

Review

Hygric Niches for Tropical Endotherms

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Biotic selective pressures dominate explanations for the evolutionary ecology of tropical endotherms. Yet, abiotic factors, principally precipitation regimes, shape biogeographical and phenological patterns in tropical regions. Despite its importance, we lack a framework for understanding when, why, and how rain affects endotherms. Here, we review how tropical birds and mammals respond to rain at individual, population, and community levels, and propose a conceptual framework to interpret divergent responses. Diverse direct and indirect mechanisms underlie responses to rainfall, including physiological, top-down, and food-related drivers. Our framework constitutes a roadmap for the empirical studies required to understand the consequences of rainfall variability. Identifying the patterns and mechanisms underpinning responses to temporal variation in precipitation is crucial to anticipate consequences of anthropogenic climate change.

Precipitation and Fitness in Endotherms: Missing Links

Precipitation and temperature are the two major axes of global climatic variation. Whereas the paramount importance of precipitation regimes in plant biology is axiomatic [1], studies associating climate with animal evolutionary ecology and conservation have focused on **thermal tolerances** (see [Glossary](#)) (e.g., [2,3]), owing to clear links between temperature and individual **animal performance**. In endotherms, as ambient temperatures deviate from thermal neutral zones, individuals compensate by actively generating or dissipating body heat; those responses are mediated by species- and individual-level traits [4]. By contrast, we have a poor understanding of the mechanistic links between rainfall and the biology of terrestrial endotherms. This gap in knowledge has major implications for our ability to interpret macroecological patterns and predict climate change impacts [5]. Precipitation is clearly critical to endotherm evolutionary ecology; for example, in **species distribution models**, the magnitude of modeled precipitation effects sometimes equals or exceeds that of temperature effects in both temperate and tropical environments (e.g., [6,7]). However, associations between precipitation and distribution represent a black box in endotherm biology. Long- and short-term fluctuations in rainfall can affect terrestrial endotherms in multiple, but largely unstudied, ways. Furthermore, rainfall regimes are changing due to anthropogenic global change ([Box 1](#)). Without understanding the basis for relationships between precipitation and fitness, we cannot predict how changing precipitation will affect tropical endotherms in future decades. Although the concepts we present here apply to endotherms living in other environments, we focus on tropical forests and other tropical terrestrial communities, because identifying responses to variation in precipitation is more tractable in tropical systems, where there is less temperature seasonality than in temperate systems.

Precipitation regimes define major plant associations, biogeographic provinces, and seasonality over most tropical regions [8,9]. Distributions of terrestrial animals closely match those of plant communities, and are likely shaped by combinations of direct, physiological responses to rainfall (analogous to thermal tolerances) and indirect responses mediated by species interactions [10,11]. Food availability is the most-commonly invoked mediator of indirect responses (e.g., [12,13]); rainfall seasonality influences plant phenology, which shapes temporal patterns of food availability [14]. For example, during the driest and hottest months, tropical dry forest

Highlights

Precipitation regimes define patterns of tropical biogeography and seasonality, and are a strong selective force on tropical taxa.

The mechanistic links between anomalies in rainfall and endotherm responses are poorly known, in contrast to an extensive literature on thermal physiology.

Mounting evidence documents both positive and negative behavioral, physiological, and demographic responses to temporal variation in precipitation in birds and mammals.

Anthropogenic changes in precipitation are spatially heterogeneous, involving increases or decreases in total rainfall combined with shifts in the timing and magnitude of rainfall events with unknown consequences for the majority of affected taxa.

We fill a conceptual gap to expand the dimensionality of climatic niches required to interpret and predict precipitation responses based on organismal processes and thermal niche theory.

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trees bloom and lose their leaves, producing fruits and new leaves with the onset of rains; these bottom-up processes define the phenology of pollinators, herbivores, and frugivores [15]. Particularly in arid tropical regions, food abundance clearly underlies demographic responses to interannual variation in rainfall, as seen, for example, in African savanna ungulate populations [16]. Yet even in far wetter tropical regions, precipitation is still paramount in shaping biotic seasonality for producers and endotherm consumers [17–19]. Ongoing phenological changes in the tropics are more strongly linked to changing precipitation regimes than to rising temperatures [20]. Tropical regions are also subject to cyclical interannual variation in rainfall driven by the **El Niño Southern Oscillation** (ENSO), which manifests as changes in daily rainfall amounts, severity of storms, and duration of dry and wet seasons. Furthermore, endotherm physiology and energetics are affected by changes in humidity associated with precipitation [21].

Although tropical animals are clearly sensitive to both spatial and temporal variation in rainfall, the reasons for their responses are largely unknown [22]. Here, we articulate a framework for understanding how, when, and why rain affects endothermic animals. The foundation of this framework is the concept of the 'hygric niche'. As with thermal **niches**, different mechanisms likely underlie relationships between performance and deviations from average conditions at opposite ends of the distributional limits of a species. However, mechanisms underlying hygric niches are diverse and not driven by physiological traits to the same extent as are thermal niches. Rather, they comprise multiple physiological, behavioral, and ecological processes, and myriad interspecific interactions (Table 1). We suggest that identifying underlying drivers is crucial to reconciling evidence of apparently individualistic functional relationships between rain and individual- or population-level performance, and for understanding and predicting responses to changing climates.

Hygric Niches for Endotherms

How do endotherms fare when conditions are drier or wetter than average? The evidence is mixed; wetter years are often 'good' years for some endotherms, whereas, for others, survival or fecundity increases in drier-than-average years [23–26]. Moreover, populations of a single species can respond differently to variation in rainfall across their range [27] (Table 1); indeed, 70 years ago, Skutch documented differences in phenology of yellow-faced grassquits (*Tiaris olivaceus*) associated with rainfall regime, with reproduction starting during the dry season in wet areas, and during the wet season in dry areas [28]. We propose a hygric niche concept in hope of reconciling divergent responses to temporal variation in rainfall among populations, and among species within the same community (Figure 1). We follow Chase and Leibold ([29] p. 19) in defining a species' niche as 'the environmental conditions that allow a species to satisfy its minimum requirements so that the birth rate of a local population is equal to or greater than its death rate along with the set of per capita impacts of that species on these environmental conditions' and follow in the footsteps of Whittaker [30] in the graphical depiction of niches along environmental gradients. We adopt a mechanistic approach to describing ecological hygric niches, amenable to testing using experimental and statistical distributional approaches [31].

