

What Is an Elevational Range?

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Submitted August 12, 2024; Accepted May 19, 2025; Electronically published August 12, 2025

Online enhancements: supplemental PDF.

ABSTRACT: Elevational distributions have long fascinated scientists, an interest that has burgeoned with studies of predicted up-slope range shifts under climate change. However, this body of work has yielded conflicting results, perhaps due to varied conceptual and statistical approaches. Here I explore how ecological processes and researcher decisions shape the patterns characterized by elevational ranges. I use community science data to illustrate (1) that elevational ranges include variation in abundance; (2) that elevational ranges are usually estimated, not observed directly; (3) that elevational ranges are dynamic across short distances and time intervals; and (4) that how we describe elevational ranges has consequences for inference of range shifts. I present a conceptual framework for understanding elevational ranges across multiple spatial scales and propose that elevational distributions are governed by scale-dependent processes. This framework implies that accurately quantifying elevational ranges and learning how they are formed or maintained requires matching questions to their appropriate scale domain. I provide a list of best practices for studying elevational ranges and highlight promising directions for future research into these complex phenomena.

Keywords: species distribution, geographic range, range shifts, range limits, zonation, niche.

Like attempts to define and classify species, efforts to characterize geographic ranges of species necessarily involve reducing a complex phenomenology to a greatly simplified abstraction. (Brown et al. 1996, p. 599)

Introduction

Studies of the elevational distribution of organisms have influenced the development of the natural sciences for six centuries. Conrad Gessner's (1555) pioneering description of plant life from the base to the summit of Switzerland's Mount Pilatus was followed by Linneaus's *Flora Lapponica* in 1737, which drew the first parallel between

elevational zonation and latitudinal zonation and established an enduring framework to link climate with broad-scale patterns of diversity (Fattorini et al. 2019; Fattorini 2021). Von Haller's 1742 description of vegetation belts in the Alps included the observation that elevational gradients permit high structural diversity in a small area, anticipating their eventual importance to studies of beta diversity. Most famously, von Humboldt and Bonpland's *Essai sur la géographie des plantes* (1807) and its accompanying *Tableau physique* precisely quantified a range of abiotic and biotic variables across an elevational gradient in Ecuador—among them, the lower and upper elevational range limits of many Andean plants (Morueta-Holme et al. 2015).

In the nineteenth and twentieth centuries, elevational ranges continued to fascinate naturalists interested in general principles governing the distribution of life on Earth (Lomolino 2001). Both Wallace (1876, 1878) and Darwin et al. (1839) frequently remarked on the elevation of plants and animals in their travelogs, speculating how climate, geological history, and biotic interactions might determine their position. In *Origin* (1859), Darwin suggests that competition is more pervasive in warm and damp environments, an enduring hypothesis for what forms lower elevation range limits (e.g., Freeman 2020). Later, Merriam and Stejneger's (1890) description of the "Life Zones" of the San Francisco Peaks of Arizona brought montane geographical ecology to North America, emphasizing the impacts of aspect and latitude.

As ecology and evolutionary biology matured into quantitative sciences in the twentieth century, elevational distributions both inspired and were used to test novel theories of community ecology and biogeography. MacArthur (1984) addressed patterns of montane species richness and competitive exclusion across elevational gradients, drawing on Diamond's (1973) extensive fieldwork and hypotheses for processes impacting the distribution of New Guinea birds. Terborgh and Weske's (Terborgh 1971, 1977, 1985; Terborgh and Weske 1969, 1975) articles on factors shaping

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avian distributions across an elevational gradient in the Cordillera Vilcabamba of Peru have influenced decades of empirical study, including an increasing focus on mechanism (Londoño et al. 2017; von May et al. 2017; Linck et al. 2023). The emergence of “model” systems in evolutionary ecology amenable to experimental manipulation—such as the wildflowers *Clarkia* and *Mimulus*—further pushed the study of elevational ranges from describing to explaining (Jonas and Geber 1999; Angert and Schemske 2005).

In the past two decades, accelerating climate warming and growth of global change biology have led to a renaissance of interest in elevational ranges after what Lomolino (2001) identifies as a late-century shift in interest to latitudinal gradients and species-area relationships. The hypothesis that species and populations will track their thermal niche in response to climate warming (Parmesan and Yohe 2003) has led to an explosion of tests of its predictions. This vast body of work indicates elevational distributions have changed (or not changed) in idiosyncratic, taxon-dependent, or region-dependent ways. Although some resurveys of elevational transects have found widespread upslope movement (e.g., Chen et al. 2009; Freeman et al. 2018), others report shifts of varied direction and magnitude across assemblages, with individual species responses best predicted by changes in precipitation and temperature (Tingley et al. 2012). Importantly, the absence of upslope shifts (Holzman et al. 2023) and even downslope movement (reviewed in Lenoir et al. 2010) appear common.

A major source of this heterogeneity may be that despite their importance to empirical biology, elevational distributions have received scant conceptual attention, leading to a literature rife with widely varied definitions, methodological approaches, and statistical implementations. Elevational ranges are alternatively described solely by their limits (Parker et al. 1996; Freeman and Class Freeman 2014; Linck et al. 2023; Holzman et al. 2023), by some measure of their central tendency (Sheldon et al. 2015), by limits as well as central tendency (Raxworthy et al. 2008; Koide et al. 2017), by presence or absence at sites along a standardized transect (McCain 2004), by relative abundance across elevation (Diamond 1972; McCain 2006), by abundance- or abundance and mass-weighted elevational range mean (Chen et al. 2009; Feely et al. 2011), by the 5th and 95th percentiles of a set of elevational observations (Freeman et al. 2022), or, more rarely, with formal occupancy models (Moritz et al. 2008; Tingley et al. 2012; Burner et al. 2020). The impact of this lack of standardization is variable but inevitably harms our understanding of general patterns and processes.

Overly simple descriptions of elevational ranges also limit understanding. For example, variation across space is often ignored (Telwala et al. 2013; Linck et al. 2023; but see Grubb 1971; Smith et al. 2019; Diamond and Bishop 2022). The situation is similar for temporal variation in elevational ranges,

where few studies have attempted to describe interannual fluctuations in detail (although for a possible exception, see Johnston et al. 2019), and our understanding of seasonal shifts is dominated by known elevational migrants (particularly birds and bats; Boyle 2017; Hsiung et al. 2018; Williamson and Witt 2021a). Finally, statistical analyses of range evolution, range shifts, and species turnover frequently neglect (Raxworthy et al. 2008; Freeman and Class Freeman 2014; Ménendez et al. 2014; Holzman et al. 2023) and only sometimes incorporate uncertainty in range definitions (Rowe et al. 2010) or observed shifts (Koide et al. 2017), likely inflating the literature with both false positives and false negatives.

Although pragmatism and the constraints of historic datasets are understandable drivers of these limitations, conflicting approaches may also reflect historic fissures between ecological versus historical biogeography (Brown et al. 1996). Ecological biogeography has traditionally treated species distributions as geographic manifestations of the Hutchinsonian niche, emphasizing traits and their interaction with abiotic and biotic variables projected on the landscape over metrics such as raw altitude or latitude (Hutchinson 1957; Dansereau 1957; Blonder 2018). In contrast, historical biogeography has often taken a more spatially centric approach, viewing ranges as fixed quantities that may be the result of evolutionary contingency and evolve in the matter of other traits (Wiens et al. 2007; Cadena et al. 2020; Linck et al. 2021). The advent of species distribution modeling has partially bridged this gap and made descriptions of the bioclimatic envelope of species ranges commonplace (e.g., Borokini et al. 2023), but their pattern-based approach to prediction suffers from a limited ability to account for dispersal, biotic interactions, demography, and genetic and phenotypic variation, let alone evolution (Jiménez-Valverde et al. 2008; Guisan and Rahbek 2011; Engler et al. 2017). The fundamental question of whether and how frequently geographic range limits reflect realized niche limits (Sexton et al. 2009; Hargreaves et al. 2014; Lee-Yaw et al. 2016) remains unresolved.

