


Do ectotherms partition thermal resources? We still do not know

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Received: 19 November 2015 / Accepted: 26 October 2016
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Abstract Partitioning of the niche space is a mechanism used to explain the coexistence of similar species. Ectotherms have variable body temperatures and their body temperatures influence performance and, ultimately, fitness. Therefore, many ectotherms use behavioral thermoregulation to avoid reduced capacities associated with body temperatures far from the optimal temperature for performance. Several authors have proposed that thermal niche partitioning in response to interspecific competition is a mechanism that allows the coexistence of similar species of ectotherms. We reviewed studies on thermal resource partitioning to evaluate the evidence for this hypothesis. In almost all studies, there was insufficient evidence to conclude unequivocally that thermal resource partitioning allowed species coexistence. Future studies should include sites where species are sympatric and sites where they are allopatric to rule out alternative mechanisms that cause differences in thermal traits between coexisting species. There is evidence of conservatism in the evolution of most thermal traits across a wide range of taxa, but thermal performance curves and preferred temperatures do respond to strong selection under laboratory conditions. Thus, there is potential for selection to act on thermal traits in response to interspecific competition. Nevertheless, more stringent tests

of the thermal resource partitioning hypothesis are required before we can assess whether it is widespread in communities of ectotherms in nature.

Keywords Character displacement · Interspecific competition · Niche partitioning · Thermal physiology

Introduction

An organism's fundamental niche is the range of conditions under which it can successfully survive and reproduce (Hutchinson 1959). Typically, only a subset of a species' fundamental niche space is occupied due, for instance, to dispersal barriers or to biotic interactions such as interspecific competition, predation, and parasitism. This occupied subset of the fundamental niche is the realized niche. The definition of niches according to resource dimensions revolutionized the fields of ecological biogeography, community ecology, and evolution in response to competition because it created a conceptual model to test hypotheses about species coexistence, competitive exclusion, and changes in niche space over time.

Resource partitioning refers to natural selection driving species that are competing with one another to diverge in resource use and eventually to occupy distinct niches (Schoener 1965, 1974). Although whether resource partitioning also refers to pre-existing differences between species that promote coexistence has been debated (Walter 1991), we retained the original definition (Schoener 1965) here and specifically refer to resource use differences that evolved in situ as a response to interspecific competition. Behavioral modifications in habitat use to reduce competition could also be considered resource partitioning, but behavioral modifications are often plastic, and

Communicated by Hannu J. Ylonen.

Electronic supplementary material The online version of this article (doi:10.1007/s00442-016-3762-7) contains supplementary material, which is available to authorized users.

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stronger evidence for resource partitioning would come from subsequent evolution of different phenotypes in response to the use of distinct habitats. Partitioning available resources allows the coexistence of previously competing species, because different species occupy different niches. Resource partitioning has often been invoked to explain the persistence of communities with very similar species (Hutchinson 1959; Martin 1988; MacArthur and Levins 1967; Chesson 2000) and as an answer to Hutchinson's (1959) famous question of why there are so many species of animals. Alternative mechanisms proposed to explain different resource use and coexistence of similar species include intraguild predation (Polis and Holt 1992) and species sorting (Cottenie 2005). Recent reviews have outlined numerous cases in which the evidence was consistent with resource partitioning in response to interspecific competition (Dayan and Simberloff 2005; Stuart and Losos 2013), but few studies have ruled out alternative mechanisms. Testing competing hypotheses that explain the coexistence of similar species remains a major challenge in ecology and evolution.

Resource (or niche) partitioning is related to character displacement, which is the observed difference in functional traits between closely related species that arise through specialization on different resources (Brown and Wilson 1956). Character displacement can be considered the phenotypic and genetic response to selective pressures that favor resource partitioning. A classic example of character displacement and resource partitioning is the evolution of different beak sizes in Darwin's finches (*Geospiza* sp.) in response to specialization on different seed sizes (Grant and Grant 2006) following the colonization by a second species of an island previously occupied by a single species. While resource partitioning can occur between any species in the same community, it is more likely to occur between closely related species because they are more likely to overlap in their fundamental niches.

Strong evidence for resource partitioning should meet Schluter and McPhail's (1992) six proposed criteria for evaluating ecological character displacement. These six proposed criteria rule out alternative mechanisms that can explain interspecific differences in resource use and in traits related to resource use. The six criteria are:

1. The pattern of resource partitioning could not have arisen by chance.
2. Interspecific phenotypic differences have arisen from evolved genetic differences.
3. The pattern of resource partitioning is the result of an evolved difference between species and not of species sorting.
4. Changes in phenotype match the changes in resource use.

5. Sites where the species occur in allopatry and in sympatry do not differ appreciably in resource availability.
6. There is evidence of competition between similar phenotypes.

