



Models for assessing local-scale co-abundance of animal species while accounting for differential detectability and varied responses to the environment

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ABSTRACT

We developed a new modeling framework to assess how the local abundance of one species influences the local abundance of a potential competitor while explicitly accounting for differential responses to environmental conditions. Our models also incorporate imperfect detection as well as abundance estimation error for both species. As a case study, we applied the model to four pairs of mammal species in Borneo, surveyed by extensive and spatially widespread camera trapping. We detected different responses to elevation gradients within civet, macaque, and muntjac deer species pairs. Muntjac and porcupine species varied in their response to terrain ruggedness, and the two muntjac responded different to river proximity. Bornean endemic species of civet and muntjac were more sensitive than their widespread counterparts to habitat disturbance (selective logging). Local abundance within several species pairs was positively correlated, but this is likely due to the species having similar responses to (unmodeled) environmental conditions or resources rather than representing facilitation. After accounting for environment and correcting for false absences in detection, negative correlations in local abundance appear rare in tropical mammals. Direct competition may be weak in these species, possibly because the ‘ghost of competition past’ or habitat filtering have already driven separation of the species in niche space. The analytical framework presented here could increase basic understanding of how ecological interactions shape patterns of abundance across the landscape for a range of taxa, and also provide a powerful tool for forecasting the impacts of global change.

Key words: Borneo; competition; co-occurrence; global change; Southeast Asia; species interactions.

DETERMINING WHICH SUBSETS OF REGIONAL SPECIES POOLS ASSEMBLE INTO LOCAL COMMUNITIES HAS BEEN A CENTRAL THEME THROUGHOUT THE HISTORY OF COMMUNITY ECOLOGY (Darmon *et al.* 2012, HilleRisLambers *et al.* 2012, Cazelles *et al.* 2016). Certain species may consistently occur with or not occur with other species based on contemporary species interactions and environmental conditions (Morueta-Holme *et al.* 2016), a history of past interactions (Connell 1980, Silvertown 2004), or chance alone (Connor & Simberloff 1979, Gotelli 2000).

The influence of climate and other environmental conditions on species distributions at large spatial scales is clear (Lomolino *et al.* 2006). But how conditions at smaller scales, and species interactions at any scale, influence distributions is poorly understood and still debated (Araujo & Rozenfeld 2014, Cazelles *et al.* 2016). A critical question is whether, once environmental factors

are accounted for, species interactions still influence distribution or abundance (Bullock *et al.* 2000, van Beest *et al.* 2014).

The reason that ecologists’ understanding of how environment and interactions shape local-scale distributions remains poor is that, despite a vast literature on species co-occurrence, detecting such patterns can be difficult (Mod *et al.* 2016, Morueta-Holme *et al.* 2016). The gold standard is to experimentally remove one species and test for changes in the abundance of others (*e.g.*, Munger & Brown 1981, Segre *et al.* 2014). This is exceedingly difficult (and potentially unethical) for many animals, particularly species living at low densities in complex habitats. Co-occurrence has also been assessed through observational occurrence data, embodied in the search for ‘checkerboard’ distribution patterns and the debate over whether such patterns are driven by species interactions (Diamond 1975, Connor & Simberloff 1979). Such datasets often consist of species presence × site matrices (Meyer & Kalko 2008, Gotelli & Ulrich 2010, Ulrich & Gotelli 2013), and their analysis catalyzed the growth of statistical null models (Gotelli 2000, Ulrich & Gotelli

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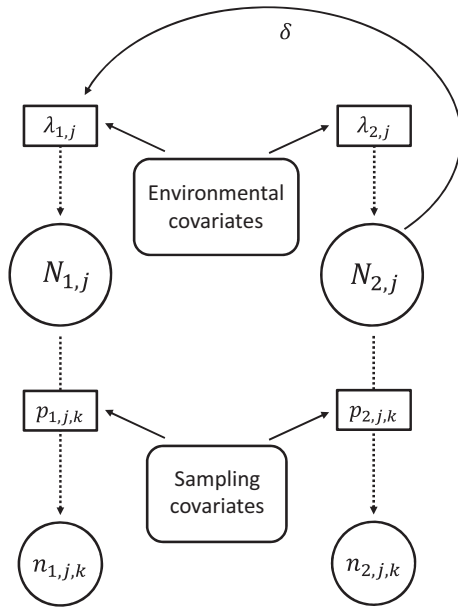


FIGURE 1. Conceptual diagram of the two-species N-mixture models to assess co-abundance patterns while controlling for differential responses to environmental resources or conditions and imperfect detectability of both species

2013, Veech 2013) that have since been widely applied throughout ecology. Other observational approaches to detecting and interpreting co-occurrence patterns include joint species distribution modeling (Lois *et al.* 2015, Ovaskainen *et al.* 2016), covariance matrices (Morueta-Holme *et al.* 2016), network analysis (Morales-Castilla *et al.* 2015, Cazelles *et al.* 2016), differential equation-based competition models (Godsoe *et al.* 2015), multivariate analyses (Collinge *et al.* 2003, Azeria *et al.* 2009), or combinations of these frameworks (Morueta-Holme *et al.* 2016).

Nearly all the of diverse quantitative approaches to understanding co-occurrence or co-abundance patterns assume that species can be detected or counted perfectly. For example, checkerboard pattern analysis was developed for thorough surveys of birds on small islands (Diamond 1975) while network and covariance matrix analysis can be robustly applied to trees on study plots (Morueta-Holme *et al.* 2016). But many animals are very difficult to detect, particularly those in structurally complex ecosystems such as tropical rainforests. This makes co-occurrence analysis problematic because it can be difficult to separate true absence of a species from situations where the species was present but undetected (MacKenzie *et al.* 2004), and biases imposed by false-absences are rarely addressed. Hierarchical models can circumvent this problem by estimating occurrence (MacKenzie *et al.* 2004, Waddle *et al.* 2010, Rayan & Linkie 2016) or abundance (Dorazio & Connor 2014) while accounting for imperfect detectability.

Here, we develop an approach to assess possible competitive interaction effects using Bayesian hierarchical models of local abundance (rather than presence-absence) while accounting for

differential environmental effects and imperfect detection. As a case study, we apply the models to four pairs of tropical rain forest mammal species in Borneo; as in most tropical ecosystems (but see Rayan & Linkie 2016), no published information exists on whether interactions with co-occurring species affect local-scale mammal distribution or abundance. This analytical approach can provide important basic information on how species interactions shape populations and communities. It also presents a methodological advance for predicting the responses of organisms to alterations in both abiotic conditions and the distributions of interacting species. While mammals could potentially be affected by competition from a large number of sympatric species (including other taxa such as birds), our method serves as a first-pass approach to detecting competition by focusing on potential effects from the most similar (phylogenetically and ecologically) species, from whence competition should be strongest. While point estimates of the local abundance of one species could simply be used as a covariate in the abundance function of a second species (Brodie & Giordano 2013), this would not address the (often substantial) uncertainty in the abundance estimates of the first species. The method that we present here incorporates such error and propagates uncertainty throughout the model.

