Developing tools for improved population and range estimation in support of extinction risk assessments for Neotropical birds

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One of the two objects of my Peruvian journey and of our last passage over the Chain of the Andes failed; but on the other hand I had, at the critical moment, the rare good fortune of a perfectly clear day, during a very unfavourable season of the year, on the misty coast of Low Peru. I observed the passage of Mercury over the Sun at Callao, an observation which has become of some importance towards the exact determination of the longitude of Lima, and of all the south-western part of the New Continent. Thus in the intricate relations and graver circumstances of life, there may often be found, associated with disappointment, a germ of compensation.

Aspects of Nature. 1849. Alexander von Humboldt

General Abstract

Species abundance and distribution metrics are cornerstones of conservation planning, for example, in establishing extinction risk and selecting priority areas, but abundance data are scarce and costly to obtain in comparison to those on species occurrence. Occurrence records, often from citizen science or non-systematic surveys, are increasingly used to model species' distributions using environmental predictors. Methods to relate occurrence models to abundance, and therefore, provide greater understanding of patterns of abundance across species' ranges and population size estimates could bring important benefits for conservation decisions.

This thesis aims to develop tools, combining different analytical techniques, field data and GIS, to provide improved estimates of species distribution and abundance in support of extinction risk assessments in threatened Neotropical bird species. To achieve this aim, a case study was implemented over the ranges of 14 dry forest birds from the Tumbesian region of Peru –an area of critical conservation importance due to high endemism and severe anthropogenic threats– with the following objectives: to model the distribution of study species (Chapter 2); to estimate local abundance of species across their ranges using covariate Distance sampling (Chapter 3); to explore range-wide variation in abundance (Chapter 4); to explore the relationship between relative probability of occurrence, derived from modelling, and bird abundance, derived from field studies (Chapter 5).

First, ensemble species distribution models, using four modelling methods, were built with a median of 150 occurrence records per species, bioclimatic variables and vegetation indices. Modelled Extent of Occurrence, using a 5% omission error threshold to define presence and absence, was compared to existing range estimates used in extinction risk assessment. Additionally, field data were obtained on the local abundance of the study species and habitat characteristics along four 2.5 km transects at 26 sites over the study area. Covariate Distance sampling was used to estimate bird abundances at each site. Where sites represented discrete or delimited units (e.g. protected areas), specific population sizes were estimated. Local abundance was compared across sites and by range core versus edge; spatial autocorrelation was examined with multivariate Mantel tests; and, relationships with environmental variables were examined using Generalised Additive Models. Finally, relationships between abundance estimates, obtained from the field study, and relative probability of occurrence, obtained from distribution models, were tested using correlations, and where significant relationships were found, these were modelled using hierarchical logistic regression.

Individual species distribution modelling methods performed adequately and coincided highly in terms of ranked correlation but differed in the distribution of their predicted values. Range size estimates, from thresholded models, were generally smaller than, but coincided spatially with, published ranges, with the exception of three species of conservation interest. Local abundance varied by one or two orders of magnitude across sites for almost all species, with abundance not necessarily highest at the centre of species' ranges. Sites of maximum abundance for individual species did not coincide – nine different sites held the highest densities of at least one species. Eleven of 14 species showed significant positive correlations between their abundance and modelled occurrence for at least one modelling technique.

Modelling techniques are discussed in light of complementing existing techniques to estimate Extent of Occurrence for extinction risk assessments. Abundance estimates, using methods that incorporate detectability, can be obtained for rare species over very patchy habitats with relatively low survey effort, using a suitably designed sampling protocol. The extreme variation in species' abundances and the complexity in relationships with environmental variables has conservation implications, for example, in the design of conservation-motivated surveys and regarding the need for multiple reserves to capture high local abundances of key species. The relationship between modelled species' occurrence and local abundance is a promising area of research with a view to obtaining better abundance information with less survey effort. In terms of biodiversity conservation in north Peru, critical sites are recommended for urgent protection, and updated extinction risk categories are given for threatened species.

Resumen general

La información sobre la abundancia y distribución de las especies son componentes claves en la planeación para la conservación y más específicamente, en la evaluación de riesgo de extinción y en la selección de áreas prioritarias. Sin embargo, frente a los datos de ocurrencia de especies, los datos de abundancia son escasos y difíciles de obtener. Los registros de ocurrencia provenientes de la ciencia ciudadana o de muestras no sistemáticas son los más usados para modelar la distribución de especies utilizando predictores ambientales. Encontrar métodos para relacionar los modelos de ocurrencia con la abundancia ofrecería grandes beneficios para la toma de decisiones para la conservación, generando un mayor conocimiento de los patrones de abundancia a lo largo de las áreas de distribución de especies o para estimar sus tamaños poblacionales.

El objetivo de esta tesis fue desarrollar herramientas para mejorar los estimativos de la distribución y abundancia de especies a través de diferentes técnicas analíticas, sistemas de información geográfica y trabajo de campo. Esto permite dar un mejor soporte a las evaluaciones de riesgo de extinción para las aves amenazadas del Neotrópico. Para lograr este objetivo, se realizó un estudio a lo largo del área de distribución de 14 especies de aves de bosque seco de la región Tumbesina de Perú. Esta es un área de importancia para la conservación debido a la alta tasa de endemismo y la alta presión antropogénica. Los objetivos de la tesis fueron: modelar la distribución de las especies de estudio (Capítulo 2); estimar la abundancia local de las especies a lo largo de sus áreas de distribución usando el muestreo Distance por covariados (Capítulo 3); explorar la variación de abundancia a lo largo del área de distribución (Capítulo 4); explorar la relación entre la probabilidad de ocurrencia relativa derivada de los modelos y la abundancia de aves derivada del trabajo de campo (Capítulo 5).

Primero, se hizo un ensamblaje de cuatro métodos de modelos de distribución de especies usando una mediana de 150 registros de ocurrencia por especie, variables bioclimáticas e índices de vegetación. La Extensión de Ocurrencia, modelada con un umbral de 5% de error de omisión para definir presencia y ausencia, fue comparada con el área de distribución actual usada en las evaluaciones de riesgo de extinción de la IUCN. Adicionalmente, se obtuvieron datos de campo acerca de la abundancia local de las especies de estudio y las características de hábitat a lo largo de transectos de 2.5 km en 26 sitios del área de estudio. Se empleó el método de muestreo Distance para estimar la abundancia de las aves en cada sitio. En sitios donde había unidades delimitadas específicas (por ejemplo, áreas protegidas), se estimaron tamaños poblacionales por sitio. Se comparó la abundancia local entre el centro y los márgenes de las áreas de distribución; se examinó la autocorrelación espacial con pruebas multivariadas Mantel y se analizaron las relaciones entre abundancia y variables ambientales con Modelos Aditivos Generalizados. Finalmente, la relación entre la abundancia estimada, obtenida del trabajo de campo, y la probabilidad de ocurrencia relativa, obtenida de los modelos de distribución, fue evaluada usando correlaciones y en caso de encontrarse relaciones significativas se modeló con regresiones logísticas jerárquicas.

Los modelos de distribución de especies individuales dieron resultados aceptables y coincidieron altamente en términos de correlación no paramétrica entre los valores predichos pero no en su distribución. Las áreas de distribución estimadas, que fueron calculadas aplicando un umbral a los modelos, resultaron generalmente más pequeñas que las áreas de distribución publicadas con excepción de tres especies de interés para la conservación. La abundancia local varió por uno o dos órdenes de magnitud entre sitios para casi todas las especies, además la abundancia máxima no necesariamente estuvo localizada en el centro del área de distribución de las especies. Los sitios de abundancia máxima para cada especie no coincidieron, ya que en nueve sitios diferentes se encontró la abundancia máxima de por lo menos una especie. Once de 14 especies tuvieron una correlación positiva significativa entre su abundancia y la ocurrencia modelada en por lo menos uno de los métodos de modelamiento.

Se discutieron los métodos de modelamiento con el fin de complementar técnicas existentes para estimar la Extensión de Ocurrencia para las evaluaciones de riesgo de extinción de la IUCN. Estimar abundancia con métodos que incorporan la detectabilidad es viable con relativamente bajo esfuerzo de muestreo en hábitats muy fragmentados para especies raras, empleando un protocolo de muestreo adecuado. La variación extrema entre la abundancia de las especies y la complejidad de las relaciones con las variables ambientales tiene implicaciones para la conservación, por ejemplo, en el diseño de muestreos con fines de conservación, y en la necesidad de tener múltiples áreas de conservación para capturar la abundancia máxima local de diferentes especies claves. La relación entre la ocurrencia modelada de las especies y la abundancia local es un área prometedora para la investigación con el fin de obtener mejor información sobre la abundancia con menos esfuerzo de trabajo de campo. En cuanto a la conservación de la biodiversidad del norte de Perú se proponen sitios críticos para ser protegidos urgentemente para las especies estudiadas y se actualizan las categorías de riesgo de extinción para las especies amenazadas.

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At each of the 26 sites during fieldwork we knocked on doors of strangers to ask for board and lodging. We never had to ask twice. Despite fears that we were goat rustlers, petrol smugglers, hunters or land surveyors (who would be crazy enough just to watch birds?), my field assistant and I were made welcome on their floors, spare beds, porches and at their tables. The hospitality and way of life of the rural people across northwest Peru is not documented in this thesis but is a critical part of the challenges set out here.

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Chapter 1

Introduction

1 Biodiversity loss and the need for conservation ecology

In recent times, the rate of biodiversity loss has surpassed the natural base rate of extinction (Pimm et al., 1995; Mace et al., 2005) to such an extent that there is consensus the world is on the verge of a sixth mass extinction event (Thomas et al., 2004; Barnosky et al., 2011). The underlying causes for changes to the planet's biodiversity – habitat loss, degradation and fragmentation, overexploitation, invasive species, pollution and global climate change (Groom et al., 2006) – are all fuelled by a rapid rate of increase of human economic activity (Steffen et al., 2015). Efforts to stem this increasing biodiversity loss, such as the Convention on Biological Diversity and its 2010/2020 Targets, and the Millennium Goals, have largely been unsuccessful (Rands et al., 2010; Tittensor et al., 2014) as development across the globe continues to be unsustainable (UN, 2010). Even recognising that biodiversity conservation is a fundamental part of poverty reduction – given the higher dependence on ecosystem services of the poorest sectors of society (Roe & Elliott, 2004; MEA, 2005) – and one of the three pillars of sustainable development, has not triggered a concerted global effort to change the way natural resources are used (UN, 2012).

Conservation biology, as an academic discipline, was founded to provide principles and tools resulting from scientific research to counteract these threats and preserve biological diversity (Soulé, 1985). Building on environmental movements, such as those responding to bird feather fashions of the late 1890s (Chapman, 1886; Doughty, 1975), and utilitarian de facto conservation, for instance, hunting preserves (Grove, 1992), the conservation ethic of the 20th century was consolidated in wildlife management. Although perspectives within conservation biology have changed, most recently in debates over fundamental principles, exemplified in conserving ecosystem services above biodiversity (Kareiva et al., 2011; Soulé, 2013), a defining quality of a crisis discipline remains that decisions need to be made before all the information is at hand (Soulé, 1985). Seven key gaps in biodiversity data were recently identified (Cardoso et al., 2011;

Hortal et al., 2015), two of which play crucial roles in a large number of conservation decisions and are at the crux of ecology: knowledge of species' distribution and abundance (Ladle & Whittaker, 2011).

2 The importance of distribution and abundance data in conservation decisions

Given the shortfall in funding available to conserve biodiversity (McCarthy et al., 2012), setting priorities is a fundamental part of conservation planning and management. This involves at least three basic questions (Redford et al., 2003; Game et al., 2013): What to focus conservation efforts on? Where to focus efforts? And, how to do this? An additional, and vital, follow up involves evaluating the effectiveness of the conservation process. With the exception of priority setting at the global scale (Brooks et al., 2006), all of these stages rely heavily on distribution and abundance data, either measured directly, or in surrogate form where data gaps exist (Table 2.1). The importance of the sub-global scale is that conservation management is usually implemented at this level. Resolving questions of what and where to conserve often include extinction risk assessment, value appraisals (e.g. biological, phylogenetic, economic or cultural) analyses of complementarity or irreplaceability, reserve selection mechanisms, priority area identification, and metapopulation models, among others (Pullin, 2002; Moilanen et al., 2009).

The most widely used measure of species extinction risk is the IUCN Red List (Lamoreux et al., 2003; Rodrigues et al., 2006). Both distribution (range size) and abundance (population size and trends) represent the basic building blocks of species' data for assessments (IUCN, 2001). In four of the five principal criteria, standardised thresholds of range or population size, in combination with other sub-criteria, are used to assess extinction risk directly. However, measuring population size reductions is far more data demanding than range size, and may be inferred from declines in area or quality of habitat (IUCN, 2001). The fifth criterion makes use of population data indirectly through population viability analysis and is used in a tiny number of taxa. IUCN Red List categories are an integral part of single species conservation programmes (IUCN/SSC, 2008), area-based conservation priority setting schemes (Eken et al., 2004), multilateral environmental agreements (e.g. CITES, 1973), among others.

Alternative measures of extinction risk, based on population and occurrence data have also been developed. The much-debated Species' Ability to Forestall Extinction (SAFE) index is calculated by subtracting the logarithm of minimum viable population (MVP) size from the logarithm of population size to rank ’distance from extinction’ among species (Clements et al., 2011). If MVP is set at a constant 5,000, then the index essentially ranks population size among species. However, the index, lacks aspects such as fluctuations in population size, fragmentation, and measures of population decline which are also symptoms of a species’ extinction risk (Akçakaya et al., 2011; McCarthy et al., 2011). Probabilistic methods of measuring extinction risk, based purely on sightings or occurrence records (e.g. from museum specimens) have also been developed (Boakes et al., 2015). As well as shedding light on whether species are actually extinct or not (e.g. Solow et al., 2012), they provide methods of prioritising threat when data on range size and population are lacking, but museum specimens are present (Robbirt et al., 2006).

Many initiatives have attempted to prioritise sites for conservation as a preliminary step to establishing protected areas. As such, most schemes designate areas without an initial conference of protection status or commitment on the part of the landowner. Sites are typically identified at national or international level, based mainly on biological criteria, although their potential for conservation management is taken into account when delimited (e.g. current use, size and protection status). These initiatives may be taxon based (e.g. shorebirds: Myers et al., 1987; plants: Plantlife International, 2004; butterflies: van Swaay & Warren, 2006; birds: Devenish et al., 2009; hoverflies: Vujić et al., 2016) multi taxa (all taxa: Eken et al., 2004; freshwater biodiversity: Darwall & Vié, 2005) or based on last remaining populations of highly threatened species (Alliance for Zero Extinction - AZE sites; Ricketts et al., 2005). Different methods exist amongst them, but generally follow a conservation planning framework of balancing vulnerability with irreplaceability (Margules & Pressey, 2000), both of which require distribution and abundance data at site and regional level. Typically, species are first assessed for vulnerability through extinction risk or a vulnerability inherent in their life cycle (e.g. migration bottlenecks, congregatory behaviour). Second, an initial network of sites containing populations of these species above certain thresholds may be assessed for complementarity to ensure geographic and taxonomic representation. Finally, given that most are site-based initiatives, the feasibility of site management is a further important criterion (e.g. Myers et al., 1987; Ricketts et al., 2005; Devenish et al., 2009).

Table 2.1. Uses of abundance and distribution data in principal conservation planning schemes. Asterisks indicate which metric is the main focus of criteria where more than one is given. Parenthesis indicate optional criteria. Schemes marked $^{+}$ require more than abundance and distribution data.

	Abundance		**Distribution**	
Conservation planning scheme	Population trend	Population size	Range size	Presence/ absence
Extinction risk assessment				
IUCN Red List – Criterion A	X*		X	
– Criterion B	X		X*	
– Criterion C	X	X*		
– Criterion D		X	X	
SAFE index $^{+}$		X		
Probabilistic (sighting records)				X
Population viability analysis^{+}		X		
Priority area identification				
Important Bird areas^{+} – Criterion A1		X		X
– Criterion A2			X*	X
– Criterion A3				X
– Criterion A4		X		
AZE sites^{+}	X	X	X	X
Reserve selection algorithms				
Marxan^{+}, C-plan^{+}		(X)		X
Multilateral environmental agreements				
CITES	X	X	X	
Ramsar		X		
CBD (2010/2020 targets)$^{+}$	X	X	X	
EU Habitats & Birds directive	X	X	X	X
Species /site management	X			X

Multilateral environmental agreements to use abundance and distribution data include CITES, Ramsar and the Convention on Biological Diversity (CBD). CITES use criteria based on the IUCN Red List criteria to specify which species are included in Appendix 1 (CITES, 2013), which strictly regulates international trade in the listed species. The Ramsar Convention identifies wetlands of conservation importance, and includes criteria based on population numbers of congregatory and migratory birds (Ramsar, 2007). The Aichi 2020 targets of the CBD employ indicators based on abundance and distribution of threatened species (target 12; CBD, 2011). Other conservation planning mechanisms to use abundance and distribution data include minimum viable population analysis, harvest models, and metapopulation models (e.g. to prioritise sites), among many other local or national schemes and proposed mechanisms in the scientific literature.

Conservation decision-making should be adaptive, responding to feedback from the system being conserved (McCarthy & Possingham, 2007; Lindenmayer & Likens, 2009). Population data from conservation targets, for example, collected through monitoring programmes for protected areas, is a direct information source to assess effectiveness of conservation programmes over time and guide site or species management plans (Hockings et al., 2006). Although such a mechanism is favoured within an evidence-based conservation management (Pullin & Knight, 2001), monitoring programmes are notoriously difficult to implement well (Legg & Nagy, 2006; Nichols & Williams, 2006), and published evidence of species population trends within protected areas is scarce (Geldmann et al., 2013). Notwithstanding, indirect evidence for the effectiveness of protected areas, ultimately based on population trend and range size data, comes from the Red List index. This indicator measures change in extinction risk across multiple species/taxa over time (Butchart et al., 2007). When applied to birds, mammals and amphibians with differing representation in protected areas, it showed that the general increase in extinction risk over the last two decades was significantly lower for those species with most coverage within protected areas (Butchart et al., 2012).

In some conservation planning mechanisms, distribution data is reduced to presence/absence information, either due to lack of abundance data, but also to facilitate analysis (e.g. presence/absence data in reserve selection), especially at larger scales (e.g. species richness in hotspot identification; Myers et al., 2000). However, some recent studies have shown that abundance data may improve, or provide different results to presence/absence data (Johnston et al., 2015; Veloz et al., 2015).

3 Research on species' distribution and abundance

3.1 Defining the determinants of species’ distributions and abundance

Determining the factors controlling species distribution and abundance has been a fundamental objective of ecology since its inception as a scientific discipline (Elton, 1927; Begon et al., 2006). Such factors are often represented in a hierarchical, nested order, where distribution and abundance are first determined by responses to the environment (e.g. topography and climate), and then modified by biotic interactions and disturbance, among other factors (Figure 3.1a; Hutchinson, 1978; Wiens, 1992). The differentiation between these two (or more) types of factors has been varied, with several authors proposing different ways of categorising them, including whether they are biotic or abiotic, whether they are consumed by the species, or the spatial scale at which they are measured. Peterson et al., (2011) proposed a differentiation, following on from Hutchinson’s concept of the fundamental niche (Hutchinson, 1978), of whether factors are dynamically affected by a species. For those that are not, such as climate and topography, there is no density dependent process (e.g. consumption, predation) affecting them. These variables were termed *scenopoetic* by Hutchinson, from the Greek for ‘setting the scene’ and are typically, but not exclusively, large scale environmental factors (Franklin, 2009). The other set of variables are those that are dynamically linked, and include biotic interactions, such as competitors, predators, resources that are consumed and disturbance factors. When these are taken into account, then a subset of the fundamental niche is reduced to the occupied or realised niche (Figure 3.1b). Hutchinson originally described the realised niche as that which remains after a species is limited by competition from other species. This niche model has subsequently been expanded to include other factors, beyond competition, which influence species' observed distributions, such as niche width, habitat availability and dispersal (Pulliam, 2000).

The difference between types of factors influencing distribution is important, given that variables dynamically linked to a species' population will require a different representation in mathematical modelling to those which are not linked (Peterson et al., 2011). However, most models of species distributions and, to a lesser extent, abundance, consider a 'snap shot' of a single time period, rather than attempting to approximate the true dynamic nature of distributions. The Hutchinsonian model of the niche, as an n-dimensional hypervolume, set at a single point in time, has become a standard representation within statistical modelling of niche relationships, including species distribution modelling. Nevertheless, there is disagreement as to whether that being modelled is a fundamental or realised niche (Araújo & Guisan, 2006). Complications arise as to the role of positive biotic interactions (e.g. mutualism) and dispersal in defining the realised niche. In fact, Araújo & Guisan (2006) question the usefulness of the fundamental and realised niche concepts for modelling and suggest reverting to the Grinnellian niche, as updated by Chase & Leibold (2003), as the environmental conditions allowing a species to persist where the species' impacts on those conditions is taken into account. Debate will no doubt continue over how to define and represent those factors determining species' distributions and abundance. Clearly stating the purpose and the expected conceptual outcome of a study will help clarify definitions. If the interest is in representing a species' actual distribution at a given moment in time, then both linked and non-linked factors must be taken into account, and can be achieved at different scales (Pearson et al., 2004).

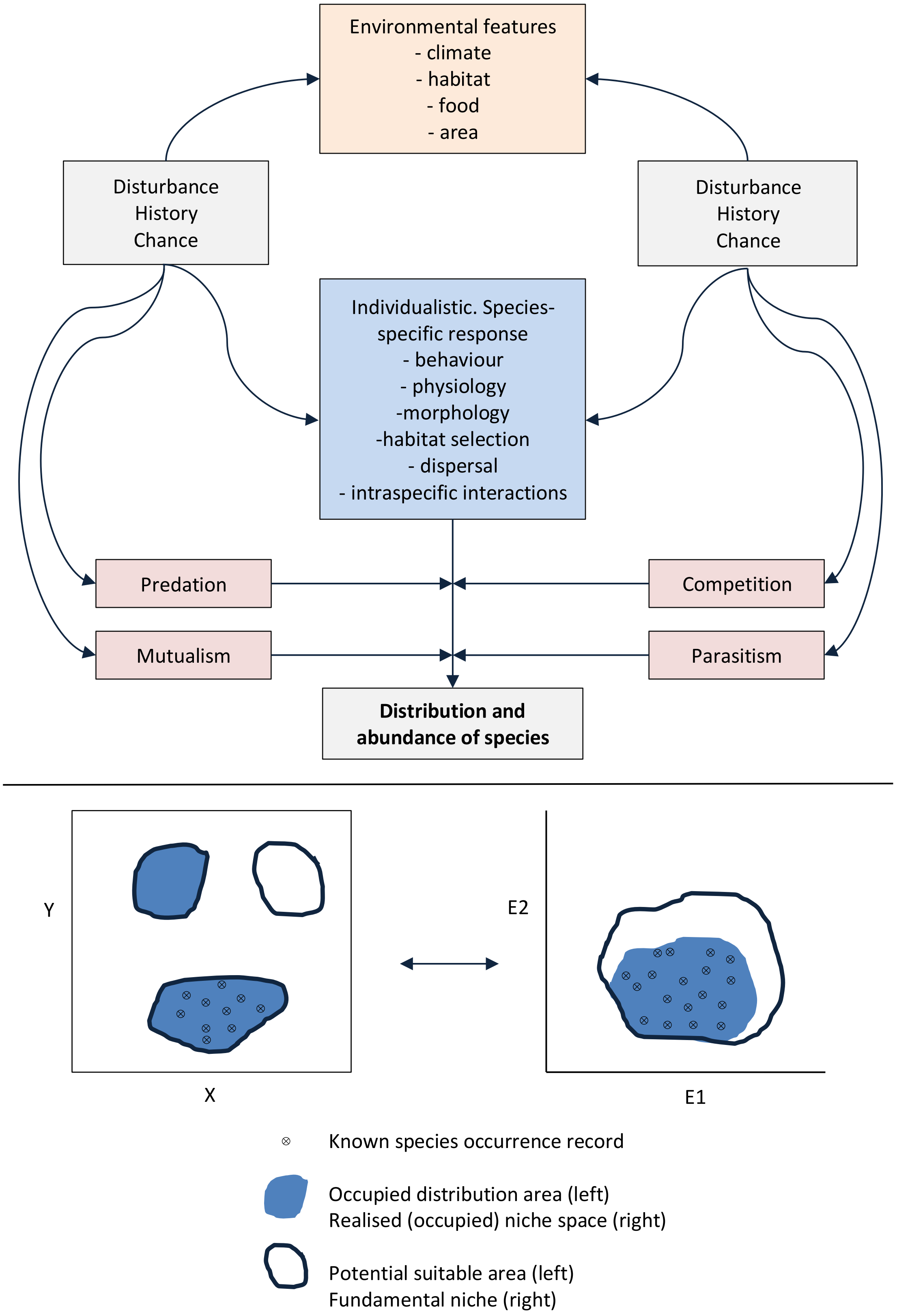

Figure 3.1. a) Factors and processes influencing the distribution and abundance of species. Individualistic responses to environmental factors are modified by other processes such as biotic interactions. Figure redrawn from Wiens (1992). b) Fundamental and realised niches in geographic (axes x, y) and environmental space (axes E1, E2). Figure redrawn from Peterson et al., (2011).

Research on niche relationships may be considered as 'bottom-up' (cf. mechanistic) or 'top-down' (cf. correlative), with the former representing individualistic, species-specific responses to niche axes, typically measured in the field or laboratory (Figure 3.1a) and the latter representing population level relationships between species occurrence points and gridded layers of niche axes, typically from remotely sensed data (Figure 3.1b). Ecological studies on the former make up a large body of research, for example, of small-scale ecological studies describing species-habitat relations (James et al., 1984; Wiens, 1992). Research on the latter, in the form of species distribution modelling has increased exponentially in the last 15 years (see below), with models increasingly used for conservation decision making (Guisan et al., 2013). An active area of current research aims to integrate such mechanistic approaches into species distribution modelling (Buckley et al., 2010; Kearney et al., 2010), including the use of more dynamically linked variables, such as biotic interactions and demographic data (Trainor & Schmitz, 2014; Pletterbauer et al., 2016). Further areas of development include combining different spatial scales (McGarigal et al., 2016) and temporal scales, including factors such as migration, dispersal, and historical events (Franklin, 2010; Génard & Lescourret, 2013).

3.2 Defining and delimiting species ranges

Defining and delimiting a species' range is not an easy task. For most purposes (e.g. atlases, IUCN Red List categorisation), a complex spatial and temporal pattern is reduced to an irregular two-dimensional outline (Brown et al., 1996; Fortin et al., 2005). Mapping ranges this way reduces the range edge, a dynamic space of repeated colonisation and local extinction of huge evolutionary importance (Sexton et al., 2009), to a binary threshold. Furthermore, such two-dimensional polygons (e.g. Extent of Occurrence, see below) are typically based on species occurrence points (or occupied grid squares), but without qualification of the frequency of occurrence or demographic rates associated with them. As such, an occurrence point may represent a regular occurrence, a vagrant record, from a population in decline or growth. In demographic terms, a species is delimited within an area where its growth rate exceeds zero (Lawton, 1993; Holt et al., 1997), provided that the species is not in decline. However, such a definition requires much more data to map the range than one based on occurrence records.

Currently, two approaches are used to map range sizes as polygons for IUCN extinction risk assessments: Extent of Occurrence (EOO) and Area of Occupancy (AOO; Gaston, 1991; IUCN, 2001). EOO and AOO can be seen as different scales of measuring range size, with EOO as the geographical space encompassed by the outermost bounds of all locality records at one end of the scale, and AOO as the actual space used by a species within those limits at the other extreme (Maurer, 1994). Alternatively, the AOO may be considered as the sum of individual home ranges. Each method has different implications, and each is suited to different applications. For example, EOO can be useful in assessing the vulnerability of a species to threats across its entire range, including all subpopulations (IUCN, 2016), whereas AOO is more suited to ecological analyses, where habitat occupancy is an important factor (Gaston, 1991).

3.2.1 Measuring Extent of Occurrence

The simplest way of measuring EOO is to draw around the outer bounds of locality records of a species' occurrence. The IUCN uses a definition (IUCN, 2001) based on the shortest continuous boundary drawn to encompass all the known, inferred or projected sites of present occurrence of a taxon, often measured as a minimum convex polygon. Further refinements can be made by changing the method of joining the occurrence points or using techniques giving similar techniques, for example, alpha hulls, merged buffers surrounding each point, kernel density methods or non-linear regression (Rapoport, 1975; Fortin et al., 2005). According to the IUCN definition, EOO can exclude discontinuities in the species' distribution (IUCN, 2016), but is not recommended when EOO is used to assess the impact of a single threatening process over the entire range of species.

3.2.2 Measuring Area of Occupancy

This measure is based on the occupancy of habitats by a particular species and is necessarily a subset of EOO. However, calculating AOO depends very much on the scale at which occupancy is measured. AOO can be a sum of the number of localities where the species is found, or more commonly, the number of grid cells occupied across an area of interest encompassing the range of the species. The IUCN has attempted to standardise the measurement of AOO by defining it as the area within the EOO occupied by a taxon (IUCN, 2001). A recommended scale at which to measure occupancy of grid cells across the EOO has been set at a size of 2 km (4 km^2) for many taxa (IUCN, 2016).

Mechanisms controlling the limits of species ranges are intrinsically linked to those controlling distribution and abundance (see above). These include physical barriers, such as coastlines, rivers and mountains; climate factors, such as gradients of precipitation and temperature; habitat factors (mainly for animal species); biotic factors such as interspecific relations (e.g. competition, predation, mutualism, parasitism) and dispersal ability (Gaston, 2003; Sexton et al., 2009). A further major impact on current range sizes is human activity, this may be direct (e.g. resource exploitation, land use change) or indirect (anthropogenic climate change, introduction of non-native species). Functionally, the above factors can be seen as either limiting dispersal to unoccupied areas or representing environments for which adaptation is limited (Eckhart et al., 2011).

3.3 Inside ranges: patterns and drivers of abundance

That species' densities are heterogeneous across their ranges is well established (e.g. Grinnell, 1914; Klomp, 1963; Hengeveld & Haeck, 1981; Brown et al., 1995; Sagarin et al., 2006). Species tend to have low abundances throughout most of their range, but with small areas of high density, i.e. a positively skewed intraspecific abundance distribution (Gaston, 1990; Brown et al., 1995; McGill & Collins, 2003). How the peaks of abundance are spatially distributed remains a key question for research, with important implications for evolutionary studies and conservation science. The most widely described pattern of abundance distributions is the ‘abundant centre hypothesis’ (Rapoport, 1975; Brown, 1984; Hengeveld, 1990) which suggests that species have greater abundances in the centres of their ranges than at the range margins. The hypothesis encompasses both unimodal and multimodal distributions (Brown, 1984, 1995; Hengeveld, 1990; McGeoch & Price, 2004), in the sense that abundance may have one or multiple peaks, but within a central region (Figure 3.2a).

Theoretical frameworks describing patterns in species’ local abundances rely on correlations with underlying environmental variables. The optimum surface model, as consolidated by Hengeveld and Haeck (1981), describes the relationship between a species' occurrence and spatial trends in environmental variables. As relationships are not necessarily linear, complex variation in local abundance across a species' geographical range can be expected. Similarly, Brown (1984) described the ‘abundant centre’ pattern as a reflection of local abundance, determined by species’ responses to local conditions meeting niche requirements. Additionally, metapopulation models predict that local abundance is positively correlated with the number of patches occupied (Lawton, 1993) so if the number of patches occupied decreases with increasing distance from the range centre (Figure 3.1c), then a concomitant reduction in density would be expected. Despite theoretical grounding for the above hypothesis (Brown, 1984; Guo et al., 2004), there is general acknowledgement that it is an oversimplification, too reliant on geography rather than species’ ecology and the spatial patterns of responses to environmental conditions (Lawton et al., 1994; Sagarin & Gaines, 2002; Sagarin et al., 2006). Further, there are many examples of species that do not conform to this pattern (Sagarin & Gaines, 2002; Gaston, 2003; Samis & Eckert, 2007). Factors that may alter the general pattern predicted by the abundant centre hypothesis can include the shape of ranges, particular barriers, or 'sharp' edges to ranges (e.g. mountain ranges, coasts), and biotic interactions, such as competition (Brown, 1995).

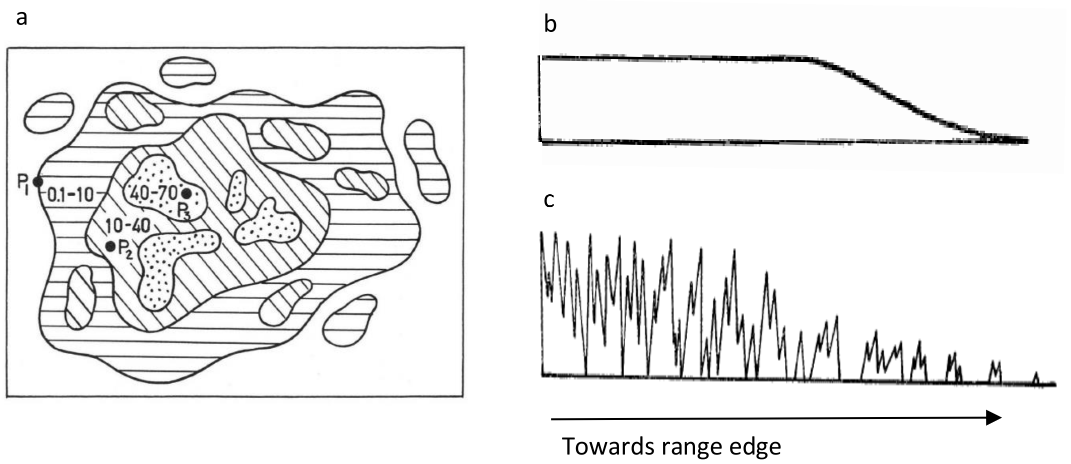

Figure 3.2. Depiction of spatial variation in species' density, a) across a model species range; across a section from the centre to edge in terms of b) average density, and c) real density. After Figure 1 (Klomp, 1963) and Figures 67 and 68 (Rapoport 1975), respectively.

Drivers of variation in abundance across a species' range come from a range of factors acting at different scales (see above; Pearson & Dawson, 2003; Guisan & Thuiller, 2005), to which, anthropogenic factors are occasionally added separately (e.g. Smith, 1868; Yackulic et al., 2011). The spatial pattern of these factors, including, for example, autocorrelation of environmental variables, will show through in patterns of local abundance. Several authors have investigated the pattern in the spatial autocorrelation of density as distances increase between sites (Brown et al., 1995; Brewer & Gaston, 2003; McGeoch & Price, 2004). A commonality is that significant autocorrelation exists at small distances between density estimates. However, at larger distances, relationships become less clear, with only some studies showing autocorrelation, which Brown et al (1995) attribute to similarly low densities of species occurring at the range margins.

3.4 State of knowledge and limitations of occurrence and abundance data

Knowledge of biodiversity is of course incomplete. For many extant species, their numbers and distribution will never be known (May & Beverton, 1990), not to mention all those that are now extinct (Erwin, 2008). A lack of knowledge of seven key aspects of biodiversity information (taxonomy, distribution, abundance, evolution, function, response and interaction) has been cited as one of the current challenges of conservation biology (Hortal et al., 2015). For the conservation biologist, this shortfall is confounded further by the fact that less information exists precisely where it is needed most, in the most biodiverse, and threatened areas of the planet (Meyer et al., 2015), such as the Neotropics.

In contrast, more data are now available on bird occurrences than ever before, as a result of online initiatives to collect new data and through making historic data available (Graham et al., 2004; Soberón & Peterson, 2004). Historic occurrence data, mainly from museum specimens, is widely available, albeit with some issues of quality, taxonomy, ease of use and completeness (Graham et al., 2004). Although the Global Biodiversity Information Facility data (GBIF; www.gbif.org) was found to be a useful source of information on invertebrate species' ranges, manual collation of data from literature and museums was more effective (Beck et al., 2013). VertNet (Constable et al., 2010) goes a long way to fill this role for vertebrates, including birds, but still lacks completeness due to absence of some museums, or incomplete data provided by some participants. eBird is the largest of several online observation recording systems focused entirely on birds (Sullivan et al., 2009, 2014). By mid-2013, more than 140M records from 150,000 observers had been accumulated in the decade since the project was started. However, the data set remains geographically biased towards north America, where its target recorders –birdwatchers– are most active (Sullivan et al., 2014).

Fewer data exist on species population sizes or abundance than on occurrence, especially in the Neotropics. Long term data sets, such as the Breeding Bird Survey in north America (50 years of data in 2016 representing over 100,000 surveys; Downes et al., 2016) and Europe (18 country surveys by 2003, with the earliest from 1980; Gregory et al., 2005) are used to monitor population trends. However, comparable data sets are not available for the Neotropics. The longest term data sets are likely to be the Christmas Bird Counts lead by Audubon Society (since mid 1980s at > 50 sites; Pashley & Martin, 1988; Boyle & Sigel, 2015) and Neotropical waterbird Census, organised by Wetlands International (average of 300 sites per year in 9 countries since 1990; Blanco & Carbonell, 2001; López-Lanus et al., 2005). However, data, especially from the earlier years are patchy, and coverage is low compared to the size of the region. The Living Planet Index is a global database of species population time series for vertebrates, extracted from literature and unpublished reports (Loh et al., 2005). Currently, the database holds over 6,500 records of terrestrial species, of which, 66% are from North America and Europe. A total of 533 records are from Latin America, of which just 18 (five from birds) are from Ecuador and Peru, from just five sites (LPI, 2016).

Occurrence data for birds has been used to produce Extent of Occurrence range maps for all extant species (BirdLife International & NatureServe, 2012) which are used in conservation assessments. The more complete nature of this data set, compared to that on population sizes, has placed greater reliance on range size to determine relative extinction risk (Gaston, 2003). However, such measures of range size have certain limitations, related to bias or errors in the original occurrence points, the method used to draw the range, and the frequency with which it is updated. Museum and observer records may be geographically biased towards areas of greater accessibility or interest, e.g. near roads or within protected areas; may be taxonomically biased against rarer species; may have georeferencing errors, and may be affected by historical events, such as military conflicts (Hijmans et al., 2000; Graham et al., 2008; Hortal et al., 2008; Newbold, 2010). How range maps are drawn will affect errors of omission and commission with respect to species occurrences, especially with respect to excluding discontinuities within a range (IUCN, 2016). Extent of Occurrence maps have been shown to overestimate ranges in a study with more than 1000 bird species (Jetz et al., 2008). Another study found both overestimation and underestimation of species occurrences in a control data set when compared to EOO maps adjusted for suitable habitat (Beresford et al., 2011). It is important that EOO data is used cautiously in conservation planning, and that coarse resolutions are not used for fine-scale solutions (Rodrigues, 2011). An estimation of both omission and commission errors from occurrence data could provide an important additional component of conservation planning (Rondinini et al., 2006). Lastly, using overlapping species range maps to determine spatial patterns of functional traits assumes that a particular trait, e.g. body mass, is unrelated to abundance, which varies across a range. Although one study found mostly positive correlations between methods adjusting for abundance and those that did not, relationships were weak for some traits. The authors conclude that local abundance data are urgently needed to provide better estimates of functional diversity (Newbold et al., 2012).

Abundance, that is, measures of individuals per unit area, rather than population counts, are less common still. A recent literature survey found abundance data for only 25% of 356 parrot species, of which only 22 species had estimates from more than a single study (Marsden & Royle, 2015), and multiple density estimates, allowing comparison across space or time, in only 23% of species. This is concerning given the spatial variation in abundance over the geographical range of a species (Brown et al., 1995); single, or few estimates over large ranges (e.g. > 50,000 $km^{2)}$, are not likely to be representative. The Red List relies on abundance estimates, as part of most criteria (see above; IUCN, 2001), but allows population decline to be inferred from reduction in habitat area. Given the lack of detailed information on population trends in South American birds, range loss, especially as a surrogate for population decline, has acquired greater importance in quantifying degree of threat in the region. For instance, of the 121 threatened birds in South America classified under present or past population change (i.e. IUCN criteria A1, A2, A4), 98 were inferred from measures such as range loss rather than directly from population decline (IUCN, 2015). Furthermore, threat categories for 40% of all globally threatened birds in 2004 were classified based on 'poor' quality data, that is, population size and trend was based on qualitative but not quantitative data (Butchart et al., 2005).

Use of remotely sensed data and habitat change models are increasingly used in conservation and recent studies have linked changes, or projected changes, in forest cover to extinction risk (Buchanan et al., 2008; Bird et al., 2011; Tracewski et al., 2016). However, despite the biological and conservation importance of dry forests, these habitats remain relatively little studied, both in terms of flora and fauna (Linares-Palomino, 2006; Pizano & García, 2014) and with regard to using remote sensing to detect changes (Hesketh & Sánchez-Azofeifa, 2014), especially compared to other forest types. Despite recent advances in global, fine resolution, deforestation data sets (Hansen et al., 2013; Chen et al., 2015), coverage of dry forest is often inadequate due to dry forest not qualifying within the 'forest' definitions employed, as well as general difficulty in the supervised classification of this type of habitat. Dry forest has been mapped with MODIS data (Miles et al., 2006), but to date, a global data set of change in dry forest cover has not been produced.

3.5 Tools for modelling species' occurrence

In species distribution models (SDM), a species' occurrence is predicted from its response to variation in multiple environmental factors through a statistical relationship. Due to the scarcity of data on species' absences (and the difficulty of defining certain absences; Peterson et al., 2011), methods focus on using presence-only data, that is, records of species' known occurrences. Environmental values at presence points are compared to a random background sample or from values at 'pseudoabsences' (selected from areas of non-presence) to produce a relative probability of occurrence (Guisan & Zimmermann, 2000).

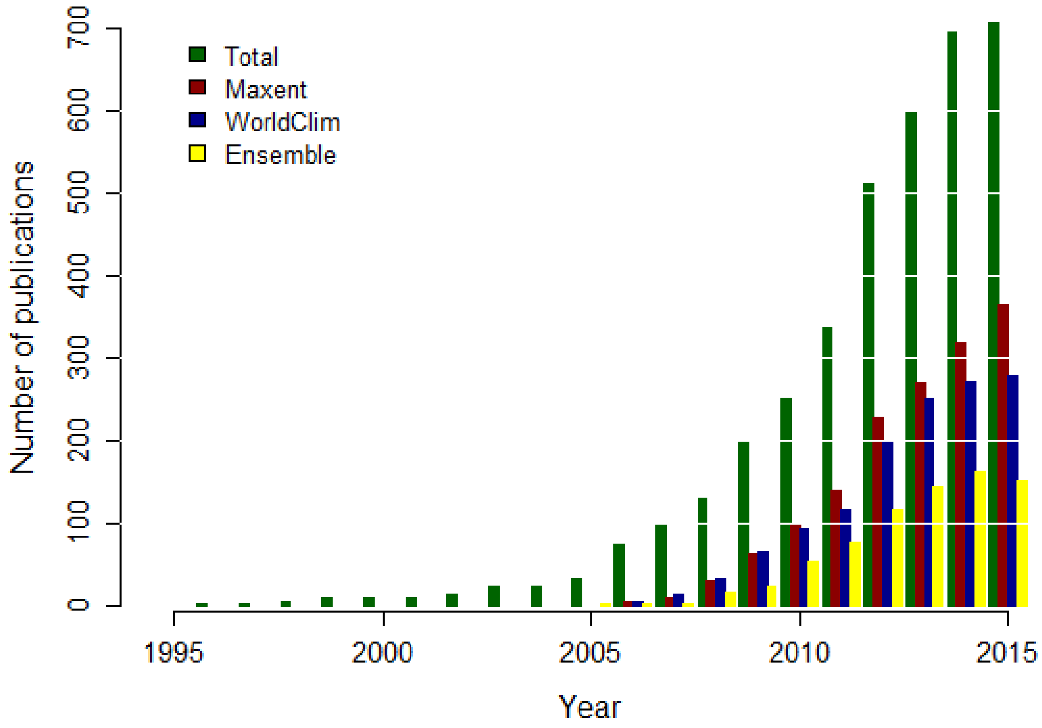

Figure 3.3. Increase in use of species distribution modelling 1995 – 2015, as the total number of publications, and those referencing 'Maxent' or 'Ensemble' in the title, abstract or keywords and those citing the WorldClim data base in references.

The contribution of species distribution models to the ecological literature has increased exponentially over the last 20 years, in part, due to the improved accessibility of species' occurrence data (see above), gridded predictors, and software (Figure 3.3). Remotely sensed data, such as global gridded climate layers (Hijmans et al., 2005), digital elevation models (e.g. SRTM, Aster), vegetation indices (e.g. from MODIS or Landsat) have recently been made available globally (e.g. Landsat archive freely available since 2008, with pre-processed vegetation indices since 2015[1]). Additionally, many national data sets, including land use and cover, geology and soils have recently become available (e.g. through national military geographical institutes in Colombia, Ecuador and Peru). Dedicated software for species distribution modelling has proliferated over the last 10 years, with user-friendly, standalone software, such as Maxent, used in half of all publications (Phillips & Dudík, 2008; Figure 3.3), and openModeller (de Souza

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[1] http://landsat.usgs.gov//high_level_science_data_access.php

Muñoz et al., 2011), several R packages (e.g. dismo: Hijmans et al., 2016; biomod2: Thuiller et al., 2016), and GIS plugins (e.g. SDMtoolbox for ArcGIS[2], DIVA-GIS).

Methods for species distribution modelling fall into broad categories including statistical regression methods (e.g. Generalised Linear Models, Generalised Additive Models), machine learning techniques (e.g. Boosted Regression Trees, Random Forests, Maximum Entropy), and bioclimatic envelope methods (e.g. bioclim, Mahalanobis distance; Franklin, 2009). Ensemble methods have been proposed to combine results from different methods, in part due to lack of consensus on which method performs best (Araújo & New, 2007). Critical decisions within the modelling process include choosing the modelling method itself (Elith et al., 2006), defining the size of the study area (Barve et al., 2011); selecting the number and location of pseudoabsences or background points (Barbet-Massin et al., 2012); selecting predictor variables (Parra et al., 2004; Peterson & Nakazawa, 2007); defining the resolution of the model (Guisan et al., 2007); choosing the evaluation metric (Fielding & Bell, 1997; Allouche et al., 2006; Lobo et al., 2008); and selecting an occupancy threshold, if a binary presence/absence map is required (Liu et al., 2013).

Species distribution models can be traced back to studies of habitat suitability and resource selection functions (Scott et al., 2002). Since then, their purpose has diversified on a par with their increased use in ecology and models are now frequently used in conservation planning and decisions (Guisan et al., 2013; McShea, 2014). Examples from the Neotropics include: guiding field expeditions to find new populations (Ferreira de Siqueira et al., 2009); conservation planning (e.g. Fajardo et al., 2014); predicting changes in distribution resulting from climate change (e.g. Ramirez-Villegas et al., 2014); range reductions (Ferrer-Paris et al., 2014); assessing range sizes for extinction risk assessment (Syfert et al., 2014); species reintroductions (Hendricks et al., 2016), and assessment of non-native species (Devenish & Arzuza, 2007). Recently, research using species distribution models has focused on the internal structure of species ranges, including how spatial variation in probability of occurrence is related to changes in abundance across a range (e.g. Legault et al., 2013). Of at least 20 research papers on this

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[2] http://sdmtoolbox.org/

topic, the overwhelming majority conclude that a significant positive relationship exists between modelled occurrence and abundance (see full review in Chapter 5).

3.6 Tools for measuring abundance

To date, most methods to count animal populations involve large investments of time and effort in the field. To minimise costs, indices of abundance (e.g. encounter rates, or counts using a standardised field protocol) are often used instead of actual abundance (e.g. density of individuals per unit area or total population size). However, comparing such indices over space (e.g. between habitats) or over time may lead to inaccurate inferences by not taking into account variations in detectability (Buckland et al., 2008). Such variability primarily depends on distance from the observer, but also, on species traits (e.g. frequency and amplitude of vocalisations changing between seasons), habitat characteristics changing over space (e.g. dense or open habitat) or differential experience between observers (Marques et al., 2007; Johnston et al., 2014). If measuring detectability is not incorporated into the study design, then either detectability must be assumed to be homogeneous across the study, or all individuals must be counted (e.g. spot mapping). Neither of these is easy to ensure (Buckland et al., 2008). Over the last 20 years, Distance sampling, has become one of the most widely used methods to estimate animal abundance. Despite being most popular in North America and Europe, approximately 10% of studies have been from the Neotropics over recent years (Figure 3.4; Thomas et al., 2010). In recent survey of density estimates of parrots worldwide, Distance sampling was found to be the method of choice for 84% of all the density estimates (Marsden & Royle, 2015).

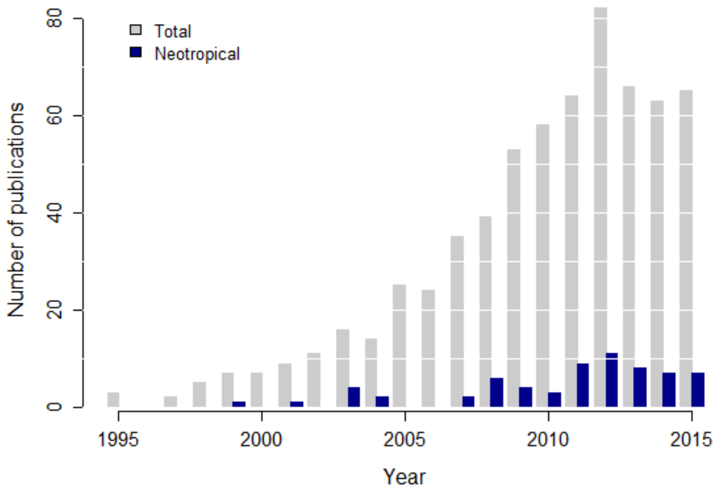

Figure 3.4. Increase in publications using Distance sampling to measure abundance 1995 – 2015, showing proportion of studies in Neotropical realm.

Distance sampling (Buckland et al., 2001; Thomas et al., 2010) is an extension of line transect abundance estimation (e.g. Emlen, 1971) where a correction factor is introduced to account for the expectation that objects at greater distances from the transect line are less likely to be detected (Buckland et al., 2001). The fundamental concept in distance sampling is the incorporation of an estimate of the proportion of objects detected into the calculation of the density estimate. For example, in strip transect sampling where all objects, n, within a specified distance, w, from the transect line of total length, L, are counted, then the estimate, $\widehat{D}$, of the population density, D, is given by

$$\widehat{D} = \frac{n}{2wL}$$

Incorporating an estimate of the proportion of objects detected (probability of detection), $\hat{P}_a$, gives

$$\widehat{D} = \frac{n}{2wL\hat{P}_a}$$

The detection function, *g(x)* is the probability of detecting an object at distance, *x*, from the transect line, which generally decreases with increasing distance from the transect line. A critical assumption of distance sampling is that objects on the line are always detected, that is, $g(0) = 1$ (Buckland et al., 2001). The detection function can be estimated from the probability density function rescaled to 1, *f(x)* of the detection distances. Then

$$\hat{P}_a = {}^{\hat{\mu}}/_{w}, \text{ where } \hat{\mu} = {}^{1}/_{\hat{f}(0)}$$

The effective strip width, μ, is the distance from the transect at which as many objects are detected beyond μ as missed within μ (Thomas et al., 2002).

