Title: Measuring the edges of species' geographic ranges

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Data availability statement: All data and code are available at https://github.com/afredston/range-edge-methods and will be archived in a repository with a DOI when the manuscript is accepted for publication.

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 have never been formalized.
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. An anonymized link to the repository can be found here: https://anonymous.4open.science/r/range-edge-methods-48BD/.

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). Here I define range edges as geographical limits outlining the boundaries of a species' range (Figure 1).

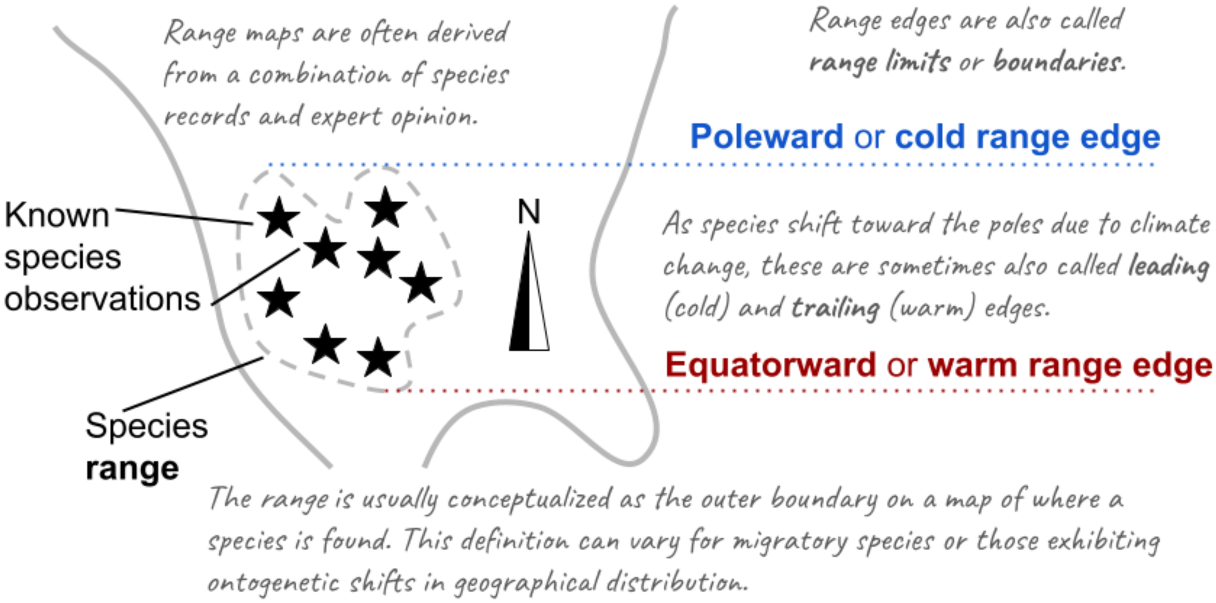

Figure 1. Illustration of terms and concepts relevant to species range edges, using a Northern Hemisphere orientation (*i.e.*, the poleward edge is toward the north). Note that the present study focused only on geographical range edges (not depth or elevational edges).

To measure the position of a species' range, studies commonly use some version of an abundance-weighted geographical center, i.e., a range centroid (La Sorte & Thompson, III 2007; Perry *et al.* 2005). No such universal metric exists for range edges, and their quantification is far more variable in literature (Lawlor *et al.* 2024). Further, because centroid metrics are mean statistics and range edge metrics are extreme value statistics, greater variation may be expected in the latter. 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—each using bespoke methods that are not standardized within fields or among studies (Gaston 2003; Guisan & Thuiller 2005). 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. 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.

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].

Here I applied a suite of range edge metrics that are common in the biogeography literature (Table 1) 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.