A core assumption of the hygric niche model is that endotherms exhibit curvilinear performance responses along precipitation gradients, just as they do along temperature gradients [32]. Thus, performance should peak near the center of the precipitation conditions that the species tolerates, and performance should decline toward wetter and drier extremes (Figure 1A). Precipitation–performance curves may be roughly Gaussian, asymmetric, or exhibit thresholds or neutral responses over portions of the gradient. The aggregate of individual performances contributes to shaping population-level demographic responses to interannual variation in rainfall (subject to several assumptions [33]). In our model, we depict the niches of species (Figure 1B)

Glossary

Animal performance: relationship between some environmental variable (typically temperature) on a core biological process or activity having direct implications for fitness.

Carbon forcing: changes to global climatic regimes due to anthropogenic emissions of greenhouse gases, most notably carbon dioxide, from the burning of fossil fuels.

El Niño Southern Oscillation

(ENSO): an important global index of multiyear cycles in climatic conditions over large areas of the tropics. Extreme El Niño years are those with above-average sea surface temperatures (SST) in the Pacific Ocean represented by negative Southern Oscillation Indices (SOIs), which contrast with La Niña years characterized by below-average SST (and positive SOIs) or more typical conditions. ENSO cycles strongly affect rainfall regimes in tropical regions.

Niche: a fundamental, but still disputed ecological concept referring to the relationship between an organism and its environment (including other species). The meaning we imply in this review is the Hutchinsonian concept of the multidimensional set of conditions that are required for survival and reproduction. The hygric niche comprises a subset of the entire niche, consisting of those dimensions describing the range of precipitation conditions under which a species can persist.

Species distribution model:

algorithms used to predict the current or future distribution of a species based on the environmental conditions in the locations where it is currently or historically found.

Thermal tolerance: range of ambient temperatures over which an organism can survive and reproduce. Tolerances are shaped by both adaptation and acclimation, and are dependent upon the duration of temperature extremes. As temperatures approach both the upper (hot) and lower (cold) extremes of an endotherm's tolerance, energy expenditure increases as the animal attempts to maintain stable internal temperatures.

Table 1. Studies Exemplifying the Diversity of Endotherm Responses to Temporal Variation in Precipitation

Taxa	Study region	Response variable	Nature of response (standardized relative to positive deviations in rainfall)	Precipitation metric	Refs
Individual-level responses					
Lance-tailed manakin (<i>Chiroxiphia lanceolata</i>)	Panama	Nestling growth rate	Positive	Southern Oceanic Niño Index (SOI)	[101]
American redstart (<i>Setophaga ruticilla</i>)	Jamaica	Size-corrected body mass	Positive	Dry season rainfall	[111]
Galápagos mockingbird (<i>Mimus parvulus</i>)	Galápagos Islands	Response to parasitism: nestling condition, parental provisioning	Positive	Breeding season and annual rainfall	[112]
Sowell's short-tailed bat (<i>Carollia sowelli</i>)	Costa Rica	Metabolic rate	Negative	Wet (vs dry) experimental manipulation	[57]
Silvery mole-rat (<i>Heliophobius argenteocinereus</i>)	Malawi	Daily energy expenditure	Negative	Onset of heavy rains	[106]
Population-level responses					
Purple-crowned fairy-wren (<i>Malurus coronatus coronatus</i>)	Northern Australia	Clutch size	Positive	Rainfall 3 weeks before egg-laying	[42]
Six species of cave-roosting insectivorous bats	Malaysia	Reproductive phenology: proportion of females lactating	Positive	Rainfall in previous month	[113]
Verreaux's sifaka (<i>Propithecus verreauxi</i>)	Madagascar	Infant survival, fertility rates	Positive	Monthly rainfall, Indian Ocean Dipole (IOD)	[25]
Milne Edward's sifaka (<i>Propithecus edwardsi</i>)	Madagascar	Fecundity	Negative	ENSO	[26]
Wire-tailed manakin (<i>Pipra filicauda</i>)	Ecuador	Survival, condition, recruitment, lek size	Negative	ENSO phase (lower survival and condition following La Niña years)	[102]
Lowland moist forest birds	Panama	Population growth rates of multiple species	Mixed responses; more negative than positive	Dry season length	[67]
Community-level responses					
Mid-elevation arid forest mammals	India	Abundance	Positive	ENSO	[114]
Lowland wet forest terrestrial mammals	Peru	Density of individuals	Negative	Flooding, measured as meters above sea level	[50]
Trophic cascades involving wildebeest (<i>Connochaetes taurinus</i>) ^a	Serengeti	Wildebeest recruitment; lion prey intake	Positive	SOI	[39]
Lowland wet forest birds	Ecuador	Abundance: estimated from captures and observations	Negative	SOI, dry-season rainfall	[115]
Lowland dry forest small mammals	Mexico	Species richness	Positive	Rainfall during previous wet season	[116]

^aThis paper evaluated the consequences of rainfall on three sets of trophic relationships. We highlight here interactions involving wildebeest, but in all cases where relationships were statistically significant, rain was positively associated with density, foraging rates, recruitment, and other demographic parameters.

to be narrower than individual hygric tolerances in part because the conditions required for successful reproduction are more stringent than those under which an individual can potentially survive [34]. Species and individual curves also differ in shape or breadth due to the differences between requirements for populations to persist (allowing for demographic rescue via dispersal) and conditions required for populations to thrive (i.e., persistence vs. establishment niches [31]). Conversely, local adaptation could lead to flatter and broader species-specific hygric response curves relative to individual performance curves. Regardless of their shape and breadth, near

the middle of species-level hygric niches, we expect populations to exhibit weak or inconsistent responses to temporal deviations in rainfall because neither modest increases nor decreases in rain will result in conditions approaching the extremes tolerated by that species (Figure 1B). However, populations living near dry extremes of the niche should respond strongly and positively to wetter-than-average conditions, because wet years will approximate environments closer to species-specific optima. Those same populations should respond negatively to drier-than-average conditions, because drought years will approximate environments located at or beyond those in which individuals can survive and reproduce. Populations near the wet extreme of the niche will exhibit opposite responses to temporal variation in rainfall. The important axes of inter-annual variation in rainfall may manifest as overall precipitation totals, the timing and duration of rainy and dry seasons, and/or the intensity of wet and dry periods. Just as each species exhibits unique demographic responses to thermal gradients, we expect them also to exhibit species-specific responses to precipitation regimes (Figure 1C).

