PNAS COMMENTARY

The importance of habitat heterogeneity

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Organisms often occur in variable numbers across temporally and spatially heterogeneous landscapes with different sets of interacting organisms and environmental conditions, as well as varying combinations of natural and anthropogenic disturbances. Effective nature stewardship in the Anthropocene will require a detailed understanding of species responses to varied and changing environmental conditions and wise management actions to preserve their viability. For example, while most current prescribed fire intervals are planned considering local fuel attributes and average rates of regeneration of dominant and/or rare endemic species (1), there is still great potential to improve management plans to accommodate fine-scale responses to fire. Notwithstanding the critical importance of population density and interactions among organisms on population dynamics, (2) there are scarce accounts of their role in population recovery after fire or of the spatial and temporal distributions of these processes.

Anthropogenic actions are increasingly fragmenting and reducing habitats and populations while changing climate and disturbance patterns. Fire is a prevalent ecological disturbance worldwide with major roles in the ecology and evolution of many species (3). Fires had growing economic and social impacts in many regions and prescribed fire is commonly used by managers to attempt to restore critical ecological processes while reducing fuel loads and burn intensity (4). Fire patterns affect and are affected by the structure of the landscape (5, 6). In PNAS, Beck et al. (7) document an interaction between fire and population density across the landscape that changes the demographic potential benefits of fire and may even cancel them. Habitat fragmentation can exacerbate these types of impacts.

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The positive effect of postfire conditions on flowering of many species is relatively well known. However, for species depending on pollinators to set seeds, changes in the strength of these interactions across the landscape can modulate final seed production after fire. Beck et al. (7) demonstrate the value of assessing reproductive variation among populations with different population densities in response to fire. They found that fire increases annual reproductive effort (number of flowers and fruits) across studied populations of *Echinacea angustifolia*, but the reproductive outcome (seed set) was much higher for large, burned populations than for small, burned populations, diminishing the overall positive effect of fire. They attribute the differences in reproductive output to density-dependent pollination influencing the population outcome.

Lack of consideration of heterogeneity among targeted populations can exaggerate the effect of management. Particularly concerning are human-altered environments where anthropogenic actions can alter, reduce, and fragment suitable habitats while isolating and decreasing the populations inhabiting them. Beck et al. (7) performed their carefully planned six-year study of 32 populations of *E. angustifolia* (18 of them burned) in the highly fragmented remnants of tallgrass prairies of western Minnesota. Their detailed account found that populations with lower than 20 individuals do not offer enough mating opportunities, failing to increase seed availability and benefit from the post-fire conditions.

Historically, available datasets and theory steered population ecology to focus on average patterns and overlooked heterogeneity. Most demographic studies have concentrated on few populations (1 to 2 populations) during a short term (<3 y) (8). It is also concerning that many studies have not related the variation of population vital rates to environmental drivers (9, 10). Based on these historical constraints, it is difficult to predict realistic long-term population dynamics, let alone extrapolate to other conditions (11). Responding to challenges brought by Global change in the Anthropocene will require more serious consideration of heterogeneity to adapt to varying conditions due to habitat transformation and environmental alteration.

It is paramount to assess interacting drivers when evaluating population dynamics of endangered or nuisance species (12–15). The frequently nonadditive interaction among ecological drivers challenges the understanding of population dynamics when studies focus on a single driver, in a single population, or when the interactive drivers are considered independently (14, 15). For example, Tye et al. (14) documented the interactive effects of fire with herbivory and habitat (roadside or scrub) on the population growth of *Liatris ohlingerae*, a Florida scrub endemic. If only fire, or herbivory, or habitat had been the focus, the population ecology of this threatened endemic would be more opaque, and resulting management strategies would likely be less successful.

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Examining the responses to fire in multiple populations allowed Beck et al. (7) to alert that studying the effects of fire or other disturbances in a single or few populations may not provide enough information for effective management. Convincingly, Gurevitch et al. (16) proposed that most distributions for the expected success of populations (measured as λ) will be skewed (lognormal or gamma) and so it is virtually impossible to predict species viability based on studies in only one population. Single average estimates without estimates of other moments preclude our ability to characterize these distributions. It is likely that even species with relatively isolated populations may require assessments from multiple populations. The importance of including multiple populations is more obvious among species with metapopulation dynamics connected by dispersal. *Hypericum cumulicola*, for example, is endemic to the pyrogenic Florida scrub. Its populations have high genetic isolation (measured with F_{ST}) (17) and a long-term seed bank. Models including habitat heterogeneity, strong seed banks, and limited dispersal among populations were more likely to predict observed occurrence and population numbers than simpler models with assumed discrete populations or without environmental variables (18, 19). These studies stress the importance of studying multiple populations and environmental heterogeneity to evaluate species viability.

Spatial and temporal habitat heterogeneity are critical features in the environment but have been frequently overlooked in population studies. There are many logistic reasons constraining the ability to address these issues. Grant terms and graduate program durations limit the number of years available for research. Traveling and other expenses challenge the possibility to include multiple populations. However, creative ways to overcome these problems will be required to improve understanding of the population dynamics and management recommendations. Detailed consideration of simultaneous processes in multiple temporally and spatially varying environments will be paramount to improving our ability to effectively steward natural resources in the Anthropocene. Collaborative research, creative research programs, and longer grant terms are promising strategies to address these obstacles.

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