

PROJECT DESCRIPTION

STATEMENT OF THE PROBLEM: POPULATION AND COMMUNITY EFFECTS OF INDIVIDUAL VARIATION & SPATIAL PATTERN

The importance of individual variability in driving both population and community dynamics has been increasingly recognized by ecologists and is at the heart of several strands of current ecological research (e.g., Pfister & Stevens 2003, Kendall & Fox 2003, Agrawal et al. 2007, Kendall et al. 2011). Genetic, developmental, behavioral, and spatial differences in individual performance have recently been shown to exert strong influences on population growth, spatial spread, and extinction rates (e.g., Fox 2005, Zuidema et al. 2009, Kendall et al. 2011, de Valpine 2009, Jongejans et al. 2011); on responses to fluctuating environments (e.g., Pfister & Wang 2005, Landis et al. 2005); and on interactions with other species (e.g., Pfister & Peacor 2003, Crutsinger et al. 2006, Tinker et al. 2008, Utsumi et al. 2011, Dugaw & Ram 2011). Established demographic approaches in population ecology have traditionally emphasized the importance of obvious differences between individuals in age, size, or developmental stage (Caswell 2001); similarly, metapopulation and meta-community approaches have emphasized broad spatial differences in performance. In contrast, the emerging research on individual variability focuses on differences that are typically harder to quantify, such as consistent variation in growth rates, age-corrected survival probabilities, time to maturity, and defensive chemistry. These new approaches to the question of how differences among individuals drive dynamics thus both complement and build on older bodies of work—including those on life-history variation, source-sink dynamics, and metapopulation dynamics—which have established that seemingly identical individuals can have very different effects on population or community dynamics due to differences (both intrinsic and extrinsic) in their demographic rates and other traits.

While this expanding field has not yet been well-synthesized, two discrete processes (**Fig. 1A-C**) appear to drive most of the theoretical and empirical examples of effects arising from individual variation that have been documented to date: (a) **Jensen's Inequality** (Ruel & Ayres 1999), in which non-linear responses to varying individual traits by other variables (e.g., population growth rate, feeding efficiency of an herbivore) result in a shift of the overall mean of the responding variable (e.g., Kendall et al. 2011); and (b) **Variance Reduction**, in which individual variation, by creating differences in the degree of susceptibility to environmentally-driven variation in performance and by reducing the correlations among individuals' responses or susceptibility to extrinsic factors, reduces population-wide variance and its attendant effects (e.g., risk of extinction; Fox 2005). Our goal here is to use a well-studied system with strong patterns of individual variation to dissect the relative importance of these two phenomena and to derive general conclusions about how individual variation shapes community structure and dynamics when individuals vary in multiple, correlated, and complex ways (which is true in most real systems, but has not been adequately addressed in past studies).

Our work will explicitly focus on individual variation that is driven by strong local-scale spatial patterning: in doing so, we will also use individual variation as a lens through which to view the question of when and why spatial structure in landscapes actually *matters* for ecological functioning. Both theoretical and empirical studies have shown that spatial location is likely to be among the strongest drivers of individual variation (e.g. Gates & Gysel 1978, Winter et al. 2000, Holyoak et al. 2005, Okullo & Moe 2011, Boulding & Van Alstyne 1993, Menge et al. 1994, Franklin et al. 2000, Manolis et al. 2002, Bollinger & Gavin 2004, Landis et al. 2005). However, little work has gone beyond this to predict when and why this variation will have strong population or community-level effects. In addition, the literature on spatially-driven individual variation has to date emphasized only one aspect of spatial patterning (variance, the second moment), whereas in all but the most spatially random or homogeneous ecological systems, the **Spatial Structure of Individual Variation** is striking. This additional property of individual variation—which may mask or amplify the effects of variance alone, and which may work in concert with either Jensen's Inequality or Variance Reduction—is the third focus of our proposed work.

Although purely abiotic forces (e.g., geology and precipitation) can obviously generate spatial structure and patterning in ecological systems, another current theme in ecological research is the ability

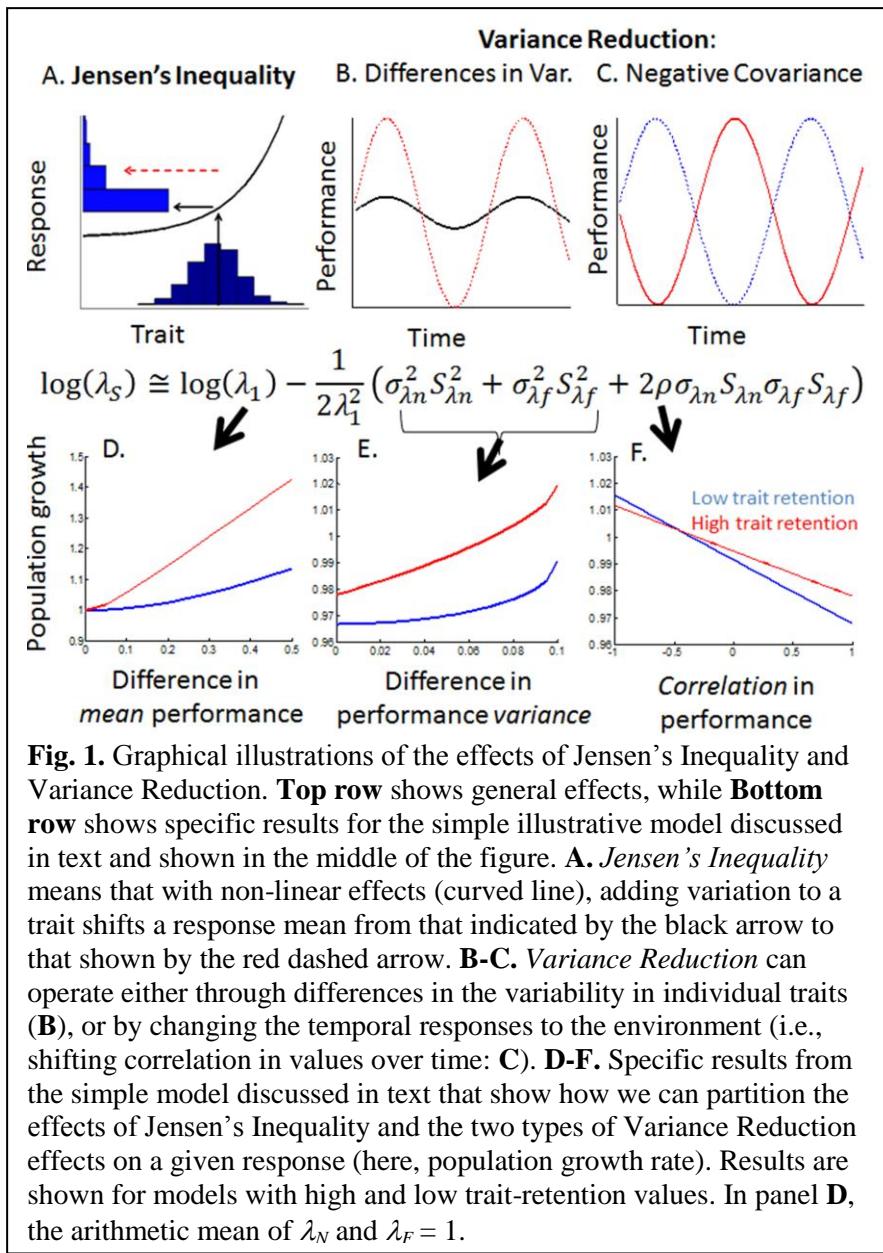
of biotic interactions to generate strong spatial patterning at scales highly relevant to the fate of individuals. A central claim of this body of work is that patterning has strong and pervasive effects at multiple levels of ecological communities – in short, that biotically-generated spatial pattern is critical for certain ecological processes and is therefore relevant to ecologists who are not necessarily focused on patterning for its own sake (e.g., Sleeman et al. 2005, van de Koppel et al. 2008, Pringle et al. 2010). However, while there is growing evidence that such patterning is extremely widespread in many ecosystems (reviewed in Rietkerk & van de Koppel 2008; see also our **Fig. 5**), the broader importance of biotically generated patterning for overall community structure and ecosystem functioning remains unclear. To borrow a memorable phrase from one prominent review (Rohani et al. 1997), we still do not understand the extent to which these effects merely result in “pretty patterns,” as opposed to being potent ecological forces. We will use the perspective of individual variation to bring powerful and generalizable methods to bear on this important issue.

