

Title: Measuring the edges of species' geographic ranges

Author name: Alexa L. Fredston

Corresponding author email: fredston@ucsc.edu

Institutions and addresses: Department of Ocean Sciences, University of California, Santa Cruz, 1156 High Street, Santa Cruz, CA, 95064

Acknowledgments: A. Marm Kilpatrick, Zoë Kitchel, Owen R. Liu, and Montague H. C. Neate-Clegg provided valuable feedback on earlier drafts of the manuscript.

Author contributions: ALF conceived of, drafted, and revised the manuscript, and conducted all analyses.

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 there are many methods for measuring range edges and quantifying their displacement.
2. Here I describe 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 show 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 standardized 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 standardized metrics.

Data/code

The data and code for this project are available on GitHub.

Keywords

Range edges; range boundaries; range limits; biogeography; range shifts; non-random resampling; 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). 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 standardized metrics exist for defining 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 (here I use “abundance-weighted” to describe range metrics that are weighted by abundance or density where the species is present, instead of being calculated based on presence and absence alone). 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, although typically with the aim of quantifying range size and shape, rather than the position of the edges (Burgman & Fox 2003; Yalcin & Leroux 2017). Researchers have also developed range edge metrics tailored to specific biological contexts, such as demographic parameters of range edge populations (Gaston *et al.* 2009), the extent of a metapopulation distribution (Watts *et al.* 2013), or by excluding mobile foragers (Krkošek *et al.* 2007).

These varying methodological choices each arose from valid scientific and/or statistical rationales. 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 understand where the vast majority of a species’ density is found, abundance-weighted metrics may provide the most relevant description of equatorward edge

dynamics. Studies 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 (Bates et al. 2014, Wolfe et al. 2025). Regardless, the consequences for the field of such unstandardized range edge metrics and reporting across studies have been little-explored (but see Hughes *et al.* 2024).

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 (Fredston-Hermann *et al.* 2020, Stuble *et al.* 2021). Longitudinal studies with more time points for studying range edge dynamics are rare, and those that exist underscore the problem: for example, Fredston-Hermann *et al.* (2020) and Fredston *et al.* (2021) used alternative methods applied to the same dataset to measure range edge dynamics, and came to different conclusions about which species' range edges had shifted and how far. Such 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, simulations have shown 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 may be underpowered.

While the exact threshold for statistical power varies by system and study, analyses 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.

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

I used data from two species' range edges as focal examples: the equatorward range edge of *Urophycis tenuis* (white hake) in the Northwest Atlantic and the poleward range edge of *Coragyps atratus* (Black Vulture) in North America. Both of these range edges have been described as shifting northward by previous studies (Fredston-Hermann *et al.* 2020; La Sorte & Thompson, III 2007). I downloaded data on the white hake 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). I downloaded historical data on the Black Vulture from the National Audubon Society Christmas Bird Count, or CBC (National Audubon Society 2023) via 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. 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 trend if it is occurring. 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). This method subsets time-series data into shorter continuous intervals of a given length but starting at a random time point, and then tests the power of each subset to reveal the trend present in the original time-series (i.e., the “broken window” algorithm; Bahlai *et al.* 2021). In doing so, this approach leverages long time-series to develop a

quantitative understanding of the statistical power of short time-series. I simulated the position of a range edge over a century given some shift rate and error:

$$edge\ position_{year} = shift\ rate \times year + e_{year}$$

where e represented an error term. Using realistic values from literature (Lenoir *et al.* 2020), I tested range edge shift rates from 0.001 – 0.1 °lat/year in 0.001 °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 for 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 time-series into different length “windows”, as if an observer were only able to record n continuous years of data, where n ranged from three to 100 (*sensu* White and Bahlai 2021). For each window, I fitted linear regressions of position on time to every possible subset of the simulated time-series. For example, for a four-year window, I fitted a regression to the simulated time-series from years 1-4; another to years 2-5; another to years 3-6 and so on. Then for each combination of window length, standard deviation, and edge shift rate, I estimated power as how often the regressions found the “correct” result (a significant positive shift, using a significance threshold of 0.05). Calculating statistical power at this step was possible because, with the exception of the case where $n = 100$ (i.e., the window was the size of the entire time-series), each parameter combination led to a pool of subsetted datasets to which I could fit regressions and thus estimate power.

I repeated this entire workflow (simulating edge shifts, subsetting the time-series, and calculating power) 100 times. I then calculated the mean power across iterations for every

parameter combination. In interpreting the results, I considered a power value of 0.8 or higher to indicate that the analysis was adequately powered.