Method	**Description**	**Examples**
Most distal point	Edge is identified at the most distal point observation or occupied grid cell along a single dimension (typically latitude)	(La Sorte & Thompson, III 2007; Schoeman *et al.* 2015)
Mean of distal points or grid cells	Mean of *n* most distal point observations or occupied grid cells along a single dimension (typically latitude)	(Hällfors *et al.* 2021; Hickling *et al.* 2006; Kerr *et al.* 2015)
Abundance-weighted mean of distal points or grid cells	Abundance-weighted mean of *n* most distal point observations or occupied grid cells along a single dimension (typically latitude)	(Perry *et al.* 2005)
Quantile of observations	Quantile of observations 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	(Fredston-Hermann *et al.* 2020; Sittaro *et al.* 2017; Zhu *et al.* 2012)
Quantile of modeled distribution	Species distribution model is fitted to data, and then quantiles of presence or abundance are extracted from the models	(Fredston *et al.* 2021)

Table 1. Summary of common methods for measuring range edge positions, typically for use in studying climate-related range shifts. This does not represent an exhaustive review of the literature. Many other examples of these approaches exist, as do many other bespoke methods.

Methods

This manuscript uses two species 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 a subset of the methods in Table 1: the three methods based on distal points, and quantiles of observations (0.9, 0.95, and 0.99 for a poleward edge, and 0.01, 0.05, and 0.10 for an equatorward edge). For the metrics based on a mean of points, I used n=3, i.e., a mean of the three most distal points. 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.

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 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:

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

Where *t* represented year and *e* represented an error term. The error term was drawn each year from a normal distribution with a mean of 0 and a standard deviation of 0.65, which was derived from the mean conditional standard deviations of the linear regressions previously fitted to white hake and black vulture data. 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.

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 and edge shift rate. 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). Interannual variability was also 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 were all within one standard deviation of one another (most distal point: 0.097 ± 0.013 °lat/year, $p < 0.001$; mean of most distal points: 0.085 ± 0.0052 °lat/year, $p < 0.001$; abundance-weighted mean of most distal points: 0.081 ± 0.0051 °lat/year, $p < 0.001$). By contrast, the shift rates using quantile edge metrics were much slower, especially the 0.95 quantile method (0.9 quantile: 0.038 ± 0.0075 °lat/year, $p < 0.001$; 0.95 quantile: 0.028 ± 0.0035 °lat/year, $p < 0.001$; 0.99 quantile: 0.036 ± 0.0017 °lat/year, $p < 0.001$).

For the equatorward edge of the white hake, the three methods using abundance-weighted quantiles found a significant northward shift in edge position from 1972-2019, and the methods calculated using most distal points did not (Figure 2). The rates of shift estimated by the three quantile methods all fell within one standard error of each other (0.1 quantile: 0.0086 ± 0.0036 °lat/year, $p = 0.02$; 0.05 quantile: 0.015 ± 0.0046 °lat/year, $p = 0.003$; 0.01 quantile: 0.016 ± 0.0054 °lat/year, $p = 0.004$).

