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If you can't stand the heat, stay out of the city: Thermal reaction norms of chitinolytic fungi in an urban heat island

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Abstract

Elevated soil and air temperatures in urban heat islands have been exerting evolutionary pressure on organisms for decades in some cities. We measured thermal reaction norms (18–26 °C) for growth rate of four species of common chitinolytic fungi from an oak forest in an urban heat island and a corresponding rural area. Urban isolates of *Chrysosporium pannorum* and *Trichoderma koningii* grew faster than rural isolates at 26 °C, but grew slower than rural isolates at 18 °C. Urban isolates of *Torulomyces lagena* and *Penicillium bilaii* grew as fast or faster than rural isolates at all temperatures. These differences in thermal reaction norms between urban and rural isolates suggest that urbanization has caused both thermal specialization and counter-gradient variation in the fungal community.

Keywords: Chitinolytic fungi; Growth rate; Microfungi; Temperature; Urban heat island

1. Introduction

For most organisms, growth proceeds best over a relatively narrow range of temperatures and is greatly retarded outside of this range (Brett, 1979; Huey and Stevenson, 1979). The temperatures that enable relatively rapid growth can vary among genotypes, and natural selection is expected to favor particular variants given spatial and temporal patterns of environmental temperature (reviewed by Angilletta et al., 2002). Theory on the evolution of thermal reaction norms for physiological performance, such as growth rate, is based on the assumptions that (1) performance contributes additively to fitness and (2) a trade-off exists between performances at different temperatures. Based on these assumptions, this theory predicts that thermal specialists will outperform thermal generalists under most patterns of environmental variation. Thus, organisms should tolerate a wide range of environmental conditions (via diapause, hibernation, dormancy, etc.), but should restrict growth to specific environmental conditions. In fact, generalists are only expected to outperform specialists when the environmental temperature is relatively stable within generations but varies among generations (Gilchrist, 1995).

The relatively recent urbanization of our planet has created rapid changes in climate that are particularly challenging for ectothermic organisms. Over the past 100 years, air and soil temperatures have been increasing in urban areas compared to their surroundings, a phenomenon that is known as the urban "heat-island" effect. Causes include both the greater absorption of heat by pavement and buildings, and the greater

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production of heat by air conditioners, traffic and factories in urban areas. Typically, urban heat islands are characterized by greater minimal, mean and maximal temperatures (Balling and Brazel, 1987; Karl et al., 1988; Brazel et al., 2000; Tereschenko and Filonov, 2001). For example, in urban Baltimore, the minimal and maximal monthly air temperatures have increased by 5 and 2 °C, respectively, relative to those of a comparable rural area (Brazel et al., 2000). While the daily minima and maxima have slowly shifted upwards in urban areas, diurnal and seasonal variations in temperature have remained large; hence the range of temperatures experienced by organisms has increased in urban environments. Urban heat islands have been exerting an evolutionary pressure on organisms for at least 50 years, and for more than 100 years in some cities.

Fungi that inhabit soil are useful subjects for assessing the evolutionary consequences of urbanization for the thermal physiology of ectotherms. Fungi cannot thermoregulate, and are thus subject to the full range of temperatures observed in soil. As assumed by theory, the growth of fungi seemingly contributes additively to fitness because fungi can enter dormant or inactive phases during unfavorable conditions. Furthermore, many species occur in both urban and rural environments, enabling intraspecific comparisons of thermal reactions norms in a suite of species. Given the gradual increase in temperatures that has been associated with urbanization, we expect that fungi have begun to adapt to the warmer conditions of urban soils. One of two responses of thermal physiology to urbanization is anticipated (Fig. 1). First, a species can shift its thermal optimum for growth rate toward higher temperatures, resulting in specialists for high and low temperatures in urban and rural soils, respectively (see Huey and Kingsolver, 1993). Alternatively, a species can increase its growth rate at all temperatures, resulting in patterns called counter-gradient variation in growth rate (see Conover and Schultz, 1995). Both responses have been observed in ectothermic animals, particularly in response to adaptation to colder environments (Angilletta et al., 2002; Yamahira and Conover, 2002). Since each of these strategies involves different mechanisms and imposes different tradeoffs (Angilletta et al., 2003), one might expect both responses to have occurred in diverse ecological communities, such as organisms inhabiting soil.