Here I attempt to answer a deceptively simple question: what is an elevational range? More specifically, which features of James Brown’s (1996) “greatly simplified abstraction” of the geographic (elevational) range are necessary for biological understanding? I use community science data to make four points, showing (1) that elevational ranges include variation in abundance; (2) that elevational ranges are estimated, not observed directly; (3) that elevational ranges are dynamic at small spatial and temporal scales; and (4) that how we describe elevational ranges has consequences for inference of range shifts. I then present a conceptual framework for understanding elevational ranges at multiple spatial scales. This framework hypothesizes that different range-limiting processes are scale dependent and suggests that approaches to quantifying elevational distributions should be matched with the question at hand. I conclude with a list of best practices

for studying elevational ranges and highlight promising directions for future research into these complex phenomena.

Methods

The following discussion draws on examples from a characterization of the breeding distribution of Yellow-eyed Junco (*Junco phaeonotus*) in the Madrean Sky Island region of Arizona, where they occur in high-elevation pine-oak forests and adjacent habitats. In this portion of their range, the species is a partial elevational migrant. Although most birds move downslope during winters with high snow-packs, males with high fasting endurance can maintain high-elevation residence year-round, highlighting the importance of individual trait variation in structuring range limits (Horvath and Sullivan 1988; Lundblad and Conway 2020). In milder years, individuals of both sexes may move little. Yellow-eyed Juncos are easily observed, tightly associated with a habitat that is structured by a precipitation gradient that drives a canonical example of elevational zonation (Merriam and Stejneger 1890) and move only short distances throughout the annual cycle (Horvath and Sullivan 1988). For these reasons, they are a useful model of several ecologically meaningful features of elevational distributions.

I described the US range of *J. phaeonotus* in May, June, and July using observations and sampling effort from the April 2023 release of eBird's Basic Dataset. eBird is a community science platform where contributors submit "checklists" noting the presence and/or abundance of bird species detected during an observation period of arbitrary duration and distance. eBird includes automated quality filters to initiate expert review of implausible or unusual records, removing them from its data products. I used the R package *auk* (ver 0.6.0; (Strimas-Mackey et al. 2022) to apply a series of filters and manipulations that were adapted from eBird's recommendations for species distribution modeling (Johnston et al. 2021; Strimas-Mackey et al. 2023) but more stringent in maximum checklist duration (<5 h) and traveled distance (<2 km) in order to reduce the spatial uncertainty associated with individual observations. After pairing checklists with elevation and slope aspect data and assigning each observation to a 50-m elevational bin, I trained a random forest algorithm on detection/nondetection data using the R package *ranger* (ver 0.15.1; Wright and Ziegler 2015), extracting the marginal effect (or "partial dependence") of elevation on encounter rate. Additional details on data filtering and species distribution modeling are available in the supplemental PDF.

To understand how different elevational range metrics influence our understanding of climate warming-driven distributional shifts, I used the empirical mean, maximum, and minimum elevation of all *J. phaeonotus* observations to simulate hypothetical elevational ranges where relative

abundance or encounter rate fit one of two different statistical distributions (normal and skew normal). In each instance I used the corresponding density distribution function in base R (ver. 4.3.0) or *fGarch* (ver. 4031.90) to simulate the elevations of 1,000 observations before and after a 150-m upslope shift in the mean, removing all records falling above a hypothetical 3,200-m summit elevation, and again assigning each observation to a 50-m elevational bin.

Elevational Ranges Include Variation in Abundance

Elevational ranges are a reduction of the three-dimensional geographic range of a species to a single vertical axis. Because geographic ranges can be considered a spatially explicit population or metapopulation (Carter and Prince 1981; Lennon et al. 1997; Holt and Keitt 2000), an elevational range will capture a cross section of metapopulation patterns and processes. At its theoretical minimum vertical extent, elevational range breadth (i.e., the elevational distance between lower elevational range limit and upper elevational range limit) might be equivalent to the physical limits or home range size of a single individual, linked to other individuals and populations by dispersal only horizontally. At its theoretical maximum vertical extent, an elevational range might be truncated by sea level and the local altitudinal apogee, with the physical limits or territory of each individual organism adjacent to that of its upslope or downslope neighbor.

More commonly, however, the number of continuously arrayed, vertically adjacent individuals or territories—and the spacing between these entities—will vary from the lower to upper range margin. At the spatial scales commonly employed by biologists in surveys, this will produce a pattern of variation in relative and absolute abundance across elevation, with discrete elevational bands (e.g., 1,500–1,550 m) containing more or fewer individuals than others and some areas within range limits containing no individuals at all. (This pattern is also driven by the impact of sampling on inferred abundance. Although any two individuals might maintain vertically or horizontally separated territories, the foraging activities of vagile animals could bring them into a single net or pitfall trap. Imperfect transect design or survey execution would have similar effects regardless of mobility.)

Variation in abundance is intuitively linked to range-limiting processes. The observation that species are sometimes most common near the midpoint of their range (the "abundant center hypothesis"; reviewed in Sagarin et al. 2002) was first attributed to dispersal behavior (Grinnell 1922) or the effects of environmental gradients on fitness (Andrewartha and Birch 1954). James Brown (1984) later provided theoretical justification for this pattern, showing that independent, spatially autocorrelated niche axes of variable importance should result in Gaussian abundance distributions, as its probability density function is the limit

distribution for the sum of a sequence of random variables. However, violations of Brown's assumptions—for example, discontinuous gradients—are ubiquitous in nature, and recent empirical work at broad taxonomic and spatial scales has found little evidence for the abundant center hypothesis and its relatives (Dallas et al. 2017; Pironon et al. 2018; Santini et al. 2019). Contemporary approaches thus emphasize fitting nonnormal data with flexible tools, such as beta response models (Austin et al. 1994), nonparametric general additive models (Yee and Mitchell 1991), and hierarchical Huisman-Olff-Fresco models (Huisman et al. 1993; Oksanen and Minchin 2002; Freeman and Beehler 2018).

Niche axes are translated into patterns of local abundance through demographic processes. In the absence of barriers to dispersal, range limits reflect locations in which deaths (d) and departures from emigration (e) outpace births (b) and arrival from immigration (i), a scenario that can be described by a simple model for population size (N) at time $t + 1$, where $N_{t+1} = N_t + i + b - d - e$ (Gaston 2009). Elevational distributions are thus constrained by factors that drive high mortality (predation, temperatures outside critical thermal minima and maxima, or evaporative stress; see McCain and Colwell 2011), high emigration (high intra- or interspecific competition), a low birth rate (low habitat quality, stressful environmental conditions, few available mates), or low immigration (a lack of suitable habitat or distance from source populations). Of course, populations exist in more than a single dimension, and immigration and emigration may operate within (in addition to across) elevational bands. Demographic factors might also fragment continuous distributions when internal abiotic conditions and biotic interactions are patchily distributed. Regardless, cases in which N_{t+1} would be lower than N in the absence of contributions from adjacent source populations are indicative of intrinsic conditions that could shape a local, if not global, elevational minimum (see “Elevational Ranges Vary in Space and Time” below).

Across its breeding range in southeast Arizona (fig. 1a), *Junco phaeonotus* illustrates a characteristic pattern of varied relative abundance between its lower and upper range limits, with encounter rates increasing with elevation (fig. 1b) despite a likely decrease in available land area (although this pattern is not universal to all mountains; Elsen and Tingley 2015). Although I am unaware of any published distribution models for the species, its tight habitat associations offer a plausible explanation for a positive relationship between population density and elevation. As none of the Sky Islands exceeds tree line and mixed-conifer forest reaches its greatest extent and biomass near the summit of most ranges, the species' upper distributional limit is largely set by topography, not demography (at least in the absence of stand-replacing wildfire; Margolis et al. 2011). In contrast, decreasing encounter rates at low elevations suggest

declining population sizes due to some combination of unfavorable biotic and abiotic conditions—that is, a limit formed by population processes.