I also used the simulated time-series of edge positions to explore the “resurvey” method (when estimates of range edge shifts are calculated from just two surveys, typically far separated in time). For gap lengths between surveys ranging from 3 to 100 years, I drew every possible set of two endpoints from each simulated time-series. For example, for a gap length of five years, I identified resurvey endpoints in the time-series from year one to six; year two to seven; and so on, up to year 95 to 100. Between those endpoints, I then calculated two estimates of slope (representing range change) to compare their performance: using endpoints only, to simulate the resurvey method:

$$slope_{resurvey} = \frac{edge\ position_{end\ year} - edge\ position_{start\ year}}{end\ year - start\ year}$$

I also used the resurvey and intervening years to calculate the slope from an ordinary least squares regression of position on year, as if an observer had also conducted an annual survey every year between the endpoints:

$$slope_{regression} = \frac{\sum_{year} (year - \overline{year}) (edge\ position - \overline{edge\ position})}{\sum_{year} (year - \overline{year})^2}$$

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 hawk, different methods estimated dramatically different range edge positions—in some years, more than five degrees of latitude apart (Figure 1). Residual standard deviations were generally lower for quantile-based approaches than for methods using most distal points (Figure 1).

All methods tested found a significant shift in the poleward range edge position of the Black Vulture from 1975-2023 (Figure 1). 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 lower, 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 the most distal points metric did not shift significantly over time (Figure 1). 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, $p < 0.001$).

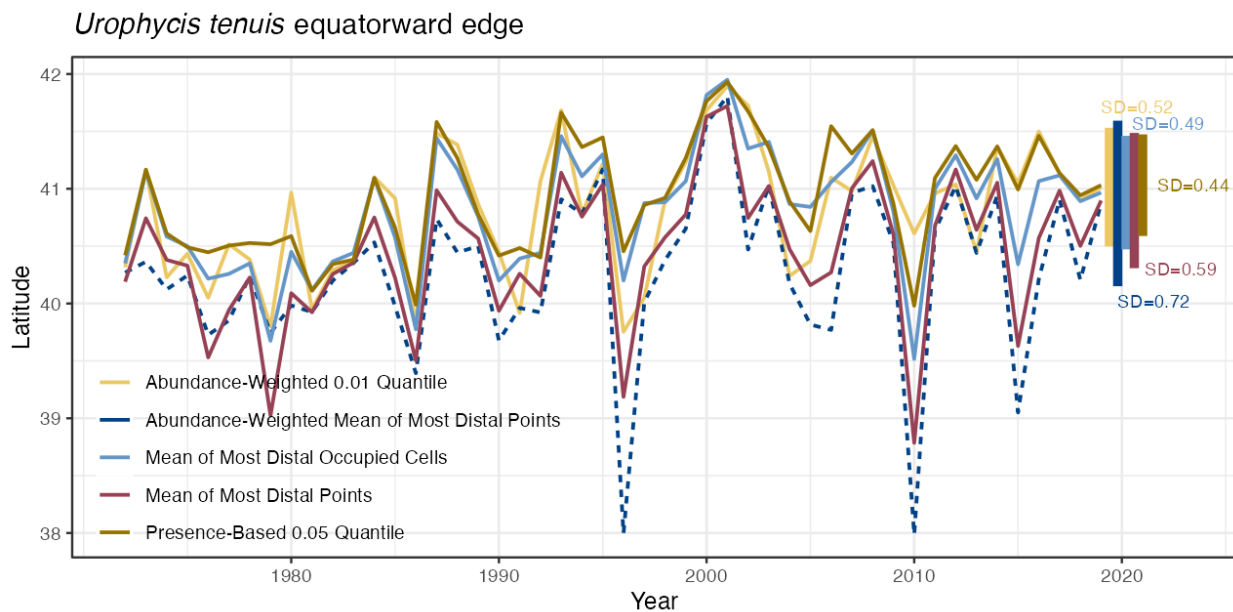
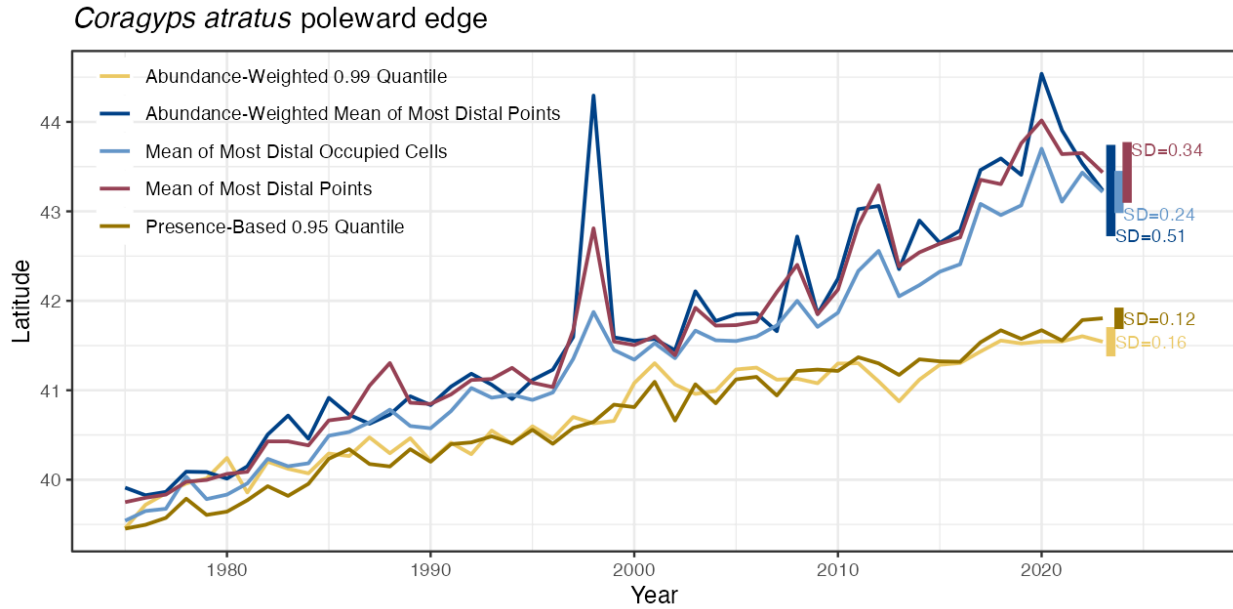


