Integrating geographic ranges across temporal scales

Simon A.F. Darroch[1,2,3], Erin E. Saupe[4], Michelle M. Casey[5] and Maria L.S.P. Jorge[1]

[1]Vanderbilt University, Department of Earth and Environmental Sciences, 5726 Stevenson Center, Nashville, TN 37240, USA.
[2]Evolutionary Studies Initiative, Vanderbilt University, Nashville, TN 37235, USA.
[3]Senckenberg Museum of Natural History, Frankfurt 60325, Germany.
[4]University of Oxford, Department of Earth Sciences, South Parks Road, Oxford, OX1 3AN, UK.
[5]Towson University, Department of Physics, Astronomy and Geosciences, 8000 York Road, Towson, MD 21252, USA.

*Author for correspondence

e-mail: simon.a.darroch@vanderbilt.edu

Keywords: geographic range, temporal scale, macroecology, macroevolution, paleontology, conservation paleobiology

Abstract

Geographic ranges are a fundamental unit of biogeography and macroecology. Increasingly, paleontologists and ecologists alike are reconstructing geographic ranges of species from fossils, in order to understand the long-term processes governing biogeographic and macroevolutionary patterns. As these reconstructions have become increasingly common, uncertainty has arisen over the equivalency of paleo-ranges and modern ranges. Here, we argue geographic ranges are time-averaged at all temporal scales, and reflect the biotic and abiotic processes operating across an equivalent range of time and space scales. This conceptual framework integrates the study of geographic ranges reconstructed using modern and ancient data, and highlights the potential for ranges to illuminate processes responsible for diversity patterns over intervals spanning days to tens of millions of years of Earth history.

What is a geographic range?

The area occupied by a species is referred to as its geographic range. Geographic ranges are fundamental to our understanding of biogeography [1], reflecting both biological and ecological attributes (including abiotic tolerances, biotic interactions, life history, dispersal mode and ability [2-6], and recent habitat loss and fragmentation in response to anthropogenic activities; see e.g. [7]). The study of geographic ranges has provided valuable insight into ecological processes and the spatial organization of biodiversity, and has been a central tenet of biogeographical research since the early 1900s [8]. Over the past ~50 years, paleontologists and ecologists have experimented with reconstructing geographic ranges from fossil locality data – termed 'paleogeographic ranges' – at a range of temporal scales. 'Temporal scale' here refers to the duration or extent of time over which a paleogeographic range is measured, acknowledging that the fossil record is **time-averaged**, and thus fossils are often grouped within temporal and **lithostratigraphic** bins; see Box 1). The study of paleogeographic ranges has revealed long-term macroecological and macroevolutionary processes responsible for the formation of biogeographic patterns (e.g. [9,10]) and the composition of present-day regional biotas [11]. For example, paleogeographic ranges possess links to rates of speciation [12-14] and extinction risk [15-17], and may therefore be crucial determinants of macroevolutionary trends. The inverse correlation between geographic range size and extinction risk over intervals in the geological past, including mass extinction events, could even help to identify at-risk species in the ongoing biodiversity crisis, termed the "6th mass extinction" [15,18-20].

Despite the surge in studies estimating paleogeographic ranges (e.g., [21]), questions remain regarding the conceptual equivalency of ranges as measured by ecologists *versus* paleontologists. Here, we argue two key points: 1) geographic and paleogeographic ranges are both time-averaged, but over a different range of temporal scales; and 2) both geographic and paleogeographic ranges reflect ecological and biological attributes of species. Consequently, the expansion or reduction of ranges – viewed at any temporal scale – ultimately represent the same intrinsic processes: the distribution of habitable conditions, and/or changing restrictions to dispersal. Ranges reconstructed at all temporal scales should thus form part of a continuum, and the specific temporal scale on which a range is reconstructed will determine the questions that can be answered using that data.

Geographic ranges vs. paleogeographic ranges

Geographic ranges attempt to describe the spatial distribution of a species at any given time interval. The area where a species is found (the 'range') is separated from areas where it is not by the range boundary, which can be mapped to illustrate the extent of species' occurrences as a two-dimensional polygon or irregular area (Figure I). The information used to construct ranges is varied, but can include species sightings data (from e.g., biological surveys), occurrence data, and museum specimens [1].