Critical decisions in a distance sampling study include choice of transects or point counts (may depend on habitat, and cost-efficiency); site selection (e.g. stratified or random sampling design; Buckland et al., 2001); placement of transects or points (e.g. on tracks or paths; Española, 2013); obtaining accurate distance measures (Alldredge et al., 2007); model selection and whether to model detection functions separately per species/site (e.g. dependent on quantity of data and availability of covariates; Marques et al., 2007). Recent developments have incorporated spatial models of density into distance sampling (Hedley & Buckland, 2004; Miller et al., 2013), allowing density surfaces to be created, conceptually similar to modelling density with environmental predictors. Such methods, as with those relating occurrence models to abundance (see above), are able to reduce survey costs by interpolating density values across non-surveyed areas. In further integrations with GIS, spatial data can also be managed directly within Distance software since version 6.0 (Thomas et al., 2010). Both density surface modelling and regular distance sampling are currently being developed as R packages.

4 Study area - Tumbesian region of Ecuador and Peru

4.1 Conservation importance of the Tumbesian region

Biological diversity is, of course, not evenly distributed over the planet (Kleidon & Mooney, 2000; Grenyer et al., 2006). Where the most biodiverse areas coincide with peaks of current anthropogenic pressures (mostly tropical, less developed areas), hotspots have been defined to focus biodiversity conservation (Brooks et al., 2002; Myers, 2003). South America contains eight biodiversity hotspots (Myers et al., 2000; Mittermeier, 2004), occupying 30% of the continental area, the largest proportion of all continents. Hotspots in South America represent 23% of the total hotspot area in 12% of the planet's area. Threatened species are also unevenly distributed throughout the continent (Beissinger et al., 1996), concentrated in certain areas, such as the Tropical Andes in the north of the continent, the Cerrado and Atlantic Forest in Brazil, and the Tumbes region on the Ecuadorian and Peruvian border (Collar et al., 1997; Devenish et al., 2009). Since the beginnings of systematic assessment of extinction risk in birds across the South American continent (Collar et al., 1992), more than 10% of species have been threatened with extinction (BirdLife International, 2015), with the degree of threat increasing over this period (Devenish, 2012).

The Tumbesian Endemic Bird Area (EBA), a lowland coastal region, straddling the Ecuadorian-Peruvian border (Figure 4.1a), is a global priority for conservation (Stattersfield et al., 1998), lying within the Magdalena-Chocó-Tumbes Biodiversity Hotspot (Mittermeier, 2004). The latter designation, by definition, implies that the area has lost more than 70% of its natural habitat. The study area also includes two priority habitats within the Global 200 ecoregions (Olson & Dinerstein, 2002).

In a Latin American forerunner to the global ecoregion analysis, the conservation status of the Ecuadorian Dry Forests and Tumbes/Piura Dry Forests was classified as Critical and Endangered, respectively. Together, these two ecoregions were included in the highest categories for both biological distinctiveness and conservation priority as part of the same analysis (Dinerstein et al., 1995). The Tumbesian region stands out among EBAs as holding one of the largest numbers of restricted-range species (4th in the world). Of the 55 species restricted to this EBA, 18 are globally threatened (Stattersfield et al., 1998; Devenish et al., 2009).

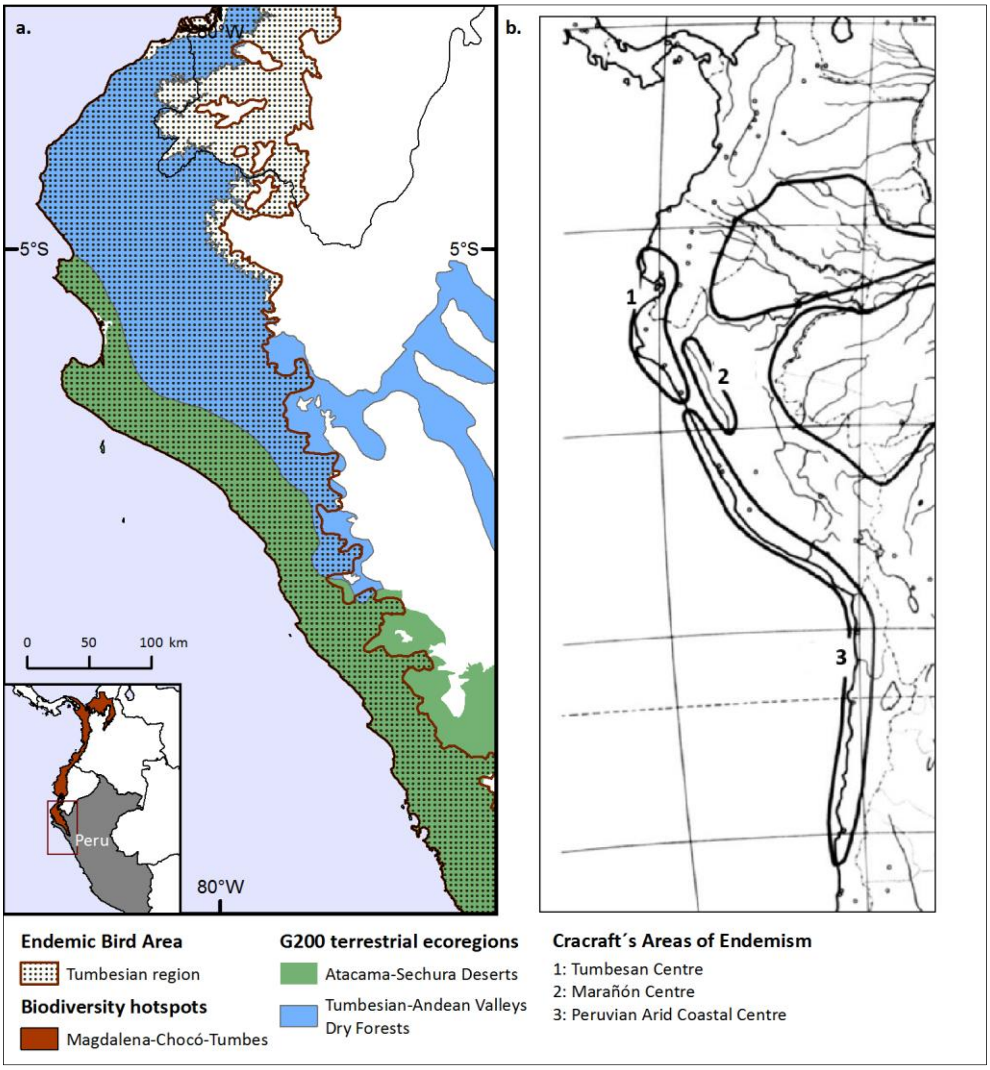

Figure 4.1. Northwest Peru in the context of a) priority conservation designations and b) Cracraft's areas of endemism. From Cracraft (1985).

The Tumbesian area is of great evolutionary importance in South America, representing a centre of endemism and dispersal for fauna (Chapman et al., 1926; Cracraft, 1985) as well as having a high proportion of evolutionary distinct species

(Jetz et al., 2014). In his seminal work, Chapman (1926), attempted to characterize bird distributions in Ecuador, with a view to clarifying evolutionary patterns. Based on a classification of elevational life zones populated by unique bird species, Chapman defined an Equatorial Arid zone, representing a transition area between the more humid forests of northwestern Ecuador and the deserts of Peru. Subsequently, Cracraft (1985)**,** building on work by Müller (1972), defined the 'Tumbesian Center' as one 33 areas of bird endemism in South America, with geographical scope similar to the present day definition of the EBA (Figure 4.1b).

4.2 Geography of the Tumbesian region

The Tumbesian region is sandwiched between the Andes and the Pacific coast and represents a transition zone between one of the wettest places (Chocó rainforests of the Colombian Pacific coast) and one of the driest places on earth (Atacama desert in South Peru and Chile). The cold Humboldt current running northwards up Peru's coast until close to the Ecuadorian border, together with the north-south Andean range, are largely responsible for an abrupt change in precipitation patterns, and thus, the region's terrestrial ecosystems (CDC, 1992; Kricher, 2008). The cold current is also responsible for an almost permanent layer of cloud and fog over the drier, southern part of the region, providing humidity, although there is virtually no precipitation in the south (Ferreyra, 1983). The region has a single wet season in the north, approximately from December to May, with practically no rain at other times of the year (Figure 4.2a). Temperature is slightly higher during the wet season (CDC, 1992). Precipitation, and temperature, show a decreasing north-south gradient in the lowland plains (Figure 4.2a,b), with average annual precipitation in Tumbes at 45.6 mm (range: 0.4 – 139.8 mm), and in Ancash, approximately 650 km to the southeast, at 0.5 mm (range: 0.01 – 2.0 mm). Similarly, annual average temperature in Tumbes is 25.5°C while Ancash is 21.6°C (SENAMHI, 2013). A west-east gradient in temperature and precipitation also exists, with increasing elevation over the Andes. Temperature decreases with height, and precipitation increases, although, even the higher western slopes of the Andes in the study region are much drier than the corresponding eastern, Amazonian, slopes (Figure 4.2). The region is also strongly impacted by the El Niño–Southern Oscillation phenomenon. El Niño is defined by an anomalous warming of the Pacific Ocean around the equator, to the west of Peru, caused by a break down in the high-pressure system approximately every 8-15 years (CDC, 1992; Hanley et al., 2003). Its major impact is an increase in precipitation and temperature over northern Peru, with considerable impact on the region's economy, livelihoods and biodiversity (Rodríguez et al., 2005). Cycles of traditional agriculture, forest growth (Ektvedt et al., 2012), and possibly bird populations, are all dependent on this climate phenomenon. Strong El Niño phenomena occurred most recently prior to fieldwork in 1982-83 and 1997-98.

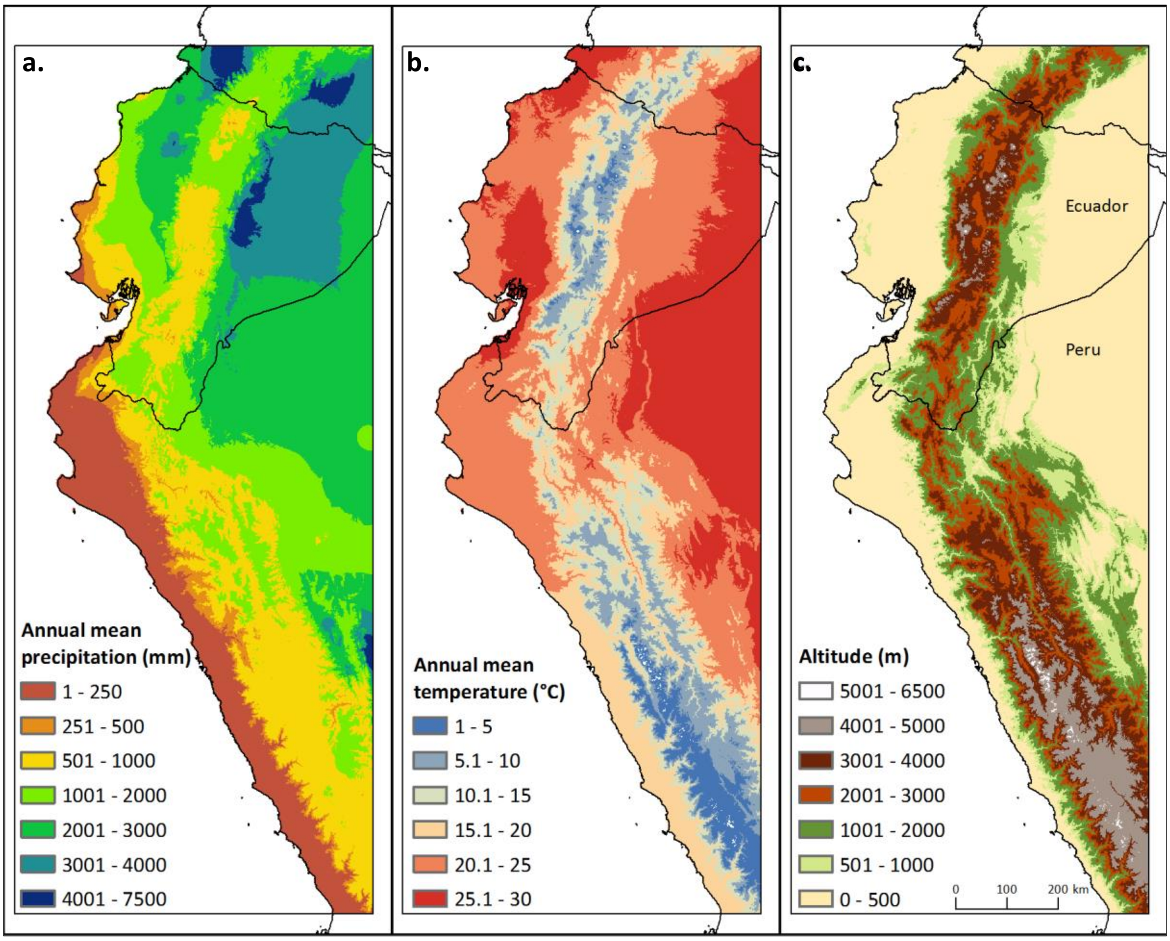

Figure 4.2. Variation in a) precipitation, b) temperature, and c) elevation across the study area, north Peru.

Peru's northern coast has a long history of human exploitation, boasting the oldest civilisation in the Americas at Caral, established some 5000 years ago (Solis, 2006). Since this time, irrigation and farming have constantly changed the landscape: from the early beginnings of farming on the continent at Caral to large-scale, permanently irrigated cropland just before the Spanish Conquest (Netherly, 1984; Haas et al., 2004; Dillehay et al., 2005). As a result of the expansion, and collapse of human populations due to earthquakes, historic climate change and El Niño events (Sandweiss et al., 2009; Beresford-Jones et al., 2011), areas of dry forest –habitat to the birds of this study– have been lost to agriculture, and subsequently recovered during these millennia (Hocquenghem, 1999).

Figure 4.3. Vegetation on Peru's north coast. a) Looking over the vast area of scrub forest in eastern Piura (e.g. site 11, see Chapter 3); b) desert scrub (site 22); c) dunes and coastal desert scrub (site 16); d) lower montane dry forest (site 2); e) Lowland savannah forest (site 3); Lowland savannah forest – wet season (site 9). See Figure 2.1 (Chapter 3) for key to sites. Photos, a-e: C. Devenish; f: E. Nuñez.

Furthermore, ecosystems in the region are naturally fragmented, with large patches of desert and low scrub between more fertile river valleys with seasonal dry forest (Figure 4.3, Figure 4.4). Vegetation gradients from forest to low desert scrub run east-west, with increasing distance from the Andes, and away from the rivers (north-south, south-north) coming down from the Andes. Plant richness increases towards the equator and with increasing elevation (Tarazona Reyes & Proyecto Algarrobo, 1998). However, endemism is equally high in both lowland and montane dry forests, with 19 of 103 and 36 of 193 species endemic to these forest types, respectively, across Ecuador and Peru (Linares-Palomino, 2006). Characteristic woody species of the equatorial lowland seasonal dry forests (Figure 4.3a, e, f) include spiny Acacia trees and scrub, *Acacia* sp., trees of the mesquite family, Algorrobo *Prosopis* sp., the green-barked Palo Verde *Parkinsonia* sp., Sapote and Bichayo *Capparis* sp., Overo *Cordia lutea* and cactus in drier areas, e.g. *Armatocereus cartwrightianus*. Species composition and structure changes with elevation, with larger trees present in montane dry forests (Figure 4.3d), such as Gualtaco *Loxopterygium huasango* and Palo Santo *Bursera graveolens* (Ferreyra, 1983; Linares-Palomino, 2006).

Although habitat is naturally fragmented, the wider Tumbesian area, to which northwest Peru belongs, has suffered massive deforestation and is considered one of the most severely threatened areas on earth in terms of biological extinction (Dodson & Gentry, 1991). Less than 5% of the original forest is estimated to remain in the Tumbes region (Best & Kessler, 1995). Currently, north Peruvian dry forests have one of the highest rates of conversion to agriculture in South America (Jarvis et al., 2010), with selective logging for charcoal production (Figure 4.5), firewood gathering (Ektvedt, 2011), and grazing also among the main threats (Best & Kessler, 1995; More, 2002; Linares-Palomino, 2006; Flanagan et al., 2009). All of these pressures are associated with the high accessibility to the dry forests in north Peru (Jarvis et al., 2010) due to high human population densities in cities and important road networks along the coast. Major transport routes not only connect coastal cities, but also Lima to Andean cities in the north. Habitat alteration and destruction comes both from large-scale industrial plantations (e.g. fruit and vegetables for export) encouraged by national and regional governments, and local scale, traditional farming. Several projects exist or are planned, to bring water through the Andes in tunnels to irrigate vast areas of desert scrub (see Chapter 3; ECSA Ingenieros, 2011; Gobierno Regional de Lambayeque, 2016). Mineral resource exploitation, such as oil and gas exploration and mining are also threats to biodiversity (Flanagan et al., 2009; Jarvis et al., 2010). Legal mining impacts biodiversity at large-industrial scales and informal, small-scale mines, often lacking in adequate mitigation measures. Additionally, illegal mining, and illegal industries associated with resource exploitation such as informal oil refining and smuggling represent further, unregulated threats.

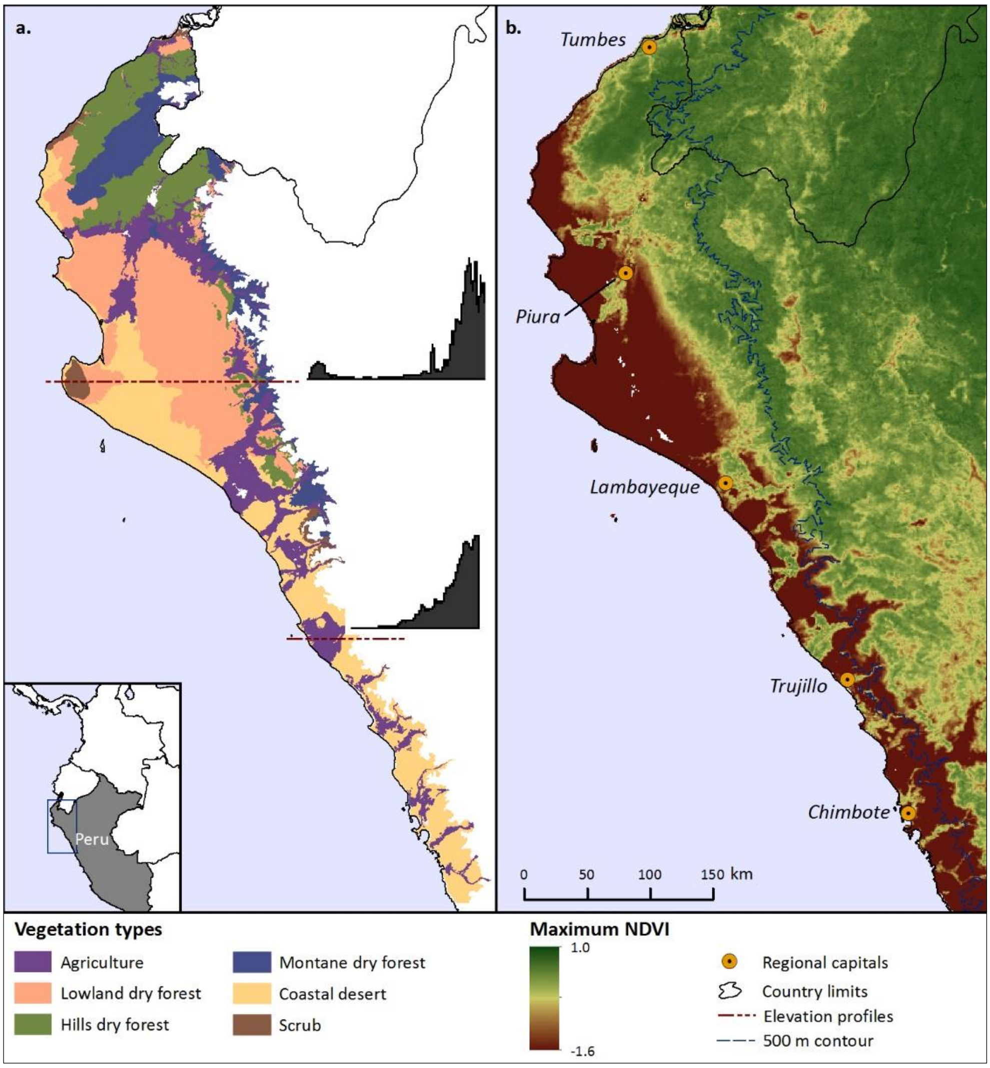

Figure 4.4. Vegetation over the north Peru coast. a) Categories of land cover and use under 500 m elevation (MINAM, 2012); b) Maximum Normal Difference Vegetation Index, showing greatest extent of vegetation (including crops) during 2013.

Protected area coverage in the region is poor, both geographically (in northwest Peru), and by ecosystem type (in dry forest). A 2008 study estimates that just 5% of the remaining 55,000 km of seasonally dry forest from the Equatorial region is protected (Linares-Palomino et al., 2009). National protected areas in the region with significant areas of lowland dry forest are Santuario Histórico Bosque de Pomac, Illescas Reserve (currently pending final category) and Coto de Caza Los Angolos (Figure 4.6). Pomac, at just 58 km^2, is currently the largest single extent of protected lowland dry forest in the region. New protected areas have recently been designated at regional level by Piura and Lambayeque local governments (e.g. Gerencia de Recursos Naturales del Gobierno Regional de Lambayeque, 2009), but both these areas, and projects to identify priority areas (e.g. More Cahuapaza et al., 2014) tend to focus on foothill regions rather than dry forest on the plains. However, a process to designate a further dry forest regional protected area at Talara, Piura is underway. Other conservation initiatives include designation of Important Bird Areas and Alliance for Zero Extinction sites (Figure 4.6), some of which have been important precursors of regional protected areas (Angulo, 2009).

Figure 4.5. The informal charcoal industry is a major cause of habitat destruction in Peru´s dry forests. a) Algarrobo *Prosopis* sp. trees are targeted; b) Only the larger trunks and branches are used. c) Charcoal production is also a fire risk to the rest of the forest. d) Carbon is transported as far as the capital Lima, for use in restaurants. Photos: C. Devenish.

Few resources are available for the management of protected areas in Peru. Encroachment into the region's only national park, protecting lowland dry forest, occupied almost a third of its area over a period of years, with a village and farmland established during this time. Biodiversity conservation on the coast is necessarily a social and economic problem, where often small scale use of biodiversity is part of subsistence livelihoods in isolated communities, lacking in basic services (Hocquenghem & Dammert Ego Aguirre, 1999; Linares-Palomino, 2006).

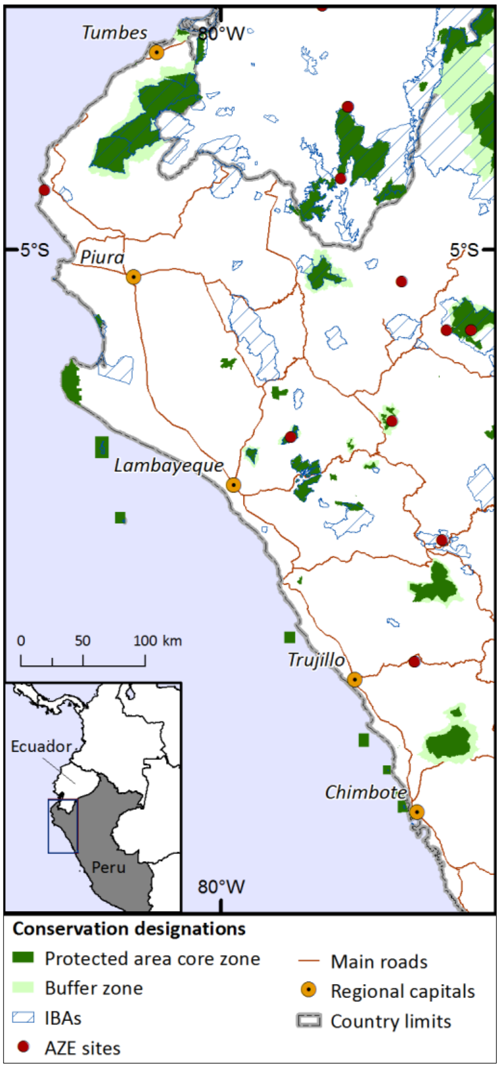

Figure 4.6. Protected areas, Important Bird Areas (IBAs), Alliance for Zero Extinction (AZE) sites in south Ecuador and north Peru.

4.3 Study species

A subset of the Tumbesian EBA restricted-range species are mostly found in the drier lowland forest or scrub habitats, corresponding to a decreasing elevational and latitudinal gradient in precipitation (Figure 4.2). These species have most of their distributions in northern Peru (typically > 50% of total range) where these habitats dominate, and are generally found below an elevation of 500 m above sea level (Ridgely, 2001; Schulenberg et al., 2007; Figure 4.7, 4.8). Although some of these species are known to exceed this elevation (Table 4.1), the majority of their distributions are below this limit. An additional factor to choosing species was to include both species of conservation interest and common species. Several Tumbes species have sister species in the Marañon valley, Peru (Chapman et al., 1926) whereas others remain at subspecies following current taxonomy (Remsen et al., 2016). For this study, geographically isolated subspecies, on Isla de la Plata, Ecuador (*Mimus longicaudatus platensis*) and in the Marañón valley (*Phaeomyias murina maranonica, Synallaxis stictothorax chinchipensis, Mimus longicaudatus maranonicus*) were not treated here. In fact, Mouse-coloured Tyrannulet *Phaeomyias murina* and Necklaced Spinetail *Synallaxis stictothorax* have recently been split into several species in the forthcoming Illustrated Checklist of the Birds of the World (N. Collar, pers. comm.).

Scant published information is available for the 14 study species (Figure 4.9). A search on the Scopus database, using species' scientific names and 17 synonyms as key words returned just 12 publications related to eight species in the study area. However, additional published information is available but not indexed. For example, for the Endangered Peruvian Plantcutter *Phytotoma raimondii* and Rufous flycatcher *Myiarchus semirufus*, the Scopus search turned up two and one articles, but at least 14 and 7 further papers exist for these species, respectively. Most of these unindexed articles are focused specifically on the species (e.g. nesting, diet, population, threats, phylogenetics), of which eight were published before 1990, and 13 post 2000, in local journals (e.g. BOC bulletin, Revista Peruana de Biología, Boletín UNOP, Ornithologisher Anzeiger). Further information is available in grey literature, for example, project reports and management plans, but even less easily than unindexed journals.

Table 4.1. Bird species included in study, showing threat status and typical altitudinal limits. Threat status: EN - Endangered, NT - Near Threatened, LC - Least Concern (BirdLife International, 2014). For further criteria on species selection and subspecies, see Chapter 2.

Taxon	**English Name**	**Family**	**IUCN Red List Category**	**Altitudinal range (m above sea level)**	**Average weight (g)**[3]	**Generation length**[4]
Myrmia micrura	Short-tailed Woodstar	Trochilidae	LC	0 – 1000	-	4.2
Forpus coelestis	Pacific Parrotlet	Psittacidae	LC	0 – 2000	22.9	4.1
Synallaxis stictothorax maculata & S. s. stictothorax	Necklaced Spinetail	Furnariidae	LC	0 - 300	8.6	3.8
Phaeomyias murina inflava & P. m. tumbezana	Mouse-coloured Tyrannulet	Tyrannidae	LC	0 - 2000	9.6	3.6
Pseudelaenia leucospodia	Grey-and-white Tyrannulet	Tyrannidae	LC	0 - 800	11.5	3.6
Tumbezia salvini	Tumbes Tyrant	Tyrannidae	NT	0 - 1000	-	3.6
Myiarchus semirufus	Rufous Flycatcher	Tyrannidae	EN	0 - 500	22.3*	5.1
Phytotoma raimondii	Peruvian Plantcutter	Cotingidae	EN	0 - 600	39.8+	4.6
Campylorhynchus fasciatus	Fasciated Wren	Troglodytidae	LC	0 - 1500	30.0+	3.6
Cantorchilus superciliaris	Superciliated Wren	Troglodytidae	LC	0 - 1000	20.3	3.9
Mimus longicaudatus albogriseus & M. l. longicaudatus	Long-tailed Mockingbird	Mimidae	LC	0 - 2400	66.6+	5.3
Piezorina cinerea	Cinereous Finch	Thraupidae	LC	0 - 200	-	3.8
Sicalis taczanowskii	Sulphur-throated Finch	Thraupidae	LC	0 - 300	9.7	3.8
Rhynchospiza stolzmanni	Tumbes Sparrow	Emberizidae	LC	0 - 1000	-	3.7

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[3] Weight sources: + BirdLife International (2016); * Lanyon 1975, all others: Diego García Olaechea (pers. com)

[4] BirdLife International (2016)

The breeding season for birds in the dry forest is highly correlated with rainfall, tending to start after the beginning of the rainy season (Marchant, 1959). The breeding period generally lasts between six weeks and three months with most breeding records for the study species from February/March to April through to June. The longest breeding season is for Tropical Mockingbird *Mimus longicaudatus*, between December and June (Marchant, 1959, 1960; Lanyon, 1975; Williams, 1981a, 1981b; Flanagan & Millen, 2008; Barrio et al., 2015). Breeding may be earlier towards the south of the ranges of most these species, and later in the north, following precipitation patterns (Lanyon, 1975). No published breeding records are known for Tumbes Tyrant *Tumbezia salvini* (Heming et al., 2013). The Peruvian Plantcutter was suggested to have a bimodal nesting period in Pomac National Park, with 19 active nests found in February and April, but not between 1-28 March (Nolazco & Roper, 2014). However, nesting records exist in March and December in other areas (Rosina & Romo, 2012). All species for which breeding records exist nest within bushes or small trees, except for the Rufous Flycatcher which appears to use both cavities (e.g. tree cavities and nest boxes) and very dark, thickets (Lanyon, 1975; F. Angulo, pers. com; Figure 4.6). The only information on nesting success is for Peruvian Plantcutter. A low success rate was found (Nolazco & Roper, 2014); of 19 nests, only two were successful, with most nests failing due to predation by birds (White-tailed Jay *Cyanocorax mystacalis*, Superciliated Wren *Cantorchilus superciliaris*, Peruvian Pygmy-Owl *Glaucidium peruanum*) and Guayaquil squirrel (*Sciurus stramineus*).

Figure 4.7. Site of first nest description (*Acacia macracantha* bush to right) and typical habitat of *Myiarchus semirufus*, as reported by Lanyon (1975). Note the proximity of the Pan-American Highway.

None of the study species are known to make migratory movements but few data are available. Migratory movements are known for some non-resident species (e.g. Black and White Tanager *Conothraupis speculigera* and Snowy-throated Kingbird *Tyrannus niveigularis*; Barrio et al., 2015), but not for seasonal movements of residents. A congener of the threatened Peruvian Plantcutter *Phytotoma raimondii*, White-tipped Plantcutter *Phytotoma rutila* was found to change food source according to availability in dry and wet seasons, but remained resident in one study (López-Calleja & Bozinovic, 2000). Peruvian Plantcutters seem to be able to adapt to novel food sources, and may be less dependent on certain food plants than previously thought (see Chapter 3). Some movement to adapt to changing food availability may be a possibility. Published information on diet for most species is also scant, but most is known about Peruvian Plantcutter. It has been suggested that certain plants are vital to its diet, including *Prosopis pallida* and *Grabowskia boerhaviifolia*, with young leaves, flowers and fruit eaten (Rosina & Romo, 2012; Nolazco et al., 2014). However, sites with high abundance of Plantcutters exist without a significant presence of these two species (data from this study) and at least 10 further plant species are listed in its diet (Romo & Rosina, 2012; Rosina & Romo, 2012). It is not known to eat any non-vegetable matter. In a laboratory trial, the congener, Rufous-tailed Plantcutter *Phytotoma rara*, consumed between twice and five times its body weight in wet vegetable matter per day, according to the dietary quality of the food source (Bozinovic, 1999).

Figure 4.8. Illustrations of a) Rufous Flycatcher and b) Peruvian Plantcutter from original species descriptions (Sclater & Salvin, 1878; Taczanowski, 1882); holotypes were collected towards southern (a) and northern extremes (b) of each species' range where they are now locally extinct. Illustrations: J. Smit

All endemic species are threatened to a certain extent by habitat loss, however, two of the most threatened are Peruvian Plantcutter *Phytotoma raimondii* and Rufous Flycatcher *Myiarchus semirufus* (Figure 4.8). Both species are classified as Endangered (BirdLife International, 2015) and currently documented only from scattered localities on the dry coastal plain (Schulenberg et al., 2007; Flanagan et al., 2009; Romo et al., 2015). Records are especially lacking in the southern limits of both species' former ranges. Nevertheless, the Rufous Flycatcher was described as uncommon in 1975, with never more than two adults seen at any one site (Lanyon, 1975), and 'wary of humans' at the time of its description (Taczanowski, 1882), indicating that it may always have been scarce. Both species are singular in many aspects; the plantcutters were formerly classified within their own family, Phytotomidae, but now are the only non-forest members of the Cotingidae (Remsen et al., 2016) with a primary diet of leaves (Snow, 2004). Rufous Flycatcher has recently been shown to be phylogenetically different to all other species of *Myiarchus*, hinted at by Zimmer (1938), and may even belong in a monotypic genus (Joseph et al., 2004). Specific threats to the Plantcutter include informal squid processing camps and other forest disturbance near Talara, one of its population strongholds (More 2002; Flanagan et al. 2009), conversion of forest belonging to an industrial food company to agriculture at Paiján, La Libertad. In the case of the Rufous Flycatcher, lack of nesting cavities, especially in large Algarrobo *Prosopis* sp. trees, as well as removal of dead limbs used as perches (Taczanowski, 1884), may be limiting factors to its survival (Lanyon, 1975; Joseph et al., 2004).

Figure 4.9. Study species (not to scale)[5]. a) Short-tailed Woodstar *Myrmia micrura*; b) Pacific Parrotlet *Forpus coelestis*; c) Necklaced Spinetail *Synallaxis stictothorax*; d) Mouse-coloured Tyrannulet *Phaeomyias murina*; e) Grey-and-white Tyrannulet *Pseudelaenia leucospodia*; f) Tumbes Tyrant *Tumbezia salvini*; g) Fasciated Wren *Campylorhynchus fasciatus*; h) Superciliated Wren *Cantorchilus superciliaris*; i) Long-tailed Mockingbird *Mimus longicaudatus*; j) Cinereous Finch *Piezorhina cinerea*; k) Sulphur-throated Finch *Sicalis taczanowskii*; l) Tumbes Sparrow *Rhynchospiza stolzmanni*.

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[5] Photo credits (all Creative Commons license). (a,i) Amy McAndrews; (b) peterdehaas2317; (c) Ardeola; (d) budgora; (e) Jorge Montejo; (f,h,l) David Cook; (g) Francesco Veronesi; (j) Richard Gibbons; (k) L. Ordóñez-Delgado.

5 Map of the thesis

5.1 Thesis aims and objectives

The overall aim of the thesis is to develop tools, combining different analytical techniques, field data and GIS, to provide improved estimates of species distribution and abundance in support of extinction risk assessments in threatened Neotropical bird species.

To achieve this aim, the following specific objectives will be implemented:

Chapter 2.	Estimate the ranges of study species with ensemble species distribution models
Chapter 3.	Estimate local abundance of study species across their ranges using covariate distance sampling
Chapter 4.	Explore range-wide variation in abundance across ranges of study species
Chapter 5.	Explore the relationship between relative probability of occurrence, derived from modelling and bird abundance, derived from field studies
Chapter 6.	Discuss findings and implications for conservation

5.2 Chapter outlines

Chapter 2

Modelling distributions of Tumbesian endemic birds: how well do species distribution models match our current understanding of species ranges?

Overview: Species distributions are modelled using ensemble species distribution models created from GLMs, GAMs, Maxent and Bioclim. Data for the models consist of species occurrences records, obtained from museum records and observation records, and environmental data, obtained from the worldclim database, and vegetation (Normal Difference Vegetation Index; NDVI) from MODIS. Modelling methods are compared, and predicted ranges are compared to existing ranges maps created by BirdLife International and NatureServe for extinction risk assessment.

Chapter 3

Estimating local abundance in patchy habitats: a case study on dry forest endemic birds of the Tumbes region

Overview: Covariate Distance sampling is used to estimate local abundance of 14 dry forest endemic bird species at 26 sites over their ranges in northern Peru. The sampling protocol is designed to maximise chances of obtaining bird records while ensuring geographical coverage based on a preliminary distribution model. Four parallel transects are used to count birds and evaluate vegetation characteristics at each site. Population sizes at discrete sites are calculated and discussed in light of threats and opportunities for conservation.

Chapter 4

Extreme variation and complex correlates of local abundance – lessons from a range-wide, multispecies survey

Overview: Patterns in abundance across the ranges of 14 dry forest species are explored, including variation in abundance across range and between range edge and core; congruence of abundance hotspots across species (i.e. do sites of highest abundances coincide?); spatial autocorrelation of abundance; and the nature and strength of correlates of local abundance. Correlates of abundance are regressed against species' densities, represented as Non-metric Multidimensional Scaling axes, using GAMs. Recommendations for surveys and conservation management are made.

Chapter 5

The relationship between occurrence modelling and abundance estimates

Overview: The relationship between local abundance (from field surveys) and relative probability of occurrence (from species distribution models) is explored using correlations. Hierarchical regression models between field-based abundance and modelled occurrence are built where relationships exist. Species- and site-level factors are explored to assess why model predictions may differ from field data. Species' global population sizes are estimated using the above regression models.

Chapter 6

General conclusions and future directions

Overview: Findings from the above chapters are discussed in a wider context of conservation research. Specific recommendations for future work are made to further explore methods treated here. Specific conservation assessments based on results are discussed for the study area and study species, e.g. changes in IUCN categories, population sizes, and key sites for conservation.

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Chapter 2

Modelling distributions of Tumbesian endemic birds: how well do species distribution models match our current understanding of species ranges?

1 Abstract

Species distribution models (SDMs) are an increasingly important tool supporting critical conservation decisions. Diverse modelling techniques, using species occurrence data from a variety of non-systematic surveys, together with climate and remote-sensed environmental data, facilitates the creation of distribution models for rare or endangered species lacking in field work and published literature. However, models are not routinely used to establish species range limits, despite the ubiquitous application of range sizes (Extent of Occurrence and Area of Occupancy) in establishing extinction risk. As a first step to comparing modelled occurrence and abundance, this study aims to provide the most up to date range size estimates for 14 endemic Tumbesian birds, including three threatened or near threatened species, using an extensive database of current occurrence records (2000-2015) and environmental layers. A median of 150 records (range: 68 - 791) per species was used to model species' occurrence over their entire Tumbesian ranges, without spatial duplicates within 1 km. An ensemble model was built using Generalised Additive Models, Generalised Linear Models (ridge regression), Maxent, and Domain, using a 5% omission error threshold to define presence and absence. A species-specific study area was restricted to just 25 km around the convex hull of all the species' occurrence points. Modelled ranges were compared to existing range estimates used in extinction risk assessment. Model AUC values of the ensemble model ranged from 0.81 to 0.87. The different modelling methods coincided highly in terms of ranked correlation but differed in the distribution of their predicted values. Range size estimates were generally smaller than, but coincided spatially with, published ranges, with the exception of the three species of conservation interest. Two threatened species (Peruvian Plantcutter *Phytotoma raimondii* and Rufous Flycatcher *Myiarchus semirufus*) had modelled ranges an order of magnitude larger than those published which were limited to the areas around known occurrences. A further species, the Near threatened Tumbes Tyrant *Tumbezia salvini* coincided

over only 18% of the published range. I suggest that published ranges are likely to underestimate the presence of rare and threatened species and that distribution models are included as additional tools to check inconsistencies and improve the process of establishing ranges for red listing purposes.

2 Introduction

The ability to predict the probability of occurrence of a species across its entire range is a desirable quantity for many conservation related problems (Guisan et al., 2013; Guillera-Arroita et al., 2015). Applications of species distribution models (SDMs) in this area already include ecological and biogeographical inference (including effects of climate change on biodiversity, determinants of range limits); species management (including invasive species, and guiding surveys); ecological restoration (including species reintroductions); and conservation planning/priority setting (Franklin, 2009; Peterson et al., 2011; Guillera-Arroita et al., 2015).

The use of species distribution models in the ecological literature has increased exponentially over the last 20 years (see Figure 3.3, Chapter 1), in part, due to the improved accessibility of predictors, such as global gridded climate layers (Hijmans et al., 2005); more extensive online species occurrence data, such as eBird or VertNet (Graham et al., 2004; Soberón & Peterson, 2004); and user-friendly software, such as Maxent (Phillips & Dudík, 2008; see Figure 3.3, Chapter 1). New methods are also constantly being developed or adapted from other disciplines, within the main groups of envelope methods, statistical regression techniques and machine learning (e.g. Blonder, 2015; Chen, 2015; Renner et al., 2015). However, despite comparisons between methods (Segurado & Araújo, 2004; Elith et al., 2006), no clear best method prevails, which has led researchers to suggest ‘ensemble’ approaches. These aim to reduce the uncertainty across different modelling methods by combining model outputs from a variety of methods to produce a consensus model based on a weighted summary (Araújo & New, 2007).

Despite the advances in SDMs, modelling methods are not routinely used to corroborate or support the establishment of range sizes for conservation processes, such as red listing. Changes in range sizes are a fundamental part of establishing extinction risk in species, acting as a signal of a reducing population (IUCN, 2001). Methods to determine range sizes as part of IUCN guidelines have been in place for at least 25 years (Mace et al., 1992; IUCN, 1994). Mapping the range of a species involves reducing a complex spatial and temporal pattern to an irregular two-dimensional outline (Brown et al., 1996). Differences in method and approach, can therefore lead to different results, often dependent on purpose. In establishing extinction risk of species, two different measures are employed to measure range size, Extent of Occurrence (EOO) and Area of Occupancy (AOO) (Gaston, 1991; IUCN, 2001). However, the difference between the two can be subject to interpretation of definitions, with uncertainty liable to be introduced at different stages, for example how an 'occurrence' is interpreted (Akçakaya et al., 2000). Each measure could be considered to lie at either end of a continuum, with EOO as the geographical space encompassed by the outermost bounds of all locality records at one end of the scale, and AOO as the actual space used by a species within those limits (Maurer, 1994) at the other extreme. EOO is based on the shortest continuous boundary drawn to encompass all the known, inferred or projected sites of present occurrence of a taxon (IUCN, 2001), often measured as a minimum convex polygon. The IUCN definition allows discontinuities in the species' distribution to be excluded. The scale and degree of such exclusions can be seen as a factor to distinguish both measures.

This chapter aims to define the ranges of 14 Tumbesian endemic birds using a comprehensive data set of recent occurrence records, as an essential first step for comparing occurrence probability with abundance. Specifically, it will:

- use a range of distribution modelling methods to map relative probability of occurrence of study species;
- validate models and compare resultant distributions across modelling methods;
- compare modelled distributions to mapped ranges (BirdLife International & NatureServe, 2015) and examine where differences occur.

3 Methods

3.1 Species occurrence points

Distribution models were built for fourteen Tumbesian species (see Table 4.1, Chapter 1). Geographically isolated subspecies, for example, on Isla de la Plata, Ecuador (*Mimus longicaudatus platensis*) and in the Marañón valley, Peru (*Phaeomyias murina maranonica, Synallaxis stictothorax chinchipensis, Mimus longicaudatus maranonicus*) were not included. In fact, Mouse-coloured Tyrannulet *Phaeomyias murina* and Necklaced Spinetail *Synallaxis stictothorax* have recently been split into several species in the Illustrated Checklist of the Birds of the World (del Hoyo & Collar, 2016).

Species occurrences at point localities were collated from observation records and museum specimens through literature searches, museum visits and online databases (principally VertNet, Xenocanto and eBird). In the case of eBird, observations were excluded where survey effort exceeded 5 km (linear route) or 500 ha (area count), given that a single location is given for the whole survey. Where occurrence records did not have geographic coordinates, but contained detailed locality data, an attempt was made to georeference the records, using online tools (e.g. GEOLocate[1]), gazetteers for Peru (Stephens & Traylor, 1983) and Ecuador (Paynter, 1993), national digital cartography and georeferenced records at the same locality. Records without detailed locality data, coordinates or dates were removed from the data set. Occurrence records were checked for correct positioning of coordinates using ArcGIS and R (within country land boundaries, 1st degree administrative boundaries or elevational limits, Table 4.1 Chapter 1). Records failing to meet these checks were flagged for manual processing. Records were also checked with known species distributions, e.g. distribution shapefiles (BirdLife International & NatureServe, 2015) and guide books (Schulenberg et al., 2007). Records at known distributional or elevational limits were evaluated using criteria such as reliability of observer, frequency/presence of nearby records and distance from known limits. Furthermore, to avoid sampling bias, exact spatial duplicates and records within 1 km of each other were removed so that only one record per grid cell was used in the models given that the predictors were at 1 km

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[1] http://www.museum.tulane.edu/geolocate/default.html

resolution (Stockwell & Peterson, 2002; Graham et al., 2004). Spatial duplicates do not necessarily correspond to areas with higher frequency of occurrence of birds, but may represent areas most visited by collectors or birdwatchers (e.g. close to roads). Spatial filtering of data, by removing observations within a certain distance of each other, has been shown to improve model performance by counteracting the inflation of validation metrics such as AUC as a result of spatial autocorrelation of presence points (Boria et al., 2014; Radosavljevic & Anderson, 2014). Occurrence records prior to 2000 were removed from the data set in order to match the temporal scale of some predictors and the field work. Occurrence records obtained from the PhD fieldwork to estimate density for this study were not used in building the species distribution models, although previous occurrence records from similar localities were included.

3.2 Selection of environmental predictors

Three types of environmental variables are readily available over the whole study area at 1 km spatial resolutions, topographical measures based on Digital Elevation Models (e.g. slope, altitude), climatological indices based on interpolated ground station data (e.g. annual temperature, precipitation) and remotely sensed data (e.g. vegetation indices; Figure 3.1). The latter two are available at monthly temporal resolutions, allowing bioclimatic variables (Xu & Hutchinson, 2013) to be processed for each, such as annual and/or periodic means, minimums and maximums, and seasonality indices. For this study, the hole-filled SRTM Digital Elevation Model (Jarvis et al., 2008) was used to create calculate derived variables, such as slope and associated variability. Calculations were performed at a scale of 100 m and subsequently averaged at 1 km resolution. Climatological data were obtained from the updated version of the Worldclim data base (Hijmans et al., 2005), including temperature, precipitation and solar radiation data, averaged over the period 1970-2000. Although regional climate layers exist, their resolution of 5 km was not adequate for this study (Manz et al., 2016). For vegetation indices, Normalised Difference Vegetation Index (NDVI) was used from the monthly MODIS product, MOD13A3 (Didan, 2015), averaged across the period 2010-2015. This

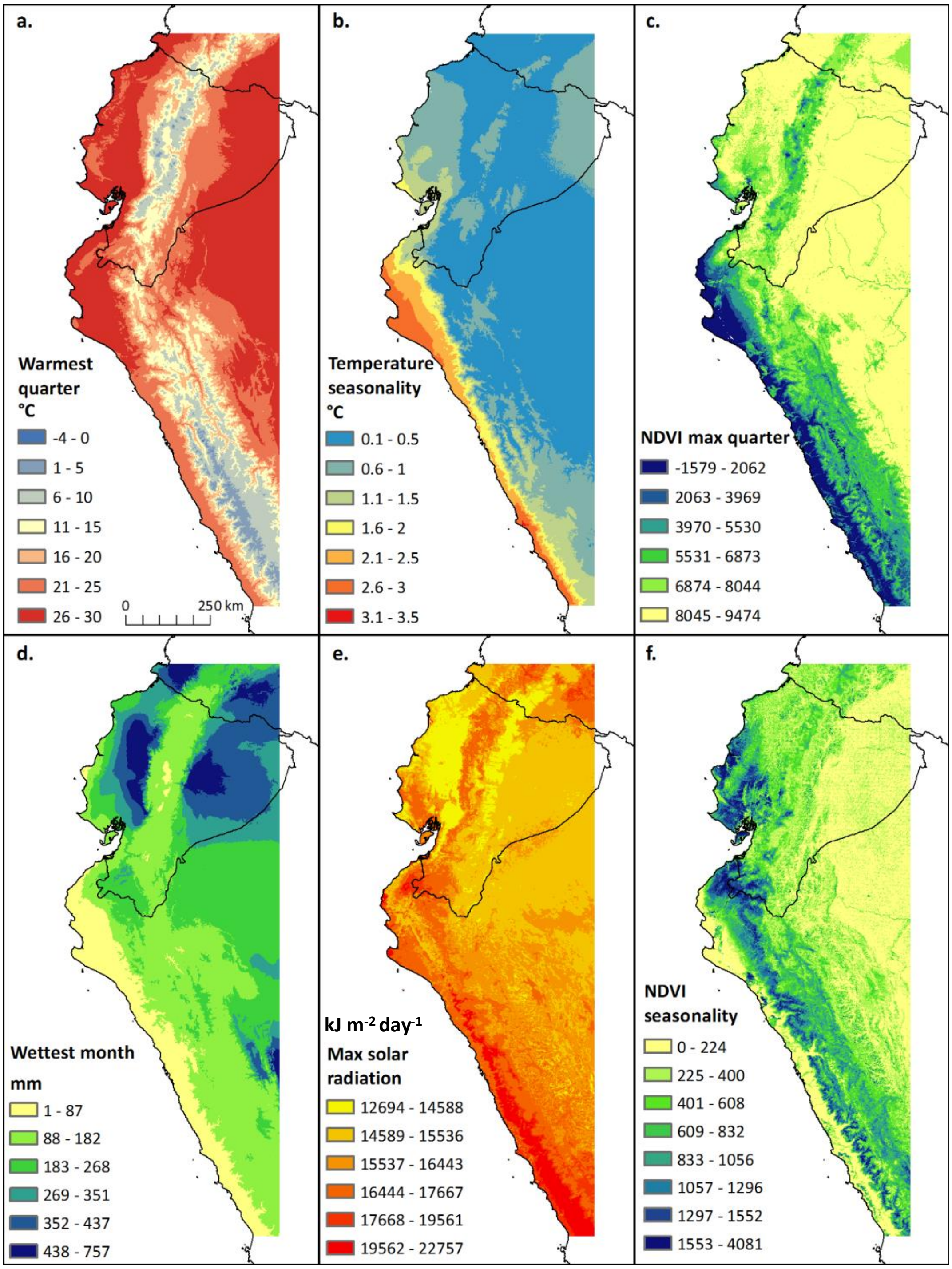


Figure 3.1. Environmental variables used for species distribution modelling over the study area, north Peru. Bioclimatic variables (a, b, d) are based on monthly values of precipitation and temperature and vegetation indices (c, f) are derived from monthly values of NDVI obtained from MODIS. a) Temperature of the warmest quarter; b) Temperature standard deviation; c) Highest quarter of NDVI values; d) Precipitation during wettest month of the year; e) Maximum solar radiation throughout year; f) Standard deviation of NDVI.

allowed for almost complete coverage of the region (only 0.05% of land pixels had cloud cover for every month during this period), whilst data were also collected within three years either way of the field study in 2013. Monthly precipitation across the study area is very seasonal, following a unimodal distribution, peaking in March. Monthly NDVI follows a similar pattern, but with a lag, that is, its peak extends into April (Figure 3.2). A recognised wet season extends from January through to April and a dry season from May to December (CDC, 1992).