Importantly, the left-hand skew of the relative abundance distribution of *J. phaeonotus* is poorly described by common summary statistics of elevational ranges (fig. 1b). In the Santa Catalina Mountains, estimates of elevational range breadth derived from the lowest and highest observations or the middle 90th percentile of all observations obscure low (<0.60) encounter rates below 2,200 m. Similarly, the mean and median elevation of all observations fall below the peak of the species abundance. Abundance-weighted mean elevation provides a better description of where encounter rates are highest but is uninformative about range edges and their dynamics. Although suitable for some questions, simplified descriptions of elevational ranges hinder a mechanistic understanding of species distributions, while field- or taxon-specific conventions for describing elevational ranges hinder comparative approaches.

The presence and importance of variation in local density across elevation has been recognized in the literature, if sometimes overlooked, for at least five decades. Brown's 1984 synthesis of abundance and geographic distributions drew heavily on data from R. H. Whittaker's (1956, 1960) descriptions of the flora of the Smoky and Klamath-Siskiyou Mountains as well as similar work by Edward Beals (1969) in Ethiopia. In 1970s ornithology alone, articles by Diamond (1972), Terborgh (1977), Terborgh and Weske (1975), and Able and Noon (1976) followed suit, describing relative abundance across a diverse set of elevational gradients and testing nascent theories in community ecology and biogeography. Although this practice continues (e.g., Samson et al. 1997; Siebert 2005; McCain 2006; Röder et al. 2017; Freeman and Beehler 2018; Sandoya et al. 2021), examples of articles in the last 15 years that do not incorporate any measure of abundance into definitions of elevational range are easy to find in fields from macroecology (Kozak and Wiens 2010) to phylogenetics and historical biogeography (Hutter et al. 2013; Cadena et al. 2020) to ecophysiology (Sheldon and Tewksbury 2014; Maccagni and Willi 2022; Linck et al. 2023). Even among studies of elevational range shifts, where the importance of local abundance for accurate inference is well known (Shoo et al. 2006), crude definitions of elevational ranges are not unusual. In a recent meta-analysis of where range shifts are occurring most rapidly, for example, 5 of 15 included articles relied only on point estimates of elevational limits or central tendencies (Mamantov et al. 2021).

In some cases, variation in abundance across a gradient may be difficult to characterize at relevant timescales, such as when irruptive or otherwise highly vagile species may range widely between upper and lower elevational range limits during daily activity. At the other end of the spectrum,

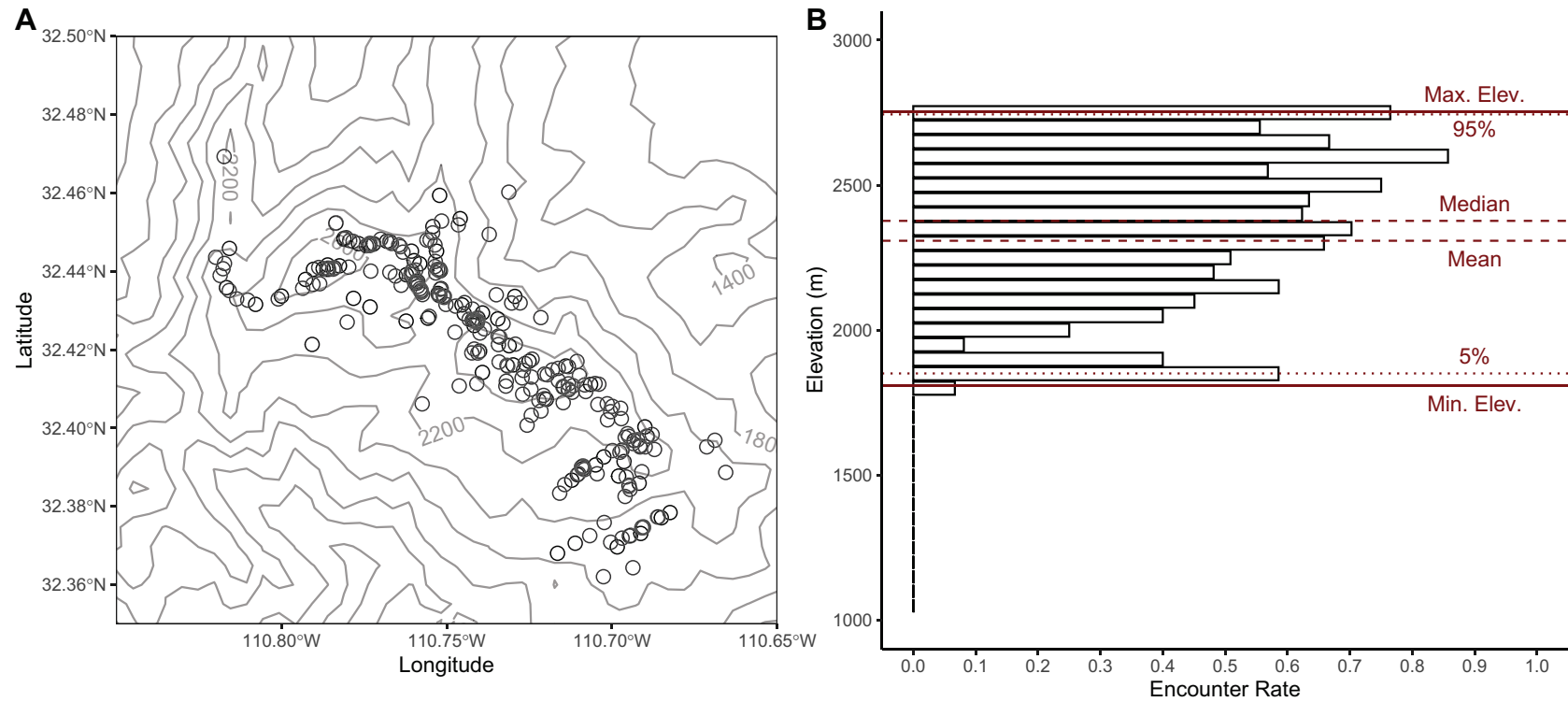


Figure 1: A, Subsampled eBird records of *Junco phaeonotus* within the Santa Catalina Mountains, Arizona (see “Methods”). B, Two-dimensional depiction of the elevational distribution of *J. phaeonotus* in the Santa Catalinas. This figure and others like it elsewhere in the article illustrate variation in a metric of relative abundance (encounter rate; the proportion of eBird checklists with at least one *J. phaeonotus* observation) across elevation in discrete bins of constant width (here 50 m each). The annotated horizontal lines indicate the value of common elevational range descriptors: “Max. Elev.” and “Min. Elev.” refer to the absolute maximum and minimum elevation of any observation of the species, “Median” and “Mean” refer to the median and mean elevation of all observations, and “95%” and “5%” refer to the 95th and 5th percentiles of all observations.

geographic range evolution may render patterns produced by short-term ecological processes irrelevant. Practical concerns ranging from the need to compare results with historical surveys to the suitability of presence/absence data for some questions will also always have a heavy influence on study design. Still, there are likely few scenarios in which abundance data and the demographic perspective they provide would fail to add valuable signal.

Elevational Ranges Are Usually Estimated, Not Observed Directly

There are some instances in which the elevational distribution of a particular organism may be characterized precisely. Down the hill from my office, for example, I can see the entire southwestern aspect of Montana's Bridger Mountains, including the lower and upper extent of Douglas fir (*Pseudotsuga menziesii* var. *glauca*). Satellite imagery or field transects could likely provide an exact location for every extant Douglas fir in some portion of the range, a situation in which elevational range metrics could be known with complete confidence down to the spatial grain of the individual.

In many cases, however, elevational distributions are estimated from sampling, not directly observed. Our knowledge is imperfect because we are not omnipresent and because organisms differ in how readily they are detected. Although the detection probability for mature Douglas fir is ~1 for an observer with a modest amount of training, a Northern Pygmy Owl perched on its branches might be noticed only by an experienced birder under rare circumstances. Intuition would thus suggest that imperfect detection is a concern restricted to studies of vagile animals (Kellner and Swihart 2014). Although this assumption is widespread, detectability appears to rarely be perfect in plants and may be as low as 0.1, even for medium-sized trees and shrubs (Chen et al. 2009, 2013; Hauser et al. 2022; Perret et al. 2023). Beyond mobility, detection probabilities will be influenced by a variety of other ecologically relevant traits (size, phenology, seasonal and diel activity patterns, life history, crypsis, vocalizations) that may be phylogenetically conserved. In most cases, it will also be positively correlated with a species' local abundance (McCarthy et al. 2013). Failing to incorporate detectability into multispecies surveys can thus lead to systematic biases in patterns in comparative studies of their elevational ranges.