METHODS

STUDY SYSTEM AND SPECIES.—We compiled an extensive collection of data from motion-triggered camera traps at 16 study areas across Sabah and Sarawak in Malaysian Borneo (Fig. S1). In total, we had 303 functional camera trap stations (Table S1). Sampling at seven of the study areas has been previously described in detail (Brodie *et al.* 2015b,c). To this dataset, we added data from Imbak Canyon (Bernard *et al.* 2013a,b) and Danum Valley (A. Granados, unpubl. data) in Sabah, and seven study areas in southern and central Sarawak (J. Mohd-Azlan, unpubl. data). The sampling protocol was similar at all sites—cameras were attached to trees, usually ~30–60 cm above the ground, and recorded photographs 24 h per day for a period of usually several weeks to months at each site. (The modeling framework that we employ, discussed below, readily accounts for unequal sampling effort across sites.) We truncated the dataset at 5 months of sampling at any given site—this cutoff was arbitrary (as in all such analyses) and was chosen to balance maximizing detections while satisfying the population closure assumption.

We sought pairs of mammal species on Borneo where the members of each pair were closely related, similar in body size and foraging ecology, and distinguishable in camera trap photographs. These criteria excluded the two species of chevrotains (*Tragulus* spp.) because they were often not distinguishable. Of the five species pairs that met these criteria, interaction models (described below) for mongooses did not converge. We were left with four species pairs: the banded (*Hemigalus derbyanus*) and Hose’s (*Diplogale hosei*) civets, long-tailed (*Macaca fascicularis*) and southern pig-tailed (*M. nemestrina*) macaques, southern red (*Muntiacus muntjak*) and Bornean yellow (*M. atberodes*) muntjac, and Malayan (*Hystrix brachyura*) and thick-spined (*H. crassispinis*)

porcupines. Other species of civets occur on Borneo but they differ in body size, morphology, and diet from the two assessed here and so were not considered to be potential close competitors. There is also a third species of porcupine on Borneo, but it is much smaller and very different morphologically from the two assessed here. In most of the pairs, species identification from photographs was straightforward. In muntjac it was somewhat more difficult; generally yellow muntjac had tails that were much darker than the body (versus about the same shade in red muntjac), lower legs that were the same shade as the body (versus darker in the red muntjac), and females lacked the dark black eyebrow markings of red muntjac females (J. Ross, pers. comm). Male yellow muntjac also has straighter, smaller antlers with shorter and narrower pedicels. We discarded records where we were not confident of identification (17.8% of total).

COUNT AND COVARIATE DATA.—We grouped the data into five-day sampling intervals to decrease the number of zeroes in the dataset (i.e., sampling occasions with no detections). For any given sampling interval, the count statistic was the total number of unique individuals observed during the occasion. The count statistic was conservative in that fewer individuals would have been recorded during a given sampling occasion than actually were there if the individuals were not uniquely distinguishable (e.g., by size, sex, or markings), so our results should be viewed as estimating minimum local abundance. For macaques and porcupines, we conducted the analysis somewhat differently. Although individuals are often distinguishable, they often live in groups and so detections would not be independent. Therefore, for these species the count statistic was the number of groups rather than the number of individuals. For all of the species, the count statistics for most of the sampling occasions were either 0 or 1; however there were enough counts >1 to warrant the use of N -mixture models rather than binary occupancy models (Fig. S2).

A large number of environmental covariates potentially affect the abundance of any given species. Because a primary goal was to assess whether similar species responded to the environment differently, rather than to accurately estimate local abundance per se, we focused our analysis on a suite of environmental variables along which partitioning might plausibly occur. These included elevation, which is known to strongly affect species distributions (Janzen 1967, Jankowski *et al.* 2013), terrain roughness, as some mammals may choose steep areas to avoid potential competitors (Pedrana *et al.* 2010), distance to rivers, as forest composition and habitat structure change across riparian-upland gradients (Corlett 2009), and habitat alteration (logging), because species often vary strongly in their tolerance of disturbance (Brodie *et al.* 2015a,c). We included quadratic terms for elevation and roughness because mammals may select middle elevations (Brodie *et al.* 2015c) or slopes (Pedrana *et al.* 2010). We did not explicitly incorporate hunting into our models. Hunting is known to strongly affect mammal abundance (Brodie *et al.* 2015c), but we thought it unlikely that species would partition habitat based on hunting pressure as there is no evidence that related or ecologically similar species in our system differ in their

demographic or behavioral responses to hunting (Brodie *et al.* 2015c). However, because hunting pressure (as well as other unmeasured factors) differed strongly across our study areas (Brodie *et al.* 2015c) and would likely alter baseline mammal abundance, we included study area as a random intercept in our multispecies models.

We downloaded a 90 m resolution elevation map of the region (Farr *et al.* 2007) and used a geographical information system to measure the average elevation and standard deviation of elevation (our metric of terrain roughness) within 100 m, 200 m, 300 m, . . . , 1000 m radii of each camera station. We then used single-species N -mixture models (Royle 2004) to assess the spatial scale at which each species pair responded most strongly to elevation and terrain roughness, choosing the spatial scale with the lowest AIC value to use in the multispecies N -mixture models described below (ESM). We measured the distance from each camera station to the nearest river using the HydroSHEDS dataset (Lehner *et al.* 2006) as a baseline for approximate river locations, corrected by visually inspecting the 90 m elevation model to determine the exact positions of the streambeds. Finally, as a metric of habitat disturbance we used binary determinations as to whether each camera station was in forest that had been selectively logged or not (“logged” covariate) or (analyzed separately) selectively logged within 10 years of our sampling (“newly logged”). Previous work in the system has suggested that some mammals respond differently to recent versus older logging (Brodie *et al.* 2015c).

Collinearity among continuously distributed covariates in our analysis was relatively low, with $|r| \leq 0.5$ for all pairs of variables.

TWO-SPECIES N -MIXTURE MODELS.—The objective of our model was to estimate the abundances of species pairs relative to each other and environmental covariates from repeated counts. To that end, we expanded upon the N -mixture modeling framework of Royle (2004) by including a term for an effect of the latent abundance of a competitor. N -mixture models estimate population abundance for species i at location j , denoted $N_{i,j}$, through repeated counts of the population over a time frame during which the population is closed to birth, death, immigration, and emigration. We assume that $N_{i,j} \sim \text{Pois}(\lambda_{i,j})$ and model the expected count of species i at location j , $\lambda_{i,j}$, relative to covariates using a log-link function (Royle 2004). For development of our two species modeling framework, we add an additional effect of the abundance of one species on the other such that:

$$\log(\lambda_{2,j}) = \alpha_2 * \text{covariate}_j + \delta * N_{1,j}$$

where α_2 is a vector of covariate effects for a target species ($i = 2$) and δ represents the effect of the site-specific abundance of another species ($i = 1$) on the target species (Fig. 1). Thus, an estimated value of $\delta \leq 0$ would suggest a negative impact of species 1 on species 2, providing evidence for competition or at least local avoidance. Similarly, a positive estimate (e.g. $\delta \geq 0$) would suggest that the abundance of species 2 increases with increasing local abundance of species 1. Estimates for δ that overlap zero indicate no interaction among the two species. Assuming that

appropriate covariates are chosen for the model, this approach allows us to tease apart the additional impacts of a species on the abundance of a target or focal species.