We will investigate these questions using a study system in Kenyan black-cotton soil savannas, where striking spatial

pattern is generated by the direct and indirect effects of termite mounds, and where there are weak effects of other pattern-forming processes (e.g., topography: **Fig. 2**). Within this system, we will focus on (a) the mono-dominant Acacia species (*Acacia drepanolobium*, or “*A. drep.*”, accounting for >97% of trees), which displays strong biochemical and demographic variation in response to termite-mound proximity, and (b) the arboreal food web that this tree population supports. Our research will address seven specific questions:

Population-level effects:

1. What is the relative strength of different factors in determining individual variability? Whereas researchers in other systems have often analyzed variation in a single trait or variation arising from a single state variable, we will attempt to dissect



variation caused by both standard effects (e.g., size-structure) and more cryptic effects (small-scale variation due to termite mounds), as well as testing for genetic determination of individual variation.

2. How does individual variation caused by termite mounds alter tree demography via Jensen's Inequality? By constructing a demographic model with and without termite-mound effects, we will estimate the extent to which mound-based variation modifies population dynamics and structure.
3. Does spatial patterning in individual variation strengthen or weaken the influences of Jensen's Inequality? By creating spatial autocorrelation in traits, spatial patterning might alter the non-linear population responses that govern the ecological influence of Jensen's Inequality; we will test for such effects using both implicitly spatial integral projection models and spatial simulations.
4. How does Variance Reduction shape stochastic tree dynamics? We will similarly test for effects of individual variation in reducing temporal variance in population performance using analytical and simulation models, and we will ask how spatial patterning influences these effects.

Community-level effects:

5. How does spatially structured individual variation in *A. drepanolobium* influence the arboreal food web via Jensen's Inequality? By examining how arboreal herbivore and predator assemblages are influenced by characteristics of their host trees, we will analyze the extent to which small-scale variance in tree traits alters faunal community structure and productivity.

6. Does regular spatial structure of tree traits lead to stronger or weaker community-level effects, relative to a random distribution? We will ask whether effects of individual tree variation on the arboreal animal community are stronger when individual variation is spatially non-random—and in particular whether this allows stronger propagation of Jensen's Inequality effects, which could arise from either (a) reduced ‘washing-out’ of incipient spatial structure by non-directed animal movements or (b) enhanced ability/tendency of animals to aggregate.

7. Does individual variation in trees promote community stability due to Variance Reduction? Our study system experiences marked climatic fluctuations, both within and between years, and we will use these fluctuations to ask whether individual variability in trees, via Variance Reduction, buffers temporal fluctuations in the arboreal food web.

Our ability to accomplish these goals relies on our complementary team of PIs. **Kena Fox-Dobbs**, an expert in geochemical techniques, will lead field work involving tracer studies and tissue analyses of trees, herbivores, and predators, which will enable us to quantify trophic interactions, movement dynamics, and nutrient flows. **Rob Pringle**, an experimental community ecologist with nine years’

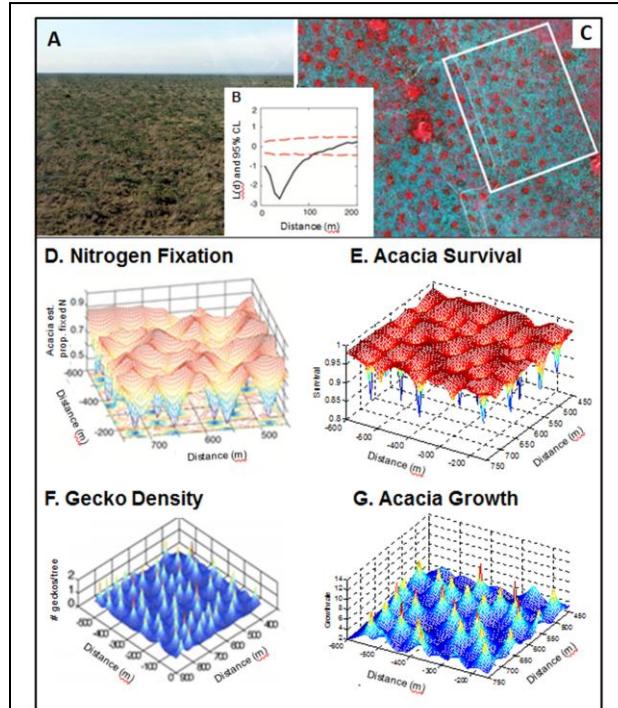


Fig. 2. Ecological pattern in the study system (black-cotton soil savanna). **A.** Aerial view of the study system: there is almost no topographic or geologic variation to complicate study of termite mound effects. **B.** Statistically significant over-dispersion of termite mounds (transformed Ripley's K values: dashed lines indicate 95% CIs for random landscape). **C.** Regular variation in NDVI created by termite mounds (red dots), as seen from Quickbird satellite image. **D-G.** Interpolated landscape patterns for some of the documented ecological responses to termite mounds. For each panel, X and Y axes are landscape position in meters, and surfaces show predicted values for a ~3600m² section of real termite-mound locations (shown in white box in panel C).

experience working on the arboreal fauna of our study system, will lead experimental and observational studies to quantify the abundance, diversity, and movement dynamics of arboreal animals. **Dan Doak**, a population ecologist and demographic modeler, will lead observations and experiments to quantify the demography of the focal tree species and will also develop and run the statistical and modeling analyses of tree demography and community structure. This team has worked together productively in the past, generating much of the preliminary knowledge that makes the proposed work feasible (Pringle & Fox-Dobbs 2008, Fox-Dobbs et al. 2010, Pringle et al. 2010, Palmer et al. 2010).

RESPONSES TO PRE-PROPOSAL REVIEWS

Reviewers of the pre-proposal were enthusiastic about the general questions being addressed and our approach to addressing them. However, the reviewers also raised several concerns and questions. We have addressed these issues throughout the proposal and summarize our responses here:

1. Feasibility of planned data collection and modeling. We now provide clear time budgets, based on our own extensive past work in this system, for the most labor-intensive aspects of our study, which demonstrate the feasibility of the planned field work. We also give far more details of the proposed modeling strategy than was possible in the preliminary proposal.
2. Generality of the patterning and processes created by termites, and necessity of working in Kenya. These two points are linked, in that they question whether our study system is a suitable model for addressing broad ecological questions. In *Study System and Prior Work* we describe the many scientific and logistical advantages of this system. Another essential advantage is our extensive experience with, and integrated understanding of, this study system; this, more than anything else, makes our ambitious field program feasible. Moreover, in *Background* we discuss more fully the globally widespread occurrence of regular patterning like that found in our system. Finally, we have added a *Broader Impact* activity (see point 5 below) in which citizen scientists will gather data to directly address and quantify the occurrence and frequency of such patterned landscapes worldwide.
3. Generality of results from the modeling. Reviewers asked, reasonably, whether our planned simulation modeling, tailored to our study system, could provide general insights. Although we believe that linking models to a real system with well-characterized parameter values is both necessary and important, we agree that the ability to extrapolate these results to other systems would be aided by developing a set of more generalized models. Therefore, as described in *Planned Research*, we have added the development of more generalized population and community models that will aid in assessing the general conditions needed for either individual variation or spatial patterning to affect population- and community-level processes.
4. Ability to distinguish sources of individual variation. In different ways, all reviewers commented on our treatment of this issue. Some reviewers seemed to interpret ‘individual variation’ as meaning only genetically-based phenotypic differences, whereas others understood our use of the phrase (consistent with that of most authors in this field: e.g., de Valpine 2009, Kendall et al. 2011) to imply *all* differences in probabilistically-defined functions of individual performance (specifically, demographic rates and probabilities). In response, we have added discussion under *Prior Work* that clarifies (a) the evidence suggesting that spatial effects arising from termites are a powerful determinant of individual variation in our system, and (b) why we consider it extremely unlikely that genetic differences among individual trees at small scales contributes substantively or systematically to the spatial effects that we observe. Furthermore, we have added two components to *Planned Research* to address these concerns: a transplant experiment and simple genetic assays to estimate effects of genetic variation at early life stages.
5. Broader Impacts activities. While the reviewers did not raise explicit concerns about our broader impacts plans and activities, their comments have prompted us to consider how to best capitalize on the opportunities our work creates for substantial educational impacts in both the US and Kenya. We have now developed a more creative plan to increase our outreach impacts, including (a) collaboration with two US charter schools and a Kenyan girls school, and (b) establishment of a Google Earth-based crowd-sourcing program to identify and quantify landscape patterning in natural systems.

BACKGROUND

In light of space limitations, we give here only brief overviews of the most central topics and concepts that underpin our proposed work:

Types of Individual Variation. Our concern here is with the population- and community-level effects of trait variation between individuals. In this context, there are two important distinctions between types of individual variation and the differences in how and why they create larger-scale effects. The most obvious difference is between genetically vs. non-genetically determined trait variation. Both types of variation are ubiquitous and undoubtedly important in nearly all populations. Unlike work by evolutionary biologists, most past ecological work on the population and community implications of individual variation has not probed deeply into these differences, instead attempting to estimate the effects of overall phenotypic variation from all causes. In our work, we will test for genetic effects that might contribute to spatial differences between individuals, but (as discussed below), we expect that other factors (tree size and spatial location) are much stronger drivers of individual variation.

The second difference in types of individual variation is gradation along a continuum of what we will call the ‘**trait retention**’ of individual traits: some trait variation is highly transitory, whereas in other cases there is high autocorrelation in this variation either within individual lifetimes and/or from one generation to the next. Examples of high retention include the strong, life-long individual differences in reproductive performance seen in many seabirds (e.g., ‘cohort effects’: Wooller et al. 1992, Rebke et al. 2010) or correlation between mothers and offspring due to genetics, social status, or simply location (reviewed in Kendall et al. 2011). As several modeling studies have shown (Pfister & Stevens 2003, Kendall et al. 2011), individual variation that has higher retention within an individual’s life or across generations generally has far stronger effects on population dynamics. Weaker (or non-existent) scaled-up effects of individual variation are expected when individual differences are less permanent, because of rapid switching of which individuals have better or worse performance. This important distinction has been well developed theoretically, but there are few empirical examples to support the generality of these effects. Another major lesson from this past work is that although trait variation and its retention can in some cases strongly influence population dynamics, there are not analytical solutions for these effects (de Valpine 2009, Kendall et al. 2011). Nonetheless, de Valpine has (2009) has recently developed computational approaches that allow analysis of well-defined models containing multiple, complex aspects of trait variation without excessive simulation. These effects and analytical approaches all relate to the influence of Jensen’s Inequality on populations. It is not clear whether there are similarly strong effects of trait retention on the influence of Variance Reduction. Finally, the influence of trait retention on effects at the community level are also unclear, but we expect that there will be distinctions in the effects occurring via Jensen’s Inequality vs. Variance Reduction that are similar to those occurring at the population level.

Dissecting Effects of Individual Variation: a simple example. To illustrate how Jensen’s Inequality and Variance Reduction can each result in population effects—and how these influences rely on trait retention—we present results from a simple population model. We consider a population with two regions (we call them ‘near’ and ‘far’, with reference to termite mounds). The model has three basic parameters: net annual growth rates (encompassing both survival and reproduction) in each region (λ_N and λ_F) and the proportion of individuals who move between regions each year (p), which is inversely related to trait retention. The deterministic model can be represented as a single matrix, with an overall deterministic growth rate (the dominant eigenvalue) of $\lambda_1 = 0.5(1 - p)(\lambda_N + \lambda_F) + 0.5(4p^2\lambda_N\lambda_F + (1 - p)^2(\lambda_N - \lambda_F)^2)^{1/2}$. Plotting λ_1 against the difference between λ_N and λ_F , and doing so for different values of movement (**Fig. 1D**), shows Jensen’s Inequality (i.e., $\lambda_1 \neq$ the mean of λ_N and λ_F) and how it depends on trait retention (higher values of p mean less retention and weaker effects of individual variation).

Next, we can ask how temporal variance in λ_N and λ_F will influence λ_S , the stochastic growth rate of the population. Using Tuljapurkar’s (1990) approximation: $\log(\lambda_S) \cong \log(\lambda_1) - \frac{1}{2\lambda_1^2}\tau^2$, where

$\tau^2 = \sum_i \sum_j \rho_{i,j} \sigma_i \sigma_j S_i S_j$; here, $\rho_{i,j}$ is the correlation between demographic rates i and j ; σ_i is the standard deviation of rate i ; and S_i is the deterministic sensitivity of λ_1 to rate i . Through its effects on λ_1 , individual variation (the difference between λ_N and λ_F) will also influence $\log(\lambda_S)$. Moreover, differences between the variance in λ_N and λ_F values and/or lower correlation between the variation in the two habitats will also alter $\log(\lambda_S)$: these effects, which in this simple model reduce the value of τ^2 and hence increase $\log(\lambda_S)$, represent the way in which Variance Reduction influences population growth (**Fig. 1E-F**). **Although highly simplified, this toy model illustrates how we can answer our research questions by incorporating and then dissecting the influences of Jensen's Inequality and Variance Reduction on metrics of population performance or community responses.**

Spatial Variation and Spatial Patterning. An important driver of individual variation is spatial patchiness, including regular (non-random) patterning in local environments. The importance of spatial scaling and patterning of individual variation arises from both (a) how it determines the distribution of individual variation and (b) its effects on the degree of retention in individual variation. Extremely fine-scale patchiness will result in low trait retention, even for sedentary species. In contrast, large-scale patchiness may lead to the formation of what are essentially subpopulations—even in a seemingly continuous population—if individual traits differ strongly enough across environments, and if patch sizes are much larger than typical movement distances at any life stage of an organism.

Similarly, the interaction between mobility and the grain size of spatial patchiness will strongly influence whether individual variation at one trophic level propagates to other parts of the community. This is similar to reaction-diffusion analyses of predator-prey interactions, in which too much movement of a predator prevents it from responding to small-scale patchiness in the prey, whereas restricted movement allows this patchiness to ‘propagate’ to the predator trophic level (Murray 2002). Analyzing the trophic effects of spatial patchiness in our system and how these effects are determined by movement rates of herbivores and predators is one specific goal of our work (Question #6 above).

Beyond random patchiness, we now know that regular patterning of ecological systems is common to an extremely wide range of species and ecosystems (Rietkerk & van de Koppel 2008; see also **Figs. 2 and 5**). Such patterning is important for two reasons. First, the patterning of a driving variable in a landscape will alter the frequency distribution of traits in responding species, and thus can determine the shape and ecological influence of individual variation (**Fig. 3A**). Second, regular patterning allows for tractable analysis and modeling of the effects of individual variation. And, with estimated response surfaces that show the effects of this variation on a particular trait (e.g., **Fig 2D-G**), we can identify likely generalities about how particular response curves and different pattern configurations will shift mean responses via Jensen’s Inequality (as we did in Pringle et al. 2010) or Variance Reduction.