Occupancy modeling provides a robust framework for predicting the proportion of sites occupied by a species of interest—that is, estimating a local or global range from observations and geographic or habitat variables—while allowing for incorporation of imperfect detection (MacKenzie et al. 2002). Although their application to studies of elevational ranges is intuitive and not uncommon (e.g., Moritz et al. 2008; Tingley et al. 2012; Mizel et al. 2016; Campos-

Cerqueira et al. 2017; Cheng et al. 2019), data requirements for estimating detection probability pose an obstacle for many studies (e.g., Menéndez et al. 2014; Burner et al. 2019, 2020). Alternative approaches include species distribution models that account for variation in detectability by controlling for survey effort (Guillera-Arroita et al. 2015; Strimas-Mackey et al. 2023) or modeling uncertainty around range limits (Rowe et al. 2010). Nonetheless, many studies make no effort to distinguish between the unobserved “true” elevational distribution of a species and range metrics based on a necessarily limited set of observations (e.g., Raxworthy et al. 2008; Freeman and Class Freeman 2014; Linck et al. 2021, 2023; Holzman et al. 2023).

A consequence of ignoring the uncertainty inherent to most descriptions of elevational distributions is that downstream analyses rely on potentially erroneous range descriptions with false precision. In Yellow-eyed Juncos, estimates of elevational range minima and maxima based on encounter rate change as different numbers of checklists are randomly sampled from eBird's full dataset (fig. 2). As expected, more data lead to better estimates of range limits from the underlying species distribution model (fig. 2). A naive description of elevational occupancy based on direct observation and not the marginal effect of elevation on encounter rate performs better, albeit at the expense of ignoring detection probability. Focused surveys of elevational gradients, although unable to match the scale of citizen science datasets, can likely achieve satisfactory accuracy at lower sample sizes (Jackson et al. 2015).

Ultimately, the choice of whether to treat elevational range metrics as estimates—quantities calculated from observations, with associated error—is both practical and philosophical. Practically, investigators will have to weigh the quality and type of their data along with constraints of field effort and funding. They should also examine the consequences of an error in range limit estimation on their study question, ideally with tools such as power analysis (Johnson et al. 2015). Philosophically, treating a description of an elevational range as fundamentally uncertain is likely to have epistemological benefits in most cases. As discussed further below, multidimensional variability is inherent to species' ranges, which are themselves the product of multiple complex factors. It may also help keep attention focused on variables directly impacted by range-limiting processes, such as local abundance or presence/absence, rather than a one-dimensional interval between two numbers. Geographic ranges are, after all, an abstraction (Brown et al. 1996). We should ensure it is one that serves us.

Elevational Ranges Vary in Space and Time

Earlier, I described elevational ranges as a cross section of a population or metapopulation in the vertical axis. This

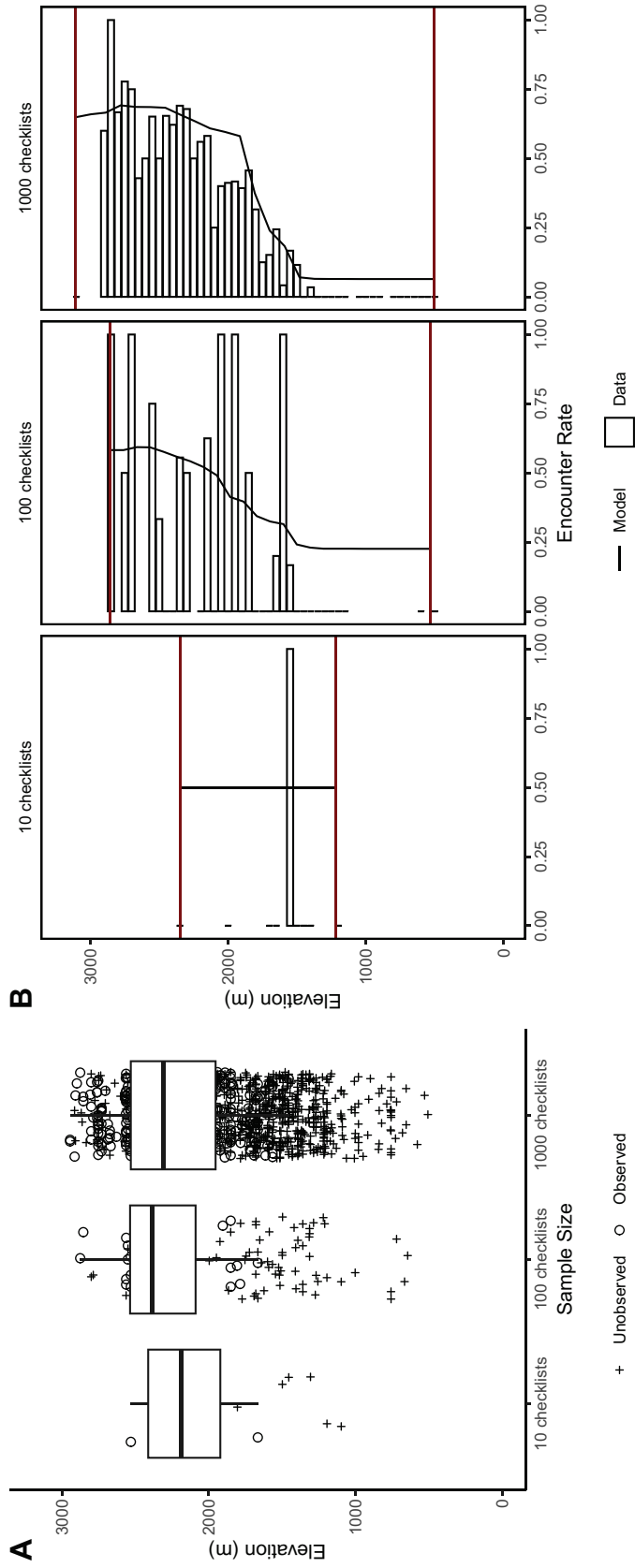


Figure 2: Impact of subsampling *Junco phaeonotus* observations on inferred elevational range characteristics. *A* shows the elevational distribution of different-sized subsamples of eBird checklists from across Arizona, with open circles indicating that the species was observed and crosses indicating that the species was unobserved. *B* illustrates variation in relative abundance (encounter rate) across elevation in the same subsamples. The black line in each panel is the marginal effect of elevation on the encounter rate, as estimated from a random forest algorithm trained on each subsampled dataset. Elevational range maximums and minimums (solid red horizontal lines) are defined as the maximum or minimum elevation with a modeled encounter rate of >0.05, respectively.

simplification elides the fact that for any given taxon there are infinitely many such cross sections across the latitudinal and longitudinal extent of its range, varying in terrain. For certain taxa and climates or at smaller geographic scales, defining the elevational range of an organism with one cross section as opposed to another may reveal no meaningful difference. But for others, particularly when other environmental gradients cut perpendicularly to elevation across their range, different cross sections may lead to markedly different estimates of range minima, maxima, central tendencies, and elevational abundance distributions.

The sources of this spatial variation in elevational ranges will themselves vary across space and phylogeny. The difference in the elevation of vegetation bands (“life zones”) between northeast- and southwest-facing aspects of the San Francisco Peaks and a nearby volcanic cone was noted and illustrated by Merriam and Stejneger (1890), who connected the pattern to slope exposure and solar radiation. Whittaker (1960) presented a similar diagram of the elevational extent of forest types in the Klamath-Siskiyous across a soil moisture gradient, showing upward displacement of habitats in the most xeric portions of the range. For plant species in particular, systematic variation in the elevation of substrates such as serpentine soil due to orogeny may lead to different elevational ranges in areas of their distribution with different geological histories (Burge and Salk 2014).

