

DISTRIBUTIONAL ECOLOGY AND DIVERSITY PATTERNS OF  
TROPICAL MONTANE BIRDS

By

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To my parents, Mike and Laverne, and my loving and adorable partner in crime, Aaron

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The distributions that species exhibit along environmental gradients are geographical expressions of the range of ecological conditions that allow species persistence. My dissertation research used elevational gradients in the Peruvian Andes and in Central America to study range boundaries of birds along mountainsides and to understand implications of ecological reinforcement of range boundaries for landscape patterns of diversity. This includes description and modeling of elevational range size, position, and response shapes, community-level analysis of species turnover and composition, and experimental approaches with single species. Bird survey data collected along a 2700-m elevational gradient in Peru showed that most species exhibited symmetric response curves with elevation; however, 16% of species showed asymmetric response curves. Congeners typically showed little range overlap, and many were separated by elevational gaps. The prominence of gaps and symmetric responses suggests that biotic interactions such as competition rarely enforce range boundaries along this gradient. Bird surveys matched to plots with measured vegetation structure and tree inventory plots showed that birds had lower richness,

broader distributions, and lower turnover compared to trees, but patterns of turnover were largely congruent between taxa. Tree composition, vegetation structure and elevation together explained 82% of variation in bird dissimilarity. Covariation among vegetation structure, trees, and elevation made the largest contribution to explained variation, suggesting that vegetation structure and composition are highly linked to bird composition and diversity. Single-species approaches to range limits used heterospecific song playback experiments to test the hypothesis that interspecific competition between congeners with elevational replacements constrains range boundaries. Playbacks conducted in the Tilarán Mountains of Costa Rica showed that individuals at replacement zones exhibited aggressive territorial behavior in response to songs of congeners. As distance from replacement zones increased, aggression towards congener song decreased, suggesting a learned component to interspecific aggression and an important role of species' densities in development of these interactions. While competitive interactions appear weak in determining range limits in the Andes, these interactions are apparently important among species tested in Central America. These results invite future investigation into potentially varying conditions along elevational gradients that influence the strength of biotic interactions in limiting species.

## CHAPTER 1 INTRODUCTION

Ecologists have long been challenged to understand the ecological factors that maintain species range limits. Tropical mountain ranges, because of their high species diversity and density of range limits at small spatial scales, have enormous potential as study systems for understanding species distributions and the ecological factors that maintain them. My dissertation research uses elevational gradients in the Peruvian Andes and in Central America to explore and test several alternative ecological mechanisms that could determine range limits of montane birds.

Chapter two is an essay that places the study of range limits of montane birds in a context of alternative mechanisms and explores ways to independently assess the effects of abiotic and biotic factors on bird species distributions. This discussion centers on considering elevational distributions of species as a representation of species' fundamental and realized niches and outlines a species distribution modeling framework that can be applied to test the combination of factors that best predict distributions along gradients.

Chapter three uses an extensive database of bird surveys collected along the 2700-m elevational gradient in Manu National Park, Peru to examine the ranges and response curves of breeding birds with elevation. Huisman-Olff-Fresco models are employed to evaluate the shape of species responses and assess the long-held assumption of species' exhibiting symmetric, bell-shaped distributions along ecological gradients. Modeled species' responses are also used to make inferences on the influence of abiotic versus biotic interactions, with particular attention to the role of competitive interactions, in maintaining species distributions in this landscape.

Chapter four explores the association between bird communities and vegetation along the elevational gradient in Manu to determine whether patterns of species richness and turnover in bird and tree taxa are congruent and whether tree composition, vegetation structure, elevation, or a combination of variables best predict bird composition. These analyses are conducted for all birds and also within avian foraging guilds. The dataset consists of bird surveys and vegetation structure measurements conducted at a subset of sites in Manu that were spatially matched to 15 1-ha tree inventory plots. The analysis describes species richness and occurrence patterns for trees, all birds, and separately for avian guilds. Dissimilarity matrices and cluster dendrograms are used to present patterns of species turnover and nestedness with elevation and to examine cross-taxon congruence. Multiple regression on distance matrices and variation partitioning were employed to determine the unique and covarying contributions of trees, vegetation structure, and elevation to explaining variation in bird composition.

Chapter five presents a direct test of the role of biotic processes in maintaining range boundaries of tropical montane birds. One historically popular hypothesis, especially for birds, is that interspecific competition constrains ranges of closely related species that “replace” each other along elevational gradients. Supporting evidence, however, is based on patterns of occurrence and does not reveal potential mechanisms. This study, located in the Tilarán Mountains of Costa Rica, uses heterospecific playback experiments to test a prediction of this hypothesis in two genera of tropical songbirds, *Catharus* (Turdidae) and *Henicorhina* (Troglodytidae), in which species have non-overlapping elevational distributions along the Pacific slope. Behavioral responses to

song playbacks are evaluated to determine whether species respond aggressively to songs of congeners where their ranges meet. Additionally, species' reactions to congener songs were analyzed at increasing distances from replacement zones to determine whether responses were learned or, alternatively, whether they might reflect misdirected intraspecific aggression. Finally, the level of asymmetry in aggressive responses of species pairs at the replacement zone was evaluated to assess the likelihood of interspecific behavioral dominance.

Tropical mountains have been targeted as regions where climate change will have high impacts on narrowly distributed flora and fauna. Over the next century, tropical montane species may be forced to undergo upslope range shifts as large as the width of their elevational distributions. Any constraints on species' ability to shift their ranges, whether abiotic or biotic in nature, will likely reduce population sizes and increase their risk of extinction. This dissertation introduces a variety of approaches that can be used to understand ecological constraints on species' range boundaries in these landscapes so that the potential risks to species with climate change can be better evaluated.

## CHAPTER 2 A MECHANISTIC APPROACH TO ELEVATIONAL RANGES OF TROPICAL BIRDS

### **Introduction**

Ecologists have often used environmental gradients to understand the range of conditions associated with species occurrence and the reinforcement of species' boundaries (Whittaker 1975, Brown et al. 1996, Case and Taper 2000, Case et al. 2005, Holt and Keitt 2005, Holt et al. 2005). Elevational gradients, in particular, have been widely adopted as model systems for understanding range limits, in part because they provide large changes in abiotic conditions and habitats over relatively small spatial scales (Whittaker 1975, Terborgh 1971, Diamond 1973). Such changes go hand-in-hand with high beta diversity or species turnover, which describes the rate at which species composition changes across space, and high regional richness, or the total number of species occurring in a larger area (Magurran 2004, McKnight et al. 2007, Jankowski et al. 2009, see also Tuomisto 2010).

Elevational gradients worldwide differ considerably in both the typical breadth of species' ranges and levels of beta diversity, with gradients in tropical regions generally being characterized by species with narrower distributions than those of temperate species (McCain 2009). Likewise, elevational gradients in the tropics typically have higher beta diversity than those in the temperate zone (Buckley and Jetz 2008, Melo et al. 2009). These patterns are found across vertebrate taxa, although vagile, endothermic taxa (e.g., birds) tend to have lower rates of species turnover than sedentary, ectothermic taxa (e.g., amphibians; Buckley and Jetz 2008). This feature of tropical mountains—high species turnover generated by narrow ranges—can lead to levels of richness that rival tropical lowland rainforest at regional scales, making tropical

montane landscapes hotspots of global biodiversity (Myers et al. 2000). Revealing the mechanisms that underlie the narrow ranges of montane species in the tropics can help reveal mechanisms that maintain regional diversity.

The study of mechanisms underlying tropical montane species distributions takes on a new, practical importance in the face of climate change. Montane landscapes are expected to undergo vast changes and reorganization of community structure as species are pushed upslope in response to warming temperatures (Parmesan 2006). Even under moderate climate change scenarios (e.g., 3°C increase in the next century; Solomon et al. 2007), simply tracking the thermal environment would require species to shift hundreds of meters upward in elevation, given typical adiabatic lapse rates in the tropics of ~5-6°C/1000m (Colwell et al. 2008, Bush et al. 2004, J. M. Rapp, pers. comm.). In many cases, these distances are larger than the current width of species' elevational distributions. Moreover, there is mounting evidence that tropical species could be intolerant of even relatively small shifts in thermal environments, at least in ectothermic animals (e.g., Deutsch et al. 2008, Tewksbury et al. 2008, Huey et al. 2009). It has also been suggested that the tropical montane climate itself may be endangered, as it is predicted to be among the climates that may no longer exist after a century of projected climate change (Williams et al. 2007). The combination of these three strikes—restricted elevational ranges of species, high sensitivity of species to change, and major predicted shifts in environmental conditions—suggest that these regions of immense biodiversity will be especially vulnerable to changes in climate. Yet, for most taxa, we lack the fundamental data (see below) that will allow us to predict how communities will respond to shifting climate regimes, or what the key drivers may be.

One response to the growing urgency of predicting effects of future climate change on species has been the development and widespread application of species distribution models (SDMs; Peterson et al. 2002, Guisan and Thuiller 2005, Elith et al. 2006, Hijmans and Graham 2006, Guisan et al. 2007). One class of SDMs called 'bioclimatic envelope' models are built using climate variables that represent the range of sites where species occur. Climate envelopes are then projected onto present or future climate landscapes to generate predicted species distributions. Though widely employed, bioclimatic envelope models have been called into question for their ability to accurately predict species' ranges (see Pearson and Dawson 2003). The most widely held criticism is that the climate models do not explicitly incorporate biotic interactions, even though many such interactions could constrain species' ranges (e.g., competition, predation, mutualisms; Araújo and Luoto 2007, Cunningham et al. 2009, Chapter 5). When applied to species distributions in montane regions, however, an important limitation is the mismatch in spatial scale on which bioclimatic envelope models are most successful (e.g., regional spatial scales > 200 km: Pearson and Dawson 2003) and the scales important to mapping distributions of montane birds (e.g., site, local or landscape scales of 100 m - 10 km; Graves 1988, Stotz et al. 1996). Bioclimatic envelope models therefore may not perform well for species with either exceedingly small geographic ranges, or species with narrow dimensions to their range, such as those exhibited by many montane species. Moreover, the approach adopted by bioclimatic models is not designed to reveal potential drivers of species range boundaries. Yet, distinguishing among alternative underlying abiotic and biotic factors is critical to understanding why elevational ranges of species' vary among gradients,

how this influences variation in beta diversity, and how we should expect montane species to respond to climate change.

More recently developed techniques in species distribution modeling may offer promising avenues for testing the roles of abiotic and biotic forces on species ranges. At their core, SDMs are necessarily linked to ecological niches of species. As Hutchinson described, the niche space of an organism includes the range of all environmental conditions and factors that permit the persistence of that organism over time (Brown 1984, Holt 2009). The fundamental niche includes the range of abiotic environments suitable for a species in the absence of competition and other biotic interactions, whereas the presence of both abiotic and biotic factors in the environment restricts a species to its realized niche (Silvertown 2004). As the literature on species distribution modeling has expanded (see Guisan and Thuiller 2005 and Elith and Leathwick 2009 for reviews), so has discussion of the representation of species' fundamental and realized niches in SDMs (e.g., Pearson and Dawson 2003, Kearney and Porter 2009). Most have concluded that SDMs largely reveal species' realized niches because the models are based on observed occurrences of species, which are influenced by both abiotic conditions and biotic interactions (Guisan and Thuiller 2005). By contrast, a more recently developed approach to species distribution modeling, called "mechanistic niche modelling", determines the sites suitable for species based on species' measured physiological responses to a range of environmental conditions, rather than the values of climate variables where species occur (e.g., Kearney et al. 2008). Such mechanistic models of species' physiological tolerances may therefore reflect the fundamental niche rather than the realized niche (Kearney and Porter 2009,

see also Holt 2009). The combination of such mechanistic models with more traditional SDMs, by predicting species distributions based on aspects of their fundamental and realized niches, respectively, may provide new opportunities for testing hypotheses of the role of abiotic factors and biotic factors in species distributions.

In this essay, we propose an approach to understanding range boundaries that considers the interplay of both abiotic and biotic constraints on avian elevational distributions. Our aim is to develop a framework that incorporates empirical data as predictors within SDMs so that the relative influence of abiotic and biotic factors can be evaluated. The abiotic aspects of species' distributions, representing the range of conditions within the fundamental niche of a species, are considered through identifying physiological responses of species to changes in ambient conditions with elevation. A species' hypothesized "physiological niche" can be further modified or constrained by the biotic environment in various ways, forcing species to occupy only a subset of the locations that are physiologically suitable. We begin by outlining a method to estimate the physiological niche of montane birds, with special considerations for physiological limitations during different life history stages and possible physiological adaptations of species at different altitudes. This is followed by a discussion of potential biotic forces that could limit species to regions within their physiological niche, and a description of how these attributes can be incorporated into SDMs. We conclude by exploring various scenarios for responses of species to climate change in montane regions, given these potential abiotic and biotic forces on range boundaries.

### **Defining the Physiological Niche for Montane Species**

The physiological response of organisms to their environment, and the ability of organisms to maintain homeostasis, is perhaps the most important consideration in

defining a species' fundamental niche (Kearney and Porter 2009). On mountainsides, the most apparent and consistent changes with increasing altitude are declining ambient temperatures and reduced oxygen availability due to declines in barometric pressure, air density, and partial pressure of oxygen. Elevational trends in solar radiation, wind speeds and vapor pressure (i.e., a measure of atmospheric moisture that is independent of temperature) can be highly variable across seasons (e.g., J. M. Rapp, pers. comm.), and elevational patterns in annual precipitation are highly dependent upon the geographic position of montane slopes (e.g., windward versus leeward gradients; Lomolino et al. 2006). All of these conditions can combine to influence basic physiological processes of respiration, temperature regulation and water balance, as well as behaviors such as foraging, reproduction, and, in volant animals, flight physiology and mechanics (McNab 2002, see also Altshuler and Dudley 2006).

Efforts to understand the range of physiological conditions that tropical species can tolerate have stemmed, in part, from the classic hypothesis proposed by Janzen (1967). This hypothesis posits that "mountain passes are higher in the tropics" because tropical species have limited exposure to varying thermal regimes across seasons, and therefore should be adapted to a narrower range of physiological conditions compared to temperate-zone species. This hypothesis further predicts that tropical species should have narrower elevational ranges and tropical mountains should show higher species turnover (see also Ghalambor et al. 2006). Additionally, because daily temperatures undergo greater fluctuations at higher elevations in the tropics (e.g., above 3000m; Soobramoney et al. 2003) high-elevation species should have broader physiological tolerances than low-elevation species. As predicted by this hypothesis, elevational

ranges of species match location-specific thermal regimes (Ghalambor et al. 2006, McCain 2009) and at least ectotherms have narrower thermal tolerances in the tropics (Tewksbury et al. 2008, Huey et al. 2009). Few studies, however, have tested the actual physiological tolerances of tropical species (e.g., McNab 2001, Huey et al. 2009), with even fewer examining tolerances in tropical montane species (Soriano et al. 2002).

If species' elevational distributions were governed by their physiological capacity to tolerate the breadth of ambient conditions they experience, then species' distributions along gradients should reflect measured traits of their metabolic functions in varying climatic conditions (Kearney and Porter 2009, Monahan 2009). Energy expenditure under different thermal conditions, for example, is a commonly used physiological metric to evaluate the ability of organisms to persist in or colonize thermally distinct environments (Alexander 1999, McNab 2002, Angilletta 2009). For endotherms, the range of temperatures in which individuals do not need to expend additional energy to regulate body temperature is called the thermal neutral zone (TNZ; Schmidt-Nielsen 1997). If the physiological niche, as defined by the TNZ (e.g., Lindsay et al. 2009), matches the thermal range of species' observed elevational distributions, then it would suggest that elevational distributions are determined largely by thermal tolerances. Alternatively, if local habituation or acclimation to thermal environments occurs within species, the TNZ of a species could vary within its elevational range. The thermal tolerance of ectotherms, because their body temperature is subject to changes in ambient temperature, can instead be measured using thermal performance curves (Huey and Bennet 1987, Angilletta 2009), which plot the the relationship between some

fitness-related measure (e.g., survival, growth, reproduction, or capacity for movement) and body temperature (see Kearney and Porter 2009).

In montane environments, temperature may act in combination with reduced oxygen availability and lower air density, which vary systematically with altitude, to determine species' physiological tolerances. Because changing air densities alter the power requirements of flight, species may face important energetic or morphological constraints at these elevations, especially those species with high activity requirements (e.g., hummingbirds: Altshuler et al. 2004, Altshuler and Dudley 2006). While birds demonstrate particularly efficient respiratory and circulatory systems, high-elevation species can possess additional adaptations for enhanced gas exchange (e.g., higher baseline affinities of hemoglobin for oxygen; Altshuler and Dudley 2006). Thus, lower oxygen availability may constrain upper range boundaries of low-elevation species if the adaptive plasticity for anatomical or physiological traits to cope with hypoxia is constrained. Furthermore, limitations in dealing with oxygen concentrations may act independently or in combination with thermal tolerances to restrict species' metabolic performance. Perhaps, for endotherms, a temperature-oxygen concentration neutral zone, which reflects both the changes in temperature and oxygen availability with altitude, would be a better descriptor of a species fundamental physiological niche.

### **Physiological Constraints on Range Limits at Different Life History Stages**

For organisms with complex life histories, we may also need to consider physiological constraints at different stages of the life cycle. For example, although adult birds are endotherms, for much of their development, in particular during the egg and most of the nestling stages, avian embryos are essentially ectothermic. Embryonic development in birds is unique among oviparous vertebrates because it typically

requires direct transfer of body heat from incubating adults (Deeming 2002, Turner 2002). The energetic costs of incubation have generally been overlooked because they are thought to be far lower than the more obvious costs of feeding young. Recent studies suggest, however, that incubation is more energetically costly than previously realized (Williams 1966, Thomson et al. 1998, Tinbergen and Williams 2002). Because time and energy invested in incubation translate to less time and energy for foraging and self-maintenance, incubating birds face a tradeoff between parental care and self-care (Williams 1996, Tinbergen and Williams 2002, Turner 2002, Londoño et al. 2008). Elucidating this life history trade-off requires understanding what influences incubation rhythms (i.e., the length and temporal pattern of incubation bouts; Martin 2004), which, in turn, may shed light on the ability of different species to exist at certain elevations or habitats (Webb 1987). McCain (2009), for example, found that elevational ranges of tropical birds appear more constrained by temperature during nesting than during the rest of the year, which suggests that the physiological needs of young and limitations on incubation behavior of adults may contribute to limitations of elevational ranges in tropical birds. More generally, we predict that the elevational distributions of birds, especially at the upper limit of the elevational range where physiological conditions are most extreme, will be constrained to areas where species can no longer regulate egg temperature by varying any of the parameters that birds use to ensure proper embryonic development (e.g., nest insulation, location, incubation rhythm, egg size; Collias and Collias 1984, Martin et al. 2007).

### **Predicted Adaptations in Physiological Tolerances along Elevational Gradients**

Because physiological pressures change with elevation, we predict that species with different elevational ranges should vary predictably in their capacity to tolerate

environmental conditions. For example, when considering species at their resting metabolic rate (RMR), we might expect high-elevation species to use energy more efficiently when exposed to lower oxygen concentrations than species that only occur at lower elevations. Because reduced air density at high elevation may also constrain species, especially in foraging capacity, we might further expect high-elevation species that rely heavily on flight to exhibit morphological adaptations that enhance flight performance and reduce wing loading (e.g., Altshuler et al. 2004).

In the case of embryos, species occurring at higher elevations may be better able to develop at lower ambient temperatures than those occurring at lower elevations. The cooler the ambient environment, the more quickly eggs will cool during parental recesses from incubation (Webb 1987, Cresswell et al. 2004). Although embryonic exposure to cold temperatures during incubation is not as lethal as excessive upper temperatures (Webb 1987), embryos that grow at temperatures below optimum experience slower growth. Accordingly, embryos developing under cool temperatures should have low metabolic rates (Olson et al. 2006, Nikkilson 2007), which will allow slow transformation of egg resources into embryonic tissue rather than using them for self-maintenance. In this way, embryos in cold temperatures may avoid depletion of their resources and successfully complete development before hatching. Alternatively, parents of embryos that develop in cool temperatures could provide additional resources for the embryo (e.g., proportionately more yolk), to avoid the probability of resource depletion (Martin 2008), or modify their behavior to sustain an egg temperature closer to the optimum (e.g., by reducing length of trips or increasing nest insulation). Of course, the length of development is also affected by vulnerability to nest

predation (e.g., Ghalambor and Martin 2002), which also varies strongly with elevation (see below).

If oxygen concentrations constrain species' distributions at the level of embryonic development, then embryo performance curves should be affected by altered oxygen concentrations, and high-elevation species should perform better under lower oxygen levels. At high elevations, a larger functional pore area of egg shells would allow more oxygen diffusion into the shell, but would also increase water vapor loss from the egg, which occurs more readily at high elevations (Rahn et al. 1977, Carey et al. 1983). There is evidence that pore area of shells is lower in high-elevation species (Carey et al. 1989), suggesting that preventing desiccation may be more important than increasing oxygen transfer. Oxygen concentrations, however, may still constrain metabolic performance. Testing whether high-elevation species outperform those at lower elevations in reduced oxygen environments would address this possibility.

### **Biotic Challenges for Montane Species**

The underlying premise that the realized niche of species can differ from the fundamental niche was that biotic interactions (e.g., competition) may shape a species' distribution within its fundamental niche (Soberón 2007). In this section, we outline a variety of biotic interactions that, based on preliminary evidence, could be important determinants for range boundaries of montane birds. The evidence for each of these interactions is presented, followed by predictions for how observed species' distributions may be constrained within their physiological niche.

### **Predation Risk along Elevational Gradients**

In birds, nest predation is the primary source of mortality and is an important selective pressure on avian life history traits and nesting behavior (Ricklefs 1969, Martin

1993, Conway and Martin 2000). High levels of nest predation, for example, favor species with long incubation bouts to minimize activity around the nest that could attract predators and possibly shorter overall incubation periods (Ghalambor and Martin 2002, Martin et al. 2006, Massaro et al. 2008). Experimental evidence suggests that nest predation risk can influence nesting habitat choice (Fontaine and Martin 2006). The characteristically high rate of nest predation in the tropics, relative to the temperate zone, is also suspected to select for smaller clutch sizes in tropical birds (Skutch 1985) or smaller eggs (Martin et al. 2006), such that investment in any given brood is reduced and the ability to re-nest is increased.

Given the strong selection pressure imposed by nest predators, the distributions of montane birds could be determined by elevational variation in the risk of nest predation and in the kinds of predators present. Little is known about changes in nest predation risk along elevational gradients in the tropics, but existing studies suggest that predation pressure declines linearly with increasing elevation as diversity and abundance of avian nest predators decrease (Skutch 1985, Boyle 2008). Preliminary data from southeastern Peru (G. Londoño, unpubl. data) also suggest that rates of nest predation decline with elevation; however, change in daily survival rate across elevations is not linear. Rather, rates of nest predation decline dramatically over a short elevational range, from over 15% daily nest loss near 1000m to approximately 5% daily nest loss near 1500 m. Given a typical 25-35 day nesting period, these rates translate into losses > 97% near 1000m, but only 50-80% above this elevation. This abrupt change in nest predation rates may correspond with dramatic decreases in some of the major nest predators such as monkeys and snakes. Given these patterns in nest

predation, it is likely that the extremely high levels of nest loss found at lower elevations may prevent high-elevation species from extending their ranges down slope because their suite of life history characteristics would not have been evolutionarily shaped by such severe nest predation pressures. Moreover, if nest predation decreases nonlinearly with elevation, then we may predict that high-elevation species show realized distributions with truncated lower boundaries, despite being physiologically capable of occupying lower portions of the gradient. Low-elevation species, being tolerant of the highest of predation levels, should occupy their entire physiological niche, unless limited by other biotic interactions at high elevations.

### **Competitive Interactions and Species Replacements**

One of the most comprehensive studies of montane birds in the tropics concluded that competition is an overriding force limiting species distributions along elevational gradients (Terborgh 1971, Terborgh and Weske 1975). Direct competitive interactions, in particular, were used to explain observations of species' range limits that coincide along elevational gradients. This pattern of "species replacement" has been most commonly noted for closely related, usually congeneric species. The hypothesis that interspecific competitive interactions prevent the coexistence of strong competitors along elevational gradients was supported by the observation of species' range expansion along replicate gradients in which one of the competitors was absent (Terborgh and Weske 1975); however, community-wide patterns suggesting competition have not been experimentally verified.

For territorial animals such as birds, interspecific competition is often expressed as interspecific territoriality (i.e., territorial defense against individuals of other species; Orians and Willson 1964). Interspecific territoriality has been experimentally shown to

reflect the outcome of interspecific competition, such that the habitat segregation of species resulting from this behavior confers higher fitness compared to individuals whose territories overlap with those of competitors (Martin and Martin 2001). Numerous studies have used song playback experiments to elicit aggressive responses in territory holders and evaluate the strength of territorial behaviors (Martin et al. 1996, Trillo and Vehrencamp 2005, de Kort et al. 2009). Likewise, *heterospecific* song playbacks (e.g., playing songs of one species to another) have been used to detect aggressive interactions between species. In the lowland tropics of Peru, heterospecific playback experiments demonstrated interspecific aggression between species that partition early- and late-succession habitats, shaping local distributions in multiple genera of birds (Robinson and Terborgh 1995).

Heterospecific song playbacks experiments have recently been applied to species showing replacements along elevational gradients, allowing measurements of behavioral responses of interspecific aggression and evaluation of interspecific interactions that may underlie abrupt replacements. Recent work in the Tilarán mountain range in Costa Rica found that interspecific territoriality occurs at range boundaries separating congeners along large-scale elevational gradients (Chapter 5). For four of five species tested, individuals located near replacement zones (i.e., where territories of congeners are found within 100m of each other) showed aggressive territorial responses to congener song playbacks. These results support the hypothesis that interspecific aggression maintains range limits in congeners with elevational replacements.

Two other results from the same study system provide further insight into how interspecific aggression can constrain species' distributions. First, two of three species pairs tested in the Tilarán Mountains showed asymmetry in their responses toward congener songs, in which one species responded more aggressively than the other. This is common in many interspecifically aggressive species (e.g., Robinson and Terborgh 1995, Martin and Martin 2001). Second, species with interspecific territorial responses only expressed this behavior near replacement zones; when playbacks were conducted with individuals at increasing distances from replacement zones, the aggression of territory holders towards congener songs decreased. These results suggest that interspecific aggression has a learned component that depends upon levels of contact with heterospecific competitors; if species rarely encounter competing congeners, they do not develop a territorial response towards these species.

These biotic interactions should have consequences for the realized distributions of species along elevational gradients. Specifically, species that have interspecific territorial responses toward congeners at replacement zones should exhibit narrower, truncated elevational distributions compared to the range predicted by their physiological tolerances. Additionally, when considering elevational distributions of all species along the gradient, species that co-occur with congeners on a mountainside should, on average, occupy smaller portions of their physiological niches than species of monotypic genera, assuming that congeners are more often competitors than species from other genera.

Symmetric and asymmetric interspecific aggression will be expressed differently in the degree to which realized distributions of species match their physiological niches.

If aggressive interactions between species are symmetric, then both species should show narrower realized distributions than what their physiology would allow.

Alternatively, if aggressive interactions between species at replacement zones are asymmetric, dominant species should be able to successfully exclude congeners from sections of the gradient that it prefers. We would therefore expect dominant species to occupy a greater portion of their physiological niche along gradients, whereas subordinate species should occupy a smaller fraction of the areas where they could persist based on their physiology alone.

Local densities of interacting species at range boundaries will influence the strength of aggressive interactions and the degree to which realized distributions of species reflect their physiological niches. If the development of interspecific aggression depends upon the level of contact with heterospecific competitors, then we predict that any environmental factors or traits that influence species' densities would also affect the strength of interspecific aggression in maintaining range limits. When both interacting species are abundant at their replacement zone, they should exhibit strong territorial responses to congener songs, resulting in limited range overlap. When both species have low densities, territorial responses by either species should be comparatively weak and range overlap should be greater, perhaps allowing for closer matching between physiological and realized elevational ranges. When one species is more common than the other, the less common species should show stronger interspecific territorial responses, because it experiences a higher encounter rate of its competing congener, but it is unclear how much range overlap should be observed in these cases.

## **Mutualistic Interactions in Mixed-Species Flocks**

Birds are players in a wide variety of mutualistic interactions, with some spanning different trophic levels, as in the roles of birds as pollinators and seed dispersers of flowering plants, and others operating within trophic levels, as in the case of mixed-species foraging flocks. In the temperate zone, mixed-species flocks are largely transitory, but in lowland tropical forests, such flocks can be impressively stable, maintaining the same composition of individuals throughout the year. These flocks are organized around “nuclear” species, and other “core” species, which actively defend a joint flock territory against conspecifics, resulting in flocks primarily composed of single mated pairs of each species (Munn and Terborgh 1979, Powell 1979, Munn 1985). Tropical species differ in the extent to which they participate in such flocks. Previous studies of mixed-species flocks have ranked species’ by “flocking propensity”, including basic categories of obligate (>85% of the detections of a species), frequent (50-85%), and occasional flockers (Buskirk et al. 1972, Munn and Terborgh 1979, Jullien and Thiollay 1998). While studies of high-elevation flocks suggest a more dynamic structure than flocks in the lowlands (Buskirk et al. 1972, Poulsen 1996), no study has yet examined patterns of change in flock composition or the associations of flocking species’ ranges along elevational gradients.

If flocking species in montane forests are dependent upon mixed-species flocks for their foraging needs, then flocking behaviors may impose constraints on species’ distributions along gradients, causing interacting species to reach their range boundaries at the same elevations and, potentially, limiting them to subsets of their physiological ranges. Generally, we should expect species that depend most on mixed-species flocks to be those most likely limited by these mutualistic interactions. Obligate

flocking species, for example, should have range boundaries that coincide along gradients, whereas facultative or occasional flocking species should show independent range limits that are independent of other flock member species. In terms of the realized distributions of species along gradients, nuclear species would be expected to express elevational ranges that are constrained compared to what their physiological tolerances would allow. Species with lower flock propensities would not be expected to have range limits that coincide with nuclear or core species boundaries. Data from Weske (1972) from the Vilcabamba range of Peru provide preliminary evidence that discrete communities, where species have similar range boundary locations along elevational gradients, may occur in tanager flocks. Many of the same insectivorous species that depend upon flocks in the lowlands have upper range limits in foothills or cloud forest, but their reliance on mixed-species flocks at these elevations has not been investigated.

### **Habitat Structure and Vegetation**

The relationship between birds and vegetation has been a natural starting point for understanding the influence of biotic interactions on bird species' distributions (Wiens 1989, Block and Brennan 1993). Vegetation structure provides important cues that guide habitat selection in terrestrial birds (Rotenberry 1985, Lee and Rotenberry 2005) and also provides food resources and substrates used for shelter, nesting and foraging (Robinson and Holmes 1982, Cody 1985, Lee and Marsden 2008). Likewise, many plants rely upon birds for pollination and seed dispersal (Stiles 1985, van Schaik et al. 1993). In tropical lowland and montane forests, the variation in type and structural complexity of habitats has been shown to influence bird diversity and composition

(MacArthur and MacArthur 1961, Karr and Freemark 1983, Terborgh 1985), especially for some foraging guilds (e.g., insectivores; Terborgh et al. 1977; Chapter 4).

In tropical montane landscapes, vegetation undergoes striking changes from low to high elevations, shifting from lower montane rainforest to cloud forest to puna grassland above treeline (Richards 1996, Terborgh 1971, Patterson et al. 1998). Distinctive patches of vegetation can be found within each of these forest classifications. For example, bamboos, including *Guadua* spp. at low elevations and *Chusquea* spp. at high elevations, can form dense stands within forest. At higher elevations, exposed, windswept ridges are covered in dense, shrub-like vegetation with a short canopy, and landslides leave scars in various stages of succession across the landscape. Thus, even tropical montane landscapes that are largely unaltered by human activity can be extremely disturbance-mediated, resulting in a patchwork of low and high-canopy forest with distinct structural elements. Effects of this variation are readily seen in patterns of site richness in birds, and, at higher elevations, vegetation type influences levels of nestedness in bird composition (i.e., the degree to which species occur in nested subsets across sites) depending on canopy cover, canopy height, and ground cover (Chapter 4). Vegetation structure and composition can also influence patchiness of species within their elevational ranges. For example, bamboo stands and regenerating landslides are microhabitats that harbor specialist species in montane landscapes (Stotz et al. 1996). Such associations to particular vegetation types or to a range of structural elements in forest may shape the realized distributions of species along elevational gradients, limiting species to a subset of the range where species should occur based on physiological tolerances.

## **Modeling Species Distributions to Test Abiotic and Biotic Effects on Ranges**

Incorporating only physiology-based traits of a species into SDMs is useful because doing so portrays predicted distributions uninfluenced by the multitude of biotic factors that can affect species occurrence. If all physiological responses of a species to climatic conditions are represented, then SDMs should provide an accurate assessment of a species' fundamental niche (Kearney 2006, Kearney et al. 2008, La Sorte and Jetz 2010). These mechanistic niche models can be used, by themselves, to test hypotheses of the relevance of physiological tolerances to species range limits. For example, if mechanistic models underpredict occurrence (i.e., if a species is found at sites where the model predicts absence), then perhaps behavioral or genetic flexibility within a species may allow it to occupy a wider range of climates or, alternatively, spatial variation in climate parameters may create patches suitable for species persistence. If mechanistic models overpredict species occurrence (i.e., if a species is not found at sites where the model predicts presence), then additional variables may need to be incorporated to improve model results. This may include information on previously unmeasured physiological response parameters (improving the mechanistic model) or information on biotic pressures in the environment.

A primary difficulty with prediction of species distributions relying on mechanistic modeling of species' physiology is in how well the measured responses to abiotic conditions by species can be matched to conditions species would experience in the landscape. Spatial variation in abiotic conditions may be particularly important. For example, along elevational gradients, temperature decreases predictably with elevation, but microclimatic variation in the landscape at similar elevations can be caused by differences in solar radiation, forest structure, and cloud cover. The influence of daily as

well as seasonally varying conditions in temperature and moisture on species should also be considered when outlining areas that, climatically, should lie within a species' distribution. Moreover, behavioral and habitat use patterns may restrict species to a narrower range of microclimates than what is available in the landscape. The challenge is therefore to translate and map the physiological tolerances of species to the landscape such that the resulting model is useful for interpreting the role of physiology in species distributions.

Combining mechanistic niche modeling with variables that represent biotic interactions offers a robust approach to hypothesis testing of species range boundaries. Until recently, SDMs rarely explicitly included variables reflecting biotic interactions, despite widespread acknowledgment of their potential role in limiting species distributions (Pearson and Dawson 2003, Guisan et al. 2005, Elith and Leathwick 2009). Several studies have recently attempted to include such effects by incorporating predictors of the occurrence or abundance of interacting species, such as a critical host plant (Araujo and Luoto 2007) or a potential competitor (Ritchie et al. 2009), and determining whether including these variables improves model predictions. Other studies have inferred biotic interactions such as competition by demonstrating a lack of overlap in the distributions of potential competitors when models based solely on climate variables predicting co-occurrence (Anderson et al. 2002, Costa et al. 2008). Ideally, independently collected empirical data or experiments should support the role of biotic predictor variables on species occurrence (e.g., Cunningham et al. 2009). It is this data-driven framework that we recommend for examining the distributions of

montane birds, where the role of physiological and biotic response variables can be evaluated for both upper and lower range boundaries.

As they are described elsewhere, the output of mechanistic niche models and more traditional SDMs differ (Kearney and Porter 2009). Mechanistic niche models provide some measure of species' fitness (e.g., survival, performance, reproductive capacity) in response to variation in environmental conditions; thereafter, portions of the area of interest can be included within or excluded from the species' range based on whether site-specific climate variables allow suitable levels of the species' response. SDMs, by contrast, typically produce output in terms of probability of occurrence or abundance given values of environmental parameters across sites. Combining these techniques to test hypotheses on the roles of abiotic and biotic processes can be achieved in at least two ways. First, predicted distributions from mechanistic niche modeling and models built on biotic variables could be compared directly in their predictive accuracy (e.g., see also Hijmans and Graham 2006). Alternatively, a species' physiological response could be represented as a predictor that represents the abiotic conditions (e.g., metabolic rates associated with site thermal environments), and multiple models including abiotic and biotic predictors, or interactions of these, could be compared in their ability to predict species occurrence (Kearney and Porter 2009).

### **Scenarios of Climate Change Impacts for Tropical Montane Species**

Species may respond to future climate change in numerous ways in montane landscapes, and predicting the most likely scenario is important for prudent planning of biodiversity conservation. Overall, montane species are expected to show upslope range shifts to track optimal climatic conditions (Hughes 2000, Wilson et al. 2005, Parmesan 2006), which in tropical montane areas, should equate to movements of 150

- 200 m elevation for each 1°C increase (using adiabatic estimates from Bush et al. 2004, Colwell et al. 2008). This may be more plausible for birds, which have the capacity to shift quickly in response to changing climates (Thomas and Lennon 1999, Hickling et al. 2006, Tingley et al. 2009, Zuckerberg et al. 2009) than for more sedentary taxa such as trees, which may shift more slowly due to their shorter dispersal ranges and longer generations times (Huntley 1991, Iverson et al. 2004, Thuiller et al. 2008, Ibanez et al. 2009). These shifts also assume that temperature changes of this magnitude (e.g., changes in maximum and minimum temperatures, daily and seasonal variation and relative humidity) will make high- elevation, unoccupied sites suitable for a species and make previously occupied sites at lower elevations unsuitable.

Alternatively, if appropriate habitat microclimates can still be found within the current elevational ranges of species, then species may respond successfully by changing the spatial use of their current environment (e.g., Huey et al. 2009) rather than exhibiting elevational shifts. Another possibility is that elevational shifts, if governed by climate, will be asymmetric, with species expanding into new suitable environments and seeking appropriate microclimates through behavior in locations already occupied. Potentially, the range of thermal environments that species already experience may dictate the extent of range shifts that species will undergo. For example, high-elevation species in the tropics, which experience a large range of temperatures on a daily basis (Ghalambor et al. 2006; McCain 2009), may be less subject to range shifts compared to low-elevation species. Whether shifts, either locally or with elevation, are likely from a climate tracking perspective, is contingent upon the range of physiological tolerances of species.

Colonization of new suitable sites by species tracking changing climates may effectively shuffle the composition of local biotas, bringing species into contact that have not coexisted in the recent past. In this way, a wide range of species may experience shifting biotic pressures. Understanding what the current biotic pressures on species ranges are may make the consequences of novel combinations of species more predictable. For example, we expect that changes in the nest predator community along elevational gradients could introduce particularly intense selection pressures on nesting birds, in part because the current disparity in nest predation is so drastic between foothill and cloud forest elevations (see above). Upslope shifts in nest predators with climate change could have wide-ranging effects on the reproductive success of cloud forest birds. Additionally, direct competitive interactions between closely related species that currently show elevational replacements present a biotic hurdle for species range expansions that will likely depend on whether changes in the abiotic environment alter species' resource acquisition, the capacity of individuals to hold territories, and whether interspecific aggression is symmetric or asymmetric (Chapter 5). Dominant low-elevation species could effectively track climate changes, relegating subordinate species to higher elevations, whereas dominant high-elevation species may prevent upward range expansion of subordinate low-elevation species. Vegetation structure represents an important environmental feature used in avian habitat selection (e.g., Lee and Rotenberry 2005), but it is unclear to what extent bird distributions, if unhindered by other biotic interactions, will track rapidly changing abiotic conditions versus potentially slow changes in vegetation structure and plant distributions. If empirical data can be collected to map physiological tolerances of

species and assess biotic interactions at range boundaries, then more informed scenarios of range shifts can be explored.

While we have focused much of our discussion on abiotic and biotic pressures along intact elevational gradients, anthropogenic alteration of montane landscapes is widespread in the tropics and could present major barriers to range expansion of species in response to climate change. In the Andes, one of the most formidable barriers, even along most continuously forested gradients, is the human-maintained treeline at high elevations (Feeley and Silman 2010). In birds and many other taxa, this inflexible shift from high-elevation cloud forest to fire-generated puna grassland will likely squeeze cloud forest species into narrower elevational distributions. Though some studies show that cloud forest birds have broad elevational distributions in the Andes, there is a suite of species with narrow distributions in upper cloud forest that might be particularly susceptible to a treeline-climate change pinch (see Chapter 4, Patterson et al. 1998).

### **Conclusions**

The narrow distributions of montane species in the tropics make these communities exceptionally susceptible to global climate changes (Parmesan 2006), where species may be faced with upslope range shifts to track warming temperature regimes (Colwell et al. 2008). In total, nearly 30% of the world's threatened birds are restricted to narrow elevational ranges in tropical montane regions. Projections of such range shifts have typically taken the form of climate-envelope models, but these models make critical assumptions that species will track shifting temperature regimes. The degree to which we can rely on these models depends upon understanding how species will physiologically tolerate changing temperatures. Measurements of metabolic

traits in tropical birds worldwide are currently limited to fewer than 100 species (e.g., Wiersma et al. 2007), and only 13 are montane (McNab 2009). Yet, not even these studies have measured thermal or oxygen tolerances; they are virtually unknown for any tropical montane birds. Biotic interactions also likely serve as important limiting factors to tropical species' distributions, constraining species in ways not predicted by physiological tolerances alone. Empirical data on species' distributions, physiological traits and species interactions will allow multiple mechanisms potentially influencing range limits to be tested simultaneously for tropical birds. In addition to allowing more informed predictions of how species are likely to respond to climate change, these data will allow testing of numerous questions on the elevational distributions of birds: Are physiological tolerances of species greater at high elevations compared to low elevations? Are upper and lower range boundaries of montane species affected differently by abiotic and biotic pressures? Accordingly, are biotic pressures on species' ranges more likely at low elevations, or are abiotic pressures more common at high elevations? Where along elevational gradients are particular biotic pressures more intense? Can disturbance-mediated heterogeneous landscapes of tropical mountains affect patchiness of species distributions, or, alternatively, select for species that tolerate a broader range of habitats and microclimates? Are high and low elevation tropical species equally likely to show upslope range shifts with climate change? The possibility of addressing these and other questions continue to make elevational gradients exciting frontiers for future research on the ecology of species distributions.

## CHAPTER 3 RANGE SIZES AND RESPONSE SHAPES OF TROPICAL BIRDS ALONG AN ANDEAN ELEVATIONAL GRADIENT

### **Introduction**

Species distributions along environmental gradients represent the interaction of multiple ecological and evolutionary processes and have long served as systems to understand patterns in species' ranges and boundaries. Elevational gradients in particular, have been central to the study of species distributions and community organization (Terborgh 1971, Diamond 1973, Whittaker 1975) and, especially in the last decade, have been important venues for studies of diversity (Patterson et al. 1998, Navas 2003, Brehm et al. 2005, Herzog et al. 2005, McCain 2005, Jankowski et al 2009, Romdal and Rahbek 2009), constraints on and shifting of range boundaries (Chapter 5, Wilson et al. 2005, Merrill et al. 2008, Moritz et al. 2008, Tingley et al. 2009), and determinants of patterns in range size (Ghalambor et al. 2006, McCain 2009). Each of these areas is pertinent to predicting how climate change in montane landscapes will affect regional biodiversity (Shoo et al. 2006, Colwell et al 2008, Sekercioglu et al. 2008). In particular, determining the forces acting to shape the distributions of individual species will be key to making informed predictions for how those species will respond to future climate change (Chapter 2).

Hypotheses for the abiotic and biotic forces that influence species' distributions along elevational gradients can be informed by three basic characteristics of species distributions: (1) the size of the elevational distribution, which indicates the extent of species occurrence and the range of conditions species can tolerate; (2) the shape of the distribution, showing the way that species respond to conditions along the gradient through changes in abundance; and (3) the position of the distribution with respect to

other species, which can reveal potential interspecific interactions, when informed by species natural history.

Numerous mechanisms have been proposed to predict patterns of species' elevational range sizes along gradients. Janzen (1967) suggested greater seasonal variation and overlap in climate conditions across altitudes in temperate mountains compared to tropical mountains and proposed that temperate species should have broader physiological tolerances and wider elevational range sizes than tropical species. An extension of this hypothesis can be applied to single elevational gradients, predicting that elevational range sizes of species should increase with elevation to reflect the larger variation in daily temperature patterns at exposed upper elevations compared to lowlands (Ghalambor et al. 2006, McCain 2009). An alternative hypothesis for the same pattern is that mountain tops exhibit an "island effect", such that lower diversity and greater isolation at high elevations results in broader niches and larger elevational distributions through ecological release (McNaughton and Wolf 1970, MacArthur 1972). Finally, the mid-domain effect hypothesis, best known for its predictions of a hump-shaped pattern in species richness along environmental gradients, predicts that range sizes will be largest for species in the center of a bounded gradient due to constraints on the maximum attainable range size of species with midpoints close to gradient boundaries (Colwell and Lees 2000, Colwell et al. 2004).

Whereas elevational range sizes describe the extent of species' occurrence along gradients and patterns in environmental tolerance across species, they provide little information about how species respond to gradients within their range through changes in probability of occurrence or abundance. Ecological niche theory predicts

Gaussian unimodal distributions along environmental gradients; species reach their highest abundance at the center of their range and decline gradually toward the periphery (Austin 2005, 2007). This view of a bell-shaped, symmetric species' response has become a practical assumption for statistical treatment of species-environment relationships (e.g., ordination techniques: Palmer 1993, ter Braak 1985, Oksanen and Minchin 2002) and a conceptual foundation for testing ecological and evolutionary hypotheses related to species' ranges, referred to as the abundant-center assumption (Brown et al. 1996, Sagarin and Gaines 2002, Sagarin 2006). It is now recognized, however, that species interactions and extreme environmental stress along gradients may result in asymmetric species response curves (e.g., Austin and Smith 1989, Austin and Gaywood 1994). Describing the shape of these curves and relating curves of different species to each other can reveal when and why deviations from symmetric bell-shaped distributions occur and can direct further testing on the role of abiotic and biotic forces on species boundaries. Furthermore, knowing the underlying response shapes is of practical importance when modeling species distributions in relation to the environment (Oksanen and Minchin 2002, Austin 2007, Santika and Hutchinson 2009).

The position of a species distribution with respect to other species along gradients can be used as an additional line of evidence to test hypotheses on the abiotic or biotic factors that enforce range limits (Whittaker 1975). This aspect goes hand-in-hand with properties of a species' response shape. For example, species with elevational replacements, if maintained by competitive interactions, would be expected to show segregated distributions along gradients and perhaps truncated boundaries in the direction of a competitor's range (Terborgh 1971, Whittaker 1975). Alternatively,

comparisons of species with similar range positions and coincident range boundaries may indicate groups of species that are limited by similar underlying conditions (e.g., habitat boundaries, ecotones) or species with strong mutualistic interactions (see Chapter 2).

In this study, we provide survey data of 395 species of breeding birds along a 2700-m elevational gradient in the tropical Andes to describe the size of species' elevational ranges, evaluate the shape of species response curves with elevation, paying special attention to their symmetry, and, assess the position of species distributions with respect to other species along the gradient. To our knowledge, this is the first statistical analysis of species responses along an elevational gradient for any tropical vertebrate. From these analyses, we infer the role of abiotic and biotic interactions in maintaining species distributions along the gradient. In particular, we address the potential for competitive interactions to maintain boundaries between closely related species and the role of habitat association in determining species distributions.

## **Methods**

### **Study Site**

The study area is located on the eastern slope of the Andes in the Department of Cuzco, southeastern Peru (S13°03'20", W071°32'49") along an elevational gradient from 800 - 3500 m. Temperature decreases with elevation along this gradient, following an adiabatic lapse rate of approximately 5.2°C/km, and annual precipitation declines monotonically with elevation at a rate of approximately 1250 mm km<sup>-1</sup> (J. M. Rapp, pers. comm.). Whereas temperatures show little seasonal variation, there is strong seasonality in precipitation, with a dry season lasting from April through October (driest

periods in June and July) and a rainy season from November through March (with precipitation peaks in January and February; J. M. Rapp, pers. comm.). Avian nesting behaviors, including territory establishment and singing, generally begin during the late dry season (August) and continue at least through December.

Vegetation along the gradient shifts from montane rainforest to cloud forest to puna grassland (Terborgh 1971, Patterson et al. 1998), with patches of distinctive vegetation occurring within each of these broad habitat classifications (Chapter 4). Most notably, these vegetation patches include exposed ridge tops with stunted vegetation, patches of bamboo (*Guadua* spp. below 1500 m and *Chusquea* spp. above 1500 m) and vegetation in various stages of recovery following landslides, which are particularly common in mid- to high elevations where topography is steepest. The elevation of the cloud base, which marks the transition from montane forest to cloud forest, is located between 1400 - 2100 m, although this depends on season and time of day (J. M. Rapp, pers. comm.). Above ~2100m, biomass of mosses and other epiphytes increases markedly, serving as a biotic indicator of the saturation of forest by clouds and mist. Above ~2800 m, the cloud forest gives way to a stunted canopy, classified as “elfin forest” elsewhere (Patterson et al. 1998). In Manu, the transition between elfin forest and puna grassland varies from 3000 - 3500 m and is largely set by anthropogenic factors, specifically the history and extent of burning in puna grasslands for cattle grazing by high-elevation farming communities (Feeley and Silman 2010c). We sampled forest habitats along this gradient, stopping at treeline.

### **Bird Surveys**

The regional species pool within Manu National Park, including lowland and montane forest birds, non-forest species, and migrants, comprises nearly 1100 species

(Patterson et al. 1998, Walker et al. 2006). In this study, we focused on resident montane forest birds. Audio-visual point-count surveys were conducted during field seasons in 2006 - 2009 at 185 forested points along the elevational gradient, with an average of 18 - 19 points within each 250-m elevational zone. Surveys took place during the first half of the breeding season (July - November), when birds were most easily detected by song, in 2006 - 2009. Points were separated by at least 130 m along narrow trails and marked with a Garmin GPSMap 60CSx GPS unit and flagging tape. Sets of ten ten-minute counts were conducted between 5:00 and 9:00 hours on mornings without heavy winds or rain. Sites were revisited a total of four times throughout the study period (2006 – 2009), usually with two or more visits occurring within a single breeding season. Revisiting points a fourth time yielded 14% new species detections on average, whereas visiting more than four times resulted in only 6% new species detections, even in the most diverse parts of the gradient (J. Jankowski, unpubl. data). Thus, four visits to a given point typically provided a representative sample of detectable species while maximizing efficiency. Order of visitation to each set of points was reversed between visits to reduce biases due to temporal variation in species' detectability. During each count, all individuals detected were identified and their distances from the point were estimated. Individuals detected >100 m from the center of the point were not included in analyses because birds detected at longer distances may be at substantially different elevations from the elevation at the point in this steep landscape. All counts were recorded using an Edirol R-09 WAV/MP3 digital recorder with a built-in omnidirectional microphone for later review of species identifications.

We supplemented audio-visual counts with mist netting of birds to provide presence-absence information on cryptic species or species that vocalize infrequently. Netting was conducted using ten nets per group. An average of 5-6 groups were run within each 250-m elevational zone throughout the breeding seasons from 2005 to 2009 (total mist net hours = ~10,000). Mist nets were placed along or near trails at forested sites and were run for three days from approximately 6:00 to 17:00 hrs during favorable weather conditions (Chapter 4).

### **Data Analyses**

Species occurrence data from audio-visual survey points and from mist netting sites were combined to describe elevational ranges of each species. A species was considered present at a site if it was detected during any visit, or absent if it was never detected during the entire sampling history of that site. To visualize trends in range size along the gradient, species were ranked by the midpoint of their elevational range and plotted with elevation.

Species response curves along the elevational gradient were fitted to presence-absence data using Huissman-Olff-Fresco (HOF) models (Oksanen and Minchin 2002, Wilson et al. 2007). HOF models enable five hierarchical models to be fit to species presence-absence or abundance data along environmental gradients. These include, from most complex to simplest functions, V) skewed, or asymmetric, IV) symmetric, III) plateau, II) monotone, and I) uniform response forms. The most complex model, which fits a skewed or asymmetric response, is written:

$$\mu = M \frac{1}{1 + \exp(a + bx)} \frac{1}{1 + \exp(c - dx)}$$

where,  $\mu$  is the expected value (e.g., probability of occurrence, when using presence-absence information),  $M$  is the maximum possible value (e.g., equal to 1 when using probability of occurrence),  $x$  is the gradient of interest (elevation), which can be scaled from 0 to 1 for analysis, and  $a$ ,  $b$ ,  $c$ , and  $d$  are estimated parameters of the function (Oksanen and Minchin 2002). The simpler response forms can be derived from the asymmetric model by fixing one or more of the estimated parameters to constant values. HOF models were fitted to species presence-absence data using program JUICE v. 7.0 (Tichý 2002, Tichý and Holt 2006), which calculates species responses within the R software environment utilizing the 'gravy' package (R development Core Team 2010). A non-linear maximum likelihood procedure was used to estimate the parameters for the set of hierarchical models (Oksanen and Minchin 2002), and the final HOF model (I - V) was selected using AIC. JUICE allows fitting of species response curves using alternative models, including general additive models (GAM) using R package 'mgcv', general linear models (GLM) and bell-shaped, Gaussian responses. For visual comparison of species' response curves, data were fitted using GAM and Gaussian responses, in addition to HOF models (see Oksanen and Minchin 2002). All species detected at ten or more point-count locations or mist-netting sites were modeled. Species responses were calculated using either audio-visual count data or mist-netting data on occurrence, and relied on data from the survey method that resulted in a larger number of detections across sites.

Response curves with elevation were summarized in terms of shape, elevational range size and the placement of upper and lower range boundaries. Several species groups were examined for general trends to allow inferences about potential ecological

forces operating on species' ranges. These include lowland, cloud forest, and highland species, bamboo specialists, and species that share the elevational gradient with congeners versus monotypic genera. Two methods were used to assess evidence for direct competitive interactions among congeners: compression of elevational range size in multi-species genera compared to monotypic genera; and in the case of species replacement patterns, evaluation of asymmetric shapes to response curves with range boundary truncations adjacent to congeners.

## **Results**

### **Elevational Range Sizes**

Our surveys generated 13,415 audio-visual detections and 4,298 mist-net captures for 421 resident breeding bird species, 395 of which were found in forested sites (Appendix A). Of these, 351 species (89%) were detected during audio-visual surveys, whereas 269 species (68%) were detected during mist-netting. The mean elevational range size of species detected at ten or more sites within the study area was 865 m, and ranged between 83 m and 2525 m. This mean value, however, is biased towards smaller ranges by lowland (< 800 m) and highland species (> 3500 m) with elevational ranges marginally included within the study area. When considering only species whose complete elevational range falls within 800 – 3500 m (Walker et al. 2006, Schulenberg et al. 2007), the mean range size was 1021 m (ranging from 322 – 2173 m).

Species with narrower elevational ranges were found mostly at low and high extremes of the gradient, whereas most species occupying the middle portions of the gradient had relatively large range sizes (Figures 3-1a). This pattern remains even after species whose ranges extend beyond the study area were removed (Figure 3-1b). In

this restricted set of species, average elevational ranges of species (detected at  $\geq 10$  sites) with midpoints in the lowest third (800 – 1700 m) and highest third (2600 – 3500 m) of the gradient were 728 and 815 m, respectively, whereas the average elevational range of species with midpoints between 1700 – 2600 m was at least 500 m larger (1352 m). Likewise, a plot of the elevational range sizes of species versus their midpoints shows a lack of species with narrow ranges in the central portion of the gradient (Figure 3-2). This plot typically exhibits a pyramid shape due to geometric constraints on the attainable range sizes of a species given its elevational midpoint. For example, a species whose midpoint is located near a gradient boundary necessarily has a smaller range size along the gradient, whereas a species whose midpoint lies in the middle of the gradient could exhibit a variety of range sizes.

Most species were detected at very few sites (Figure 3-3). For example, no species occurred at even 50% of the 236 forest survey sites (including 185 audio-visual survey points and 51 net-group sites). Eighty-three percent of species ( $n = 326$ ) were detected at 30 sites or fewer, and 54% of species ( $n = 215$ ) occurred at 10 or fewer sites. Rarity found within this group of 215 species can be attributed to several potential causes (Appendix B). Nearly half (47%) of these species had lowland distributions that extended upslope no more than 300 m into the study area. One species had a broad highland range above the study area and just reached our high-elevation sites. Twenty-four species (11%) had rather inconspicuous behavior or resided in forest strata that were difficult to sample (e.g., high canopy) and were likely “rare” due to low detection probability. Another 17% of species were either habitat specialists with patchy distributions within the study area ( $n = 21$ ; e.g., streamside residents, bamboo

specialists), or were common in open or heavily-disturbed habitats and rarely sampled in forest (n = 14). One-fourth of the rare species (26%, n = 56) were generally detectable with netting or were conspicuous when present during counts, but nevertheless occurred at low densities across the landscape or had an especially narrow elevational zone where they are found. Much of this group was composed of small insectivores (mostly suboscines), hummingbirds, and large-bodied birds belonging to various foraging guilds.

### **Species Response Curves and Position of Range Boundaries**

Response curves were modeled for 164 species; 144 of these were modeled using count data and 20 were modeled using netting data (Appendix C). Of the total species modeled, 98 species (60%) exhibited symmetric response curves with elevation (HOF model IV; Fig 3-4), and 26 species (16%) showed asymmetric responses, in which one elevational boundary was more sharply truncated than the other (HOF model V).

Truncations were equally likely to occur on the lower or upper elevational range boundary for species with asymmetric responses (13 upper and 13 lower truncations).

Plateau responses from the upper or lower gradient boundary (HOF model III) were exhibited by only seven species, five highland and two lowland. Thirty-one species (18%) showed monotonic responses (HOF model II), in which probability of occurrence declined from one boundary of the gradient; 28 of these were lowland or lower foothill species and three were highland species. Only two species showed flat response shapes along the gradient (HOF model I). Response curves were generally similar between HOF and GAM models across species, showing similar range sizes, boundary locations, and symmetry for 85% of the 164 modeled species. In cases where the two

approaches differed, GAM models typically fitted more complex shapes than possible through the hierarchical HOF models (Appendix C).

Lowland species (i.e., species occurring down to 250 m; Walker et al. 2006) with ranges extending upslope into our study area always reached their upper elevational limits within the lower third of the gradient (800 – 1700 m). Of 43 lowland species with modeled ranges, 58% dropped out in a narrow elevational zone between 1000 – 1300 m, and 84% reached their upper range boundaries below 1400 m. There were comparatively few highland species (i.e., species occurring in forest or puna above 3500 m) that showed similar declines in occurrence moving downslope. Of the six modeled species with highland distributions, four had plateau response curves that did not reach lower boundaries until 2000 - 2500 m. Only two species showed a monotonic decline in occurrence from the highlands, one of which did not reach its lower boundary until 2000 m.

Cloud forest species included 75 modeled species with range optima, (i.e., the peaks of their modeled response curves) between 1400 – 2800 m, following the designation of Manu cloud forest in Patterson et al. (1998). Upper and lower range boundaries of these species were found between 1000 – 3300 m. Over half of cloud forest species showed lower range boundaries between 1100 – 1700 m (29% from 1100-1400 m and 28% from 1400 - 1700 m). Another 23% of species showed lower range boundaries farther upslope, between 2100 - 2500 m. Likewise, upper range boundaries of cloud forest birds were concentrated in two areas, with 50% occurring in lower cloud forest, between 1700 – 2200 m, and another 30% of upper limits occurring at high elevations, between 3000 – 3300 m. These patterns tend to characterize two

groups of cloud forest birds: those with optima occurring above and below approximately 2200 m. One-fourth of cloud forest birds ( $n = 18$ ) showed asymmetric response shapes, and there was an equal proportion of species with upper and lower range boundary truncations. The locations of these range truncations were not concentrated at any particular elevation.

Bamboo habitat specialists that were modeled included 12 species found in *Guadua* and one species found in *Chusquea*. Seven of the *Guadua* species showed upper range boundaries coincident or within 100 m elevation of the upper limits of *Guadua*, and three of these showed asymmetric response shapes with truncated upper range boundaries. The single *Chusquea* specialist that could be modeled (*Drymophila caudata*) showed a lower range limit within 50 m elevation of the lower limits of *Chusquea*.

A comparison of range sizes between species with and without congeners along the elevational gradient showed that the median range size for species sharing the gradient with congeners was only slightly narrower than the median range size for species in monotypic genera (689 m versus 757 m), and this difference between the groups was not statistically significant (Mann-Whitney test,  $Z = 0.8$ ,  $p = 0.21$ ).

Visualizing modeled species response curves of congeners along the gradient allows additional assessment of the potential role of competitive interactions at range boundaries. Generally, congeners partitioned the gradient, showing a rather uniform distribution of species optima with elevation (e.g., species in *Grallaria*; Appendix D, Figure D-13). Unexpectedly, most congeners that were modeled were separated by elevational gaps or showed little overlap (Table 3-1; see example in Figure D-21). Gaps

between congeners ranged from 50 - 700 m elevation, and were usually over 250 m elevation. Many of these congeners are easily detected by audio-visual counts (e.g., *Formicarius*, *Chamaeza*, *Anisognathus*), so the gaps are likely not due to low detection probability. Repulsion interactions at range boundaries between congeners, where the range boundary that is adjacent to a congener range shows truncation, were uncommon. Species in only five of 26 genera with multiple species exhibited asymmetric distributions with a truncated boundary abutting that of a congener. Truncations were reciprocal among these congeners in only one genus (*Myioborus*; Figure D-25).

### **Discussion**

Our results show several overriding features of montane bird distributions along this Andean elevational gradient. We find that elevational range sizes of species generally increase from foothill to cloud forest elevations, but decline toward the upper end of the gradient. The considerable majority of species have symmetric, bell-shaped responses to elevation, consistent with ecological theory. Asymmetric responses, however, were not uncommon, and at least a portion of these may be attributable to biotic interactions. Our analyses of range boundary position and response shapes across species groups suggest that both habitat association and competitive interactions may set range boundaries for selected species, but for many others, these particular biotic factors appear to be weak in determining elevational range limits. Congeners that partition the gradient, for example, have ranges separated by elevational gaps in the majority of cases. Below we discuss of each of these results in relation to predictions from the literature.

## **Elevational Range Sizes**

On average, range sizes of species were close to a kilometer wide (1021 m). This is generally larger than the average range sizes found by other avian studies on this and nearby gradients (e.g., averages between 710-807 in Patterson et al. 1998 and approximately 741 m in Terborgh 1971). Both of these studies, however, sampled lower elevations more extensively than in this study, and the inclusion of lowland species would certainly reduce the average range size. No species along the Manu gradient had an elevational range of more than 2200 m. Species with the most restricted ranges tended to occur in foothills and highland elevations, whereas species with the broadest ranges tended to occur in cloud forest. This pattern of larger range sizes in cloud forest is consistent with that reported by Patterson et al. (1998). This range-size trend is also consistent with patterns that would be generated by a mid-domain effect, in which species with range midpoints found near gradient boundaries necessarily have limited range sizes. Still, the nearly complete lack of species with narrow ranges in the middle of the gradient, and the association of these elevations with cloud forest habitat may also reflect biological phenomena. For example, it is possible that cloud forests, due to their frequent saturation by clouds and mist, contain key structural characteristics in vegetation that a core group of montane birds use when foraging (e.g., epiphytic growth), and the large elevational extent of these structural characteristics allows montane bird species to attain correspondingly large elevational distributions. To be conclusive, the frequency distribution of range sizes could be tested against expectations under a mid-domain effect (MDE; Colwell and Lees 2000) to assess the degree to which observed patterns in elevational range distributions reflect

biological processes versus geometric constraints on species ranges by gradient boundaries.

Our results do not support Janzen's (1967) hypothesis that species exposed to a wider range of climatic conditions (e.g., greater diurnal temperature variation at high elevations) show broader elevational distributions, except when comparing low-elevation and foothill species to cloud-forest species. Species in the highest third of the study area had relatively narrow distributions, which is contrary to this hypothesis. It is possible, however, that the reduced range size of species in the highest third of the gradient is a product of the severe habitat alteration above treeline. Anthropogenic disturbance, in the form of deforestation, fire, and grazing pressures maintains the high-elevation puna grassland throughout much of the high Andes and presents a hard boundary for forest species that require more than scattered patches of montane scrub for persistence (Stotz et al. 1996, Feeley and Silman 2010c). Thus, anthropogenic modifications confound the evaluation of range size patterns in forest birds along these gradients. Independent measurements of species' physiological tolerances (e.g., thermal tolerances) would be a more direct test of the mechanisms underlying Janzen's hypothesis (Chapter 2). This assessment would also allow this physiology-based hypothesis for increased range size at higher elevations to be distinguished from alternative mechanisms that are expected to produce similar patterns, such as the competition-based island effect proposed to affect species residing in low-diversity, high-elevation communities (MacArthur 1972).

A large proportion of the species detected in our study region were uncommon or rare. Although describing species' rarity was not an initial objective of this study, it is

noteworthy that approximately half of species detected could not be modeled effectively, despite extensive sampling; fifty-four percent of species (n=215) were detected at ten or fewer sampling points. Whereas some of these species are rare because of some sampling artifact (e.g., incompletely sampling the species' elevational range or low detection probability), a substantial number of species, 77, occurred at low-densities, had highly restricted elevational distributions, or were habitat specialists. Furthermore, another 102 forest species that are known to occur within the elevational range of our study area were never detected (Chapter 4; Walker et al. 2006). This suggests that rarity is a prevailing characteristic of the bird communities along this Andean gradient, much as it is in the neighboring Amazonian lowlands (Terborgh et al. 1990). Practically, the rarity of Andean birds makes the study of their natural history, range attributes and abundance patterns extremely challenging.

### **Species Response Shapes and Positions of Range Boundaries**

The majority of species (60%) had symmetric, unimodal responses to the elevational gradient, consistent with assumptions of ecological niche theory (Austin 2005, Austin 2007, Heikkinen and Mäkipää 2010). Asymmetric responses, however, were not uncommon (16% of species modeled), and response shapes in this more limited group may reflect biotic interactions or physiological stresses at range boundaries. Truncated boundaries of species with asymmetric responses were not confined to a particular elevation, nor were they more likely to occur at upper or lower limits of species distributions.

Our analysis of low-elevation species indicates that many species in this group reach upper limits at a similar elevational zone. At the community level, this transition from lowland to montane avifauna pinpoints the region of highest species turnover along

the gradient (Chapter 4). Given that along latitudinal gradients, southern range boundaries of species are often determined by biotic factors whereas northern boundaries are set by abiotic factors (MacArthur 1972, Gross and Price 2000), we may expect that along elevational gradients, biotic pressures should be more influential at lower limits of species' elevational distributions and abiotic or physiological pressures more significant at upper boundaries. Overall, physiological tolerances of tropical birds are still poorly known (but see Wiersma et al. 2007), but it has been shown that metabolic capacity for cold tolerance is more restricted for suboscines, which dominate the lowland bird community in Manu, in comparison to oscines, which represent a greater portion of the community at higher elevations (see McKechnie and Swanson 2010). Such limited flexibility in thermal tolerances, if widespread, may play a role in setting the upper limits of this lowland avifauna.

Analysis of range boundary positions for cloud forest birds, including species with optima between 1400-2800 m, indicate that these species can generally be divided into two groups with range optima below and above the location of the cloud base in the breeding season. This result is also consistent with community-level analyses along the gradient, which show increased species turnover in bird composition near 2250 m (Chapter 4). Within this general division of upper and lower cloud forest birds, species generally had scattered range boundaries, rather than concentrated boundaries at any single elevation. This suggests that, to some extent, montane species distributions reflect the physical changes in climate or vegetation (or both) along the elevational gradient. The cloud base effect in Manu, however, does not impose any sharp boundaries or truncations on species' ranges. Such "cloud forest ecotone" effects on

bird communities have been found along other elevational gradients in the tropics (e.g., Terborgh 1985a, Jankowski et al. 2009), though the degree to which avian elevational limits are affected is variable. Perhaps elevational gradients with more drastic changes in moisture over small spatial scales (e.g., rainshadow gradients; Jankowski et al. 2009) would be more likely to show montane species with truncated and spatially coincident range boundaries located at the cloud base.

Among the most distinctive microhabitats along the Manu gradient are the stands of bamboo that grow within forest, which are known to host avian specialists in the lowlands (Kratler 1997) and highlands (Stotz et al. 1996, Schulenberg et al. 2007). In montane areas, these stands often occur as a successional stage following landslides or treefalls. The upper limits of *Guadua* bamboo in Manu occur near 1500 m, and *Chusquea* extends from this elevation upward to treeline. Our results show that approximately half of the common *Guadua*-associated species reached their upper range limits well below the limits of this habitat type. It is possible that patches of *Guadua* found near its upper limits are very limited in extent and only attract species that can persist in smaller stands (e.g., *Hypocnemis cantator*, *Myrmotherula longicauda*, *Basileuterus bivittatus*, all of which drop out at 1500m). The only common *Chusquea* specialist seems to have its lower limit set by the existence of appropriate habitat.

Congeners that share the elevational gradient collectively showed little evidence for competitive interactions in maintaining range boundaries. Species within multi-species genera did not exhibit compressed elevational ranges compared to species in monotypic genera, and the majority of distributions of congeners along the gradient were separated by elevational gaps or co-occurred at range boundaries at low densities

(< 10% overlap of congener ranges). Repulsion interactions, evaluated by asymmetric response shapes with range truncation toward congeners, were relatively uncommon, occurring decidedly in three of 26 genera. Two other genera each contained one species that exhibited this pattern. Evidence of interspecific competitive interactions at range boundaries in mountain ranges elsewhere suggests that higher densities and sufficient contact between congeners may be a prerequisite for active or behavioral exclusion at range boundaries (Chapter 5, see also Terborgh 1971). Based on this, it is unlikely that the congeners partitioning the Manu gradient that were too rare to be modeled are limited by direct (interference) competitive interactions. While these results suggest that direct competitive interactions are not likely to maintain range boundaries at present, one cannot rule out the influence of historical interactions, nor can we assess the impacts of diffuse competition in these communities (see Terborgh and Weske 1975). Indeed, the well defined segregation and overdispersion in the range optima of most of these congeners along the gradient is highly suggestive of patterns resulting from selective niche divergence and resource partitioning described by ecological theory (e.g., Whittaker 1975).

Patterns of elevational gaps between avian congeners have been found elsewhere (Terborgh 1971), yet few hypotheses have been proposed to explain them. MacArthur (1972) suggested that along low-productivity resource gradients, competing species that partition this gradient may be separated by a zone where neither species could occur if levels of species' primary resources were sufficiently low. An alternative explanation, proposed by Cornell (1974), suggests that if species showing such replacements are more susceptible to parasites or pathogens of their congeners, and

fitness consequences are sufficiently negative, then elevational ranges of congeners could be separated by an intermediate region that neither species could colonize, and the size of this gap would correspond to the dispersal distance of the parasite via its vectors. Any local selection in the host for genetic variants for increased tolerance of the congener's parasites would likely be swamped by gene flow from the central portion of each species' range. It would also be useful to test physiological alternatives for the range boundaries of congeners exhibiting this elevational separation to determine whether these species' boundaries may be better explained by physiological specialization to the climatic conditions experienced within their ranges (see Chapter 2).

## **Conclusion**

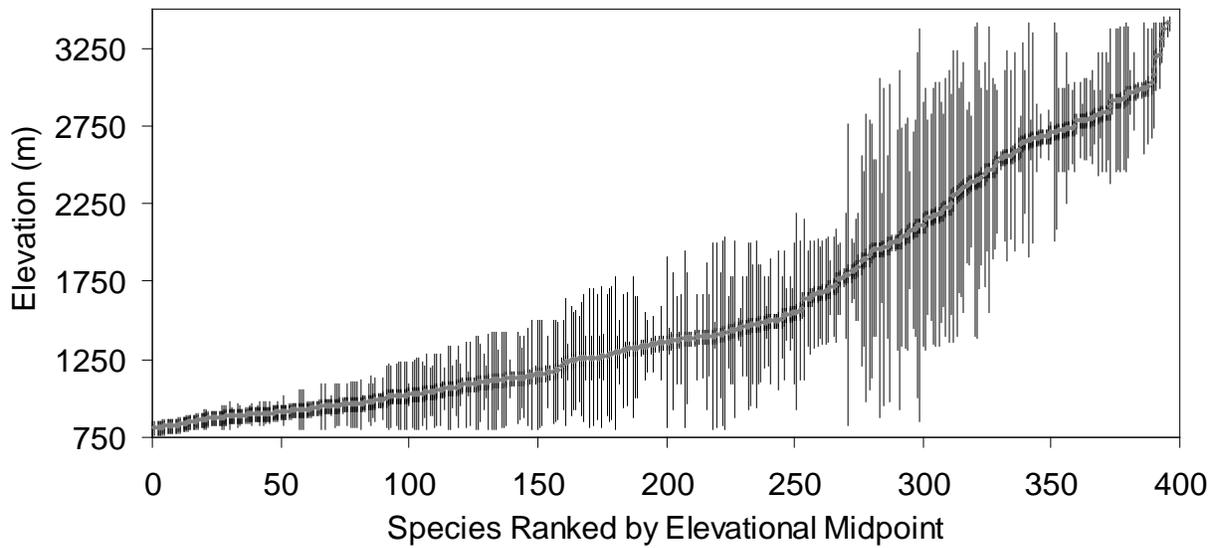
Our study makes an important step toward defining the underpinnings of species' range sizes, response shapes, and the potential roles of abiotic and biotic interactions along tropical elevational gradients. Range sizes of species show trends toward larger ranges at middle (cloud forest) elevations, and future analyses, including measurements of species' physiological tolerances and tests against mid-domain effects can be used to test alternative hypotheses for this pattern. Our analysis of species response shapes along elevational gradients in the tropics calls attention to several notable patterns in both the shape and position of species range boundaries that may present fruitful areas of focused research. These include understanding the mechanisms that cause lowland species to drop out within a narrow elevational window and the existence of elevational gaps separating congeners that partition the gradient. Finally, species-habitat associations and direct competitive interactions between closely related species may influence the overall position of species distributions with elevation, but they do not appear to maintain species' range boundaries along this gradient.

Table 3-1. Summary of elevational range overlap of species within multi-species genera. Only genera with >1 modeled species are shown. “Gap” indicates an elevational gap separates congeners along the gradient. “Low Density” indicates overlap with < 10% co-occurrence of congener ranges. “Overlap” indicates congener range overlap with ≥ 10% co-occurrence. “Repulsion” denotes an asymmetric response shape of at least one congener and range truncation in the direction of the other congener. Congeners separated by elevational gaps are assumed not to have repulsion due to competitive interactions (even if they exhibit asymmetric response shapes).

Genus	Gap	Low Density Overlap	Overlap	Repulsion
<i>Tinamus</i>	X			
<i>Patagioenas</i>	X			
<i>Geotrygon</i>	X			
<i>Phaethornis</i>	X			
<i>Trogon</i>		x		x
<i>Pharomachrus</i>	X			
<i>Aulacorhynchus</i>		x		
<i>Colaptes</i>	X			
<i>Xiphorhynchus</i>	X			
<i>Thamnophilus</i>	X			
<i>Chamaeza</i>	X			
<i>Formicarius</i>	X			
<i>Grallaria</i>			x	*
<i>Scytalopus</i>		x		x
<i>Mecocerculus</i>			x	
<i>Mionectes</i>			x	
<i>Ochthoeca</i>			x	
<i>Pipreola</i>			x	
<i>Turdus</i>			x	
<i>Hemispingus</i>	X			
<i>Anisognathus</i>	X			
<i>Diglossa</i>		x		
<i>Chlorospingus</i>		x		
<i>Arremon</i>	X			
<i>Myioborus</i>		x		x
<i>Basileuterus</i>			x	*

\* genera with > 3 species, where only one species shows asymmetry in response shape

a)



b)

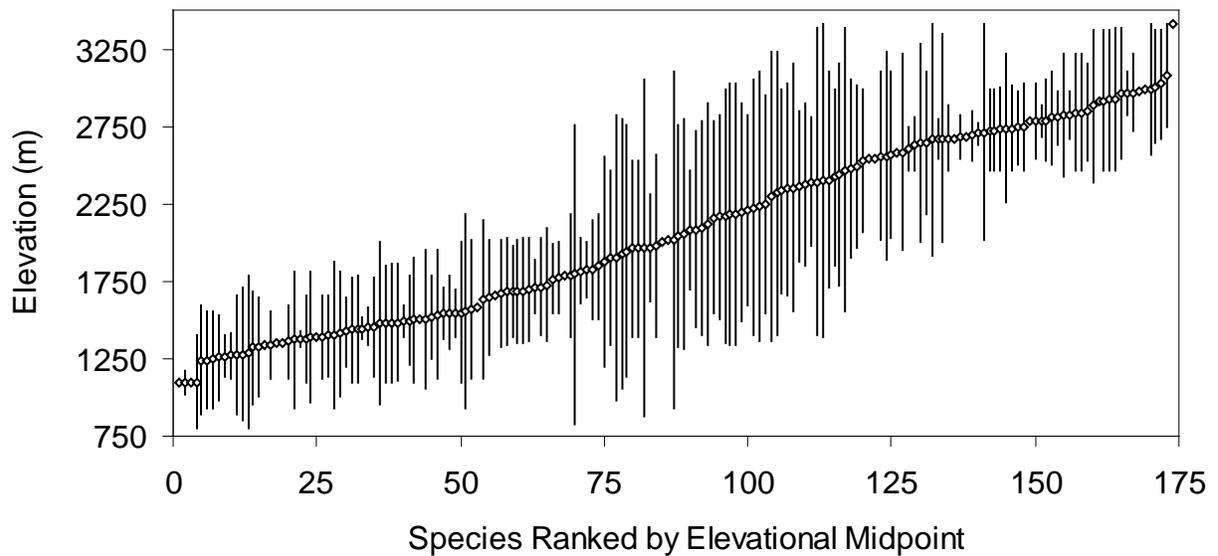


Figure 3-1. Elevational range profiles for birds netted or detected during point counts within the Manu study area. Species are ranked along the x-axis by their elevational midpoint. Bars indicate the maximum and minimum elevation for a) all species detected and b) the subset of montane species whose complete elevational ranges lie within the study area.

