Title: Measuring the edges of species' geographic ranges

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Abstract

1. The fundamental unit of spatial ecology is a species range: the geographic area that it occupies. Species ranges are delineated by range edges (also known as boundaries or limits). Why range edges occur where they do and not elsewhere, and what makes them move, has been an active area of research since the 19th century. In the present day, range edge dynamics are an important metric of biodiversity's response to climate change, as species shift toward the poles to track their climatic niches. Yet methods for measuring range edges and quantifying their displacement are often applied *ad hoc*.
2. Here I described common methods for describing range edge positions and applied them to example data for a bird species and a fish species, using some of the most popular datasets in climate biogeography: the Audubon Society Christmas Bird Count and a National Oceanic and Atmospheric Administration bottom trawl survey.
3. I showed that the choice of range edge metric influences where range edge positions are estimated to occur; whether they are estimated to be shifting over time; and the estimated rate of shift. The lack of universal metrics for range edges has likely shaped statistics reported in synthesis studies that measured overall biodiversity responses to climate change and global rates of range shifts. Through simulation, I found that reliably detecting range edge shifts may require decades of data or more, suggesting that many global change studies in this field are underpowered.
4. Pairing metrics to research questions, sharing raw data and code, and conducting power analyses before reporting statistically significant results will all help to minimize this issue. Going forward, the field of biogeography should confront the degree to which *ad hoc* methods have influenced our understanding of range edge dynamics, and move toward universally accepted metrics.

Data/code

The data and code for this project are available on GitHub and in an anonymized repository at: https://anonymous.4open.science/r/range-edge-methods-96E1/

Keywords

Range edges; range boundaries; range limits; biogeography; range shifts; non-random subsampling; time-series; power analysis

Introduction

Range edges (or limits, or boundaries) are a fundamental unit of spatial ecology. Range edges are commonly understood to delineate where a species' geographic range ends on a map (Gaston 2003). They have fascinated ecologists and evolutionary biologists since the origins of our field (MacArthur 1972; Wallace 1876). Range edges are dynamic, over short and long time scales (Boisvert-Marsh *et al.* 2014; Williams & Blois 2018). In recent decades, many species' range edges have begun to shift polewards in concert with global climate change (Hickling *et al.* 2006; Parmesan & Yohe 2003). These recent shifts have underscored how range edges are part of humanity's relationship with nature; they influence our management boundaries and conservation plans, and are embedded in our culture and history (Pecl *et al.* 2017). Range edges are also where we often test foundational hypotheses in ecology and evolutionary biology—about dispersal, population genetics, species interactions, species invasions, and of course biogeography (Sexton *et al.* 2009; Willi & Van Buskirk 2019).

However, no universal metrics exist for range edges. Range edges have been characterized using expert opinion, species distribution models, or through metrics based on species' abundance or presence, in one, two, or three spatial dimensions—all using bespoke methods that are not standardized within fields or among studies (Gaston 2003; Guisan & Thuiller 2005). For example, some studies measure the range edge as the most distal point observation or occupied grid cell along a single dimension such as latitude (La Sorte & Thompson, III 2007; Schoeman *et al.* 2015). Others average these most distal records to measure range edges: Hällfors *et al.* (2021) and Hickling *et al.* (2006) used the mean latitude of ten most distal occupied grid cells and Kerr *et al.* (2015) used the mean latitude of five, ten, and 20 most distal point observations. Perry *et al.* (2005) measured range edges as the abundance-weighted mean of the three most distal point observations. Quantiles of observations or densities in a single dimension (usually latitude), often 0.01, 0.05, or 0.1 for equatorward edges, and 0.9, 0.95, or 0.99 for poleward edges, are also common (Fredston-Hermann *et al.* 2020; Sittaro *et al.* 2017; Zhu *et al.* 2012). These point- or grid-based methods may also be applied to the outputs of statistical species distribution models that estimate abundance (Fredston *et al.* 2021) or probability of occurrence (Yalcin & Leroux 2017) over space and time. Hulls or polygons are often used to characterize range edges in two dimensions, but typically with the aim of quantifying range size and shape, rather than the position of the edges (Burgman & Fox 2003; Yalcin & Leroux 2017). The effect of these methodological choices on analytical conclusions has been little-explored, although a recent study illuminated how user decisions influence the delineation of species range maps (Hughes *et al.* n.d.).

