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Symposium

Temperate Assumptions: How Where We Work Influences How We Think*

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abstract: Scientists have been observing the natural world for centuries and have long been intrigued by the high biodiversity and complexity of the tropics. They also usually had North American or European—in other words, outsider—perspectives and frequently concluded that the tropics were qualitatively different from the temperate regions in their ecology, evolution, and behavior. In particular, the tropics were seen as having a more benign abiotic environment, which in turn fostered more complex biotic relationships, with increased competition and other interactions. This may or may not be the case. Regardless, these ideas establish the temperate regions of the world as a kind of model system, a norm to which the tropics are compared and seen as different or unusual. The tropics are warmer or more diverse, rather than the temperate zone being cooler or less diverse. Such an attitude makes it difficult both to appreciate the scope of variation in nature and to develop accurate and general models for ecological and evolutionary processes.

Keywords: temperate bias, tropical biology, model system.

Introduction

Although people have always observed the world around them wherever they lived, until recently most formal examination of nature took place in Europe and, later, North America, where scientists naturally gravitated to the species and habitats around them. Many early works cataloged the details of biological life in Europe, and when Europeans began to settle in the New World, they likewise formulated ideas about nature based on the local flora and fauna. In some parts of the world, efforts to replicate European flora and fauna led to the introduction of dozens of what are now called invasive species, with enormous consequences for biodiversity.

The tropics, however, here conventionally defined as the area between the Tropics of Cancer and Capricorn, have particularly fascinated biologists for centuries. Starting with the earliest European explorers in the sixteenth century, Westerners eagerly devoured the accounts of voyages to Africa, Asia, or Central and South America, with their descriptions of novel and exotic flora and fauna (Chazdon and Cranbrook 2002). Early figures such as Linnaeus relied on specimens sent from around the world for developing their ideas about the diversity of life and marveled at the strange plants and animals from tropical regions. Later, both the Dutch East India Company and the British East India Company fostered expeditions that led to greater understanding of the world's biota (Chazdon and Cranbrook 2002).

Western biologists who did travel to the tropics often found themselves overwhelmed by the experience, as this passage from the memoir of noted naturalist Alexander Skutch (1987) reveals:

> The eager young naturalist who, from the less richly endowed temperate zone, plunges into the midst of tropical splendor may almost be overwhelmed by the multitude of strange and fascinating things clamoring for his attention, to be named and classified, to be studied, to be photographed or drawn. He may find it all too much for him and return to his distant homeland, where he feels more secure, where more knowledge is readily accessible through books and journals and the experience of his colleagues, where the unknown does not so press upon him. (P. vii)

Along similar lines, Dobzhansky (1950) states:

> Plants and animals of temperate lands seem to us somehow easy to live with, and this is not only because many of them are long familiar. Their style is for the most part subdued, delicate, often almost inhibited . . . In contrast, tropical life seems to have flung all restraints to the winds. It is exuberant, luxurious, flashy, often even gaudy, full of daring and abandon. (P. 209)

This notion of the tropics as far away, strange, and an onslaught on the senses because of their many differences from temperate ecosystems recurs in many other writings about tropical regions. Throughout the long history of the

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tropics and their biota influencing major figures in ecology and evolution, from Banks to Humboldt to Wallace to Darwin, all of these naturalists struggled to explain why the forests and jungles between the Tropics of Cancer and Capricorn were so alien, so different from home. Darwin (1839) noted, "Nothing can be more improving to a young naturalist, than a journey in distant countries" (p. 607). He was, of course, highly influenced by his own travels on the *HMS Beagle* but clearly also viewed the tropics as distant and, by definition, not part of the standard way the world worked.