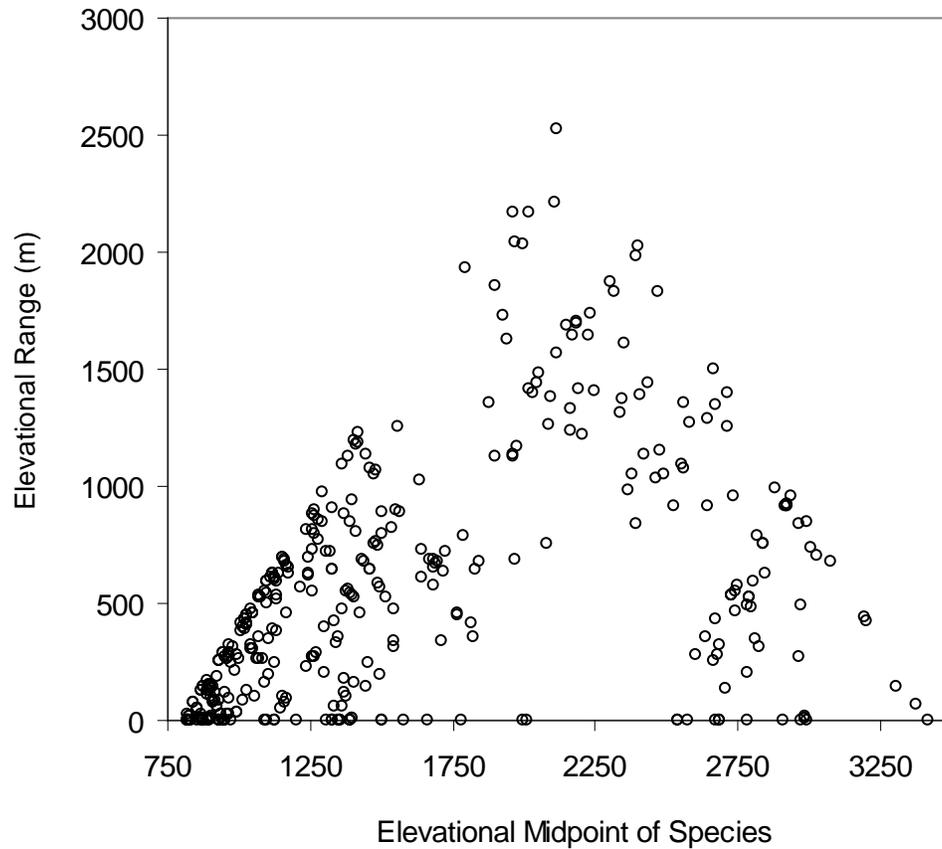


Figure 3-2. The elevational ranges of species that are completely encompassed within the study area are plotted against species' elevational midpoints. The pyramid shape of points demonstrates constraints on range size according to species' locations along the gradient, a product of the mid-domain effect. Empty regions within this pyramid indicate range sizes that are not exhibited by species with those elevational midpoints.

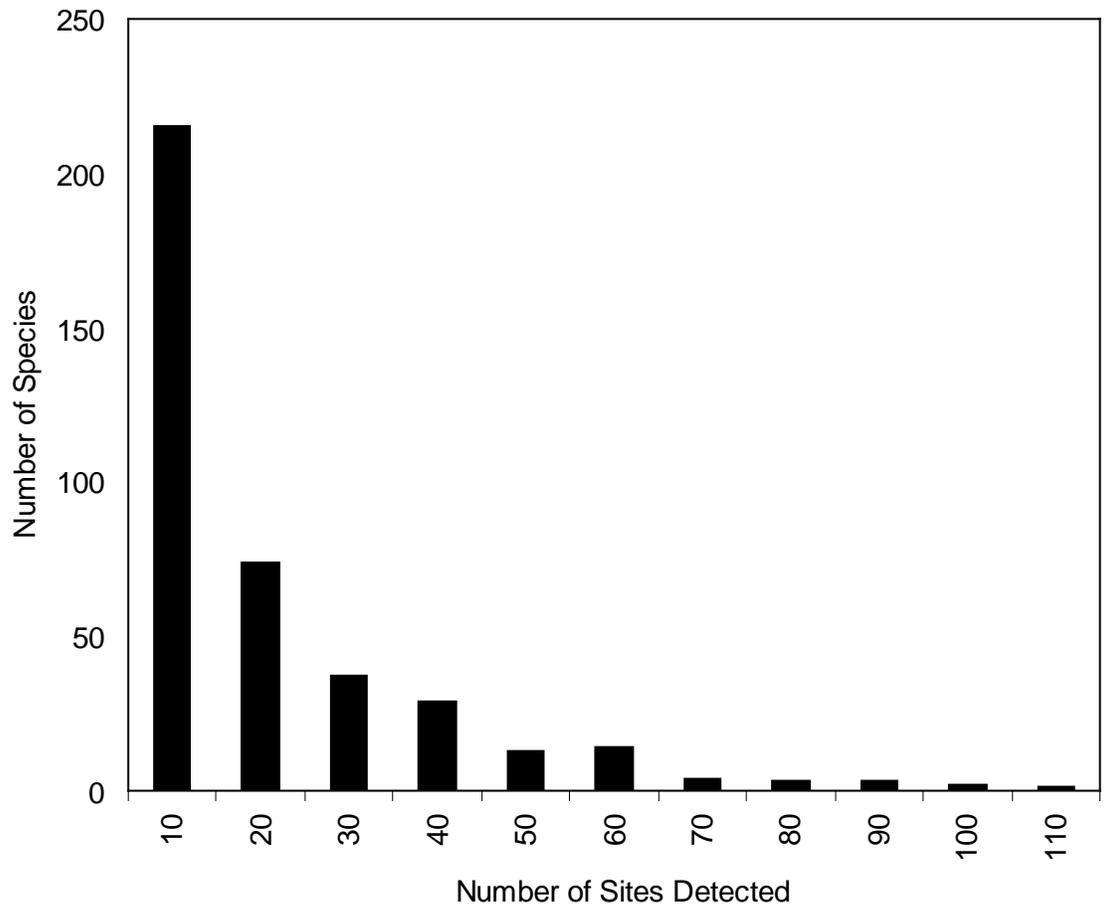


Figure 3-3. Frequency histogram for the number of sites where species were detected during netting (n = 51 sites) and point counts (n= 185 sites).

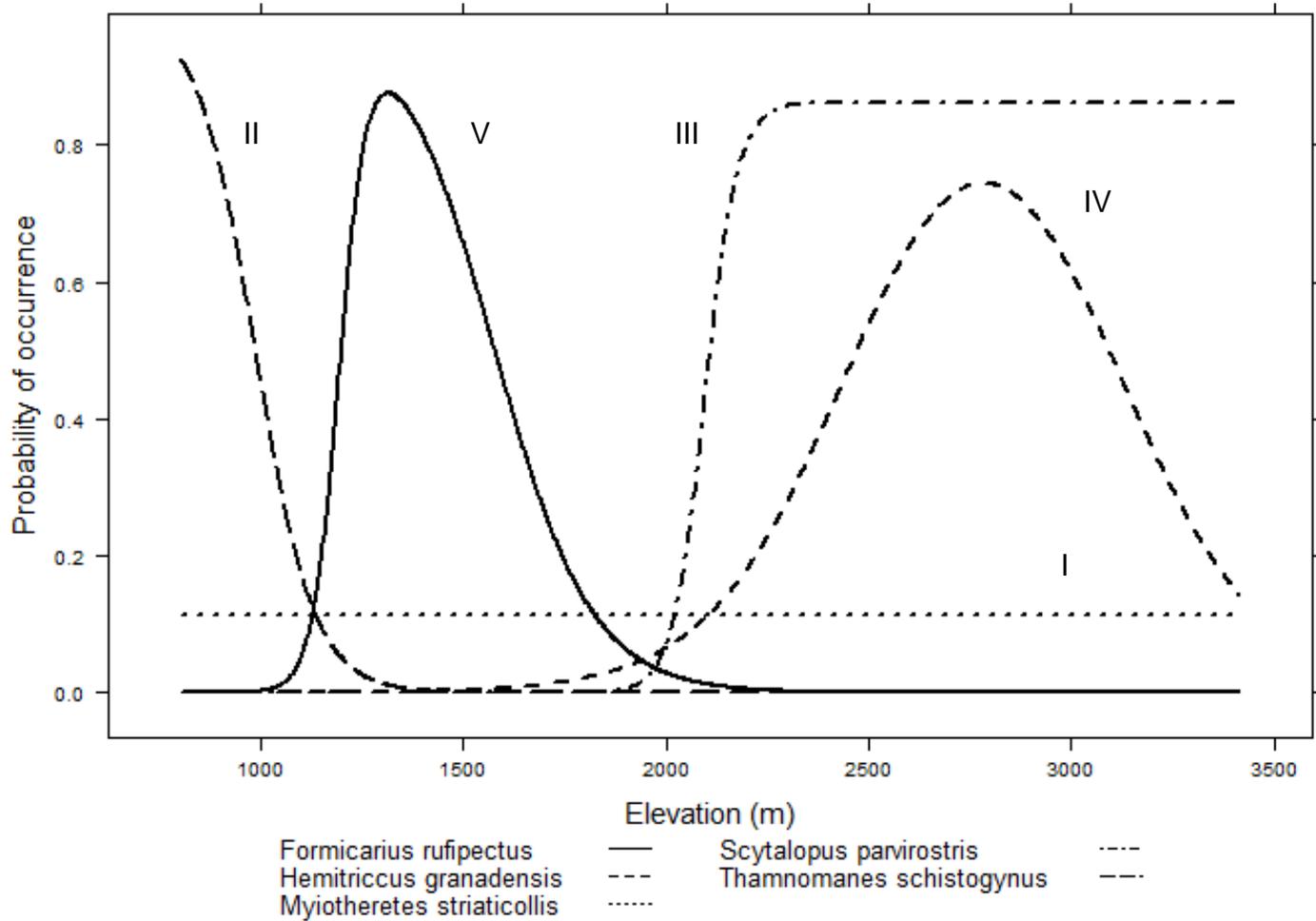


Figure 3-4. Examples of Huissman-Olff-Fresco (HOF) model types used to estimate species responses (as probability of occurrence) with elevation. The model types include: Asymmetric (V); Symmetric (IV); Plateau (III); Monotonic (II); and Flat (I). Species used to demonstrate each model type in the figure are listed below the x-axis.

## CHAPTER 4 THE RELATIONSHIP OF TROPICAL BIRD COMMUNITIES TO TREE COMPOSITION AND VEGETATION STRUCTURE ALONG AN ANDEAN ELEVATIONAL GRADIENT

### **Introduction**

Tropical montane species are especially vulnerable to future climate change (Parmesan 2006, Williams et al. 2007, Colwell et al. 2008, Tewksbury et al. 2008, Feeley and Silman 2010a). In tropical montane regions, plants and animals are often confined to narrow elevational ranges, producing belt-like distributions that may extend hundreds to thousands of kilometers in distance, but span only a few hundred meters in elevation (Stotz et al. 1996, Vázquez G. and Givnish 1998, Haber 2000, Jankowski et al. 2009). In response to warming climates, montane species are generally expected to show upslope range shifts in order to track optimal abiotic conditions (Hughes 2000, Wilson et al. 2005, Parmesan 2006, Colwell et al. 2008, Feeley and Silman 2010b). In birds, such shifts in geographic distributions could potentially occur rapidly, as has been noted in some Palearctic species (Thomas and Lennon 1999, Hickling et al. 2006, Parmesan 2006, Visser et al. 2009, Zuckenberg et al. 2009). Trees, on the other hand, may shift distributions more slowly than birds, due to substrate specificity, shorter dispersal distances, and longer generation times (Huntley 1991, Clark 1998, Iversen et al. 2004, Takahashi and Kamitani 2004, Thuiller et al. 2008, Ibanez et al. 2009). Even under scenarios of rapid plant migration, given that bird and plant distributions are set by factors that differ in intensity and kind, it is unclear to what extent bird distributions will track rapidly changing abiotic conditions versus changing tree distributions, which at least in part determine features of the environment used in avian habitat selection (e.g., Lee and Rotenberry 2005).

The relationship between birds and vegetation has been a natural starting point for understanding the influence of biotic interactions on bird species' distributions (Weins 1989a,b, Block and Brennan 1993). Vegetation forms a fundamental component of terrestrial avian habitats and provides important cues that guide habitat selection in birds (Wiens 1989a,b, Rotenberry 1985, Lee and Rotenberry 2005). Plants provide birds with food resources as well as habitat structure and substrates used for shelter and foraging (Holmes and Robinson 1981, Robinson and Holmes 1982, Cody 1985, Lee and Marsden 2008), and, likewise, many plants rely upon birds for pollination and fruit dispersal (Terborgh 1977, Stiles 1985, van Schaik et al. 1993, Burns 2004). In temperate regions, previous studies have shown a strong correspondence between avian assemblages and both the composition and structure of vegetation (Rotenberry 1985, Fleishmann et al. 2003, Lee and Rotenberry 2005, Fleishmann and Mac Nally 2006). While both aspects of vegetation are likely important, it has been suggested that structural differences best explain variation in bird species occurrence at larger spatial scales, while floristic differences best explain variation at smaller scales (Bersier and Meyer 1994, Lee and Rotenberry 2005). Such assessment of plant composition within structurally similar environments may occur if birds preferentially forage in particular tree species (e.g., Gabbe et al. 2002), perhaps responding to fine-scale structural differences that favor specialized avian foraging strategies (Robinson and Holmes 1984).

In contrast to temperate regions, the level of correspondence between tropical bird and plant communities is poorly studied, though generally, the type and structural complexity of habitats are known to influence bird species diversity and composition

(MacArthur and MacArthur 1961, Karr and Freemark 1983, Terborgh 1985b). Most studies addressing tropical avian-vegetation associations have adopted broad classification schemes for vegetation, using distinctive structures or dominant plant species to examine bird distributions (Terborgh 1985a,b, Robinson and Terborgh 1995, Kratter 1997). It has been proposed that different guilds of birds should be more sensitive to structural versus compositional changes in vegetation (Terborgh 1985b), with insectivorous birds that rely on specific foraging substrates responding to structural changes and frugivores being more directly linked to plant community composition (Hasui et al. 2007).

Along tropical elevational gradients, vegetation changes dramatically in both structure and composition (Grubb et al. 1963, Grubb 1977, Richards 1996). The coincidence of range limits in birds with distinctive habitat shifts along gradients (e.g., ecotones) suggests that vegetation may influence avian species distributions (Terborgh and Weske, 1975, Terborgh 1985a, Jankowski et al. 2009). In their survey of avian distributions along an elevational gradient in the Vilcabamba range of Peru, Terborgh and Weske (1975) reported that one-sixth of elevational range limits coincided with vegetation ecotones, affecting either upper or lower range boundaries of 28% of bird species in the study. This work suggests that, at least to some degree, birds respond to recognizable changes in vegetation along elevational gradients, but the level of correspondence of birds and plants, and the relative influence of vegetation structure and plant species composition on avian communities remains unknown.

Here we provide the first analysis, to our knowledge, of the correspondence of bird and tree assemblages for an environmental gradient in the tropics, focusing on a

forested elevational gradient from 800 – 3500 m in the Andes of southeastern Peru, one of the world's biodiversity hotspots. Using datasets of bird and tree species composition and information on vegetation structure along the same gradient, we describe the change in species richness and community composition for these taxa with elevation and determine the extent to which their patterns of species turnover are congruent. Then we ask how well species composition of birds across sites can be predicted by composition of trees, vegetation structure, elevation, or a combination of these factors. We also examine particular feeding guilds of birds, testing the hypothesis that foraging guilds that rely on plants directly for food resources (i.e., frugivores, nectarivores, granivores) are more closely linked to plant composition, whereas insectivorous birds are more influenced by structural changes in vegetation. If relationships between birds and vegetation are weak in these environments, which would be indicated by incongruent patterns of species turnover or low explanatory power of bird species composition by vegetation structure or floristic composition, then we would expect greater flexibility in bird-tree interactions, and range shifts of birds with climate change would be likely to occur more independently of vegetation changes on tropical mountains. If we find evidence for high correspondence of bird and tree communities, then range shifts in bird communities might be constrained by selective forces in birds for particular characteristics of vegetation.

## **Methods**

### **Study Region**

Our survey sites are distributed along an elevational gradient on the eastern slope of the Andes in the Department of Cuzco, southeastern Peru (S13°03'20", W071°32'49"). The study area is accessible from the Cuzco-Pilcopata highway, an

unpaved road on the eastern border of Manu National Park which descends from above treeline through the Andean montane forest of the Kosñipata Valley and into the Amazon basin. Our highest survey sites at ~3500 m elevation are located 15 km northwest of Acjanaco pass (S13°11'49.0", W071°37'11.5") and the lowest sites are found at ~800 m elevation in the Andean foothills, 5 km from the park guard station of Tono (S12°57'22.4", W071°28'53.9"). Survey sites are located on trails in primary forest or older secondary growth forest contiguous with primary forest, accessed either by foot or by wading through stream beds (Figure 4-1).

Vegetation along the gradient undergoes striking changes within this elevational range, including montane rainforest, cloud forest, and puna grassland as one proceeds from lower to higher elevations (*sensu* Terborgh 1971; Patterson et al. 1998). Within each of these broad forest classifications are patches of distinctive vegetation. Bamboos, including *Guadua* spp. at elevations below 1500 m and *Chusquea* spp. above 1500 m, are common across the landscape and in many areas form dense stands within forest. At middle and high elevations, some exposed, windswept ridges are covered in elfin forest -- short, dense shrub-like vegetation with a canopy less than 3 m high. Landslides are ubiquitous, leaving scars in various stages of succession across the landscape. Their incidence and return frequency vary with slope and geological substrate, which also contributes to overall habitat heterogeneity. The result is a patchwork of low and high-canopy forest with distinct elements of vegetation structure, even at similar elevations. While logistical constraints prevented us from surveying all of these vegetation types within each elevational zone, we were able to represent most of them in our survey sites.

## **Tree Censuses**

Trees were censused in 15 1-ha plots, established approximately every 250 m elevation within primary forest. Plots at 1500 m, 1750 m and 3000 m had two replicates on different transects that were separated by approximately 3 – 9 km. Within each 1-ha plot, every individual  $\geq 10$  cm diameter at breast height (dbh) was measured, tagged and identified to species or to morphospecies (Silman et al. in review).

## **Bird Surveys**

Prior to bird surveys, we used field seasons from 2004 - 2005 for mist netting (> 10,000 net-hours, see below) and for training in identification of bird vocalizations using a combination of personal song recordings, an online song database for Neotropical birds (xeno-canto.org), published recordings, and expert knowledge (D. Lane, R. Yaber, pers. comm.). During field seasons from 2006 - 2008, we established 172 permanent sites to conduct audio-visual counts along the elevational gradient, with an average of 17 (ranging from 7 to 34) forest bird survey sites per 250-m elevation. Due to steepness of the terrain and restricted accessibility, some elevational zones were sampled more broadly than others. Approximately half of these sites were associated with the 1-hectare tree census plots (see below).

Sites of audio-visual counts were placed at least 130 m apart (horizontal distance) along narrow trails and marked with a Garmin GPSMap 60CSx or 76Cx GPS unit and flagging tape. All counts were conducted between 5:00 and 9:00 hours by C. L. Merkord or myself on mornings without heavy wind or rain. Sites were revisited between four and eight times throughout the study period (2006 - 2008), with most visits occurring in the avian breeding season (July - November). Sets of 10 - 12 counts were conducted each morning, and the order of visitation to points was reversed between

visits to reduce biases due to temporal variation in species' detectability. Counts lasted for either 5 or 10 minutes, depending on the observer. During each count, all individuals detected were identified and their distances from the point were estimated. We did not use detections beyond 100 m from the point because birds detected at longer distances may be at substantially different elevations from the elevation at the point. Counts were recorded using a digital recorder with a built-in omnidirectional microphone (Edirol R-09 WAV/MP3 digital recorder) for later review of species identifications.

We supplemented audio-visual counts with mist netting of birds to provide presence-absence information on cryptic species or species that vocalize infrequently. Mist netting surveys were conducted within or immediately adjacent to all 1-ha tree census plots. Mist nets (2.5 by 6 to 12 m, 34 mm mesh) were placed both along and off trail and were run for three days from approximately 6:00 to 17:00 hrs during favorable weather conditions.

### **Vegetation Structure**

Vegetation structure was measured at each bird audio-visual count site within square plots of 10 by 10 m using a protocol adapted from Martin et al. (1997). Variables summarized from vegetation structure data generally describe aspects of forest vertical structure or understory vegetation density. Forest vertical structure variables included average canopy height, number of trees > 10 cm dbh (tallied within a 20 by 20 m plot surrounding each 10 by 10 m plot), total tree basal area, and percent canopy cover, obtained from hemispheric photos taken 1 m above ground level using a Nikon D-50 digital SLR camera and fish-eye lens mounted on a tripod and analyzed using Gap Light Analyzer v.2 (Frazer et al. 1999). Understory vegetation variables included density of

small stems (< 2.5 cm dbh; ≥1 m in height), density of large stems (≥ 2.5 cm dbh), percent cover by shrubs or saplings and bamboo (*Chusquea* spp. and *Guadua* spp.), and percent vegetation cover < 50 cm.

### **Avian Feeding Guild Classification**

Birds were classified into feeding guilds using references on diets of tropical birds, first-hand observations of foraging in the field, and fecal samples of birds captured with mist nets. Our classification primarily follows Terborgh et al. (1990) for species occurring in lowland and foothill tropical forest and a number of studies with diet information of highland species (Parker and O'Neill 1980, Poulin et al. 1994, Restrepo and Gomez 1998, Herzog et al. 2003). We designated species as frugivorous, nectarivorous, granivorous, omnivorous, or insectivorous. Carnivorous species, such as raptors, and piscivorous species, such as kingfishers, were not included in foraging guild analyses. Such guild classifications are admittedly crude, because very few species are strictly limited to a single food type. For example, even “specialized” nectarivores such as hummingbirds (Trochilidae) supplement their diets with insects for protein (Stiles, 1995). We expect that this guild classification, however, generally reflects each species' principal foraging method and dietary requirement.

### **Data Summary and Analyses**

Analyses were performed at the level of 1-ha tree plots (N = 15; hereafter “plot level”) and, for particular questions, at the level of bird survey sites (N = 172; “site level”). For plot-level analyses, bird survey data and vegetation structure data collected at bird survey sites were assigned to a 1-ha tree plot if the sites were located within 500 m horizontal distance or within 150 m elevation of the tree plot. If a survey site could be assigned to more than one tree plot by those criteria, then it was assigned to the plot

closest in elevation. Mist-netting locations were assigned to a tree plot if the netting occurred on or within 100 m of the edge of the tree plot. Bird species presence-absence data from associated survey sites and mist-netting locations were then combined to create a plot-species matrix. Tree occurrence data for each plot were used to create a presence-absence plot-species matrix of tree species composition. To summarize plot-level vegetation structure, values of variables were averaged across bird survey sites associated with each plot. Site-level analyses used bird audio-visual survey and vegetation structure data only. Bird occurrences at survey sites were used to create a presence-absence site-species matrix.

We examined patterns of species richness in trees and in birds (overall and within each guild) across plots. We then used several approaches based on species dissimilarity matrices to examine variation in bird species composition and to evaluate correspondence of bird and tree communities. Measurements of change in species composition across sites (e.g., beta diversity) that are expressed as dissimilarities can reflect two separate processes: change due to species loss (i.e., nestedness) and change due to replacement of one set of species by another (i.e., turnover; Koleff et al. 2003, Baselga 2010). Because our sites are distributed along an elevational gradient with a large disparity in richness across sampling locations, it is important to distinguish between these processes. We accomplish this by adopting an approach proposed by Baselga (2010) that partitions total beta diversity into contributions by spatial turnover and nestedness. In this approach, Sorenson's dissimilarity index ( $\beta_{sor}$ ), a common measure of total beta diversity, is broken down into two additive indices: Simpson dissimilarity ( $\beta_{sim}$ ; Lennon et al. 2001), which describes spatial turnover without the

influence of richness gradients, and nestedness-resultant dissimilarity ( $\beta_{nes}$ ), which is derived as the difference between  $\beta_{sor}$  and  $\beta_{sim}$  (see Baselga, 2010). In the absence of nestedness,  $\beta_{sor}$  is equal to  $\beta_{sim}$ . Each index varies between 0 and 1, with lower values indicating a greater proportion of shared species and larger values indicating greater dissimilarity between two locations. Dissimilarity matrices for  $\beta_{sim}$  and  $\beta_{nes}$  were calculated in R v. 2.11.0 (R Development Core Team 2010) using functions provided by Baselga (2010). At the site level, we summarized pairwise bird dissimilarity values of species turnover ( $\beta_{sim}$ ) and nestedness ( $\beta_{nes}$ ) for survey sites within four 650-m elevational zones to determine whether either beta-diversity metric changed along the elevational gradient. At the plot level, we examined dissimilarity values between adjacent plots for birds and trees to assess congruency in species turnover and nestedness between taxa. In cases with replicate tree plots at each elevation, the dissimilarity values of those plots with adjacent higher and lower plots were averaged. We also performed separate cluster analyses of bird and tree dissimilarity matrices using the  $\beta_{sim}$  index and an agglomerative hierarchical clustering algorithm (Legendre and Legendre 1998). Several grouping methods (e.g., single, complete, average, Ward's) were used to create cluster dendrograms. The dendrogram with cophenetic distances (i.e., the distance at which sites are clustered) that best corresponded to the original distances among sites was selected.

Finally, we addressed the statistical relationship of bird species composition to tree composition, elevation and vegetation structure through multiple regression on distance matrices (MRM; Legendre and Legendre 1998, Lichstein 2007), where the dissimilarity matrix of tree species composition ( $\beta_{sim}$ ), and distance matrices of elevation

and vegetation structure variables were used as predictors to explain variation in bird species dissimilarity ( $\beta_{\text{sim}}$ ). Models with all possible combinations of predictor matrices were examined to determine which combination explained the most variation in bird species composition across plots. We then used variance partitioning methods to divide the variation explained in bird dissimilarity into fractions representing unique contributions by each predictor alone and variation coexplained by a combination of predictors (Appendix E; Macía et al. 2007, Linares-Palomino and Kessler 2009). In the case of vegetation structure, we began with all structural variables in the model, then used backward elimination to remove variables without a statistically significant ( $p > 0.05$ ) contribution to explaining variation in bird dissimilarity. These structural variables were thereafter retained in more complicated models that included vegetation structure (e.g., vegetation structure and elevation). MRM analyses at the plot level were performed for all birds and independently for each foraging-guild. MRM analysis was also performed at the site level for the four 650-m elevational zones along the gradient to determine the variation of  $\beta_{\text{sim}}$  and  $\beta_{\text{nes}}$  explained in each zone, where predictor matrices included vegetation structure and elevation. All analyses were performed in R 2.11.0 using functions within packages *vegan* (Oksanen et al. 2008), *stats* and *ecodist* (R Development Core Team 2010).

## **Results**

### **Species Richness**

Our surveys revealed high regional richness across the 15-ha plots in both bird and tree communities (Table 4-1). Overall, 894 species of trees were identified from the plots, while 353 species of birds were identified from survey sites and mist-netting locations associated with plots. Per plot richness for trees was nearly 25% higher than

that of birds; the average number of tree species per plot was 99.4 (ranging from 38 to 171), and the average number of bird species per plot was 75.1 (ranging from 27 to 130). Species richness across plots was highly correlated between birds and trees (Figure 4-2a,b;  $r = 0.83$ ;  $p < 0.0001$ ), and the number of species per plot generally decreased with elevation for both taxa, although there was a low-elevation plateau in tree richness between 800 - 1750 m, above which the number of species dropped considerably (Figure 4-2a). When richness within foraging guilds of birds was analyzed, we found that the pattern of decreasing richness with elevation was driven primarily by loss of insectivores along the gradient (Figure 4-3a). Species richness in frugivores, granivores, nectarivores and omnivores also decreased with elevation, but only marginally in comparison with the loss of insectivores. Similar patterns across guilds are shown when species richness is plotted with canopy height (Figure 4-3b). Canopy height decreases with elevation ( $r = -0.68$ ;  $p < 0.0001$ ) and correspondingly, species richness increases with increasing canopy height, especially in insectivores.

### **Patterns of Species Occurrence, Nestedness and Turnover**

Individual species in both taxa showed narrow distributions along the elevational gradient, generating high species turnover at the community level. On average, individual tree species occurred on 1.75 of the 15 plots (12%), and bird species, on average, were associated with 3.1 plots (21%). Over half of tree species (55%) and one-third of bird species (30%) in our study were restricted to a single plot, and 82% of tree species and 50% of bird species were restricted to two or fewer plots. Only 5% of bird species, and not a single tree species, occurred on half or more of the plots.

At the plot level, pairwise dissimilarity values of species turnover ( $\beta_{sim}$ ) ranged from 0.15 to 0.98 in birds (mean =  $0.65 \pm 0.28$  s.d.) and from 0.49 to 0.98 in trees (mean

=  $0.86 \pm 0.13$ ). For both taxa, nestedness dissimilarity ( $\beta_{nes}$ ) made up a much smaller component of change in species composition, compared to species turnover. Values of  $\beta_{nes}$  across plots ranged from 0 to 0.38 (mean =  $0.07 \pm 0.08$ ) in birds and from 0 to 0.12 (mean =  $0.03 \pm 0.02$ ) in trees.

At the site level, pairwise bird dissimilarity values varied more than at the plot level, with  $\beta_{sim}$  ranging from 0 to 1 (mean =  $0.76 \pm 0.24$ ) and  $\beta_{nes}$  ranging from 0 to 0.86 (mean =  $0.05 \pm 0.09$ ). Mean pairwise dissimilarity values within 650-m elevational zones were not constant across zones (Table 4-2). Dissimilarity attributed to turnover ( $\beta_{sim}$ ) declined with elevation, such that pairwise points in high-elevation zones, on average, reached only two-thirds of the levels of dissimilarity found in the low-elevation zone. Dissimilarity due to nestedness of species ( $\beta_{nes}$ ), however, was between two to four times greater in the high-elevation zones and negligible between points in low-elevation zones. This indicates that variation in species composition at high elevations, to a greater extent, is determined by differences in richness, where the birds found at less diverse sites are subsets of the species found at more diverse sites. At low elevations, differences in composition across sites are largely due to replacement of one set of species by another, and richness across sites varies less.

### **Taxonomic Congruence in Birds and Trees with Elevation**

Analysis using dissimilarity indices of adjacent plots revealed several patterns in species turnover of bird and tree communities with elevation. Across 250-m intervals, trees showed much higher turnover, with adjacent-zone dissimilarity ranging from 0.5 to 0.75, compared to birds, whose dissimilarity values ranged from 0.2 to nearly 0.5 (Figure 4-4). Points of particularly high species turnover are apparent in both communities and occur in similar locations: (1) foothill elevations between 1000-1250 m;

(2) the middle of the gradient or “cloud forest” between 2000 - 2500 m (this turnover point occurs between 2000 - 2250 m for trees and between 2250 - 2500 m for birds); and (3) at treeline between 3250 - 3450 m (this zone also shows high turnover in trees, with the loss of all stems > 10 cm dbh above 3450 m). With the highest elevation plots’ comparison removed (due to spatial mismatch of habitat types sampled between birds and trees at treeline), dissimilarity in  $\beta_{sim}$  between adjacent plots was positively correlated between taxa ( $r = 0.65$ ,  $p = 0.02$ ). Dissimilarity of adjacent plots due to nestedness was generally higher in birds than in trees, with relatively high nestedness in cloud forest elevations (1750 - 2250 m) and in high-elevation forest > 3000 m. Dissimilarity due to nestedness in trees was consistently low along the elevational gradient, with slightly higher values in lower cloud forest (1750 - 1850 m). Dissimilarities in  $\beta_{nes}$  were not significantly associated in birds and trees in comparisons of adjacent plots ( $r = 0.17$ ,  $p = 0.30$ ).

Cluster analyses of bird and tree communities were constructed using the “average” grouping method, which produced dendrograms with cophenetic correlations of 0.84 and 0.85 for birds and trees, respectively. Bird and tree dendrograms contained three and four clusters, respectively, that generally separated plots by elevation (Figure 4-5). Birds and trees each contained a foothill elevation group (800 - 1000 m), but plots within middle elevations (i.e., lower cloud forest; 1250 - 2250 m) were clustered differently between birds and trees. Both taxa showed clusters identifying higher elevation plots (2500 - 3450 m)—in birds, groupings within this high-elevation cluster were not easily distinguished, compared to trees. Generally, compositional dissimilarities among tree plots were greater than among bird plots, as shown by the

'distance' at which clusters formed in these taxa. For example, in trees, no tree plots shared more than 60% of species (i.e., no pair of plots was joined with a 'distance' below 0.40; Figure 4-5), whereas in birds, the majority of plots were paired at 40% dissimilarity or lower, indicating, overall, that birds shared more species between plots, compared to trees.

Because bird survey sites assigned to each plot are located up to 150 m elevation above or below the plot itself, our bird sites sample a larger area and slightly broader elevational range compared to trees. It is therefore possible that higher species turnover in trees is generated by a sampling artifact, where narrower spatial sampling makes adjacent plots less likely to share species. To address this, we restricted our analysis to bird sites within 50 m horizontal distance and 25 m elevation of the tree plot. This resulted in slightly higher bird species turnover, as expected, with adjacent-plot dissimilarities ranging from 0.3 to 0.7 (compared to a range of 0.2 to 0.45 in the original dataset). Turnover in trees, however, was still substantially higher than in birds, with an average of 15% greater dissimilarity between adjacent zones in trees compared to birds, suggesting that taxonomic differences are also biological. We proceed with our original sampling design, as it better represents the regional bird diversity.

### **Explanation of Bird Dissimilarity by Vegetation Structure, Elevation and Trees**

Multiple regression on distance matrices (MRM) showed that a combination of vegetation structure, elevation, and tree dissimilarity best explained variation in bird dissimilarity across plots (Table 4-3). For the group 'all birds', and for all but one guild, this combination included all three predictors; however, models with only two of the three predictors often performed nearly as well. In granivores, the best combination included only elevation and vegetation structure variables. Overall, a large proportion of

the total variation in bird species dissimilarity was explained across groups (ranging from 44% in granivores to 82% in all birds). All groups except granivores had > 70% of variation explained.

Variation partitioning of MRM showed that co-contributions by vegetation structure, elevation, and trees explained between 14 - 31% of variation in bird dissimilarity across groups (Table 4-4). For 'all birds', frugivores, insectivores, and nectarivores, the remaining variation was largely explained by co-contributions of elevation and trees (29 - 32%), and uniquely by elevation (10 - 21%). In granivores, the remaining variation was explained by vegetation structure (13%) as well as covariation in vegetation structure and elevation (10%). In omnivores, unique contribution by trees (10%) as well as covariation in trees and elevation (26%) explained most of the remaining variation.

Bird species turnover ( $\beta_{sim}$ ) and nestedness ( $\beta_{nes}$ ) at the site level within 650-m elevational zones along the gradient was always best explained by a combination of vegetation structure and elevation (Table 4-5). Variation in species turnover patterns across sites was generally better explained than nestedness patterns; the total variation explained in turnover ranged from 12 - 74% across zones while the variation explained in nestedness ranged from 6 - 23%. The unique contribution by elevation and vegetation structure varied across elevational zones (Table 4-6). Elevation explained more variation in species turnover and nestedness in low-elevation zones and explained relatively little variation in high-elevation zones. Conversely, the unique contribution of vegetation structure to species turnover and nestedness was greater at high elevations.

## Discussion

Our surveys along an elevational gradient in Southeastern Peru include nearly 900 tree species and 350 bird species. For trees, there is little information beyond this study on regional diversity in the area, except in lowland communities (Terborgh et al. 1996, Pitman et al. 1999, 2001). For birds, a published list from this landscape by Walker *et al.* (2006) indicates that 582 resident species occur between 800 - 3500 m on the eastern slope of the Andes, with 562 species found within forest or along forest edges. Of the 209 species missing from our dataset, 58 were detected at other sites that were not associated with tree or vegetation plots (J. E. Jankowski and C. L. Merkord, unpubl. data). Three-quarters (74%) of the remaining missing species come from lower elevations (800-1700 m), and were likely missed due to differences in location and sampling intensity between this study and Walker et al. (2006). In particular, lowland species might show higher upper elevational range limits on slopes in closer proximity to the Amazon basin compared to their distributions in our study area (D. Stotz, pers. comm.). Additionally, Walker et al. (2006) present an accumulation of records from expeditions and surveys spanning three decades. Nevertheless, our avian dataset includes 63% of known resident species in this elevational range.

### Species Richness Patterns in Birds and Trees

Our results show that, generally, species richness in trees and birds decreased with elevation, resulting in a strong positive correlation of richness between taxa. A notable deviation from this correlation occurs at middle elevations, where trees maintain high, lowland-level richness and bird richness continues to decline. This discrepancy could be explained by several changes that occur independently of tree diversity at these plots. First, the foothill elevation of 1250 m marks the loss of canopy emergent

trees, greatly reducing the complexity of forest canopy structure, with consequences for richness of canopy birds and foraging flocks. In addition, this elevation marks a decrease in overall tree growth rates and fruit crop production (M. Silman, unpubl. data), reflecting decreases in above-ground net primary productivity. Reduced productivity could have strong consequences for the resource base of many avian guilds, and especially for insectivores, which can have specific, inflexible, and time-consuming foraging behaviors for seeking out cryptic prey (Naoki 2007). From an energetic perspective, increasing the foraging area to compensate for lower productivity should be comparably easier for frugivores and granivores (often large-bodied), and traplining nectarivores, which can travel widely in search of food (Stiles 1975).

Our results also clearly indicate that the loss of insectivores dominates the pattern of decreasing bird richness with elevation; changes in richness of other guilds are relatively slight. These patterns match those found by Terborgh (1977) in the Vilcabamba range of Peru. In addition to potential effects of decreasing productivity, discussed above, declining vertical forest structure with elevation may explain reduced diversity at high elevations, following the widely accepted association between habitat complexity and bird species diversity (e.g., MacArthur and MacArthur 1961; Cody 1985, Kissling et al. 2008). Canopy height may be important for insectivore diversity, in particular, with less space in forest vertical structure at higher elevations to support a large range of specialized foraging strategies. Understanding mechanistic ecological correlates of vegetation structure and elevation and their impacts on richness of foraging guilds needs further investigation, but at least in Neotropical birds, any

explanation for decreasing richness with elevation should address the overwhelming loss of insectivores.

### **Species Turnover, Nestedness and Patterns of Compositional Similarity**

While species richness of trees is generally higher than birds within each plot, these differences alone do not account for the much larger discrepancy in regional diversity found between montane trees and birds; regional richness in trees is more than 2.5 times that of birds. These differences may instead be explained by differences in beta-diversity of trees and birds along the gradient. Measures of dissimilarity between adjacent plots in bird and tree communities show that, overall, trees experience higher turnover with elevation than do birds. Because of the short distances between plots along this steep elevational gradient, and the high dispersal capacity of trees (Clark et al. 1999), the higher turnover in trees is not likely a result of dispersal limitation. Rather, increased turnover may result from higher diversity in tree communities combined with greater specialization to environmental conditions along gradients (e.g., temperature and rainfall), limiting establishment and growth to a narrow elevational range. Indeed, patterns of floristic composition in tree communities have been linked to edaphic characteristics in numerous studies (Potts et al. 2002, Ruokolainen et al. 2007, Bohlman et al. 2008), and specialization to edaphic characteristics has been identified as a likely driver of divergence among closely related species (Fine et al. 2005). Across our study area, one line of evidence suggests that soil and tree composition are associated. The lowest dissimilarity (or highest similarity) observed between adjacent plots occurred between those at 1850 and 2000 m ( $\beta_{sim} = 0.49$ ), with values equivalent or more similar than pairs of plots at the same elevation (e.g., replicate plots at 1500m and 3000m have values of 0.68 and 0.49, respectively).

These two plots are located on soils derived from granite, whereas other plots lie on Paleozoic shales and slates (M. Silman, unpubl. data). These results are consistent with results from elevational transects on distinct geologies from Mount Kinabalu, Borneo (Aiba and Kitayama 1999).

Despite differences in levels of species turnover in birds and trees, we found similar regions of punctuated turnover between these taxa along the gradient, suggesting that birds and trees are either associated, or both communities respond in parallel fashion to some other aspect of the elevational gradient. The matching peaks of species turnover of birds and trees in the foothills (1000-1250 m) are especially notable (Figure 4-4a); adjacent-plots are approximately 10% more dissimilar, followed by a steady decline in adjacent plot dissimilarity until 2000 m. In birds, the foothill peak in turnover is likely driven by the loss of species in insectivorous families (e.g., Furnariidae, Thamnophilidae, Tyrannidae) and increased representation from other families (e.g., Trochilidae). A second region of elevated turnover occurs in the middle of the gradient. In trees, the high turnover between 2000-2250 m is likely influenced by the soil type differences, mentioned above. In birds, high turnover between 2250-2500 m is likely influenced by the location of the 2250-m plot on an exposed ridge with truncated vegetation. The cluster dendrogram, however, also suggests a prominent division between low and high elevation flora and fauna at this location. In birds, for example, this zone marks the appearance of genera with high-elevation diversity centers (e.g., *Ochthoeca*, *Diglossa*, *Conirostrum*) and replacements within genera (e.g., *Grallaria*, *Scytalopus*, *Myioborus*). This zone roughly corresponds to the elevation of the cloud base during the dry season, which may be responsible for shifts in moisture

levels, with consequences for vegetation structure and composition. The third region of higher turnover occurs at treeline, where bird composition turnover is equivalent to the foothill peak in dissimilarity. This marks a primary ecotone transition in vegetation that birds appear to recognize, although this treeline shift could not be detected in the tree censuses due to the loss of stems  $\geq 10$  cm dbh above this ecotone boundary.

Compared to species turnover, nestedness contributed much less to dissimilarity in birds and trees across plots or to dissimilarity in birds across survey sites. There was, however, variation in the relative contributions of turnover and nestedness to site-level bird dissimilarity along the gradient. Specifically, nestedness was more prominent at higher elevations (e.g., > 2100 m), whereas dissimilarity due to turnover was greater at low elevations. Such a pattern in birds may be linked to variation in landscape characteristics along the elevational gradient. Exposed, windswept ridges and landslides are more frequent at middle to high elevations, creating patches of truncated or regenerating vegetation across the landscape. Accordingly, our results show that vegetation structure uniquely explained more site-level variation in bird dissimilarity (for both nestedness and turnover) in high-elevation zones. This suggests that high-elevation bird communities, at least to some degree, are composed of species specialized to structural aspects of vegetation, and generalist species that inhabit a wider range of vegetation types. Low-elevation bird communities, on the other hand, tend to show a larger component of species turnover (with little nestedness) across sites, which is attributable to elevational differences or co-varying effects of elevation and vegetation structure.

## Importance of Tree Composition, Vegetation Structure and Elevation

Multiple regression on distance matrices (MRM) and variation partitioning analysis revealed that vegetation structure, tree composition and elevational position of plots are all important predictors of bird community composition along the gradient. Moreover, these predictors covary — for all bird groups, the largest fraction of variation in bird dissimilarity was either co-explained by vegetation, trees and elevation, or co-explained by trees and elevation. Thus, while patterns of species turnover in birds were successfully predicted across study sites (up to 82% of variation explained), it is difficult to attribute the major fraction of explained variation to one variable over another. Within avian guilds, however, there was a moderate fraction of additional variation explained (e.g.,  $\geq 10\%$ ), beyond the covarying effects of vegetation, trees, and elevation, and this varied across groups. Granivore composition, more than other guilds, contained the most variation explained uniquely by vegetation structure, particularly by density of large stems, basal area of trees, and canopy height. Most granivores in our dataset forage on the forest floor (e.g., tinamous, wood-quail) or in the canopy, moving over large distances (e.g., parrots). It is possible that understory vegetation structure could influence occurrence of ground-foraging species, while canopy height likely influences occurrence of parrots. That said, most variation in this group remained unexplained, perhaps due to the rarity of granivores. All but two species occurred at 1% of bird survey sites (well below the average of 21% for all birds). Omnivore composition was more associated with tree dissimilarity compared to other guilds. Notably, this guild contained the greatest proportion of canopy species (87% versus 23-68% in other guilds). Based on these results, we find little support for the hypothesis that avian foraging guilds with diets based on plants are more closely associated with plant

composition. Moreover, variation in insectivore composition was not more associated with vegetation structure compared to other guilds.

### **Prospects for Montane Birds and Trees with Climate Change**

Most projections of species range shifts with climate change have used abiotic variables (e.g., temperature and moisture) to predict future “climate landscapes” in which species will likely be distributed with new temperature regimes. Given the climate-change predictions of a change of 4-6 °C for the study region over the next century (Cramer et al. 2004, Urrutia and Vuille 2009), and given an adiabatic lapse rate of approximately 5.6 °C per 1000 m elevation for tropical montane landscapes (e.g., Bush et al. 2004), we should predict that within a hundred years, a given elevation should reflect the present-day temperature environment of areas 500 m lower in elevation. Given their high mobility and dispersal abilities, we might expect birds to keep up with changing climates better than sessile taxa such as trees, but only provided that birds disperse and undergo habitat selection independent of tree composition or structural characteristics of vegetation. Our analysis has demonstrated a strong statistical correspondence between birds and aspects of both vegetation structure and tree species composition, although these effects were heavily confounded with each other and with elevation. Still, the congruence between bird and tree communities suggests that these taxa respond to the elevational gradient in similar ways, such that changes in birds may not occur independently of trees or vegetation. If this correspondence is driven by avian habitat selection, tropical birds may not show expected upslope range shifts in montane landscapes for a long time after climate change, perhaps at the expense of tolerating lower reproductive success within suboptimal thermal environments.

Patterns of vegetation structure with elevation may also impose community-wide constraints on shifts in bird distributions, especially if a multitude of bird species shift upslope in response to warming. Our results show that bird diversity was positively associated to canopy height along the elevational gradient. If structural complexity is indeed linked to bird diversity, there may not be sufficient space for numerous lower elevation species to shift their ranges into smaller forests. Lower canopies at higher elevations may impose an inflexible ceiling on the number and types of species that can share more truncated forests, and birds may collectively face a fundamental constraint on the structural space available to accommodate increasing diversity.

In conclusion, our analyses suggest that understanding birds' relationship to vegetation structure and composition will be important for predicting responses to climate change. Avian range shifts will likely rely on how climate change affects forest dynamics, successional pathways, and major physiognomic vegetation types found along these mountainsides. Where information on vegetation structure is available, models of species' projected distributions could incorporate vegetation parameters of future habitats that species will likely occupy, allowing alternative projections of species responses to climate change to be explored under varying scenarios of habitat constraints. In addition, understanding the variation in vegetation types occupied by bird species could be useful for projections. For example, vegetation generalists will likely be the best responders to climate change, and may reliably track physiological optima as thermal and moisture regimes change, whereas vegetation specialists will be more constrained by specific habitat requirements. With the narrow elevational distributions that so many Andean species exhibit in these heterogeneous montane

landscapes, such local scale projections that include information on habitat association will be necessary for precise evaluations of the threats that tropical montane species face.

Table 4-1. Plot names and elevation, study transects, and number of bird auditory-visual survey points and vegetation structure areas associated with each plot. Number of species of birds (detected by counts and netting or by counts only) and trees found on each plot is shown.

Plot Name	Study Region	Elevation (m)	Bird survey points/plot	No. bird species (counts & netting)	No. bird species (counts only)	No. tree species
TO_800	Tono	850	5	121	87	171
TO_1000	Tono	950	5	126	66	151
SI_1250	San Isidro	1250	8	130	95	163
SP_1500	San Pedro	1500	4	83	61	166
SI_1500	San Isidro	1500	8	99	61	168
SP_1750	San Pedro	1750	4	79	60	148
TU_1850	Trocha Union	1850	3	50	40	90
TU_2000	Trocha Union	2000	7	72	54	70
TU_2250	Trocha Union	2250	7	51	43	73
TU_2500	Trocha Union	2500	5	77	47	62
TU_2750	Trocha Union	2750	7	66	55	56
TU_3000	Trocha Union	3000	4	48	38	39
WA_3000	Wayqecha	3000	8	70	51	52
TU_3250	Trocha Union	3250	3	28	21	44
TU_3450	Trocha Union	3450	3	27	17	38

Table 4-2. Pairwise dissimilarity values for  $\beta_{sim}$  and  $\beta_{nes}$  across bird survey sites within 650-m elevational zones along the gradient. Number of sites per zone, mean (with standard deviation), minimum, and maximum dissimilarity values are shown for each index.

Elevational Zone	No. of Sites	Simpson's index ( $\beta_{sim}$ )			Nestedness-resultant index ( $\beta_{nes}$ )		
		Mean (sd)	Min.	Max.	Mean (sd)	Min.	Max.
800 - 1450 m	42	0.70 (0.17)	0.24	1	0.03 (0.03)	0	0.24
1450 - 2100 m	38	0.52 (0.12)	0.12	1	0.07 (0.07)	0	0.48
2100 - 2750 m	52	0.44 (0.15)	0	0.83	0.14 (0.15)	0	0.85
2750 - 3400 m	36	0.44 (0.15)	0	0.83	0.13 (0.12)	0	0.72

Table 4-3. Proportion of explained variation ( $R^2$ ) in bird species dissimilarity ( $\beta_{sim}$ ) in models from multiple regression on distance matrices (MRM). Models were performed for all birds and separately for each guild. Significance was evaluated based on 1,000 permutations.

Predictors in model	All birds	Frugivores	Insectivores	Nectarivores	Granivores	Omnivores
Vegetation Structure (VS)	0.36**	0.20*	0.34*	0.28*	0.37**	0.33**
Elevation	0.76**	0.72**	0.71**	0.70**	0.31**	0.55**
Trees	0.65**	0.52**	0.62**	0.60**	0.18*	0.61**
VS + Elevation	0.78**	0.73**	0.73**	0.74**	0.44**	0.61**
VS + Trees	0.70**	0.53**	0.67**	0.63**	0.41**	0.68**
Elevation + Trees	0.80**	0.73**	0.76**	0.74**	0.31**	0.66**
VS + Elevation + Trees	0.82**	0.74**	0.77**	0.78**	0.44**	0.71**

\*  $P < 0.01$ , \*\*  $P = 0.001$

Table 4-4. Percent of variation in bird dissimilarity ( $\beta_{sim}$ ) for all birds and for each guild explained uniquely by each predictor or co-explained by multiple predictors. Values were obtained by variation partitioning of model  $R^2$  values from multiple regression on distance matrices.

Predictors	All birds	Frugivores	Insectivores	Nectarivores	Granivores	Omnivores
Vegetation structure (VS)	2	1	1	4	13	5
Elevation	12	21	10	15	3	3
Trees	4	1	4	4	0	10
VS + Elevation	3	1	4	0	10	2
VS + Trees	0	0	0	1	0	1
Elevation + Trees	30	32	29	32	4	26
VS + Elevation + Trees	31	19	28	24	14	24
Unexplained	18	26	23	21	56	29

Table 4-5. Proportion of explained variation ( $R^2$ ) in bird species dissimilarity (using  $\beta_{sim}$  and  $\beta_{nes}$ ) in models from multiple regression on distance matrices (MRM). Models were performed at the site level for all birds within four elevational zones along the gradient. Significance was evaluated based on 1,000 permutations.

Simpson's index ( $\beta_{sim}$ )				
Predictors	800-1450 m	1450-2100 m	2100-2750 m	2750-3400 m
Vegetation structure	0.22***	0.31***	0.05**	0.27***
Elevation	0.73***	0.44***	0.07***	0.11***
VS + Elevation	0.74***	0.56***	0.12***	0.30***
Nestedness-resultant index ( $\beta_{nes}$ )				
Predictors	800-1450 m	1450-2100 m	2100-2750 m	2750-3400 m
Vegetation structure	0.04**	0.04*	0.10*	0.17***
Elevation	0.15***	0.04***	0.01	0.09***
VS + Elevation	0.18***	0.06*	0.12*	0.23***

\*  $P < 0.05$ , \*\*  $P < 0.01$ , \*\*\*  $P = 0.001$

Table 4-6. Percentage of variation in bird dissimilarity (using  $\beta_{sim}$  and  $\beta_{nes}$ ) explained uniquely by each predictor or co-explained by multiple predictors. Models were performed at the site level, for all birds within four elevational zones. Values were obtained by variation partitioning of model  $R^2$  values from multiple regression on distance matrices.

Simpson's index ( $\beta_{sim}$ )				
Predictors	800-1450 m	1450-2100 m	2100-2750 m	2750-3400 m
Vegetation structure	2	11	5	19
Elevation	52	25	7	3
VS + Elevation	20	20	0	8
Nestedness-resultant index ( $\beta_{nes}$ )				
Predictors	800-1450 m	1450-2100 m	2100-2750 m	2750-3400 m
Vegetation structure	3	3	11	14
Elevation	14	3	0	6
VS + Elevation	2	1	0	3

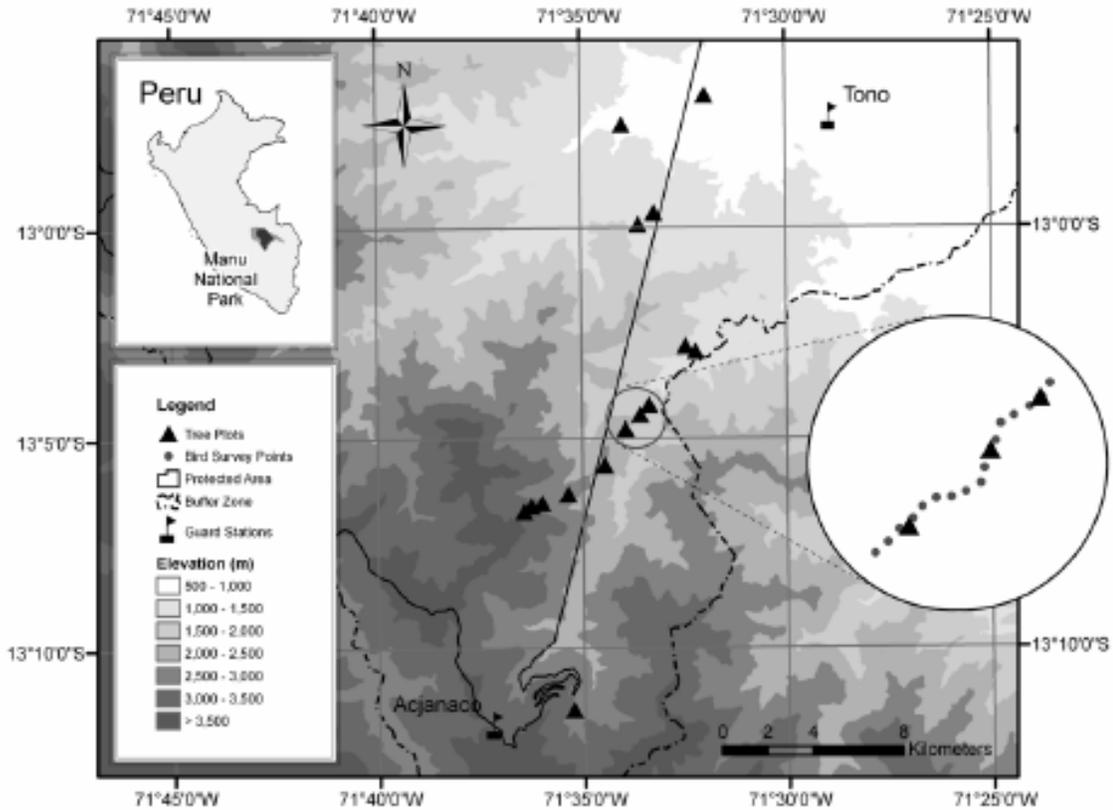


Figure 4-1. Map of the study area in Manu National Park, with locations of 1-ha tree plots along the elevational gradient (triangles). Bird survey sites (circles; see magnification) were located within 500 m horizontal distance (or 150 m elevation) of each tree plot.

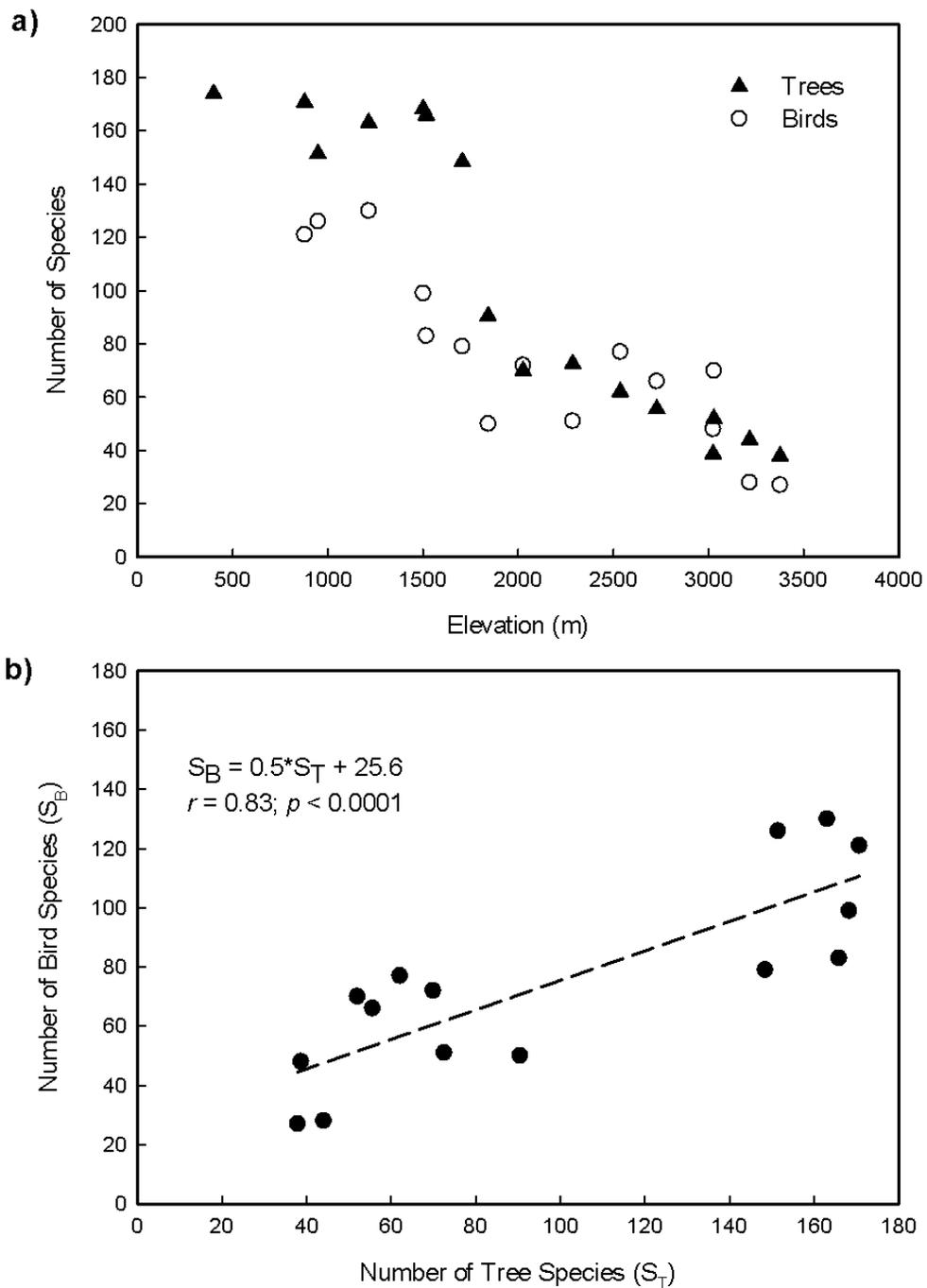


Figure 4-2. (a) Species richness for trees and birds with elevation for 15 1-ha plots and (b) the relationship between species richness of birds ( $S_B$ ) and trees ( $S_T$ ). An estimate of tree species richness for lowland *terra firme* in Manu National Park (approximately 400 m elevation) is given as a reference (from Pitman et al. 2001; averaged across 20 1-ha plots). The equation for the linear relationship, Pearson correlation coefficient ( $r$ ) and  $p$ -value are shown.

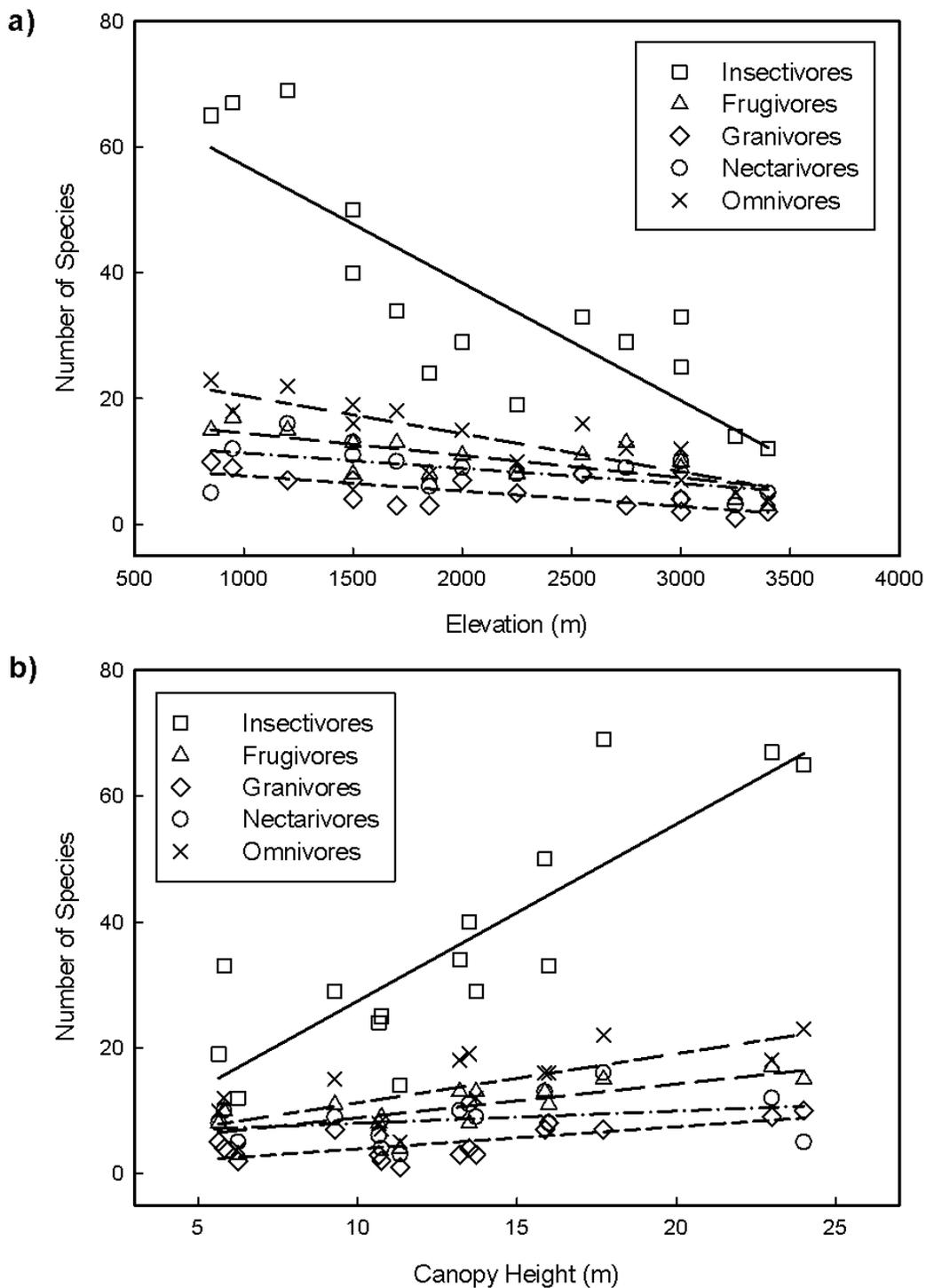
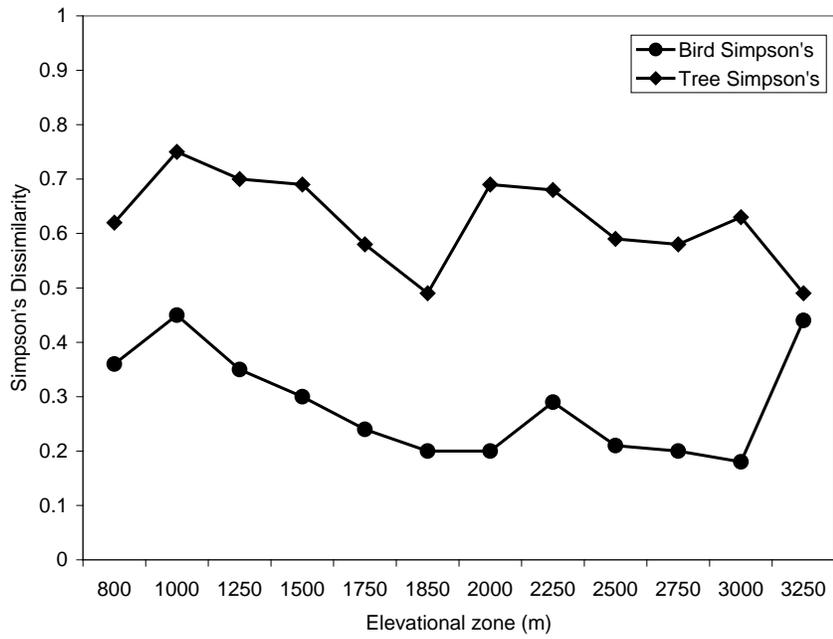


Figure 4-3. Species richness of avian foraging guilds across plots varying in (a) elevation and (b) average canopy height. Best fit lines are shown for each guild, including nectarivores, granivores, omnivores, frugivores and insectivores.

a)



b)

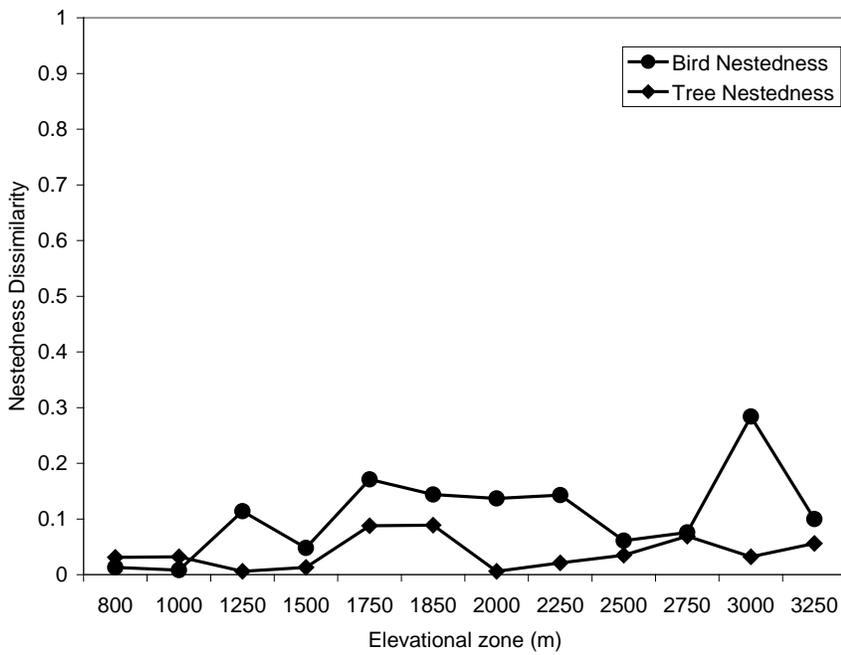
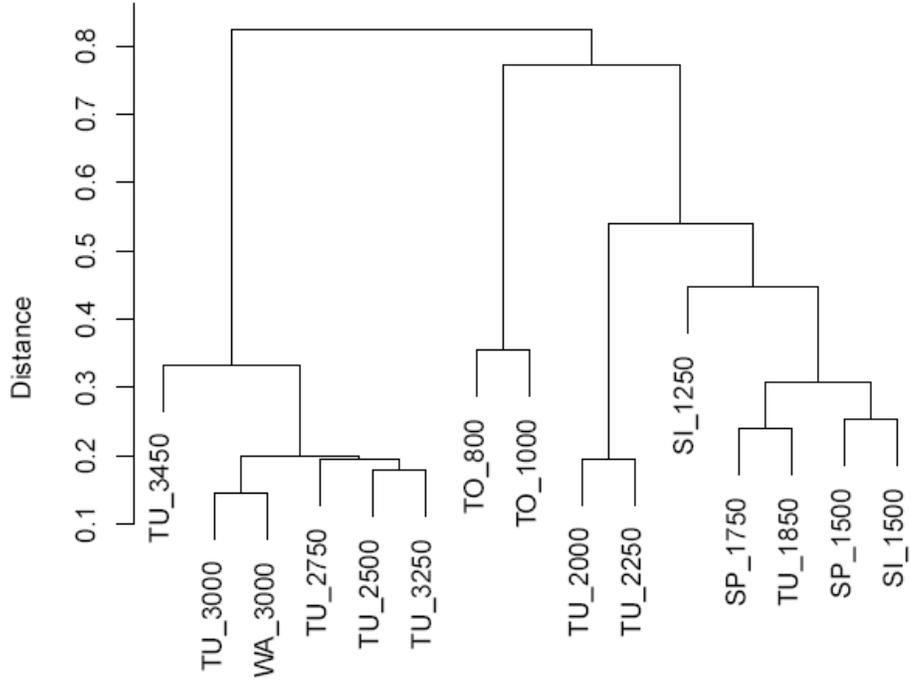


Figure 4-4. Dissimilarity values of  $\beta_{sim}$  (a) and  $\beta_{nes}$  (b) for adjacent plots along the elevational gradient for birds (circles) and trees (diamonds). The x-axis indicates the name of the lower of the two adjacent plots compared.

a)



b)

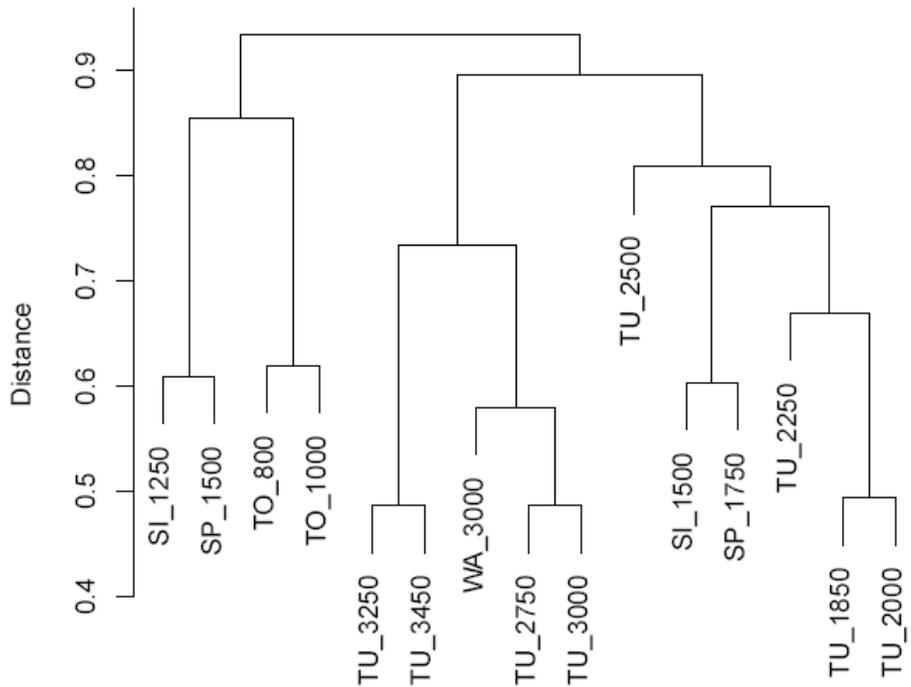


Figure 4-5. Cluster dendrograms for birds (a) and trees (b) across 1-hectare plots (labels show plot code and elevation), using the average linkage method.

CHAPTER 5  
SQUEEZED AT THE TOP: INTERSPECIFIC COMPETITION MAY CONSTRAIN  
ELEVATIONAL RANGES IN TROPICAL BIRDS

**Introduction**

Tropical montane plants and animals are typically restricted to narrow, belt-like elevational distributions, often only a few hundred meters wide (Stotz et al. 1996, Vásquez & Givnish 1998, Jankowski et al. 2009). This elevational specialization of species leads to high species turnover or “beta-diversity” along tropical elevational gradients, making these landscapes important centers of global biodiversity and endemism (Stotz et al. 1996, Myers et al. 2000). Although distributions of tropical montane species are becoming increasingly well documented through investigation of species richness and turnover patterns (Patterson et al. 1998, Herzog et al. 2005, Jankowski et al. 2009, Romdal and Rahbek 2009), there is little understanding of the processes acting at range boundaries to maintain these species’ narrow elevational distributions. Research focused on understanding species’ range limits, however, is of immediate importance in the context of climate change; our ability to predict how climate changes will drive range shifts and possible extinctions hinges on understanding the factors that determine where a given species occurs. In particular, species with restricted distributions along elevational gradients may be highly vulnerable (Parmesan 2006, Colwell et al. 2008, Sekercioglu et al. 2008).

Range boundaries are generated by multiple abiotic and biotic factors that influence the persistence of populations (see Holt and Keitt 2005); a combination of such factors could lead to narrow distributions of tropical montane species. Recent studies have emphasized abiotic, physiologically based explanations, in which small seasonal variation in thermal regimes leads to physiological specialization, as

classically proposed by Janzen (1967; Ghalambor et al. 2006, McCain 2009). Tropical ectotherms, for example, appear less able than temperate ectotherms to tolerate widely varying thermal conditions and may be at greater risk from global climate change (Tewksbury et al. 2008, Huey et al. 2009).

Likewise, range boundaries may be influenced by biotic interactions (Case et al. 2005, Price and Kirkpatrick 2009). In the tropics, direct interspecific competitive interactions at range boundaries constitute another classic hypothesis of what limits species' distributions in montane landscapes (Terborgh 1971, Diamond 1973). Such interactions should result in elevational gradients that are partitioned into non-overlapping ranges of competing species, compressing the distributions of any single competitor. Along many tropical mountainsides, there is strong evidence for such "replacements" between closely related species (Bull 1991), especially in birds (Terborgh 1971). Demonstration of range compression of species in areas with competitors present, and range expansion where competitors are absent, is consistent with this hypothesis (Terborgh and Weske 1975, Remsen and Graves 1995), but experimental support for competitive interactions between species in replacement zones is still lacking.

Here we test a prediction of the hypothesis that competitive interactions, in the form of interspecific aggression, determine species' range limits along an elevational gradient in the Tilarán Mountains of Costa Rica. We focus our study on two passerine genera with species that show distinct elevational replacements: wood-wrens (*Henicorhina*, Troglodytidae) and nightingale-thrushes (*Catharus*, Turdidae). Using a series of song playback experiments to detect aggressive territorial behaviors, which

may reflect underlying competitive interactions (Martin and Martin 2001), we tested whether territorial individuals in species with elevational replacements respond aggressively to songs of congeners where their ranges meet. We analyzed each species' reaction to congener songs at increasing distances from replacement zones to determine whether responses were learned or, alternatively, whether they might reflect misdirected intraspecific aggression (the "mistaken identity" hypothesis of Murray 1971). Finally, we evaluated whether interspecific responses of species pairs at the replacement zone were asymmetric in their level of aggression, a likely indication of interspecific behavioral dominance (Robinson and Terborgh 1995).

