Towards a unified conceptual framework for studies of altitudinal migration: linguistic nuances, taxonomic prevalence, and emerging opportunities

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Abstract

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Abstract

The study and importance of altitudinal migration has attracted increasing interest among zoologists. Altitudinal migrants are taxonomically widespread and move across environmental gradients that transect altitudinal and latitudinal gradients as partial or complete migrants, subjecting them to a wide array of environments and ecological interactions. Here, we present a brief synthesis of recent development and suggest future directions towards a more taxonomically inclusive conceptual framework for the study of altitudinal migration. Our framework centers on a working definition of altitudinal migration that highlights the biological relevance and scale of movement for a given taxon and its life history. Even with a revised definition,

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Keywords

Altitudinal migration, animal movement, elevational migration, vertical migration, latitudinal migration

Introduction

Since the Upper Paleolithic age more than 20,000 years ago, humans have been fascinated by animal movement, as evidenced by early rock art depicting animal migration (Bacon et al., 2023). From this long-standing interest in animal movement has come a rich history in studying animal migration. Most studies of animal migration have primarily focused on latitudinal migration, although altitudinal migration—the seasonal movement of populations across elevational or bathymetric gradients (Hsiung et al., 2018; Milligan et al., 2020)—has garnered increasing attention across taxonomic groups. Altitudinal migrants often pass through multiple habitats with different environmental conditions and experience a similar or even greater breadth of ecological interactions (e.g., predation, interspecific competition, interactions with parasites, etc.) compared to strict latitudinal migrants (Williamson & Witt, 2021). As the taxonomic representation of studies on altitudinal migration has grown, so too have inconsistencies in the language used to describe this phenomenon. Here we propose a functional definition of altitudinal migration and provide guidelines towards a unified conceptual framework of altitudinal migration that highlights its biological importance and prevalence across taxa (Figure 1). We also discuss emerging opportunities and challenges, outstanding questions in the field, and future directions to advance its study. Collective thought towards an improved conceptual framework will enable researchers to better compare and contrast emergent patterns and identify idiosyncrasies of altitudinal migration behavior among taxa and biogeographic regions.

Definitions and nuances:

A shared language for discussing altitudinal migration has not been used consistently in the literature. Both the term used and the definition of the phenomenon itself lack a standardized definition (Barçante et al., 2017), which makes it difficult to find and compare studies across disciplines and taxonomic groups. In fact, the patterns and processes that constitute altitudinal migration and the taxa considered altitudinal migrants have differed widely among studies, with most definitions focused heavily on birds (Burgess & Mlingwa, 2000, Boyle, 2017; Hsiung et al., 2018; Tsai et al., 2021; Williamson & Witt, 2021). A conceptual framework for studying altitudinal migrations needs to start with a standardized definition and understanding of the use of the term. Here, we suggest a revised definition for altitudinal migration as**a seasonal round trip between breeding and non-breeding ranges for part or all of a population along an elevational or bathymetric gradient that results in a biologically relevant shift in distribution** . But then what do we mean by "biologically relevant"?

We believe biological relevance depends on the taxon in question and whether the vertical movement directly impacts an organism's fitness—either by ensuring successful migration and subsequent reproduction, or by harming their chances for survival. Challenges to an organism's fitness can fall under two, non-mutually exclusive categories: seasonal elevational movements that impart (1) physiological and/or (2) ecological changes on migrants. Physiological challenges can occur when individuals move across extreme elevational gradients (i. e. Bar-headed Geese; Scott et al., 2015), which requires adaptations for the extreme differences in partial oxygen pressure (Williamson & Witt, 2021). Vertical physical barriers, such as waterfalls or mountains, or dams, can also impose physiological challenges to survival by blocking migratory routes or requiring physical exertion to cross (Cosgrove et al., 2018). Physical barriers may present different strengths of physiological or ecological change; in some instances, certain taxa may move across a given physical barrier daily, while other taxa may only do so once a season or only once in their lifetime. Ecological challenges may include changes in habitat, intraspecific competition, predation risk, climatic changes, trophic interactions and/or resource availability (Alerstam & Bäckman, 2018). The distance covered by altitudinal migrants varies among taxa, but the migration event typically involves movement between breeding and non-breeding ranges that extend far beyond the organism's home range in either site (Teitelbaum et al., 2015). On one extreme, more vagile species may move more than 2000 m in elevation and thousands of kilometers in latitude, which presents clear physiological challenges for survival in dramatically different environments across their annual cycle (Williamson & Witt, 2021). In contrast, some snails undertake amphidromous migrations from saltwater to freshwater habitats that cover less than a hundred meters of elevational change (Villeneuve et al., 2019), while some terrestrial species only move a few hundred meters in elevation (i.e. some Drosophila; Mitsui et al. 2010 or Trochilidae; Tinoco et al., 2009). These may seem like trivial elevational changes for more vagile taxa, yet represent dramatic shifts in ecology and physiological conditions between breeding and non-breeding sites. Thus, although physiological and ecological changes are difficult to quantify and observe directly, they are nevertheless more important than changes in elevation that meet a numerical or statistical threshold between breeding and non-breeding territories. Imposing a strictly numerical definition to identify altitudinal migrants without considering the biological relevance of the migration event may erroneously include or omit altitudinal migrants and bias the inferences drawn from such studies.