The predictors were selected using three criteria. First, in terms of ecological significance, second, in their predictive ability, and third, to avoid multicollinearity. Given the seasonality of the rainfall and the generally dry environment (the maximum monthly mean rainfall is just over 150 mm, Figure 3.1, 3.2), areas retaining some moisture over the dry period could be important to dry forest birds. Minimum rainfall and minimum NDVI may provide an indication of this, in particular, NDVI, given the generally low quality of rainfall data in this region (Manz et al., 2016). However, if NDVI is used to predict species occurrence, care must be taken with the extent of irrigated crops over the study area. As such, NDVI should be in such a format as to be able to separate between crops and natural habitat. The NDVI variables were assessed for their ability to differentiate between different land cover types (MINAM, 2012), both visually through boxplots, and using Kruskal-Wallis tests (Appendix 1).

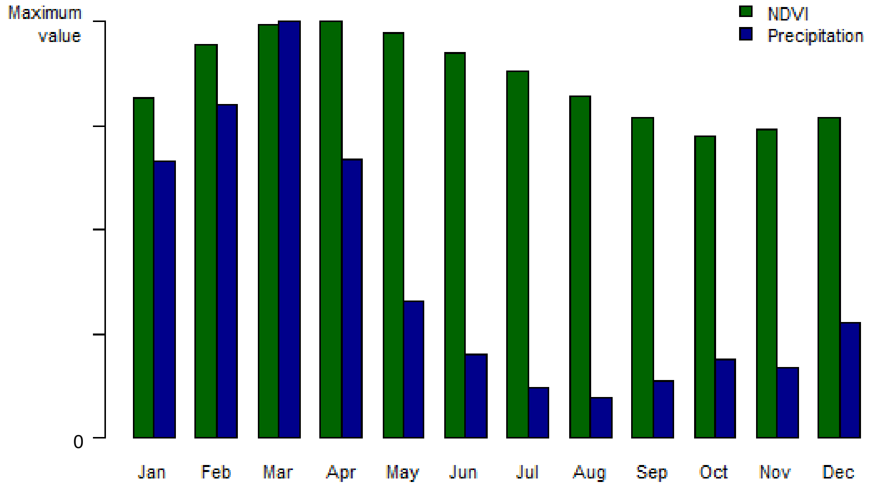


Figure 3.2. Standardised monthly precipitation and NDVI across the study area. NDVI peaks after rainfall has peaked. Range of precipitation and NDVI values correspond to 14.6 to 151.6 mm, and 0.41 to 0.56, respectively.

Variables were assessed for predictive ability by running univariate Generalised Linear Models for each species (binomial with logit link) and each of 35 potential predictors, with and without quadratic terms, and averaging the explained deviance over species. In all cases, predictive performance improved with the addition of a quadratic term, therefore quadratics were always included (GAMs excepted). Potential predictors were also assessed for collinearity using scatterplots and pairwise Spearman's correlation coefficients. Predictive ability and pairwise correlations were combined graphically (Appendix 2). Using this graphic, a selection was made whilst bearing in mind ecological rationale, attempting to maximise total explained deviance from the combined predictors, and avoiding predictors with absolute pairwise correlation coefficients greater than 0.7. In a review of methods to counter collinearity, Dormann et al., (2013) found that this method was almost as effective as some of the other more complex methods to counter collinearity. Predictors were chosen for all species simultaneously to aid comparison among species, and because all species are endemic to the same broad habitat.

3.3 Modelling methods

Four modelling methods were used: regression based techniques Generalised Linear Models (GLMs) and Generalised Additive Models (GAMs), the machine learning 'Maxent' (Phillips & Dudík, 2008), and the climate envelope, or similarity metric-based method 'Domain' (Carpenter et al., 1993). The first three are popular species distribution modelling techniques which perform well in method comparisons (Elith et al., 2006). The latter is distance-based, and of interest to the comparison of modelled occurrence with field-based density estimates (Chapter 5) given that a similar method was recently shown to be important in species distribution model - abundance comparisons (Martínez-Meyer et al., 2012). The methods below provide for a variety of species response distributions, including unimodal, using quadratic terms in GLM, and more flexible distributions with Maxent and GAMs.

For all modelling methods, a species-specific study area was constructed from which to select background points. A convex hull, with a 25 km buffer, was drawn round all presence points, representing the species' effective area utilised (Barve et al., 2011; Peterson et al., 2011). Then, 5000 background points were randomly selected from this area for all modelling methods except for Domain, which uses presence records only. Finally, species' distributions were predicted using each modelling method over the same study area with a further 25 km buffer applied, allowing maps to show relative probability of occurrence up to 50 km beyond all known presences. For all methods, predictor values were extracted at presence and background locations using the R package raster (Hijmans, 2016). For the regression techniques (GLM and GAM), observation weights were included in the model specification to the effect that the sum of presence weights was equal to the sum of absence weights (Hirzel et al., 2006; Barbet-Massin et al., 2012) . This technique effectively adjusts the sample prevalence to a value of 0.5, rather than letting the model be strongly influenced by the high ratio of background to presence points, given that as the number of background points increases to infinity, the predicted occurrence tends to zero (Warton & Shepherd, 2010). Maxent software also assumes a sample prevalence of 0.5. In all cases, the true prevalence (the ratio of presences to absences) is unknown.

3.3.1 Regularised Generalised Linear Models

Regularisation of GLMs was used to include an element of variable selection within this regression method. Ridge and lasso regression employ a shrinkage penalty which is added to the residual sum of squares during the fitting procedure. As with least squares regression, coefficients are chosen that minimise this value. This has the effect of shrinking coefficient estimates towards zero, depending on a tuning parameter, λ (James et al., 2013). The R package glmnet (Friedman et al., 2010) employs cross validation to find the value of λ which gives the minimum mean squared error. Furthermore, the package provides a link between ridge regression (coefficients approach zero) and the lasso (coefficients may be equal to zero) through a further parameter, α, which can be set exclusively for either type of shrinkage or at intermediate values between them. Cross validation with 10 folds were used to select λ, with presences and absences selected randomly, but in the same proportion as the full dataset (Guillera-Arroita et al., 2014). Different values of α were trialled, and final models were built with $\alpha = 0$ (i.e. ridge regression).

3.3.2 Generalised Additive Models

GAMs represent a flexible approach to modelling allowing species' responses to environmental variables to take on non-linear, asymmetric forms (Austin, 2007). GAMs were implemented using the R package mgcv, using thin plate regression splines with a modified smoothing penalty allowing the whole term to be shrunk to zero (Wood, 2006), thus allowing a degree of variable selection. Additionally, both the x and y coordinates of each presence and background point were included within an isotropic smooth term.

3.3.3 Maxent

Maxent is a machine-learning method that fits a distribution to the environmental predictors most closely approximating a uniform distribution (maximum entropy), subject to the constraint of the empirical distribution of the environmental variables at the presence points (Franklin, 2009). Maxent also implements a type of variable selection through its regularisation coefficient (Merow et al., 2013). Maxent was implemented through the R package dismo (Hijmans et al., 2016), using the same randomly selected background points as the other methods. Default settings were employed apart from omitting threshold and product features.

3.3.4 Domain

Domain assigns a classification between 0 and 1 to each grid cell based on the value of the Gower distance (a similarity metric) to the nearest presence point in climate space, that is, the maximum similarity between a particular grid cell and all presences (Carpenter et al., 1993). As such, it does not use background points, but rather, evaluates the similarity metric over the full set of grid cells. Domain was implemented in the R package dismo (Hijmans et al., 2016), which follows the original specification with the exception of truncating values below 0, so that the output is in the range 0-1.

3.4 Model validation

For each modelling method, 5-fold cross validation was performed and the validation metric (Area under the Receiver Operating Curve - AUC) were averaged across all folds. Each fold was chosen with the same proportion of presences and absences as in the full data set. For the final prediction, all presence points were used to build the model. Despite criticisms of the use of AUC to validate models (Lobo et al., 2008), no universally accepted alternatives exist, and it remains the most widely used evaluation metric for species distribution models. Despite suggested benefits of alternatives to AUC, such as partial AUC, where AUC is evaluated only over part of a modified ROC curve (Peterson et al., 2008), or AUC with ‘spatial sorting bias’ removed (Hijmans, 2012), these were not included in this analysis. All methods here predict values over the whole range between 0 and 1, and used a standard method to set the size of the study area, which justifies use of the standard AUC. Even though a validation metric based on the error associated with presence points (partial AUC; Peterson et al., 2008) is of interest, it still requires setting a subjective threshold over which AUC is to be evaluated, which complicates comparison (Liu et al., 2011) among models or species. Models with AUC values over 0.7 are considered to have good model accuracy (Manel et al., 2001).

3.5 Consensus model

To assess similarity between individual modelling methods, models were compared with pairwise correlations of 2500 random points across the predicted areas of each species between all four model types (i.e. resulting in 14 4x4 matrices of correlation coefficients). The mean and standard deviation of the pairwise correlation coefficients across all species were compared to evaluate similarity between models.

A consensus model was then created as a weighted average of the four individual models. Weights were constructed to overcome the difficulty that different modelling techniques do not produce absolute values of probability of occurrence (Hastie & Fithian, 2013) and are therefore not directly comparable. Therefore, weights provide a measure of the relative difference in predicted values at presence points between the models. Weights, *w*, equal the median predicted value, *p*, at *n* presence points, averaged over *m* models, divided by median.

$$w_{1\ldots m} = \frac{\sum_1^m \tilde{x}}{m} / \tilde{x}_{1\ldots m}\,, \quad \text{where } \tilde{x}_{1\ldots m} = \ median(p_{1,} \ldots p_n)$$

Therefore, models with generally higher value at presence points than others are penalised ($w < 1$), whereas models with generally lower values at presence points are weighted favourably ($w > 1$).

Models were compared among methods (including the consensus model) in terms of ranked correlation and distribution of model values. Spearman's correlation coefficient was used to compare across values from 10,000 random samples from each model. To compare the distribution of model values, index plots of ranked values by species were made for each method (i.e. ranked model value against proportion of area covered). Species were grouped according to a measure of rarity/commonness, approximated by creating four groups using hierarchical clustering with standardised values of modelled range size (see below) and average abundance (see Chapter 3).

3.6 Threshold

Multiple methods exist for applying thresholds to species distribution models to define likely species presence or absence. A method shown to have good performance is the threshold at which sensitivity (True Positive Rate) + specificity (True Negative Rate) reaches a maximum (Jiménez-Valverde & Lobo, 2007; Liu et al., 2013). However, other authors (Peterson et al., 2011) prefer thresholds not calculated with absences when background data, rather than true absences, are used in models. One such measure, relates to an acceptable omission rate defined for the species occurrence data, based on its perceived or measured quality, while minimising the predicted area (Engler et al., 2004; Peterson et al., 2008). A threshold is calculated as the percentile of predicted values at presence points, corresponding to the omission rate for the occurrence data. This limit has previously been used to define Extent of Occurrence from distribution models (Fivaz & Gonseth, 2014). If occurrence data are deemed perfect, e.g. with no geographic or taxonomic errors, then a 0% omission rate can be used, conceptually similar to a convex hull method for establishing Extent of Occurrence, and the threshold corresponds to the minimum predicted value at presence points. For this study, a 5% error rate was chosen, which was considered to balance the high quality data verification process, and yet allow for some location errors and vagrancy (i.e. individuals recorded at atypical locations). Therefore, a threshold was set for each species where 95% of occurrence points remained within a minimal predicted area. The thresholded models were compared to published range maps (BirdLife International & NatureServe, 2015). BirdLife ranges were plotted over model outputs, and percentage differences in area and overlap between the two were calculated in R (R Core Team, 2016).

4 Results

4.1 Species occurrence records

A total of 13,423 species occurrence records were collated (Appendix 3), of which over 7,400 were spatial duplicates. Of the total data set, 93% of records came from observations, with 7% from specimens and recordings. Sources of the final data set, after elimination of duplicated records, in decreasing numbers of records were eBird, literature and unpublished fieldwork, VertNet and other museums, and xenocanto (Table 4.1). The final selection had a median of 150 records per species, with a minimum of 68 for Sulphur-throated Finch *Sicalis taczanowskii* and a maximum of 791 for Long-tailed Mockingbird *Mimus longicaudatus* (Table 4.2).

Table 4.1. Summary of data sources for species occurrence points

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 (Museums visited - Ecuador: Museo Ecuatoriano de Ciencias Naturales, Instituto de Ciencias, Biológicas Escuela Politécnica Nacional; Peru: Museo de Historia Natural, Universidad Nacional Mayor de San Marcos, Colección de Aves, CORBIDI)
Xenocanto	Sound recordings	2	http://www.xeno-canto.org/

Table 4.2. Species occurrence points collated, showing final number of points used in models and numbers of spatial duplicates and records within 1000 m

Species	Points used in models	Spatial duplicates within 1000 m	Spatial duplicates exact	Total
Myrmia micrura	141	73	191	405
Forpus coelestis	572	326	1,221	2,119
Synallaxis stictothorax	241	117	369	727
Phaeomyias murina	181	71	325	577
Pseudelaenia leucospodia	148	99	258	505
Tumbezia salvini	81	50	132	263
Myiarchus semirufus	123	78	153	354
Phytotoma raimondii	140	97	146	383
Campylorhynchus fasciatus	518	312	1,338	2,168
Cantorchilus superciliaris	321	272	644	1,237
Mimus longicaudatus	791	662	2,182	3,635
Piezorina cinerea	157	67	181	405
Sicalis taczanowskii	68	13	57	138
Rhynchospiza stolzmanni	145	130	232	507
Total	**3,627**	**2,367**	**7,429**	**13,423**

4.2 Species distribution models

Species distribution models were produced for 14 species, using four different methods. GAMs scored highest mean AUC, followed by Maxent, GLM and finally Domain. AUC values were consistent within methods, with less than 4% variation observed in each (Table 4.3). AUC was not significantly correlated with numbers of species presence points used in models ($r_s = -0.10$, $p = 0.74$, $n = 14$), with Peruvian Plantcutter *Phytotoma raimondii* and Tumbes Tyrant *Tumbezia salvini* both scoring high AUC values but with low numbers of presence points (Table 4.2).

Table 4.3. Model validation metrics: mean (± standard deviation) AUC value per species with 5-fold cross validation for individual methods and consensus model

Species	**GLM**	**GAM**	**Maxent**	**Domain**	**Mean per species**	**Consensus**
Myrmia micrura	0.76	0.8	0.78	0.72	0.76±0.03	0.83
Forpus coelestis	0.82	0.85	0.83	0.75	0.81±0.04	0.84
Synallaxis stictothorax	0.78	0.86	0.81	0.76	0.80±0.04	0.86
Phaeomyias murina	0.72	0.82	0.75	0.72	0.75±0.05	0.82
Pseudelaenia leucospodia	0.78	0.84	0.8	0.76	0.80±0.03	0.84
Tumbezia salvini	0.8	0.86	0.82	0.78	0.81±0.03	0.87
Myiarchus semirufus	0.76	0.8	0.78	0.75	0.77±0.02	0.83
Phytotoma raimondii	0.81	0.86	0.83	0.76	0.81±0.04	0.87
Campylorhynchus fasciatus	0.79	0.85	0.82	0.75	0.80±0.04	0.84
Cantorchilus superciliaris	0.76	0.82	0.77	0.75	0.78±0.03	0.81
Mimus longicaudatus	0.81	0.87	0.83	0.74	0.81±0.05	0.85
Piezorina cinerea	0.77	0.86	0.79	0.76	0.80±0.05	0.86
Sicalis taczanowskii	0.76	0.76	0.77	0.73	0.76±0.02	0.83
Rhynchospiza stolzmanni	0.78	0.83	0.82	0.78	0.80±0.03	0.85
Mean per method	**0.78±0.03**	**0.83±0.03**	**0.80±0.03**	**0.75±0.02**		**0.84**

Modelling methods produced systematic differences in relative probability of occurrence, with GAMs generally producing the highest values, and Maxent and Domain, generally the lowest (Appendix 4, Appendix 5) and is also reflected in the response curves (Figure 4.1). Species response curves for each species showed similar patterns across methods for each predictor (Figure 4.1), especially in the case of GAMs and Maxent, both of which allow most flexibility in modelling responses. GAMs showed the strongest degree of variable selection, with several coefficient values almost unchanging across the range of a particular predictor.

Variables showing least contribution (that is, least positive or negative responses across the predictors) were seasonality of NDVI, and maximum solar radiation. The remaining four predictors showed similar levels of contribution, with mean temperature of warmest quarter, precipitation of wettest month, mean NDVI of highest quarter showing most variation (Figure 4.1). In general, patterns between models were similar for each species and each predictor.

Table 4.4. Similarity across modelling methods. Mean (upper triangle) and standard deviation (lower triangle) of correlation coefficients

	GLM	**GAM**	**Maxent**	**Domain**
GLM		+0.86	+0.94	+0.87
GAM	0.08		+0.89	+0.82
Maxent	0.02	0.07		+0.88
Domain	0.04	0.10	0.03	

Species distribution maps, predicted across the study areas showed similar patterns (Figure 4.2) across methods. In general, GAMs produced less pixels (i.e. smaller areas) with higher probabilities and reflecting the higher flexibility of GAMs to overfit (Figure 4.2a). In contrast, Domain produced the largest areas of higher probabilities (Figure 4.2d). GLMs (Figure 4.2b) and Maxent (Figure 4.2c) produced the most visually similar patterns but with GLMs showing higher absolute values of relative probability of occurrence. This similarity between models was borne out by pairwise comparisons between modelling methods across all species (Table 4.4). Maxent and GLM were most strongly correlated with the smallest standard deviation in correlation coefficients, followed by Maxent and GAM. All individual correlations were highly significant ($p < 0.001$). Mean correlation coefficients by species (across all models) ranged from 0.74 in Mouse-coloured Tyrannulet *Phaeomyias murina*, through six species > 0.80, to seven > 0.90, including the three threatened species in the latter group.

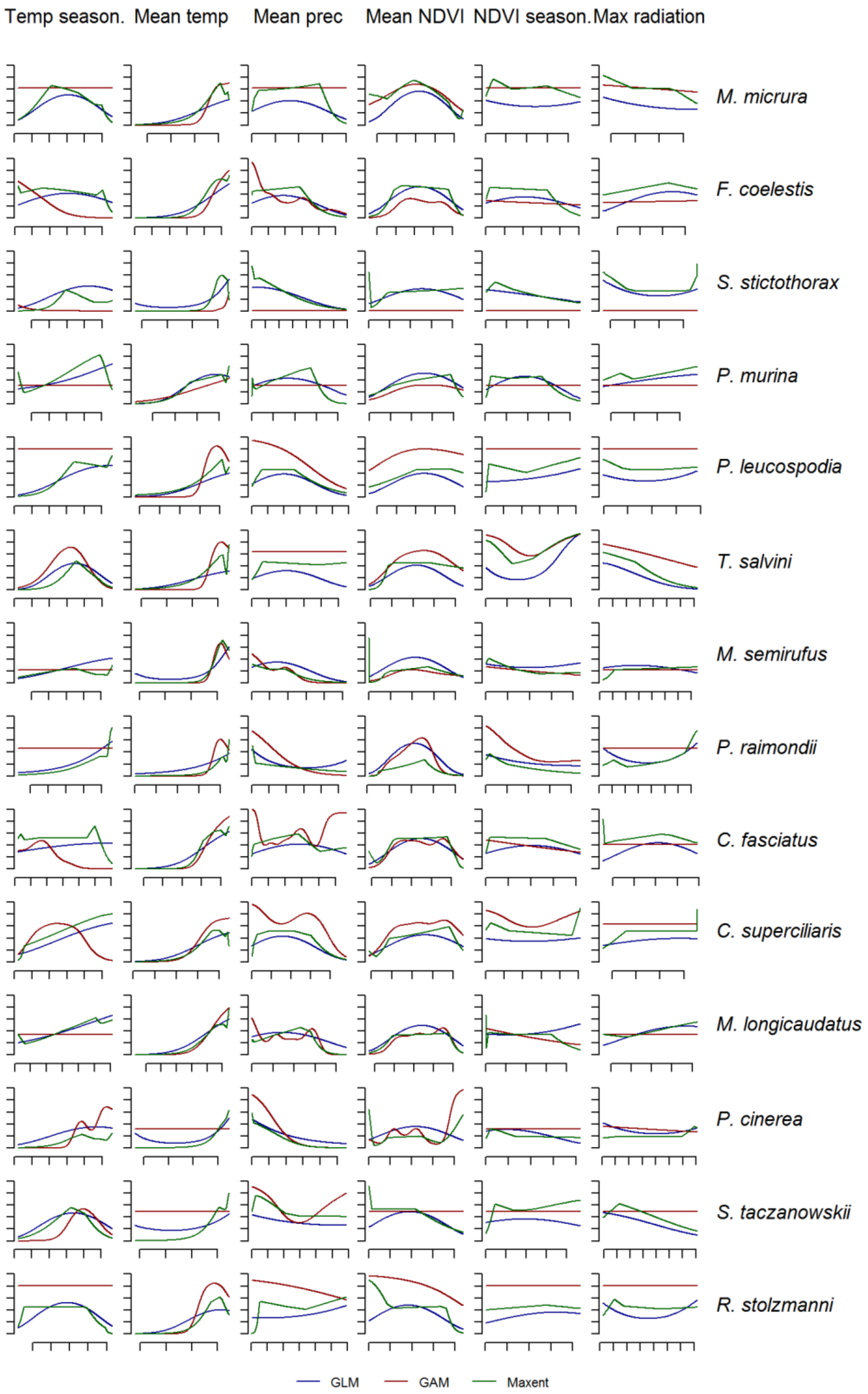


Figure 4.1. Response curves for each predictor variable by species for three modelling methods. Predictors (from left to right): mean annual temperature, mean annual precipitation, minimum solar radiation, maximum solar radiation, NDVI seasonality, minimum NDVI.

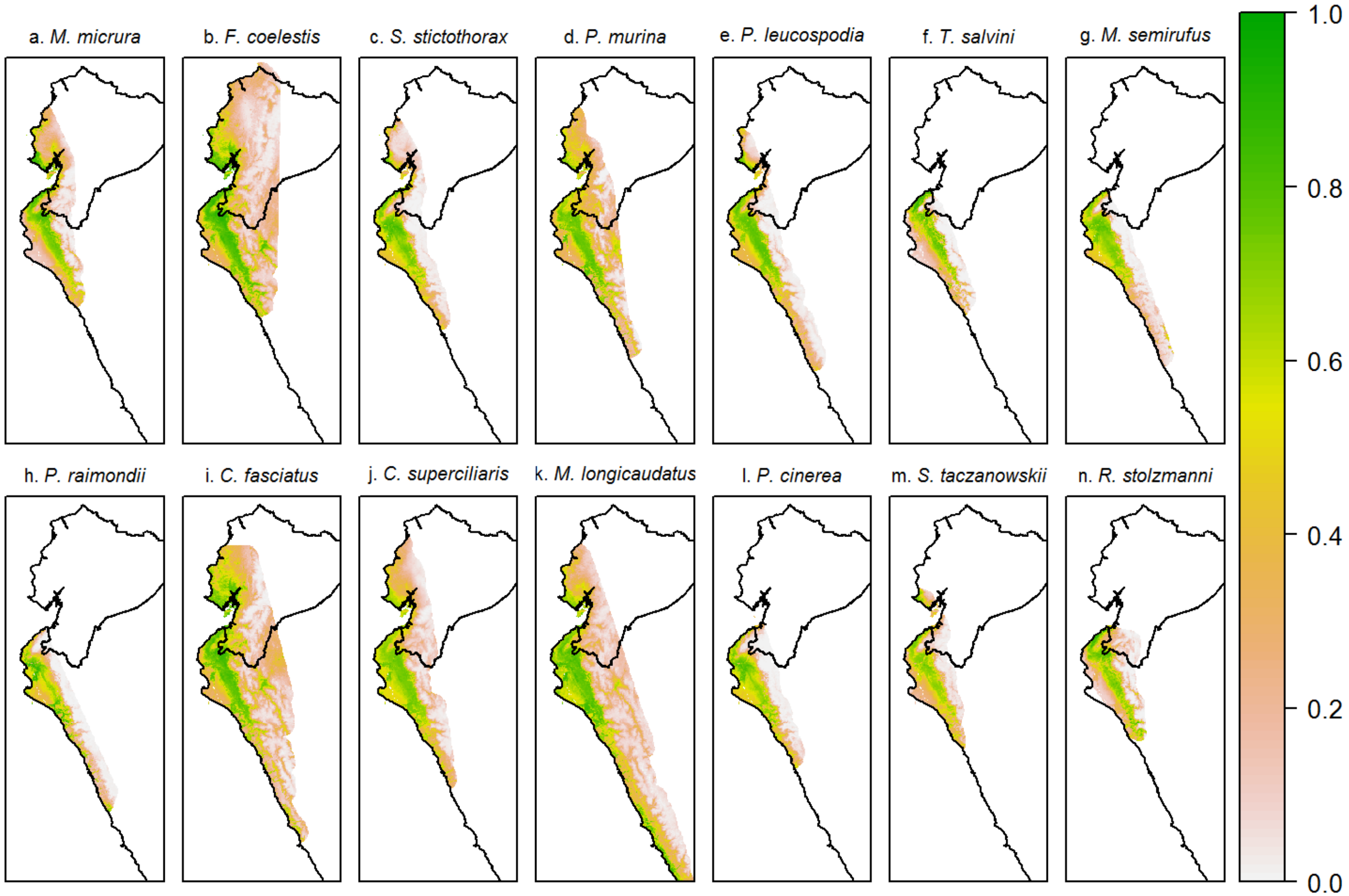
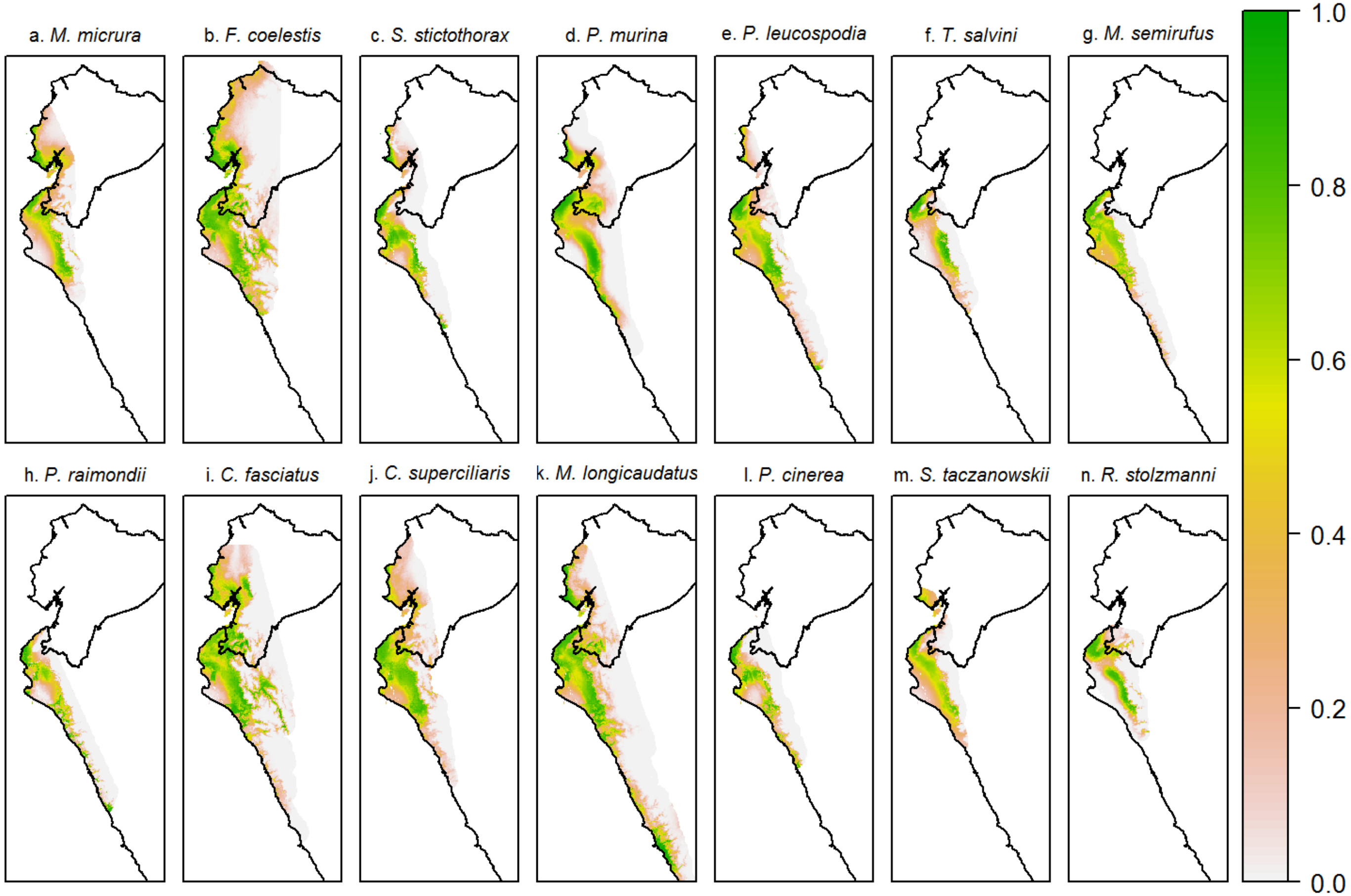
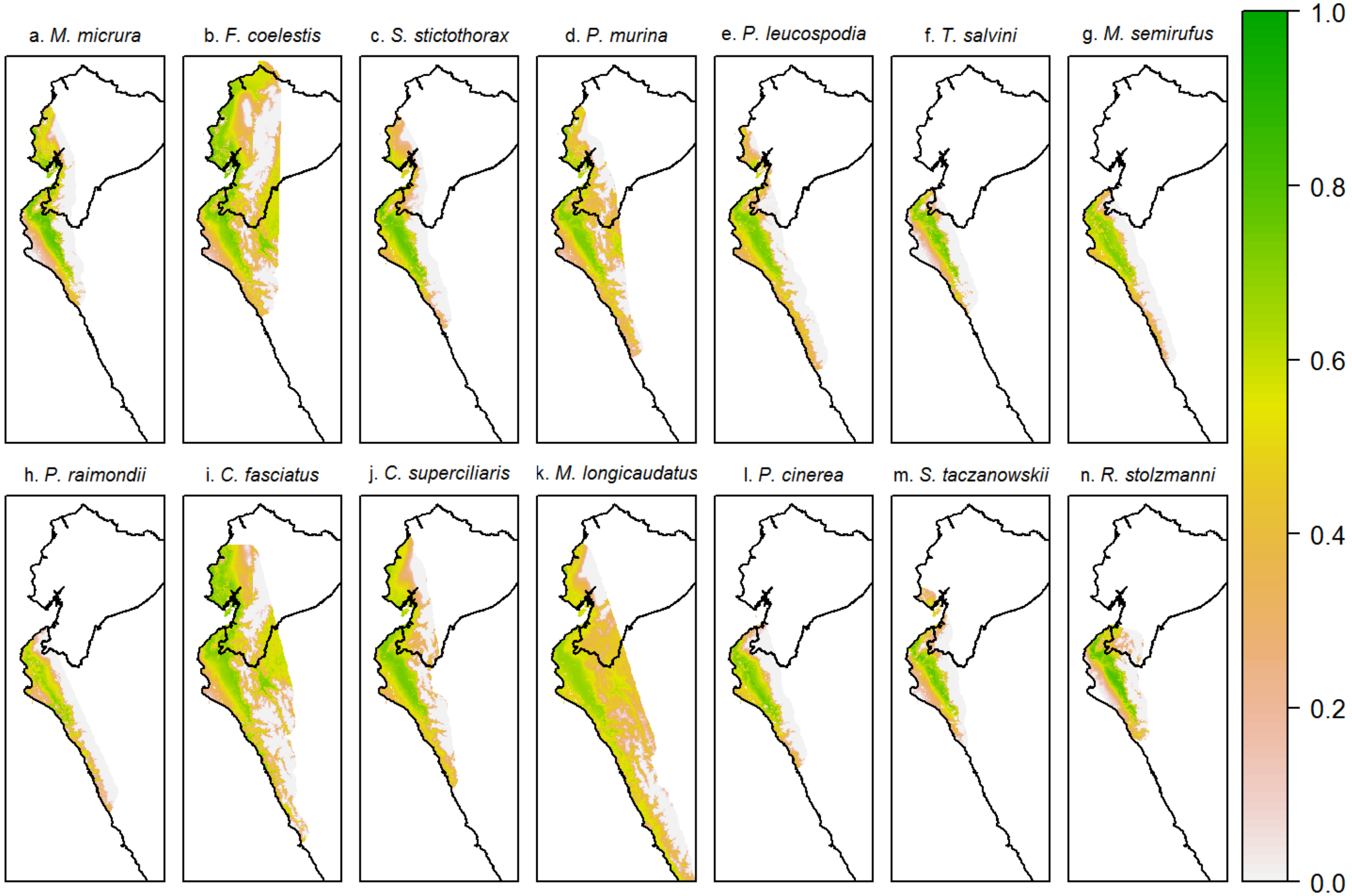


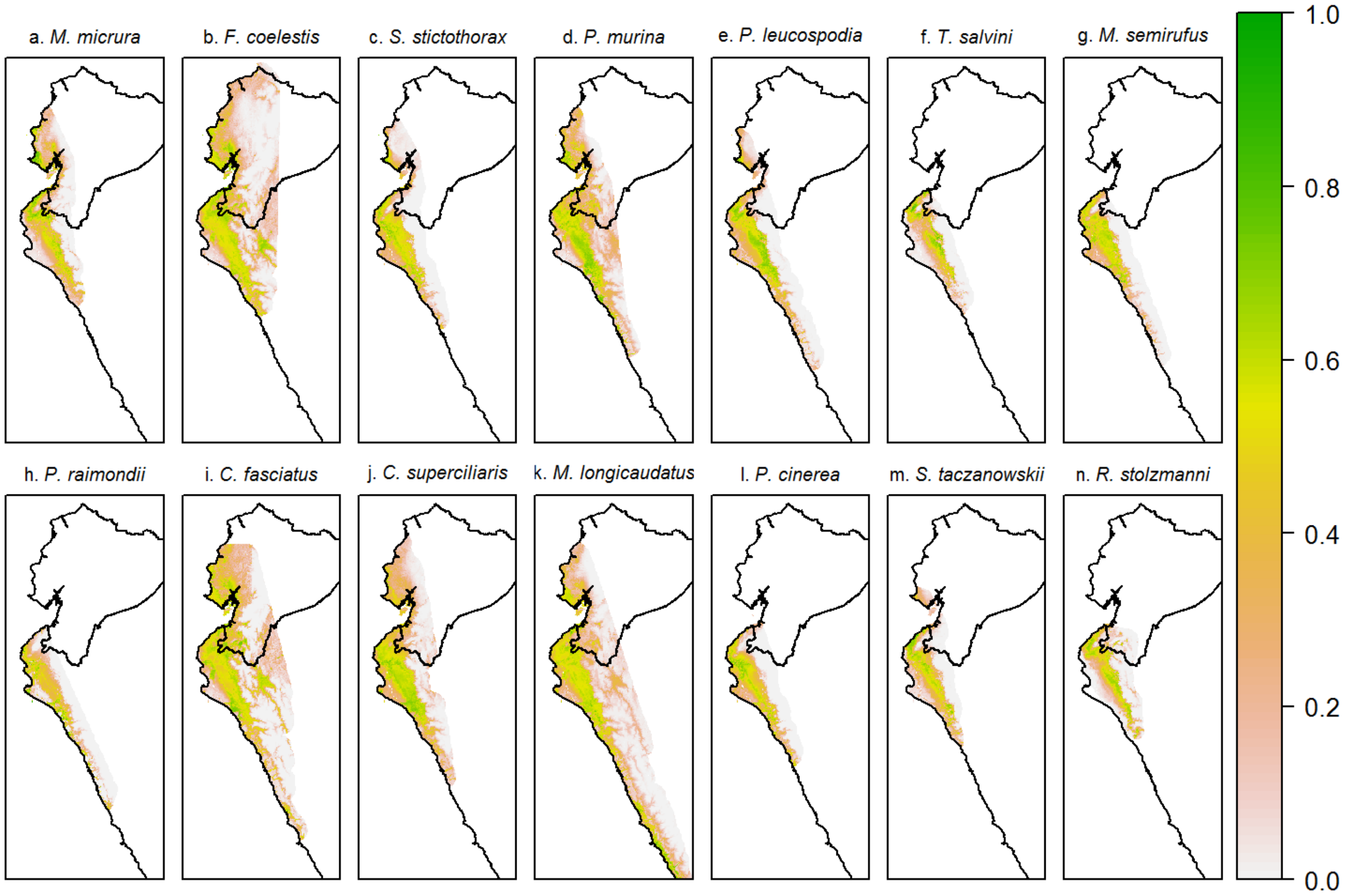
Figure 4.2. Predicted species distribution maps – a) GLM


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
1.0
0.8
0.6
0.4
0.2
0.0

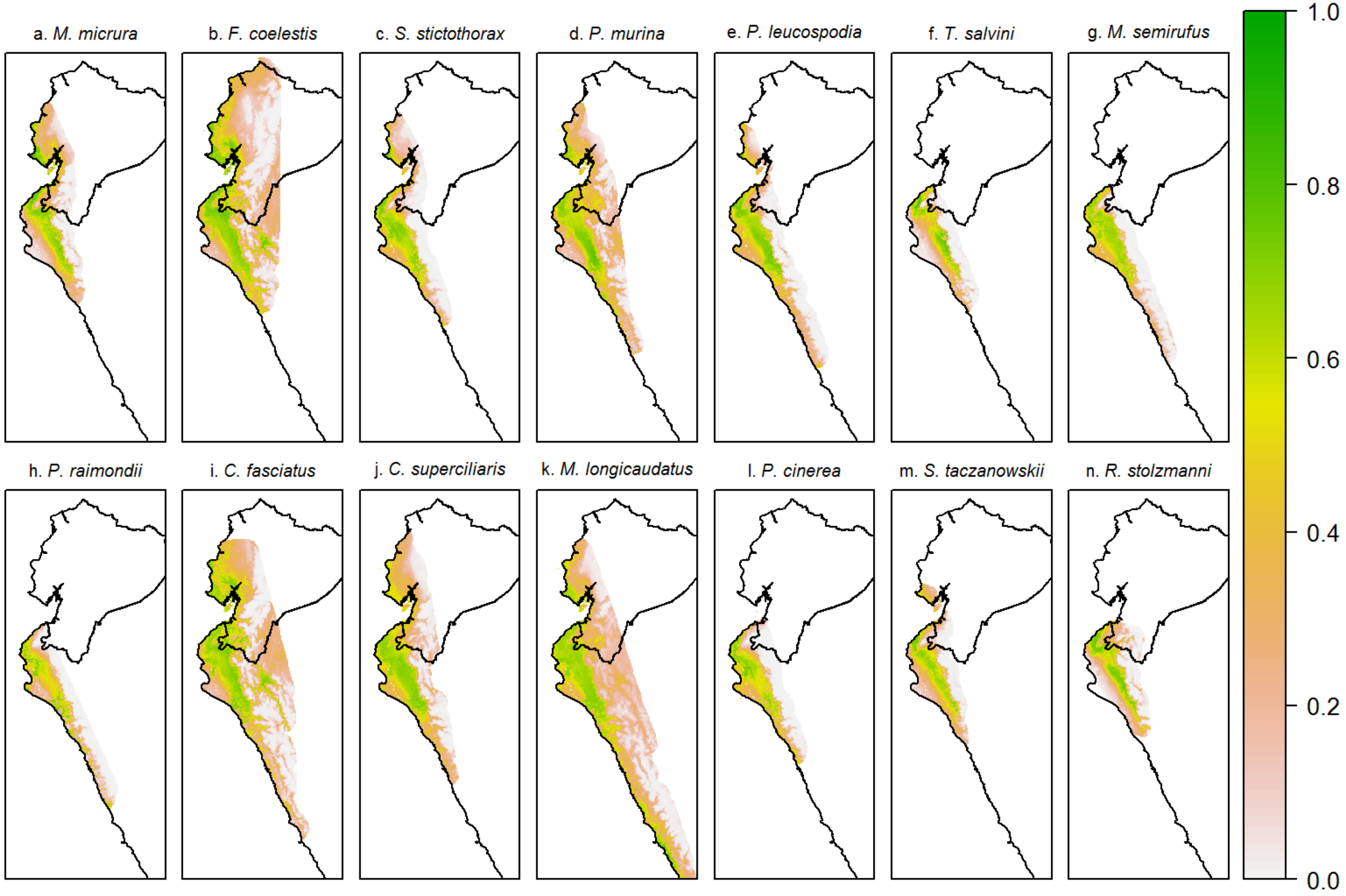
b). GAM


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
1.0
0.8
0.6
0.4
0.2
0.0

c). Maxent


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
1.0
0.8
0.6
0.4
0.2
0.0

d). Domain



e). Consensus model

Although models were very similar to each other overall (i.e. ranked correlation), the distributions of model values were different among modelling methods, and between species (Figure 4.3, Appendix 5). GAM and Maxent values tended to drop off faster than all other methods, whereas Domain maintained higher values across a larger area, in other words, Domain created areas of more homogenous model values. Within species, all distributions were significantly different to a common distribution function as assessed by a k-sample Anderson Darling test ($p < 0.001$ for all species). Both between methods and species, predicted values appear to coincide more at higher than lower values. For some species, differences between models were marked. For example, in Long-tailed Mockingbird *Mimus longicaudatus*, there is a difference of almost 50% of the total area between the lowest and highest model values when applying the same threshold value (Figure 4.3).

4.3 Comparison to published range maps

Species ranges, calculated with a 5% omission error threshold produced generally smaller range estimates than those published by BirdLife International and NatureServe (2015) but coincided spatially, except for notable differences in the three threatened species in the study (Table 4.4, Figure 4.4). Peruvian Plantcutter *Phytotoma raimondii* and Rufous Flycatcher *Myiarchus semirufus* were the only species to have (considerably) larger ranges in the models than the expert drawn areas. Both species were over 10 times larger than the published range areas (Table 4.4). In the case of Tumbes Tyrant *Tumbezia salvini*, this species showed the least overlap of all the species, with the modelled range coinciding with less than 20% of the area of the published range. Conversely, almost all the modelled ranges of Peruvian Plantcutter and Rufous Flycatcher were contained within the modelled range (Figure 4.4).

Figure 4.3. Ranked values for GLM, GAM, Maxent, Domain and Consensus models for each species. The consensus threshold value, used to create presence/absence range maps, is shown as a horizontal, grey, dotted line.

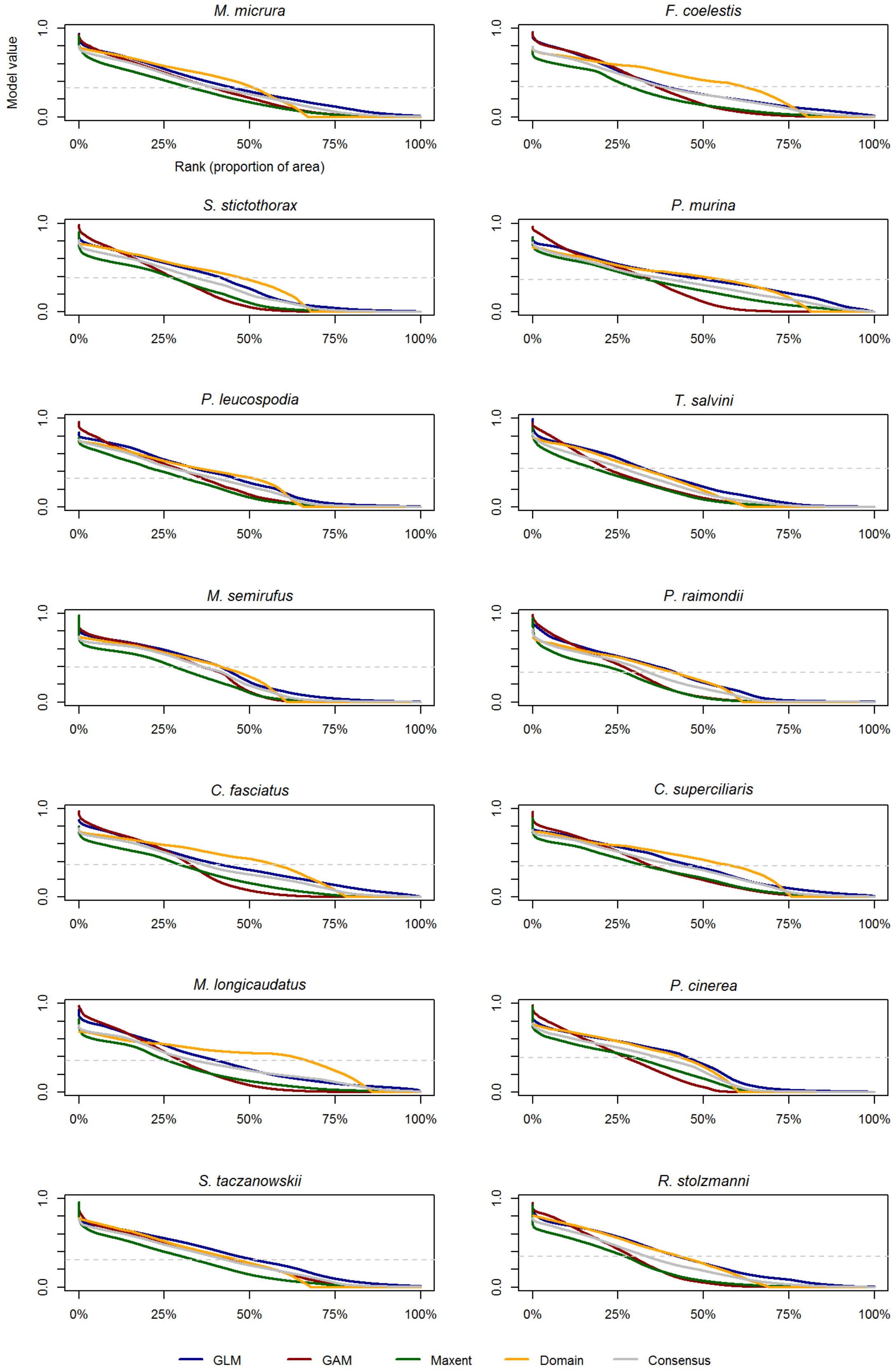
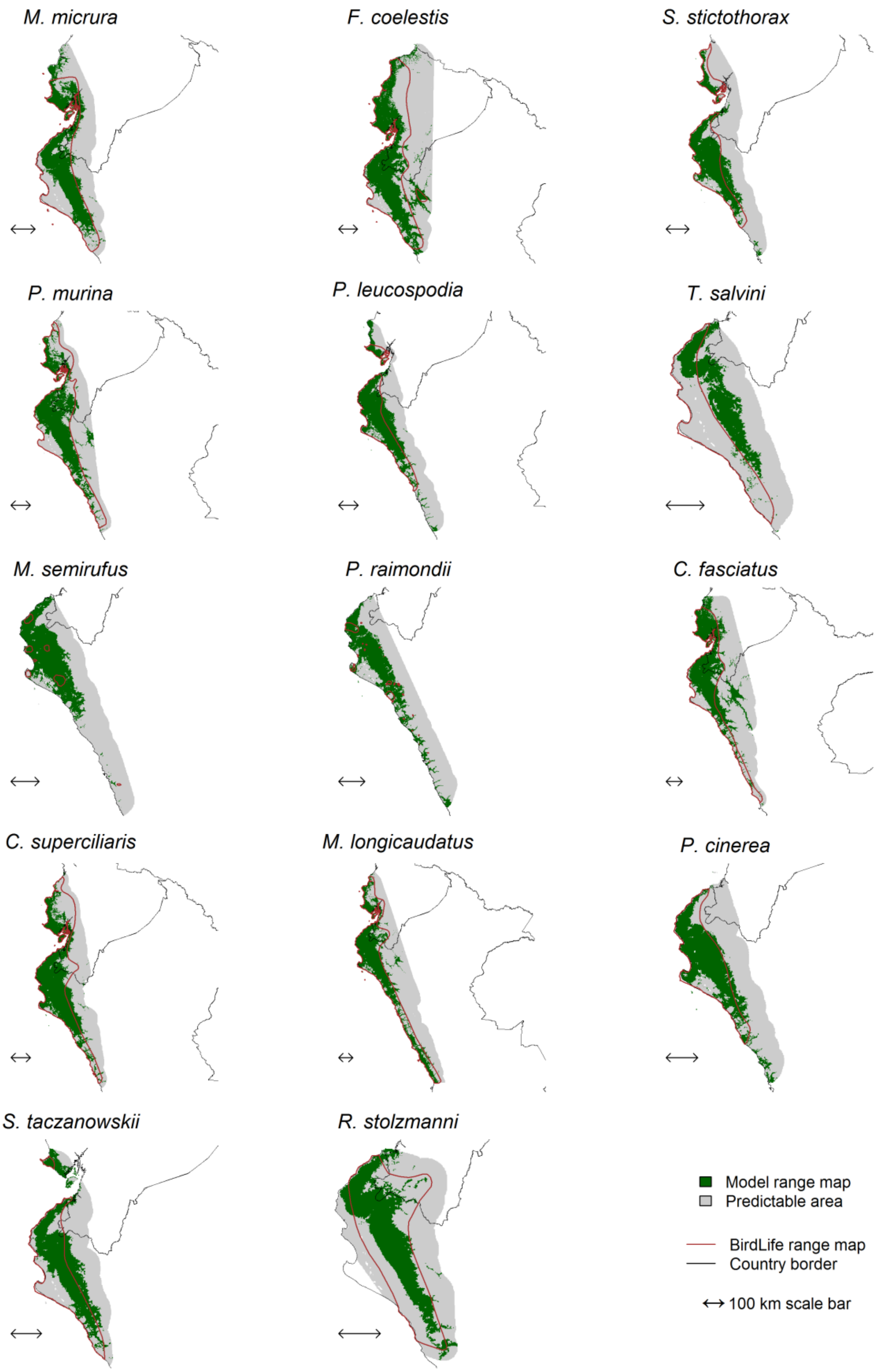


Figure 4.4. Comparison of EOO range maps produced by species distribution models in this study and BirdLife International EOO range maps, used to establish extinction risk. Note different scale of each map.



M. micrura

F. coelestis

S. stictothorax

P. murina

P. leucospodia

T. salvini

M. semirufus

P. raimondii

C. fasciatus

C. superciliaris

M. longicaudatus

P. cinerea

S. taczanowskii

R. stolzmanni

Table 4.5. Comparison of position and size of thresholded consensus model and BirdLife ranges. Comparisons (final two columns) are with respect to BirdLife ranges; e.g. -50% difference implies that the model range is half the size of the BirdLife polygon, whereas 100% overlap implies that model range is entirely within the BirdLife polygon.