## Methods

### Study Area and Target Species

The Tilarán Mountains of northwestern Costa Rica (10°18'N, 84°45'W; max. altitude 1850 m) run northwest to southeast, with the continental divide separating the leeward Caribbean slope from the drier Pacific slope. The 36 km<sup>2</sup> study area ranges from 1000-1700 m altitude on the Pacific slope within 3.6 km of the continental divide. The study area shows dramatic changes in moisture, averaging 4000-6000 mm rainfall annually at the ridgetop cloud forest and declining approximately 1000 mm km<sup>-1</sup> downslope (see Jankowski et al. 2009 for more details).

Congeneric species with adjacent, non-overlapping elevational distributions in the study area were selected for their patterns of replacement, relatively high local population densities, and accessibility of their replacement zones along the mountainside. Our focal species were two wood-wrens, *Henicorhina leucosticta* (White-breasted Wood-Wren), and *H. leucophrys* (Gray-breasted Wood-Wren), and three nightingale-thrushes, *Catharus aurantiirostris* (Orange-billed Nightingale-Thrush), *C.*

*mexicanus* (Black-headed Nightingale-Thrush), and *C. fuscater* (Slaty-backed Nightingale-Thrush). All of these species are largely restricted to forest understory and are partially to entirely insectivorous (Stiles et al. 1989). Along the elevational gradient, *H. leucosticta* and *C. aurantirostris* inhabit drier, more seasonal low-elevation forest, whereas *H. leucophrys* and *C. fuscater* inhabit high-elevation moisture-saturated cloud forest. *C. mexicanus* has a narrow elevational distribution on the Pacific slope of 75-125 m (max. 600 m horizontal distance) between the other two nightingale-thrushes.

### **Territory Mapping, Playback Stimuli and Experiments**

Territories of target species were located at their replacement zones, where individuals of each species are in daily contact with congeners, and at varying distances from replacement zones, up to 1.5 km (horizontal distance) within species' elevational ranges. For *C. mexicanus* no territories were more than 600 m from the replacement zone because of this species' extremely narrow range. Territories of *C. fuscater* were not studied away from the replacement zone because of the lack of behavioral responses toward its lower elevation congener, *C. mexicanus*, at the replacement zone (see Results). Prior to playback experiments, transects within the study site were walked daily, and the locations of singing individuals of target species were marked using a GPSMap 60CSx GPS unit (with an accuracy of  $\pm 6$  m in forest). These territory locations were revisited on multiple days thereafter. During this time, individuals' movements within their territory and simultaneous singing events with neighbors were noted to estimate the territory's center and to approximate its boundaries. Because our target species regularly sing throughout the morning from well-defined areas, we are confident that our method of territory mapping by simultaneous singing events with neighbors, coupled with observations of individuals' movements, is a reliable approach

to distinguish territories of unbanded birds. Each territory along the gradient was assigned a proximity value to the replacement zone, defined by the distance between the territory center and that of the nearest congener using ArcGIS 9.2 (ESRI 2007).

Songs used for playback stimuli were recorded within the study area in May of 2007 and 2008. Recordings were made from within 20 m of singing individuals not involved in interactions with neighbors, using a parabolic dish and microphone and an Edirol R-09 digital recorder. Songs were filtered to remove low-frequency noise, generally below 750 Hz, and other unwanted noises such as other singing birds using Raven Pro 1.3 (Cornell Lab of Ornithology 2003). Waveforms in some recordings were amplified so that all recordings could be broadcast at equal volume. Each recorded song was presented as a playback stimulus to only one individual per species following recommendations by Kroodsma et al. (2001).

Playback experiments were conducted in May-June of 2007-2008 during the peak of the local breeding season when birds are actively singing and defending established territories. Each individual was tested on two days, usually within a five-day period. Tests consisted of an 8-minute observation period of the focal bird, during which no stimulus was given, followed immediately by either an 8-minute heterospecific (hereafter “congeneric”) or conspecific playback broadcast by a speaker within the territory. The second test consisted of another 8-minute observation period followed by whichever playback was not performed on the first visit. The order of presentation of congener and conspecific playback stimuli was randomized. Observation and playback periods for each trial were recorded using an Edirol R-09 digital recorder and Sennheiser ME-66 microphone mounted on a tripod. Playback songs were played from

a second recorder connected to a playback speaker (Dean Markley GT1000 Micro Amp) placed 5 m from the observers and approximately 15 m from the focal individual. Song stimuli were broadcast at approximately 70-80 dB SPL at 5 m (varying slightly across species) for up to 3 min or until the focal bird approached to within 5 m of the speaker.

Playbacks were conducted from 05:30 to 14:00, avoiding periods of heavy wind or rain. First, territorial males were located, usually by song. If the individual was involved in a counter-singing bout with a neighbor, we delayed the trial for several hours. If disputes persisted, no trials with that individual were attempted that day. If non-target individuals (congeneric or conspecific neighbors) approached the territory in response to the playback stimulus, we were thereafter unable to distinguish whether the target individual was responding to our playback or the presence of a non-target bird. In these situations, the playback was aborted and attempted on a different day. During the 8-minute observation and playback periods, all movements of the focal bird were mapped by noting the distances of the bird from the speaker and the amount of time spent in each location. Behavioral variables summarized from these data included closest approach to speaker and latency to approach the speaker to within 10 m.

In 2008, we used the same protocol as in 2007, except that we also conducted “control playbacks” for target individuals to evaluate use of pre-playback observation periods as a negative control. Stimuli for control playbacks used locally recorded songs from one of two common species: *Basileuterus culicivorus* (Golden-crowned Warbler, Family Parulidae) or *Hylophilus decurtatus* (Lesser Greenlet, Family Vireonidae). These species have wide elevational distributions and are sympatric but not known to

interact with the target species. For all behavioral variables examined, we found no differences between control playbacks and observation periods prior to control playbacks nor between control playbacks and observation periods prior to congener or conspecific playbacks (Kruskal-Wallis non-parametric ANOVA; for all species and variables,  $\chi^2$  values range from 0.28 – 6.0, d.f. = 3, *P*'s range from 0.11 - 0.96).

Therefore, we pooled the behavioral data recorded during observation periods prior to congener and conspecific playbacks to use as a comparative stimulus type (hereafter “control”) in statistical models of behavioral response to playback.

### **Statistical Analysis**

We analyzed behavioral response to playbacks for each species pair using both general and generalized linear mixed models performed in SAS/STAT v. 9.2 (SAS Institute 2008) for two groups: 1) individuals close to the replacement zone (wood-wrens  $\leq 100$  m; nightingale-thrushes  $\leq 200$  m) and 2) all individuals, at varying distances from the replacement zone. Each response variable (i.e., closest approach to speaker, and latency to approach to within 10 m) was analyzed separately for each pair of congeners sharing a range boundary. The response variable ‘closest approach to the speaker’ was square-root transformed to achieve normality and was modeled using a general linear mixed model for individuals close to the replacement zone and for all individuals. The response variable ‘latency to approach the speaker’ was analyzed using a logistic regression, which modeled the probability of a response during the playback period, given the explanatory variables. We used this procedure because many individuals did not approach to within 10 m (i.e., no response). Then, using only responding individuals close to the replacement zone, we performed a second analysis using a general linear

mixed model to examine the time to approach to within 10 m (log transformed), given the explanatory variables. We report mixed-model results for time to approach for individuals close to the replacement zone, and we report logistic regression results for the probability of a response during the playback period when including all individuals. Explanatory variables for all models included stimulus (congener, conspecific or control), species of the target individual, distance of the target individual's territory from the replacement zone (only for models including all individuals), and interaction terms. Individual was included as a repeated subject. For models with all individuals, if species was a significant term in the model ( $P < 0.05$ ), each species was then analyzed separately to avoid modeling three-way interactions. Post-hoc tests for direct effects or interactions with categorical explanatory variables used least squares mean difference with a Tukey adjustment to test for significant differences among levels. Contrast statements were used to test for significant differences among levels in the distance-stimulus interaction term, with distance as a continuous variable. See Table 5-1 for sample sizes of individuals tested for each species.

## Results

Individuals of each genus (*Henicorhina* and *Catharus*) responded aggressively to playbacks of congener songs. In wood-wrens, individuals with territories close to the replacement zone responded aggressively to playbacks of their congeners' songs, approaching on average 71% closer to the speaker and responding 85% faster compared to the control period (Figure 5-1; Table 5-2;  $t_{11} = 6.8$  and  $7.8$ , respectively,  $p$ 's  $< 0.0001$ ). Wood-wrens responded to congener songs by approaching the speaker quietly with short flights through the understory, then singing near the speaker for several minutes. These responses to congener songs were not significantly different

from responses to conspecific songs (closest approach:  $t_{11} = 2.2$ ,  $p = 0.11$ ; latency to approach:  $t_{11} = 1.04$ ,  $p = 0.32$ ). When considering individuals at varying distances from the replacement zone, we found that wood-wrens located farther from the replacement zone showed a decreased response to congener playbacks (Figure 5-2; Table 5-3; contrasts of congener to control and conspecific playbacks: for closest approach,  $F_{1,49} = 39.01$ ,  $p < 0.0001$ ; for latency:  $F_{1,141} = 12.2$ ,  $p < 0.0006$ ). At distances  $> 1$  km from the replacement zone, responses to congener playback did not differ from the control period (for closest approach and latency,  $t_8 = -1.7$ ,  $p$ 's  $> 0.26$ ).

The low-elevation *C. aurantirostris* and its middle-elevation congener, *C. mexicanus*, likewise responded to congener playbacks (Figure 5-1; Table 5-2). These responses were strongest for *C. aurantirostris*, which approached 69% closer to the speaker and responded 75% faster compared to control periods ( $t_{11} = 5.8$  and  $t_{22} = 3.5$ , respectively,  $p$ 's  $< 0.02$ ). In this species, responses to congener and conspecific playbacks were similar, in both the closest approach and latency to respond ( $t_{12} = 0.83$  and  $t_{22} = -0.06$ , respectively,  $p$ 's  $> 0.95$ ). *C. mexicanus*, on average, approached 27% closer and responded 57% faster to congener playbacks compared to controls ( $t_{11} = 4.0$  and  $t_{22} = 3.2$ , respectively,  $p$ 's  $\leq 0.04$ ), but the response to congener playback in this species was not as aggressive as the response to conspecific playback (closest approach:  $t_{12} = 4.0$ ,  $p = 0.02$ ; latency:  $t_{22} = 4.27$ ,  $p = 0.004$ ). When considering individuals at varying distances from the replacement zone, we found that these two species of nightingale-thrushes showed weaker responses to congener playbacks farther from the replacement zone (Figure 5-2; Table 5-3; closest approach *C.*

*aurantiiostris*:  $F_{1,25} = 10.8$ ,  $p = 0.0003$ , *C. mexicanus*:  $F_{1,25} = 7.8$ ,  $p = 0.01$ ; latency to approach significant for *C. aurantiiostris* only:  $F_{1,50} = 7.1$ ,  $p = 0.01$ ).

The middle-elevation *C. mexicanus* and its high-elevation congener, *C. fuscater*, responded differently to congener playbacks. Compared to control periods, *C. mexicanus* approached on average 28% closer and responded 51% faster to congener playbacks (Figure 5-1; Table 5-2;  $t_{21} = 3.6$  and  $t_{41} = 4.5$ , respectively;  $p$ 's  $\leq 0.0008$ ). Its response to congener playbacks was nonetheless weaker than its response to conspecific playbacks (Figure 5-1; closest approach:  $t_{21} = 4.9$ ,  $p = 0.001$ ; latency:  $t_{41} = 7.5$ ,  $p < 0.0001$ ). In this species, there was no change in the strength of the response to congener playbacks farther from the replacement zone (Table 5-3). In *C. fuscater*, response to congener playbacks did not differ from the control period (Figure 5-1; Table 5-2; closest approach:  $t_{21} = 0.6$ ; latency:  $t_{41} = -0.28$ ;  $p$ 's = 0.99), indicating no detectable aggressive response of this species toward *C. mexicanus*.

## Discussion

These results demonstrate aggressive interactions between species that replace each other along elevational gradients, consistent with the hypothesis that such biotic interactions are important in determining species' range limits in tropical montane landscapes (Terborgh and Weske 1975). The influence of interspecific competition on the spatial arrangement of species in sympatry has been suggested for many taxa, including fish (Bay et al. 2001), amphibians (Cunningham et al. 2009), reptiles (Langkilde and Shine 2004) and mammals (Brown 1971). In birds, such interactions can determine local habitat selection (Martin and Martin 2001), settlement patterns of migrants arriving to breeding grounds (Fletcher 2007), and spatial partitioning of closely-related species along successional gradients (Robinson and Terborgh 1995). In

particular, song playback experiments in birds have been shown to be an appropriate method to assess underlying competitive interactions between species; indeed, habitat segregation of species resulting from this behavior can confer higher fitness compared to individuals whose territories overlap with those of congeneric competitors (Martin and Martin 2001). Our observations of interspecific territorial aggression at range boundaries of species with replacements support the presence of competitive interactions and the importance of this biotic interaction in maintaining segregated distributions. Our study is the first to provide experimental support for the hypothesis that such interspecific competitive interactions could reinforce range boundaries that segregate species along large-scale elevational gradients in the tropics.

Our results are also unique in demonstrating that interspecific aggression varies greatly over small spatial scales. In particular, we discovered that interspecific aggression occurs primarily when individuals are in close contact with congeners and weakens with increasing distance from zones of replacement. This pattern is not consistent with the alternative hypothesis of response to congener song – that the responses simply reflect mistaken identity of congeners and misdirected intraspecific aggression (e.g., Murray 1971). Rather, assuming that our populations are not genetically divergent within the 4-km gradient of our site (which would be unlikely at this spatial scale in a primarily forested landscape lacking major dispersal barriers), our results suggest a learned component to aggressive interactions at range boundaries and a behavioral flexibility that allows finely tuned responses corresponding to the likelihood of encountering heterospecifics (see also Richards 1979). In this situation,

the development of such behavioral interactions likely depends upon local densities of interacting species along gradients.

Species pairs tested at their replacement zone did not respond equally to playbacks of their congeners' songs. Whereas wood-wrens exhibited symmetric levels of interspecific aggression, nightingale-thrushes showed asymmetry in their territorial responses to congeners. The high-elevation *C. fuscater* showed no response toward songs of the middle-elevation *C. mexicanus*, whereas *C. mexicanus* responded aggressively to *C. fuscater* songs. Such asymmetries suggest that interspecific dominance in the aggressive species could limit some species to portions of the elevational gradient.

In light of climate change, interspecific aggression could have important implications for species with behavior-mediated elevational range limits, especially if high-elevation species were subordinate. If warming in montane climates allows upslope range expansion by dominant competitors, then high-elevation species could be forced to still higher elevations and become dependent on progressively smaller land areas to sustain viable populations. If interspecific aggression between congeners is widespread, many species could face such a scenario. Considering only species that are currently threatened with extinction, we estimate that 108 of 334 tropical montane species occurring at high elevations (approximately 9% of the 1184 threatened species, worldwide) have elevational ranges that are bordered by widespread low-elevation congeners (data from BirdLife International 2000). Dominant congeners at higher elevations could similarly prevent upslope expansion of subordinate species, squeezing middle-elevation species between an expanding suboptimal abiotic environment at the

lower boundary and a resistant biotic upper boundary. In this scenario, dominant high-elevation species would be able to hold off upslope movement of lower-elevation species as true “kings of the hill” for much longer than predicted by climate models alone.

In conclusion, our results point to the importance of including biotic interactions in predicting community responses to climate change; doing so may be particularly important for diverse tropical systems. In the Tilarán Mountains, there is already evidence for climate-driven population declines and elevational range shifts across many taxa, including birds (Pounds et al. 1999). Under a moderate warming scenario of 3° C over the next century (Solomon et al. 2007), montane species can be expected to shift their ranges 500 m upslope in response to rising temperatures (assuming an adiabatic lapse rate of 6° C/1000 m altitude; Colwell et al. 2008; Gasner et al. 2010). For the high-elevation species in our study, this corresponds to shifts nearly as large as their elevational distributions. While range shifts in tropical montane regions will undoubtedly be affected by a changing abiotic environment and species’ physiological tolerances (Tewksbury et al. 2008), the constraints imposed by biotic interactions will likely limit the ability of many species to track optimal abiotic conditions.

Table 5-1. Number of playback trials conducted per species (includes control, congener, and conspecific trials) and number of individuals tested per species. Two groups of individuals are distinguished: individuals close to the replacement zone (wood-wrens  $\leq 100$  m; nightingale-thrushes  $\leq 200$  m) and individuals at all distances from the replacement zone. Playback trials for *C. mexicanus* are divided into playbacks associated with *C. aurantirostris* (low-elevation congener) and those associated with *C. fuscater* (high-elevation congener). Playbacks with *C. fuscater* were not conducted more than 200m from the replacement zone.

Target species	Number of Trials		Number of Individuals Tested	
	Close to Replacement Zone	All Distances from Replacement Zone	Close to Replacement Zone	All Distances from Replacement Zone
<i>Henicorhina leucosticta</i>	28	100	8	25
<i>Henicorhina leucophrys</i>	24	108	6	27
<i>Catharus aurantirostris</i>	16	108	5	27
<i>Catharus mexicanus</i> (vs. <i>C. aurantirostris</i> )	40	108	10	27
<i>Catharus mexicanus</i> (vs. <i>C. fuscater</i> )	72	88	18	22
<i>Catharus fuscater</i>	24	---	6	---

Table 5-2. Mixed model results for each species pair for closest approach to speaker and latency to approach speaker for individuals close to the replacement zone ( $\leq 100$  m for wood-wrens,  $\leq 200$  m for nightingale-thrushes). Variables in the model include Stimulus, or the song stimulus delivered to the target individual, and Species, which is the species of the target individual. “Total N” shows the total sample size followed by the number of individuals tested (including both species). Statistics from post-hoc tests are provided in text.

	Closest Approach	Latency to Approach
	<i>H. leucosticta/H. leucophrys</i>	<i>H. leucosticta/H. leucophrys</i>
Stimulus	$F_{2,11} = 142.0$ ; $P < 0.0001$	$F_{2,11} = 49.4$ ; $P < 0.0001$
Species	$F_{1,11} = 1.93$ ; $P = 0.19$	$F_{1,11} = 1.05$ ; $P = 0.33$
Total N	50 obs, 13 ind	50 obs, 13 ind
	<i>C. aurantiirostris/C. mexicanus</i>	<i>C. aurantiirostris/C. mexicanus</i>
Stimulus	$F_{2,12} = 42.1$ ; $P < 0.0001$	$F_{2,22} = 29.7$ ; $P < 0.0001$
Species	$F_{1,12} = 20.7$ ; $P = 0.0007$	$F_{1,11} = 0.06$ ; $P = 0.81$
Stimulus x Species	$F_{2,12} = 4.3$ ; $P = 0.04$	$F_{2,22} = 3.0$ ; $P = 0.07$
Total N	56 obs, 14 ind	52 obs, 13 ind
	<i>C. mexicanus/C. fuscater</i>	<i>C. mexicanus/C. fuscater</i>
Stimulus	$F_{2,21} = 71.4$ ; $P < 0.0001$	$F_{2,41} = 63.5$ ; $P < 0.0001$
Species	$F_{1,21} = 1.5$ ; $P = 0.24$	$F_{2,21} = 7.0$ ; $P = 0.02$
Stimulus x Species	$F_{2,21} = 3.1$ ; $P = 0.07$	$F_{2,41} = 2.9$ ; $P = 0.06$
Total N	88 obs, 23 ind	90 obs, 23 ind

Table 5-3. Mixed model results for each species pair for closest approach to speaker and latency to approach speaker for individuals at varying distance from the replacement zone (shown as “Distance” below). Other variables in the model include Stimulus, the song stimulus delivered to the target individual, and Species, which is the species of the target individual. “Total N” shows the total sample size followed by the number of individuals tested (including both species). Statistics from post-hoc tests are provided in text.

	Closest Approach		Latency to Approach	
	<i>H. leucosticta/H. leucophrys</i>		<i>H. leucosticta/H. leucophrys</i>	
Stimulus	$F_{2,49} = 24.7; P < 0.0001$		$F_{1,141} = 8.9; P = 0.0002$	
Species	$F_{1,49} = 0.1; P = 0.73$		$F_{1,141} = 2.2; P = 0.14$	
Distance	$F_{1,49} = 14.0; P = 0.0005$		$F_{1,141} = 0.14; P = 0.70$	
Stimulus x Distance	$F_{2,49} = 19.5; P < 0.0001$		$F_{2,141} = 8.20; P = 0.0004$	
Total N	198 obs, 52 ind		198 obs, 52 ind	
	<i>C. aurantirostris</i>	<i>C. mexicanus</i>	<i>C. aurantirostris</i>	<i>C. mexicanus</i>
Stimulus	$F_{2,25} = 43.2; P < 0.0001$	$F_{2,25} = 25.5; P < 0.0001$	$F_{1,50} = 9.4; P = 0.003$	$F_{1,52} = 5.8; P = 0.02$
Distance	$F_{1,25} = 4.7; P = 0.04$	$F_{1,25} = 0.02; P = 0.89$	$F_{1,50} = 2.0; P = 0.16$	$F_{1,52} = 0.02; P = 0.9$
Stimulus x Distance	$F_{2,25} = 9.0; P = 0.001$	$F_{2,25} = 4.1; P = 0.03$	$F_{1,50} = 7.1; P = 0.01$	$F_{1,52} = 1.5; P = 0.2$
Total N	105 obs, 27 ind	108 obs, 27 ind	79 obs, 27 ind	81 obs, 27 ind
	<i>C. mexicanus</i>	( <i>C. fuscater</i> )	<i>C. mexicanus</i>	( <i>C. fuscater</i> )
Stimulus	$F_{2,20} = 25.5; P < 0.0001$	----	$F_{1,40} = 12.1; P < 0.0001$	----
Distance	$F_{1,20} = 2.2; P = 0.15$	----	$F_{1,41} = 0.08; P = 0.78$	----
Stimulus x Distance	$F_{2,20} = 0.34; P = 0.72$	----	ns*	----
Total N	84 obs, 22 ind	----	64 obs, 22 ind	----

\* Interaction term not significant; without this term, stimulus is significant in simpler model.

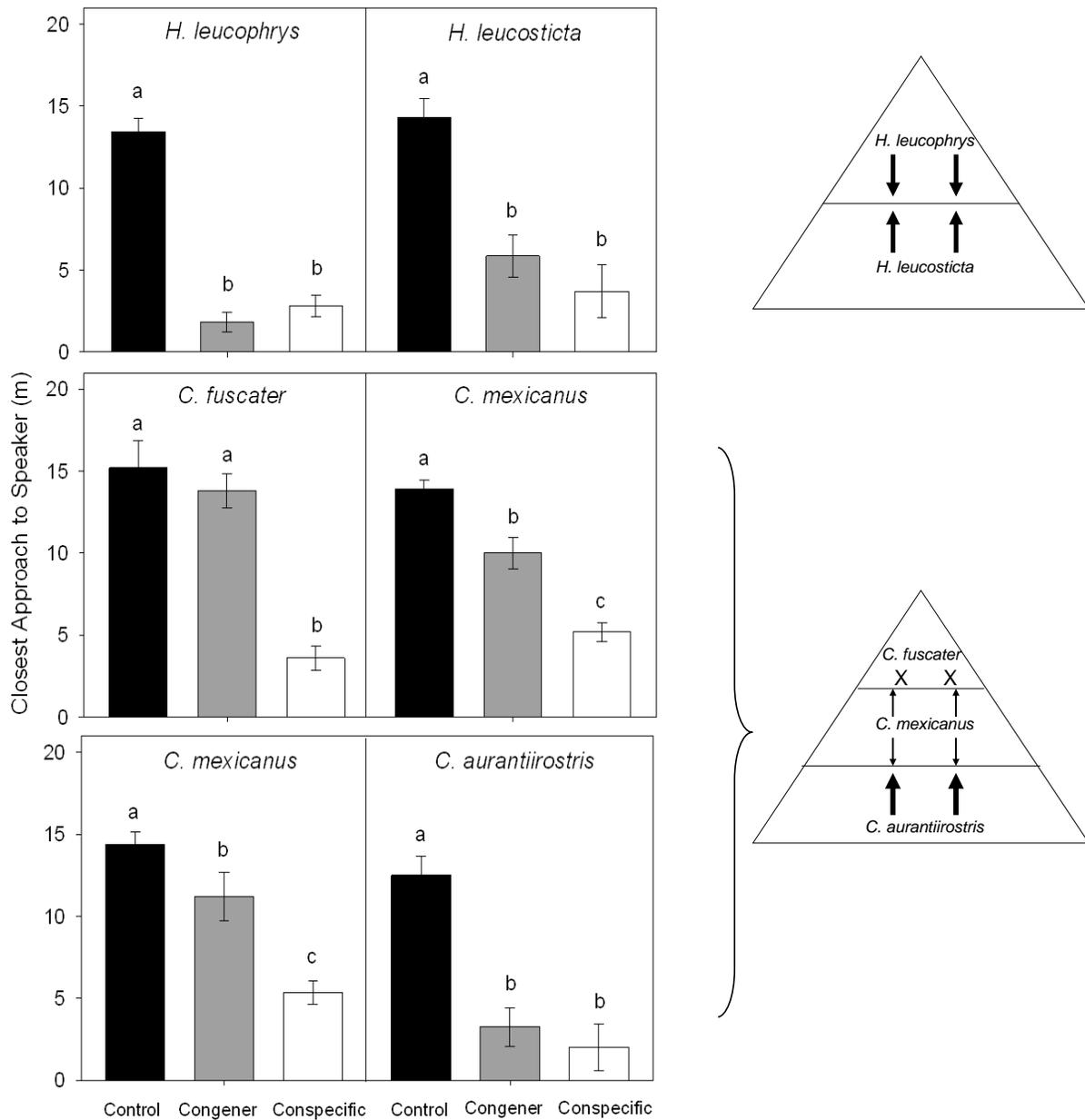


Figure 5-1. Response to playback trials by individuals with territories near replacement zones ( $\leq 100$  m for wood-wrens,  $\leq 200$  m for nightingale-thrushes). Bars show closest approach to the speaker (means  $\pm$  SEM) during control (black), congener (gray) and conspecific (white) trials for each pair of species tested. Values with different letters are significantly different for that species ( $p < 0.02$ ; least squares mean difference with Tukey adjustment). Schematics to right depict the elevational location of species, with arrows of different thickness indicating the relative strength of response to congener playbacks between species pairs at the replacement zone and “x” to indicate species with no response to congeners.

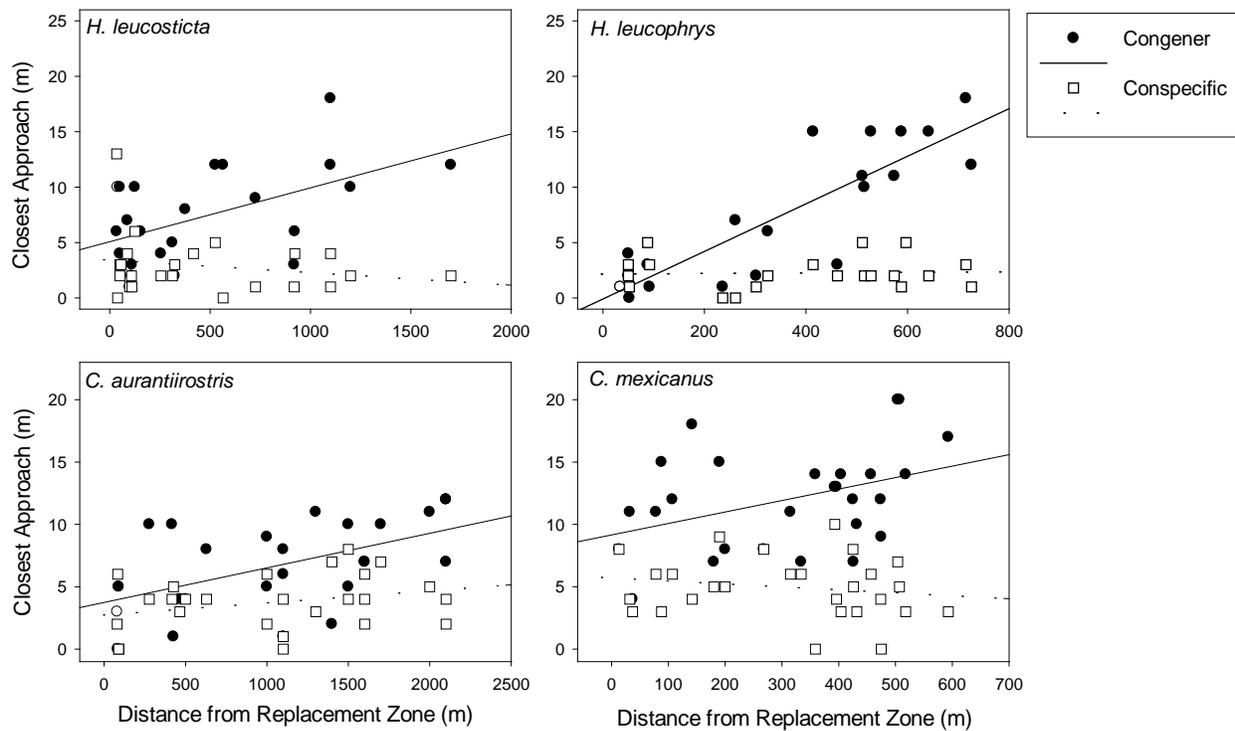


Figure 5-2. Closest approach to the speaker in response to congener and conspecific stimuli for individuals at increasing distances from the replacement zone. Filled circles show responses of each individual to congener playbacks (with solid best fit lines), and hollow squares show responses of individuals to conspecific playback trials (with dashed best fit lines). Species pairs shown have significant stimulus-distance interactions, where post hoc contrasts of congener response to combined control and conspecific response for each species are significant with  $p$ 's  $\leq 0.01$ .

## CHAPTER 6 CONCLUSION

The overarching goal of this dissertation is to develop ways to study the causes and maintenance of range boundaries along elevational gradients, and to understand the implications of ecological reinforcement of ranges for patterns of diversity at the landscape level. The mechanistic approach to understanding range boundaries outlines a target for future work. The underlying conceptual framework of this approach is based on classic concepts of the fundamental and realized niches of species. It proposes a way to estimate the physiological niche of bird species in response to elevation, based on metabolic rates and thermal tolerances. This working physiological niche describes the species' idealized distribution if it were limited only by the range of physical conditions it could tolerate. Using these hypothesized distributions as a baseline, it is then possible to determine whether species show different realized distributions along gradients. Using a combination of field experiments and intensive data collection on life-history and behavioral traits, researchers can begin to evaluate additional biotic constraints that could be acting on species' range limits. We highlight the forces of interspecific competition, mutualistic interactions, and nest predation and consider how each of these factors may be important in maintaining range boundaries of Neotropical montane birds.

Analysis of elevational range sizes, response shapes and position of species distributions along the gradient revealed that elevational range sizes were largest for cloud forest birds, and these were nearly twice as large as those of species found in foothill and highland elevations. Additional tests against mid-domain-effect models should be conducted to determine whether this pattern is biological. Most species

exhibited symmetric response curves with elevation, consistent with the expectations of ecological niche theory. A moderate proportion of species showed asymmetric response curves, which were truncated at one range boundary; however, there was no tendency for truncations to occur at lower or upper boundaries. Our analyses suggest that both habitat association and competitive interactions may set range boundaries for selected species, but for many others, these particular biotic factors appear to be weak in determining elevational range limits along the Andean gradient. Congeners found along the gradient, for example, typically showed little range overlap, and many congeners were separated by elevational gaps. Only two pairs of congeners showed evidence of repulsion interactions through range truncations at replacement zones.

The lack of strong competitive interactions maintaining the range boundaries of congeners in the Andes contrasts sharply with results from field experiments conducted in the Tilarán Mountain range of Costa Rica. Results of heterospecific playbacks along this gradient with *Henicorhina* and *Catharus* spp. showed that individuals at replacement zones exhibit aggressive territorial behavior in response to songs of congeners. As distance from replacement zones increased, aggression towards congener song decreased, suggesting a learned component to interspecific aggression. Additionally, aggressive responses in *Catharus* were asymmetric, indicating interspecific dominance. These results provide experimental evidence consistent with the hypothesis that interspecific competitive interactions restrict ranges of Neotropical birds. They also suggest that densities of congeners at range boundaries play an important role in the development of these interactions. The contrasting results of the strength of competition in maintaining range boundaries between Central America and the Andes

invites future investigation into the conditions along elevational gradients that influence these biotic interactions.

Few assessments of diversity patterns and congruence in species composition across different taxonomic groups exist, especially for such diverse biological systems. Furthermore, examination of associations of bird species to vegetation structure and composition has rarely been attempted in the tropics. The assessment of cross-taxon congruence in bird and tree communities along the Manu gradient found that species richness was generally higher in trees than in birds. While diversity in both taxa decreased with elevation, tree richness showed a low-elevation plateau before declining at higher elevations. Tree species had narrower distributions and higher turnover compared to birds, but patterns of turnover along the gradient were congruent between taxa. Nestedness contributed much less to bird and tree dissimilarity, though in birds, the nestedness component of dissimilarity increased at higher elevations and was best explained by vegetation structure. Multiple regression of distance matrices showed that tree composition, vegetation structure and elevation were all important predictors of bird composition, explaining 82% of variation in bird dissimilarity across plots. For all groups of birds, covariation between vegetation structure, trees, and elevation made the greatest contribution to explained variation, though additional variation was explained uniquely by tree composition (in omnivores), vegetation structure (in granivores) and by elevation (in frugivores, insectivores and nectarivores). While trees appear to be more specialized than birds along the elevational gradient, the patterns of change with elevation in birds and trees are similar.

This research on the distributions and range boundaries of species along montane gradients is highly relevant to understanding the response of these montane communities to future climate change. Nearly 30% of the world's threatened birds are restricted to narrow elevational ranges in tropical mountains, and species are expected to shift their ranges upslope to follow optimal climate conditions as warming continues. Projections of such species' range shifts typically assume that species will track changing thermal regimes. The degree to which we can rely on these projections, however, also depends upon understanding how species respond physiologically to changing temperatures, but such thermal tolerances are virtually unknown for tropical birds. Species interactions also likely impose limits to species' elevational distributions, constraining ranges in ways not predicted by physiological tolerances alone. Future research in distributional modeling should be directed not only toward collection of data on species' occurrence or abundance, but also on physiological traits and species interactions. While filling the data void will be a difficult task for tropical birds, and even more so for poorly known taxa, increasing data availability through focused empirical research will allow multiple mechanisms potentially influencing range limits to be assessed simultaneously.

APPENDIX A  
ELEVATIONAL RANGES OF SPECIES IN MANU

Table A-1. Species detected in forested sites along the elevational gradient in the Manu study area. The number of sites where each species was detected (by netting or counts) is indicated, with each species' observed elevational minimum, maximum, midpoint and range. For species with sufficient detections to model response shapes, the modeled minimum, maximum, optimum, probability of occurrence, elevational range, and HOF model type is given. The optimum indicates the elevation where species show their maximum probability of occurrence. Species are listed in taxonomic order with nomenclature following the American Ornithologists' Union South American species classification (Remsen et al. 2010).

Species	No. Sites Detected		Observed Elevational Range				Modeled Elevational Range				HOF Type	
	Netted	Counts	Midpoint	Min.	Max.	Range	Optimum	Prob. of Occurrence	Min.	Max.		Range
<i>Nothocercus nigrocapillus</i>	0	8	2377	1852	2901	1049						
<i>Tinamus tao</i>	0	14	933	805	1061	256	975	0.79	881	1069	188	IV
<i>Tinamus osgoodi</i>	0	12	1423	1194	1651	457	1476	0.36	1251	1702	451	IV
<i>Tinamus guttatus</i>	0	8	968	923	1013	90						
<i>Crypturellus soui</i>	0	8	894	818	969	151						
<i>Crypturellus obsoletus</i>	0	35	1994	975	3013	2038	1590	0.51	1246	2394	1148	V
<i>Penelope montagnii</i>	0	17	2334	1676	2992	1316	2511	0.18	1877	3143	1265	IV
<i>Penelope jacquacu</i>	0	4	895	829	960	131						
<i>Aburria aburri</i>	0	9	1639	1332	1945	613						
<i>Ortalis guttata</i>	0	1	1331	1331	1331	0						
<i>Odontophorus speciosus</i>	0	13	1504	1061	1947	886	1397	0.28	1063	1729	665	IV
<i>Odontophorus balliviani</i>	0	4	2664	2537	2791	254						
<i>Odontophorus stellatus</i>	0	2	901	893	909	16						
<i>Elanoides forficatus</i>	0	1	818	818	818	0						
<i>Accipiter striatus</i>	0	1	2010	2010	2010	0						
<i>Buteo magnirostris</i>	0	1	823	823	823	0						
<i>Micrastur ruficollis</i>	0	16	1418	823	2012	1189	805	0.28	805	1877	1072	II
<i>Ibycter americanus</i>	0	1	895	895	895	0						
<i>Claravis mondetoura</i>	0	1	2673	2673	2673	0						
<i>Patagioenas fasciata</i>	0	28	2715	2087	3342	1255	2650	0.36	2175	3122	947	IV
<i>Patagioenas plumbea</i>	0	48	1382	818	1945	1127	1369	0.75	946	1791	845	IV

Table A-1. Continued

Species	No. Sites Detected		Observed Elevational Range				Modeled Elevational Range				HOF Type	
	Netted	Counts	Midpoint	Min.	Max.	Range	Optimum	Prob. of Occurrence	Min.	Max.		Range
<i>Patagioenas subvinacea</i>	0	4	1021	805	1236	431						
<i>Leptotila rufaxilla</i>	0	1	892	892	892	0						
<i>Geotrygon frenata</i>	1	20	2164	1501	2828	1327	1995	0.27	1371	2616	1244	IV
<i>Geotrygon montana</i>	7	10	1136	877	1395	518	1225	0.90	1126	1322	196	IV
<i>Ara ararauna</i>	0	1	829	829	829	0						
<i>Ara militaris</i>	0	4	1169	1124	1213	89						
<i>Ara severus</i>	0	15	1027	818	1236	418	805	0.69	805	1105	300	II
<i>Primolius couloni</i>	0	5	899	837	960	123						
<i>Aratinga mitrata</i>	0	22	2663	1911	3414	1503	3414	0.63	2699	3414	715	II
<i>Aratinga leucophthalma</i>	0	6	842	805	878	73						
<i>Bolborhynchus lineola</i>	0	14	2467	1551	3383	1832	3414	0.12	2029	3414	1385	III
<i>Pionus menstruus</i>	0	20	1021	805	1236	431	805	0.68	805	1251	446	II
<i>Pionus tumultuosus</i>	0	5	2345	1657	3032	1375						
<i>Amazona mercenaria</i>	0	33	1793	826	2760	1934	805	0.24	805	2297	1492	III
<i>Amazona farinosa</i>	0	2	828	818	837	19						
<i>Piaya cayana</i>	0	9	1328	876	1780	904						
<i>Dromococcyx pavoninus</i>	0	4	1367	1279	1454	175						
<i>Ciccaba albitarsis</i>	0	1	2908	2908	2908	0						
<i>Glaucidium bolivianum</i>	1	2	2725	2458	2992	534						
<i>Lurocalis rufiventris</i>	0	1	2575	2575	2575	0						
<i>Eutoxeres condamini</i>	20	1	1461	923	1998	1075	1373	0.65	982	1767	785	IV
<i>Threnetes leucurus</i>	4	1	1072	893	1250	357						
<i>Phaethornis ruber</i>	5	11	890	805	975	170	805	0.70	805	980	175	II
<i>Phaethornis hispidus</i>	1	1	892	837	946	109						
<i>Phaethornis guy</i>	22	11	1305	946	1663	717	1280	0.85	1002	1560	558	IV
<i>Phaethornis koepckeae</i>	3	0	976	853	1100	248						
<i>Phaethornis superciliosus</i>	4	2	1048	893	1202	309						
<i>Doryfera ludovicae</i>	15	1	1382	1100	1663	563	1461	0.64	1194	1731	538	IV
<i>Doryfera johannae</i>	3	0	1215	930	1501	571						
<i>Schistes geoffroyi</i>	13	4	1293	805	1781	976	1499	0.46	1098	1898	800	IV
<i>Colibri thalassinus</i>	3	34	2194	1486	2901	1415	1755	0.90	1562	2243	681	V

Table A-1. Continued

Species	No. Sites Detected		Observed Elevational Range				Modeled Elevational Range				HOF Type	
	Netted	Counts	Midpoint	Min.	Max.	Range	Optimum	Prob. of Occurrence	Min.	Max.		Range
<i>Colibri coruscans</i>	3	0	2151	1309	2992	1683						
<i>Heliathryx auritus</i>	1	0	1129	1129	1129	0						
<i>Heliangelus amethysticollis</i>	7	56	2921	2458	3383	925	2968	0.82	2553	3385	832	IV
<i>Phlogophilus harterti</i>	17	25	1278	893	1663	770	1100	0.95	972	1355	384	V
<i>Adelomyia melanogenys</i>	25	13	1942	1129	2756	1627	1936	0.93	1338	2531	1194	IV
<i>Aglaiocercus kingi</i>	5	1	1961	1396	2527	1131						
<i>Lesbia nuna</i>	0	1	2685	2685	2685	0						
<i>Chalcostigma ruficeps</i>	3	33	2643	2184	3101	917	2540	0.52	2183	2897	715	IV
<i>Metallura tyrianthina</i>	7	21	2936	2458	3414	956	3414	0.33	2712	3414	702	III
<i>Haplophaedia assimilis</i>	2	0	1960	1393	2527	1134						
<i>Aglaeactis cupripennis</i>	0	1	2991	2991	2991	0						
<i>Coeligena coeligena</i>	22	4	1878	1202	2554	1352	1746	0.90	1302	2193	891	IV
<i>Coeligena torquata</i>	4	6	2673	2458	2887	429						
<i>Coeligena violifer</i>	9	10	2918	2458	3377	919	2931	0.20	2608	3257	650	IV
<i>Boissonneaua matthewsii</i>	1	4	2740	2507	2972	465						
<i>Ocreatus underwoodii</i>	25	40	1557	930	2184	1254	1713	0.88	1369	2060	691	IV
<i>Heliodoxa schreibersii</i>	4	1	1300	1100	1501	401						
<i>Heliodoxa aurescens</i>	1	0	1129	1129	1129	0						
<i>Heliodoxa leadbeateri</i>	22	15	1500	1100	1899	799	1434	0.80	1110	1757	646	IV
<i>Chaetocercus mulsant</i>	1	1	2091	1401	2781	1380						
<i>Chlorostilbon mellisugus</i>	1	1	1105	1007	1202	195						
<i>Klais guimeti</i>	1	0	1202	1202	1202	0						
<i>Campylopterus largipennis</i>	3	0	1039	877	1202	325						
<i>Thalurania furcata</i>	8	2	1101	853	1350	498						
<i>Taphrospilus hypostictus</i>	4	0	1265	1129	1401	272						
<i>Amazilia viridicauda</i>	1	0	1501	1501	1501	0						
<i>Chrysuronia oenone</i>	3	0	1151	1100	1202	102						
<i>Pharomachrus auriceps</i>	0	21	2474	1899	3049	1150	2535	0.25	1963	3106	1143	IV
<i>Pharomachrus antisianus</i>	0	11	1766	1541	1991	450	1721	0.50	1525	1919	394	IV
<i>Trogon melanurus</i>	0	6	852	826	878	52						
<i>Trogon viridis</i>	0	2	872	866	878	12						

Table A-1. Continued

Species	No. Sites Detected		Observed Elevational Range				Modeled Elevational Range				HOF Type	
	Netted	Counts	Midpoint	Min.	Max.	Range	Optimum	Prob. of Occurrence	Min.	Max.		Range
<i>Trogon violaceus</i>	0	6	948	805	1090	285						
<i>Trogon curucui</i>	0	3	984	878	1090	212						
<i>Trogon collaris</i>	1	10	1178	866	1489	623	1079	0.29	844	1311	467	IV
<i>Trogon personatus</i>	1	60	2171	1350	2992	1642	1734	0.60	1575	3015	1440	V
<i>Chloroceryle aenea</i>	1	0	930	930	930	0						
<i>Baryphthengus martii</i>	3	13	1257	892	1621	729	1251	0.39	1003	1499	496	IV
<i>Momotus aequatorialis</i>	2	0	1337	1309	1365	56						
<i>Galbula cyanescens</i>	1	3	1030	805	1255	450						
<i>Nystalus striolatus</i>	0	2	997	980	1013	33						
<i>Malacoptila fulvogularis</i>	4	8	1497	1213	1781	568						
<i>Micromonacha lanceolata</i>	0	2	1459	1139	1779	640						
<i>Nonnula ruficapilla</i>	1	0	946	946	946	0						
<i>Capito auratus</i>	0	6	1025	960	1090	130						
<i>Eubucco versicolor</i>	4	13	1485	1110	1859	749	1580	0.31	1267	1893	626	IV
<i>Ramphastos tucanus</i>	0	1	818	818	818	0						
<i>Aulacorhynchus prasinus</i>	0	8	1128	826	1429	603						
<i>Aulacorhynchus derbianus</i>	2	11	1435	1090	1779	689	1554	0.27	1249	1859	611	IV
<i>Aulacorhynchus coeruleicinctis</i>	0	15	2085	1454	2716	1262	2464	0.33	2175	2754	579	IV
<i>Andigena hypoglauca</i>	0	17	2844	2528	3159	631	2874	0.34	2582	3164	582	IV
<i>Selenidera reinwardtii</i>	1	8	1264	826	1702	876						
<i>Pteroglossus azara</i>	1	0	950	950	950	0						
<i>Picumnus aurifrons</i>	0	1	837	837	837	0						
<i>Melanerpes cruentatus</i>	0	3	953	892	1013	121						
<i>Veniliornis affinis</i>	0	1	951	951	951	0						
<i>Colaptes rubiginosus</i>	1	32	1567	1124	2010	886	1781	0.91	1431	1958	527	V
<i>Colaptes rivolii</i>	1	22	2525	2067	2982	915	2788	0.36	2415	3158	744	IV
<i>Dryocopus lineatus</i>	0	4	1064	934	1194	260						
<i>Campephilus rubricollis</i>	0	1	878	878	878	0						
<i>Campephilus melanoleucos</i>	0	3	1044	893	1194	301						
<i>Sclerurus mexicanus</i>	1	0	930	930	930	0						
<i>Schizoeaca helleri</i>	1	6	3193	2972	3414	442						

Table A-1. Continued

Species	No. Sites Detected		Observed Elevational Range					Modeled Elevational Range				HOF Type
	Netted	Counts	Midpoint	Min.	Max.	Range	Optimum	Prob. of Occurrence	Min.	Max.	Range	
<i>Synallaxis azarae</i>	18	78	2225	1401	3049	1648	2081	0.94	1682	2809	1127	V
<i>Synallaxis cabanisi</i>	1	3	1101	805	1397	592						
<i>Cranioleuca marcapatae</i>	1	1	2705	2636	2774	138						
<i>Cranioleuca curtata</i>	3	23	1391	969	1813	844	1355	0.45	998	1713	715	IV
<i>Premnornis guttuligera</i>	2	0	2080	1702	2458	756						
<i>Premnoplex brunnescens</i>	22	6	1480	1100	1859	759	1487	0.82	1153	1817	664	IV
<i>Margarornis squamiger</i>	4	20	2670	1998	3342	1344	3414	0.34	2754	3414	660	III
<i>Pseudocolaptes boissonneautii</i>	2	35	2438	1716	3159	1443	2063	0.34	1877	3255	1378	V
<i>Anabacerthia striaticollis</i>	20	24	1476	1100	1852	752	1525	0.60	1243	1807	564	IV
<i>Syndactyla rufosuperciliata</i>	7	17	1645	1279	2010	731	1783	0.72	1567	2003	436	IV
<i>Simoxenops ucayalae</i>	4	3	1118	923	1313	390						
<i>Ancistrops strigilatus</i>	0	4	903	826	980	154						
<i>Hyloctistes subulatus</i>	3	5	991	853	1129	276						
<i>Philydor ruficaudatum</i>	1	4	1070	938	1202	264						
<i>Philydor erythrocerum</i>	1	1	865	853	878	26						
<i>Philydor erythropterum</i>	0	3	922	892	951	59						
<i>Philydor rufum</i>	2	1	1129	1007	1250	243						
<i>Anabazenops dorsalis</i>	1	14	1021	805	1236	431	805	0.69	805	1055	250	II
<i>Thripadectes melanorhynchus</i>	15	13	1245	930	1561	631	1204	0.77	974	1431	457	IV
<i>Thripadectes holostictus</i>	5	6	1682	1354	2010	656						
<i>Automolus ochrolaemus</i>	7	24	1028	805	1250	445	805	0.87	805	1115	310	II
<i>Automolus rubiginosus</i>	2	2	1105	930	1279	349						
<i>Automolus rufipileatus</i>	0	7	899	829	969	140						
<i>Lochmias nematura</i>	5	1	1093	818	1367	549						
<i>Xenops minutus</i>	4	2	1049	818	1279	461						
<i>Xenops rutilans</i>	0	2	958	826	1090	264						
<i>Dendrocincla tyrannina</i>	3	8	2688	2527	2849	322						
<i>Dendrocincla fuliginosa</i>	4	12	1142	829	1454	625	1082	0.48	894	1269	376	IV
<i>Deconychura longicauda</i>	0	1	975	975	975	0						
<i>Glyphorhynchus spirurus</i>	9	7	1169	837	1501	664						
<i>Dendrexetastes rufigula</i>	0	10	1167	938	1395	457	1186	0.60	1035	1337	303	IV

Table A-1. Continued

Species	No. Sites Detected		Observed Elevational Range				Modeled Elevational Range				HOF Type	
	Netted	Counts	Midpoint	Min.	Max.	Range	Optimum	Prob. of Occurrence	Min.	Max.		Range
<i>Xiphocolaptes</i>												
<i>promeropirhynchus</i>	3	26	1963	876	3049	2173						
<i>Dendrocolaptes certhia</i>	0	3	1084	951	1217	266						
<i>Dendrocolaptes picumnus</i>	2	9	1153	805	1501	696						
<i>Xiphorhynchus obsoletus</i>	1	0	853	853	853	0						
<i>Xiphorhynchus ocellatus</i>	3	20	1159	818	1501	683						
<i>Xiphorhynchus guttatus</i>	3	12	997	866	1129	263	959	0.66	868	1053	185	IV
<i>Xiphorhynchus triangularis</i>	14	20	1549	1100	1998	898	1786	0.71	1429	1914	485	V
<i>Lepidocolaptes lacrymiger</i>	2	10	2052	1309	2795	1486	2634	0.25	2477	2790	313	IV
<i>Campylorhamphus pucherani</i>	0	1	2542	2542	2542	0						
<i>Campylorhamphus trochilirostris</i>	5	16	1117	805	1429	624	1076	0.39	818	1337	519	IV
<i>Cymbilaimus sanctaemariae</i>	0	12	1051	823	1279	456	805	0.59	805	1074	269	II
<i>Thamnophilus palliatus</i>	1	4	1352	1173	1531	358						
<i>Thamnophilus schistaceus</i>	2	23	1021	805	1236	431	805	0.87	805	1121	316	II
<i>Thamnophilus caerulescens</i>	6	18	1828	1507	2148	641	1739	0.85	1601	2000	399	V
<i>Thamnophilus aethiops</i>	1	2	851	826	877	51						
<i>Dysithamnus mentalis</i>	13	27	1260	818	1702	884	1069	0.57	805	1371	566	IV
<i>Thamnomanes schistogynus</i>	2	20	1011	805	1217	412	805	0.93	805	1016	211	II
<i>Epinecrophylla spodionota</i>	5	9	1162	823	1501	678						
<i>Epinecrophylla ornata</i>	8	11	1117	805	1429	624	805	0.38	805	1282	477	II
<i>Epinecrophylla erythrura</i>	1	0	877	877	877	0						
<i>Myrmotherula brachyura</i>	0	3	1031	826	1236	410						
<i>Myrmotherula longicauda</i>	2	12	1133	837	1429	592	1301	0.47	1016	1405	389	V
<i>Myrmotherula axillaris</i>	1	0	1501	1501	1501	0						
<i>Myrmotherula schisticolor</i>	14	6	1545	1309	1781	472	1522	0.71	1282	1762	480	IV
<i>Myrmotherula menetriesii</i>	0	2	907	904	909	5						
<i>Herpsilochmus axillaris</i>	0	19	1256	980	1531	551	1209	0.77	1022	1400	378	IV
<i>Microrhoptias quixensis</i>	2	16	1042	805	1279	474	805	0.66	805	1134	329	II
<i>Drymophila caudata</i>	4	20	2247	1541	2952	1411	1820	0.63	1522	2115	592	IV
<i>Hypocnemis subflava</i>	4	27	1117	805	1429	624	1262	0.71	909	1366	457	V
<i>Terenura sharpei</i>	1	3	1242	934	1550	616						

Table A-1. Continued

Species	No. Sites Detected		Observed Elevational Range				Modeled Elevational Range				HOF Type	
	Netted	Counts	Midpoint	Min.	Max.	Range	Optimum	Prob. of Occurrence	Min.	Max.		Range
<i>Cercomacra cinerascens</i>	0	1	823	823	823	0						
<i>Cercomacra serva</i>	3	11	1110	805	1415	610	805	0.55	805	1076	271	II
<i>Cercomacra manu</i>	1	7	870	805	934	129						
<i>Pyriglena leuconota</i>	12	33	1478	946	2010	1064	1846	0.84	1335	1963	629	V
<i>Myrmoborus leucophrys</i>	4	24	933	805	1061	256	805	0.99	805	1006	201	II
<i>Myrmoborus myotherinus</i>	2	9	964	818	1110	292						
<i>Percnostola lophotes</i>	1	15	1070	805	1335	530	805	0.54	805	1217	412	II
<i>Schistocicla leucostigma</i>	2	2	1080	818	1341	523						
<i>Myrmeciza hemimelaena</i>	8	32	1100	805	1395	590	805	0.97	805	1173	368	II
<i>Myrmeciza atrothorax</i>	0	4	817	805	829	24						
<i>Myrmeciza goeldii</i>	1	9	948	805	1090	285						
<i>Myrmeciza fortis</i>	0	2	997	980	1013	33						
<i>Rhegmatorhina melanosticta</i>	4	2	913	876	950	74						
<i>Hylophylax naevius</i>	7	18	1030	805	1255	450	805	0.93	805	982	177	II
<i>Phlegopsis nigromaculata</i>	2	2	937	923	950	27						
<i>Formicarius analis</i>	3	10	933	805	1061	256	805	0.81	805	925	120	II
<i>Formicarius rufipectus</i>	1	30	1459	1139	1779	640	1316	0.88	1183	1632	449	V
<i>Chamaeza campanisona</i>	2	13	1338	1124	1551	427	1280	0.52	1095	1468	373	IV
<i>Chamaeza mollissima</i>	0	14	2392	1972	2811	839	2462	0.22	2003	2926	924	V
<i>Grallaria squamigera</i>	0	3	2990	2566	3414	848						
<i>Grallaria guatemalensis</i>	0	11	1340	1173	1506	333	1267	0.63	1131	1405	274	IV
<i>Grallaria albigula</i>	0	26	1845	1506	2184	678	1859	0.89	1596	2123	527	IV
<i>Grallaria erythroleuca</i>	1	50	2489	1965	3013	1048	2637	0.81	2198	2864	665	V
<i>Grallaria rufula</i>	0	23	3077	2739	3414	675	3414	1.00	2981	3414	433	II
<i>Myrmothera campanisona</i>	0	3	899	893	904	11						
<i>Grallaricula flavirostris</i>	3	1	1819	1640	1998	358						
<i>Grallaricula ferrugineipectus</i>	4	12	2727	2458	2995	537	2921	0.35	2704	3137	433	IV
<i>Conopophaga ardesiaca</i>	15	20	1320	960	1679	719	1310	0.59	1022	1598	575	IV
<i>Liosceles thoracicus</i>	1	16	964	818	1110	292	805	0.73	805	1074	269	II
<i>Scytalopus parvirostris</i>	5	79	2713	2012	3414	1402	3414	0.86	2282	3414	1132	III
<i>Scytalopus atratus</i>	4	41	1668	1324	2012	688	1744	0.97	1444	2044	600	IV

Table A-1. Continued

Species	No. Sites Detected		Observed Elevational Range				Modeled Elevational Range			HOF Type		
	Netted	Counts	Midpoint	Min.	Max.	Range	Optimum	Prob. of Occurrence	Min.		Max.	Range
<i>Scytalopus schulenbergi</i>	0	1	3414	3414	3414	0						
<i>Phyllomyias cinereiceps</i>	0	2	1445	1373	1517	144						
<i>Phyllomyias plumbeiceps</i>	0	1	1578	1578	1578	0						
<i>Elaenia albiceps</i>	1	6	1971	950	2991	2041						
<i>Elaenia pallatangae</i>	1	19	2788	2527	3049	522	2965	0.65	2767	3164	397	IV
<i>Mecocerculus stictopterus</i>	1	53	2924	2465	3383	918	2837	0.78	2558	3310	751	V
<i>Mecocerculus leucophrys</i>	1	14	2797	2553	3040	487	2801	0.39	2621	2981	360	IV
<i>Anairetes parulus</i>	0	1	2972	2972	2972	0						
<i>Serpophaga cinerea</i>	1	0	1357	1357	1357	0						
<i>Pseudotriccus ruficeps</i>	1	12	2920	2463	3377	914	3059	0.21	2634	3414	780	IV
<i>Corythopsis torquatus</i>	2	4	962	948	975	27						
<i>Zimmerius bolivianus</i>	4	54	2118	1335	2901	1566	2000	0.66	1361	2639	1278	IV
<i>Phylloscartes poecilotis</i>	1	0	1392	1392	1392	0						
<i>Phylloscartes ophthalmicus</i>	6	21	1329	1007	1651	644	1301	0.59	1045	1554	509	IV
<i>Phylloscartes orbitalis</i>	1	0	946	946	946	0						
<i>Phylloscartes ventralis</i>	6	3	1770	1541	1998	457						
<i>Phylloscartes parkeri</i>	0	4	1260	1124	1395	271						
<i>Mionectes striaticollis</i>	47	13	2115	853	3377	2525	2115	0.92	1105	3125	2019	I
<i>Mionectes olivaceus</i>	17	0	1177	853	1501	649	853	1.00	853	1254	401	II
<i>Mionectes oleagineus</i>	6	0	914	853	975	123						
<i>Leptopogon amaurocephalus</i>	2	2	922	893	950	57						
<i>Leptopogon superciliaris</i>	16	27	1291	866	1716	850	1353	0.64	1063	1642	579	IV
<i>Myiopiccus ornatus</i>	5	9	1010	818	1202	384						
<i>Myiomis ecaudatus</i>	0	3	918	876	960	84						
<i>Lophotriccus pileatus</i>	15	40	1372	930	1813	883	1395	0.88	1100	1689	590	IV
<i>Hemitriccus flammulatus</i>	0	5	909	866	951	85						
<i>Hemitriccus granadensis</i>	5	55	2737	2258	3215	957	2783	0.74	2355	3210	856	IV
<i>Hemitriccus ruficularis</i>	0	1	1090	1090	1090	0						
<i>Poecilotriccus albifacies</i>	0	2	887	823	951	128						
<i>Poecilotriccus plumbeiceps</i>	3	7	1816	1610	2023	413						
<i>Poecilotriccus latirostris</i>	0	1	895	895	895	0						

Table A-1. Continued

Species	No. Sites Detected		Observed Elevational Range				Modeled Elevational Range				HOF Type	
	Netted	Counts	Midpoint	Min.	Max.	Range	Optimum	Prob. of Occurrence	Min.	Max.		Range
<i>Rhynchocyclus fulvipectus</i>	4	3	1360	1124	1597	473						
<i>Tolmomyias assimilis</i>	1	8	1097	826	1367	541						
<i>Tolmomyias flaviventris</i>	1	0	1324	1324	1324	0						
<i>Platyrrinchus mystaceus</i>	10	2	1518	1255	1781	526	1537	0.48	1249	1822	573	IV
<i>Myiophobus inornatus</i>	7	0	1474	950	1998	1048						
<i>Myiophobus ochraceiventris</i>	0	5	2969	2723	3215	492						
<i>Myiobius villosus</i>	6	0	1258	853	1663	811						
<i>Terenotriccus erythrurus</i>	3	1	906	837	975	138						
<i>Pyrrhomyias cinnamomeus</i>	5	54	2233	1365	3101	1736	3414	0.43	1807	3414	1607	III
<i>Lathrotriccus euleri</i>	7	16	1267	818	1716	898	805	0.55	805	1243	438	II
<i>Contopus fumigatus</i>	0	28	2016	930	3101	2171	2770	0.45	2436	3104	668	IV
<i>Knipolegus aterrimus</i>	0	1	2685	2685	2685	0						
<i>Myiotheretes striaticollis</i>	0	21	2182	1332	3032	1700	2110	0.11	1066	3153	2087	I
<i>Ochthoeca frontalis</i>	2	1	3306	3235	3377	142						
<i>Ochthoeca pulchella</i>	8	45	2562	2023	3101	1078	2790	0.76	2490	3090	600	IV
<i>Ochthoeca cinnamomeiventris</i>	3	8	2725	2458	2992	534						
<i>Ochthoeca rufipectoralis</i>	2	15	3007	2637	3377	740	2986	0.60	2817	3156	339	IV
<i>Legatus leucophaeus</i>	0	7	964	818	1110	292						
<i>Conopias cinchoneti</i>	1	4	1380	1331	1429	98						
<i>Myiodynastes chrysocephalus</i>	1	6	2034	1334	2734	1400						
<i>Tyrannus melancholicus</i>	0	8	2015	1307	2723	1416						
<i>Rhytipterna simplex</i>	0	2	872	866	878	12						
<i>Myiarchus tuberculifer</i>	2	31	2111	1007	3215	2208	2420	0.28	1658	3182	1524	IV
<i>Ramphotrigon megacephalum</i>	0	6	878	805	951	146						
<i>Ramphotrigon fuscicauda</i>	1	3	937	923	951	28						
<i>Attila spadiceus</i>	0	2	1149	1124	1173	49						
<i>Pipreola intermedia</i>	4	38	2405	1709	3101	1392	2858	0.57	2279	3077	798	V
<i>Pipreola arcuata</i>	1	43	2581	1947	3215	1268	2918	0.68	2530	3310	780	IV
<i>Pipreola frontalis</i>	1	0	1781	1781	1781	0						
<i>Ampelion rubrocristatus</i>	0	3	2786	2685	2887	202						
<i>Rupicola peruvianus</i>	7	8	1265	866	1663	797						

Table A-1. Continued

Species	No. Sites Detected		Observed Elevational Range				Modeled Elevational Range				HOF Type	
	Netted	Counts	Midpoint	Min.	Max.	Range	Optimum	Prob. of Occurrence	Min.	Max.		Range
<i>Cephalopterus ornatus</i>	0	1	1307	1307	1307	0						
<i>Tyranneutes stolzmanni</i>	0	1	866	866	866	0						
<i>Machaeropterus pyrocephalus</i>	9	16	1124	818	1429	611	805	0.61	805	1186	381	II
<i>Lepidothrix coronata</i>	0	2	1018	975	1061	86						
<i>Lepidothrix coeruleocapilla</i>	22	12	1281	853	1709	857	853	0.98	853	1406	553	II
<i>Manacus manacus</i>	2	0	963	950	975	25						
<i>Chiroxiphia boliviana</i>	31	45	1401	930	1872	942	1428	0.96	1032	1825	793	IV
<i>Pipra fasciicauda</i>	3	4	902	853	951	99						
<i>Pipra chloromeros</i>	4	2	921	829	1013	184						
<i>Schiffornis turdina</i>	3	10	954	818	1090	272	805	0.51	805	1071	266	II
<i>Pachyramphus versicolor</i>	0	2	2965	2828	3101	273						
<i>Piprites chloris</i>	1	0	930	930	930	0						
<i>Vireolanius leucotis</i>	0	5	1059	1007	1110	103						
<i>Vireo leucophrys</i>	1	7	1541	1373	1709	336						
<i>Vireo olivaceus</i>	0	2	828	818	837	19						
<i>Hylophilus hypoxanthus</i>	0	5	852	826	878	52						
<i>Hylophilus ochraceiceps</i>	3	15	981	823	1139	316	995	0.83	891	1100	209	IV
<i>Cyanolyca viridicyanus</i>	1	37	2738	2463	3013	550	2710	0.62	2420	2997	577	IV
<i>Cyanocorax violaceus</i>	0	9	878	805	951	146						
<i>Cyanocorax yncas</i>	0	19	1716	1398	2033	635	1823	0.86	1619	2026	407	IV
<i>Pygochelidon cyanoleuca</i>	2	0	1395	1392	1397	5						
<i>Microcerculus marginatus</i>	7	33	1069	805	1332	527	805	0.97	805	1183	378	II
<i>Odontorchilus branickii</i>	1	6	1456	1334	1578	244						
<i>Troglodytes aedon</i>	0	2	2987	2982	2991	9						
<i>Troglodytes solstitialis</i>	8	45	2559	1883	3235	1352	2754	0.65	2365	3140	775	IV
<i>Campylorhynchus turdinus</i>	0	8	1051	823	1279	456						
<i>Pheugopedius genibarbis</i>	4	15	1151	805	1496	691	1136	0.33	836	1434	597	IV
<i>Cinnycerthia fulva</i>	8	34	2642	1998	3286	1288	2780	0.46	2321	3203	882	V
<i>Henicorhina leucophrys</i>	19	52	2044	1324	2764	1440	1742	0.97	1447	2261	814	V
<i>Cyphorhinus thoracicus</i>	10	23	1394	1124	1663	539	1251	0.81	1121	1525	404	V
<i>Myadestes ralloides</i>	25	23	1902	975	2828	1853	1416	0.80	1017	1815	798	IV

Table A-1. Continued

Species	No. Sites Detected		Observed Elevational Range				Modeled Elevational Range				HOF Type	
	Netted	Counts	Midpoint	Min.	Max.	Range	Optimum	Prob. of Occurrence	Min.	Max.		Range
<i>Catharus fuscater</i>	1	0	1350	1350	1350	0						
<i>Catharus dryas</i>	7	7	1261	1124	1398	274						
<i>Entomodestes leucotis</i>	10	43	2161	1541	2781	1240	1956	0.98	1721	2438	717	V
<i>Turdus leucops</i>	2	15	1536	1124	1947	823	1684	0.36	1337	2029	691	IV
<i>Turdus hauxwelli</i>	1	0	1392	1392	1392	0						
<i>Turdus ignobilis</i>	7	8	1235	829	1640	811						
<i>Turdus fuscater</i>	1	7	3025	2673	3377	704						
<i>Turdus chiguanco</i>	1	1	2983	2974	2992	18						
<i>Turdus serranus</i>	6	36	2355	1550	3159	1609	2780	0.54	2250	3044	793	V
<i>Creurgops dentatus</i>	2	3	1712	1541	1883	342						
<i>Hemispingus atropileus</i>	3	10	2465	1947	2982	1035	2715	0.14	2292	3135	843	IV
<i>Hemispingus superciliaris</i>	1	5	2681	2542	2820	278						
<i>Hemispingus frontalis</i>	3	3	2363	1872	2854	983						
<i>Hemispingus melanotis</i>	13	16	2300	1365	3235	1870	1739	0.45	1423	2052	629	IV
<i>Hemispingus xanthophthalmus</i>	0	1	2781	2781	2781	0						
<i>Hemispingus trifasciatus</i>	0	3	3378	3342	3414	72						
<i>Cnemoscopus rubrirostris</i>	1	7	2635	2458	2811	353						
<i>Thlypopsis ruficeps</i>	0	3	2825	2668	2981	313						
<i>Trichothraupis melanops</i>	18	1	1396	1129	1663	534	1497	0.83	1259	1736	477	IV
<i>Lanio versicolor</i>	2	17	964	818	1110	292	805	0.89	805	1027	222	II
<i>Ramphocelus carbo</i>	7	3	1369	1309	1429	120						
<i>Thraupis episcopus</i>	1	2	1362	1331	1392	61						
<i>Thraupis cyanocephala</i>	4	27	2184	1335	3032	1697	2616	0.34	2104	3127	1023	IV
<i>Buthraupis montana</i>	1	63	2821	2426	3215	789	2905	0.97	2563	3247	684	IV
<i>Anisognathus igniventris</i>	0	22	2963	2542	3383	841	3119	0.75	2866	3372	506	IV
<i>Anisognathus somptuosus</i>	2	24	1966	1621	2310	689	1943	0.91	1684	2198	514	IV
<i>Chlorornis riefferii</i>	4	54	2837	2458	3215	757	2809	0.80	2443	3174	731	IV
<i>Delothraupis castaneiventris</i>	0	8	2804	2507	3101	594						
<i>Iridosornis analis</i>	16	23	1636	1124	2148	1024	1763	0.63	1447	2081	634	IV
<i>Iridosornis jelskii</i>	1	3	2880	2383	3377	994						
<i>Pipraeidea melanonota</i>	3	0	1405	1324	1486	162						

Table A-1. Continued

Species	No. Sites Detected		Observed Elevational Range				Modeled Elevational Range				HOF Type	
	Netted	Counts	Midpoint	Min.	Max.	Range	Optimum	Prob. of Occurrence	Min.	Max.		Range
<i>Chlorochrysa calliparaea</i>	12	10	1440	1100	1780	680	1406	0.41	1030	1782	752	IV
<i>Tangara cyanicollis</i>	6	1	1298	1194	1401	207						
<i>Tangara xanthogastra</i>	1	0	877	877	877	0						
<i>Tangara punctata</i>	3	2	1487	1194	1781	587						
<i>Tangara vassorii</i>	2	3	2745	2458	3032	574						
<i>Tangara nigroviridis</i>	6	1	1547	1392	1702	310						
<i>Tangara chilensis</i>	3	33	1365	818	1911	1093	1142	0.63	818	1465	647	IV
<i>Tangara gyrola</i>	1	1	1163	1124	1202	78						
<i>Tangara chrysotis</i>	1	1	1492	1392	1591	199						
<i>Tangara xanthocephala</i>	1	2	1682	1392	1972	580						
<i>Tangara parzudakii</i>	1	0	1998	1998	1998	0						
<i>Tangara schrankii</i>	2	5	903	826	980	154						
<i>Tangara arthus</i>	12	1	1376	1100	1651	551	1269	0.51	1002	1540	538	IV
<i>Cyanerpes caeruleus</i>	2	1	1239	1124	1354	230						
<i>Chlorophanes spiza</i>	1	1	963	826	1100	274						
<i>Iridophanes pulcherrimus</i>	1	0	1663	1663	1663	0						
<i>Hemithraupis flavicollis</i>	0	1	826	826	826	0						
<i>Conirostrum albifrons</i>	0	1	2542	2542	2542	0						
<i>Diglossa mystacalis</i>	1	4	3203	2991	3414	423						
<i>Diglossa brunneiventris</i>	2	9	2788	2527	3049	522						
<i>Diglossa glauca</i>	15	32	1926	1061	2791	1730	1885	0.99	1622	2149	527	IV
<i>Diglossa caerulescens</i>	4	7	1788	1392	2184	792						
<i>Diglossa cyanea</i>	10	84	2403	1392	3414	2022	3414	1.00	2464	3414	950	II
<i>Catamblyrhynchus diadema</i>	2	2	2808	2636	2981	345						
<i>Chlorospingus ophthalmicus</i>	4	35	1977	1392	2561	1169	1919	0.87	1554	2284	731	IV
<i>Chlorospingus parvirostris</i>	7	0	1686	1350	2023	673						
<i>Chlorospingus flavigularis</i>	17	18	1410	1007	1813	806	1272	0.60	1053	1491	438	IV
<i>Chlorospingus canigularis</i>	1	0	1100	1100	1100	0						
<i>Coereba flaveola</i>	6	7	1134	866	1401	535						
<i>Saltator grossus</i>	0	10	870	805	934	129	805	0.93	805	894	89	II
<i>Saltator maximus</i>	5	7	1124	818	1429	611						

Table A-1. Continued

Species	No. Sites Detected		Observed Elevational Range				Modeled Elevational Range				HOF Type	
	Netted	Counts	Midpoint	Min.	Max.	Range	Optimum	Prob. of Occurrence	Min.	Max.		Range
<i>Ammodramus aurifrons</i>	2	0	1399	1397	1401	4						
<i>Haplospiza rustica</i>	3	4	2208	1597	2820	1223						
<i>Sporophila schistacea</i>	0	7	842	805	878	73						
<i>Sporophila luctuosa</i>	1	0	1392	1392	1392	0						
<i>Oryzoborus angolensis</i>	3	0	1135	946	1324	378						
<i>Arremon taciturnus</i>	6	12	909	837	980	143	922	0.70	849	993	143	IV
<i>Arremon brunneinucha</i>	5	14	1727	1367	2087	720	1765	0.58	1538	1989	451	IV
<i>Arremon torquatus</i>	0	12	2786	2539	3032	493	2725	0.35	2577	2877	300	IV
<i>Arremon castaneiceps</i>	1	0	1354	1354	1354	0						
<i>Atlapetes melanolaemus</i>	15	56	2318	1401	3235	1834	2535	0.67	1987	3083	1096	IV
<i>Piranga flava</i>	0	3	1093	1013	1173	160						
<i>Piranga leucoptera</i>	1	2	1270	1124	1415	291						
<i>Chlorothraupis carmioli</i>	5	21	958	826	1090	264	933	0.93	834	1032	198	IV
<i>Cyanocompsa cyanoides</i>	4	6	1016	818	1213	395						
<i>Parula pitiayumi</i>	1	32	1329	1007	1651	644	1361	0.82	1105	1616	511	IV
<i>Myioborus miniatus</i>	17	68	1408	818	1998	1180	1802	0.97	1074	1937	864	V
<i>Myioborus melanocephalus</i>	7	83	2392	1401	3383	1982	2316	0.97	2073	3111	1038	V
<i>Basileuterus bivittatus</i>	15	33	1242	893	1591	698	1311	0.89	993	1462	470	V
<i>Basileuterus chrysogaster</i>	1	21	965	805	1124	319	805	0.93	805	1029	224	II
<i>Basileuterus luteoviridis</i>	7	28	2837	2458	3215	757	2770	0.47	2456	3080	624	IV
<i>Basileuterus signatus</i>	9	49	2422	1852	2992	1140	2292	0.81	1856	2728	871	IV
<i>Basileuterus coronatus</i>	20	34	1896	1334	2458	1124	1718	0.95	1457	1979	522	IV
<i>Basileuterus tristriatus</i>	15	10	1681	1340	2023	683	1605	0.84	1348	1860	512	IV
<i>Phaeothlypis fulvicauda</i>	0	1	818	818	818	0						
<i>Psarocolius angustifrons</i>	4	20	1419	805	2033	1228	805	0.54	805	1397	592	II
<i>Psarocolius atrovirens</i>	3	10	1696	1358	2033	675	1637	0.25	1314	1961	647	IV
<i>Psarocolius decumanus</i>	0	9	1020	823	1217	394						
<i>Psarocolius bifasciatus</i>	0	10	934	892	975	83	943	0.78	894	995	102	IV
<i>Cacicus chrysonotus</i>	1	36	2556	2010	3101	1091	2736	0.53	2352	3117	764	IV
<i>Cacicus cela</i>	0	1	934	934	934	0						
<i>Amblycercus holosericeus</i>	2	1	2599	2458	2739	281						

Table A-1. Continued

Species	No. Sites Detected		Observed Elevational Range				Modeled Elevational Range			HOF Type		
	Netted	Counts	Midpoint	Min.	Max.	Range	Optimum	Prob. of Occurrence	Min.		Max.	Range
<i>Euphonia mesochrysa</i>	7	3	1401	1139	1663	524						
<i>Euphonia xanthogaster</i>	32	70	1402	805	1998	1193	805	0.82	805	1760	955	III
<i>Chlorophonia cyanea</i>	2	50	1443	876	2010	1134	1656	0.89	1149	1924	775	V

APPENDIX B  
SUMMARY OF RARE SPECIES

Table B-1. Species detected at ten sites or fewer (with netting and counts) in the Manu study area. The total number of detections is given for each species with the proposed cause for its rarity across surveys. A species is assigned to only one of the categories described. “Lowland” species are those not detected above 1200 m and whose distribution extends below 500 m; “Highland” species are those not found below 3200 m and whose distribution extends above 3800 m. “Detection” indicates that species rarely sings, has inconspicuous behavior, or resides in areas that are difficult to survey. “Habitat specific” denotes species that are found within easily identifiable habitat types within forest (see Habitat Notes for details). “Non-forest” species are those common along forest edges, second growth, and clearings within the study area. “Low density” species is a catch-all category for easily detected forest species with no known habitat specificity.

