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Extreme and complex variation in range-wide abundances across a threatened Neotropical bird community

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Abstract

Aim

Understanding patterns and drivers of variation in abundance across full species ranges is crucial in conservation science, but our knowledge of these forms and processes is limited, especially in the tropics. This study aims to; a) identify patterns in variation of abundance across sites; b) examine congruence of abundance hotspots across species and spatial autocorrelation of abundance within species; c) assess the nature and strength of environmental correlates of abundance (topography, habitat and human pressure).

Location

Twenty-six sites across the full ranges of 14 dry forest bird species in northern Peru.

Methods

Study sites in this patchy habitat were selected within strata derived from species distribution models, while also ensuring geographic representation. Species abundance data from variable-width transects were compared across sites and across range core versus edge; relationships between abundance and environmental variables were examined using GAMs, and spatial autocorrelation was examined with multivariate Mantel tests.

Results

Although most species were recorded at most sites, local abundance varied by one or two orders of magnitude. Several species showed a humped rather than the classic skewed abundance distribution, with abundance not necessarily highest at the centre of species' ranges. Spatial autocorrelation in species' local abundance was evident only at distances less than 55 km. Sites of maximum abundance for individual species did not coincide - nine different sites held highest

densities of at least one species. Relationships between local abundance and almost all environmental correlates were non-linear.

Main conclusions

The extreme variation in species abundances and the complexity in their relationships with environmental variables have important implications, both for design of conservation-motivated surveys for which we offer some recommendations, and for the need for multiple reserves to capture high local abundances of key species.

(A) **Introduction**

That local abundance varies across species' ranges is well established (e.g. Grinnell, 1914; Hengeveld & Haeck, 1981; Brown et al., 1995; Sagarin et al., 2006), but how precisely it varies, and what drives this variation, remain key questions for research, with important implications for macroecology, evolutionary studies and conservation science. The majority of species are believed to have low abundance throughout most of their range with small areas of high density (Gaston, 1990; Brown et al., 1995; McGill & Collins, 2003). According to the 'abundance centre hypothesis', these hotspots of high abundance tend towards the centre, or multiple core areas, of species' ranges with local abundance lower at the range margins (Rapoport, 1975; Brown, 1984; Hengeveld, 1990). However, despite some theoretical and empirical support for this hypothesis (Brown, 1984; Guo et al., 2004), there are examples of species that do not conform to the pattern (Sagarin & Gaines, 2002; Gaston, 2003; Samis & Eckert, 2007), for example, when there are multiple hotspots of abundance (e.g. Maurer, 1994). There is general acknowledgement that it is an oversimplification (Sagarin et al., 2006), relying on the geographical centre rather than the niche centre, as well as omitting factors such as biogeographical barriers and species interactions (Brown, 1995), and demographic variability (Williams et al., 2003). Drivers of local abundance are likely to be complex, arising from a range of non-biotic (e.g. climate and habitat) and biotic factors (e.g. competition and dispersal; Pearson & Dawson, 2003; Guisan & Thuiller, 2005), to which, anthropogenic factors are occasionally added separately (e.g. Smith, 1868; Yackulic et al., 2011).

Understanding the above patterns and drivers is of particular importance in conservation science, for example, for effective population estimation or detection of abundance trends, identification of key sites, or identification of environmental pressures that limit abundance (Lawton, 1993; Mace et al., 2008). However, our understanding is severely limited by a lack of range-wide data on actual abundance (Sagarin & Gaines, 2002; Marsden & Royle, 2015), especially for threatened species and multiple species within important areas (Brooks et al., 2006). From a conservation viewpoint, there

are great benefits if we are able to predict local abundance from local environmental measures, or even from spatial patterns of abundance themselves. Scarce resources for conservation (McCarthy et al., 2012) can also be saved by taking similar approaches for multiple species. With this in mind, we ask the following questions

- How does local abundance vary across species' ranges, and is this variation consistent across species? Is local abundance at nearby sites autocorrelated and does abundance relate predictably to location within range?
- Do local hotspots of abundance exist for multiple species sharing broad habitats and ranges? If so, can this congruence help in protected area selection?
- How does local abundance across the assemblage respond to environmental correlates? If so, can these relationships be used to reliably predict abundance or threats to species?

(A) **Methods**

(B) Study species and site selection

The study focused on 14 lowland dry forest bird species, all but one of which have their entire ranges

within the study area. The exception is Long-tailed Mockingbird *Mimus longicaudatus* Tschudi, 1844

which has a geographically isolated subspecies in the Marañon Valley (Chapman 1926). Two further

species (Mouse-coloured Tyrannulet *Phaeomyias murina* Spix, 1825 and Necklaced Spinetail

Synallaxis stictothorax Sclater, 1859) that also have Marañon populations have recently been split

into sister species (del Hoyo & Collar, 2016). Thus, we consider that our analyses for all 14 species

are range-wide. The median range size of the 14 bird species was just over 50,000 km^2 (min = 2,726

km^2, max = 146,892 km^2). These ranges sit at a mean percentile of 22% of all Neotropical birds, as

mapped by BirdLife International & NatureServe (2012).

We selected 26 sites across these ranges within dry forest and scrub habitat, below an

altitude of 500 m, in northwest Peru (Figure 1). Given the size of the study area (approximately

600 km from northern to southern extreme), it was logistically unfeasible to implement a random

sampling strategy and obtain sufficient species records. Therefore, to meet the requirements of

obtaining sufficient bird records from a wide geographic spread of sites across species' ranges, we

selected sites randomly from within three strata representing higher probabilities of species

occurrences, and a 50 km grid geographic stratum across the study area (see Figure S1 in Supporting

Information). To identify the 'occurrence probability' stratum, we created species distribution

models using occurrence records from four target bird species, representative of study species'

habitat requirements and distributions within the study area (Schulenberg et al., 2007).

Environmental predictors used in the model were climate based: mean annual rainfall, mean annual

temperature (Hijmans et al., 2005), and habitat-based: maximum and minimum Normalized

Difference Vegetation Index from the dry and wet seasons (processed from MODIS product,

MOD13QA1). Maxent software (Phillips et al., 2006), run through the R package Dismo (Hijmans et

al., 2013), was used to create distribution models for each species, and were evaluated with mean AUC from 5-fold cross validation. The final models were constructed using all the data points, and then summed to create a single composite surface, providing regions of high and low probability of occurrence for study species. Despite criticisms of using AUC as a means to validate models (Lobo et al., 2008), it is still the most widely used threshold-independent method of judging model performance. To create the geographic strata, we created a regular 50 km grid across the study area and identified the top 25 cells in terms of highest average model scores. We randomly selected sites only from the top three deciles of the probability of occurrence from the final model, using double weights for the top decile, i.e. sampling was restricted in order to avoid the large areas of high unsuitability for the species, including desert and urban areas. Sampling was repeated until at least one site fell in the top 25 grid cells. In the field, sites were chosen as close as possible to the randomly selected sites, and were only moved when access or safety issues prevented the researchers from reaching the site. All sites, except for the southernmost, were within the extant or former ranges of all study species as mapped by BirdLife International & NatureServe (2012). Median distance between sites was 150 km (range: 5-625 km).