To begin to understand thermal adaptation of fungal communities in soil, we measured thermal reaction norms for growth rate of four species of fungi from an oak forest in an urban heat island and a corresponding rural area. Previous studies of fungi in natural environments have provided abundant evidence that the active fungal community depends on thermal conditions (e.g., Bissett and Parkinson, 1979; Widden, 1986; Carreiro and Koske, 1992a, b). Fungi present in extreme environments, including those found on refrigerated or frozen food, are often specialized for activity or growth at relatively low or high temperatures (Hesseltine and Anderson, 1957; Tansey and Brock, 1972; Chapman, 1974; Ivarson, 1974; Palmer, et al., 1987; Carreiro and Koske, 1992c; Smith, 1993; Tibbett et al., 1998). However, our study is unique in that we examine thermal adaptation in a suite of sympatric species that share a common resource.

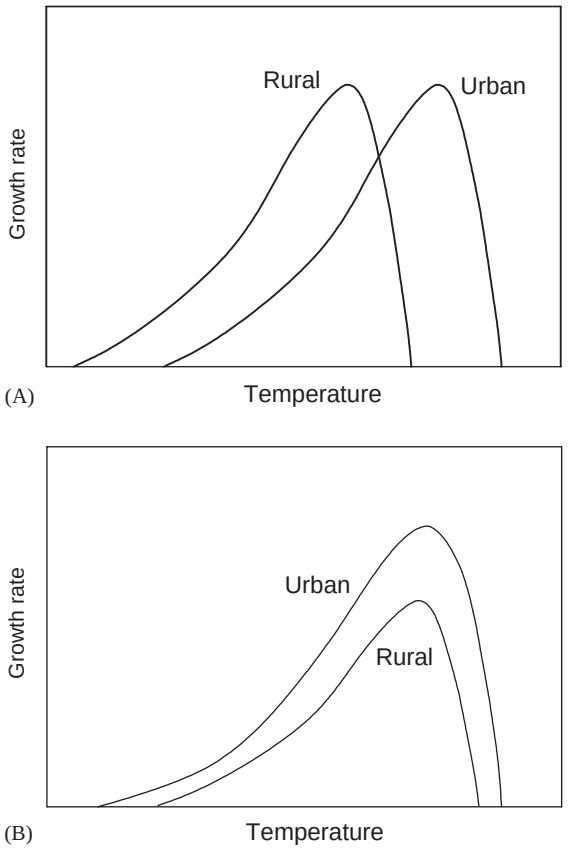

Fig. 1. Thermal adaptation along gradients of urbanization could result in either of two patterns: thermal specialization and counter-gradient variation. (A) Natural selection could produce urban genotypes that grow faster than rural genotypes at high temperatures but slower than rural genotypes at low temperatures (thermal specialization). (B) Natural selection could produce urban genotypes that grow faster than rural genotypes at all temperatures (counter-gradient variation).

2. Materials and methods

2.1. Experimental sites

Fungi were isolated from a rural and an urban oak forest with similar vegetation, slope, aspect, and soils

(M. M. Carreiro, unpublished data). The rural site was in Bernheim Arboretum and Research Forest in Clermont, KY, 30 miles south of Louisville, KY. The urban site was in Iroquois Park, Louisville, KY. These sites were chosen to be as similar as possible in terms of soil characteristics, including texture, bulk density, pH, % organic matter content, nitrogen and phosphorous content, and C:N ratio. These sites also had similar coverages of *Quercus* spp., ground flora and exotic plants. However, the two sites differed in their matrix land use (developed land and road length within radii of 2 km), population densities and environmental temperatures. During a 2-week period in July of 2002, temperatures of these sites differed according to our expectations (M. M. Carreiro, unpublished data). Mean daily temperature at the soil surface was 1 °C higher in the urban forest than it was in the rural forest. Moreover, the urban forest exhibited a greater range of temperatures at the surface of the soil (16.8 vs. 12.8 °C) and at a depth of 10 cm (9.2 vs. 3.7 °C).