Ecologists, however, have long recognized that any attempt to map or describe ranges suffers from reduction of a complex phenomenon to a simple abstraction that can be easily mapped and quantified [1,21-23]. Range boundaries are one illustration of the complexity of this reduction. Although the center of the range may be more or less continuously occupied by individuals, occupancy tends to become more diffuse closer to range boundaries, leading to large areas where individuals are typically never found (range 'holes') [24], and to areas where species can be found but are isolated from the main range (range 'fragments' or 'outliers') [25,26]. Holes and fragments are often not depicted on range maps [1], and they illustrate the issues in depicting range boundaries as simple lines showing presence *versus* absence that can be largely subjective [23]. Because of this inherent complexity, ecologists and biologists map geographic ranges using a wide array of methods [1,23] that attempt to estimate the spatial spread of areas currently occupied by the species (**EOO** - 'extent of occurrence') or the area over which a species is actually found (**AOO** - 'area of occupancy').

Similar to geographic ranges defined by ecologists, paleogeographic ranges measured by paleontologists attempt to describe the spatial distribution of a species at a given interval of time. However, paleogeographic ranges are constructed using fossil or **geohistorical** data, rather than 'modern' occurrence records, although both temporal scales still incorporate occurrences aggregated on a range of timescales (see Box 1, Figure I; Box 2). The sizes and shapes of these paleogeographic ranges have been reconstructed using a variety of methods, including **convex hulls** drawn around mapped occurrences (incorporating the position of modern or ancient coastlines), maximum distance between occurrences, maximum latitudinal or longitudinal range between occurrences, and number of occupied latitude/longitude grid cells [24]. Given the movement of geological plates on million-year timescales (plate tectonics), measurement of paleogeographic ranges is almost always performed after rotating fossil occurrence sites back to their original locations. More recently, paleontological studies have begun to develop probability-based estimates of both (i) fossil occupancy within reconstructed ranges (e.g., [28-30], which are important given the complex processes involved in fossil preservation (see Box 1), and (ii) suitable conditions for species, referred to as species distribution modelling (SDM) or ecological niche modelling (ENM), which can augment estimation of past geographic distributions [31].

Regardless of methodology, however, recent simulation-based approaches [20,27] have shown the relative rank order of range sizes can be detected with remarkable fidelity in the fossil record (Figure 1), illustrating that paleogeographic range reconstruction is a valid method for addressing macroecological and macroevolutionary questions.

To what extent are geographic and paleogeographic ranges equivalent?

Both geographic ranges and paleogeographic ranges attempt to measure the spatial distribution of taxa during any one interval of time. Similarly, both geographic and paleogeographic ranges are used to address fundamental questions in biogeography, including the factors that influence the distribution of species, the effects of ranges on ecological and evolutionary processes, and how such insights may be brought to bear on predicting and remediating the effects of ongoing global change. The only practical difference between geographic and paleogeographic ranges is the latter are reconstructed using fossil (rather than recent) material, and will therefore be subject to a broadly different set of time- and space-specific processes influencing their shape and character. Defining a strict age-based criterion for fossil vs. extant material (and thus a boundary between what we refer to as ‘geographic’ vs. ‘paleogeographic’ ranges) is, however, not straightforward. Our definition of ‘geographic’ range occasionally incorporates historical surveys or museum records that can be 100s of years old, especially for studies focused on quantifying range shifts due to anthropogenic activities (e.g., [32]). Similarly, ‘paleogeographic’ ranges can incorporate **subfossil** or geohistorical material as young as 1000s or even 100s of years old. Thus, we emphasize that there can be a degree of temporal overlap between these two terms.

Paleontologists typically measure paleogeographic ranges of fossil species after grouping occurrence data within temporal and lithostratigraphic bins, most frequently at the scale of geological Stages (typically ~0.5-10 million years in duration), although some studies have reconstructed ranges at finer temporal scales [33,34]. Consequently, paleogeographic ranges can be substantially time averaged, representing the distribution of species over an interval that can span millions of years that amalgamates range expansions, contractions, and shifts, and which are affected by issues of non-preservation (i.e., false absences) and erosional processes that control the distribution of fossiliferous sediments at the surface of the Earth.

