modelling efforts to temporally static presence-only modelling (e.g. Jaberg & Guisan, 2001), but in this study, drawing on an extensive monitoring dataset, we advanced the application of species distribution and occupancy modelling frameworks to much broader spatial and temporal scales than has been possible in the past for bats. Our approach represents a substantial increase in capacity for bat conservation efforts, particularly as developing bat monitoring programmes provide much needed data to fuel similar analyses across broader regions of North America (Loeb *et al.*, 2015) and on other continents (Barlow *et al.*, 2015). The ability to integrate and test hypotheses motivated by an understanding of the taxon's unique energetic constraints is a particularly appealing aspect of the approach, explicitly linking evolutionary and ecological theory to bat conservation via distribution models (Guisan & Thuiller, 2005). Our model performances and prediction uncertainties indicate the need for cautious inferences about some species and point to opportunities for future improvements. Nonetheless, important ecological insights were revealed from models, even for the rarest and most infrequently encountered species, and we present our set of probabilistic range maps (Appendix S5) and accompanying maps of prediction uncertainty as conservation baselines that can be updated over time as new data become available (e.g. Fig. 6); the Bayesian inferential paradigm provides a conceptually straightforward way for doing so.

The species we investigated are widespread in western North America and existing range maps are static and uninformative about the spatio-temporal variation within range boundaries. Assessments of species rarity and commonness for bats within our study area have historically been based largely on local, small-sample studies and anecdote (Verts & Carraway, 1998; Hayes & Wiles, 2013). The autoregressive 1st-order Markov structure of our models makes our maps explicitly dynamic, with mapped probabilities of occurrence in 2010 conditional on probabilities estimated in prior years. Other results can be mapped as well, for example, for earlier study years or dynamic parameters (e.g. sample unit survival and extinction probabilities), although occurrence

Table 2 Comparison of parameter estimates (mean and 95% credible intervals) for distribution models of seven forest-associated species in Oregon and Washington that included either % forest cover or snag density covariates. Snag models with substantially lower (e.g. < 2) deviance information criterion (DIC; Spiegelhalter *et al.*, 2002) and with substantial increases in the magnitude of coefficient estimates are suggestive of a strong relationship between patterns of bat species distribution and snag density across the study region. Three species, silver-haired bat (LANO), California myotis (MYCA) and long-legged myotis (MYVO), show a particularly strong relationship to snag density, consistent with findings from previous telemetry-based studies. Compelling evidence is also evident for long-eared myotis (MYEV) and big brown bat (EPFU).

	Forest cover model				Snag density model			
	DIC	Mean	2.5%	97.5%	DIC	Mean	2.5%	97.5%
<i>Myotis evotis</i>	2125	1.36	0.45	2.38	2143	2.55	1.17	4.24
<i>Myotis thysanodes</i>	1288	0.49	-0.09	1.20	1286	0.45	-0.06	1.06
<i>Myotis lucifugus</i>	2093	0.46	-0.16	1.20	2092	0.55	-0.42	1.80
<i>Myotis volans</i>	1562	1.74	0.99	2.69	1432	3.08	1.80	4.61
<i>Myotis californicus</i>	1940	0.90	0.28	1.60	1920	2.15	0.77	3.80
<i>Lasionycteris noctivagans</i>	2413	1.77	0.93	3.06	2338	2.30	0.99	4.00
<i>Eptesicus fuscus</i>	2042	2.08	1.13	3.40	2086	2.50	0.98	4.40