2.2. Fungal isolations

On 5 October 2002, we took ten soil cores from each site. The cores (2.5 cm in diameter × 10 cm in depth) were taken at 2–5 m intervals within an area of 2500 m^2. Soil from each site was combined in a ziploc bag and transported to the laboratory in a cooler. In the laboratory, samples were stored overnight at 4 °C and fungi were isolated from these samples the following day. A washing technique was used to remove spores and permit isolation of active hyphae (Parkinson, 1994). Samples were sieved to 4 mm and a 0.5 g subsample was placed in a 100 ml bottle with 50 ml of deionized water. The samples were washed 30 times; previous experiment had shown this to be the optimum number of washings (K. S. Williams, unpublished data). During each washing, samples were shaken for 2 min on a wrist-action shaker, the water was poured off through a 45 μm sieve, and fresh water was added. After washing, particles of soil (160–250 μm size fraction) from each site were plated on chitin medium (2 g L^{-1}, Hsu and Lockwood, 1975) plus antibiotics (0.1% streptomycin + 0.05% aureomycin). One hundred plates from each site were incubated at each of three temperatures (4, 15 and 30 °C) to obtain chitinolytic fungi that were active over a broad range of temperatures. Chitin medium is semi-opaque, and a zone of clearing is seen around the colony when fungi degrade the chitin. Chitinolytic fungi (i.e., those showing a cleared zone around the colony) isolated from both sites at one or more temperatures were used in the following experiments. These fungi included *Penicillium bilaii* (Chalabuda), *Trichoderma koningii* (*sensu* Rifai), and *Torulomyces lagena* (Delitsch) isolated at 15 °C, and *Chrysosporium pannorum* (Link) isolated at both 4 and 15 °C.

2.3. Experiment I: Thermal sensitivity of growth

The first experiment was conducted to quantify the thermal sensitivity of growth of each fungal isolate. We selected a range of temperatures that encompassed the mean soil temperature in the summer at these sites. Prior to the experiment, each isolate was pure-cultured onto chitin medium and maintained at the isolation temperature until use in the experiment. Twenty replicate plates of each fungal isolate were incubated at each of the following temperatures: 18, 20, 22, 24, and 26 °C. After 7 days of growth, the diameter of the colonies was measured to the nearest ± 0.5 mm with a digital caliper, with the exception of isolates of *T. koningii*. Since *T. koningii* filled the plates within 7 days, it was measured after 2 days.

2.4. Experiment II: Thermal sensitivity of acquisition and growth efficiency

Since growth is limited by the acquisition of resources and the efficiency with which these resources are metabolized, we conducted a second experiment to quantify rates of chitinolytic activity and resource acquisition. A practical measure of resource acquisition is the diameter of the cleared zone in the semi-opaque medium. *C. pannorum* was chosen for use in this experiment because its zone is clearly defined and develops relatively rapidly. For each site and isolation temperature, 15 plates were incubated at each of the five temperatures used in Experiment I. To allow zones to clear completely through the depth of the agar, growth and cleared zones were measured after 25 days.

2.5. Statistical analyses

In both experiments, we were interested primarily in the difference in thermal reaction norms between urban and rural sites within each species. Therefore, we used a General Linear Model to examine the main effects of site and incubation temperature (T_{inc}) on growth rate (G) of each species and the interaction between site and incubation temperature: $G = \mu + \text{Site} + T_{inc} + (\text{Site} \times T_{inc}) + \in$. Because *C. pannorum* was isolated at 4 and 15 °C; we used a model for this species that included the main effect of isolation temperature (T_{iso}): $G = \mu + \text{Site} + T_{isol} + T_{inc}(T_{isol}) + (\text{Site} \times T_{inc}) + \in$. A significant interaction between site and incubation temperature would indicate variation in the thermal reaction norm resulting from thermal specialization by fungi in rural and urban sites. In the absence of an interaction, a significant main effect of site would indicate either a co-gradient or a counter-gradient variation in growth rate between fungi from rural and urban sites.