More generally, prevailing winds that blow counter to the dominant axis of a mountain range can generate precipitation and relative humidity differences between its windward and leeward sides, impacting microclimate, the steepness of temperature and humidity gradients, and the elevational distributions of organisms (Jankowski et al. 2009; Minder et al. 2010). On islands and in coastal or otherwise isolated mountains, life zones and the elevational distributions of species that rely on them are often compressed and shifted downslope due to some combination of increased cloud formation on exposed summits, the buffering effect of the ocean, and steeper temperature lapse rates over lowland plains than highlands (Pouteau et al. 2018). Known as the Massenerhebung effect (Richards 1952; Grubb 1971), this phenomenon appears to explain a significant portion of local variation of avian elevation ranges in New Guinea (Diamond and Bishop 2022).

In Arizona, the elevational distribution of Yellow-eyed Juncos varies with both slope and mountain range. In the high Pinalenos (3,627 m), the middle 50th percentiles of all breeding season observations are lower from the northwest to east aspects than west to southeast, mirroring patterns in spruce-fir and ponderosa forest (fig. 3a; Merriam and Stejneger 1890). Although uneven sampling adds noise to observed elevational limits, geography itself is responsible: with a relatively limited extent of high-elevation conifer forest but several sheltered, low-elevation canyons with

moist microclimates (McLaughlin and Bowers 1990), *Junco phaeonotus* habitat in the Santa Ritas largely occurs below its analogs in other Sky Islands.

A second dimension of variation in elevational ranges are changes in vertical abundance at short temporal scales, that is, cross sections taken day to day, month to month, or one year to the next. The most dramatic and best-known example of this variation is the irruptive or seasonal elevational migration of vagile animals such as birds (e.g., Loiselle and Blake 1991), bats (Fraser et al. 2010), ungulates (Oosenbrug and Theberge 1980), and insects (Peterson 1997). Reviewed in Boyle (2017) and Hsiung et al. (2018), elevational migration typically involves the upslope or downslope movement of individuals at scales of ~200 (Wheelwright 1983) to $\geq 2,000$ m (Williamson and Witt 2021a) and has profound implications for elevational range estimates. Yet subtler changes in abundance distributions across elevation may be common as well, as population dynamics and vital rates appear to vary more at geographic range margins than range centers (Curnutt et al. 1996; Mehlman 1997; Angert 2009). Such variability can lead to false positives in tests of range expansions and contractions but has only infrequently been incorporated into empirical work (McCain et al. 2016).

I hypothesized that variation in population size due to indirect impacts of nondirectional climate fluctuations such as the El Niño–Southern Oscillation would cause interannual changes in the elevational range limits in *J. phaeonotus*. Acknowledging the limitations of uneven sampling effort inherent to community science datasets such as eBird, this appears to be the case: the 95th, 50th, and 5th percentile of all observations of Yellow-eyed Juncos shifts from year to year in the frequently visited Santa Catalinas, on a scale ranging from the tens to hundreds of meters (fig. 3b). As a result, elevational range estimates will strongly depend on survey date, filtering procedures, and how data are aggregated across time. A study comparing solely the median, minimum, or maximum elevations of Junco observations in 2022 with those from a historic survey would infer much less upslope movement than one using data from 2021, for example. Summarizing abundance distributions with multiple descriptive statistics and samples will better reflect differences in the position of elevational ranges across space and time (fig. 3b).

Range Shift Inferences Are Sensitive to Elevational Range Concepts and Definitions

By now I hope it is apparent that our conceptualization and definition of elevational ranges will have an impact on our ability to identify range shifts and estimate their size, a major goal in global change biology. Earlier reviews

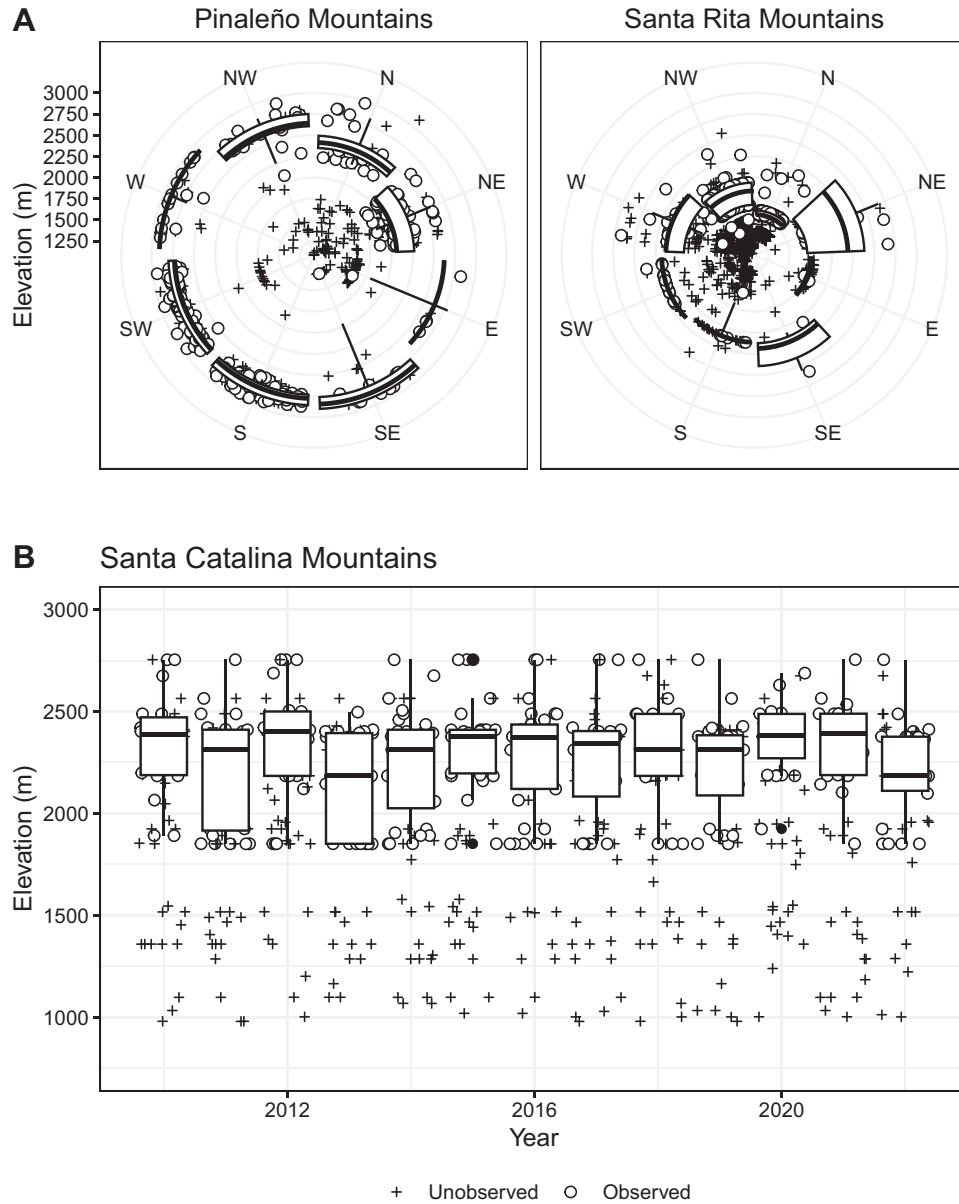


Figure 3: The observed elevational distribution of *Junco phaeonotus* varies by aspect, across mountain ranges, and from year to year. Boxplots in A show the median elevation of all observations (horizontal lines), the range between the 5th and 95th percentile (vertical lines), and the range between the 25th and 75th percentile (boxes) in the Pinaleño and Santa Rita Mountains, Arizona. Open circles show the elevation of the checklist where *J. phaeonotus* was observed; crosses reflect checklists where the species was not observed. Boxplots in B are calculated for a random sample of 50 checklists from the Santa Catalina Mountains for each year from 2010 to 2022. Percentiles and points are indicated as before.

of range shifts have discussed related issues in study design, covering the selection of focal taxa (Parmesan 2001), the influence of local abundance and choice of range metrics (Shoo et al. 2006), the problems with presence-only datasets (Tingley and Beissinger 2009), and the influence of population variability (McCain et al. 2016). To further explore this point, two questions are worth posing. First,

when we quantify an elevational range, which features are we capturing and which are we ignoring? Second, when warming temperatures have caused a shift in the geographic range of a species, how will we know?