Species	**Area (km^2)**		**Model : BirdLife comparison**	
	Model range maps	**BirdLife range maps**	**% difference**	**% overlap**
Campylorhynchus fasciatus	101,394	102,478	-1	71
Cantorchilus superciliaris	72,718	96,797	-25	66
Forpus coelestis	103,806	146,892	-29	63
Mimus longicaudatus	95,044	128,415	-26	68
Myiarchus semirufus	35,066	2,882	1117	88
Myrmia micrura	51,035	72,136	-29	61
Phaeomyias murina	71,036	108,593	-35	60
Phytotoma raimondii	31,720	2,726	1063	79
Piezorina cinerea	32,850	37,227	-12	74
Pseudelaenia leucospodia	53,823	51,890	4	77
Rhynchospiza stolzmanni	29,172	48,974	-40	53
Sicalis taczanowskii	36,462	41,412	-12	61
Synallaxis stictothorax	42,920	49,643	-14	69
Tumbezia salvini	20,867	30,227	-31	18

5 Discussion

Distribution models were made for 14 Tumbesian species, as a first step in comparing modelled occurrence with field-based abundance (see Chapter 5). Different modelling methods were combined in a consensus ensemble model to produce the final estimates of species' range sizes and habitat suitability. Although the values of individual component models of the ensemble method were highly correlated, their distributions were different. Given the low sample size, discerning patterns among species is preliminary. Species that show less area under the curve (a faster drop off), may tend towards having more fragmented distributions, i.e. a multimodal distribution of hotspots of suitability across their range, given that larger extents of unsuitable areas are predicted within the full predictable area (convex hull around presence points). However, only in Domain, did variability in abundance appear to show any agreement with this suggestion (Appendix 5). If the distribution of relative probability of occurrence is linked to the distribution of abundance across a range (e.g., Legault et al., 2013; see Chapter 5), then some patterns such as these might be expected. Differences in distributions also have potential to effect range size estimates when applying thresholds to different modelling methods. Such effects could be taken into account when choosing thresholding methods (Liu et al., 2013). These differences also lend more importance to the methods used to combine individual models in a consensus model. The method used here aimed to compensate for systematic differences between individual models, for example, values of relative probability of occurrence for GAMs were generally higher than values of other methods. The consensus models presented here performed better than individual components. Other studies have found that using average functions to combine models performed well compared to other methods (Marmion et al., 2009), although weights in the aforementioned study were based on model performance.

This study found that species distribution models can highlight inconsistencies and improve upon published range maps. Several studies have recently compared species distribution models to published ranges of Neotropical species, used in red listing (Herzog et al., 2012; Mota-Vargas & Rojas-Soto, 2012; Fourcade et al., 2013; Fivaz & Gonseth, 2014; Syfert et al., 2014; Peterson et al., 2016). The authors agree about the utility of using species distribution models as tools in defining ranges, although opinions are divided as to the extent of reliance on models (Sérgio et al., 2007; Attorre et al., 2013). Herzog et al., (2012), assessing the ranges of Bolivian endemics, found a similar pattern to this study in that EOOs of non-threatened species were larger than modelled ranges while EOOs of threatened species were smaller.

It may be expected that modelled ranges are slightly smaller than published EOOs in this study due to the threshold method excluding 5% of presence points. However, modelled range sizes of two threatened species was more than an order of magnitude larger than published EOOs. In both Peruvian Plantcutter *Phytotoma raimondii* and Rufous Flycatcher *Myiarchus semirufus*, larger range size estimates could lead to a change in IUCN Red List category. Both species are currently listed under criteria B1ab (BirdLife International, 2016a, 2016b), due to a fragmented EOO estimated at less than 5,000 km^2, showing continuing decline (IUCN, 2001). Downgrading the current Red List category, to Vulnerable or Near Threatened, would depend on how much area is excluded from the final EOO estimate. At present, the published range maps exclude much potential habitat that is likely to be, or is actually occupied, resulting from different methods employed to map threatened and non-threatened birds. Threatened birds have more areas excluded than would be the case based on habitat preference and elevation range alone. The size of the estimated EOO for Rufous Flycatcher warrants downgrading its current threat category (see also comments on population size in Chapter 3). For the Plantcutter, the highly fragmented distribution and its scarce nature make discontinuities or unsuitable habitat within its EOO more difficult to define (see Chapter 3 and 4).

Species' geographic ranges consist of complex, dynamic spatial and temporal patterns (Maurer, 1994; Fortin et al., 2005). Current methods to map species' ranges (e.g. Extent of Occurrence and Area of Occupancy) are still focused on 2-dimensional outlines yet modelling methods are better able to approximate the true nature of species ranges as probability surfaces, for example, taking into account dispersal, patchiness and disturbance over specific periods of time (Franklin, 2010). I do not suggest using species distribution models to replace current methods to estimate species ranges for IUCN red listing. However, models are a useful tool to check inconsistencies and improve published ranges (Fourcade et al., 2013) and their (backward-compatible) integration into red listing warrants further exploration. It would therefore be timely to urge their routine use within existing guidelines for employing models within the Red List process (IUCN, 2016). Also, tools commonly employed in validating species distribution models, could also be employed to validate EOOs produced by other methods, such as checking omission rates of current occurrence records (Peterson et al., 2016). A careful combination of modelling and topological methods, as well as assessment techniques, including internal (e.g. cross validation), independent (e.g. testing data collected separately) and expert validation could yield important improvements to extinction risk prediction. Some key points to complement guidelines provided by the IUCN on using models with respect to climate change and extinction threat, but also of wider relevance, are provided below.

- Quality of species data, selection of background or pseudoabsence points, the spatial extent of the study area and thresholds to create binary models from probability surfaces interdependent aspects that need to be considered simultaneously. Using IUCN established methods to construct EOO (i.e. convex hull or alpha hull) is a useful starting point in providing a spatial extent for using species distribution models to estimate ranges (Sangermano & Eastman, 2012; Attorre et al., 2013; Fivaz & Gonseth, 2014;

Syfert et al., 2014). However, this utility is dependent on the threshold used; a hull based on presence points will necessarily include the whole model output with a zero omission threshold. Furthermore, if using a threshold based on a percentage omission (including 0), then the degree of filtering of species occurrence data will directly relate to this, i.e. the more confident one is about data quality, the lower the omission percentage can be used as a threshold.

- Range-wide occurrence data should be used, even if categorising extinction risk at the national level, to ensure full response curves are included in training models (Kadmon et al., 2003). However, the study area must be limited sensibly to the area considered reachable by species (Peterson et al., 2011), and in a standardised way between species to increase comparability, for example, by using buffered convex hulls constructed around presence points. This latter method will, again, be influenced by the filtering of presence points.

- Use of recent species occurrence data, and temporal coincidence between occurrence data and predictors is important given that EOO should provide current range estimates (IUCN, 2016). This study used data from the last 15 years. Although land use may change considerably during such a period, a balance must be sought between having sufficient data and appropriate temporal resolution, e.g. based on three generation lengths of the species in question. Data from different time periods can give large differences in range estimates (Fivaz & Gonseth, 2014).

- Using expert opinion to complement the model validation process (Sérgio et al., 2007; Marcer et al., 2013; Syfert et al., 2013) increases the information input, especially since this type of information is difficult to use within predictor layers. Online services provide useful platforms for engaging experts to validate models (e.g. BioModelos in Colombia[2]). Post-model validation is a common format for expert input, but it is also valuable at earlier stages such as selecting predictors and verifying occurrence records.

- Predictors not included in models that influence distribution often include biotic and anthropogenic factors. Land cover or use has been recommended as a measure of the latter (IUCN, 2016), however, it may be difficult to obtain high resolution layers of land use at required time periods. NDVI, or other vegetation indices (e.g. Enhanced Vegetation Index, Leaf Area Index, Soil Humidity) may provide useful proxies with high spatial and temporal resolution data freely available globally (van Ewijk et al., 2014). In this study seasonal NDVI indices proved to be important in modelling, and were also capable of distinguishing types of land cover.

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[2] http://biomodelos.humboldt.org.co/

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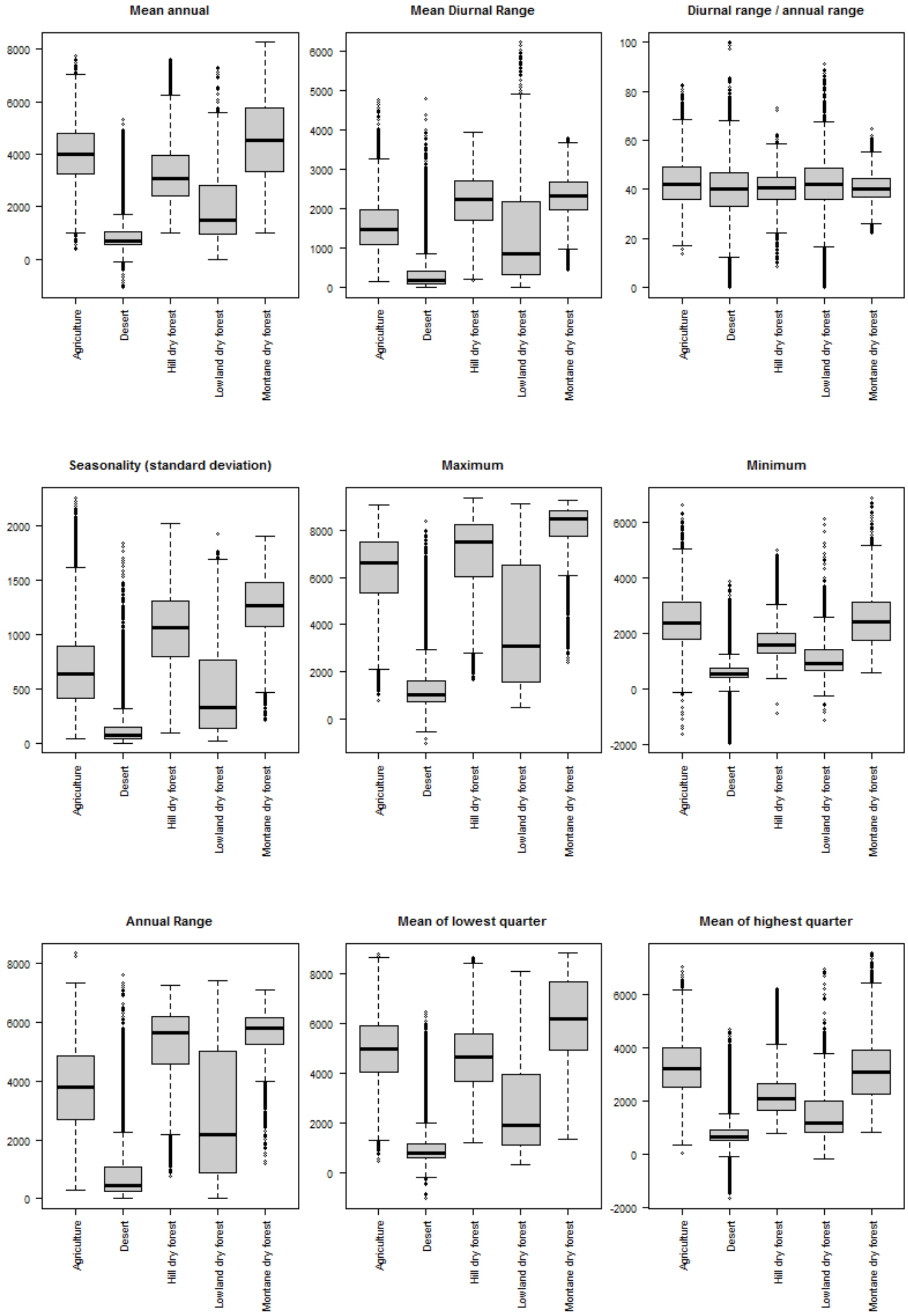
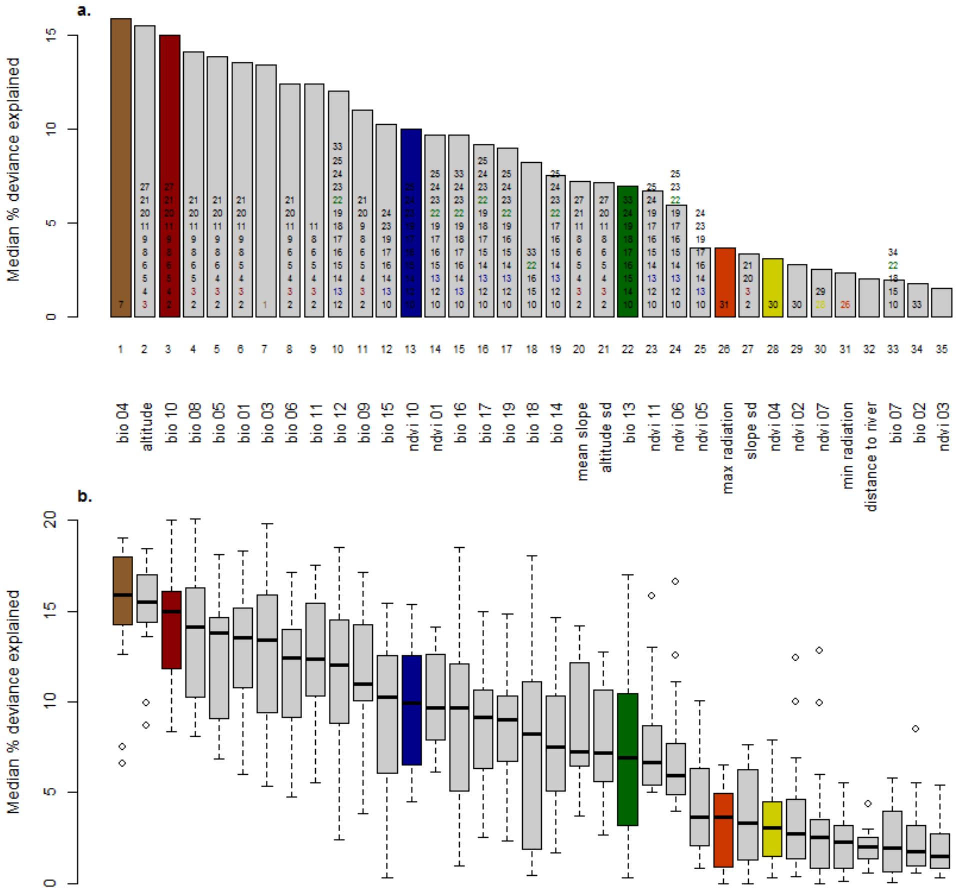
7 Appendices

Appendix 1. Different measures of NDVI (following the 'bioclimatic' indices) across different land cover types. In all cases, Kruskal-wallis and post-hoc multiple comparison tests showed significant differences (at α = 0.05) between crops and natural forest types.



Appendix 2. Predictor selection. a) Median percentage deviance explained from univariate models across all species for all potential predictors. Numbers show those predictors with absolute values of pairwise Spearman's correlation coefficients > 0.7; for example, the first predictor (bio 04) is correlated to the seventh predictor (bio 03), and vice versa. See table below for predictor codes. Coloured bars (and numbers) correspond to final predictors selected for models.

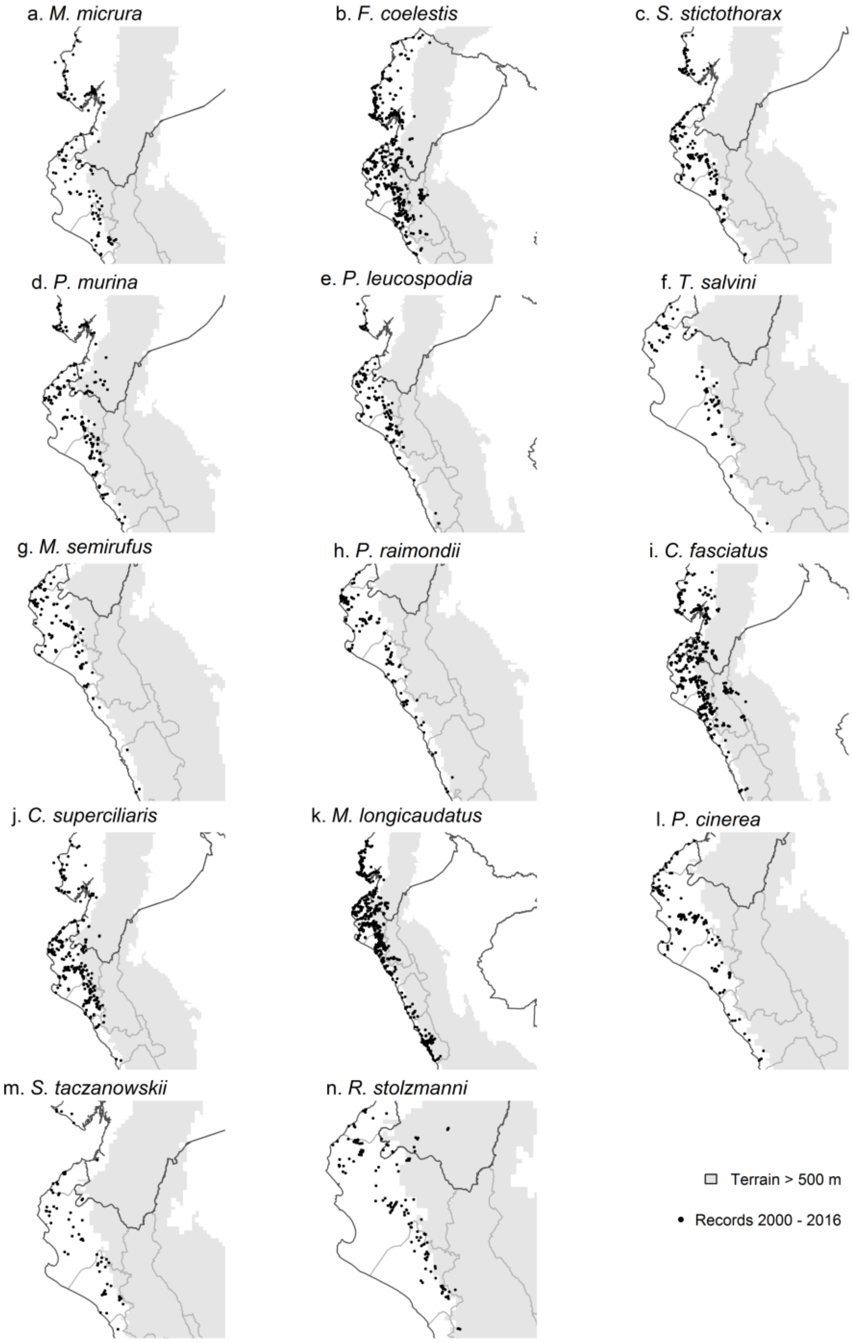


c. Predictor codes

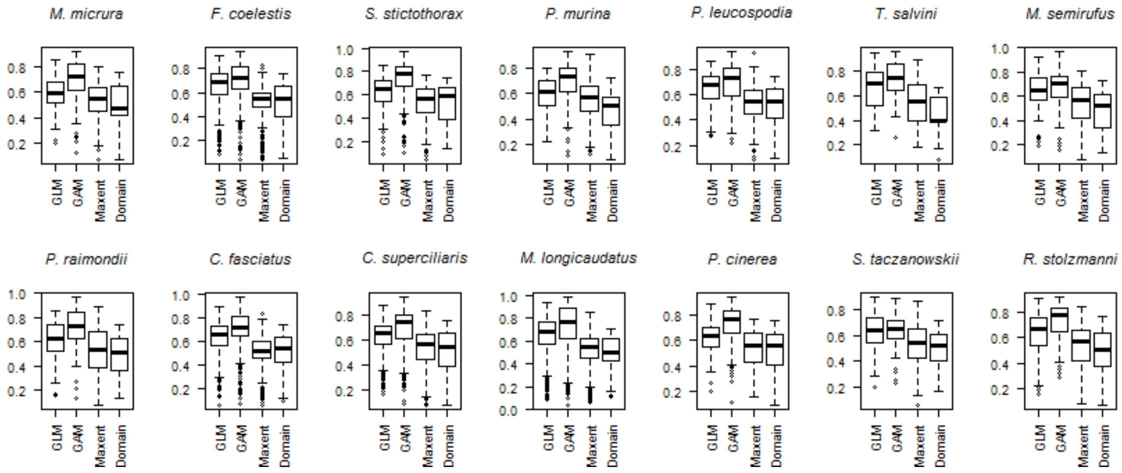
	Code	Predictor
Topographic	altitude	Altitude above sea level
	altitude sd	Standard deviation of altitude
	mean slope	Slope of altitude
	slope sd	Standard deviation of slope
	roughness	Topographic Roughness Index
	distance to river	Distance to nearest river (km)
Vegetation indices	ndvi01	Annual mean NDVI
	ndvi02	Mean diurnal range NDVI (as bio02)
	ndvi03	ndvi02 / ndvi07
	ndvi04	Seasonality (standard deviation)
	ndvi05	Max NDVI of month with highest NDVI
	ndvi06	Min NDVI of month with lowest NDVI
	ndvi07	NDVI annual range (ndvi05 – ndvi06)
	ndvi10	Mean NDVI of quarter with highest NDVI
	ndvi11	Mean NDVI of quarter with lowest NDVI
Radiation	max radiation	Maximum solar radiation
	min radiation	Minimum solar radiation

	Code	Predictor
Bbioclimatic	bio01	Annual Mean Temperature
	bio02	Mean Diurnal Range (Mean of monthly (max temp - min temp))
	bio03	Isothermality (bio02/bio07) (* 100)
	bio04	Temperature Seasonality (standard deviation *100)
	bio05	Max Temperature of Warmest Month
	bio06	Min Temperature of Coldest Month
	bio07	Temperature Annual Range (bio05-bio06)
	bio08	Mean Temperature of Wettest Quarter
	bio09	Mean Temperature of Driest Quarter
	bio10	Mean Temperature of Warmest Quarter
	bio11	Mean Temperature of Coldest Quarter
	bio12	Annual Precipitation
	bio13	Precipitation of Wettest Month
	bio14	Precipitation of Driest Month
	bio15	Precipitation Seasonality (Coefficient of Variation)
	bio16	Precipitation of Wettest Quarter
	bio17	Precipitation of Driest Quarter
	bio18	Precipitation of Warmest Quarter
	bio19	Precipitation of Coldest Quarter

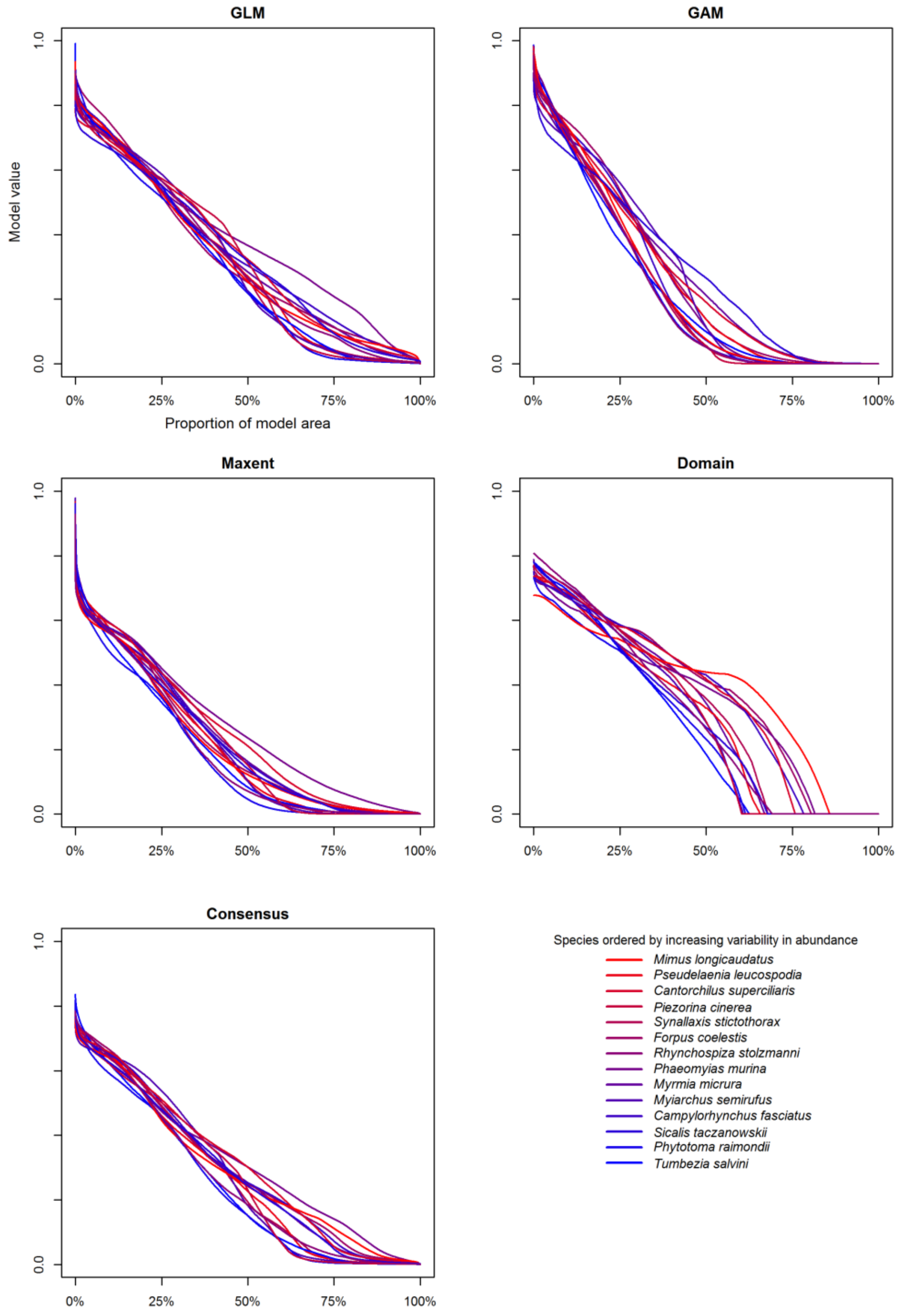
Appendix 3. Occurrence records per species used in models



Appendix 4. Variation in predicted values at presence points within and between modelling methods per species. GAMs generally show highest values, with Maxent and Domain generally lower.



Appendix 5. Differences in distribution of GLM, GAM, Maxent, Domain and Consensus model values for each species. Species are coloured in order of increasing variability in abundance from red to blue (see key for indicative species order). The x-axis can be read as a cumulative proportion of area (i.e. number of pixels) covered by the model at each value.



Chapter 3

Estimating local abundance in patchy habitats: a case study on dry forest endemic birds of the Tumbes region

1 Abstract

Estimating local abundance (population densities) of species in tropical environments is often logistically and economically challenging. However, local abundance, and derived metrics, such as population sizes, are a vital part of many conservation planning mechanisms, including priority area selection and red listing. Patchy environments across extents of occurrences add to challenges in estimating local abundance, especially in terms of selecting study sites given limited resources for fieldwork. This case study, on birds of conservation importance from the dry forests of the Tumbes region in Peru, aims to estimate local abundance and site-specific population sizes using novel methods for site selection. In all, 26 sites were selected across the ranges of 14 bird taxa using criteria to maximise chances of encountering target species while encompassing most of species' ranges. Sites were selected using two criteria, to obtain records among large areas of unsuitable habitat and across the ranges of the study species. Samples were randomly selected from strata based on a geographical division of the study area, and on the relative probability of occurrence of study species obtained from exploratory species distribution models. At each site, I walked four parallel 2.5 km transects to evaluate bird abundance and habitat characteristics. Bird densities were estimated per species with distance sampling, using type of record (auditory/sight) and habitat characteristics as covariates. A total of 7,505 bird records were obtained, with local abundances ranging from 0.9 to 340 individuals km^{-2} across all species. Site areas were estimated using existing boundaries of management areas, suitable vegetation extent, or arbitrary 10 km^{2} plots around transects. The summed population sizes of the threatened Peruvian Plantcutter and Rufous Flycatcher from just the study sites alone were greater than current estimates of their whole populations. Major strongholds of Peruvian Plantcutter, especially in the south of its range, are currently unprotected, and proposed protected areas fail to capture important populations of both species lying just outside their boundaries. Key sites are recommended for urgent

protection, and a vast area of lowland dry savannah forest, that may hold important populations of key species, is highlighted as the last remaining expanse of dry forest in the northwest of Peru, already threatened by urbanisation and large-scale irrigated agriculture.

2 Introduction

Local abundance (population density) is an essential building block in constructing reliable estimates of population size, itself, a cornerstone of conservation instruments such as IUCN Red Lists and priority area designation (IUCN 2001; Rodrigues et al. 2006). However, quantitative data on population sizes and trends are lacking, including in birds – one of the best known taxonomic groups (Marsden and Royle 2015). For example, 121 birds are currently listed as threatened (CR, EN, or VU) in South America based, in part, on past reductions of population size, however, data comes from direct observation in just five of these species, and from abundance indices in 18 (IUCN 2015). The remainder were inferred from other sources, such as changes in extent of habitat.

Distance sampling (Thomas et al. 2010) has been widely used to estimate bird abundance in temperate regions (Buckland et al. 2000) but is still relatively underemployed in tropical areas where so many threatened taxa occur. In biodiverse regions such as the Neotropics, mainly comprising so-called developing countries, obtaining density estimates from the field, and then translating these to population sizes, is a challenging process (Danielsen et al. 2003). The logistics of data collection are complicated by factors such as local social and political conditions, climate and topography, while lack of training can encumber data analysis (Danielsen et al. 2005). The nature of the species' population and distribution can also create additional methodological challenges, for example, in the case of rare or very patchily distributed species (Thompson 2004), that is, where the area of occupancy is much smaller than the extent of occurrence (see for example, Attorre et al. 2013). Surveying vast areas under these circumstances requires setting up surveys carefully to maximise detections of target species and ensure efficiency, using techniques such as stratification based on occurrence probability (Guisan et al. 2006; Aizpurua et al. 2015) and accounting for spatial variation (Yoccoz et al. 2001).

The northwest of Peru is a global priority for conservation, with several rare, threatened and patchily distributed species(Stattersfield et al. 1998; Rodríguez and Young 2000; Olson and Dinerstein 2002; Mittermeier 2004). The area is strongly influenced by the cold Humboldt current along the coast of Peru, reducing precipitation on the coastal areas (CDC 1992). As a consequence, the distribution of vegetation closely follows river valleys crossing the dry plains from east to west as they descend from the Andes (Figure 2.1). Vegetation is predominantly patches of dry forest or scrub savannah, among desert areas, dominated by *Prosopis* sp. *Acacia* sp. *Cordia* sp. and *Capparis* sp., among others (Schulenberg et al. 2007). Although habitat is naturally fragmented, the wider Tumbesian area, to which northwest Peru belongs, has suffered from massive deforestation and is considered one of the most severely threatened areas on earth in terms of biological extinction (Dodson and Gentry 1991). The area lies within three major conservation priority-setting schemes (Figure 2.1): the Magdalena-Chocó-Tumbes Biodiversity Hotspot (Mittermeier 2004), which, by definition, implies that more than 70% of its natural habitat has been lost; the Global 200 ecoregions (Olson and Dinerstein 2002), a priority ranking of the world's most threatened habitats; and the Tumbes Endemic Bird Area (Stattersfield et al. 1998), a region delimited by 55 restricted-range species, of which, 18 are globally threatened (Devenish et al. 2009). The area had previously been identified by Chapman et al., (1926) and Cracraft (1985) as a centre of bird endemism. The principal threats to bird species are from degradation or loss of habitat, with the main causes including conversion of dry forest to agriculture, mining, grazing by goats and logging for firewood or charcoal (Best and Kessler 1995; More 2002; Flanagan et al. 2009). Trees outside protected areas are seldom left to grow large, which could affect nesting habitat, especially of obligate cavity nesters, such as the Rufous Flycatcher *Myiarchus semirufus* (Lanyon 1975).

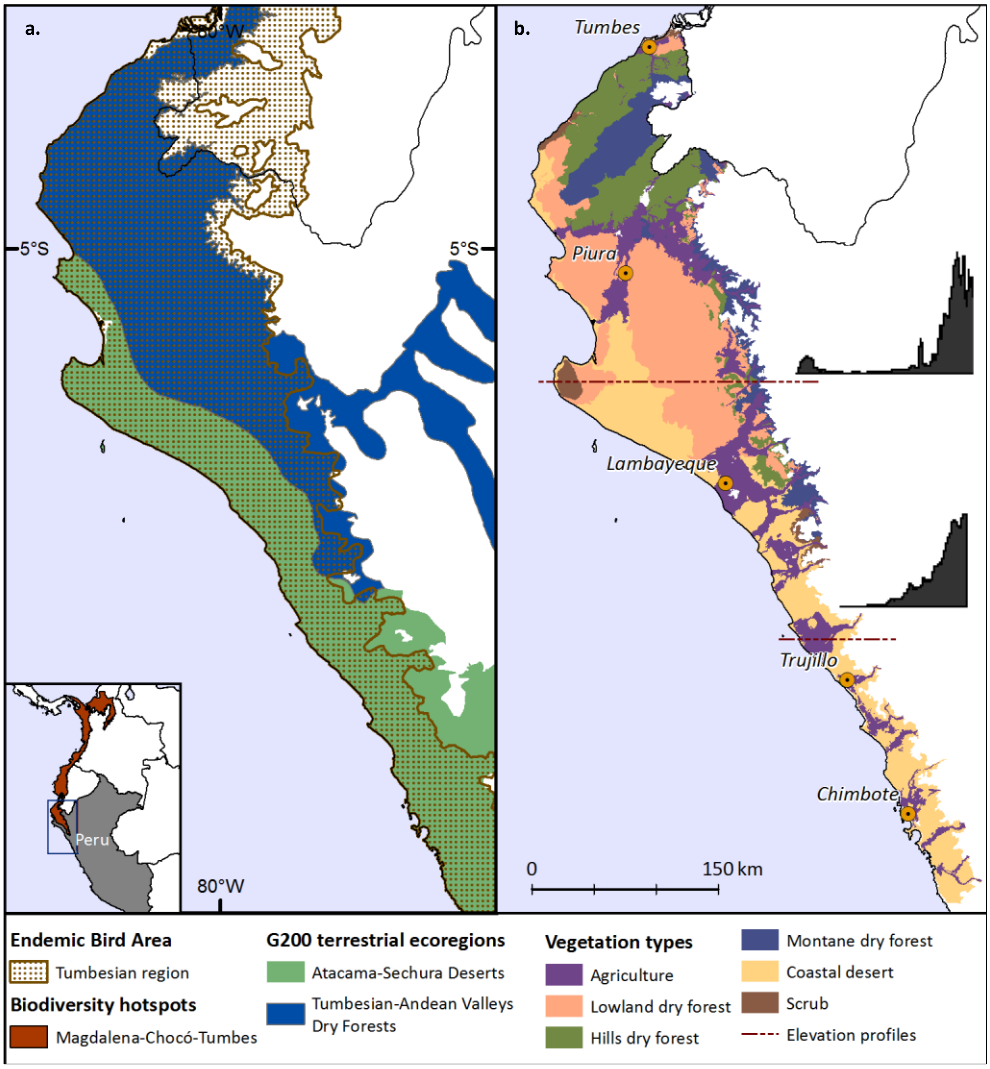


Figure 2.1. Northwest Peru in the context of a) conservation designations and b) vegetation types below elevations of 500 m. Major cities are shown in b).

This study aims to cover a shortfall in abundance data for a region of high conservation importance using recent innovations in distance sampling and survey design. It provides local abundance and site-specific population estimates for a suite of endemic birds, including rare and threatened species, in a patchy habitat. Specifically, this chapter will:

- develop a practical method for survey site selection in patchy populations;
- estimate local abundances of dry forest endemic birds using covariate distance sampling, constituting the first ever range-wide survey of these species;
- produce population size estimates at important and discrete sites, and discuss threats and opportunities for their conservation in the region.

3 Methods

3.1 Step 1 - Field site selection

The study area was located along the north Peruvian coast, comprising most of the known ranges of the study species, from approximately 3.5° to 9° S, representing a distance of over 600 km (Figure 3.2). Bird habitat for the study species consists mainly of dry forest and scrub savannah amongst larger desert areas, located in a narrow band between the Andes and the coast below an elevation of approximately 500 m (CDC 1992). Given the size of the study area, it was logistically impossible 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, sites were selected randomly from within two strata layers. Strata were defined according to the relative probability of obtaining species records and geographically by dividing the study area into a 50 x 50 km grid. To identify the 'occurrence probability' strata, a species distribution model was created using occurrence records of four bird species, whose distributions and broad habitat associations were representative of the community as a whole and for which there were good numbers of presence points (Grey-and-white Tyrannulet *Pseudelaenia leucospodia*, Rufous Flycatcher *Myiarchus semirufus*, Cinereous Finch *Piezorina cinerea*, Peruvian Plantcutter *Phytotoma raimondii*). Environmental predictors (Appendix 1) used in the model were climate based: eight bioclimatic variables based on precipitation and temperature (Hijmans et al. 2005) and habitat based: maximum and minimum Normalized Difference Vegetation Index from the dry and wet seasons. Maxent (Phillips et al. 2006), run through the R package Dismo (Hijmans et al. 2013), was used to create a distribution model for each species, and these were evaluated with mean AUC from 5-fold cross validation. AUC ranged from 0.89 to 0.95 for the individual species models. The final models were constructed using all the data points, and then summed to create a single surface, providing regions of high and low suitability for the four 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, in part, due to lack of more appropriate alternatives (Merow et al. 2013). To create the geographic strata, a regular 50 km grid was drawn across the study area and identified the top ten cells in terms of highest average model scores. Twenty-six sites were selected randomly from only the top three deciles of the probabilities of occurrence from the final model, using double weights for the top decile, i.e. sampling was restricted to avoid areas of high unsuitability for the species, including desert and urban areas. Sampling was repeated until at least one site fell in the top ten 50 km grid cells. In the field, sites were chosen as close as possible to the randomly selected sites, and were only moved when safety or access issues prevented the researchers from reaching the site. Two additional sites at Pomac National Park were added. All sites, except for the southernmost, were within the current or former ranges of all study species as mapped by BirdLife International & NatureServe (2012). Sites ranged from 27 to 369 m above sea level, from 3 to 101 km from the coast, and with a median distance between sites of 150 km (interquartile range: 161 km).

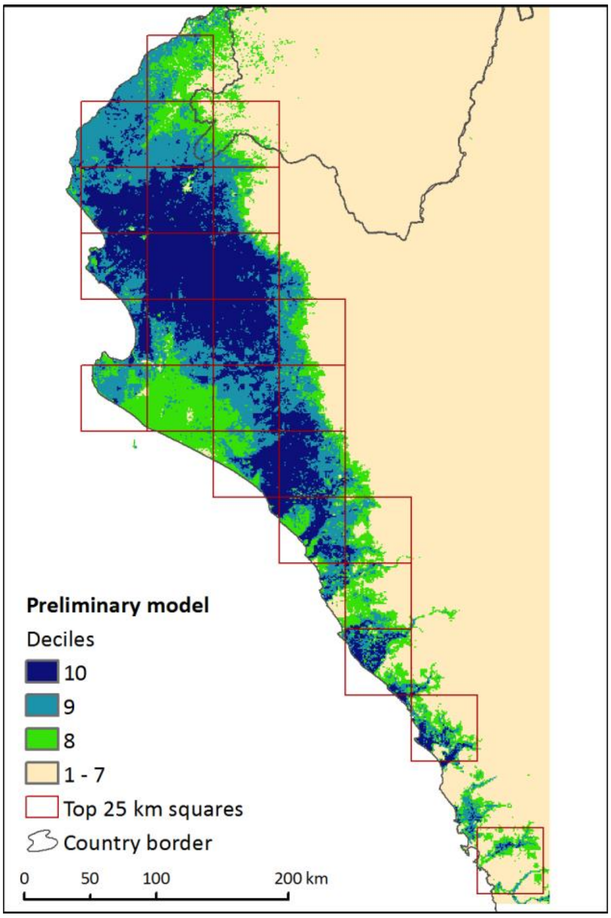
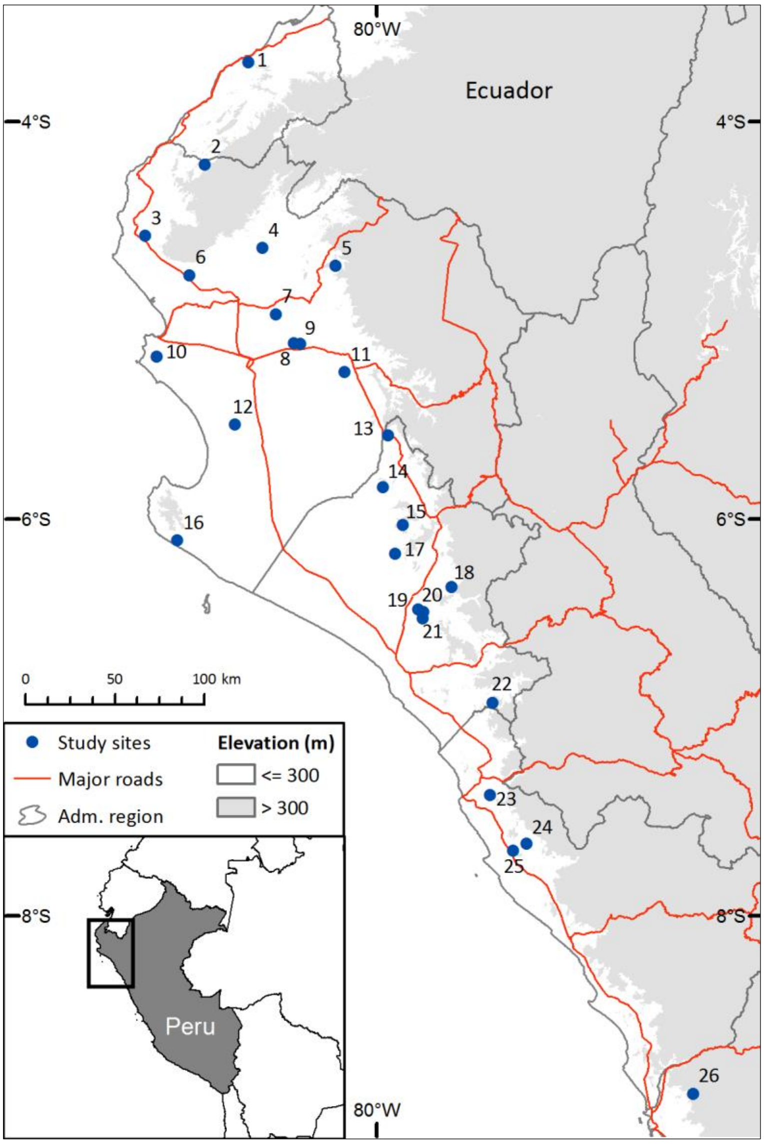


Figure 3.1. Model results for exploratory species distribution models, showing stratification of study area based on probability of occurrence of sampled species.

3.2 Step 2 - Field surveys

Surveys were implemented from June to October 2013, by CD and Elio Nuñez Cortez, an undergraduate student from the Universidad Nacional de Piura, Peru. Fieldwork was only conducted during the dry season (outside the main breeding season) to avoid environmental seasonality affecting bird abundance as a result of changing resources within their habitat (Tinoco 2009). Both observers participated in pilot studies at six sites in 2012 to practise distance estimation, learn bird calls and trial field methods. Local abundances of 14 dry forest endemic bird species (see Table 4.1, Chapter 1), without known seasonal movements and small ranges (< 115,000 km^2), were estimated at each site. The survey design consisted of four 2.5 km parallel, straight transects, separated by 500 m at each site. Habitat was sufficiently open to allow transects to be walked without major difficulty and did not require previous clearing of vegetation. Transects were not located on paths or tracks, and were occasionally moved to avoid them falling along the length of features such as irrigation canals or stream beds (Buckland et al. 2001). The two observers walked the transects together, using preloaded way markers on GPS for guidance. Each transect was walked once at a speed of 1-1.5 km h^{-1} to gather bird data, and once to measure habitat characteristics at twelve plots located 200 m apart on each transect.

Distances to birds were estimated either by eye, or for distances greater than around 25 m, with laser rangefinders. Two transects were completed per day where conditions permitted, with bird data collected between 6:15 and 11:00. For each bird encounter, the following were noted: species; number of individuals; type of detection (aural or visual); and perpendicular distance from transect line to individual or to the centre of a group of birds. Habitat characteristics were taken within a 10 m radius circular plot and included tree species present; % vegetation cover at two vertical strata (<3 m, >3 m; estimated visually); diameter at breast height (dBH; with tape measure) and height (estimated visually) of three largest trees; total number of stems with dBH > 10 cm; and presence/absence of grass. Topographic measurements at each plot included elevation above sea level (using a barometric GPS) and slope, average of two measurements using an inclinometer at 90° to each other. Human pressure on the habitat was also measured at each plot as a count of felled trees (cut tree trunks) and a count of livestock dung (goat, cow, horse, donkey).



No.	Site name	Administrative region
1	Tucillal	Tumbes
2	Fernandez Bajo	Tumbes/Piura
3	Enace	Piura
4	Lancones	Piura
5	Puerta Pulache	Piura
6	Pampa Larga	Piura
7	Progreso Bajo	Piura
8	Cruz de Caña	Piura
9	Sagrado Corazón	Piura
10	Islilla	Piura
11	Ancajima	Piura
12	Ñapique	Piura
13	Ñaupe	Piura
14	Piedra Mora	Lambayeque
15	Las Norias	Lambayeque
16	Illescas	Piura
17	Pañalá	Lambayeque
18	La Peña	Lambayeque
19	Pomac - Poma III	Lambayeque
20	Pomac - Zona Recuperada	Lambayeque
21	Pomac - Salinas	Lambayeque
22	La Viña	Lambayeque
23	Cañoncillo	La Libertad
24	Mocan	La Libertad
25	La Arenita	La Libertad
26	Monte Zarumo	Ancash

Figure 3.2 . Study area with study sites

3.3 Bird density estimation

Distance sampling is a method of estimating density of biological populations (Buckland et al. 2001; Thomas et al. 2010) that takes account of the detectability of the objects under survey to adjust the encounter rates in estimating density. Detectability is modelled as a function of distance from the transect to the object (Buckland et al. 2001) employing the fundamental basis that detectability decreases with increasing distance from the transect line. It is also possible for covariates to be included in modelling the detection function (Buckland et al. 2004; Marques et al. 2007), that is, those that may affect the detectability of a species. These can be related to the species itself (e.g. temporal frequency and volume of calling; Alldredge et al. 2007), to its environment (e.g. density of habitat cover or factors affecting food availability; Winiarski et al. 2013), or to the fieldwork process itself (e.g. observer differences, time of observation; Marques et al. 2007). A disadvantage of using distance sampling for rare species is that a minimum number of records, e.g. 60-80 (Buckland et al. 2001), are required to be able to fit a detection function. When attempting to estimate abundance at different sites, ideally, site-specific detection functions should be used, given that differences may exist in detectability between sites. However, this is often logistically difficult, therefore, site-level covariates were included in the detection function fitted to the complete dataset (Buckland et al. 2004; Marques et al. 2007), effectively taking into account site level variation.

Data were analysed in Distance 6.0 (Thomas et al. 2010) as clusters, i.e. modelling the detectability of groups of one or more individuals of the same species. Distance data were grouped into bins of equal intervals prior to analysis and truncated, following guidelines to improve fit of detection functions (Buckland et al. 2001). Preliminary analyses with different truncation distances and numbers of intervals were trialled and a truncation distance, number of intervals and candidate model key function type (e.g. half-normal, uniform, hazard-rate) were set for each species based on visual inspection of histograms and goodness of fit tests (Appendix 2). To maximise the number of records used in the analysis, both aural and visual records were used, with a covariate included to account for any differences in detectability between these two detection modes. To estimate group size (numbers of individuals) for groups that were heard only, a random group size was taken from the visual records of the same species. To account for a possible effect of detection distance on size of groups, all recorded distances per species were divided into two bands, above and below the median, and the group size was randomly sampled by species and distance band. Whether the frequency of aural records changed as the field season progressed was also evaluated by plotting percentage of aural records against month (Appendix 3).

The suitability of habitat variables as candidate covariates was assessed with respect to collinearity, effect on detection distance and variability across sites. Also, a maximum of two or three covariates to minimise failure rates in computing model likelihood were chosen. First, correlations between covariates were visually inspected using scatterplots; variation of covariates across sites using boxplots; and the effect of covariates on the distances recorded per species or number of detections using linear regression (Appendix 3). All exploratory analyses were implemented in R (R Core Team 2014). Final covariates were chosen to avoid correlated covariates and to favour those showing variability between sites and those perceived to affect detection distances or number of detections. For each species, models were built using the established key function type, with different combinations of covariates and series expansions. Of these, a final model was selected through AIC minimisation, after checking χ^2 goodness of fit. Density was estimated at the site level, using the global detection function, adjusted with the site-level covariates. As well as site-specific density estimates, an overall, region-wide estimate was produced by combining the site level estimates. Given that the site level density estimates are calculated using the same global detection function, they are not independent, obligating variance to be calculated via bootstrapping (Thomas et al. 2010). Finally, density of groups km^{-2} was converted to individuals km^{-2} using average cluster size per site. Given that correlations between cluster size and detection distance were not significant at $\alpha = 0.05$ for all species, a regression-based method to eliminate bias in cluster size affecting detectability was not applied (Thomas et al. 2010).

In the case of two rare species (Rufous Flycatcher *Myiarchus semirufus* and Tumbes Tyrant *Tumbezia salvini*), individuals were not observed on the transects at six sites and one site, respectively, but were observed within the transect area when walking from one transect to another. Given their presence, they were given arbitrarily low density values of 0.5 ind. km^{-2} (lower than the minimum estimated density for both species) for subsequent analysis, following Brewer & Gaston (2002).

3.4 Local population size estimation

Population sizes were calculated for species at each field site by multiplying the density of individuals km^{-2} by the area of the site, calculated in one of three ways. In the case of sites having an official or proposed protection category corresponding to a formally delimited area, this was intersected with ArcGis 10.2 with a vegetation cover map (MINAM 2012) and the area of suitable habitat types within the conservation area was summed. Habitats were deemed suitable if they occurred over the transects themselves at the study site (Table 3.2). If study sites did not have a delimited area, then one of two approaches were taken. If existing patches of vegetation were delimited by landscape features (such as valleys, surrounding agriculture or desert), then these areas were summed, using the vegetation cover map. Alternatively, if study sites were part of a much larger area of continuous vegetation of suitable habitat type, then a circular plot of 10 km^2 around the transects was used (Appendix 4). In one case (Enace), two such circular plots were used, corresponding to the study site from this study and from the 2012 pilot site less than 5 km away, were similar densities of birds were recorded (Appendix 4). Rapid Eye 5 m resolution, multispectral satellite images were used to further guide the delimitation by vegetation types. Finally, a site importance index was created. Population size by site was ranked for each species, and for each site, the number of species with a top three rank was assigned as the importance index. Thus, the index ranges from 0 to 14, where a site with a value of 14 would imply that the site holds one of the top three population sizes for all species.

Table 3.1. Habitat types within circular plot of 10 km^2 at study sites according to 2011 vegetation map (MinAm 2013).

Broad vegetation type	Original vegetation type	Area (km^2)	%
Agriculture	Coastal and Andean agriculture	38.8	15
Desert	Coastal desert	39.5	15
Dry forest	Savannah dry forest	77.8	70
	Foothills dry forest	32.7	
	Upper hills dry forest	26.0	
	Slope dry forest	17.3	
	Lower hills dry forest	9.7	
Riverine dry forest	Riverine *Prosopis* sp. dry forest	17.0	
Total		**260**	

4 Results

4.1 Species presence and encounter rates at sites

In total, 7,505 records of the 14 study species were recorded over a total of 104 transects at 26 sites. At least five species endemic to the Tumbesian region (Stattersfield et al. 1998) were present at each site, with a maximum of 16 at Ñaupe (site 13, Figure 1). Encounter rates (groups km^{-1}) at individual sites ranged from 0.09 (Baird's Flycatcher *Myiodynastes bairdii*, Short-tailed Woodstar *Myrmia micrura*, Tumbes Tyrant *Tumbezia salvini*) to a maximum of 15.80 (Mouse-coloured Tyrannulet *Phaeomyias murina*; Appendix 5). Overall encounter rates per species ranged from 0.3 to 6.3 (Table 4.1). In terms of individuals of all species, encounter rates averaged 28.7 individuals per km, equivalent to approximately 7 birds every 10 minutes at the average walking speed.