While biogeography in the 20th century focused on describing species ranges (Gaston 2000; MacArthur 1972), the field is increasingly focused on range *shifts* in light of human impacts on the planet (Parmesan & Yohe 2003). A large and growing literature has documented recent shifts in species' ranges and range edges, often tracking local climate velocities and/or moving toward the poles (Lenoir *et al.* 2020). Many of these studies have compared a historic dataset to a modern "resurvey" to measure range edge shifts. Unfortunately, this approach may lead to misleading inferences about global change impacts (Stuble *et al.* 2021), and longitudinal studies with more time points for studying range edge dynamics are rare (although see Fredston-Hermann *et al.* 2020 and Fredston *et al.* 2021). Inconsistencies in global change metrics used by individual studies and researchers have ripple effects in synthesis science, making it difficult to accurately estimate large-scale patterns and trends (Brown *et al.* 2016; Lenoir *et al.* 2020). Further, simulation testing found that many years of data are often required to accurately estimate population trends (White 2019); if the same is true of range trends, many range edge shift studies are possibly underpowered.

While the exact threshold for statistical power varies by system and study, the implication remains that studies with just a few time points are unlikely to reflect true rates of edge shifts (Stuble *et al.* 2021). Publishing under-powered interpretations of ecological time-series is not uncommon, despite statistical evidence that doing so may lead to misleading inferences about trajectories of populations and ecosystems with complex dynamics (Bahlai *et al.* 2021; McCain *et al.* 2016; White 2019). With high interannual variability being a common feature of range edges, and few large-scale, long-term, and high-resolution datasets available (Thomas *et al.* 2006), it remains an open question if and how the field is ready to accurately quantify range edge dynamics.

The challenge of measuring range edge dynamics is evident in my own work. Using a 50-year annual time-series of marine bottom trawl surveys with hundreds of samples per year, colleagues and I found that it was still difficult to separate the signal of a putative range edge shift from noise [CITATION REDACTED FOR DOUBLE-BLIND PEER REVIEW]. A follow-up study that used alternative methods to measure range edge dynamics came to very different conclusions about which species' range edges had shifted and how far [CITATION REDACTED FOR DOUBLE-BLIND PEER REVIEW].

To diagnose the extent of this problem and propose possible solutions, I applied a suite of range edge metrics that are common in the biogeography literature to standardized biodiversity data. I found substantial heterogeneity in the edge positions measured and the resulting estimates of range edge shifts. I showed that methodological choices in measuring range edges can influence not only the rate of inferred shifts, but whether shifts are identified at all. I also simulated range edge data to demonstrate that for realistic values of shift rates and interannual variability, many decades of data are likely to be needed to reliably quantify edge shifts.

Methods

This study uses two range edges as focal examples: *Urophycis tenuis* (white hake), a marine fish whose distribution in the Northwest Atlantic includes an equatorward range edge that falls within the Northeast US continental shelf, and *Coragyps atratus* (black vulture), a bird species with a poleward range edge in the continental US. Both of these range edges—the equatorward edge of the white hake and the poleward edge of the black vulture—have been described as shifting northward by previous studies (Fredston-Hermann *et al.* 2020; La Sorte & Thompson, III 2007).