We used a similar model to analyze data from Experiment II, except that cleared zone was used as a covariate. By adjusting growth rates by the size of the cleared zone, we were able to determine whether differences in growth rate between isolates reflected differences in the efficiency of growth or merely differences in the rates of resource acquisition. A significant effect of site in this analysis would suggest a difference in growth efficiency between isolates from urban and rural sites. All analyses were performed with Statistica 6.0 (StatSoft, Inc., 2003).

3. Results

3.1. Experiment I: Thermal sensitivity of growth

As predicted, thermal reaction norms for growth rate differed between isolates from urban and rural sites (Table 1). Two of the four species exhibited patterns that are consistent with our prediction that urban isolates would have specialized for growth at higher temperatures than rural isolates; urban isolates of *T. koningii* and *C. pannorum* grew faster than rural isolates at 26 °C, but grew slower than rural isolates at 18 °C (Fig. 2). In some cases, the exact value of the thermal optimum could not be distinguished with certainty because it was either equal to or greater than the highest temperature in our experiment. However, we presume that thermal adaptation involved divergence in thermal optima when reaction norms for urban and rural isolates crossed at an intermediate temperature (see Fig. 1). The other two species exhibited patterns that are consistent with either co-gradient or counter-gradient variation in growth rate. In *T. lagena*, isolates from urban sites grew faster than those from rural sites at all five incubation temperatures. In *P. bilaii*, isolates from urban sites grew faster than those from rural sites at 20 and 24 °C, and equally fast at the other incubation temperatures. Since we do not know whether the growth rate of fungi at the urban site is higher or lower than that of fungi at the rural site, we cannot determine whether this variation was co-gradient or counter-gradient. We isolated samples of *C. pannorum* from urban and rural sites at both 4 and 15 °C, and samples isolated at 4 °C grew faster at all incubation temperatures than those isolated at 15 °C (Fig. 3).

3.2. Experiment II: Thermal sensitivity of acquisition and growth efficiency

The patterns of growth exhibited by *C. pannorum* in Experiments I and II were similar (see Tables 1 and 2). Urban isolates grew faster than rural isolates at 26 °C, but grew slower than the rural isolates at 18 °C. Also, isolates from 4 °C grew more quickly at all incubation temperatures than those from 15 °C. Much of the variation in growth was explained by the rate of resource acquisition, as growth was significantly related to the diameter of cleared zone. However, differences in growth between rural and urban isolates, as well as differences between isolates from 4 and 15 °C, resulted partly from variation in the efficiency of growth because these patterns persisted even after adjusting growth for the diameter of cleared zone (Table 2, Fig. 4).

Table 1
Results of Generalized Linear Models describing the effects of site, isolation temperature (for *C. pannorum*), and incubation temperature on the growth of four species of chitinolytic fungi

Species/effect	Degrees of freedom	MS	*F*	*P*
Chrysosporium pannorum				
Site	1	15.0	8.5	0.0038
Isolation temperature (site)	2	654.7	369.0	0.0000
Incubation temperature	4	170.0	95.9	0.0000
Site × incubation temperature	4	116.7	65.8	0.0000
Penicillium bilai				
Site	1	50.0	22.5	0.0000
Incubation temperature	4	844.4	380.8	0.0000
Site × incubation temperature	4	8.4	3.8	0.0058
Torulomyces lagena				
Site	1	95.6	49.5	0.0000
Incubation temperature	4	151.4	78.4	0.0000
Site × incubation temperature	4	4.9	2.5	0.0456
Trichoderma koningii				
Site	1	516.4	14.1	0.0002
Incubation temperature	4	5895.3	161.5	0.0000
Site × incubation temperature	4	333.2	9.1	0.0000