In some cases, spatial patterning has strictly abiotic origins, but it appears that the more common situation is synergistic effects of both physical and biotic processes, or for biotic forces to dominate the creation of patterning (Rietkerk & van de Koppel 2008, van de Koppel et al. 2008, McKey et al. 2010). It is also the case that social insects appear to be extremely common generators of strong, well-patterned variation in natural communities. While we do not know of a comprehensive review of this topic, multiple papers have directly or indirectly addressed patterned social-insect colonies as organizing forces in terrestrial ecosystems (MacMahon et al. 2000, Schooley & Wiens 2003, Eldridge et al. 2009, Jones 1990, Vandermeer et al. 2008, Perfecto & Vandermeer 2008, McKey et al. 2010, Okullo & Moe 2011, Darlington 1985, Glover et al. 1964, Korb & Linsenmair 2001). These include studies of termites in arid woodlands, grasslands, and humid tropics in Australia, Africa, and South America, as well as research on ants in arid North America and humid tropical sites on multiple continents. Our own experience of flying over eastern and southern Africa suggests that patterned arrays of termite mounds are nearly ubiquitous in savannas and drylands. In short, the type of spatial patterning that we are examining, although perhaps not *identical* in other areas, is nonetheless common to an extraordinarily broad range ecological settings worldwide.

RESULTS OF PRIOR NSF SUPPORT

Past NSF support has allowed us to investigate multiple aspects of our study system, setting the stage for

the work we are now proposing:

NSF DEB-0812824. A Brody, T Palmer, & DF Doak. Collaborative Research: Interactions among keystone species: effects of termites and ungulates on biodiversity in East African savannas. 2005-2011. Two of the current PIs were supported from this award (Doak as PI, Fox-Dobbs as postdoc). This work focused on whether and why termite mounds have strong community effects in black-cotton soil savannas. Our findings, especially on the strength of termite effects are central to our planned work here. **Publications** to date from this award include 6 papers on our study system, including 1 *PNAS*, 1 *PLoS Biology*, and 2 *Ecology* papers, and 8 other papers on projects partially supported by this award (see References Cited). **Human Resource Development**: This award provided support for 3 M.S. (one Kenyan, all woman) and 3 Ph.D. students (all women), 3 postdocs (one Kenyan, two woman), and 3 undergraduates (1 woman). It also trained and employed three full-time Kenyan research assistants. Two REU awards to this grant supported exemplary undergraduates. After accepting her faculty position, Fox-Dobbs has involved 3 undergraduates at her (primarily undergraduate) institution in this project.

NSF-DDIG-0709880. GC Daily, RM Pringle. Dissertation Research: Indirect regulation of aboveground ecological processes by a belowground ecosystem engineer. 2007-2009.

NSF-OISE-0852961. RM Pringle. International Research Fellowship: Ecological consequences of large-herbivore declines under different rainfall regimes. 2009-2011. These two awards supported Pringle's doctoral and post-doctoral research in Kenya, the former on the trophic and pattern-generating roles of termites and the latter on the context-dependence of large herbivores' ecological impact along a rainfall gradient. **Scientific output.** These doctoral and post-doctoral awards supported 11 publications (one of which, on termite patterning, was featured on NSF's website), in addition to Pringle's PhD thesis.

Human Resource Development &

Outreach. Under these awards, Pringle trained and employed three full-time Kenyan research assistants; involved three undergraduates (2 women); co-advised one undergraduate woman's undergraduate thesis and one master's thesis; and assisted a grade-school teacher with field-based curriculum development. He has been active in disseminating results in local, national, and international settings, for both scientific and non-scientific audiences.

THE STUDY SYSTEM AND PRIOR WORK

Characteristics and Advantages of the

Study System. We will conduct this work at our long-term study site (2004-present), Mpala Research Centre in the semi-arid Laikipia County of central Kenya (0°N , 37°E , 1800 m elevation). Mpala comprises two soil types: red sand soils in low-lying areas, and high-clay, poorly drained, and topographically uniform 'black-cotton' vertisols (derived from basaltic lava flows) on plateaus (Ahn & Geiger 1987). Our work will be situated on these plateau vertisols, which characterize >40% of Laikipia and large areas elsewhere in East Africa, (e.g., large parts of Serengeti and Nairobi National Parks).

A key advantage of black-cotton soil

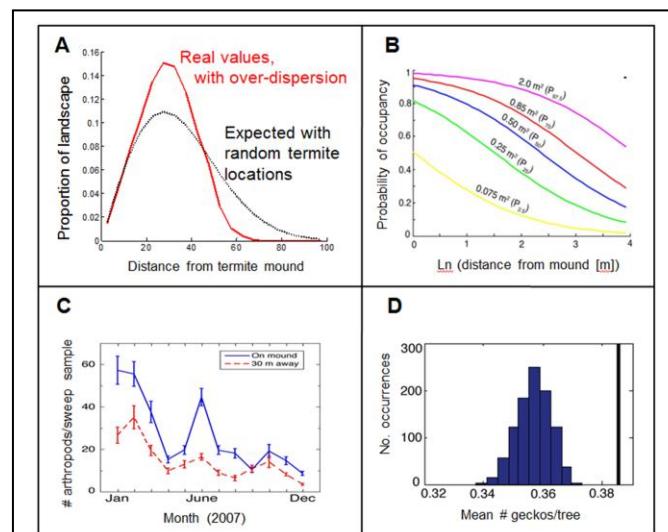


Fig. 3. Termite-mound effects and landscape patterning. **A.** Over-dispersion of termites alters the fraction of the landscape at different distances to termite mounds, shifting the distribution of termite-driven ecological effects. **B.** Non-linear responses in the probability of geckos occupying *A. drepanoides* as a function of tree size (curves) and mound proximity (x axis). **C.** Arthropod abundance is higher, but more variable, on termite mounds (blue) than off (red dashed). **D.** Observed landscape densities of geckos (vertical black bar) is higher than predicted in 1,000 simulated landscapes with randomized mound locations (blue histogram).

savannas for our work is their physical and biological simplicity. One source of this simplicity is homogeneity in the underlying parent material and hence the soils. Another is their topographic simplicity: over large areas, the ground is essentially flat, reducing variation in drainage or other topographically-determined features to very low levels (**Fig. 1C**). Together, these features limit the complexity of spatial variation and the forces producing it, greatly improving the signal-to-noise ratio when looking for effects of patterning. Black-cotton habitats throughout upland East Africa also feature strongly over-dispersed arrays of termite mounds (*Odontotermes montanus*; Darlington 1985) (**Fig. 1A-B**). These mounds have multiple important ecological properties and have been a major focus of prior work by ourselves and our colleagues (e.g., Palmer 2003, Brody et al. 2010, Fox-Dobbs et al. 2010, Pringle et al. 2010). We have found no evidence that abiotic factors (such as ‘gilgai’ or human activities) interact with termites to create or maintain this patterning, giving credence to the single-causative-agent hypothesis. Termite mounds in this system are also believed to be long-term features, lasting multiple decades (Darlington 1985) and perhaps up to 700 years (Watson 1967). Thus, mound patterning, once established, likely becomes an almost permanent landscape feature.