Similar ideas about the tropics being qualitatively different in ecological and evolutionary processes from the temperate regions were commonly seen as more and more biologists began to spend time in Asia, Africa, and Central and South America. Still, the academic study of tropical biology has been relatively recent. Although the Bombay Natural History Society was founded in 1883, the more broad-based International Society for Tropical Ecology did not get its start until 1956, and the Association for Tropical Biology was begun only in 1963, long after societies such as the American Society of Naturalists were founded. Even today, the literature on tropical biology may be fragmented in its ease of access and reach. Pitman et al. (2007) surveyed over 2,000 accounts, including books, government reports, and articles on biology and conservation of the department of Madre de Dios, Peru, in southwestern Amazonia over the last 450 years. They confirmed that "the tropical literature has a notorious split personality" (p. 254), with roughly half the documents written in Spanish and virtually inaccessible outside Peru. The other half were in English and similarly inaccessible inside many parts of Peru. The authors further noted that their survey "does puncture three frequently encountered myths about the tropical literature: (1) that it is skimpy, (2) that most of it is written in English by nontropical biologists, and (3) that the most valuable information for conservation practitioners is published in developed-world journals" (p. 258).

This view of tropical organisms being "different" can have more practical and immediate repercussions for researchers trying to publish work from those regions; Pauly (1994) recounts a single-sentence review of a manuscript he wrote in 1984 on measuring age in fishes: "Rubbish, may apply in the tropics but not here." Aside from being, at best, unhelpful, such a review suggests, of course, that findings from tropical ecosystems are not generally applicable and that "here" is a temperate area. Pauly (1994) also notes how biologists working on fish in tropical oceans have had to counter then prevailing wisdom that tropical fish age could not be determined by rings in scales and that spawning in the tropics was continuous, both of which turned out to be questionable (Mohr 1921). Temperate biologists, in other words, make temperate assumptions and extend them to nontemperate regions.

The tropics, then, are distinct. But how? And what does it mean to view them as different, as strange, as not "here"? In this article I explore the ways that the tropics have been seen as qualitatively different from the temperate regions in their biology. I then argue that, whether or not such differences exist, biologists have tended to view processes and patterns of the temperate zones as a model system in ecology and evolutionary biology, much as *Drosophila* or *Caenorhabditis elegans* are model systems in genetics or neuroscience. This notion of biology makes certain taxa or processes normative and can make them appear to be a standard, with others seen as exceptions to the rule (Zuk et al. 2014). Finally, I explore some examples of myths about tropical biology that are now being debunked. My hope is that biologists will reexamine their assumptions about a tropical versus temperate dichotomy, potentially raising new questions about their systems regardless of their location.

Is Tropical Biology Real?

Perhaps the first biologist to discuss whether the tropics are unique was Theodosius Dobzhansky (1950) in his classic article "Evolution in the Tropics." Dobzhansky shared the view of tropical biota as exotic and different, as the quotation above indicates, but he further suggested that the difference lies in the nature of biotic versus abiotic interaction in temperate and tropical regions. Though he recognized that the tropics still have seasons, albeit not as marked as those of the temperate zones, he speculated that the greater stability and age of the tropics made the physical environment relatively benign. The climate is less harsh, and moisture is rarely limiting. In contrast, biotic interactions such as competition evolved to become more important in the tropics, and such interactions, he suggested, are more complex in the tropics (Dobzhansky 1950). Although I suspect that few biologists nowadays believe that the tropics are truly benign, Dobzhansky's attempts to generalize about what evolutionary processes might prevail in the two types of habitat are still relevant. In his words, "Tropical environments provide more evolutionary challenges than do the environments of temperate and cold lands" (p. 220).

Robinson (1978) picked up this theme with his bluntly titled article "Is Tropical Biology Real?" He wondered whether it is legitimate to set aside an area of biology simply because of where its major players live. He also pointed out that biologists have long been fascinated with the high biodiversity near the equator and that behavior links ecology and evolution, perhaps nowhere more so than in the tropics. After some consideration, however, Robinson (1978) also argued that biological interactions among and within species make life in the tropics qualitatively different. He was particularly taken with the idea that interactions among, rather than within, species are critical in the tropics. Robinson suggested that social and reproductive behavior may be similar in tropical and temperate species but that complex interspecific interactions are more common in the former. Within-species communication, he argued, has the same repertoire the world over, but the potential for complicated relationships among taxa is greater in the tropics. For example, army ants (*Eciton* spp.) travel long distances in their raids, and their trails are followed by a wide variety of other organisms, including antbirds specialized on eating the insects flushed up by the raiders as well as a host of terrestrial arthropods that either parasitize the ants themselves or opportunistically eat the prey left behind. Robinson (1978, 1979) also suggested that mixed-species foraging flocks of birds attain a complexity in the tropics that is unequaled elsewhere.