(B) **Field methods**

All fieldwork was carried out from June to October 2013 by the first author and Elio Nuñez Cortez. Both observers participated in pilot studies at six sites in 2012 to practise distance estimation, learn bird calls and trial other field methods. To estimate bird abundances, we used a variable-width transect method, with two observers walking four 2.5 km parallel, straight transects at each site (not located on trails), separated by 500 m, using just GPS for guidance. We walked each transect once at a speed of 1-1.5 km h^{-1} to gather bird data. Distances to birds were estimated either by eye, or for distances greater than approximately 25 m, with laser rangefinders. Two transects were completed per day where conditions permitted, with bird data collected between 6:00 and 11:00. For each bird encounter, the following were noted: species; number of individuals; type of detection (aural or

visual); and perpendicular distance. We measured habitat characteristics within 10 m radius circular

plots at twelve points positioned 200 m apart on each transect. Characteristics included tree species

present; % of vegetation cover at two vertical strata (<3 m, >3 m); diameter at breast height (dBH)

and height of three largest trees; total number of stems (dBH > 10 cm); grass cover; presence of

epiphytes. Topographic characteristics measured were altitude and slope. Human pressure was

assessed at each plot as presence of felled trees (cut tree trunks) and a count of ungulate dung. An

additional human pressure index was later calculated to combine urban and rural population

pressure, road proximity and protection status of sites as

$$(Pop_{urban} + Pop_{rural}) \times (1/Road\ dist) \times Protection\ status$$

where Pop_{urban} is the number of inhabitants of cities within 25 km; Pop_{rural} is rural population size of

the 2nd degree administrative region containing the study site; Road dist is distance to nearest main

road (km); and unfavourable protection status is penalised as follows, 1: non-protected, 0.5:

protected.

FIGURE 1

(B) **Data analysis**

(C) **Local abundance estimation**

We used the multiple covariates engine of Distance 6.1 to estimate local abundance at sites

(Buckland et al., 2001; Marques et al., 2007). An advantage for rare species is that this method

enables a single detection function to be fitted across all sites and adjusted with site-specific

covariates. Data were analysed as clusters and distance data were binned and truncated, following

guidelines (Buckland et al., 2001) to improve fit of detection functions. Preliminary analyses with

different truncation distances and intervals were trialled and a truncation distance, number of

intervals and candidate model families (e.g. half-normal, uniform, hazard-rate) were set for each

species based on visual inspection of histograms and goodness of fit tests. We selected covariates

for density estimation by assessing correlations between potential covariates, variation between

sites, and their effect on the distances recorded per species. Covariates were selected based both on

previous studies of those most likely to influence detectability generally (e.g. Marques et al., 2007),

and on the nature of habitat within the study area specifically. We used mode of bird detection

(heard or not heard) and habitat features (percentage of low cover and tree height) as covariates.

Full details of covariate selection are given in Devenish (2017). Final models were selected per

species using AIC minimisation. Density of groups per km^2 was converted to individuals per km^2

using average cluster size, given that correlations between cluster size and detection distance were

not significant at $\alpha = 0.05$ for all species.

(C) **Variation in abundance**

We plotted histograms of species densities across all sites and measured symmetry of the

distribution via skewness (Zar, 1999). Species abundance distributions were considered skewed

when this value was significantly different from zero, following tables of critical values of the skew

measure (Zar, 1999). To assess differences in abundance between the centre and periphery of

species' distributions, we represented species' ranges as convex hulls constructed from post-1970

occurrence records from museum specimens and observations (following manual and automated

validation; see Table S1 in Supporting Information). The coastline and upper altitudinal limits were

used to exclude areas from each convex hull to approximate range shape further (see Figure S2 in

Supporting Information). Although convex hulls have their limitations (Rapoport, 1975), the method

facilitates comparison between species, in that each range was constructed following a standardised

method. We compared local abundance between core and edge areas using Wilcoxon (Mann-

Whitney) two sample tests (Zar, 1999) which is robust to different sample sizes, and small numbers

in each group (Fowler & Cohen, 1992). Core areas were defined as the inner polygon occupying 50%

of the total convex hull area with a perimeter equidistant to the full range perimeter. Sites with absences were only included in the analysis if they lay within the convex hull range.

(C) **Spatial autocorrelation in abundance**

To examine spatial autocorrelation of local abundance across sites for all species, we used a multivariate Mantel correlogram (Legendre & Legendre, 1998). First, pairwise distances between all sites were grouped into six bands between 0 and 650 km, with sample sizes of 204, 236, 122, 52, 26, and 10 respectively. Correlation coefficients were then calculated between a similarity matrix of all species' densities (using the Jaccard metric) and the matrix of geographical distances between sites in each band. Significance of correlations was evaluated using permutation tests, as implemented in the R package, vegan (Oksanen et al., 2015). Spatial autocorrelation was also evaluated for each species separately, using Moran's I, over the same six distance bands. Given the general lack of spatial autocorrelation (only significant at < 55 km in six of 14 species; see Results), we continued with the following analyses. To identify congruence of local abundance hotspots across species, we identified the sites holding maximum density and the highest three densities for each species. To assess whether species' densities varied in similar ways across sites, we calculated Spearman's rank correlation coefficients for density between all species pairs at all sites (n = 91).

(C) **Environmental correlates of local abundance**

We evaluated the nature and strength of ten environmental correlates of bird abundance, across the dry forest bird community as a whole, using separate Generalised Additive Models (GAMs), where each correlate was modelled as a function of community density. This approach was favoured over a full multivariate model because in this analysis we are more interested in the complexity of the relationships of the community with individual environmental measures (e.g. Taylor et al., 2014) than with identifying suites of habitat variables that together might drive abundance of individual species (e.g. for conservation management). This said, we made a preliminary selection of

uncorrelated variables to reduce the total number of models built. We first assigned these to one of three groups: topography (altitude, slope); habitat structure and composition (understorey cover, tree height, number of stems, grass cover, tree species richness); and anthropogenic pressures (grazing pressure, logging pressure, human population pressure). Variables in each group were inspected for collinearity using pairwise scatterplots and Variance Inflation Factors (VIF). Any variable with VIF > 5 was removed (Zuur et al., 2007), and the group checked again until all VIF values were < 5.

GAMs were used to model the relative strength and degree of complexity (non-linearity) of the relationship between each correlate and local bird abundances. First, an ordination based on the abundances of the 14 study species at each site was performed using non-metric multidimensional scaling (NMDS; Legendre & Legendre, 1998; as implemented in R package, vegan Oksanen et al., 2015). Each environmental correlate was then modelled as a function of the site scores on both ordination axes simultaneously and a spatial term, consisting of the x and y coordinates of the sites (Hefley et al., 2017), using thin plate spline isometric smoothers with fixed degrees of freedom in R package mgcv (Wood, 2006). Best models for each correlate, from the three combinations of terms (NMDS scores; spatial term; NMDS + spatial term) were chosen using AIC minimisation (Anderson et al., 2000). In cases where the difference in AIC between models was less than 2.0, the least complex model was chosen. To evaluate the complexity of the relationship between density and correlates, models were repeated with increasing basis dimension values of 4, 6 and 8, effectively increasing the amount of smoothing within each model (Wood, 2006). We expected correlates with more complex relationships to show steeper increases in explained deviance as basis dimension increases. Where the best models included the NMDS term, we plotted predicted values as contours over the species ordination to visualise the relationship between the species' density and correlate. Species centroids, weighted by density values at each site, were plotted on the NMDS axes (Oksanen et al., 2015). We used R (R Core Team, 2014) for all analyses.