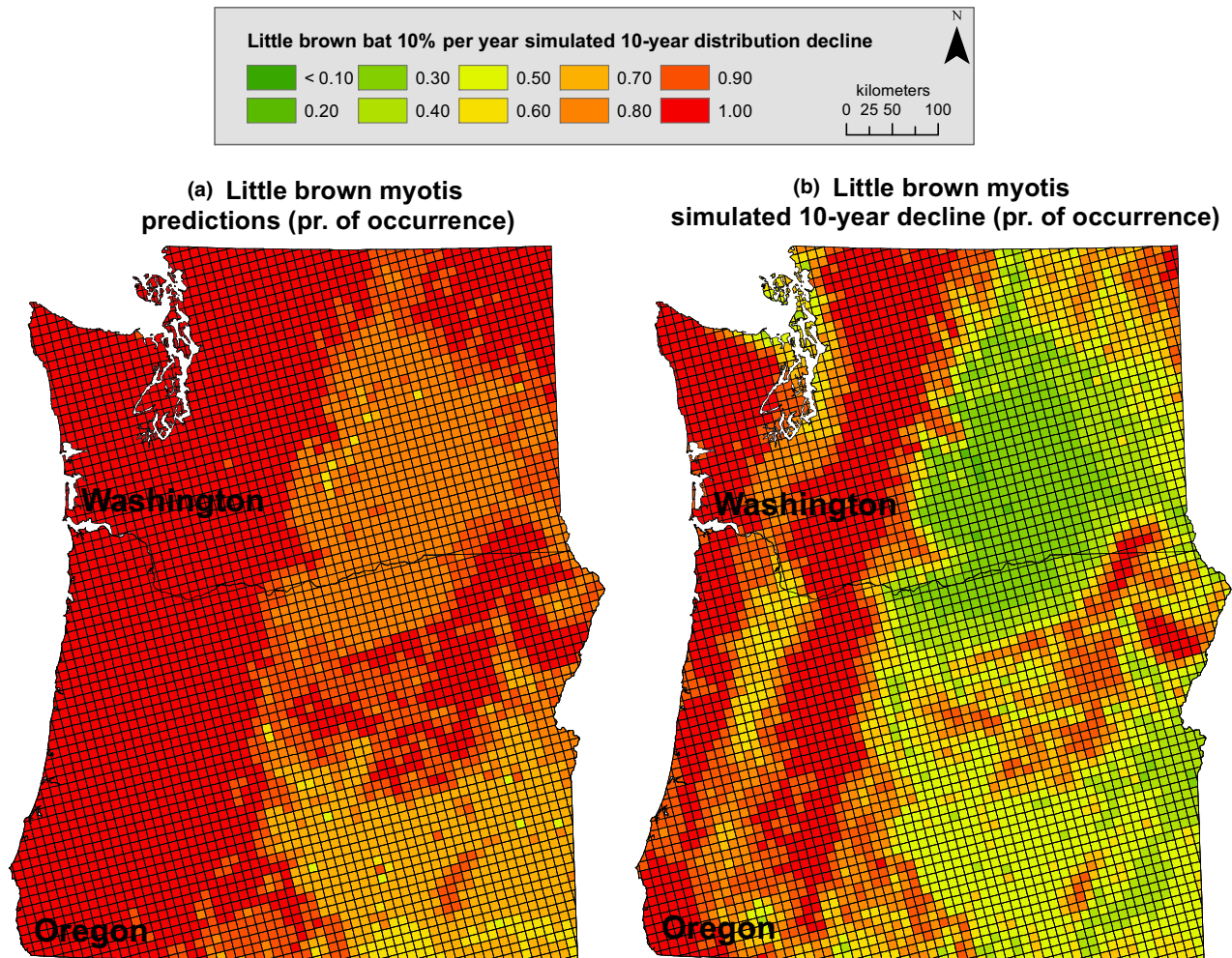


Figure 6 (a) Contemporary little brown myotis predicted distribution and (b) a contrasting scenario of simulated predicted distribution probabilities after imposing a 10% year⁻¹ decline over 10 years. This map is just one realization of the 100 posterior predictions examined in this study (Fig. 2).

probabilities of the most recent year available are the most intuitive and relevant.

Our maps align with prior belief (e.g. Verts & Carraway, 1998; Hayes & Wiles, 2013) that the majority of species appear to be widespread and common across the region. However, after accounting for imperfect detection and biogeographic influences, estimated occurrence probabilities for species such as the big brown bat and Yuma myotis, presumed to be omnipresent, exhibited consistent patterns of spatial variation along environmental gradients (e.g. availability of roosting habitat (Humphrey, 1975) and productivity (McCain, 2007; Rodhouse *et al.*, 2012)).