Data on the white hake was downloaded from FISHGLOB, an international effort to collate, harmonize, and publish scientific bottom trawl surveys (“FishGlob_data” 2023; Maureaud *et al.* 2024). I used data from the Northeast US, where a biannual survey has been operated since the 1960s by the National Oceanic and Atmospheric Administration, NOAA (Azarovitz 1981; Despres-Patanjo *et al.* 1988). Consistent with other publications using this dataset, I used data from the fall survey from 1972 onward (Fredston-Hermann *et al.* 2020;

Pinsky *et al.* 2013). Data on the black vulture was downloaded from the National Audubon Society Christmas Bird Count, or CBC (National Audubon Society 2023). I downloaded historical data on the black vulture from the CBC online data portal. Consistent with other publications using this dataset, I used data from 1975 onward (La Sorte & Thompson, III 2007).

For each of these species, I calculated annual range edge positions using an array of methods published in the range shift literature, specifically: mean latitude of the five most distal points (Kerr *et al.* 2015), abundance-weighted latitude of the three most distal points (Perry *et al.* 2005), mean latitude of the ten most distal occupied grid cells (here, 1/12 degree cells; *sensu* Hällfors *et al.* 2021 and Hickling *et al.* 2006), 0.05 (equatorward) / 0.95 (poleward) quantile of latitude of observations (Fredston-Hermann *et al.* 2020), and 0.01 / 0.99 abundance-weighted quantile of latitude of observations (Fredston *et al.* 2021). I estimated whether edges had shifted over time using linear regression of edge position (in degrees latitude) on year with a significance threshold of 0.05. P-values less than 0.001 are reported as “< 0.001” in-text. I also calculated the residual standard deviation of each edge position time-series after detrending.

Regardless of which edge metric is chosen, researchers must also ensure that their study has sufficient power to detect a “true trend”. I conducted a set of simulations to evaluate which combinations of edge shift rates, residual standard deviations, and time-series lengths have sufficient power to detect significant shifts when they occur, using non-random resampling (White & Bahlai 2021). I simulated the position of a range edge over a century given some shift rate and error:

$$edge\ position_t = shift\ rate \times year + e_t$$

Where *t* represented year and *e* represented an error term. Using realistic values from literature (Lenoir *et al.* 2020), I tested range edge shift rates from 0.01 – 0.1 °lat/year in 0.01

°lat/year steps. The error term was drawn each year from a normal distribution with a mean of 0 and a standard deviation that was fixed in each simulation at 0.12, 0.47, and 0.72 °lat. These standard deviation values were the minimum, median, and maximum residual standard deviations from the linear regressions previously fitted to white hake and black vulture data, and were used to represent low, medium, and high interannual variability in the simulated time-series (referred to as low, mid, and high SD).

I then subsetted the simulated data into different time-series lengths, as if an observer were only able to record *n* continuous years of data, where *n* ranged from three to 100. For each time-series length, I fitted linear regressions of position on time to every possible subset of the simulated data. For example, for a time-series length of four years, I fitted a regression to the simulated data from years one, two, three, and four; another to years two, three, four, and five; another to years three, four, five, and six; and so on. Then for each time-series length, I estimated its power as how often the regressions found the “correct” result (a significant positive shift, with a significance threshold of 0.05). I repeated the workflow above 100 times to generate a distribution of power values for every combination of time-series length, standard deviation, and edge shift rate. For each iteration I then calculated the minimum time-series length that reached the power threshold of 0.8, and reported the minimum, median, and maximum of those time-series length values across the 100 iterations in each parameter combination. In interpreting the results, I considered a power value of 0.8 or higher to mean that the analysis accurately captured the “true trend” of the simulated data.

All data analysis was conducted in R version 4.1.1 (R Core Team 2021). Code and data to reproduce the results can be found online at [*GitHub link to be inserted after peer review*].

Results

For both the poleward edge of the black vulture and the equatorward edge of the white hake, different methods estimated dramatically different range edge positions—in some years, more than five degrees of latitude apart (Figure 2). Residual standard deviations were generally lower for quantile-based approaches than for methods using most distal points (Figure 2).