For our analysis of the Borneo mammalian data, we defined species 1 as the competitively dominant species of the pair based on known ecological information (when possible). However, the choice of which species in a pair was set to 1 or 2 was not critical to our inference because we essentially measured correlations in abundance between the two species rather than actual dominance versus subordination. For macaques and porcupines, we assumed that the smaller-bodied member of the pair, the long-tailed macaque and thick-spined porcupine (species 2), respectively, would be influenced by the abundance of their larger counterparts, the southern pig-tailed macaque and the Malayan porcupine (species 1), respectively. For civets and muntjac, we set the relatively rarer, Bornean endemic, member of each pair, Hose’s civet and yellow muntjac, respectively, as species 2 and the widespread banded civet and red muntjac, respectively, as species 1. For species 1, we modeled the expected abundance relative to the environmental covariates at each survey site j as follows:

$$\log(\lambda_{i,j}) = \alpha 0_i + \alpha 1_i * \text{ruggedness}_j + \alpha 2_i * \text{ruggedness}_j^2 + \alpha 3_i * \text{elevation}_j + \alpha 4_i * \text{elevation}_j^2 + \alpha 5_i * \text{river}_j + \alpha 6_i * \text{newly_logged}_j + \alpha 7_i * \text{study area}_j$$

where $\alpha 0_i$ is the intercept, $\alpha 1_i - \alpha 6_i$ are the effects of the covariates described in the previous section, standardized to have a mean of zero and a standard deviation of one, and $\alpha 7_i$ is a categorical random effect accounting for the highly clustered nature of the sampling whereby camera traps were grouped into study areas straddling the region (Brodie *et al.* 2015b,c). The model for the second species ($i = 2$) included an additional parameter estimating the effect of the latent local abundance of the first species: $\delta * \hat{N}_{1,j}$.

We assume that the true latent abundance of both species is detected imperfectly during sampling (Royle 2004). Because abundance cannot be directly observed at survey locations, sampling biases are accommodated in estimates of $N_{i,j}$ by assuming that the detections of species i at location j during survey replicate k , denoted $n_{i,j,k}$, follow a binomial distribution with species-level detection probability $p_{i,j,k}$: $n_{i,j,k} \sim \text{Bin}(N_{i,j,k}, p_{i,j,k})$. The detection model for both species included covariates for whether the camera was located on a trail, and for the number of hours during which the camera was operational during a given sampling interval (“camera”). We also included an effect of sampling day (since camera deployment) to account for potential trends in trap avoidance (“day”), and included logging to allow for differences in gross vegetation structure on detection:

$$\text{logit}(p_{i,j,k}) = \beta 0_i + \beta 1_i * \text{camera}_j + \beta 2_i * \text{trail}_j + \beta 3_i * \text{day}_{j,k} + \beta 4_i * \text{logging}_j$$

We estimated model parameters using a Bayesian approach with Markov chain Monte Carlo (MCMC) with the programs R (Core Team 2013) and WinBUGS (Lunn *et al.* 2000). Bayesian analysis is particularly useful for our model structure because it explicitly estimates the latent $N_{1,j}$ values, which are used to estimate the $N_{2,j}$ values. For each species pair, we ran three chains of

70,000 iterations and discarded the first 30,000 as a burn-in. The remaining 40,000 iterations of each chain were thinned by 20, which left 6,000 values to quantify the posterior distribution of each parameter. These values were chosen to balance robust parameter estimation with computational efficiency (they are the same decision values as in Brodie *et al.* 2015c). To determine if parameter estimates were different between species in a pair, we subtracted one parameter value from another for each iteration of the MCMC (e.g., $\alpha 6_1 - \alpha 6_2$ to determine if the effect of logging was larger on one species in a pair) and then examined the credibility intervals of these differences (see SM for model code).

We considered that a given coefficient or derived parameter (i.e., difference in parameter values for a particular covariate between species in a pair) was statistically significant if its 95% credibility interval did not include zero. Our model had the same assumptions as a standard N -mixture model, including independence among sites, population closures over all replicate sampling events, independent and equal detection probabilities among individuals (within a species), and that site-level abundance was a random variable with $E(N_j) = \lambda$ (Royle 2004).

LOCAL ABUNDANCE AND SPATIAL INDEPENDENCE.— N -mixture models estimate the local abundance of a given species, which can be difficult to interpret ecologically in camera trapping studies where the area surveyed by a given camera is small relative to the home ranges of the species surveyed. Thus, we define local abundance in this context as the number of individuals that use the small area (on the order of 100 m²) surveyed by a given camera during the course of the study, similar to metrics of home range overlap used in studies of breeding birds (e.g., Warning & Benedict 2015). We view the local abundance estimates as relative indices that are comparable within species pairs but not across taxa with widely divergent spatial sorting behaviors.

Our models also assume independent detections among sites. The median camera station density within study areas was 1 camera per 2.66 km². To determine whether, given that spacing, camera stations could be considered independent, we examined the spatio-temporal pattern of detections of individual Sunda clouded leopards (*Neofelis diardi*) in a previous study (Brodie *et al.* 2015c). We found that in Maliau Basin (with density of 1 camera station per 2.68 km²), detections of this species could be considered independent among even adjacent cameras because detections of the same individual did not follow a spatially contagious pattern. Being large-bodied carnivores, clouded leopards are almost certainly more wide-ranging than any of the species analyzed here, so we feel that our camera spacing should not violate the assumption of independent detections.

RESULTS

Of a total of 24,289 camera trap days across 303 camera trap stations in 16 study areas, we obtained records of each species ranging from 29 (Hose’s civet) to 747 (pig-tailed macaque; Table 1) detections. The spatial scale analysis revealed that for macaques, muntjac, and porcupines the most parsimonious model had

TABLE 1. Summary data and parameter estimates for landscapes level factors for the eight species that were modeled.