Species	No. Sites Detected	Lowland	Highland	Detection	Habitat Specific	Non-forest	Low Density	Habitat notes
<i>Nothocercus nigrocapillus</i>	8						x	
<i>Tinamus guttatus</i>	8	x						
<i>Crypturellus soui</i>	8	x						
<i>Penelope jacquacu</i>	4	x						
<i>Aburria aburri</i>	9						x	
<i>Ortalis guttata</i>	1					x		
<i>Odontophorus balliviani</i>	4						x	
<i>Odontophorus stellatus</i>	2	x						
<i>Elanoides forficatus</i>	1	x						
<i>Accipiter striatus</i>	1						x	
<i>Buteo magnirostris</i>	2	x						
<i>Ibycter americanus</i>	1	x						
<i>Claravis mondetoura</i>	1				x			Nomadic, <i>Chusquea</i>
<i>Patagioenas subvinacea</i>	4	x						
<i>Leptotila rufaxilla</i>	1	x						
<i>Ara ararauna</i>	1	x						
<i>Ara militaris</i>	4						x	
<i>Primolius couloni</i>	5	x						
<i>Aratinga leucophthalma</i>	6	x						
<i>Pionus tumultuosus</i>	5						x	
<i>Amazona farinosa</i>	2	x						
<i>Picumnus aurifrons</i>	1	x						

Table B-1. Continued

Species	No. Sites Detected	Lowland	Highland	Detection	Habitat Specific	Non-forest Areas	Low Density	Habitat notes
<i>Piaya cayana</i>	9						x	
<i>Dromococcyx pavoninus</i>	4	x						
<i>Ciccaba albitarsis</i>	1						x	
<i>Glaucidium bolivianum</i>	3						x	
<i>Lurocalis rufiventris</i>	1			x				
<i>Threnetes leucurus</i>	5				x			Gaps, River-edges
<i>Phaethornis hispidus</i>	2	x						
<i>Phaethornis koepckeae</i>	3	x						
<i>Phaethornis superciliosus</i>	6	x						
<i>Doryfera johannae</i>	3						x	
<i>Colibri coruscans</i>	3					x		
<i>Heliostyris auritus</i>	1						x	
<i>Agelaiocercus kingi</i>	6			x				
<i>Lesbia nuna</i>	1						x	
<i>Haplophaedia assimilis</i>	2						x	
<i>Aglaeactis cupripennis</i>	1				x			Montane scrub
<i>Coeligena torquata</i>	10						x	
<i>Boissonneaua matthewsii</i>	5						x	
<i>Heliodoxa schreibersii</i>	5						x	
<i>Heliodoxa aurescens</i>	1	x						
<i>Chaetocercus mulsant</i>	2			x				
<i>Chlorostilbon mellisugus</i>	2	x						
<i>Klais guimeti</i>	1	x						
<i>Campylopterus largipennis</i>	3	x						
<i>Thalurania furcata</i>	10						x	
<i>Taphrospilus hypostictus</i>	4						x	
<i>Amazilia viridicauda</i>	1						x	
<i>Chrysuronia oenone</i>	3						x	
<i>Trogon melanurus</i>	6	x						
<i>Trogon viridis</i>	2	x						
<i>Trogon violaceus</i>	6	x						
<i>Trogon curucui</i>	3	x						

Table B-1. Continued

Species	No. Sites Detected	Lowland	Highland	Detection	Habitat Specific	Non-forest Areas	Low Density	Habitat notes
<i>Chloroceryle aenea</i>	1	x						
<i>Momotus aequatorialis</i>	2				x			Streamsides
<i>Galbula cyanescens</i>	4	x						
<i>Nystalus striolatus</i>	2	x						
<i>Micromonacha lanceolata</i>	2			x				
<i>Nonnula ruficapilla</i>	1	x						
<i>Capito auratus</i>	6	x						
<i>Ramphastos tucanus</i>	1	x						
<i>Aulacorhynchus prasinus</i>	8						x	
<i>Selenidera reinwardtii</i>	9	x						
<i>Pteroglossus azara</i>	1	x						
<i>Melanerpes cruentatus</i>	3	x						
<i>Veniliornis affinis</i>	1	x						
<i>Dryocopus lineatus</i>	4				x			River-edge forest
<i>Campephilus rubricollis</i>	1	x						
<i>Campephilus melanoleucos</i>	3						x	
<i>Sclerurus mexicanus</i>	1	x						
<i>Schizoeaca helleri</i>	7				x			Montane scrub, Treeline
<i>Synallaxis cabanisi</i>	4					x		
<i>Cranioleuca marcapatae</i>	2						x	
<i>Premnornis guttuligera</i>	2			x				
<i>Simoxenops ucayalae</i>	7				x			Guadua
<i>Ancistrops strigilatus</i>	4	x						
<i>Hyloctistes subulatus</i>	8	x						
<i>Philydor ruficaudatum</i>	5	x						
<i>Philydor erythrocercum</i>	2	x						
<i>Philydor erythropterum</i>	3	x						
<i>Philydor rufum</i>	3	x						
<i>Automolus rubiginosus</i>	4	x						
<i>Automolus rufipileatus</i>	7	x						
<i>Lochmias nematura</i>	6				x			Streamsides
<i>Xenops minutus</i>	6	x						
<i>Xenops rutilans</i>	2	x						

Table B-1. Continued

Species	No. Sites Detected	Lowland	Highland	Detection	Habitat Specific	Non-forest Areas	Low Density	Habitat notes
<i>Deconychura longicauda</i>	1	x						
<i>Dendrexetastes rufigula</i>	10	x						
<i>Dendrocolaptes certhia</i>	3	x						
<i>Xiphorhynchus obsoletus</i>	1	x						
<i>Campylorhamphus pucherani</i>	1						x	
<i>Thamnophilus palliatus</i>	5					x		
<i>Thamnophilus aethiops</i>	3	x						
<i>Epinecrophylla erythrura</i>	1	x						
<i>Myrmotherula brachyura</i>	3						x	
<i>Myrmotherula axillaris</i>	1	x						
<i>Myrmotherula menetriesii</i>	2	x						
<i>Terenura sharpei</i>	4						x	
<i>Cercomacra cinerascens</i>	1	x						
<i>Cercomacra manu</i>	8	x						
<i>Schistocicla leucostigma</i>	4				x			Streamsides
<i>Myrmeciza atrothorax</i>	4	x						
<i>Myrmeciza goeldii</i>	10	x						
<i>Myrmeciza fortis</i>	2	x						
<i>Rhegmatorhina melanosticta</i>	6	x						
<i>Phlegopsis nigromaculata</i>	4	x						
<i>Grallaria squamigera</i>	3						x	
<i>Myrmothera campanisona</i>	3	x						
<i>Grallaricula flavirostris</i>	4						x	
<i>Scytalopus schulenbergi</i>	1				x			Treeline
<i>Phyllomyias cinereiceps</i>	2						x	
<i>Phyllomyias plumbeiceps</i>	1						x	
<i>Elaenia albiceps</i>	7			x				
<i>Anairetes parulus</i>	1				x			Montane scrub
<i>Serpophaga cinerea</i>	1				x			River-edge forest, Islands
<i>Corythopsis torquatus</i>	6	x						
<i>Phylloscartes ventralis</i>	9						x	
<i>Phylloscartes orbitalis</i>	1						x	
<i>Phylloscartes parkeri</i>	4						x	

Table B-1. Continued

Species	No. Sites Detected	Lowland	Highland	Detection	Habitat Specific	Non-forest Areas	Low Density	Habitat notes
<i>Phylloscartes poecilotis</i>	1						x	
<i>Mionectes oleagineus</i>	6	x						
<i>Leptopogon amaurocephalus</i>	4	x						
<i>Myiomis ecaudatus</i>	3	x						
<i>Hemitriccus flammulatus</i>	5	x						
<i>Hemitriccus rufularis</i>	1				x			Outlying ridges
<i>Poecilotriccus latirostris</i>	1	x						
<i>Poecilotriccus plumbeiceps</i>	10						x	
<i>Rhynchocyclus fulvipectus</i>	7						x	
<i>Tolmomyias assimilis</i>	9	x						
<i>Tolmomyias flaviventris</i>	1						x	
<i>Poecilotriccus albifacies</i>	2	x						
<i>Myiophobus inornatus</i>	7			x				
<i>Myiophobus ochraceiventris</i>	5			x				
<i>Myiobius villosus</i>	6			x				
<i>Terenotriccus erythrurus</i>	4	x						
<i>Knipolegus aterrimus</i>	1				x			Montane scrub
<i>Ochthoeca frontalis</i>	3			x				
<i>Legatus leucophaeus</i>	7	x						
<i>Conopias cinchoneti</i>	5					x		
<i>Myiodynastes chrysocephalus</i>	7						x	
<i>Tyrannus melancholicus</i>	8					x		
<i>Rhytipterna simplex</i>	2	x						
<i>Ramphotrigon megacephalum</i>	6	x						
<i>Ramphotrigon fuscicauda</i>	4	x						Guadua
<i>Attila spadiceus</i>	2	x						
<i>Piprites chloris</i>	1	x						
<i>Pipreola frontalis</i>	1						x	
<i>Ampelion rubrocristatus</i>	3			x				
<i>Cephalopterus ornatus</i>	1						x	
<i>Tyranneutes stolzmanni</i>	1	x						
<i>Lepidothrix coronata</i>	2	x						
<i>Manacus manacus</i>	2	x						

Table B-1. Continued

Species	No. Sites Detected	Lowland	Highland	Detection	Habitat Specific	Non-forest Areas	Low Density	Habitat notes
<i>Pipraeidea melanonota</i>	3						x	
<i>Pipra fasciicauda</i>	7	x						
<i>Pipra chloromeros</i>	6	x						
<i>Pachyramphus versicolor</i>	2						x	
<i>Piranga flava</i>	3						x	
<i>Vireolanius leucotis</i>	5	x						
<i>Vireo leucophrys</i>	8						x	
<i>Vireo olivaceus</i>	2	x						
<i>Hylophilus hypoxanthus</i>	5	x						
<i>Cyanocorax violaceus</i>	9					x		
<i>Pygochelidon cyanoleuca</i>	2			x				
<i>Odontorchilus branickii</i>	7						x	
<i>Troglodytes aedon</i>	2					x		
<i>Campylorhynchus turdinus</i>	8	x						
<i>Catharus fuscater</i>	1				x			Streamsides
<i>Turdus hauxwelli</i>	1						x	
<i>Turdus fuscater</i>	8		x					
<i>Turdus chiguanco</i>	2					x		
<i>Creurgops dentatus</i>	5						x	
<i>Hemispingus superciliaris</i>	6			x				
<i>Hemispingus frontalis</i>	6						x	
<i>Hemispingus xanthophthalmus</i>	1			x				
<i>Hemispingus trifasciatus</i>	3				x			Treeline
<i>Cnemoscopus rubrirostris</i>	8						x	
<i>Thlypopsis ruficeps</i>	3					x		
<i>Ramphocelus carbo</i>	10					x		
<i>Thraupis episcopus</i>	3					x		
<i>Delothraupis castaneiventris</i>	8						x	
<i>Iridosornis jelskii</i>	4						x	
<i>Tangara cyanicollis</i>	7			x				
<i>Tangara xanthogastra</i>	1			x				
<i>Tangara punctata</i>	5			x				
<i>Tangara vassorii</i>	5			x				

Table B-1. Continued

Species	No. Sites Detected	Lowland	Highland	Detection	Habitat Specific	Non-forest Areas	Low Density	Habitat notes
<i>Tangara nigroviridis</i>	7			x				
<i>Tangara gyrola</i>	2	x						
<i>Tangara chrysotis</i>	2			x				
<i>Tangara xanthocephala</i>	3			x				
<i>Tangara parzudakii</i>	1			x				
<i>Tangara schrankii</i>	7	x						
<i>Cyanerpes caeruleus</i>	3	x						
<i>Chlorophanes spiza</i>	2	x						
<i>Iridophanes pulcherrimus</i>	1			x				
<i>Hemithraupis flavicollis</i>	1	x						
<i>Conirostrum albifrons</i>	1			x				
<i>Diglossa mystacalis</i>	5				x			Montane scrub
<i>Catamblyrhynchus diadema</i>	4						x	
<i>Chlorospingus parvirostris</i>	7						x	
<i>Chlorospingus canigularis</i>	1						x	
<i>Saltator grossus</i>	10	x						
<i>Ammodramus aurifrons</i>	2					x		
<i>Haplospiza rustica</i>	7				x			Landslides, <i>Chusquea</i>
<i>Sporophila schistacea</i>	7	x						
<i>Sporophila luctuosa</i>	1					x		
<i>Oryzoborus angolensis</i>	3	x						
<i>Arremon castaneiceps</i>	1				x			Streamsides
<i>Piranga leucoptera</i>	3						x	
<i>Cyanocompsa cyanoides</i>	10	x						
<i>Phaeothlypis fulvicauda</i>	1				x			Streamsides
<i>Psarocolius decumanus</i>	9	x						
<i>Psarocolius bifasciatus</i>	10	x						
<i>Cacicus cela</i>	1	x						
<i>Amblycercus holosericeus</i>	3				x			<i>Chusquea</i>
<i>Euphonia mesochrysa</i>	10						x	

APPENDIX C  
SPECIES RESPONSE CURVES ALONG THE MANU GRADIENT

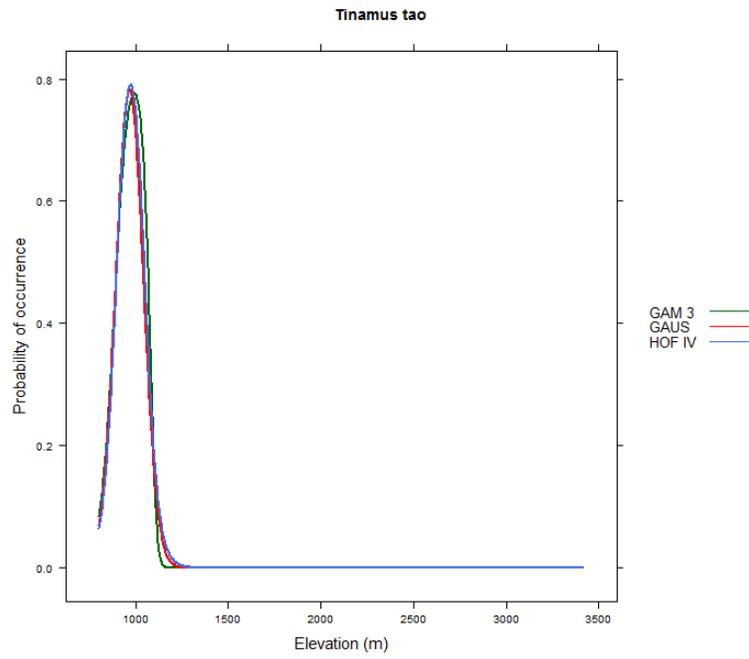


Figure C-1.

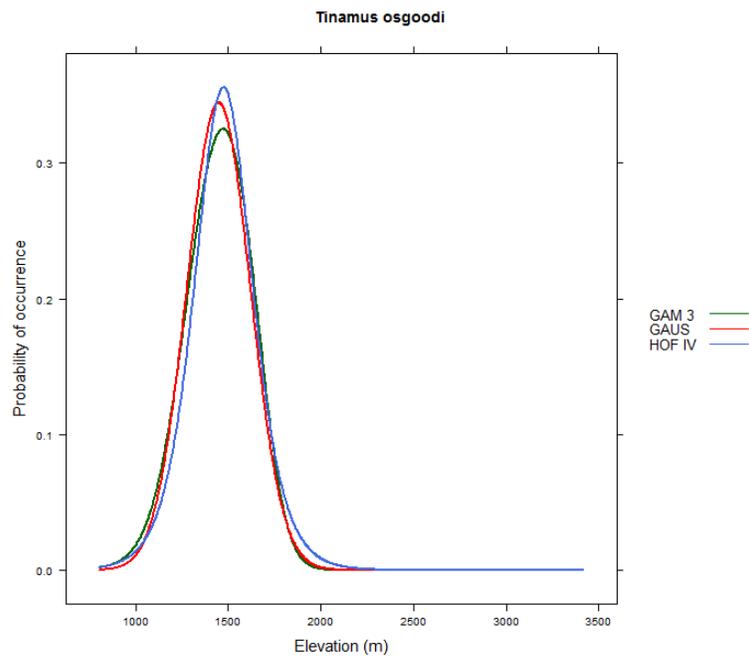


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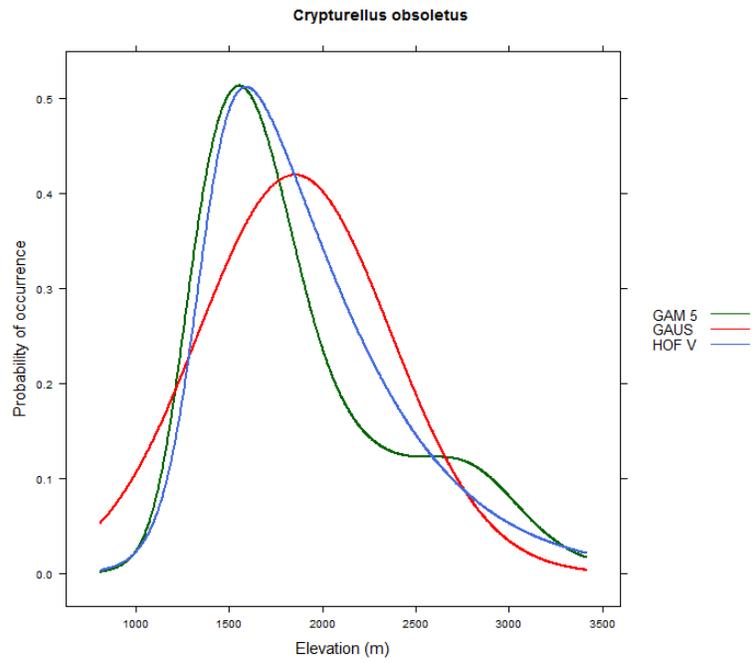


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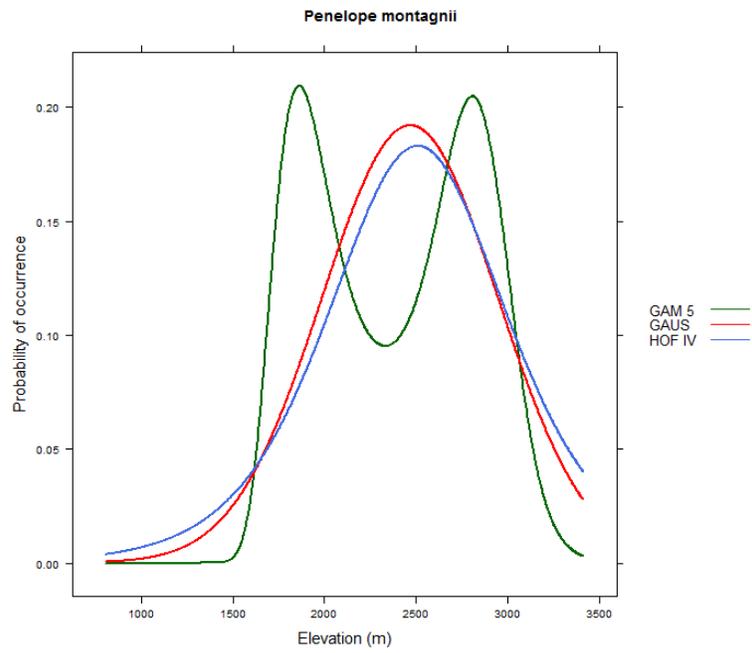


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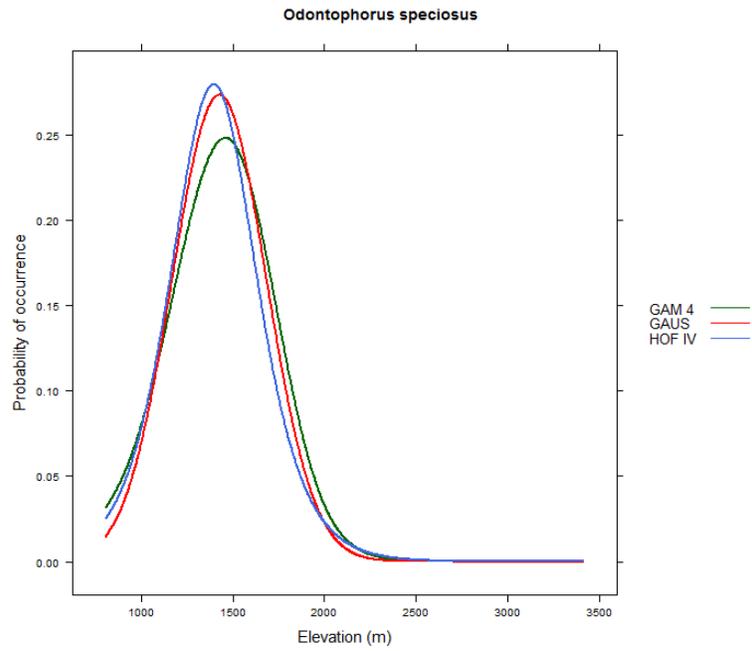


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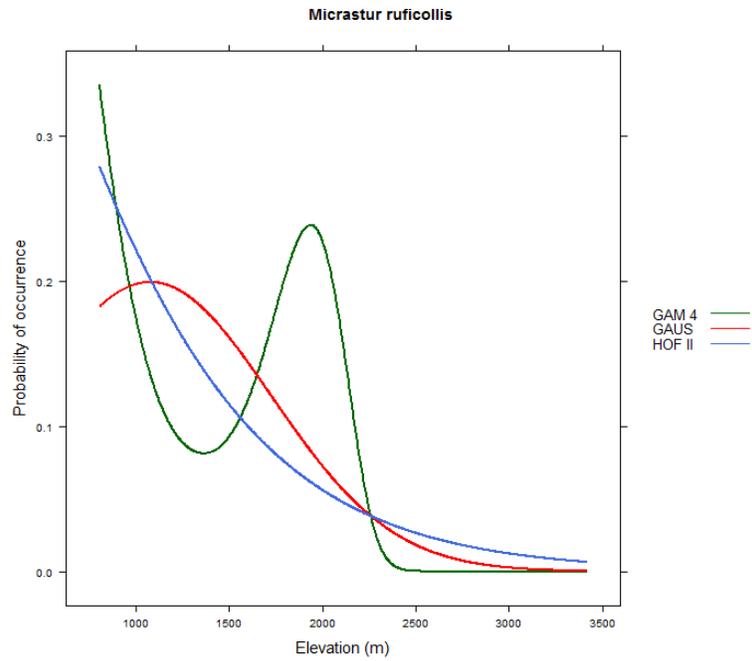


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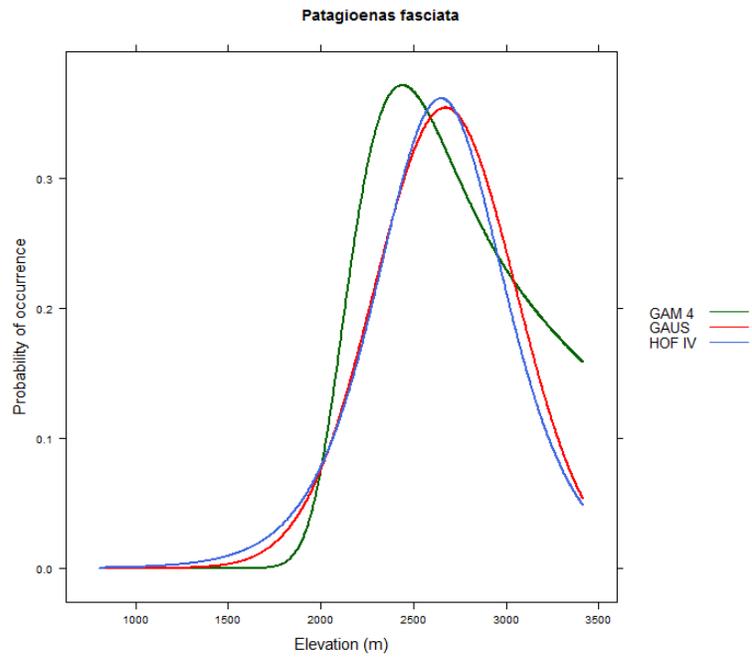


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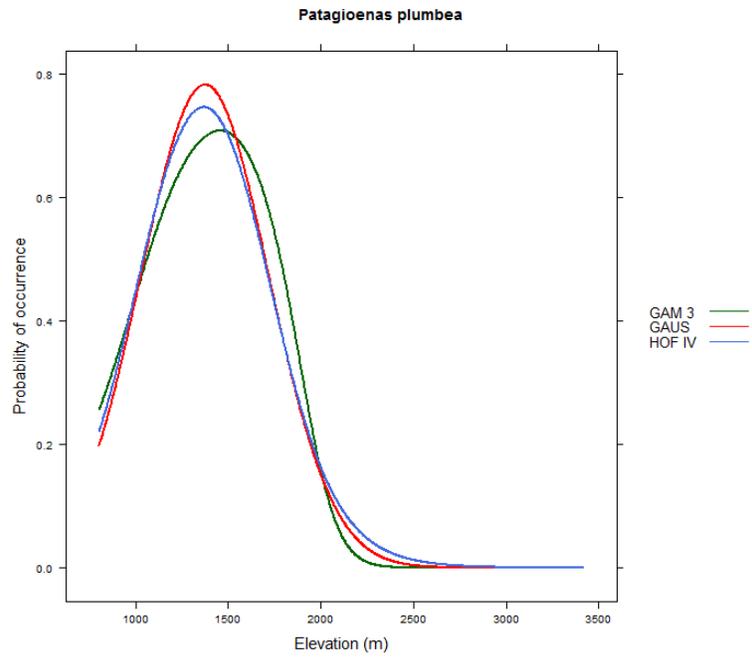


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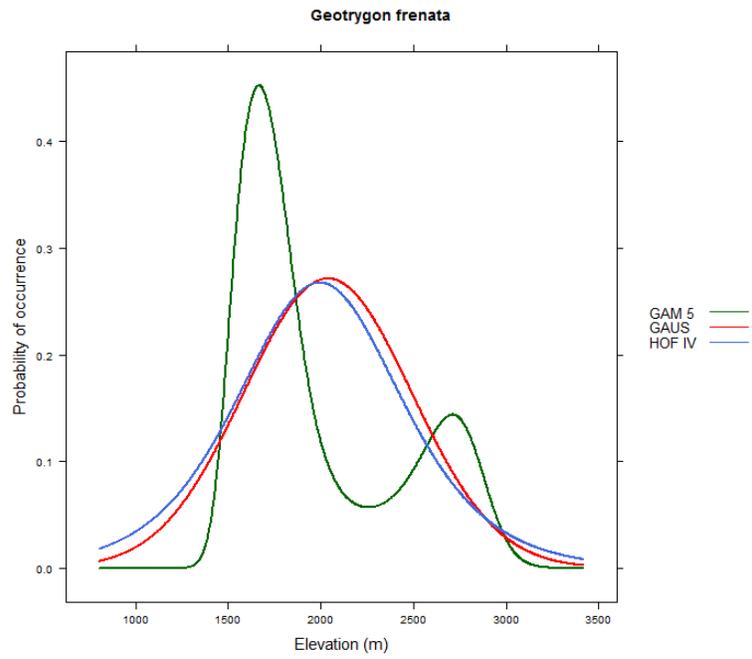


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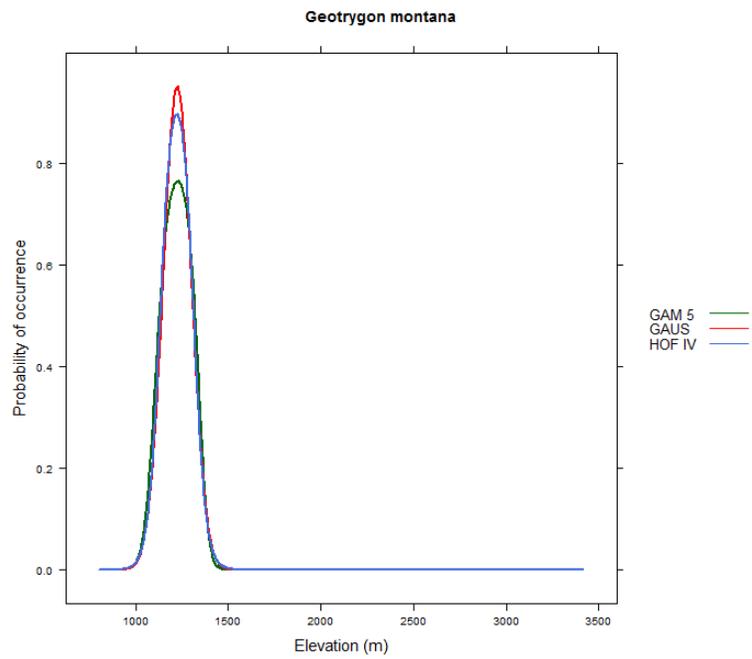


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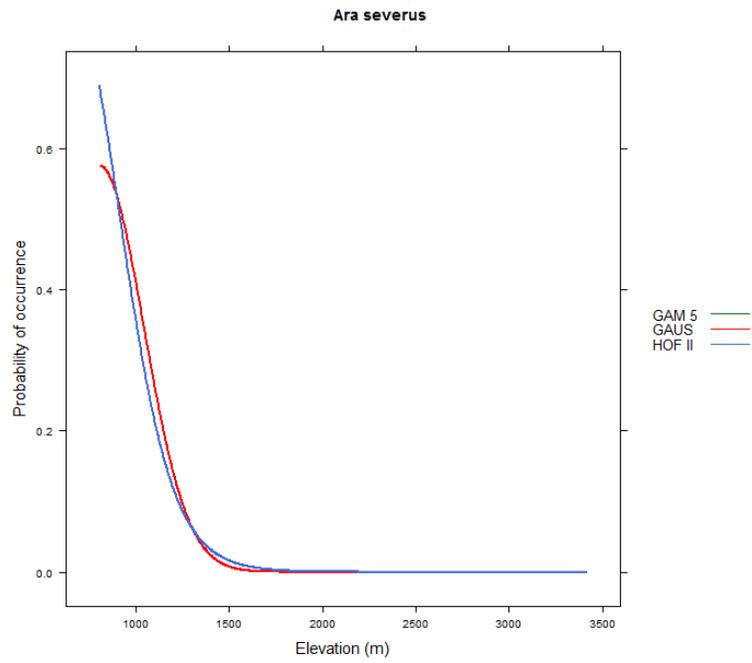


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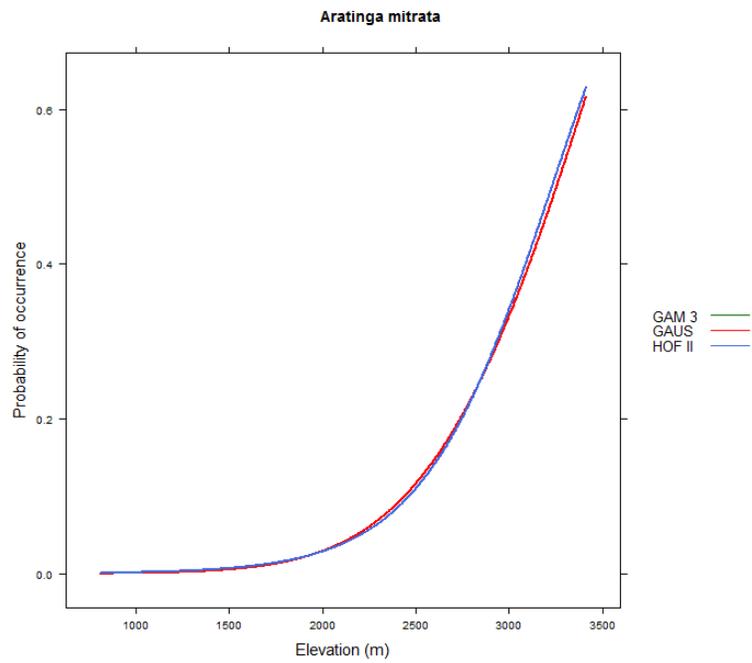


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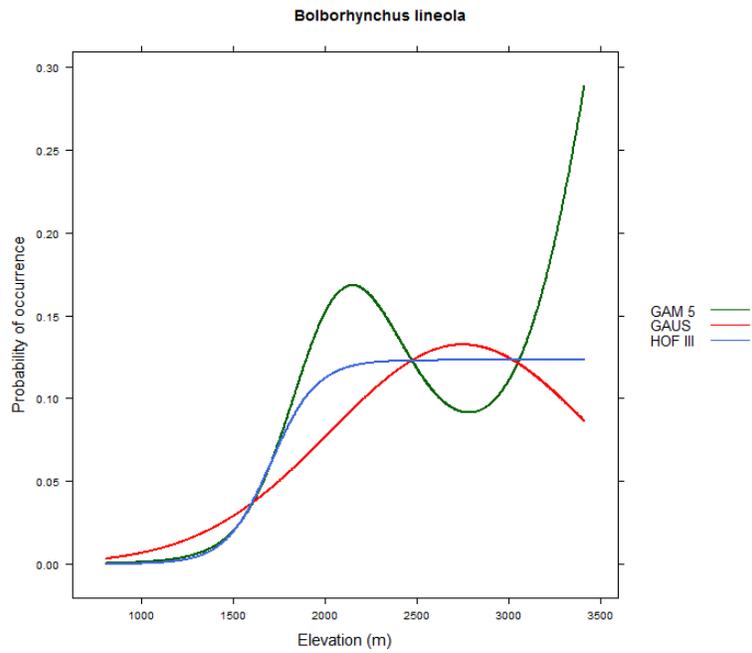


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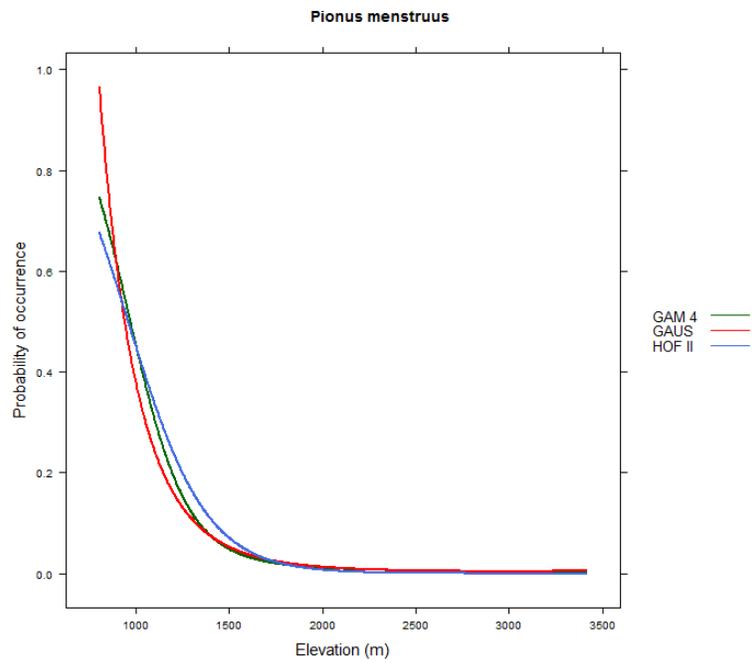


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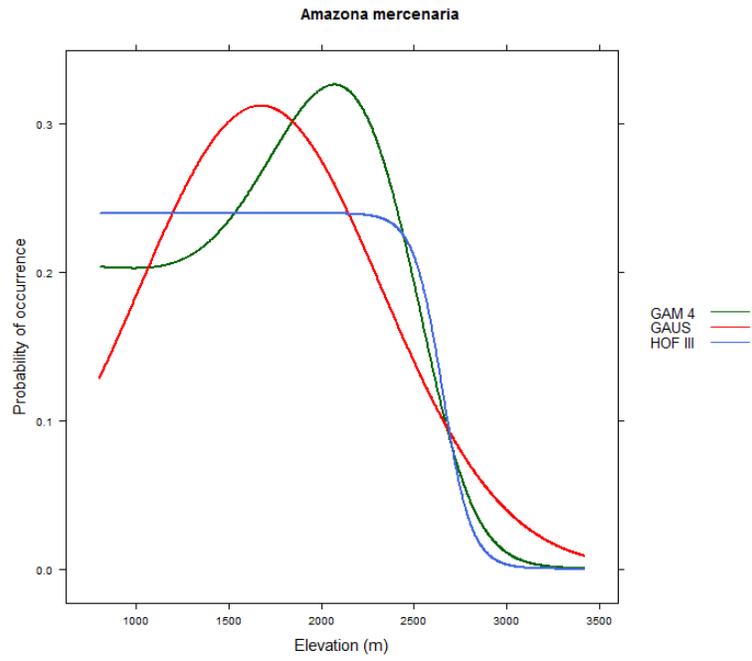


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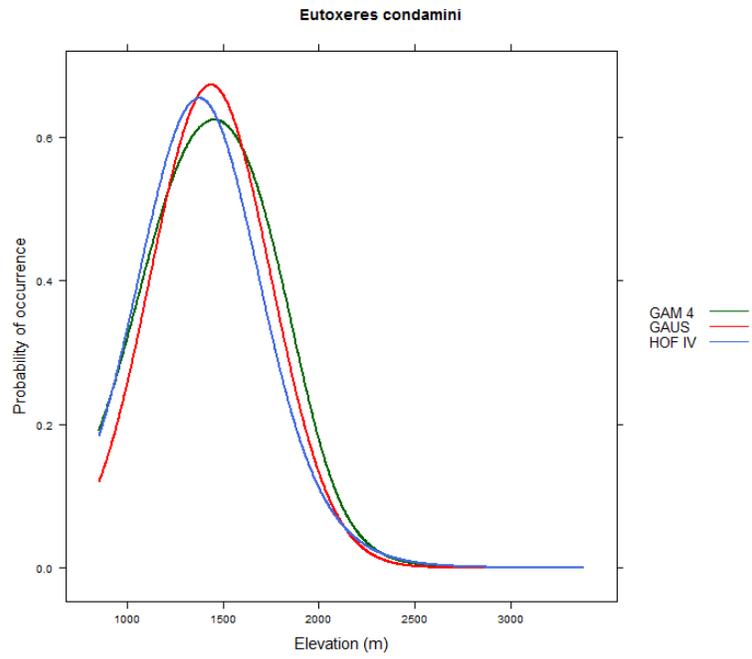


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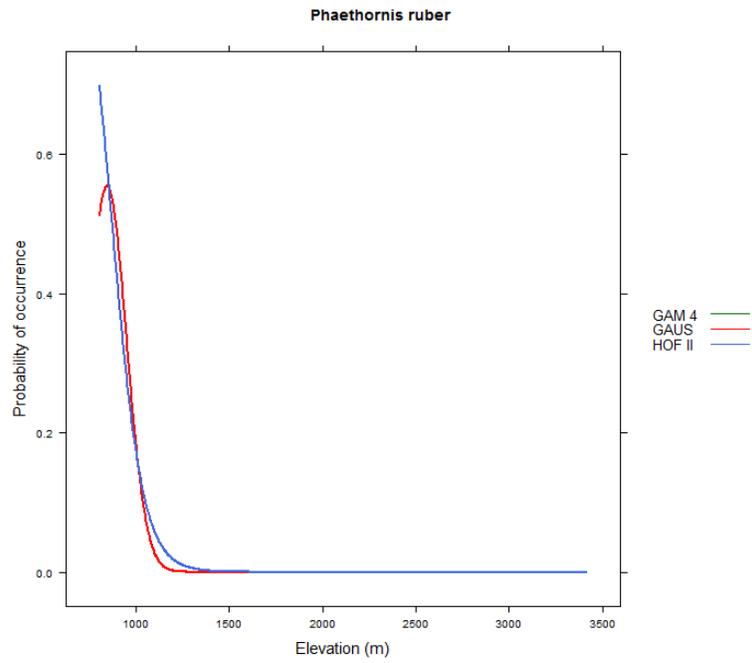


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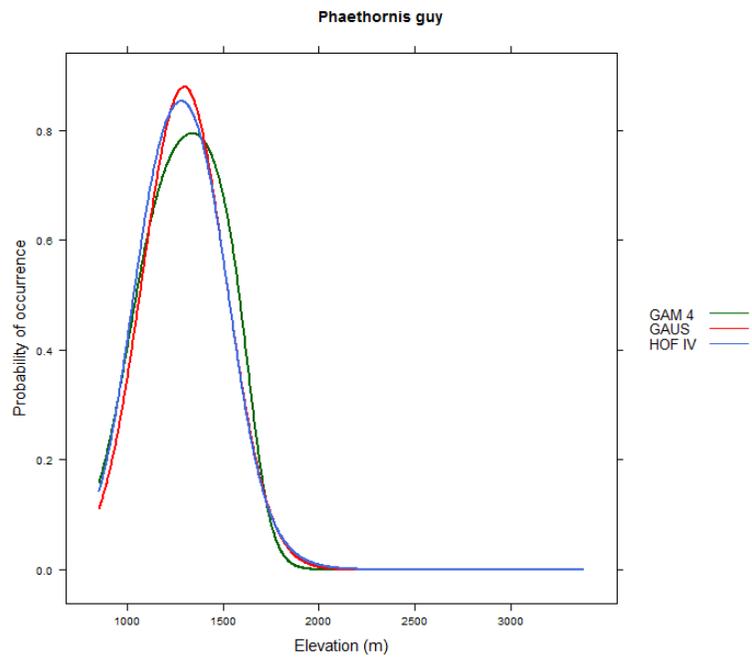


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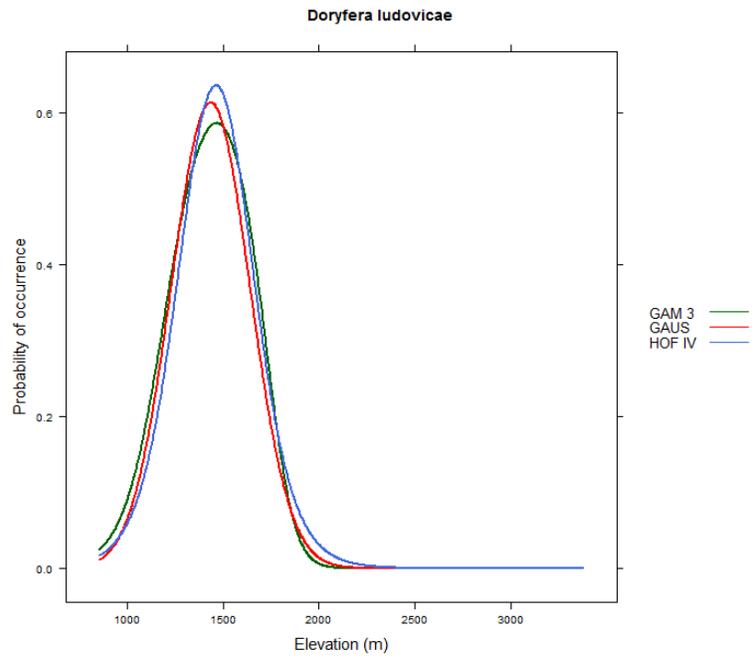


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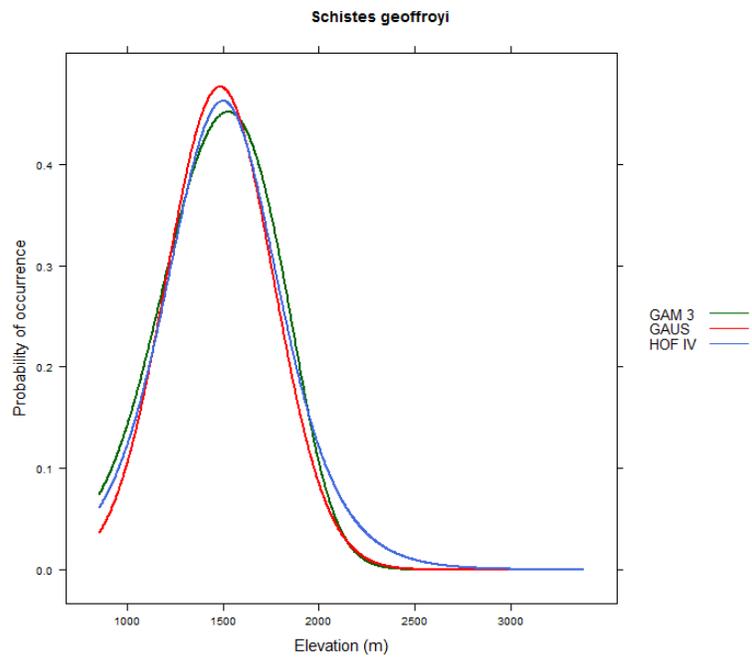


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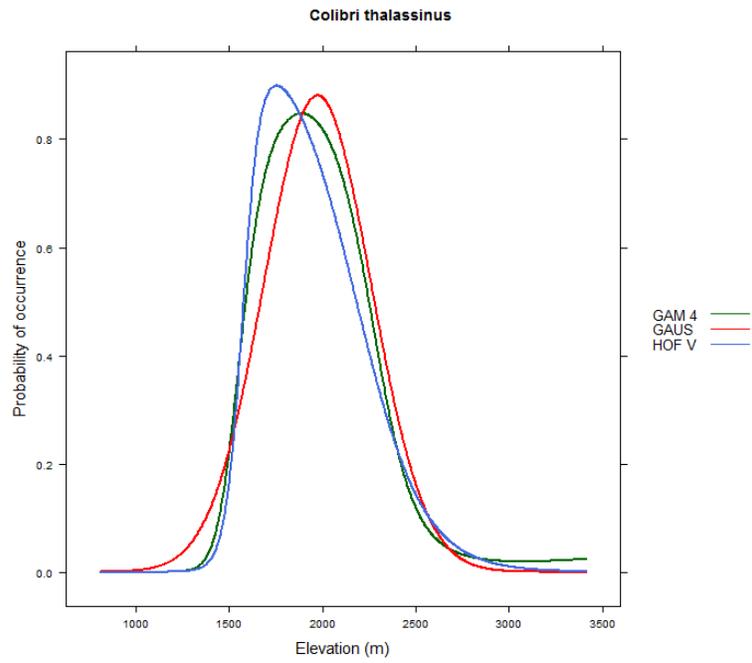


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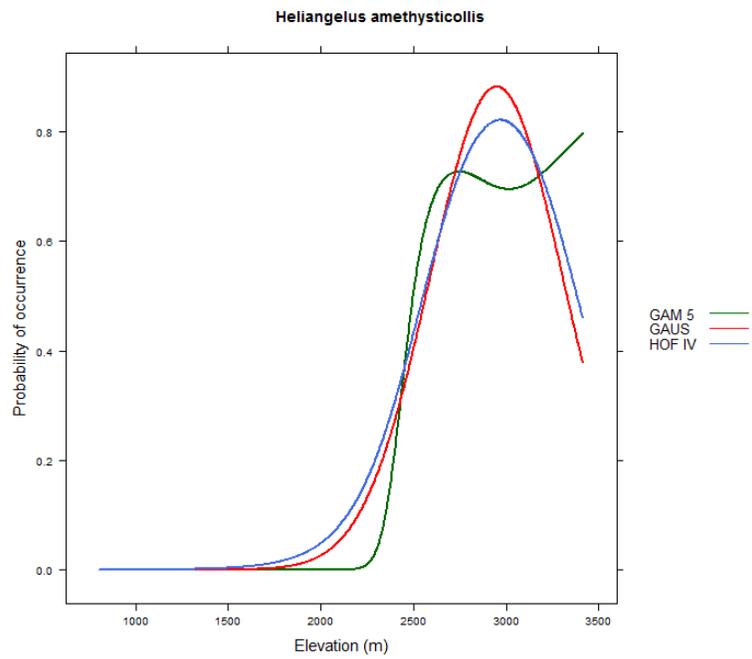


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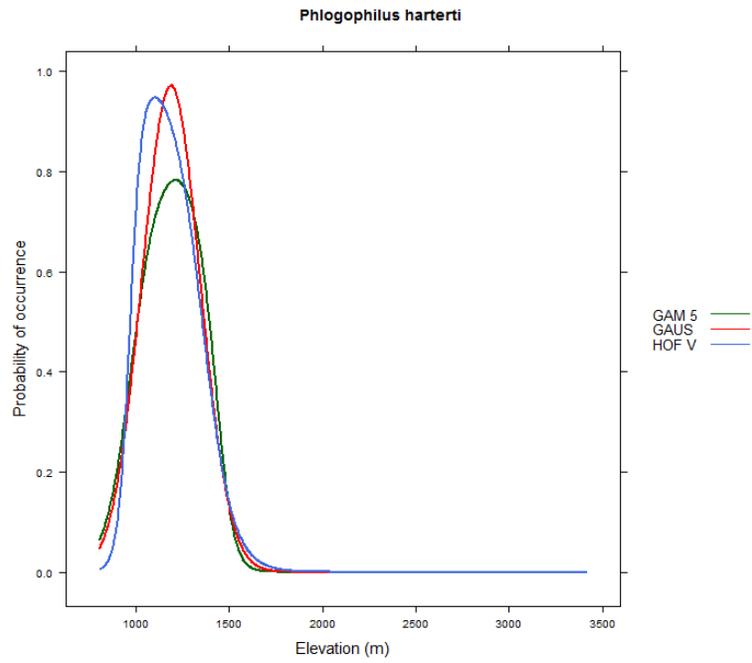


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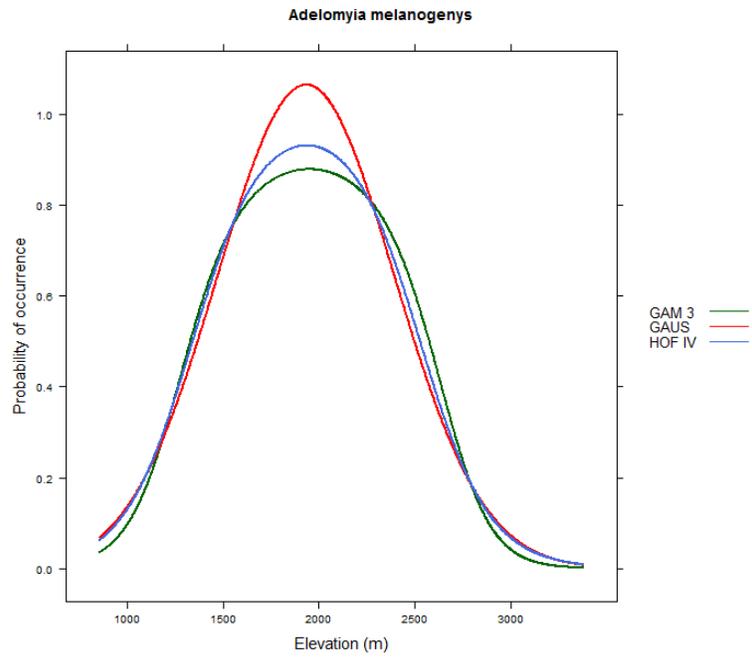


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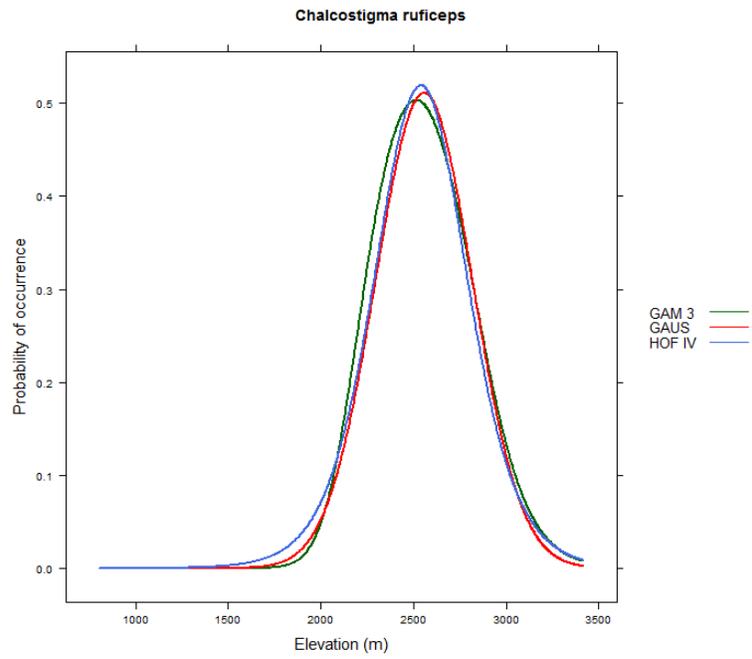


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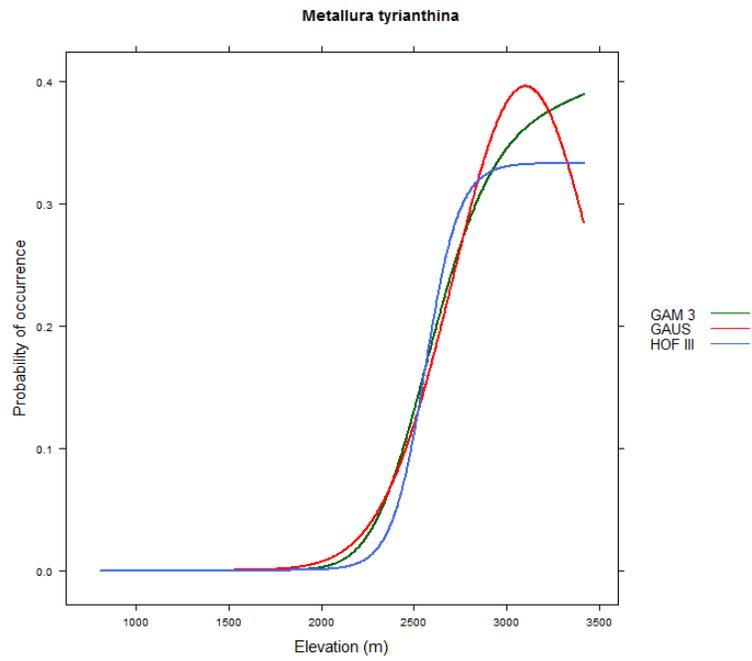


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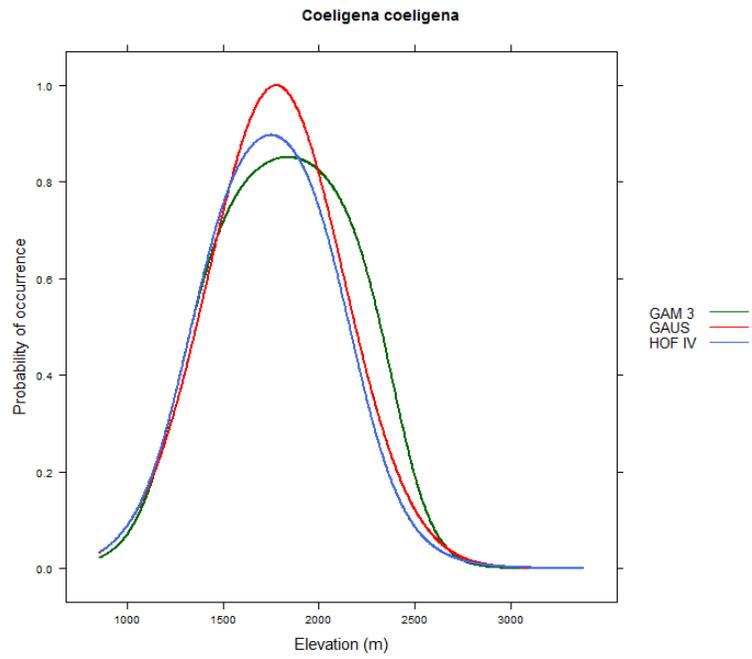


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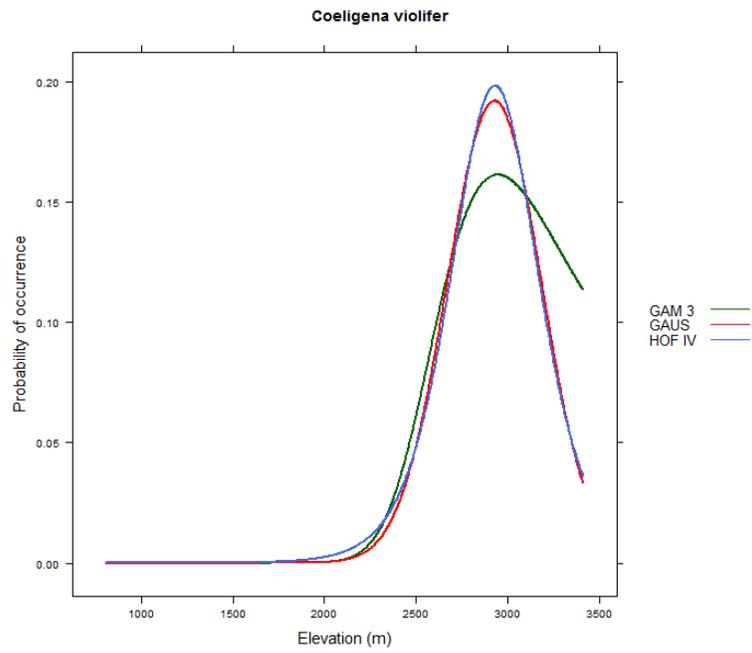


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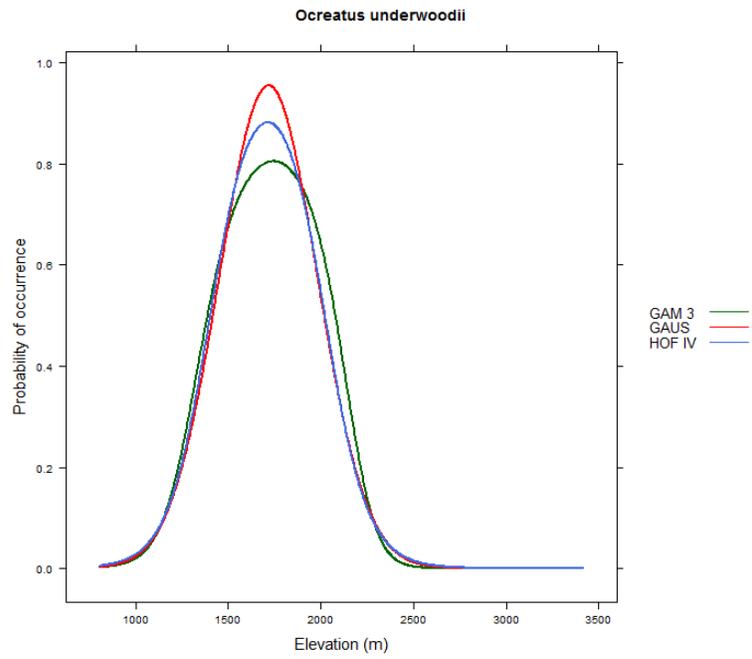


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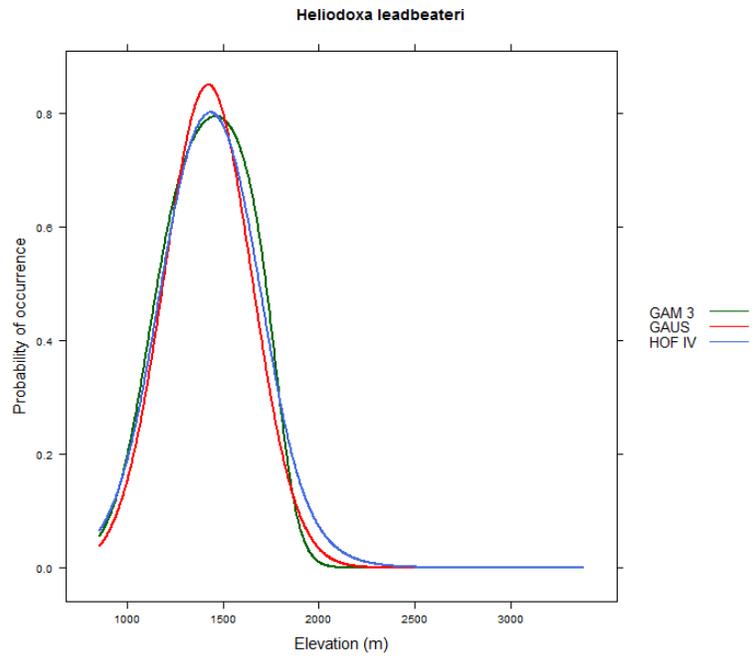


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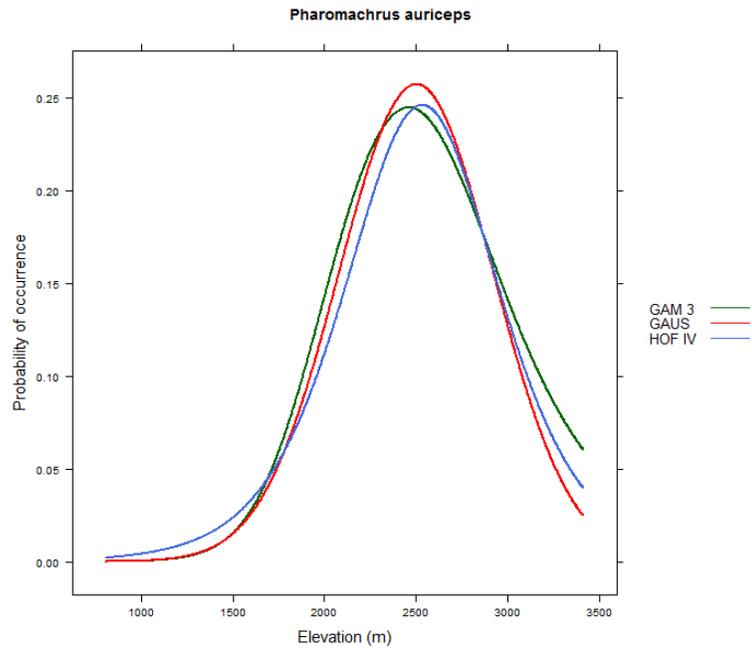


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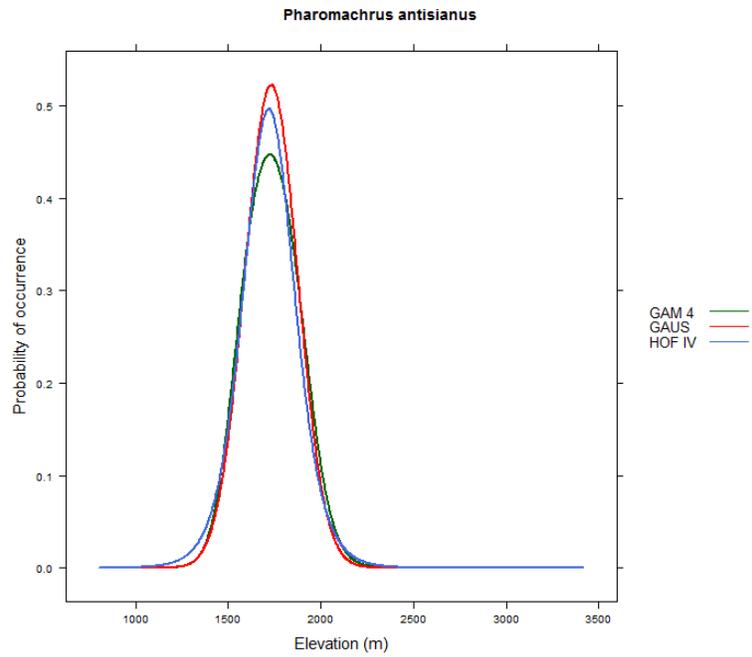


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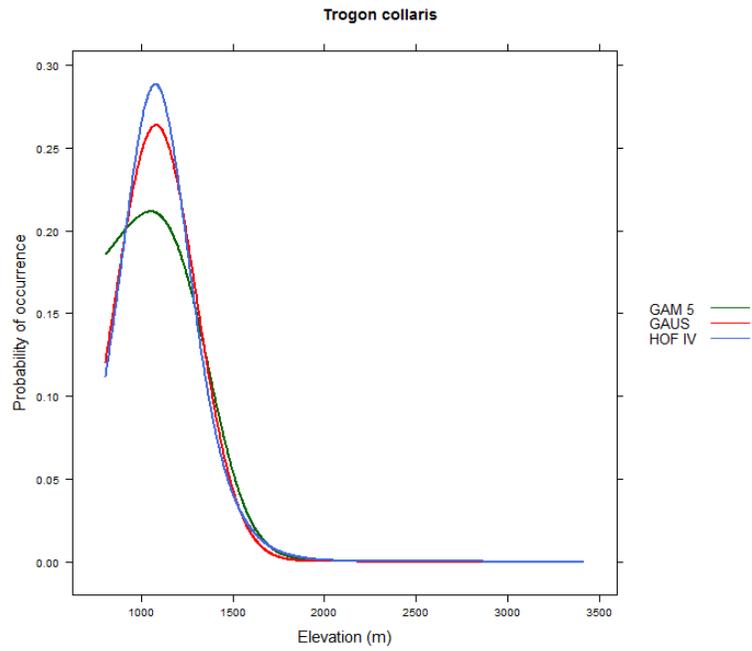


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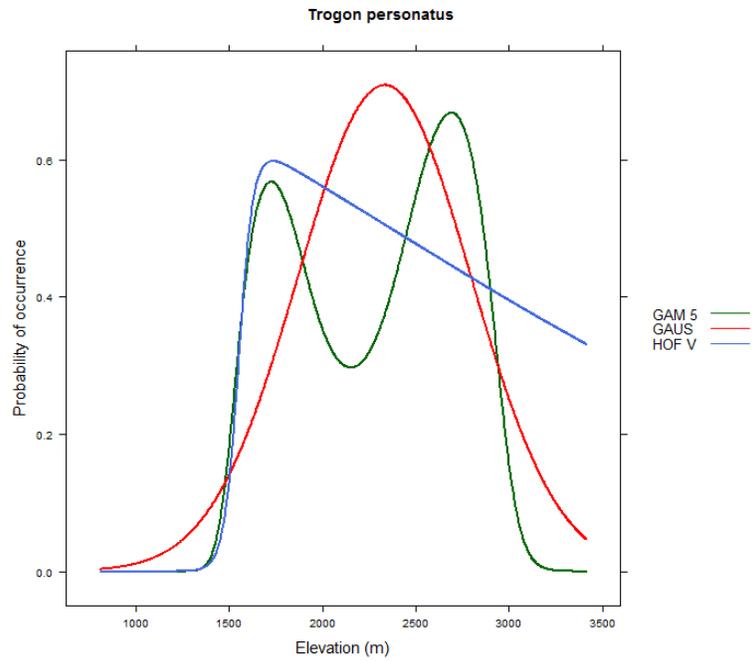


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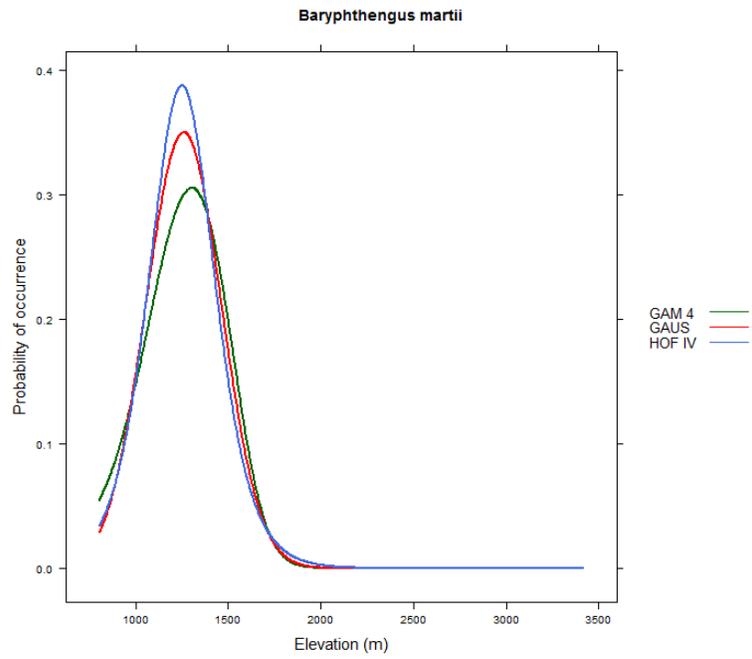


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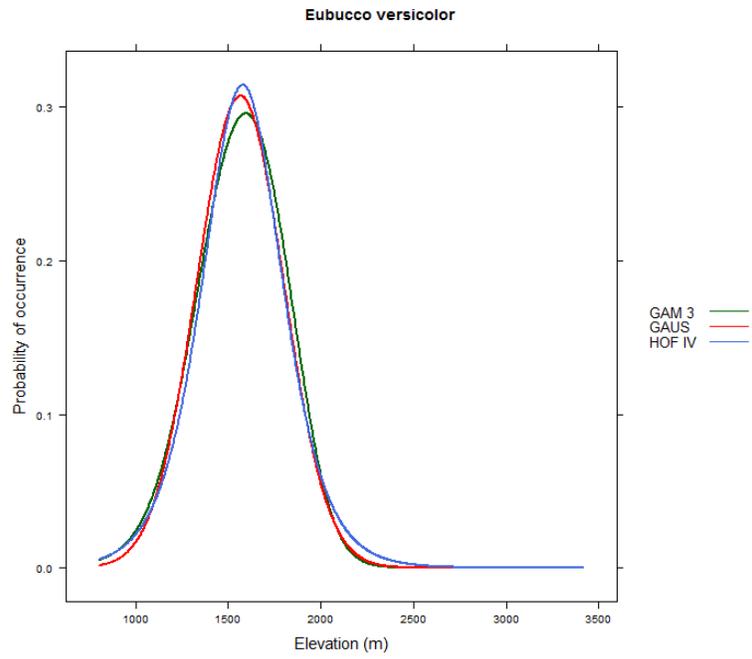


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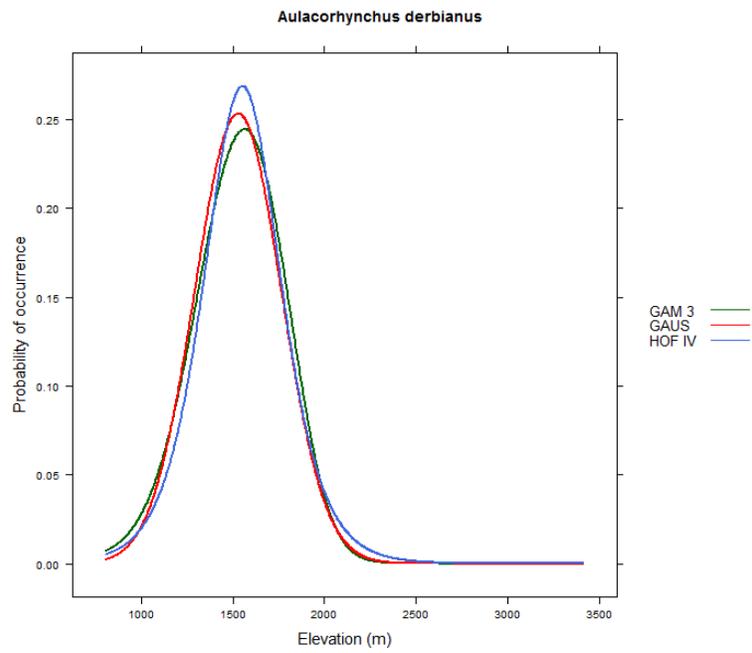


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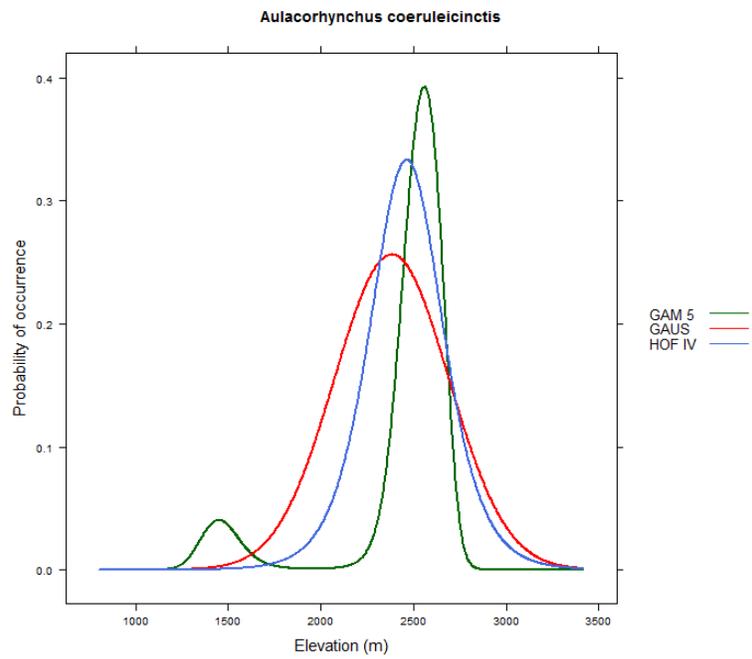


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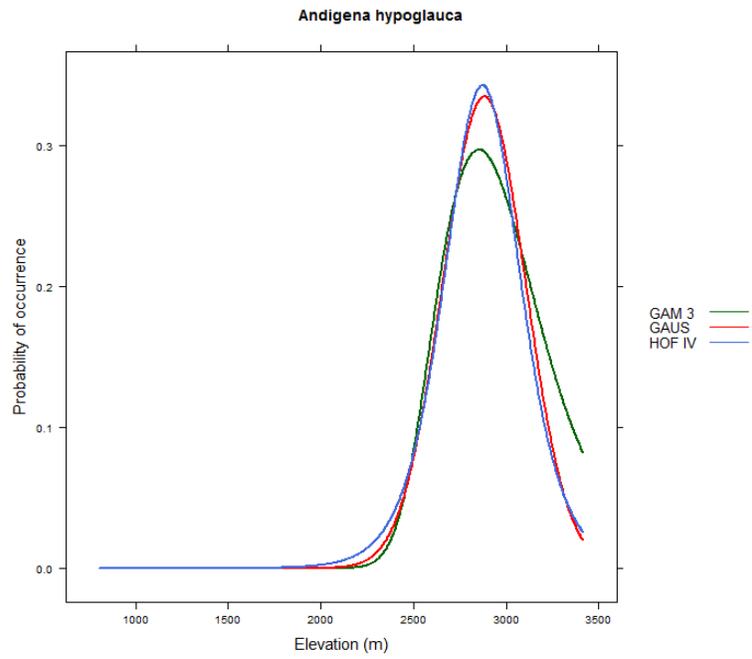


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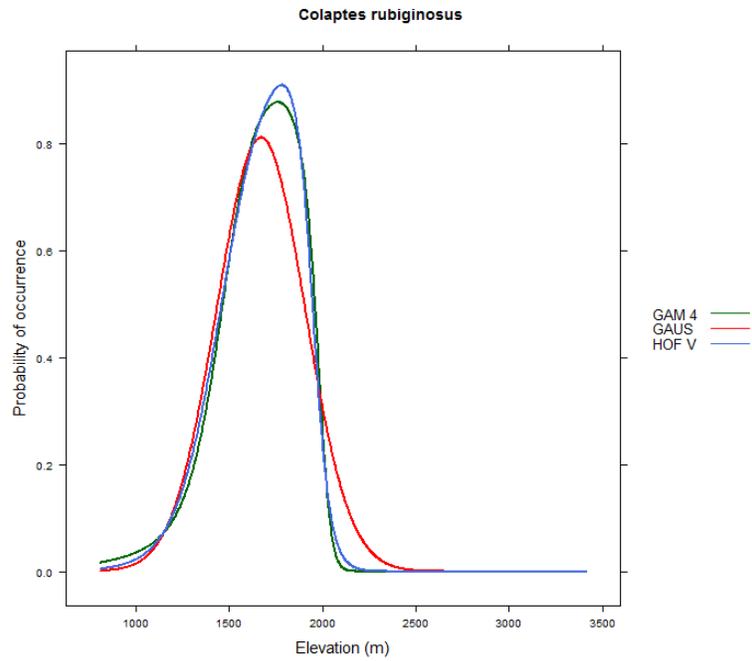


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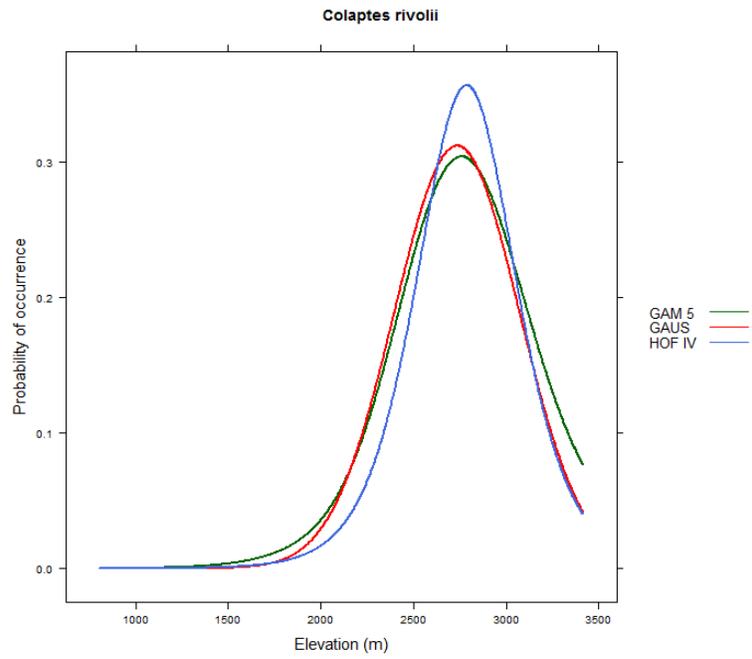