All methods tested found a significant shift in the poleward range edge position of the black vulture from 1975-2023 (Figure 2). However, the methods differed markedly in the estimated shift rates. Shift rates using edge metrics that were based on most distal points or cells all fall within one standard deviation of one another (mean of five most distal points: 0.080 ± 0.0034 °lat/year, $p < 0.001$; abundance-weighted mean of three most distal points: 0.081 ± 0.0052 °lat/year, $p < 0.001$; mean latitude of ten most distal occupied cells: 0.075 ± 0.0024 °lat/year, $p < 0.001$). By contrast, the shift rates using quantile edge metrics were much slower, particularly the abundance-weighted one (presence-based 0.95 quantile: 0.047 ± 0.0012 °lat/year, $p < 0.001$; abundance-weighted 0.99 quantile: 0.039 ± 0.0017 °lat/year, $p < 0.001$).

For the equatorward edge of the white hake, the abundance-weighted mean of most distal points metric did not shift significantly over time (Figure 2). The other metrics did show significant shifts and estimated shift rates that were all within one standard deviation of each other (mean of five most distal points: 0.014 ± 0.006 °lat/year, $p = 0.03$; mean latitude of ten most distal occupied cells: 0.015 ± 0.0052 °lat/year, $p = 0.005$; abundance-weighted 0.01 quantile: 0.017 ± 0.0054 °lat/year, $p = 0.003$; presence-based 0.05 quantile: 0.016 ± 0.0046 °lat/year, $p < 0.001$).