Many direct (physiological) and indirect (biotically mediated) mechanisms underlie rainfall-demographic relationships. Even within species, different mechanisms may link precipitation to survival or reproduction at opposite ends of the hygric niche. The idea that bottom-up processes, specifically food availability, drives endotherm population dynamics pervades most interpretations of individual, population-level, or distributional responses to precipitation in tropical communities (e.g., [35]). At low elevations in the tropics, plant productivity is often constrained by soil moisture [36]; locations having pronounced dry seasons experience deficits in soil moisture for periods of days to months, reducing primary productivity [37]. Thus, in a wetter-than-average year, the severity and duration of moisture deficits will typically decline [9], leading to increasing primary productivity; the reverse will occur in dry years [38]. Such bottom-up processes are fundamental to structuring endotherm communities in tropical grassland systems (most notably in the Serengeti [39]). In forests, interannual variation in precipitation affects leaf production and flower, fruit, and seed production, which in turn affects food availability at higher trophic levels [40]. Elevated food availability affects endotherm foraging efficiency, which can influence reproductive investment and survival at all life stages. Such cascading implications of rainfall-mediated fluctuations in food and competition underlie well-known examples of trait evolution in Darwin's finches [41] and drive rapid, plastic reproductive responses to the onset of rains in tropical grasslands and savannas (e.g., [42]).

The assumption that food-driven, bottom-up mechanisms lead to positive responses in wetter years and negative responses in drier years is not universally true. For example, in Panama, plants produce synchronous crops of higher-quality leaves and increase energy allocation to flowers and fruits in dry years with less rain and more sunlight. The increase in leaf nutrients and reproductive structures results in more arthropod prey for endotherm consumers [43,44]. Furthermore, factors other than food availability may regulate populations. For example, changes in predation pressure and parental vigilance may underlie associations between precipitation and fledging success of understory tropical birds [45]. Therefore, rainfall-driven demographic or behavioral changes in predator communities could influence fecundity more strongly than could bottom-up processes. Finally, direct risks of dehydration under arid conditions can influence the behavior of tropical primates [46] and birds [47], indicating the potential for physiologically mediated direct responses to rain. Thus, even at the dry end of the hygric niche of a species, it is not safe to assume that food-driven processes underlie all positive associations between demography and rainfall.

Negative relationships between rain and fitness at the wet ends of hygric niches are less intuitive and likely involve a broad suite of direct and indirect mechanisms. Direct consequences of rain

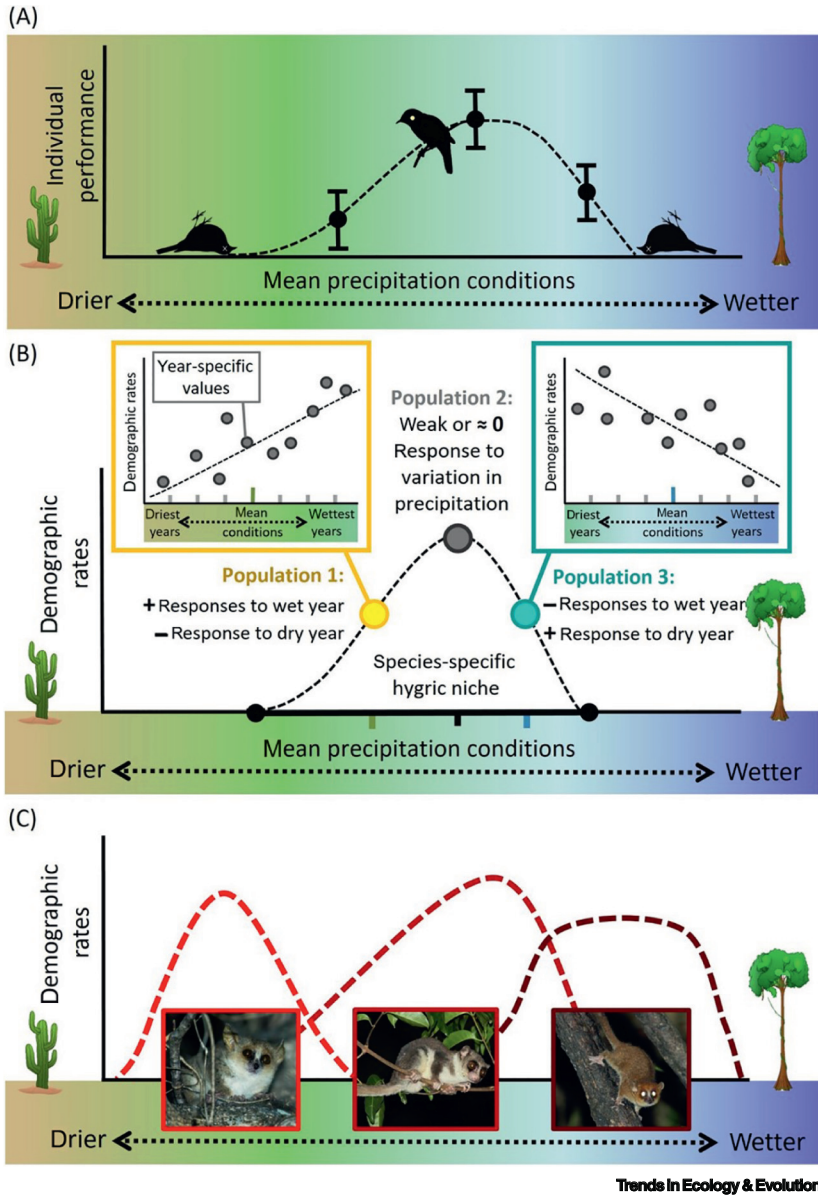


Figure 1. Hygric Niches for Endotherms.