The first question relates to the multidimensional nature of elevational ranges as dynamic populations or meta-populations in space and time. The minimum data required

to infer an elevational range shift are summary statistics of a population's elevational distribution at two points in time, for example, a measure of the central tendency of the elevation of observations in each dataset. In the simplest scenario, this might be the arithmetic mean of presence-only data in elevational bands. If so, the researcher is implicitly assuming that the biologically meaningful features of an elevational range are captured in a single data point: that calculating the mean elevation of observations taken on a different day or different slope or different mountain range would make no difference, that patterns of abundance are irrelevant to the study's goals, and that the observations are precise and complete.

Few would endorse such assumptions! More realistically, the researcher might calculate several summary statistics. Even so, the success of her work depends on her data providing a representative snapshot of reality. When experimental design is unconstrained by comparability with historical data—as should be the case for future ecological monitoring or with some large-scale biodiversity datasets—developing a hypothesis for the drivers and underlying process of an elevational range shift can help guide priorities. In some situations, such as elevational shifts in recruitment in long-lived tree species, accurately describing patterns of abundance may be most important. In others, sampling additional time points to compensate for population variability could take precedence (McCain et al. 2016).

How to detect true range shifts depends on the method used to assess confidence in observed patterns and the nature of the underlying process itself. Because most range shift studies to date have relied on imperfect historical data from a single year or short span of years, often lacking any record of absences or effort, statistical tests are often performed at the level of communities (e.g., Freeman and Class Freeman 2014). A scenario in which 50% of species moved their entire range upslope 150 m and 50% of species moved their entire range downslope 150 m would lead to a failure to reject a null hypothesis of a change in the community's elevational means but would not eliminate the possibility that half of all taxa were showing true responses to warming temperatures. Detecting range shifts with this study design therefore depends on either a concerted response across focal species or trait data that can explain variation in shift size and direction. More complicated cases—such as when the range shift process primarily involves changes in the elevational distribution of abundance, occurs across geography with complex microclimates (Breshears et al. 2008; Kelly and Goulson 2008), or involves a species with irruptive fluctuations in population size—may go undetected.

At other times, such as when data permit the use of occupancy models (Cheng et al. 2019) or confidence intervals

around range limits are provided (Rowe et al. 2010), analysis at the species level is possible. Each taxon-specific range shift can be qualified with its associated uncertainty, and downslope movement in some species will not weaken evidence for upslope movement in others (although attributing any particular response to warming will require climatic or physiological data). In these circumstances, our ability to detect shifts will depend on the interaction of the range shift process, choice of summary statistics, and sample size and location. Detailed, ecologically informed hypotheses will increase the odds of effective study design.

Simulating encounter rate data for *Junco phaeonotus* under a 150-m mean elevational range shift illustrates the impact of choice of summary statistics and the underlying elevational distribution of abundance on inferred upslope movement (fig. 4). When both historic and modern encounter rates are normally distributed—as would be expected under Brown's (1984) model of local abundance across an uninterrupted environmental gradient—the lower elevational range limit shows the greatest change in the fact of the 100-m mean retraction, jumping from 1,014 to 1,248 m, while the upper elevational range limit, constrained by geography, shows little change (+21 m). Changes in the median (+149 m), 5th (+134), and 95th (+112) percentiles are more representative of the population's "true" range shift. Under a transition from a left-skewed to a right-skewed distribution—as might be expected if marginal low-elevation habitat is no longer suitable while marginal high-elevation habitat opens up, but the range center remains most suitable—lower and upper range limits and the bottom 5th percentile show large jumps (+784, +332, and +373 m, respectively), while the median remains nearly stationary (+5 m).

These toy examples are consistent with the idea that different shift processes may have underlying different causes and can lead to different ecological consequences. A shift driven by niche tracking might indicate consistent responses to warming temperatures across interacting taxa and thus result in little community reassembly across an elevational gradient. In contrast, a shift process that involves niche deformation or niche truncation might indicate idiosyncratic responses across taxa and lead to significant community reassembly.

Elevational Ranges Are Shaped by Scale-Dependent Processes

The discussion above is haunted by issues of scale. If variation in relative abundance is an informative property of elevational ranges, how should species with different dispersion patterns, home range sizes, and densities be compared? Does accounting for detection probability matter equally at great and small spatial scales? And if elevational

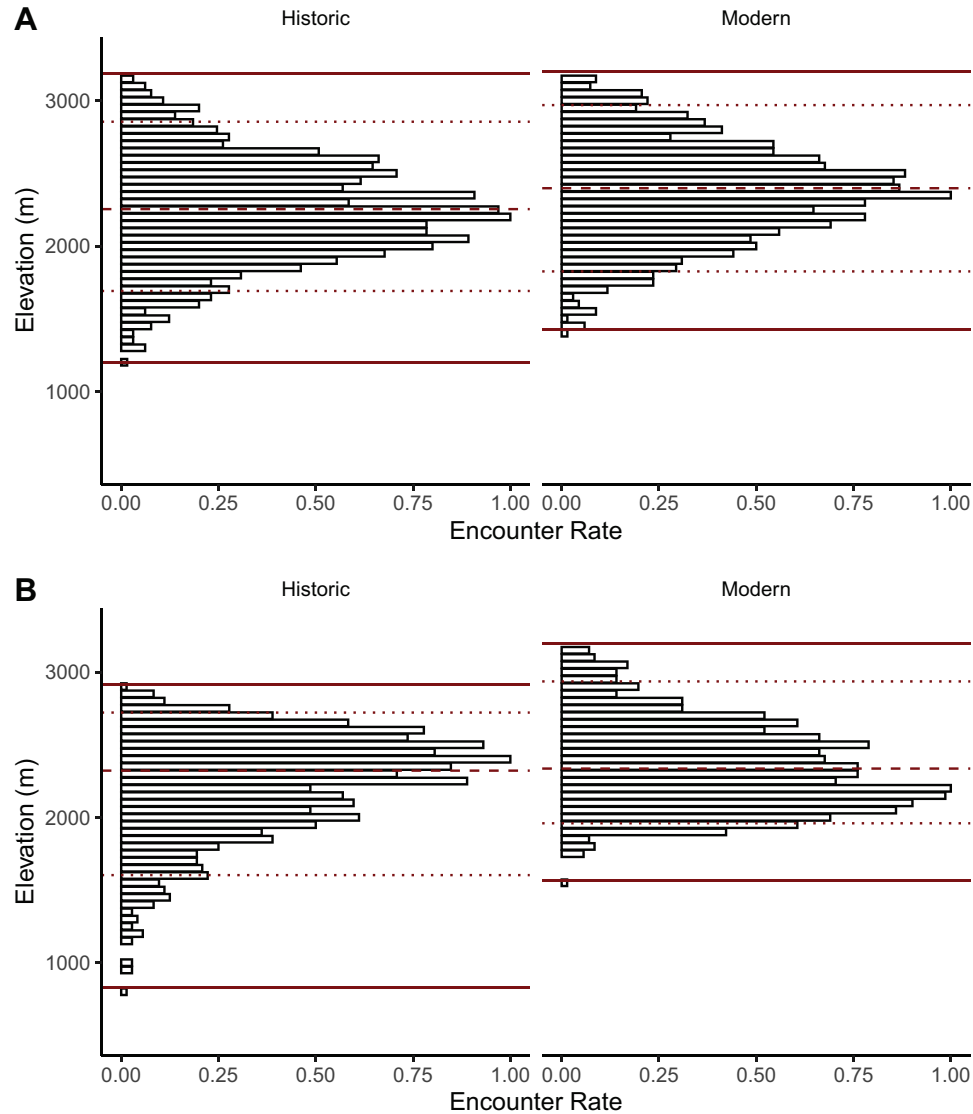


Figure 4: Inferred elevational range shifts are sensitive to the shape of elevational distributions. Each panel from top to bottom shows simulated elevational range data before (“Historic”) and after (“Modern”) a 150-m upslope shift in the mean of the underlying distribution of encounter rates, with observations assigned to 50-m elevational bins. In *A*, both historic and modern distributions are normally distributed, with a mean and variance derived from *Junco phaeonotus* eBird records. In *B*, the historic data have a skew normal distribution with a shape parameter of 2, while the modern data have a skew normal distribution with a shape parameter of -2 . Solid lines show the minimum and maximum of elevations of simulated observations, dotted lines show the 5th and 95th percentiles, and dashed lines show medians.

ranges vary across aspects, how great a geographic sample is required to accurately describe them? Although answers to these questions will vary across taxa and geography, they highlight the importance of developing a framework to understand how scale impacts descriptions of elevational distributions and inferences about the processes that shape them.