Even with a revised definition grounded in biological relevance and scale, there are still many nuances and potential points of confusion when discussing and classifying altitudinal migrants. For instance, animals can move both latitudinally and vertically during seasonal movements, as exhibited by monarch butterflies (*Danaus plexippus*), which migrate over the course of multiple generations from high-elevation mountains in the Transvolcanic Belt of central Mexico to breed at low-elevation sites in the eastern United States and Canada during warmer spring and summer months (Kimura, 2021). There is not widespread agreement in the literature if altitudinal migration is strictly a short-distance migration phenomenon or if it encompasses such long-distance migration events as well. Some comparative studies or syntheses either do not address this explicitly, or allow for some but not all latitudinal migrants that also move in elevation to be classified as altitudinal migrants (Boyle, 2017; McGuire & Boyle, 2013; Pageau et al., 2020). Other studies state it is strictly a short-distance phenomenon (Hsiung et al., 2018), or may encompass long-distance latitudinal migration as well (Barçante et al., 2017a; Rappole, 2013; Williamson & Witt, 2021). Migrants that move across large latitudinal expanses while also changing elevations experience similar or greater physiological and ecological changes as short-distance altitudinal migrants. As such, we feel that work on altitudinal migration should encompass both long- and short-distance migrants, and that authors should explicitly state their criteria and rationale for classifying altitudinal migration.

The complex migratory patterns of monarch butterflies illustrate another nuance of altitudinal migration: partial altitudinal migration. Not all monarch populations are migratory (Chowdhury et al., 2021), as opposed to obligate migrants where all populations within a species are migratory. Here, we follow the broader definition of partial migration (Terrill & Able, 1988), where partial altitudinal migration (including differential migration; Dingle & Drake, 2007) not only includes distinct migratory and non-migratory populations, but also encompasses within-population variation in migration strategies, including taxa wherein only certain ages, sexes, or other demographic subunits of a population migrate (e.g. White-ruffed manakin *Corapipo altera*, Boyle et al., 2011). The majority of altitudinal migrants are also partial migrants (Hsiung et al., 2018), such that some subpopulation or demographic group does not participate in each annual migration event. Conversely, many long-distance latitudinal migrants undertake 'obligate' or complete migration, in which each demographic class of each population participates in seasonal movements (Newton, 2012).

Although altitudinal migration is a specific type of and part of the broader study of animal movement, 'movement' is not synonymous with 'migration'. Rather, migration is a specific form of animal movement.

Importantly, altitudinal migration is seasonal and cyclic with individuals and populations moving between distinct breeding and non-breeding areas at different elevations, which distinguishes it from other forms of movement where populations may shift their elevational distribution, but do so non-annually (i.e., dispersal, irruptions). Some cyclic daily movements may occur across vertical gradients, such as "hilltopping" in some insects, in which they form daily leks on top of hills or mountains (Kimura, 2021), and aquatic animals undergoing "diel vertical migration", in which individuals change water depth between night and day (Chapman et al., 2012). However, these are daily rather than seasonal movements at different elevations or depths, and therefore do not fall under our working definition of altitudinal migration.

Migration and movement exist along a behavioral and ecological continuum, and distinguishing migration from the broader study of movement is not always straightforward (e.g. some flies in the family Calliphoridae; Kimura 2021). For example, two polar breeding birds—Ivory Gull *Pagophila eburnea* in the Arctic, and Snow Petrel *Pagodroma nivea* in the Antarctic—both breed on high remote rocky outcrops (up to 2000 m and 2500 m, respectively) and make regular foraging trips to the ocean (Carboneras et al., 2020; Mallory et al., 2020). Under our definition, these daily behaviors of adults are best categorized as 'movements'. However, the young that are born at high-elevation nesting sites and return to breed after spending the non-breeding season at sea level could be considered altitudinal migrants. Despite the similar movement ecology of these two species, only the Ivory Gull is considered an altitudinal migrant, whereas no Antarctic birds—including the Snow Petrel—are considered altitudinal migrants (Barçante et al., 2017a; Hsiung et al., 2018). The study of migration is embedded within the broader study of animal movement, but determining where the narrower study begins is sometimes difficult due to complex life histories involving seasonal and/or ontological changes in elevation. A unified conceptual framework for altitudinal migration will help unpackage these complexities and alleviate this confusion. One can envision a multivariate space to describe the how organisms vary in their migratory behavior; for example, it may be helpful to place organisms along continua that describe variation whether organisms exhibit latitudinal migration, altitudinal migration, or both in conjunction with whether or not those taxa are complete or partial migrants (Figure 2).