Geographic ranges are often considered an emergent trait of species [1] and are quantified most often at this level (although populations and individual ranges can also be estimated [35]). In the fossil record, however, higher taxa (i.e., genera or families) are often used as proxies for species, including for range estimation (e.g., [12,16]). This is because higher taxa are considered easier to diagnose and recognise than fossil species, show greater taxonomic stability, and their sampling is considered more complete [36]. Nevertheless, their use as proxies for species is not without issue, and the extent to which they can be used as proxies for the purposes of reconstructing macroecological and macroevolutionary processes requires deeper investigation [36]. It may be sensible, therefore, to aggregate modern occurrence data at the same taxonomic level (e.g., genus *versus* species) when the goal is to compare geographic and paleographic ranges.

Processes influencing the size and shape of ranges

We argue all ranges, measured for either modern or fossil species, are to some extent time-averaged, and the size, shape, and location of these ranges are governed by processes operating on nested temporal scales. Geographic and paleogeographic ranges should therefore be viewed as a continuum, reflecting processes operating on the temporal scale at which the ranges are measured. We address specific processes that influence ranges here in order of lengthening temporal scale. Arranged in this way, we emphasize two points: first, it is nearly impossible to determine the spatial distribution of a species at any given moment, except over small areas for relatively long-lived and immobile organisms, such as trees and corals. Thus, all distributional information related to the reconstruction of ranges is integrated over time [1]. Second, changes in the spatial distribution of any biological group are driven by processes operating on a continuous range of timescales spanning up to 12 orders of magnitude (summarized in Figure 2).

On the very shortest timescales, defined here as hours to 10s of years, the spatial distribution of a species reflects the availability of basic individual needs (e.g. food, shelter and mates), with motile organisms moving to fulfill those needs. For example, individual white-lipped peccaries (*Tayassu pecari*) move an average of ~3-5 km in a day, ~100 km in a month, and (cumulatively) ~40,000 km in one year [37]. Thus, convex hulls drawn around individuals may differ substantially on a day-to-day basis. What is typically mapped as the range of the species is instead equivalent to the sum of individual home ranges (i.e., the range an individual animal will occupy over its lifetime), which represents a time-averaged approximation of the range over months to decades, depending on the lifespan of the individual. Population-level processes (e.g., the dispersal of individuals away from their place of birth, birth/death rates, and local extinction/extirpation) will also result in expansions or contraction of the range [38], instigating range changes that can be maintained across generations [39]. Biological invasions are another process linked to change in ranges on these timescales, especially those resulting from accidental introduction (see, for example, the European Zebra mussel *Dreissena polymorpha* [40]).

Bridging these short timescales to intermediate and long timescales are processes that fall broadly into the category of 'climate change'. As climate warms or cools, the conditions suitable for the persistence of given species shifts across the surface of the Earth, prompting species to move as they attempt to track preferred climatic conditions [32,41,42]. Both global and local climates are subject to processes operating across temporal scales and have been shown to drive changes in species' distributions (see, for example [43-45) in order of lengthening temporal scale).

On monthly to annual timescales, natural climate perturbations such as drought, heat waves, and storms can have a large effect on ranges. For example, *Pinus ponderosa* and *Pinus edulis-Juniperus monosperma* (i.e. piñon-juniper) forests in northern New Mexico shifted ~2 km in less than 5 years due to drought [43]. Short-term climate oscillation phenomena, such as the El Niño Southern Oscillation ('ENSO'), can also shift ranges over weeks to months. This led, for example, to the regional-scale extirpation of *Merluccius gayi* hake from shallow-water environments along the coast of northern Peru [46]. On decadal to centennial timescales, anthropogenic-driven climate change has initiated changes in the distributions of both plant and animal groups [32,47-51], and these changes are forecast to become more dramatic as the planet continues to warm [52-55]. For example, all but one demersal North Sea fish species have shifted their distributions northwards in response to warming over the past 25 years by an average of 174 km [56]. Indeed, marine species may shift their ranges polewards in response to anthropogenic warming at rates six times faster than terrestrial groups [32].