Typically, research investigating resource partitioning focuses on three main niche axes: food, space, and time (Pianka 1973). While each of these niche axes can be important, they are clearly not always independent. For instance, food is usually not equally distributed in space; so, competition for food could also be perceived as competition for space. Similarly, the mechanism driving spatial resource partitioning could be competition for thermal resources. For example, partitioning of perch height (Roughgarden et al. 1981) and of structural habitat (Ruibal 1961) between anole species (*Anolis* sp.) also partitions realized body temperatures. Did competing anole species evolve different preferred body temperatures that are achieved by using different habitats, or did competing anole species evolve to use different habitats for other reasons and the differences in body temperatures are simply a by-product?

Thermal resources

Most animals (including reptiles, amphibians, fish, and arthropods) are ectotherms and, by definition, have variable body temperatures. Body temperature has a strong impact on performance (Huey and Stevenson 1979) and, ultimately, on fitness (Huey and Berrigan 2001; Halliday et al. 2015). Therefore, many ectotherms use habitat selection to maintain body temperatures that optimize performance (Huey 1991; Blouin-Demers and Weatherhead 2001). It has been suggested that species can compete for thermoregulatory opportunities if they are limited in space or in time (Magnuson et al. 1979; Tracy and Christian 1986). If species can compete for thermal resources, then thermal niche partitioning is a potential mechanism allowing the coexistence of similar species. In fact, several authors have explicitly suggested that thermal resources should be regarded as a niche dimension that ectotherms can partition and compete for (summarized in Table 1). In addition, this hypothesis could explain the large diversity of thermal traits displayed in some taxonomic groups (Labra et al. 2009; Hertz et al. 2013). But how strong is the evidence for thermal niche partitioning?

Thermal resource partitioning refers to species having evolved specialization on thermal resources to limit interspecific competition. Species can partition thermal resources spatially or temporally (Tracy and Christian 1986), but the competitive mechanism is likely not exploitative since thermal resources cannot be 'depleted' in most

Table 1 Quotes from authors suggesting that sympatric species partition thermal resources in response to interspecific competition

References	Taxon	Quote
Tracy and Christian (1986)	Ectotherms	“While there can be no competition for any particular ambient temperature (Hutchinson 1978), the time or space in which an organism can attain optimal heat exchange can be objects of competition (Magnuson et al. 1979; Mushinsky et al. 1980; Roughgarden et al. 1981)”
Crowder et al. (1981)	Fish	“The apparent partitioning of food and [thermal] habitat resources by the current Lake Michigan fish community should allow them to reduce competition”
Crowder and Magnuson (1982)	Fish	“The idea that the altered thermal distribution of alewife results from competitive interactions with bloaters is favored by existing data”
Attrill and Power (2004)	Fish	“The temporal migration pattern of fish in estuaries is therefore interpreted as a response to resource separation along the temperature axis which limits potential competition between functionally or taxonomically similar species”
Magnuson et al. (1979)	Fish	“We will argue animals compete for and partition thermal resources....Thermal niche shifts in the face of interspecific competition for preferred temperature appear supported by one laboratory study”
Roughgarden et al. (1981)	Lizards	“It is shown that the two lizard species in Grenada partition space as a resource with respect to GBTI [grey body temperature index] and that the two species in St. Kitts do not”
Buckley and Roughgarden (2005)	Lizards	“In the case of microclimate partitioning, the interaction results from the use of thermal physiology to partition habitat at multiple scales”
Melville (2002)	Lizards	“When these species occur in sympatry, <i>N. microlepidotus</i> was found to shift its habitat occupation to the heathlands, which provide less thermal opportunities”
Rummel and Roughgarden (1985)	Lizards	“The presence of <i>A. bimaculatus</i> at normal perch heights caused <i>A. watsi</i> to use perch positions with hotter microclimates and to be active at different times of day than when <i>A. bimaculatus</i> was absent.... this further establishes that there is an inverse relationship between interspecific competition and resource partitioning”
Ruibal (1961)	Lizards	“The three closely related species (<i>sagrei</i> , <i>homolechis</i> , and <i>allogus</i>) have different temperature preferences but similar perching preference. The species occupying the same thermal habitat are not closely related and differ in perching habits. It is concluded that in the evolution of the Cuban species of <i>Anolis</i> perching habits have been conservative within related species, while the thermal habitat selected (or temperature preference) has diverged”
Jenssen et al. (1984)	Lizards	“In complex anoline faunas, the occurrence of interspecific competition seems likely. On close inspection, however, it has been found that anoles diverge along a number of niche dimensions. Some basic examples are climatic habitat (differing mean body temperature as proposed by Ruibal 1961), structural habitat (differing perch height and diameter as proposed by Rand 1964), and food resource (differing prey size with covarying lizard mouth and body size as proposed by Schoener 1968)”
Losos (2009)	Lizards	“Species co-occur by partitioning climatic microhabitats. In Cuba, for example, the widespread trunk-ground anoles <i>A. sagrei</i> and <i>A. homolechis</i> co-occur throughout the island, with <i>A. sagrei</i> always using hotter and more open microhabitats than <i>A. homolechis</i> (Ruibal 1961; Hertz et al., in prep)”
Losos (2009)	Lizards	“First, sympatric anole species exhibit ecological differences. This resource partitioning generally involves differences along one of three axes of resource use: structural microhabitat, thermal microhabitat, or prey size”
Mushinsky et al. (1980)	Snakes	“When the thermal axis of the fundamental niche is considered in light of available data on the food, time, and space axes, the influence of temperature on this ectothermic community appears to be significant. In summary, we maintain that the underlying mechanism for the asynchronous daily and seasonal patterns of habitat use is specific differences in thermal niches. The two most ecologically similar species do not appear to be in competition for thermal niche space, but rather partition the thermal resource to reduce interference competition”

