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Ecography

Seasonality, niche management, and vertical migration in landscapes of relief

Abstract

Landscapes of vertical relief, such as mountains and continental slopes, intensify ecological and climatological variation within narrow spatial windows. Seasonal vertical migrants exploit this variation during their residence in, and movements between, vertically stratified seasonal ranges. Animals in terrestrial, marine, and even human-ecological systems undergo similar patterns of seasonal vertical movements. The diversity of arenas in which vertical migration evolved lends insight to the factors promoting seasonal use of landscapes of relief. Because animals must contend with both endogenous circannual rhythms and exogenous environmental seasonality, vertical migrants may be sensitive to inconsistent change across stratified seasonal ranges under climate change. To better understand how ongoing and future climatic and environmental changes are likely to impact vertical migrants, we examine vertical migration in the context of niche tracking and niche switching. Whereas niche trackers minimize variation in realized environmental conditions throughout their seasonal movements, niche switchers undergo seasonal transitions in realized niche space. These strategies mediate the relationship between migrants and their changing environment, and can be used to forecast impacts of future change and effectively conserve systems of vertical migration. Niche tracking may be hindered by inconsistent or unpredictable environmental change along a single niche axis across strata, while niche switching may be sensitive to incongruous spatiotemporal change across factors. We suggest that climate change will affect seasonal patterns in vertical environments discontinuously across time, space, and strata, and that vertical migrants are likely to face additional anthropogenic threats that interact with environmental seasonality. Conservation of vertical migrants should prioritize the availability of, and facilitate movement between, stratified seasonal ranges.

Keywords

altitudinal, bathymetric, migration, seasonality, climate change, niche breadth

biotopic space. Axes of positions in a physical environment, such as elevation or depth.
fundamental niche. The range of biotic and abiotic conditions over which an organism can, theoretically, survive and produce viable offspring.
geographic migration. Long-distance seasonal movements, such as latitudinal migration.
landscape. Any environment with a substrate, including terrestrial and marine settings.
niche space. Axes of positions in an n-dimensional hypervolume of conditions that define an organism's suitable environment.
realized niche. The range of biotic and abiotic conditions over which an organism actually survives and produces viable offspring. This is a sub-set of the organism's fundamental niche constrained by realized environmental conditions at a specific location and time and by positive and negative interactions with other organisms.
season. An intra-annual subset of any annual cycle, such as tropical precipitation patterns, Arctic sea ice formation and depletion, or endogenous rhythms in hormone release.
strata. Two or more positions separated by vertical biotopic space, as in the case of movement along topographic or bathymetric slopes.
vertical migration. Short-distance seasonal movements across strata such as altitudinal or bathymetric migrations.

Glossary

Introduction

Migration is a taxonomically and geographically widespread adaptation to temporal variation in the environment. Migration is characterized by movements between spatially isolated ranges, on a much greater scale than typical day-to-day movements (Dingle and Drake 2007). Seasonal ranges may be separated by hundreds or thousands of kilometers across geography, as is the case in long-distance migrations, or just a few hundred meters across topography or bathymetry, as is the case in vertical migrations. Whereas long-distance migrants face significant energetic demands and risks of mortality during their journeys, vertical migrants minimize costs of travel while still realizing considerable ecoclimatic variation. Amphibians, birds, and crustaceans are but a few of the taxa represented among Earth's vertical migrants (Aguzzi et al. 2013, Boyle 2017, Hsiung et al. 2018). These climbing creatures seasonally traverse mountain sides and marine canyons alike, in pursuit of resources, shelter, and mating opportunities.

Mountains cover a quarter of Earth's land surface, and shallow seas comprise over a tenth of the total global seabed area (Costello et al. 2010, Karagulle et al. 2017). While vast distances must be traveled to realize significant changes in ecology or climatology across latitudinal gradients, comparable variation can be experienced by traversing only a few hundred meters up or down a mountainside (Körner 2007, Klinges and Scheffers 2020). Similarly, physical properties of the water column generate abiotic and biotic gradients over small distances in depth, compared to the thousands of kilometers that would be required for the same apparent change across latitude (Sprintall and Cronin 2001). Together, elevation and depth constitute a continuous, 1-dimensional biotopic space which vertical migrants can navigate in order to realize or mitigate seasonal change in their environment (Figure 1).