The canyon bat and fringed myotis were the rarest among the suite of mapped species. The canyon bat is strongly associated with the desert canyons of eastern Oregon and south-eastern Washington (Verts & Carraway, 1998; Hayes & Wiles, 2013), and our model reflected this in the very steep gradient of mapped occurrence probabilities, from near certain occurrence along the major cliff and canyon complexes to near certain absence elsewhere (Fig. 4a). Our model for the fringed myotis described the species as being associated with low- to moderate-elevation dry forestlands, particularly in Washington's Mountains and Plateau regions and in Oregon's Blue and Klamath Mountains (Fig. 4b). A band of high occurrence probabilities was also estimated for the Olympic Mountains' rain shadow region in Washington's Puget Lowland (Fig. 4b). This description is consistent with the fringed myotis species accounts from Oregon (Verts & Carraway, 1998) and Washington (Hayes & Wiles, 2013), although our model predicts higher occurrence probabilities in western Washington than is indicated by county records summarized by Hayes & Wiles (2013).

Three species, the spotted bat, Townsend's big-eared bat and pallid bat, were so infrequently encountered that detection history matrices were too sparse to develop reliable predictive models. The Townsend's big-eared bat and spotted bat are difficult to catch and record (Rodhouse *et al.*, 2005; WBWG, 2005), and it was not surprising that the omnibus methods employed in our study were not effective. The results for the pallid bat were surprising, however. This species is readily captured and recorded, making the sparse pallid bat encounter history conspicuous and concerning. The species was not encountered west of the Cascade Range, where it was historically found, during our study and in other recent surveys (e.g. Weller, 2008).

The pattern of forested versus non-forested lands emerged as a particularly distinct driver of bat community assembly in the region. A large suite of otherwise widespread species had lower occurrence probabilities in xeric south-eastern Oregon and Columbia Plateau of south-eastern Washington (Appendix S5). The majority of these species were more likely to occur in forested landscapes (Fig. 5a). Of these, the California myotis, silver-haired bat and long-legged myotis were also strongly associated with abundances of large diameter snags, as were long-eared myotis and big brown bat (Table 2). This is consistent with telemetry studies of these

same species that have documented dependence on snags for maternity colonies (Ormsbee & McComb, 1998; Barclay & Brigham, 2001; Arnett & Hayes, 2009; Lacki *et al.*, 2010). Our study brings a unique regional perspective to this relationship, adding evidence to the importance of snags as keystone structures (Tews *et al.*, 2004) and underscoring the conservation implications of snag retention and other forest management practices in the Pacific Northwest and elsewhere (Hayes, 2003).

Our models provided evidence of the importance of cliffs and canyon complexes to the four arid-land species in the region, although, surprisingly, this pattern was weaker than expected for the cliff-roosting pallid bat (Verts & Carraway, 1998). This may be a possible reflection of low detectability and model uncertainty or perhaps of broader niche breadth for this species (e.g. reports of snag roosting; Baker *et al.*, 2008). The aptly named canyon bat exhibited very tight association with the large canyon complexes in the region (Fig. 4a) as did the western small-footed myotis and spotted bat. These three species are well-established obligate cliff roosters (Luce & Keinath, 2007; Hayes & Wiles, 2013; Rodhouse & Hyde, 2014). We included the cliff and canyon covariate in the fringed myotis model because some studies have indicated an association (Lacki & Baker, 2007; Hayes & Wiles, 2013). Our results suggest no clear relationship with these features. Rather, regional plasticity in the species' summer roosting habits is likely a reflection of availability of suitable features (Verts & Carraway, 1998; Weller & Zabel, 2001; Lacki & Baker, 2007; Hayes & Wiles, 2013).

Elevation and precipitation patterns were moderately negative influences on occurrence probabilities, with few exceptions (e.g. long-eared myotis). This is an intriguing pattern and, when considered within the context of species-energy theory, suggests that bat species richness in the region follows a hump-shaped pattern, peaking at moderately productive conditions in a mix of forest (and snags) and rock habitat, especially east of the Cascade Range where historical constraints (i.e. geographic ranges) are not limiting. The hump-shaped pattern has been widely observed at regional scales similar to our study across a range of taxa (Rosenzweig & Abramsky, 1993) including for bats (McCain, 2007). Although we leave a more thorough investigation of patterns of richness for future work, the results of our study suggest the potential to identify the regional bat community assembly rules.