Species	Total detections	Number of camera stations at which species was detected	Model coefficients (95% CI)						
			Elevation (linear)	Elevation (quadratic)	Topography (linear)	Topography (quadratic)	Distance to river	Selective logging	
Civets									
Hose's civet (species 1)	29	16	4.96 (1.8, 9.59)	-2.36 (-4.45, -0.77)	0.88 (-0.25, 2.18)	-0.03 (-0.5, 0.42)	-2.5 (-6.2, 0.56)	-9.82 (-24.25, 0.11)	
Banded civet (species 2)	192	54	0.07 (-0.2, 0.34)	-0.11 (-0.3, 0.07)	0.21 (-0.03, 0.45)	-0.09 (-0.21, 0.01)	0.1 (-0.11, 0.31)	0.89 (0.14, 1.98)	
Macaques									
Long-tailed macaque (species 1)	143	21	-0.72 (-1.65, 0.11)	-0.28 (-1.01, 0.39)	-0.2 (-0.63, 0.21)	-0.18 (-0.65, 0.22)	-0.03 (-0.47, 0.33)	0.14 (-0.92, 1.25)	
Southern pig-tailed macaque (species 2)	747	127	0.25 (-0.07, 0.54)	-0.2 (-0.35, -0.05)	0.08 (-0.07, 0.24)	-0.08 (-0.17, 0.01)	-0.02 (-0.19, 0.16)	-0.06 (-0.57, 0.52)	
Muntjacs									
Bornean yellow muntjac (species 1)	336	59	-2.35 (-3.52, -1.35)	-0.28 (-1.17, 0.48)	-0.31 (-0.81, 0.1)	0.25 (0.05, 0.49)	0.45 (0.09, 0.82)	-1.96 (-3.31, -0.5)	
Southern red muntjac (species 2)	706	105	0.63 (0.34, 0.91)	-0.27 (-0.43, -0.12)	0.24 (0.08, 0.4)	-0.1 (-0.19, -0.01)	-0.04 (-0.19, 0.1)	0.36 (-0.06, 0.77)	
Porcupines									
Thick-spined porcupine (species 1)	242	43	0.06 (-0.73, 0.83)	-0.58 (-1.19, -0.01)	-0.14 (-0.53, 0.25)	0.06 (-0.17, 0.26)	-0.62 (-1.19, -0.09)	-0.3 (-1.2, 0.58)	
Malayan porcupine (species 2)	329	52	0.59 (0.27, 0.91)	-0.27 (-0.44, -0.1)	0.46 (0.23, 0.7)	-0.09 (-0.19, 0)	0.24 (0.04, 0.43)	1.49 (0.64, 2.6)	

elevation and terrain roughness averaged at the 100 m scale; for civets the most parsimonious spatial scales was 200 m (Fig. S3). Model results from the analysis using “logged” as a disturbance covariate were very similar to those using “newly logged”, based on correlations among model coefficients (civets: $r = 1.00$, macaques: $r = 0.97$, muntjacs: $r = 0.93$, porcupines: $r = 0.99$). We report all subsequent results from the analysis with “logged” as the disturbance covariate as they were slightly more precise (i.e., narrower credibility intervals). The model for civets gave unrealistic local abundance estimates when using the random effect term, so for this species pair we report model results without the random effect.

Three species pairs—civets, muntjac, and porcupines—showed correlations in local abundance (all positive) at fine spatial scales (i.e., the credibility intervals for the α_8 coefficient did not include zero; Table 2; Fig. 2).

The local abundance of Hose’s civet generally increased with elevation (i.e., there was a significant, positive, linear elevation coefficient; Table 1; Fig. S4), but with a significant mid-elevation peak in local abundance (negative elevation quadratic coefficient, Table 1) at ~1000 m (Fig. 3). The responses to elevation differed between the species in both general trend (linear coefficient) and curvature (quadratic coefficient; Table 2). Although logging reduced the detection rates of banded civets, estimated local abundance of this species was higher in logged areas (Table 2). Hose’s civets responded more negatively than banded civets to logging.

The macaque species had contrasting responses to elevation (Table 2); the local abundance of pig-tailed macaque groups peaked at about 800 m, while the local abundance of long-tailed macaque groups was unrelated to elevation (Table 1).

Yellow muntjac local abundance decreased with elevation while red muntjac local abundance increased with elevation generally, with a peak at about 1200 m (Fig. 3). The species differed significantly in their linear elevation terms (Table 2) and their responses to terrain roughness, where red muntjac local abundance generally peaked at mid rugged values (Fig. 4; SM, Fig. S5). They also differed in their response to river proximity—yellow muntjac local abundance increased slightly with distance from the nearest river while red muntjac local abundance was unaffected (Figs 5 and S6). The species differed in their response to habitat disturbance, with yellow muntjac local abundance negatively affected by selective logging and red muntjac local abundance unaffected (Fig. 6).

The local abundance of groups of both porcupine species peaked at mid-elevations (Fig. 3). The species differed in their response to river proximity, with local abundance being highest near rivers for thick-spined porcupines and unaffected by river proximity for Malayan porcupines (Fig. 5). The species also differed in their response to terrain roughness and habitat disturbance, with Malayan porcupines responding positively to roughness and selective logging while thick-spined porcupines were unaffected by both.

TABLE 2. Estimates of the local-level species-pair correlation term (α_8) and derived parameters (i.e., difference in landscape level covariate estimates between the two species in a given pair). Designations of species 1 and species 2 shown in Table 1.

Species pair	Model coefficients (95% CI)							
	Effect of species 2 local abundance on species 1 local abundance	Difference in linear elevation coefficients (species 1–species 2)	Difference in linear topography coefficients (species 1–species 2)	Difference in quadratic elevation coefficients (species 1–species 2)	Difference in quadratic topography coefficients (species 1–species 2)	Difference in quadratic topography coefficients (species 1–species 2)	Difference in distance to river coefficients (species 1–species 2)	Difference in logging coefficients (species 1–species 2)
Civets	0.39 (0.16, 0.7)	4.89 (1.69, 9.52)	0.68 (–0.52, 2.02)	–2.26 (–4.36, –0.62)	0.07 (–0.43, 0.53)	–2.61 (–6.3, 0.47)	–10.71 (–25.39, –0.54)	
Macaques	0.14 (–0.05, 0.32)	–0.97 (–1.98, –0.06)	–0.27 (–0.76, 0.18)	–0.07 (–0.84, 0.63)	–0.1 (–0.58, 0.31)	–0.01 (–0.49, 0.41)	0.2 (–1.14, 1.55)	
Muntjac	0.45 (0.28, 0.71)	–2.98 (–4.22, –1.89)	–0.55 (–1.12, –0.06)	–0.01 (–0.94, 0.81)	0.35 (0.1, 0.62)	0.49 (0.05, 0.93)	–2.32 (–3.81, –0.69)	
Porcupines	0.03 (–0.06, 0.13)	–0.53 (–1.41, 0.3)	–0.6 (–1.05, –0.14)	–0.31 (–0.94, 0.29)	0.15 (–0.1, 0.38)	–2.61 (–6.3, 0.47)	–1.79 (–3.2, –0.53)	