More recently, Schemske et al. (2009) surveyed a wide variety of biotic interactions and found that many, including herbivory and insect predation, are indeed more important at low latitudes, while others, such as cleaning symbioses and ant-plant interactions, are predominantly tropical. Macías-Ordóñez et al. (2014) examined the literature on sexual selection from various regions in the world. They examined articles on sexual selection and reproduction in four journals on animal behavior published since 2000 and found that both arid-zone and tropical species were underrepresented. In keeping with the notion that complex interspecies interactions are more frequently found near the equator, their study found that parasitism was more common in the tropics, and Macías-Ordóñez et al. (2014) suggested that the prevalence of parasitism might lead to different selective trade-offs than those found in temperate regions.

Temperate Assumption: Warmer Is Better

It is perhaps understandable that temperate biologists working through a long, cold winter would think wistfully of foliage and tropical breezes and assume that the climate closer to the equator will make life easier for the organisms living there. But the notion that a warmer climate is necessarily more benign or that it makes adaptation to increasing temperatures more likely for tropical species has been challenged recently by scientists studying the effects of climate change on ectotherms.

Janzen (1967) noted that tropical organisms should be expected to have a more limited capacity to acclimate to large temperature changes, simply because they evolved in more stable climatic regimes. Although it might seem that they would also be more heat tolerant, tropical ectotherms turn out to have relatively narrow thermal tolerances (Tewksbury et al. 2008; Logan et al. 2015). Therefore, if the climate warms by even a small amount, tropical ectotherms may become less able to function, while higher-latitude species are unaffected, because the changes still permit the latter to remain in their tolerance range. Long-term demographic data from studies of frogs and lizards in Costa Rica show declines in density over a 35-year period, a change potentially attributable to decreases in leaf litter due to warming climate (Tewksbury et al. 2008).

Ectotherms are, of course, not passive "prisoners of climate warming," as Huey and Tewksbury (2009) point out. By moving between sun and shade, terrestrial ectotherms can effectively keep their internal temperatures within a narrow range, and such behaviors might be expected to at least partially ameliorate the effects of climate change. Availability of shade, however, is crucial. Because tropical and desert ectotherms often need to actually cool off rather than warm up, such species may be at higher risk of moving outside their thermal tolerance if the climate warms but shade is less available (Huey and Tewksbury 2009).

Kearney et al. (2009) modeled the effects of climate variation in lizards that were allowed to behaviorally thermoregulate. Their results suggested that behavior helps species only in certain sites, such as coastal temperate zones, to deal with increased temperature. In the tropics, however, the lizards will be able to persist only in sites with deep shade. Tropical forest lizards are thus likely to be at high risk with even slight climate warming (Huey et al. 2009). Furthermore, if temperate species are not at a disadvantage when the temperature rises because they have wider temperature tolerances, they may be positioned to invade habitats previously occupied by tropical ectotherms (Huey et al. 2009). Some Puerto Rican forest lizards, for example, are already at risk of becoming displaced (Huey et al. 2009).

Reptiles and amphibians are not the only ectotherms potentially affected by climate change, of course, and aquatic organisms may respond very differently than terrestrial ones, perhaps because thermal plasticity is higher in aquatic taxa (Gunderson and Stillman 2015). Interestingly, in a survey of thermal tolerance in a broad range of taxa from around the world, Gunderson and Stillman (2015) did not find a relationship between latitude and plasticity in upper thermal tolerance, and they caution against assuming a greater vulnerability of tropical organisms to climate change. In addition, a taxon's thermal tolerance was not related to its plasticity. A similar cautionary note was sounded by Logan et al. (2015), who examined two species of lizards from Honduras, finding that although such tropical ectotherms may be sensitive to temperature increases, other abiotic factors such as wind speed were also important in shaping the lizards' activity patterns. In conclusion, the notion that the tropics are benign and that the animals in them are widely tolerant of high temperatures is not necessarily grounded in fact.