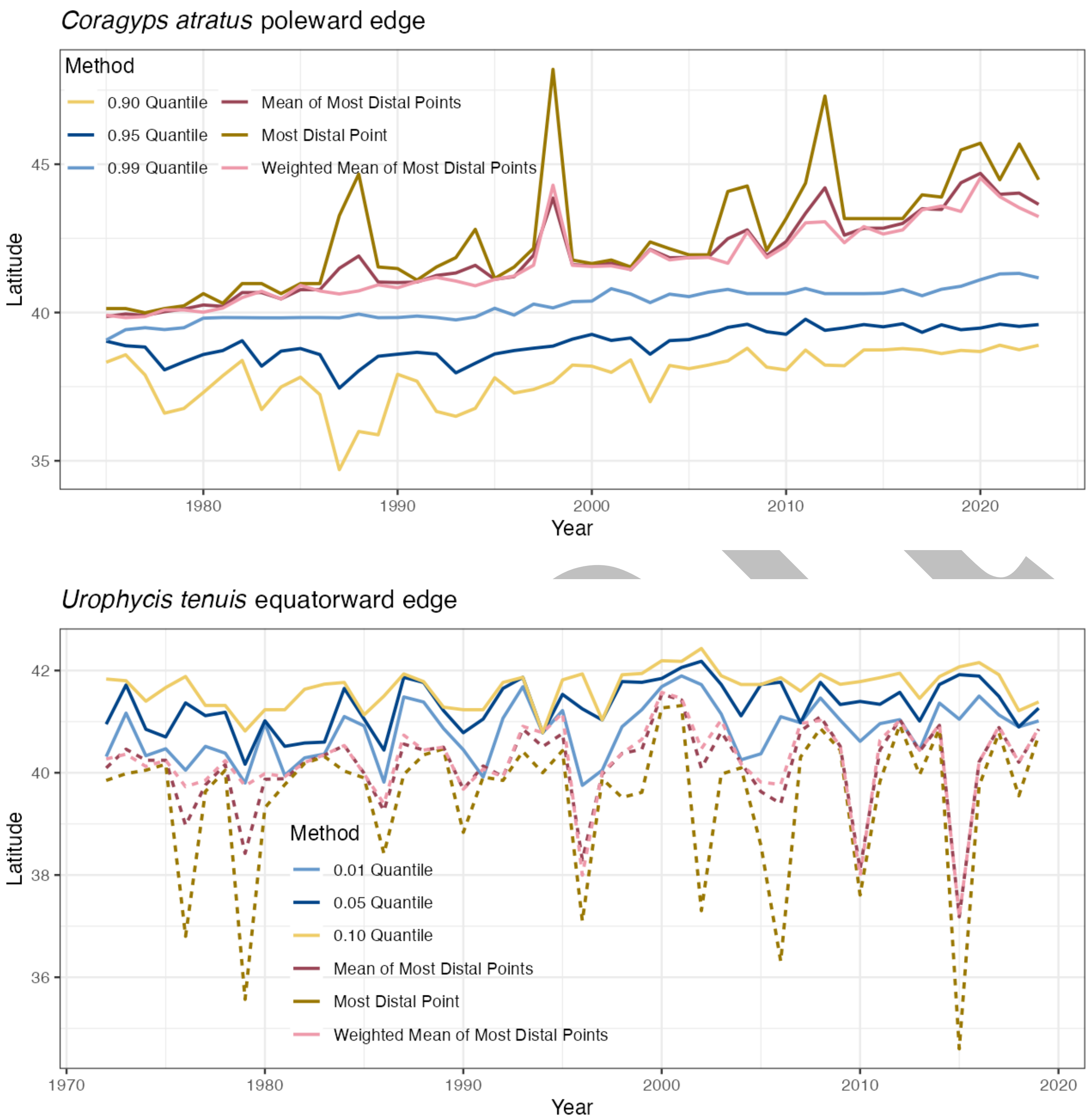

Figure 2. Positions of the poleward edge of the black vulture (*Coragyps atratus*) estimated from the Christmas Bird Count (top) and the equatorward edge of the white hake (*Urophycis tenuis*) in the Northwest Atlantic estimated from an annual NOAA survey (bottom) using various methods that are common 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.

Using realistic time-series lengths, shift rates, and error terms, I simulated that many decades of data would often be needed to reliably detect range edge shifts (Figure 3). The median minimum time-series length required to accurately detect a significant shift ranged from 94 years (in the third-slowest range edge shift rate tested, 0.003 °lat/year) to 59 years (for edge shift rates of 0.085 – 0.1 °lat/year). Across all time-series subsets and simulation iterations, the shortest time-series to reach the statistical power threshold of 0.8 was 14 years long, in a simulation where the range edge shift rate was 0.099 °lat/year—the second-fastest shift rate I tested. Conversely, for the slowest rates of range edge shifts tested (0.001 – 0.011 °lat/year), at least one iteration of the simulation never reached the statistical power threshold of 0.8 after 100 years (Figure 3).