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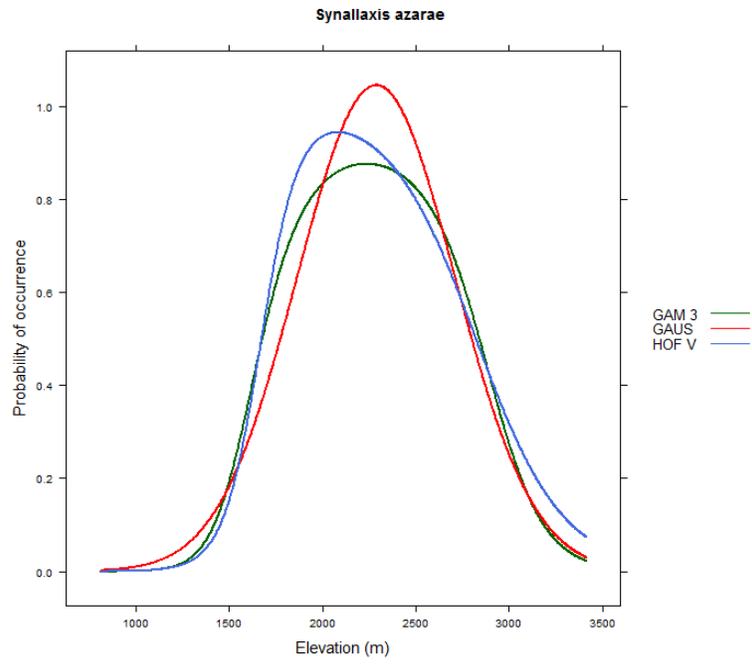


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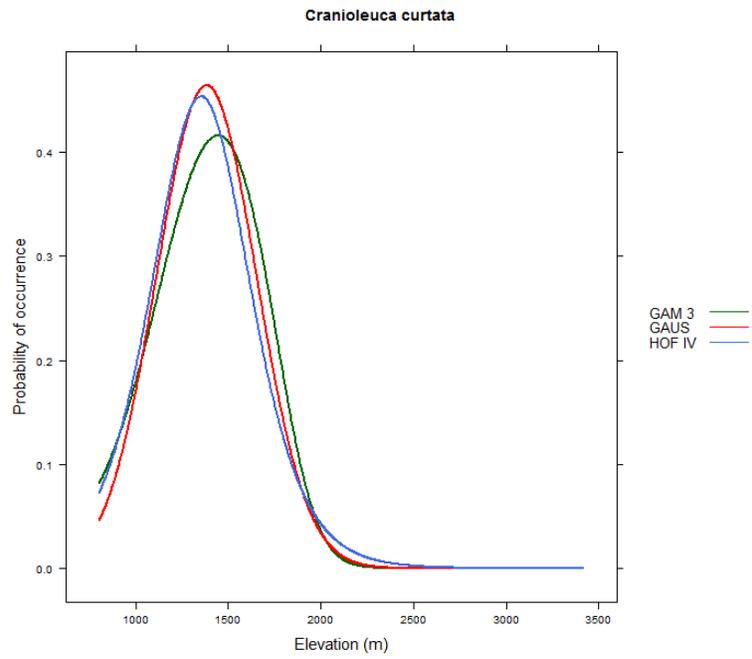


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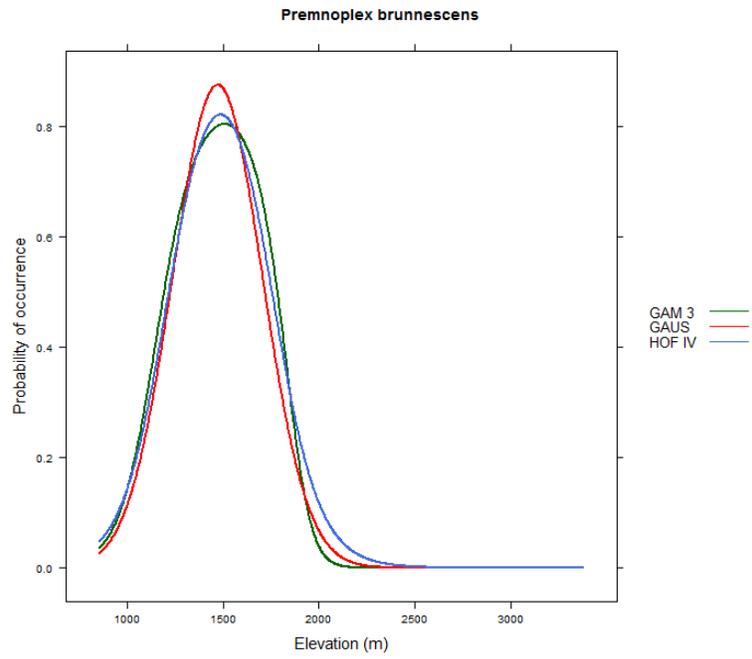


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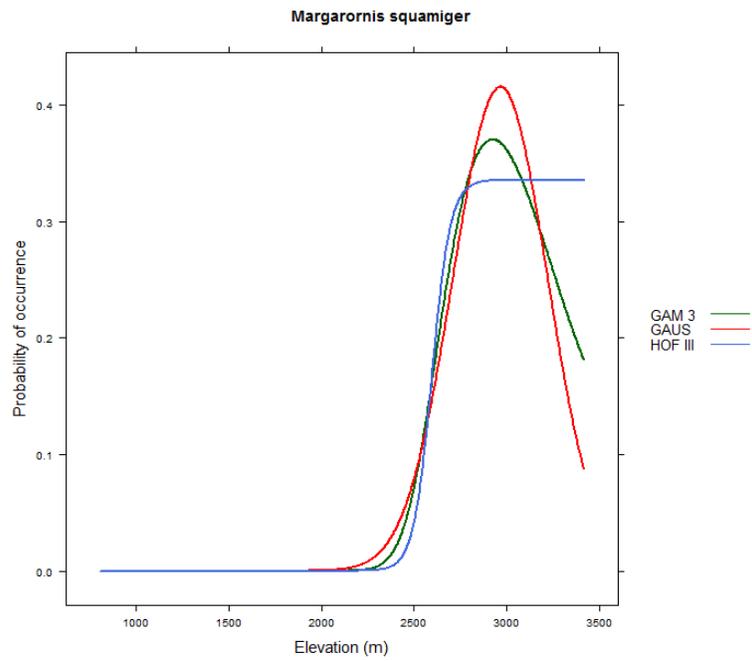


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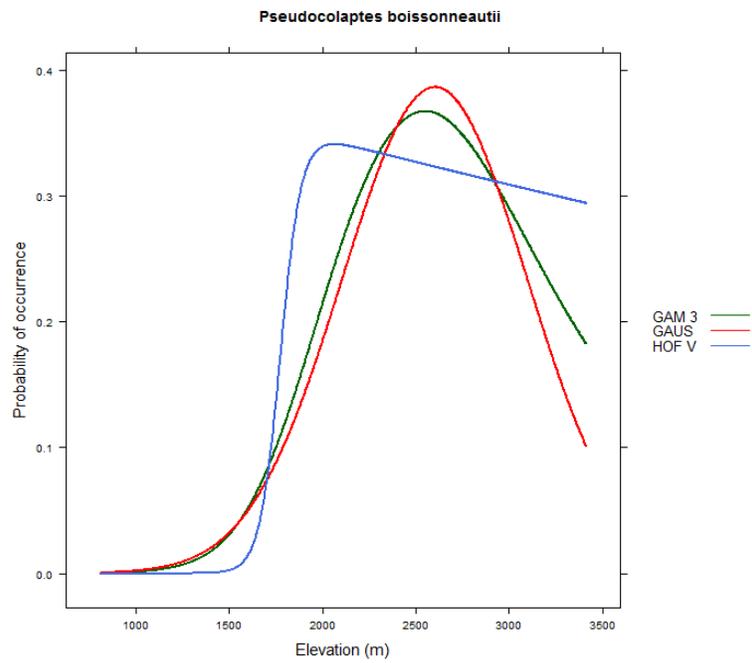


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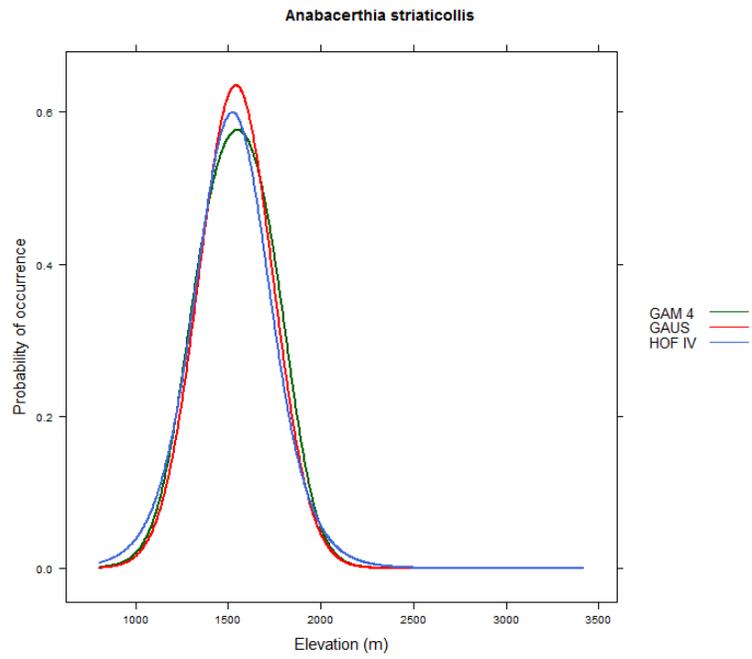


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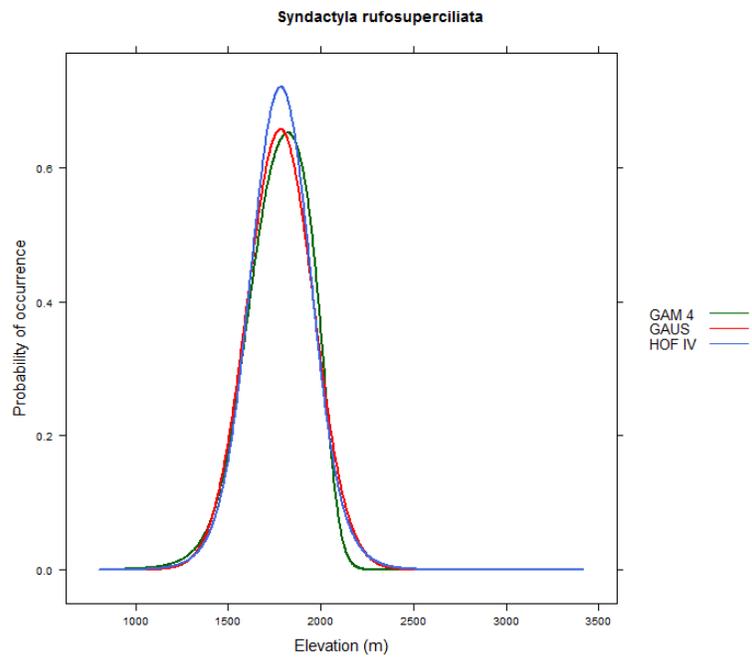


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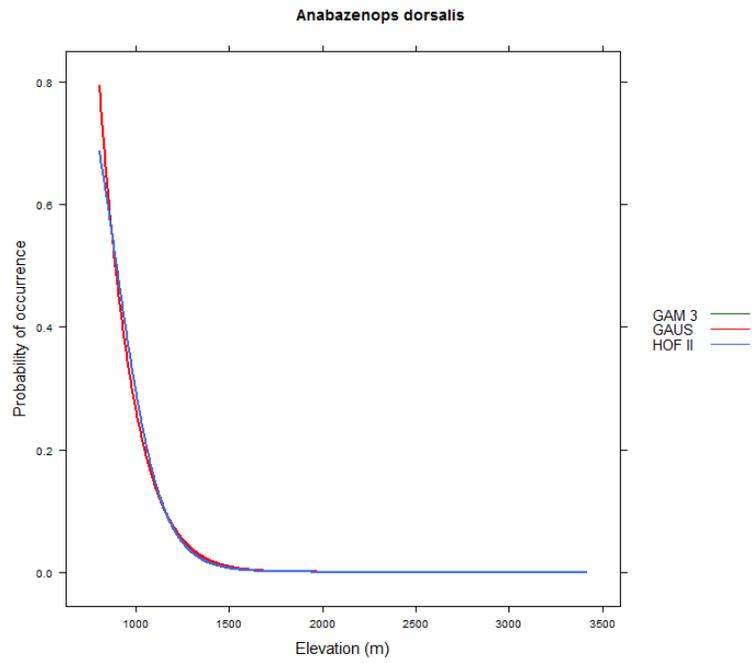


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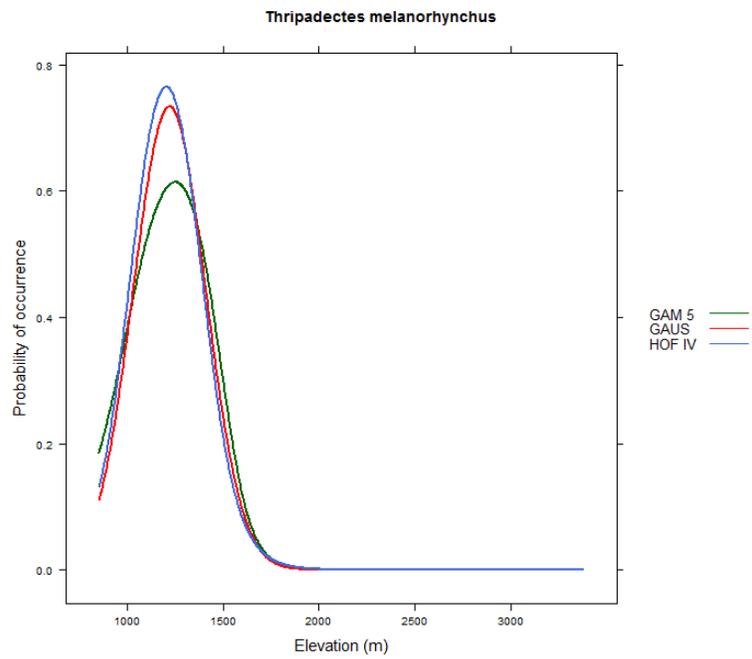


Figure C-50.

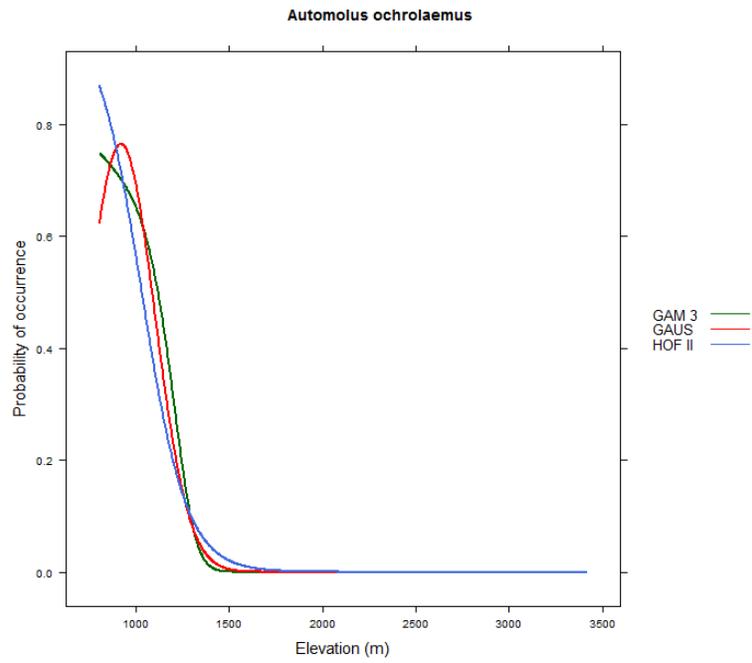


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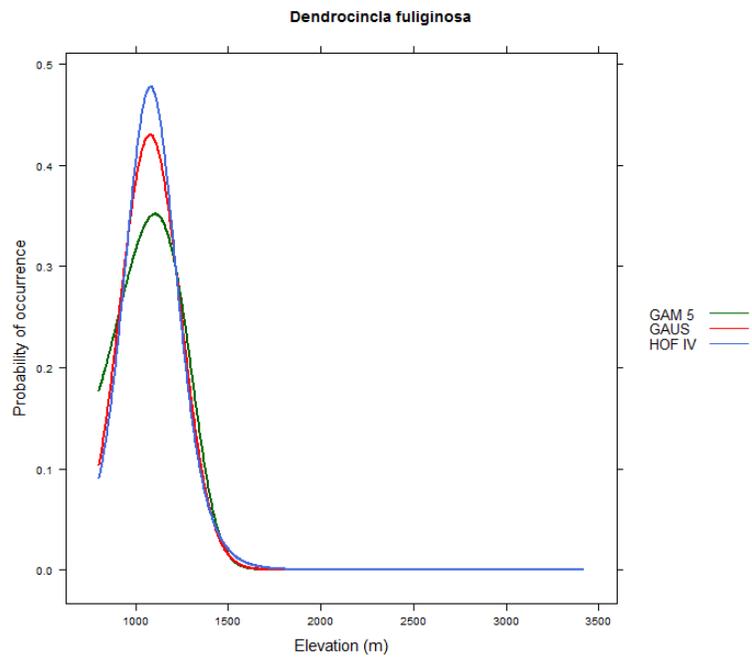


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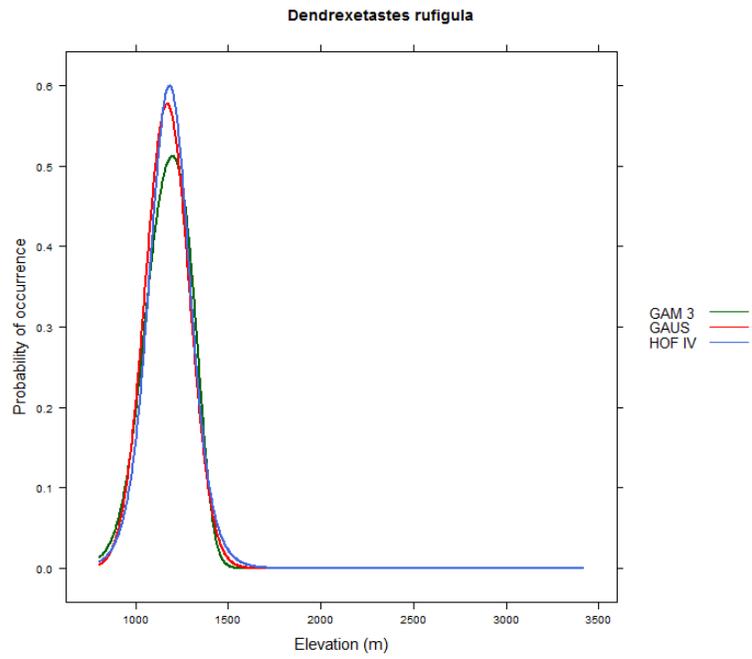


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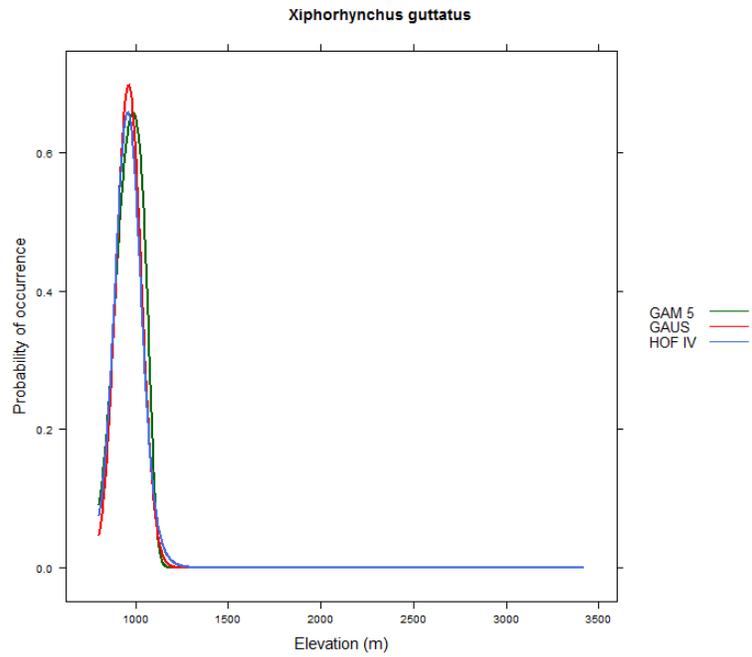


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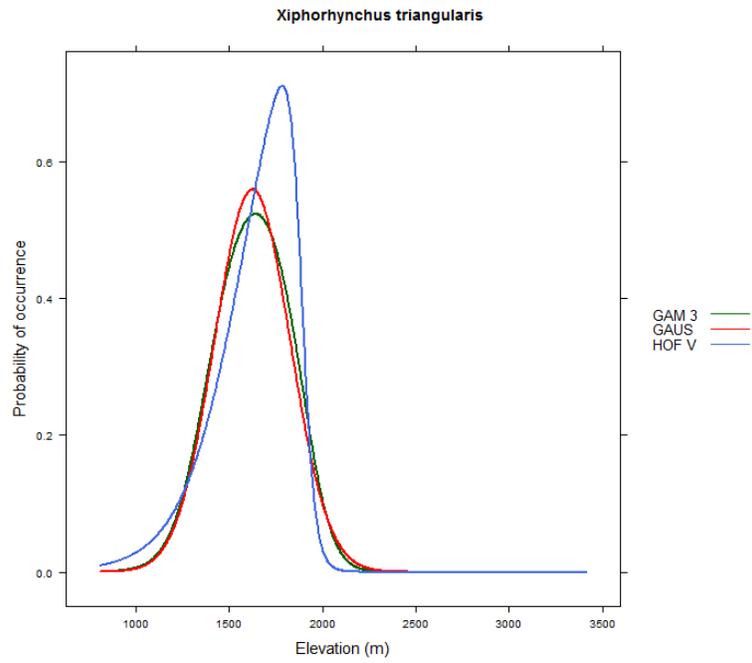


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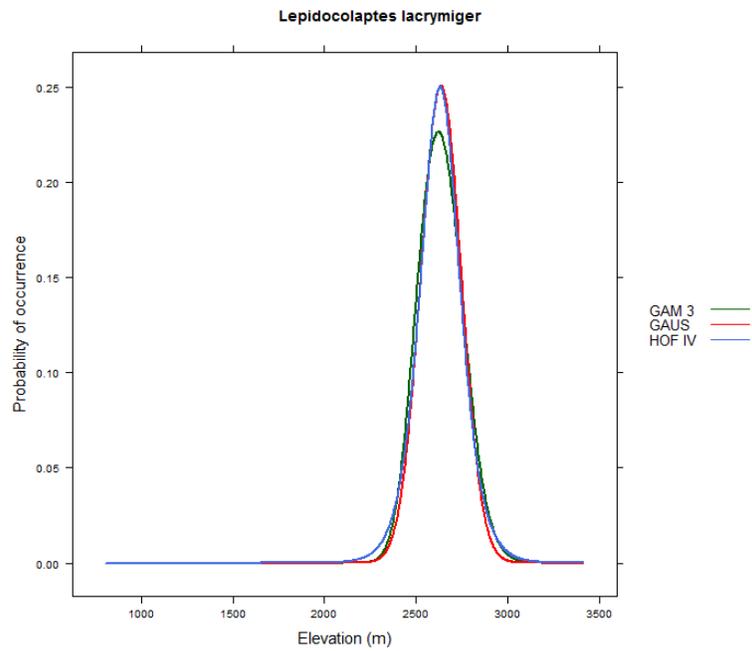


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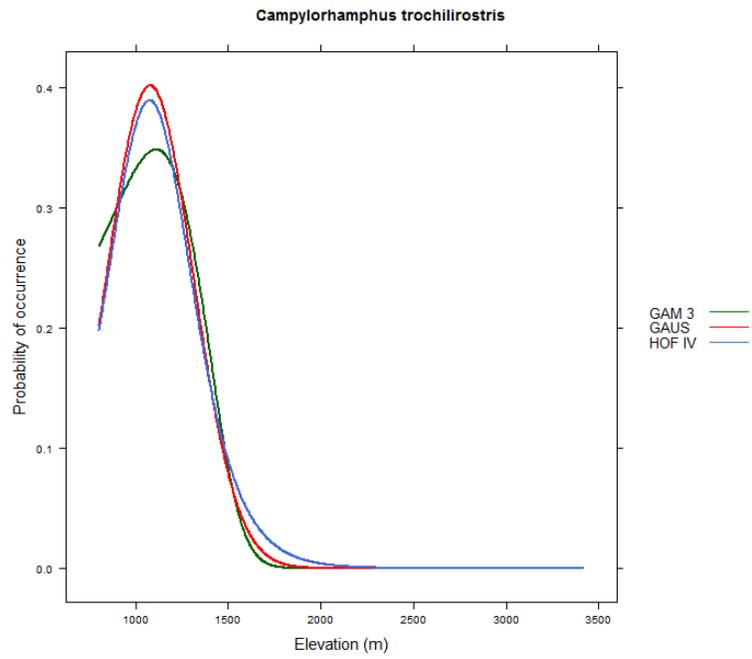


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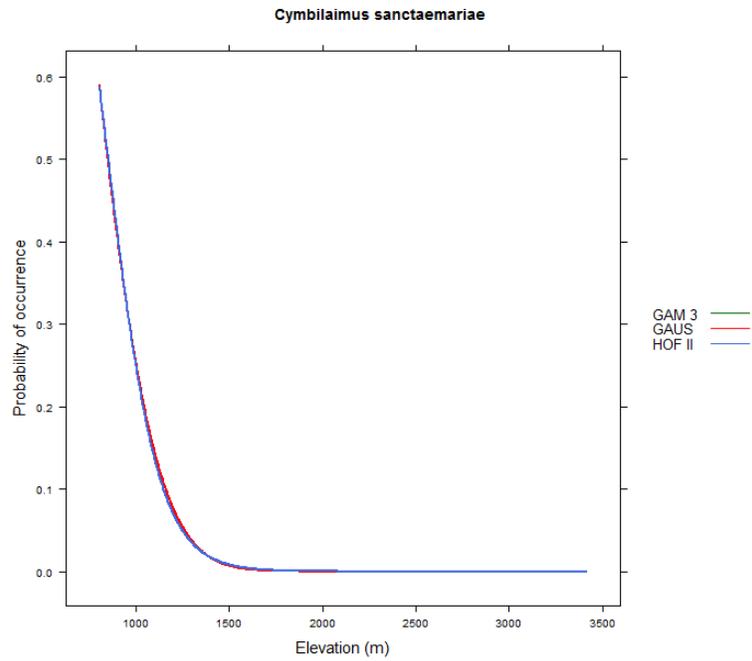


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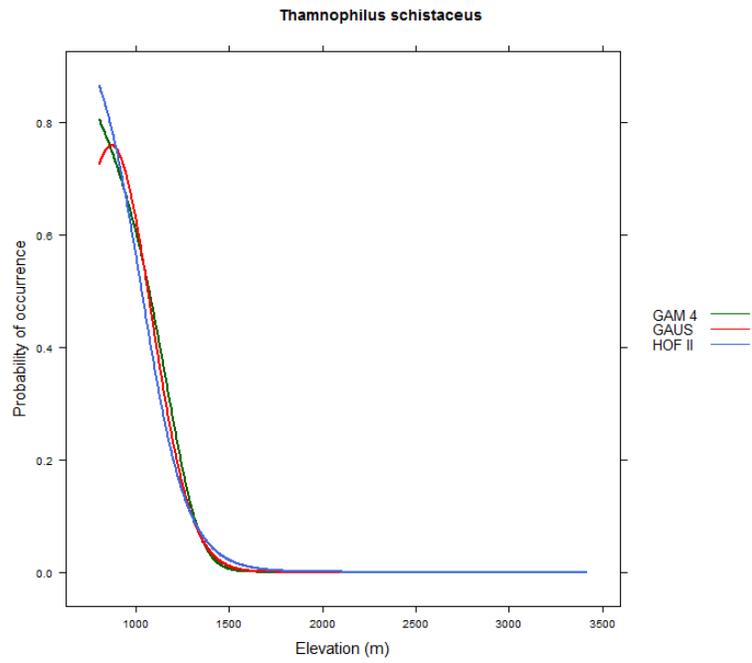


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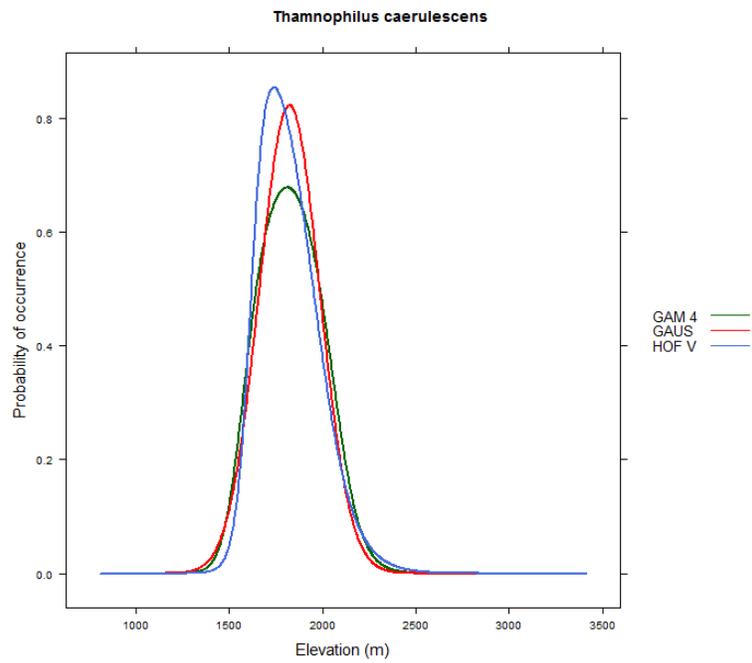


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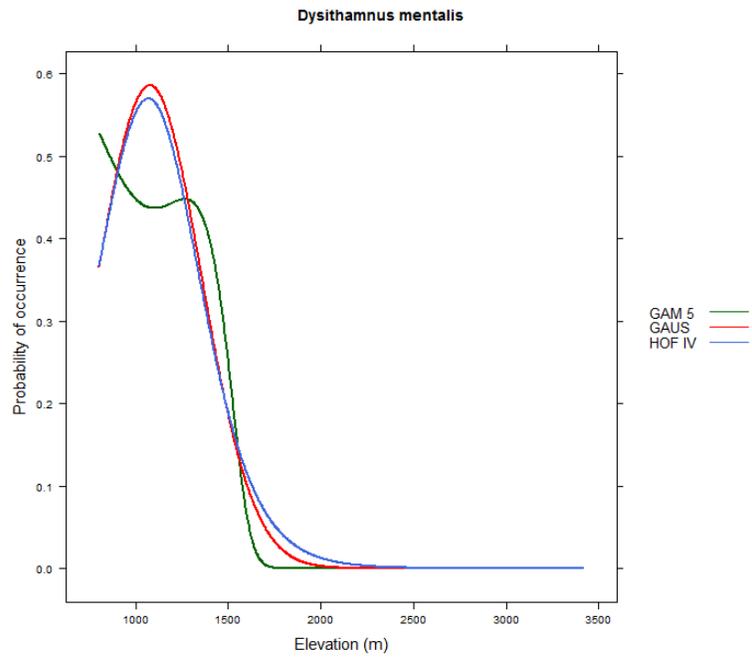


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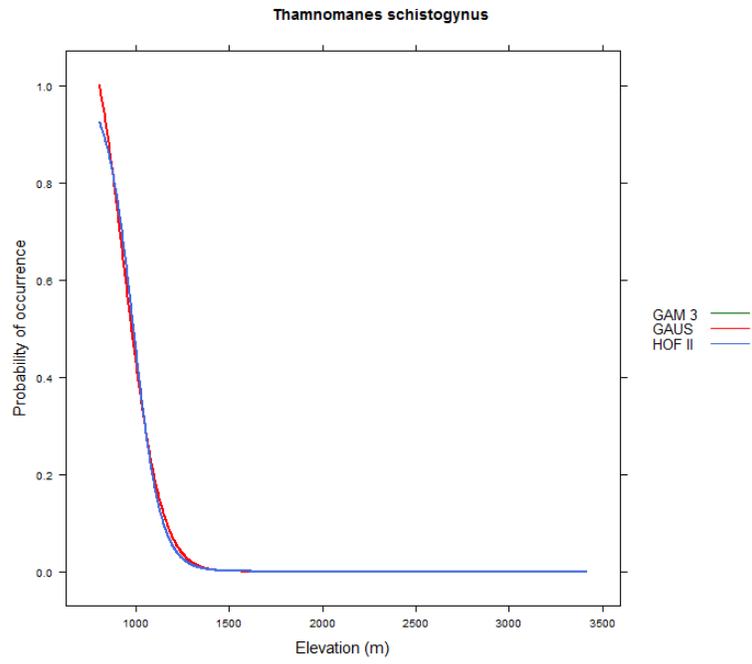


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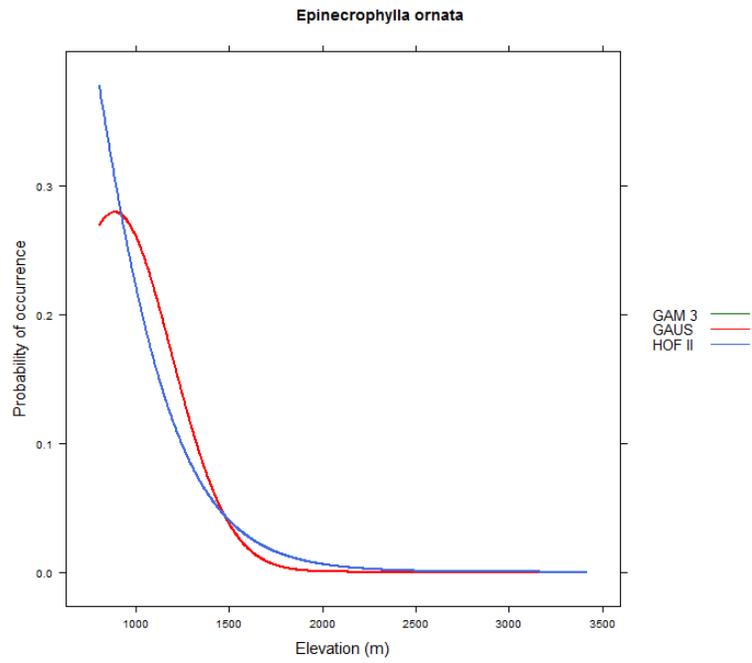


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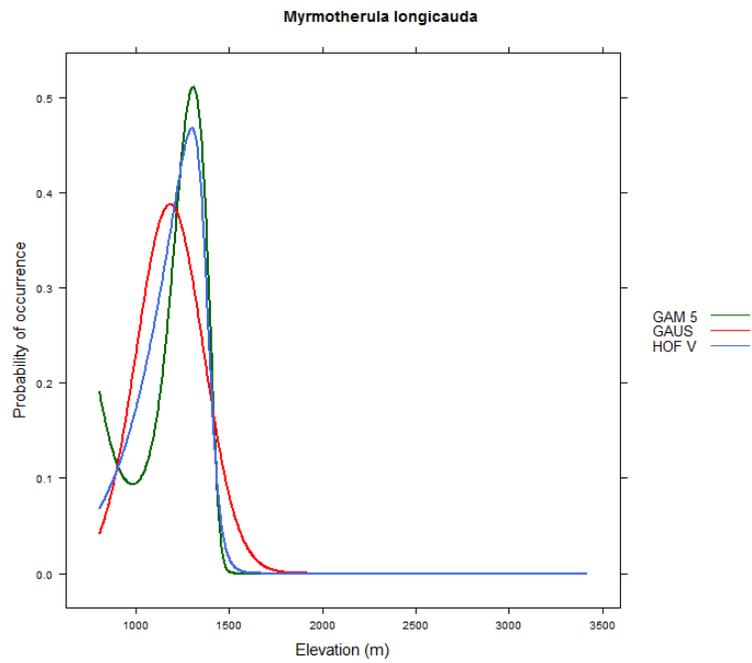


Figure C-64.

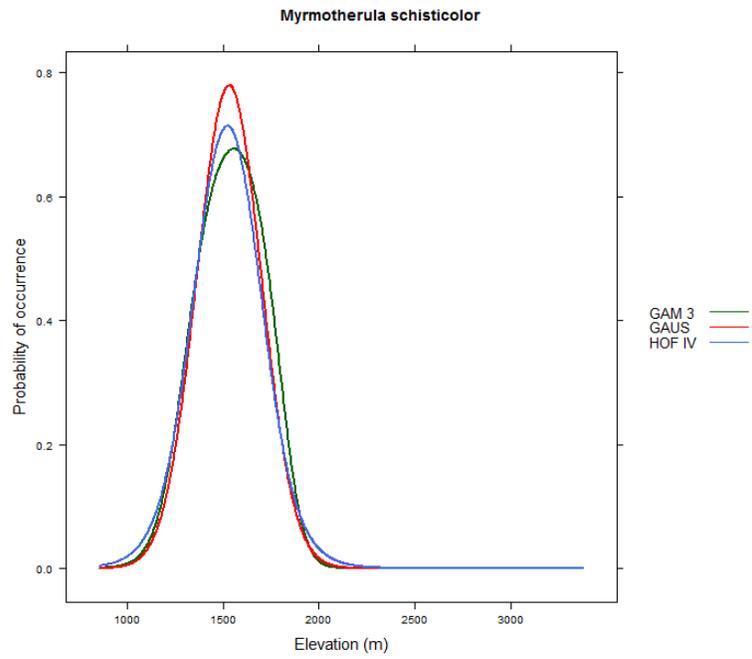


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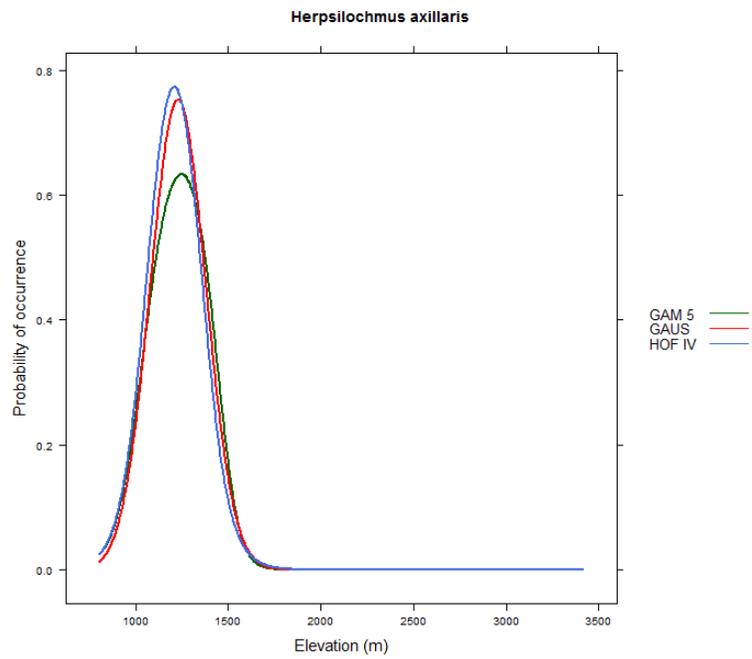


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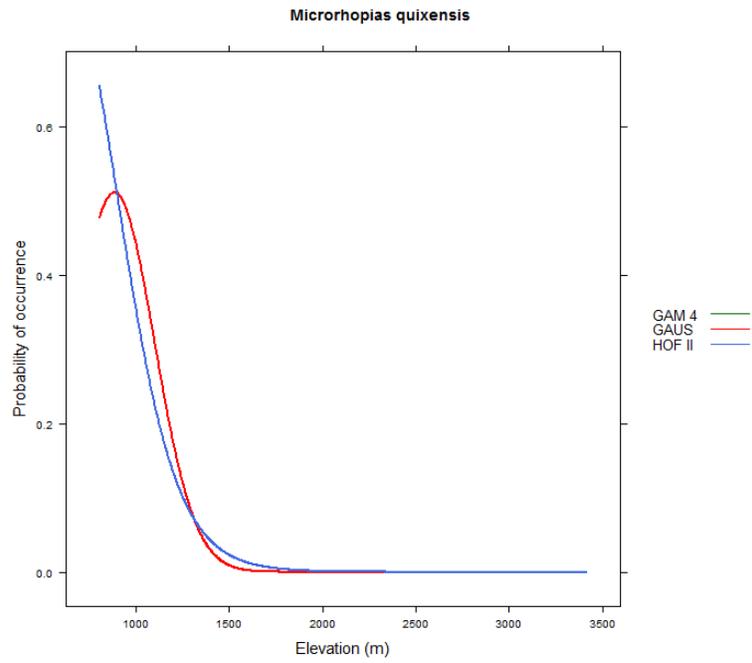


Figure C-67

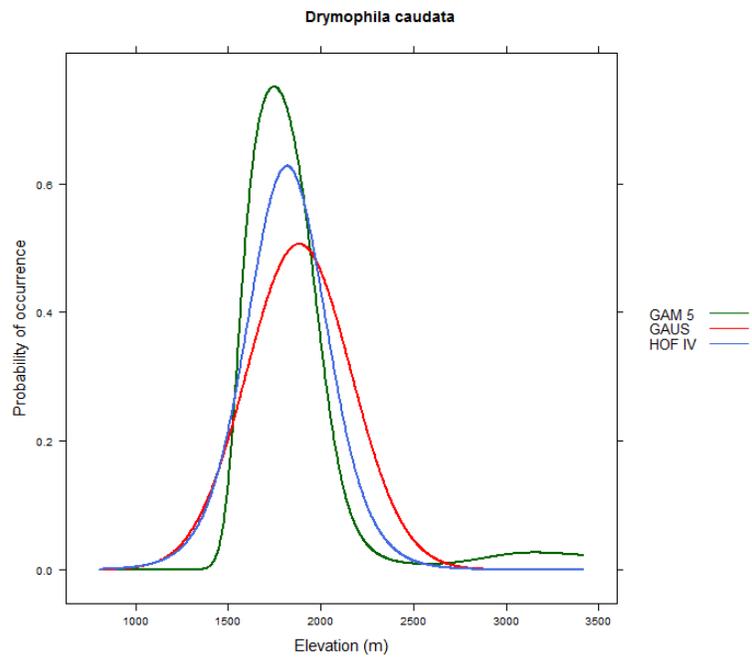


Figure C-68.

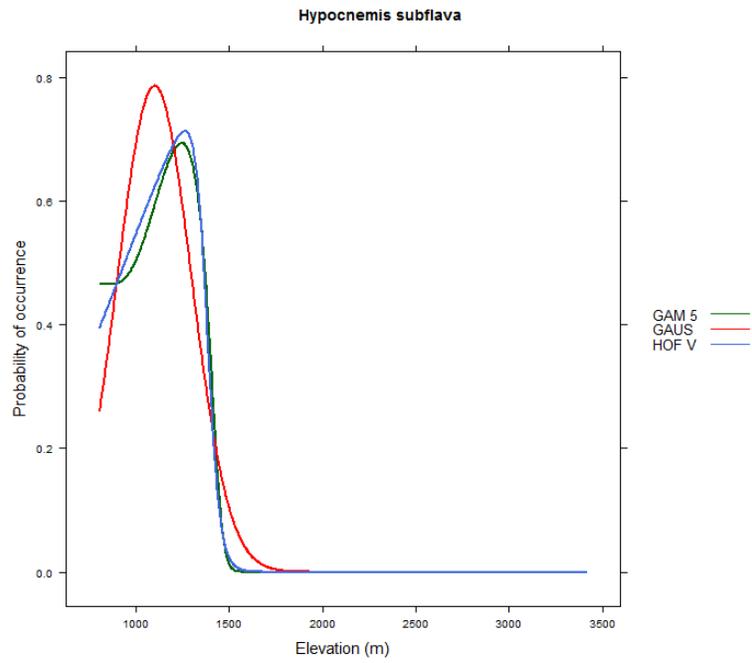


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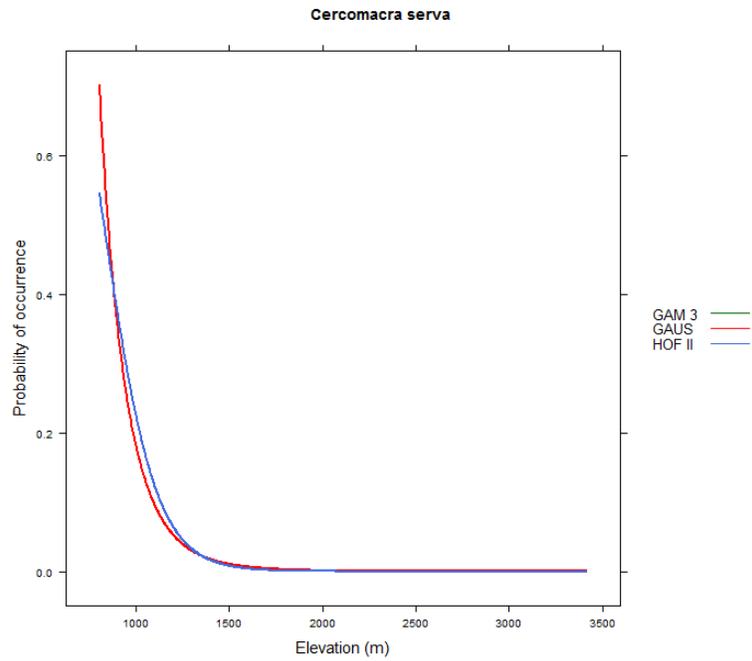


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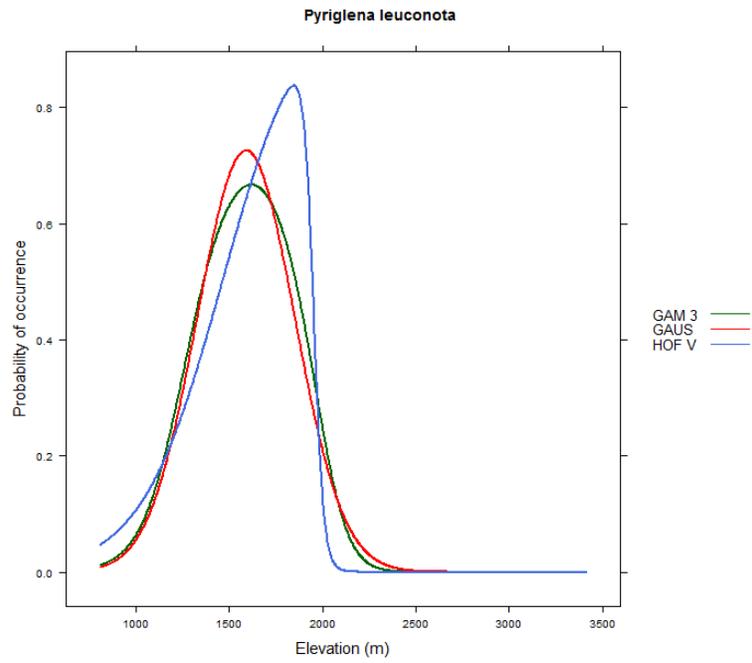


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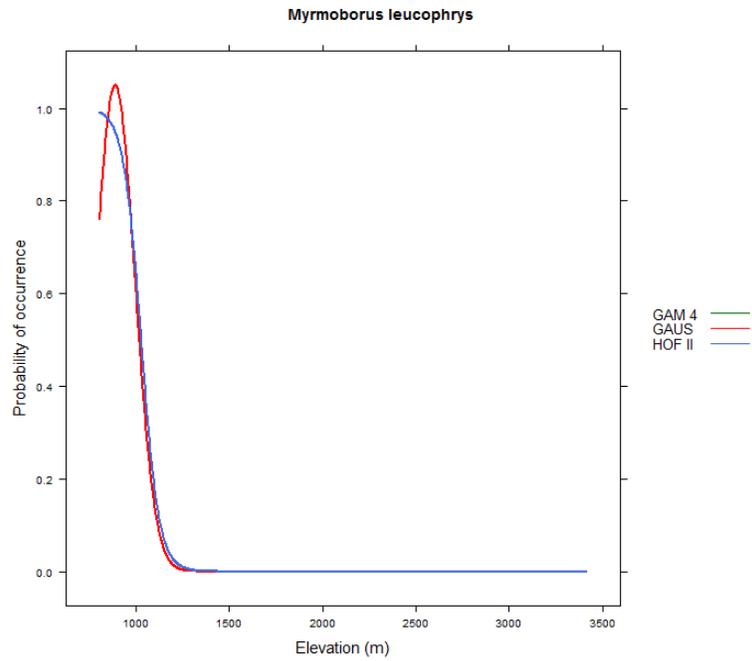


Figure C-72.

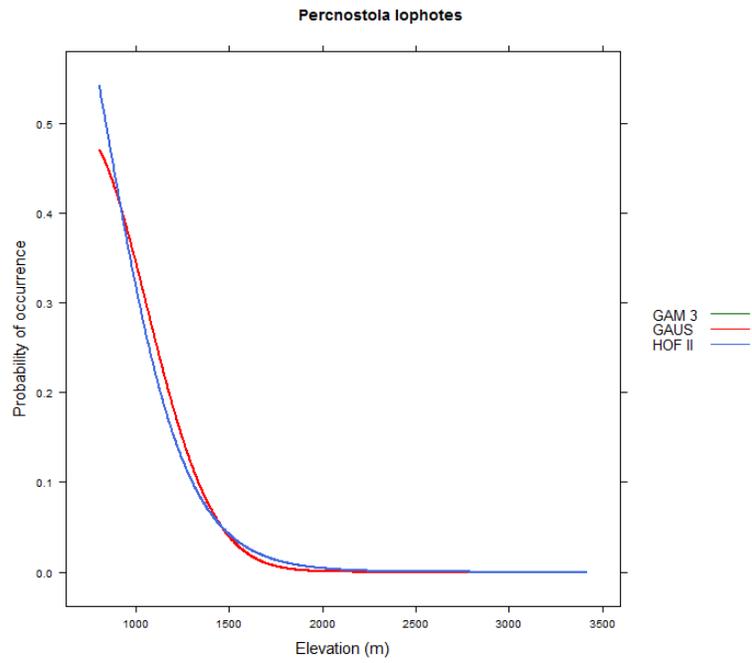


Figure C-73.

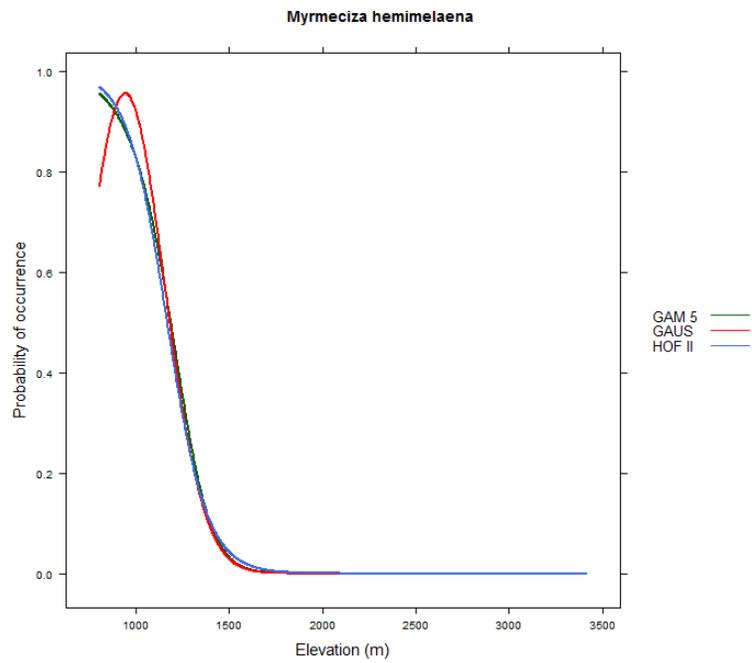


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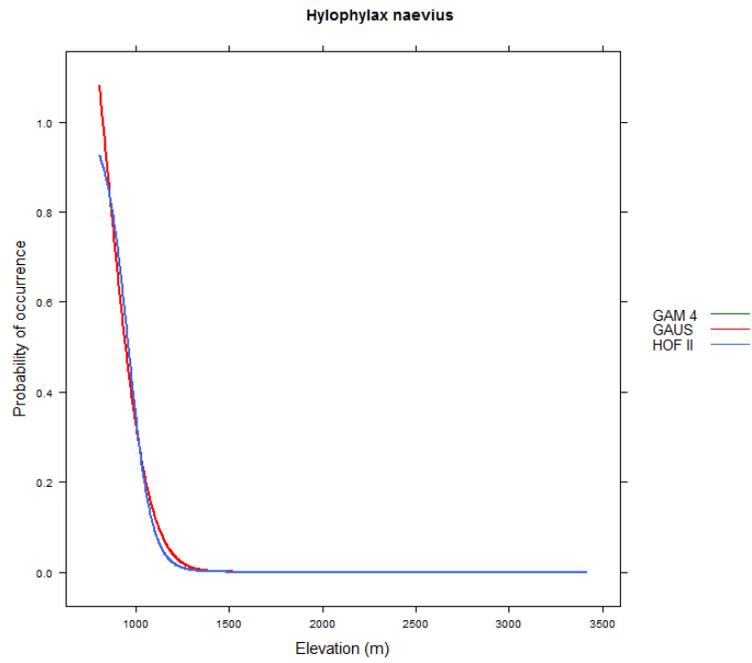


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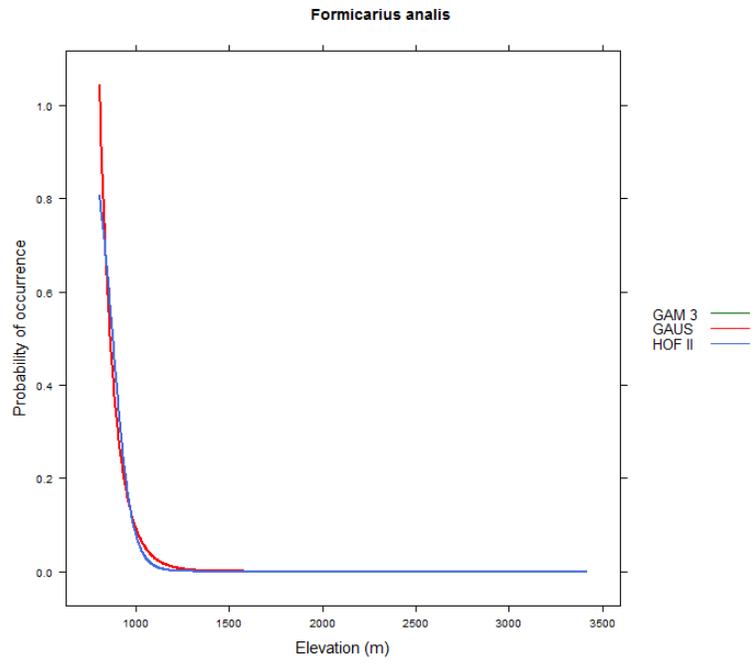


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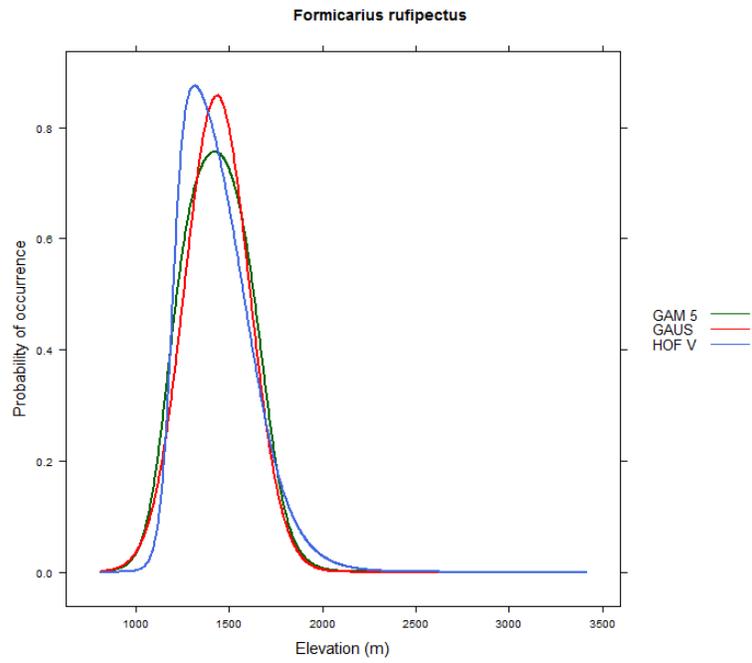


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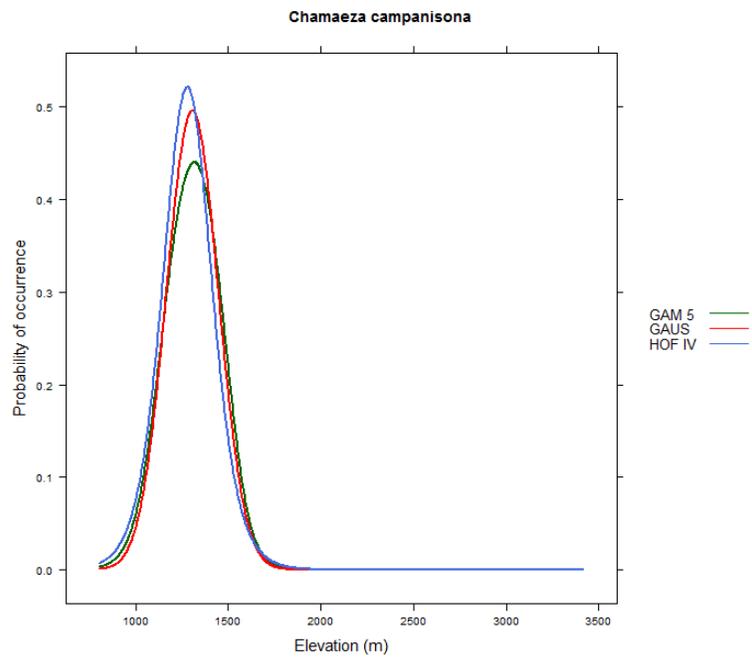


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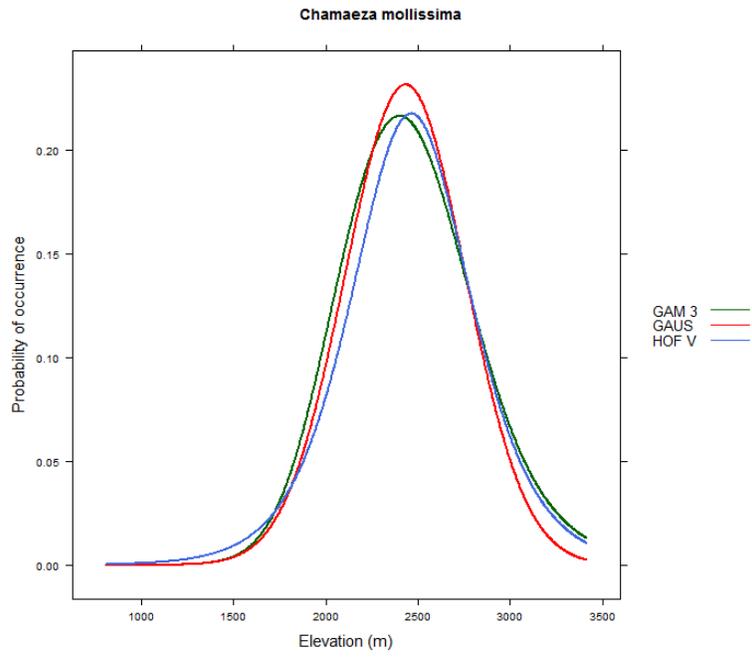


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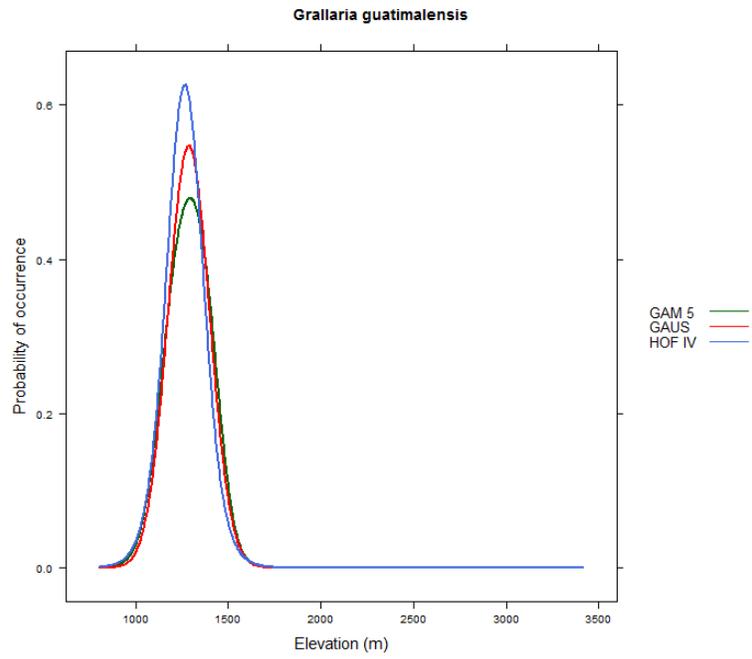


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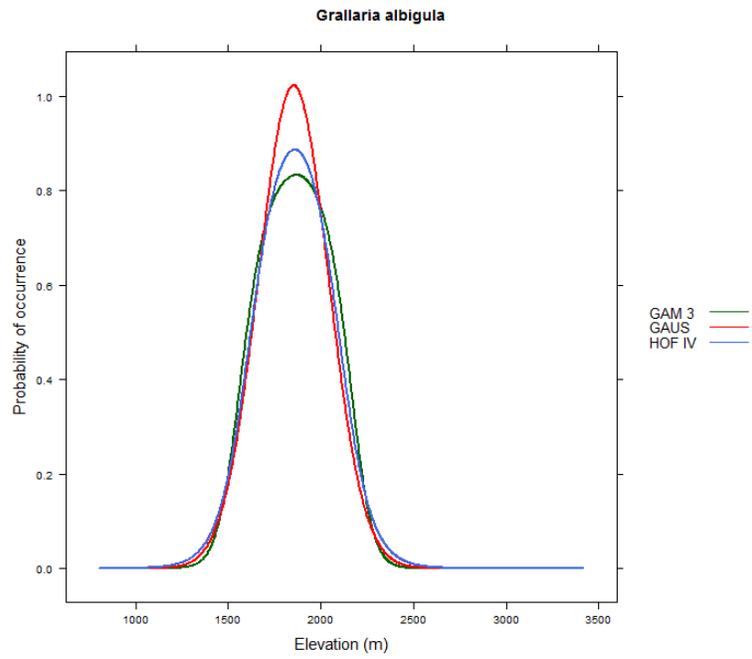


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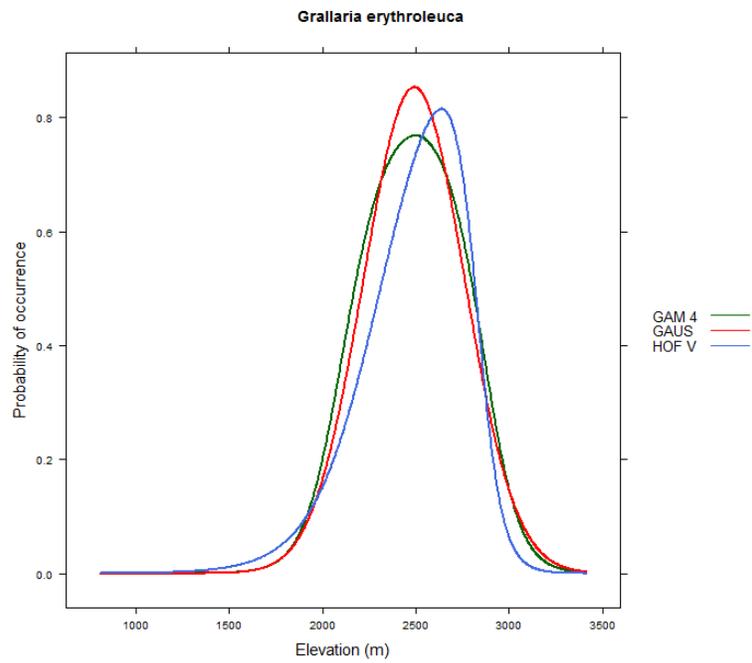


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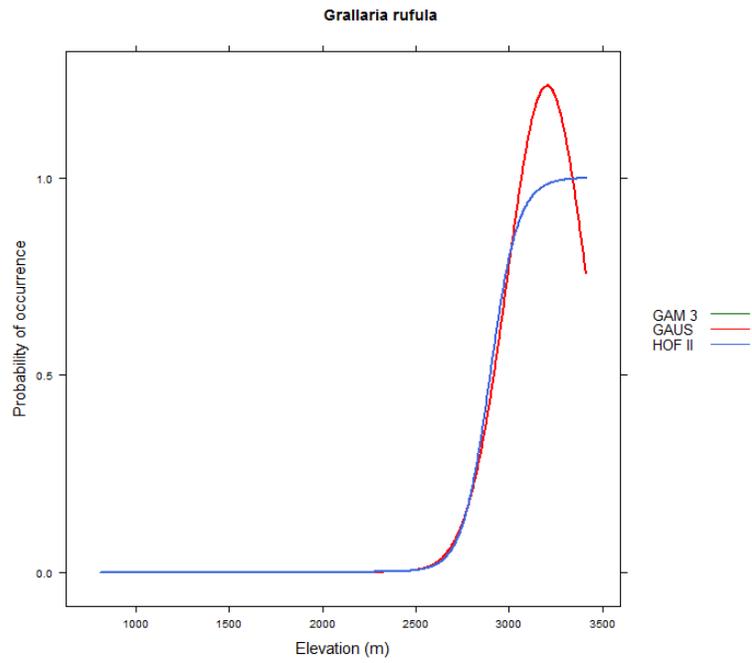


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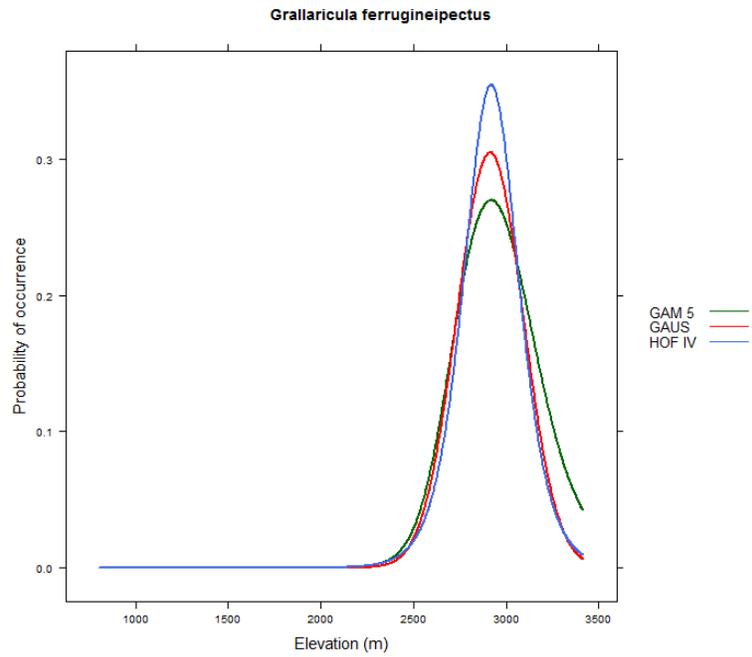


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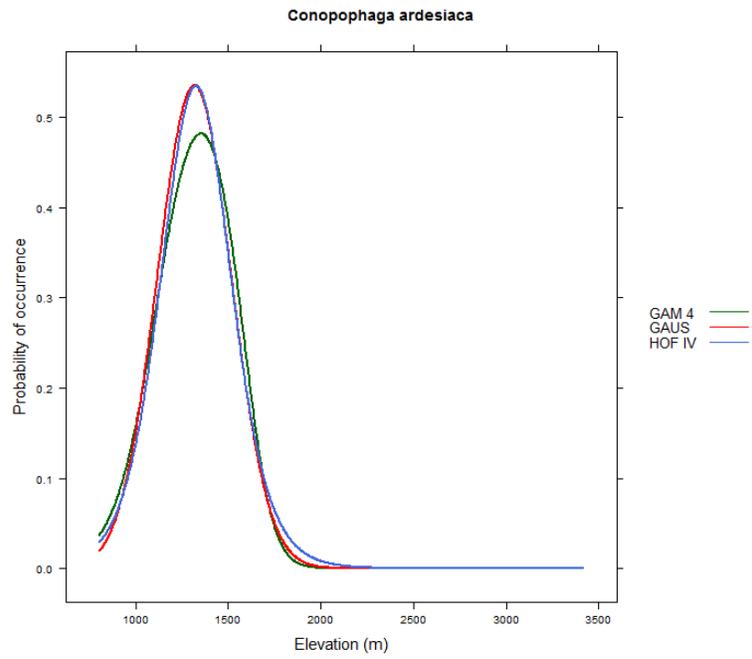


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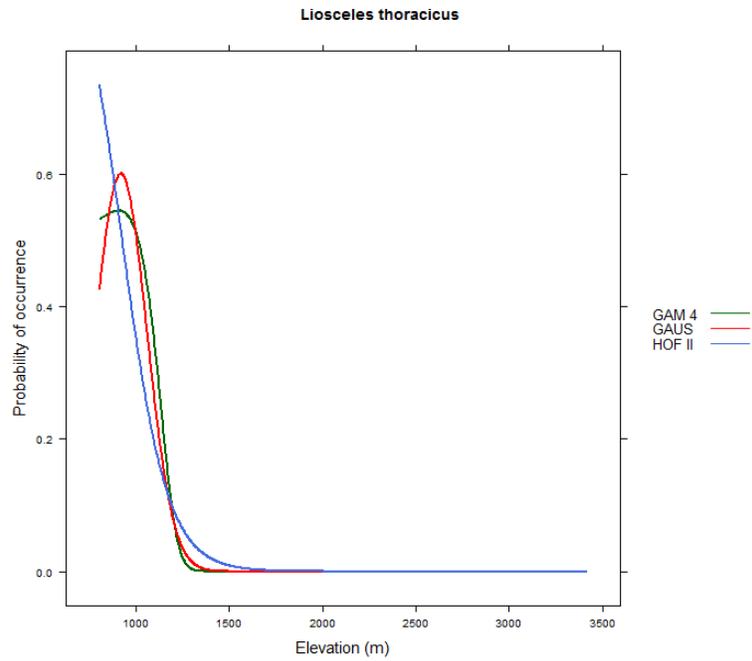


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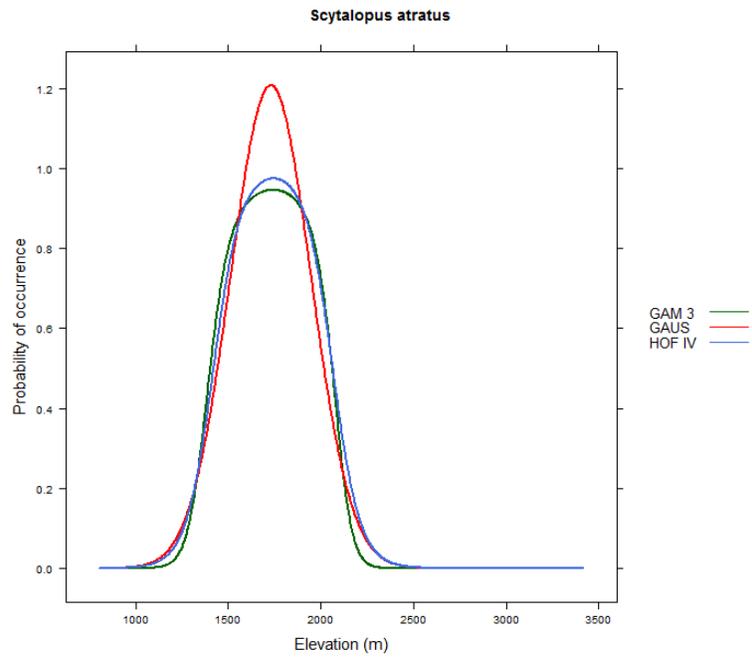


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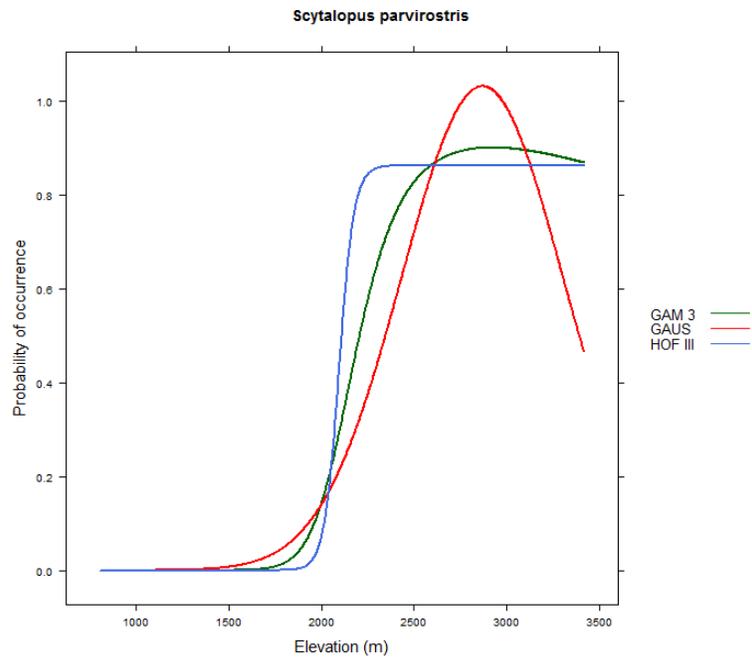


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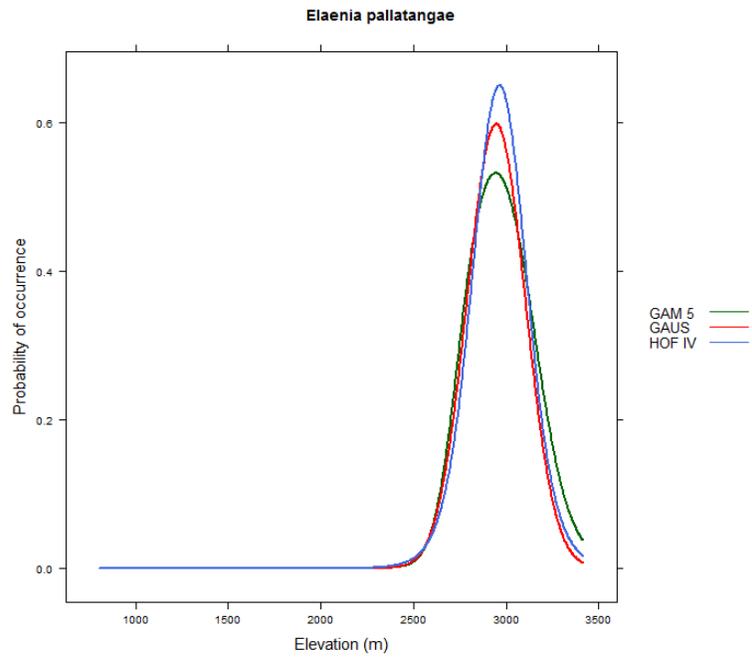


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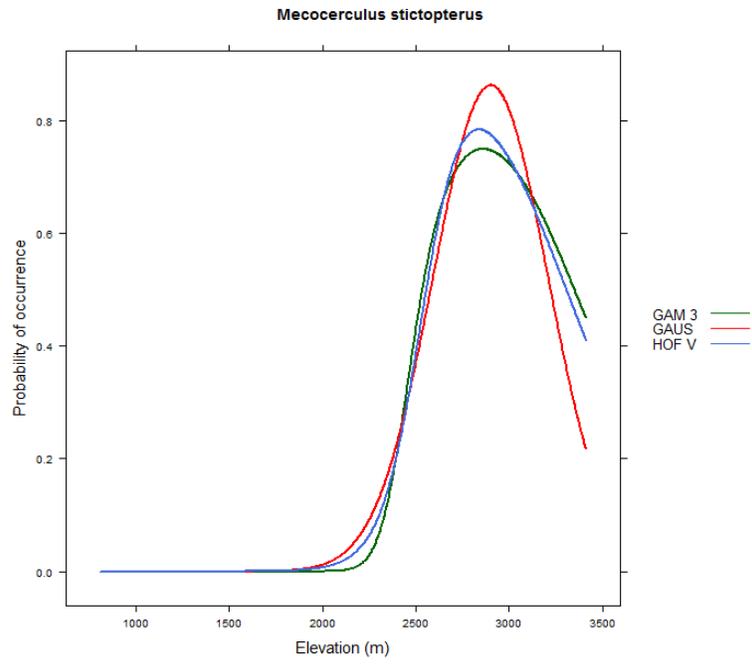