Table 4.1. Summary encounter rates and group sizes by species (see Appendix 5 for encounter rates by site)

Species	Mean encounter rate (groups km^{-1} ± standard error)	Mean group size (individuals ± standard error)	Total number of groups observed
Myrmia micrura	0.5 ± 0.08	1.1 ± 0.04	132
Forpus coelestis	1.0 ± 0.09	4.3 ± 0.44	253
Phytotoma raimondii	1.4 ± 0.30	1.2 ± 0.05	379
Phaeomyias murina	3.3 ± 0.47	1.2 ± 0.02	858
Pseudelaenia leucospodia	3.3 ± 0.22	1.0 ± 0.01	876
Tumbezia salvini	0.4 ± 0.09	1.1 ± 0.04	103
Myiarchus semirufus	0.3 ± 0.05	1.1 ± 0.04	70
Synallaxis stictothorax	2.9 ± 0.24	1.4 ± 0.03	761
Campylorhynchus fasciatus	0.8 ± 0.11	1.8 ± 0.06	199
Cantorchilus superciliaris	2.9 ± 0.20	1.1 ± 0.02	768
Mimus longicaudatus	6.3 ± 0.37	1.4 ± 0.03	1651
Rhynchospiza stolzmanni	1.7 ± 0.20	1.8 ± 0.04	443
Piezorina cinerea	3.1 ± 0.24	1.7 ± 0.05	811
Sicalis taczanowskii	0.8 ± 0.10	31.2 ± 7.56	201

4.2 Covariate selection

Following the selection procedure, three covariates were chosen for inclusion in models. These were: mode of detection (vocalising or non-vocalising, following Marques et al. 2007); tree height; and percentage of vegetation cover < 3 m (low cover). Bird records on transects were evenly split between vocalising and non-vocalising, with 41.5% of records exclusively aural and 40.5% exclusively visual

(18% were both seen and heard). Non-vocalising records had a median detection distance greater than vocalising records (Appendix 3a), justifying its inclusion as a covariate. This was also apparent on the detection function, with vocalising birds more detectable than non-vocalising individuals (Figure 4.1). Survey month did not appear to affect numbers of vocalising records (Appendix 3b) and was not included as a covariate. Given that surveys were conducted outside the main breeding season, numbers of vocalising birds was not expected to change over the four months of the survey.

As with other multivariate regressions, it is not recommended to include strongly correlated variables, therefore, of the habitat variables, high cover, and basal area were excluded (due to correlations with low cover and tree height; Appendix 3c). Number of stems (as a measure of habitat density) was excluded due to lack of perceived effect on detection distance (Appendix 3d), as evidenced by a lack of significant linear regression coefficients between detection distance and number of stems for each species. Tree species richness was excluded because it did not vary greatly across sites (Appendix 3e). Additionally, low cover and tree height were among the most variable across sites, an important characteristic, given that the main objective of using covariates was to improve site level density estimates without using separate detection functions at this level.

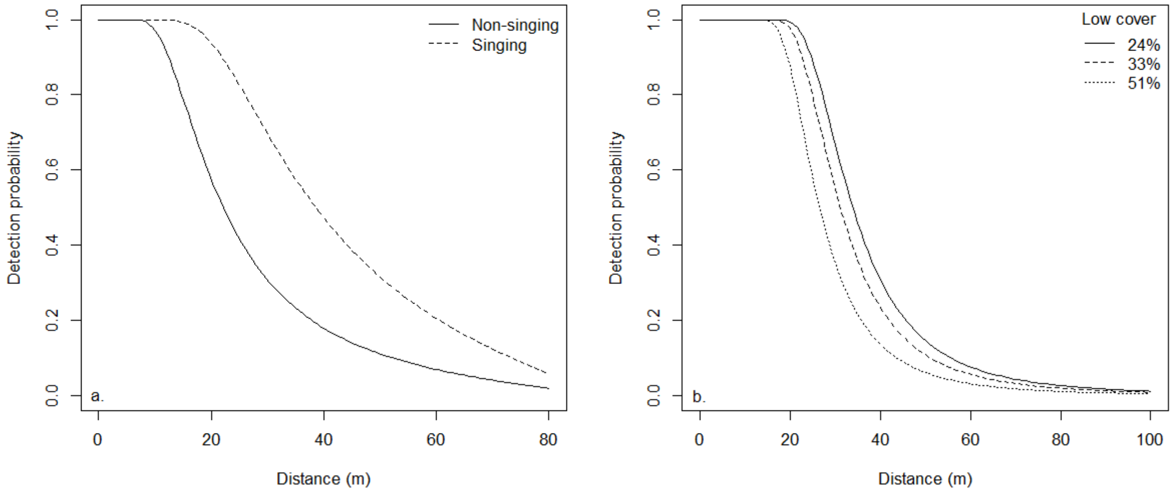


Figure 4.1. a) Illustrative detection function for non-vocalising and vocalising records for all species showing composite detection function. Species were analysed separately, but detection functions are typically as shown here. b) Detection function for *Phytotoma raimondii* for different values of low cover, with remaining covariates kept constant (non-vocalising and tree height at mean of 3.7 m).

Covariate coefficients from species-specific detection functions showed similar patterns among species (Figure 4.2). In all species, non-vocalising records compared to vocalising records had a negative effect on detectability. In the case of Rufous Flycatcher *Myiarchus semirufus*, over 95% of records were visual, with the coefficient almost at zero. In contrast, Peruvian Plantcutter *Phytotoma raimondii* was detected aurally 54% of the time, and the absolute value of the coefficient is larger. In terms of habitat covariates, low cover negatively affected detectability in almost all cases, i.e. higher percentages of low cover decreased detectability (Figure 4.1b). Exceptions include Rufous Flycatcher *Myiarchus rufus* and Tumbes Tyrant *Tumbezia salvini*, both of which can occur in habitats with larger trees. Finally, tree height also negatively affected detectability. However, coefficient values are calculated by maintaining the remaining covariates at a stable value (as non-vocalising for the categorical covariate, and at the mean values of the continuous covariates). In the case of the habitat covariates, this could produce variable effects depending on the interaction between both, for example, birds vocalising from tree tops, and should therefore be interpreted with care.

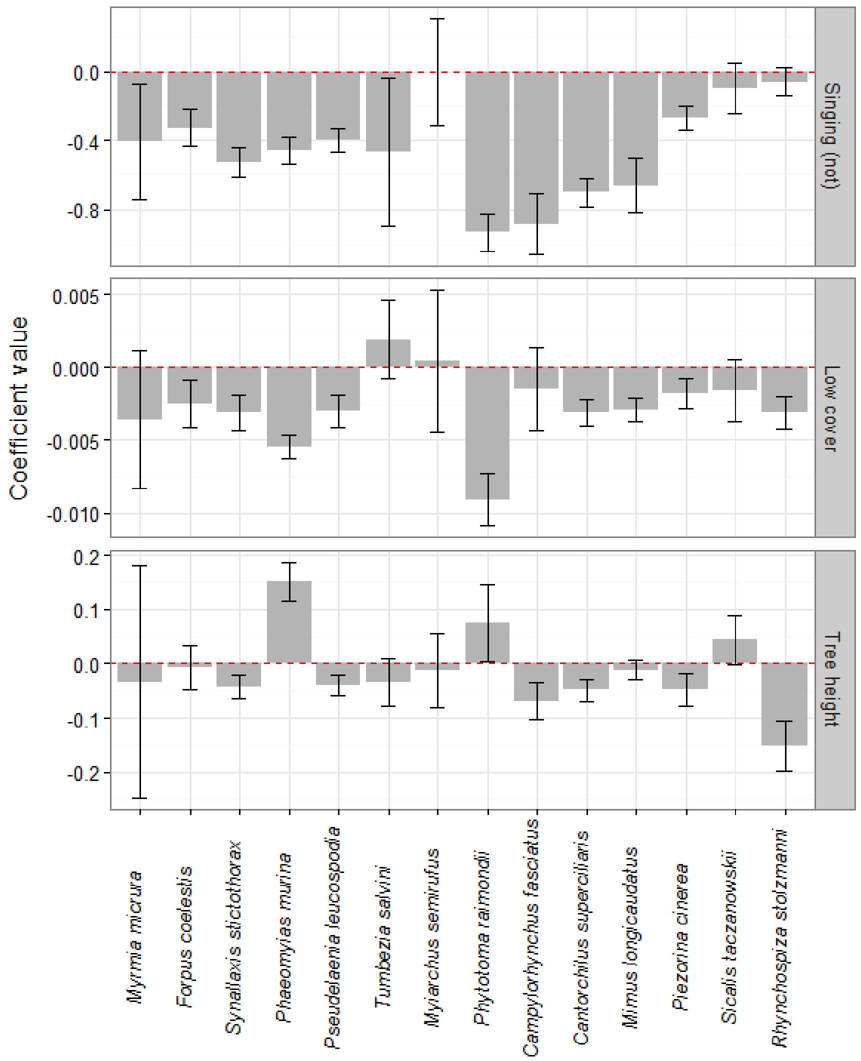


Figure 4.2. Covariate coefficient values for species; error bars show standard errors. Vocalising is a factor covariate with two levels (vocalising, non-vocalising), coefficient value compares 'non-vocalising' to 'vocalising' as a baseline.

4.3 Local abundance estimates

Local abundance by site varied greatly within and between species, with non-zero values ranging from 0.9 to over 340 individuals km^{-2}. Confidence limits ranged from 5% to 24% of the overall estimates of density, but with much greater variation on the lower estimates (Table 4.2). Variance of the encounter rate contributes the highest component of the overall variance; where there were very low numbers of records at sites, species were not always observed on all four transects, greatly inflating the variance of the encounter rate. Sites where species registered particularly high coefficients of variation did not generally coincide (Figure 4.3). The highest density estimate comes from Sulphur-throated Finch *Sicalis taczanowskii*, a species commonly found in flocks numbering in the 100s or even 1,000s (Schulenberg et al. 2007). The lowest mean density estimates are from two threatened flycatchers, Tumbes Tyrant *Tumbezia salvini* and Rufous Flycatcher *Myiarchus semirufus*. The latter had low density estimates across almost all sites, although its distribution is widespread. At least four species reach the limits of their distributions within the study area and have zero abundance at the southernmost sites (Figure 4.3).

Table 4.2. Summary density estimates per species (see Appendix 5 for local abundance by site). The combined estimate represents the overall density estimate for all sites. Minimum values represent minimum density where present.

Species	**Density estimate: ind. km^{-2} (% coefficient of variation)**		
	Combined (across all sites)	**Minimum (where present)**	**Maximum**
Myrmia micrura	19.1 (23.3)	2.3 (91.9)	113.9 (46.2)
Forpus coelestis	51.2 (13.1)	0.9 (92.0)	210.7 (44.4)
Phytotoma raimondii	27.5 (18.3)	1.8 (87.2)	104.7 (31.9)
Phaeomyias murina	60.1 (10.3)	3.8 (59.2)	284.4 (42.3)
Pseudelaenia leucospodia	44.5 (6.3)	3.0 (95.7)	103.2 (10.3)
Tumbezia salvini	4.1 (18.1)	0.9 (102.9)	38.4 (16.1)
Myiarchus semirufus	5.9 (19.9)	1.9 (89.9)	44.6 (25.6)
Synallaxis stictothorax	63.2 (5.9)	4.6 (53.5)	157.1 (18.4)
Campylorhynchus fasciatus	12.9 (15.2)	0.7 (85.4)	97.6 (34.7)
Cantorchilus superciliaris	38.8 (5.8)	1.0 (92.0)	90.0 (15.6)
Mimus longicaudatus	142.9 (5.5)	22.9 (28.6)	305.5 (10.5)
Rhynchospiza stolzmanni	77.4 (7.2)	5.0 (52.5)	344.9 (14.7)
Piezorina cinerea	65.1 (5.0)	4.4 (84.8)	161.7 (8.1)
Sicalis taczanowskii	341.6 (24.4)	6.6 (89.7)	3060.2 (53.8)

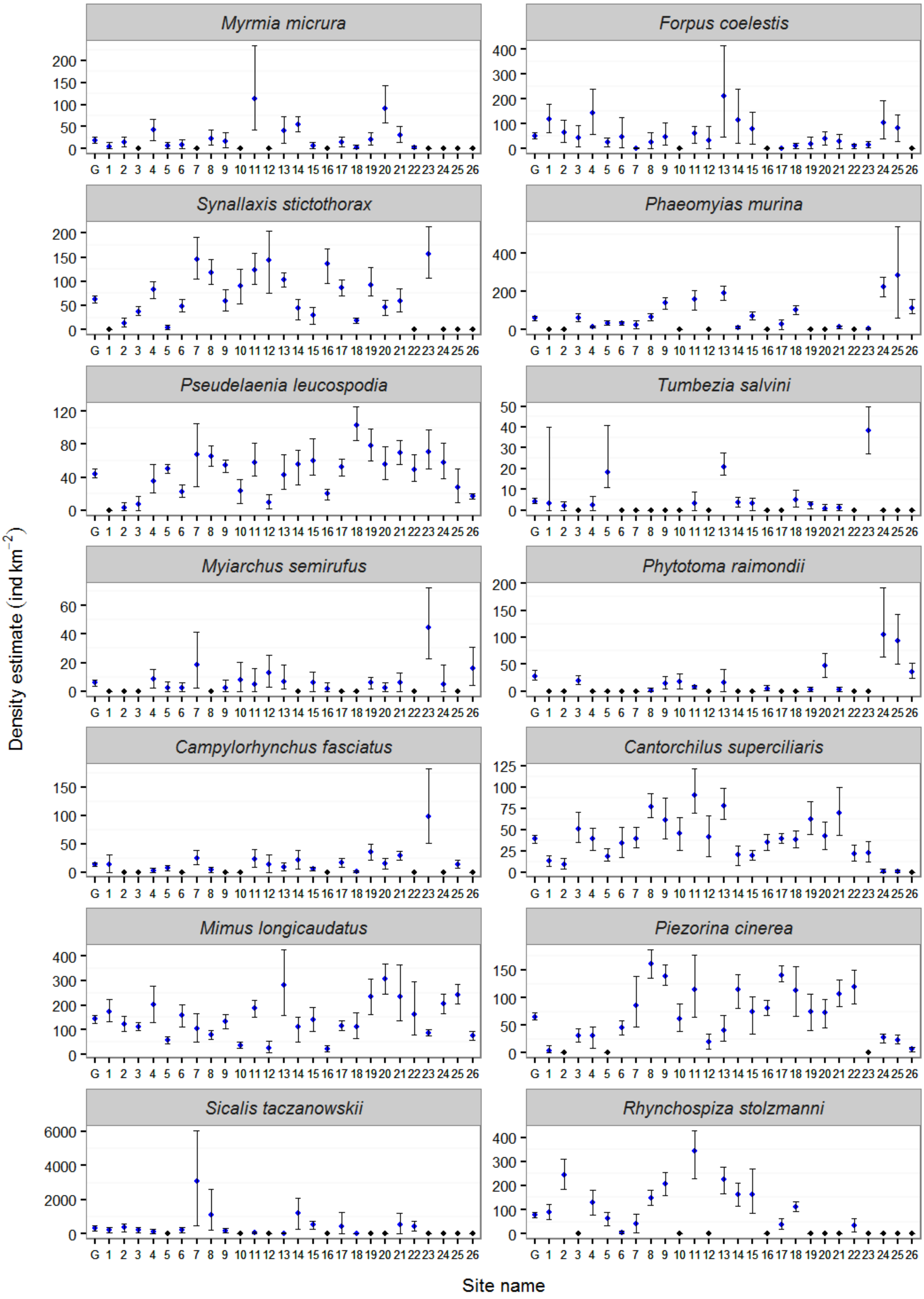


Figure 4.3. Density estimates with lower and upper confidence limits by species and study sites. Site names refer to labels in Figure 3.1 and are ordered north to south. The first estimate (G) is the combined (or global) estimate across all sites. Densities of 0 (absence from a site) are shown by black dots.

4.4 Local population size estimates

Areas were calculated for 13 sites, using suitable habitat within management areas at five, landscapes features at four, and circular plots at four (Table 4.3, Appendix 4). In two cases (Enace, Illescas) the bird surveys were conducted just outside the limits of the management area. Population sizes for the Peruvian Plantcutter ranged from 50 to 890 individuals, and for the Rufous Flycatcher from 20 to 280 individuals per site (Table 4.4). Three species (Long-tailed Mockingbird, *Mimus longicaudatus*, Tumbes Sparrow *Rhynchospiza stolzmanni* and Sulphur-throated Finch *Sicalis taczanowskii*) had estimated population sizes over 10,000 at five different sites (Table 4.4). Larger sites generally had higher population estimates and therefore scored higher in the site importance rank. Fernandez Bajo, as the largest site, held the highest number of species within their top three population size estimates (Table 4.3). However, Huacrupe regional protected area and the proposed conservation area at La Peña, both less than half the size of Fernandez Bajo, had very similar site importance scores. That is, they held almost the same number of species with population estimates within their top three (Table 4.3).

Table 4.3. Site areas and protection status.

No	Site name	Region	Conservation area name (IUCN category)	Suitable area (km^2)	Total size of conservation area	Site importance index
2	Fernandez Bajo	Piura	Coto de Caza El Angolo (VI)	116.1	653.4	8
3	Enace	Piura	Área de Conservación Regional Estribaciones al Sur de los Amotapes (proposed)	20.0	274.9	0
10	Islilla	Piura		10.0		0
13	Ñaupe	Lambayeque		10.0		3
14	Piedra Mora	Lambayeque	Área de Conservación Regional Bosque Huacrupe - La Calera (VI)	35.8	72.7	8
15	Las Norias	Lambayeque		24.9		4
16	Illescas	Piura	Zona Reservada (Illescas)	10.0		0
18	La Peña	Lambayeque	Área de Conservación Privada San Francisco de Asís (proposed)	67.7	107.9	7
19,20,21	Pomac	Lambayeque	Santuario Histórico Bosque de Pómac (III)	49.8	58.9	6
23	Cañoncillo	La Libertad	Área de Conservación Privada Bosque Natural El Cañoncillo (VI)	5.3	14.9	2
24	Mocan	La Libertad		4.1		1
25	La Arenita	La Libertad		4.3		0
26	Monte Zarumo	Ancash		17.2		3
7,8,9,11	Chulucanas - La Matanza	Piura		> 2500		n/a

Table 4.4 Population sizes (95% confidence intervals) at case study sites. A '+' means that the species was observed at the site, but not during the transect census.

Site Name	*Campylorhynchus fasciatus*	*Cantorchilus superciliaris*	*Forpus coelestis*	*Mimus longicaudatus*	*Myiarchus semirufus*	*Myrmia micrura*	*Phaeomyias murina*	*Phytotoma raimondii*	*Piezorina cinerea*	*Pseudelaenia leucospodia*	*Rhynchospiza stolzmanni*	*Sicalis taczanowskii*	*Synallaxis stictothorax*	*Tumbezia salvini*
Fernandez Bajo		1037 (490-1839)	7726 (2887-13338)	14067 (11012-18141)	+	1771 (562-3042)				351 (0-1097)	28107 (21343-36071)	41434 (16496-70334)	1588 (610-2798)	224 (0-471)
Enace		1011 (703-1410)	850 (135-1907)	2256 (1955-2575)	+		1265 (852-1731)	397 (265-581)	619 (411-872)	148 (0-334)		4279 (1333-7572)	742 (583-946)	
Islilla		453 (256-642)		367 (267-494)	80 (0-204)			174 (44-323)	609 (396-887)	232 (87-378)			912 (527-1263)	
Ñaupe	90 (21-161)	779 (623-989)	2106 (479-4165)	2816 (1591-4261)	67 (15-184)	398 (133-737)	1912 (1534-2311)	159 (0-403)	408 (218-682)	427 (261-677)	2236 (1673-2784)	202 (0-570)	1030 (880-1177)	209 (169-277)
Piedra Mora	745 (205-1389)	713 (284-1107)	4069 (758-8588)	3975 (1854-5369)	+	1943 (1356-2634)	416 (229-656)		4126 (2923-5099)	1975 (1126-2618)	5838 (4077-7588)	42984 (9580-74881)	1596 (756-2243)	143 (62-233)
Las Norias	132 (43-234)	494 (363-645)	2014 (455-3684)	3466 (2369-4718)	150 (0-331)	162 (0-344)	1762 (1258-2366)	+	1863 (857-2522)	1495 (1076-2160)	4035 (2082-6668)	13692 (6685-18441)	752 (272-1127)	83 (0-148)
Illescas		354 (254-445)		229 (113-368)	19 (0-58)			52 (9-119)	804 (680-958)	200 (132-253)			1362 (961-1670)	
La Peña	50 (0-148)	2616 (1978-3319)	742 (0-1611)	7500 (4351-11476)	+	185 (0-524)	6886 (5379-8455)		7633 (4523-10535)	6994 (5756-8473)	7487 (6207-8964)	448 (0-1409)	1256 (866-1654)	351 (108-660)
Pomac	1330 (1015-1735)	2875 (2250-3675)	1485 (815-2710)	12845 (10775-15310)	230 (115-450)	2385 (1585-3595)	205 (90-465)	865 (560-1335)	4205 (3300-5365)	3370 (2930-3880)		8570 (1640-44755)	3265 (2535-4205)	85 (45-165)

Site Name	*Campylorhynchus fasciatus*	*Cantorchilus superciliaris*	*Forpus coelestis*	*Mimus longicaudatus*	*Myiarchus semirufus*	*Myrmia micrura*	*Phaeomyias murina*	*Phytotoma raimondii*	*Piezorina cinerea*	*Pseudelaenia leucospodia*	*Rhynchospiza stolzmanni*	*Sicalis taczanowskii*	*Synallaxis stictothorax*	*Tumbezia salvini*
Cañoncillo	513 (270-958)	118 (64-187)	82 (25-158)	454 (390-527)	234 (120-380)		20 (0-47)			374 (264-513)			826 (562-1128)	201 (143-260)
Mocan		4 (0-13)	424 (168-803)	854 (688-1011)	20 (0-75)		920 (706-1133)	431 (261-791)	115 (75-140)	236 (157-334)				
La Arenita	59 (33-91)	4 (0-13)	356 (133-594)	1046 (887-1225)			1226 (258-2343)	405 (215-618)	101 (69-139)	121 (39-215)				
Monte Zarumo				1298 (992-1604)	280 (71-527)		1965 (1417-2729)	613 (420-894)	128 (42-183)	300 (242-357)				

5 Conservation implications: population size estimates, priority sites and threats to endemic birds in northwest Peru

The north coast of Peru, comprising the regions of Tumbes, Piura, Lambayeque, La Libertad and Ancash, is one of the most economically important areas of the country, representing less than 10% of Peru's area, but home to 25% of the country's urban population (INEI 2007). The region is responsible for 15% of GDP, with large-scale, irrigated agriculture and mining making up significant components of the region's economy (INEI 2014). Conservation issues affecting the northwest region revolve around habitat loss and habitat degradation. Dry forests are being lost to urban development, large-scale irrigated agriculture, open cast mining and at a smaller scale, smallholder farming. Habitat degradation is also serious, with selective logging effectively wiping out large individual trees, especially *Prosopis* sp., for the production of charcoal (CDC 1992). The following sections discuss population size estimates for key species and priority sites in light of challenges facing biodiversity conservation, including creation of protected areas, urban development, large- and small-scale agriculture and mining.

5.1 Populations of key species across the Tumbesian region

Three bird species in northwest Peru are listed on the IUCN Red List: Peruvian Plantcutter *Phytotoma raimondii* (Endangered), Rufous Flycatcher *Myiarchus semirufus* (Endangered) and Tumbes Tyrant *Tumbezia salvini* (Near Threatened). The latter two both had the lowest mean and the lowest maximum abundance across sites. Published estimates of population size or population density for these species are scarce; estimates only exist in literature for Peruvian Plantcutter in a small part of its range, Pomac National Park (Nolazco et al. 2014). Results from the present study and Nolazco et al., (2014) show a similar geographic distribution of the species in the National Park. An area with recovering habitat (i.e. a mix of abandoned farmland, scrub and small patches of trees) held the highest local abundances. This sector of the park was reclaimed by the authorities in 2009 after an illegal invasion of settlers had cleared, farmed and built houses over most of this area (SERNANP 2011). The overall population estimate of 865 (95% CI 560 – 1,335) obtained in the present study (Table 4.4) was larger than the 488 individuals of the previous estimate (confidence intervals not given). Higher encounter rates, and greater numbers of females were found during the present study. An unpublished study in 2006 to assess presence of both Peruvian Plantcutter and Rufous Flycatcher visited nine sites over a period of 20 days in the northern part of the present study area (Chávez Villavicencio et al. 2006). Encounter rates found by Chávez et al. were highly variable, as in this study, but mean values were remarkably similar to this study (correlation of mean encounter rates for 11 species: $r_s = 0.91$, p-value < 0.001;Appendix 7), providing some evidence for a recent stability in species presence and abundance at sites.

Locations of known sites for Peruvian Plantcutter *Phytotoma raimondii* were published for the whole of Peru in 2009 (Flanagan et al. 2009) and updated in 2015 with a population estimate of less than 500 individuals (Romo et al. 2015). The present study has found more individuals at eight sites than the above global population estimate. The methods used by Romo et al., (2015) did not include systematic surveys and did not take into account detection probability; rather, they were mostly limited to summing individual plantcutters sighted on field visits or from casual observations. As a result, there are large differences in population sizes at sites common to this study and Romo et al., (2015). For example, La Arenita in the province of Paiján, La Libertad, has one of the highest abundance estimates from the present study (94.1 ind. km^{-2} ± 23.2; Appendix 6) with an estimated population of 450 individuals, whereas Romo et al. estimated a population of 40.

The Endangered Rufous Flycatcher *Myiarchus semirufus* (IUCN 2015), was observed at all but three study sites. The flycatcher's distribution was described shortly after its description as covering most of the study area, with records ranging from Tumbes to Chimbote (Zimmer 1938). The species is still widespread throughout the nortwest of Peru, but generally at low densities. The current population estimate (used for red listing purposes) stands at 1,500-7,000 (BirdLife International 2016). This is undoubtedly an underestimate given that there are more than 25,000 km^2 of dry forest savannah and desert scrub (MINAM 2012) –suitable habitats for the species– within its range as defined by this study. Average local abundance across the study area was 5.9 (95% CI 3.5 - 8.2). A population of approximately 1,500 individuals is estimated from the study sites alone (485 km^2 of suitable habitat), but its global population size could well be one or two orders of magnitude larger. Factors limiting its abundance may be connected to nesting sites, i.e. a lack of tree cavities (Lanyon 1985) or at least, very dark, thick thorny thickets (Lanyon 1975). Large trees are largely absent across the lowland plains forest in northwest Peru. Density was highest at the private reserve of Cañoncillo, the site with the largest *Prosopis* sp. 'Algarobo' trees recorded. Further evidence of a lack of nesting sites comes from a project on Tumbes Swallow *Tachycineta stolzmanni* at Pomac National Park (Stager et al. 2012) where at least four nestboxes put out for swallows were first occupied by Rufus Flycatchers (F. Angulo, pers. comm).

Population density estimates for Sulphur-throated Finch *Sicalis taczanowskii* may suffer from higher uncertaintly than other species given their life history. This species tends to form large flocks numbering 100s of individuals (Schulenberg et al. 2007). Distance sampling is more effective when there are many smaller clusters than few large clusters, as is mostly the case in this species, due to less detections made per given effort for large clusters, leading to less precise estimates of encounter rate (Buckland et al. 2001). When a species is almost entirely found in a single group, then estimation techniques such as complete counts may be more appropriate. However, a median of 14 encounters per site was recorded (range: 1 - 30) at the 16 sites were the species was found, compared to 17 per site across all species. Furthermore, the species had a very large variability in flock size (from 1 to 400 individuals), which also contributes to the density estimate variance, although not as much as the contribution of the encounter rate variance.

5.2 Key sites for conservation

The Pacific Equatorial Coast and Subtropical Pacific biomes, covering the study area, have the lowest representation of protected areas in Peru, at 6.4% and 5.1% of their area, respectively. In contrast, 34% of the Southern Amazon biome is protected (calculated from Olson et al. 2001; IUCN and UNEP-WCMC 2016). Additionally, lowland dry forest is generally underrepresented in site-based conservation priority setting schemes (e.g. CDC 1992; Rodríguez and Young 2000; Peralvo et al. 2007; Véliz Rosas et al. 2008; SERNANP 2009; Gobierno Regional Piura 2009; Arnillas et al. 2011; More Cahuapaza et al. 2014; Fajardo et al. 2014), sometimes used to implement new protected areas (Gerencia de Recursos Naturales del Gobierno Regional de Lambayeque

2009). This lack of protection is highlighted by the fact that several hotspots of local abundance for important species occur at unprotected and/or threatened sites. Three main issues occur: a lack of protection at key sites for the patchily distributed Peruvian Plantcutter, lack of a large continuous block of protected lowland dry forest, and a general lack of protected sites in the southern parts of the ranges of the Tumbes endemics.

For the Peruvian Plantcutter, of particular importance are the sites at Mocan and La Arenita (sites 24, 25; Figure 3.2), in La Libertad. Density estimates at these very small sites are among the highest estimates for this species (Appendix 6). The sites are owned by a large food company with extensive sugar cane plantations across the area. Although the site at La Arenita is not currently planned for conversion to agriculture, the site at Mocan is, and neighbouring fields have already been cleared. These sites are important strongholds for the plantcutter in the southern part of its range, along with Monte Zarumo, another unprotected site, further south still, in Ancash. Population sizes at each of the three sites are over 400 individuals. Additionally, the sites near the town of Paiján, La Libertad, demonstrate how different models of agriculture affect biodiversity. To the south of the town, agriculture generally corresponds to smallholdings, interspersed with small patches (i.e. < 5 ha) of scrub and dry forest. Among these, plantcutters have been found regularly (Pollack Velásquez 2011). To the north, industrial scale monocultures dominate, where Plantcutters have formerly been recorded (Flanagan et al. 2009) but are now restricted to the sites at La Arenita and Mocan. Furthermore, at La Arenita, the Plantcutter was observed to use olive plantations next to the small area of dry scrub as a novel food source. Population densities within the olive plantation were similar to those in the dry scrub. Habitat mosaics of small-scale agricultural and natural habitats could be exploited as part of conservation initiatives aimed at protecting threatened species beyond protected areas. Two other geographically important sites, Illescas and Enace (sites 3, 16; Figure 3.2), hold significant populations of Plantcutters, but remain just outside proposed conservation areas. At both sites, it was not possible to extend the limits of the protected areas, despite information on Plantcutter distributions being available. A major obstacle to establishing new conservation areas in Peru lies in navigating permissions related to land use, for example, with holders of mining concessions and peasant farmer communities (e.g. land for goat grazing), both of which have rights to land use, although often not ownership (see Figure 5.3).

A notable region, outstanding for its lack of roads, villages and settlements, but also for its lack of biodiversity information lies between the new and old Panamerican highways, straddling the regions of Piura and Lambayeque (Figure 5.1). The conservation value of this area, given its continuous habitat, is exceptional, providing connectivity between numerous protected areas and important sites, especially along the base of the Andes, and with Ñapique (site 12; Figure 5.3). The biodiversity value of this area could be enormous, and could represent the largest contiguous populations of many of the low altitude dry forest endemics of the Tumbes region. A combined abundance estimate from study sites within the same habitat type of dry forest savannah surrounding this area (sites 7, 8, 9, 11,14, 15, 17; Figure 5.1) was calculated for Rufous Flycatcher as 4.6 ind. km^{-2} (95% CI 2.2-9.6), which over an area well in excess of 5,000 km^2 implies a significant population. This region is threatened by large-scale agriculture in the south and along the base of the Andes, (see below) and by urban sprawl from the city of Piura in the north. A site on the northern edge of this area, on the outskirts of the city of Piura, with a previously studied population of Peruvian Plantcutters *Phytotoma raimondii*, has already been cleared for construction (Chávez Villavicencio et al. 2006). This vast area should be taken into account in projects to define new protected areas.

Many of the endemic species have lost more of their former ranges at their southern extremes than at the north. Further south, as the coastal plains are reduced in area with the increasing proximity of the Andes to the sea, two changes occur in land cover. First, as the climate becomes drier, desert becomes the dominant natural land cover (Figure 2.1). Second, the proportion of agriculture to natural land cover increases sharply. Small fragments of dry forest in the river valleys among the desert, where not already lost to agriculture, need to be conserved and connected, including for example, the study site at Monte Zarumo (Appendix 4l), where one of the highest population densities of Peruvian Plantcutter is found (Table 4.2). A network of sites should be protected here to maintain populations of endemic species at the present range extremes and to prevent further range loss.

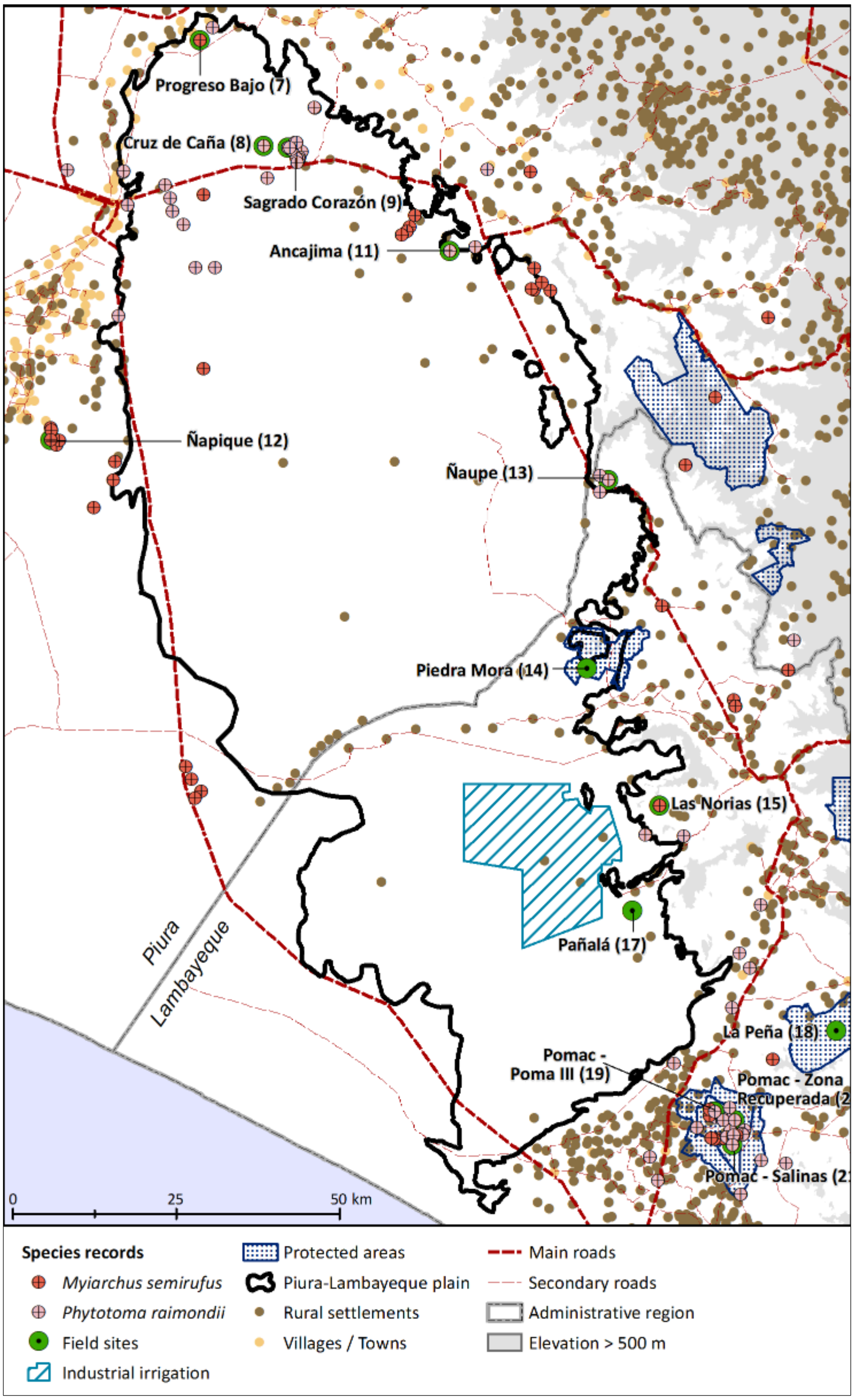


Figure 5.1. Area of lowland plains dry forest with very low population and road density, showing study sites and occurrence records of threatened species.

5.3 Major threats to biodiversity conservation in northwest Peru

Large-scale irrigation projects along the coast involve bringing water from the Amazonian basin, east of the Andes, via reservoirs, canals and tunnels to feed export agriculture on the drier coastal plains. Engineering projects such as these have been planned since at least the 1920s (Gobierno Regional de Lambayeque 2016), and irrigation canals feeding coastal agriculture from rivers on the west side of the Andes have existed in places for several millennia (Hocquenghem 1999). At least three large irrigation projects are at different stages of completion in the present study area: Alto Piura, Olmos-Tinajones in Lambayeque and Chavimochic in La Libertad, promising development and improved local economies (Figure 5.1, Figure 5.2). The Olmos project has already constructed a reservoir on the Rio Huancabamba east of the Andes, and canals now bring water to the region around Olmos (study sites 15 and 17; Figure 5.1). An area of 38,000 ha is due to be irrigated for industrial use, while smaller areas totalling 5,500 ha will be irrigated for community use, including the whole of the study area of Las Norias, implying the loss of most of its avifauna (Table 4.4). At average densities of sites surrounding this area, this conversion could entail the loss of approximately 1,730 (95% CI: 820-3,665) Endangered Rufous Flycatchers *Myiarchus semirufus*. However, the global population is probably an order of magnitude higher than current estimates (see above), therefore this number, although alarming, does not represent such a drastic population decline as would be calculated with current global population estimates.

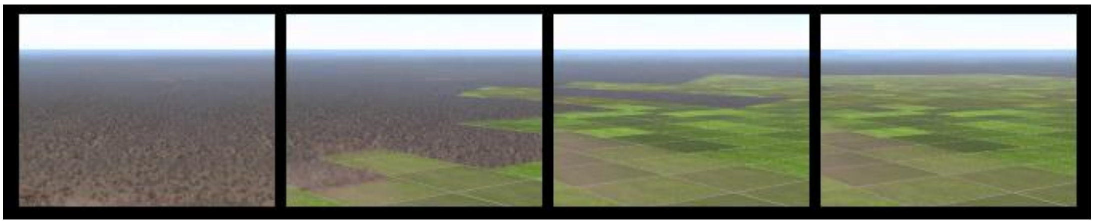


Figure 5.2. A series of stills from a promotional video showing the proposed benefits of the Olmos large-scale irrigation project. The 'desert' on the left, i.e. a vast lowland savannah dry forest, is transformed to green monocultures.

A worrying aspect of these large-scale projects is not only the habitat loss, but also how mitigation and offsets are managed within the framework of environmental impact assessments. Peru has recently developed legislation requiring ecological equivalence within environmental mitigation measures (MINAM 2014; MINAM 2016). Currently, the bird components of environmental impact assessments are mostly limited to very short field surveys with reports providing species lists and diversity indices, such as Shannon and Simpson (for example, see official guidelines; MINAM 2015). The environmental impact assessment for the industrial irrigation area did not report any of the threatened bird species found by this study at the same sites (ECSA Ingenieros 2011). This is very worrying. Furthermore, mitigation measures, in terms of equivalent area of habitat reforested or protected, are evidently less than the area impacted (ECSA Ingenieros 2011) and include recommendations for reforestation with species of economic interest for local communities. A similar pattern is seen in the environmental impact assessment at Illescas (site 16; Figure 3.2) with regard to the Bayovar mine (Golder Associates Perú S.A. 2008). Surveys during impact assessments need to be improved and ecological equivalence calculations improved, for example with bird abundance data.

Mining is on the increase in Peru (Devenish and Gianella 2012) and large areas of the country are given over to mining concessions (Figure 5.3). Mining takes place at both industrial and artisanal scales, with different legislation controlling each, whilst illegal mining, given its lack of regulation, represents an additional threat to biodiversity conservation. Mining, in any of its forms, was occurring at seven sites during the study. Although the total area of any one concession will likely not be exploited, land use is restricted for the duration of the concession, making the establishment of new protected areas difficult. A strip of dry forest at the base of the Illescas Cerros, currently outside the proposed national reserve (Appendix 4g) but within the mining concession, holds around 450 Plantcutters and over 150 Rufous Flycatchers as estimated by this study, comparable to some of the highest population estimates at other protected areas. Furthermore, both these species have not been recorded within the limits of the proposed area itself, mostly made up of rocky scrub with very low, or absent vegetation.

A further site, Islilla (site 10; Figure 3.2), completely covered by an active Andalusite mining concession, represents a geographically important site on the coast, with an estimated 80 individuals of Rufous Flycatcher and around 175 Peruvian Plantcutters in just the 10 km^2 plot around the transects. The area of desert scrub here actually benefits from the water discharged from the mining operation, and apparently is free from chemical waste due to the mechanical nature of the mining operation. Furthermore, the area of vegetation, although within the concession, is not under active exploitation, and currently represents a *de facto* reserve, albeit, without long-term protection (compare to similar cases, e.g. Forero-Montaña et al. 2003). Opportunities exist to work with mining companies to protect habitat within the areas of mining concessions, but requires forging agreements and long-term commitments on the part of industry, conservation NGOs and regional governments.

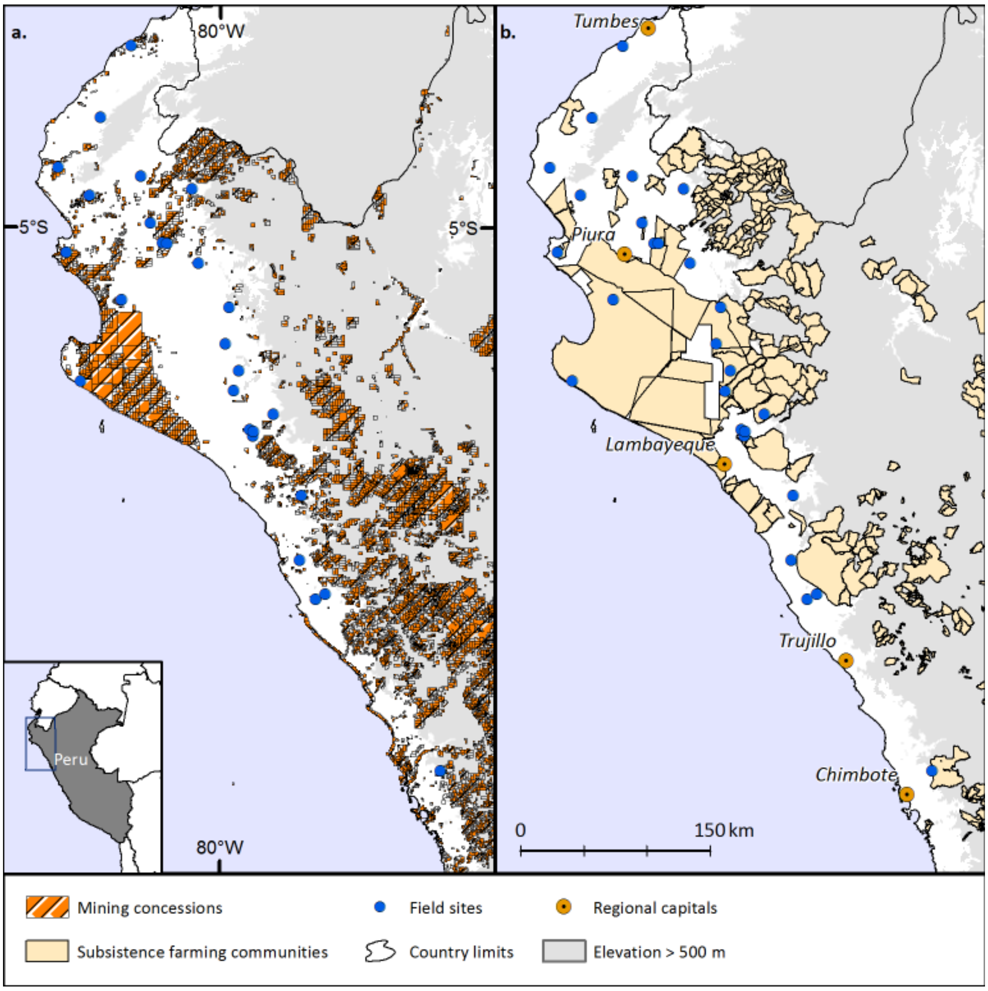


Figure 5.3. Location of mining concessions and subsistence farming community territories in northwest Peru.

6 Key recommendations

- Incorporate key sites for Peruvian Plantcutter into regional government biodiversity strategies as proposed sites for protection.
- Work with industry to protect key sites within mining concessions and to incorporate natural habitat patches within large-scale agriculture.
- Safeguard the vast area of lowland dry forest savannah, currently used as grazing areas, through cooperative agreements with farming communities and protect from large-scale industrial development.
- Establish a network of proposed protected areas in the southern extreme of the Tumbes region, working with the regional governments of La Libertad, Ancash and Lima.
- Support existing initiatives, such as private conservation areas, that conserve key populations of important species, for example, by increasing effectiveness of site protection.
- Improve survey techniques within environmental impact assessments to include a measure of abundance and employ this in ecological equivalence calculations for mitigation measures.

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8 Appendices

Appendix 1. Predictors used in exploratory species distribution model for defining sampling strata.