For a Figure360 author presentation of Figure 1, see the figure legend at <https://doi.org/10.1016/j.tree.2020.06.011>.

The hygric niche model provides a conceptual framework for understanding and predicting how endotherms living in different locations with varying precipitation conditions respond to temporal variability in rainfall. Just as individuals perform optimally within specific temperature ranges, they are hypothesized to also exhibit peak performance in the middle of the range of precipitation conditions they can tolerate (A). At the population level (B), drought-related stressors in arid regions (e.g., population 1) are expected to reduce demographic rates relative to those of population 2 at the middle (i.e., optimum) of the hygric niche. Similarly, rainfall-related stressors will reduce demographic rates in population 3. Populations 1 and 3 will also vary in the nature of their response to interannual variation in rainfall [(B) inset figures]. Given that population 1 is located near the arid extreme of conditions that the species can tolerate, demographic rates will increase in a wetter year, during which conditions approximate locations in more mesic regions (to the right along the x-axis) and decrease in a drier year, when conditions approximate locations in even more arid regions (to the left along the x-axis). Conversely, demographic rates in population 3 will decrease in a wetter year and increase in a drier year. Each species will vary in the location and shape of their rainfall response curves (C), even among closely related and ecologically similar species, such as Malagasy lemurs (*Microcebus gireourufus*, *Cheirogaleus medius*, and *Microcebus rufus*, respectively; reproduced with permission from Nick Athanas).

include mortality during storms due to elevated energetic costs under wet conditions [48,49], drowning [50], or physical damage to nests or shelters [51]. Direct, but sublethal, consequences of storms include elevated thermoregulatory costs [52] affecting condition. Compromised condition may cumulatively influence apparent survival [53] by elevating susceptibility to disease, predation, or propensity to emigrate [54]. Additionally, sublethal effects of wet years can negatively affect subsequent reproductive success [55]. Heavy rain can impede the foraging ability of birds [56] and bats [57]. In small endotherms requiring high energy intake rates [58], short-term foraging reductions of only a few hours represent potentially lethal energetic challenges [59] and can reduce fecundity [60].

Negative responses to increased rain can also result from indirect, biotically mediated processes, including food limitation. In wetter, less seasonal tropical forests, productivity is not usually limited by soil moisture [61]. Instead, solar radiation typically limits the capacity of plants to capture carbon from the air and grow the leaves, flowers, and fruits forming the base of terrestrial food webs [37,62]. Given that elevated rainfall is associated with increased cloud cover, primary productivity declines in wetter years, which reduces food at higher trophic levels [63]. Other consequences of excess rain that may reduce primary productivity include nutrient leaching and reduced root respiration in waterlogged soils. Even where elevated precipitation does not reduce productivity, rain affects arthropod behavior, reducing prey activity and availability [64]. Variation in precipitation also influences ecto- and endoparasite populations [65]; for example, endotherm blood parasites and botfly infestations are often more prevalent in wetter conditions [66].

Scaling Up: From Populations to Communities

The hygric niche framework can be scaled up to interpret community-level patterns and generate biogeographic predictions. Communities comprise co-occurring species, each located at different points along their hygric niche (Figure 2A). Thus, within a community, the direction and strength of precipitation–fitness relationships vary in species-specific ways. Diverse responses to temporal variation in precipitation within communities is exemplified by the divergent responses to interannual variation in rain of bird species in Panamanian seasonal moist forest. Over 34 years, the population growth rates of some species decreased under drier conditions, others experienced little net change, and a few increased [67]. Similarly, within a Mexican small mammal community, population growth rates varied in response to deviations in rainfall; five species increased in wetter years, while two were unaffected. Additionally, in response to extreme rainfall events, one species increased and three decreased [68].

The hygric niche framework predicts that population-level responses to temporal increases in rainfall should become consistently more negative in communities located in the wettest regions and, conversely, consistently more positive in communities located in the driest regions (Figure 2B). Although we frame our model graphically in terms of responses to wetter-than-average conditions, we expect opposite responses to drier conditions. Local precipitation gradients will typically span only a portion of the total range of mean precipitation conditions existing within the tropics. Community-level patterns would arise because, in communities located near environmental extremes, most or all populations comprising the community will be located near the same edge of species-specific niches; consequently, all rainfall–demography relationships will either exhibit positive slopes (dry extremes) or negative slopes (wet extremes). Species turnover in bird communities along a Colombian precipitation gradient provides evidence of aridity constituting a stronger biotic filter for wet forest birds than precipitation is for dry forest birds [69].

Biogeographic predictions emerge when we summarize expected net responses to temporal variation in rainfall as the means and variances of component demographic responses within communities (i.e., β -values; Figure 3A). Whereas the magnitude of variances among species is likely to be similar over most precipitation conditions, we expect them to converge (i.e., responses of species to be more consistent) approaching both the arid and pluvial extremes. Over a broad central range of conditions, variances of population-specific responses within communities are expected to overlap zero; some species responding positively, some negatively, and others not responding in a consistent manner to temporal increases in rainfall. However, moving geographically along precipitation gradients to communities located nearer arid extremes, mean responses to increased rain become more positive to a point where the variance around community means does not overlap zero. Conversely, toward the wet end, at some point the variance around mean responses within a community will fall below zero. These points delineate three broad regions useful for developing and testing predictions of the hygric niche framework (visualized in Figure 3A as points i and ii). For instance, if bottom-up, food-mediated mechanisms underlie demographic responses to deviations in rainfall, we expect point ii (where responses become net-negative) to be located where primary productivity is no longer limited by rainfall and begins to be limited by solar radiation (although, if alternative mechanisms are more important, then this threshold may be located at higher or lower mean precipitation amounts). Likewise, to the left of i (where responses become net-positive), rainfall-mediated food limitation leads to the prediction of reproductive phenology being more synchronous among species within the community and timed to exploit seasonally abundant food resources than in regions between i and ii. Additionally, communities located in regions of intermediate precipitation amounts (i.e., between i and ii) should be those most strongly structured by biotic interactions and least subject to abiotic filtering; this prediction mirrors the hypothesis that biotic interactions are relatively more important sources of selection in tropical relative to temperate latitudes [70]. We note that this model does not take into consideration local geographical factors that may modulate responses to precipitation conditions. For instance, the moisture-holding capacity and nutrient composition of soils have major roles in the distribution of tropical tree species [71]; drought more strongly affects trees where soils are porous, especially those along steep slopes with thin soil layers [72].