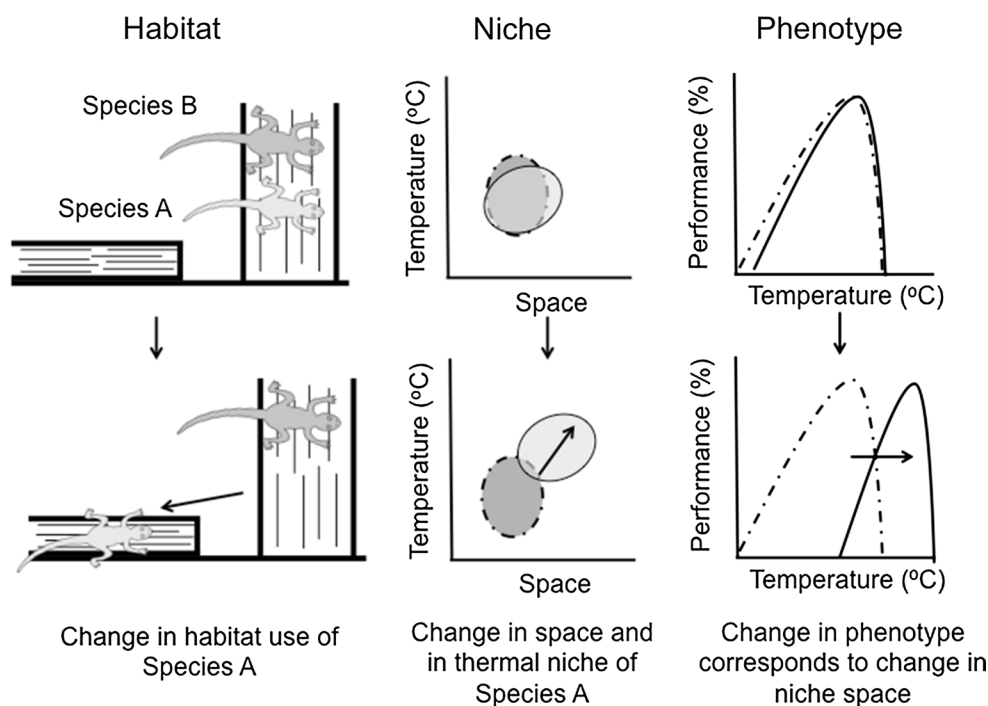
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circumstances. Instead, interference competition for thermal resources could lead to partitioning. Large temporal shifts in habitat use may not necessarily reduce exploitative competition, as demonstrated for food in diurnal

versus nocturnal predatory birds (Jaksic 1982), but it would decrease interference competition.

A hypothetical example will help illustrate how two competing species could undergo thermal resource

Fig. 1 Conceptual model for two competing lizard species that partition thermal resources and evolve phenotypes that reduce competition and allow coexistence



partitioning to reduce interspecific competition (Fig. 1). Imagine two lizard species (species A and B) that occupy forest habitats with sunny patches. Originally, both species have similar thermal traits (e.g., optimal and preferred body temperatures) and live on tree trunks where they defend small territories. Species A occupies a forest patch that is subsequently invaded by species B that is slightly larger and thus dominant in competitive interactions. Following the invasion by species B and in response to strong interspecific competition for space (access to basking sites on tree trunks to reach their optimal body temperature), species A starts occupying fallen trees in sunny patches of the forest. Interspecific interference competition is highest between individuals with the most overlap in habitat selection and in thermal preference, thus causing selective pressure for individuals of species A to diverge more towards using the warmer, fallen tree habitat. After several generations, species A evolves warmer optimal and preferred body temperatures to match the change in resource use from mostly shaded tree trunks to mostly sunny fallen trees. The presence of genetic changes in thermal traits after several generations could be verified with a common garden experiment or by demonstrating heritability of the traits along with selection differentials. In forests where species B is absent, species A still prefers cooler temperatures on tree trunks rather than sunny fallen trees, providing evidence from allopatric and sympatric sites that the change in habitat use is likely due to competition between the two species and not to alternative mechanisms. In this hypothetical example, we have competition for a resource (space to