Sex in the Tropics

Robinson (1978, 1979) suggested that social behavior and other intraspecific interactions were unlikely to be different in tropical regions, in contrast to the greater degree of complexity in interspecific relationships such as the antbirds following army ant columns mentioned above. Other scientists, however, have disagreed. In particular, Macías-Ordóñez et al. (2014) point out that because so many aspects of behavior, perhaps especially reproductive behavior, vary with environmental characteristics such as temperature and seasonality, it is only reasonable to expect differences between the tropics and temperate regions in mating systems, reproductive strategies, and other within-species traits. They propose an approach, further detailed in Machado et al. (2016), that they term the macroecology of sexual selection, examining how spatial variation influences the behavioral ecology of sexual traits (Macías-Ordóñez et al. 2014). For example, they predict that arthropods in hot, humid environments are under weaker selection to develop quickly, since resources are available over a longer period. In turn, male-male competition is expected to increase, with concomitant selection for greater weaponry (Macías-Ordóñez et al. 2014). Along similar lines, Peixoto and Mensoza-Cuenca (2014) outline a general framework for the effect of climatic conditions on territorial mating system evolution in butterflies, focusing not on a tropics versus temperate dichotomy but on a more encompassing view of abiotic influences on behavior.

The discovery that many socially monogamous birds mated outside the pair bond and that many clutches were of mixed paternity significantly changed views about sexual selection (Griffith et al. 2002). Such extrapair paternity (EPP), like many other behaviors, was first documented in the temperate zone, using migratory birds (Stutchbury and Morton 2001), and researchers soon sought generalizations about the circumstances under which EPPs were most likely to occur, including whether tropical species exhibited similar patterns. Variation in EPPs has been attributed to a number of life-history characteristics, including adult mortality rate (high mortality rates should lead to higher EPP because of the costs associated with abandoning a current reproductive attempt and the reduced value of long-term pairing), amount of parental care needed (EPPs are more risky and hence expected to be rarer in species in which paternal care is crucial), breeding density (denser populations lead to greater opportunities for EPPs), and breeding synchrony (opportunities for seeking EPPs depend on the number of available partners; Stutchbury and Morton 1995; Tarwater et al. 2013).

Stutchbury and Morton (2001) proposed that while a temperate bias could be seen in research on EPPs, tropical birds were likely to show a lower rate overall. Some of the biases may have arisen because “for many years, ornithologists regarded migratory birds as ‘invaders’ or ‘interlopers’ in tropical habitats” (Forsyth and Miyata 1984, p. 141). However, Macedo et al. (2008) reviewed the available data on EPPs in a range of tropical species and found that the rates were roughly comparable to those in temperate birds; they advised caution in drawing conclusions, because the sample size is still limited and may not be representative of the diversity of reproductive behaviors. In addition, some tropical species are actually highly seasonal in reproduction, contrary to the temperate assumption of year-round breeding (Manica et al. 2014). A detailed examination of the tropical black-crowned antshrike (*Thamnophilus atrinucha*) in Panama revealed low rates of EPP (3% of offspring sired by extrapair males), but in contradiction to the hypotheses above, a high-density population that varied in breeding synchrony over the course of the study did not exhibit simultaneous changes in EPP (Tarwater et al. 2013). The distinction between temperate and tropical species has not proven to be productive in understanding variation in EPP among taxa.

Sexually selected behavior and morphology depend on physiological parameters such as hormones and components of the nervous system. But in addition to the lack of information about the rates of EPP in many tropical bird species, the relationship between endocrine changes and reproduction in tropical species is relatively unexplored and may challenge some of the conventional wisdom about the relationship between hormones and behavior. For example, tropical birds tend to have lower levels of circulating testosterone but may possess other attributes that enhance the action of the hormone, such as greater androgen receptor expression in the brain (Wingfield et al. 2014). Similarly, cooperatively displaying tropical species such as manakins may have elevated testosterone without the concomitant increase in aggression commonly seen in temperate species, and it is possible that the way that the hormone responds to social stimuli differs in tropical and temperate birds (Wingfield et al. 2014).