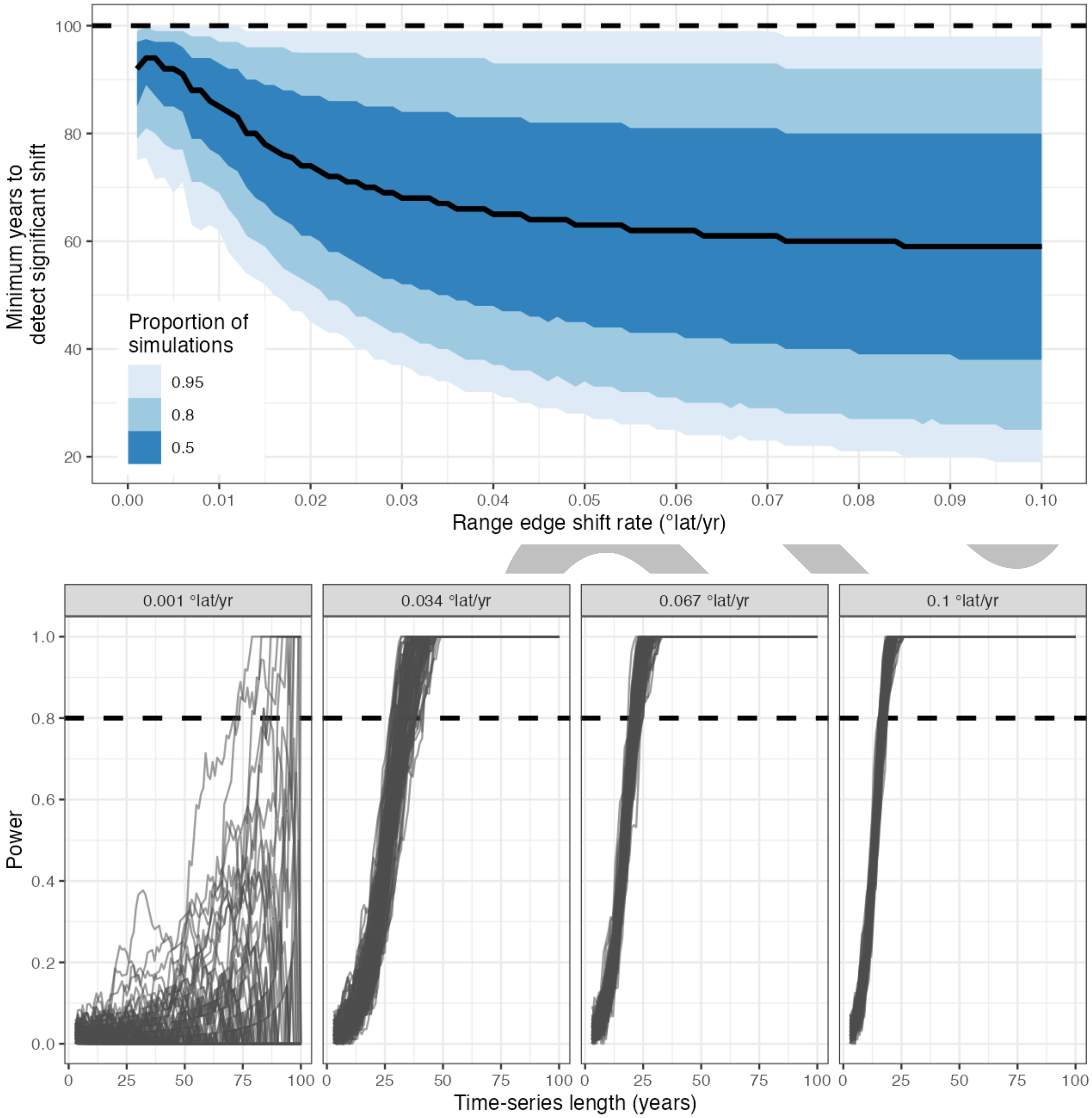

Figure 3. Results of a non-random subsampling analysis exploring statistical power in analyses of simulated range edge data, showing the number of years required to accurately identify significant shifts in the simulation, i.e., when the simulated analysis reached a power level of 0.8 (top) and the relationship between time-series length and statistical power for four example rates of range edge shift (bottom). The dashed line represents the end of the simulation after

100 years (top) and the power threshold of 0.8 (bottom). Both plots show results for simulations run 100 times. In the top plot, the color fill represents what proportion of those iterations falls within each band, and the black line is the median value. In the bottom plot, each line is an iteration of the simulation.