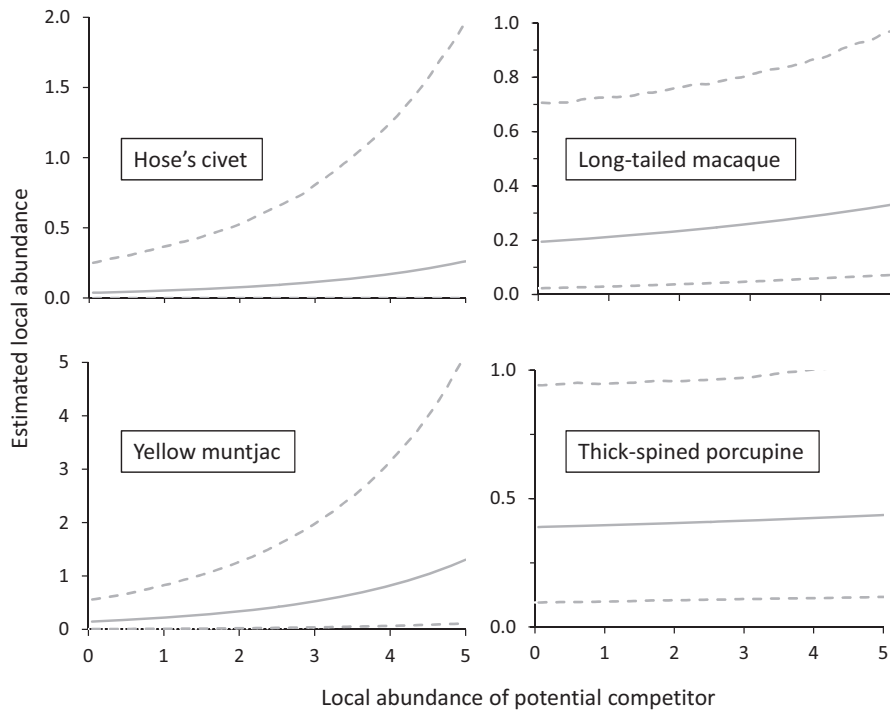


FIGURE 2. Correlations in local abundance between members of species pairs, accounting for habitat effects and imperfect detection in all species. Mean estimates and 95% credibility intervals (solid and dashed lines, respectively) shown.

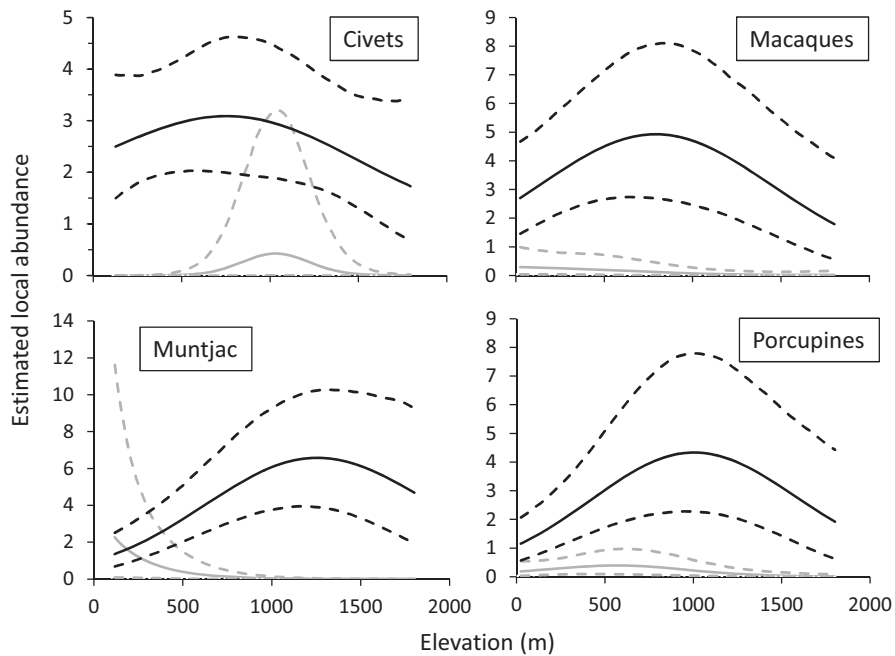


FIGURE 3. Variation in local abundance with elevation, holding other environmental covariates at their mean values and assuming no effect of the other species in the pair. Banded civet, pig-tailed macaque, red muntjac, and Malayan porcupine are shown in black; Hose's civet, long-tailed macaque, yellow muntjac, and thick-spined porcupine are shown in gray. Mean estimates and 95% credibility intervals (solid and dashed lines, respectively) shown.

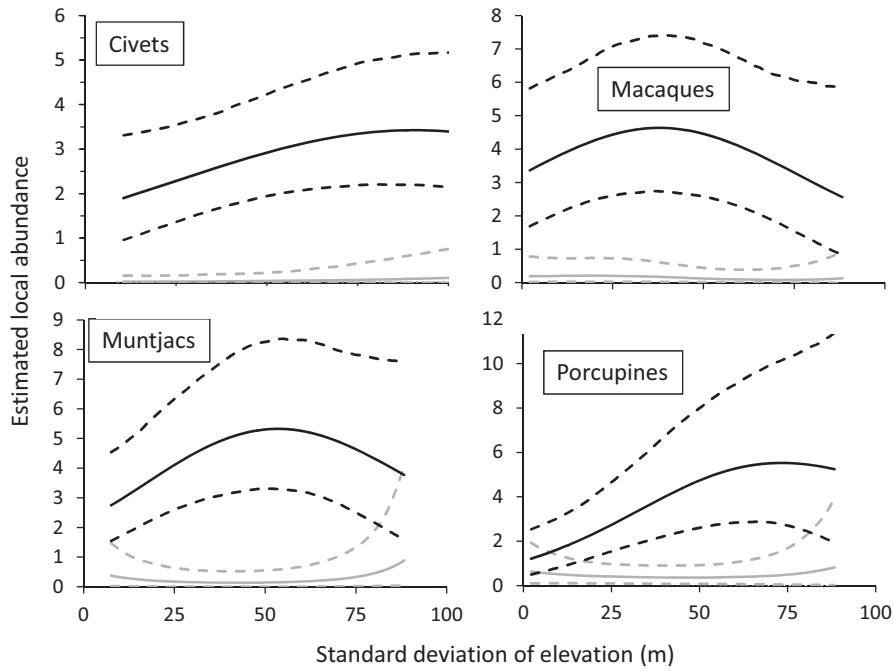


FIGURE 4. Variation in local abundance with terrain roughness, holding other environmental covariates at their mean values and assuming no effect of the other species in the pair. Banded civet, pig-tailed macaque, red muntjac, and Malayan porcupine shown in black; Hose's civet, long-tailed macaque, yellow muntjac, and thick-spined porcupine shown in gray. Mean estimates and 95% credibility intervals (solid and dashed lines, respectively) shown.