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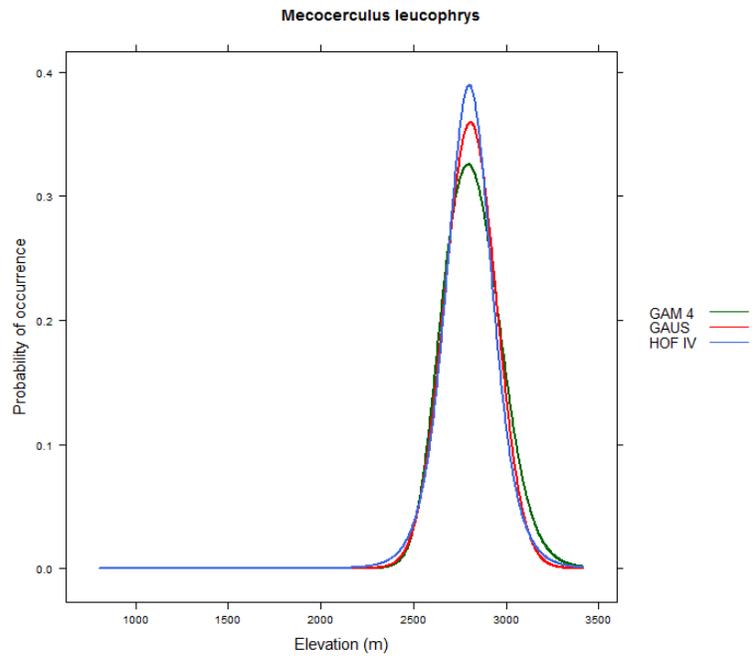


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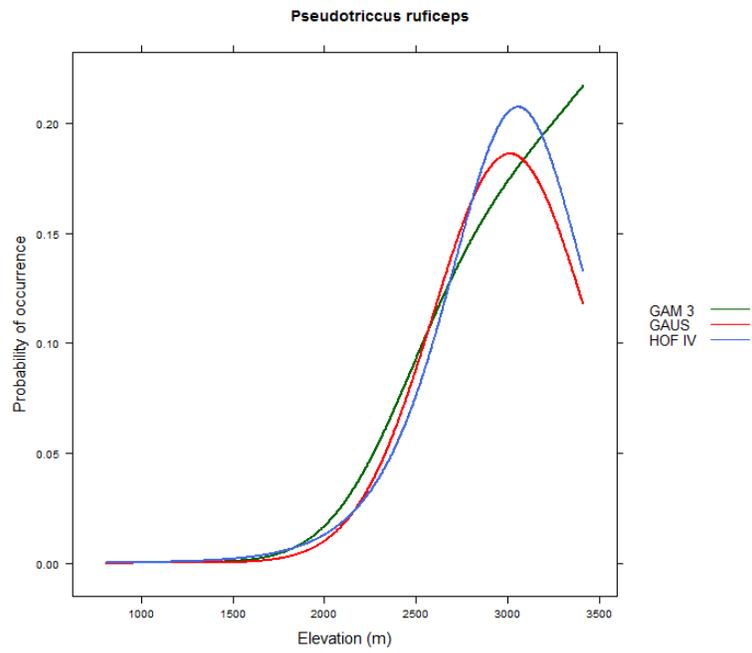


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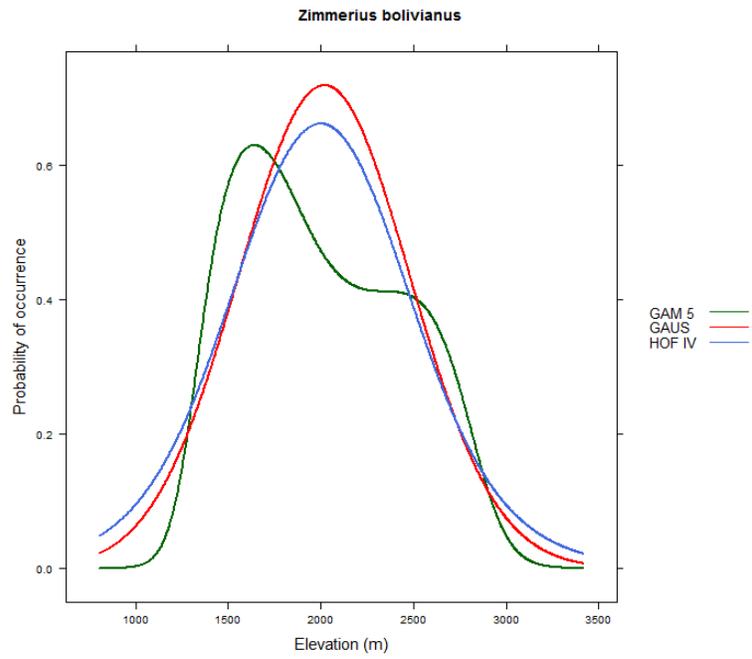


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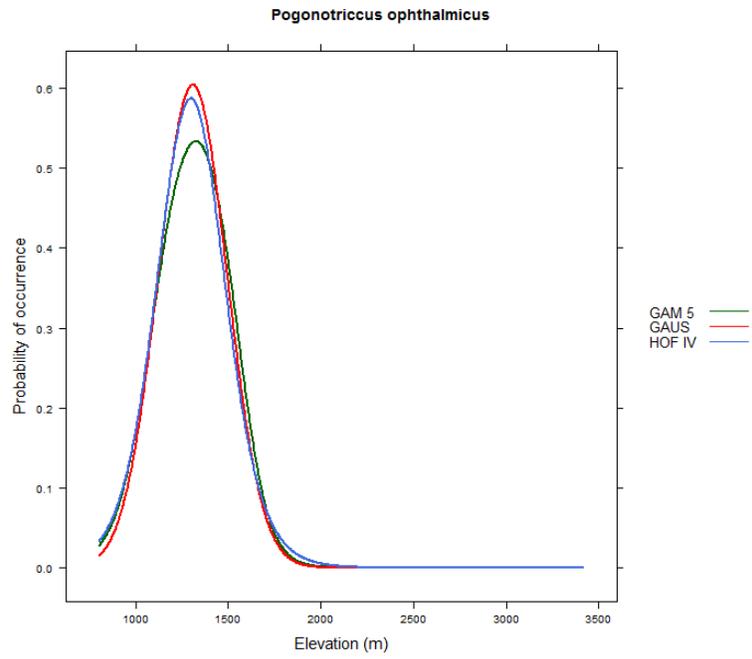


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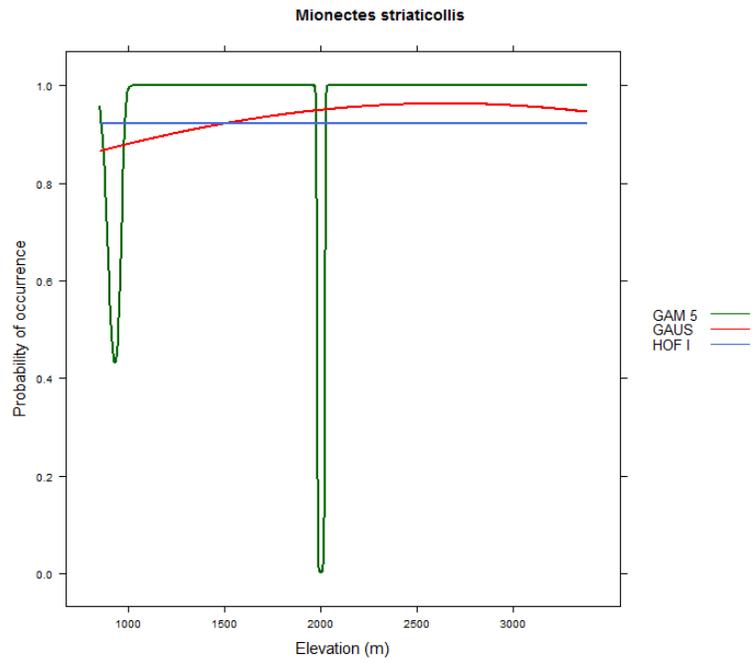


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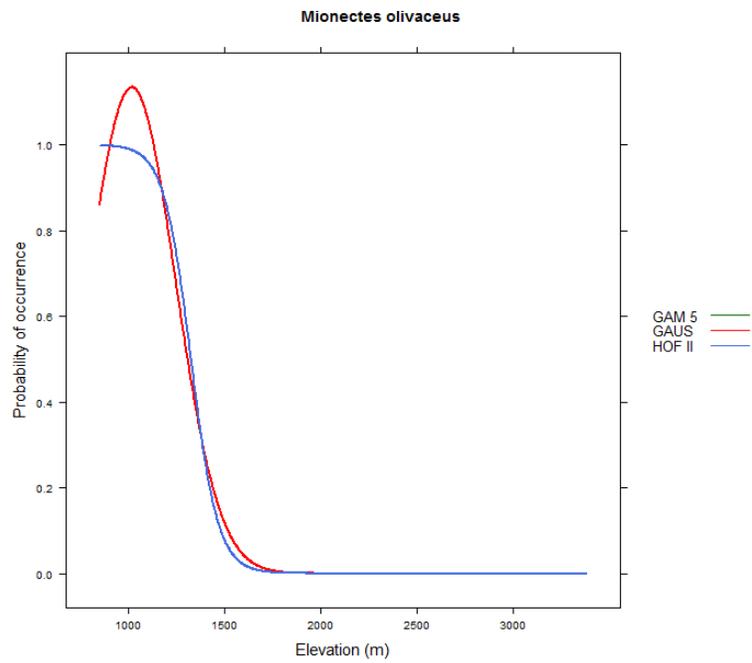


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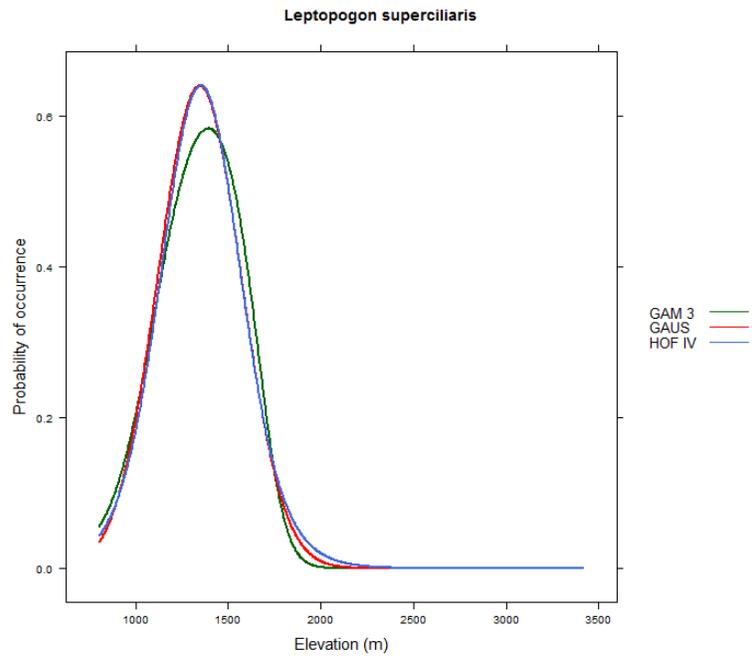


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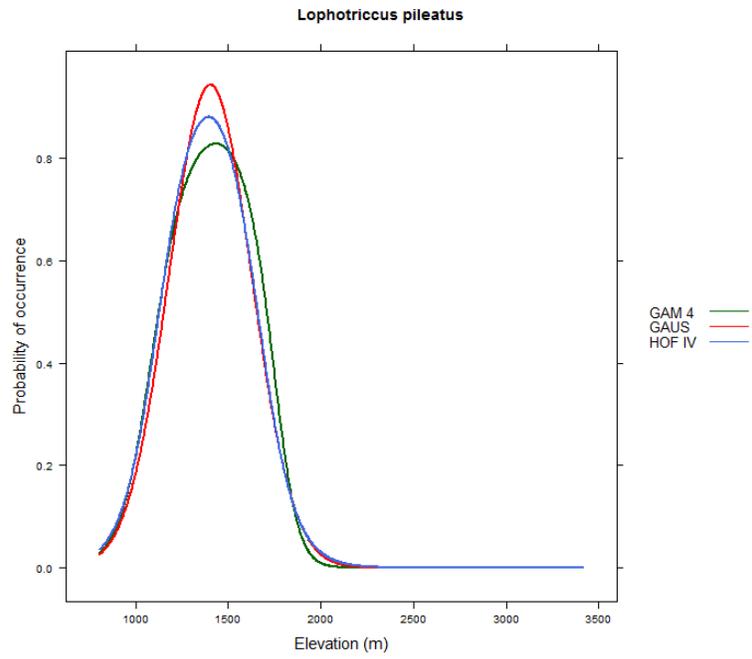


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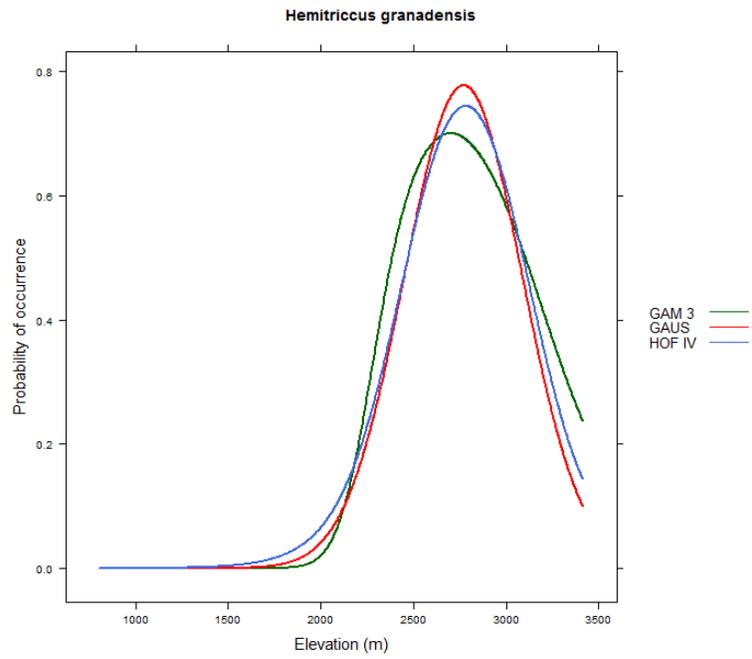


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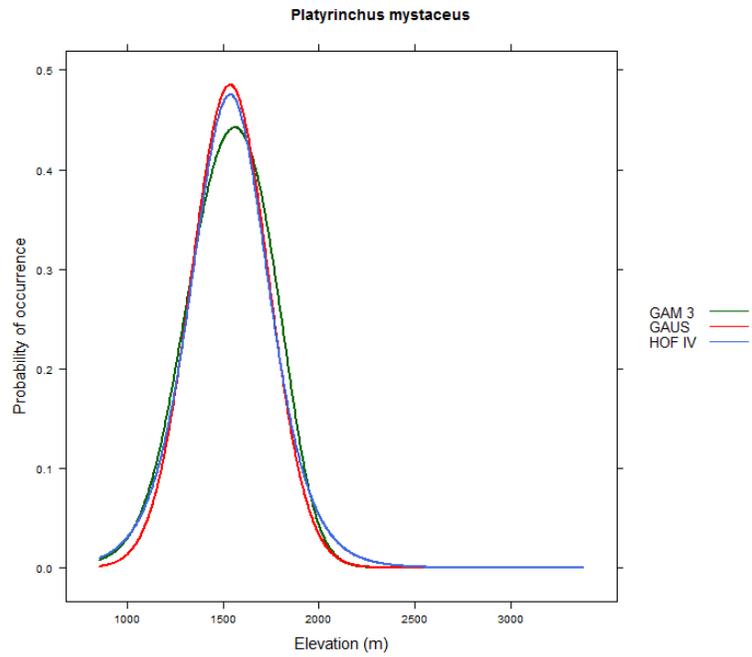


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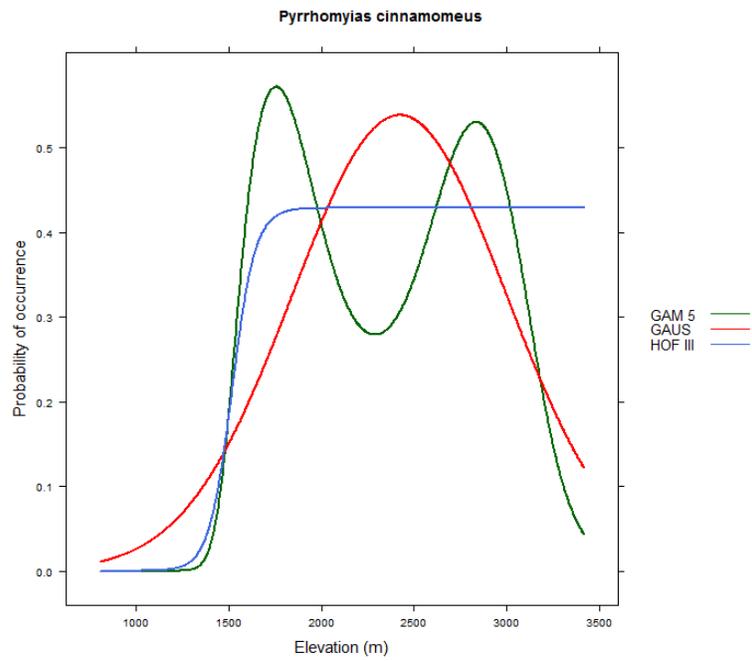


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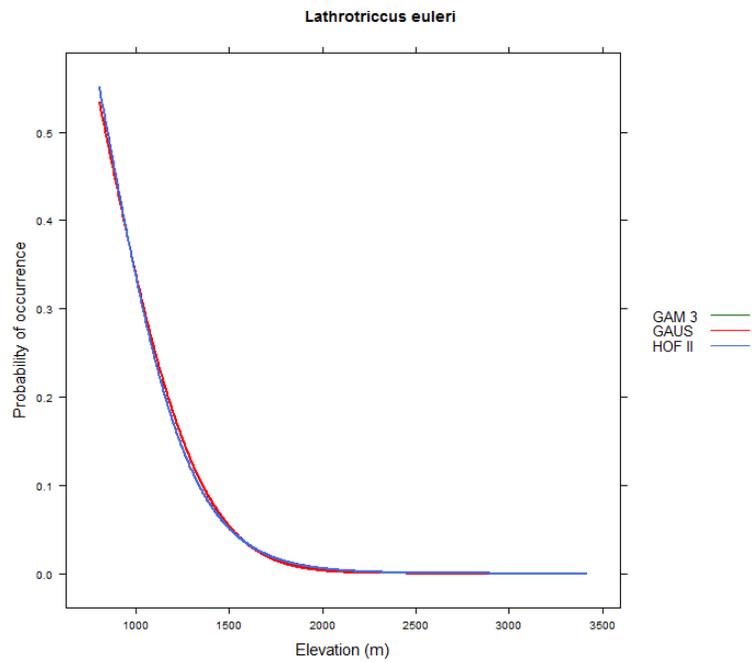


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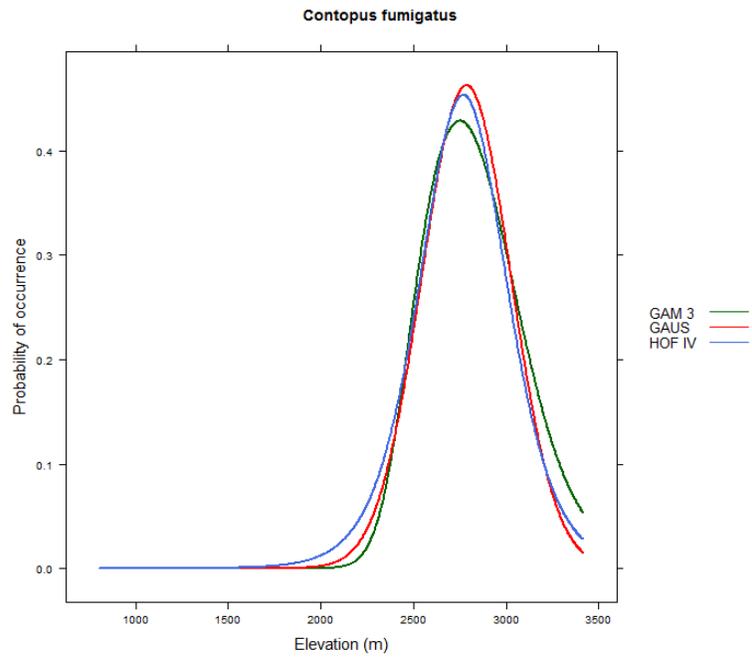


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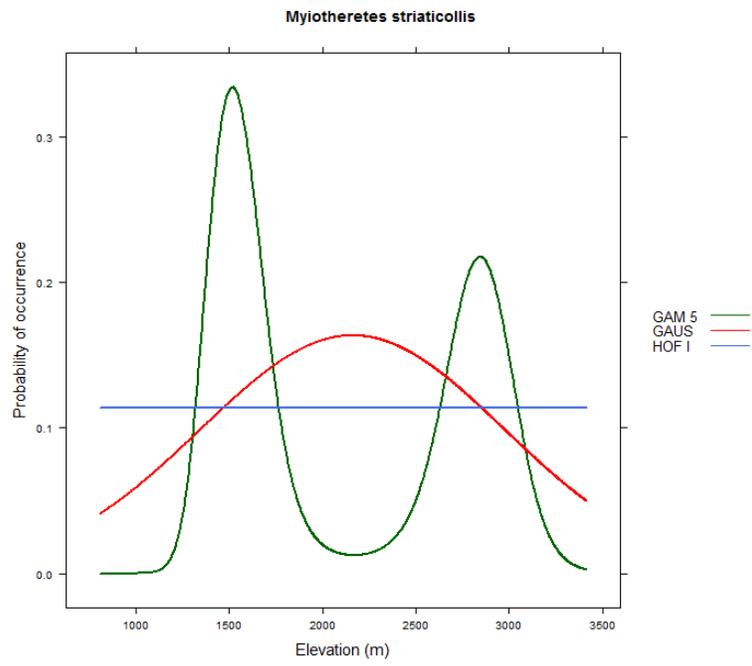


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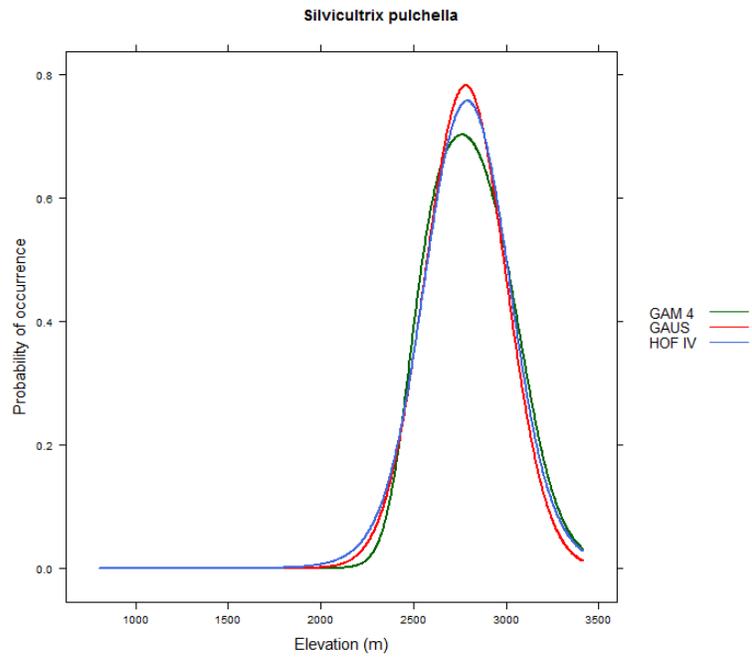


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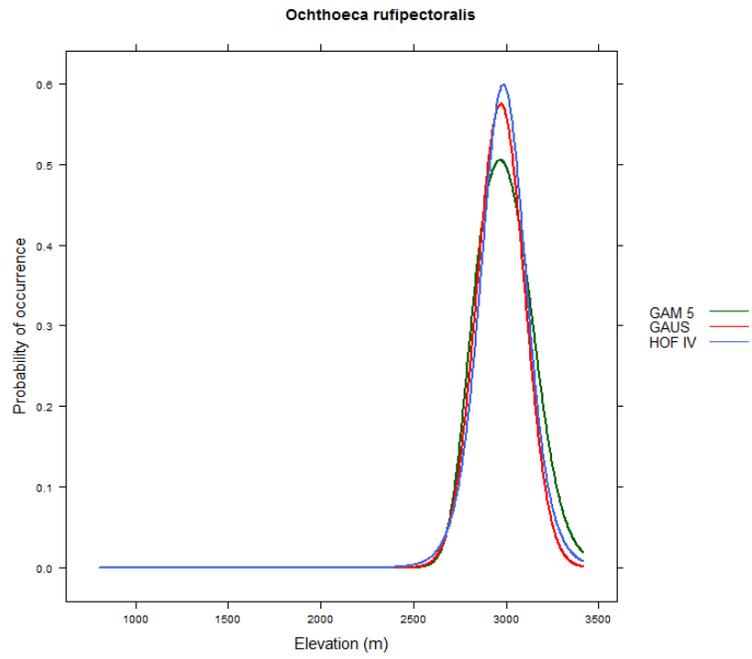


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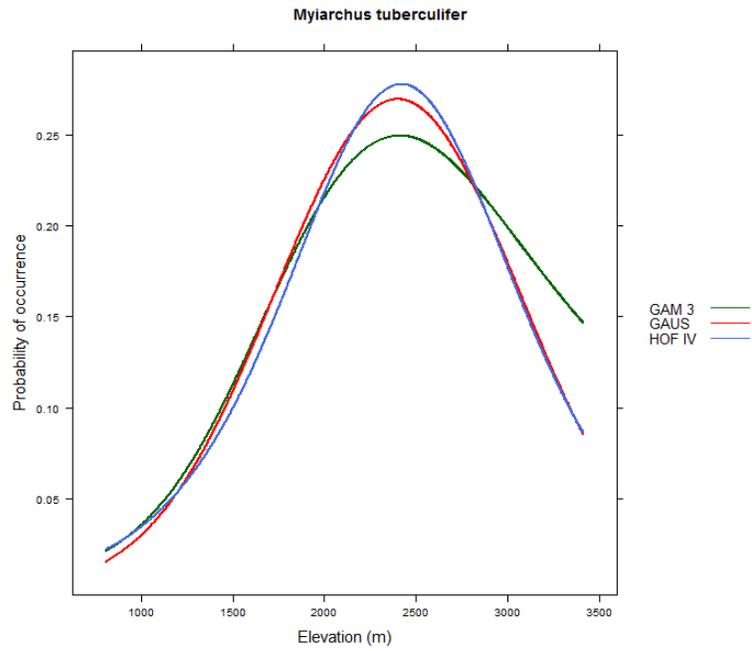


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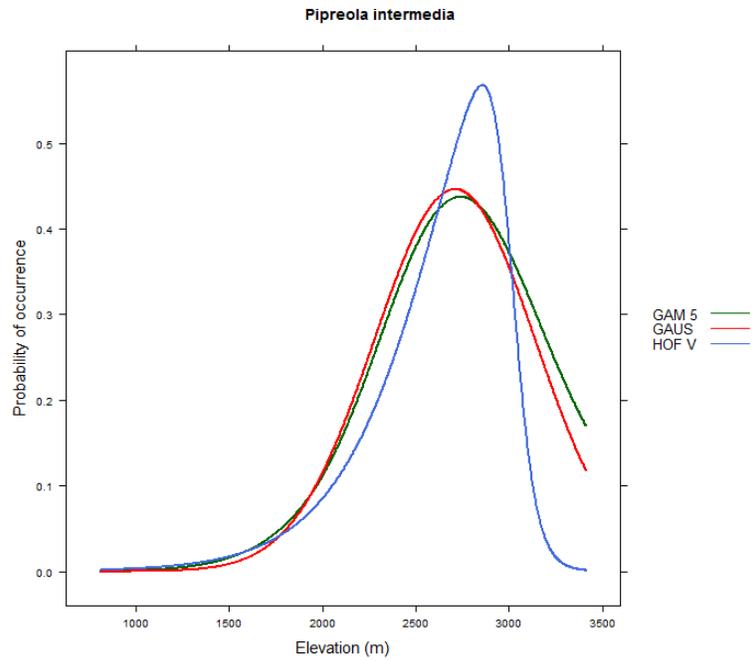


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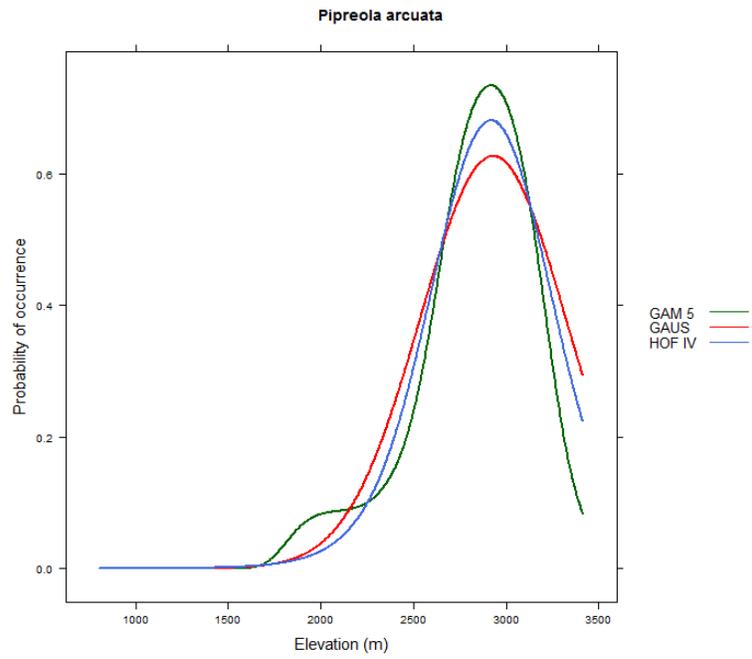


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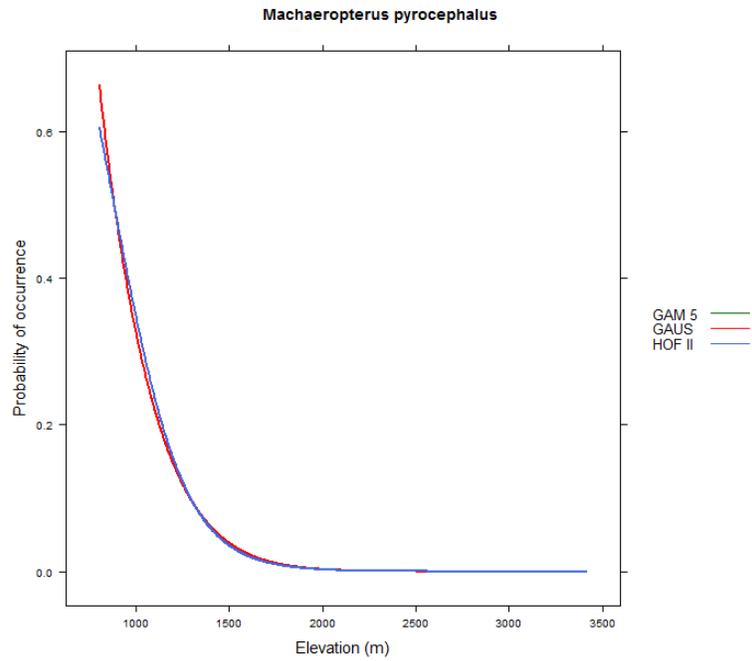


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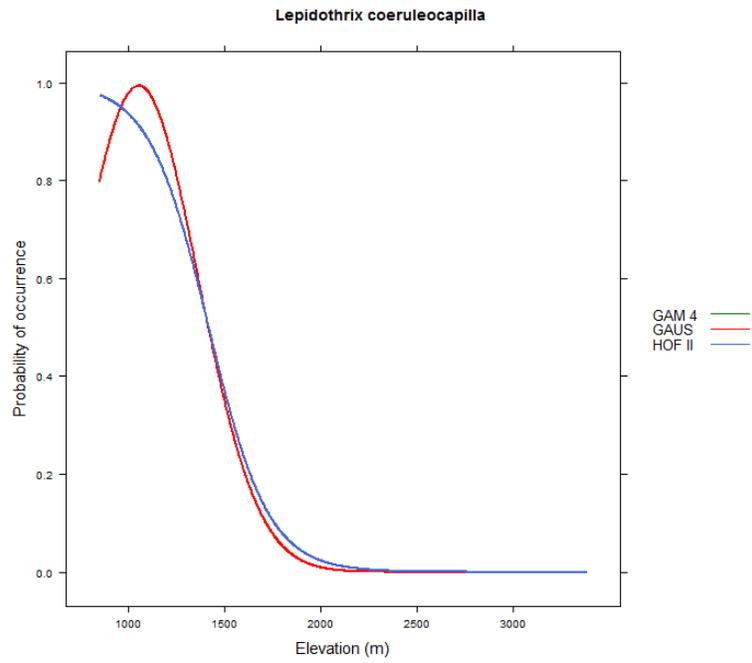


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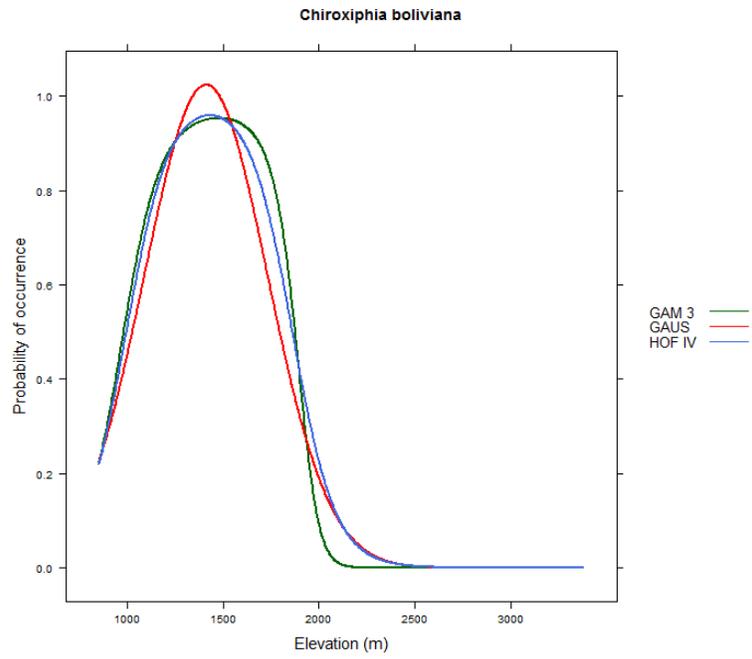


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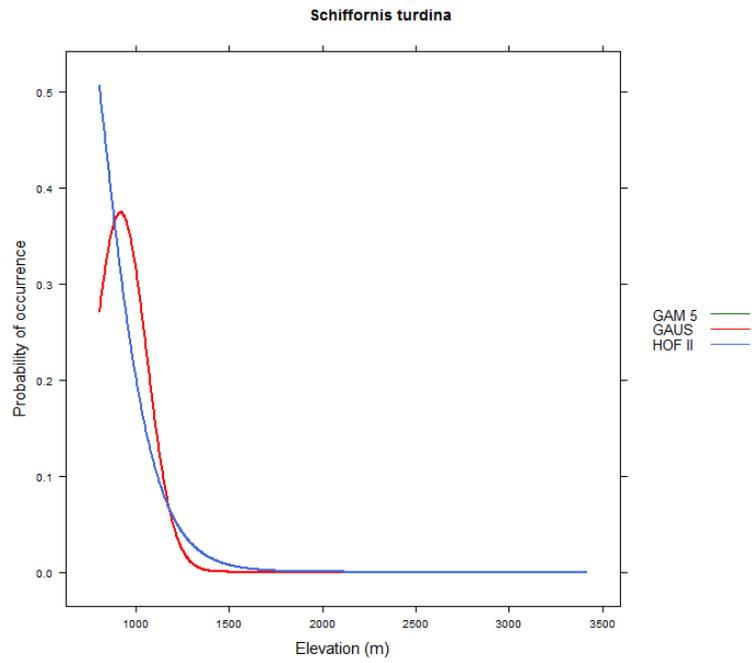


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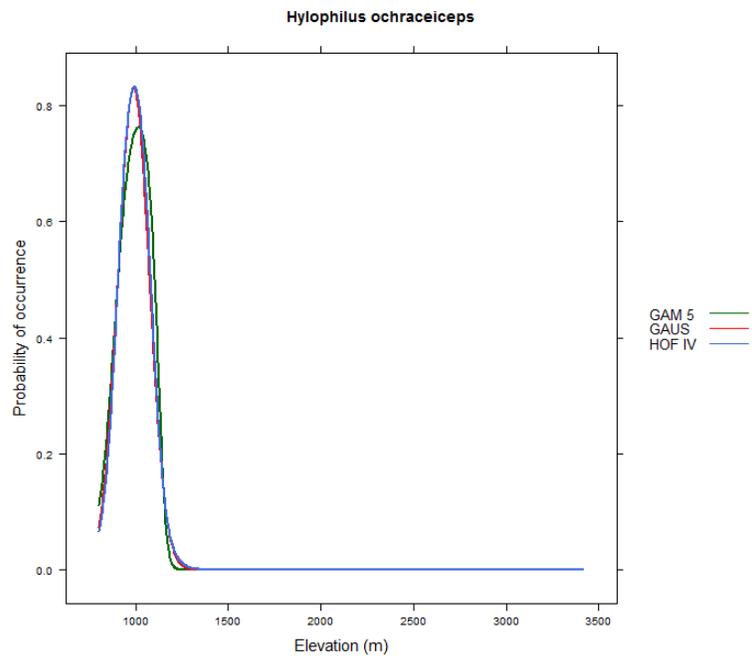


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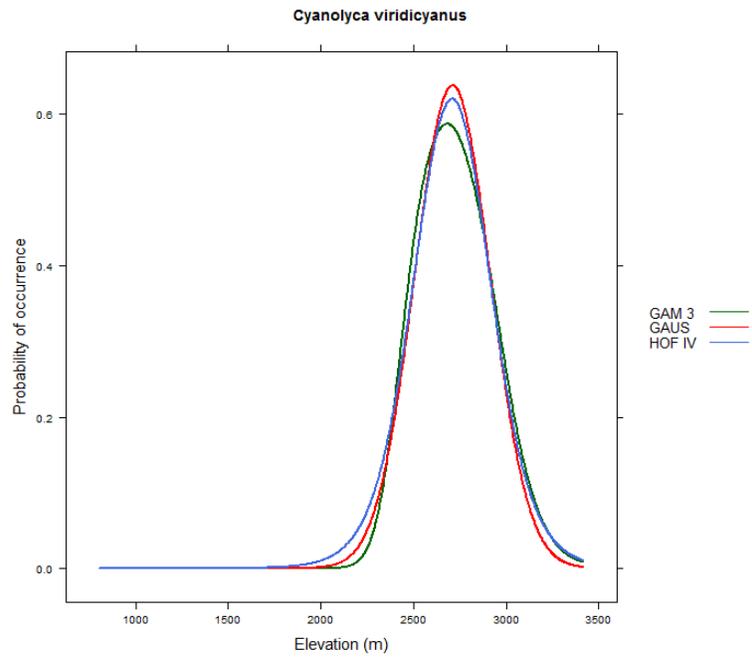


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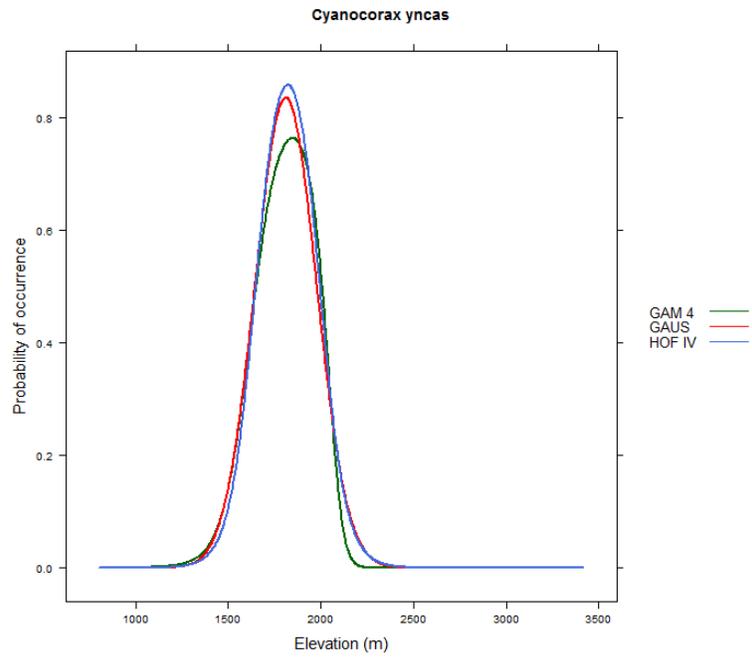


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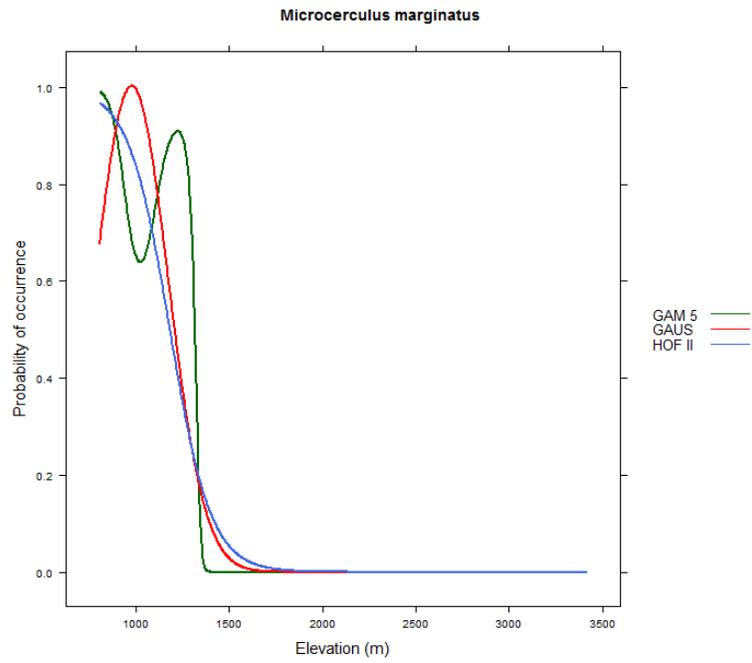


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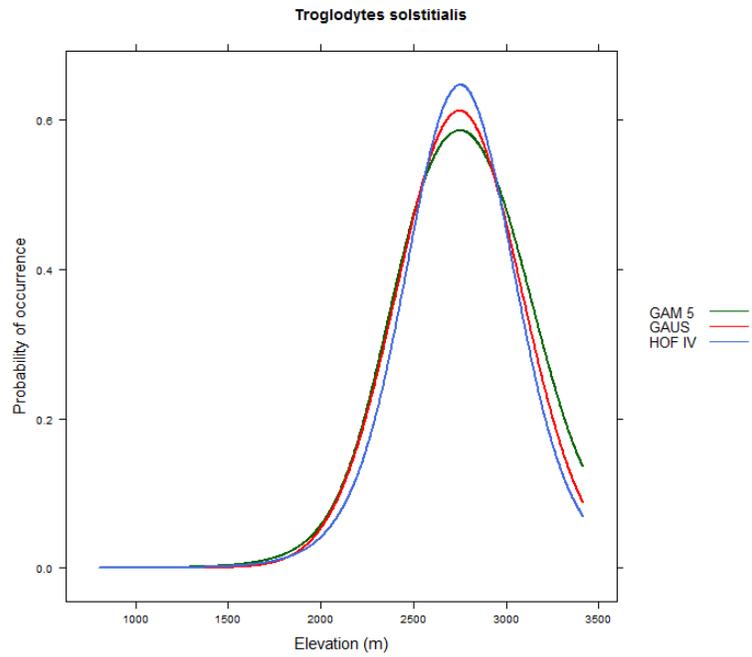


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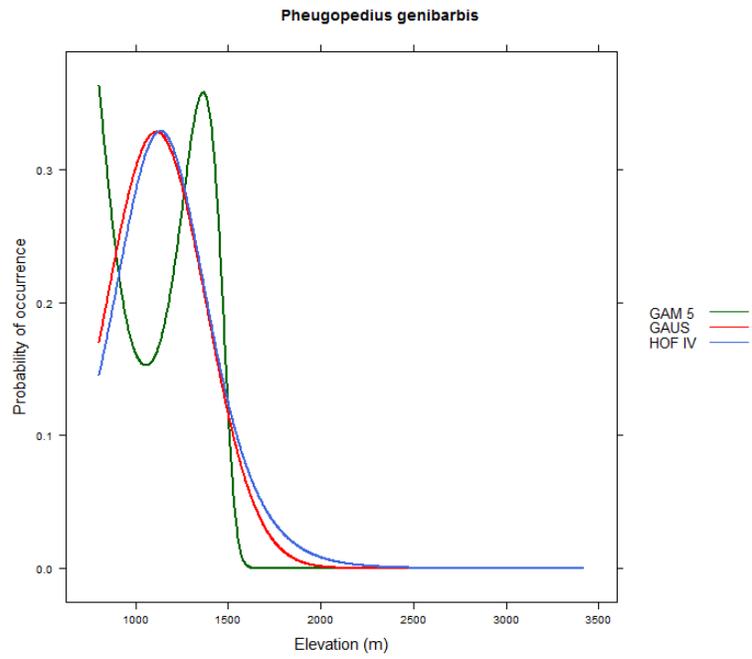


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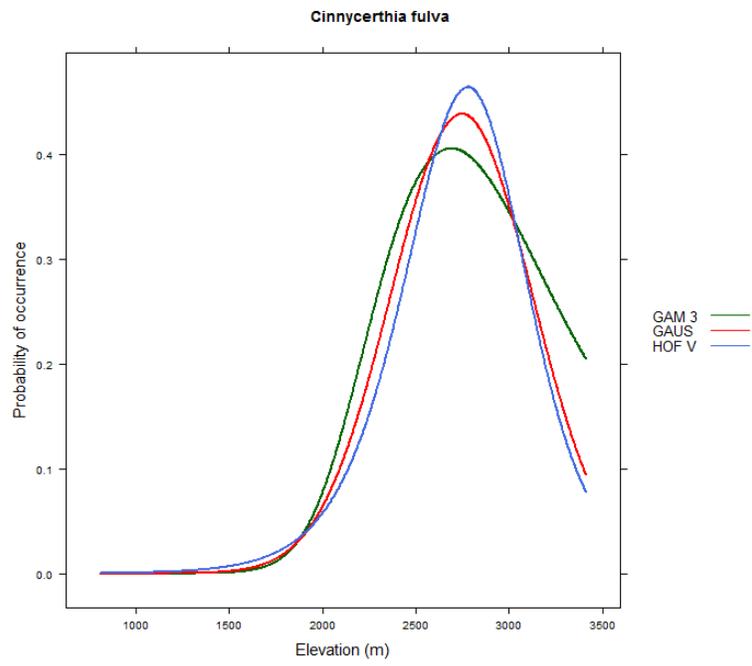


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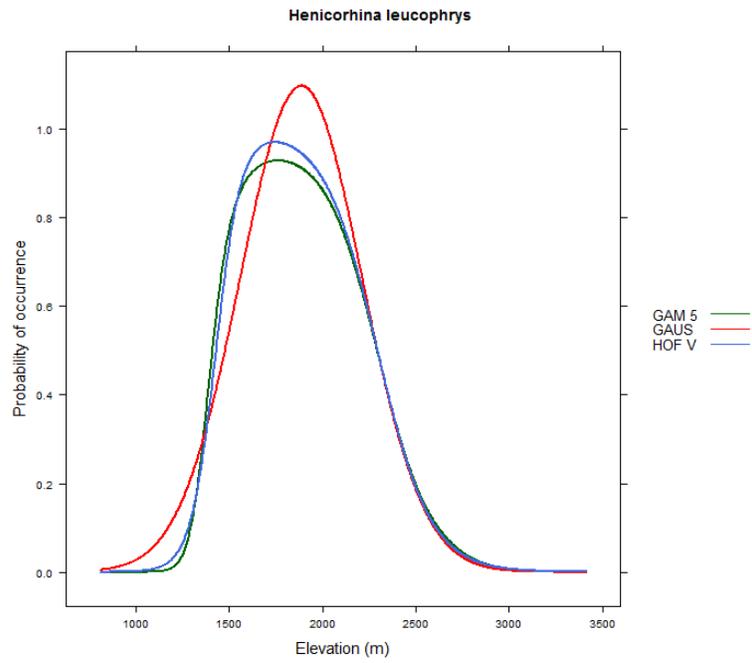


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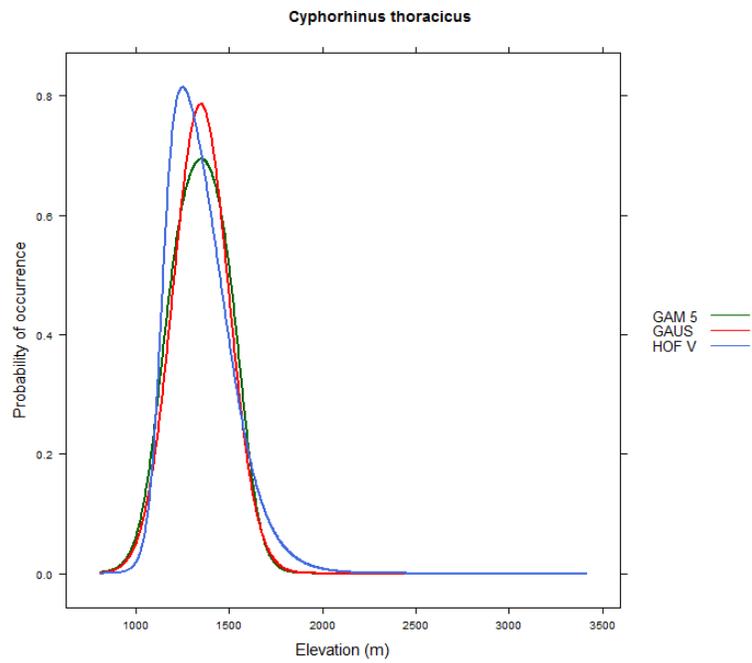


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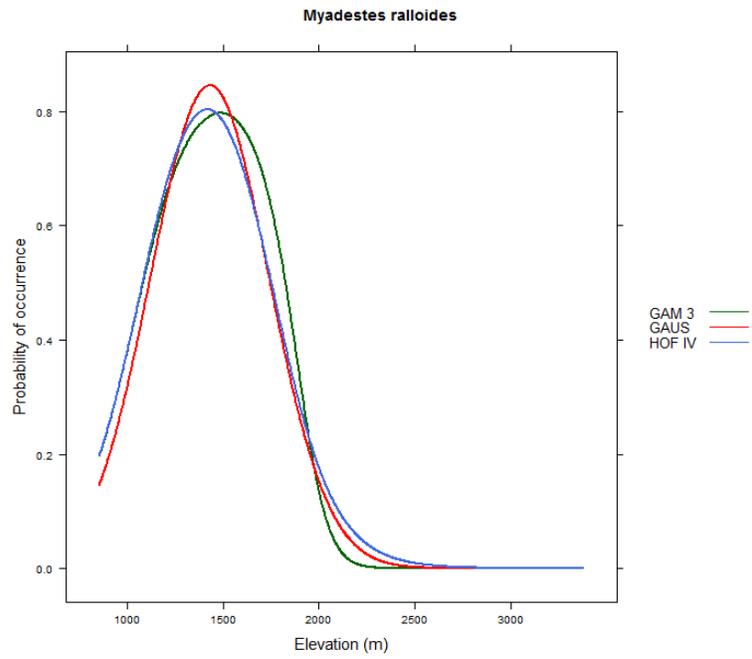


Figure C-123.

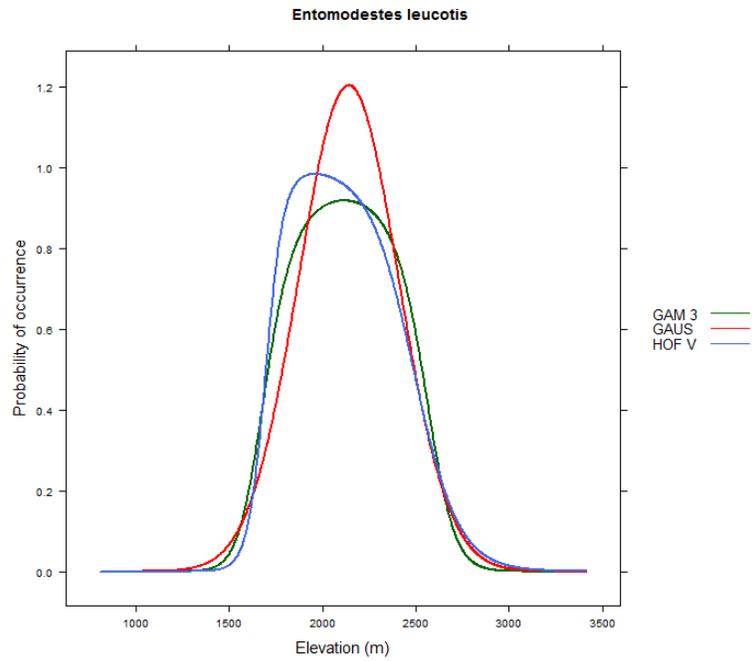


Figure C-124.

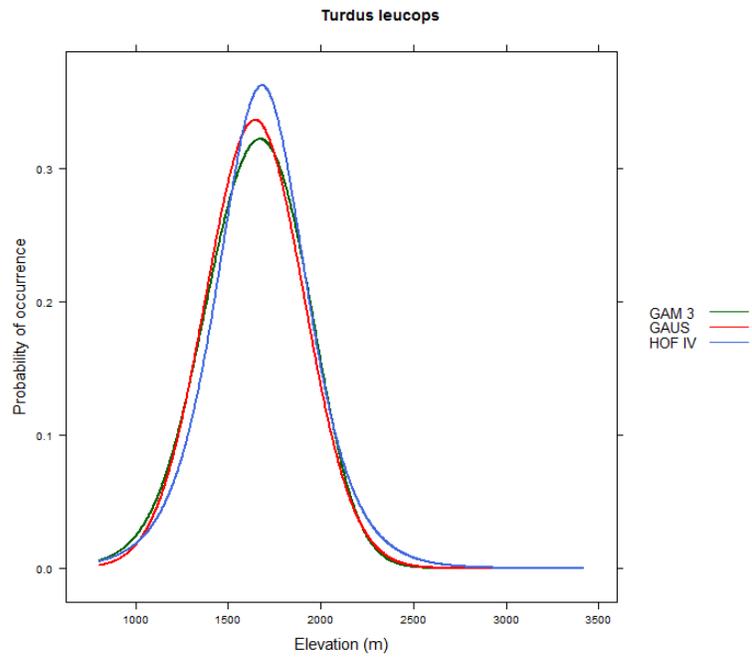


Figure C-125.

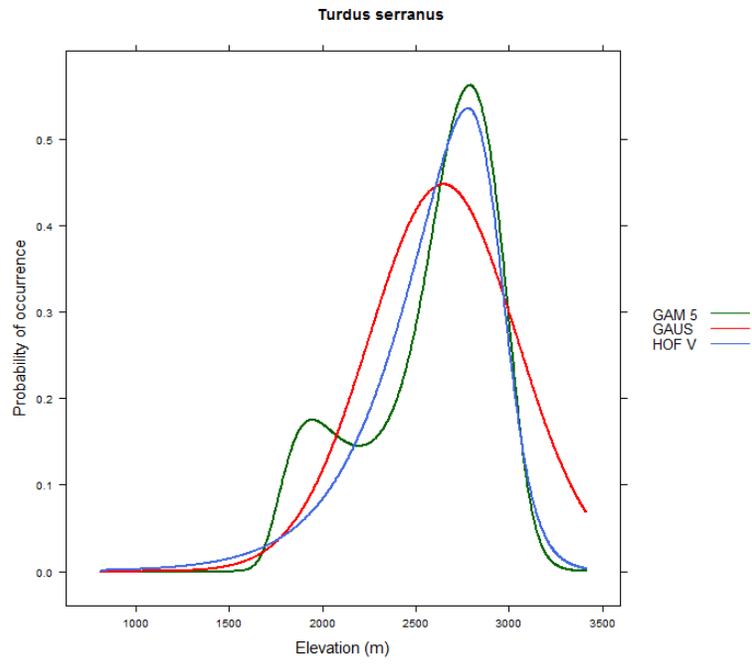


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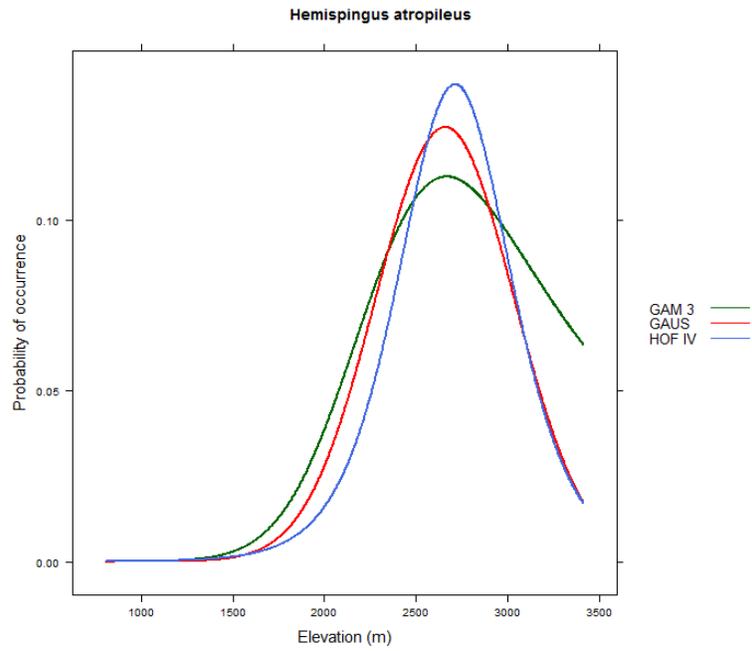


Figure C-127.

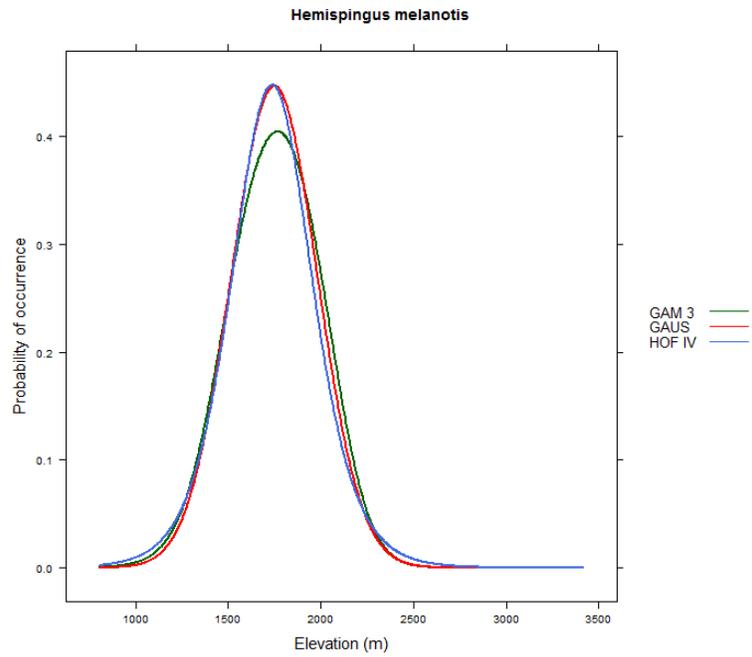


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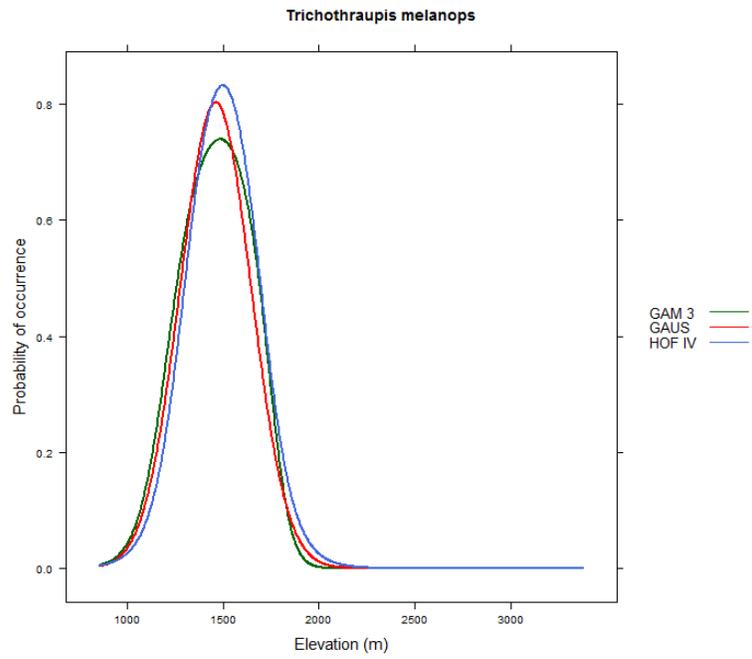
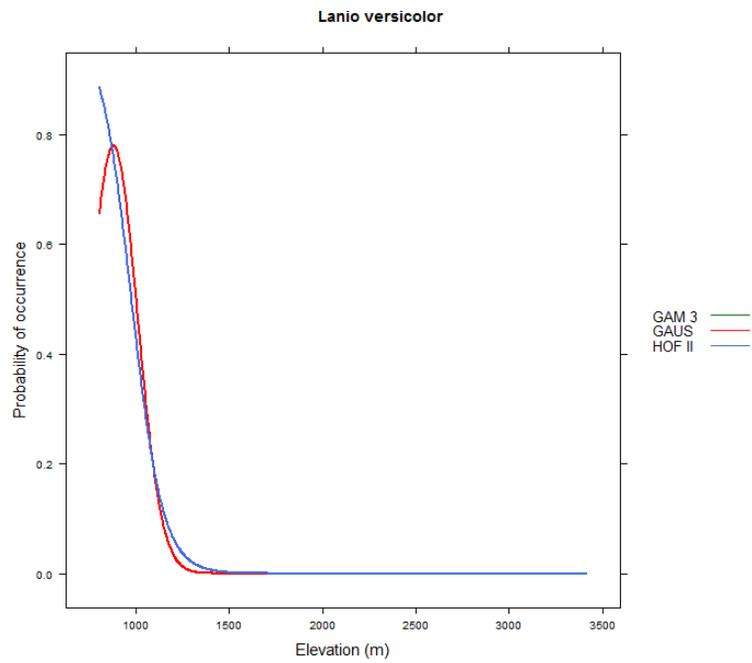


Figure C-129.



Figuer C-130.

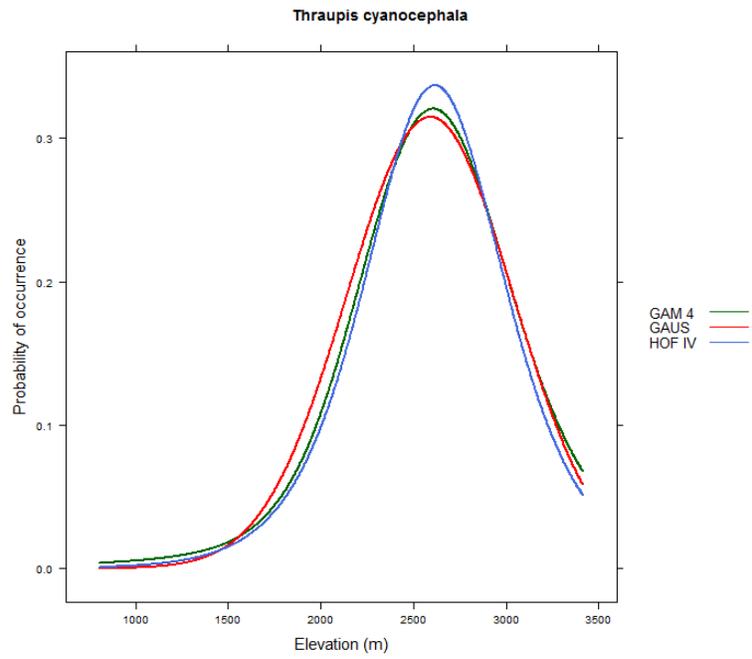


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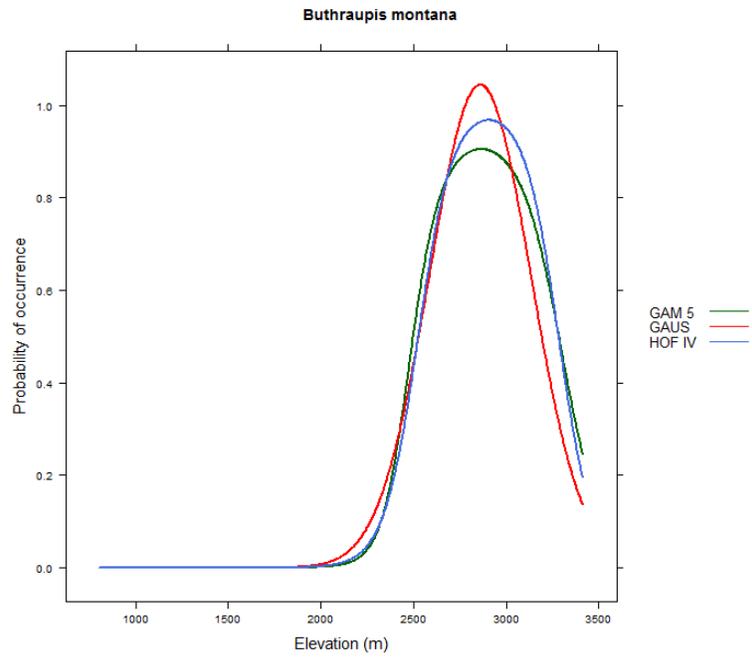


Figure C-132.

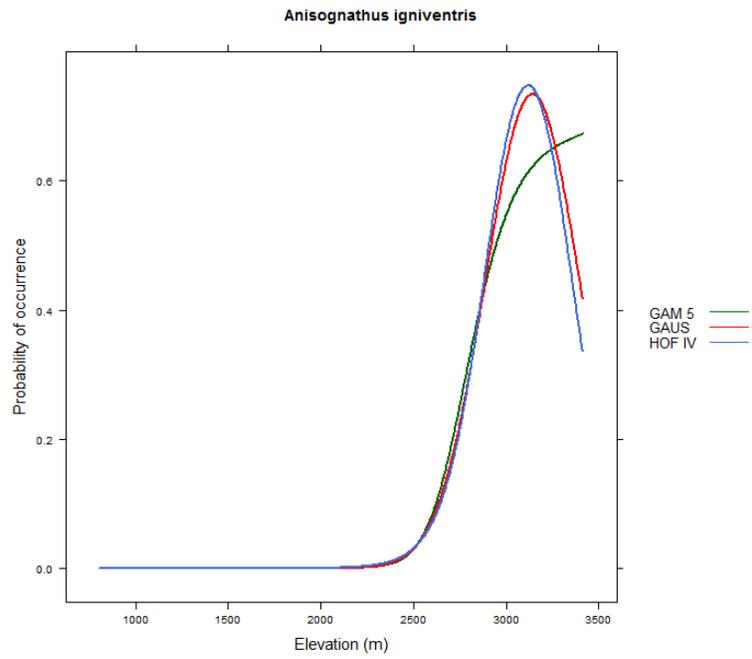


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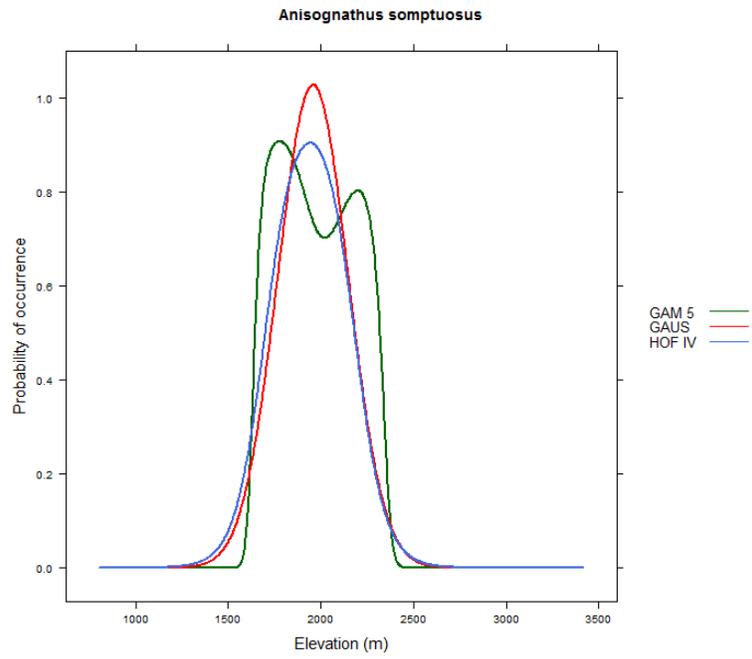


Figure C-134.

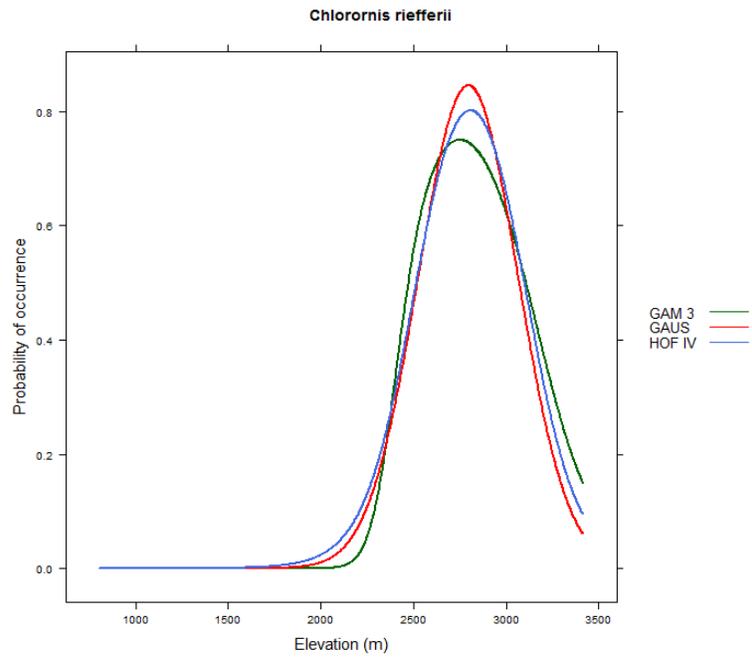


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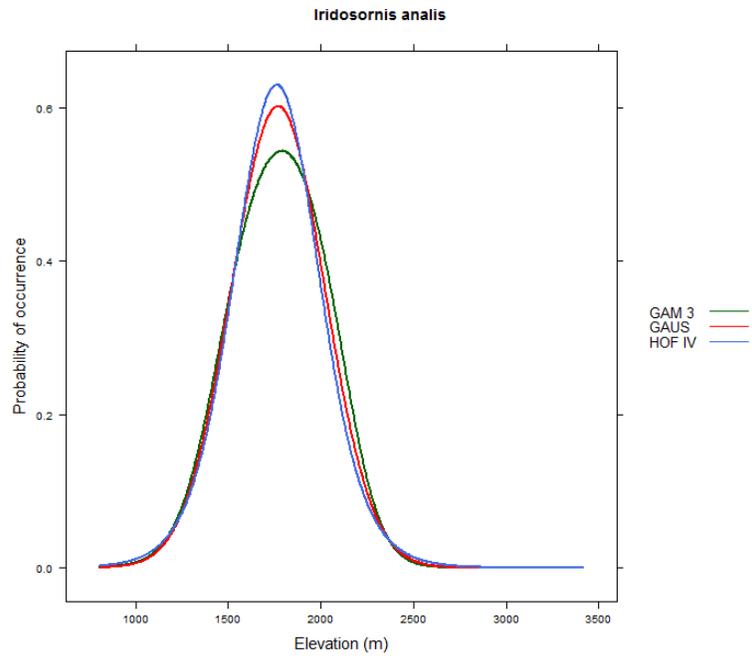


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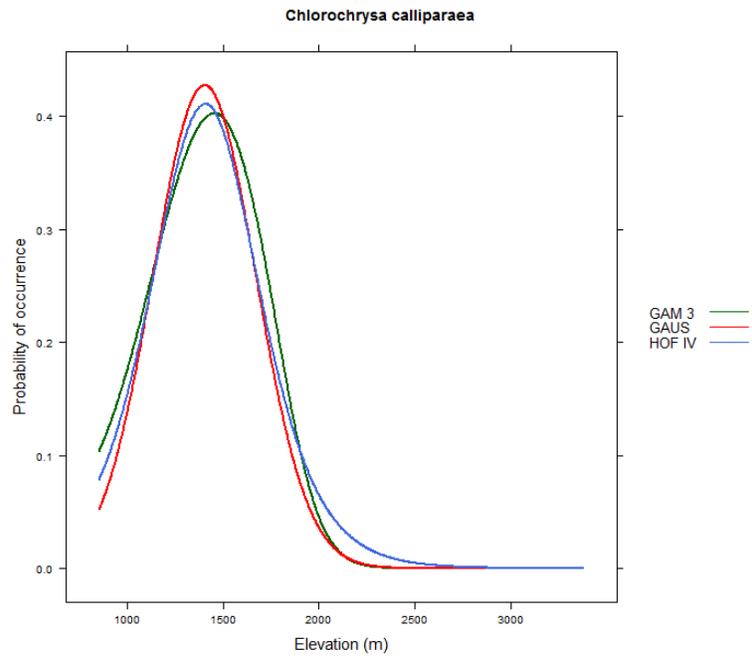


Figure C-137.

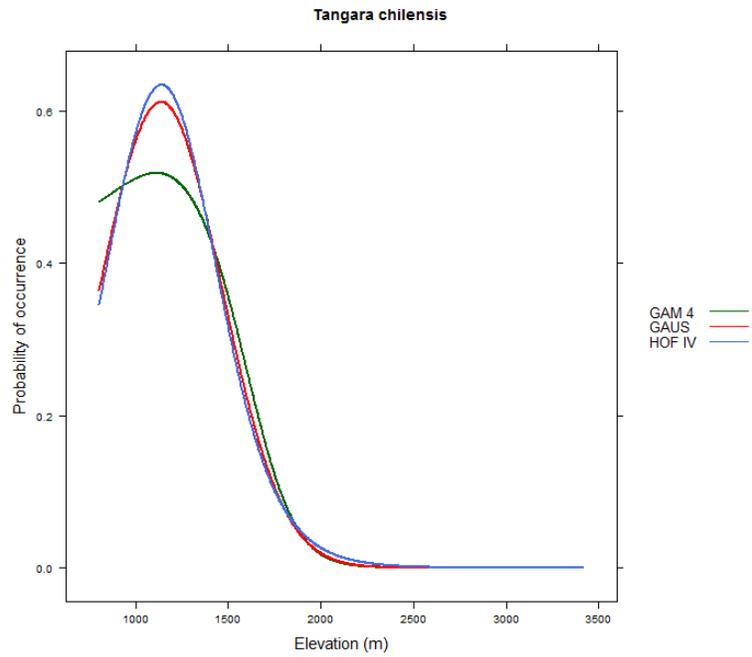


Figure C-138.

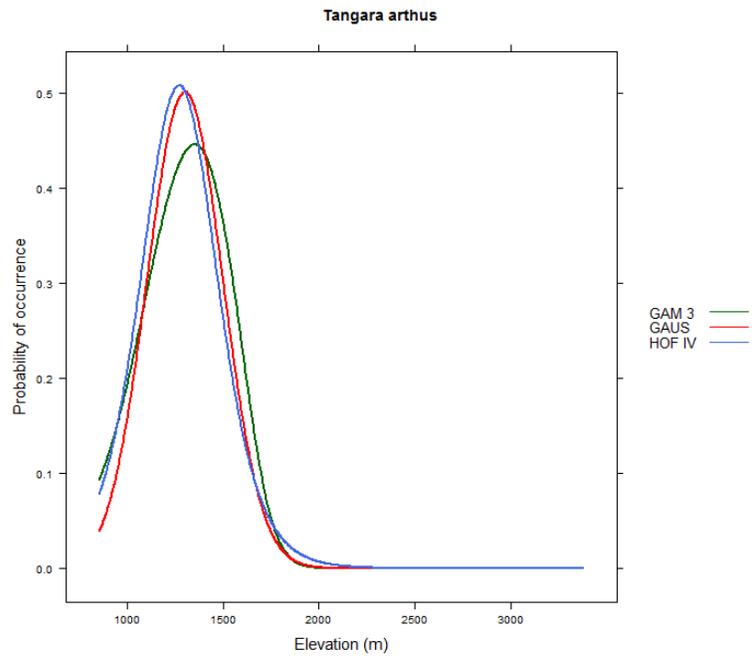


Figure C-139.