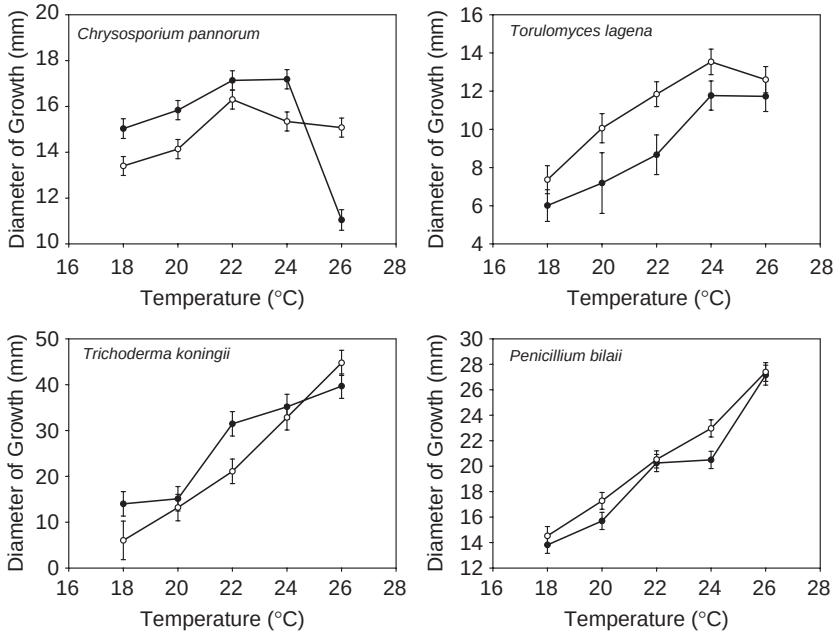

Fig. 2. Thermal reaction norms for growth rate in four species of chitinolytic fungi: *Chrysosporium pannorum*, *Penicillium bilaii*, *Torulomyces lagena* and *Trichoderma koningii*. Urban isolates of *C. pannorum* and *T. koningii*, grew faster than rural isolates at 26 °C, but grew slower than rural isolates at 18 °C. In *P. bilaii* and *T. lagena*, urban isolates grew as fast or faster than rural isolates at all incubation temperatures. Filled circles (●) represent rural isolates, and open circles (○) represent urban isolates. Error bars denote 95% confidence intervals.

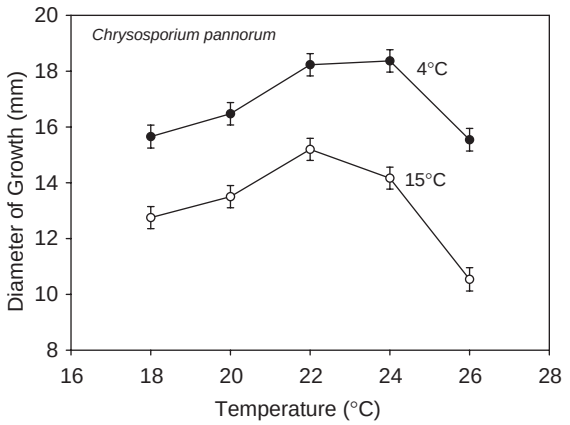

Fig. 3. At all incubation temperatures, growth of 4 °C *Chrysosporium pannorum* isolates was faster than that of 15 °C isolates. Error bars denote 95% confidence intervals.

Table 2
Results of the Generalized Linear Model describing the effects of site, isolation temperature, and temperature on the growth of *Chrysosporium pannorum*

Effect	Degrees of freedom	MS	*F*	*P*
Cleared zone	1	5231.8	684.3	0.0000
Site	1	52.8	6.9	0.0089
Isolation temperature (Site)	4	1285.3	168.1	0.0000
Incubation temperature	4	318.0	41.6	0.0000
Site × Incubation temperature	4	79.3	10.4	0.0000

4. Discussion

Based on the historical increase in the mean and variance of soil temperature in urban environments, we hypothesized that fungi from our urban site would exhibit different thermal reaction norms than those from our rural site; specifically, we thought that fungi from the urban site would exhibit higher thermal optima for growth than fungi from the rural site. Ideally, we would evaluate this hypothesis by directly comparing the thermal optima of these fungi. For *C. pannorum*, we were able to distinguish the thermal optimum of rural isolates (22 °C; see Fig. 2), which was within the range of values reported previously for this species (Azmi and Seppelt, 1997; Domsch et al., 1993). In the other cases, however, we were unable to determine thermal optima

