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THREATENED SPECIES

SEE ENDANGERED AND THREATENED SPECIES

TOLERANCE LIMITS, ANIMAL

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Ecophysiological constraints prevent species from occupying the entirety of abiotic gradients present in nature and restrict them to just a portion lying between certain environmental bounds (i.e., their tolerance limits) beyond which they cannot survive. The fact that every species shows specific environmental adaptations that allow it to grow and reproduce is the basis of the niche concept. These environmental restrictions are the first factor that demarcates the geographic regions that a species can inhabit. Therefore, knowledge of tolerance limits is crucially important in order to assess the risk that a species will become invasive in a new site. Are environmental tolerance limits fixed? What role is played by these environmental restrictions in delimiting geographic range limits? Are invasive species characterized by broader tolerances than native ones? To what extent is their survival and spread limited by tolerances? These and related questions are essential to understanding the potential invasiveness of species as well as their abundance and distribution.

PHYSIOLOGICAL LIMITS

Temperature is probably the most important environmental factor influencing the performance of species, especially in ectotherms, the majority of species on Earth. Thermal performance curves are typically asymmetrically bell-shaped, with a progressive increase in fitness from the lowest limit of temperature tolerance to an optimum, after which a sharp decline occurs (Fig. 1A). Denaturation of proteins and degradation of enzymatic processes are believed to be among the main determinants of maximum
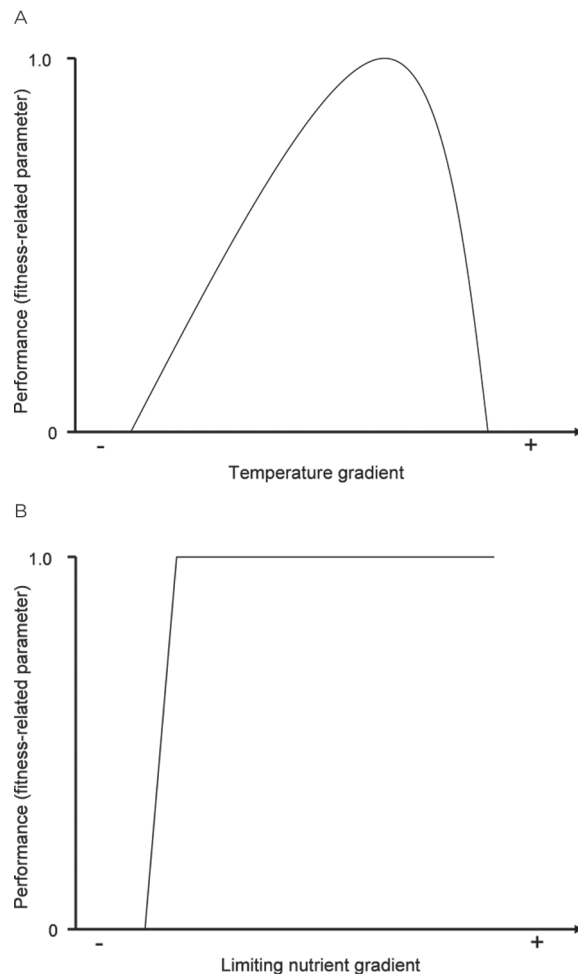

FIGURE 1 (A) Theoretical thermal performance curve in which the performance of the organism increases slowly with temperature and eventually reaches an optimum from which the performance sharply decreases. (B) Theoretical performance curve of an organism in relation to limiting nutrient availability. Below a certain threshold, the organism has a severe deficit of that nutrient and is unable to survive.

lethal limits. The need for oxygen when an increase in the metabolic rate occurs may also be an important additional determinant of these maximum lethal limits. Insufficient aerobic capacity of mitochondria also plays a significant role in setting low thermal tolerance limits, although the freezing of body fluids is probably the main determinant. Physiological adaptations to low temperatures have been extensively studied, and we know that several strategies in response to freezing have evolved in animals. Some amphibians, reptiles, and invertebrates are freeze-tolerant (i.e., they can survive a certain amount of extracellular ice formation in their tissues), while freeze-avoiding species synthesize antifreezing molecules that decrease the temperature at which the formation of ice starts.

Besides temperature, many other factors such as humidity, salinity, and limiting nutrient availability influence the fitness of species, with each factor producing a different shape of performance curve (Fig. 1B). Laboratory experiments provide the underlying explanation for physiologically imposed tolerance limits and the mechanisms behind their respective curve shapes. However, laboratory experiments are usually performed over short periods, and their results are often difficult to extrapolate to real-world situations. Moreover, the mismatch between laboratory theory and field observations—species living above or below reported tolerance limits—highlights the importance of taking into account interactions between different factors and demonstrates the complexity of the phenomenon.