Finally, establishing a consistent language for the field is important to help improve the visibility and searchability of the primary literature involved. Though "vertical" or "elevational" migration may be seen as more accurate descriptors of this type of seasonal movement across biomes and taxonomic groups, the term "altitudinal migration" has historical precedence (i. e. Todd and Carriker 1922; Presnall, 1935) and is more frequently used in the literature (2840 Google Scholar search hits for "altitudinal migration" compared to 464 for "elevational migration"; searches done on 15 August 2023). We used the program Publish or Perish (Harzing 2007) to quantify temporal trends in Google Scholar hits for publications that use the terms "altitudinal migration" and "elevational migration", finding that altitudinal migration was established as a term far earlier and is used far more often than "elevational migration" (Figure 3). Thus, although these terms have often been used interchangeably,we recommend using the more commonly used term altitudinal migration. We do not just advocate for its use because it is the more commonly used and historical term, but also because it better encompasses terrestrial and aquatic migrations. In that regard, "vertical migration" is perhaps a more accurate term, but is used predominantly in aquatic systems (over 141,000 Google Scholar search hits on 15 August 2023) to describe a different phenomenon of daily movement across multiple trophic levels up and down the water column rather than the seasonal movements we focus on here (Chapman et al., 2012). Use of a single term not commonly used elsewhere in the literature will aid researchers and search engines in identifying information on this phenomenon rather than often-conflated terms (Leeming 2023). 'Altitudinal migration' may seem a misnomer due to the definition of altitude in aviation as the distance above the Earth's surface as opposed to above sea level, yet we nonetheless recommend its use to promote a consistent vocabulary to facilitate dialogue across disciplines and taxonomic groups.

Taxonomic Prevalence:

Across the tree of life, from ocean depths to mountain peaks, various animals change their elevational distribution and/or depth between seasons (Figure 1; Hsiung et al., 2018; Milligan et al., 2020). Studies on altitudinal migration have largely focused on insects (Kimura, 2021), mammals (primarily ungulates and bats;

McGuire & Boyle, 2013), and especially birds (Barçante et al., 2017), whereas studies on other terrestrial organisms (e.g. reptiles, amphibians, and non-insect invertebrates) are comparatively scarce (Hsiung et al., 2018). Altitudinal migration is widespread and can even bridge aquatic and terrestrial biomes in some species (e.g., salmon *Oncorhynchus spp.*). Although salmon and other diadromous taxa are not typically included in discussions of altitudinal migration, or are mentioned only in passing (e.g., Hsiung et al., 2018), they do undertake altitudinal migration as some species move from sea-level up to ~2000 m in elevation in the mountains of western North America over the course of their breeding cycle (Crossin et al., 2004). Correspondingly, they experience many of the same challenges and drivers as "traditional" (i.e., terrestrial) altitudinal migrants, such as changes in air pressure, habitat type, and predation risks. Anadromous and catadromous fish also connect the study of altitudinal migration to aquatic species that may seasonally move across bathymetric gradients (Milligan et al., 2020). Many of these bathymetric movements are also seasonal (not to be confused with diel vertical migration) and involve a biologically relevant shift in distribution, and thereby would be included in our broad definition of altitudinal migration. An expanded conceptual framework for altitudinal migration that includes all species that undergo seasonal vertical movement will facilitate communication among researchers of different taxonomic groups.

Ignoring the nuances that we outline here risks misclassifying the altitudinal migratory status of the taxa at hand. We believe that most reviews or databases concerning altitudinal migration consistently underestimate the number of species that are altitudinal migrants (Barçante et al., 2017). This underestimation is in part due to a lack of data on many species, but is also related to how altitudinal migration is defined. We suspect this is especially true when studies exclude populations that are altitudinal migrants as well as latitudinal migrants, which would constitute a type II error or a 'false negative'. However, the reverse pattern also occurs: sometimes species' irruptive movements (i. e. Pine Siskin, *Spinus pinus,*Boyle, 2017) or opportunistic movements to avoid inclement weather (O'Neill & Parker, 1978) are sometimes classified as altitudinal migration, or a type I error. Without a consistently applied definition, studies of altitudinal migration—especially macroevolutionary studies that incorporate hundreds or even thousands of taxa—may inaccurately classify migratory behavior, which could lead to erroneous inferences and biases. Regional biases also exist: some geographic regions have received more attention than others (Boyle, 2017), both in terms of the number of publications and the rigor of scientific study (Schunck et al., 2023). A consistent definition also allows comparisons among regions that may have heretofore been using different definitions of what constitutes an altitudinal migrant.