Figure 1. Positions of the poleward edge of the Black Vulture (*Coragyps atratus*) estimated from the Christmas Bird Count (top) and the equatorward edge of the white hake (*Urophycis tenuis*) in the Northwest Atlantic estimated from an annual NOAA survey (bottom) using different methods that are common 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 2). 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 2). However, it took substantially longer for parameter combinations 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 22 years was required to reach the power threshold of 0.8 (Figure 3). With a high residual standard deviation and slow shift rates, most simulations never reached the power threshold of 0.8 even with 100 years of data (Figures 2, 3).

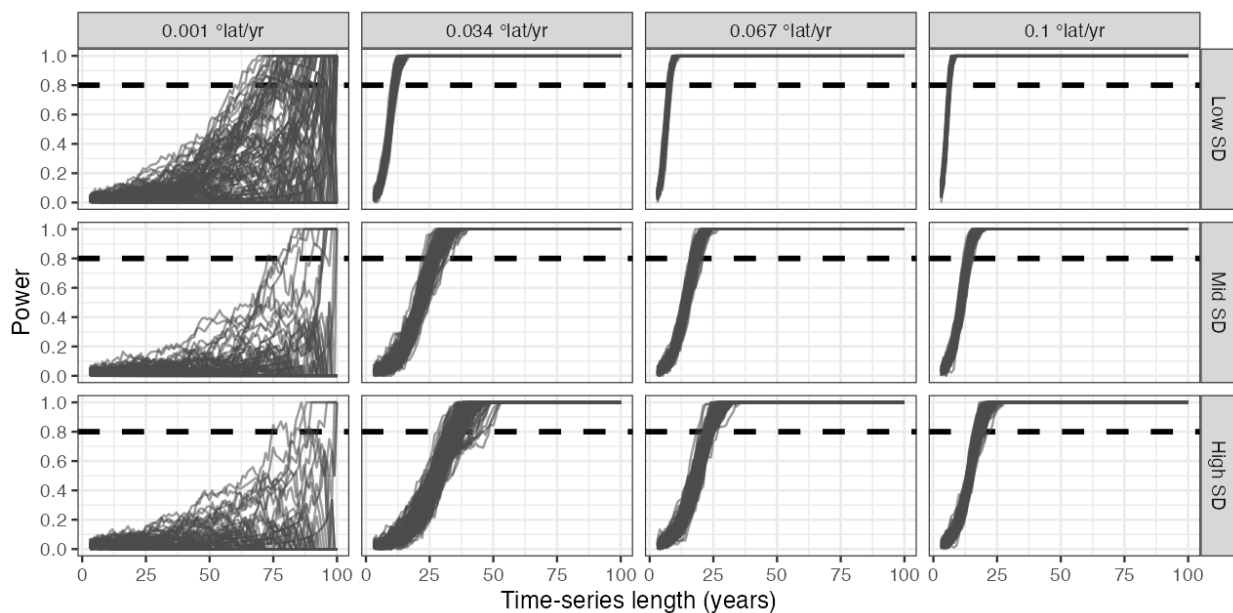


Figure 2. Relationship between four example edge shift rates (columns), time-series length (x-axis), residual standard deviation (rows), and statistical power (y-axis) in the sequential resampling analysis (for time series length 5, years 1-5, 2-6, 3-7, etc.). The dashed line represents the power threshold 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).

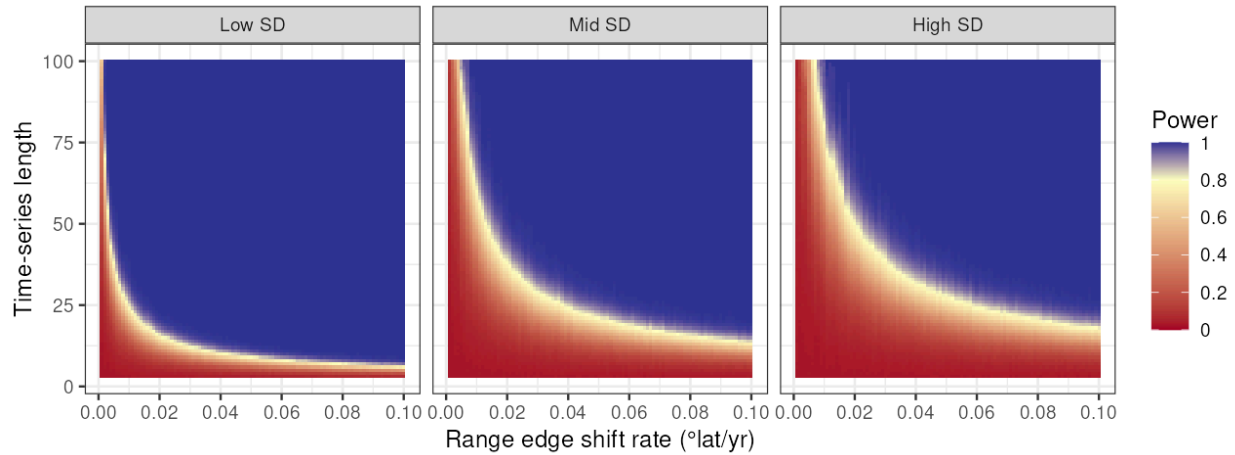


Figure 3. Statistical power as a function of simulated range edge shift rate, time-series length, and lower residual standard deviation. The low, mid, and high SD values correspond to simulations with standard deviations of 0.12, 0.47, and 0.72 °lat, respectively (see Methods). Each grid cell represents a mean of power estimates across 100 iterations; inside each iteration, I estimated power by calculating the proportion of subsetted time-series in which a regression found a significant positive range edge shift.

For long intervals between start and end years and low standard deviation, the resurvey method always captured not only the direction of range edge shifts but also the magnitude that was calculated via ordinary least squares regression using the full intervening time-series (Figure 4). However, with higher standard deviations or smaller intervals, the agreement between the resurvey and regression methods decreased—not just in their estimates of how fast edges were shifting, but also in what direction (Figure 4).