Black-cotton savannas are also fairly simple ecological systems, characterized by relatively few dominant species. The ant-mutualist tree *A. drepanophylla* comprises >95% of canopy cover (and 97% of all individual trees). *A. drepanophylla* is also the only common N₂-fixing species in this habitat, and there is also a low-diversity understory (five grasses account for 90% of cover). These features, along with the dominance of exclusively C₄ grasses in the understory, make the black-cotton community exceptionally tractable for stable-isotope analyses of food-web structure: we can easily quantify the relative contribution of C₃ and C₄ plants to herbivore diet (Pringle & Fox-Dobbs 2008), and it is also possible to characterize spatial patterns in N₂ fixation and animal foraging (Fox-Dobbs et al. 2010; **Fig. 2D**). As with plants, the animal guilds in this habitat are also low in species diversity, often with one or a few numerically dominant taxa. One focal species of our work, the diurnal, insectivorous dwarf gecko *Lygodactylus keniensis*, represents ~94% of the lizard fauna, making it the most abundant vertebrate in the area (Pringle et al. 2007).

Prior Work. Our prior work has explored several aspects of how termites influence the biochemistry and ecology of *A. drepanophylla*, the mono-dominant tree in our system, and how this in turn affects the ecology of multiple trophic levels to produce rippling, community-wide indirect effects. Key published and unpublished results of this work, and their implications for our planned research, are:

Termite mounds show highly uniform arrangement (i.e., are highly over-dispersed) over large areas in otherwise extremely homogeneous landscapes (Pringle et al. 2010; **Fig. 2A-C**).

Proximity to termite mounds drives variation in multiple other aspects of the savanna community. Soil N and P concentrations are higher near mounds, as are large-mammal activity levels (Brody et al. 2010), NDVI values (**Fig. 2C**), the diversity and productivity of understory plants (AK Brody, *unpub. data*), and the diversity and productivity of arthropods on *A. drepanophylla* (Pringle et al. 2010). Most termite-mound influences attenuate sharply between 10 and 15 meters from the mound center (Pringle et al. 2010, Fox-Dobbs et al. 2010).

The individual ecology of *A. drepanophylla* trees is strongly influenced by termite mound proximity. Among the most striking features that vary with mound proximity are foliar N concentration (higher near mounds) and the percent of foliar N derived from atmospheric N₂ fixation (higher *far* from mounds; Fox-Dobbs et al. 2010 and **Fig. 2D**). In addition, preliminary analyses of four years of demographic data from ~2500 mapped trees show strong effects of mound proximity on growth and survival rates of *A. drepanophylla* (**Fig. 2E-F**) and on the transition dynamics and occupancy rates of its four obligate ant symbionts (Doak, *unpub. results*). We have also shown (Palmer et al. 2010) that the species of ant mutualist on a tree has potent demographic effects that will lead to indirect mound effects on tree traits. Finally, mound effects are *strong*: for example, of variables tested, only size and ant mutualist exert stronger effects than mound proximity on *A. drepanophylla* growth rates. This preliminary work also allows us to gauge the feasibility of our proposed work (e.g., it required 13 days for six researchers to set up our 2500 tree study, and 10 days for four researchers to re-census these trees each year), and gave us experience in constructing and simulating

complex demographic models of *A. drepanophylla* (e.g., Palmer et al. 2010, for which Doak did all demographic data analysis and modeling).

Mound effects on *A. drepanophylla* are likely due to phenotypic changes, not genetic differentiation. We do not yet have data to directly test this assertion, but *A. drepanophylla* canopies are large relative to mound spacing, making genetic differentiation at the scale of mounds unlikely: large trees have canopy diameters >8 m, and the maximum distance from nearest mound is ~28 meters. Furthermore, the strongest differences in *A. drepanophylla* traits are concentrated at even smaller scales, very near to mounds (Fox-Dobbs et al. 2010).

There are strong and non-linear effects of mound proximity on the arboreal community living on *A. drepanophylla*. The abundance and diversity of arboreal herbivores and predators is higher near to mounds, as is the fecundity of a major predator guild, spiders (Pringle et al. 2010). These mound effects attenuate in a non-linear fashion (*ibid.*), suggesting the possibility of Jensen's Inequality effects. We have used simulation studies to show that the regular spacing of termite mounds, coupled with these non-linear faunal responses, lead to landscape-scale faunal abundances and fecundities that are higher than would be the case if mounds had identical local effects, but were not strongly patterned (Fig. 3D; Pringle et al., 2010). The arboreal food web is a largely self-contained compartment of the broader savanna community, with minimal energetic input from the grass-forb layer (~5% for geckos, ~15% for spiders: Pringle & Fox-Dobbs 2008); thus, we can reasonably analyze this assemblage as a discrete sub-community.

Some components of the *A. drepanophylla* community are not strongly influenced by termite-mound patterning. Most notably, *A. drepanophylla* does not consistently differ in density or size distribution with distance from mound centers (Doak, *unpub. results*). This lack of response is especially surprising given that the nitrogen economy and demography of individual trees is strongly influenced by proximity to termite mounds. Thus, at least some of effects of termite mounds appear to cancel out, while others propagate to create population- and community-level effects (e.g., densities of arboreal herbivorous arthropods and their predators). These contrasting patterns provide a cautionary note to the many claims and extrapolations about the importance of individual variability and spatial patterning, and suggest the need for the type of work we propose here to understand when and why these effects will occur.

Fertilization can be used to manipulate spatial structure in this system. Through persistent (and painful) long-term effort, we have found that it is essentially impossible to manipulate (i.e., kill) termite colonies as a way of experimentally altering spatial structure in this system (at least without entirely disrupting the rest of the ecosystem). However, in early 2012 we conducted a **pilot experiment** that showed that fertilization can be used to rapidly simulate the effects of mound proximity on *A. drepanophylla*. Six months following localized application of N-P-K fertilizer, mature *A. drepanophylla* far (>20 m) from mounds showed foliar N concentrations and C/N ratios that were as high or higher than those of unfertilized trees close (<5 m) to mounds (e.g., for %N: linear mixed model, ΔAIC for treatment*before/after = 4.5; likelihood ratio test $P = 0.011$; Fig 4).

PLANNED RESEARCH

Our research questions require us to (a) quantify individual variation and how it is driven by termite-mound proximity at the local scale for both *A. drepanophylla* and the arboreal community, and (b) simulate and also manipulate key features of the system to estimate how these effects are regulated by Jensen's Inequality and/or Variance Reduction. An added goal is to understand how different ecological processes increase or reduce trait retention, thus mediating the population and community effects of individual variation. To meet these goals, we will employ a large, multi-faceted observational study, plus six

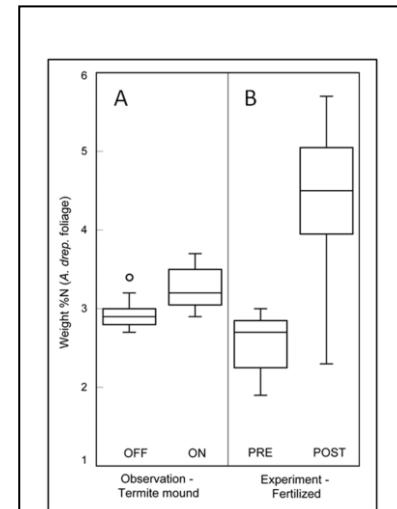


Fig. 4. A. Weight percent nitrogen (%N) is naturally higher in *A. drepanophylla* trees close to termite mounds. **B.** After a 6-month fertilization experiment, we replicated this effect, with strong increases in %N in treatment trees located far from mounds.

experiments and ancillary observations to add detail and test key processes. This field work will provide the information needed to parameterize models that we will use to dissect the influences of individual variation, and will also provide direct tests of some of the processes, especially at the community level, that may control these influences.