Because of 'slow' life-history traits and fidelity to roosting and foraging areas, annual changes in regional population size and hence in occurrence patterns are also likely slow in the absence of acute extrinsic sources of mortality such as WNS. Verifying this is of practical importance for conservation monitoring (Jones *et al.*, 2009), particularly in advance of the anticipated arrival of WNS (Maher *et al.*, 2012). As expected, our models provided estimates of low annual turnover in occurrence and flat trends in most of the 11 species examined. Encouragingly, several species showed modest increases in occurrence probabilities from 2003 to 2010, most

notably the long-eared myotis. The canyon bat and hoary bat showed notable increases but low precision made the magnitude of increase unclear. Only fringed myotis showed evidence of decline. Because this species was relatively uncommon throughout the region (Fig. 4b), we call attention to it, along with the pallid bat, as being potentially the most at risk based on our results.

We hypothesized that turnover rates among the studied species would covary with the relative 'riskiness' of species' roosting and migratory behaviours. We found modest evidence for such covariation. The lowest and most precise estimates of turnover were for species that ostensibly use more secure roosts and are less migratory: the long-eared myotis, little brown myotis, small-footed myotis, Yuma myotis and big brown bat. Species exhibiting higher turnover included the tree-roosting long-legged myotis and the rarest species. The migratory species hoary bat and silver-haired bat were estimated with moderate rates of turnover of indeterminate biological significance due to lower precision. Sample size limitations and imprecision require our results to be interpreted cautiously (McKann *et al.*, 2013), but our results suggest this topic warrants further study.

Against annual background fluctuation represented in our turnover estimate, our 10-year simulation for the little brown myotis showed evident decline in occurrence probability (Fig. 6) and 92% of iterations from parameter posteriors provided upper 95% credible intervals for trend < 1.0 (i.e. as declining). While not a statistical power analysis per se, our result, when placed within the context of bat life-history strategies and site fidelity, establishes a framework for doing so. Furthermore, this result suggests that further suggests that meaningful declines can be revealed from regional bat monitoring programmes, as recently found by Barlow *et al.* (2015). This is particularly likely if sufficient investments are made to increase the sample size and geographic extent of surveys. Monitoring programmes that can accommodate data contributions from a broad community of citizen scientists and partnering organizations is one strategy recommended to achieve this because resources can be leveraged and costs distributed broadly among partners (Ormsbee *et al.*, 2006; Barlow *et al.*, 2015; Loeb *et al.*, 2015; Meyer, 2015).

Our study demonstrates an integrated way to simultaneously address the concerns of monitoring and conservation as well as more fundamental questions about regional biogeography and community assembly. Although it does not resolve the ultimate need to acquire more quantitative estimates of abundance, the positive correlations between abundances and occurrences across many taxa (Holt *et al.*, 2002) add to the utility of monitoring to generate probabilistic distribution maps for bats, particularly for the 'overdispersed' species that do not congregate in large conspicuous colonies. Even though WNS and wind turbine collisions exert mortality outside of summer, summertime populations are most accessible in our study region and therefore monitoring them emerges as an effective way to assess net changes in populations resulting from these stressors. This is due in part to the

developing technology of ultrasound acoustic detection and recording, which will enable broader participation in monitoring (e.g. Barlow *et al.*, 2015; Meyer, 2015) and rapid accumulation of large datasets.

ACKNOWLEDGEMENTS

Funding for the Bat Grid was provided by the U.S. Forest Service, Bureau of Land Management, and Department of Defense Legacy Program. The National Park Service provided additional funding and support. We thank the contributors to the Bat Grid. L. Cousineau provided data management support. J. Hobson provided GIS support. J. Sauer provided helpful comments during preparation of this manuscript. Any use of trade, product, or firm names is for descriptive purposes only and does not imply endorsement by the U.S. Government.