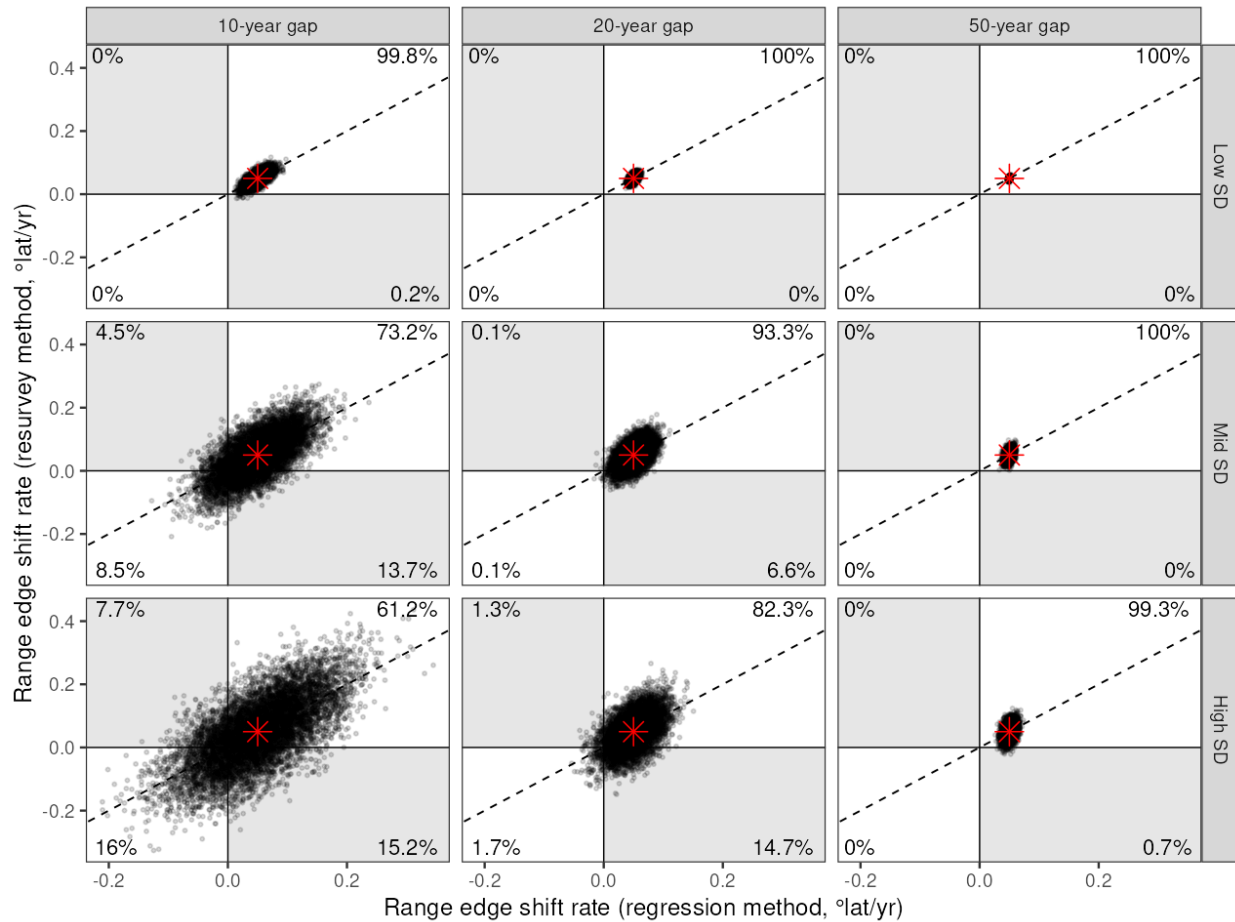


Figure 4. Range edge shift rates estimated by an ordinary least squares regression using annual data (x-axis) *versus* a “resurvey” method with only two time points (y-axis) for different time intervals (columns) and standard deviation values (rows), based on a simulated time-series that used an intermediate “true” shift rate (0.05 °lat/yr, plotted here as a red star). The percentage of points falling in each quadrant is labeled; the dashed line is a 1:1 line.

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 1). 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 1). For the equatorward edge species, one of the distal points-based methods failed to identify a significant shift (Figure 1). While all methods found a significant northward shift in the poleward edge species, their estimated magnitudes were very different (Figure 1).

Methods matter in measuring range edge dynamics, but so does statistical power. Resampling time-series 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 2, 3). This analysis was not designed to establish a single minimum time-series length required for all range edge studies. Instead, researchers can explore or adapt this simulation to estimate their own statistical power at different time-series lengths. The example values I used suggest that decades of data may often be needed to reliably detect range edge shifts (Figure 3).

Statistical power was also diminished by having only a few estimates of species’ distributions (e.g. resurveys, with 2 time points). The resurvey method most accurately described range edge shifts when the gap between start and end years was long and the range edge had low interannual variability around the trend (represented as standard deviation) (Figure 4). With high standard deviation and shorter gaps between start and end years, simulations revealed that resurvey methods may fail to capture the magnitude or even the direction of range edge shifts (Figure 4).