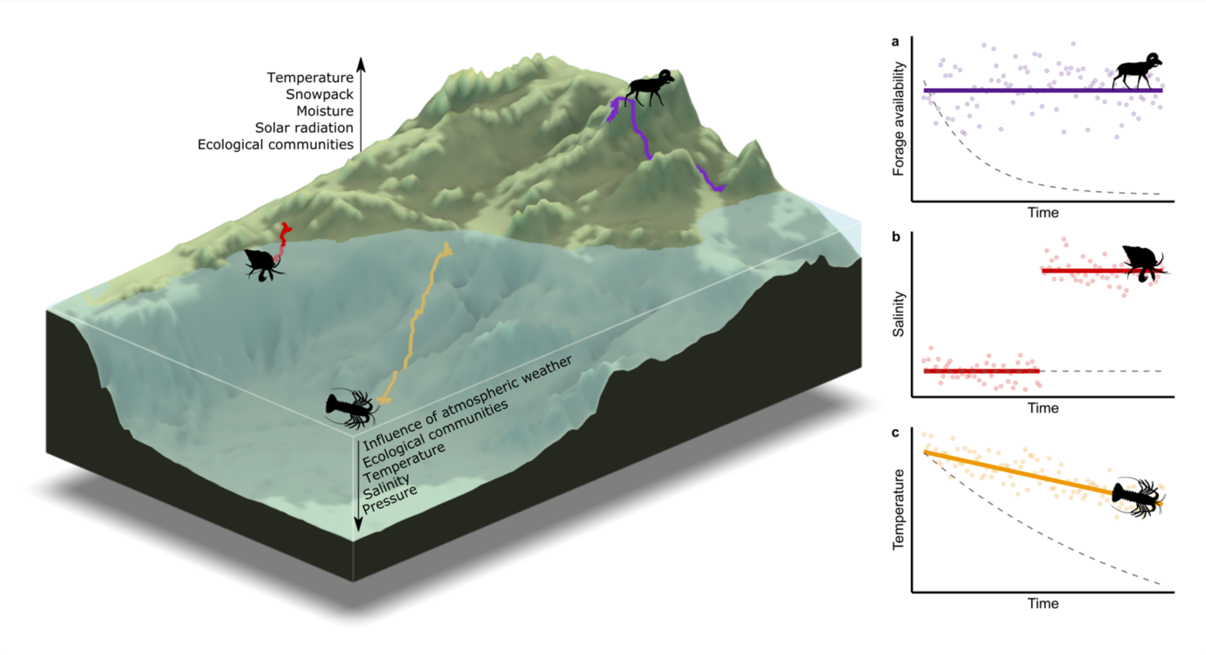


Figure 1. Landscapes of relief introduce multiple axes of environmental variation over short distances, which can be exploited by mobile organisms. In this conceptual illustration, exemplar species are shown at the destination end of their seasonal movement path in both the perspective landscape plot and niche panels (a-c). Environmental factors that vary vertically are indicated along arrows in the perspective plot. In a-c, one axis of niche space is plotted against time, with environmental conditions realized by seasonal migration shown in color, and environmental conditions realized by non-migration shown by a dashed line. Bighorn sheep track springtime plant growth as vegetation green-up progresses uphill (“niche tracking”, a). Soldier hermit crabs face a massive shift in realized salinity when they move from their terrestrial non-reproductive environment to their marine reproductive and developmental environment (“niche switching”, b). Other decapod crustaceans, such as some lobsters, dampen wintertime shifts in temperature by migrating to deeper waters (“dampened niche tracking”, c). Data are for illustrative purposes only; terrain data from ETOPO1 (Amante and Eakins 2009), movement paths generated using directed random steps, and niche space generated using normal distributions with shifting center across time (R version 3.6.1). Animal silhouettes adapted from phylopic; illustrated by Scott Harmon, Ekaterina Kopeykina, and Joanna Wolf; and under public domain and creative commons licenses CC0 1.0 and CC 3.0.

The magnitude of seasonal rhythms with which migrants contend often varies across strata. For example, snowpack is deeper and the snow season is longer in temperate alpine regions than in the foothills below. Similarly, deep seafloors are more protected from seasonal storms than shallow coastal waters. Two strategies are available to migrants for coping with spatially structured seasonal environmental variation: they can track spatiotemporal variation along niche axes ("niche tracking," Figure 1a,c) or undergo seasonal transitions in the niche space they occupy ("niche switching," Figure 1b) over the course of their migratory journey (Martínez-Meyer et al. 2004, Gómez et al. 2016). Whereas niche trackers maintain constancy or dampen seasonal oscillations in their realized niche (e.g. Somveille et al. 2019, Bay et al. 2021), niche switchers abandon niche space at the turn of the season and exacerbate variation along some niche axes (e.g. Ponti et al. 2020). If seasonal ranges undergo inconsistent environmental change, past strategies of niche tracking and niche switching may fail to accommodate novel conditions.

Prevailing patterns of seasonal change across stratified environments may be threatened by changes in the climate regime. Inconsistent change in the timing and magnitude of seasons across strata, as well as long-term trends in bioclimatic and species distributions, modify the pattern of emergence of seasons across landscapes of relief. If phenological shifts in exogenous seasonal factors are inconsistent across elevation or depth (e.g. Inouye et al. 2000), the ability of both niche trackers and niche switchers to cope with forecasted environmental change may be compromised. Inconsistent trends among axes of fundamental niche space may lead to the loss of suitable niche space within a range. Simultaneously, direct human impacts such as land use change and fencing infrastructure limit migrants' historical access to seasonal ranges. Effective conservation management plans for vertical migrants will account for the spatiotemporal complexities of landscapes of relief.

In this review, we ask the following questions: 1) *Why migrate vertically rather than geographically*? 2) *In what vertical migratory systems do niche tracking and switching emerge*? and 3) *How will anthropogenic change affect systems of vertical migration*? To answer these questions, we identify how landscapes of relief modify seasonal variation in limiting factors across vertical space, and examine the means by which vertical migrants cope with seasonal variation in the environment. We then explore how climate shapes the progression of seasons across strata, and discuss the mechanisms through which ongoing and future change are likely to affect vertical migrants. We conclude by outlining conservation priorities that will help protect vertical migrants in the face of forecasted change.

Environmental variation in landscapes of relief

Seasonal movements such as migration arise in response to temporal variation in endogenous or exogenous factors. Relative to the scale of seasonal migration, some environmental factors that vary spatially appear to be constant through time, with a similar spatial pattern of variation persisting across years. Migrants that experience significant seasonal endogenous variation (such as breeding or molting) may exploit temporally “static” variation by moving between disparate ranges as the need for - or challenges posed by - different conditions arises. Conversely, other environmental factors vary both spatially and seasonally due to Earth’s axial tilt and position along its revolution around the Sun. Such dynamic exogenous variation may promote migratory movements regardless of the migrant's endogenous state if the relative favorability of seasonal ranges varies across seasons.