achieve a preferred body temperature), a change in phenotype that matched the change in resource use, a genetic response of thermal traits to interspecific competition, and it is unlikely that these differences evolved by chance, because in similar forests where species B is absent, species A still occupies cooler tree trunks. Although hypothetical, this example is plausible because it is consistent with the biology of many lizard species. We can envision similar scenarios for other ectotherm communities. Plastic behavioral modifications to occupy different habitats in response to competition may alter the thermal environment a species experiences, but the strongest evidence for thermal resource partitioning would comprise the evolution of different thermal traits to match the change in habitat use. Although thermal resource partitioning is plausible and invoked (Table 1), is there evidence for this phenomenon actually occurring in ectotherm communities?

To determine how prevalent thermal resource partitioning is in ectotherm communities, we searched the Web of Science and Google Scholar databases using the terms [interspecific competition AND (thermal OR temperature)]. We retained the 22 studies in which at least two species were examined, and some aspects of sympatric competition or habitat use differences were measured in relation to thermal biology. For each study, we determined which of the six criteria proposed by Schluter and McPhail (1992) to infer character displacement were met (Table 2). Our review is complementary to that of Stuart and Losos (2013) on the strength of evidence for ecological character displacement because these authors did not consider thermal

Table 2 Summary of studies that evaluated whether species partition thermal resources indicating which of the six criteria proposed by Schluter and McPhail (1992) for character displacement are met

References	Taxon	Number of species	Some evidence of TRP?	1. Could not arise by chance	2. Genetic differences	3. Evolved differences in situ	4. Change in phenotype to match resource use	5. Allopatric and sympatric resource availability similar	6. Competition between similar phenotypes	Number of criteria met
Stuble et al. (2013)	Ants	12	N	N	N	N	N	N	N	0
Torres (1984)	Ants	8	Y	Y	N	N	Y	N	N	3
Taylor (1981)	Beetles	2	Y	Y	N	N	N	N	N	2
Helland et al. (2007)	Fish	2	Y	Y	N	Y	N	N	N	2
Brandt et al. (1980)	Fish	6	Y	Y	N	N	Y	N	N	2
Crowder et al. (1981)	Fish	5	Y	N	N	N	N	N	N	0
Crowder and Magnuson (1982)	Fish	4	Y	Y	N	N	N	Y	Y	3
Atrill and Power (2004)	Fish	16	Y	Y	N	N	Y	N	N	2
Gillis and Possai (1983)	Grasshoppers	2	Y	Y	N	N	N	N	N	2
Schoener and Gorman (1968)	Lizards	3	Y	Y	N	N	Y	N	N	2
Roughgarden et al. (1981)	Lizards	4	Y	Y	N	N	N	N	N	1
Buckley and Roughgarden (2005)	Lizards	4	Y	Y	N	N	N	N	N	1
Hertz (1992)	Lizards	2	Y	N	N	N	N	N	Y	1
Melville (2002)	Lizards	2	Y	Y	N	Y	Y	Y	Y	5
Huey and Webster (1976)	Lizards	3	Y	Y	N	N	Y	N	N	2
Salzburg (1984)	Lizards	2	Y	Y	N	N	N	Y	Y	3
Kolbe et al. (2008)	Lizards	3	Y	Y	N	N	N	N	Y	2
Hertz et al. (2013)	Lizards	62	Y	Y	N	N	N	N	N	2

Table 2 continued

References	Taxon	Number of species	Some evidence of TRP?	1. Could not arise by chance	2. Genetic differences	3. Evolved differences in situ	4. Change in phenotype to match resource use	5. Allopatric and sympatric resource availability similar	6. Competition between similar phenotypes	Number of criteria met
Rummel and Roughgarden (1985)	Lizards	2	Y	Y	N	N	N	N	Y	2
Ruibal (1961)	Lizards	5	Y	Y	N	N	Y	N	N	2
Jenssen et al. (1984)	Lizards	2	N	N	N	N	N	N	N	0
Mushinsky et al. (1980)	Snakes	5	Y	Y	N	N	N	N	N	1
Sum			20	18	4	2	7	3	6	-

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traits, even though thermal traits are of paramount importance for ectotherms, which constitute the vast majority of animal species, and even though thermal traits have been inferred to be subjected to resource partitioning (Table 1).