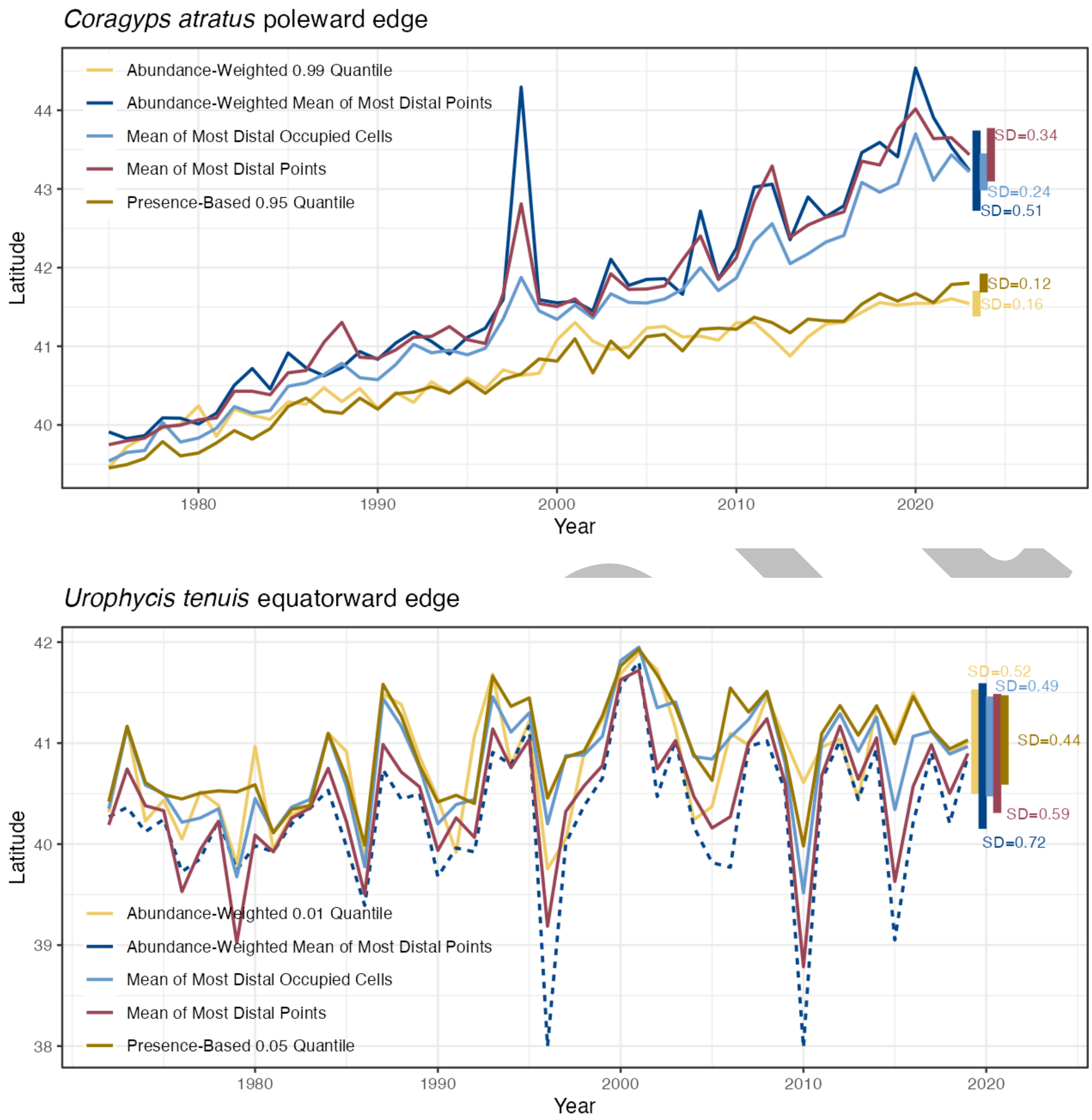

Figure 2. Positions of the poleward edge of the black vulture (*Coragyps atratus*) estimated from the Christmas Bird Count (top) and the equatorward edge of the white hake (*Urophycis tenuis*) in the Northwest Atlantic estimated from an annual NOAA survey (bottom) using various methods that are common in the biogeography literature. Solid lines indicate that a linear regression of latitude on year found a significant shift ($p \leq 0.05$) over the time-series; dashed

lines indicate no significant shift. Vertical bars on the right-hand side represent the residual standard deviation of each time-series after detrending.

Using realistic time-series lengths, shift rates, and residual standard deviations, I simulated that many decades of data would often be needed to reliably detect range edge shifts (Figure 3). Individual iterations of the simulation sometimes detected significant shifts quickly: at rapid edge shift rates (≥ 0.086 °lat/yr) and a low standard deviation, some time-series revealed significant shifts after only six years (Figure 4). However, it took substantially longer for all iterations of a simulation to meet the power threshold of 0.8 (Figure 3). For example, for an intermediate shift rate (0.050 °lat/yr) and the middle residual standard deviation value tested, a time-series length of 27 years was required for 100% of simulations to reach the power threshold of 0.8 (Figure 3). With a high residual standard deviation and slow shift rates, many iterations of the simulation never reached the power threshold of 0.8 after 100 years (Figures 3, 4).