Novel discussion and comparisons may reveal new insights into the evolutionary drivers, ecological interactions, conservation implications of seasonal shifts in vertical distributions, and contextualize altitudinal migration alongside other types of animal movement. By using a common definition for altitudinal migration, new comparisons and questions can be made under a more unified conceptual framework. For example, are certain taxonomic groups more inclined to be altitudinal migrants, or are these groups just better studied (i. e. birds)? Are certain ecological or morphological traits associated with evolutionary gains or losses in altitudinal migration? Across mammals and birds, migrants are on average more similar to each other for numerous ecological traits than they are to their more closely related resident counterparts, suggesting evolutionary constraints on migratory phenotypes (Soriano-Redondo et al., 2020), but does this pattern hold for ectotherms? Does this vary regionally (i.e frugivore/nectavore are under-represented in the Palearctic; Pageau et al., 2020)? Do terrestrial and aquatic altitudinal migrants share similar comparative evolutionary associations, such as body size differences between residents and migrants, or differences in tempo of life history traits? With a rapidly changing climate our understanding of the traits or lack thereof of altitudinal migrants may allow for a better understanding of species response. How do differences in mobility and physiology impact the capacity for altitudinal migration among different animal groups? Animal movement across ecosystems affects food webs, nutrient recycling, and resource availability, such as when diadromous fish bring nutrients from the ocean to the terrestrial realms. But what is the broader role of altitudinal migration in such ecosystem services and how does this vary among different groups of altitudinal migrants? While habitat loss and broad-scale global change have disrupted many ecosystems (Brodie et al., 2021; Wootton et al., 2023), how have changes in the migratory routes and abundances of altitudinal migrants affected ecosystem services? Using a united definition improves our comparative framework by recognizing potentially confounding variables when contrasting taxa and biomes.

Future opportunities: addressing the challenges

With a more unified definition that includes both terrestrial and aquatic species of divergent animal lineages, we have outlined an improved conceptual framework for the study of altitudinal migration, but multiple challenges and questions still exist:

1. What is the full taxonomic extent of altitudinal migration? Whether or not many taxa undertake altitudinal migration remains unknown, especially in the global south (i.e Rappole et al., 2011; Maicher et al., 2020; Guaraldo et al., 2022). Many studies and sources on altitudinal migration have lacked scientific rigor, are descriptive, or are from "gray" literature and are not easily found (Schunck et al., 2023), all of which hampers our knowledge of the true extent of altitudinal migration. Combining macroevolutionary analyses in a phylogenetic comparative framework with population-level studies will reveal how altitudinal migration contributes to diversification at different taxonomic scales. A deeper understanding of the taxonomic diversity of altitudinal migration will also clarify how ecological and evolutionary drivers may overlap and contrast with latitudinal migrants (Barçante et al., 2017; Hobson et al., 2019; Hsiung et al., 2018; Pageau et al., 2020).
2. How do the drivers of altitudinal migration differ among regions? Each mountain range has a unique geological history and evolutionary pressures driving the gain and loss of altitudinal migration may vary substantially among mountains that vary in latitude or their surrounding biome (Rahbek et al., 2019). The distinct age and origin of each mountain or bathymetric feature can contribute to differences in elevational zonation, climate, and the potential for altitudinal migration to evolve. Studies of altitudinal migration have been highly concentrated in a few select biogeographic realms and counties, especially in North America (Hsiung et al., 2018; Pageau et al., 2020, Schunck et al., 2023). Expanding the geographic scope of altitudinal migration studies will undoubtedly reveal novel patterns and comparisons among regions with altitudinal migrants.
3. What impacts does altitudinal migration have on diversification? Various studies have considered how the evolution of different migratory states may impact speciation, both empirically at the population level (Gómez-Bahamón et al., 2020) and through a more theoretical lens (Winker, 2010). However, little is known regarding how altitudinal migration may impact rates of speciation or diversification. One might hypothesize that changes in altitudinal migration may lead to a reduction in gene flow—as is seen in latitudinal migration—but there are few empirical papers that have explicitly tested this hypothesis (but see Tigano & Russello, 2022). Future studies could clarify how changes in altitudinal migration impact patterns of gene flow and whether there are generalizable or idiosyncratic patterns across lineages regarding whether altitudinal migration character states or transition rates are associated with speciation rates.
4. How is anthropogenic change impacting altitudinal migration and migrants? Migrants and especially altitudinal migrants experience such a wide breadth of environmental conditions, they are severely impacted by anthropogenic change at different elevations and may be more subjected to declines caused by forest fragmentation (Loiselle & Blake, 1992, Runge et al. 2014). For example, many altitudinal migrants are reliant on high-elevation habitat, which is rapidly shifting upslope as our planet warms (Chen et al., 2011; Maicher et al., 2020). Changes in the elevational distributions of ecosystems and their constituents may induce new ecological interactions, such as the introduction of avian malaria to the Hawaiian Honeycreepers, many of which are altitudinal migrants and become infected with malaria during their non-breeding season at lower elevations (Eggert et al., 2008). Anthropogenic change has also induced various phenological shifts, which can harm altitudinal and latitudinal migrants due to a mismatch in the timing of resource availability (Green, 2010; Inouye et al., 2000). Despite the potentially pernicious impacts of land use and climate change on altitudinal migrants, empirical studies that address this harm and our general understanding of anthropogenic impacts on altitudinal migrants are still sorely lacking (but see Adams, 2018).
5. What comparisons can we draw between altitudinal and latitudinal migration? Migration is taxonomi-