(A) **Results**

(B) **Variation of abundance across species' ranges**

We recorded a total of 7,505 bird encounters over the 26 transects for 14 species. Encounter rates averaged 28.7 individuals km^{-1}, equivalent to approximately 7 birds every 10 minutes at the average walking speed. Overall, non-zero local abundances ranged from less than one to over 3,000 individuals km^{-2} (Table 1, see Table S2 in Supporting Information). Two broad patterns of variation in species' densities across their ranges are distinguishable. Nine species showed extreme variation in local abundance across sites, with species having low densities at most sites and higher densities at relatively few. These species have a positively skewed intraspecific abundance distribution (Figure 2a-i) with skew significantly different from zero (skew, g_1 = 1.19 to 3.37, n = 26, p < 0.05). Median densities for these species are less than 10% of their maximum density (Table 1).

FIGURE 2

A second group (five species; Figure 2j-m) showed a humped density distribution, that is, species had consistently high densities across their ranges, with relatively few sites with extreme high or low local abundance. Median density values were generally > 40% of the maximum density value. Species' abundance distributions were not significantly skewed (skew, g_1 = 0.01 to 0.38, n = 26, p > 0.20) and excess kurtosis was negative, implying that distribution of abundance is relatively flat. This group also shows generally high and less variable densities (Table 1). The presence of sites with zero density did not affect the groupings of the species' abundance distributions.

TABLE 1

In all species, maximum and minimum densities (> 0) varied by at least an order of magnitude, and by two orders of magnitude in three species. Where densities showed most variability between sites, the interquartile range was over five times greater than the median (Table 1). We found a significant positive correlation between number of sites occupied and median local abundance (r_s = 0.57, p = 0.02, n = 26). Additionally, species with higher numbers of sites occupied had lower variability between local abundances (r_s = -0.92, p < 0.01, n = 26; Table 1). Different spatial arrangements of local abundance were found, with the highest species' densities not always occurring at the centres of their geographical ranges. Three species had significantly higher local abundances within the central areas of their ranges compared to the periphery (Figure 3, see Table S3 in Supporting Information) while all the others showed no significant relationship.

FIGURE 3

(B) **Spatial autocorrelation in local abundances**

Spatial autocorrelation in species' densities across sites was significant only within the smallest distance band, < 55 km (r_s = 0.19, n = 204, p = 0.004). Correlation coefficients decreased with increasing distance between sites, but were weak for the remaining five distance bands, varying between 0.1 and -0.2. Correlograms for individual species also showed a generally decreasing pattern with larger distance bands; significant correlations were found in six of fourteen species at the smallest distance band (see Figure S3 in Supporting Information).

(B) **Congruence of abundance hotspots across species**

Sites of maximum abundance for individual species did not coincide. Nine different sites held highest densities of at least one species, and 20 of 26 sites held 'top three' abundances for at least one species. Of 91 pairwise correlations between species' densities, 21 species' pairs were significantly correlated, but only ten correlation coefficients were > 0.5 (Figure 4). The highest correlation

coefficient was 0.68, for Necklaced Spinetail *Synallaxis stictothorax* and Superciliated Wren *Cantorchilus superciliaris* Lawrence, 1869, both of which occupy lower strata of the dry scrub. Local abundances of two species pairs had significant negative correlations.

FIGURE 4

(B) **Environmental correlates of species' local abundances**

Ordination on two axes of species' densities at sites using non-metric multidimensional (NMDS) had a final stress value of 0.14. McCune et al (2002) state that most ecological data produce stress values between 0.10 and 0.20, with values of < 0.15 being satisfactory.

TABLE 2

Best supported (lowest AIC) GAMs for nine of the ten environmental correlates included the NMDS scores, with only that for understorey cover including the spatial term alone (see Table S4 in Supporting Information). For the above nine models, explained deviance varied from 62% to 90% with the maximum basis dimension (Table 2). All relationships between correlates and density were non-linear, although mean number of stems most approximates a linear response (Figure 5).

In simpler models (basis dimension = 4), the three anthropogenic pressure variables explained least variability in densities. However, two of these (logging and human pressure) had the highest gains in explained deviance with more complex models (basis dimension = 8; Table 2; Figure 5).

FIGURE 5

(A) **Discussion**

(B) **Variation in density across species' ranges**

Variation in local abundance was extreme across the ranges of most species. Although differences in abundance of at least one order of magnitude have been found in other studies encompassing the

whole ranges of species (e.g. Curnutt et al., 1996; Brewer & Gaston, 2003; Filloy & Bellocq, 2006), most studies evaluating spatial variation in abundance do not cover full ranges (Samis & Eckert, 2007). In general, we found that species with lower median densities showed more variation in density. Nine of fourteen species in our study showed the classic skewed distribution of local abundances, where species are rare at most sites but abundant at a few sites (Gaston, 1990; Brown et al., 1995; Brewer & Gaston, 2003; McGill & Collins, 2003). The other five, showing humped local abundance distributions, were among the commonest species. Common species across a number of taxonomic groups have been found to occupy more central niche positions (e.g. habitat dimensions) than rare species (e.g. Gregory & Gaston, 2000; Marsden & Whiffin, 2003; Heino, 2005). Martínez-Meyer et al. (2012) found a decline in abundance as distance from central niche positions increased. For such species, density can fall away on all sides, whereas for species with niche positions at one extreme, it cannot. The five species with humped abundance distributions did tend to occupy mid-range conditions within our study area, at least for some environmental variables (Figure 5).

Hotspots of local abundance were, as found in other studies, often multiple rather than singular (Maurer & Villard, 1994; Sagarin & Gaines, 2002; Sagarin et al., 2006), and not necessarily concentrated in the centres of species' ranges (Sagarin & Gaines, 2002; Kluth & Bruelheide, 2005; Murphy et al., 2006). The 'abundant centre hypothesis' is more likely to refer to the niche centre than the geographic centre of the range (Blackburn et al., 1999; McGeoch & Price, 2004; Martínez-Meyer et al., 2012), or as Hengeveld and Haeck (1981) termed it, ecologically 'central' rather than geographically 'central'. Carter and Prince (1981) noted that many plants are abundant at their limits, implying an abrupt response to the climatic gradients that control the distribution. Brown (1984) hypothesised that contributing factors to this response may include abrupt changes in availability of resources, such as caused by coastlines and mountains, important features within our study area.

Despite sharing similar ranges and broad habitats, different species did not tend to occur at their highest local densities at the same sites. This result is also consistent both with the lack of grouping of species when plotted on the two NMDS axes, and with findings elsewhere. For example, Mehlman (1994), working with US Breeding Bird Survey data, reported little overlap between sites of species' highest abundances. A study comparing pairwise density of 14 shrubsteppe species in northwest US found just eight species with significant correlations between density values at sites (Wiens & Rotenberry, 1980). If species in our study had been clumped within hotspots of coincident high density, then we might expect that certain drivers of density acted on different species in similar ways, but this was not the case leading to the conclusion that determinants of local density are generally distinct for each species. A useful extension would be to identify trait attributes that influence differences in local abundances at sites, patterns of habitat associations across species, and inter-specific interactions between species. However, such a study would require a very large survey effort to obtain sufficient data to identify patterns, especially with rare species.