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 variation in 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), although note that range edge extensions may not be detected if populations are small and/or monitoring effort is low (Robinson *et al.* 2015). Frequent reporting of range extensions is not necessarily an issue; early detection of species spreading into new areas is often a priority in conservation and natural resource management, and can be accomplished via large-scale community science programs (Pecl *et al.* 2019). In ecological analyses, however, the fact that scientific surveys have more power to detect range

extensions relative to contractions is frequently overlooked (Bates *et al.* 2014; Hampe & Petit 2005). Further, 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).

Species experiencing global change are expected to track their climatic niches, which may not always lead them toward the poles (Burrows *et al.* 2014)—particularly because they can shift along environmental gradients that exist at small scales as well as large (i.e., latitudinal) ones (Fredston *et al.* 2025). 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), and/or along custom “rulers” that correspond to coastlines, isotherms, contours, or other features that range-shifting species might follow (Fredston *et al.* 2021). The study of range edges would likely also 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 in one dimension: latitude. 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. Further research is needed into these methods, as well as into the power needed to estimate the correct *rate* of shift; here I focused on the power needed to detect a shift *at all* if it is occurring. 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 routinely conduct power analyses when testing for shifts in range edge positions and should leverage simulation approaches to ensure that their studies are not under-powered. The simulation results presented here can be reused or adapted for this purpose.
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 (Ivimey-Cook *et al.* 2025).

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 standardized metrics. It is time for range edges to get their due.

References

- Azarovitz, T.R. (1981). A brief historical review of the Woods Hole Laboratory trawl survey time series. *Can. Spec. Publ. Fish. Aquat. Sci.*, 58, 62–7.
- Bahlai, C.A., White, E.R., Perrone, J.D., Cusser, S. & Stack Whitney, K. (2021). The broken window: An algorithm for quantifying and characterizing misleading trajectories in ecological processes. *Ecol. Inform.*, 64, 101336.
- Bates, A.E., Pecl, G.T., Frusher, S., Hobday, A.J., Wernberg, T., Smale, D.A., *et al.* (2014). Defining and observing stages of climate-mediated range shifts in marine systems. *Glob. Environ. Change*, 26, 27–38.
- Boisvert-Marsh, L., Périé, C. & de Blois, S. (2014). Shifting with climate? Evidence for recent changes in tree species distribution at high latitudes. *Ecosphere*, 5, 1–33.
- Brodie, S., Smith, J.A., Muhling, B.A., Barnett, L.A.K., Carroll, G., Fiedler, P., *et al.* (2022). Recommendations for quantifying and reducing uncertainty in climate projections of species distributions. *Glob. Change Biol.*, 28, 6586–6601.
- Brown, C.J., O'Connor, M.I., Poloczanska, E.S., Schoeman, D.S., Buckley, L.B., Burrows, M.T., *et al.* (2016). Ecological and methodological drivers of species' distribution and