Static variation: space

Elevation and depth generate environmental variation over short distances through static influences on abiotic environmental factors. In general, solar radiation increases while air density and temperature decrease with increasing altitude (Körner 2007). Other factors such as precipitation and wind may vary across altitude but the pattern of their variation is locally or regionally idiosyncratic. For example, temperate latitudes tend to experience increasing annual precipitation at higher elevations, while in polar and equatorial latitudes the opposite trend is observed. Within regions, relationships among precipitation and elevation are nonlinear, and vary across seasons (Körner 2007). Water depth similarly imposes stratified abiotic variation: incoming light and solar radiation dramatically decrease through the photic zone, while buffering from atmospheric weather is increased. Conversely, temperature, oxygen concentration, and salinity vary with depth, but their profiles can be nonlinear and locally idiosyncratic (Paulmier and Ruiz-Pino 2009, Shadwick et al. 2015).

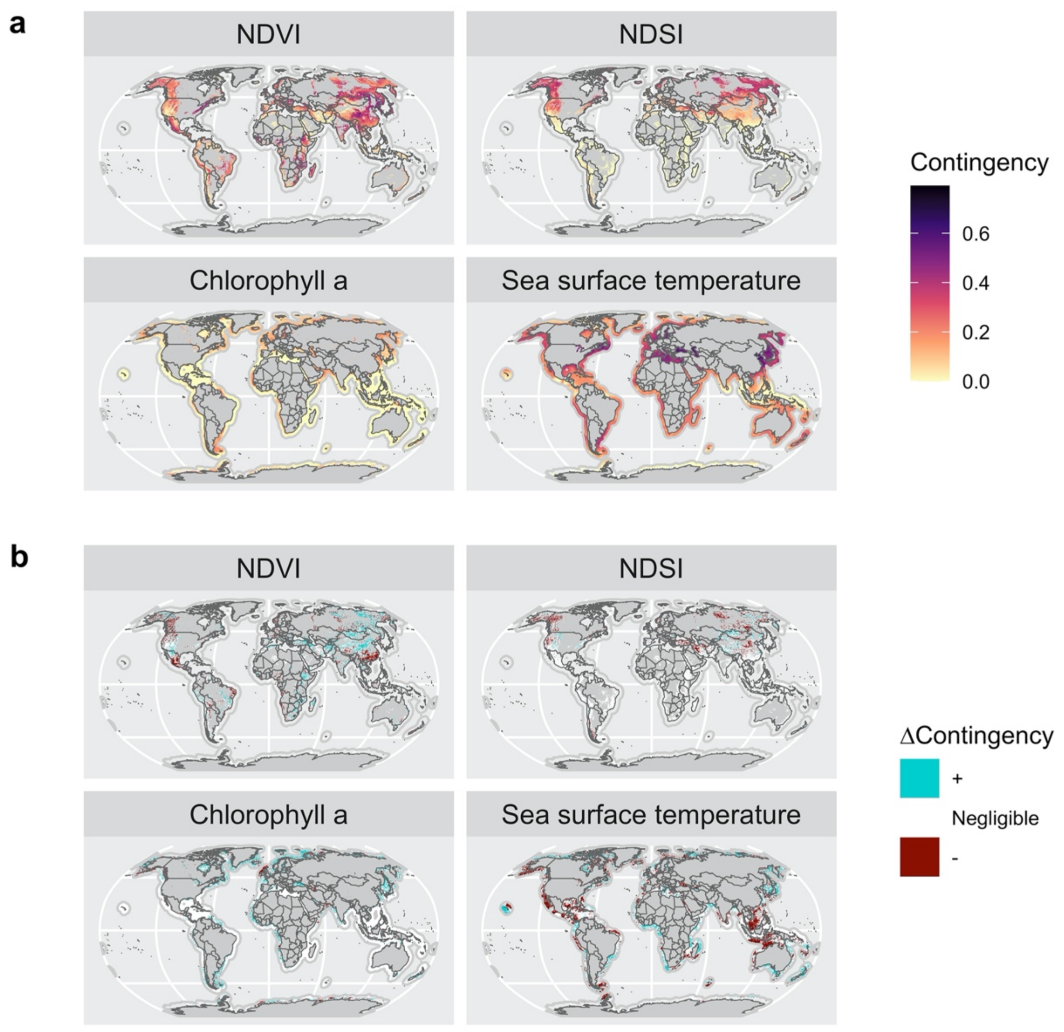
Stratified variation in abiotic factors drives vertical zonation in ecological communities, composed of species that are simultaneously adapted to a window of conditions and interspecific interactions. Physiological limits of animals and plants determine the vertical range of habitat available to them on both mountains (Janzen 1967) and in oceans (Carney 2005). The process through which relief generates community stratification is perhaps most famously illustrated by the upper limit of tree growth on mountainsides (Körner and Paulsen 2004). In the ocean, primary production is largely limited to the shallowest reaches, where sunlight is able to penetrate and the rate of photosynthesis is greater than that of respiration (Dennison 1987). Consequently, a steep decline in forage availability emerges for primary consumers with increasing ocean depth. Similarly, a balance of pressure tolerance, temperature, and oxygen availability dictates the bathymetric range of many marine animals (e.g. Brown and Thatje 2011, Brown et al. 2017).

Dynamic variation: space-time

Seasonal variation in abiotic factors drives seasonal variation in ecological communities (Post 2019). Just as accumulated temperature and precipitation regulate plant growth in many terrestrial systems (Cleland et al. 2007), so too do these factors impact the timing, magnitude, and species composition of marine phytoplankton blooms (Thompson et al. 2015). Temperature, precipitation, and primary productivity cycles underlie the adaptive benefits of dormancy and emergence by many terrestrial animals. Seasonal pulsed reproduction by plants and animals alike are linked to cascading effects of abiotic seasons (e.g. madwort flowering: Gómez 1993, caribou and muskox parturition: Kerby and Post 2013, bivalve spawning: Philippart et al. 2014). When seasonal variation follows predictable cycles (e.g. Box 1), migrants can rely on temporal cues such as photoperiod to coordinate movements with anticipated change at the destination.