Of the 22 studies identified, only one met more than three of the six criteria proposed to infer character displacement (Table 2). The criteria that were met the least were criteria three (species evolved differences in situ as opposed to prior to contact) and five (resource availability is similar in sympatry and in allopatry). Meeting both of these criteria requires studying sites where species are allopatric and sites where species are sympatric, but the vast majority of studies only included sites where the species of interest occurred in sympatry. The criterion that was met the most was criterion one (difference could not have arisen by chance) since most studies demonstrated interspecific differences in thermal resource use and/or phenotype that were unlikely to have arisen by chance. On its own, however, this is weak evidence that interspecific competition caused a shift in thermal resource use and in phenotype. Most studies that tested for thermal resource partitioning failed to demonstrate that it was an evolved trait difference in response to competition. Therefore, it is possible that there is thermal resource partitioning in communities of ectotherms, but the current evidence is insufficient to rule out alternative explanations, such as species sorting according to pre-existing interspecific differences in thermal physiology. It should be noted, however, that very few examples of resource partitioning on other niche axes can pass the same six criteria (Stuart and Losos 2013).

Species could partition thermal resources by altering their habitat use in space or in time, since these are the dimensions along which thermal resources vary. Environmental temperature usually varies spatially and this provides one way by which species could partition this niche dimension. For example, Brandt et al. (1980) found evidence consistent with thermal resource partitioning in a fish community in Lake Michigan where each species occupied a different section of the thermocline. Fish species in this system tracked spatial shifts in the thermocline, suggesting that it is the thermal resource and not habitat structure (space per se) that is partitioned. Davis et al. (1998) used a laboratory thermal gradient and found that the occupied space (and thus the range of body temperatures experienced) by *Drosophila* fruit flies depended on the presence of other species. When more *Drosophila* species were present in the thermal gradient, interspecific competition compressed the realized thermal niche of each species. Although this response was due to plasticity, we would expect selective pressure on thermal traits to be strong if those competitive environments were maintained across generations. Schoener and Gorman (1968) observed differences in perch height (spatial segregation), and,

consequently, in body temperature in two sympatric *Anolis* lizards in the Lesser Antilles. Many other similar examples exist for *Anolis* assemblages on islands with circumstantial evidence of competition for and partitioning of thermal resources based on structural habitat (Schoener 1970; Lister 1976a). Although these are examples of observed differences in space use in ectotherm communities that were associated with species experiencing different body temperatures, it is unclear whether thermal resource partitioning was causing differences in space use or, alternatively, whether spatial habitat partitioning for other reasons (e.g., different food preferences) was causing differences in experienced body temperatures (see discussions in Schoener 1970; Buckley and Roughgarden 2005). In addition, these examples demonstrate a difference in resource use between species, but do not necessarily present strong evidence for competition between similar phenotypes. Finally, the observed differences in thermal resource use may not have evolved in situ in response to interspecific competition because habitat use could be plastic or because distinct habitat use could have evolved before species came in contact for reasons other than interspecific competition.

Thermal resources could also be partitioned temporally. Kronfeld-Schor and Dayan (2003) suggested that time is an ecological resource, but like space, the actual resource for which individuals are competing could be temperature. Similar to temperature, time cannot be consumed and depleted by organisms, but interference competition could cause species to be active at different times. There are several examples of ectotherms using the same space at different times with different experienced body temperatures. Pianka (1973) described how different North American flatland lizard species emerge at different times, and how this is associated with different realized body temperatures. Attrill and Power (2004) found evidence for temporal partitioning of temperature in an estuarine fish community. Fish species that overlapped more in niche axes other than temperature (e.g., food) were more likely to partition thermal resources temporally. Like spatial partitioning of thermal resources, temporal partitioning of thermal resources could be driven by differences in temperature preference or result from competition over another resource that results in observed differences in body temperature because of different activity times (Jaksic 1982).

Can thermal physiology evolve in response to competition?

An important question for determining whether thermal resource partitioning could occur is whether thermal physiology could evolve rapidly in response to interspecific competition. There are several examples of thermal

performance curves or of preferred body temperatures that have evolved within a taxonomic group (van Berkum 1986; Labra et al. 2009; Hertz et al. 2013). The preferred body temperature of individuals is heritable in some species, although only maternally in at least one lizard (Paranjpe et al. 2013). In addition, selection can act on thermal performance curves even when the temperatures experienced by populations vary significantly within a single generation (Kingsolver and Gomulkiewicz 2003; Logan et al. 2014). On the other hand, there also appears to be considerable conservatism in thermal trait evolution, especially for critical thermal maxima (Araújo et al. 2013; Grigg and Buckley 2013). Strong selection imposed under laboratory conditions can increase population mean values for thermal traits, but upper thermal limits appear largely constrained (Gilchrist and Huey 1999). Another potential limitation to the evolution of thermal traits is the observation that individuals that experience higher body temperatures have higher reproductive outputs (Angilletta 2001; Du et al. 2005; Meiri et al. 2012). Species with higher optimal temperatures also have higher intrinsic rates of population increase (Savage et al. 2004; Frazier et al. 2006). Therefore, it may be unlikely for species to evolve a decreased optimal temperature if it decreases reproductive output of individuals. Although the degree to which species can evolve differences in thermal physiology depends on phylogeny, it appears that some aspects of thermal biology are heritable and respond to selection (Angilletta et al. 2002). Therefore, the available evidence suggests that thermal physiology traits could respond to selection in response to interspecific competition, but responses could potentially be small due to physiological limits on the upper critical thermal maxima. In addition, there are currently no documented examples of natural populations evolving differences in thermal traits in response to interspecific competition.