Variation in local bird abundances covaried in a non-linear way with all of the environmental correlates. Relatively few studies have investigated correlates of local abundance, with most focusing on species richness or occupancy. Nevertheless, habitat variables were found to influence bird abundance more than climate variables at a mesoscale (1,700 km latitudinal gradient) in a study of 88 grassland species in Argentina (Filloy & Bellocq, 2013). Marsden and Whiffin (2003) found no relationship or weak correlations between local bird abundance and three composite habitat axes in a Neotropical forest. In our study, the least complex responses, indicative of similarity across species' responses, were found among the habitat-based correlates. Therefore, factors such as mean number of stems, tree height, and tree species richness may be useful as general indicators of avifaunal health, especially as they are relatively easy to measure in the field. No single group of environmental correlates (habitat, topography and human pressure) stood out as particularly useful predictors, although more complex relationships with local abundances were found for pressure-

based than for habitat correlates. Other authors have also found variability in response of abundance to pressure-based predictors in the Neotropics: Piana and Marsden (2014) found opposing responses to cattle grazing among different raptor species, and Filloy and Bellocq (2006) found mixed responses among *Sporophila* seedeaters to agricultural development. There is a long history of human alteration of environments on the Peruvian coast with cycles of agricultural expansion and contraction (Shimada & Shimada, 1985; Hocquenghem, 1998, 1999), which have surely influenced current patterns of distribution and abundance.

(B) **Implications for conservation**

A shortfall in conservation funding (James et al., 1999; McCarthy et al., 2012), especially in the most biodiverse countries (Brooks et al., 2006), has led to conservation prioritisation schemes such as Red Listing (IUCN, 2001; Rodrigues et al., 2006), often informed by data on population sizes and trends. Extreme heterogeneity in local abundances across species' ranges has important implications for the generation of such data. Many species of conservation importance lack even a single density estimate from anywhere within their range (Marsden & Royle, 2015). For example, one of the best-studied parrot species, the Scarlet Macaw *Ara macao* has just four density estimates from an extent of occurrence greater than 5 million km^2. Single density estimates cannot reflect the likely complex variation in local abundance across species' ranges, and scaling up from such estimates runs the risk of local data not being representative of the species as a whole (Hengeveld & Haeck, 1981). In terms of survey design, the more local abundance varies across the range of a species, the more field sites will be needed to capture this variability. The negative relationship between proportion of sites occupied and variability in local densities indicates that a desk-based survey of presence/absence of the target species (e.g. using online occurrence databases) may help to inform how many sites need to be visited. It may also be useful to examine encounter rates/density estimates for the target species at sites as the survey progresses or during pilot studies. Again, high variability may indicate that a greater number of sites needs to be surveyed. We argue that this study obtained high

numbers of records for the target species despite covering a tiny proportion of the 50,000 km^2 study area. This was achieved by disregarding many areas of unsuitable habitat by stratifying the study area using probability of occurrence from species distribution models and adjusting survey effort in areas of low probability accordingly (see also Aizpurua et al., 2015). Finally, our study indicated that survey sites at geographically marginal sites should not be neglected and may contribute significantly to overall abundance, given that range margins do not always coincide with ecological margins (Chardon et al., 2015).

Spatial autocorrelation of local abundance was strong only very locally (typically < 55 km), a pattern found in most, but not all, studies (e.g. Eber & Brandl, 1994; Brewer & Gaston, 2003; Murphy et al., 2006). Distances over which spatial autocorrelation of local abundances is significant could be determined from a pilot study and guide minimum distances between survey sites to reduce survey effort. This distance may also be useful when evaluating the effect of disturbance on species' abundance. Such studies often designate 'natural' or control (undisturbed) sites as baselines and then compare them with disturbed sites at different locations (e.g. Barthlott et al., 2001) rather than comparing the same sites before and after disturbance. However, extreme variation in local abundance could confound changes in abundance attributed to disturbance (Gardner et al., 2007). For example, despite a heavily altered study area, Jones et al (2003) found that habitat variables were more important in controlling abundance than pressure variables. In these kind of studies, sites should be positioned within distances where spatial autocorrelation makes them comparable.

There was little congruence in local abundance hotspots across species due to complex responses to environmental correlates, as found among communities elsewhere (Garrido et al., 2003; McGeoch & Price, 2004). This means that multiple protected/management areas will be required to capture large proportions of the populations of each species, given the large differences in abundance between sites. Most conservation planning algorithms are based on species' presence

and/or species richness (e.g. site selection algorithms, priority site identification; Brooks et al., 2006; Fleishman et al., 2006). This may lead to an insufficient network of proposed sites when patterns of species' presence or absence is similar but local abundance varies greatly. Recent studies provide further evidence for improving systematic conservation planning and site selection algorithms with site-based abundance estimates (Johnston et al., 2015; Veloz et al., 2015). However, the added costs of collecting abundance data may not always outweigh the benefits, especially in the case of more common species (Joseph et al., 2006). Further research is still needed to find cost-efficient methods to determine patterns of range-wide abundance in species without implementing full surveys. Promising results in quantifying changes in abundance, which may be possible to adapt to the above needs, have been shown with a widespread, poorly known species (Senyatso et al., 2013). Other techniques, such as interpolating density surfaces from several local abundance estimates across a range (e.g. Thomas et al., 2010), combined with carefully planned surveys, may also increase the utility and cost-efficiency of using local abundance to inform conservation.

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Biosketch

Christian Devenish is interested in describing species distributions, including factors that limit ranges and control abundance, using field work and analytical methods. He is also interested in applying research results to bird conservation, and has worked extensively in this field in northern South America.

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

Table S1 Data sources of species occurrence points

Table S2 Bird density estimates per site

Table S3 Wilcoxon two sample tests between local abundance in centre and edge of species' ranges

Table S4. AIC values for GAMs of environmental correlates as a function of NMDS scores and spatial terms.

Figure S1 Overview of site selection methods

Figure S2 Occurrence records used to construct convex hulls for centre-periphery analysis.

Figure S3 Spatial autocorrelation of density over five distance bands per species

Table 1. Maximum, minimum, median and coefficient of dispersion (interquartile range/median) of species abundance across 26 sites. Species are ordered by increasing variability in density.