Interactions between Hygric and Thermal Niches

Given that the mean annual temperature at sea level does not change between the tropics of Cancer and Capricorn, the framework described herein is applicable over large, lowland regions of the tropics. However, temperature decreases predictably with increasing elevation [73] and, whenever energetic mechanisms underlie responses of endotherms to variation in rainfall, those responses will be temperature dependent for two physiological reasons. First, wet animals lose heat in cool environments more quickly than do dry animals [74]. Consequently, a high elevation endotherm will incur higher thermogenic costs resulting from the same amount of rain at high elevations relative to low elevations. Second, rain increases humidity; an exercising endotherm must dissipate body heat to maintain homeothermy via evaporative cooling, which becomes more difficult as both temperature and humidity increase [4].

Elevational temperature variation should also affect rainfall–fitness relationships due to indirect, food-related mechanisms and plant physiological processes. With ample soil moisture, plant productivity increases with temperature [75]. However, at higher, cooler elevations, evaporation and evapotranspiration rates are slower, meaning that less rain is required to maintain a positive water balance when ambient temperatures are lower [76]. Thus, given the same precipitation amounts, high elevations will be relatively less susceptible to water limitation and more likely to experience reduced primary production in a wet year, decreasing invertebrate abundance, and affecting other trophic links between plants and endotherm consumers. Associations between rain,

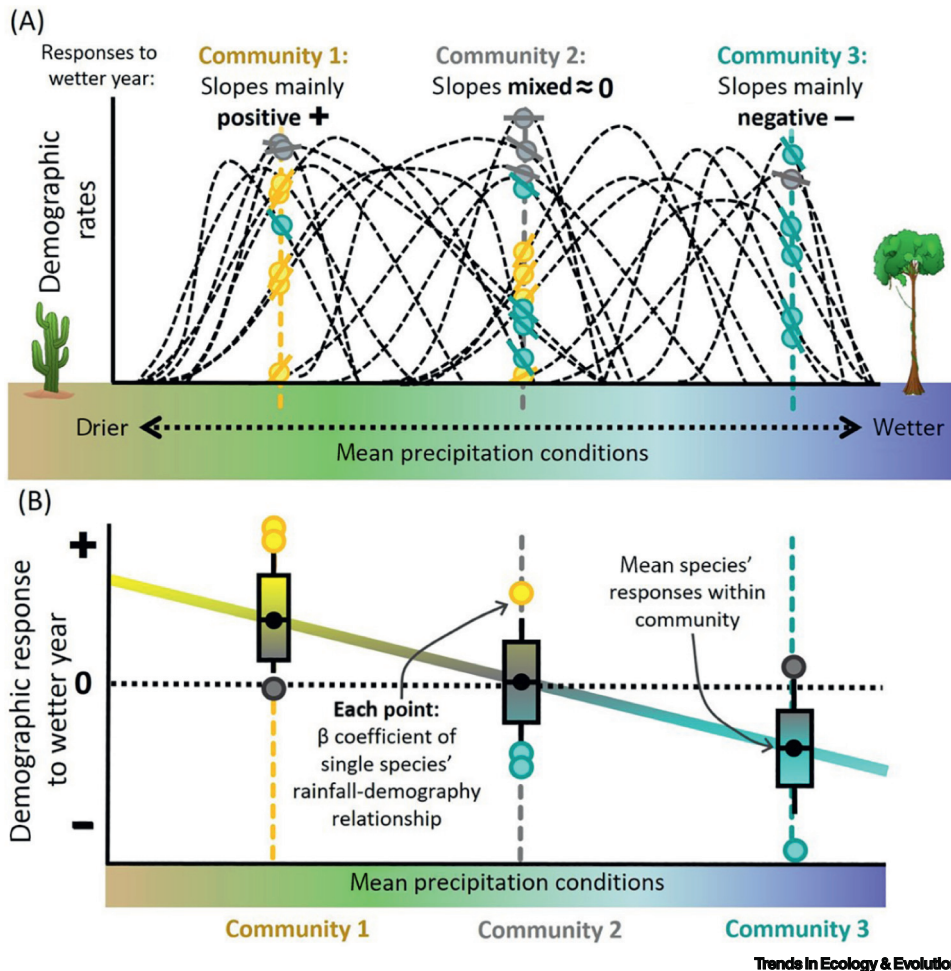
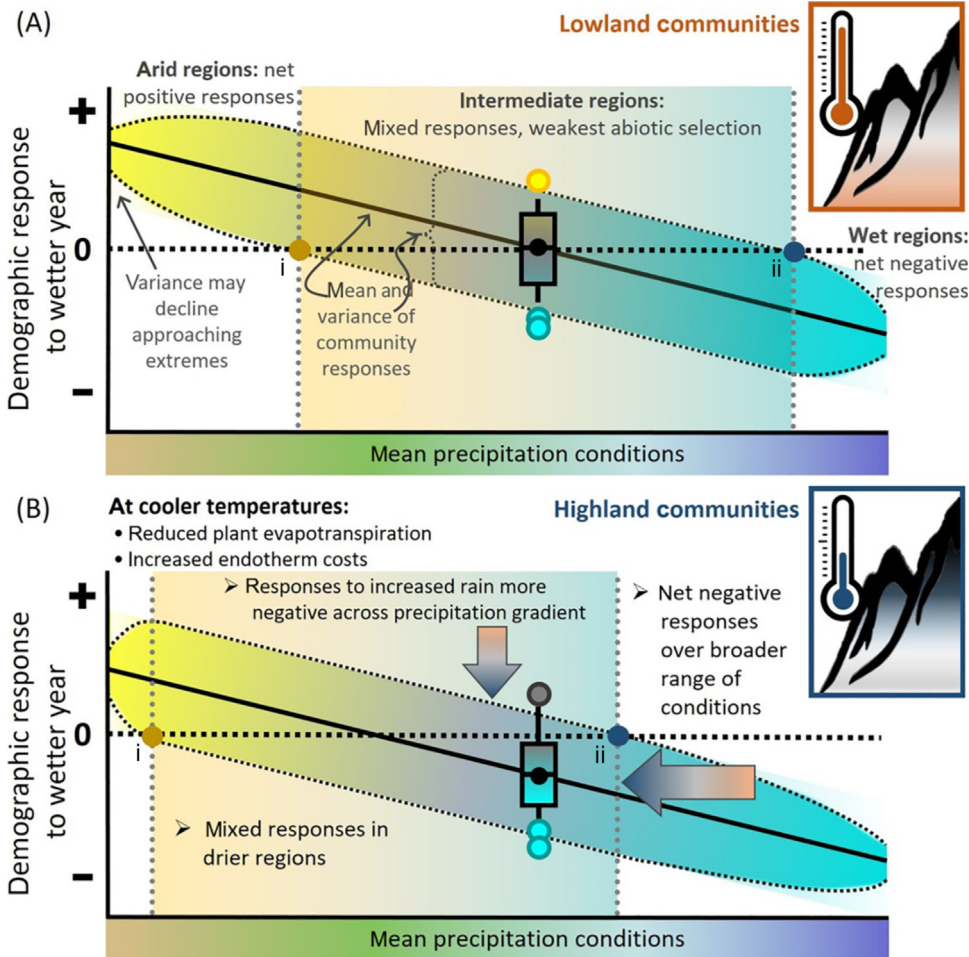