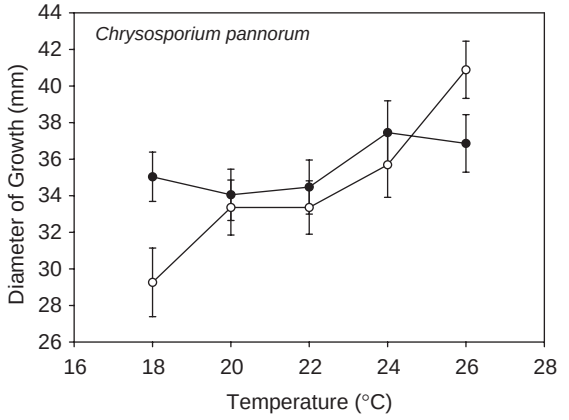

Fig. 4. The growth of *Chrysosporium pannorum* differed between urban and rural isolates even after growth was adjusted for the rate of acquisition (estimated by the diameter of cleared zone). Adjusted growth rates are the residuals of growth rate when regressed onto the diameter of cleared zone. Filled circles (●) represent rural isolates, and open circles (○) represent urban isolates. Error bars denote 95% confidence intervals.

because we only examined growth at temperatures within the range of daily mean temperatures experienced during the summer. In most cases, growth rate was maximal at the highest temperature used in our experiment (26 °C), indicating that the thermal optimum for growth was equal to or greater than this temperature. Because thermal reaction norms for growth rate are generally unimodal (Huey and Stevenson, 1979; Huey and Kingsolver, 1993; Angilletta et al., 2002), we were able to use the main effect of site and the interaction between the effects of site and incubation temperature to assess significant differences in the shape and position of thermal reaction norms between urban and rural isolates. For example, a crossing of thermal reaction norms reflects different abilities of urban and rural isolates to grow at thermal extremes. Furthermore, our measures are ecologically relevant because the thermal extremes in our experiment corresponded to the extreme daily mean temperatures observed in the natural environments.

Interestingly, four fungal species using the same resource—chitin, have apparently responded to increased temperature in the urban site in two different ways. Two of the species appear to have undergone divergences in thermal optima for growth rate between urban and rural populations. The other two species appear to have evolved patterns of co-gradient or counter-gradient variation in growth rate, depending on the patterns of growth that exists in the two natural environments. In both cases, though, the difference in thermal reaction norms suggests that fungi in the urban environment have acquired physiological adaptations that enhance growth at high temperatures relative to fungi in the rural environment. These differences are probably the result of genetic divergences rather than adaptive phenotypic plasticity because fungi from urban and rural sites were maintained in a common environment through several transfers before being used in the experiment. Adaptation might have been caused by the gradual increase in both the mean and the variance of environmental temperature in the urban site.

Thermal adaptation of soil fungi is similar to that observed in other ectothermic organisms. Comparative studies of invertebrates (e.g. fish, amphibians, and reptiles) suggest that both thermal specialization and counter-gradient variation in growth rate are common (reviewed by Conover and Schultz, 1995; Angilletta et al., 2002). As with *C. pannorum*, both higher rates of acquisition and higher efficiencies of growth account for the faster growth of some genotypes relative to others (Angilletta et al., 2003). Natural selection in laboratory experiments has been used to demonstrate that environmental temperature can cause patterns like those documented by comparative studies. For example, Bennett et al. (1992) exposed *Escherichia coli* to different mean temperatures for 2000 generations, and noted that the selected lines had a higher fitness relative to the ancestral lines with the difference in fitness being greatest at their selected temperature.

For the two species that exhibited intraspecific divergence in the thermal optimum for growth rate, the mechanism of thermal adaptation probably involved changes in the activities of chitinolytic enzymes. Chitin, the (1–4)-β-linked homopolymer of *N*-acetyl-D-glucosamine, is a complex substrate that is cross-linked to wall components such as β-glucans and proteins in fungi and insects, respectively. The degradation of chitin is also complex, involving the action of several enzymes (Gooday, 1994). Studies of fungal enzymes show that many fungi produce multiple isozymes of each enzyme (Haran et al., 1995), some of which are active at different temperatures (e.g., see Bradner et al., 1999; Tibbett et al., 1999). The faster growth of urban isolates of *C. pannorum* and *T. koningii* at higher temperatures may reflect increased activity at higher temperatures by all of some of the chitinolytic enzymes.