	Grey-and-white Tyrannulet *Pseudelaenia leucospodia*	Superciliated Wren *Cantorchilus superciliaris*	Long-tailed Mockingbird *Mimus longicaudatus*	Cinereous Finch *Piezorina cinerea*	Necklaced Spinetail *Synallaxis stictothorax*	Pacific Parrotlet *Forpus coelestis*	Fasciated Wren *Campylorhynchus fasciatus*	Rufous Flycatcher *Myiarchus semirufus*	Short-tailed Woodstar *Myrmia micrura*	Mouse-coloured Tyrannulet *Phaeomyias murina*	Tumbes Sparrow *Rhynchospiza stolzmanni*	Sulphur-throated Finch *Sicalis taczanowskii*	Tumbes Tyrant *Tumbezia salvini*	Peruvian Plantcutter *Phytotoma raimondii*
Maximum	103.2	90.0	305.5	161.7	157.1	210.7	97.6	44.6	113.9	284.4	344.9	3060.2	38.4	104.7
Minimum (>0)	3.0	1.0	22.9	4.4	4.6	0.9	0.7	1.9	2.3	3.8	5.0	6.6	0.9	1.8
Median	51.5	38.7	126.8	66.9	54.1	38.0	5.9	2.2	6.6	26.6	35.7	76.9	0.5	0.9
IQR/median	0.7	0.8	0.8	1.3	1.6	1.7	2.8	3.0	3.4	3.5	4.0	5.5	7.4	16.8
Percentage of sites occupied	96	96	100	88	81	88	65	88	65	69	57	62	54	50

Table 2. Complexity of relationships between environmental correlates and bird densities represented by change in explained deviance with increasing basis dimension (smoothing) in GAMs. Correlates are ordered by decreasing complexity as measured by difference in explained deviance between models with basis dimension 8 and 4. Correlates marked [+] are those where the best models included the spatial term, the remainder only included the NMDS scores.

Correlate	Explained deviance		
	Basis dimension: 4	Basis dimension: 6	Basis dimension: 8
Logging pressure[+]	22.69%	66.63%	79.22%
Human pressure[+]	33.26%	59.11%	80.17%
Altitude[+]	54.26%	82.75%	90.08%
Grass presence[+]	56.49%	70.65%	85.45%
Grazing pressure[+]	35.41%	52.05%	62.18%
Tree height	46.51%	69.29%	71.41%
Tree species richness[+]	64.45%	79.01%	85.06%
Slope	47.03%	54.11%	65.59%
Mean no. stems	53.68%	56.26%	61.73%

Figure 1. Study sites in northern Peru, with maximum NDVI values over the wet season (December to May) to illustrate extent of ground vegetation cover and desert/scrub areas. See Table S2 for key to site names.

Figure 2. Distribution of species' local abundance at 26 sites, ordered by decreasing skewness. The first bar (black) shows zeros at sites, the following bars are of equal width in each histogram.

Figure 3. Variation in local abundance across species' ranges. Minimum convex polygons show core and edge areas (see methods) with abundance at sites expressed in quartiles to facilitate comparison. Boxplots show difference in abundance (individuals km^{-2}) between the two regions, those bordered in dashed red lines are significantly different ($\alpha = 0.05$) according to the Wilcoxon two sample test. Note different scale of each map.

Figure 4. Frequency of Spearman's rank correlation coefficients for pairwise correlations between densities at 26 sites (n = 91). Red (dashed) and blue (dotted) lines show critical values of Spearman's correlation coefficient for p values corresponding to 0.05 and 0.01.

Figure 5. NMDS ordination (stress = 0.14) based on species densities across 26 sites with fitted GAM surfaces (using a basis dimension of six for each plot) representing smooth trends between species densities and habitat-based, topographic, and pressure-related correlates. The plots are ordered according to decreasing complexity. Key to species (see Table 1 for English names): Mm - *M. micrura*; Fc - *F. coelestis*; Ss - *S. stictothorax*; Pm - *P. murina*; Pl - *P. leucospodia*; Ts - *T. salvini*; Ms - *M. semirufus*; Pr - *P. raimondii*; Cf - *C. fasciatus*; Cs - *C. superciliaris*; Ml - *M. longicaudatus*; Pc - *P. cinerea*; St - *S. taczanowskii*; Rs - *R. stolzmanni*.

Supporting Information

Devenish, C., Buchanan, G. M., Smith, G. R. & Marsden, S. J. 2017. Extreme and complex variation in range-wide abundances across a threatened Neotropical bird community. Diversity and Distributions.

Table S1. Data sources of species occurrence points used to make convex hulls

Source	Record type	Percentage of records	Online references
eBird	Observations	66	http://ebird.org/content/ebird/
Literature and unpublished reports	Observations and specimens	30	n/a
Museum databases (VertNet and other museums)	Museum specimens	2	http://vertnet.org/ http://www.lsu.edu/mns/collections/ornithology.php
Xenocanto	Sound recordings	2	http://www.xeno-canto.org/

Table S2. Bird density estimates (individuals km^{-2}) ± standard error and sample size (in parentheses) per site. See Figure 1 for location of numbered sites.