Figure 2. Scaling Up the Hygric Niche. The hygric niche framework can be used to understand community-level responses to precipitation variability. We visualize communities as vertical cross-sections across the hygric niche curves of multiple species, with each community located at a specific location along a gradient of precipitation conditions (A). Each community comprises populations (dots) of species located at different positions within their hygric niche. Thus, within communities, species should respond individually to temporal variation in rainfall, with some responding positively to a wetter year (yellow dots, positive slopes), some responding little (gray dots, slopes close to zero), and some responding negatively (teal dots, negative slopes). In relatively arid regions (i.e., near the dry extremes of precipitation conditions; community 1), species responses to temporal increases in rain should typically be positive. Conversely, in very wet regions, responses to a wetter-than-average year should average negative (community 3). Over a large central span of precipitation regimes, responses to temporal variation in rainfall would be more variable, including positive, negative, and neutral responses (community 2). (B) Box plots of the slope values (β coefficients of rainfall-demographic relationships) of species within the three representative communities in (A) to visualize net community responses and the overall negative relationship between mean precipitation (x-axis) and the net responses of species within communities (y-axis).

productivity, and consumers mean that, under the same precipitation regime, food-mediated endotherm responses to increased rain will average more negative in high-elevation communities than low-elevation communities.

Both the thermogenic and plant-driven food-mediated mechanisms make the same predictions regarding the consequences of lower temperatures at high elevations on precipitation–demography relationships; the net effects of a wetter year should be more negative at high relative to low elevations (Figure 3B). Indeed, evidence of physiological costs of high



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Figure 3. Hygric Niches over Elevational Gradients. Within the lowland tropics (A), mean responses (unbroken black line) of all community-level responses to wetter-than-average conditions (e.g., box plot) decline from communities located in arid areas (L) to those located in very wet areas (R). Visualizing net responses this way reveals three graphical regions defined by whether net demographic responses within communities are consistently positive (L of i), negative (R of ii), or overlap zero (between i and ii). To the left of i, where biotic responses to seasonal and interannual increases in precipitation are consistently positive, we expect the most costly activities in the annual cycle (e.g., reproduction) to coincide with wet seasons. Conversely, to the right of ii, where negative biotic responses reflect elevated costs of increased rain, we expect costly activities to be concentrated during dry seasons. Over broad central regions of mean precipitation conditions (shaded area between i and ii), precipitation-mediated sources of selection are expected to be inconsistent, with communities comprising species exhibiting individualistic behavioral, demographic, and phenological responses. The magnitude of variances (shaded area around the mean line) likely remain fairly constant except near environmental extremes, where we expect them to decrease as abiotic constraints result in species-level responses becoming more similar to one another. Cooler temperatures at higher elevation (B) can influence rain–demography relationships via (i) food-mediated; and (ii) physiologically mediated mechanisms. First, at cooler temperatures, plant evapotranspiration slows; less precipitation is required to maintain a positive water balance, and solar radiation limits productivity more often. Thus, in a wetter year, high-elevation forests will be less productive (with less food available to endotherms) compared with low-elevation forests receiving the same amount of rain. When food-mediated mechanisms underlie endotherm demographic response to rainfall, this temperature dependency of evapotranspiration will mean that endotherm–rainfall responses will shift to being more negative. Second, rainfall affects associations between temperature and endotherm thermoregulatory costs. Over the temperature ranges that most tropical forests experience, energetic costs increase with decreasing temperature. Additionally, wet endothermic animals expend more energy to maintain homeothermy than do dry ones. Thus, at colder, higher elevations, endotherms will experience greater costs of elevated rainfall than at low elevations. When physiologically mediated mechanisms underlie responses to rainfall, the added costs of staying warm while wet will also shift the slopes of responses to being more negative. Under both mechanisms, net responses shift downward and points i and ii will be located in more arid regions.