Scale is a perennial theme in ecology and the study of geographic distributions. In a 1989 review in *Functional Ecology*, J. A. Wiens highlighted the correlated nature of

spatial scale and the temporal scale of processes of interest, how the extent and grain (resolution) of a study determine its ability to detect patterns, and the need for nonarbitrary ways to define scale based on the biology of organisms themselves. Soon after, Levin (1992) emphasized the importance of matching scale with methods for quantifying patterns. Among studies of elevational distributions, lessons from these influential articles and a related literature have primarily been applied to studies of alpha and beta diversity. Both extent (Nogués-Bravo et al. 2008) and grain size (Rowe

and Ligard 2009) can impact the shape of elevational species richness curves and estimates of species turnover (Martínez-Villa et al. 2020), although other studies report coarsely consistent patterns regardless (Bhatta et al. 2018). Grain size can also impact inferred drivers of species richness patterns (Rowe et al. 2015) and affect estimates of the volume, position, and shape of environmental niches (Lu and Jetz 2023). Consistent with suggestions from Wiens, Levin, and others, this body of work indicates that choice of study extent and grain should be aligned with the hypothesized mechanism behind the pattern under consideration. I follow this tradition to argue that scale is crucial to accurately characterizing and understanding the drivers of elevational ranges of individual taxa. Elevational distributions exist at multiple scale domains, each of which is shaped by unique processes (i.e., show scale dependency; fig. 5). At local scales—across a single slope or within a drainage with a consistent aspect—an elevational range can be summarized through the direct observation of most or all individuals from valley floor to ridgeline. Range limits are simply the locations of the lowest and highest recorded individuals, and the range itself can be easily described in its entirety as a collection of elevations, as survey grain should be small enough to capture the radius of individual territories. An individual organism's location on the gradient at any point in time will be determined by natal dispersal, diel movement (if vagile), physiological tolerance and abiotic conditions, and biotic interactions. These processes will lead to high temporal variance in range metrics at short time intervals and predict that organismal performance will decline with increasing distance from distributional minima and maxima. A local scale is therefore best suited for studies with *a priori* mechanistic hypotheses, especially those that can be tested experimentally: reciprocal transplants, tests of critical thermal limits, and manipulations of parasite load or potential symbionts.

One level up in a scale domain hierarchy, a species' regional elevational range—here defined as a logically discrete subsection of its overall geographic range, such as a single mountain range or a genetic deme—will encompass elevational variation in the abiotic and biotic variables that directly influence occupancy. As discussed above, its limits will reflect demography at a temporal scale of multiple generations. Although an individual organism may survive beyond range limits for a relatively short period, successful recruitment will require remaining within a geographic projection of its realized niche. This scenario predicts that deaths and emigration will exceed births and immigration at or past range limits, leading to relatively stable correlations between occupancy and abiotic and biotic conditions across gradients. Regional-scale elevational ranges should be studied with an intermediate survey grain that captures local variation in abundance and are best suited for tasks

such as prediction or casual inference using multivariate data (e.g., species distribution models). Because the impacts of climate change on distributions are most meaningfully identified as changes in patterns of abundance in heterogeneous landscapes where correlated drivers can be disentangled, studies at a regional scale are well suited to test for range shifts.

The broadest-scale domain is the entirety of a species' distribution. For many taxa, this will involve systematic variation in range metrics across geography because of local adaptation or historical contingency (e.g., the chance colonization of a competitive congener; Cadena 2007). Elevational ranges in this “global” sense are formed by niche evolution and the historical biogeographic processes of dispersal, vicariance, and extinction. Consequently, they should vary coarsely across geography, with variation partitioned across the boundaries of demes, correlated with broad trends in abiotic conditions across latitude and longitude or constrained by the consequences of past dispersal events and range expansion and contraction. Grain size choice should reflect these predictions, as finer-scale assessments of distributions will add noise generated by largely irrelevant factors such as microtopographic variation. In some cases, ranges of phylogeographic clades will show phylogenetic signal, reflecting either niche conservatism or adaptive divergence.

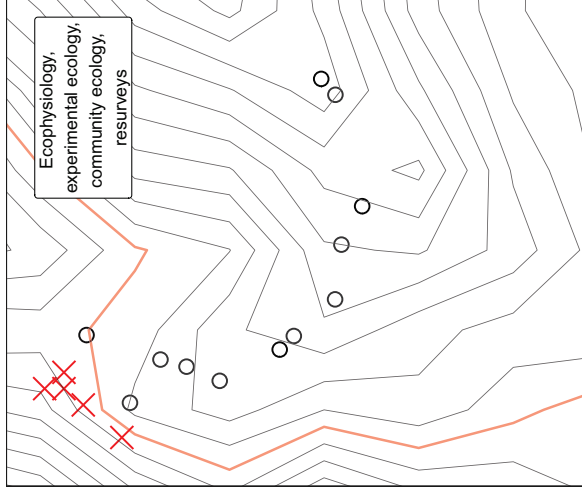
Although the scale domain categories discussed here are arbitrary, they provide a guide for aligning research questions to their appropriate extent and grain. The spatial extent of an elevational distribution is positively related to the temporal scale of the processes that shape it, and mixing space and timescale domains to address a research question can hamstring otherwise well-designed studies. Trivially, using species-wide measurements of the minimum and maximum elevation of occurrence in a study of range shifts along a single slope may lead to a false negative, while using limits from a single slope in a study of niche evolution may exaggerate rates of change if unrepresentative of its global elevational range. Metrics downstream of elevational range descriptions are similarly sensitive to scale alignment. Calculating beta diversity from global range limit data will likely be more informative of community assembly processes than estimates derived from local range limit data, while population modeling will likely be more successful when grounded in fine-scale occupancy data.

Conclusions

In this synthesis I have argued that elevational ranges include variation in abundance that reveals the impact of niche limits on fitness; that elevational ranges are usually estimated, not directly observed; that elevational ranges

Local

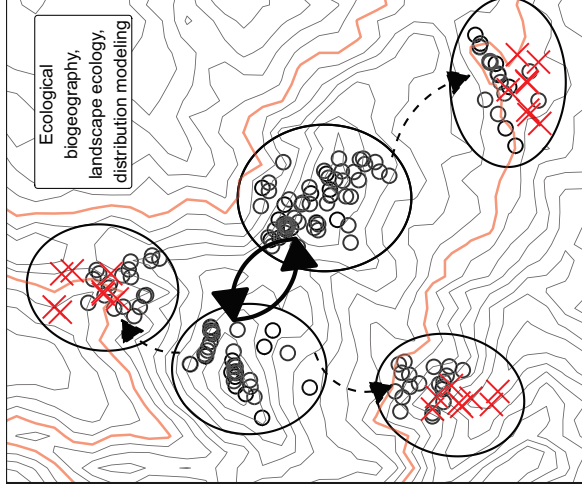
Hypothesis: Range limits reflect fundamental niche limits and dispersal



Prediction: Poor performance past range limits

Regional

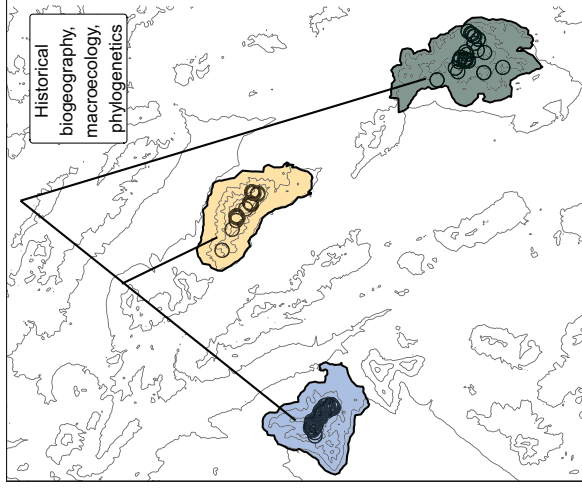
Hypothesis: Range limits reflect metapopulation dynamics