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, and different approaches estimated notably disparate edge positions—sometimes differing by up to five degrees of latitude (Figure 2). For the equatorward edge species, only quantile-based methods found a significant northward shift. While all methods found a significant northward shift in the poleward edge species, their estimated magnitudes were very different (Figure 2).

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 (Table 1), 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 over range edge retractions. 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)). Researchers aiming to identify the full geographical area occupied by a species—i.e., a range map—may prefer to use presence-only metrics for precisely the reason that they capture the most distal occupied sites. However, 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. Alternatively, researchers may want to combine these metrics in a single study 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 very 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). It may be that measuring demographic parameters in range edge populations is a more reliable predictor of their trajectories than abundance (Gaston *et al.* 2009). Researchers may also consider more biologically relevant metrics that exclude adult migration and foraging from range measurement. For example, 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.

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.

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 the long time-series that may be needed to reliably detect the signal of a range edge shift (Figure 3). This analysis was not intended to provide quantitative rules of thumb, and did not explore the effects of different range edge metrics on estimated shift rates and statistical significance. Rather, it is the type of simulation that could be conducted by researchers analyzing novel empirical data to test whether their study is underpowered. By adapting the shift rate, time-series length, and error rate parameters to their own study systems, researchers can simulate how likely they are to detect a significant shift should one exist. The example values I used suggest that decades of data may be needed to reliably detect modern range edge shifts (Figure 3).

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 such as the CBC and NOAA surveys available (Thomas *et al.* 2006), it remains an open question if and how the field is ready to accurately quantify range edge dynamics.

The simulation presented here did not address additional sources of uncertainty, such as observer error and the abundance and detectability of a species. These can be quantified and partitioned from biological processes using species distribution models (Brodie *et al.* 2022). Another advantage of using species distribution models is that they can quantify uncertainty associated with range edge positions (Fredston *et al.* 2021). However, the degree to which species distribution models accurately predict biological parameters (e.g., presence, abundance) is widely debated (Lee-Yaw *et al.* 2022), and their usefulness in projecting future species distributions—one primary focus of modern biogeography—is unclear (Fourcade *et al.* 2018; Sofaer *et al.* 2018). Mechanistic models may provide an alternative path toward forecasting range edge dynamics while accounting for observation error (Briscoe *et al.* 2019).

Syntheses of edge shift rates across studies, systems, and taxa is facilitated by researchers sharing their raw data, which allows future re-analysis or meta-analysis with different methods and motivating questions (Carpenter *et al.* 2009). Ecological synthesis is especially important in the context of global change biology, because the field-collected datasets researchers use to study biogeography in a warming world are each irreplaceable (Wolkovich *et al.* 2012). In addition to open data, open code will make it possible to investigate the effect of methodological choices on reported measurements of range edges. Openly sharing data and code has many other advantages that are well-described (Cheruvelil & Soranno 2018; Fredston & Lowndes 2024; McKiernan *et al.* 2016; O'Dea *et al.* 2021).

Species range edges are a core concept in biogeography, and range edge shifts are among the most common metrics of "species on the move" in a warming world (Lenoir *et al.* 2020). Predicted future range edge shifts are already influential in biodiversity conservation and natural resource management, as models project when species will shift out of protected areas or across jurisdictional boundaries (Pinsky *et al.* 2018). Yet range edges lack a universally accepted measurement, and the *ad hoc* approach taken by global change studies to date makes it impossible to accurately synthesize—let alone forecast—the true rates of range edge shifts in the Anthropocene. 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. Range edge metrics should be chosen to match a research question, and care should be taken when comparing poleward and equatorward edge dynamics—especially when using presence-based approaches. Sensitivity analyses can reveal whether results are driven by the choice of metric.

2. Researchers should conduct simulations to ensure that their studies are not under-powered, especially when testing for shifts in range edge positions.
3. 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.
4. 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.

The methods that I tested here (Table 1) are simple statistics, and it is likely that none of them are an ideal metric for range edges. Far more sophisticated approaches exist that could be applied to measuring the boundaries of species' ranges. For example, kernel densities, contour estimation, and two- and three-dimensional range edge metrics all merit much greater attention in the biogeography and global change biology fields. 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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