On the order of 1000's to 100,000's of years, Earth's climate is governed by **Milankovich cycles** that control the timing of glacial and interglacial cycles throughout Earth's history. These cycles have had a profound effect on the distribution of species, to the extent that Dynesius and Jansson [57] referred to them as 'orbitally-forced range dynamics'. Some of the best-studied examples include shifts in the ranges of north-temperate tree species [58], molluscs [59], and marine bivalves [45] over Pleistocene glacial-interglacial cycles – some on the order of 100s of kms.

Finally, global climate is subject to forcing on million-year timescales by a variety of Earth-system-scale processes that affect the composition of atmospheric gasses and thus temperature. For example, the onset of the Late Paleozoic Ice Age ('LPIA', ~360 million years ago) marked the transition from greenhouse to icehouse conditions, leading to equator-wards contraction of ranges in various taxonomic groups – particularly bryozoan and brachiopod species – and to a long-term re-organization of range-size distributions [60].

Changes in ranges on thousand- to million-year timescales have also been shown to be driven by a variety of processes that, although potentially related to climate, do not fit easily in the category of 'climate change'. One of these processes is the sinking or uplift of continental crust as it re-establishes **isostatic equilibrium**, leading to changes in topography and regional sea level. Species ranges can expand and contract in response to these changes, for example during the late Ordovician (~446 mya) Richmondian invasion, where sea level changes in present-day North America allowed marine invertebrates to disperse to a shallow marine basin located in present-day Ohio [61]. Not only did the ranges of invading taxa increase significantly, but competition amongst invaders and native species led to the extinction of native species with small ranges, and thus a long-term reorganization of range-size distributions [61].

Finally, on the very longest timescales (millions of years), the movements of tectonic plates can have a profound effect on the distribution of species within clades. One well-studied example is the formation of the Isthmus of Panama ~3 million years ago, which allowed range expansion in a large number of terrestrial mammals as part of the 'Great American Biotic Interchange', which simultaneously cut the ranges of many marine species that were distributed on both sides of the Isthmus [62]. Continental collision can also diminish the amount of habitable area for shallow marine species, thus reducing range sizes while forcing new biotic interactions—an effect once thought responsible for driving mass extinction events [63]. Since tectonic plate movement occurs on the timescale of multi-millions of years, it can affect multiple lineages over that time span and promote or inhibit speciation.

This account is not meant as an exhaustive list of the processes that govern the size and shape of species' ranges, but rather illustrates the temporal scales over which ranges can be reconstructed, and over which ranges can be dynamic. This, in turn, emphasizes that geographic *versus* paleogeographic ranges form part of a continuum, and thus the temporal scale at which a range is studied will reflect processes operating over that same scale (Figure 2).

Applications in evolutionary ecology and conservation paleobiology

Although treating geographic and paleogeographic ranges as part of a continuum is arguably intuitive, we stress there remain key questions regarding both the accuracy with which fossil data can reconstruct past distributions, and how these data should be applied. For example, the rank order of range sizes may be preserved, but reconstructing absolute range sizes may only be possible if, once preservational biases and the distribution of fossil localities are considered, ranges are truncated in a consistent fashion among species, biomes, and timescales. Addressing this question will require not only simulation studies (e.g., [20,27]), but detailed **taphonomic** work that quantifies the preservation potential of organisms in a range of environments.