Main Observational Study. We will build a series of observations of the spatial dynamics of *A. drepanophyllum* and its attendant small-animal community by establishing twelve 30x30m plots in which we will map and monitor every *A. drepanophyllum* tree. One edge of each plot will bisect the center of a termite mound: the 30-m size is based on the mean distance between mound centers of ~60 meters (**Fig. 2**), such that each plot will span the typical range of distances from mound centers. Six similar (though slightly smaller) plots have been mapped and followed since 2007; these will be expanded so that the data they have already generated can contribute to our planned research. Based on these data, we estimate that our 12 plots will collectively contain ~6000 total trees—sufficient for accurate estimation of survival, growth, and recruitment rates.

To measure basic demographic rates, we will record the survival, size, and mutualist ant species of each tree in each year in every mapped plot. We will also search for new recruits, mapping and tagging all new individuals. Mapping, using laser rangefinders, is accurate to 10 cm. We will survey for fruiting following rain events, which occur unpredictably in this system and generate episodic flowering events. Based on our past work, we estimate that only a month will be required for a team of eight to establish and map these plots, and roughly three weeks per year will be required to collect the basic re-survey data.

The second facet of our observational study consists of biogeochemical assays. Specifically, we will (a) collect *A. drepanophyllum* leaf tissue for C and N analyses and (b) use stable isotope and elemental data to estimate nutritional quality and atmospheric N₂ fixation rates. The logistics of sample transport and preparation for these analyses are not trivial; our sampling will be designed to maximize information yield from a workable number of samples. In four of our 12 mapped plots, we will sample 25% of the *A. drepanophyllum* trees and nearby reference plants at the beginning and end of our study, allowing us to finely map the biogeochemical spatial landscape. In addition, we will randomly subsample 50 trees in each of the other eight mapped plots for C and N isotopic and elemental analyses. δ¹⁵N values measured in plant tissues provide insight into the relative contributions of N sources (i.e., fixed atmospheric N₂ vs. soil N) if the sources are isotopically discreet. While estimation of fixation by N-fixing trees in the field is difficult (reviewed in Höglberg 1997), we have already established the use of the ¹⁵N natural-abundance method at our sites (Fox-Dobbs et al. 2010). To strengthen our inferences, we will also include two additional components: we will increase the number of non-fixing C₃ reference plants (2-3 species) that are concurrently sampled with *A. drepanophyllum* (thus constraining the soil-N endmember in our fixation model); and, we will conduct a small ‘calibration’ study with a select set of *A. drepanophyllum* and non-fixing reference plants to directly measure the δ¹⁵N values of the plant-available (NO₃ and NH₄) soil N pool (following methods in Révész & Casciotti 2007 and Révész & Qi 2007; see letter of collaboration from Calla Schmidt).

Finally, we will measure herbivory rates and characterize the abundance and diversity of herbivorous arthropods living on *A. drepanophyllum*. Herbivory rates will be measured at two scales. At a broad scale, the % of leaves damaged on each tree will be visually estimated, as will % of total leaf area removed, the % of branch tips damaged by mammalian browsers, and the loss of large branches due to elephant feeding. For greater detail at a smaller scale, we will make digital micrographs of ten randomly selected mature leaves from each tree and count the number of leaflets lost to herbivores, thereby estimating leaf area lost; if and when possible, we will identify the insect herbivore guild responsible for the consumption. These surveys will each require ~ 10 person-days.

To characterize seasonal changes in arthropod communities, and how these changes relate to tree traits, we will conduct arthropod surveys at two-month intervals on a subset of 20 of our biogeochemically sampled trees in each plot (240 trees total; ~20 person-days/census). Arthropod abundance will be assessed using (a) visual surveys, which are particularly effective for cursorial and web spiders, and (b) beating surveys, which have been shown by Kuria et al. (2010) to be effective for herbivorous insects in this system. We will take particularly detailed data on three guilds of predators: cursorial spiders (mostly Salticidae), web-spinning spiders (mostly Araneidae), and the most common

vertebrate in our system, the arboreal gecko *Lygodactylus keniensis*. Once per year, ***outside the experimental plots***, we will calibrate our visual surveys on 25 randomly selected trees by first conducting visual surveys and then destructively sampling all arthropods using insecticide mist (Kuria et al. 2010). Gecko abundance will be assessed at the level of individual trees every 6 months, using exhaustive surveys (as in Pringle et al. 2010), and plot-level gecko censuses will be conducted using the Heckel and Roughgarden (1979) mark-resight method (as in Pringle et al. 2007; ~ 36 person-days/census). Finally, we will use stable-isotope analyses ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) to monitor seasonal changes in predator diet—particularly any short-term changes in the contribution of understory prey that might result from pulses of C₄ grass productivity in response to rainfall. We will collect samples of common spider species from each tree during surveys, along with tail tissue from geckos; these samples will subsequently be identified to species (for spiders) and analyzed for $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ following methods in Pringle & Fox-Dobbs (2008).

Additional experiments and observations:

1) We will use rubidium (Rb) and strontium (Sr) tracer studies to follow movement of biomass through trophic levels and across the termite proximity gradient (e.g., Berry et al. 1972, Hagler & Jackson 2001). A **pilot test** in our study site (March 2010), in which concentrated RbCl solution was applied to *A. drep.* leaves, confirmed both the uptake and the persistence for 3-4 months of an Rb label that was approximately five-fold greater than background levels in plants (K. Fox-Dobbs, *unpub. data*). Some of these tracer studies will be combined with fencing (see Expt. 2 below) to further refine estimates of movement. We will also use these tracer experiments to estimate the dispersal kernels for *A. drep.* seeds (Carlo et al. 2009, Waitman et al. 2012). For these studies, we will label (in year 1) the leaves of 12 groups of 5 trees (all within 3 m of one another), for a total of two groups at half of our focal mounds. One group will be close to the mound center (<5 meters), and one far (>20 meters); we will label one group of trees with Rb, and another group with Sr (Stadelbacher 1991, Fernandes et al. 1997). On half the mounds, we will use Rb on trees near to the mound center, and Sr far away, and on half we will reverse these positions. We will follow each mound with labeled trees for the duration of the study. Because tracer concentrations will decrease with time, we will reapply Rb and Sr labels three times per year. Around each group of labeled trees, we will establish one 20-m transect oriented directly towards and away from the nearest mound center, and another perpendicular to this. Sampling will be conducted at ~ 2, 4, 6, 10, 15, and 20 meters from the labeled group of trees (exact distances will depend on spacing of trees to sample). On the transects, we will collect *A. drep.* leaf samples and arboreal arthropods twice a year, as well as establish seed traps following fruiting events (~ 4 person-days/sampling).

2) We will use mesh fencing to reduce movement of arboreal species across the mound proximity gradient, allowing estimation of the extent to which movement of animals amplifies or dampens responses to tree traits. This manipulation will be nested within the tracer experiment (with 6 mounds randomly chosen for a movement-reduction treatment and 6 more chosen for a procedural control) and will consist of erecting 5-m high semicircular fences at a radius of 7 meters from mound centers (i.e., approximately on the mound edge). Fences will be covered with green nylon fine mesh, as is used around tennis courts to block wind. Although these barriers will not *eliminate* animal movement between near-mound and far-mound trees, they will significantly reduce movement between areas ‘near’ and ‘far’ from the mound edge. Procedural controls will consist of identical fencing infrastructure, but with only narrow horizontal strips of the same nylon mesh. If diffusive movement of herbivores or predators dampens the effects arising from spatial patterning of *A. drep.* characteristics, then these barriers should lead to more pronounced spatial differentiation in the arboreal community. Conversely, if aggregation onto trees near to mounds (via taxis, area-restricted search or other mechanisms) heightens community responses, barriers should lead to decreased differentiation; either response is possible for different components of the community. We will sample trees exhaustively twice yearly to investigate food web structure via $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ analyses (Pringle & Fox-Dobbs 2008) and will use Rb and Sr tracer data to more directly infer effects on movement rates (~ 10 person-days/sampling).