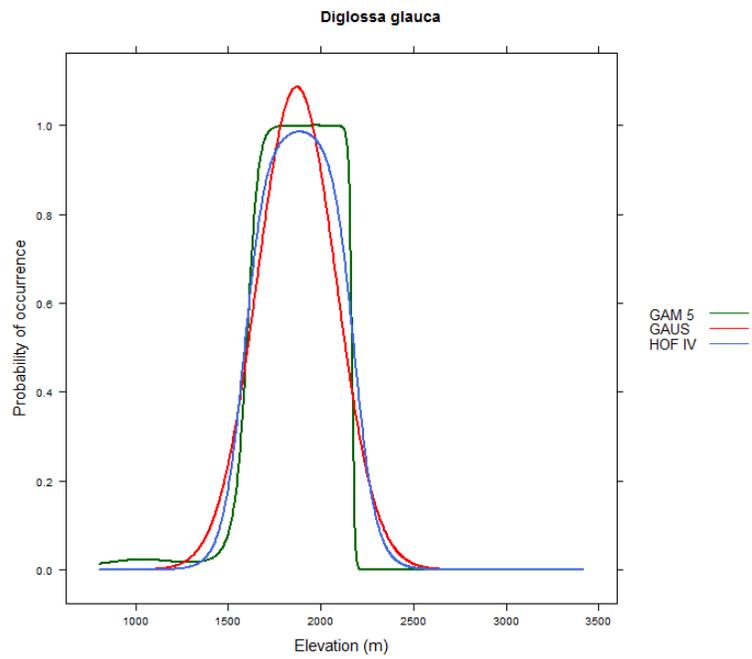


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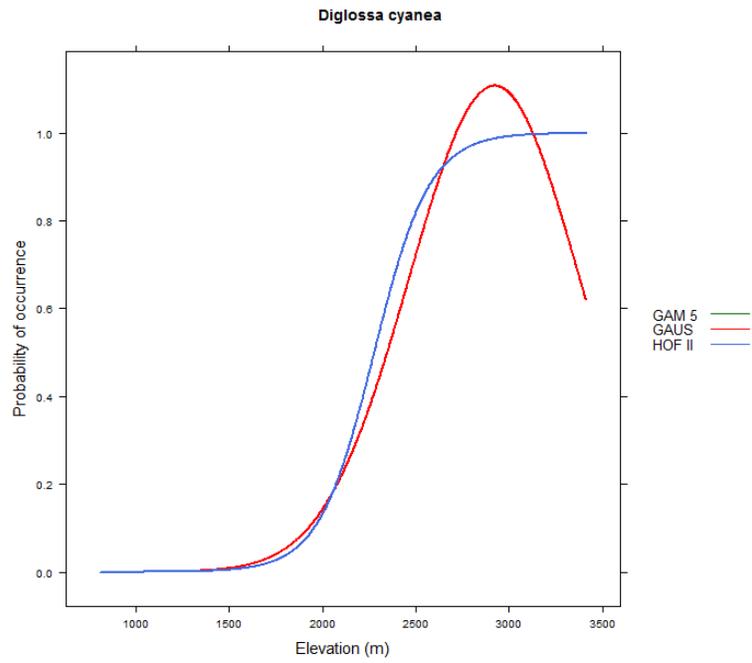


Figure C-141.

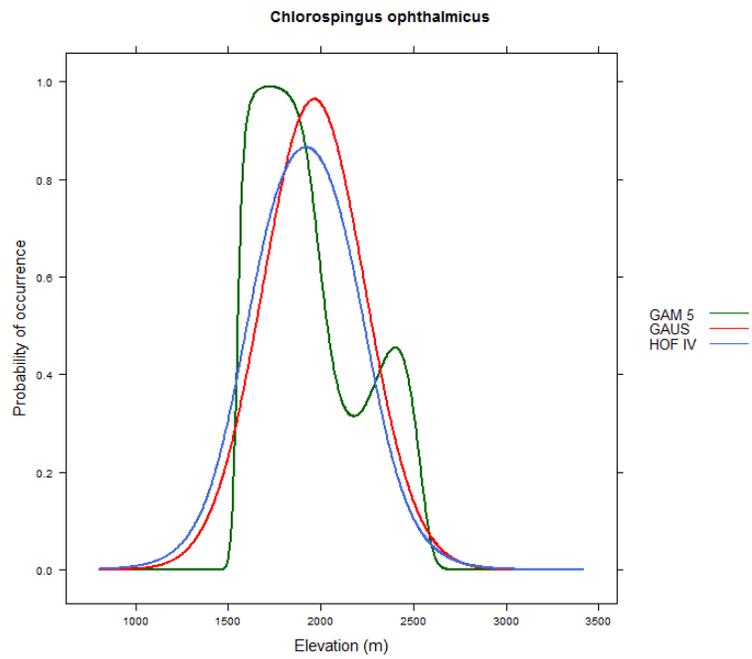


Figure C-142.

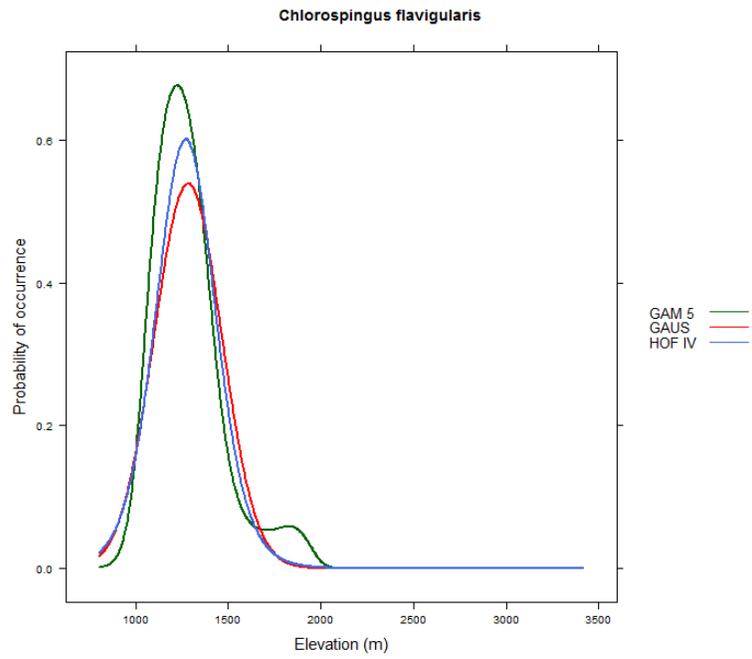


Figure C-143.

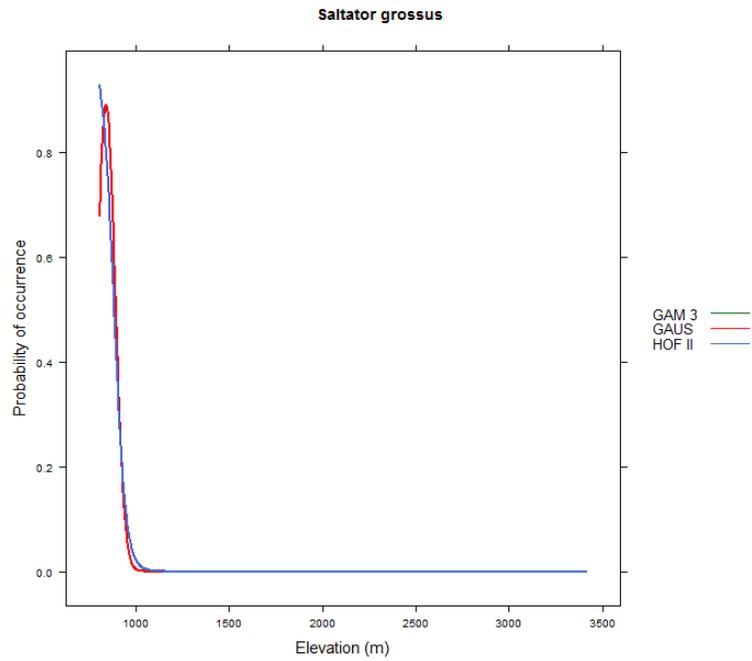


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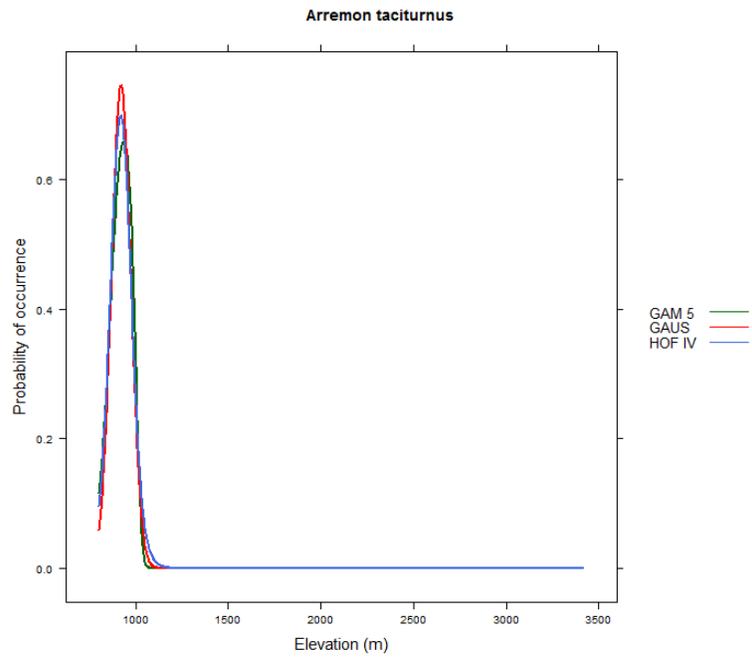


Figure C-145.

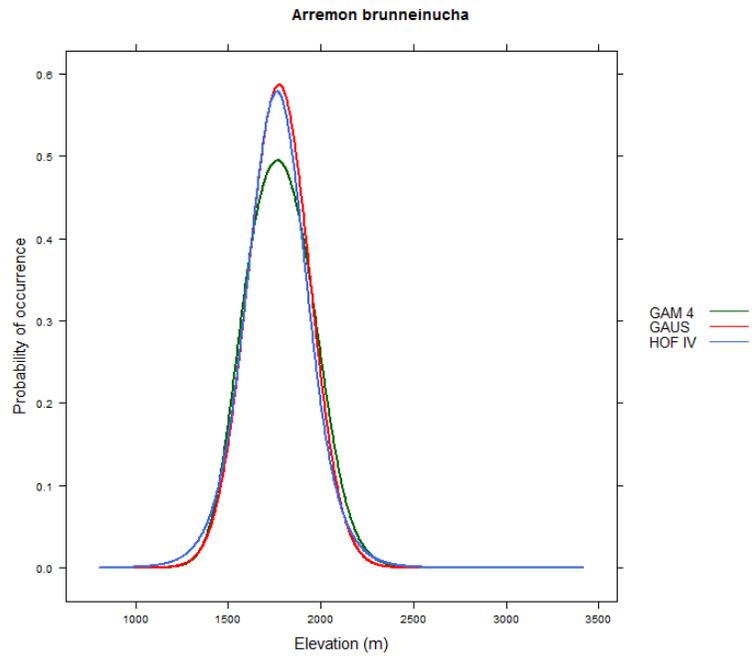


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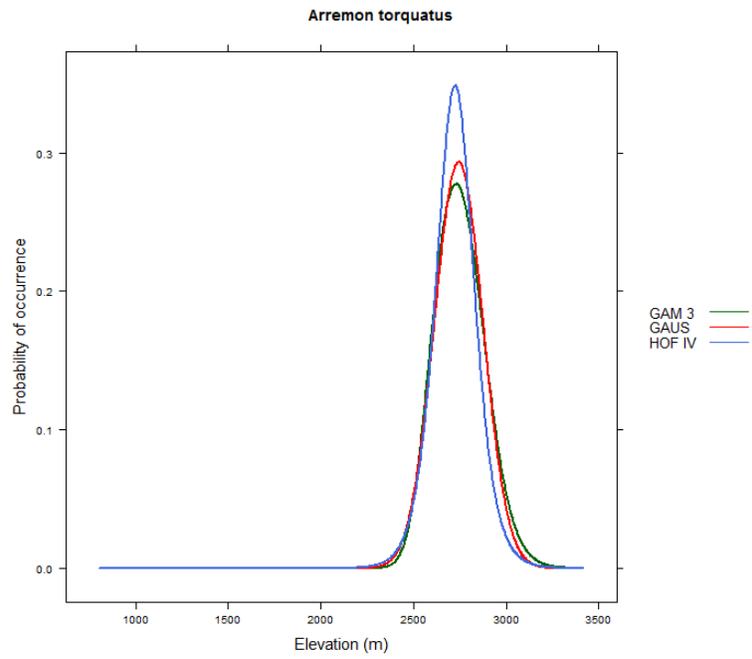


Figure C-147.

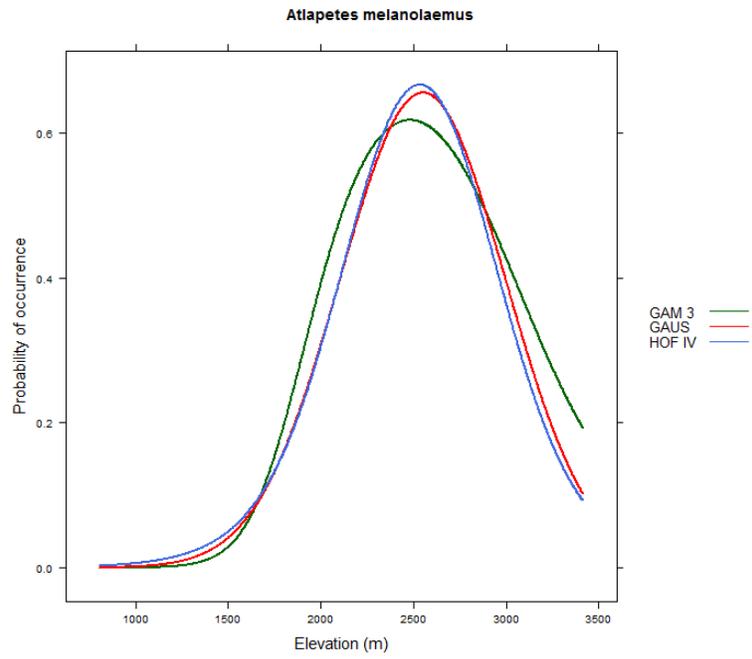


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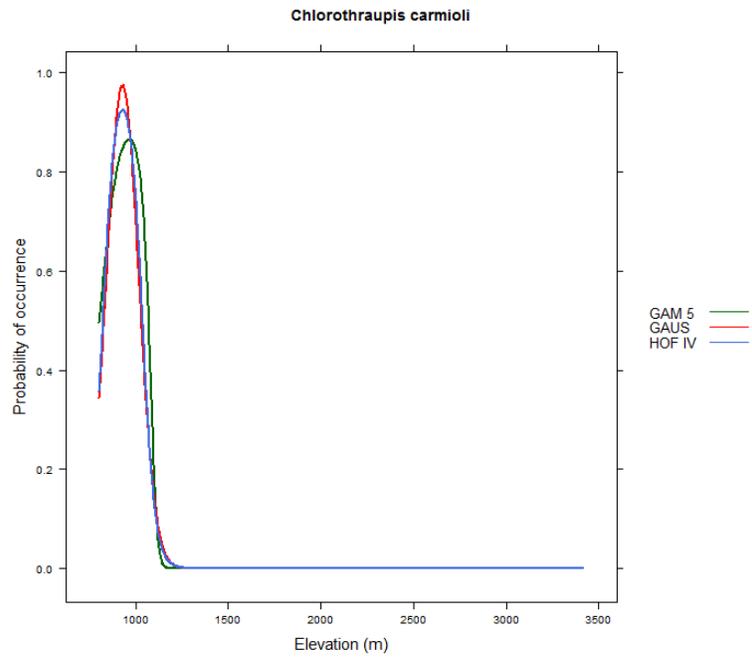


Figure C-149.

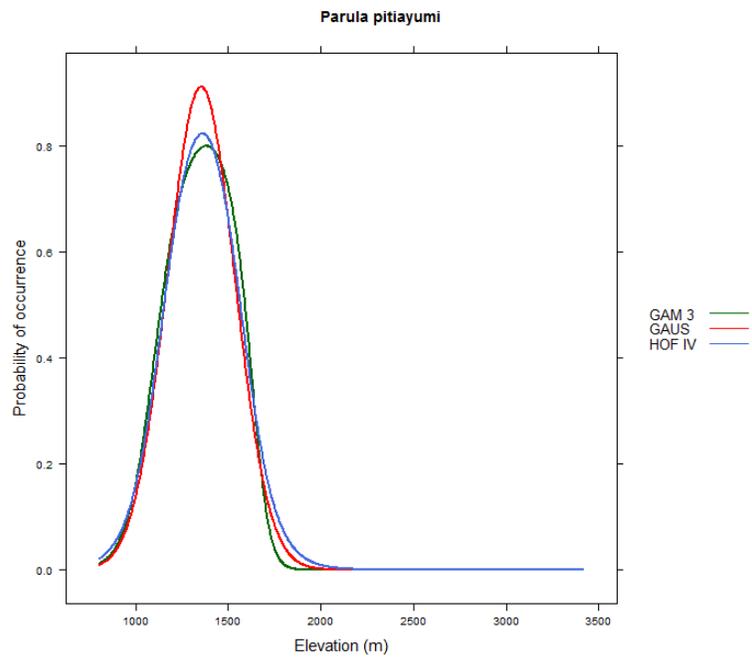


Figure C-150.

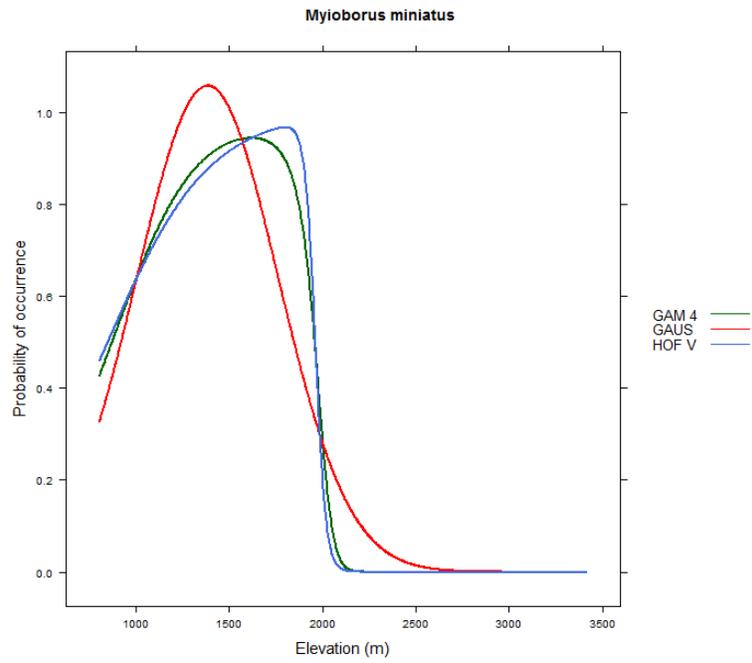


Figure C-151.

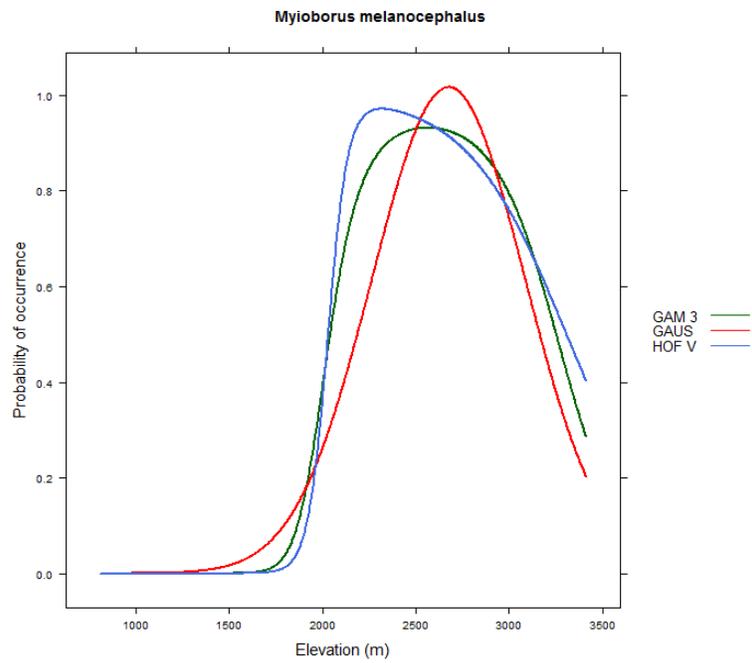


Figure C-152.

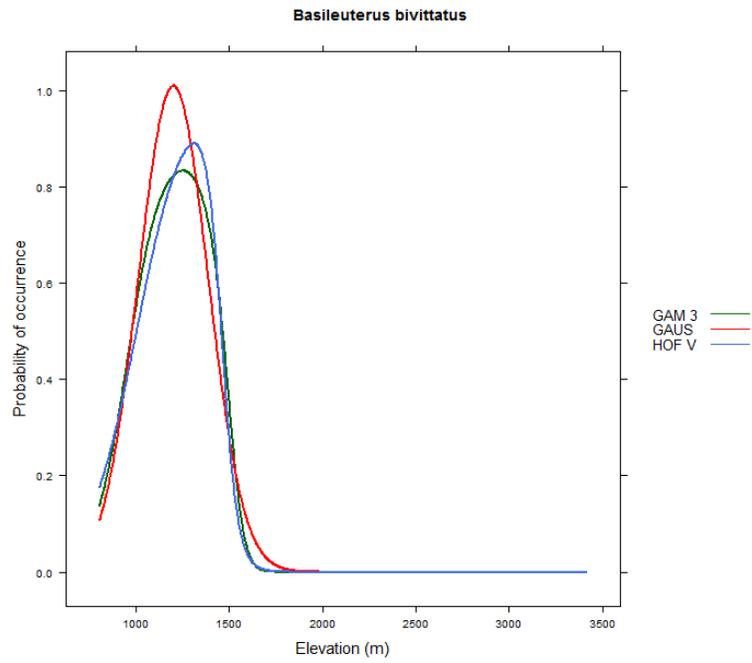


Figure C-153.

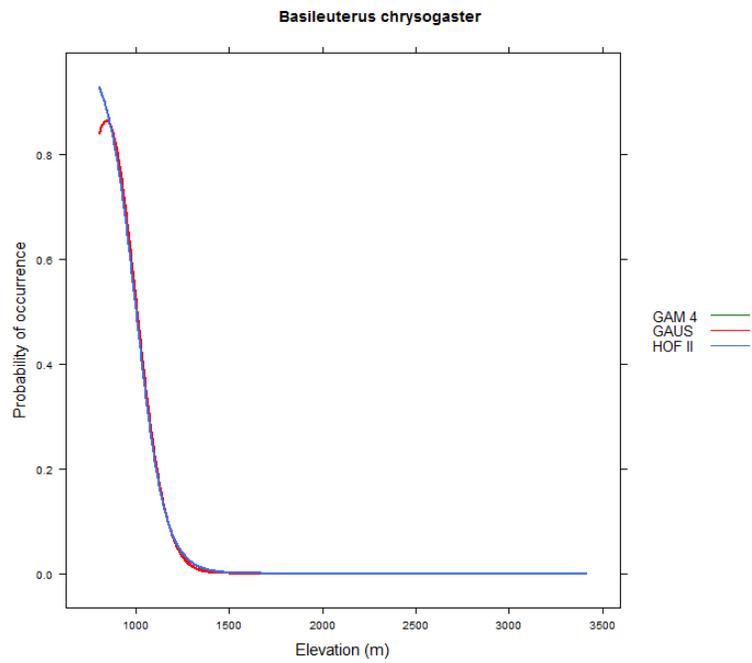


Figure C-154.

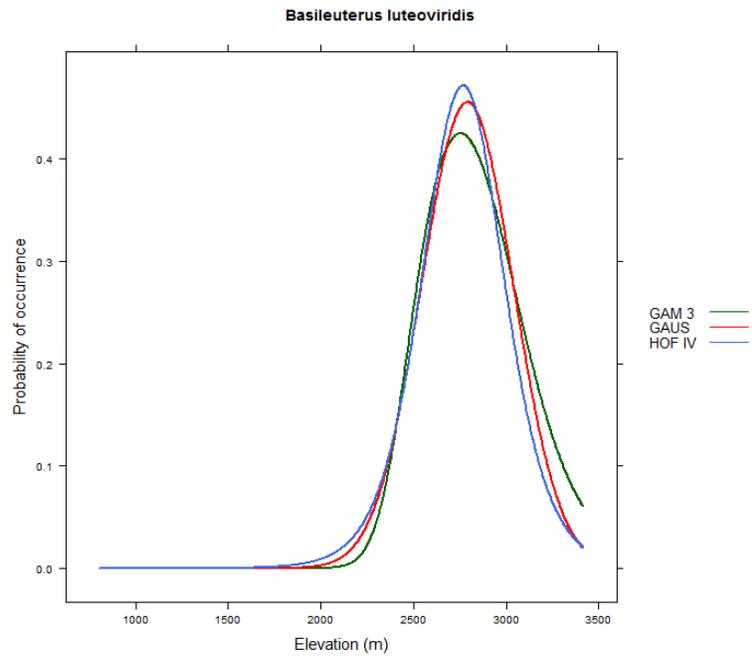


Figure C-155.

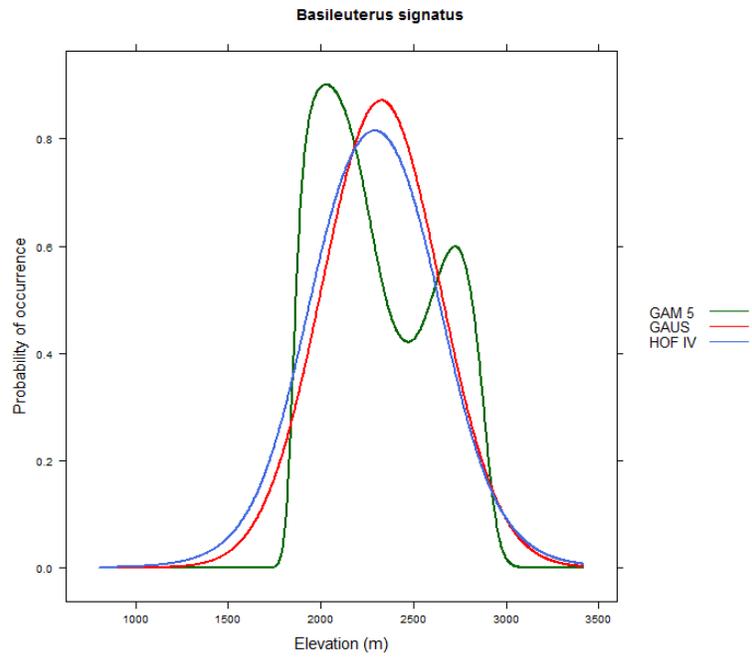


Figure C-156.

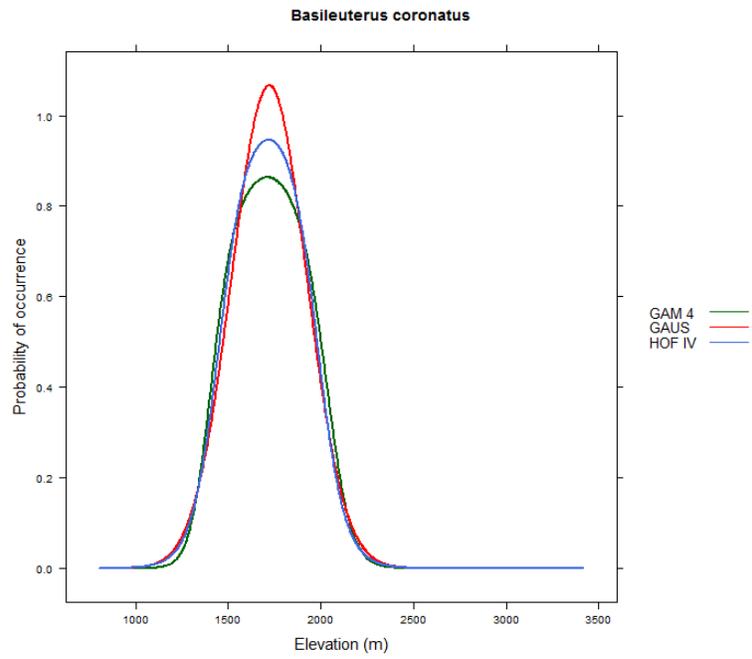


Figure C-157.

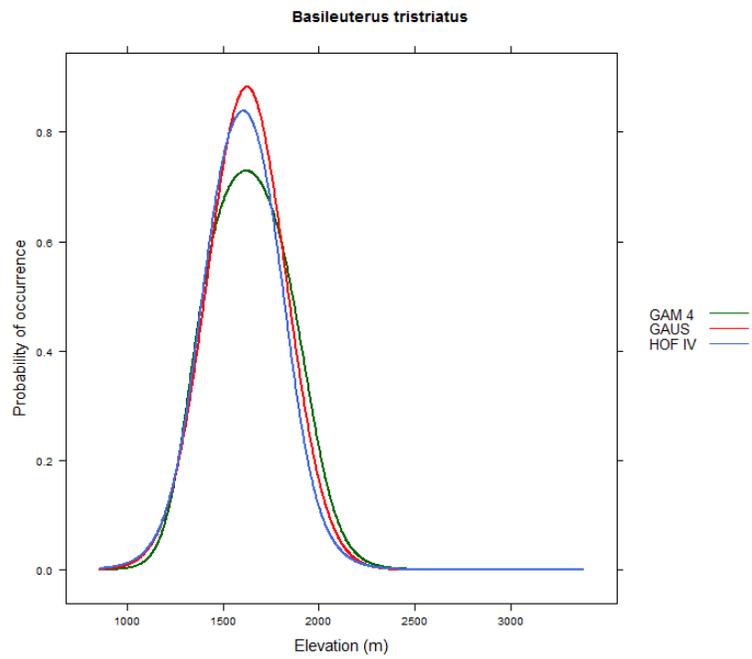


Figure C-158.

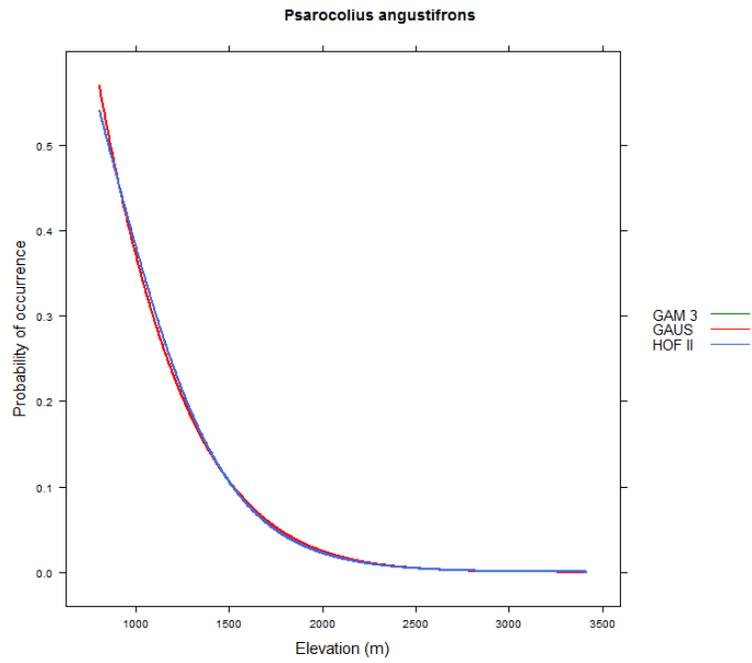


Figure C-159.

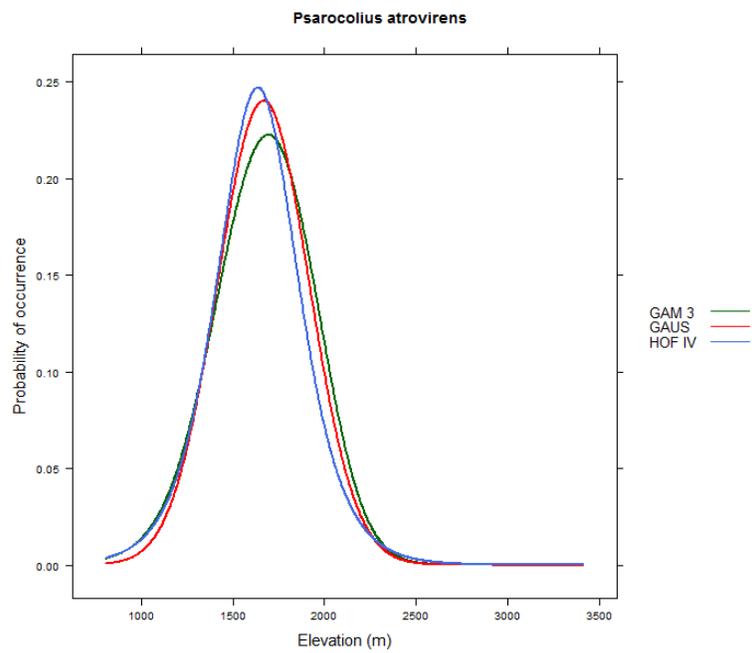


Figure C-160.

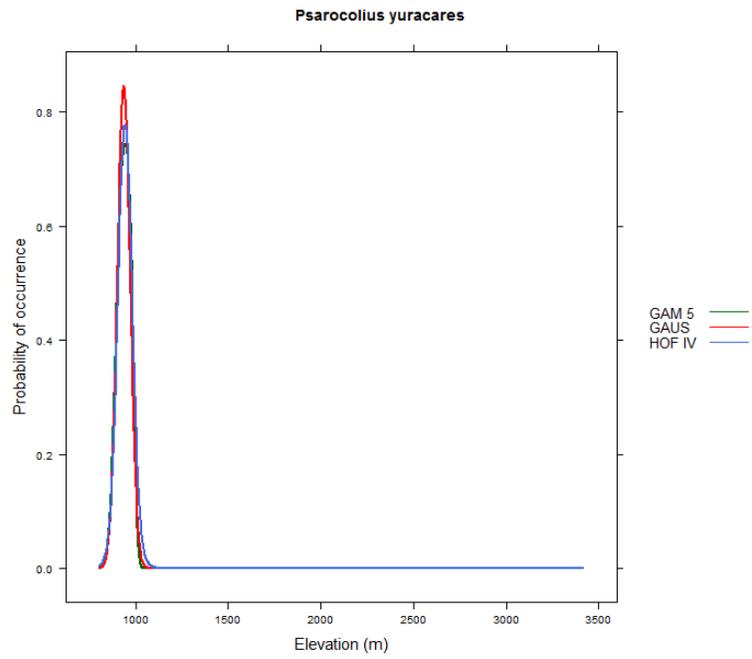


Figure C-161.

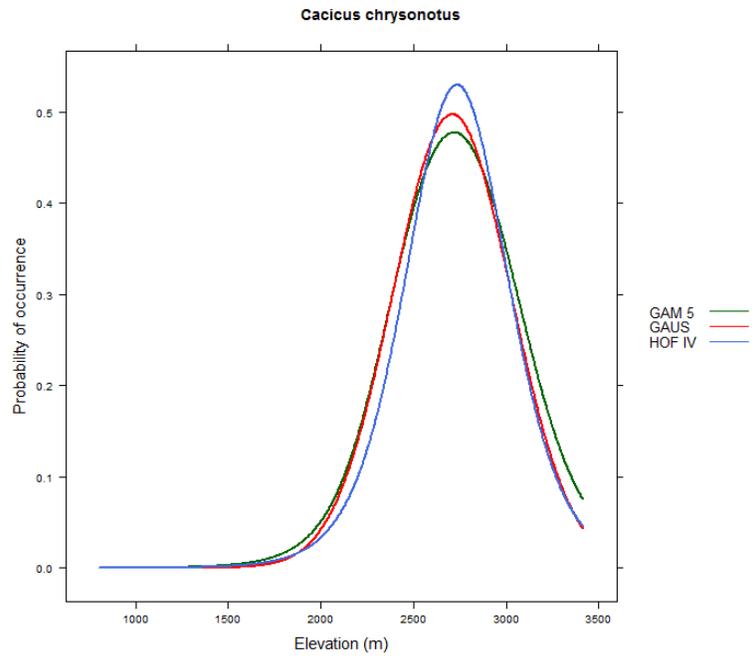


Figure C-162.

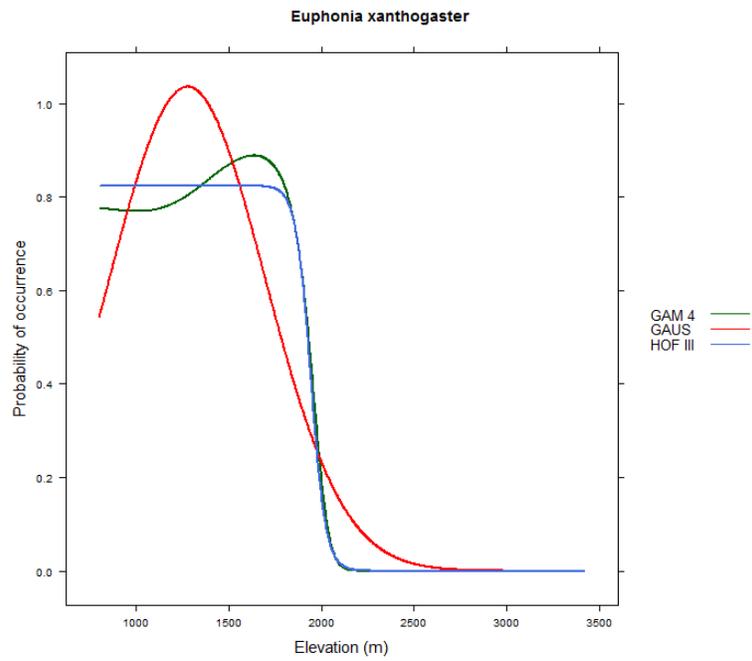


Figure C-163.

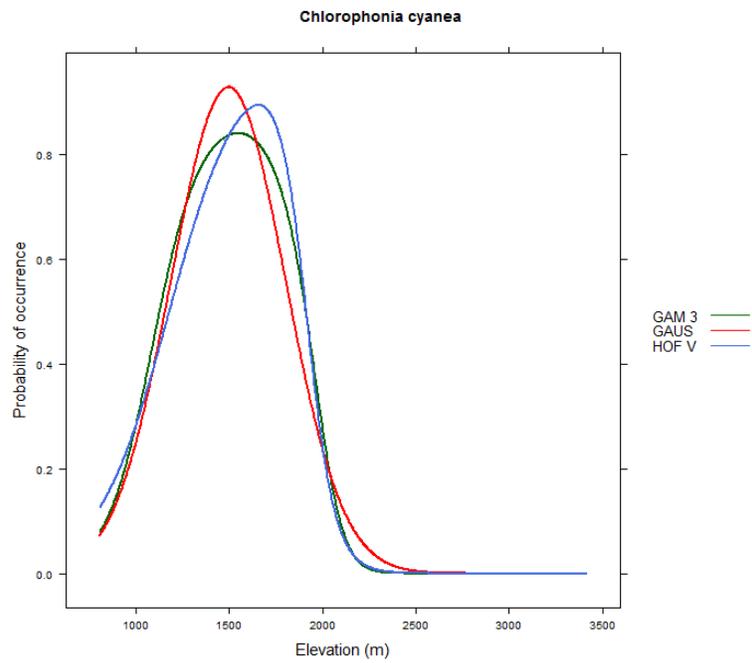


Figure C-164.

APPENDIX D  
RESPONSE CURVES OF CONGENERS ALONG THE MANU GRADIENT

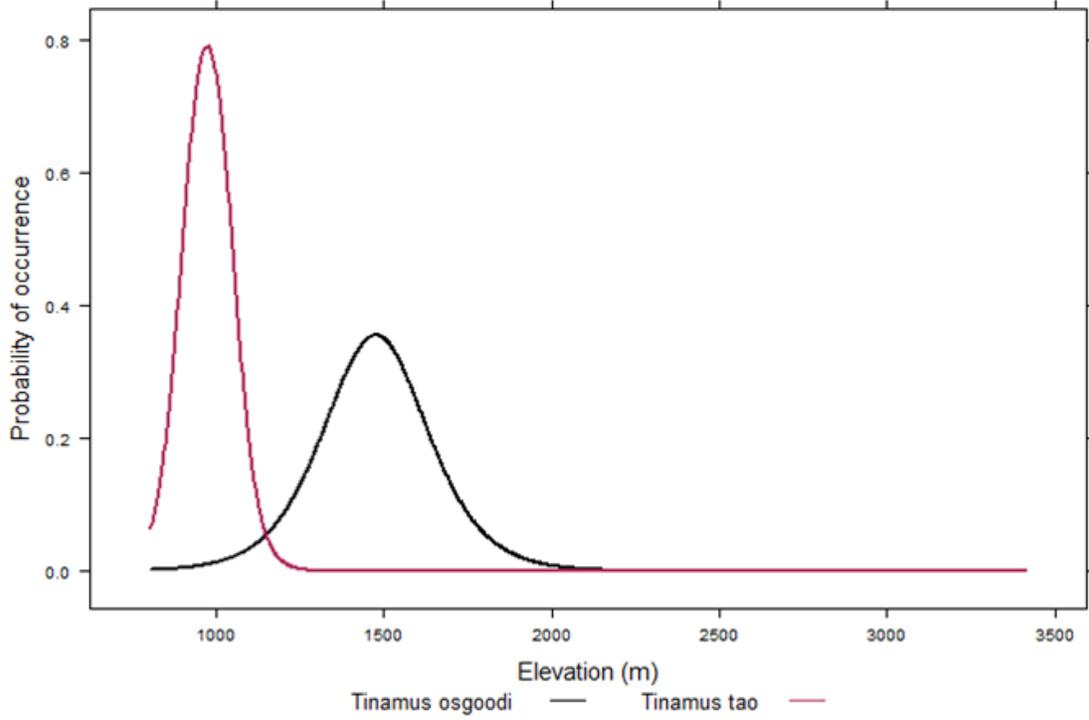


Figure D-1.

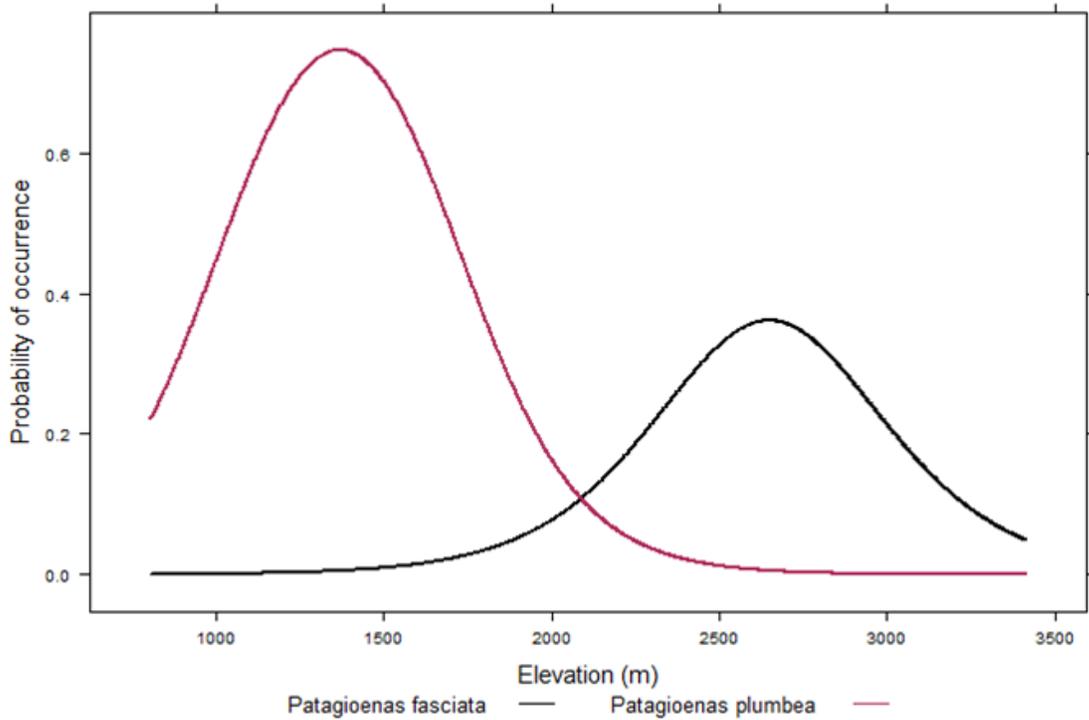


Figure D-2.

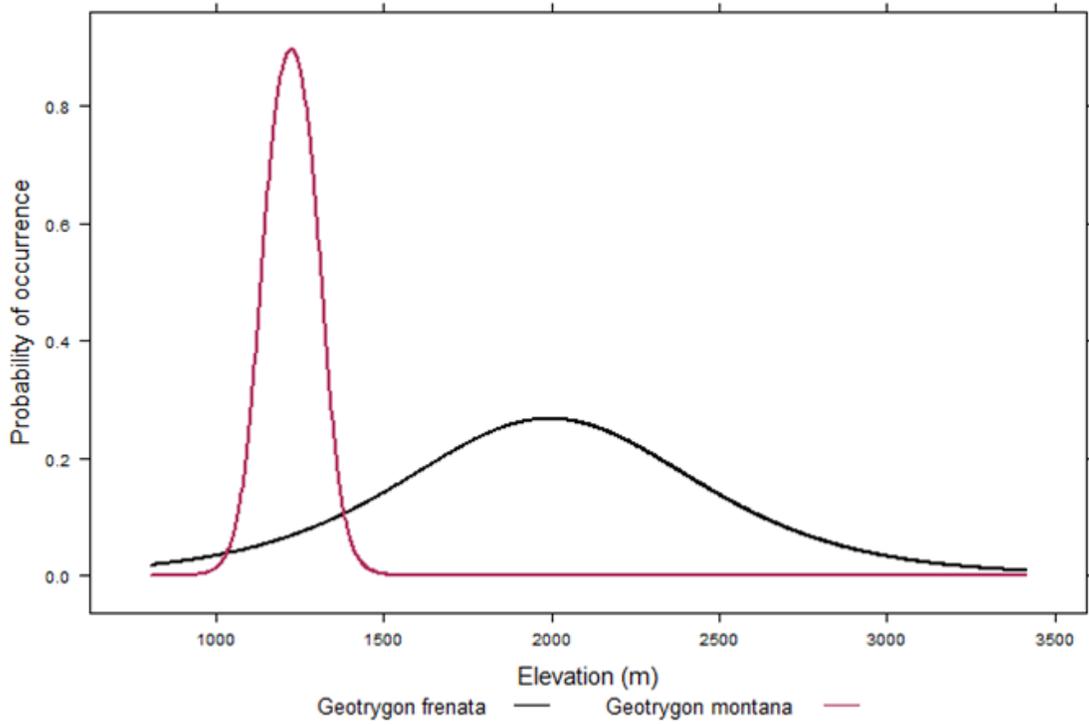


Figure D-3.

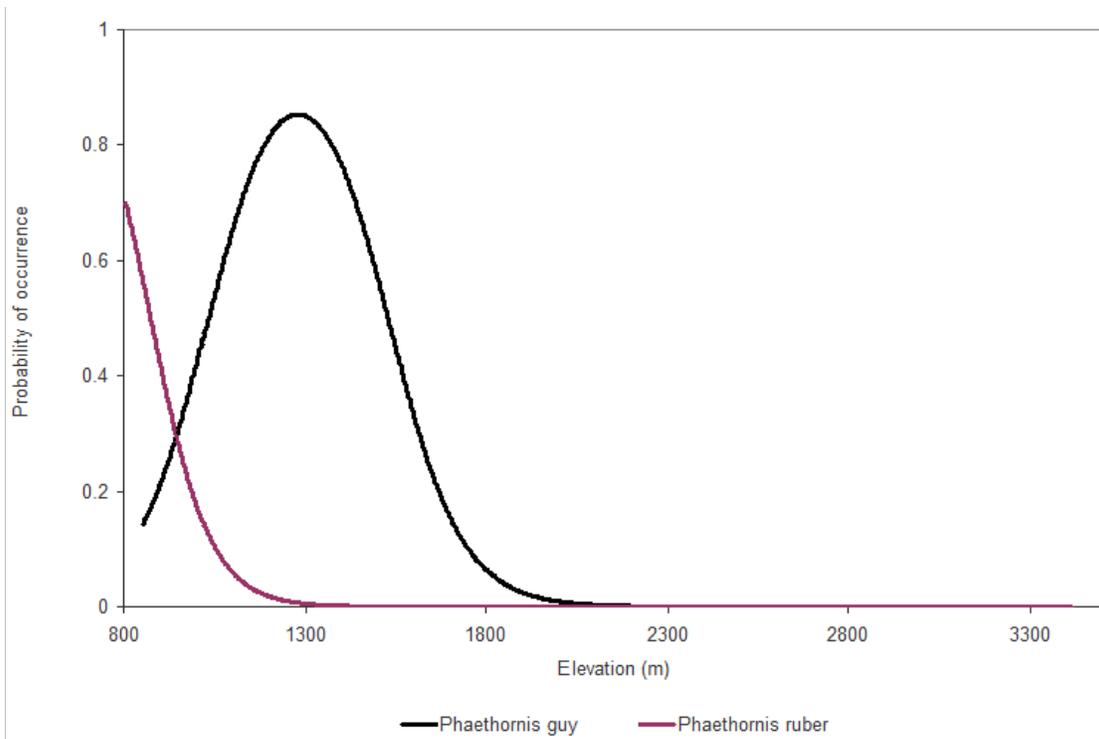


Figure D-4.

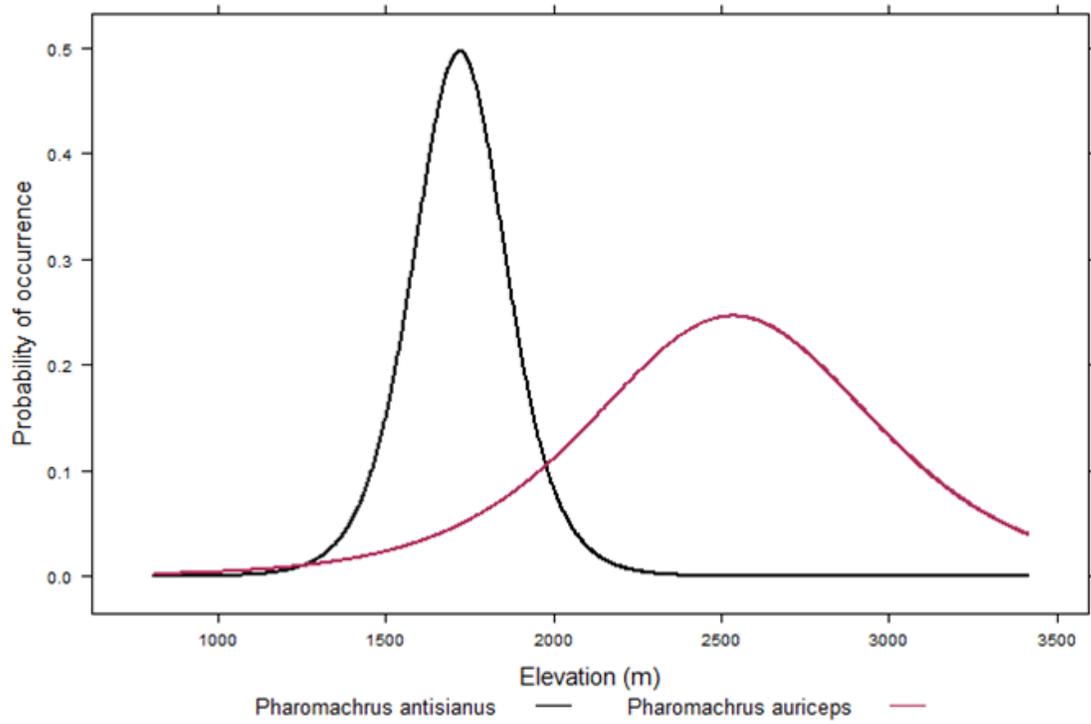


Figure D-5.

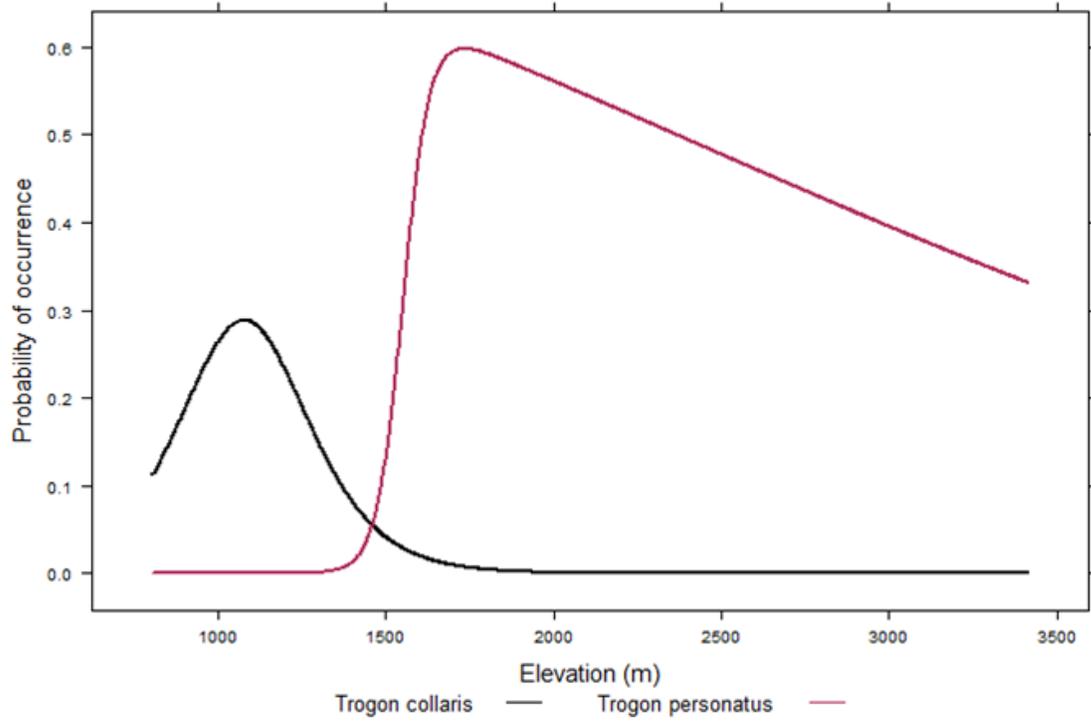


Figure D-6.

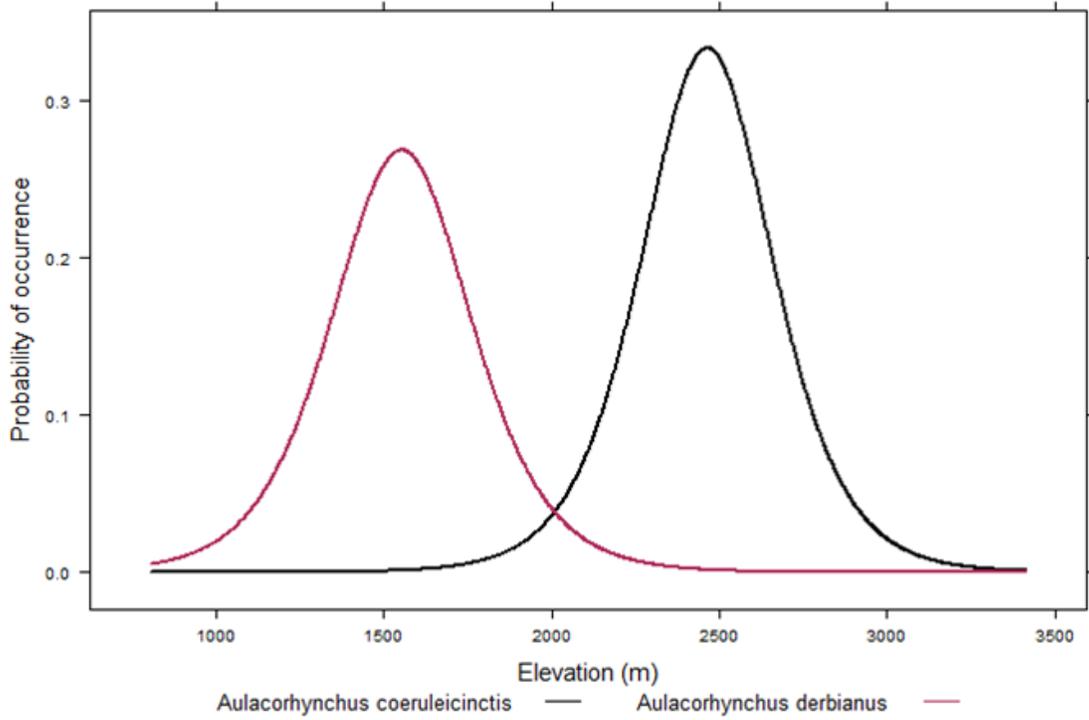


Figure D-7.

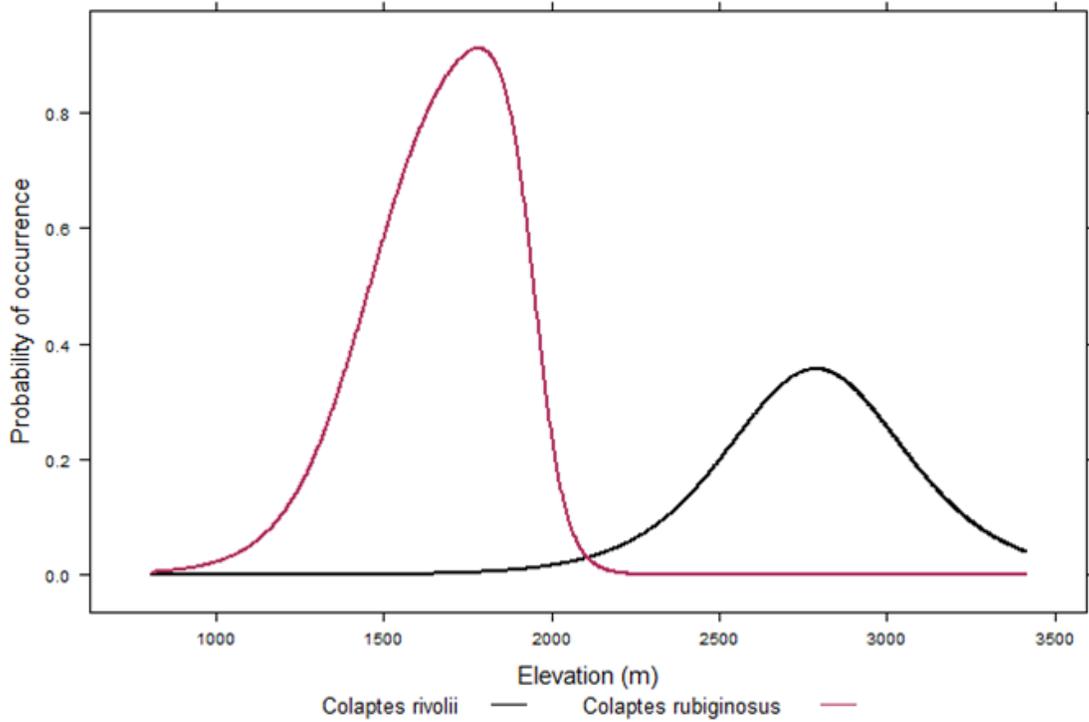


Figure D-8.

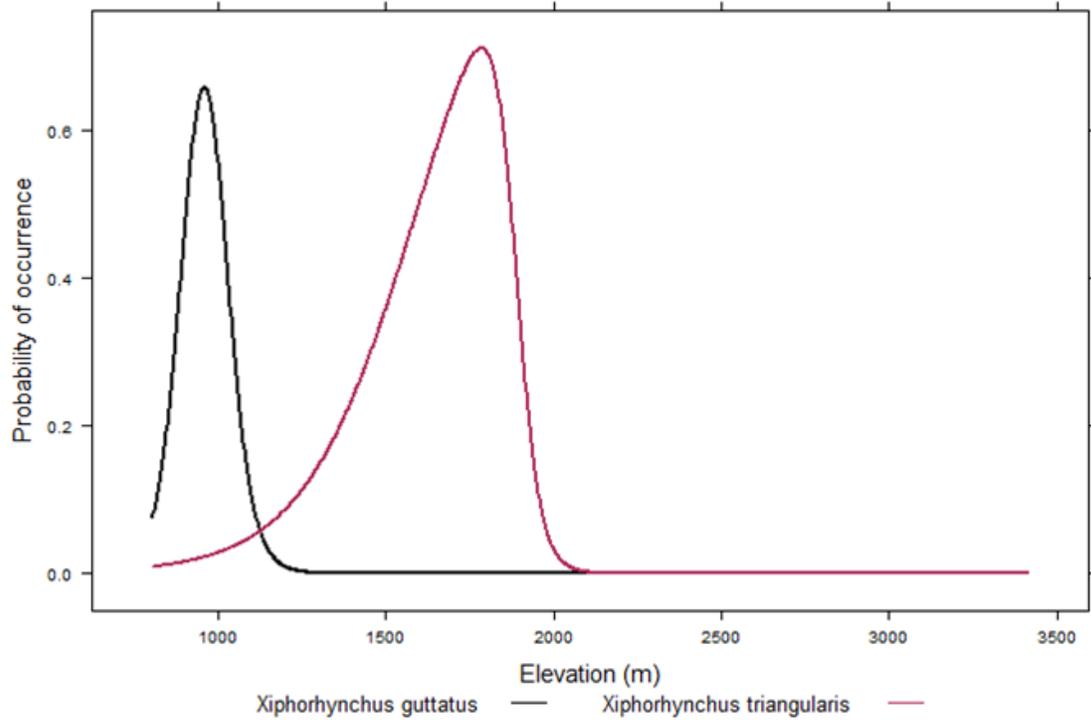


Figure D-9.

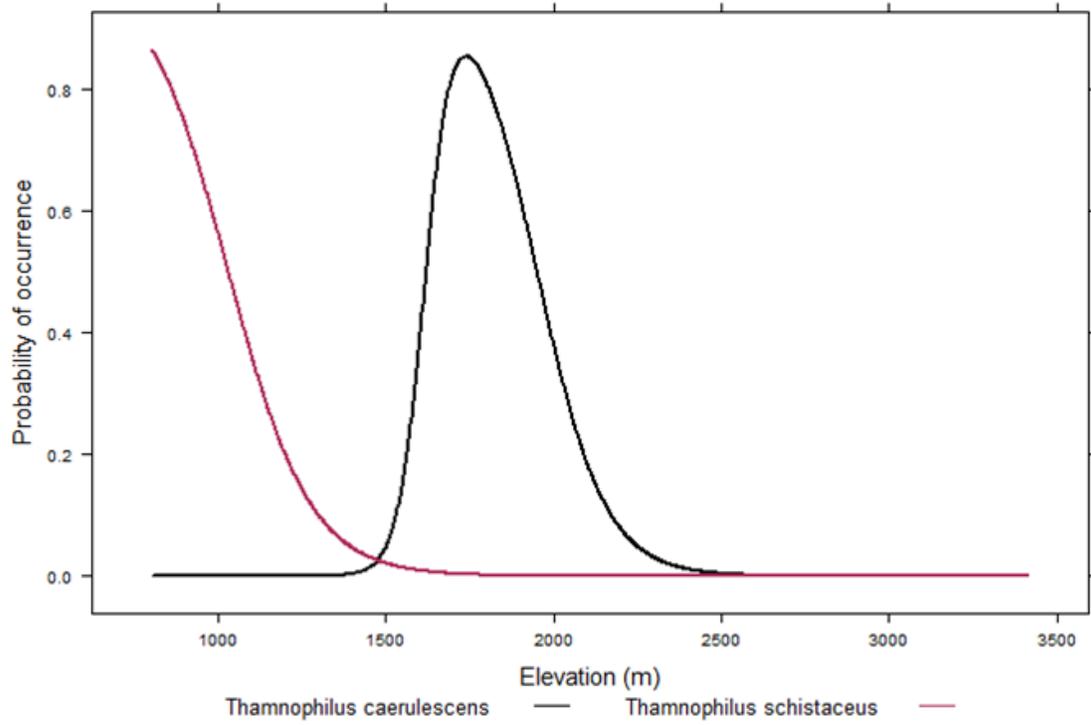


Figure D-10.

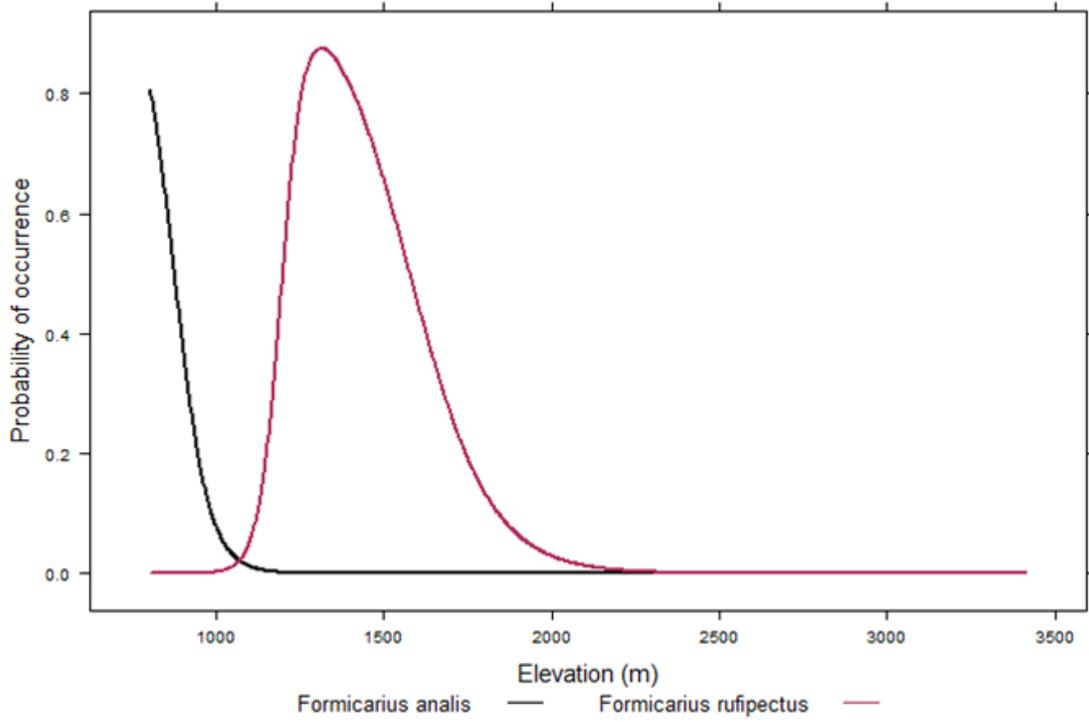


Figure D-11.

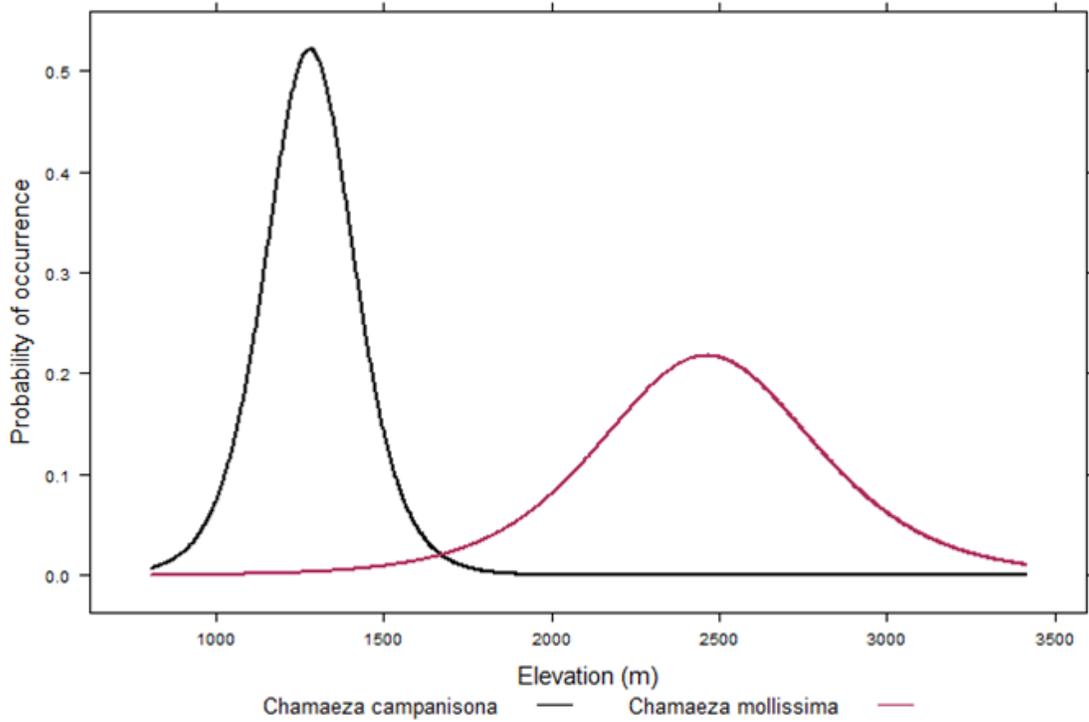


Figure D-12.

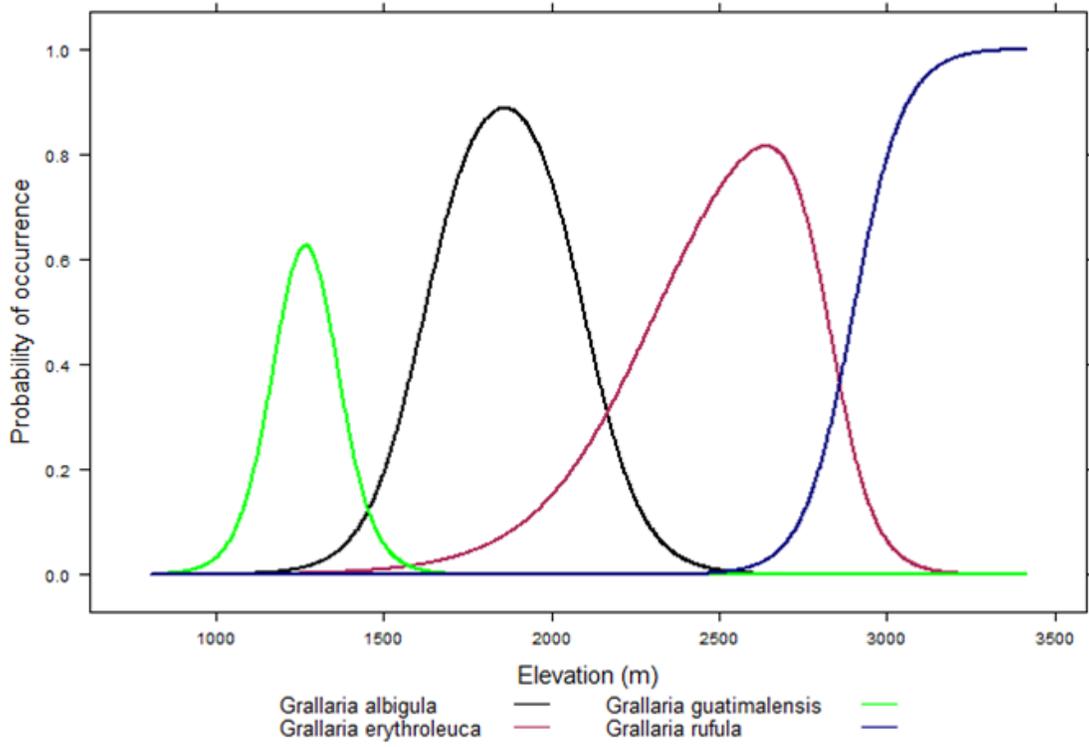


Figure D-13.

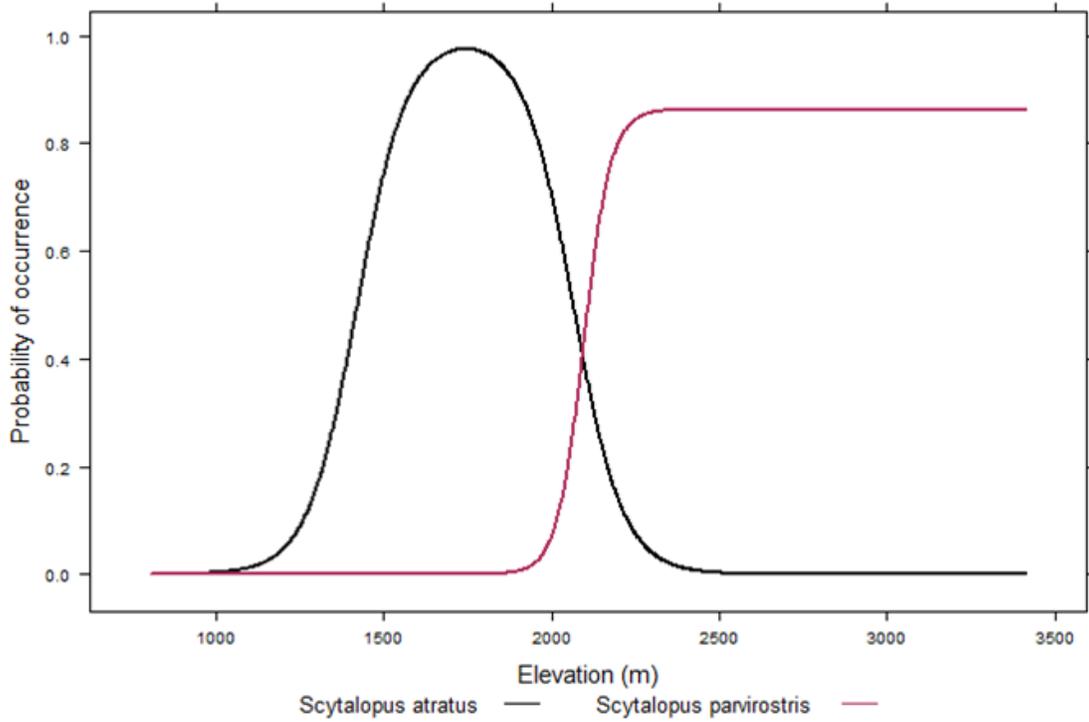


Figure D-14.

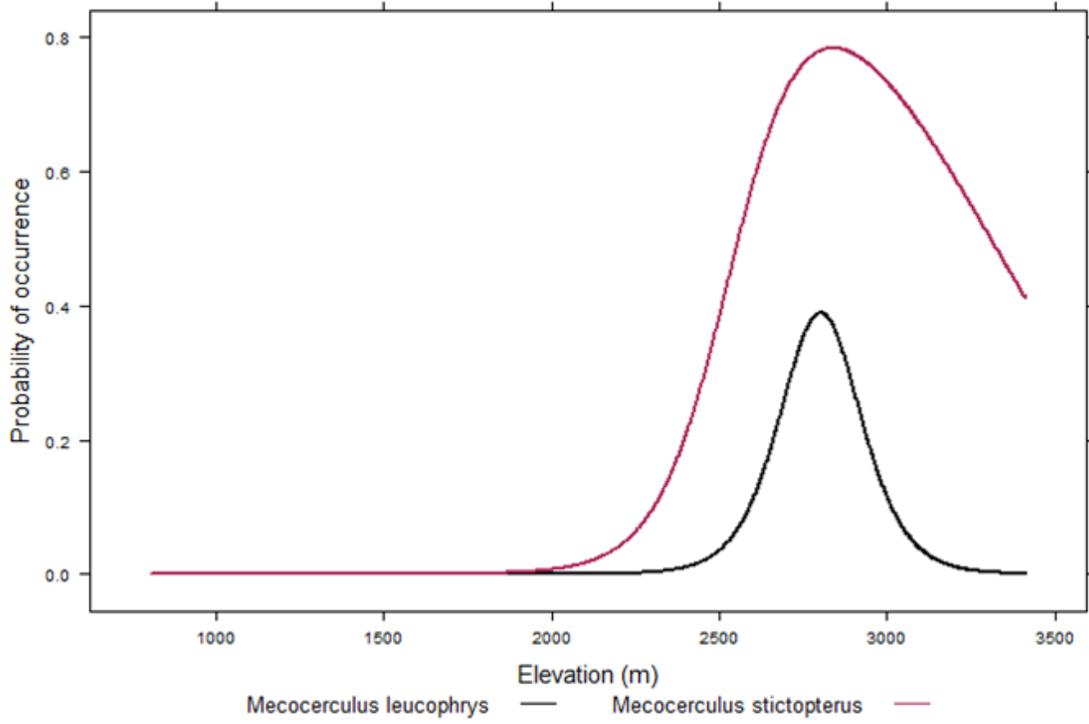


Figure D-15.