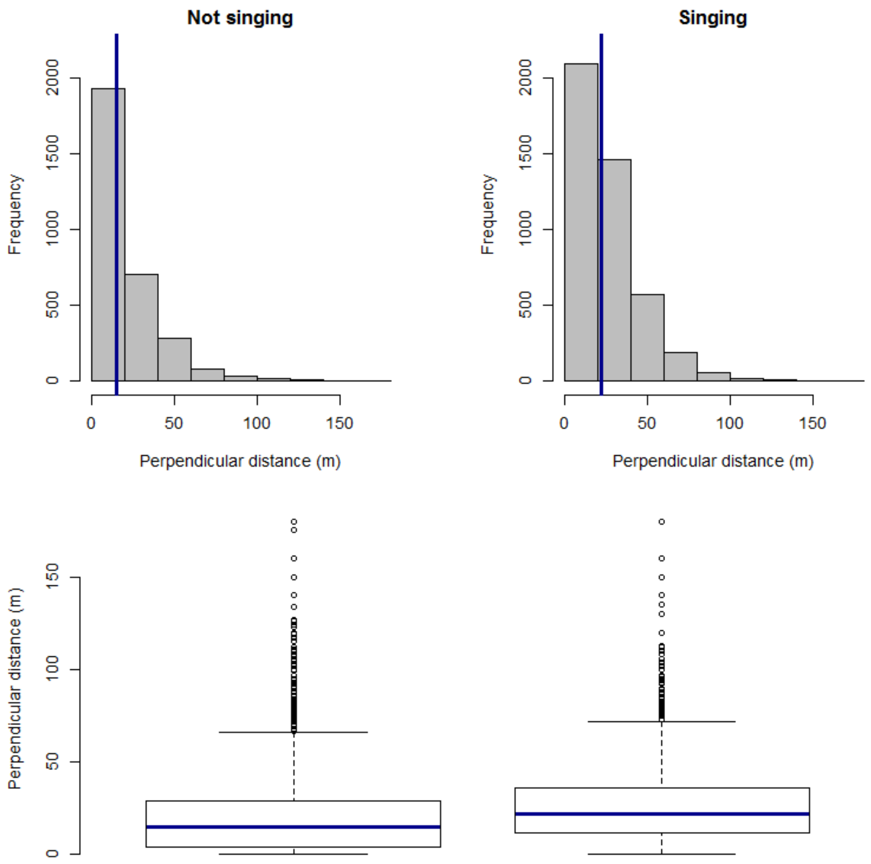
Model variable	Source
Annual Mean Temperature	bio1: Hijmans et al. 2005
Mean Temperature of Warmest Quarter	bio10: Hijmans et al. 2005
Mean Temperature of Coldest Quarter	bio11: Hijmans et al. 2005
Annual Precipitation	bio12: Hijmans et al. 2005
Precipitation of Driest Month	bio14: Hijmans et al. 2005
Precipitation Seasonality (Coefficient of Variation)	bio15: Hijmans et al. 2005
Precipitation of Wettest Quarter	bio16: Hijmans et al. 2005
Precipitation of Driest Quarter	bio17: Hijmans et al. 2005
Dry season maximum NDVI	MODIS product: MODQ13A1, 5 year average 2007-2012
Dry season minimum NDVI	MODQ13A1
Wet season maximum NDVI	MODQ13A1
Wet season minimum NDVI	MODQ13A1

Appendix 2. Interval and truncation distances per species for distance sampling analysis

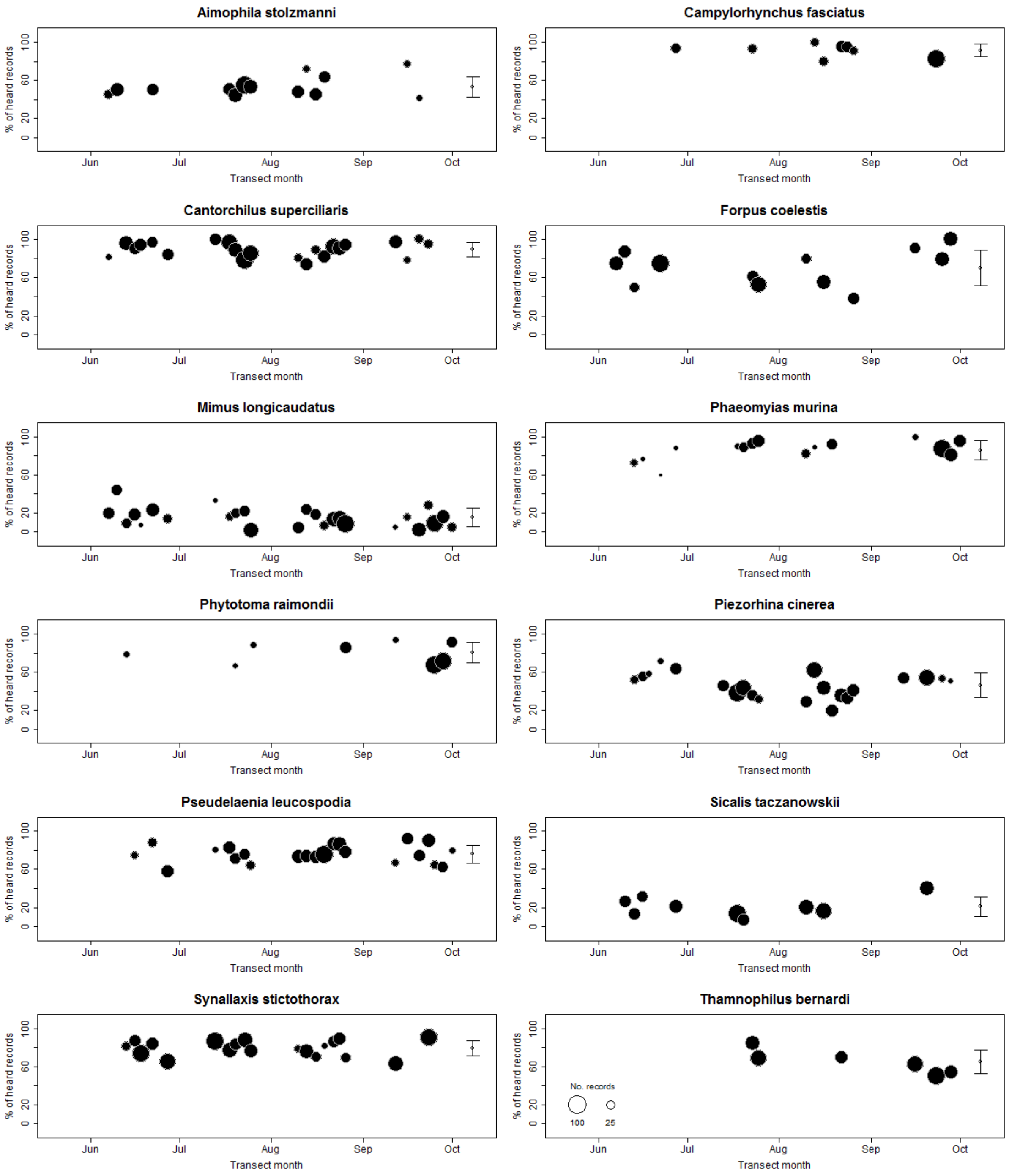
Species	Number of records (groups)	Intervals	Truncation distance	Key function	Adjustment terms
Myrmia micrura	132	7	60	Hazard rate	-
Forpus coelestis	244	7	90	Half normal	-
Synallaxis stictothorax	758	9	80	Hazard rate	Simple polynomial
Phaeomyias murina	851	9	80	Hazard rate	-
Pseudelaenia leucospodia	871	9	80	Hazard rate	Simple polynomial
Tumbezia salvini	101	7	80	Hazard rate	-
Myiarchus semirufus	69	6	60	Half normal	-
Phytotoma raimondii	370	6	100	Hazard rate	-
Campylorhynchus fasciatus	196	7	90	Hazard rate	-
Cantorchilus superciliaris	752	6	80	Hazard rate	-
Mimus longicaudatus	1578	10	70	Half normal	Cosine
Piezorina cinerea	780	7	80	Half normal	-
Sicalis taczanowskii	197	7	80	Half normal	Cosine
Rhynchospiza stolzmanni	440	6	60	Half normal	Cosine

Appendix 3. Covariate exploratory analysis

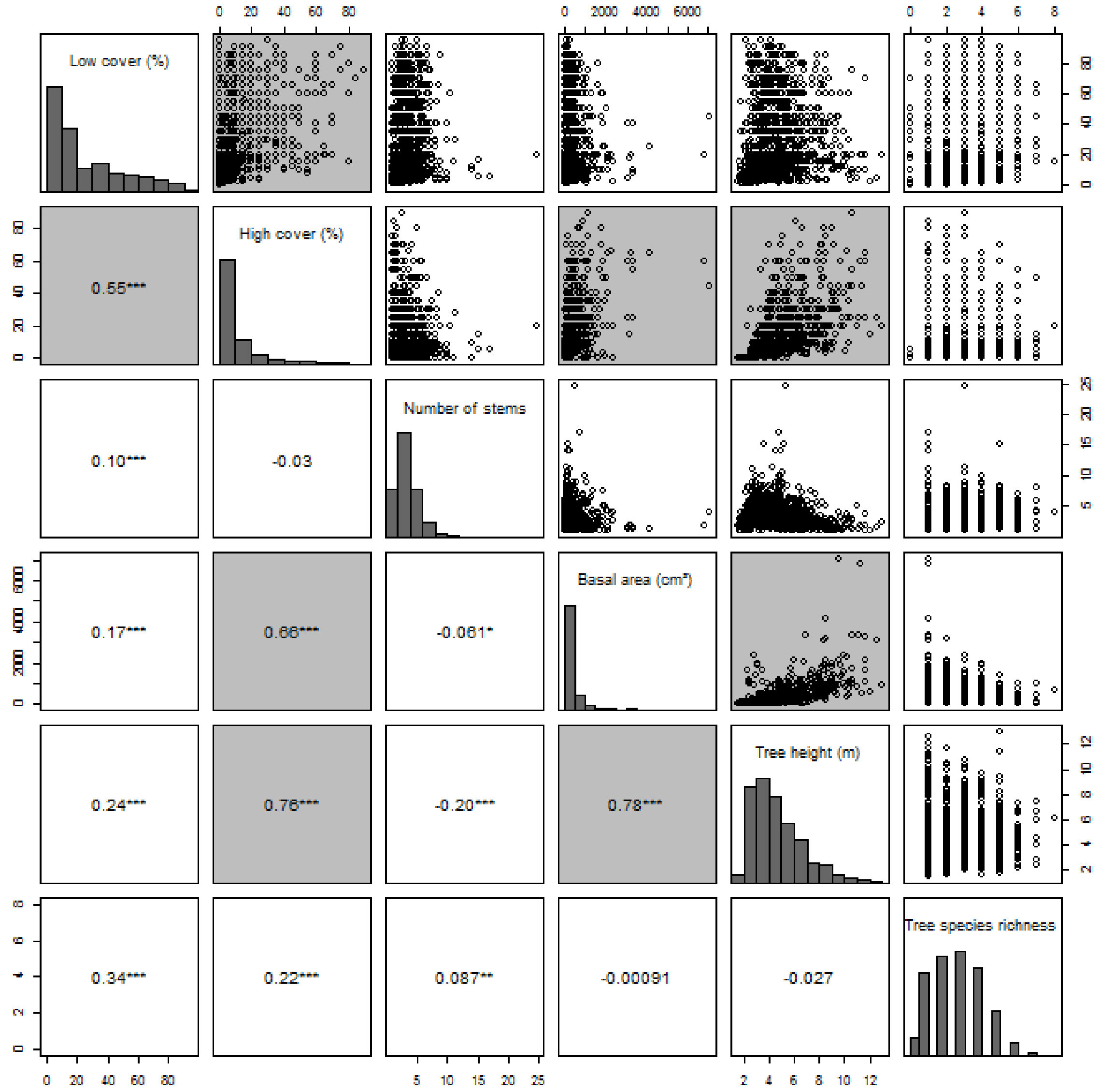
a). Perpendicular distance by aural and non-aural records; the blue line marks median distance.



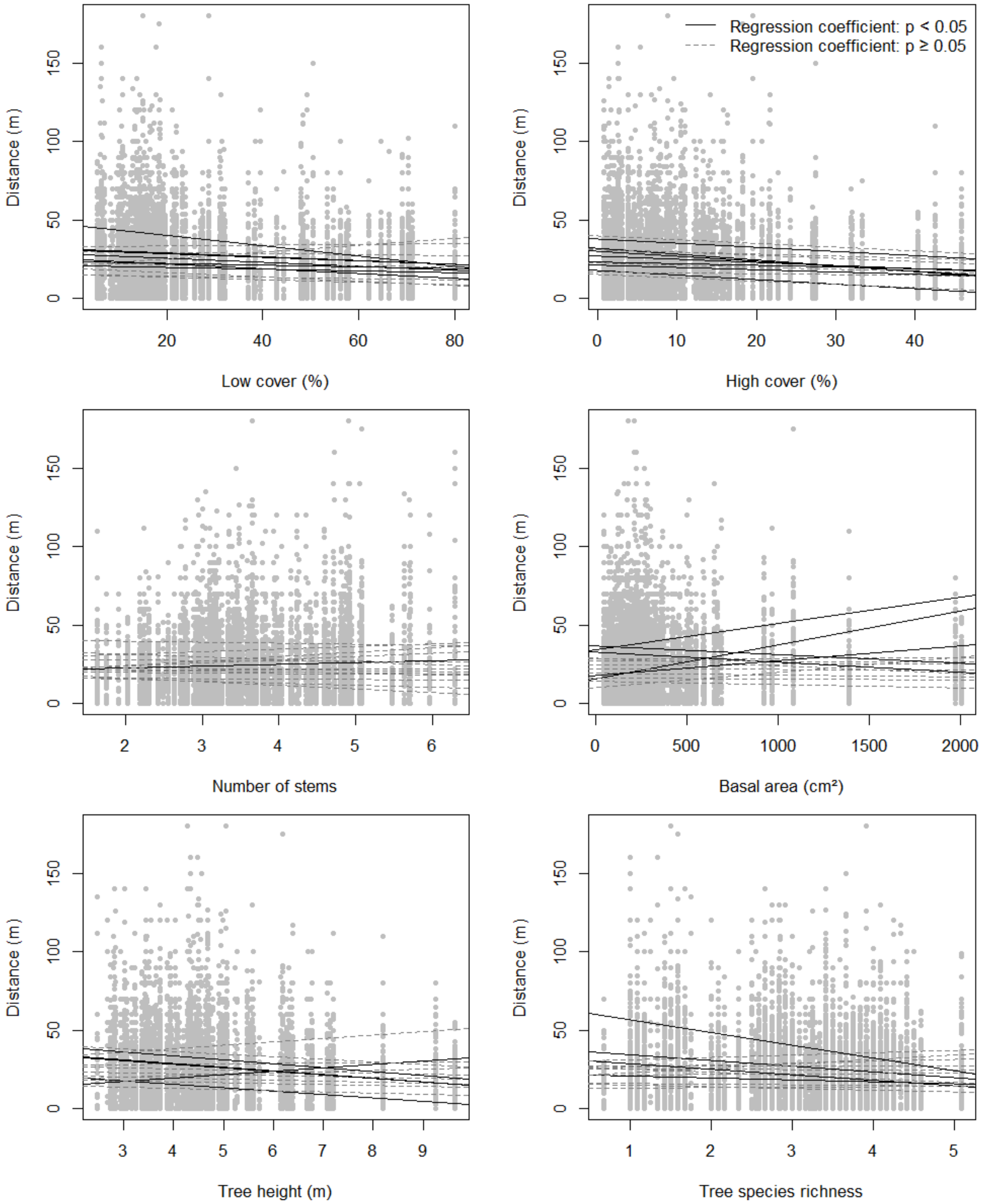
b). Percentage of heard records per species at each study site, plotted in chronological order of field surveys. Point area is proportional to sample size (see (l) for key), sites are only included where sample size is ≥ 10. Mean percentage ± standard deviation bar shown at right of each series.



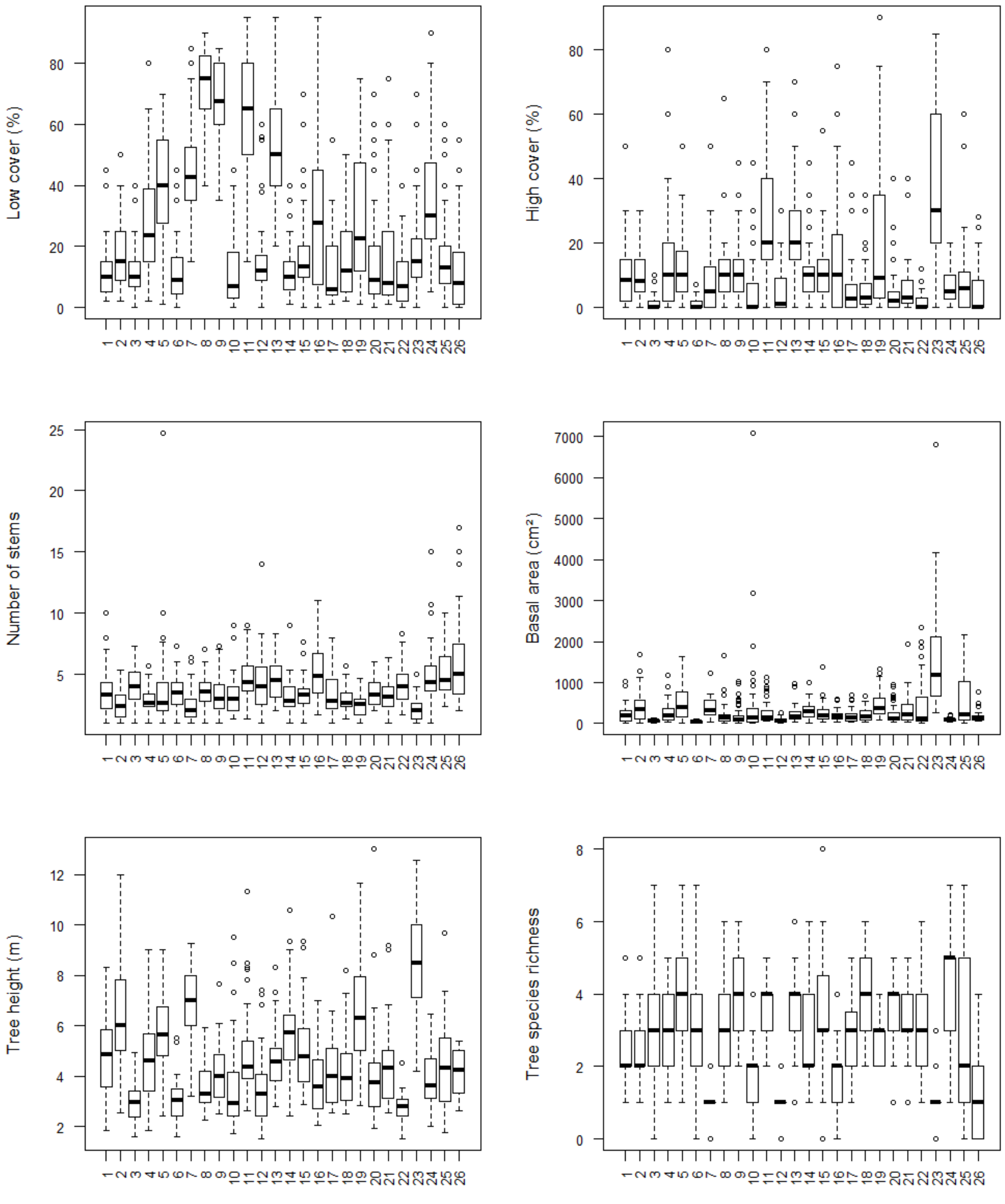
c) Correlations among potential habitat covariates. Lower diagonal shows spearman correlation coefficients (stars indicate significance as follows: *** $p \leq 0.001$; ** $p \leq 0.01$; * $p \leq 0.05$); diagonal panel shows distribution of covariate. Panels are shaded where correlations are significant ($p < 0.05$) and where coefficients indicate strong correlations ($r_s > |0.5|$)



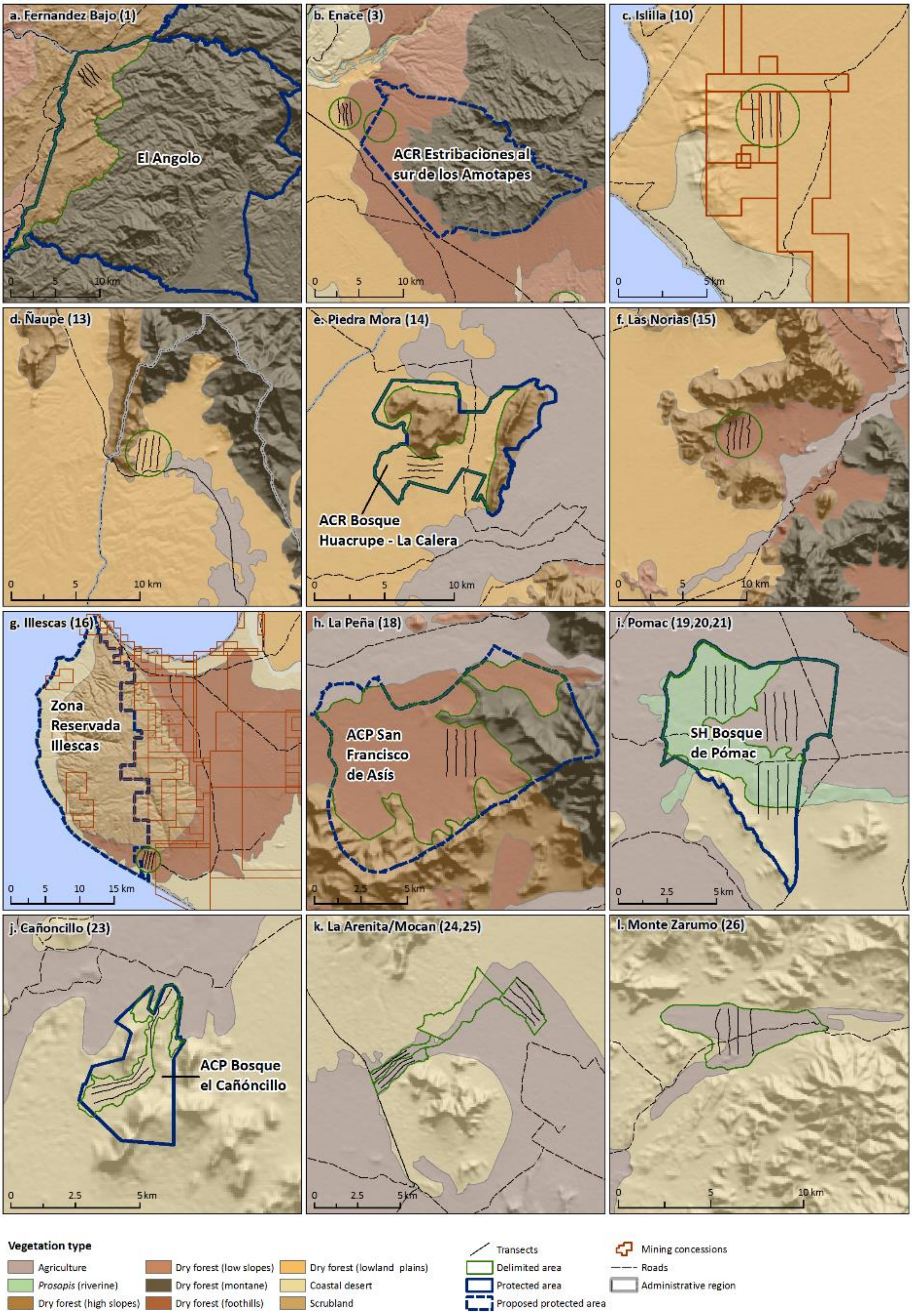
d) Effect of potential habitat covariates on distances recorded. Perpendicular distances recorded for birds along transects are plotted against six potential habitat covariates. Linear regression lines (and whether they are significantly different to zero) are shown for each bird species separately.



e) Variation of covariates across sites. Site numbers on x-axis follow those in Appendix 5 and Figure 3.2.



Appendix 4. Study sites showing areas used in population size case studies. See Figure 3.1 for location of sites (site numbers in brackets as in Figure 3.1). See Table 4.3 for full names of protected areas. Vegetation types follow MINAM (2012).



Appendix 5. Encounter rates (± standard error) expressed as groups km^{-1} for all records of all species across sites. See Figure 3.2 for location of numbered sites.

No.	**Name**	***Myrmia micrura***	***Forpus coelestis***	***Synallaxis stictothorax***	***Phaeomyias murina***	***Pseudelaenia leucospodia***	***Tumbezia salvini***	***Myiarchus semirufus***	***Phytotoma raimondii***	***Campylorhynchus fasciatus***	***Cantorchilus superciliaris***	***Mimus longicaudatus***	***Piezorhina cinerea***	***Sicalis taczanowskii***	***Rhynchospiza stolzmanni***
1	Tucillal	0.09 ± 0.09	1.90 ± 0.52	0 ± 0	0 ± 0	0 ± 0	0.09 ± 0.10	0 ± 0	0 ± 0	0.66 ± 0.45	1.04 ± 0.33	6.07 ± 1.30	0.28 ± 0.29	0.85 ± 0.32	1.90 ± 0.14
2	Fernandez Bajo	0.48 ± 0.19	1.55 ± 0.52	0.68 ± 0.29	0 ± 0	0.19 ± 0.19	0.19 ± 0.11	0 ± 0	0 ± 0	0 ± 0	0.68 ± 0.19	5.72 ± 0.94	0 ± 0	1.45 ± 0.29	4.07 ± 0.57
3	Enace	0 ± 0	0.96 ± 0.37	2.02 ± 0.34	3.07 ± 0.59	0.48 ± 0.36	0 ± 0	0 ± 0	1.82 ± 0.45	0 ± 0	4.32 ± 0.77	5.09 ± 0.61	2.02 ± 0.39	1.44 ± 0.23	0 ± 0
4	Lancones	1.47 ± 0.38	2.93 ± 0.54	3.98 ± 0.42	1.05 ± 0.25	2.62 ± 0.63	0.10 ± 0.11	0.31 ± 0.11	0 ± 0	0.21 ± 0.12	2.93 ± 0.59	8.48 ± 1.41	1.47 ± 0.51	0.42 ± 0.25	3.14 ± 0.35
5	Puerta Pulache	0.20 ± 0.11	1.09 ± 0.30	0.20 ± 0.11	2.59 ± 0.24	3.88 ± 0.27	1.59 ± 0.29	0.10 ± 0.10	0 ± 0	0.40 ± 0.16	1.39 ± 0.12	3.18 ± 0.18	0 ± 0	0 ± 0	1.29 ± 0.31
6	Pampa Larga	0.20 ± 0.11	0.80 ± 0.24	3.09 ± 0.35	1.69 ± 0.20	1.99 ± 0.34	0 ± 0	0.10 ± 0.10	0 ± 0	0 ± 0	3.09 ± 0.81	7.67 ± 1.10	2.69 ± 0.26	1.29 ± 0.22	0.30 ± 0.09
7	Progreso Bajo	0 ± 0	0.10 ± 0.10	5.46 ± 0.86	1.63 ± 0.66	4.31 ± 1.30	0 ± 0	0.86 ± 0.50	0 ± 0	1.53 ± 0.20	3.06 ± 0.15	4.21 ± 1.13	3.45 ± 0.78	1.82 ± 0.07	0.77 ± 0.32
8	Cruz de Caña	0.60 ± 0.20	0.30 ± 0.10	5.31 ± 0.69	2.90 ± 0.44	4.51 ± 0.53	0 ± 0	0 ± 0	0.10 ± 0.10	0.30 ± 0.19	5.61 ± 0.38	3.70 ± 0.40	7.71 ± 0.55	3.00 ± 0.82	3.60 ± 0.37
9	Sagrado Corazón	0.40 ± 0.16	0.79 ± 0.16	3.08 ± 0.91	5.66 ± 0.59	3.48 ± 0.30	0 ± 0	0.10 ± 0.10	1.49 ± 0.76	0 ± 0	4.37 ± 0.77	5.06 ± 0.61	6.26 ± 0.68	1.39 ± 0.47	4.77 ± 0.42
10	Islilla	0 ± 0	0 ± 0	4.86 ± 1.03	0 ± 0	1.78 ± 0.58	0 ± 0	0.50 ± 0.30	1.68 ± 0.66	0 ± 0	3.96 ± 0.77	1.98 ± 0.29	3.47 ± 0.76	0 ± 0	0 ± 0
11	Ancajima	2.59 ± 0.66	1.30 ± 0.34	4.98 ± 0.86	6.98 ± 1.26	3.69 ± 0.38	0.40 ± 0.28	0.20 ± 0.12	0.60 ± 0.11	1.50 ± 0.41	6.28 ± 0.73	6.08 ± 0.58	3.39 ± 1.01	0.30 ± 0.19	6.58 ± 0.49
12	Ñapique	0 ± 0	0.42 ± 0.18	6.88 ± 1.49	0 ± 0	0.85 ± 0.43	0 ± 0	0.53 ± 0.25	0 ± 0	0.95 ± 0.64	3.49 ± 0.89	1.38 ± 0.58	1.27 ± 0.42	0 ± 0	0 ± 0
13	Ñaupe	1.09 ± 0.38	2.28 ± 0.56	4.26 ± 0.56	9.12 ± 0.70	2.77 ± 0.58	2.48 ± 0.30	0.30 ± 0.10	1.68 ± 1.32	0.30 ± 0.10	5.55 ± 0.76	10.01 ± 2.10	1.88 ± 0.60	0.20 ± 0.11	4.46 ± 0.74
14	Piedra Mora	1.56 ± 0.16	1.95 ± 0.49	2.34 ± 0.53	0.88 ± 0.25	4.29 ± 0.96	0.39 ± 0.16	0 ± 0	0 ± 0	1.46 ± 0.61	1.76 ± 0.60	5.46 ± 1.20	5.17 ± 0.79	2.44 ± 0.34	3.71 ± 0.47
15	Las Norias	0.19 ± 0.11	0.97 ± 0.12	1.36 ± 0.44	4.87 ± 0.81	4.87 ± 0.80	0.39 ± 0.23	0.29 ± 0.19	0 ± 0	0.29 ± 0.10	1.56 ± 0.28	6.04 ± 1.27	3.70 ± 1.02	2.34 ± 0.46	3.70 ± 1.16
16	Illescas	0 ± 0	0 ± 0	6.55 ± 0.62	0 ± 0	1.59 ± 0.28	0 ± 0	0.10 ± 0.10	0.60 ± 0.34	0 ± 0	3.18 ± 0.43	1.49 ± 0.41	3.87 ± 0.41	0 ± 0	0 ± 0

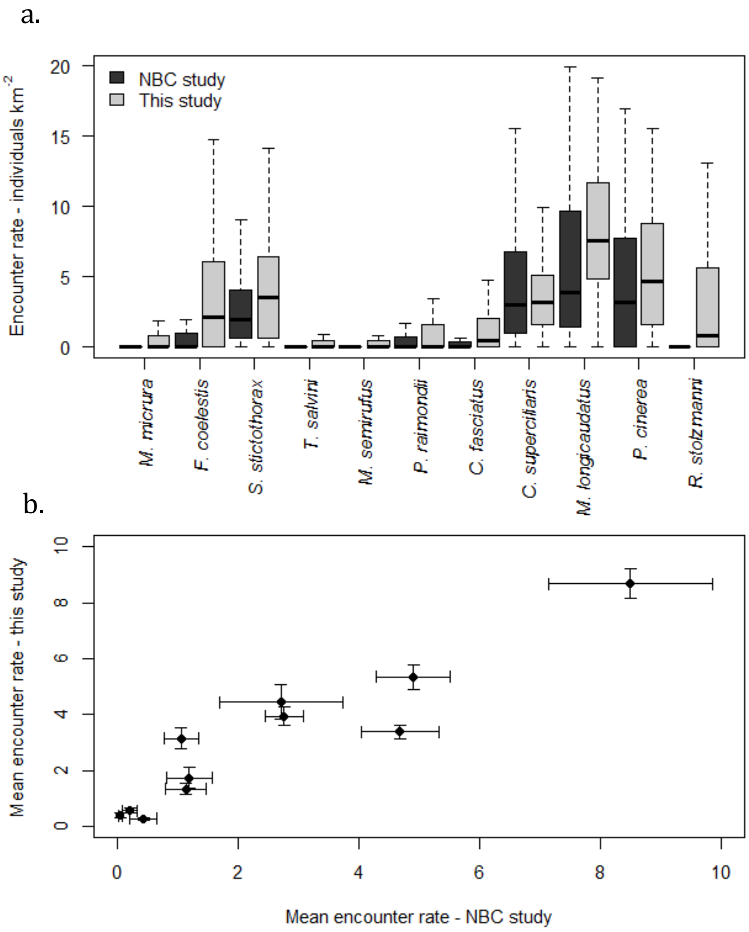
No.	Name	***Myrmia micrura***	***Forpus coelestis***	***Synallaxis stictothorax***	***Phaeomyias murina***	***Pseudelaenia leucospodia***	***Tumbezia salvini***	***Myiarchus semirufus***	***Phytotoma raimondii***	***Campylorhynchus fasciatus***	***Cantorchilus superciliaris***	***Mimus longicaudatus***	***Piezorhina cinerea***	***Sicalis taczanowskii***	***Rhynchospiza stolzmanni***
17	Pañalá	0.59 ± 0.25	0.10 ± 0.10	4.41 ± 0.48	1.86 ± 0.97	4.50 ± 0.58	0 ± 0	0 ± 0	0 ± 0	1.27 ± 0.33	3.33 ± 0.24	5.87 ± 0.58	6.66 ± 0.49	0.39 ± 0.28	1.37 ± 0.34
18	La Peña	0.10 ± 0.10	0.30 ± 0.19	1.09 ± 0.19	6.95 ± 0.99	8.44 ± 0.76	0.50 ± 0.25	0 ± 0	0 ± 0	0.10 ± 0.10	3.28 ± 0.41	4.47 ± 0.98	4.07 ± 0.59	0.10 ± 0.10	2.98 ± 0.20
19	Pomac - Poma III	0.50 ± 0.10	0.30 ± 0.19	3.69 ± 0.64	0 ± 0	5.78 ± 0.60	0.30 ± 0.10	0.30 ± 0.10	0.30 ± 0.30	1.89 ± 0.34	4.39 ± 0.81	10.37 ± 1.20	3.99 ± 1.04	0 ± 0	0 ± 0
20	Pomac - Zona Recuperada	2.09 ± 0.38	1.29 ± 0.34	2.28 ± 0.50	0 ± 0	4.47 ± 0.75	0.10 ± 0.10	0.10 ± 0.10	4.87 ± 1.12	1.19 ± 0.36	3.48 ± 0.75	13.61 ± 0.83	4.37 ± 1.02	0 ± 0	0 ± 0
21	Pomac - Salinas	0.90 ± 0.19	0.80 ± 0.43	2.99 ± 0.70	0.80 ± 0.33	5.38 ± 0.38	0.10 ± 0.10	0.30 ± 0.19	0.30 ± 0.30	2.19 ± 0.20	5.48 ± 1.05	10.07 ± 2.24	5.08 ± 0.69	0.30 ± 0.19	0 ± 0
22	La Viña	0.10 ± 0.10	0.40 ± 0.23	0 ± 0	0 ± 0	4.28 ± 0.82	0 ± 0	0 ± 0	0 ± 0	0 ± 0	1.89 ± 0.41	8.95 ± 3.22	6.46 ± 1.19	1.99 ± 0.54	1.19 ± 0.56
23	Cañoncillo	0 ± 0	0.78 ± 0.17	6.27 ± 1.12	0.49 ± 0.29	5.20 ± 1.06	3.53 ± 0.72	1.86 ± 0.19	0 ± 0	4.51 ± 0.20	1.96 ± 0.49	3.92 ± 0.25	0 ± 0	0 ± 0	0 ± 0
24	Mocan	0 ± 0	2.09 ± 0.37	0 ± 0	11.43 ± 1.20	4.07 ± 0.66	0 ± 0	0.22 ± 0.25	10.55 ± 2.46	0 ± 0	0.11 ± 0.11	8.90 ± 0.83	1.10 ± 0.33	0 ± 0	0 ± 0
25	La Arenita	0 ± 0	1.88 ± 0.34	0 ± 0	15.80 ± 6.40	2.27 ± 0.97	0 ± 0	0 ± 0	10.07 ± 2.38	0.89 ± 0.19	0.10 ± 0.10	12.24 ± 0.90	1.68 ± 0.30	0 ± 0	0 ± 0
26	Monte Zarumo	0 ± 0	0 ± 0	0 ± 0	8.22 ± 0.86	1.49 ± 0.11	0 ± 0	0.79 ± 0.33	4.46 ± 0.29	0 ± 0	0 ± 0	4.26 ± 0.29	0.40 ± 0.16	0 ± 0	0 ± 0

Appendix 6. Bird density estimates per site: (ind km^{-2}) ± standard error, sample size (in parentheses). '+' means species was observed at site but not on transect.

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

Appendix 7. Comparison of abundances over a seven-year period: NBC study (Villavicencio et al, 2006) and this study (2013) across all sites, showing a), variation and b), comparison of mean (± se) encounter rates by species.



Chapter 4

Extreme variation and complex correlates of local abundance – lessons from a range-wide, multispecies survey

1 Abstract

Understanding patterns and drivers of variation in abundance across species full ranges is crucial in conservation science and macroecology but remain little studied, especially in the tropics. It is generally expected that species will have few hotspots of high abundance within large areas of low abundance, with hotspots concentrated at geographical range centres. This study looked across 14 endemic birds of the Tumbesian region with a view to; a) identifying patterns in variation of abundance across sites; b) examining congruence of abundance hotspots across species and spatial autocorrelation of abundance within species; and c) assessing the nature and strength of environmental correlates (topography, habitat and human pressure) of abundance. Data were collected from 26 sites, separated by a maximum distance of c.600 km, in dry forest habitat, covering most of the species' ranges. Sites in this patchy habitat were selected randomly from strata derived from species distribution models and a 50 km grid. At each site, four parallel 2.5 km transects were used to evaluate bird abundance and habitat characteristics. Local abundance, or bird densities, was estimated using covariate Distance sampling methods. Abundance was compared across sites and by range core versus edge, relationships with environmental variables were examined using GAMs, and spatial autocorrelation was examined with multivariate Mantel tests. Although most species were recorded at most sites, abundance varied by one or two orders of magnitude across sites. 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 50 km. Sites of maximum abundance for individual species did not coincide – nine different sites held the highest densities of at least one species. The relationship between local abundance and environmental predictors was generally non-linear, with some evidence that current habitat measures were stronger predictors of abundance than human pressure. 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 some recommendations are offered, and regarding the need for multiple reserves to capture high local abundances of key species.

2 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). These 'hotspots' of high abundance tend towards the centre or multiple core areas of species' ranges with local abundance lower at the range margins (the abundance centre hypothesis: Rapoport, 1975; Brown, 1984; Hengeveld, 1990). Despite both 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), while 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). 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 local abundance can be predicted 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, this chapter has the following specific objectives:

- 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?

3 Methods

3.1 Site selection

A total of 26 sites were selected in dry forest and scrub habitat, below an altitude of 500 m, in northwest Peru (Figure 3.1) Given the size of the study area, 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, sites were randomly selected from three strata representing higher probabilities of species occurrences and 25 geographic strata across the study area. To identify the 'occurrence probability' stratum, species distribution models were built 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 a distribution model 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, in part, due to lack of alternatives (Merow et al., 2013). To create the geographic strata, a regular 50 km grid was drawn across the study area and the top ten cells were identified in terms of highest average model scores. Sites were randomly selected from 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 ten 50 km 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).

3.2 Field methods

All fieldwork was carried out from June to October 2013 by CD 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. A variable width transect method was used to estimate bird abundances, 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. Each transect was walked 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. Habitat characteristics were measured within 10 m radius circular plots at twelve points positioned 200 m apart on each transect. Features 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

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

where Popurban is the number of inhabitants of cities within 25 km; Poprural 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: 1: non-protected, 0.5: protected.

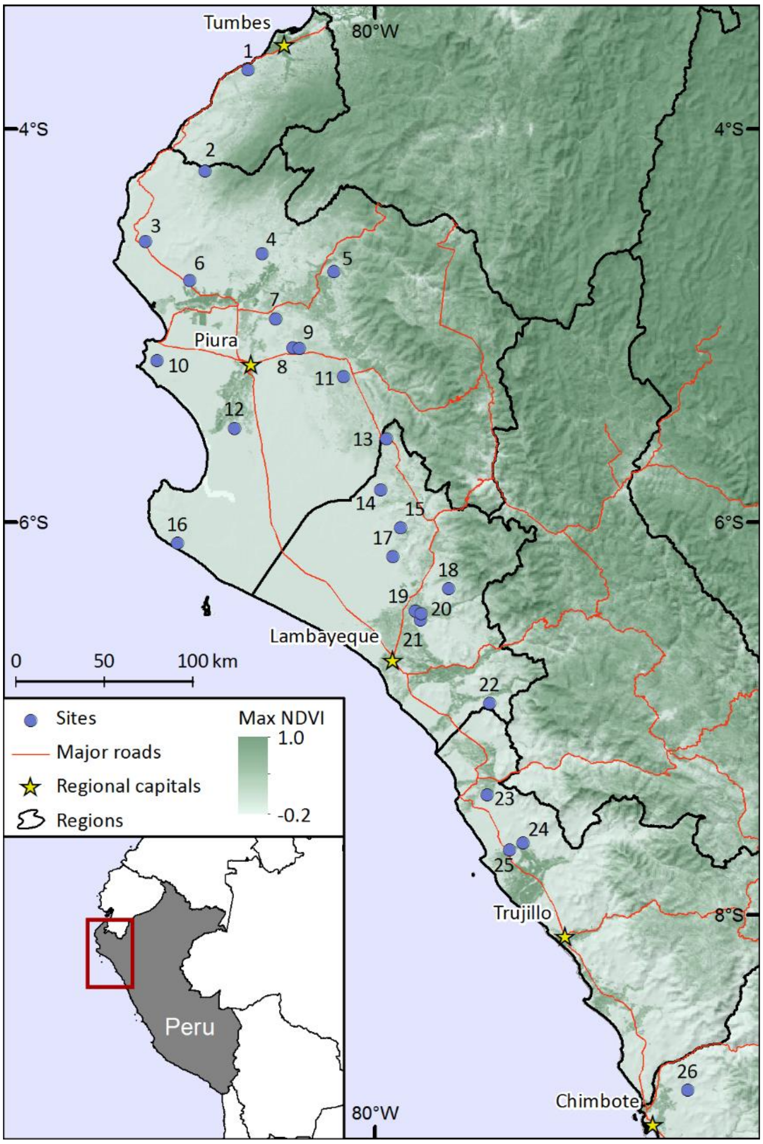


Figure 3.1. Study sites in northern Peru, with maximum NDVI values over the wet season (December to May) to illustrate extent of ground vegetation cover and desert/scrub areas. See Figure 3.2, Chapter 3 for key to site names.

3.3 Data analysis

Local abundance at sites was estimated using the multiple covariate engine of Distance 6.1 (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. Covariates were selected by assessing correlations between potential covariates, variation between sites, and their effect on the distances recorded per species. Detection functions with type of detection (heard or not heard) and habitat density (total number of stems) as covariates were trialled. 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.

Histograms were plotted of species densities across all sites and symmetry of the distribution was measured 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, species' ranges were represented as convex hulls constructed from post-1970 occurrence records from museum specimens and observations (following manual and automated validation). The coastline and upper altitudinal limits were used to exclude areas from each convex hull to further approximate range shape. Although convex hulls have their limitations (Rapoport, 1975), the method facilitates comparison between species, in that each range was constructed following a standardised method. Local abundance was compared 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.

To identify congruence of local abundance hotspots across species, sites holding maximum density and the highest three densities were identified for each species. To assess whether species' densities varied in similar ways across sites, Spearman's rank correlation coefficients were calculated for density between all species pairs at all sites ($n = 91$). A multivariate Mantel correlogram (Legendre & Legendre, 1998) was used to examine spatial autocorrelation of local abundance across sites for all species. First, distances between sites were grouped into seven 50 km distance bands between 0 and 350 km, with sample sizes of 34, 57, 71, 47, 36, 25 and 25, respectively (sample size per band was insufficient beyond this distance). A correlogram then plots each correlation between a similarity matrix of all species' densities (calculated with the Jaccard metric) and the matrix of geographical distances between sites in each band. Significance of correlations was evaluated using permutation tests. Spatial autocorrelation was also evaluated for each species separately, using Moran's I over five distance bands.

The nature and strength of ten environmental correlates of local bird abundance were evaluated. First, predictors were assigned 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 multiple 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. Generalised Additive Models (GAMs) were used to evaluate the linearity and relative strength of the relationship between each predictor and local bird abundances. First, an ordination based on species abundances at each site was performed using non-metric multidimensional scaling (NMDS; Legendre & Legendre, 1998; as implemented in R package, vegan Oksanen et al., 2015) in order to examine correlates of local abundance across the dry forest bird community as a whole. Each predictor was then modelled as a function of the site scores on both ordination axes simultaneously using a thin plate spline isometric smoother in R package mgcv (Wood, 2006) with varying numbers of smoother parameters. Deviance changes with respect to these increasing numbers of smoother parameters were examined as a way to approximate the complexity of the relationship between density and predictors. Predictors with more complex relationships were expected to show increases in explained deviance with increasing numbers of smoother parameters. Models were evaluated for fit, significance of smoother term and an appropriate number of knots using techniques suggested by Wood (2006). For models with a significant smooth term ($\alpha < 0.05$), predicted values were plotted as contours over the species ordination to visualise the relationship between the species' density and predictors. Species centroids, weighted by density values at each site, were plotted on the NMDS axes (Oksanen et al., 2015). R (R Core Team, 2014) was used for all statistical analyses and all significance tests were evaluated at $\alpha = 0.05$.

4 Results

4.1 Variation of abundance across species' ranges

A total of 7,505 bird encounters were recorded over the 26 transects for 14 species. Encounter rates averaged 28.7 individuals per km, equivalent to approximately 7 birds every 10 minutes at the average walking speed. Overall, non-zero local abundances ranged from less than 1 to over 3,000 individuals per km^2 (Table 4.1, see Appendix 6, Chapter 3). 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 4.1a-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 4.1).

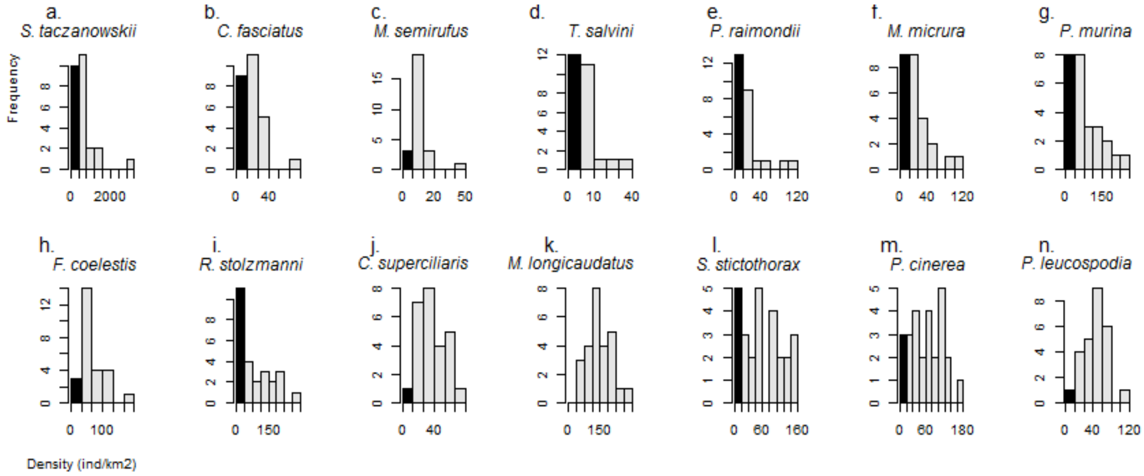


Figure 4.1. Distribution of species' local abundance at 26 sites, ordered by decreasing skewness. The first bar (black) shows zeros at sites, the following bars are of equal width in each histogram.

A second group (five species; Figure 4.1j-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 4.1). The presence of sites with zero density did not affect the groupings of the species' abundance distributions.

Table 4.1. 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

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 4.1). A significant positive correlation was found 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 4.1).

Different spatial arrangements of local abundance were found, with the highest species' densities not always occurring at the centres of their geographical ranges. Four species had significantly higher local abundances within the central areas of their ranges compared to the periphery (Figure 4.2, Appendix 1) while all the others showed no significant relationship. Two species showing significant relationships (Cinereous Finch *Piezorina cinerea* and Grey-and-white Tyrannulet *Pseudelaenia leucospodia*) were among the most abundant overall, and among those with highest overall presences at sites (Figure 4.1m-n, Table 4.1).

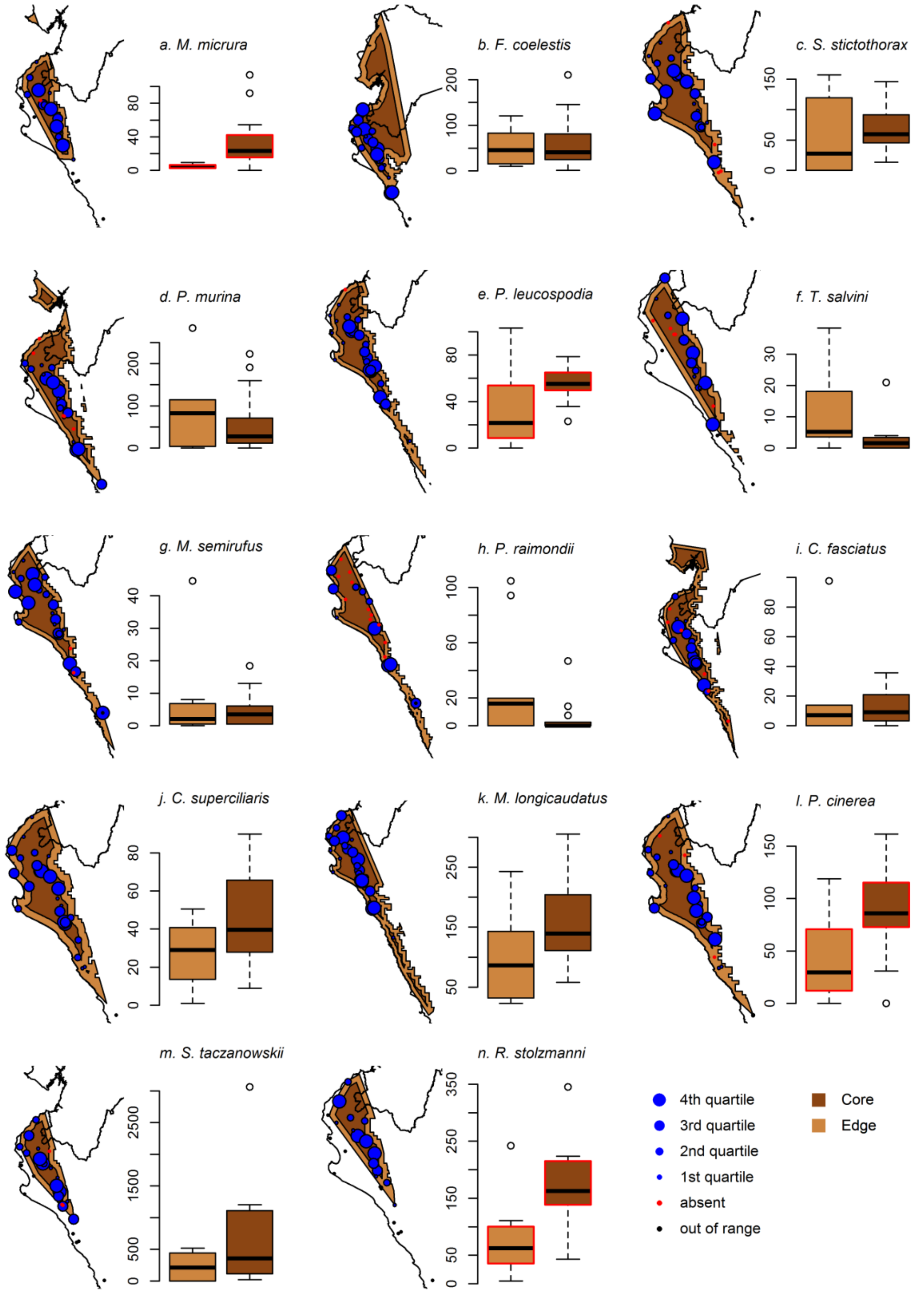


Figure 4.2. Variation in local abundance across species' ranges. Minimum convex polygons show core and edge areas (see methods) with abundance at sites expressed in quartiles to facilitate comparison. Boxplots show difference in abundance (individuals km^{-2}) between the two regions, those bordered in red are significantly different (α = 0.05) according to Wilcoxon two sample test.

4.2 Spatial autocorrelation in local abundances

Spatial autocorrelation in species' densities across sites was significant only at the smallest distance band of 0–50 km ($r_S = 0.18$, $n = 34$, $p = 0.003$). Correlation coefficients decreased with increasing distance between sites, but were weak for the remaining six distance bands, varying between 0.2 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 (Appendix 2).

4.3 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 (Appendix 3). Of 91 pairwise correlations between species' densities, 21 species' pairs were significantly correlated, but only ten correlation coefficients were > 0.5 (Figure 4.3). The highest correlation coefficient was 0.68, for Necklaced Spinetail *Synallaxis stictothorax* and Superciliated Wren *Cantorchilus superciliaris*, both of which occupy lower strata of the dry scrub. Local abundances of two species pairs had significant negative correlations.

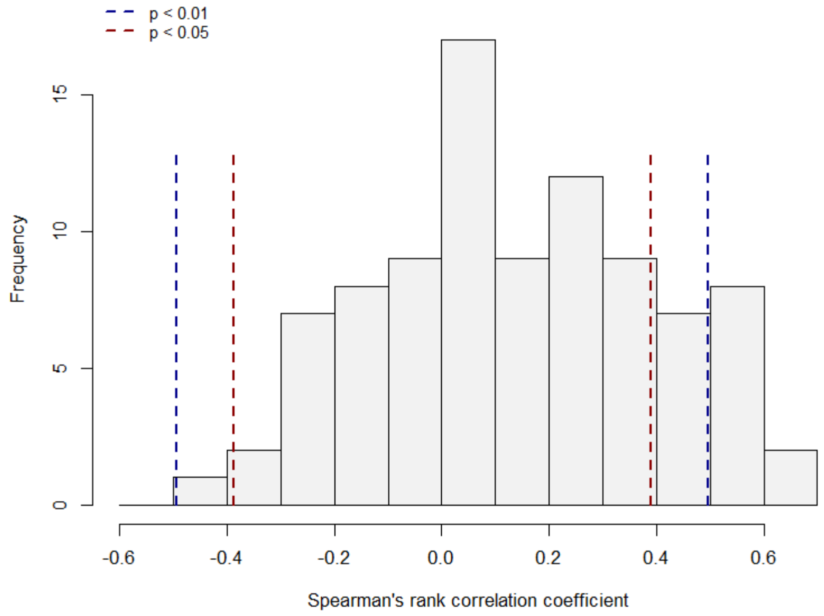


Figure 4.3. Frequency of Spearman's rank correlation coefficients for pairwise correlations between densities at 26 sites (n = 91). Red and blue lines show critical values of Spearman's correlation coefficient for p values corresponding to 0.05 and 0.01.

4.4 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 0.145. 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. Eight of the ten predictors were significantly related to densities, that is, GAMs showed significant smooth terms ($p < 0.001$ in all cases). Explained deviance varied from 55-75% when the maximum number of spline terms was employed Table 4.2). All relationships between predictors and density were non-linear with the exception of 'mean number of stems'.

Table 4.2. Complexity of relationship between predictors and bird densities represented by change in explained deviance with increasing number of smooth terms in GAMs. Approximate significance of smooth terms indicated as follows: * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$.

Predictor	**Link family**	**Deviance explained (rank)**			**Range:**
		3 smooth terms	**6 smooth terms**	**9 smooth terms**	**max - min (rank)**
Understorey cover	Gaussian	6.8% (9)	8.3% (9)	7.7% (9)	5.4 (9)
Tree height	Gaussian	43.0% (5)**	66.9% (1)***	65.6% (4)***	36.4 (4)
Mean no. stems	Gaussian	51.6% (2)***	51.6% (6)***	51.6% (8)***	0.0 (10)
Grass cover (presence)	Binomial	47.3% (3)***	49.6% (7)***	58.5% (6)***	32.0 (5)
Tree species richness	Gaussian	58.8% (1)***	60.2% (3)***	71.2% (3)***	16.0 (7)
Slope	Gaussian	44.0% (4)**	56.5% (5)**	62.6% (5)**	23.2 (6)
Altitude	Gaussian	16.6% (6)	60.0% (4)**	74.8% (1)***	66.7 (2)
Grazing pressure	Poisson	16.1% (7)***	47.2% (8)***	56.7% (7)***	49.3 (3)
Logging pressure (presence)	Binomial	5.7% (10)***	65.3% (2)***	74.8% (2)***	76.7 (1)
Human pressure	Gaussian	9.7% (8)	6.9% (10)	3.2% (10)	7.6 (8)

The non-habitat based predictors, 'altitude', 'grazing pressure' and 'logging pressure' showed the most complex relationship with density (Figure 4.4), with sharp gains in explained deviance as additional smoothing parameters were added. This group of predictors also had the largest range between minimum and maximum explained deviance with increasing numbers of parameters. Explained deviance was more stable with increasing smoothing parameters in 'tree height', 'tree species richness', 'grass cover' and 'grazing pressure' (Table 4.2). Neither 'understorey cover' nor 'human pressure' showed a significant smooth term with any number of splines.