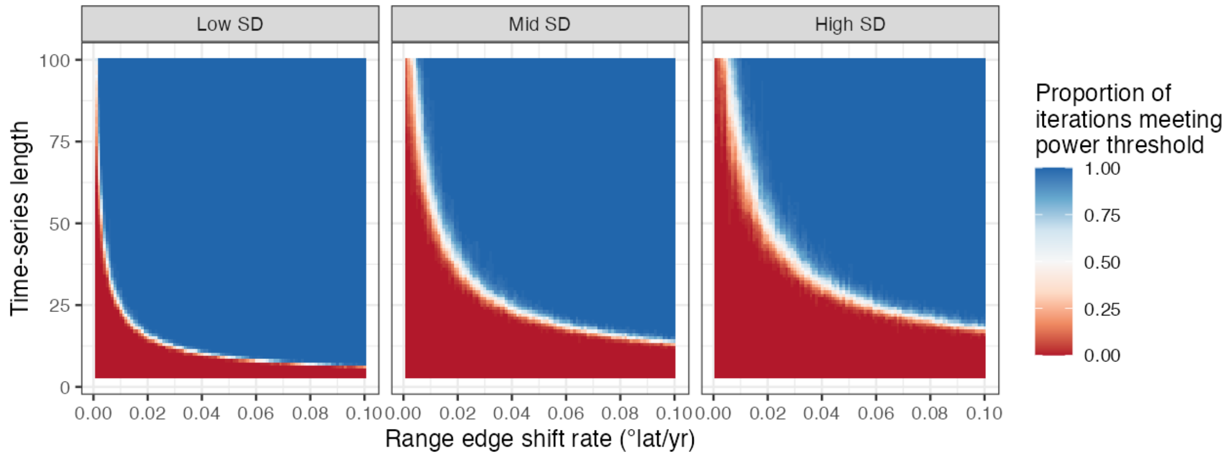

Figure 3. The proportion of iterations meeting the power threshold of 0.8 increased with simulated range edge shift rate, time-series length, and lower residual standard deviation. The low, mid, and high SD values correspond to simulations with standard deviations of 0.12, 0.47, and 0.72 °lat, respectively (see Methods). Simulations were run 100 times for each unique combination of standard deviation, shift rate, and time-series length.

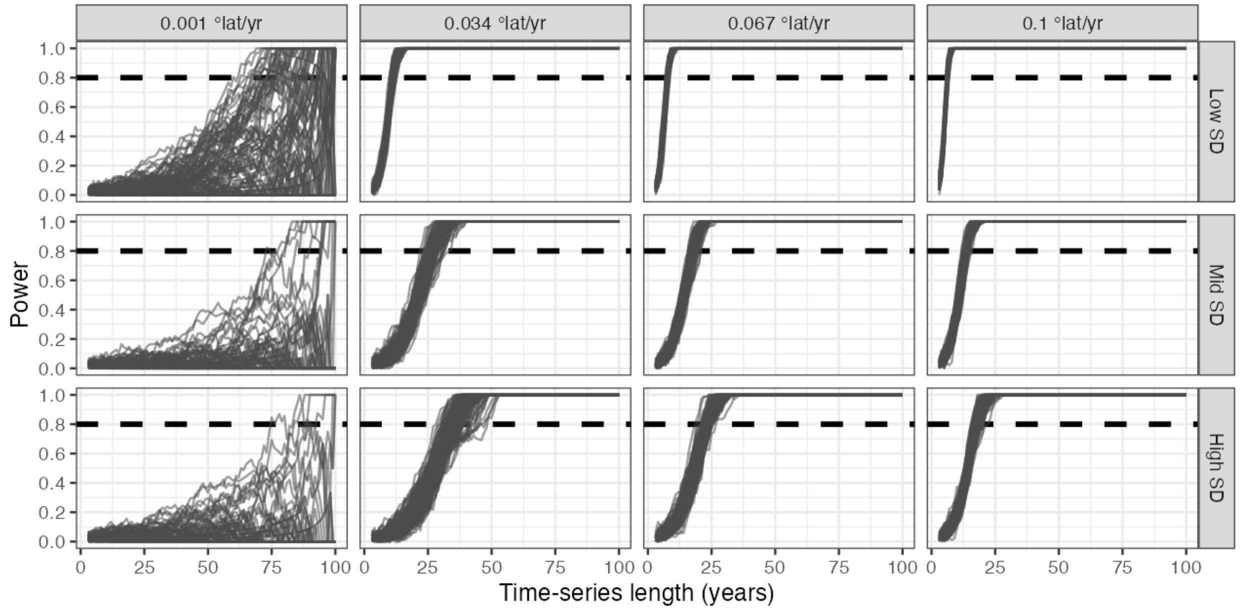

Figure 4. Relationship between four example edge shift rates (columns), time-series length (x-axis), residual standard deviation (rows), and statistical power (y-axis) in a non-random

subsampling analysis. The dashed line represents the power threshold of 0.8 (bottom). Each line is an iteration of the simulation, which was run 100 times for every parameter combination. The low, mid, and high SD values correspond to simulations with standard deviations of 0.12, 0.47, and 0.72 °lat, respectively (see Methods).