3) We will conduct fertilization experiments to experimentally create spatial variation in tree demography and in the arboreal community, as well as changing the spatial scale and patterning of tree

traits. These experiments will allow us to directly test some of the likely effects of termites on trees, as well as to perturb both the degree and patterning of individual tree variation and measure the effects on the arboreal community. We know from our **pilot data** that we can simulate termite mound proximity on *A. drepanolobium* through small-scale fertilization (**Fig. 4**). Although we cannot eliminate existing termite mounds and their effects, we will use fertilization to add new high-fertility areas that are (a) positioned to reinforce strong spatial pattern or (b) positioned to create a more random distribution. Either approach would independently accomplish the principal goal of experimentally manipulating the degree of spatial patterning, but our design provides a comprehensive test by creating opposite extremes of patterning. We will choose ten 200x200 m areas (enough to encompass ~15 real mounds) and map the locations of all *real* mounds within each area. We will then assign each area to have either randomizing additions of fertilization treatments or regularly patterned additions ($n=5$ additions in each treatment). To choose locations for randomizing fertilization patches, we will generate random coordinates and use Ripley's K statistics to choose the most randomizing set of positions (including both fertilization patches and real mounds in the analysis). To pick locations for fertilization in the regular-pattern treatment, we will similarly find positions that maximize the uniformity of fertilization patches and mounds. We will sample *A. drepanolobium* leaves, arboreal arthropods, and geckos at 50 random points within each plot before the manipulation to obtain a baseline, and twice annually after the fertilization treatments have been established (~60 person-days to establish the experiment).

4) Given a prior study showing that seed establishment can have strong effects on *A. drepanolobium* population dynamics (MacLean et al. 2011), but that was not conducted with reference to termite-mound location, we will out-plant seeds and seedlings both near (<5 m) and far (>20 m) from mound centers to test for patterns of establishment and the possible limits on seed and seedling survival in both locations. Out-planting will be done in years 1 and 2, and we will follow growth and mortality for up to 3 years.

5) Testing for genetic patterning of *A. drepanolobium* around termite mounds. We will conduct a second out-planting experiment to look for genetic effects on early survival and growth, and in particular for interactions between genetics and performance near or far from termite mounds. We will collect seeds from parent trees growing either at termite mound centers, or at least 25 meters from any mound. We will then out-plant both seeds and seedlings in caged common-garden plots, again placed either very near mounds or far from them. Our goal will be to collect a minimum of 1000 seeds from each of 20 parents for this experiment. Each set of seeds will be divided into 200 for greenhouse germination and outplanted as seedlings, and 800 for outplanting as seeds. We will outplant around 4 mounds, resulting in 8 caged gardens. This design is the best compromise that we can afford between (a) statistical power to detect family*treatment interactions and (b) logistical feasibility. We will retain tissue samples for determination (using microsatellite genotypes of mothers and offspring) of the relatedness of experimental individuals (as has been done for a related *Acacia* species at our study site: Ruiz-Guajardo et al. 2010).

6) Finally, we will leverage an 11-year-and-counting dataset on *A. drepanolobium* demography collected by our long-term collaborator Todd Palmer, which one of us (Doak) has already analyzed for other purposes (Palmer et al. 2010), by using high-resolution GPS to map the locations of the 1800 trees and all neighboring termite mounds, so that we can estimate how temporal variance in vital rates of trees and long-term dynamics of mutualistic ants is governed by termite mound proximity.

Population Model Development and Analysis: To build a population model for *A. drepanolobium*, we will first use generalized mixed models to quantify effects of size, termite proximity effects, ant mutualists and varying environment (e.g., rainfall) on survival, growth, and reproduction, and ant succession (cf. Palmer et al. 2010). We will also test for neighbor effects using spatial autoregressive methods, and will include neighbor densities as another state variable if supported. These analyses will result in continuous state variable functions for each vital rate, as well as estimation of a covariance structure for these rates. Analyses of Palmer's long term data set, in conjunction with our own data, will help estimate the covariance structure of rate parameters, which is necessary for building stochastic models and thus addressing population stability. Finally, we will fit dispersal kernels using our isotope data: these will

generate dispersal estimates that can be expressed as spatial movement, and also (with data from real or simulated termite mound distributions) as dispersal between regions of varying termite-mound effects.

With these vital rate functions, we will first construct an implicitly spatial integral projection model (IPM: Easterling et al. 2000, Ellner & Rees 2006, Rees & Ellner 2009). The approach taken in IPMs is to combine the functions for each vital rate into a single “kernel” that describes the expected number of individuals in a certain *state* next year from each *state* this year, where *state* can include multiple aspects of individual condition. For example, we can define a kernel $K(ht, tp; ht', tp')$ as the number of individuals generated by a tree of height ht and proximity to termite mound of tp that will be of height ht' and proximity tp' in the following year (most values will be zero, since trees don't move, and except for recruitment, all non-zero values will be probabilities). The resulting population model is then:

$$N(ht, tp, t + 1) = \int_{ht} \int_{tp'} K(ht, tp; ht', tp') N(ht', tp', t) dht' dtp'$$

For our actual system, state variables used to index tree state will include not only height and termite-mound proximity, but also species of ant mutualist and the random effects of annual climate variation (or climate indices: see Rees & Ellner 2009, Bakker et al. 2009). We will follow the approach of de Valpine (2009) to analyze the effects of individual variation on mean population growth rate. The de Valpine method is explicitly aimed at analyzing variation at development times, but is readily adaptable to the incorporation of other aspects of individual variation. This Monte Carlo numerical integration approach to calculating long-term growth rate, its sensitivities, stable age-stage distributions, and reproductive values makes for highly time-efficient model analysis and precludes the need for exhaustive simulations. Inclusion or removal of different effects in our vital-rate functions will allow us to test the strength of their effects on population growth and hence to address Questions 1-4. We will also use the approaches suggested in Rees and Ellner for analysis of the stochastic versions of this model.

In addition to our fully-parameterized IPM, we will construct two other sets of models. First, to look at the development and also the dampening of spatial structure in the *A. drepanoides* population, we will use our same vital-rate functions, along with our seed-dispersal kernel, to simulate the explicit spatial structure of trees on landscapes with realistically patterned mounds and different degrees of spatial randomness. These models will allow us to address Question 3, and will also provide a template upon which we can simulate community effects, as described below. Second, we will construct a series of reduced models, which will retain the IPM structure but reduce or eliminate size- and mutualist-generated structure, to arrive at more general results about the factors influencing Jensen's Inequality and Variance Reduction effects, and about how spatial patterning mediates these effects. We will adopt the approach of Vindenes et al. (2011) to formulate such reduced models from stochastic IPMs.

Community Effects Model and Analysis: In parallel with our population modeling, we will construct two models, one detailed and one more generalized, describing the propagation of individual variation and patterning effects in trees to the arthropod community. We will use the real and modeled landscapes of trees (including distances from mounds, sizes, densities) as a template upon which to simulate herbivore and predator responses. The results of our tracer and fencing experiments will provide us with estimates of intrinsic population growth rates near and far from mounds and also with movement probabilities. The approach we will take to these models is similar to those of population-level IPMs: we will define a kernel that is the expected number of individuals in a guild, or in some cases a species, found in a given *state* in each year. For these models, *state* will be defined as tree size and proximity to mounds. The models will of necessity be more phenomenological than the IPMs we develop for *A. drepanoides*, but will nonetheless share most of the same features and be amenable to similar analysis methods. We will also use tracer experiments and stable-isotope variation to estimate predator consumption rates. The model will therefore include growth rates of key herbivore guilds (e.g., chewing, sucking, and galling insects) on *A. drepanoides* of different quality (foliar N concentration), and the consumption of herbivores by at least three predator guilds (geckos, web-spinning, and cursorial spiders). We will simulate these dynamics to address Questions #5-7, focusing on how local effects of tree quality vs. movement at each trophic level serve to

dampen or reinforce patterning and mean abundance. We will also construct a much less detailed reaction-diffusion model for an idealized pair of predator-prey groups, living in a landscape with spatially determined prey growth rates. The goal of the analyses with these models will be to test how the shape and strength of spatial (which will determine prey growth rates) regulate both the patterning and the landscape-mean abundances of herbivores and their predators (addressing Questions 6 & 7).