Prediction: Negative population growth past range limits

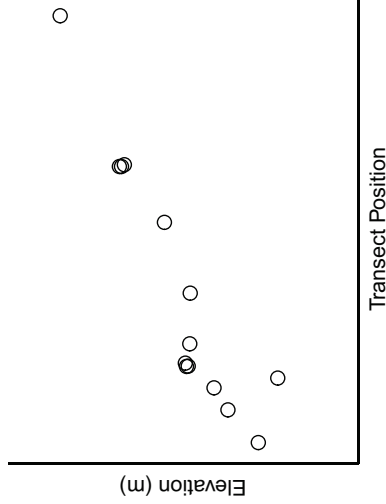
Global

Hypothesis: Range limits reflect historical contingency and adaptive evolution

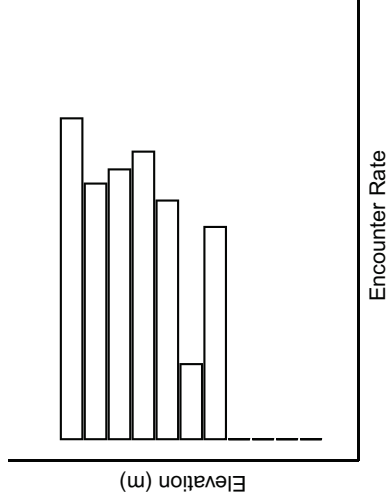


Prediction: Phylogenetic signal in elevational ranges

Data: Raw elevations of observations



Data: Binned relative abundances



Data: Summary statistics across populations

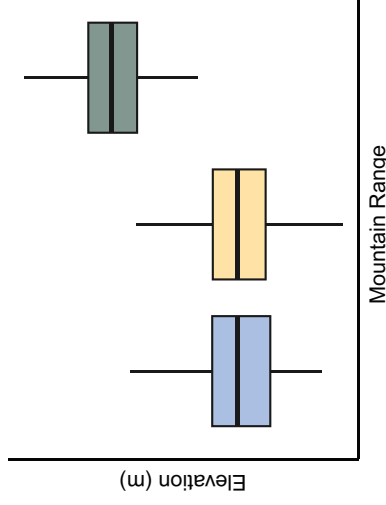


Figure 5: Elevational ranges exist at different spatial scales and are limited by scale-dependent phenomena. At a local scale (i.e., a single mountainside), raw data on the elevation and position of each individual is feasible to collect and useful for testing hypotheses about organismal performance, abiotic variables, and biotic interactions. At a regional scale (i.e., an entire mountain range), relative abundance across elevation ("Encounter Rate") is informative about the metapopulation dynamics that limit distributions, such as immigration, emigration, mortality, and births. At a global scale (i.e., all mountain ranges in a species' distribution), elevational range summary statistics can be used to understand latitudinal and longitudinal variation and are informative about biogeographic and macroecological processes.

vary across small spatial and temporal scales; and that how we quantify elevational ranges influences our ability to detect range shifts. I have also proposed that elevational ranges are best understood as hierarchical phenomena, with range limits formed by scale-dependent processes.

These arguments have implications for best practices in studying elevational ranges. First, the spatial grain and extent of surveys should align with the process under investigation. Generally, evolutionary questions will require descriptions of ranges from larger areas than ecological questions (fig. 5). Second, surveys should document the number of individuals of each focal species at each elevation (as well as absences and effort), as this will allow researchers to describe patterns of abundance as well as simple summary statistics (Billman et al. 2024). Third, investigators should employ replication. Spatial replicates will help link occupancy and abundance to niche axes, while temporal replicates are essential for contextualizing short-term stochasticity and seasonal movements. Last, surveys should pair occurrence records with other data types. Trait measurements, fine-scale measurements of abiotic conditions, and estimates of the abundance of interacting species will all increase the long-term value of datasets, especially when associated with vouchered specimens (Webster 2017).

My recommendations stand to help us determine the degree to which heterogeneity in range shifts reflects biological responses to climate change versus measuring error (e.g., Holzmann et al. 2023), help understand the connection between functional traits and range characteristics (e.g., Linck et al. 2023), and improve our understanding of elevational range evolution (e.g., van Els et al. 2021). Both descriptions of elevational occupancy and mechanistic studies of range limits will also benefit from novel data streams. Although still impractical for many species, technologies to track individual movement are advancing rapidly (e.g., Williamson and Witt 2021b; Williamson et al. 2024) and will complement repeated transect surveys to describe short-term changes in elevational ranges. Long-term monitoring of communities along elevational gradients should begin now, aided by citizen science initiatives (Freeman et al., in prep.; <https://benjamingfreeman.com/mountainbirdnetwork>), autonomous recording units (Drake et al. 2021), and camera traps (Snider et al. 2024). Of particular importance are efforts to quantify demographic rates across gradients, still a frontier for most nonplant taxa (Conlisk et al. 2017; Caruso and Rissler 2019; Ordoñez et al. 2024). Genomic data have shed light on patterns of speciation and hybridization across elevation (Culumber et al. 2011; Aizawa and Iwaizumi et al. 2020; Linck et al. 2020; Luzuriaga-Aveiga et al. 2021), but dense, landscape-scale sampling remains uncommon (Waterhouse et al. 2018), particularly in concert with trait and environmental data (Bachman et al. 2020).

Climate warming is accelerating, and the study of elevational distributions is thus likely to retain its central role for a wide range of questions in ecology and evolutionary biology and deserves continued critical examination. Pragmatism will no doubt continue to govern the design of studies of elevational range limits and shifts. However, careful consideration of study design and statistical approach can help reduce bias and maximize inference in the face of constraints. In doing so, we may begin to understand the most important features of the complex phenomenology that is an elevational range.

Acknowledgments

The ideas in this article began to germinate while I was supported by a National Science Foundation Postdoctoral Research Fellowship in Biology at the University of New Mexico (DBI-1907353). I thank Ben Freeman, Chris Witt, Erik Beever, and Zac Cheviron for providing feedback on the manuscript; Ernesto Gallardo and Daniel Cadena reviewed my translation of the abstract. This article is dedicated to Eva Wallace Schimel, who was born on December 31, 2024.

Data and Code Availability

Data and a digital notebook with code to reproduce all figures and analyses are available from the Dryad Digital Repository and Zenodo (<https://doi.org/10.5061/dryad.ht76hddr1>; Linck 2025).

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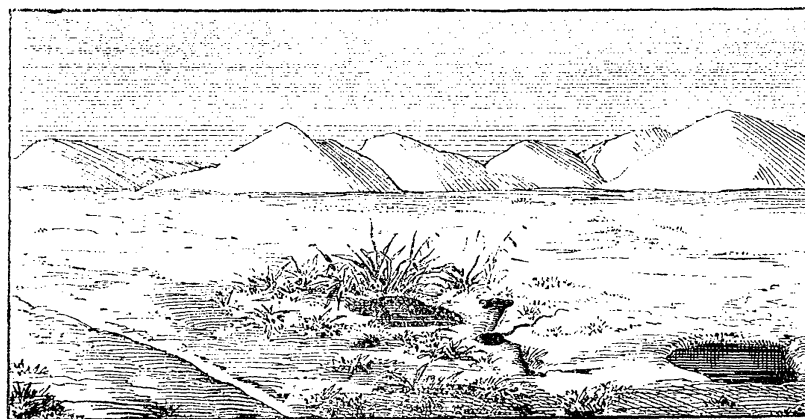
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Associate Editor: Vincent M. Eckhart
Editor: Jill T. Anderson



“Just north of this is found a cluster of springs; the largest and most central one is called Saturn.” From “The Springs of Southern Nevada” by D. A. Lyle (*The American Naturalist*, 1878, 12:18–27).