Birdsong is a well studied aspect of animal communication in the context of sexual selection, but here, too, the focus has been primarily on either temperate zone species or tropical species kept in captivity, such as the zebra finch (Podos 2014). From studies of such taxa, scientists had long concluded that, with rare exceptions, only male birds sang (Odom et al. 2014). A recent survey of 323 species of songbirds, many of them from tropical regions, revealed that in fact 71% of females also sang and that female song appears to be the ancestral state, calling into question some commonly held assumptions about the evolution of elaborate traits (Odom et al. 2014). Similarly, Podos (2014) noted that the enormous diversity of body and bill shapes as well as habitats and life history among tropical bird species shows great promise in elucidating the way in which song evolves, given the often opposing forces of natural and sexual selection. This diversity also holds promise for examining hypotheses about EPP and other aspects of sexual selection.

Model Systems and the Tropics

Model systems are a cornerstone of biology. We use them because they allow us to understand broad concepts without having to constantly reinvent the wheel of husbandry, methodology, or technique. As Kunkel (2006) put it, "We are unlikely to ever know everything about every organism. Therefore, we should agree on some convenient organism (s) to study in great depth, so that we can use the experience of the past (in that organism) to build on in the future. This will lead to a body of knowledge in that 'model system' that allows us to design appropriate studies of non-model systems to answer important questions about their biology."

Indeed, while less common in ecology and evolution than in biomedical research, model species such as *Arabidopsis*, *Tribolium*, and sticklebacks have been crucial to our understanding of how organisms evolve and interact. Once a few researchers began working on these taxa, more scientists became attracted to them and the storehouses of knowledge accumulated. Such organisms are usually easy to rear, are abundant, or are relatively easy to manipulate in the field or laboratory. More recently, the genomics revolution has allowed scientists to enlarge the list of tractable model systems and species, because genetic details and complete genome sequences can be obtained at lower and lower effort and cost, enabling the use of previously obscure organisms.

At the same time, the use of model systems has its drawbacks. Or as the title of a 2012 *Nature* opinion piece by developmental biologist Jessica Bolker put it, "There's More to Life than Rats and Flies." Bolker (2012) pointed out that the inadvertent selection on certain characteristics that occurs in laboratory-derived lines of animals can alter the generality of the results. As she notes, "studying only a few organisms limits science to the answers that those organisms can provide" (p. 31). Model systems can pose the risk of canalizing our thinking, so that all fish are assumed to be like sticklebacks or guppies or all flies like *Drosophila*. Taxonomic bias, in which a few groups are studied and others ignored, has become a concern among conservation biologists, who note that emphasis on charismatic megafauna can skew the perceptions of both scientists and the public. Insects and other arthropods, for instance, are often understudied and underrepresented in the conservation literature (Clark and May 2002).

Perhaps even more seriously, model systems can become more than representatives—they can be seen as the norm or the standard, with other systems (or organisms) viewed as less important variations or something to be studied once the main exemplars are understood. Such a hierarchy of study subjects can be detrimental to understanding biological variation. For example, males have been the standard experimental subject for biomedical research for over a century, whether humans or nonhuman animals were being used (Zuk 2002). Various reasons have been given for this bias, including the difficulty of controlling for female mammals' reproductive cycles or the construction of equipment for male bodies (Zuk 2002). More recently, however, scientists are beginning to realize the importance of including a more diverse range of subjects in such research (Clayton and Collins 2014; Sorge et al. 2015), in no small part because if drugs or other medical interventions are to be effective in both men and women it stands to reason that we should understand their action in both sexes. Indeed, new guidelines from the National Institutes of Health emphasize the use of both males and females in research (Clayton and Collins 2014).

In an example more closely tied to ecology and evolutionary biology, research on sexual conflict in insects has focused primarily on just a few species, including water striders (*Aquarius* spp.), bean beetles (*Callosobruchus maculatus*), and *Drosophila melanogaster* (Zuk et al. 2014). Many of the studies using these insects have revealed antagonistic coevolution between the sexes, with multiple mating leading to increased fitness for males but physical damage or reduced longevity or fecundity in females (Arnqvist and Rowe 2005). But are the results biased because of the focus on a few model systems? Similar taxonomic bias appears more generally in research on sexual selection in insects, with just three genera providing the study system for over a quarter of 363 published articles in a sample from 1989 to 1990, 1999 to 2000, and 2009 to 2010 (Zuk et al. 2014). Zuk et al. (2014) suggest that this concentration skews the perception of typical insect mating behavior toward female harm, when in reality females from many insect taxa benefit from multiple mating.