PHYSIOLOGY AND GEOGRAPHIC DISTRIBUTION

Physiological tolerances clearly influence species distributions, and the match between the geographic ranges of species and climate has long been recognized by naturalists and biogeographers. Also, observed range shifts in response to past and present climate changes indicate the undeniable influence of climate on species distributions. However, as explained above, critical lethal limits observed in the laboratory are not likely to limit species ranges. We now know that a slight departure from optimal conditions can cause important adverse effects on the populations of species even before lethal limits are reached. For example, many species die if exposed repeatedly to moderately low temperatures. A decrease in the activity rate can lead to fasting periods that eventually may kill the organism by the indirect effect of temperature on starvation. Similarly, a rise in temperature increases the amount of energy required to maintain a given metabolic rate, compromising growth and reproduction. Low temperatures may also

affect dispersal rates, while high temperatures can increase the activity of predators, competitors, and parasites, jeopardizing the long-term persistence of populations.

The interaction between different climatic factors also has a decisive influence on organisms' survival. For example, the response to winter temperatures depends on the temperature of the former season. The capacity to survive low temperatures is also highly dependent on the rate of thermal change—rapid changes offer fewer opportunities for acclimatization—or on the length of the cold period. Snow may enhance the opportunities to survive cold extremes by creating an insulating surface, and the presence of water in the environment may promote tissue-freezing by inoculation. However, behavior is probably the most important and flexible factor that modifies tolerance limits. For instance, selection of overwintering places with higher temperatures than the surrounding area and aggregation of individuals are strategies to avoid exposure to harmful cold conditions. Researchers must also consider that tolerance limits and functions describing the relationship between performance and environmental factors can change between the different life stages of the same species, and so the distribution will then be determined by the most constrained stage.

PHENOTYPIC PLASTICITY AND EVOLUTION

Physiological limitations are not fixed but rather vary among individuals and populations of the same species, giving phenotypic plasticity an important role in the processes of adaptation to new environments. The capacity to change the phenotype may differ between life stages of the same species. Similarly, not all traits are equally plastic. For example, upper thermal tolerances are usually quite constant; on the contrary, lower thermal limits are quite flexible, and individuals can more readily adapt to decreases in temperature. Interestingly, it has been shown that even specialist species that are at present restricted to very specific climatic conditions retain the capacity to respond to environmental changes. Changes due to phenotypic plasticity can take place very quickly; a few days of acclimation in insects may be enough to alter their thermal limits. These phenotypic changes can promote genetic adaptation, which, together with the effect of either genetic drift owing to bottlenecks or genetic diversity caused by multiple source populations, makes rapid physiological evolution an important process in colonization events. In fact, the available evidence is sometimes contrary to what would be expected, and there is no general rule that invasion success is the direct consequence of having higher environmental tolerances or wider phenotypic plasticity.

The capacity to adapt to new environments allows both generalist and specialist species to increase their geographic ranges. Invasiveness should thus be viewed as a species-specific characteristic affected by many different (unknown) factors that interact in complex ways.

PREDICTING THE GEOGRAPHIC DISTRIBUTION OF INVADERS

Because the control of populations of already-established invasive species can be extremely costly and difficult, prevention is the most important strategy. Risk maps showing invasiveness potential are thus a valuable tool for environmental managers. As we have seen, the complexity of the responses of species to the environment, interactions among factors, and the ability to adapt make the prediction of the potential areas of establishment challenging. Prediction of areas susceptible to invasion is usually done using distribution data of the focal species, several bioclimatic variables, and correlative techniques that establish a relationship between both kinds of data: the so-called species distribution models (or ecological niche models). However, these techniques have been criticized because they do not rely on any mechanistic basis for the response of the species to the environment. Thus, for exercises such as predicting the potential distribution of a species in a new territory, models that incorporate physiological and biological knowledge of the species are recommended, and ideally, a combination of both approaches (mechanistic and correlative—which may not be mutually exclusive but complementary) is preferred when possible. Unfortunately, physiological information is lacking for most species, so correlative models will continue to be a necessary tool. Correlative models must be parameterized, and this step should avoid, as much as possible, blind procedures that rely on automatic variable-selection techniques that ignore the basic knowledge about the response of organisms to environmental gradients. Similarly, because the distribution data do not reflect the fundamental niche of a species but only a part, and because interactions between environmental factors are not stationary but vary geographically, simple techniques that account for extreme and rare data should be preferred over complex overfitting methods.

SEE ALSO THE FOLLOWING ARTICLES

Climate Change / Evolution of Invasive Populations / Genotypes, Invasive / Range Modeling / Tolerance Limits, Plant

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TOLERANCE LIMITS, PLANT

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Plants, including invasive species, vary immensely in tolerance of the extremes of abiotic factors such as temperature, moisture, light, nutrient availability, and toxic substances. Such tolerance sets the ultimate limits of species' distributions, and the reaction of plants to the complex of abiotic factors present in any habitat strongly affects productivity and abundance. Different combinations of physiological mechanisms, developmental patterns, and morphology at a variety of scales allow plants to exploit habitats that differ in the combination of stresses present. The ability of plants to adjust to variable conditions during growth (i.e., to acclimate) is critical for tolerance of abiotic extremes and for maximizing growth and reproduction under different growing conditions. Usually growth and reproduction are very limited when abiotic conditions are near tolerance limits, yet some examples of exceptional tolerance can explain invasive success.