This question is also crucial when we consider where paleogeographic range data can be applied. There are many pressing questions in macroecology and macroevolution that should be addressed using ranges reconstructed at all temporal scales (see 'Outstanding questions'), but a particularly critical one hinges on the relevance of paleogeographic ranges to conserving present-day biodiversity. Paleontological studies [15,64-66] have demonstrated an inverse correlation between paleogeographic range size and extinction risk over one or more of the **'Big 5' mass extinction** events. This relationship suggests range studies focused on past extinction events can help to predict those species most at risk from future global change [15,19]. Establishing whether relatively small- or large-ranged taxa are more vulnerable over, for example, intervals of climatic warming is undoubtedly useful. However, the IUCN currently defines specific range size thresholds for determining the extinction risk status of species. Thus, for paleogeographic ranges to have more specific predictive power, the consistency with which ranges are truncated (and thus our ability to reconstruct paleogeographic range size) needs detailed investigation (see, e.g., [67]). Predictive fossil-based studies may be most plausible in the **Neogene** and **Quaternary**, where range truncation is likely less severe, and the durations of lithostratigraphic bins are typically much shorter. More promisingly, reconstructing ranges through successive warming and cooling cycles over the last ~23 million years may provide a sense for how we expect the ranges of specific species to shift (i.e., expand, contract, or move) in response to a variety of scenarios. These reconstructions may also provide ecological and conservation insight not available from ‘modern’ geographic ranges, including environments not currently occupied by species, but shown to be suitable (i.e., potentially providing estimates closer to the fundamental rather than realized niche [54,68,69]). In addition to identifying at-risk species, the information provided by paleogeographic ranges could be crucial to predicting the long-term impacts of biotic invasions [25] and to designing the size and location of conservation areas [70].

Concluding remarks

In summary, recent research shows the preservation potential of many aspects of ranges is remarkably high, even in the distant past where fossiliferous sediments are scarce. We argue that ranges as measured by both ecologists and paleontologists represent broadly the same ecological phenomenon – the area occupied by a species – which ultimately reflects the distribution of ideal abiotic and biotic conditions and barriers to movement. Moreover, despite the fundamental differences in data sources (i.e., modern vs. fossil) used to reconstruct them, all ranges are time averaged to some extent. By averaging over shorter or longer intervals of time, we gain insight into how species’ distributions respond to processes operating on a range of timescales from hours to hundreds of thousands and even millions of years. Our conceptual framework thus integrates the study of ranges across temporal scales, and highlights the potential for ranges to illuminate processes responsible for structuring diversity over long swathes of Earth history.

Acknowledgments

S.A.F.D. acknowledges generous support from the Alexander von Humboldt Foundation, which is sponsored by the Federal Ministry for Education and Research in Germany. E.E.S. is grateful for funding from the Leverhulme Trust (Leverhulme Prize and grant #DGR01020) and NERC (NE/V011405/1). We thank Andrew Flick (Evolutionary Studies Institute, Vanderbilt University) for providing constructive feedback on an earlier version of this manuscript. This manuscript was considerably improved after constructive comments from Jonathan Lenoir and two anonymous reviewers.

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Figures captions

Figure 1: The preservation potential of relative range size is surprisingly high (modified from [20]). A) Results are presented from simulations that assess how well range sizes are preserved in deep time using the present-day distribution of 341 terrestrial mammal species in the contiguous United States (data taken from the IUCN Redlist). B) Frequency distribution of range sizes within this species pool. We superimposed a hypothetical distribution of fossiliferous sediments (C), taken from the Paleozoic record of North America, and randomly generated fossil localities within these sedimentary areas. We then assessed how well we could reconstruct the “actual” distribution of range sizes using the simulated fossil record. D) Right panels show the rank agreement between actual and reconstructed range sizes under these scenarios; note that agreement is still fairly high ($\rho = 0.46$) even when the area of preserved sediment is vanishingly small (6818 km^2).

Figure 2: The biotic and abiotic processes affecting range sizes and range size distributions of species and/or taxonomic groups on timescales ranging from hours to millions of years.

Box 1 – How are geographic ranges vs. paleogeographic ranges measured?

Figure I caption: Key differences between ranges as measured by ecologists *versus* paleoecologists. A) Present-day distribution of individuals belonging to a hypothetical species. The range of this species (blue) is estimated by an irregular area drawn around individuals. B) Example of paleo-range reconstruction. The distribution of the same species time-averaged over an arbitrary number of years (i.e., comprising range expansions, contractions, and shifts) is given in light blue. The distribution of fossiliferous sediments from the same interval is shown in orange. Fossil localities preserving the species (in red) occur at the intersection between the range and preserved sediment. The paleogeographic range for this species in this interval is reconstructed using a convex hull drawn around the outside of fossil occurrences.