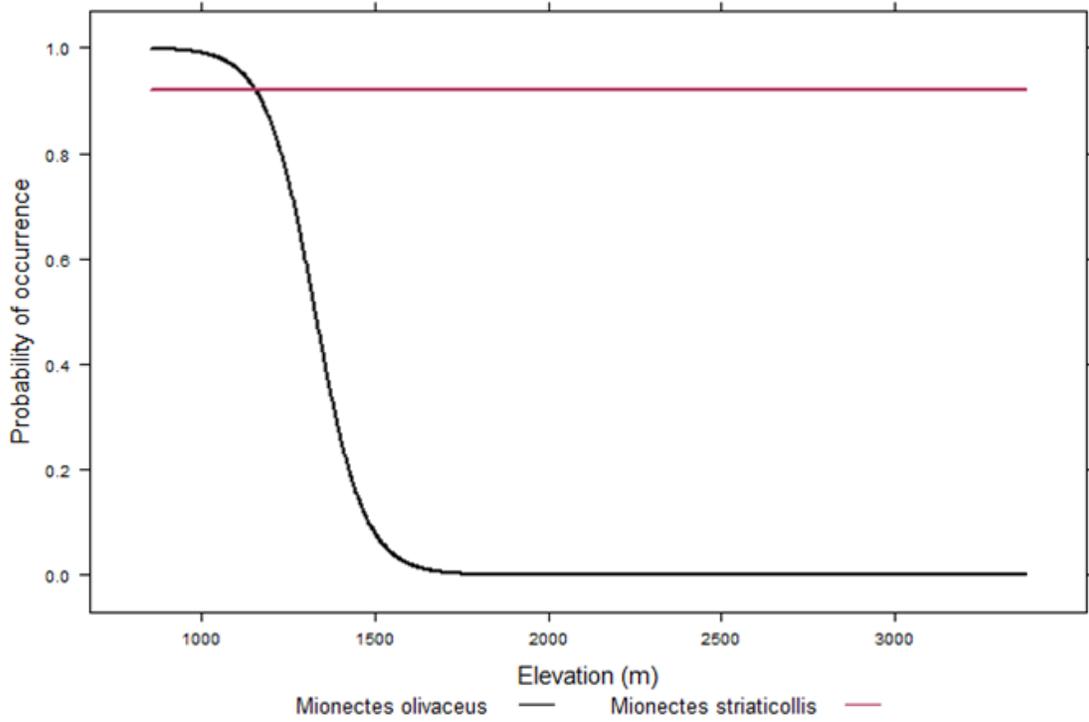


Figure D-16.

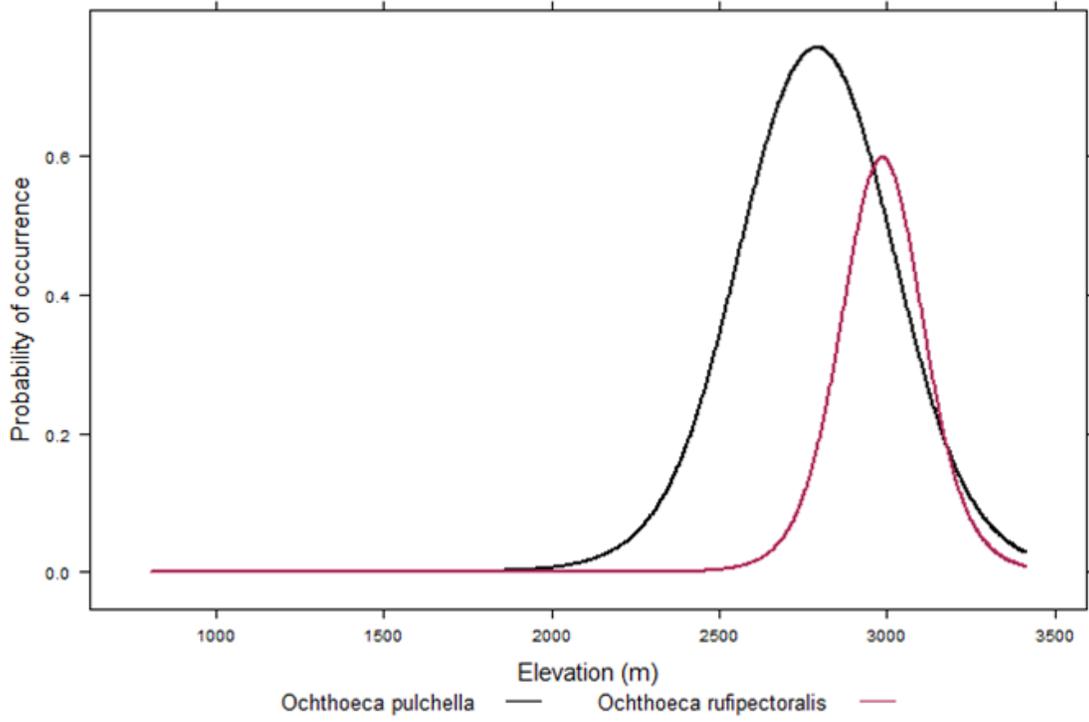


Figure D-17.

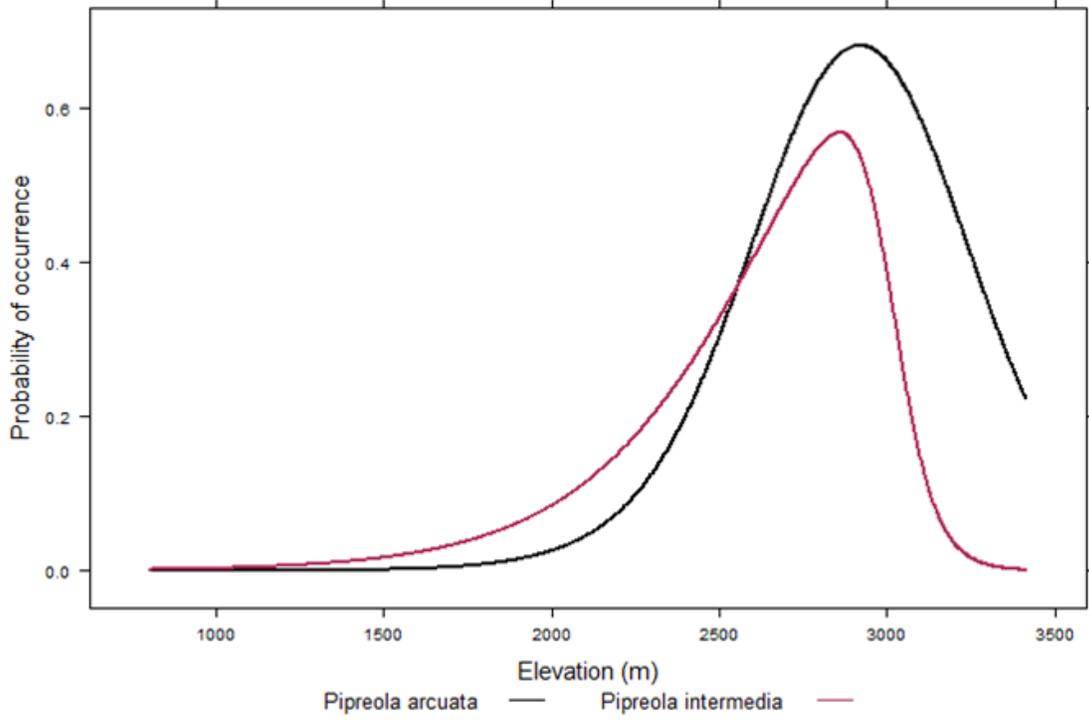


Figure D-18.

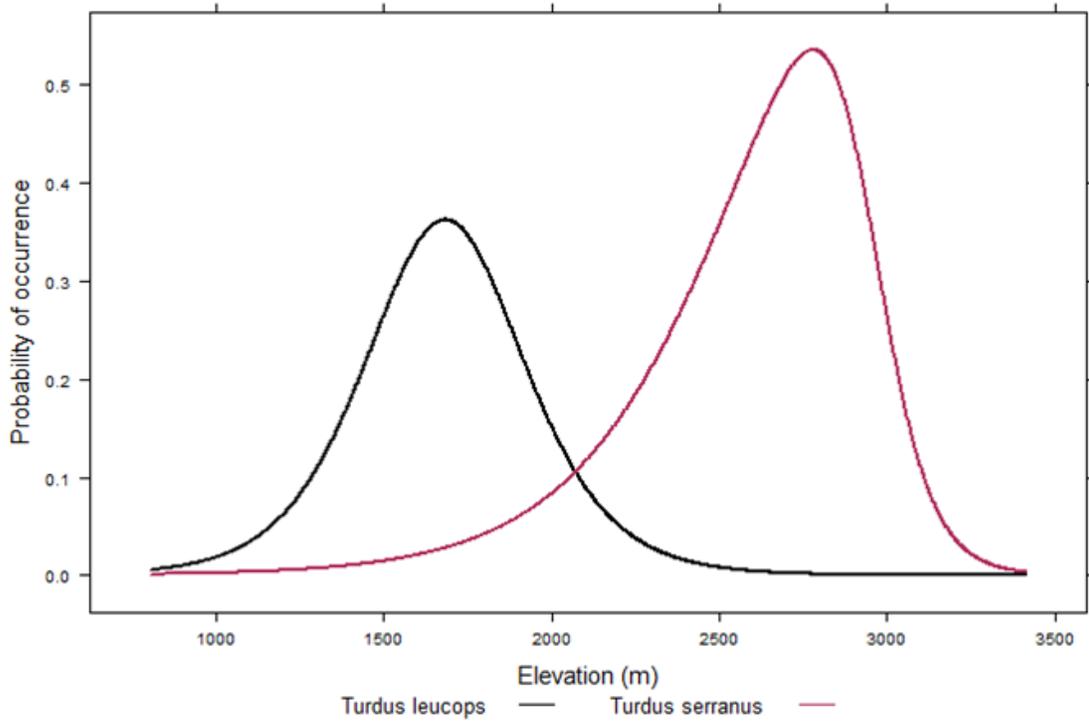


Figure D-19.

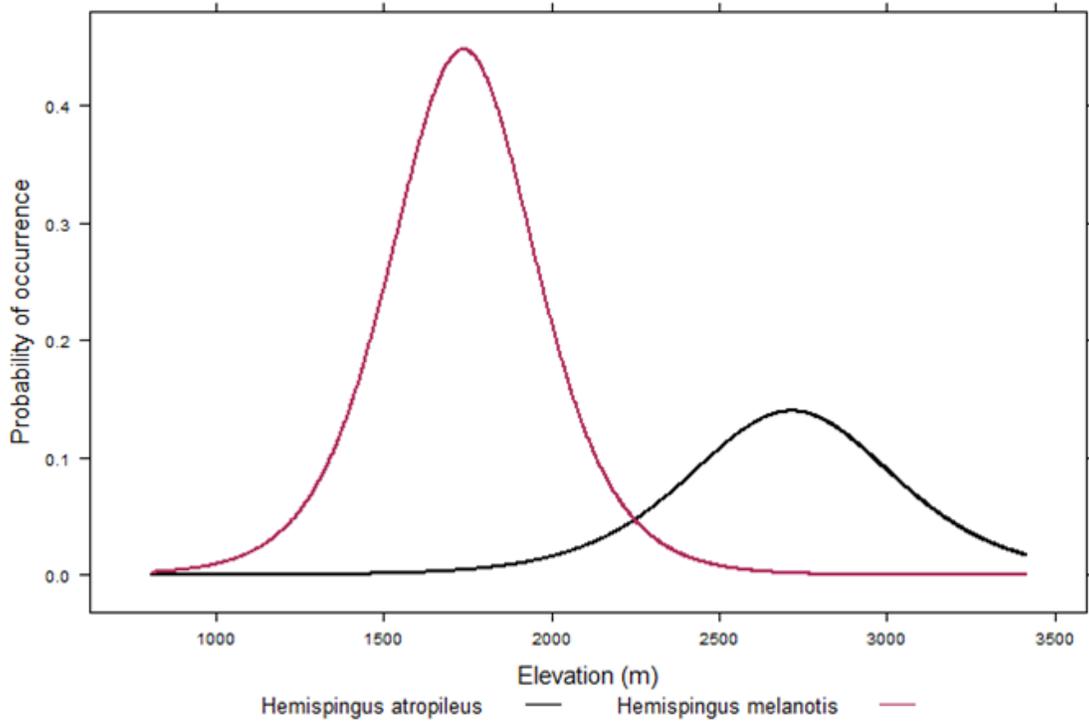


Figure D-20.

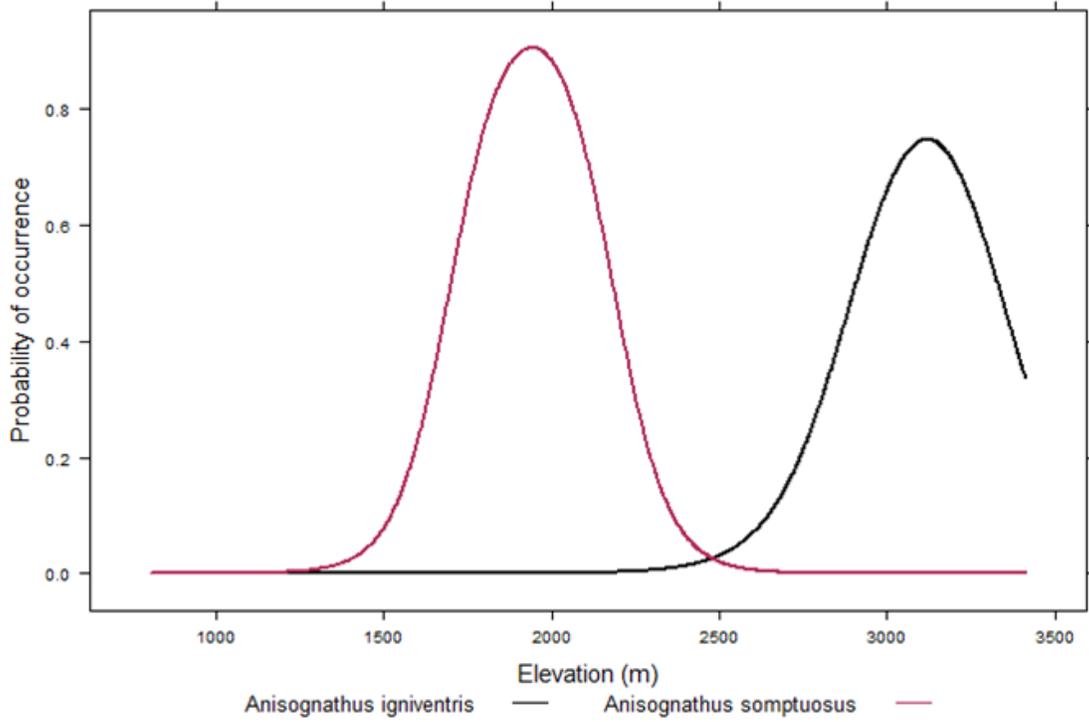


Figure D-21.

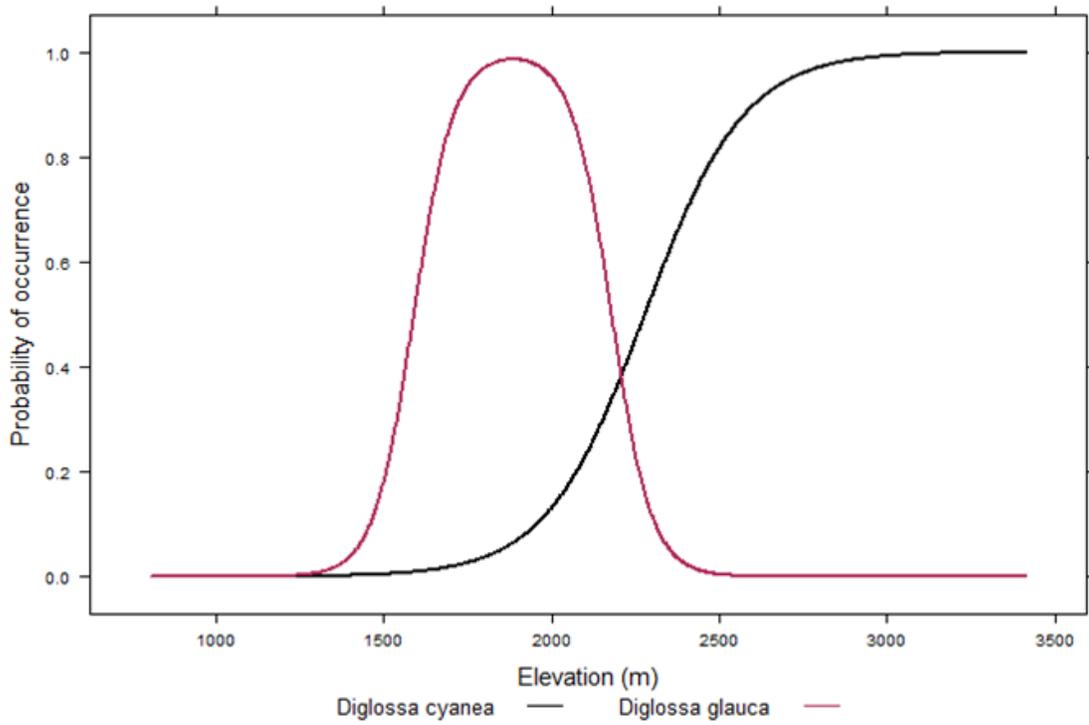


Figure D-22.

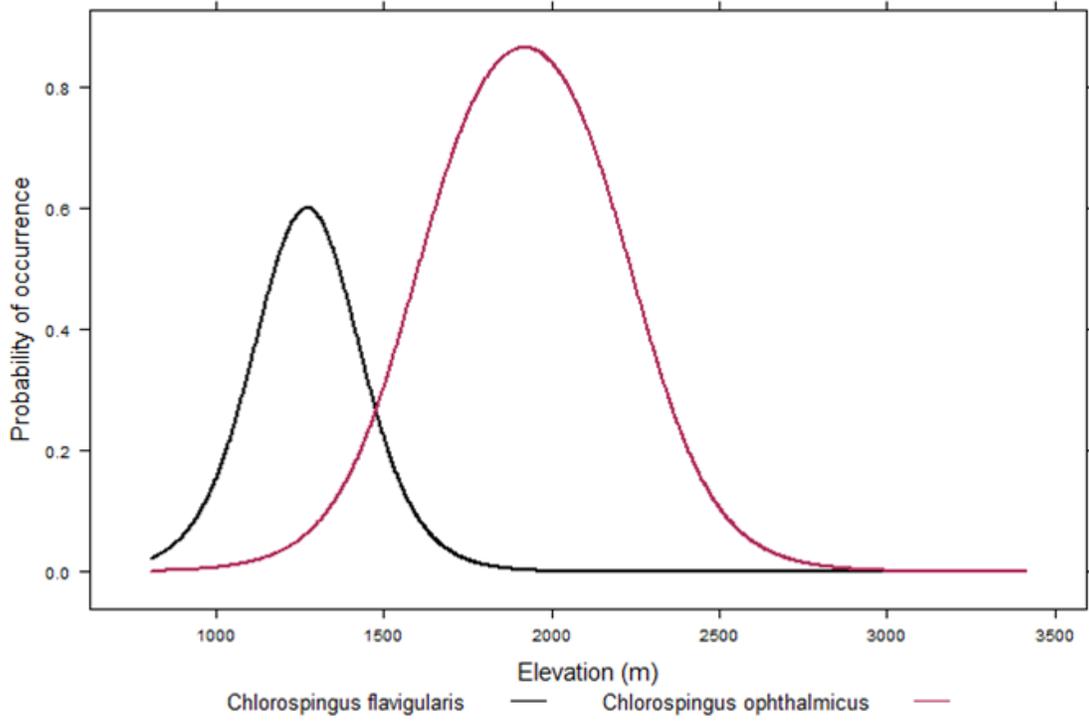


Figure D-23.

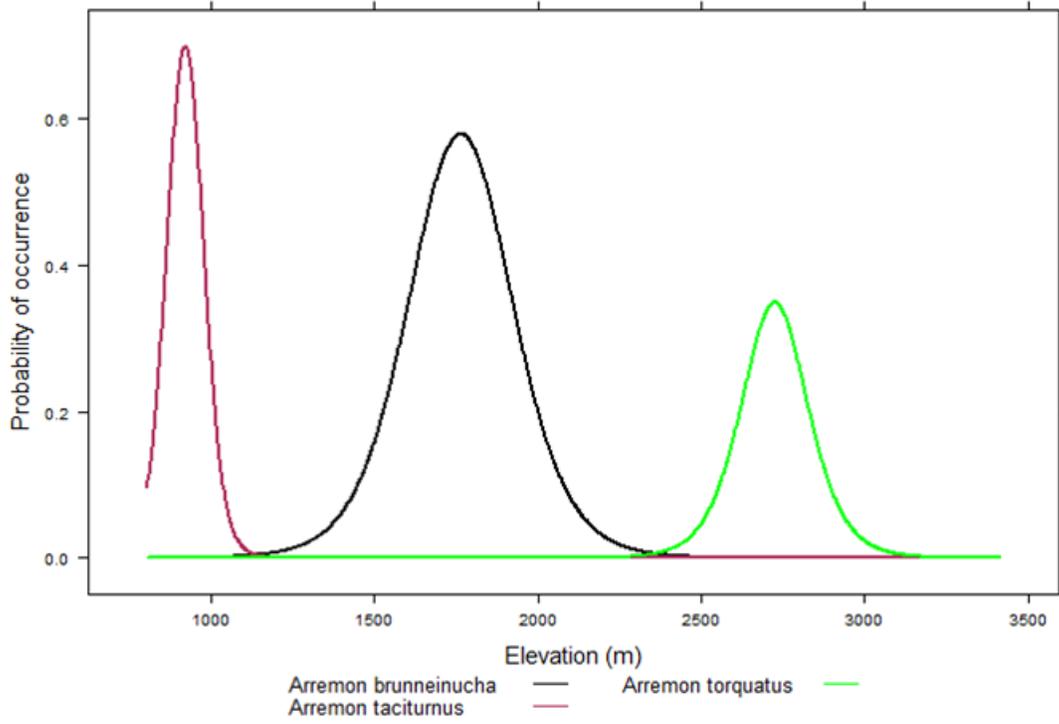


Figure D-24.

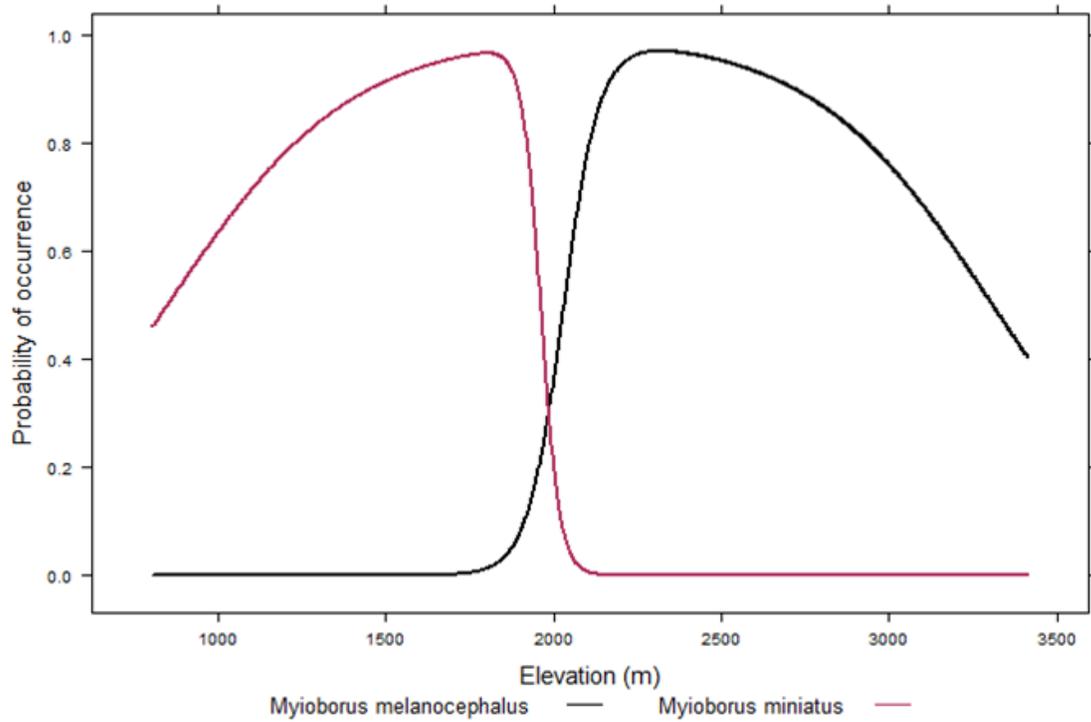


Figure D-25.

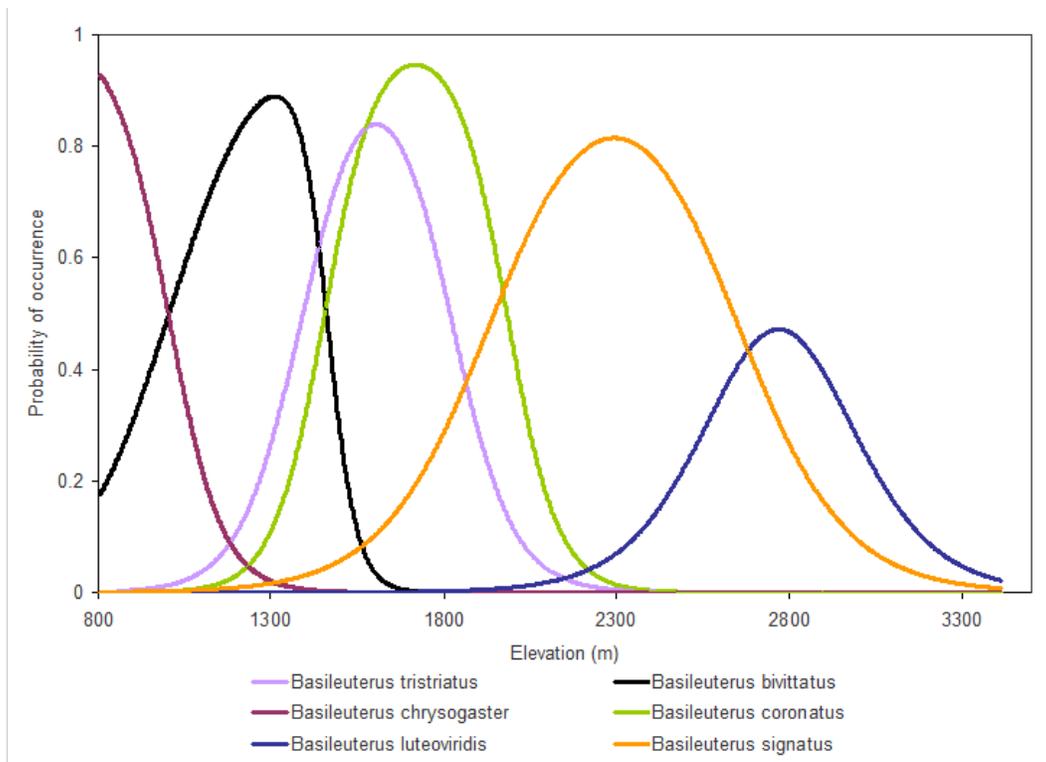


Figure D-26.

## APPENDIX E VARIATION PARTITIONING METHODS BASED ON MULTIPLE REGRESSION ON DISTANCE MATRICES

Variation partitioning of the multiple regression on distance matrices (MRM) analysis was used to determine the percentage of the variation in bird dissimilarity matrices that was explained uniquely by each of the predictor variables, and the variation that was co-explained by multiple predictors as a result of intercorrelation (e.g., Macía et al. 2007). This procedure examines variation explained in a response matrix by a series of models using all possible combinations of predictor variables. For cases with three predictors, the total variation can be partitioned into eight fractions:

- a) uniquely explained by vegetation structure
- b) uniquely explained by elevation
- c) uniquely explained by tree dissimilarity
- d) co-explained by vegetation structure and elevation
- e) co-explained by vegetation structure and tree dissimilarity
- f) co-explained by elevation and tree dissimilarity
- g) co-explained by vegetation structure, elevation, and tree dissimilarity
- h) unexplained variation

The following models were performed (shown below), representing all possible combinations of the three predictors. The variation explained by each model can be represented by the sum of a subset of lettered categories above. For example, variation explained by a model relating bird composition to elevation (Model II below) is the sum of the variation uniquely explained by elevation (b), co-explained by elevation

and vegetation structure (d), co-explained by elevation and trees (f), and co-explained by all three (g).

Model I included effects of vegetation structure on bird dissimilarity. This model included all vegetation structure variables initially, after which backwards elimination was used to remove variables that were not significant at the  $P < 0.05$  level. The significant structure variables retained in the model were thereafter used in more complex models with the other predictors of elevation and tree dissimilarity (see below). Variation explained by this model can be represented by  $R^2 = a+d+e+g$ .

Model II included effects of elevation on bird dissimilarity. Variation explained by this model can be represented by  $R^2 = b+d+f+g$ .

Model III included effects of tree dissimilarity on bird dissimilarity. Variation explained by this model can be represented by  $R^2 = c+e+f+g$ .

Model IV (vegetation structure and elevation) included variables retained in models I and II, giving  $R^2 = a+b+d+e+f+g$ .

Model V (vegetation structure and trees) included variables retained in models I and III, giving  $R^2 = a+c+d+e+f+g$ .

Model VI (elevation and trees) included variables retained in models II and III, giving  $R^2 = b+c+d+e+f+g$ .

Model VII (vegetation structure, elevation and trees) included all variables retained in models I - III, giving  $R^2 = a+b+c+d+e+f+g$ .

By subtracting the  $R^2$  values of one model from another, the percentage of variation attributed to each lettered category can be calculated:

- a) unique contribution by vegetation structure: Model VII – Model VI
- b) unique contribution by elevation: Model VII – Model V
- c) unique contribution by tree dissimilarity: Model VII – Model IV
- d) co-contribution by vegetation structure and elevation: Model V – Model III – (a)
- e) co-contribution by vegetation structure and tree dissimilarity:  
Model IV – Model II – (a)
- f) co-contribution by elevation and tree dissimilarity: Model IV – Model I – (b)
- g) co-contribution by vegetation structure, elevation, and tree dissimilarity:  
Model VII – (a + b + c + d + e + f)
- h) unexplained variation:  $100 - (a + b + c + d + e + f + g)$

Letter categories should sum to 100%. See Macía et al. (2007) for a similarly structured analysis of variation partitioning based on multiple regression on distance matrices.

## LIST OF REFERENCES

- Aiba, S., and K. Kitayama. 1999. Structure, composition and species diversity in an altitude-substrate matrix of rain forest tree communities on Mount Kinabalu, Borneo. *Plant Ecology* 140:139-157.
- Alexander, R. M. 1999. *Energy for animal life*. Oxford University, Cambridge University Press, USA.
- Altshuler, D. L., F. G. Stiles, and R. Dudley. 2004. Of hummingbirds and helicopters: Hovering costs, competitive ability, and foraging strategies *American Naturalist* 163:16-25.
- Altshuler, D. L., and R. Dudley. 2006. The physiology and biomechanics of avian flight at high altitude. *Integrative and Comparative Biology* 46:62-71.
- Anderson, R. P., A. T. Peterson, and M. Gómez-Laverde. 2002. Using niche-based GIS modeling to test geographic predictions of competitive exclusion and competitive release in South American pocket mice. *Oikos* 98:3-16.
- Angilleta, M. 2009. *Thermal Adaptation: A theoretical and empirical synthesis*. Univeristy of Chicago Press.
- Araújo, M. B., and M. Luoto. 2007. The importance of biotic interactions for modelling species distributions under climate change. *Global Ecology and Biogeography* 16:743-753.
- Austin, M. P., and T. M. Smith. 1989. A new model for the continuum concept. *Vegetatio* 83:34-47.
- Austin, M. P., and M. J. Gaywood. 1994. Current problems of environmental gradients and species response curves to continuum theory. *Journal of Vegetation Science* 5:473-482.
- Austin, M. P. 2005. Vegetation and environment: Discontinuities and continuities. Pages 52–84 *in* E. van der Maarel, editor. *Vegetation Ecology*. Blackwell Science Ltd., Oxford, UK.
- Austin, M. 2007. Species distribution models and ecological theory: A critical assessment and some possible new approaches. *Ecological Modelling* 200:1-19.
- Baselga, A. 2010. Partitioning the turnover and nestedness components of beta diversity. *Global Ecology and Biogeography* 19:134-143.
- Bay, L. K., G. P. Jones, and M. I. McCormick 2001. Habitat selection and aggression as determinants of spatial segregation among damselfish on a coral reef. *Coral Reefs* 20:289-298.

- Bergen, K. M., A. M. Gilboy, and D. G. Brown. 2007. Multi-dimensional vegetation structure in modeling avian habitat. *Ecological Informatics* 2:9-22.
- Bersier, L-F., and D. R. Meyer. 1994. Bird assemblages in mosaic forests: the relative importance of vegetation structure and floristic composition along the successional gradient. *Acta Oecologica* 15:561-576.
- BirdLife International. 2000. Threatened birds of the world. Lynx Editions and BirdLife International, Barcelona and Cambridge, UK.
- Block, W. M., and L. A. Brennan. 1993. The habitat concept in ornithology: theory and application. *Current Ornithology* 11:35-91.
- Bohlman, S. A., W. F. Laurance, S. G. Laurance, H. E. M. Nascimento, P. M. Fearnside, and A. Andrade. 2008. Importance of soils, topography and geographic distance in structuring central Amazonian tree communities. *Journal of Vegetation Science* 19:863-874.
- Boyle, A. W. 2008. Can variation in risk of nest predation explain altitudinal migration in tropical birds? *Oecologia* 155:397-403.
- Brehm, G., L. M. Pitkin, N. Hilt, and K. Fiedler. 2005. Montane Andean rain forests aer a global hotspot of geometrid moths. *Journal of Biogeography* 32:1621-1627.
- Brown, J. H. 1971. Mechanisms of competitive exclusion between two species of chipmunks. *Ecology* 52:305-311.
- Brown, J. H. 1984. On the relationship between abundance and distributions of species. *American Naturalist* 124:255-279.
- Brown, J. H., G. C. Stevens, and D. M. Kaufman. 1996. The geographic range: Size, shape, boundaries and internal structure. *Annual Reviews in Ecology and Systematics* 27:597-623.
- Buckley, L. B., and W. Jetz. 2008. Linking global turnover of species and environments. *Proceedings of the National Academy of Sciences* 105:17836-17841.
- Buermann, W., S. Saatchi, T. B. Smith, B. R. Zutta, J. A. Chaves, B. Milá, and C. H. Graham. 2008. Predicting species distributions across the Amazon and Andean regions using remote sensing data. *Journal of Biogeography* 35:1160-1176.
- Bull, C. M. 1991. Ecology of parapatric distributions. *Annual Review of Ecology and Systematics* 22:19-36.

- Burns, K. C. 2004. Scale and macroecological patterns in seed dispersal mutualisms. *Global Ecology and Biogeography* 13:289-293.
- Bush, M. B., M. R. Silman, and D. H. Urrego. 2004. 48,000 Years of Climate and Forest Change in a Biodiversity Hot Spot. *Science* 303:827-829.
- Buskirk, W. H., G. V. N. Powell, J. F. Wittenberger, R. E. Buskirk, and T. U. Powell. 1972. Interspecific bird flocks in tropical highland Panama. *Auk* 89:612-624.
- Carey, C., S. D. Garber, E. L. Thompson, and F. C. James. 1983. Avian reproduction over an altitudinal gradient. II. Physical characteristics and water loss of eggs. *Physiological Zoology* 56:340-352.
- Carey, C., F. Leon-Velarde, O. Dunin-Borkowski, and C. Monge-C. 1989. Shell conductance, daily water loss, and water content of Puna Teal eggs. *Physiological Zoology* 62:83-95.
- Case, T. J., and M. L. Taper. 2000. Interspecific competition, environmental gradients, gene flow, and the coevolution of species' borders. *American Naturalist* 155:583-605.
- Case, T. J., R. D. Holt, M. A. McPeck, and T. H. Keitt. 2005. The community context of species' borders: ecological and evolutionary perspectives. *Oikos* 108:28-46.
- Chambers, J. Q., G. P. Asner, D. C. Morton, L. O. Anderson, S. S. Saatchi, F. D. B. Espirito-Santo, M. Palace, and C. Souza, Jr. 2007. Regional ecosystem structure and function: ecological insights from remote sensing of tropical forests. *Trends in Ecology and Evolution* 22:414-423.
- Chase, J. M., and M. A. Leibold. 2003. *Ecological Niches: Linking Classical and Contemporary Approaches*. University of Chicago Press, Chicago, Illinois, USA.
- Clark, J. S. 1998. Why trees migrate so fast: Confronting theory with dispersal biology and the paleorecord. *American Naturalist* 152:204-224.
- Clark, D. B., M. W. Palmer, and D. A. Clark. 1999. Edaphic factors and the landscape-scale distributions of tropical rain forest trees. *Ecology* 80:2662-2675.
- Cody, M. L. 1985. *Habitat selection in birds*. Academic Press, New York, New York, USA.
- Collias, N. E., and E. C. Collias. 1984. *Nest Building and Bird Behavior*. Princeton University Press, Princeton, New Jersey, USA.
- Colwell, R. K., and D. C. Lees. 2000. The mid-domain effect: geometric constraints on the geography of species richness. *Trends in Ecology and Evolution* 15:70-76.

- Colwell, R. K., C. Rahbek, and N. J. Gotelli. 2004. The mid-domain effect and species richness patterns: What have we learned so far? *American Naturalist* 163:E1-E23.
- Colwell, R. K., G. Brehm, C. L. Cardelús, A. C. Gilman, and J. T. Longino. 2008. Global warming, elevational range shifts, and lowland biotic attrition in the wet tropics. *Science* 322: 258-261.
- Conway, C. J., and T. E. Martin. 2000. Effects of ambient temperature on avian incubation behavior. *Behavioral Ecology* 11:178-188.
- Cornell, H. 1974. Parasitism and distributional gaps between allopatric species. *American Naturalist* 108:880-883.
- Cornell Lab of Ornithology, Bioacoustics Research Program. 2003. Raven Pro 1.3. Cornell University, Ithaca, New York.
- Costa, G. C., C. Wolfe, D. B. Shepard, J. P. Caldwell, and L. J. Vitt. 2008. Detecting the influence of climatic variables on species distributions: a test using GIS niche-based models along a steep longitudinal environmental gradient. *Journal of Biogeography* 35:637-646.
- Coudun, C., and J. Gégout. 2006. The derivation of species response curves with Gaussian logistic regression is sensitive to sampling intensity and curve characteristics. *Ecological Modelling* 199:164-175.
- Cramer, W., A. Bondeau, S. Schaphoff, W. Lucht, B. Smith, and S. Sitch. 2004. Tropical forests and the global carbon cycle: Impacts of atmospheric carbon dioxide, climate change and rate of deforestation. *Philosophical Transactions of the Royal Society of London: Series B* 359:331-343.
- Cresswell, W., S. Holt, J. M. Reid, D. P. Withfield, R. J. Mellanby, D. Norton, and S. Waldron. 2004. The energetic costs of egg heating constraint incubation attendance but do not determine daily energy expenditure in the pectoral sandpiper. *Behavioral Ecology* 15:498-507.
- Cunningham, H. R., L. J. Rissler, and J. J. Apodaca. 2009. Competition at the range boundary in the slimy salamander: using reciprocal transplants for studies on the role of biotic interactions in spatial distributions. *Journal of Animal Ecology* 78:52-62.
- Deeming, D. C. 2002. Embryonic development and utilization of egg components. Pages 43–53 *in* D. C. Deeming, editor. *Avian incubation behaviour, environment, and evolution*. Oxford University Press, New York, New York, USA.

- de Kort, S. R., E. R. B. Eldermire, E. R. A. Cramer, and S. L. Vehrencamp. 2009. The deterrent effect of bird song in territory defense. *Behavioral Ecology* 20:200-206.
- Deutsch, R. B., J. J. Tewksbury, R. B. Huey, K. S. Sheldon, C. K. Ghalambor, D. C. Haak, and P. R. Martin. 2008. Impacts of climatic warming on terrestrial ectotherms across latitude. *Proceedings of the National Academy of Sciences* 105:6668-6672.
- Diamond, J. 1973. Distributional ecology of New Guinea birds. *Science* 179:759-769.
- Elith, J., C. H. Graham, R. P. Anderson, M. Dudík, S. Ferrier, A. Guisan, R. J. Hijmans, F. Huettmann, J. R. Leathwick, A. Lehmann, J. Li, L. G. Lohmann, B. A. Loiselle, G. Manion, C. Moritz, M. Nakamura, Y. Nakazawa, J. M. Overton, A. T. Peterson, S. J. Phillips, K. Richardson, R. Scachetti-Pereira, R. E. Schapire, J. Soberón, S. Williams, M. S. Wisz, and N. E. Zimmermann. 2006. Novel methods improve prediction of species' distributions from occurrence data. *Ecography* 29:129-151.
- Elith, J., and J. R. Leathwick. 2009. Species distribution models: Ecological explanation and prediction across space and time. *Annual Review of Ecology Evolution and Systematics* 40:677-697.
- Environmental Systems Research Institute. 2007. ArcView GIS, V. 9.2. Redlands, California.
- Feeley, K. J., and M. R. Silman. 2010a. Modelling the responses of Andean and Amazonian plant species to climate change: the effects of georeferencing errors and the importance of data filtering. *Journal of Biogeography* 37:733-740.
- Feeley, K. J., and M. R. Silman. 2010b. Biotic attrition from tropical forests correcting for truncated temperature niches. *Global Change Biology* 16:1830-1836.
- Feeley, K. J., and M. R. Silman. 2010c. Land use and climate change effects on population size and extinction risk of Andean plants. *Global Change Biology* doi:10.1111/j.1365-2486.2010.02197.x
- Fine, P. V. A., D. C. Daly, G. V. Muñoz, I. Mesones, and K. M. Cameron. 2005. The contribution of edaphic heterogeneity to the evolution and diversity of Burseraceae trees in the Western Amazon. *Evolution* 59:1464-1478.
- Fleishman, E., N. McDonal, R. Mac Nally, D. D. Murphy, J. Walters, and T. Floyd. 2003. Effects of floristics, physiognomy and non-native vegetation on riparian bird communities in a Mojave Desert watershed. *Journal of Animal Ecology* 72:484-490.

- Fleishman, E., and R. Mac Nally. 2006. Patterns of spatial autocorrelation of assemblages of birds, floristics, physiognomy, and primary productivity in the central Great Basin, USA. *Diversity and Distributions* 12:236-243.
- Fletcher, R. J. 2007. Species interactions and population density mediate the use of social cues for habitat selection. *Journal of Animal Ecology* 76:598-606.
- Fontaine, J. J., and T. E. Martin. 2006. Experimental test of nest predation influences on adult habitat selection in a breeding bird community. *American Naturalist* 168:811-818.
- Frazer, G. W., C. D. Canham, and K. P. Lertzman. 1999. Gap Light Analyzer (GLA): Imaging software to extract canopy structure and gap light transmission indices from true-colour fisheye photographs. Simon Fraser University, Burnaby, British Columbia, and the Institute of Ecosystem Studies, Millbrook, New York, USA.
- Gabbe, A. P., S. K. Robinson, and J. D. Brawn. 2002. Tree-Species Preferences of Foraging Insectivorous Birds: Implications for Floodplain Forest Restoration. *Conservation Biology* 16:462-470.
- Gasner, M. R., J. E. Jankowski, A. L. Ciecka, K. O. Kyle, and K. N. Rabenold. 2010. Projecting impacts of climate change on Neotropical montane forests. *Biological Conservation* 143:1250-1258.
- Ghalambor, C. K., and T. E. Martin. 2002. Comparative manipulation of predation in incubating birds reveals variability in the plasticity of responses. *Behavioral Ecology* 13:101-108.
- Ghalambor, C. K., R. B. Huey, P. R. Martin, J. J. Tewksbury, and G. Wang. 2006. Are mountain passes higher in the tropics? Janzen's hypothesis revisited. *Integrative and Comparative Biology* 46:5-17.
- Goetz, S., D. Steinberg, R. Dubayah, and B. Blair 2007. Laser remote sensing of canopy habitat heterogeneity as a predictor of bird species richness in an eastern temperate forest, USA. *Remote Sensing of Environment* 108:254-263.
- Graves, G. R. 1988. Linearity of geographic range and its possible effect on the population structure of Andean birds. *Auk* 105:47-52.
- Gross, S. J., and T. D. Price. 2000. Determinants of the northern and southern range limits of a warbler. *Journal of Biogeography* 27:869-878.
- Grubb, P. J. 1977. Control of forest growth and distribution on wet tropical mountains with special references to mineral nutrition. *Annual Review of Ecology and Systematics* 8:83-107.

- Grubb, P. J., J. R. Lloyd, T. D. Pennington, and T. C. Whitmore. 1963. A comparison of montane and lowland rain forest in Ecuador. 1. The forest structure, physiognomy and floristics. *Journal of Ecology* 51:567-601.
- Guisan, A., and W. Thuiller. 2005. Predicting species distribution: offering more than simple habitat models. *Ecology Letters* 8:993-1009.
- Guisan, A., C. H. Graham, J. Elith, F. Huettmann, and NCEAS Species Distribution Modelling Group. 2007. Sensitivity of predictive species distribution models to change in grain size. *Diversity and Distributions* 13:332-340.
- Haber, W. A. 2000. Plants and vegetation. Pages 39-70 in N. M. Nadkarni and N. T. Wheelwright, editors. *Monteverde: Ecology and conservation of a tropical cloud forest*. Oxford University Press, New York, New York, USA.
- Hasui, É., V. Sousa da Mota Gomes, and W. R. Silva. 2007. Effects of vegetation traits on habitat preferences of frugivorous birds in Atlantic rain forest. *Biotropica* 39:502-509.
- Heikkinen, J., and R. Mäkipää. 2010. Testing hypotheses on shape and distribution of ecological response curves. *Ecological Modelling* 221:388-399.
- Herzog, S. K., A. R. Soria, and E. Matthysen. 2003. Seasonal variation in avian community composition in a high-Andean *Polylepis* (Rosaceae) forest fragment. *Wilson Bulletin* 115:438-447.
- Herzog, S. K., M. Kessler, and K. Bach. 2005. The elevational gradient in bird species richness at the local scale: a foothill peak and a high-elevation plateau. *Ecography* 28:209-222.
- Hickling, R., D. B. Roy, J. K. Hill, R. Fox, and C. D. Thomas. 2006. The distributions of a wide range of taxonomic groups are expanding polewards. *Global Change Biology* 12:450-455.
- Hijmans, R. J., and C. H. Graham. 2006. The ability of climate envelope models to predict the effect of climate change on species distributions. *Global Change Biology* 12:2272-2281.
- Holmes, R. T., and S. K. Robinson. 1981. Tree species preferences of foraging insectivorous birds in a northern hardwoods forest. *Oecologia* 48:31-35.
- Holt, R. D., and T. H. Keitt. 2005. Species borders: a unifying theme in ecology. *Oikos* 108:3-6.
- Holt, R. D., T. H. Keitt, M. A. Lewis, B. A. Maurer, and M. L. Taper. 2005. Theoretical models of species' borders: Single species approaches. *Oikos* 108:18-27.

- Holt, R. D. 2009. Bringing the Hutchinsonian niche into the 21<sup>st</sup> century: Ecological and evolutionary perspectives. *Proceedings of the National Academy of Sciences* 106:19659-19665.
- Huey, R. B., and A. F. Bennett. 1987. Phylogenetic studies of coadaptation: Preferred temperatures versus optimal performance temperatures of lizards. *Evolution* 41:1098-1115.
- Huey, R. B., C. A. Deutsch, J. J. Tewksbury, L. J. Vitt, P. E. Hertz, H. J. Álvarez Pérez, and T. Garland, Jr. 2009. Why tropical forest lizards are vulnerable to climate warming. *Proceedings of the Royal Society B-Biological Sciences* 276:1939-1948.
- Hughes, L. 2000. Biological consequences of global warming: is the signal already apparent? *Trends in Ecology and Evolution* 15:56-61.
- Huntley, B. 1991. How plants respond to climate change. Migration rates, individualism and the consequences for plant communities. *Annals of Botany* 67:15-22.
- Ibanez, I., J. S. Clark, and M. C. Dietze. 2009. Estimating colonization potential of migrant tree species. *Global Change Biology* 15:1173-1188.
- Iverson, L. R., M. W. Schwartz, and A. M. Prasad. 2004. How fast and far might tree species migrate in the eastern United States due to climate change? *Global Ecology and Biogeography* 13:209-219.
- Jankowski, J. E., A. L. Ciecka, N. Y. Meyer, and K. N. Rabenold. 2009. Beta diversity along environmental gradients: implications of habitat specialization in tropical montane landscapes. *Journal of Animal Ecology* 78:315-327.
- Janzen, D. H. 1967. Why mountain passes are higher in the tropics. *American Naturalist* 101:233-249.
- Jullien, M., and J. Thiollay. 1998. Multi-species territoriality and dynamic of Neotropical forest understorey bird flocks. *Journal of Animal Ecology* 67:227-252.
- Karr, J. R., and K. E. Freemark. 1983. Habitat selection and environmental gradients: dynamics in the "stable" tropics. *Ecology* 64:1481-1494.
- Kearney, M. 2006. Habitat, environment and niche: what are we modelling? *Oikos* 115:187-191.
- Kearney M., B. L. Phillips, C. R. Tracy, K. A. Christian, G. Betts, and W. P. Porter. 2008. Modelling species distributions without using species distributions: the cane toad in Australia under current and future climates. *Ecography* 31:423-434.

- Kearney, M., and W. Porter. 2009. Mechanistic niche modelling: combining physiological and spatial data to predict species' ranges. *Ecology Letters* 12:334-350.
- Kissling, W. D., R. Field, and K. Böhning-Gaese. 2008. Spatial patterns of woody plant and bird diversity: functional relationships or environmental effects? *Global Ecology and Biogeography* 17:327-339.
- Koleff, P., K. J. Gaston, and J. J. Lennon. 2003. Measuring beta diversity for presence-absence data. *Journal of Animal Ecology* 72:367-382.
- Kratter, A. W. 1997. Bamboo specialization by Amazonian birds. *Biotropica* 29:100-110.
- Kroodsma, D. E., B. E. Byers, E. Goodale, S. Johnson, and W. C. Liu. 2001. Pseudoreplication in playback experiments, revisited a decade later. *Animal Behavior* 61:1029-1033.
- Langkilde, T., and R. Shine. 2004. Competing for crevices: interspecific conflict influences retreat-site selection in montane lizards. *Oecologia* 140:684-691.
- La Sorte, F. A., and W. Jetz. 2010. Avian distributions under climate change: toward improved projections. *Journal of Experimental Biology* 213:862-869.
- Lee, D. C., and S. J. Marsden. 2008. Increasing the value of bird-habitat studies in tropical forests: choice of approach and habitat measures. *Bird Conservation International* 18:S109-S124.
- Lee, P.-Y., and J. T. Rotenberry. 2005. Relationships between bird species and tree species assemblages in forested habitats of eastern North America. *Journal of Biogeography* 32:1139-1150.
- Legendre, P., and L. Legendre. 1998. *Numerical Ecology*. 2nd edition. Elsevier Science, Amsterdam.
- Lennon, J. J., P. Koleff, J. J. D. Greenwood, and K. J. Gaston. 2001. The geographical structure of British bird distributions: diversity, spatial turnover and scale. *Journal of Animal Ecology* 70:966-979.
- Lichstein, J. W. 2007. Multiple regression on distance matrices: a multivariate spatial analysis tool. *Plant Ecology* 188:117-131.
- Linares-Palomino, R., and M. Kessler. 2009. The role of dispersal ability, climate, and spatial separation in shaping biogeographical patterns of phylogenetically distant plant groups in seasonally dry Andean forests of Bolivia. *Journal of Biogeography* 36:280-290.

- Lindsay, C., C. Downs, and M. Brown. 2009. Physiological variation in Amethyst Sunbirds (*Chalcomitra amethystina*) over an altitudinal gradient: A seasonal comparison. *Comparative biochemistry and physiology A-molecular and integrative physiology* 152:22-45.
- Lomolino, M. V., B. R. Riddle, and J. H. Brown. 2006. *Biogeography*. Sinauer Associates Inc., Sunderland, Massachusetts, USA.
- Londoño, G. A., D. J. Levey, and S. K. Robinson. 2008. Effects of temperature and food on incubation behavior of the Northern Mockingbird (*Mimus polyglottos*). *Animal Behavior* 76:669-677.
- MacArthur, R. H., and J. W. MacArthur. 1961. On Bird Species Diversity. *Ecology* 42:594-598.
- MacArthur, R. H. 1972. *Geographical ecology: Patterns in the distribution of species*. Harper & Row, Publishers, Inc., New York, NY, USA.
- Macía, M. J., K. Ruokolainen, H. Tuomisto, J. Quisbert, and V. Cala. 2007. Congruence between floristic patterns of trees and lianas in a southwest Amazonian rain forest. *Ecography* 30:561-577.
- Magurran, A. E. 2004. *Measuring Biological Diversity*. Blackwell Science Ltd., Oxford, UK.
- Martin, P. R., J. R. Fotheringham, L. Ratcliffe, and R. J. Robertson. 1996. Response of American redstarts (suborder Passeri) and least flycatchers (suborder Tyranni) to heterospecific playback: the role of song in aggressive interactions and interference competition. *Behavioral Ecology and Sociobiology* 39:227-235.
- Martin, P. R., and T. E. Martin. 2001. Behavioral interactions between coexisting species: song playback experiments with wood warblers. *Ecology* 82:207-218.
- Martin, T. E. 1993. Nest predation and nest sites: New perspectives on old patterns. *BioScience* 43:523-532.
- Martin, T. E., C. R. Paine, C. J. Conway, W. M. Hochachka, P. Allen, and W. Jenkins. 1997. BBIRD field protocol. Montana Cooperative Wildlife Research Unit, University of Montana, Missoula, Montana, USA.
- Martin, T. E. 2004. Avian life-history evolution has an eminent past: does it have a bright future? *Auk* 121:289-301.

- Martin, T. E., R. D. Bassar, S. K. Bassar, J. J. Fontaine, P. Lloyd, H. A. Mathewson, A. M. Niklison, and A. Chalfoun. 2006. Life-history and ecological correlates of geographic variation in egg and clutch mass among passerine species. *Evolution* 60:390–398.
- Martin, T. E., S. K. Auer, R. D. Bassar, A. M. Niklison, and P. Lloyd. 2007. Geographic variation in avian incubation periods and parental influences on embryonic temperature. *Evolution* 61:2558-2569.
- Martin, T. E. 2008. Egg size variation among tropical and temperate songbirds: An embryonic temperature hypothesis. *Proceedings of the National Academy of Sciences USA* 105:9268-9271.
- Massaro, M., A. Starling-Windhof, J. V. Briskie, and Martin, T. E. 2008. Introduced mammalian predators induce adaptive shifts in parental behaviour in an endemic New Zealand bird. *PLoS ONE* 3:e2331. doi:10.1371/journal.pone.0002331.
- McCain, C. M. 2005. Elevational gradients in diversity of small mammals. *Ecology* 86:366-372.
- McCain, C. M. 2009. Vertebrate range sizes indicate that mountains may be ‘higher’ in the tropics. *Ecology Letters* 12:550-560.
- McKechnie, A. E., and D. L. Swanson. 2010. Sources and significance of variation in basal summit and maximal metabolic rates in birds. *Current Zoology* in press.
- McKnight, M. W., P. S. White, R. I. McDonald, J. F. Lamoreux, W. Sechrest, R. S. Ridgely, and S. N. Stuart. 2007. Putting beta-diversity on the map: Broad-scale congruence and coincidence in the extremes. *PLoS Biology* 5:e272.doi:10.1371/journal.pbio.0050272.
- McNab, B. K. 2001. The energetics of toucans, a barbet, and a hornbill: Implications for avian frugivory. *Auk* 118:916-933.
- McNab, B. K. 2002. *The physiological ecology of vertebrates*. Cornell University press, Ithaca, New York, USA.
- McNab, B. K. 2003. Ecological factors affect the level and scaling of avian BMR. *Comparative biochemistry and physiology A-molecular and integrative physiology* 152:22-45.
- McNaughton, S. J., and L. L. Wolf. 1970. Dominance and the niche in ecological systems. *Science* 167:131-139.

- Melo, A. S., T. F. L. V. B. Rangel, and J. A. F. Diniz-Filho. 2009. Environmental drivers of beta-diversity patterns in New-World birds and mammals. *Ecography* 32:226-236.
- Merrill, R. M., D. Gutiérrez, O. T. Lewis, J. Gutiérrez, S. B. Díez, and R. J. Wilson. 2008. Combined effects of climate and biotic interactions on the elevational range of a phytophagous insect. *Journal of Animal Ecology* 77:145-155.
- Monahan, W. B. 2009. A mechanistic niche model for measuring species' distributional responses to seasonal temperature gradients. *PLoS ONE* 4:e7921. doi:10.1371/journal.pone.0007921.
- Moritz, C. M., J. L. Patton, C. J. Conroy, J. L. Parra, G. C. White, and S. R. Beissinger. 2008. Impact of a century of climate change on small-mammal communities in Yosemite National Park, USA. *Science* 322:261-264.
- Müller, J., C. Moning, C. Bäessler, M. Heurich, and R. Brandl. 2009. Using airborne laser scanning to model potential abundance and assemblages of forest passerines. *Basic and Applied Ecology* 10:671-681.
- Munn, C. A., and J. W. Terborgh. 1979. Multi-species territoriality in Neotropical foraging flocks. *Condor* 81:338-347.
- Munn, C. A. 1985. Permanent canopy and understory flocks in Amazonia: Species composition and population density. Pages 683-712 in P. A. Buckley, M. S. Foster, E. S. Morton, R. S. Ridgely, and F. G. Buckley, editors. *Neotropical Ornithology. Ornithological Monographs No. 36.* The American Ornithologists' Union, Washington D.C., USA.
- Murray, B. G. 1971. The ecological consequences of interspecific territorial behavior in birds. *Ecology* 52: 414-423.
- Myers, N., R. A. Mittermeier, C. G. Mittermeier, G. A. B. da Fonseca, and J. Kent. 2000. Biodiversity hotspots for conservation priorities. *Nature* 403:853-858.
- Naoki, K. 2007. Arthropod resource partitioning among omnivorous tanagers (*Tangara* spp.) in Western Ecuador. *Auk* 124:197-209.
- Navas, C. A. 2003. Herpetological diversity along Andean elevational gradients: links with physiological ecology and evolutionary physiology. *Comparative Biochemistry and Physiology Part A* 133:469-485.
- Nikkilson, A. M. 2007. Influence of embryonic metabolic rate and incubation temperature on incubation length variation in Neotropical passerines. M.Sc. Thesis. University of Montana, Missoula, Montana, USA.

- Oksanen, J., and P. R. Minchin. 2002. Continuum theory revisited: What shape are species responses along ecological gradients? *Ecological Modelling* 157:119-129.
- Oksanen, J., R. Kindt, P. Legendre, R. B. O'Hara, G. L. Simpson, M. H. H. Stevens, and H. Wagner. 2008. *Vegan: community ecology package, version 1.17-2*. Available at: <http://vegan.r-forge.r-project.org/>.
- Olson, C. R., C. M. Vleck, and D. Vleck. 2006. Periodic cooling of birds eggs reduces embryonic growth efficiency. *Physiological and Biochemical Zoology* 79:927-936.
- Orians, G. H., and M. F. Willson. 1964. Interspecific territories of birds. *Ecology* 45:736-745.
- Palmer, M. W. 1993. Putting things in even better order: The advantages of canonical correspondence analysis. *Ecology* 74:2215-2230.
- Parker, T. A., III, and J. P. O'Neill. 1980. Notes on little known birds of the upper Urubamba valley, southern Peru. *Auk* 97:167-176.
- Parmesan, C. 2006. Ecological and evolutionary response to recent climate change. *Annual Review of Ecology Evolution and Systematics* 37:637-669.
- Patterson, B. D., D. F. Stotz, S. Solari, J. W. Fitzpatrick, and V. Pacheco. 1998. Contrasting patterns of elevational zonation for birds and mammals in the Andes of southeastern Peru. *Journal of Biogeography* 25:593-607.
- Pearson, R.G., and T. P. Dawson. 2003. Predicting the impacts of climate change on the distribution of species: are bioclimate envelope models useful? *Global Ecology & Biogeography* 12:361-371.
- Peterson A. T., M. A. Ortega-Huerta, J. Bartley, V. Sánchez-Cordero, J. Sorberón, R. H. Buddemeier, and D. R. B. Stockwell. 2002. Future projections for Mexican faunas under global climate change scenarios. *Nature* 416:626-629.
- Pitman, N. C. A., J. W. Terborgh, M. R. Silman, and P. Núñez V. 1999. Tree species distributions in an upper Amazonian forest. *Ecology* 80:2651-2661.
- Pitman, N. C. A., J. W. Terborgh, M. R. Silman, P. Núñez V., D. A. Neill, C. E. Cerón, W. A. Palacios, and M. Aulestia. 2001. Dominance and distribution of tree species in upper Amazonian terra firme forests. *Ecology* 82:2101-2117.
- Potts, M., P. S. Ashton, L. S. Kaufman, and J. B. Plotkin. 2002. Habitat patterns in tropical rain forests: A comparison of 105 plots in Northwest Borneo. *Ecology* 83:2782-2797.

- Poulin, B., G. Lefebvre, and R. McNeil. 1994. Characteristics of feeding guilds and variation in diets of bird species of three adjacent tropical sites. *Biotropica* 26:187-197.
- Poulsen, B. O. 1996. Structure, dynamics, home range and activity pattern of mixed-species bird flocks in a montane Alder-dominated secondary forest in Ecuador. *Journal of Tropical Ecology* 12:333-343.
- Pounds, J. A., M. P. L. Fogden, and J. H. Campbell. 1999. Biological response to climate change on a tropical mountain. *Nature* 398:611-615.
- Powell, G. V. N. 1979. Structure and dynamics of interspecific flocks in a Neotropical mid-elevation forest. *Auk* 96:375-390.
- Price, T. D., and M. Kirkpatrick. 2009. Evolutionarily stable range limits set by interspecific competition. *Proceedings of the Royal Society B-Biological Sciences* 276:1429-1434.
- R Development Core Team. 2010. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. Available at: <http://www.r-project.org/> (accessed April 10, 2010).
- Rahn, H., C. Carey, K. Balmas, B. Bhatia, and C. Paganelli. 1977. Reduction of pore area of the avian eggshell as an adaptation to altitude. *Proceedings of the National Academy of Sciences USA* 74:3095-3098.
- Remsen, J. V., Jr., and W. S. Graves. 1995. Distribution patterns and zoogeography of Atlapetes Brush-Finches (Emberizinae) of the Andes. *Auk* 112:225-236.
- Remsen, J. V., Jr., C. D. Cadena, A. Jaramillo, M. Nores, J. F. Pacheco, M. B. Robbins, T. S. Schulenberg, F. G. Stiles, D. F. Stotz, and K. J. Zimmer. Version [June 2010]. A classification of the bird species of South America. American Ornithologists' Union. <http://www.museum.lsu.edu/~Remsen/SACCBaseline.html>
- Restrepo, C., and N. Gómez. 1998. Responses of understory birds to anthropogenic edges in a neotropical montane forest. *Ecological Applications* 8:170-183.
- Richards, D. G. 1979. Recognition of neighbors by associative learning in Rufous-sided Towhees. *Auk* 96: 688-693.
- Richards, P. W. 1996. *The tropical rain forest: An ecological study*. Cambridge University Press, Cambridge, UK.
- Ricklefs, R. E. 1969. An analysis of nesting mortality in birds. *Smithsonian Contribution to Zoology* Number 9.

- Ritchie, E. G., J. K. Martin, C. N. Johnson, and B. J. Fox. 2009. Separating the influences of environment and species interactions on patterns of distribution and abundance: competition between large herbivores. *Journal of Animal Ecology* 78:724-731.
- Robinson, S. K., and R. T. Holmes. 1984. Effects of plant species and foliage structure on the foraging behavior of forest birds. *Auk* 101:672-684.
- Robinson, S. K., and J. Terborgh. 1995. Interspecific aggression and habitat selection by Amazonian birds. *Journal of Animal Ecology* 64:1-11.
- Romdal, T. S., and C. Rahbek. 2009. Elevational zonation of afro-tropical forest bird communities along an homogeneous forest gradient. *Journal of Biogeography* 36:327-336.
- Rotenberry, J. T. 1985. The role of habitat in avian community composition: physiognomy or floristics? *Oecologia* 67:213-217.
- Ruokolainen, K., H. Tuomisto, M. J. Macía, M. A. Higgins, and M. Yli-Halla. 2007. Are floristic and edaphic patterns in Amazonian rain forests congruent for trees, pteridophytes and Melastomataceae? *Journal of Tropical Ecology* 23:13-25.
- Saatchi, S., R. Houghton, R. Avala, Y. Yu, and J-V. Soares. 2007. Spatial Distribution of Live Aboveground Biomass in Amazon Basin. *Global Change Biology* 13:816–837.
- Sagarin, R. D., and S. D. Gaines. 2002. The ‘abundant centre’ distribution: To what extent is it a biogeographic rule? *Ecology Letters* 5:137-147.
- Sagarin, R. D., S. D. Gaines, and B. Gaylord. 2006. Moving beyond assumptions to understand abundance distributions across the ranges of species. *Trends in Ecology and Evolution* 21:524-530.
- Santika, T., and M. F. Hutchinson. 2009. The effect of species response form on species distribution model prediction and inference. *Ecological Modelling* 220:2365-2379.
- SAS Institute. 2008. SAS/STAT Users Guide, version 9.2. SAS Institute, Cary, North Carolina.
- Schmidt-Nielsen, K. 1997. *Animal Physiology: Adaptation and Environment*. Cambridge University Press, Cambridge, UK.
- Schulenberg, T. S., D. F. Stotz, D. F. Lane, J. P. O’Neill, and T. A. Parker III. 2007. *Birds of Peru*. Princeton University Press, Princeton, New Jersey, USA.

- Sekercioglu, C. H., S. H. Schneider, J. P. Fay, and S. R. Loarie. 2008. Climate change, elevational range shifts, and bird extinctions. *Conservation Biology* 22:140-150.
- Silvertown, J. 2004. Plant coexistence and the niche. *Trends in Ecology and Evolution* 19:605-611.
- Skutch, A. F. 1985. Clutch size, nesting success, and predation on nests of tropical birds, reviewed. Pages 575–594 *in* P. A. Buckley, M. S. Foster, E. S. Morton, R. S. Ridgely, and F. G. Buckley, editors. *Neotropical Ornithology*. Ornithological Monographs No. 36. The American Ornithologists' Union, Washington D.C., USA.
- Soberón, J. 2007. Grinnellian and Eltonian niches and geographic distributions of species. *Ecology Letters* 10:1115-1123.
- Solomon, S., D. Qin, M. Manning, Z. Chen, M. Marquis, K. B. Averyt, M. Tignor, and H. L. Miller. 2007. A Contribution of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change. Cambridge University Press, New York, New York, USA.
- Soobramoney, S., C. T. Downs, and N. J. Adams. 2003. Physiological variability in the Fiscal Shrike (*Lanius collaris*) along an altitudinal gradient in South Africa. *Journal of thermal biology* 28:581-594.
- Soriano, P. J., A. Ruiz, and A. Arends. 2002. Physiological responses to ambient temperature manipulation by three species of bats from Andean cloud forests. *Journal of Mammalogy* 83:445-457.
- Stiles, F. G. 1975. Ecology, flowering phenology, and hummingbird pollination of some Costa Rican *Heliconia* species. *Ecology* 56:285-301.
- Stiles, F. G. 1985. Seasonal patterns and coevolution in the hummingbird-flower community of a Costa Rican subtropical rainforest. Pages 757-787 *in* P. A. Buckley, M. S. Foster, E. S. Morton, R. S. Ridgely, and F. G. Buckley, editors. *Neotropical Ornithology*. Ornithological Monographs No. 36. The American Ornithologists' Union, Washington D.C., USA.
- Stiles, F. G., A. Skutch, and D. Gardner. 1989. *A Guide to the Birds of Costa Rica*. Cornell University Press, Ithaca.
- Stiles, F. G. 1995. Behavioral, ecological and morphological correlates of foraging for arthropods by the hummingbirds of a tropical wet forest. *Condor* 97:853-878.
- Stotz, D. F., J. W. Fitzpatrick, T. A. Parker III, and D. K. Moskovits. 1996. *Neotropical Birds*. Ecology and Conservation. University of Chicago Press, Chicago.

- Takahashi, K., and T. Kamitani. 2004. Effect of dispersal capacity on forest plant migration at a landscape scale. *Journal of Ecology* 92:778-785.
- Terborgh, J. 1971. Distributions on environmental gradients: Theory and a preliminary interpretation of distributional patterns in the avifauna of the Cordillera Vilcabamba, Peru. *Ecology* 52:23-40.
- Terborgh, J., and J. S. Weske. 1975. The role of competition in the distribution of Andean birds. *Ecology* 56:562-576.
- Terborgh, J. 1977. Bird species diversity on an Andean elevational gradient. *Ecology* 58:1007-1019.
- Terborgh, J. 1985a. The role of ecotones in the distribution of birds. *Ecology* 66:1237-1246.
- Terborgh, J. 1985b. Habitat selection in Amazonian birds. Pages 311-338 *in* M. L. Cody, editor. *Habitat selection in birds*. Academic Press, New York, New York, USA.
- Terborgh, J., S. K. Robinson, T. A. Parker III, C. A. Munn, and N. Pierpont. 1990. Structure and organization of an Amazonian forest bird community. *Ecological Monographs* 60:213-238.
- Terborgh, J., R. B. Foster, and P. Núñez V. 1996. Tropical tree communities: A test of the nonequilibrium hypothesis. *Ecology* 77:561-567.
- Ter Braak, C. J. F. 1985. Correspondence analysis of incidence and abundance data: Properties in terms of a unimodal response model. *Biometrics* 41:859-873.
- Tewksbury, J. J., B. H. Raymond, and C. A. Deutsch. 2008. Putting the heat on tropical animals. *Science* 320:1296-1297.
- Thomas, C. D., and J. J. Lennon. 1999. Birds extend their ranges northwards. *Nature* 399:213.
- Thomson, D. L., P. Monaghan, and R. W. Furness. 1998. The demands of incubation and avian clutch size. *Biological review of the Cambridge philosophical society* 73:293-304.
- Thuiller, W., C. Albert, M. B. Araújo, P. M. Berry, M. Cabeza, A. Guisan, T. Hickler, G. F. Midgley, J. Paterson, F. M. Schurr, M. T. Sykes, and N. E. Zimmerman. 2008. Predicting global change impacts on plant species' distributions: Future challenges. *Perspectives in Plant Ecology Evolution and Systematics* 9:137-152.
- Tichý, L. 2002. JUICE, software for vegetation classification. *Journal of Vegetation Science* 13:451-453.

- Tichý, L., and J. Holt. 2006 JUICE: Program for management, analysis and classification of ecological data. Vegetation Science Group, Masaryk University Brno, Czech Republic.
- Tinbergen, J. M., and J. B. Williams. 2002. Energetics of incubation. Pages 300–313 *in* Avian incubation Behaviour, Environment, and Evolution (D. C. Deeming, Editor). Oxford University Press, New York, USA.
- Tingley, M. W., W. B. Monahan, S. R. Beissinger, and C. Moritz. 2009. Birds track their Grinnellian niche through a century of climate change. *Proceedings of the National Academy of Sciences* 106:19637-19643.
- Trillo, P. A., and S. L. Vehrencamp. 2006. Song types and their structural features are associated with specific contexts in the banded wren. *Animal Behavior* 70:921-935.
- Tuomisto, H. 2010. A diversity of beta diversities: straightening up a concept gone awry. Part 2. Quantifying beta diversity and related phenomena. *Ecography* 33:23-45.
- Turner, J. S. 2002. Maintenance of egg temperature. Pages 119–142 *in* D. C. Deemin, editor. Avian incubation Behaviour, Environment, and Evolution. Oxford University Press, New York, USA.
- Turner, W., S. Spector, N. Gardiner, M. Fladeland, E. Sterling, and M. Steininger. 2003. Remote sensing for biodiversity science and conservation. *Trends in Ecology and Evolution* 18:306-314.
- Urrutia, R., and M. Vuille. 2009. Climate change projections for the tropical Andes using a regional climate model: Temperature and precipitation simulations for the end of the 21st century. *Journal of Geophysical Research* 114:D02108.
- van Schaik, C. P., J. W. Terborgh, and S. J. Wright. 1993. The phenology of tropical forests: adaptive significance and consequences for primary consumers. *Annual Review of Ecology and Systematics* 24:353-377.
- Vásquez G., J. A., and T. J. Givnish. 1998. Altitudinal gradients in tropical forest composition, structure, and diversity in the Sierra de Manantlán. *Journal of Ecology* 86:999-1020.
- Vierling, K. T., L. A. Vierling, W. A. Gould, S. Martinuzzi, and R. M. Clawges. 2008. Lidar: Shedding new light on habitat characterization and modeling. *Frontiers in Ecology and the Environment* 60:90-98.
- Visser, M. E., A. C. Perdeck, J. H. van Balen, and C. Both. 2009. Climate change leads to decreasing bird migration distances. *Global Change Biology* 15:1859-1865.

- Walker, B., D. F. Stotz, T. Pequeño, and J. W. Fitzpatrick. 2006. Birds of the Manu Biosphere Reserve. *Fieldiana Zoology* 110:23-49.
- Webb, D. R. 1987. Thermal tolerance of avian embryos: a review. *Condor* 89:874–898.
- Weske, J. S. 1972. The distribution of the avifauna in the Apurimac valley of Peru with respect to environmental gradients, habitat, and related species. PhD Dissertation, University of Oklahoma, Norman, Oklahoma, USA.
- Whittaker, R. H. 1975. *Communities and Ecosystems*. MacMillan, New York, USA.
- Wiens, J. A. 1989a. *The ecology of bird communities: volume 1: foundations and patterns*. Cambridge University Press, Cambridge, UK.
- Wiens, J. A. 1989b. *The ecology of bird communities: volume 2: processes and variations*. Cambridge University Press, Cambridge UK.
- Wiersma, P., A. Muñoz-García, A. Walker, and J. B. Williams. 2007. Tropical birds have a slow pace of life. *Proceedings of the National Academy of Sciences USA* 104:9340-9345.
- Williams, G. C. 1966. Natural selection, the cost of reproduction, and a refinement of Lack's principle. *American Naturalist* 100:687–690.
- Williams, J. W., S. T. Jackson, and J. E. Kutzbach. 2007. Projected distributions of novel and disappearing climates by 2100 AD. *Proceedings of the National Academy of Sciences* 104:5738-5742.
- Wilson, R. J., J. Gutiérrez, D. Martínez, R. Agudo, and V. J. Monserrat. 2005. Changes to the elevational limits and extent of species ranges associated with climate change. *Ecology Letters* 8:1138-1146.
- Zuckerberg, B., A. M. Woods, and W. F. Porter. 2009. Poleward shifts in breeding bird distributions in New York State. *Global Change Biology* 15:1866-1883.

## BIOGRAPHICAL SKETCH

Jill Emily Jankowski was born in June of 1980 and grew up in Southwestern Indiana near the Ohio River basin. Her parents own property adjacent to a large tract of forest, which served as her favorite stomping grounds throughout childhood. The close ties she developed with the natural world later inspired her to study ecology in far away places and close to home. Jill graduated in 1998 from F.J. Reitz High School on the west side of Evansville, and she attended Purdue University for her undergraduate education. She began as a student in civil engineering and played soccer on the Women's Boilermaker varsity team, but her academic interests turned to biology in her second year. She graduated from Purdue with a Bachelor of Science in ecology, evolution and population biology in 2002. Jill was accepted into graduate school at Purdue, where she continued research begun with Dr. Kerry Rabenold as an undergraduate examining patterns of diversity and endemism of bird communities in the cloud forests of Costa Rica. In the spring of 2004, she obtained her Master of Science in the Department of Biological Sciences upon the completion of her thesis: "Patterns of avian diversity and the interspecific abundance-distribution relationship in the Tilarán Mountain Range, Costa Rica". Jill began her doctoral dissertation work in the fall of 2004 in the Department of Zoology at the University of Florida with her co-advisors, Dr. Doug Levey and Dr. Scott Robinson. There she continued her studies of montane birds in the tropical Andes, honing in on some of the ecological forces that determine where species live along large-scale elevational gradients. This dissertation is the product of over 20 months of data collection from field sites in Costa Rica and Peru. Outside of her field seasons, Jill has resided in Gainesville, Florida, with her fiancé, Aaron Spalding, and her two cats, Missy and Duchess.