cally widespread, and a broader definition of altitudinal migration allows for more nuanced comparisons of animal movement (Dingle & Drake, 2007). As in latitudinal migration, subcategories of altitudinal migration can be differentiated and compared, such as partial versus complete altitudinal migration, or short- versus long-distance altitudinal migration. How do these different categories compare to latitudinal migrants? Are certain types of altitudinal migration more common among certain lineages or biogeographic regions? Are there shared paths of altitudinal migration (i.e., "flyways") as there are in latitudinal migrants? Do barriers to movement impact altitudinal migrants in a similar or different way to that observed in latitudinal migrants? Comparisons between strictly altitudinal migration and latitudinal migration are lacking.

6. What can we gain from comparisons of altitudinal migration patterns across taxonomic groups? Comparative studies have been a fruitful area of research in latitudinal migration research (i.e. Soriano-Redondo et al., 2020), however this topic has received little attention for altitudinal migrants (Pageau et al., 2020). Questions such as how do ectotherms address the challenges of traveling long distances across elevational gradients compared to endotherms have yet to be addressed. Though birds are comparatively well-studied in terms of altitudinal migration, we have only scratched the surface of how they are physiologically adapted to the changes in partial pressure and oxygen levels (see Williamson & Witt, 2021). How other organisms manage these changes, and if they have physiological changes is largely unknown (but see Jacobsen, 2020). Comparative studies at different taxonomic scales will reveal how ecological, physiological, and morphological variation among lineages impacts how altitudinal migration has evolved in different animals.

Fortunately for our ability to address these challenges, the toolbox to detect and study altitudinal migration is rapidly expanding and improving. Here, we describe key advancements and resources that the field can leverage toward a deeper understanding of the taxonomic prevalence and nature of altitudinal migration. Rather than restricting themselves to a single tool, future researchers will benefit from integrating these tools to answer when, where, how, and why animals move along elevational gradients across seasons (i.e. Ruegg et al., 2017).

1. Community science is steadily growing, adding thousands of observations that can be used to determine animal movements across seasons (Tsai et al., 2021, Rueda-Uribe et al., 2023). Surveys and observational data provide a simple yet powerful way to detect changes in seasonal abundance across elevational gradients (Liang et al., 2021, Cheng et al., 2022). However, because many altitudinal migrants are partial migrants (Hsiung et al., 2018), sole reliance on presence and absence data may overlook some potential altitudinal migrants. Using abundance in combination with sex and/or age ratio data can provide information at the population level rather than describing the movement of individuals.
2. Tracking technologies are improving at a remarkable pace: biologgers using satellite, radio, or acoustic transmitters are increasingly smaller, cheaper, and easier to use (Börger et al., 2020; Holton et al., 2021). This revolution in tracking technologies has led to new discoveries in animal movement and migration (i. e. Satyr tragopan Norbu et al., 2013). New multi-sensory tags that also record atmospheric pressure are especially well-suited for short-distance altitudinal migrants, and may help in our ability to distinguish diel- or weather-related movements from seasonal migration across elevational gradients (Nussbaumer et al., 2023; Rime et al., 2023). Parasites and other symbionts offer another emerging framework to track populations as symbiont communities differ strongly across elevational gradients (Williamson & Witt, 2021).
3. Genomic data has long been used to study population connectivity among latitudinal migrants (e.g. DeSaix, et al., 2019; DeSaix et al., 2023), but has not been as extensively applied to altitudinal migrants. Genomic data could be used to study gene flow among populations that differ in altitudinal migration behavior and could also be used to link populations between their breeding and non-breeding distributions at different elevations, as has been done in many latitudinal migrants (e.g., Battey and Klicka, 2017). Comparative and population genomics have identified various loci associated with altitudinal migration (i. e. Qu et al., 2015; Tigano & Russello, 2022), yet similar studies of altitudinal migration are lacking and the degree to which altitudinal migration is an innate or learned behavior

with a genetic component is unknown (Merlin & Liedvogel, 2019; Talla et al., 2020). Various studies have identified genomic loci associated with adaptations to hypoxic conditions at high-elevation, but our general understanding of the genetic underpinnings of altitudinal migration lags behind that of latitudinal migration (Moussy et al., 2013; Merlin & Liedvogel, 2019; Toews et al., 2019; Justen & Delmore, 2022; Rougemont et al., 2023; Sokolovskis et al., 2023).