- phenology responses to climate change. *Glob. Change Biol.*, 22, 1548–1560.
- Burgman, M.A. & Fox, J.C. (2003). Bias in species range estimates from minimum convex polygons: implications for conservation and options for improved planning. *Anim. Conserv. Forum*, 6, 19–28.
- Burrows, M.T., Schoeman, D.S., Richardson, A.J., Molinos, J.G., Hoffmann, A., Buckley, L.B., *et al.* (2014). Geographical limits to species-range shifts are suggested by climate velocity. *Nature*, 507, 492–495.
- Despres-Patanjo, L.I., Azarovitz, T.R. & Byrne, C.J. (1988). Twenty-five Years of Fish Surveys in the Northwest Atlantic: The NMFS Northeast Fisheries Center's Bottom Trawl Survey Program. *Mar. Fish. Rev.*, 50, 69–71.
- FishGlob_data. (2023).
- Fredston, A., Pinsky, M., Selden, R.L., Szuwalski, C., Thorson, J.T., Gaines, S.D., *et al.* (2021). Range edges of North American marine species are tracking temperature over decades. *Glob. Change Biol.*, 27, 3145–3156.
- Fredston, A., Tingley, M.W., Neate-Clegg, M.H.C., Evans, L.J., Antão, L.H., Ban, N.C., *et al.* (2025). Reimagining species on the move across space and time. *Trends Ecol. Evol.* 40, 629–638.
- Fredston-Hermann, A., Selden, R., Pinsky, M., Gaines, S.D. & Halpern, B.S. (2020). Cold range edges of marine fishes track climate change better than warm edges. *Glob. Change Biol.*, 26, 2908–2922.
- Gaston, K.J. (2000). Global patterns in biodiversity. *Nature*, 405, 220–227.
- Gaston, K.J. (2003). *The structure and dynamics of geographic ranges*. Oxford series in ecology and evolution. University Press, Oxford.
- Gaston, K.J., Chown, S.L., Calosi, P., Bernardo, J., Bilton, D.T., Clarke, A., *et al.* (2009). Macrophysiology: A Conceptual Reunification. *Am. Nat.*, 174, 595–612.
- Gould, E., Fraser, H.S., Parker, T.H., Nakagawa, S., Griffith, S.C., Vesk, P.A., *et al.* (2023). Same data, different analysts: variation in effect sizes due to analytical decisions in ecology and evolutionary biology.
- Guisan, A. & Thuiller, W. (2005). Predicting species distribution: offering more than simple habitat models. *Ecol. Lett.*, 8, 993–1009.
- Hällfors, M.H., Pöyry, J., Heliölä, J., Kohonen, I., Kuussaari, M., Leinonen, R., *et al.* (2021). Combining range and phenology shifts offers a winning strategy for boreal Lepidoptera. *Ecol. Lett.*, 24, 1619–1632.
- Hampe, A. & Petit, R.J. (2005). Conserving biodiversity under climate change: the rear edge matters. *Ecol. Lett.*, 8, 461–467.
- Hickling, R., Roy, D.B., Hill, J.K., Fox, R. & Thomas, C.D. (2006). The distributions of a wide range of taxonomic groups are expanding polewards. *Glob. Change Biol.*, 12, 450–455.
- Hughes, A.C., Dorey, J.B., Bossert, S., Qiao, H. & Orr, M.C. (2024). Big data, big problems? How to circumvent problems in biodiversity mapping and ensure meaningful results. *Ecography*, 2024, e07115.
- Jackson, S.T. & Sax, D.F. (2010). Balancing biodiversity in a changing environment: extinction debt, immigration credit and species turnover. *Trends Ecol. Evol.*, 25, 153–160.
- Kerr, J.T., Pindar, A., Galpern, P., Packer, L., Potts, S.G., Roberts, S.M., *et al.* (2015). Climate change impacts on bumblebees converge across continents. *Science*, 349, 177–180.
- Krkošek, M., Lauzon-Guay, J.-S. & Lewis, M.A. (2007). Relating dispersal and range expansion of California sea otters. *Theor. Popul. Biol.*, 71, 401–407.
- La Sorte, F.A. & Thompson, III, F.R. (2007). Poleward Shifts in Winter Ranges of North American Birds. *Ecology*, 88, 1803–1812.
- Lai, Y.-Z., Lin, Y.-C.J. & Ko, C.-Y. (2024). How would estimation of geographic range shifts of marine fishes be different when using occurrence and abundance data? *Divers. Distrib.*,