Additional Analyses: In addition to the above analyses, we will also conduct a set of more straightforward statistical tests, including:

- Statistical characterization of the strengths of spatial structure in *A. drepanoides* physiology and demography, as well as comparison with the spatial characteristics of patterning in animal numbers/productivities. These tests will allow us to tie key traits of trees (N content, fixation rates) to demography and community dynamics. These results will also help guide development of the model just described, and depending on the results, could lead to state variables that encompass alternative measures of tree state, beyond location and size.
- Comparison of the patterning and mean landscape values obtained for various community measures in the control vs. experimental landscapes that we create in Experiment 3. We will not only test for treatment effects, but also use these results to assess the ability of our models to yield accurate, process-based descriptions of landscape-level effects of individual variation and spatial patterning
- Analysis of relatedness patterns among our sampled trees, in order to probe for evidence of local genetic adaptation. In addition, we will use straightforward tests of seed origin on location-specific growth and survival to look for local adaptation to the habitat variation created by termite mounds.

Synthesis: Our overarching goals are to provide both an empirically-based analysis of the effects of individual variation and spatial structuring, and also to develop a set of more generalized model results that predict generalities about these effects that can then be tested in a diversity of systems. Collectively, the analyses described above will provide two different ways to understand, predict, and test the effects of individual variability, spatial patterning, and their interaction. Development of population and community models will help us analyze how individual variation and its spatial structure influence population growth, population stability, and the abundance and diversity of the arboreal community. Our experimental work will generate some of the parameters needed for these models. Moreover, these experiments will allow direct tests of the strength of spatial patterning, as well as the dynamics of movement and trophic interactions, which have the potential to amplify or dampen the landscape-scale effects of individual variation. Finally, ‘down-sizing’ our parameterized models and analyzing their simpler, more general forms will generate predictions about the factors influencing the ecological importance of individual variation, and which of its aspects will exert the strongest influences in different settings.

BROADER IMPACTS

This project will have numerous broader impacts for both education and conservation.

Undergraduate and Graduate Education: One PI is at an Undergraduate Teaching Institution (U. of Puget Sound), and two are Beginning Investigators (Fox-Dobbs and Pringle). All three universities have strong undergraduate research programs, and we anticipate at least four undergraduate thesis projects *per year* associated with this grant (2 UPS, 1 Princeton, 1 Colorado). We will also use our large-scale experiments as a teaching tool in undergraduate field courses run at Mpala by Princeton, U. Wyoming, and U. Florida. We will train at least one Kenyan MS student, building scientific capacity in this developing country. Doak and Pringle will also each mentor at least one graduate student on this project.

Training of Kenyan Research Assistants: We will train and employ two local assistants at Mpala for all three years of the project. We have trained and employed a total of five such RAs since 2005.

Public Outreach: The PIs have been successful in disseminating their past results via popular media (numerous news reports, and Pringle’s work on the Kenya dwarf gecko was recently featured in the BBC’s *Secrets of Our Living World*). We will continue to work with journalists to this end, as well as participating in local outreach programs (e.g., “Discovery Days” for local Kenyan community members). Pringle will blog bi-monthly on the *Huffington Post* about emerging findings from the work.

Conservation: Despite growing recognition that individual variation and spatial structure are critical for population persistence, ecosystem stability, and ecological restoration (Zelder 2000, Sleeman et al. 2005, Brosi et al. 2008), we lack a detailed understanding in any system of how and why these effects operate and interact. Our work will build a transferrable, mechanistic understanding of these general effects, that can then be used to hasten restoration efforts.

K-12 Education: We have planned and budgeted for a clear and concrete outreach program for US students that is based (a) on the visually compelling aspect of our work (the ability to see landscape-scale spatial patterning in many communities: **Fig. 5**), as well as (b) the theme of interconnectedness within our system, in which the ecological linkages behind pattern generation are sometimes cryptic, requiring careful probing to understand (e.g., the use of stable isotope chemistry). We will utilize connections with colleagues to bring our research into three diverse educational programs that share similar missions: the Citizens of the World (CWC) school in Los Angeles (a K-3 charter school); the Tacoma Science and Math Institute (SAMI) in Tacoma, Washington (a public charter high school with high ethnic and socioeconomic diversity), and the Daraja Girls School in Nanyuki, Kenya (a secondary school for academically talented girls from impoverished families (see letters of collaboration from each institution).

Our plan comprises three sets of goals and specific activities. **First**, we will collaborate with K-12 teachers to develop age-appropriate curriculum units that emphasize interdisciplinarity, guided inquiry, and discovery-based learning (all increasingly regarded as essential by theorists of education). For example, high-schoolers might conduct in-class experiments and observations that illustrate the use of stable-isotope methods to ‘see’ underground and/or utilize the Google Earth tools we will develop (see below) to find and quantify landscape patterning in different parts of the world. **Second**, we will bring one teacher from each US school to our Kenyan sites for two summer weeks in each year. During the first week, teachers and students from Daraja will join the US visitors in participating in field work. During the second week, the PIs and postdoc will work with teachers to develop curriculum units rooted in the accessibility of patterning and individual variation as entry points into science; these units will be imported back to the US and presented to students in their classrooms. These field trips will also provide valuable professional enrichment for teachers themselves. Additional enrichment activities, such as ‘pen-pal’ exchanges of photographic science journals between US and Kenyan high school students, are possible and will be explored. Finally, 2 Tacoma students per year will be awarded 4 week paid internships to learn and complete biogeochemical analyses in Fox-Dobbs’ research laboratory at UPS. **Third**, due to the Kenyan academic schedule, Daraja students cannot proceed directly to university after graduating, but rather must take a ‘gap year,’ leading to high abandonment of collegiate ambitions by even the best students. We will hire one gap-year intern from Daraja in each year of the project, who will be trained as an RA and receive room, board, and stipend. One responsibility of these interns will be as liaisons to current Daraja students and teachers during field visits to our sites.

Citizen Science Exploration of Ecological Patterning: We will also develop a set of web-based tools to allow citizen scientists to look for, quantify, and catalogue spatial patterns on Google Earth. This activity addresses a

common concern with all work on spatial patterning (and brought up by one reviewer of our pre-proposal): How common *is* patterning, anyway? We aim to greatly expand the one existing, informal survey of patterned landscapes (Rietkerk & van de Koppel 2008) and to *quantify* these patterns. We will work with the Coordinator of Citizen Science Programs at the Univ. of Colorado’s Natural History Museum to develop the tools for this project, and after testing by our school groups, we will post it on citizen science websites (e.g., <http://www.scistarter.com/>, <http://www.citizensciencealliance.org>).

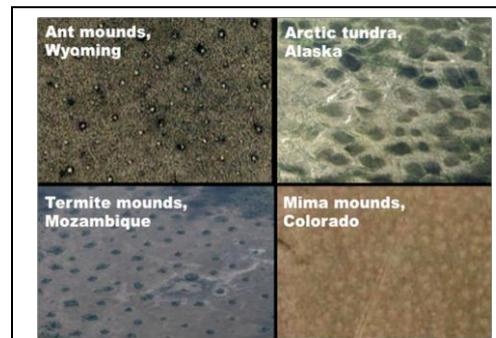


Fig. 5. Many patterned landscapes are easily visible in Google Earth and aerial photos. Four examples of patterned landscapes are shown, two created by social insects.