REFERENCES

- Adams, R.A. (2010) Bat reproduction declines when conditions mimic climate change projections for western North America. *Ecology*, **91**, 2437–2445.
- Arnett, E.B. & Baerwald, E.F. (2013) Impacts of wind energy development on bats: implications for conservation. *Bat evolution, ecology, and conservation* (ed. by R.A. Adams and S.C. Pedersen), pp. 435–456. Springer, New York.
- Arnett, E.B. & Hayes, J.P. (2009) Use of conifer snags as roosts by female bats in western Oregon. *Journal of Wildlife Management*, **73**, 214–225.
- Arnett, E.B., Brown, K.W., Erickson, W.P., Fiedler, J.K., Hamilton, B.L., Henry, T.H., Jain, A., Johnson, G.D., Kerns, J., Koford, R.R., Nicholson, C.P., O'Connell, T.J., Piorkowski, M.D. & Tankersley, R.D. Jr (2008) Patterns of fatality of bats at wind energy facilities in North America. *Journal of Wildlife Management*, **72**, 61–78.
- Baker, M.D., Lacki, M.J., Falxa, G.A., Droppelman, P.L., Slack, R.A. & Slankard, S.A. (2008) Habitat use of pallid bats in coniferous forests of northern California. *Northwest Science*, **82**, 269–275.
- Barclay, R.M.R. & Brigham, R.M. (2001) Year-to-year reuse of tree-roosts by California bats (*Myotis californicus*) in southern British Columbia. *The American Midland Naturalist*, **146**, 80–85.
- Barclay, R.M.R. & Harder, L.D. (2003) Life histories of bats: life in the slow lane. *Bat ecology* (ed. by T.H. Kunz and M.B. Fenton), pp. 209–253. University of Chicago Press, Chicago.
- Barlow, K.E., Briggs, P.A., Haysom, K.A., Hutson, A.M., Lechiara, N.L., Racey, P.A., Walsh, A.L. & Langton, S.D. (2015) Citizen science reveals trends in bat populations: the national bat monitoring programme in Great Britain. *Biological Conservation*, **182**, 14–26.
- Bellamy, C., Scott, C. & Altringham, J. (2013) Multiscale, presence-only habitat suitability models: fine-resolution maps for eight bat species. *Journal of Applied Ecology*, **50**, 892–901.