That Urban isolates of *T. lagena* and *P. bilaii* grew as fast or faster than the rural isolates at all temperatures tested (see Fig. 2), indicating that these isolates exhibit either counter- or co-gradient variation. A possible explanation for counter-gradient variation involves the growth inhibition of these isolates by high temperatures in the urban site. The maximal daily surface temperatures during 2 weeks in July and August 2002 were 37.7 and 33.0 °C in the urban and rural sites, respectively (M. M. Carreiro, unpublished data). These temperatures could be high enough to inhibit growth. The optimal

temperature for the growth of *T. lagena* has been recorded as 20 °C (Domsch et al., 1993), but our isolates appear to have an optimum at about 24–26 °C. Pitt (1979) records *P. bilaii* as usually growing at 37 °C and in our experiment, the optimal temperature for growth was $\geqslant$26 °C. The critical thermal maximum is often only a few degrees above the thermal optimum, so it is possible that high summer temperatures experienced in the urban site inhibit the growth of fungi. If so, the length of the growing season for fungi might be more restricted in urban areas, leading to the evolution of counter-gradient variation in growth rate.

The association of two distinct patterns of intraspecific variation with urbanization begs some explanation. Both scenarios involving thermal specialization and those producing counter-gradient variation would result in the faster growth of urban isolates at higher temperatures (see Fig. 1). To date, no single theory can account for the evolution of one pattern as opposed to the other. However, one possibility is that the genetic structure of the populations varied at the onset of urbanization, and this variation caused different responses to selection in each species. If genotypes that are specialized for growth at high temperatures are absent within a population, selection for faster growth at high temperatures might produce counter-gradient variation instead. Another possibility is that the specific biology of each species makes one form of adaptation more favorable than another. Thermal specialization and counter-gradient variation in growth rate involve different proximate mechanisms, which in turn lead to different evolutionary tradeoffs (Angilletta et al., 2003). If the consequences of these tradeoffs for fitness varies among species, natural selection might favor thermal specialization in some species and counter-gradient variation in others. Unlike the first possible explanation, this latter one does not implicate genetic constraints as a cause for the different patterns of intraspecific variation.

Samples of *C. pannorum* isolated at 4 °C grew faster and grew more efficiently at all five temperatures than those isolated at 15 °C. This phenomenon could have been caused by a greater synthesis of chitinolytic enzymes by the low temperature isolates. Other studies have documented that acclimation of fungi to low temperatures can cause increased enzymatic activities (e.g., see Tibbett et al., 1998, 1999). Arctic strains of *Heboloma* spp. produced more extracellular acid phosphatase than temperate strains when grown at temperatures ranging from 2 to 22 °C (Tibbett et al., 1998, 1999). Moreover, protease activity of an arctic strain of *Heboloma subsaponaceum* exceeded that of a temperate strain over a range of temperatures from 2 to 37 °C (Tibbett et al., 1998). This result could have been caused by thermal acclimation, rather than genetic variation between strains, because both arctic and temperate strains exhibited higher protease activity at 2–37 °C when stored for >100 days at 2 or 6 °C than when they were stored for 33 days at 22 °C (Tibbett et al., 1999).

The variation in thermal reaction norms that we have documented could have broader impacts on the dynamics of terrestrial communities in urban environments and the processes of ecosystems that contain such communities. The fungal species examined in our study were abundant at both the rural and the urban sites. All four species seem to have responded to urbanization, but these responses varied. Differential responses to urbanization can alter the competitive relationships between fungi (Marín et al., 1998b; Carreiro and Koske, 1992b; Naár and Kecskés, 1998), which would affect the decomposition of organic matter and cycling of nutrients. Furthermore, food webs can be altered since microbial grazers prefer certain species of fungi and avoid others (Newell, 1984; Bonkowski et al., 2000), thus affecting ecosystem processes indirectly. The dynamics of aquatic communities depend on such differential responses of organisms to variation in environmental temperature (Garvey et al., 2003), and we expect similar phenomena will be observed in terrestrial communities as ecological and evolutionary physiologists fix their gaze upon the soil.

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