Box 1. Seasonal variation is not universally predictable in landscapes of relief.

Migration is an adaptive life history strategy when seasonal variation follows a predictable schedule (high "contingency"; Colwell 1974, Shaw and Couzin 2013, Riotte-Lambert and Matthiopoulos 2020). In mountain and coastal regions, contingency of a given factor may vary across space (a). For example, although snow cover is highly contingent in the northern Canadian Rocky Mountains, reliable seasonal cycles are diminished toward the south (NDSI, a). However, seasonal variation may become more or less predictable over time (b) as factors individually respond to cascading effects of climate change. For example, sea surface temperature variation in numerous areas throughout the Malay Archipelago became less predictable in the 2010's compared to the 2000's, but the same pattern was not observed for chlorophyll concentration. In (a), contingency was calculated following Colwell (1974) for MODIS Terra NDVI and NDSI, and MODIS Aqua L3SMI Chlorophyll a and Sea surface temperature products aggregated to 10km pixel resolution. In (b), contingency of each factor during 2010-2019 was compared against contingency during 2000-2009 to identify change, with |ΔContingency | < 0.025 considered "Negligible."



Because variation in abiotic and biotic factors is neither linear across strata nor uniform among factors, temporal environmental variation is spatially structured in landscapes of relief. Landscapes of relief modify the spatial structure of seasonal environmental variation in three forms of "seasonal transformation": phase shifts, phase differences and phase products (Figure

2). In phase shifts (Figure 2a), the timing of variation in a factor is shifted with respect to strata, but the magnitude, and baseline condition of variation in that factor, remain unchanged. For example, plant growth may be delayed with respect to elevation due to the recession of the snowline and variation in accumulated temperature along an elevational gradient. In phase differences (Figure 2b), the baseline condition of a factor changes with respect to strata, but the timing and magnitude of variation in that factor remain unchanged. For example, the timing and magnitude of seasonal temperature variation may be consistent across a mountainside, while high elevations experience predictably colder temperatures than lower elevations. In phase products (Figure 2c), the magnitude of variation in a factor is adjusted with respect to strata, while the timing and baseline condition of the factor remain unchanged. For example, disturbance from seasonal atmospheric storms is greater in shallow waters than in protected waters deep below. Finally, landscapes of relief may introduce a combination of these phase modifications (Figure 2d), where two or more forms of spatiotemporal variation emerge. For example, the duration and magnitude of seasonal snow cover may be much greater in an alpine environment than the foothills below. Similarly, photosynthetic activity in the euphotic zone generates a primary productivity seasonality regime in shallow waters, while primary production in deeper waters may be negligible.

Geography and the relative role of relief

Migration may facilitate the pursuit of favorable conditions, or escape from unfavorable conditions (Winger et al. 2019). Across broad geographic distances, spatiotemporal variation in environmental conditions is generally reliable. For example, movement between a savanna and tropical rainforest ensures directional change in moisture and ecosystem structure (Whittaker

1970). This is also the case to a certain extent across topography or bathymetry (e.g. Whittaker and Niering 1968); however, regional variation in climate may predominate in spite of considerable local variation in some factors. For example, persistent snow is common at high elevations in the Arctic, while seasonal snow cover characterizes variation across elevations (Hammond et al. 2018). Vertical migration would thus be insufficient as a means of complete escape from snow in the Arctic; geographical movements are the only available option if that region is to be utilized by migrants that cannot cope with snow. At more temperate and tropical latitudes, however, persistent snow is rare, and seasonal snow at high elevations is not matched at low elevations (Hammond et al. 2018). Altitudinal movements would facilitate a response to snow at these latitudes.

Conversely, vertical retreat from unfavorable winter conditions may be adaptive in marine settings at higher latitudes, where sea surface temperatures are most dramatically seasonal in shallow waters (Box 1). This combined phase difference and amplification at high latitudes introduces a strong seasonal signal in the depth gradient in water temperature, of particular importance for ectotherms. Tropical waters face comparatively little seasonal variation in temperature, but strong seasonality in sea surface salinity due to winds and fresh water inputs by precipitation and runoff (Delcroix and Hénin 1991). While vertical migration in these waters may satisfy seasonal endogenous requirements, so too may it allow migrants to cope with temporally dynamic exogenous factors.

Terrain structure further complicates general patterns of environmental variation along elevation or depth. Slope and aspect are particularly impactful factors in terrestrial temperate and Arctic settings, where increased direct solar irradiance on slopes facing the equator leads to increased temperature, reduced moisture, and advanced phenology (Jackson 1966, Griffiths et al. 2009, Geroy et al. 2011). In marine settings, topography underlies the mixing and movement of water masses (Huthnance 1995, Shapiro et al. 2003), impacting temperature, deposition of organic matter, availability of oxygen and nutrients, and community diversity (Robertson et al. 2020). Coastal upwelling and its drivers add additional complexities to seasonal variation in environmental factors along depth, but simultaneously introduce cues that reliably predict imminent environmental change (Largier 2020). Upwelling in California (USA), for example, leads to a seasonal influx of nutrients from deeper waters, and consequently increases in production of phytoplankton and ultimately krill. Thus ensures seasonal arrival by geographically migratory blue whales (*Balaenoptera musculus*) when availability of their preferred food source is high there (Croll et al. 2005). Further from the coast, organic carbon deposition reliably follows upwelling events, leading to seasonal influxes of consumable detritus and visitation by mobile benthic species on the deep sea-floor (Smith et al. 2013). Thus, in spite of coarse regional patterns that underlie some unavoidable seasonal environmental, landscapes of relief introduce additional dimensions of local environmental variation along which migratory animals can track existing conditions, or seek out novel environments.