4. Bulk stable isotope analysis—primarily of Hydrogen but also Oxygen—has been foundational in many recent studies of altitudinal migration (Gadek et al., 2018; Newsome et al., 2015). However, interpreting stable isotope data is sometimes difficult due to potentially confounding factors of shifting isotopic baselines and the influence of trophic cascades on isotope values (Hobson et al., 2012). The use of trace element isotopes and microchemistry has been suggested as a means to better detect altitudinal migration (Chapman et al., 2012; Hobson et al., 2019), yet has seen few applications to date in part due to high monetary costs and difficulty in obtaining and analyzing samples. The advent of compound-specific stable isotope analyses of amino acids (CSIA-AA), offers new possibilities and increased power to detect altitudinal migration by more directly connecting isotopes to the landscape rather than diet (McMahon and Newsome 2019). For example, CSIA-AA was used to trace the long-distance migration of Chum Salmon (*Oncorhynchus keta*) between Okhotsk and Bering seas (Matsubayashi et al., 2020). In particular, CSIA-AA of Hydrogen could provide improved spatial resolution for tracking altitudinal migrants compared to bulk stable isotope analyses (McMahon and Newsome 2019). However, 'isoscapes' that describe spatial patterns of compound-specific isotopic variation are not yet available due to the specialized instrumentation and expenses required to process hundreds or thousands of samples at continental scales. As the technologies underlying isotopic analyses continue to improve, future studies of altitudinal migration incorporating CSIA-AA will be better able to discriminate spatial from trophic signatures of isotopic values underlying altitudinal migration.
5. Natural history collections offer spatial and temporal series of specimens that can be combined with aforementioned techniques to study how altitudinal migration may have changed over time during the Anthropocene (Schmitt et al., 2019). Many techniques used to estimate the geographic origin from contemporary samples can be applied to museum specimens, such as stable isotopes (Rocque and Winker, 2005) and historical DNA sequencing (Wandeler et al., 2007), providing a potential way to examine temporal shifts in altitudinal migration. However, differences in preservation media—especially formalin—may impact stable isotope values (Edwards et al., 2002) and our ability to accurately sequence historical DNA (Do and Dobrovic, 2015) . As natural history museums contribute specimens and metadata via continued collecting efforts and online databases (Nachman et al., 2023), additional studies of spatiotemporal change in altitudinal study will be unlocked.

ConclusionHere, we have developed a taxonomically inclusive definition as a starting point towards a conceptual framework for the study of altitudinal migration that relies on the biological importance of distribution shifts. We argue that the biological relevance of altitudinal migration hinges on the movement capacity and physiology of the taxon in question. In turn, these movements must be considered alongside the strength and nature of ecological and physiological changes imparted by movement along the vertical axis. A more unified framework for studying altitudinal migration acknowledges the complexities when classifying and comparing altitudinal migrants: many altitudinal migrants are partial migrants, and there is also a continuum between movement and migration that is sometimes difficult to partition. There is still considerable work to be done to characterize the taxonomic extent of altitudinal migration, understand regional differences in patterns of altitudinal migration among biomes, and mitigate Anthropogenic impacts on altitudinal migrants. Armed with an expanding toolbox, researchers will benefit from a more unified conceptual framework that enables comparisons across a wider breadth of taxonomic groups, thereby revealing the evolutionary drivers, ecological interactions, and conservation risks of altitudinal migrants across aquatic and terrestrial biomes.

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Figure Legends

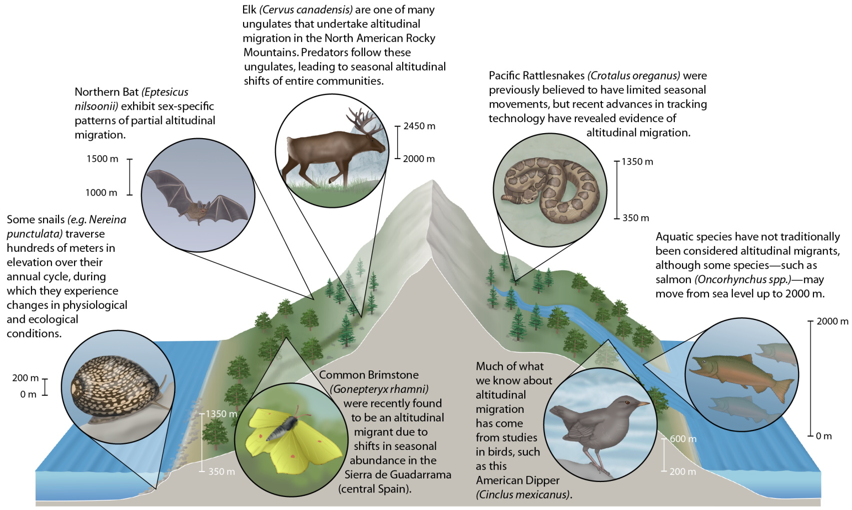
Figure 1:

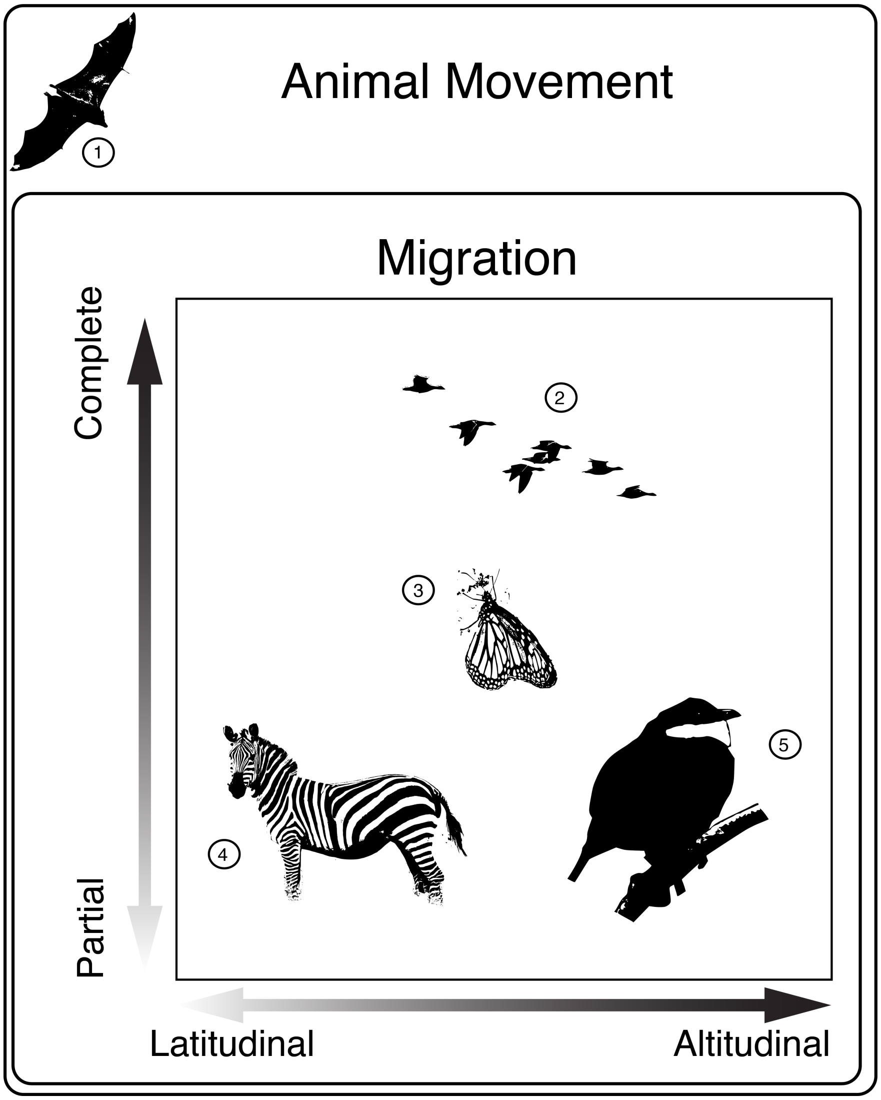
: Altitudinal migration is a widespread phenomenon that occurs in many different taxonomic groups and across habitat types. Here, we show seven different examples of altitudinal migration that illustrate differences in the magnitude of altitudinal shifts as well as physiological and/or ecological changes across seasons. These examples are taken from recent studies of altitudinal migration on snails (Villeneuve et al., 2019), Common Brimstone (Gutiérrez & Wilson, 2014), Elk (Middleton et al., 2020), Northern Bat (Holzhaider & Zahn, 2001), Pacific Rattlesnake (Gomez et al., 2015), American Dipper (Morrissey et al., 2004), and Salmon (Crossin et al., 2004). Illustrations were provided by Ann Sanderson.