No.	Site	*M. micrura*	*F. coelestis*	*S. stictothorax*	*P. murina*	*P. leucospodia*	*T. salvini*	*M. semirufus*
	Mean of all sites	19.1 ± 4.5 (132)	51.2 ± 6.7 (244)	63.2 ± 3.7 (758)	60.1 ± 6.2 (851)	44.5 ± 2.8 (871)	4.1 ± 0.7 (101)	5.9 ± 1.2 (69)
1	Tucillal	4.8 ± 4.2 (1)	120.5 ± 29.9 (20)	0	0	0	3.5 ± 9.1 (1)	0
2	Fernandez Bajo	15.3 ± 5.5 (5)	66.5 ± 23.8 (15)	13.7 ± 4.9 (7)	0	3.0 ± 2.9 (2)	1.9 ± 1.1 (2)	+
3	Enace	0	42.5 ± 23.6 (10)	37.1 ± 4.5 (21)	63.3 ± 11.6 (32)	7.4 ± 4.4 (5)	0	+
4	Lancones	42.3 ± 12.0 (14)	145.7 ± 49.7 (27)	83.6 ± 9.3 (38)	15.8 ± 2.7 (10)	35.8 ± 9.1 (25)	2.3 ± 1.8 (1)	8.2 ± 3.2 (3)
5	Puerta Pulache	6.7 ± 3.7 (2)	24.8 ± 10.0 (9)	4.6 ± 2.4 (2)	35.1 ± 6.1 (26)	50.4 ± 2.8 (39)	18.1 ± 9.0 (16)	2.2 ± 2.0 (1)
6	Pampa Larga	9.5 ± 5.6 (2)	48.5 ± 33.4 (8)	48.8 ± 7.1 (29)	33.6 ± 5.1 (17)	22.9 ± 3.9 (20)	0	2.0 ± 1.8 (1)
7	Progreso Bajo	0	2.2 ± 1.9 (1)	146.1 ± 21.7 (57)	25.4 ± 10.0 (17)	67.4 ± 19.7 (45)	0	18.5 ± 10.4 (9)
8	Cruz de Caña	23.1 ± 9.2 (6)	27.3 ± 18.3 (3)	118.8 ± 13.6 (53)	64.5 ± 10.4 (29)	65.0 ± 6.2 (45)	0	+
9	Sagrado Corazón	16.8 ± 8.9 (4)	49.0 ± 24.5 (8)	59.4 ± 11.7 (31)	138.5 ± 14.9 (57)	54.3 ± 4.0 (35)	0	2.2 ± 2.3 (1)
10	Islilla	0	0	91.2 ± 19.4 (49)	0	23.2 ± 7.2 (18)	0	8.0 ± 5.4 (4)
11	Ancajima	113.9 ± 52.6 (26)	60.7 ± 17.4 (13)	124.3 ± 16.7 (50)	159.5 ± 28.2 (70)	58.1 ± 10.9 (37)	3.5 ± 2.3 (4)	4.7 ± 4.5 (2)
12	Ñapique	0	34.9 ± 23.3 (3)	143.9 ± 34.1 (65)	0	9.6 ± 4.7 (8)	0	13.0 ± 5.8 (5)
13	Ñaupe	39.8 ± 16.6 (11)	210.7 ± 93.5 (22)	103.1 ± 7.7 (43)	191.2 ± 19.8 (92)	42.8 ± 11.6 (28)	21.0 ± 2.7 (23)	6.8 ± 4.4 (3)
14	Piedra Mora	54.3 ± 11.2 (16)	113.7 ± 59.1 (19)	44.6 ± 10.9 (24)	11.6 ± 3.2 (9)	55.2 ± 10.9 (43)	4.0 ± 1.4 (4)	+
15	Las Norias	6.6 ± 4.3 (2)	81.1 ± 32.7 (9)	30.3 ± 9.0 (14)	70.9 ± 11.7 (49)	60.2 ± 12.1 (48)	3.4 ± 1.8 (4)	6.1 ± 3.4 (3)
16	Illescas	0	0	136.3 ± 17.6 (65)	0	20.1 ± 3.2 (16)	0	1.9 ± 1.8 (1)
17	Pañalá	15.7 ± 5.9 (6)	0.9 ± 0.9 (1)	86.4 ± 8.3 (45)	27.8 ± 13.2 (19)	52.7 ± 5.9 (45)	+	+
18	La Peña	2.7 ± 2.3 (1)	11.0 ± 7.1 (3)	18.6 ± 3.0 (11)	101.7 ± 11.5 (70)	103.2 ± 10.6 (84)	5.2 ± 2.1 (5)	+
19	Pomac - Poma III	20.2 ± 7.9 (5)	17.2 ± 12.8 (3)	91.6 ± 16.0 (37)	0	78.6 ± 9.7 (58)	3.0 ± 0.9 (3)	5.9 ± 2.1 (3)
20	Pomac - Zona Recuperada	91.9 ± 23.9 (21)	41.1 ± 13.3 (12)	45.5 ± 8.1 (23)	0	55.4 ± 10.3 (45)	0.9 ± 1.0 (1)	2.1 ± 1.9 (1)
21	Pomac - Salinas	31.4 ± 9.3 (9)	31.3 ± 14.0 (8)	59.6 ± 12.6 (30)	12.4 ± 4.6 (8)	69.1 ± 7.6 (54)	1.1 ± 1.0 (1)	5.8 ± 3.5 (3)
22	La Viña	2.3 ± 2.1 (1)	10.2 ± 5.1 (4)	0	0	49.5 ± 8.5 (43)	0	0
23	Cañoncillo	0	15.7 ± 7.0 (8)	157.1 ± 28.9 (64)	3.8 ± 2.3 (5)	71.3 ± 12.1 (53)	38.4 ± 6.2 (36)	44.6 ± 11.4 (19)
24	Mocan	0	103.0 ± 38.9 (19)	0	223.2 ± 26.8 (102)	57.4 ± 11.1 (37)	0	5.0 ± 5.2 (2)
25	La Arenita	0	82.7 ± 27.4 (19)	0	284.4 ± 120.4 (159)	28.3 ± 11.0 (23)	0	0
26	Monte Zarumo	0	0	0	114.1 ± 19.9 (80)	17.4 ± 1.8 (15)	0	16.3 ± 6.9 (8)

No.	Site	*P. raimondii*	*C. fasciatus*	*C. superciliaris*	*M. longicaudatus*	*P. cinerea*	*S. taczanowskii*	*R. stolzmanni*
	Mean of all sites	27.5 ± 5.0 (370)	12.9 ± 2.0 (196)	38.8 ± 2.3 (752)	142.9 ± 7.9 (1578)	65.1 ± 3.3 (779)	341.6 ± 83.3 (197)	77.4 ± 5.6 (440)
1	Tucillal	0	13.6 ± 8.3 (7)	13.6 ± 3.5 (11)	173.2 ± 23.2 (61)	4.4 ± 3.8 (3)	221.7 ± 73.6 (9)	89.7 ± 15.1 (19)
2	Fernandez Bajo	0	0	8.9 ± 3.2 (7)	121.1 ± 15.9 (56)	0	356.7 ± 126.0 (15)	242.0 ± 33.5 (42)
3	Enace	19.9 ± 3.9 (19)	0	50.6 ± 9.4 (44)	112.8 ± 7.8 (52)	31.0 ± 5.8 (21)	214.0 ± 91.0 (15)	0
4	Lancones	0	3.3 ± 1.7 (2)	38.8 ± 7.0 (28)	200.8 ± 38.9 (80)	30.8 ± 10.1 (14)	113.5 ± 66.9 (4)	130.4 ± 24.7 (30)
5	Puerta Pulache	0	6.4 ± 2.3 (4)	18.7 ± 4.0 (14)	58.0 ± 8.1 (28)	0	0	62.3 ± 14.7 (13)
6	Pampa Larga	0	0	34.0 ± 9.2 (30)	157.1 ± 22.8 (71)	46.2 ± 6.5 (24)	210.6 ± 90.9 (13)	5.0 ± 2.6 (2)
7	Progreso Bajo	0	25.1 ± 6.4 (16)	39.0 ± 6.5 (31)	106.4 ± 29.5 (42)	85.8 ± 23.9 (36)	3060.2 ± 1645.3 (19)	42.9 ± 19.5 (8)
8	Cruz de Caña	1.8 ± 1.6 (1)	4.2 ± 2.2 (3)	76.9 ± 7.6 (56)	78.0 ± 9.4 (37)	161.7 ± 13.1 (76)	1108.1 ± 654.8 (29)	146.4 ± 17.1 (36)
9	Sagrado Corazón	14.0 ± 6.5 (14)	0	61.4 ± 12.1 (44)	132.5 ± 15.5 (50)	139.3 ± 9.0 (61)	188.6 ± 63.0 (14)	207.0 ± 26.0 (48)
10	Islilla	17.5 ± 7.0 (17)	0	45.3 ± 10.2 (37)	36.7 ± 5.9 (19)	61.0 ± 12.5 (34)	0	0
11	Ancajima	7.4 ± 1.6 (6)	22.6 ± 8.1 (15)	90.0 ± 14.1 (63)	186.0 ± 17.5 (61)	114.5 ± 29.6 (34)	40.3 ± 34.2 (3)	344.9 ± 50.7 (66)
12	Ñapique	0	14.0 ± 7.7 (9)	40.8 ± 12.8 (31)	26.8 ± 12.6 (12)	19.6 ± 6.9 (10)	0	0
13	Ñaupe	16.0 ± 10.8 (16)	9.0 ± 3.6 (3)	78.0 ± 9.2 (56)	281.6 ± 67.8 (99)	40.9 ± 12.7 (19)	20.2 ± 16.3 (2)	223.7 ± 28.4 (45)
14	Piedra Mora	0	20.8 ± 9.1 (15)	19.9 ± 6.4 (18)	111.1 ± 26.6 (54)	115.3 ± 16.2 (52)	1201.0 ± 644.5 (25)	163.1 ± 25.7 (38)
15	Las Norias	+	5.3 ± 1.9 (3)	19.9 ± 3.0 (16)	139.5 ± 25.3 (57)	75.0 ± 18.0 (38)	551.0 ± 109.4 (22)	162.4 ± 48.9 (38)
16	Illescas	5.3 ± 2.8 (6)	0	35.4 ± 5.0 (28)	22.9 ± 6.6 (14)	80.4 ± 6.8 (35)	0	0
17	Pañalá	0	16.5 ± 3.9 (12)	39.6 ± 3.1 (33)	116.0 ± 10.8 (53)	139.8 ± 7.0 (64)	441.6 ± 353.1 (4)	39.1 ± 10.8 (13)
18	La Peña	0	0.7 ± 0.6 (1)	38.6 ± 5.2 (33)	110.7 ± 28.9 (45)	112.7 ± 22.2 (40)	6.6 ± 5.9 (1)	110.5 ± 10.5 (30)
19	Pomac - Poma III	2.5 ± 2.3 (3)	35.7 ± 7.4 (19)	62.1 ± 10.5 (44)	234.1 ± 37.5 (104)	73.8 ± 17.1 (39)	0	0
20	Pomac - Zona Recuperada	46.7 ± 11.3 (49)	15.7 ± 5.0 (11)	41.9 ± 8.6 (35)	305.5 ± 32.0 (130)	72.8 ± 13.0 (41)	0	0
21	Pomac - Salinas	2.6 ± 2.3 (3)	28.7 ± 3.9 (22)	69.4 ± 14.8 (54)	233.9 ± 57.9 (99)	106.9 ± 12.6 (50)	516.7 ± 377.2 (3)	0
22	La Viña	0	0	21.7 ± 4.9 (18)	163.7 ± 58.1 (79)	119.0 ± 15.7 (57)	453.0 ± 155.6 (19)	32.4 ± 14.5 (12)
23	Cañoncillo	0	97.6 ± 33.9 (45)	22.6 ± 6.0 (19)	86.5 ± 6.7 (40)	0	0	0
24	Mocan	104.7 ± 33.4 (96)	0	1.1 ± 1.0 (1)	207.2 ± 20.6 (78)	27.9 ± 3.8 (10)	0	0
25	La Arenita	94.1 ± 23.2 (102)	13.8 ± 3.6 (9)	1.0 ± 0.9 (1)	242.7 ± 19.8 (116)	23.5 ± 4.3 (17)	0	0
26	Monte Zarumo	35.6 ± 7.1 (38)	0	0	75.4 ± 9.0 (41)	7.4 ± 2.2 (4)	0	0