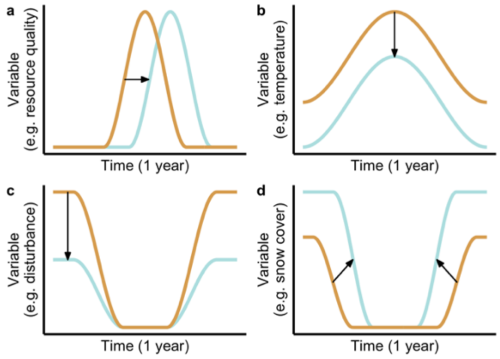


Figure 2. Landscapes of relief shape the spatiotemporal environmental variation through seasonal transformations across strata (tan and blue lines correspond to two environments of different elevation or depth). Phase *shifts* (a) involve a temporal advance or delay in the seasonal cycle without change in the intercept or magnitude of the cycle. Phase *differences* (b) arise when the cycle's intercept changes but without changing the amplitude of the cycle. Phase *products* occur where the same baseline conditions exist across space, but the magnitude of the cycle varies in the form of amplification or attenuation (c). Further spatiotemporal complexities may arise through a combination of these phase changes (d). The primary axes of phase variability are illustrated with black arrows.

Niche management in multi-season space

The environmental variation introduced by landscapes of relief can be exploited without moving across vast distances, as would be required of long-distance migrants. This reduces the endogenous cost of migration, such as energy usage and storage limitations, as well as external pressures such as unfavorable conditions faced during long-distance migrations (Alerstam et al. 2003, Boyle 2017). Migrants must navigate a gamut of exogenous seasons while simultaneously facing seasonal variation in endogenous factors such as hormone release, body condition, and reproductive status. Animals may therefore use seasonal migration as a tactic to navigate biotopic space while managing their use of niche space. For a given niche axis, migrants may maintain access to consistent conditions ("niche tracking") or seek out completely different conditions during a subset of year ("niche switching", Martínez-Meyer et al. 2004). Whereas niche tracking involves the maintenance of niche space during migration, niche switching involves a fundamental shift in the realized environmental factors during or as a result of migration. Vertical migrants may employ either or both of these strategies to cope with the numerous seasons of change they face.

Niche tracking

Niche tracking vertical migrants follow constant environmental conditions across strata in landscapes of relief. Because the phenology of seasonal factors such as forage availability and accumulated temperature may vary across strata (e.g. Hopkins 1920), niche trackers can synchronize their vertical movements with spatially predictable change in their environment (Riotte-Lambert and Matthiopoulos 2020). Migrants using this strategy can minimize physiological or behavioral adjustments that would be required for major transitions in realized environmental factors.

Many migrating ungulates follow the phase shift in spring plant growth upslope during spring in a form of niche tracking called “surfing the green wave” (Albon and Langvatn 1992, Mysterud et al. 2001, Merkle et al. 2016). Because newly emergent plant material is nutrient-rich and easily digested, these migrants can extend the window of high-quality forage access and increase fat reserves by tracking green-up through space (Middleton et al. 2018). Recent evidence indicates that ungulates are able to more effectively track resource phenology when vegetation growth is rapid and progresses sequentially across the landscape, as is the case in many mountain settings (Aikens et al. 2020). Evidence of resource tracking in landscapes of relief has also been reported in tortoises (Blake et al. 2013), hares (Rehnus and Bollmann 2020), birds (Loiselle and Blake 1991), and human-ecological systems (Beck 1991).

Niche tracking vertical migrations are also useful for coping with seasonal variation in temperature. For example, sea surface temperature off the coast of Maine (USA) is highly seasonal, generating an attenuation in temperature variation toward deeper, more insulated water. Seasonal bathymetric movements have been detected through mark-recapture of deep-sea lobsters (*Homarus americanus*) in Maine, where they use shallower waters during the summer before retreating to the continental slope for winter (Cooper and Uzmann 1971). Migratory lobsters were able to maximize their growth rate, in part because they maintained a warm narrow range of temperature across the year, while sympatric lobsters that remained resident in shallow waters year-round experienced colder temperatures that were more variable (Cooper and Uzmann 1971). In the Mediterranean Sea, similar seasonal variation in bathymetric distributions of benthopelagic fish and crustaceans appears to coincide with temperature and salinity variability introduced by seasonal subsurface water currents (Aguzzi et al. 2013).

Niche switching

Niche switching vertical migrants face major shifts in realized niche space during or as a result of their migration. Migrations associated with endogenous schedules, such as dormancy, molting, and reproduction frequently include some element of niche switching. Because seasonality in physiology and behavior may cyclically require different habitat parameters, many niche switching vertical migrants exploit stratified environmental variation that is not necessarily seasonal. By partitioning niche space over the course of the year, niche switchers can adjust habitat use to accommodate seasonal life history requirements.

Seasonal dormancy allows organisms to cope with periodically harsh conditions, and is frequently associated with vertical migratory movements. In Costa Rican dry forests, seasonal variation in rainfall generates seasonality in vegetation growth. Skipper butterfly (*Aguna* *asander*) caterpillars rely on leaves of *Bauhinia ungulata,* a shrub that produces leaves only during the rainy season (Assunção et al. 2014). In the absence of *Bauhinia* leaves, the insects migrate uphill to colder strata where they estivate in trees and among rocks. Once the seasonal rains resume, *A. asander* return to the rejuvenated lowland forests to feed and reproduce (Janzen 2004). Interestingly, a sympatric predatory paper wasp (*Polistes variabilis*) undergoes similar vertical movements to reach dry season dormancy habitat (Hunt et al. 1999). Bears and bats also undergo seasonal vertical movements to access hibernacula, which are separated from habitat used during their waking life through amplified snowpack and stratified geomorphology (Grachev 1976, Neubaum et al. 2006).