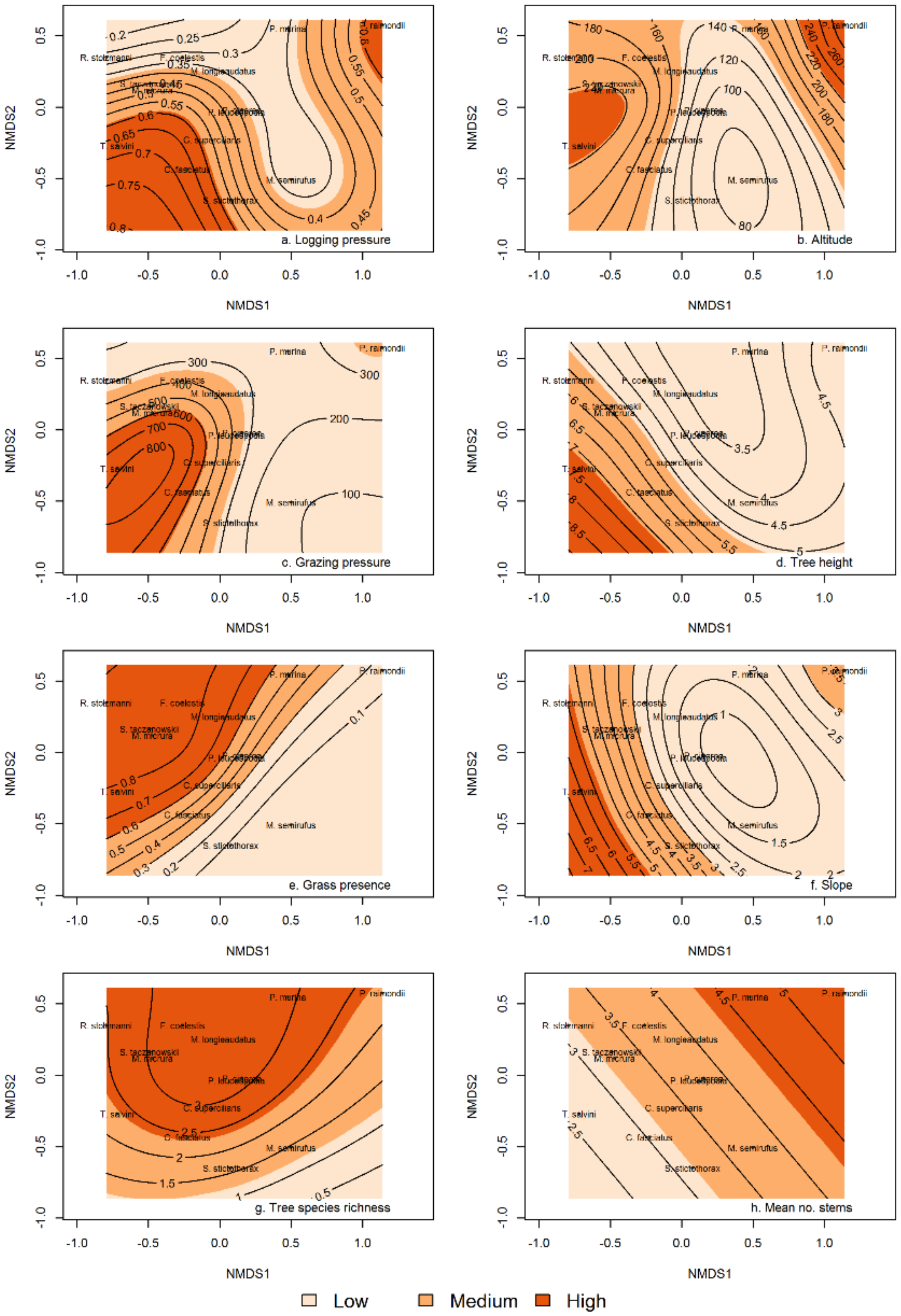


Figure 4.4. NMDS ordination (stress = 0.15) based on species densities across 26 sites with fitted GAM surfaces (using six spline terms for each plot) representing smooth trends between species densities and habitat-based, topographic, and pressure-related predictors. GAM surfaces were classified into three equal-sized groups of predicted values (low, medium and high) to facilitate interpretation. The plots are ordered according to decreasing complexity.

5 Discussion

5.1 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 the whole range of species (Samis & Eckert, 2007). In general, 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 species with niche positions at one extreme 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 4.4).

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 'marginal' or 'central' rather than geographically 'marginal' or '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 certain drivers of density that acted on different species in similar ways might have been expected, but this was not the case leading to the conclusion that determinants of local density are generally distinct for each species. A completely random sampling scheme, as opposed to that used in this study, may have increased the congruence somewhat between species. However, the sampling scheme made the majority of the occupied habitat available for selection (Figure 3.1, Chapter 3), and includes a significant gradient across habitat quality. This may be reflected in the very wide range of densities found across sites for each species. Furthermore, from a conservation perspective, sites of interest to conserve, are those that hold the largest parts of species' populations (Winston & Angermeier, 1995) rather than sites in the tail of the abundance distribution.

Variation in local bird abundances covaried in a linear way with just one of the predictors – 'mean number of stems'. 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 predictors. Therefore, factors such as 'mean number of stems', 'grass cover', 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 predictors than for habitat predictors. 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.

5.2 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. I 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 < 50 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 sites being suggested 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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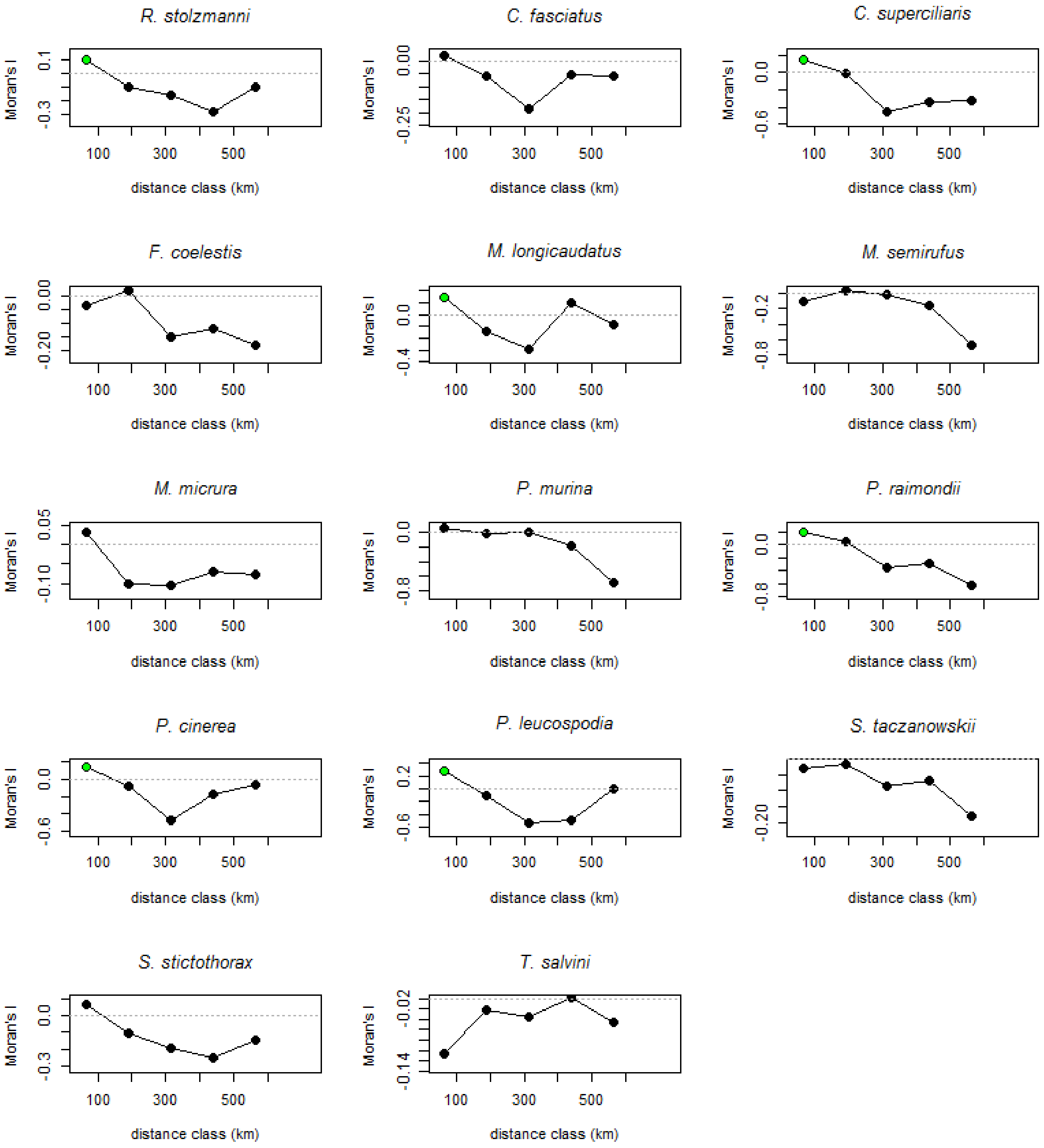
7 Appendices

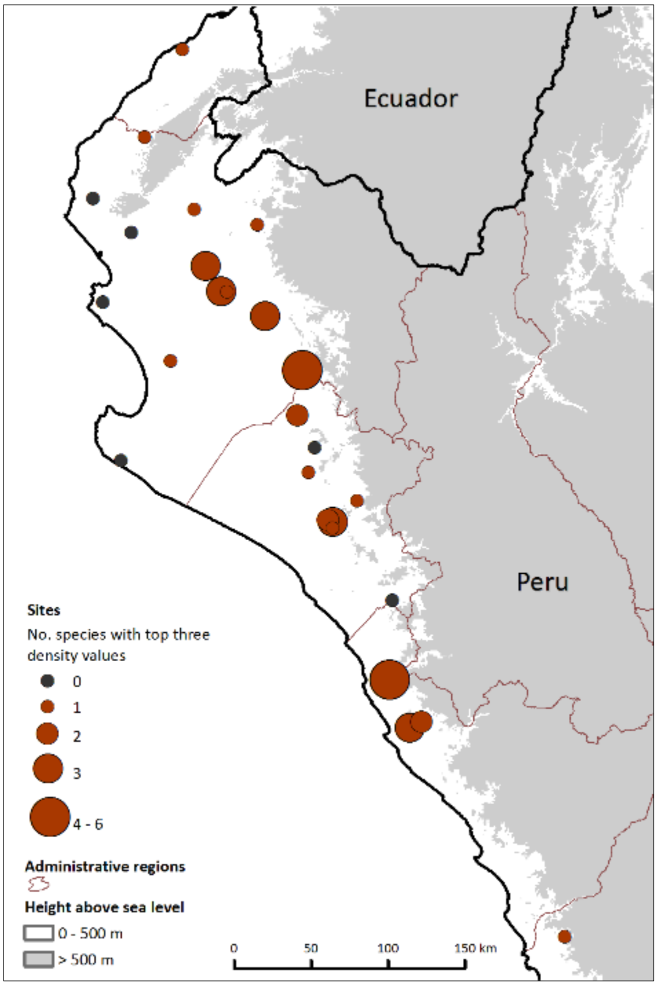
Appendix 1. Wilcoxon two sample tests between local abundance in centre and edge of species' ranges

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*	66 (10,13)	0.976	-4.5
Necklaced Spinetail *Synallaxis stictothorax*	59 (12,13)	0.313	31.8
Mouse-coloured Tyrannulet *Phaeomyias murina*	60 (6,17)	0.55	-54.7
Grey-and-white Tyrannulet *Pseudelaenia leucospodia*	41 (12,14)	0.027	33.6
Tumbes Tyrant *Tumbezia salvini*	53 (5,14)	0.102	-3.6
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*	43 (6,17)	0.596	1.9
Superciliated Wren *Cantorchilus superciliaris*	42 (10,15)	0.071	10.6
Long-tailed Mockingbird *Mimus longicaudatus*	38 (7,19)	0.107	53
Cinereous Finch *Piezorina cinerea*	36 (12,13)	0.024	56.4
Sulphur-throated Finch *Sicalis taczanowskii*	27 (10,9)	0.152	144.4
Tumbes Sparrow *Rhynchospiza stolzmanni*	32 (6,12)	0.743	62.4

Appendix 2. Spatial autocorrelation between density estimates over five distance bands (66, 190, 314, 439, 563 km) with n = 126, 120, 55, 17, 7 per band, respectively. Green points represent significant Moran's I values ($p < 0.05$) as evaluated through permutation tests.



Appendix 3. Sites holding species' top three density values.



Chapter 5

The relationship between occurrence modelling and abundance estimates

1 Abstract

Species abundance metrics are cornerstones of conservation planning, in fields such as establishing extinction risk, priority areas and harvest models. However, abundance data are scarce and costly to obtain, especially when compared to data on species' presence and absence. A growing field in conservation ecology relates such occurrence data to environmental gradients in models that predict species' distributions. Recently, an increasing number of studies have found positive relationships between occurrence model predictions and abundance estimates, with applications of this relationship including population size estimates and priority habitat selection. This chapter first reviews recent literature on using occurrence models to predict abundance, highlighting commonalities and challenges. Then, a case study, addressing certain challenges identified above, aims to establish a working relationship between occurrence and abundance in order to estimate population sizes. Local abundance estimates were obtained from range-wide surveys for 14 Neotropical bird species, taking into account detectability through distance sampling. Relationships were modelled between abundance estimates and relative probability of occurrence, obtained from four different distribution modelling techniques. Eleven of 14 species showed significant positive correlations between abundance and occurrence for at least one technique. Relationships were modelled using hierarchical logistic regressions with varying numbers of parameters, allowing for non-linearities, for eight species and used to estimate global population sizes. Differing model predictions to abundance estimates are discussed with relation to the scale and type of predictor variables, and site level pressures.

2 Introduction

2.1 The relationship between occurrence and abundance

The distribution and abundance of animals can be considered different aspects of the same 'problem' in ecology (Andrewartha & Birch, 1954). For instance, distribution can be defined in terms of net growth rate or other demographic metrics related to abundance (Lawton, 1993; Holt et al., 1997). Abundance, therefore, is an inherent ingredient of any relationship between a species' distribution and its environment, or niche dimensions. To date, models of such relationships have been dominated by environmental conditions and presence/absence distribution data (e.g. Guisan et al., 2013). Abundance, however, is a key component of conservation-related research, including protected area selection, harvest models and setting conservation priorities (Rodrigues et al., 2006), yet is a scarce and costly data resource (Marsden & Royle, 2015). If a link can be established in the relationship between those factors controlling a species' distribution and those factors controlling a species' abundance, the growing suite of methods and body of research invested in the former may provide more efficient methods for obtaining estimates of the latter.

Since 2001, at least 21 studies[1] have specifically investigated the question of whether abundance can be predicted from species distribution models using presence only data (Table 2.1). Using a variety of methods, the articles compare predictions of relative probability of occurrence with independent measurements of abundance. A brief review of these papers is provided below as a manner of introducing a case study exploring this topic in the Neotropics. Related studies have examined the relationship between abundance and occupancy or resource selection functions (Kunin, 1998; Royle & Nichols, 2003; Conlisk et al., 2009; Duff et al., 2012; Clare et al., 2015; Boyce et al., 2016) but are not considered here.

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[1] A literature search was performed in Scopus and Google Scholar, using combinations of the key terms, 'abundance', 'species distribution modelling', 'habitat suitability model', 'niche model' and 'density estimate'. The search was set to coincide with the rise of species distribution modelling methods (i.e. 2000 onwards, Figure 2.1, chapter 2).

2.1.1 Methods used to investigate occurrence – abundance relationships

Two broad types of comparison have been performed: 1) Relative probability of occurrence from species distribution models, built from independent occurrence points and environmental layers, was compared to abundance estimates at sites (17 studies); and 2) both abundance and probability of occurrence were modelled over the same set of sites with the same set of predictors, and model outputs compared (4 studies).

Most studies were based on small numbers of species (median = 3), but ranged from 1–243, with four including species from more than one taxonomic class or order (birds, reptiles, amphibians, mammals, arthropods and plants). Just over half the studies were based on data collected in Europe (11), five were from North America/Mexico, and two each from Australia and Asia. The Neotropics were only represented by a single species (Jaguar *Panthera onca*) from Central and South America (Tôrres et al., 2012). Only four studies specifically included data from the entire range of the species, implying that neither the full range of density values, nor the full range of the environmental conditions within its niche were taken into account. Yañez-Arenas et al., (2014), in a study of simulated species data, found that the sampling protocol, and whether the data came from the species' whole range, was a crucial factor in whether a relationship was found or not. Study extents ranged from 400 to 20,000,000 km^2, with pixel size ranging from 50 to 50,000 m. In one case, pixel size was set to coincide with a species' home range (Yañez-Arenas et al., 2012).

Most studies used just one method for building the occurrence model, with Maxent (9 studies) and Generalised Linear Models (GLM; 7) the most frequently used methods. Only three studies used more than one method (Oliver et al., 2012; Tôrres et al., 2012; Carrascal et al., 2015). A novel method, proposed specifically to investigate the occurrence-abundance relationship, uses the distance to the environmental niche centroid (Yañez-Arenas et al., 2012), similar to distance-based distribution modelling methods. The most frequent predictor types in models were climate (17 of 21 studies), topography (14), habitat (12) and soil (5). Other predictors included distances to landscape features such as rivers. Just over half the studies (11) included predictors that could potentially separate the realised and fundamental (potential) niche (Hutchinson, 1978), but only in one case was it part of the study design (Jiménez-Valverde et al., 2009). These latter predictors included vegetation indices (e.g. NDVI, coinciding temporarily with abundance data as oppose to long term averages), distance to urban areas, land use categories, such as agricultural areas, anthropogenic disturbance, such as logging (Pearce & Ferrier, 2001), and biotic interactions in two studies (Nielsen et al., 2005; Gutiérrez et al., 2013).

Abundance data came mainly from methods measuring encounter rates, for example, counts along transects or nest surveys (14 studies), percentage cover for plants (4), or density as simple counts per area, uncorrected for detectability. Only four studies took detectability into account in abundance estimations in some form, either using distance sampling (Legault et al., 2013); camera trap capture-recapture data (Tôrres et al., 2012); survey metrics (e.g. number of observers; Johnston et al., 2015); or two band transects (Carrascal et al., 2015). Indirect or qualitative measures of abundance were used in two cases (Real et al., 2009; Bradley, 2016). Abundance data was nearly always compiled from multiple surveys, often from different projects and over multiple periods of time, with a maximum span of 17 years (VanDerWal et al., 2009).

Studies compared occurrence and abundance estimates using either one or both of regression (17) and correlation (11 cases) analyses. Several studies performed comparisons with and without zeros in data sets as a way of evaluating whether relationships were overly influenced by differences in model predictions at occupied and unoccupied sites (Pearce & Ferrier, 2001). Regression analysis included logistic and generalised additive regression (GAM); quantile regression was used in four studies given that a triangular relationship was hypothesised.

2.1.2 Results of previous studies

Of the 21 studies listed, 14 concluded that a relationship existed between occurrence and abundance estimates. Further, five studies used the relationship to infer population sizes or establish priority habitats. However, the remaining seven studies found mixed results or non-significant relationships and concluded that factors controlling distribution are different to those controlling abundance. Both linear and non-linear relationships were found in those studies reporting positive relationships between occurrence and abundance. A triangular relationship, a result of at least four studies, suggests that occurrence models can predict maximum densities (VanDerWal et al., 2009; Tôrres et al., 2012; Carrascal et al., 2015; Muñoz et al., 2015) but that at some sites, densities are limited by factors not included in the model. Jiménez-Valverde (2009) specifically tested whether separate occurrence models for potential and realised niches showed different relationships with abundance but found poor evidence for either. Real et al., (2009) found that the strength of the relationship between occurrence predictions and abundance for Iberian Lynx *Lynx pardinus* over a 35-year period of range contraction decreased in strength in recent years, suggesting that proximate factors limiting lynx abundance were not included.

Nine studies investigated species traits or environmental factors affecting the strength or residuals of the relationship between occurrence and abundance. Abundance was underestimated in species with narrow habitat breadths and large variabilities in abundance (Carrascal et al., 2015), and overestimated with increasing agricultural intensity over the range of the Corncrake *Crex crex* (Fourcade et al., 2013). Marine birds' vulnerability to food availability, as measured by foraging ecology, increased with the strength of the relationship between climate-based occurrence model and abundance (Russell et al., 2015). Nielsen et al., (2005) obtained mixed results, with a positive relationship in one of two species tested, and suggested that differing life histories and scales of measurement of predictor data are important in determining relationships. However, the resolution of the model, that is, the scale of the environmental variables, did not appear to affect the reported outcome overall, although the extreme heterogeneity of the data set (e.g. in extent and numbers of presence points) and small sample size make formal analysis difficult. A large range in pixel size was reported for studies reporting both successful and unsuccessful relationships (50-50,000 m, 200-50,000 m respectively).

2.2 Objectives

Although the above literature shows some promising results and evidence for a positive relationship exists between occurrence and abundance, further research is needed to unravel critical aspects enabling confident use of this relationship in conservation, particularly in the Neotropics. These include effects of changes in abundance over time (where abundance is from multiple surveys), detectability between sites, the effect of using subsets of range-wide data, the effect of including predictors of the realised niche of species, and exploration of correlates of the strength of the relationship, among others. This study attempts to address some of these challenges by using data collected across the entire ranges of 14 dry forest birds in a poorly studied Neotropical habitat over a single period of time, with abundance estimated taking into account detectability.

This chapter explores the relationship between relative probability of occurrence, derived from presence/background niche modelling and bird abundance, derived from field studies using distance sampling. Specifically, it will attempt to:

- test for a relationship between density and model predictions
- build a suitable regression model where relationships are established
- explain where model predictions differ from field data using species- and site-level factors
- estimate species' global population sizes for key species using the regression models

Table 2.1. Outcome of studies investigating the relationship between occurrence model predictions and abundance

Abundance data[2] **abundance metric – species – no. sites (country)**	**Occurrence model[3]** **method (predictors) – extent – pixel**	**Relationship found - comparison method[4]**	**Correlates of relationship**
transect-ER - arboreal marsupials – 792 quadrat – reptiles – 752 cover – plants - 667 (Australia)[5]	GLM* (climate, topography, soil, habitat, disturbance, spatial) - no extent - 200 m	89% of species: all sites 18%: occupied sites - COR	
quadrat - Bracken *Pteridium aquilinum* – 296 (USA) quadrat-ER - Moose *Alces* 191 (Canada)[6]	GLM (soil, topography, habitat, snow depth, disturbance) – 35 km^2 / 13 000-km^2	1 of 2 species: occupied sites - COR	
pitfall trap-ER - 48 arthropods -67 (Azores)[7]	ANN (climate, topography, land-use, spatial) – c.400 km^2 - 500m	17% of species: climate only 4%: land-use model - COR	+ve: habitat distribution, movement capacity -ve: dependence on limiting resources
indirect/ER - Iberian Lynx *Lynx pardinus* – 323 transects (ER) - Rabbit *Oryctolagus cuniculus* – 397 (Spain)[8]	GLM (climate, topography, lithology, disturbance, spatial)- 516,700 km^2 - 10 km	Yes - COR	-ve: range contraction
transects-ER/quadrat - 59 birds, 4 amphibian, 6 reptiles – no. sites not given (Australia)[9]	MAX (climate, habitat) – c. 9,000 km^2 - 80 m	84% of species - LM, QR	
transect-ER -10 birds, 10 butterflies – 1941 (UK)[10]	ANN, GAM, MAX, RF (climate, habitat) - c.200,000 km^2 - 2000/1000 m (birds /butterflies)	80% butterflies 100% birds - COR, LME	
capture-recapture - Jaguar *Panthera onca* - 37 (Central, South America)[11]	BCL, MD, DOM, MAX, CTA, RF, GBM, MARS, MDA, ANN, GARP (climate, topography) - c.20,000,000 km^2 – 4000 m	Yes, in 2 models - LM, QR	No effect: model AUC
transects-ER White-tailed deer *Odocoileus virginianus* – 28 (Mexico) [12]	DC (MAX) (climate, topography, habitat, land use) - 10,000 km^2 – 1000 m	Yes, 1 site only - LM, SAR	
transect-ER - 61 butterflies – 14 (Germany)[13]	MAX (climate) - 31,250 km^2 - c.1000 m	8% of species – COR	

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[2] Abundance metrics: ER-encounter rate; D- density

[3] *Abundance and occurrence modelled over same sites. Occurrence models: ANN- artificial neural networks; BCL-bioclim; BRT- boosted regression trees; CRS- climate response surface; CTA-classification tree analysis ; DC-distance to niche centroid; DOM-domain; GAM- generalised additive model; GARP- genetic algorithm for rule set production ; GBM- generalised boosting models; GLM- generalised linear model; MARS- multivariate additive regression spline; MAX-maxent; MD- mahalanobis distance ; MDA- mixture discriminant analysis; RF- random forests.

[4] Comparison methods: COR: correlation, GAM: generalised additive model, GLM: generalised linear model, LM: linear model, LME: linear mixed effects model, QR: quantile regression, SAR: spatial autoregression

[5] (Pearce & Ferrier, 2001)

[6] (Nielsen et al., 2005)

[7] (Jiménez-Valverde et al., 2009)

[8] (Real et al., 2009)

[9] (VanDerWal et al., 2009)

[10] (Oliver et al., 2012)

[11] (Tôrres et al., 2012)

[12] (Yañez-Arenas et al., 2012)

[13] (Filz et al., 2013)

Abundance data[2] **abundance metric – species – no. sites (country)**	**Occurrence model**[3] **method (predictors) – extent – pixel**	**Relationship found - comparison method**[4]	**Correlates of relationship**
population size - Corncrake *Crex crex* – 38 countries (EU)[14]	MAX (climate, habitat, topography, distance to wintering area, NDVI) - 3,980,000 km^2 - c. 3500 m	Yes, R^2: 40% - LM	-ve: agricultural intensity
transects-ER - Butterfly *Parnassius apollo* - 90 sites (Spain)[15]	GLM* (climate, topography, habitat, host species) - 17,050 km^2	Yes - COR	
transect-ER/D, 3 parakeets *Cyanoramphus saisseti*, *Eunymphicus cornutus*, *Eunymphicus uvaeensis* - 39 (New Caledonia)[16]	MAX (climate, topography, habitat, soil, distance to forest) - 18,500 km^2 – 50 m	Yes - LM	
cover - 243 vascular species – 10,996 (France)[17]	GLM* (climate, soil) - 550,000 km^2	Yes - COR	
sett count - Badger *Meles meles* (Republic of Ireland)[18]	GLM (topography, soil, habitat, distance to river, land use, spatial) - 49,000 km^2 - 100 m	Yes - LM	
density - hypothetical species (different sampling strategies)[19]	DC (climate) c.2,000,000 km^2 - c.1400 m	No (mixed results) - GAM	+ve: random sampling, sample size
transect-D - 21 terrestrial birds - 437 (La Palma)[20]	MAX, BRT (topography, habitat, disturbance, spatial) - 706 km^2 - 500 m	90-100% of species – COR, QR	+ve: habitat breadth; -ve: variability in abundance. prevalence, regional maximum density
eBird-ER - 6 waterbird spp – (USA)[21]	BRR* (topography, habitat, survey effort, land cover) - 420,000 km2	No (non linear) - COR, GAM	
no. pairs - Bonelli's Eagle *Aquila fasciata* - 961(Spain)[22]	GLM (climate, habitat, topography, disturbance, spatial) - 87,600 km^2 – 10,000 m	Yes (occupied/unoccupied) – COR, QR	
no. pairs - 18 seabirds – 960 (Europe)[23]	RSM (climate) - 107,300 km^2 - 50,000 m	50% of species – LME, GLM	+ve: vulnerability to food availability
burrow count - Bolson tortoise *Gopherus flavomarginatus* – 22 (Mexico)[24]	DC (climate, topographic) - c.6000 km^2 – 1000 m	Yes – LM (10 regression methods)	
cover/indirect - 15 invasive plants (USA)[25]	MAX (climate) -50,000 m	No (compared occurrence models with high/low abundance presence points)	

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[14] (Fourcade et al., 2013)
[15] (Gutiérrez et al., 2013)
[16] (Legault et al., 2013)
[17] (Van Couwenberghe et al., 2013)
[18] (Byrne et al., 2014)
[19] (Yañez-Arenas et al., 2014)
[20] (Carrascal et al., 2015)
[21] (Johnston et al., 2015)
[22] (Muñoz et al., 2015)
[23] (Russell et al., 2015)
[24] (Ureña-Aranda et al., 2015)
[25] (Bradley, 2016)

3 Methods

3.1 Relationship between field-based density estimates and model-based predictions

Density (measured as individuals km^{-2}) was estimated from field surveys at 26 sites using distance sampling (see Chapter 3). A measure of relative probability of occurrence was estimated at a 1 km resolution using four different presence only or presence/background modelling methods, as well as a consensus model consisting of a weighted average of all four (see Chapter 2). Each model output (four modelling methods and a 'consensus' model) was averaged over a 3 x 3 km grid at each field site (see Figure 3.2 in Chapter 3), representing the area where the transects were implemented in the field. To identify significant relationships between density estimates and model predictions, Spearman's rank correlation analyses were implemented for each species and each modelling method.

To investigate further the form of the relationship between model output and density with a view to predicting abundance, regression models were built for those species showing significant correlation coefficients between the consensus model and density estimates. The type of regression analysis employed depends on the kind of data being analysed. Although both density and the species distribution model can be considered as random variables, a Model II regression (e.g. ranged axis regression) is not necessary when the purpose is prediction rather than estimating parameters (Legendre & Legendre, 1998). In previous studies (Table 2.1), 10 of 21 studies used regression techniques to investigate this relationship. In this study, the response variable, species abundance, is bounded at the lower limit by zero and at the higher limit by a carrying capacity set by environmental variables which may be further limited by biotic interactions (e.g. competition) or a disturbance process. A relationship between abundance and model output is hypothesised to be monotonically increasing, imposing a further requirement on the type of regression to be used. Finally, since the species distribution model outputs do not represent absolute probability of occurrence, rather a relative probability (given the lack of true absences in the modelling methods), the line of fit may not necessarily pass through the origin, justifying the inclusion of intercepts in the models. Linear regression, including polynomial terms, is not suitable as lower limits are not imposed, and functions are not necessarily monotonic.

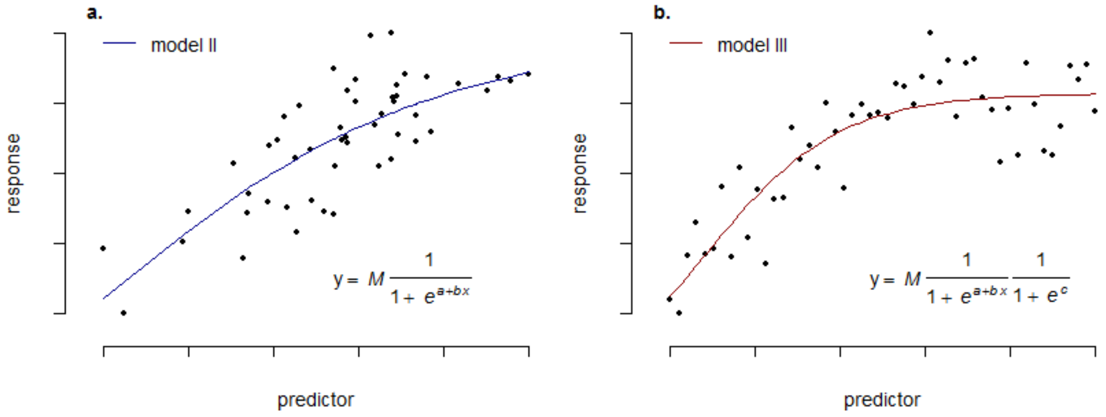

Figure 3.1. a) Type II and b) type III models, with generating equations, proposed by Huisman et al., (1993). Simulated data were produced using a) linear and b) half normal functions. In each case, model type was chosen by AIC_C. In equations, *a*, *b* and *c* are the parameters to be estimated by optimisation, *M* is the upper bound of the response value.

Huisman et al., (1993) proposed a set of five hierarchical logistic regression models, later extended to seven by Jansen & Oksanen (2013), to model species abundance patterns along environmental gradients. Of these, two types meet the above criteria: type II (following the original nomenclature of the model set) where a trend is allowed to reach an upper bound, and; type III, were a trend may be limited before the upper bound (Figure 3.1). Both models were constrained to be increasing only. A null model (type I), consisting solely of an intercept was also included. The best model for each species was chosen by AIC corrected for small samples (AIC_C; Anderson et al., 2000), and confidence intervals were implemented as the 0.05 and 0.95 percentiles of a bootstrapped sampling distribution (with 999 repetitions). A modified function from the eHOF package (Jansen & Oksanen, 2013) was used to produce the models in R (R Core Team, 2016). An R^2 value (model sum of squares/total sum of squares) approximates the amount of variation explained by the predictor, as proposed for continuous response data (i.e. density estimates; Huisman et al., 1993).

3.2 Factors influencing relationships between density estimates and model predictions

A series of species- and site-level covariates were used to evaluate where model predictions and density estimates differ. Spearman’s correlation was used to assess existence of a relationship between a) species-level factors and the correlation coefficients obtained from the occurrence-abundance relationship, and b) site-level factors and the residuals of the model describing abundance as a function of the occurrence model prediction for each species.

3.2.1 Species-level factors

Two covariates were used to assess different aspects of the performance of the species distribution models. First, AUC, or the area under the receiver operator curve, provides an indication of the predictive accuracy of the model. Second, variation among models making up the consensus model was calculated as the median range (maximum – minimum value) of the model predictions per site. Two covariates related to the species density estimates were used: the coefficient of variation of the density estimate and the variation in detectability of each species among sites. Detectability is measured as the proportion of individuals or groups of the target species that are detected in the survey area (Buckland et al., 2001). Both measures were calculated using DISTANCE sampling software (Thomas et al., 2010). Two covariates were used as general indicators of the rarity or commonness of the species: the average density of the species across its range, and the size of its range (calculated from the species distribution model in chapter 2).

3.2.2 Site-level factors

Anthropogenic pressures were measured at sites during fieldwork (see Chapter 3). These included prevalence of logging (proportion of vegetation plots with stumps present) and prevalence of grazing (proportion of vegetation plots with cattle and goat dung present). A site protection index was calculated using the number of people living in the 2nd degree administrative region where the site was located, the distance to the nearest large city (> 10,000 inhabitants), and lack of formal site protection status as penalty factors (see Chapter 4 for details).

3.3 Population estimates based on abundance-occurrence models

A global population size estimate was calculated for species with models showing a working relationship, i.e. where a model other than the null model was chosen. In the case of the Sulphur-throated Finch *Sicalis taczanowskii*, a population estimate was not calculated, given the higher uncertainty of the density estimate (see Chapter 3).The estimated model parameters were used to predict abundance for each pixel from the consensus distribution model, within the presence threshold, as established by 5% omission rate. Additionally, unsuitable areas (agriculture, urban areas, desert) were combined from land use and cover maps from Peru and Ecuador, based on Landsat images (MINAM, 2012; MINAM-EC, 2014) and masked from the consensus model after applying the threshold. Abundance estimates were summed across this masked range to estimate global population. The standard error of this total was estimated as the square root of the sum of the squared individual standard errors for each pixel from the bootstrap sample.

4 Results

4.1 Relationships between model predictions and density estimates

Eleven of fourteen species showed significant positive correlations between density estimates and occurrence predictions from at least one modelling method (Table 4.1, Appendix 1). The three species without any relationships were Rufous Flycatcher *Myiarchus semirufus*, Necklaced Spinetail *Synallaxis stictothorax*, and Mouse-coloured Tyrannulet *Phaeomyias murina*. The consensus model had the highest number of significant relationships, at 10 species, followed by Maxent at nine; GLM and Domain had the lowest with six (Table 4.1, Appendix 1). The highest correlation coefficients were found in Tumbes Sparrow *Rhynchospiza stolzmanni*, and all but one species with significant relationships had coefficients over 0.5.

Table 4.1. Spearman correlation coefficients for field based density estimates against model predictions. Number of significant (bold) relationships per species and models shown for p < 0.05.

Species	**GLM**	**GAM**	**Maxent**	**Domain**	**Consensus**	**Number of significant relationships**
Myrmia micrura	**0.64** (p<0.001)	**0.58** (p<0.001)	**0.65** (p<0.001)	**0.64** (p<0.001)	**0.62** (p<0.001)	**5**
Forpus coelestis	**0.52** (p=0.01)	0.05 (p=0.82)	0.16 (p=0.46)	**0.45** (p=0.02)	**0.47** (p=0.02)	**3**
Synallaxis stictothorax	0.28 (p=0.17)	0.29 (p=0.15)	0.16 (p=0.44)	0.30 (p=0.13)	0.33 (p=0.10)	**0**
Phaeomyias murina	0.22 (p=0.27)	0.11 (p=0.58)	0.30 (p=0.14)	0.31 (p=0.12)	0.19 (p=0.35)	**0**
Pseudelaenia leucospodia	0.34 (p=0.09)	0.23 (p=0.27)	**0.55** (p<0.001)	0.37 (p=0.06)	**0.48** (p=0.01)	**2**
Tumbezia salvini	**0.56** (p<0.001)	**0.67** (p<0.001)	**0.65** (p<0.001)	**0.53** (p=0.01)	**0.70** (p<0.001)	**5**
Myiarchus semirufus	-0.04 (p=0.85)	-0.27 (p=0.19)	-0.03 (p=0.88)	0.02 (p=0.93)	0.02 (p=0.93)	**0**
Phytotoma raimondii	-0.01 (p=0.97)	**0.51** (p=0.01)	0.34 (p=0.09)	-0.05 (p=0.81)	0.30 (p=0.13)	**1**
Campylorhynchus fasciatus	0.20 (p=0.32)	0.39 (p=0.05)	**0.46** (p=0.02)	0.16 (p=0.42)	**0.45** (p=0.02)	**2**
Cantorchilus superciliaris	0.38 (p=0.06)	**0.64** (p<0.001)	**0.52** (p=0.01)	0.23 (p=0.26)	**0.57** (p<0.01)	**3**
Mimus longicaudatus	0.29 (p=0.14)	**0.50** (p=0.01)	**0.51** (p=0.01)	0.14 (p=0.48)	**0.45** (p=0.02)	**3**
Piezorina cinerea	**0.62** (p<0.001)	0.20 (p=0.33)	**0.41** (p=0.04)	**0.61** (p<0.001)	**0.56** (p<0.01)	**4**
Sicalis taczanowskii	**0.63** (p<0.001)	**0.62** (p<0.001)	**0.63** (p<0.001)	**0.56** (p<0.01)	**0.67** (p<0.001)	**5**
Rhynchospiza stolzmanni	**0.84** (p<0.001)	**0.79** (p<0.001)	**0.87** (p<0.001)	**0.89** (p<0.001)	**0.91** (p<0.001)	**5**
Number of significant relationships	**6**	**7**	**9**	**6**	**10**	

Of the ten species showing significant correlation coefficients between the consensus model and density estimates, nine were modelled best by curvilinear relationships, with the more complex, type III model, superior in four species (Figure 4.1a, h, i, j) and the less complex, type II model, in five (Figure 4.1b, c, d, f, g). R^2 values ranged from zero (in the null model) to 0.78. The three best supported models, in terms of explained variance, were Tumbes Sparrow *Rhynchospiza stolzmanni* (78%), followed by Cinereous Finch *Piezorina cinerea* (51%) and Superciliated Wren *Cantorchilus superciliaris* (34%). Bootstrapped

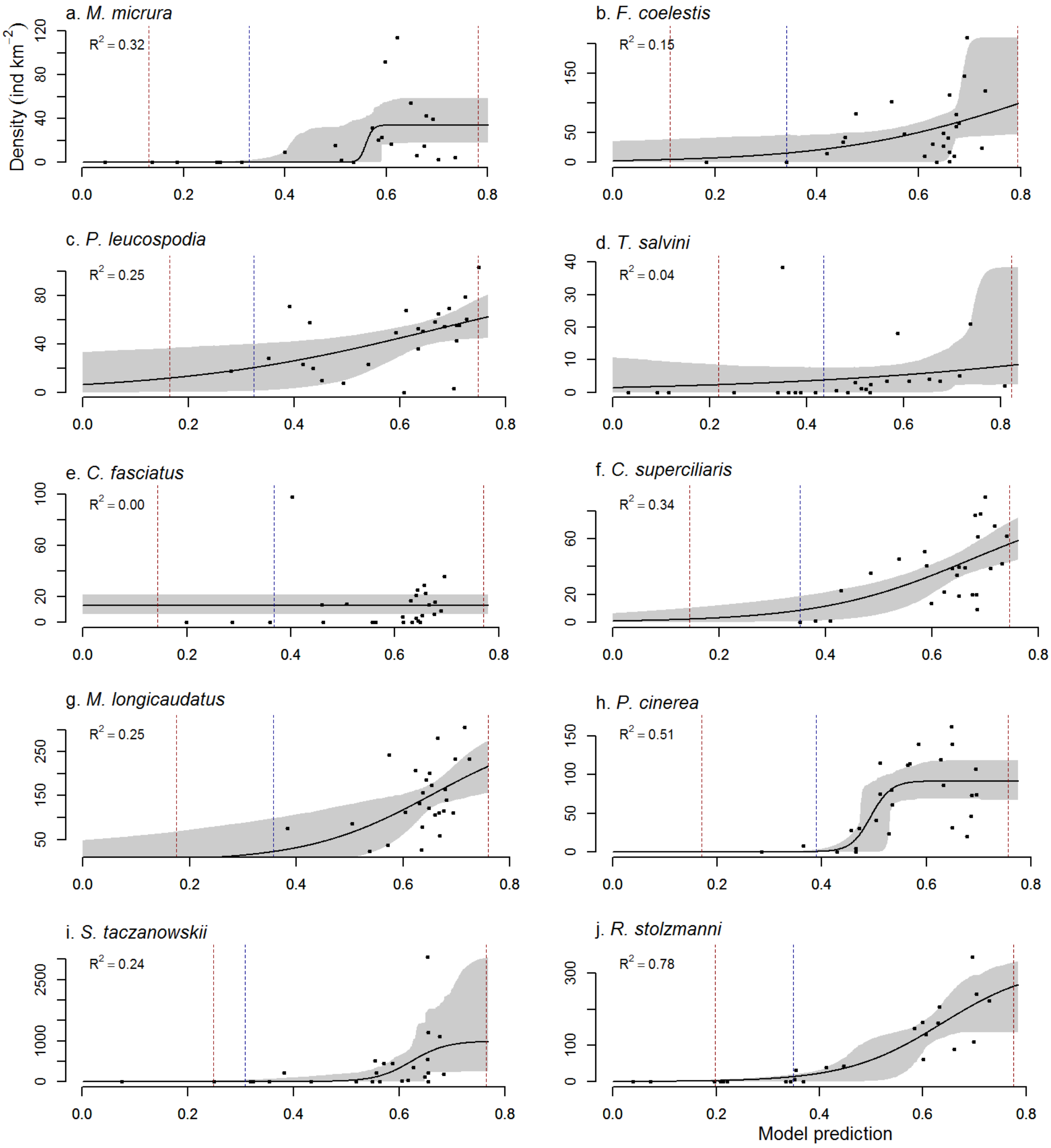

Figure 4.1. Relationships between population density (y-axis) and model predictions (x-axis) for ten species as modelled by a type of logistic regressions. Grey shading represents 95% percentile bootstrapped confidence intervals for the fitted values. Vertical red dashed lines represent the extremes of model predictions at all presence points used in the species distribution models; blue dashed line represents the presence threshold, using 5% omission.

confidence intervals on these species did not generally expand at the extremes, as in other species with more unstable models (e.g. Figure 4.1b, d, i). Models were not built for both threatened species due to a lack of relationship, and the Near Threatened Tumbes Tyrant *T. salvini* had an R^2 value of 0.04, showing instability at higher occurrence predictions (Figure 4.1d).

4.2 Factors influencing relationships

None of the species-level factors with regard to occurrence models (consensus model AUC, variability in individual models; Appendix 2) density estimate (coefficient of variation of density estimate, detectability) or species traits (average density and range size) were significantly related to the correlation coefficients between abundance estimates and model predictions (all p values > 0.2). However, significant relationships were found for site-level factors that could limit species' abundance and model residuals. Prevalence of grazing (measured by dung counts) at sites was positively correlated with residual values in Cinereous Finch *Piezorina cinerea* ($r_s = 0.43$, $p = 0.028$) and Fasciated Wren *Campylorhynchus fasciatus* ($r_s = 0.44$, $p = 0.025$). Four other species had p values < 0.06, hinting at further relationships between residuals and pressure factors (Appendix 3).

4.3 Estimating population size using density-model relationships

Preliminary population estimates were obtained from predicted values over the masked consensus models (i.e. between the blue and right-hand red dashed lines; Figure 4.1) with coefficients of variation ranging from 17% to 63% (Table 4.2). Population estimates refer to the entire global range of the species, with the exception of *Mimus longicaudatus*, for which geographically isolated subspecies (e.g. in the Marañón valley) were excluded (see 3.1, Chapter 2).

Table 4.2. Preliminary global populations (numbers of individuals) estimated from relationship between species distribution models and field-based density. Standard error and coefficient of variation are from bootstrapped samples.

Species	English name	Population estimate	Standard error	Coefficient of variation
Myrmia micrura	Short-tailed Woodstar	627,908	282,382	45%
Forpus coelestis	Pacific Parrotlet	2,872,442	1,390,939	48%
Pseudelaenia leucospodia	Grey-and-white Tyrannulet	1,408,909	260,983	19%
Cantorchilus superciliaris	Superciliated Wren	1,355,930	234,280	17%
Mimus longicaudatus	Long-tailed Mockingbird	5,404,490	1,183,043	22%
Piezorina cinerea	Cinereous Finch	1,390,227	254,267	18%
Rhynchospiza stolzmanni	Tumbes Sparrow	2,840,519	598,303	21%

5 Discussion

Significant benefits could result from a working link between distribution models and abundance. More efficient and cost-effective population estimates, and related metrics such as population trends, would constitute major advances in conservation science. This study found working relationships in the majority of bird species tested from the Tumbesian region in Peru. The sampling strategy used to select sites to obtain density estimates favoured areas of higher probability of finding the species (see Chapter 3). This may tend to reduce the correlation between density and occurrence if this implies that the relationship is not evaluated over the full breadth of a species' abundance values. Conversely, the species distribution models themselves may tend to increase the correlation due to bias in the models from unsystematic location of occurrence records (where density is higher, detectability is higher, leading to more occurrence records; Jiménez-Valverde, 2011). However, I believe that the wide variation in density estimates obtained and the steps taken to reduce bias in models (although not completely, as is the nature of presence only models) are sufficient to avoid the relationships presented from being unrepresentative.

Evidence from a review of previous work, presented above, supports the generality of these results (Table 2.1). Further evidence for common factors driving both abundance and distribution come from related studies. Howard et al., (2014) found improvements to distribution model performance when trained with abundance data rather than presence/absence data. Additionally, Serra-Diaz et al., (2013) found a positive relationship when comparing tree growth to distribution model predictions, given that growth rate is a metric related to abundance. Crucially, both landscape- and local-scale abiotic factors have been found to explain presence/absence distribution (Stewart-Koster et al., 2013). I conclude that significant overlap exists between factors controlling both abundance and distribution, as oppose to some authors who claim they are separate processes (e.g. Nielsen et al., 2005; Johnston et al., 2015). A commonly held theory of the hierarchical nature of factors controlling distribution and abundance (Wiens, 1989; Guisan & Thuiller, 2005) is not necessarily invalidated by this overlap. Rather, factors controlling distribution and abundance are not mutually exclusive, but are present at all levels of the hierarchy. This may be further clarified by considering that abundance and distribution result from individualistic species-specific responses to environmental factors (Wiens, 1989).

Notwithstanding, relationships were not found for all species in this study, and even in positive results, much unexplained variability remains. This, again, mirrors results from the review. Many studies found that models could predict upper limits of abundance or carrying capacity (VanDerWal et al., 2009; Muñoz et al., 2015). One explanation for this pattern is that predictors explaining local limiting factors, rather than broad environmental gradients (Feldman & McGill, 2014), were absent from models. Further, this pattern is also seen where the interaction of multiple limiting factors increases the unpredictability of an ecological response as environmental conditions become more favourable (Cade et al., 1999; Huston, 2002). I suggest that appropriate predictors at sensible scales of analysis are crucial to making these relationships work. First, predictors should define the realised niche of a species (Hutchinson, 1978), that is, they should describe one or more of current habitat effects, disturbance, dispersal and biotic interactions (Guisan & Thuiller, 2005; Peterson et al., 2011). In this study, NDVI, as measured at the same time as the field study, was used as such a predictor, incorporating information on current habitat conditions. Second, scales of predictors should match the scale of variation in abundance across a species' range. Variation in predictor resolution can lead to prediction resolutions that range from continuous, through ordered rank, to presence or absence (Huston, 2002). The second recommendation is especially important when data are not available to describe the realised niche (in most cases in the Neotropics) given that local-scale abiotic or habitat variables may act as proxies (Stewart-Koster et al., 2013).

This study addressed several challenges related to predicting abundance with distribution models; factors, which could affect the strength of relationships were explored. Detectability, which Jiménez-Valverde (2011) suggested could be the cause of circular reasoning in a positive relationship between model prediction and abundance, was taken into account within the density estimates. Furthermore, species' detectability was not found to be related to the correlation coefficients between model predictions and abundance estimates, suggesting that detectability was not affecting relationships in this study. Other species-levels traits were not found to affect the relationship in this study, however, niche width is known to effect how well occurrence models are supported (Tsoar et al., 2007; Attorre et al., 2013), and may influence a relationship between the model and population density. The general lack of relationships between pressure factors at sites (e.g. selective logging) and model residuals may be partly explained by NDVI already containing some of this information. A further complication relates to the time scale of this disturbance factor, which represents an accumulation of logging activity at least as far back as the last significant El Niño event (1998).