Discussion

Here I used two prominent long-term monitoring datasets—each of which encompasses decades of warming and has been previously found to reveal climate-related range edge shifts (Fredston-Hermann *et al.* 2020; La Sorte & Thompson, III 2007)—to show that estimated edge positions, shift rates, and statistical significance depend on methodological choices by researchers (Figure 2). Quantile-based methods showed less interannual variability in edge position than distal points-based methods (as measured by residual standard deviation), and different approaches estimated notably disparate edge positions—sometimes differing by up to five degrees of latitude (Figure 2). For the equatorward edge species, one of the distal points-based methods failed to identify a significant shift (Figure 2). While all methods found a significant northward shift in the poleward edge species, their estimated magnitudes were very different (Figure 2).

Methods matter in measuring range edge dynamics, but so does statistical power. Non-random resampling of time-series datasets can reveal how much data is necessary to detect a "true trend" (White 2019; White & Bahlai 2021). The simulation results presented here underscore that long time-series may be needed to reliably detect the signal of a range edge shift, and that variability in estimated edge positions—represented here as residual standard deviation—erodes statistical power (Figures 3, 4). This analysis was not designed to establish a single minimum time-series length required for all range edge studies. Rather, it demonstrates an approach that researchers can adapt to conduct exploratory power analyses with shift rates, residual standard deviations, and power thresholds that are relevant to their focal systems and use cases to determine whether future studies of range edge dynamics are likely to be underpowered. The example values I used suggest that decades of data may often be needed to reliably detect modern range edge shifts (Figure 3).

It is generally understood that individual researcher decisions affect science (Gould *et al.* 2023), and previous work in global change biology found that methodological decisions explain a large proportion of variation in estimated range shifts (Brown *et al.* 2016; Lenoir *et al.* 2020). This issue is especially salient for range edges, which are extreme value statistics that may be highly sensitive to seemingly small differences in methodology. The results presented here only represent a subset of common approaches to estimating range edge positions, and many other approaches exist in literature. Thus, the effect of *ad hoc* methods on range edge measurements and estimated shift rates may be even greater than demonstrated here with a handful of approaches. Observer error, low and/or variable probability of detection, and changes in sampling over time can further confound range edge measurements.

Studies often pool results about poleward and equatorward edge shifts as if they were comparable processes. Especially when using presence-only metrics, this approach may have the unintended consequence of biasing results toward recording range edge extensions (which we expect at poleward edges in a warming world) over range edge retractions (which we expect at equatorward edges in a warming world). This is because in order for a range edge retraction to be found using presence-only data, every individual in a population has to vanish from the most distal site(s); but for a range edge extension to occur just one individual has to spread beyond the historical range (Thomas *et al.* 2006). Indeed, a recent synthesis of evidence for range shifts revealed that poleward edge shifts are much more commonly recorded than equatorward edge shifts (Lawlor *et al.* 2024). Whether this phenomenon is considered a “feature” or a “bug” in analysis depends on the research question (and note that range edge extensions can also be difficult to detect if populations are small and/or monitoring effort is low; see Robinson *et al.* (2015)).

The degree of precision needed to characterize a species on the move, and the choice of edge metric, depend on the use case. Programs focused on early detection of climate-related range extensions or species invasions may be able to detect shifts and trigger management or conservation actions based on a few sightings beyond a species' poleward range edge (or even one), without needing statistically robust estimation of shift rates or exact edge positions (Wolfe *et al.* 2025). Researchers aiming to identify the full geographical area occupied by a species—i.e., a range map—may opt to use presence-based metrics and/or two-dimensional approaches such as hulls for precisely the reason that they capture the most distal occupied sites. If the goal is to calculate rates of range edge shifts or to understand where the vast majority of a species' density is found, abundance-weighted metrics may provide a more accurate picture of equatorward edge dynamics. Combining these metrics in a single study will allow researchers to capture both distal colonization or extinction events and changing abundance patterns.