rainfall are evident in some montane taxa. For example, Puerto Rican toadies (*Todus mexicanus*) living in high-elevation wet forests have elevated basal metabolic rates and readily utilize energy-saving reductions in body temperature relative to birds living at low-elevations [58]. In Central America, mid-elevation white-ruffed manakins (*Corapipo altera*) respond to major rain storms with larger increases in baseline corticosterone and plasma metabolites reflecting short-term fasting, than do individuals at lower elevations [59]. Phenological differences between high- and low-elevation populations also reflect elevated costs of rain under cooler temperatures; high-elevation birds in Cameroon reproduce during the driest months, whereas, in the same mountain range, low-elevation birds breed during wet months [77]. In many tropical highland communities, reproduction is more temporally constrained relative to low-elevation relatives and concentrated during dry seasons [12,78,79]. The prevalence of seasonal 'escape' from high-elevation wet season rains is likewise consistent with elevated energetic costs of precipitation under cooler conditions; in some bats and birds, heavy rains induce not only short-term physiological responses, but also periods of torpor or downhill migration [59,80]. While the occurrence of storms is typically unrelated to changes in temperature in tropical systems, in the Andes of Bolivia and Peru, and in Southern Mexico, short-term downhill movements of birds from high elevations is associated with both heavy precipitation and colder temperatures, which would exacerbate the direct costs of storms [81] (M.A. Ramos-Olmos, PhD thesis, University of Minnesota, 1983).

Interactions between the cooler temperatures at higher elevation and precipitation regime also influence indirect mechanisms shaping endotherm hygric niches. For example, rain generally dampens insect activity, but when conditions are both rainy and cool, prey availability declines further, increasing foraging costs of insectivores [82]. Likewise, temperature, rainfall, and irradiance all influence flower and fruit production in tropical systems [40,83]. Furthermore, the responses of predators to rain [84], the ability of prey to detect predators during wet conditions [85], or the risks that prey are willing to take [86] can depend upon interactions with temperature.

Axes of Rainfall Variation: Extreme Events, Seasonality, and ENSO

A foundational concept of the hygric niche framework is that species distributions are constrained by specific ranges of mean precipitation conditions. However, empirical studies (e.g., Table 1) reveal that tropical endotherms respond to multiple axes of precipitation variability, including short-term, severe weather events, variation in the length and intensity of dry seasons, and global climatic events, such as ENSO. The multidimensionality of precipitation regimes adds complexity to the hygric niche concept, but at the same time, can assist researchers in identifying mechanisms underlying responses [87]. Multiple metrics can be included in analyses based on *a priori* hypothesized mechanisms. Alternatively, when mechanistic understanding is lacking, model selection methods can be used heuristically to reveal which axes of rainfall variation are most important.

Short-term, extreme rainfall events can influence a range of biological processes [88] with disproportionate evolutionary consequences [89]. Rainfall over days to weeks is associated with changes in hormones, metabolites, breeding condition, and movement propensity in mammals [90,91] and birds [42,59]. Many tropical endotherms appear to mitigate short-term energetic challenges, such as those imposed by heavy rainstorms via facultative heterothermy (e.g., [92,93]). Some of the most extreme rainfall events occur during hurricanes when torrential rain accompanies gale-force winds. Although disentangling the direct and indirect effects of wind and rain is challenging, we know that hurricanes are a major source of selection, and the traits of species differing in their responses can help identify causal mechanisms [94].

The degree of rainfall seasonality is important in shaping biogeographical patterns and community ecology in tropical regions [20,95–97]. Typically, dry season length and intensity correlate with mean annual precipitation, and the duration of wet or dry seasons can be the precipitation metric most strongly associated with demographic rates [67]. However, the nature of seasonal effects can vary within communities. For example, the timing of reproduction of six species of Afrotropical ungulates responded to interannual variation in rain; however, fecundity peaked in response to rain in the current year in some species, while in others, fecundity peaks lagged by a year [98]. Furthermore, responses to seasonal deviations in rainfall can manifest via different vital rates among species, implicating multiple proximate drivers of demographic responses. For instance, Montserrat orioles (*Icterus oberi*) laid larger clutches and decreased re-nesting intervals following elevated prebreeding rainfall [99], whereas in spotted antbirds (*Hylophylax naevoides*), prebreeding rainfall affected the onset and duration of reproduction, but not clutch size, number of nesting attempts, or re-nesting interval [100].

A major source of interannual variability in rainfall in most areas of the tropics is ENSO, a cyclical change in tropical Pacific Ocean temperatures and the location of jet streams, measured by the Southern Oscillation Index (SOI). Sometimes, performance and demographic rates respond more strongly to variation in SOI than to local weather conditions (e.g., [26,101,102]), potentially due to this single metric capturing multiple dimensions of climatic variability. Both the nature and strength of relationships between SOI and local precipitation vary substantially among regions [103], and ENSO also influences the occurrence and intensity of storms [104]. Thus, the potential exists for independent or interactive effects of mean precipitation and oscillation in this and other global climatic indices. Indeed, in the Serengeti, SOI affects local dry- and wet-season rainfall, which, in turn, affects multiple trophic links between plant productivity, the demography of grazing mammals, densities of smaller mammals, and both lion foraging success and avian predator abundance [39].

Concluding Remarks and Future Perspectives

Although many empirical studies have documented positive or negative response of endotherms to deviations in precipitation, until now, we have lacked a framework for predicting the nature of such responses. Perhaps due to the lack of such a framework, for no tropical endotherm species can we fully identify the mechanisms underlying responses at both the dry and wet ends of their distribution. Consequently, we cannot draw general conclusions regarding the factors that most frequently constrain species' hygric niche. Although challenging, quantifying hygric niches for endotherms is within reach of the research community and will likely best be tackled using a combination of approaches [31]. For many species we already have quantitative descriptions of the statistical (distributional) hygric niche; that is, the range of conditions under which species persist. Large-scale distributional data derived from biological collections and citizen scientist databases make such descriptions ever more accurate. Experimental methods, such as are commonly applied to plants [105], will be useful to differentiate the establishment niche from the persistence niche, and have a major role to play in testing the mechanisms underlying responses to rainfall proposed here. While rainout shelters are generally impractical for most endotherm taxa, transplant experiments, captive animal studies in open-air enclosures, and tracking devices equipped to measure physiological metrics are feasible for many taxa (e.g., [106,107]). Correlative tests of some responses (such as the association between reproductive phenology and the seasonality of rainfall and consequences of variation in timing of rainfall [108]) are feasible using existing data for many species. Finally, demographic studies and investigations of life-history trait variation spanning the range of precipitation conditions under which a species occurs are crucial to elucidating hygric niches. While not technically difficult, such studies are rare and invaluable, given the time and effort they require. While core assumptions and predictions of the model

Outstanding Questions

What are the species-specific range of precipitation conditions under which endotherms thrive? The hygric niche model is founded upon the assumption of roughly curvilinear responses in individual performance and demographic rates over broad precipitation gradients. Explicit tests of this assumption are crucial and lacking; experimental studies of physiological responses to rain in outdoor enclosures and/or via reciprocal translocations, and the collection of detailed, long-term data for demographic analyses are needed.