Alternative explanations and designing stronger tests

Moving forward with our understanding of thermal resource partitioning will require ruling out alternative explanations for observed differences in thermal resource use in communities of ectotherms. This will require disentangling the roles of space, time, and temperature in delineating the realized niches of coexisting species. Temperature varies spatially and changes in time, so observed differences in body temperature can be driven by species competing for thermal resources across space and time, or by species competing directly for space and time for reasons other than temperature (e.g., food). Also, any observed differences in body temperature could be a secondary consequence of competition for another resource that is correlated with temperature.

Careful experiments will have to be designed to disentangle what is the mechanism of competition and what resource are animals actually competing for. If there is no way to disentangle the effects of these factors experimentally, then does testing for thermal resource partitioning improve our ability to predict resource use, divergence in phenotype, and community diversity in natural systems? We believe so, because if thermal resource partitioning is common in communities of ectotherms, it would generate testable predictions about community size, competition, and diversification based on the extent of thermal habitat heterogeneity in an ecosystem. For instance, we would predict ecosystems with more thermal habitat heterogeneity to harbor larger communities and to exhibit higher speciation rates.

Because of the current lack of strong evidence for the existence, or for the absence, of thermal resource partitioning in nature, what can make tests of the thermal resource partitioning hypothesis stronger? Stronger evidence would come from passing all six criteria suggested for character displacement (Schluter and McPhail 1992), but this limits strong inference to systems with a known and recent evolutionary history. The most common weakness of studies reviewed in this essay is that potentially competing species were studied only at sites where the species occurred in sympatry. The addition of study sites where potentially competing species occur in allopatry would allow ruling out the alternative mechanisms of species sorting and of evolution in response to different resource availabilities. For example, using islands with different species assemblages can provide evidence for competitive release or niche shifts in response to interspecific competition (Lister 1976a, b). In addition, range expansions of similar species that create new contact zones, such as following invasions, provide good systems to design more stringent tests of the thermal resource partitioning hypothesis, because such expansions provide allopatric and sympatric situations before and after contact with a competing species. For example, both brown anoles (*Anolis sagrei*) and cane toads (*Rhinella marina*) have multiple expanding introduced range fronts where they are coming in contact with similar species that are potential competitors (Kolbe et al. 2004; Urban et al. 2007). Can we document thermal niche shifts in native species before and after the arrival of the introduced competitor? Another line of evidence may come from laboratory or semi-natural experiments where the number of competitor species can be manipulated to observe population responses over several generations. Experiments also provide the ability to manipulate space, time, and temperature to tease apart whether phenotypic differences in thermal traits are a cause or a consequence of shifts in resource use along other niche axes. For instance, experiments could be designed in which thermal environments and the number of competing

species present are manipulated in ants of the genera *Iridomyrmex* and *Melophorus*. These ants occupy a wide range of thermal niches and are aggressive towards other species (Morton and Davidson 1988; Walters and Mackay 2004).

Conclusion

Schoener's (1974) paper on resource partitioning in communities concluded with several important questions for future work that included asking what dimensions of the niche are important, divisible, and likely to be influencing competition. The food axis has dominated in the literature on competition and niche theory. Thermal resource partitioning has received much less attention, likely because of the difficulty in conceptualizing competition for it, despite the clear effect body temperature has on fitness in ectotherms. It is plausible that thermal resource partitioning in ectotherms is widespread considering how important body temperature is to their performance and fitness, considering the large spatial and temporal variation in thermal environments (especially in terrestrial systems), and considering the large community sizes of many ectotherms. Despite many authors invoking thermal resource partitioning as a mechanism for reducing interspecific competition (Table 1), we believe there is currently insufficient empirical evidence to indicate that it occurs, because alternative mechanisms have generally not been ruled out and evidence of genetic responses to selection on thermal traits is lacking for natural populations. Stronger observational or experimental tests that can disentangle the effects of temperature, space, and time and where potentially competing species are studied in allopatry and in sympatry are required before we can determine whether thermal resource partitioning is a common mechanism allowing species coexistence. Do species shift their thermal niche in response to interspecific competition? We still do not know.