Niche switching may also facilitate reproductive tasks. A perhaps extreme example of this occurs in a transit between terrestrial and marine environments. The ecotone between land and sea is inherently stratified and delineates an impressive array of environmental conditions. Soldier crabs (*Coenobita clypeatus*) of Mona Island (Puerto Rico, USA) undergo seaward migrations during an annual summer spawning event called the *cobada* (Nieves-Rivera and Williams 2003). Adult *C. clypeatus* spend most of their time in terrestrial habitat, but migrate to the ocean where eggs are deposited, larvae develop, and juveniles claim shells. Seaward migrations by land hermit crabs are timed to coincide with seasonal peaks in water temperature, but also attuned to the lunar cycle for favorable tide and lighting conditions (Doi et al. 2016, Nio et al. 2019). Niche switching reproductive migrations are also observed among some birds, when seasonal courtship, foraging, and roosting habitat are vertically stratified (Mussehl 1960, Crawford and Pelren 2001, Zwickel and Bendell 2003), or when reproduction is seasonal and sensitive to stratified variation in predation (Boyle 2008).

Navigating the fundamental niche: the tracking-switching continuum

Across the entirety of a migrant's fundamental niche, both niche tracking and niche switching are no doubt employed over the course of a year. Any environmental condition that varies in space can be tracked or abandoned by a mobile organism, so long as relocation does not require exceeding some physiological constraint (i.e. departing from fundamental niche space). Because migrants face a crash of endogenous and exogenous seasons, they potentially realize inconsistent variation among niche axes while moving across strata. For example, ascending a marine canyon may increase access to forage, but simultaneously lead to changes in light, salinity, and hydrostatic pressure. By navigating physical space, migrants can realize considerable differentiation along one niche axis, but minimize variation along another. Incomplete migratory patterns, such as partial and facultative migrations, lend insight into how animals use vertical movements to track or switch among seasonal niche spaces.

Partial migration is common among vertically migratory species, wherein a subset of the population migrates while another does not (e.g. Cooper and Uzmann 1971, Boyle 2017). Whereas migration can facilitate tracking favorable environmental variation, remaining resident in a particular range may limit the extent to which niche tracking is possible (Laube et al. 2015, Gómez et al. 2016). For example, many Sierra Nevada bighorn sheep (*Ovis canadensis sierrae*) in California (USA) move to low-elevation slopes during winter to avoid deep snow and seek foraging opportunities, but they face increased predation pressure compared to those remaining in the barren snowy alpine zone (Spitz et al. 2020). While individuals that remain resident in the alpine zone may reduce interactions with predators, they must cope with increased seasonal variation in temperature, wind speed, snow cover, and forage availability.

Other factors favoring partial migration include seasonal intraspecific competition and conflict, intrapopulation niche differentiation, and thermal tolerance (Chapman et al. 2011). Coping with, or evading, these factors, likely underlies how individuals manage niche space: evading conditions that are sought after by conspecifics ensures a different realization of total annual niche space occupied by the individual.

Facultative and sub-seasonal movements add flexibility to migrants' seasonal distribution schedule. Niche tracking vertical migrants may be able to entrain their movements with environmental conditions by making multiple vertical movements leading up to and during the migratory season. The close geographic proximity of seasonal ranges afford vertical migrants the opportunity to scout conditions and find refuge from unfavorable weather by revisiting seasonal ranges (Horvath and Sullivan 1988, Hahn et al. 2004, Rice 2008, Boyle et al. 2010). Sub-seasonal vertical movements also arise among multiple-breeding animals, such as some birds seeking to track high-quality conditions across reproductive attempts (Brambilla and Rubolini 2009, Ceresa et al. 2020). Such fine-scale adjustments in vertical distribution may enable some migrants to buffer climate change and maintain access to tracked niche space throughout the season (Frey et al. 2016).

Tracking and switching lie on opposite ends of a continuum of strategies for managing seasonal niche space. Migrants likely employ both approaches during vertical migration because of the numerous factors that vary across strata in landscapes of relief. However, the interaction between physiology, behavior, and environmental factors governs whether a migrant generally tracks niche space across the year, or switches between seasonal subsets of niche space. For example, ectotherms that face seasonal temperature variation without going into dormancy track vertical zonation in temperature in order to maintain metabolic activity (e.g. Cooper and Uzmann 1971, Crossin et al. 1998). Conversely, species that migrate to hibernacula in order to escape unfavorable conditions undergo a massive shift in metabolism, activity, and preferred habitat (e.g. Hunt et al. 1999, Haroldson et al. 2002, Neubaum et al. 2006). Niche switching is similarly dramatic for diadromous and semi-diadromous migrants as they deposit larvae in ontogenic habitat (e.g. Elliott et al. 2007, Amorim et al. 2016). The niche management strategy employed by vertical migrants, and the faculty to use alternative approaches during migration, will likely determine their ability to persist under future climate change.

Climate shapes configuration of seasonal niche space

Climate modifies stratified environmental variation in landscapes of relief by shaping patterns within and relationships among niche axes across biotopic space (Colwell and Rangel 2009). Changes in temperature and precipitation, and the seasonality thereof, lead to ecological response across strata and through time. Common ecological responses to warming include advancing phenology due to more rapidly accumulated spring temperature, and range shifts to accommodate physiological constraints (Parmesan 2006). However, the degree of phenological change may vary across strata, as well as the propensity to shift ranges and the availability of novel, suitable habitat. Climate-induced changes in migratory propensity may influence reproductive exchange within partially migratory populations, ultimately impacting gene flow and genetic diversity, potentially driving, or limiting, evolutionary change. Vertical migrants' ability to “keep up” with climate change will depend on modifications to the spatiotemporal arrangement of environmental variation in their historic, current, and potentially future habitat, as well as change in the phenology and distribution of organisms with which migrants interact.