Table S3. Wilcoxon two sample tests between local abundance in the centre and at the edge of species' ranges.

Species	Wilcoxon two sample test between core and edge local abundance		
	W (n_{edge}, n_{core})	p	Δ median (core - edge)
Short-tailed Woodstar *Myrmia micrura*	7 (5,13)	0.01	18.4
Pacific Parrotlet *Forpus coelestis*	65 (12,11)	0.976	7.3
Necklaced Spinetail *Synallaxis stictothorax*	59 (12,13)	0.313	31.8
Mouse-coloured Tyrannulet *Phaeomyias murina*	65 (8,15)	0.77	-20.7
Grey-and-white Tyrannulet *Pseudelaenia leucospodia*	55 (9,17)	0.263	31.1
Tumbes Tyrant *Tumbezia salvini*	41 (4,15)	0.289	-2.4
Rufous Flycatcher *Myiarchus semirufus*	58 (10,14)	0.497	1.4
Peruvian Plantcutter *Phytotoma raimondii*	90 (9,14)	0.077	-16
Fasciated Wren *Campylorhynchus fasciatus*	41 (9,14)	0.172	11.6
Superciliated Wren *Cantorchilus superciliaris*	54 (8,17)	0.44	2
Long-tailed Mockingbird *Mimus longicaudatus*	51 (8,18)	0.261	36.4
Cinereous Finch *Piezorina cinerea*	36 (12,13)	0.024	56.4
Sulphur-throated Finch *Sicalis taczanowskii*	17 (5,12)	0.187	305.9
Tumbes Sparrow *Rhynchospiza stolzmanni*	4 (7,10)	0.003	130.3

Table S4. AIC and Δ AIC values for Generalised Additive Models of environmental correlates as a function of NMDS scores and spatial terms. Asterisks in the column Δ AIC show best model (in cases where Δ AIC is less than 2.0 between two or more models, the least complex model was chosen).

Correlate	Response distribution	Model		Degrees of freedom	AIC	Δ AIC
		NMDS scores	Spatial term			
Altitude	Gaussian	+	+	10	277.28	0.00*
			+	5	282.77	5.48
		+		5	288.94	11.66
Grass presence	Binomial	+	+	10	345.55	0.00*
		+		5	542.50	196.95
			+	5	548.11	202.56
Grazing pressure	Poisson	+	+	10	3701.69	0.00*
			+	5	3917.26	215.58
		+		5	4766.47	1064.78
Human pressure	Gaussian	+	+	10	8.83	0.00*
			+	5	14.04	5.21
		+		5	17.74	8.90
Logging pressure	Binomial	+	+	10	220.60	0.00*
		+		5	238.32	17.72
			+	5	354.28	133.67
Mean no. stems	Gaussian	+	+	10	57.24	0.00
		+		5	57.92	0.68*
			+	5	69.67	12.43
Slope	Gaussian	+		5	105.07	0.00*
		+	+	10	107.07	2.00
			+	5	121.15	16.09
Tree height	Gaussian	+		5	69.92	0.00*
		+	+	10	74.77	4.86
			+	5	96.90	26.99
Tree species richness	Gaussian	+	+	10	55.65	0.00*
		+		5	61.39	5.75
			+	5	74.49	18.84
Understorey cover	Gaussian		+	5	241.05	0.00*
		+	+	10	248.57	7.51
		+		5	253.28	12.23