Author contribution statement JEP and GBD conceived the study. JEP designed and executed the study. JEP and GBD wrote the manuscript.

References

- Angilletta MJ (2001) Thermal and physiological constraints on energy assimilation in a widespread lizard (*Sceloporus undulatus*). *Ecology* 82:3044–3056
- Angilletta MJ, Niewiarowski PH, Navas CA (2002) The evolution of thermal physiology in ectotherms. *J Therm Biol* 27:249–268. doi:[10.1016/S0306-4565\(01\)00094-8](https://doi.org/10.1016/S0306-4565(01)00094-8)
- Araújo MB, Ferri-Yáñez F, Bozinovic F et al (2013) Heat freezes niche evolution. *Ecol Lett* 16:1206–1219. doi:[10.1111/ele.12155](https://doi.org/10.1111/ele.12155)
- Attrill MJ, Power M (2004) Partitioning of temperature resources amongst an estuarine fish assemblage. *Estuar Coast Shelf Sci* 61:725–738. doi:[10.1016/j.eccs.2004.07.010](https://doi.org/10.1016/j.eccs.2004.07.010)

- Blouin-Demers G, Weatherhead PJ (2001) Thermal ecology of black rat snakes (*Elaphe obsoleta*) in a thermally challenging environment. *Ecology* 82:3025–3043
- Brandt B, Magnuson J, Crowder LB (1980) Thermal habitat partitioning by fishes in Lake Michigan. *Can J Fish Aquat Sci* 37:1557–1564
- Brown WL, Wilson EO (1956) Character displacement. *Syst Zool* 5:49–64
- Buckley LB, Roughgarden J (2005) Lizard habitat partitioning on islands: the interaction of local and landscape scales. *J Biogeogr* 32:2113–2121. doi:10.1111/j.1365-2699.2005.01340.x
- Chesson P (2000) Mechanisms and maintenance of species diversity. *Annu Rev Ecol Syst* 31:343–358
- Cottenie K (2005) Integrating environmental and spatial processes in ecological community dynamics. *Ecol Lett* 8:1175–1182. doi:10.1111/j.1461-0248.2005.00820.x
- Davis AJ, Jenkinson LS, Lawton JH (1998) Making mistakes when predicting shifts in species range in response to global warming. *Nature* 391:783–786
- Dayan T, Simberloff D (2005) Ecological and community-wide character displacement: the next generation. *Ecol Lett* 8:875–894. doi:10.1111/j.1461-0248.2005.00791.x
- Du WG, Lu YW, Shen JY (2005) The influence of maternal thermal environments on reproductive traits and hatchling traits in a Lacertid lizard, *Takydromus septentrionalis*. *J Therm Biol* 30:153–161. doi:10.1016/j.jtherbio.2004.09.005
- Frazier MR, Huey RB, Berrigan D (2006) Thermodynamics constrains the evolution of insect population growth rates: “warmer is better”. *Am Nat* 168:512–520. doi:10.1086/506977
- Gilchrist GW, Huey RB (1999) The direct response of *Drosophila melanogaster* to selection on knockdown temperature. *Heredity* (Edinb) 83:15–29. doi:10.1038/sj.hdy.6885330
- Grant PR, Grant BR (2006) Evolution of character displacement in Darwin’s finches. *Science* 313:224–226. doi:10.1126/science.1128374
- Grigg JW, Buckley LB (2013) Conservatism of lizard thermal tolerances and body temperatures across evolutionary history and geography. *Biol Lett* 9:20121056. doi:10.1098/rsbl.2012.1056
- Halliday WD, Thomas AS, Blouin-Demers G (2015) High temperature intensifies negative density dependence of fitness in red flour beetles. *Ecol Evol* 5:1061–1067. doi:10.1002/ece3.1402
- Hertz PE, Arima Y, Harrison A et al (2013) Asynchronous evolution of physiology and morphology in *Anolis* lizards. *Evolution* 67:2101–2113. doi:10.1111/evo.12072
- Huey RB (1991) Physiological consequences of habitat selection. *Am Nat* 137:S91–S115
- Huey RB, Berrigan D (2001) Temperature, demography, and ectotherm fitness. *Am Nat* 158:204–210
- Huey R, Stevenson RD (1979) Integrating thermal physiology and ecology of ectotherms: a discussion of approaches. *Am Zool* 19:357–366
- Hutchinson GE (1959) Homage to Santa Rosalia or why are there so many kinds of animals? *Am Nat* 93:145–159
- Jaksic FM (1982) Inadequacy of activity time as a niche difference: the case of diurnal and nocturnal raptors. *Oecologia* 52:171–175
- Kingsolver JG, Gomulkiewicz R (2003) Environmental variation and selection on performance curves. *Integr Comp Biol* 47:470–477