- 30, e13919.
- Lawlor, J.A., Comte, L., Grenouillet, G., Lenoir, J., Baecher, J.A., Bandara, R.M.W.J., *et al.* (2024). Mechanisms, detection and impacts of species redistributions under climate change. *Nat. Rev. Earth Environ.*, 5, 351–368.
- Lenoir, J., Bertrand, R., Comte, L., Bourgeaud, L., Hattab, T., Murienne, J., *et al.* (2020). Species better track climate warming in the oceans than on land. *Nat. Ecol. Evol.*, 1–16.
- Linck, E.B. (2025). What Is an Elevational Range? *Am. Nat.*
- MacArthur, R.H. (1972). *Geographical Ecology: Patterns in the Distribution of Species*. Princeton University Press.
- Maureaud, A.A., Palacios-Abrantes, J., Kitchel, Z., Mannocci, L., Pinsky, M.L., Fredston, A., *et al.* (2024). FISHGLOB_data: an integrated dataset of fish biodiversity sampled with scientific bottom-trawl surveys. *Sci. Data*, 11, 24.
- McCain, C., Szewczyk, T. & Knight, K.B. (2016). Population variability complicates the accurate detection of climate change responses. *Glob. Change Biol.*, 22, 2081–2093.
- National Audubon Society. (2023). The Christmas Bird Count Historical Results [Online].
- Oborny, B. & Zimmermann, D. (2023). Advancing and retreating fronts in a changing climate: a percolation model of range shifts. *Ecography*, 2023, e06645.
- Parmesan, C. & Yohe, G. (2003). A globally coherent fingerprint of climate change impacts across natural systems. *Nature*, 421, 37–42.
- Pecl, G.T., Araújo, M.B., Bell, J.D., Blanchard, J., Bonebrake, T.C., Chen, I.-C., *et al.* (2017). Biodiversity redistribution under climate change: Impacts on ecosystems and human well-being. *Science*, 355, eaai9214.
- Perry, A.L., Low, P.J., Ellis, J.R. & Reynolds, J.D. (2005). Climate Change and Distribution Shifts in Marine Fishes. *Science*, 308, 1912–1915.
- Pinsky, M.L., Worm, B., Fogarty, M.J., Sarmiento, J.L. & Levin, S.A. (2013). Marine taxa track local climate velocities. *Science*, 341, 1239–1242.
- Poloczanska, E.S., Brown, C.J., Sydeman, W.J., Kiessling, W., Schoeman, D.S., Moore, P.J., *et al.* (2013). Global imprint of climate change on marine life. *Nat. Clim. Change*, 3, 919–925.
- R Core Team. (2021). R: A language and environment for statistical computing.
- Robinson, L.M., Gledhill, D.C., Moltschanivskyj, N.A., Hobday, A.J., Frusher, S., N.Barrett, *et al.* (2015). Rapid assessment of an ocean warming hotspot reveals “high” confidence in potential species’ range extensions. *Glob. Environ. Change*, 31, 28–37.
- Schoeman, D.S., Schlacher, T.A., Jones, A.R., Murray, A., Huijbers, C.M., Olds, A.D., *et al.* (2015). Edging along a Warming Coast: A Range Extension for a Common Sandy Beach Crab. *PLoS ONE*, 10, e0141976.
- Sexton, J.P., McIntyre, P.J., Angert, A.L. & Rice, K.J. (2009). Evolution and Ecology of Species Range Limits. *Annu. Rev. Ecol. Evol. Syst.*, 40, 415–436.
- Sittaro, F., Paquette, A., Messier, C. & Nock, C.A. (2017). Tree range expansion in eastern North America fails to keep pace with climate warming at northern range limits. *Glob. Change Biol.*, 23, 3292–3301.
- Stuble, K.L., Bewick, S., Fisher, M., Forister, M.L., Harrison, S.P., Shapiro, A.M., *et al.* (2021). The promise and the perils of resurveying to understand global change impacts. *Ecol. Monogr.*, 91.
- Thomas, C.D., Franco, A.M.A. & Hill, J.K. (2006). Range retractions and extinction in the face of climate warming. *Trends Ecol. Evol.*, 21, 415–416.
- Tilman, D., May, R.M., Lehman, C.L. & Nowak, M.A. (1994). Habitat destruction and the extinction debt. *Nature*, 371, 65–66.
- Wallace, A.R. (1876). *The Geographical Distribution of Animals: With a Study of the Relations of Living and Extinct Faunas as Elucidating the Past Changes of the Earth’s Surface*.

- Cambridge University Press, Cambridge.
- Watts, M.J., Fordham, D.A., Akçakaya, H.R., Aiello-Lammens, M.E. & Brook, B.W. (2013). Tracking shifting range margins using geographical centroids of metapopulations weighted by population density. *Ecol. Model.*, 269, 61–69.
- White, E.R. (2019). Minimum Time Required to Detect Population Trends: The Need for Long-Term Monitoring Programs. *BioScience*, 69, 40–46.
- White, E.R. & Bahlai, C.A. (2021). Experimenting With the Past to Improve Environmental Monitoring. *Front. Ecol. Evol.*, 8.
- Willi, Y. & Van Buskirk, J. (2019). A Practical Guide to the Study of Distribution Limits. *Am. Nat.*, 193, 773–785.
- Williams, J.E. & Blois, J.L. (2018). Range shifts in response to past and future climate change: Can climate velocities and species' dispersal capabilities explain variation in mammalian range shifts? *J. Biogeogr.*, 45, 2175–2189.
- Wolfe, B.W., Champion, C., Gaston, T., Brown, J., Coleman, M.A., Davis, T.R., *et al.* (2025). Continental-Scale Assessment of Climate-Driven Marine Species Range Extensions Using a Decade of Citizen Science Data. *Divers. Distrib.*, 31, e70022.
- Yalcin, S. & Leroux, S.J. (2017). Diversity and suitability of existing methods and metrics for quantifying species range shifts. *Glob. Ecol. Biogeogr.*, 26, 609–624.
- Zhu, K., Woodall, C.W. & Clark, J.S. (2012). Failure to migrate: lack of tree range expansion in response to climate change. *Glob. Change Biol.*, 18, 1042–1052.