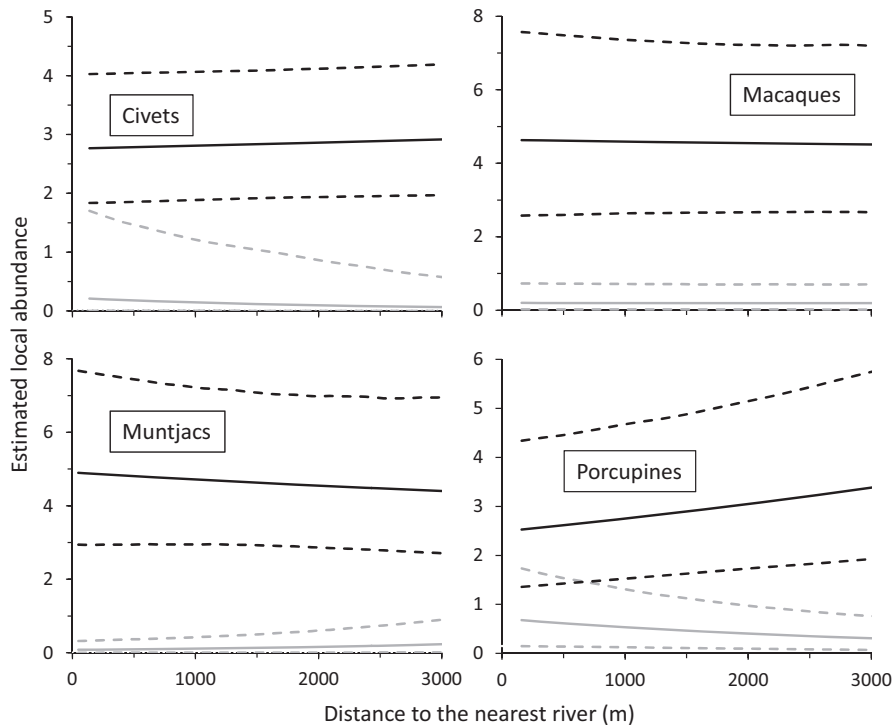


FIGURE 5. Variation in local abundance with distance to the nearest river, holding other environmental covariates at their mean values and assuming no effect of the other species in the pair. Banded civet, pig-tailed macaque, red muntjac, and Malayan porcupine shown in black; Hose's civet, long-tailed macaque, yellow muntjac, and thick-spined porcupine shown in gray. Mean estimates and 95% credibility intervals (solid and dashed lines, respectively) shown.

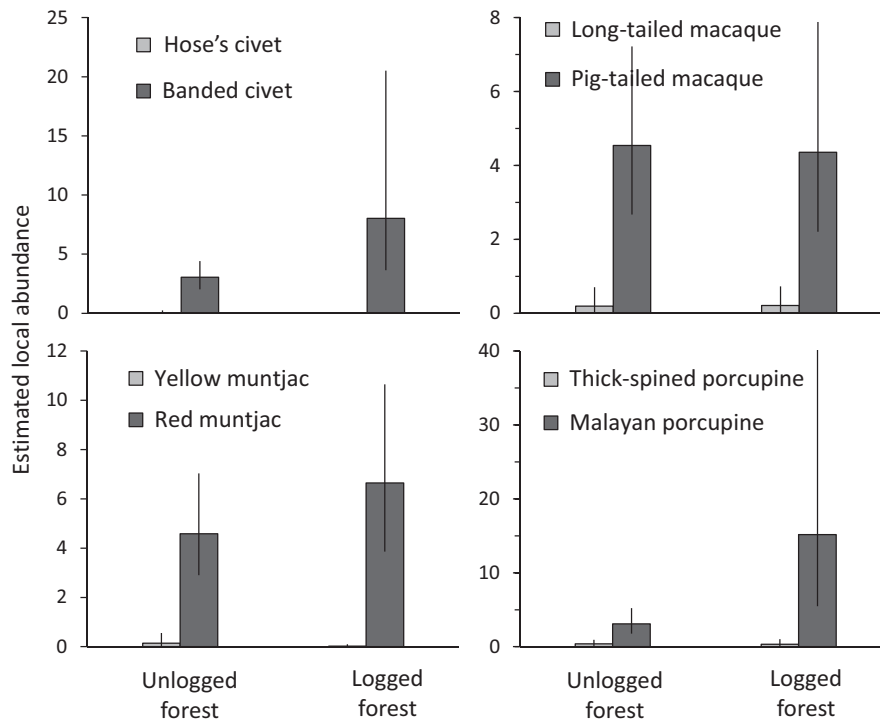


FIGURE 6. Variation in local abundance with habitat disturbance (selective logging), holding other environmental covariates at their mean values and assuming no effect of the other species in the pair. Banded civet, pig-tailed macaque, red muntjac, and Malayan porcupine shown in black; Hose's civet, long-tailed macaque, yellow muntjac, and thick-spined porcupine shown in gray. Mean estimates and 95% credibility intervals (solid and dashed lines, respectively) shown.

DISCUSSION

We developed a model to estimate species' co-abundance patterns while accounting for imperfect detectability and differential responses to environmental conditions or resources, represented here by gradients in elevation, topography, and forest structure. We found little evidence of avoidance of potential competitors. Local abundance was positively correlated for the two muntjac and civet species, despite broadly different responses within these groups in their apparent habitat preference along landscape-scale gradients. Positive correlations between potentially competing species have been found in other taxa (Richmond *et al.* 2010, Sebastian-Gonzalez *et al.* 2010, Dorazio & Connor 2014) and are difficult to interpret in terms of interspecific interactions. Such positive correlations likely arise from the species tracking the same resources (ones not included as covariates in our models), such as food availability (Akers *et al.* 2013). If the species were not at or near their combined carrying capacity, resource partitioning would not be needed (van Beest *et al.* 2014). It is also possible that one of the muntjac and civet species facilitated the other, but the mechanism for how this would occur in our system is not readily apparent.

For several of the groups we assessed, members of a species pair responded differently to environmental gradients or conditions. The two muntjac species were roughly equally abundant in the lowlands, but the local abundance of yellow muntjac declined at higher elevations where the local abundance of red muntjac

increased several fold. Such opposing responses to elevation between related species are not uncommon (Terborgh 1971, Jankowski *et al.* 2013), but have not hitherto been quantified while simultaneously accounting for imperfect detection and the explicit potential for correlations in abundance (*e.g.*, due to habitat partitioning) at fine spatial scales (Dorazio & Connor 2014). Local abundance within species pairs also differed in terms of proximity to rivers for muntjac and porcupines in that one member of each pair responded to this factor while the other did not. We found less evidence for partitioning along variation in terrain roughness or tolerance of habitat disturbance. Red muntjac preferred more rugged terrain than did yellow muntjac, and were more tolerant of logging. Banded civets were more tolerant of logged areas than were Hose's civets. Terrain roughness is known to influence habitat selection in individual species (Nellemann & Reynolds 1997), but whether it can act as an axis along which related species partition habitat has remained poorly understood (Pedrana *et al.* 2010). Likewise, many studies have shown taxon-specific responses to logging-induced forest disturbance (Gomes *et al.* 2008, Brodie *et al.* 2015c), but rarely quantified them concurrently with other habitat effects and interspecific interactions.