Even when range edges are measured with abundance-weighted metrics, it must be emphasized that colonization and extirpation are distinct processes that happen at different rates. The relatively slow rate of extirpation, which may cause "extinction debt", means that equatorward-edge populations could be declining even if their geographical shifts are slower than at the poleward edge (Hampe & Petit 2005; Jackson & Sax 2010; Tilman *et al.* 1994). This is evident in the white hake equatorward edge example: the statistically significant shift rates I calculated were less than 2 km/year, which is far slower than literature syntheses on marine range shift rates overall (Lenoir *et al.* 2020; Poloczanska *et al.* 2013). This discrepancy is well-known in the global change biology literature; one possible approach is to document range edge shifts with increasing confidence as they move through the colonization or extirpation process (Bates *et al.* 2014).

Researchers may also consider more biologically relevant metrics of range edges. For example, it may be that demographic parameters of range edge populations (Gaston *et al.* 2009), or the extent of a metapopulation distribution (Watts *et al.* 2013), are more reliable predictors of range edge trajectories than simpler presence- or abundance-based metrics. Other approaches exclude adult migration and foraging from range measurement: range expansion in California sea otters has been modeled using only abundance data on females and pups (Krkošek *et al.* 2007), since males are mobile foragers and their geographical distributions are not reflective of the species' year-round range. In addition to more biologically relevant metrics, the study of range edges would likely be improved with more sophisticated statistics. For example, the common methods in global change biology explored here may be outperformed by kernel densities, contour or hull estimation (Oborny & Zimmermann 2023), and two- and three-dimensional range edge metrics. The uncertainty associated with range edge positions can be quantified using species distribution models (Fredston *et al.* 2021), as can the uncertainty associated with observer error and species detectability (Brodie *et al.* 2022).

This study focused on geographical range edges measured primarily in one dimension: latitude. In the context of global change, species are expected to track climate velocities, which do not always point north (Burrows *et al.* 2014). Range edge dynamics in response to climate change may be better captured by measuring shifts relative to these local climate velocities (Pinsky *et al.* 2013), or along custom "rulers" that correspond to coastlines, isotherms, contours, or other features that range-shifting species might follow (Fredston *et al.* 2021). While not discussed here, depth and elevational range edges are typically studied in an *ad hoc* fashion similar to geographical range edges, and their reported positions and shifts may be similarly sensitive to researchers' methodological choices. An analogous study to this one recently explored the effect of ecological processes, spatiotemporal variability, and methodological decisions on our understanding of elevational range edges, and came to similar conclusions regarding the potential for high bias and low power in many commonly-used metrics (Linck 2025).

Improving measurements of range edge positions and shifts would enable global change researchers to better describe changes that are occurring and to more effectively relate them to important environmental variables. Several recommended best practices for quantifying range edge dynamics emerge from this study:

1. Because there is no single perfect metric of range edges, researchers should fit multiple metrics, and conduct sensitivity analyses to explore the robustness of ecological results to methodological choices. More sophisticated metrics, such as contours, multi-dimensional range edges, and edges modeled with uncertainty, should be considered.
2. Researchers should conduct simulations to ensure that their studies are not under-powered, especially when testing for shifts in range edge positions. These simulations should capture the differences in interannual variability (i.e., residual standard deviation) introduced by the different edge metrics used.
3. Care should be taken when comparing poleward and equatorward edge dynamics—especially when using presence-based approaches. Because range extensions are easier to detect than range contractions, it may be that studies have different statistical power to accurately measure poleward *vs.* equatorward edge shifts.
4. Demographically relevant parameters, such as population growth rates or abundance of reproductive females, may lead to more informative metrics of range edge dynamics than simple inventories of presence or abundance.

5. Publishing raw data and code means that range edge studies can be re-analyzed in the future to assess the effect of methodological choices on results and to conduct syntheses and meta-analyses about range edge dynamics.

How to measure other foundational properties of species—e.g., abundance, growth rates, population structure—has received extensive research attention in quantitative ecology for many years. By contrast, biogeography has yet to grapple with to what degree our understanding of range edge dynamics is driven by methods rather than biological processes, let alone to move toward universally accepted metrics. It is time for range edges to get their due.

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