Seasonal niche space

Inconsistent alteration of stratified ranges by climate change will impact the relative timing of transitions between seasons, and consequently the ability of some migrants to track spatial variation along some niche axes (Figure 3, Niche 1). For example, in the European Alps, rapid phenological advance at high elevations has led to more uniform green-up across elevation (Vitasse et al. 2018). Earlier green-up and flowering by plants related to climatic warming were not matched by parturition of roe deer (*Capreolus capreolus*) in the Alps (Rehnus et al. 2020). Roe deer are income breeders and therefore depend on forage availability during the energetically expensive parturition and fawn rearing season. Thus, exacerbation of conditions that result in trophic mismatch can be consequential for offspring production and survival (Kerby and Post 2013). However, due to the elevational gradient in green-up timing, *C. capreolus* were able to buffer the expanding mismatch by adjusting their migratory schedule to account for shifting spatiotemporal dynamics of forage quality (Rehnus et al. 2020). The advantages of such a buffer may be stymied by more spatio-temporally uniform plant phenological dynamics. A similar pattern is expected for bark beetles (*Ips typographus*), as the timing of diapause termination and swarming is expected to shift more rapidly at high elevations and on south-facing slopes in the Alps (Jakoby et al. 2019). Adjustments to the historic elevational trend in insect swarming phenology may impact insectivorous altitudinal migrants that live there (e.g. grey wagtails, Klemp 2003). Inconsistent shifts across stratified ranges can also be expected in marine settings, where effects of climate change are not constant between surface waters and deep ocean (Capotondi et al. 2012).

Inconsistent climatic change across space also modifies the historic overlap and adjacency of stratified niche spaces between seasons. Disruption of the historic relative timing of seasonal niche availability may impact the seasonal migration schedule of some niche switching vertical migrants (Figure 3, Niches 2 and 3). For example, grizzly bears (*Ursus arctos horribilis*) in the greater Yellowstone ecosystem undergo a partial downhill migration after emerging from high-elevation dens in spring (Haroldson et al. 2002). They then follow the elevational progression of snowmelt into high-elevation habitat in the summer, coincident with the summertime aggregations of Army cutworm moths (*Euxoa auxiliaris*) that migrate to the alpine from the Great Plains (Pruess 1967, Servheen 1983, French et al. 1994, White et al. 1998). This influx of forage facilitates the hyperphagia required of bears leading up to hibernation (Nelson et al. 1983, French et al. 1994). Throughout the Rocky Mountains, the predictability of seasonal variation in snow cover has changed during recent years (Box 1). Warming winters and reduced snow accumulation are expected in that area for the coming decades (Lapp et al. 2005). If emergence and departure timing of *E. auxiliaris* in the Great Plains becomes decoupled from snowmelt and den emergence by *U. a. horibilis* in the Rocky Mountains, the efficacy of migratory bears' switch from hibernating to foraging may be compromised.

Fundamental niche space

Response to climate change through range shifts is additionally limited for vertical migrants. Abiotic stressors covary with both altitude and depth, imposing novel pressures on animals that undergo distributional shifts in response to increasing temperatures (Spence and Tingley 2020). In mountains, a finite upper biotopic limit (mountain peaks and ridgelines) prohibits indefinite upslope response. The available surface area of mountains is furthermore not constant across strata (Körner 2004, Elsen and Tingley 2015) and presents an added constraint on altitudinal migrants, particularly if density dependent factors like intraspecific competition for resources underlies the elevational distribution of seasonal ranges. In marine systems, range shifts toward deeper water are a common response to warming surface waters (Pinsky et al. 2013). However, physical and chemical factors prevent an indefinite retreat to deeper waters. The twilight zone introduces an absolute maximum depth for visual animals, while the sea surface delimits a minimum depth available to marine obligates. Reduced oxygen and increased hydrostatic pressure in deep water impose limits on metabolism, introducing a barrier that can only be overcome through physiological adaption (Brown and Thatje 2015). Because hypoxia tolerance is strongly linked to temperature in some depth migrants (Bigford 1979, Deutsch et al. 2015), change in ocean temperature and oxygenation, and shifts in the depth of the oxygen minimum zone, may be especially limiting for depth shifts by seasonal vertical migrants in the ocean.

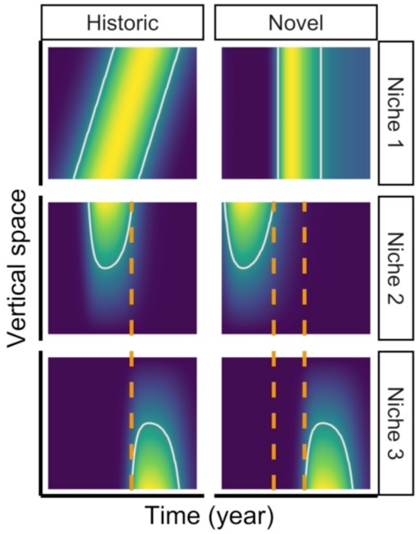


Figure 3. Inconsistent seasonal transformations across biotopic and niche axes precludes effective niche tracking and niche switching. Each panel illustrates the vertical gradient (y-axis) in niche value (color intensity) across the course of a year (x-axis). The left column of panels represents an historic climate regime, while the right column represents novel climatic conditions. Each row represents a different niche axis which may be tracked or differentially prioritized. Grey contour lines indicate an arbitrary threshold value within niche space that migrants seek out. For Niche 1, novel conditions lead to a more synchronous season across biotopic space. A tracking migrant may have historically migrated vertically to follow the spatiotemporal progression of Niche Variable 1, but under novel conditions more synchronous emergence of threshold niche access may reduce incentives to relocate in a coherent vertical pattern. For Niches 2 and 3, an advance in the timing of Niche 2 relative to Niche 3 leads to a temporal window where suitable space is not available along either niche axis under novel conditions (delineated with orange dashed lines). If a niche switcher depends on the historical synchrony of senescence in Niche Variable 2 and emergence of Niche Variable 3 during its migration, inconsistent change in the onset and termination of these factors will disrupt the pattern of environmental variation under which migration was adaptive.