A better understanding of how current environmental conditions and species interactions affect species distributions and co-occurrence patterns could greatly improve predictions of how changing environmental conditions will alter ecological communities. Responses to climate change and anthropogenic habitat disturbance are frequently measured or predicted with species

distribution models. Such models are often quantitatively sophisticated but ecologically crude in that they only estimate species presence (rather than abundance) and they rarely incorporate species interactions and detection probabilities. Our models provide a way to understand the factors related to where species occur, but because they explicitly account for interactions they may generate different insights from presence-only, single-species distribution models. In this study, our results broadly supporting the interaction-less analyses of species distribution models in that we did not find influence of competitors on local abundance in any of the species we assessed. This could suggest that not incorporating potential competitors in species distribution models still results in unbiased predictions in some instances. But interactions in other taxa are known to shape both micro- and macro-scale abundances (Buckley & Roughgarden 2005, Guillaumet & Leonard 2015). In those cases, and for species with sufficient data available for parameterization, our model could generate high resolution estimates of changes in local abundance of a given species over wide areas as a function of environmental covariates and potential interactions with other species. Being able to explicitly measure both habitat effects and the influence of potential competitors, while accounting for imperfect detectability, could greatly improve our ability to understand and predict species' responses to climatic and other global changes.

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DATA AVAILABILITY

Data available from the Dryad Repository: <https://doi.org/10.5061/dryad.fn208> (Brodie *et al.* 2017). The R and WinBUGS code for the models used here, as well as the data, are stored on <https://zipkinlab.github.io/>.

SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article:

TABLE S1. *Information on each sampling area.*

FIGURE S1. Map of camera trap locations, rivers, and elevation in Borneo.

FIGURE S2. Count statistics for each species.

FIGURE S3. Assessment of the most parsimonious spatial

scale over which to average the 90 m resolution elevation data.

FIGURE S4. Histogram of elevations of detections of each species and the total range of covariate values.

FIGURE S5. Histogram of terrain roughness of detections of each species and the total range of covariate values.

FIGURE S6. Histogram of distance to river of detections of each species and the total range of covariate values.

LITERATURE CITED

- AKERS, A. A., M. A. ISLAM, AND V. NIJMAN. 2013. Habitat characterization of western hoolock gibbons *Hoolock hoolock* by examining home range microhabitat use. *Primates* 54: 341–348.
- ARAUJO, M. B., AND A. ROZENFELD. 2014. The geographic scaling of biotic interactions. *Ecography* 37: 406–415.
- AZERIA, E. T., D. FORTIN, C. HEBERT, P. PERES-NETO, D. POTHIER, AND J. C. RUEL. 2009. Using null model analysis of species co-occurrences to deconstruct biodiversity patterns and select indicator species. *Divers. Distrib.* 15: 958–971.
- van BEEST, F. M., P. D. MCLOUGHLIN, E. VANDER WAL, AND R. K. BROOK. 2014. Density-dependent habitat selection and partitioning between two sympatric ungulates. *Oecologia* 175: 1155–1165.
- BERNARD, H., A. H. AHMAD, J. BRODIE, A. J. GIORDANO, M. LAKIM, R. AMAT, S. K. P. HUE, L. S. KHEE, A. TUUGA, P. T. MALIM, D. LIM-HASEGAWA, Y. S. WAI, AND W. SINUN. 2013a. Camera-trapping survey of mammals in and around Imbak Canyon Conservation Area in Sabah, Malaysian Borneo. *Raffles Bull. Zool.* 61: 861–870.
- BERNARD, H., J. BRODIE, A. J. GIORDANO, A. H. AHMAD, AND W. SINUN. 2013b. Bornean felids in and around the Imbak Canyon Conservation Area, Sabah, Malaysia. *Cat News* 58: 44–46.
- BRODIE, J. F., AND A. J. GIORDANO. 2013. Lack of trophic release with large mammal predators and prey in Borneo. *Biol. Cons.* 163: 58–67.
- BRODIE, J. F., A. J. GIORDANO, AND L. AMBU. 2015a. Differential responses of large mammals to logging and edge effects. *Mamm. Biol.* 80: 7–13.
- BRODIE, J. F., A. J. GIORDANO, B. G. DICKSON, M. HEBBLEWHITE, H. BERNARD, J. MOHD-AZLAN, J. ANDERSON, AND L. AMBU. 2015b. Evaluating multi-species landscape connectivity in a threatened tropical mammal community. *Conserv. Biol.* 29: 122–132.
- BRODIE, J. F., A. J. GIORDANO, E. F. ZIPKIN, H. BERNARD, J. MOHD-AZLAN, AND L. AMBU. 2015c. Correlation and persistence of hunting and logging impacts on tropical rainforest mammals. *Conserv. Biol.* 29: 110–121.
- BRODIE, J. F., O. E. HELMY, J. MOHD-AZLAN, A. GRANADOS, H. BERNARD, A. J. GIORDANO, AND E. ZIPKIN. 2017. Data from: Models for assessing local-scale co-abundance of animal species while accounting for differential detectability and varied responses to the environment. Dryad Digital Repository. <https://doi.org/10.5061/dryad.fn208>
- BUCKLEY, L. B., AND J. ROUGHGARDEN. 2005. Lizard habitat partitioning on islands: the interaction of local and landscape scales. *J. Biogeogr.* 32: 2113–2121.
- BULLOCK, J. M., R. J. EDWARDS, P. D. CAREY, AND R. J. ROSE. 2000. Geographical separation of two *Ulex* species at three spatial scales: does competition limit species' ranges? *Ecography* 23: 257–271.
- CAZELLES, K., M. B. ARAUJO, N. MOUQUET, AND D. GRAVEL. 2016. A theory for species co-occurrence in interaction networks. *Theor. Ecol.* 9: 39–48.
- COLLINGE, S. K., K. L. PRUDIC, AND J. C. OLIVER. 2003. Effects of local habitat characteristics and landscape context on grassland butterfly diversity. *Conserv. Biol.* 17: 178–187.
- CONNELL, J. H. 1980. Diversity and the coevolution of competitors, or the ghost of competition past. *Oikos* 35: 131–138.
- CONNOR, E. F., AND D. SIMBERLOFF. 1979. The assembly of species communities -chance or competition. *Ecology* 60: 1132–1140.