- Kolbe JJ, Glor RE, Rodríguez Schettino L et al (2004) Genetic variation increases during biological invasion by a Cuban lizard. *Nature* 431:177–181. doi:10.1038/nature02807
- Kronfeld-Schor N, Dayan T (2003) Partitioning of time as an ecological resource. *Annu Rev Ecol Syst* 34:153–181. doi:10.1146/132435
- Labra A, Pienaar J, Hansen TF (2009) Evolution of thermal physiology in *Liolaemus* lizards: adaptation, phylogenetic inertia, and niche tracking. *Am Nat* 174:204–220. doi:10.1086/600088
- Lister BC (1976a) The nature of niche expansion in West Indian *Anolis* lizards II: evolutionary components. *Evolution* 30:677–692
- Lister BC (1976b) The nature of niche expansion in West Indian *Anolis* lizards I: ecological consequences of reduced competition. *Evolution* 30:659–676
- Logan ML, Cox RM, Calsbeek R (2014) Natural selection on thermal performance in a novel thermal environment. *Proc Natl Acad Sci USA* 111:14165–14169. doi:10.1073/pnas.1404885111
- MacArthur R, Levins R (1967) The limiting similarity, convergence, and divergence of coexisting species. *Am Nat* 101:377–385
- Magnuson JJ, Crowder LB, Medvick PA (1979) Temperature as an ecological resource. *Am Zool* 34:331–343
- Martin TE (1988) On the advantage of being different: nest predation and the coexistence of bird species. *Proc Natl Acad Sci USA* 85:2196–2199. doi:10.1073/pnas.85.7.2196
- Meiri S, Brown JH, Sibly RM (2012) The ecology of lizard reproductive output. *Glob Ecol Biogeogr* 21:592–602. doi:10.1111/j.1466-8238.2011.00700.x
- Morton SR, Davidson DW (1988) Comparative structure of harvester ant communities in arid Australia and North America. *Ecol Monogr* 58:19–38. doi:10.2307/1942632
- Paranjpe DA, Bastiaans E, Patten A et al (2013) Evidence of maternal effects on temperature preference in side-blotched lizards: implications for evolutionary response to climate change. *Ecol Evol* 3:1977–1991. doi:10.1002/ece3.614
- Pianka ER (1973) The structure of lizard communities. *Annu Rev Ecol Syst* 1973:53–74
- Polis GA, Holt RD (1992) Intraguild predation: the dynamics of complex trophic interactions. *Trends Ecol Evol* 7:151–154. doi:10.1016/0169-5347(92)90208-S
- Roughgarden J, Porter W, Heckell D (1981) Resource partitioning of space and its relationship to body temperature in *Anolis* lizard populations. *Oecologia* 50:256–264
- Ruibal R (1961) Thermal relations of five species of tropical lizards. *Evolution* 15:98–111
- Savage VM, Gillooly JF, Brown JH et al (2004) Effects of body size and temperature on population growth. *Am Nat* 163:429–441. doi:10.1086/381872
- Schluter D, McPhail JD (1992) Ecological character displacement and speciation in sticklebacks. *Am Nat* 140:85–108
- Schoener TW (1965) The evolution of bill size differences among sympatric congeneric species of birds. *Evolution* 19:189–213
- Schoener TW (1970) Nonsynchronous spatial overlap of lizards in patchy habitats. *Ecology* 51:408–418
- Schoener TW (1974) Resource partitioning in ecological communities. *Science* 185:27–39
- Schoener TW, Gorman GC (1968) Some niche differences in three Lesser Antillean lizards of the genus *Anolis*. *Ecology* 49:819–830
- Stuart YE, Losos JB (2013) Ecological character displacement: glass half full or half empty? *Trends Ecol Evol* 28:402–408. doi:10.1016/j.tree.2013.02.014
- Tracy RC, Christian KA (1986) Ecological relations among space, time, and thermal niche axes. *Ecology* 67:609–615
- Urban MC, Phillips BL, Skelly DK, Shine R (2007) The cane toad’s (*Chaunus [Bufo] marinus*) increasing ability to invade Australia is revealed by a dynamically updated range model. *Proc Biol Sci* 274:1413–1419. doi:10.1098/rspb.2007.0114
- van Berkum F (1986) Evolutionary patterns of the thermal sensitivity of sprint speed in *Anolis* lizards. *Evolution* 40:594–604
- Walter GH (1991) What is resource partitioning? *J Theor Biol* 150:137–143. doi:10.1016/S0022-5193(05)80327-3
- Walters AC, Mackay DA (2004) Comparisons of upper thermal tolerances between the invasive Argentine ant (Hymenoptera: Formicidae) and two native Australian ant species. *Ann Entomol Soc Am* 97:971–975. doi:10.1603/0013-8746(2004)097[0971:COU-TB]2.0.CO;2