In the case of tropical biology, I argue that scientists have viewed temperate regions as a model system, the source of theory and models about ecology, evolution, and behavior. Once the basic rules were elucidated in such temperate ecosystems, scientists could move on to see how the tropics deviated from the norm. This perception has its roots in the view of the tropics as exotic that I outlined above—they were places that the prevailing scientists of the nineteenth century and prior had visited and until very recently were not the places where many scientists lived. This idea is not original—in a series of exchanges about the causes of avian clutch size variation with David Lack, the eminent tropical naturalist Alexander Skutch pointed out that if biologists had been raised in the tropics they would ask why temperate clutches were so large, not why tropical ones were so small (Skutch 1949; Stratford and Robinson 2005). Instead, the tropics are always "more diverse" or "warmer," rather than the temperate regions being "less diverse" or "cooler." In Janzen's (1967) classic article, the mountain passes are "higher." The reference point is always the temperate area, which makes the tropics seem secondary. While the source is understandable, this legacy has the potential to hamper our progress.

Biodiversity and Model Systems

The striking richness of the flora and fauna of the tropics has been a hallmark of descriptions of the region for centuries. Naturalists' notes and publications refer to the impact of such diversity on the observer with language that is nearly as florid as the descriptions themselves, from Alexander von Humboldt's "If he feel strongly the beauty of picturesque scenery, he can scarcely define the various emotions, which crowd upon his mind" (in Chazdon and Whitmore 2002, p. 36) to Connell's (1978) more terse "The great variety of species in local areas of tropical rain forests and coral reefs is legendary" (p. 1302).

This high level of biodiversity in the tropics has been substantiated many times in many different taxa, with the oft-quoted statistic of half of the world's species occurring in 7% of its area (Corlett and Primack 2010). Estimates of species numbers are still being revised upward; Slik et al. (2015) calculated that at least 40,000 and perhaps more than 53,000 tree species occur in the tropics, while just 124 are found across temperate Europe. This generalization has been important in many aspects of ecology and evolutionary biology. Studies of latitudinal diversity gradients have been key to development of theory in community ecology, leading to studies of the role of equilibrium, coexistence, and disturbance. Fischer (1960) was the first to suggest higher speciation rates in tropics (again, note the use of "higher" rather than "lower" rates elsewhere), which in turn provided fodder for many intensive studies of the nature of speciation and diversity in different parts of the world over evolutionary time (e.g., Jansson et al. 2013).

A focus on the potential for large numbers of unknown taxa in tropical regions is part of what has in turn led to recognition that old-fashioned taxonomy may still have a crucial role to play in areas ranging from medicine to biological control to conservation (Mace 2004; Smith et al. 2011). But the gap in our knowledge of what species are even present in a given habitat has other implications as well. Model systems are supposed to be representative, but what if we do not know even a substantial fraction of the taxa they are representing? The lack of information about tropical diversity makes the use of temperate species and regions as models even more problematic. Along these lines, Podos (2014) does not believe that sexual selection is different in the tropics but that "it achieves a greater range of outcomes" because of the greater diversity of habitats and the organisms living in them. Such a sentiment is likely to apply to many subfields other than sexual selection—the scope for variation given a large sample size of species in the tropics means that more evolutionary options have been explored.

In conclusion, temperate regions, for better or worse, have become our model system. This is true regardless of whether they are truly qualitatively different from the tropics, and it is not altogether bad or wrong. It is also understandable given the time lag in systematic study of tropical regions compared with that of North America and Europe and given the lack of resources available for undertaking basic research into many tropical systems. As Macedo and Machado (2014) point out, "it is naïve to assume that a centuries-old gap in scientific knowledge can be eradicated in a few years" (p. xvi). Nevertheless, seeing the tropics as normal and as much of a model of the world as the temperate regions will help expand our worldview in many ways.

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