- Clement, M.J., Rodhouse, T.J., Ormsbee, P.C., Szewczak, J.M. & Nichols, J.D. (2014) Accounting for false-positive acoustic detections of bats using occupancy models. *Journal of Applied Ecology*, **51**, 1460–1467.
- Committee on the Status of Endangered Wildlife in Canada (COSEWIC) (2013) *COSEWIC assessment and status report on the Little Brown Myotis Myotis lucifugus, Northern Myotis Myotis septentrionalis and Tri-colored Bat Perimyotis subflavus in Canada*. Committee on the Status of Endangered Wildlife in Canada. Ottawa. Available at: <http://www.registrelep-sararegistry.gc.ca/default.asp?lang=En&n=24F7211B-1> (accessed 18 August 2015).
- Daly, C., Halbleib, M., Smith, J.I., Gibson, W.P., Doggett, M.K., Taylor, G.H., Curtis, J. & Pasteris, P.P. (2008) Physiographically sensitive mapping of climatological temperature and precipitation across the conterminous United States. *International Journal of Climatology*, **28**, 2031–2064.
- Evans, K.L., Warren, P.H. & Gaston, K.J. (2005) Species-energy relationships at the macroecological scale: a review of the mechanisms. *Biological Reviews*, **80**, 1–25.
- Fenton, M.B. & Barclay, R.M.R. (1980) *Myotis lucifugus*. *Mammalian Species*, **142**, 1–8.
- Fielding, A.H. & Bell, J.F. (1997) A review of methods for the assessment of prediction errors in conservation presence/absence models. *Environmental Conservation*, **24**, 38–49.
- Frick, W.F., Pollock, J.F., Hicks, A.C., Langwing, K.E., Reynolds, D.S., Turner, G.G., Butchkowski, C.M. & Kunz, T.H. (2010) An emerging disease causes regional population collapse of a common North American bat species. *Science*, **329**, 679–682.
- Guisan, A. & Thuiller, W. (2005) Predicting species distribution: offering more than simple habitat models. *Ecology Letters*, **8**, 993–1009.
- Hayes, J.P. (2003) Habitat ecology and conservation of bats in western coniferous forests. *Mammal community dynamics in coniferous forests of western North America—management and conservation* (ed. by C.J. Zabel and R.G. Anthony), pp. 81–119. Cambridge University Press, London.
- Hayes, M.A. (2013) Bats killed in large numbers at United States wind energy facilities. *BioScience*, **63**, 975–979.
- Hayes, G. & Wiles, G.J. (2013) *Washington bat conservation plan*. Washington Department of Fish and Wildlife, Olympia, WA, USA.
- Hayes, J.P., Ober, H.K. & Sherwin, R.E. (2009) Survey and monitoring of bats. *Ecological and behavioral methods for the study of bats*, 2nd edn (ed. by T.H. Kunz and S. Parsons), pp. 112–129. Johns Hopkins University Press, Baltimore, MD, USA.
- Holt, A.R., Gaston, K.J. & He, F. (2002) Occupancy-abundance relationships and spatial distribution: a review. *Basic and Applied Ecology*, **3**, 1–13.
- Humphrey, S.R. (1975) Nursery roosts and community diversity of Nearctic bats. *Journal of Mammalogy*, **56**, 321–346.
- Humphries, M.M., Thomas, D.W. & Speakman, J.R. (2002) Climate mediated energetic constraints on the distribution of hibernating mammals. *Nature*, **418**, 313–316.
- Huso, M.M.P. & Dalthorp, D. (2014) A comment on “bats killed in large numbers at United States wind energy facilities”. *BioScience*, **64**, 546–547.
- Jaberg, C. & Guisan, A. (2001) Modelling the distribution of bats in relation to landscape structure in a temperate mountain environment. *Journal of Applied Ecology*, **38**, 1169–1181.
- Jones, K.E., Purvis, A. & Gittleman, J.L. (2003) Biological correlates of extinction risk in bats. *The American Naturalist*, **161**, 601–614.
- Jones, G., Jacobs, D.S., Kunz, T.H., Willig, M.R. & Racey, P.A. (2009) Carpe noctem: the importance of bats as bioindicators. *Endangered Species Research*, **8**, 93–115.
- Lacki, M.J. & Baker, M.D. (2007) Day roosts of female fringed myotis (*Myotis thysanodes*) in xeric forests of the Pacific Northwest. *Journal of Mammalogy*, **88**, 967–973.
- Lacki, M.J., Baker, M.D. & Johnson, J.S. (2010) Geographic variation in roost-site selection of long-legged myotis in the Pacific Northwest. *Journal of Wildlife Management*, **74**, 1218–1228.
- Landscape Ecology, Modeling, Mapping, and Analysis (LEMMA) (2014) *Gradient nearest neighbor structure maps*. Available at: <http://lemma.forestry.oregonstate.edu/> (accessed 18 August 2015).
- Lewis, S.E. (1995) Roost fidelity of bats: a review. *Journal of Mammalogy*, **76**, 481–496.
- Loeb, S.C., Rodhouse, T.J., Ellison, L.E., Lausen, C.L., Reichard, J.D., Irvine, K.M., Ingersoll, T.E., Coleman, J.T.H., Thogmartin, W.E., Sauer, J.R., Francis, C.M., Bayless, M.L., Stanley, T.R. & Johnson, D.M. (2015) *A plan for the North American Bat Monitoring Program (NABat)*. General Technical Report SRS-208. United States Department of Agriculture, Forest Service, Southern Research Station, Asheville, NC, USA.
- Luce, R.J. & Keinath, D. (2007). *Spotted bat (Euderma maculatum): a technical conservation assessment*. USDA Forest Service, Rocky Mountain Region. Available at: http://www.fs.usda.gov/Internet/FSE_DOCUMENTS/stelprdb5181916.pdf (accessed 18 August 2015).
- MacKenzie, D.I., Nichols, J.D., Royle, J.A., Pollock, K.H., Bailey, L.L. & Hines, J.E. (2006) *Occupancy estimation and modeling: inferring patterns and dynamics of species occurrence*. Academic Press Elsevier, London, England.
- Maher, S.P., Kramer, A.M., Pulliam, J.T., Zokan, M.A., Bowden, S.E., Barton, H.D., Magori, K. & Drake, J.M. (2012) Spread of white-nose syndrome on a network regulated by geography and climate. *Nature Communications*, **3**, 1306.
- McCain, C.M. (2007) Could temperature and water availability drive elevational species richness patterns? A global case study for bats. *Global Ecology and Biogeography*, **16**, 1–13.
- McKann, P.C., Gray, B.R. & Thogmartin, W.E. (2013) Small sample bias in dynamic occupancy models. *Journal of Wildlife Management*, **77**, 172–180.