- CORLETT, R. T. 2009. The ecology of tropical East Asia. Oxford University Press, Oxford, UK.
- DARMON, G., C. CALENGE, A. LOISON, J.-M. JULLIEN, D. MAILLARD, AND J.-F. LOPEZ. 2012. Spatial distribution and habitat selection in coexisting species of mountain ungulates. *Ecography* 35: 44–53.
- DIAMOND, J. M. 1975. Assembly of species communities. In M. L. Cody, and J. M. Diamond (Eds.). *Ecology and evolution of communities*, pp. 342–444. Belknap Press, Cambridge, Massachusetts.
- DORAZIO, R. M., AND E. F. CONNOR. 2014. Estimating abundances of interacting species using morphological traits, foraging guilds, and Habitat. *PLoS ONE* 9: 1–9.
- FARR, T. G., P. A. ROSEN, E. CARO, R. CRIPPEN, R. DUREN, S. HENSLEY, M. KOBRIK, M. PALLER, E. RODRIGUEZ, L. ROTH, D. SEAL, S. SHAFFER, J. SHIMADA, J. UMLAND, M. WERNER, M. OSKIN, D. BURBANK, AND D. ALSDORE. 2007. The shuttle radar topography mission. *Rev. Geophys.* 45: 1–33.
- GODSOE, W., R. MURRAY, AND M. J. PLANK. 2015. The effect of competition on species' distributions depends on coexistence, rather than scale alone. *Ecography* 38: 1071–1079.
- GOMES, L. G. L., V. OOSTRA, V. NIJMAN, A. M. CLEEF, AND M. KAPPELLE. 2008. Tolerance of frugivorous birds to habitat disturbance in a tropical cloud forest. *Biol. Cons.* 141: 860–871.
- GOTELLI, N. J. 2000. Null model analysis of species co-occurrence patterns. *Ecology* 81: 2606–2621.
- GOTELLI, N. J., AND W. ULRICH. 2010. The empirical Bayes approach as a tool to identify non-random species associations. *Oecologia* 162: 463–477.
- GUILLAUMET, A., AND G. LEOTARD. 2015. Annoying neighbors: multi-scale distribution determinants of two sympatric sibling species of birds. *Curr. Zool.* 61: 10–22.
- HILLERISLAMBERS, J., P. B. ADLER, W. S. HARPOLE, J. M. LEVINE, AND M. M. MAYFIELD. 2012. Rethinking community assembly through the lens of coexistence theory. *Annu. Rev. Ecol. Evol. Syst.* 43: 227–248.
- JANKOWSKI, J. E., G. A. LONDONO, S. K. ROBINSON, AND M. A. CHAPPELL. 2013. Exploring the role of physiology and biotic interactions in determining elevational ranges of tropical animals. *Ecography* 36: 1–12.
- JANZEN, D. H. 1967. Why mountain passes are higher in the tropics. *Am. Nat.* 101: 233.
- LEHNER, B., K. VERDIN, AND A. JARVIS. 2006. HydroSHEDS technical documentation. World Wildlife Fund US, Washington, DC.
- LOIS, S., D. E. COWLEY, A. OUTEIRO, E. SAN MIGUEL, R. AMARO, AND P. ONDINA. 2015. Spatial extent of biotic interactions affects species distribution and abundance in river networks: the freshwater pearl mussel and its hosts. *J. Biogeogr.* 42: 229–240.
- LOMOLINO, M. V., B. R. RIDDLE, AND J. H. BROWN. 2006. *Biogeography* (3rd Edition). Sinauer, Sunderland, Massachusetts.
- LUNN, D. J., A. THOMAS, N. BEST, AND D. SPIEGELHALTER. 2000. WinBUGS - A Bayesian modelling framework: concepts, structure, and extensibility. *Stat. Comput.* 10: 325–337.
- MACKENZIE, D. I., L. L. BAILEY, AND J. D. NICHOLS. 2004. Investigating species co-occurrence patterns when species are detected imperfectly. *J. Anim. Ecol.* 73: 546–555.
- MEYER, C. F. J., AND E. K. V. KALKO. 2008. Bat assemblages on Neotropical land-bridge islands: nested subsets and null model analyses of species co-occurrence patterns. *Divers. Distrib.* 14: 644–654.
- MOD, H. K., R. K. HEIKKINEN, P. C. le ROUX, M. S. WISZ, AND M. LUOTO. 2016. Impact of biotic interactions on biodiversity varies across a landscape. *J. Biogeogr.* 43: 2412–2423.
- MORALES-CASTILLA, I., M. G. MATIAS, D. GRAVEL, AND M. B. ARAUJO. 2015. Inferring biotic interactions from proxies. *Trends Ecol. Evol.* 30: 347–356.
- MORUETA-HOLME, N., B. BLONDER, B. SANDEL, B. J. MCGILL, R. K. PEET, J. E. OTT, C. VIOLLE, B. J. ENQUIST, P. M. JORGENSEN, AND J. C. SVENNING. 2016. A network approach for inferring species associations from co-occurrence data. *Ecography* 39: 1139–1150.
- MUNGER, J. C., AND J. H. BROWN. 1981. Competition in desert rodents -an experiment with semipermeable enclosures. *Science* 211: 510–512.
- NELLEMANN, C., AND P. E. REYNOLDS. 1997. Predicting late winter distribution of muskoxen using an index of terrain ruggedness. *Arct. Alp. Res.* 29: 334–338.
- OVASKAINEN, O., D. B. ROY, R. FOX, AND B. J. ANDERSON. 2016. Uncovering hidden spatial structure in species communities with spatially explicit joint species distribution models. *Methods Ecol. Evol.* 7: 428–436.
- PEDRANA, J., J. BUSTAMANTE, A. TRAVAINI, AND A. RODRIGUEZ. 2010. Factors influencing guanaco distribution in southern Argentine Patagonia and implications for its sustainable use. *Biodivers. Conserv.* 19: 3499–3512.
- RAYAN, D., AND M. LINKIE. 2016. Managing conservation flagship species in competition: tiger, leopard and dhole in Malaysia. *Biol. Cons.* 204: 360–366.
- RICHMOND, O. M. W., J. E. HINES, AND S. R. BEISSINGER. 2010. Two-species occupancy models: a new parameterization applied to co-occurrence of secretive rails. *Ecol. Appl.* 20: 2036–2046.
- ROYLE, J. A. 2004. N-mixture models for estimating population size from spatially replicated counts. *Biometrics* 60: 108–115.
- SEBASTIAN-GONZALEZ, E., J. ANTONIO SANCHEZ-ZAPATA, F. BOTELLA, AND O. OVASKAINEN. 2010. Testing the heterospecific attraction hypothesis with time-series data on species co-occurrence. *Proc. R. Soc. B Biol. Sci.* 277: 2983–2990.
- SEGRE, H., R. RON, N. De MALACH, Z. HENKIN, M. MANDEL, AND R. KADMON. 2014. Competitive exclusion, beta diversity, and deterministic vs. stochastic drivers of community assembly. *Ecol. Lett.* 17: 1400–1408.
- SILVERTOWN, J. 2004. The ghost of competition past in the phylogeny of island endemic plants. *J. Ecol.* 92: 168–173.
- Team, R. C. 2013. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.
- TERBORGH, J. 1971. Distribution on environmental gradients: theory and a preliminary interpretation of distributional patterns in the avifauna of the Cordillera Vilcabamba, Peru. *Ecology* 52: 23–40.
- ULRICH, W., AND N. J. GOTELLI. 2013. Pattern detection in null model analysis. *Oikos* 122: 2–18.
- VEECH, J. A. 2013. A probabilistic model for analysing species co-occurrence. *Glob. Ecol. Biogeogr.* 22: 252–260.
- WADDLE, J. H., R. M. DORAZIO, S. C. WALLS, K. G. RICE, J. BEAUCHAMP, M. J. SCHUMAN, AND F. J. MAZZOTTI. 2010. A new parameterization for estimating co-occurrence of interacting species. *Ecol. Appl.* 20: 1467–1475.
- WARNING, N., AND L. BENEDICT. 2015. Overlapping home ranges and micro-habitat partitioning among canyon wrens (*Catherpes mexicanus*) and rock wrens (*Salpinctes obsoletus*). *Wilson J. Ornithol.* 127: 395–401.