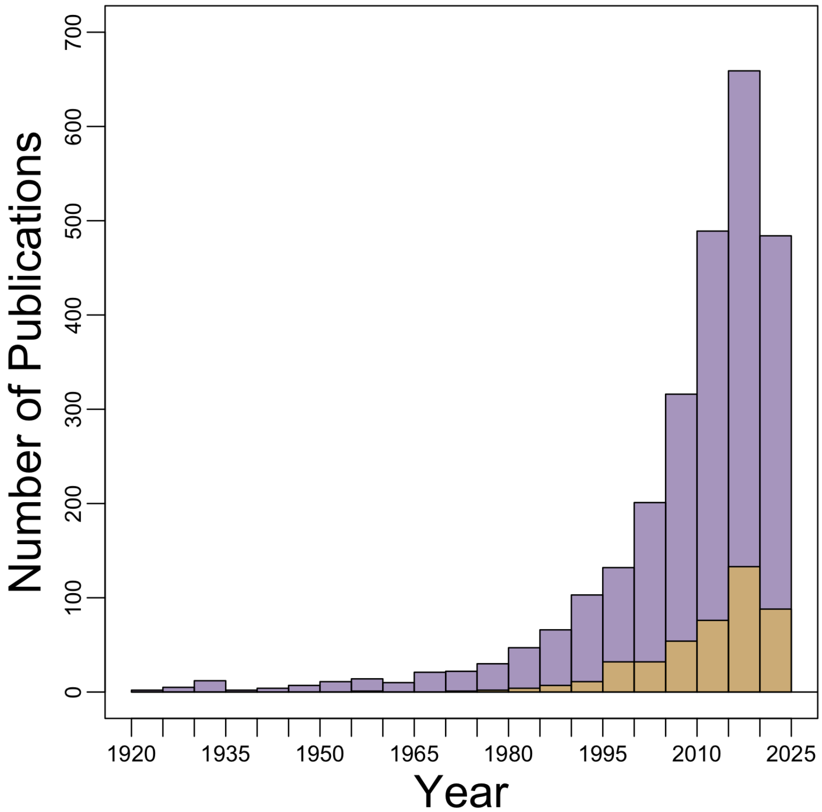
Figure 2:

A simplified, multivariate space that conceptualizes migration behavior continua. Altitudinal migration is part of the broader study of animal migration, which in turn is part of the even broader study of animal movement. Though most animal populations can be classified as either altitudinal or latitudinal migrants and obligate or partial migrants, many taxa and/or populations do not fit neatly into a single categorization. Rather, migrants may undertake both latitudinal and altitudinal migration, while populations or demographic classes within a species may vary in migratory behavior, such that species can be placed in a hypothetical “migration space” with continuous axes that describe variation in different aspects of migration. Here, we illustrate this conceptual framework with five examples: (1.) Gray-headed Flying Fox*Pteropus poliocephalus* moves irruptively as food becomes available. Although this movement is often referred to as “migration”, it is not a regular seasonal occurrence. (2.) Geese are typically thought of as “traditional” latitudinal migrants, moving from their high-latitude breeding range to a low-latitude wintering range, but may also move across large vertical distances during their migration (e. g. Bar-headed Goose *Anser indicus*). (3.) Monarchs *Danaus plexippus* show a complex partial migration pattern that transverses latitudinal and altitudinal distances, varies by population, and spans multiple generations. (4.) Plains Zebra *Equus quagga* is well known as part of the great Serengeti migration that is latitudinal but does not change in elevation. However, at the species level it is a partial migrant as some populations are resident. (5.) White-ruffed Manakin *Corapipo altera* is a partial altitudinal migrant that does not travel long longitudinal distances; only some age and sex classes migrate to lower elevations during their non-breeding season. Photos of the Gray-headed Flying Fox, White-ruffed Manakin, and Monarch were taken by David Vander Pluym, Plains Zebra photo was provided by Joachim Huber, CC BY-SA 2.0 <https://creativecommons.org/licenses/by-sa/2.0> via Wikimedia Commons. Geese photo was provided by Thermos - Own work, CC BY-SA 2.5, https://commons.wikimedia.org/w/index.php?curid=1387483.

Figure 3: Histogram comparing the number of Google Scholar hits for search terms “altitudinal migration” in purple and “elevational migration” in yellow as quantified via the program Publish or Perish. Both terms have seen a steady increase in the number of publications over time, but altitudinal migration has historical precedence and is used more often.


Elk (Cervus canadensis) are one of many ungulates that undertake altitudinal migration in the North American Rocky Mountains. Predators follow these ungulates, leading to seasonal altitudinal shifts of entire communities.
2450 m
2000 m
Northern Bat (Eptesicus nilsoonii) exhibit sex-specific patterns of partial altitudinal migration.
1500 m
1000 m
Pacific Rattlesnakes (Crotalus oreganus) were previously believed to have limited seasonal movements, but recent advances in tracking technology have revealed evidence of altitudinal migration.
1350 m
350 m
Some snails (e.g. Nereina punctulata) traverse hundreds of meters in elevation over their annual cycle, during which they experience changes in physiological and ecological conditions.
200 m
0 m
Aquatic species have not traditionally been considered altitudinal migrants, although some species—such as salmon (Oncorhynchus spp.)—may move from sea level up to 2000 m.
2000 m
0 m
Common Brimstone (Gonepteryx rhamni) were recently found to be an altitudinal migrant due to shifts in seasonal abundance in the Sierra de Guadarrama (central Spain).
1350 m
350 m
Much of what we know about altitudinal migration has come from studies in birds, such as this American Dipper (Cinclus mexicanus).
600 m
200 m


Animal Movement
1
Migration
Complete
Partial
2
3
4
5
Latitudinal
Altitudinal


Number of Publications
0
100
200
300
400
500
600
700
1920
1935
1950
1965
1980
1995
2010
2025
Year