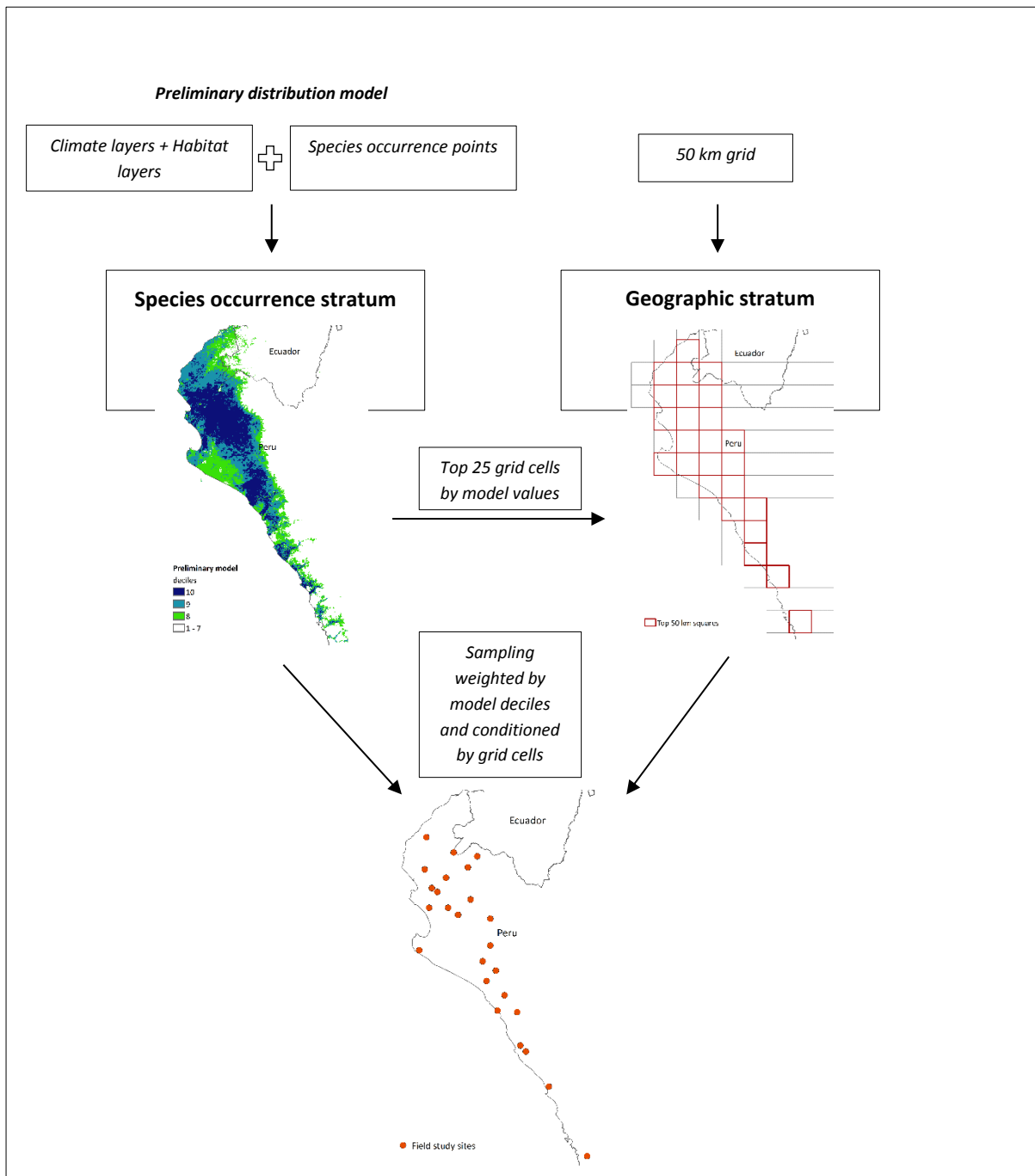**Figure S1** Overview of site selection methods

Figure S2. Occurrence records used to construct convex hulls for centre-periphery analysis. Coastline and elevations over maximum elevations at which species were recorded were cut from convex hulls.
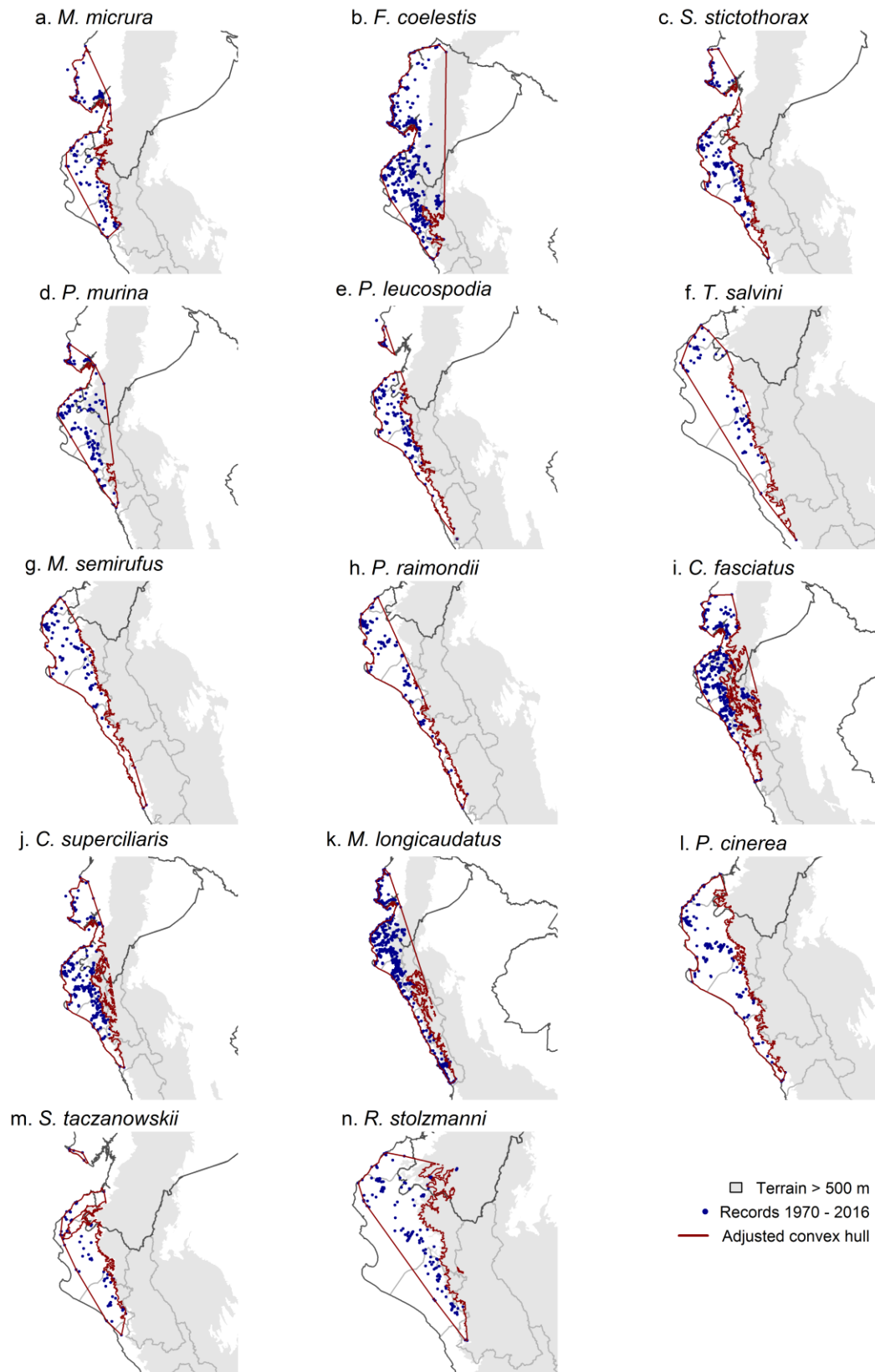

a. *M. micrura* b. *F. coelestis* c. *S. stictothorax*

d. *P. murina* e. *P. leucospodia* f. *T. salvini*

g. *M. semirufus* h. *P. raimondii* i. *C. fasciatus*

j. *C. superciliaris* k. *M. longicaudatus* l. *P. cinerea*

m. *S. taczanowskii* n. *R. stolzmanni*

☐ Terrain > 500 m
• Records 1970 - 2016
— Adjusted convex hull

Figure S3. Spatial autocorrelation of density estimates at 26 sites, evaluated over six distance bands with midpoints between 55 and 570 km (n = 204, 236, 122, 52, 26, 10 per band, respectively). Green points represent significant Moran's I values (p < 0.05) as evaluated through permutation tests.