Text: Ecologists map ranges using a wide array of methods that attempt to estimate the spatial spread of areas currently occupied by the species. Paleogeographic ranges are constructed using fossil or geohistorical data, rather than ‘modern’ occurrence records. To become fossilized, an organism typically needs to be deposited in a location where sediment is accumulating (e.g., [70]). In most environments this requires water, and thus the fossil record of marine organisms is thought to be more complete than that of terrestrial organisms [71]. After death, soft tissues typically decay and multi-element skeletons disarticulate due to post-mortem processes that can include transport, weathering, erosion (including bioerosion), and scavenging [72]. Post-mortem transport presents a potential barrier to accurate range reconstruction (e.g., if an organism were to be transported outside of its original range), but empirical studies have shown that organisms are overwhelmingly preserved within their original habitat (i.e., parautocthonous, rather than allocthonous [71,72]). Once encased in sediments, what remains of the original organism will be buried in the developing stratigraphic column, subjected to varying degrees of diagenetic alteration, and eventually re-exposed at the surface due to weathering, erosion, and tectonics. These ancient sediments are mapped at the surface of the Earth as geological formations, which are stratigraphic packages of rock grouped by lithology or paleoenvironment, and assigned an age based on index fossils and/or geochronological dating. The fossils within these sediments are identified and recorded, and added to large fossil databases (e.g., Paleobiology Database and the Global Biodiversity Information Facility).

Box 2: Resources for paleogeographic range reconstruction

Text: The data necessary to conduct geographic and paleogeographic range size analyses have become increasingly available with the advent of large, spatial datasets and data aggregators. These resources allow you to search, view, download, and map data through their web APIs. Although a comprehensive list of databases containing strictly modern distributional data is beyond the scope of this opinion piece (see, for example, a recent compilation on GBIF: https://www.gbif.org/dataset/search?q=), we briefly describe here some of the larger databases that include geohistorical and paleontological data, and which have been used to reconstruct geographic ranges in both shallow and deep time. This list is far from exhaustive, but includes many of the sources that have been used in studies cited elsewhere in this paper. Some of the most important characteristics of these databases are summarized in the table below.

The iDigBio Portal provides access to >67 million organismal occurrences curated at museums and other institutions, largely in the U.S. The ‘Basis of Record’ field indicates whether the occurrence record comes from a fossil specimen, a modern specimen, or a recorded observation. Each record also includes a geographic uncertainty radius in meters, if provided by the institution.

The PBDB is a non-governmental, non-profit open access resource for paleontological data. It contains published data on the taxonomy, temporal distribution, and geographic distribution of over 1.5 million global fossil occurrences. Data in the PBDB has been entered over the last 20+ years by Database Authorizers, mainly PhD-holding scientists in various subdisciplines of paleontology. The PBDB contains only published data, and so does not include (for example) museum specimens that have not been formally described (present in iDigBio).

The Download Generator allows you to select the output fields included in downloads, with options for both ‘coordinates’ (the location of the fossil collection in decimal degrees latitude and longitude) and ‘paleolocation’ (the reconstructed location of the fossil at the time it was deposited), precluding the need to reconstruct paleogeographic location of occurrences using other software.

Finally, GBIF is an international network and data infrastructure aimed at open access to data for all life on Earth. GBIF acts as a data aggregator, including records from a large number of other databases and sources. For that reason, GBIF is the largest database of those mentioned, including over 2 billion specimen occurrence records with latitude and longitude coordinates. GBIF also has the largest range of data types, from natural history collection specimens, fossils recorded in the PBDB, geotagged smartphone photos shared by amateur naturalists, live animals on display in zoos, and dredge, trawl and bycatch records from marine monitoring organizations. Consequently, restricting data downloads to those types most suitable to any given analysis is paramount.

Table caption: Characteristics of some commonly-used databases that contain occurrence records for geographic range reconstruction. The ‘temporal scale’ field refers to the temporal extent of occurrences (i.e., oldest/youngest records).