- McNab, B.K. (1980) Food habits, energetics, and the population biology of mammals. *The American Naturalist*, **116**, 106–124.
- Meyer, C.F.J. (2015) Methodological challenges in bat monitoring population- and assembly-level changes for anthropogenic impact assessment. *Mammalian Biology*, **80**, 159–169.
- Milne, D.J., Fisher, A. & Pavey, C.R. (2006) Models of the habitat associations and distributions of insectivorous bats of the Top End of the Northern Territory, Australia. *Biological Conservation*, **130**, 370–385.
- Northwest GAP Analysis Project (GAP) (2008) *Land cover*. Available at: <http://gapanalysis.usgs.gov/gaplandcover/featured-post-1/> (accessed 18 August 2015).
- Ntzoufras, I. (2009) *Bayesian modeling using WinBUGS*. John Wiley and Sons, Hoboken, NJ, USA.
- Ohmann, J.L. & Gregory, M.J. (2002) Predictive mapping of forest composition and structure with direct gradient analysis and nearest neighbor imputation in coastal Oregon, USA. *Canadian Journal of Forest Research*, **32**, 725–741.
- Ormsbee, P.C. & McComb, W.C. (1998) Selection of day roosts by female long-legged myotis in central Oregon Cascade Range. *Journal of Wildlife Management*, **62**, 596–603.
- Ormsbee, P.C., Zinck, J.M., Szewczak, J.M., Patrick, L. & Hart, A.H. (2006) Benefits of a standardized sampling frame: an update on the “Bat Grid”. *Bat Research News*, **47**, 4.
- PRISM Climate Group (PRISM) (2015) *PRISM climate data*. Available at: <http://www.prism.oregonstate.edu/> (accessed 18 August 2015).
- Rodhouse, T.J., McCaffrey, M.F. & Wright, R.G. (2005) Distribution, foraging behavior, and capture results of the spotted bat in central Oregon. *Western North American Naturalist*, **65**, 215–222.
- Rodhouse, T.J. & Hyde, K.J. (2014) Roost and forage site fidelity of western small-footed myotis (*Myotis ciliolabrum*) in an Oregon desert canyon. *Western North American Naturalist*, **74**, 241–248.
- Rodhouse, T.J., Vierling, K.T. & Irvine, K.M. (2011) A practical sampling design for acoustic surveys of bats. *Journal of Wildlife Management*, **75**, 1094–1102.
- Rodhouse, T.J., Ormsbee, P.C., Irvine, K.M., Vierling, L.A., Szewczak, J.M. & Vierling, K.T. (2012) Assessing the status and trend of bat populations across broad geographic regions with dynamic distribution models. *Ecological Applications*, **22**, 1098–1113.
- Royle, J.A. & Dorazio, R.M. (2008) *Hierarchical modeling and inference in ecology*. Elsevier, London, UK.
- Rosenzweig, M.L. & Abramsky, Z. (1993) How are diversity and productivity related? *Species diversity in ecological communities: historical and geographical perspectives* (ed. by R.E. Ricklefs and D. Schluter), pp. 52–65. University of Chicago Press, Chicago, IL.
- Safi, K. & Kerth, G. (2004) A comparative analysis of specialization and extinction risk in temperate-zone bats. *Conservation Biology*, **18**, 1293–1303.
- Sattler, T., Bontadina, F., Hirzel, A.H. & Arlettaz, R. (2007) Ecological niche modeling of two cryptic bat species calls for a reassessment of their conservation status. *Journal of Applied Ecology*, **44**, 1188–1199.
- Spiegelhalter, D.J., Best, N.G., Carlin, B.P. & van der Linde, A. (2002) Bayesian measures of model complexity and fit. *Journal of the Royal Statistical Society, Series B.*, **64**, 583–639.
- Tews, J., Brose, U., Grimm, V., Tielborger, K., Wichmann, M.C., Schwager, M. & Jeltsch, F. (2004) Animal species diversity driven by habitat heterogeneity/diversity: the importance of keystone structures. *Journal of Biogeography*, **31**, 79–92.
- Thogmartin, W.E., King, R.A., McKann, P.C., Szymanski, J.A. & Pruitt, L. (2012) Population-level impact of white-nose syndrome on the endangered Indiana bat. *Journal of Mammalogy*, **93**, 1086–1098.
- US Fish and Wildlife Service (USFWS). (2013) *Endangered and threatened wildlife and plants; 12-month finding on a petition to list the eastern small-footed bat and the northern long eared bat as endangered or threatened species; listing the northern long-eared bat as an endangered species; proposed rule*. FWS–R5–ES–2011–0024. United States Fish and Wildlife Service, Green Bay Field Office, Green Bay, WI, USA.
- Verts, B.J. & Carraway, L.N. (1998) *Land mammals of Oregon*. University of California Press, Berkeley.
- Weller, T.J. (2008) Using occupancy estimation to assess the effectiveness of a regional multiple-species conservation plan: bats in the Pacific Northwest. *Biological Conservation*, **141**, 2279–2289.
- Weller, T.J. & Zabel, C.J. (2001) Characteristics of fringed myotis day roosts in northern California. *Journal of Wildlife Management*, **65**, 489–497.
- Western Bat Working Group (WBWG) (2005) *Western bat species*. Available at: <http://wbwg.org/western-bat-species/> (accessed 18 August 2015).
- Wright, D.H. (1983) Species-energy theory: an extension of species-area theory. *Oikos*, **41**, 496–506.
- Yackulic, C.B., Chandler, R., Zipkin, E.F., Royle, J.A., Nichols, J.D., Campbell Grant, E.H. & Veran, S. (2013) Presence-only modelling using MAXENT: when can we trust the inferences? *Methods in Ecology and Evolution*, **4**, 236–243.

SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Appendix S1. Methodological details.

Appendix S2. Maps of covariates.

Appendix S3. AUC posterior distributions.

Appendix S4. Plots of posterior means and CIs for estimated predictor effects.

Appendix S5. Probabilistic distribution and error maps.

BIOSKETCH

This article is the result of a decade-long collaborative effort by the authors and others to establish a sustainable bat monitoring program across broad regions of North America. P.C.O. designed, developed and led the Bat Grid program, which provided the data for this study. T.J.R. and K.M.I. continue to work towards a second-generation iteration of the program, the North American Bat Monitoring Program (NABat).

Author contributions: T.J.R., P.C.O. and J.M.S. conceived of the ideas and planned the study. P.C.O. and J.M.S. collected the data and processed acoustic calls. T.J.R. and K.M.I. developed the modelling strategy. L.A.V. and K.T.V. contributed to the development of region-wide environmental predictors, including snag density. T.J.R. performed the

modelling. T.J.R. wrote the manuscript, and P.C.O., K.M.I., L.A.V., J.M.S. and K.T.V. helped to write, edit and refine the final version of the manuscript. The authors' research groups and interests can be found at the following websites:

<http://science.nature.nps.gov/im/units/ucbn/>
<http://www.fs.fed.us/r6/sfpnw/issssp/species-index/fauna-mammals-bats.shtml>
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Editor: Janet Franklin