Conserving systems of vertical migration

While the emergence of suitable niche space across vertical biotopic space is prone to adjustments by climate, migrants' access to and availability of seasonal ranges face additional threats. Direct processes such as infrastructure development and harvest may inhibit access by animals to seasonal ranges, influence population dynamics, and drive microevolutionary change in vertical migrants (Pecl et al. 2009, Pigeon et al. 2016, McInturff et al. 2020). Because migrants have more expansive annual ranges than nonmigratory animals, more opportunities arise for anthropogenic processes to disrupt their life history. Management of systems of vertical migration should account for the multifaceted spatiotemporal requirements of migrants.

Seasonal landscapes that actively face direct human-induced change such as deforestation and destructive harvest are likely to be immediate concerns for vertical migrants. For example, due to rapid and accelerating global deforestation (Hansen et al. 2013, Kim et al. 2015), habitat fragmentation is of particular concern for migrants that specialize on forests for at least part of their life history. The Eastern Arc Mountains of Tanzania house a large proportion of forest-dependent birds, but also face a high degree of deforestation (Buchanan et al. 2011). Such loss of forest habitat is concerning for both the numerous endemic tree species (Hall et al. 2009) and avian altitudinal migrants that live there (Burgess and Mlingwa 2000). One such species is the Banded green sunbird (*Anthreptes rubritorques*), a forest-dependent altitudinal migrant endemic to the Eastern Arc Mountains, which is now listed as a Threatened species due to habitat loss through deforestation (BirdLife International 2017). Conservation efforts must prioritize areas of rapidly vanishing habitat, especially where these intersect with forecasts of climate change impacts on habitat availability, and particularly in instances where highly endemic species face extinction (Post and Brodie 2015).

Parallel to habitat destruction, movement barriers limit the realized availability of seasonal ranges to migratory animals. Human infrastructure, including fencing, roads, and bridges, interrupt directed movement, thereby preventing migrants from accessing seasonal ranges. Because anthropogenic delineations between land designations rarely fall along ecological boundaries, fences bar passage across otherwise continuous niche space. Semi-permeable solutions, such as wildlife-friendly fencing, increase connectivity between seasonal ranges, while still fulfilling the original intention of the infrastructure (Paige 2008, Sawyer et al. 2013). Barrier permeability may be similarly important in marine settings. For example, many crabs undergo seasonal movements between shallow estuarine and deeper ocean waters (e.g. Bigford 1979). The construction of bridges connecting capes at the mouth of estuaries may present temporary or permanent barriers to crab migration: project scheduling and design permeability must be considerations if the conservation of marine-estuarine bathymetric migrants is a priority.

Effectively managing for the future will rely on focused consideration of the seasonal role humans play in the systems vertical migrants occupy, and the sensitivity of niche space to a changing climate. One such example lies in a climate change hotspot, the East Australian Current (EAC), which has faced changes in the strength and seasonality of its flow and poleward shifts in the distribution of species that inhabit it (Johnson et al. 2011, Champion et al. 2018). The southern rock lobster (*Jasus edwardsii*) is an economically important species that undergoes seasonal bathymetric movements to shallow water for molting (MacDiarmid 1991). *Jasus* sp. lobsters face seasonal fishery pressure in Tasmania, which is also highest in shallow waters near the coast. Lobster recruitment is expected to fall in the coming decades as sea temperature rises (Pecl et al. 2009), but they face the added threat of invading sea urchins that arrived in response to overfishing (Johnson et al. 2011). Accounting for spatiotemporal variation in lobster abundance, and determining whether effects of climate and harvest are additive or synergistic, are crucial to the success of fishery management there.

While systems of vertical transhumant pastoralism may not fit neatly under some contemporary definitions of “migration,” their seasonal structure of landscape use presents an opportunity to forecast dynamics and examine policy through analogy: transhumant pastoralism is the practice of leading livestock along seasonal routes to track pasture quality, and mountain ranges across the world have served as systems for vertical pastoralism throughout human history. A primary concern of shepherds is the condition of grazing and wintering lands; decisions about grazing timelines dictate forage quality for livestock, and frequently incite conflict (Beck 1991). Shifts in predictable forage phenology may be difficult to match by pastoralists due to the often-rigid transit schedules imposed on them through political avenues. Nepalese herders have reported earlier snowmelt and advanced plant phenology in the Himalaya, where they undergo seasonal vertical movements to maintain yaks and other ungulates (Aryal et al. 2016). Added to shifting social and cultural landscapes, environmental change amplifies the expected decline of vertical transhumant pastoralism in the coming decades (Hock et al. 2019). Protection of the routes that connect seasonal ranges, and flexibility by officials to account for changes in ecosystem dynamics, will be central to the conservation of this imperiled lifestyle.

Conclusions

The evolution of analogous patterns across ecosystems lends insight to both basic and applied research questions (Burkepile et al. 2020). One such pattern is the seasonal movement between vertically separated habitats: vertical migration. Seasonal vertical migrations have evolved not only within marine and terrestrial habitats, but in some cases they involve transit between these inherently stratified ecosystems. Vertical migrants can be found throughout the animal kingdom, including among arthropods, birds, and even human-ecological systems. The heightened environmental variation generated by landscapes of relief allows animals to exploit or mediate the seasonality of their environment in order to facilitate growth and reproduction. However, the historic pattern of variation may be sensitive to adjustment by climate and accessibility by other anthropogenic impacts. Migrants' capacity to manage seasonal niche space by navigating biotopic space may underlie their ability to persist under climate and land use change, but well-planned conservation action and policy can help ensure the longevity of vertical migrants.

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