What common patterns emerge regarding the mechanisms underlying both positive and negative constraints on hygric tolerances? How do species-level attributes, such as body size or dietary guild, mediate responses to rainfall? Do the responses of similar species parallel each other at the dry and wet ends of their hygric niches?

How important are direct versus indirect, biotically mediated links between rainfall and demographic rates? Many responses are assumed to reflect bottom-up, food-mediated processes without rigorous alternative hypothesis testing; an increasing number of studies document direct physiological challenges of rainfall extremes.

How well do population-level responses scale up? Can we predict community-level patterns of reproductive phenology and responses to climate change in tropical communities? Do community-level predictions of net responses correspond to biogeographical patterns of the factors limiting plant productivity (i.e., soil moisture or solar radiation)?

Are responses to anthropogenic climate change stronger in tropical species inhabiting areas of less seasonal rainfall relative to those subject to more pronounced wet- and dry seasons? Akin to the hypothesis that the magnitude of seasonal temperature variation shapes thermal tolerances, we predict that species tolerant of greater rainfall seasonality may be better able to cope with directional change in precipitation regimes.

must be tested before placing confidence in its explanatory value (see Outstanding Questions), for the first time, we have a hypothesis-testing framework upon which to base future empirical studies.

We acknowledge that real-world niches are complex and highly dimensional; we have necessarily avoided much of this complexity to focus attention on the rainfall-related components of the more general niche concept [29]. Temperature, particularly dry-bulb temperature, remains the predominant metric discussed in studies of climate change and physiological tolerances. When means or extremes of temperature correlate with precipitation, mechanistic discussions of endotherm responses typically focus on temperature rather than rainfall [69]. Alternative metrics, such as wet-bulb temperature, incorporate some of the energetic consequences inherent in humidity–temperature interactions [109], but cannot account for the diversity of mechanisms described here that mediate responses to precipitation. Explicitly accounting for precipitation-mediated performance, population dynamics, and community responses will move ecologists closer to biological realism in understanding and applying niche theory to the real world.

This review demonstrates that rain matters a lot to tropical taxa, shaping the geographical and temporal patterns of biodiversity over large portions of the globe. It also reveals that we know relatively little about how it matters; it is time to begin unpacking the black box of hygric niches. This need is urgent because precipitation is changing at tropical latitudes more rapidly and less predictably than is temperature [110], and other forms of anthropogenic change are exacerbating

Box 1. Changing Precipitation Regimes and the Future of Tropical Endotherm Communities

Temperatures are rising in both temperate and tropical latitudes due to elevated greenhouse gases; nevertheless, concomitant changes in precipitation may be the most direct threat to the integrity of tropical ecosystems [117]. Many tropical areas are predicted to experience changes in the amount and timing of rainfall [118], and the duration and severity of wet or dry seasons [119,120]. Although ENSO-driven severe weather has occurred for millennia [104], rising air and ocean temperatures are increasing the frequency and severity of these events [121].

Land use is a second important driver of tropical rainfall regimes [122,123]. Land use affects precipitation because up to 50% of tropical forest rainfall is derived from water recycled from the ground back to the atmosphere via evapotranspiration [124]. Small reductions in forest cover can increase local rainfall due to increases in convective heating [125], but more extensive deforestation results in soil desiccation, increased runoff, and decreased local rainfall. Importantly, such effects can alter rainfall patterns in distant, intact forests due to regional atmospheric moisture transport [126]. Thus, deforestation can fundamentally alter the hydrology of tropical systems in ways that are dependent upon both local and regional processes.

Whereas temperature changes occur gradually over large regions, rainfall regimes vary over finer spatiotemporal scales, and involve complex interactions between **carbon forcing** and land use [127]. Some places will get wetter and others drier [128]. With increasingly severe ENSO events, the tropical Eastern Pacific ocean region is predicted to get wetter and experience more extreme rainfall events [129]. By contrast, the Amazon Basin and nearly all of southeast Asia will likely get drier [130]. Levels of 40% deforestation likely constitute a tipping point, above which wet forests will be subject to extreme desiccation, frequent fire, and 'savannization', with complete loss of ecological integrity [131,132].

The hygric niche model helps interpret the consequences of changing rainfall regimes. Even where forests persist, we expect that changing rainfall will constitute important selective pressures on the life histories of tropical endotherms. Given the associations between patterns of rainfall seasonality and reproductive phenology in birds [18,100,133] and mammals [134–136], we expect either shifts in the timing of reproduction or, analogous to temperature mismatches at high latitudes, adverse consequences of phenological mismatches in species with low plasticity in phenology. Generally, the location of populations along species-specific hygric niches will determine their response to precipitation changes, and idiosyncratic responses could result in novel community assemblages affecting biotic interactions. The magnitude, nature of precipitation changes (e.g., timing, amount, and severity), and the mechanistic links between rain and fitness will mediate the strength of endotherm responses. Until we have tested assumptions of the hygric niche model and discovered repeatability in underlying mechanisms, framing reliable predictions will be challenging and complex. However, failure to tackle this complexity will likely lead to erroneous conclusions regarding the future of tropical communities and to faulty conservation strategies.

disruptions to global precipitation regimes (Box 1). The framework described here provides a way to interpret responses to spatial and temporal variation in rain, not only in the tropics, and not only in endotherms. We urge researchers tackling critical basic and applied problems in climate change research to expand the dimensionality of climatic niches, explicitly incorporating precipitation changes and population-specific responses to those changes in their studies and mitigation strategies.

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