Based on the relationship between distribution and abundance, population estimates were made for eight species using model parameters. Given the difficulty in obtaining population size estimates, especially in the Neotropics (see Chapter 2), conservation assessments need to be pragmatic. No published population size estimates exist for these species, but they are described as ‘common’ in the most recent comprehensive conservation assessment of Neotropical birds (Stotz et al., 1996). I suggest that this method represents a practical way of improving estimates using relatively small numbers of abundance estimates by taking into account variation in abundance over the range of a species (see Chapter 4; Brown et al., 1995; Sagarin et al., 2006). Furthermore, these estimates are unlikely to underpredict if negative relationships are not used. Where relationships are not found, then an intercept only model will be equivalent of scaling up a mean abundance estimate over a suitable area. However, density surfaces from spatial interpolation, given that abundance is spatially autocorrelated at small distances (see Chapter 4), may represent an improvement over intercept only models (Bahn & McGill, 2007) and spatial terms could be included within models. For intercept only models, the choice of sampling strategy for the abundance estimates must also be taken into account. For example, a sampling design stratified by relative probability of occurrence (i.e. this study) would not be suitable for scaling up mean estimates without a modelled relationship. Population estimates at local level may not always be reliable from this method, given the wide variation in observed abundance at higher levels of model prediction. Similarly, Oliver et al., (2012) concluded that population densities can be predicted over wider landscapes rather than by pixel. However, some species, e.g. Tumbes Sparrow *R. stolzmanni* did not show this amplification of variance, and local estimates should therefore be evaluated on an individual species basis. Williams (2012) commented that Sulphur-throated Finch *Sicalis taczanowski* had declined severely in recent years and is no longer ‘common’. This study (Chapter 3) observed the species in flocks numbering in the 100s at 6 of 24 sites within its range, and using methods described in this chapter, placed a population estimate in excess of 7 million individuals (Table 4.2). However, further work is needed to qualify a threshold to approximate better an area of occupancy, or to further refine predictors of presence for this species.

Similar applications of an occurrence-abundance relationship have already been applied to conservation problems. Three studies reviewed above also predict population size, but as oppose to methods here, encounter rates or similar are predicted and then converted to density taking into account detectability from field studies (Legault et al., 2013; Carrascal et al., 2015). Priority sites for conservation were established based on ranked habitat quality in two studies[26] (Escalante & Martínez-Meyer, 2013; Ureña-Aranda et al., 2015). Future applications of this relationship could include multi-temporal studies to investigate population trends and their relationship to environmental variables, especially habitat change. Existing models using future scenarios to predict distributions could be extended to abundance and measure population size effects of deforestation (Bird et al., 2011) or climate change (Ramirez-Villegas et al., 2014). Such applications could be especially important in cases where a lack of change in range size masks population declines (Wilcove & Terborgh, 1984; Chamberlain & Fuller, 2001; Rodriguez, 2002). They could also improve extinction risk assessments where linear relationships are often assumed between habitat loss and population decline (IUCN, 2016). Correlates of seasonal differences in populations (e.g. local and large-scale migration) could also be assessed for importance in distribution-based models where abundance data are not widely available. Further applications could include aggregating data from different survey protocols where bird counts are standardised by modelled habitat suitability indices (Massimino et al., 2008). In this case, models were built with

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[26] Escalante & Martínez-Meyer (2013) did not report details of the occurrence-abundance relationship and is therefore not included in Table 2.1

count data, but using the relationships outlined here, occurrence data could also be used. Finally, other regression-based methods exist for exploring the relationships between distribution and abundance, most notably, as a two stage process (first for occupancy, and then for abundance-where-present), for example, hurdle or zero inflated models (Michaud et al., 2014), or where both are incorporated into a single modelling framework (Stewart-Koster et al., 2013). Ordinal regression has also been used (Guisan, 2002), building on the fact that relative probability of occurrence can be considered ordinal data, and may be worth further exploration in the context of this study.

In conclusion, abundance-occurrence relationships are a promising tool to add to conservation science and are already being applied to improve knowledge of species' population sizes and habitat quality. Further application of these relationships have potential to improve our understanding of how abundance within a species' geographic range, and how a species' occurrence itself, changes over time and space.

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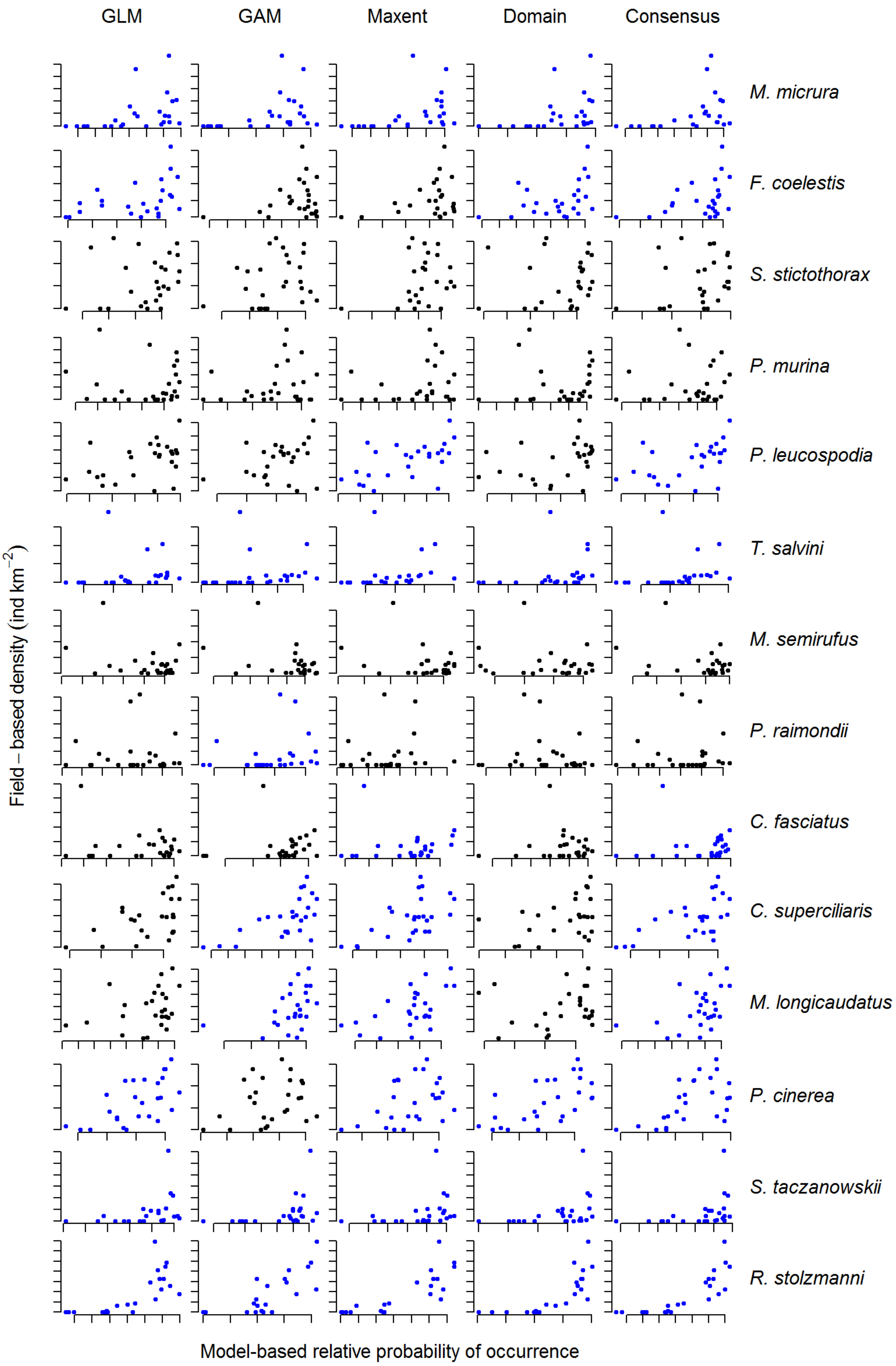
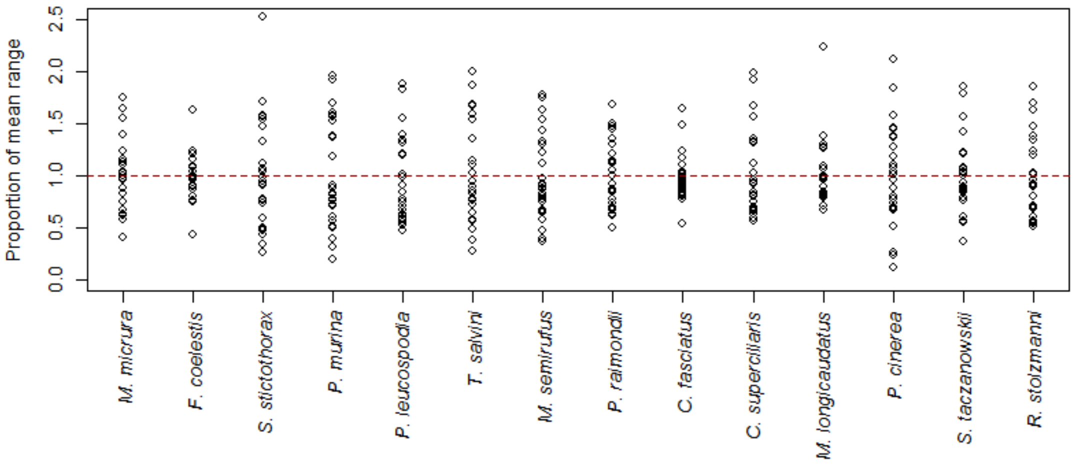
7 Appendices

Appendix 1. Comparison of model-based probability of occurrence and field-based density estimates for 14 species at 26 sites in northwest Peru. Blue points indicate that Spearman's correlation coefficients are significant at $p < 0.05$.



Appendix 2. Variation in the predictions of the four species distribution modelling methods at each field site. The range of predicted values at each site (maximum – minimum prediction) is shown as a proportion of the mean range of model values at all sites. The red dashed line represents no difference between range of predictions at a particular site and the mean value.



Appendix 3. Correlation coefficients for model residuals and site level factors, significance (< 0.05 and < 0.1 are shaded).

Species	Site-level factor	Spearman correlation coefficient	P-value
Myrmia micrura	Distance to road	0.10	0.617
	Grazing prevalence	-0.19	0.354
	Logging prevalence	-0.11	0.595
	Population pressure index	-0.12	0.556
Forpus coelestis	Distance to road	-0.17	0.411
	Grazing prevalence	-0.34	**0.099**
	Logging prevalence	-0.07	0.741
	Population pressure index	-0.12	0.556
Synallaxis stictothorax	Distance to road	-0.03	0.878
	Grazing prevalence	0.38	**0.056**
	Logging prevalence	0.18	0.389
	Population pressure index	0.03	0.899
Phaeomyias murina	Distance to road	-0.31	0.122
	Grazing prevalence	-0.03	0.895
	Logging prevalence	0.15	0.478
	Population pressure index	0.04	0.846
Pseudelaenia leucospodia	Distance to road	0.00	0.987
	Grazing prevalence	0.39	**0.051**
	Logging prevalence	0.35	**0.079**
	Population pressure index	0.00	0.984
Tumbezia salvini	Distance to road	-0.10	0.646
	Grazing prevalence	0.29	0.162
	Logging prevalence	0.00	0.997
	Population pressure index	-0.24	0.244

Species	**Site-level factor**	**Spearman correlation coefficient**	**P-value**
Myiarchus semirufus	Distance to road	0.03	0.881
	Grazing prevalence	0.38	**0.052**
	Logging prevalence	0.23	0.249
	Population pressure index	-0.01	0.969
Phytotoma raimondii	Distance to road	-0.28	0.169
	Grazing prevalence	-0.30	0.141
	Logging prevalence	0.07	0.720
	Population pressure index	0.09	0.678
Campylorhynchus fasciatus	Distance to road	-0.18	0.391
	Grazing prevalence	0.44	**0.025**
	Logging prevalence	0.30	0.132
	Population pressure index	0.04	0.862
Cantorchilus superciliaris	Distance to road	-0.34	**0.093**
	Grazing prevalence	0.07	0.739
	Logging prevalence	0.17	0.407
	Population pressure index	0.31	0.123
Mimus longicaudatus	Distance to road	-0.28	0.163
	Grazing prevalence	-0.28	0.167
	Logging prevalence	0.18	0.383
	Population pressure index	0.22	0.279
Piezorina cinerea	Distance to road	0.38	**0.057**
	Grazing prevalence	0.43	**0.028**
	Logging prevalence	-0.05	0.803
	Population pressure index	-0.33	0.105
Sicalis taczanowskii	Distance to road	0.03	0.902
	Grazing prevalence	-0.16	0.435
	Logging prevalence	0.25	0.229
	Population pressure index	0.14	0.515
Rhynchospiza stolzmanni	Distance to road	0.12	0.561
	Grazing prevalence	0.08	0.725
	Logging prevalence	-0.04	0.862
	Population pressure index	-0.08	0.697

Chapter 6

General conclusions, recommendations and future work

1 Main Findings and recommendations

This thesis aimed to develop tools, combining different analytical techniques, field data and GIS, to provide improved estimates of species distribution and abundance in support of extinction risk assessments in threatened Neotropical bird species. Given the current extinction crisis (Barnosky et al., 2011), and the lack of critical information to inform conservation decisions on the ground (Hortal et al., 2015), new methods and analytical techniques are urgently needed to counter information shortfalls that prevent or hinder efficient conservation planning and management. Information shortfalls are especially severe in terms of the abundance of species over their geographical ranges. Most species lack abundance estimates, and for those that have them, these are often singles estimates over large ranges (see Chapter 1). Inextricably linked to information on abundance is information on the extent of species ranges, critical at range edges (i.e. where does abundance become zero –and how often?), or areas where abundance is variable. Several findings from this thesis support improvements to methods aimed at providing information on species' ranges and abundances for conservation decisions.

1.1 Making use of the relationship between occurrence and abundance

Relationships between the environment and species' distributions have been a core issue of ecology since its beginnings as a discipline (Andrewartha & Birch, 1954; Begon et al., 2006). Since the time of Humboldt's graphical representation of plant distributions over altitudinal gradients and bioclimatic zones on Chimborazo in Ecuador (Humboldt & Bonpland, 1807), some 400 km north of the present study area, ecologists have attempted to explain species' responses to environmental gradients. The idea that such relationships should be linked to abundance is also not new. Chapman (1931) had already hinted at climate-based distribution maps predicting areas of normal abundance and rare occurrence in an early textbook on ecology. Over the last decade, researchers have increasingly focused on the relationship between models of species occurrence and local abundance (e.g.

Nielsen et al., 2005; Muñoz et al., 2015; see Chapter 5). This is becoming a promising area of research aimed at obtaining better, more efficient, abundance information, by incorporating information about what drives species presence. This thesis has also found a relationship between abundance and occurrence in most of the study species. However, this does not represent a quick-fix short cut to obtaining range-wide information on abundance at present. Species ranges and abundances are dynamic, spatial patterns, controlled by abiotic and biotic factors, some of which are modified by the species' life processes themselves (Gaston, 2003; Peterson et al., 2011). Such complexity has led some authors to urge caution in overvaluing the contribution of species distribution models to ecology (Aguirre-Gutiérrez et al., 2013; Jiménez-Valverde, 2014). However, given the importance of range and abundance metrics (and changes therein) to conservation decisions, the potential benefits of understanding such relationships requires further research for improving models as well as applying the relationship to conservation issues.

Population decline and habitat loss

A major application of this relationship would be to clarify the relationship between changes in population numbers and habitat area, especially population decline and range loss. This is a major factor in current extinction risk assessments, given that most threatened species are classified on the basis of changes in population inferred from habitat loss (see Chapter 1). Given the complex variation in abundance over the range of a species, as was the case in this study, the relationship between habitat loss and population decline is unlikely to be linear. IUCN guidelines urge a sensible application of this relationship (IUCN, 2016), and models using time series data (e.g. over three generation lengths of the species in question) from vegetation indices, such as NDVI used in this study, with occurrence calibrated to abundance, could provide important insights into the true relationship over specific areas. Different patterns proposed for range loss (e.g. Wilcove & Terborgh, 1984; Donald & Greenwood, 2001; Rodriguez, 2002) could also be tested and simulated through this approach.

Global change studies

Other global change studies, such as those involving climate change, could also benefit from using abundance information in predicted impacts, instead of changes in species richness or range size. Understanding how climate change might affect the internal population structure of a species' range would represent an important step forward in quantifying the risks.

Improving models

In terms of improving models, both methods and predictors require further thought and action. This study found some evidence for certain factors limiting abundance within a framework where a relationship between abundance and occurrence models predicts a carrying capacity or maximum potential abundance (VanDerWal et al., 2009; Muñoz et al., 2015). Further research is needed on these factors that can tell us more about where the relationship between abundance and occurrence models breaks down. For example, local biotic interactions (e.g. competition –abundances of other species) and local pressure factors (e.g. habitat degradation, hunting) should be incorporated into models, especially when using them to estimate population size. Collection of such variables may entail significant fieldwork but recent advances in remotely assessing local pressures may also offer real opportunities to use satellite data for this purpose (e.g. logging; Buchanan et al., 2013).

Two stage models

Other methods with similar goals, such as abundance modelling, could also be compared to this method. Techniques, such as a two stage modelling processes –zero-inflated models or hurdle regression applied to abundance data (Zuur et al., 2009)– where presence/absence is modelled first, and then abundance within areas of presence, should be assessed with data from this study. This process is conceptually similar to predicting abundance within a thresholded and calibrated species distribution model. An advantage of using the present method is the availability of additional data, e.g. museum records, used in presence/background methods, whereas zero-inflated models typically use the same data set, converted to presence absence for the first modelling stage.

Occupancy modelling

Occupancy modelling is another technique to explore, especially, where surveys to assess occupancy are replicated over space (e.g. Charbonnel et al., 2014), rather than time, as is more typically the case. For example, using the data from this study, occupancy could be assessed using data from each of the four transects per site as a replicate. Occupancy could then be compared to abundance, using a series of similar covariates, as in this study.

Abundance surface modelling

Abundance surface modelling incorporated into Distance sampling (Miller et al., 2013) represents a more sophisticated method to propagate errors from density estimates through to the population size estimates but is data intense. This method, as proposed currently, relies on Generalised Additive Models to predict abundance using spatial predictors, such as those typically used in species distribution models (Hedley & Buckland, 2004). Combining such techniques with an occurrence-abundance relationship might be a compromise to include more meaningful uncertainty measures while maintaining a pragmatic and relatively straightforward approach to improving population size estimates.

1.2 Modelling species ranges

Modelling species distributions, from its origins in relating species responses to resources and habitat relationships (Scott et al., 2002), has increased exponentially in recent years with the advent of dedicated software, expanding online data sources, and increasing ease of sharing analysis methods through statistical programming (see Chapter 2). Although species distribution models are currently an accessible and common tool for conservation planning (often at large scales), they may be underexploited for practical conservation decisions on the ground (Guisan et al., 2013) or not always the right tool for the job (Guillera-Arroita et al., 2015). This is evidenced by some reluctance for SMDs to be fully embraced within certain conservation planning mechanisms (e.g. Red List, Important Bird Areas), with issues of scale and accuracy, themselves major drivers of research in SDMs, often sticking points. Obtaining a fuller picture of a species' distribution will need models to become more dynamic, and more process-based. Incorporating process (e.g. population dynamics, interspecific interactions) into conservation planning, in addition to biodiversity patterns (based ecosystem types and species distributions), has been a recent goal (Pressey, 2004). New methods in modelling are beginning to reflect this, with several methods being developed to incorporate mechanistic modelling with correlative distribution models.

Estimating Extent of Occurrence

Modelling techniques represent a useful tool to complement existing methods of estimating Extent of Occurrence (EOO) for extinction risk assessments. Although several examples exist in the literature (e.g. Marcer et al., 2013; Syfert et al., 2014), and suggestions for their use are included in the IUCN guidelines on extinction risk assessment (IUCN, 2016), several issues still prevent their use as standard practice, of which three are highlighted. Firstly, although many stages of the process may be automated, to ensure the quality of occurrence records, manual checking is required, which for many species is time-consuming and requires expert knowledge. Secondly, thresholds are difficult to standardise across species, can be affected by the quality of the occurrence records, and are not subject to a general consensus on which method to use. Thirdly, the increasing number of modelling methods, and whether ensemble methods are an adequate solution to variability among methods, makes standardisation difficult. Notwithstanding such challenges, automated models incorporating online sources of both species occurrence records and environmental layers could highlight discrepancies with expert-based Extent of Occurrence estimates. EOO, as in this study, could be based on a percentage omission threshold. Although a 0% omission threshold conceptually conforms to a convex hull approach to EOO, excluding a small proportion of presence records equal to a low quantile (e.g. 5% as in this study) of model values allows for vagrancy (i.e. genuine, but very rare, records of species in atypical locations) and location error (likely to be present in most presence-only data sets such as those from museum records).

Area of Occupancy

Thresholds specific to modelling purpose require further research. A threshold for AOO is a more challenging proposition than EOO, where a balance must be sought between overestimating a species occupancy, albeit in suitable habitat, and excluding areas of true presence - in other words, between errors of commission and errors of omission. The difficulty with setting thresholds with relative probability of occurrence, such as that produced by presence/background SDMs, is that ‘traditional’ probability-based methods (e.g. 0.5 in logistic regression) cannot be used. Freeman & Moisen (2008) suggest using thresholds based on specificity to avoid overestimating population. However, thresholds related to commission errors are difficult to implement when ‘background’ absences, rather than true absences are used (Peterson et al., 2011). A compromise between choosing a higher threshold than 0% omission and using post-processing to exclude unoccupied areas was used in this study. Using predictors that are better able to differentiate occupied and unoccupied areas would be an advantage for modelling and standardising approaches. Also, other ways to estimate commission errors should be trialled, such as using pilot studies to approximate true prevalence, or using sites of ‘absence’ for a particular species from specimen or observation data (where sufficient records exist) as true absences in threshold or accuracy metrics.

Species occurrence records

Quality and suitability of species occurrence data in distribution models remains a key issue (Graham et al., 2004). Further work is required to process and make available species occurrence records from past collections despite the hugely significant efforts of initiatives such as VertNet and GBIF. Ultimately, greater willingness to share will bring improvements. Distributed systems can aid data sharing by avoiding issues of ownership and storage. Major collections of Neotropical birds are yet to be made fully available online, no doubt due to lack of funds for preparing data. Creative crowd-sourced help is already being used to digitise natural history collections (Beaman & Cellinese, 2012), although, of course, some funds are required to manage them (and manage data quality) but such initiatives would be worth exploring in the Neotropics. Additionally, better mechanisms are needed to be able to share corrections and comments on the quality of existing data sets. Many records of species occurrence were processed for this study, and being able to organise and share processing details, given its manual nature (in part), is still difficult.

Notwithstanding the availability of existing data, and constant sources of new data (e.g. eBird), bias in occurrence records remains an issue for models (Guillera-Arroita et al., 2015).

Improving predictors

Better predictors are key to obtaining better estimates of occurrence and abundance. This study used remote sensed data to produce annual summaries (in the style of bioclimatic indices) of a vegetation index with promising results as a proxy for habitat. This kind of fine scale data on habitat requires further exploration (e.g. based on 30 m Landsat images), especially in the Neotropics, where other high resolution data on habitat (e.g. ground mapped soils, ecosystem composition, etc.) is not available. Habitat data, if good enough, should preclude the need for using climate data in distribution models. Recent habitat change (approximately up to 30 years ago) can also be incorporated within such predictors and represents an important research area in relation to predicting species abundance (as detailed above). Other remotely sensed variables, such as cloud free radar data (e.g. ALOS – PALSAR) should also be trialled for such data poor regions.

Integrating process into models

Biotic interactions, as predictors of abundance, also require further exploration. At their simplest, other species' presence can been used in models (e.g. Leach et al., 2016), but aspects such as competition (Alexander et al., 2016) could also be included if evidence is found, for example, from pairwise correlations of abundance data, as used in this study. Research is also active in joint species modelling, for example, describing abundances across many taxa and using multiple species to fill data gaps (e.g. Warton et al., 2015; Evans et al., 2016; but see Beissinger et al., 2016). Demographic parameters are a further key data source to combine with occurrence or abundance models, already an active research topic (Schurr et al., 2012; Aben et al., 2016), but are probably the least feasible addition among Neotropical species (or in biodiverse countries in general) due to lack of data.

1.3 Obtaining local abundance estimates from the field

Obtaining local abundance estimates from the field is costly, logistically difficult and time-consuming, especially for rare species, or in regions with patchy habitats, such as the present study area. In this study, abundance estimates, using methods that incorporate detectability, were obtained for rare species over very patchy habitats with relatively low survey effort following a sampling protocol designed to maximise the number of bird records. However, further research in such methods is needed, as well as in trialling and calibrating alternative methods for density estimation.

Sampling design

Although using relative probability of occurrence in a stratified sampling design is successful in obtaining records, more research is needed in the processing of subsequent density estimates, especially in terms of converting these to range-wide population estimates. Techniques were trialled in this study using the relationship between the obtained local abundance and modelled occurrence, but other methods to statistically account for the fraction of the study area sampled, taking into account the relative probability of finding the species, also need to be developed. This proportion could be estimated using the relationship between abundance and modelled occurrence, and the distribution of modelled values across the whole study area.

Core population size estimate

This kind of sampling protocol stratified by relative probability of occurrence could also be used to obtain an estimate of core, or minimum, population size (more cost efficient than complete population) by focusing fieldwork on just the sites of highest habitat suitability (≃ highest abundance). If the spatial structure of a species' abundance across its range is typically made up of few sites of high abundance (as in this study), then by focusing on these sites for monitoring programmes or censuses could provide estimates of significant proportions of the species' population.

Validating other methods to assess abundance

Genetic methods for monitoring abundance also need further research (Schwartz et al., 2007), and need to be compared with density estimates obtained using traditional methods, such as in this study. Recent advances have been made using environmental DNA fragments in water for measuring fish abundance (Lacoursière-Roussel et al., 2016). Other creative methods to quantify numbers of terrestrial animals could entail testing material potentially containing DNA, such as feathers, excrement, scales, etc. found at roosting, nesting or feeding sites, or using blood from lice (e.g. similar to monitoring vertebrate species from leech gut contents; Schnell et al., 2015).

Other methods, such as acoustic monitoring using semi-permanent arrays of microphones(Blumstein et al., 2011), or tracking devices from which data is downloaded remotely to base stations (López-López, 2016), are also candidates for field trials in the Neotropics, but would need to be calibrated with 'traditional' field data, such as that collected for this thesis.

1.4 Variation of abundance over the range

The extreme variation in species abundances and the complexity in their relationships with environmental variables have implications for conservation planning. A single estimate of abundance is unlikely to provide a reasonable estimate of abundance over the range of a species, emphasising the need for methods to quantify abundance across a range (see above). However, further research is required with regards the variation in abundance itself.

Spatial distribution of abundance within the niche

Whether the distribution of abundance across a range is multimodal or unimodal, and the spatial arrangement of those peaks, has implications for issues, such as selecting reserves and important areas for conservation. Further research is required in describing the modality of the spatial variation in abundance, and how this relates to underlying patterns of environmental variables. For example, is there a relationship between the distance to the optima of a species' environmental niche and a species' vulnerability? This could have special relevance to studies on the impact of climate change involving species pushed to the limits of their environmental niche, or classifying the relative threat status of geographical subpopulations of a species.

Index of variation in abundance

Extreme variation in abundance, leading to patchy distributions, could also be a sign of vulnerability in a species, indicative of past disturbance to population processes (Wilson et al., 2004). Further research into an index of variation in abundance is required, especially, how this relates to a species' vulnerability, or how this could be incorporated into a species' extinction risk assessment.

Congruence of species abundance hotspots

Reserve selection algorithms often use presence/absence data for species, but given the variation in abundance, and the fact that species' highest abundances do not coincide at sites, as shown in this study, further research is needed into the benefits and costs of using abundance data in site selection methods. The relationship between a species' permanence at a site and abundance is also a relevant topic of further research here (Rodrigues et al., 2000), especially if the former could act as a proxy of the latter, in other words, the relationship between occupancy and abundance.

Monitoring

Monitoring could be made more efficient if patterns of variation of abundance over a range were better understood. Monitoring effort, in general, is most important where most heterogeneity exists (in either time or space). If such areas of heterogeneity could be identified, then monitoring efforts should be concentrated there. For example, if abundance can be linked to spatial variables (e.g. linking occurrence modelled on environmental layers to abundance, or directly modelling abundance on environmental layers), then areas of most heterogeneity in these layers could be targeted for increased monitoring effort. The complexity and species-specificity of such relationships (see Chapter 4) represents a challenge for such research, but a balance could be sought between appropriate scales of environmental variables, the scale of variation in abundance, and the scale of monitoring efforts. Fieldwork to obtain estimates of local abundance could certainly be made more efficient by ensuring that areas of most variation in abundance are covered by sample sites. Improving monitoring can further improve the economic benefit of surveys to conservation (Balmford & Gaston, 1999).

1.5 New technologies, methods and data sources

Data sources and methods in conservation biology are evolving rapidly. With technology theoretically able to connect almost real-time species occurrence data to remote sensed data, exciting possibilities exist for the future of monitoring the status of species and ecosystems. The analysis of almost real-time automated surveillance data (e.g. real time acoustic monitoring), live citizen science fed species occurrence data (e.g. eBird) with real-time remote sensed information on habitat quality has potential to highlight risk quicker than ever before. Of course, such systems are not functioning yet, but the time is right to begin incorporating and trialling these new data sources and technologies into extinction risk assessments and conservation planning and management.

2 Conservation recommendations

The study area is of international conservation importance, with high numbers of endemic species (Stattersfield et al., 1998) and high degree of threat (Mittermeier, 2004). Dry forest ecosystems around the globe, and in the Neotropics, are especially threatened habitat types (Miles et al., 2006; Pizano & García, 2014; Sánchez-Azofeifa, 2014). The dry forests of the study area have been subject to differing degrees of use during prehispanic and colonial times (Rostworowski, 2005), the effect of which is still poorly understood for this biome. However, a slow recovery of species composition in dry forests after disturbance (Derroire et al., 2016) could potentially affect species with greatest habitat specificity. Conservation measures within the study area include the designation of protected areas, at international, national and local level, as well as recent large-scale projects using ecosystem approaches in an attempt to balance resource use with biodiversity conservation (e.g. Proyecto Algarrobo; Darwin Initiative for the dry forests of Peru and Ecuador). Academic research on biodiversity in the study area is lacking, as is capacity for implementing evidence-based conservation. Cooperation, in terms of capacity-building with regional state universities, in collaboration with national and regional environmental authorities (e.g. local government, National Parks Authority – attached to Ministry of Environment, Forestry and Wildlife Service – attached to Ministry of Agriculture & Irrigation) will surely play an important role in furthering sustainable development in one of Peru's most populous and economically important regions (see Chapter 1 and 3).

2.1 Species related conservation findings: case studies on IUCN threat categories

Rufous flycatcher *Myiarchus semirufus*

The Rufous flycatcher (Figure 2.1) is currently listed as Endangered under criteria B1ab(i,ii,iii,iv,v), corresponding to a severely fragmented Extent of Occurrence of 2,800 km^2 (< 5,000 km^2 to meet EN criterion) with inferred continuing decline in range, habitat and subpopulations. Its population is estimated at 1,500-7,000 mature individuals. The IUCN text account accompanying the threat classification describes a population decline, range contraction and a genuinely patchy distribution, but clarifies that the species may be more widespread and common than currently believed (BirdLife International, 2016a). This study has shown that the species is certainly more widespread than currently believed, not just from fieldwork, but also from a careful compilation of existing occurrence records. This study suggests that the species is rare throughout its range, but widespread, with an Extent of Occurrence (without exclusions) approximately 10 times larger than currently listed. This estimated range size, with a population density at just 1 individual km^{-2} (the average density from this study was 5.9 individual km^{-2}; 95% CI 3.5 - 8.2) would place the species beneath the threshold for Vulnerable under criterion B1a and C (i.e. in terms of range and population size). Although habitat has declined in area in the last 15 years (three generations), there is no evidence that reductions have amounted to more than 30-50% to trigger criterion A (this criterion is currently not applied in the species' assessment). However, this could be assessed using remote sensing. The only evidence for temporal trends shows similar encounter rates over the last 10 years approximately (Chapter 3).

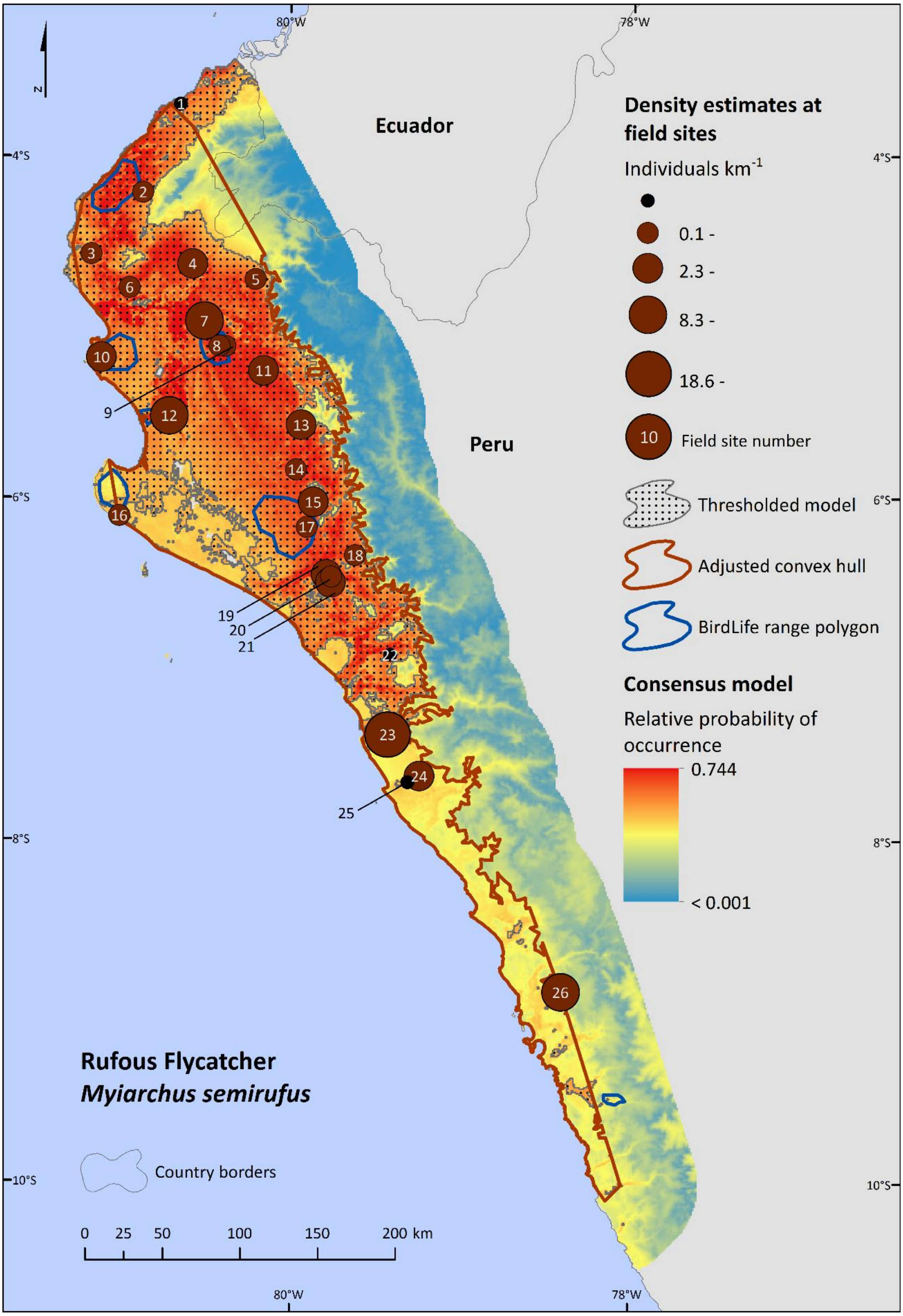


Figure 2.1. Consensus species distribution model for Rufous Flycatcher *Myiarchus semirufus*, showing field sites, sized proportionally to field-based density estimates (see Chapter 3), with overlays of thresholded model (estimated Extent of Occurrence; see Chapters 2) and current BirdLife range polygon. The elevation-adjusted convex hull around occurrence points was used as the species specific accessible area for the model (see Chapter 2).

Peruvian Plantcutter *Phytotoma raimondii*

The Peruvian Plantcutter (Figure 2.2) is also listed as Endangered under criteria B1ab(i,ii,iii,v), corresponding to a severely fragmented extent of occurrence of 4,900 km^2 (< 5,000 km^2 to meet EN criterion) with inferred continuing decline in range, habitat and subpopulations. Its population is estimated at 670-1,600 mature individuals in just two subpopulations. The text account describes a severely fragmented range, with recent records from just four locations (BirdLife International, 2016b). This study found the Peruvian Plantcutter to have a severely fragmented range, but with very high population densities at several sites –more than seven sites have densities exceeding 15 individuals km^{-2}, and four sites over 30 individuals km^{-2} (Appendix 6, Chapter 3). Population estimates at just the eight sites where the Plantcutter was present during this survey total more than 3,000 mature individuals, already more than the global population estimate currently held for this species. With these extra populations, the EOO would exceed 5,000 km^2, but not 20,000 km^2, corresponding to threat category VU. Other criteria for VU would include C2ai, but not D1, as currently listed.

2.2 Site related conservation findings and recommendations

The threats to Peruvian Plantcutter are more severe than for Rufous Flycatcher given the fragmented nature of its population and the concentration of at least 50% of its population at less than ten sites. While one key site, Enace (Talara), is currently being designated as a regional protected area, the small site at Paiján (Mocan and Arenita), with the highest recorded Plantcutter density from this study, is under threat from expanding agriculture. The site is owned by a large food company, and although they have shown willing to conserve the Arenita area, Mocan is still under threat. An urgent need is to work with the food company towards creating a private protected area. Legislation is provided for these types of areas in Peru and they become part of the National System of Protected Areas. Furthermore, the local village, already subject to several educational campaigns concerning the Plantcutter, especially among schools (Figure 2.3), is well placed to facilitate such a process. A similar situation is faced by the southernmost site for the Plantcutter in this study, Monte Zarumo, but here the threat from agriculture is from the local peasant farmer community. Other examples exist of communities

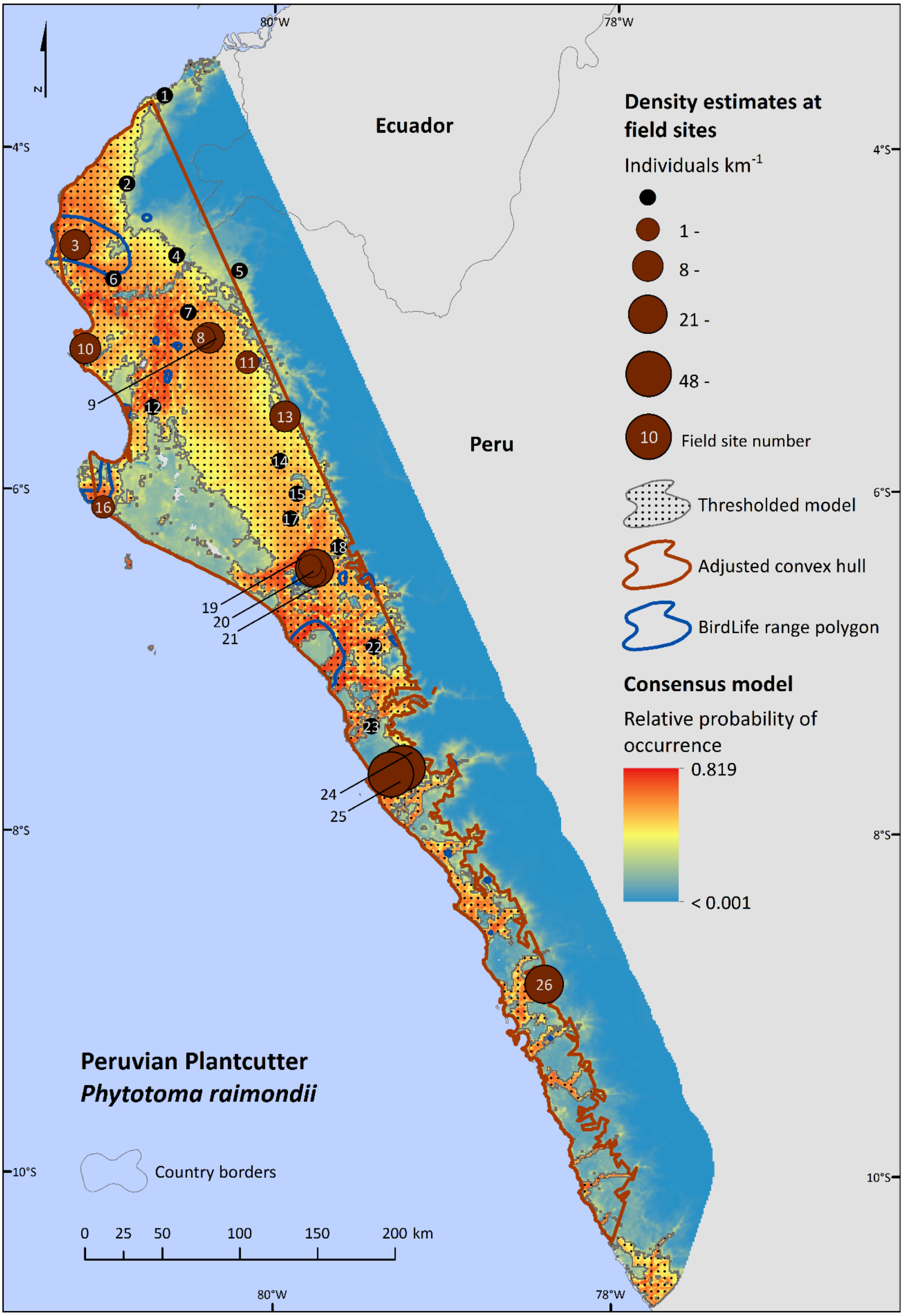


Figure 2.2. Consensus species distribution model for Peruvian Plantcutter *Phytotoma raimondii*, showing field sites, sized proportionally to field-based density estimates (see Chapter 3), with overlays of thresholded model (estimated Extent of Occurrence; see Chapters 2) and current BirdLife range polygon. The elevation-adjusted convex hull around occurrence points was used as the species specific accessible area for the model (see Chapter 2).

creating private reserves (e.g. project funded by Kew Gardens at the study site La Peña) and this remains a possibility here, but urgent work is also required.

Figure 2.3. The author participating in educational programmes on the Plantcutter at local schools in Paiján during fieldwork for this study. a, b) Talks and field trips with local schools, c, d) Mayor of Paiján (third from right; c) and representatives of food company (first and second from right; c) at a ceremony to donate bird guides and educational material to local 'wildlife' clubs.

The current provision of protected areas for the two threatened species above, the Near Threatened Tumbes Tyrant (), and biodiversity in general over the northwest of Peru is poor (Figure 2.4). A simple visual representation of modelled occurrence hotspots for the three bird species of conservation interest in this study was created by summing standardised consensus models, excluding areas outside the threshold values for each species. This shows that protected areas and proposed priority sites (More Cahuapaza et al., 2014) do not generally coincide with these hotspots, except at Pomac, in the mid study area, and around the lower slopes of Amotapes/Angolo National Park in the north (Figure 2.4). Two kinds of areas are urgently needed, first, specific sites for the Peruvian Plantcutter, as mentioned above (dispersal studies are also required for this species), and secondly, larger areas for the suite of the lowland Tumbes endemic species, including the Rufous Flycatcher, especially in the vast area of scrub forest between Piura and Chiclayo at the foot of the Andes. This area is currently threatened by large-scale irrigation projects (see Chapter 4), but is large enough to also afford some protection, and important connectivity, to the dryland biodiversity of north Peru.

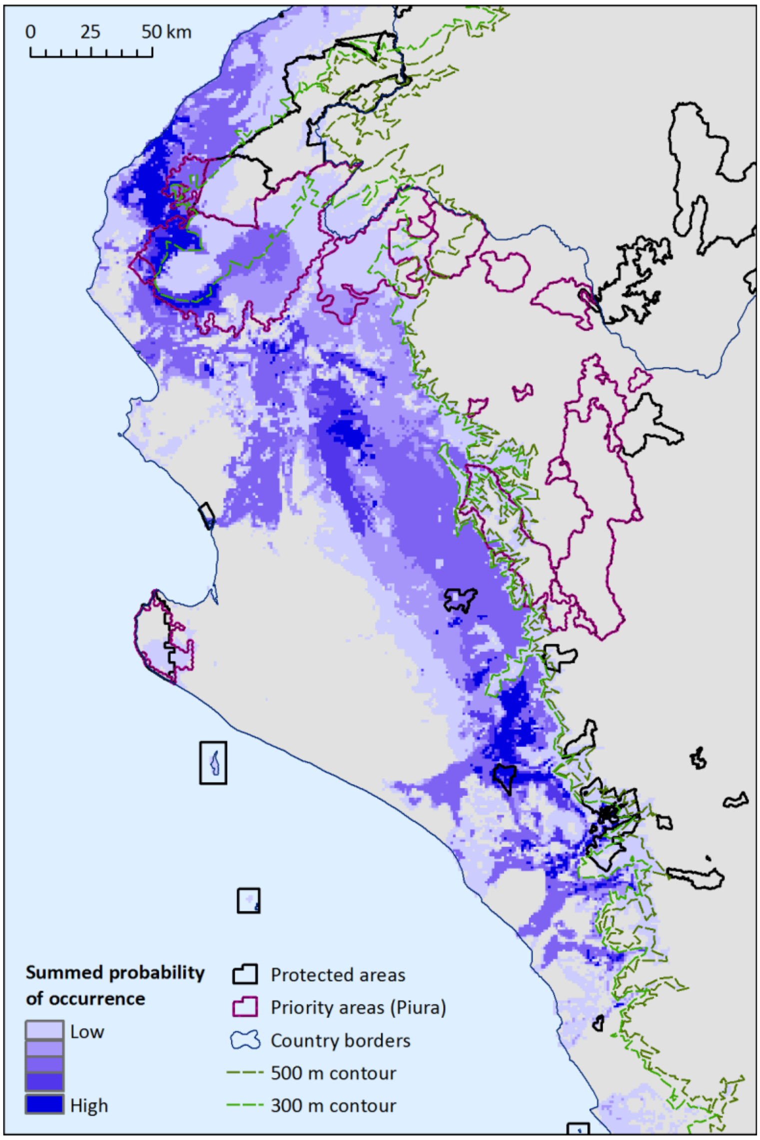


Figure 2.4. Summed species distribution models for Threatened and Near Threatened species showing protected areas and priority sites for conservation in Piura region. Model values were standardised prior to summing.

The north coast of Peru is home to a substantial part of the Peruvian population, and responsible for a significant part of the country's GDP, which will increase with new industrial agricultural development. Yet, at distances of no more than 30 km from the principal cities, rural communities farm the land as they have done for centuries, in some places, without electricity, and where water is still collected by mule cart. Of course, such communities welcome development, in terms of better accessibility, better educational infrastructure, running water, electricity, and the possibility of stable income. However, the choice between working 10 hours shifts on plantations without shade, earning a small but steady income, compared to growing what is needed for the family on small holdings, is not always a welcome choice to make. Today, while some look to progress in the form of conquering the desert, others lament the loss of traditional ways of life. For biodiversity, keeping development in check has been a longer fought battle. Despite millennia of changes in land use over the course of human history at civilisation's birthplace in the Americas, the extension of forests on the north coast may be at its lowest. Not only do these fragile habitats and their biodiversity depend on the balance between development and conservation, but ultimately, continued development may depend on the persistence of these natural ecosystems.

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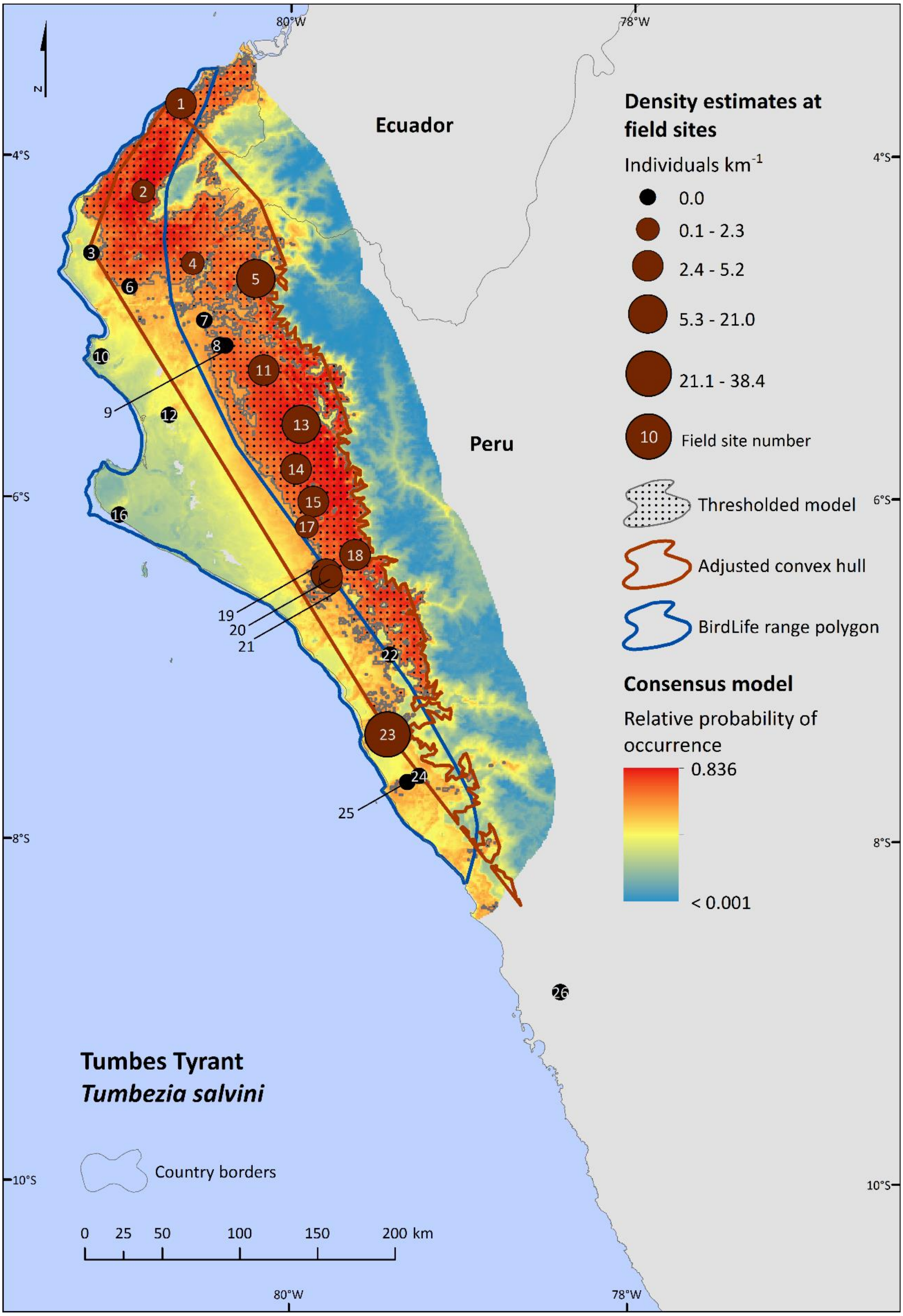
4 Appendices



Appendix 1. Consensus species distribution model for Near Threatened Tumbes Tyrant *Tumbezia salvini*, showing field sites, sized proportionally to field-based density estimates (see Chapter 3), with overlays of thresholded model (estimated Extent of Occurrence; see Chapters 2) and current BirdLife range polygon. The elevation-adjusted convex hull around occurrence points was used as the species specific accessible area for the model (see Chapter 2).

Piezorhina cinerea Photo: Murray Cooper