Interaction Cascades in Anthropogenic Glades

Adding Habitat Heterogeneity in an Otherwise Homogenous Landscape Across Multiple Spatial Scales and Trophic Levels

By

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ABSTRACT

Pastoralism was traditionally, and is currently, one of the most pervasive and widespread livelihoods throughout East African savannas. After abandonment, livestock corrals in East African savannas develop into nutrient-rich, treeless “glades” that persist for decades. Other research has shown that glades have significantly higher concentrations of soil nutrients including nitrogen, potassium and carbon, which support several specialist grass species, and turning these patches long-term primary productivity hotspots. Using detailed observations, extensive sampling, and experimental methods, we demonstrate that these effects on primary productivity cascade up two trophic levels to increase abundance of insects and the gecko *Lygodactylus keniensis*. Extending previous research, we find that *Acacia drepanolobium* trees close to glade edges are larger and grow faster than those farther from the glade. Furthermore, we demonstrate experimentally that grasshoppers grow significantly faster inside glades than far away from glade edges and that arboreal insect abundance, biomass and diversity show the same significant trend. Finally, we find that geckos are significantly more abundant in trees close to the glade edge than far away. Our results show that traditional pastoral methods have significant impacts on multiple trophic levels at multiple scales and add important habitat heterogeneity to an otherwise homogenous landscape.

KEYWORDS: Trophic interaction cascades, indirect effects, bomas, glades, gecko, *Lygodactylus keniensis*, Laikipia, Kenya.

INTRODUCTION

Interaction Cascades

Interaction cascades between species within and across trophic levels are critical to the composition and function of natural communities. Trophic cascades especially, which by convention occur when changes in the abundance of a carnivore affect the distribution and abundance of a plant community (Polis 1999, Schmitz et al. 2000), have been the subject of much interest, research, and debate over the last 40 years. These debates have largely taken two forms, one summarized by Strong's pithy question "Are trophic cascades all wet?" (Strong 1992) and the other, more fundamental to this research: "When is a trophic cascade a trophic cascade?" (Polis et al. 2000) Our study adds a new aspect to the literature on interaction cascades, and informs both of these questions.

Literature definitions of trophic cascades have varied over the last 40 years, sometimes encompassing more cases, and sometimes becoming narrower. Some authors have suggested that trophic cascades occur whenever there are indirect effects between two species mediated by an intermediate trophic level (Pace et al. 1999). This broad definition is the one that is most often taught in introductory ecology classes and includes a range of trophic interactions, but extends beyond the original intent of the term, to describe a strong effect of predators on vegetation communities by mediating herbivore populations (Strong 1992, Polis 1999, Chase 2000, Polis et al. 2000, Schmitz et al. 2000).

Polis (1999) suggested that there should be a distinction between species-level and community-level cascades. Species-level cascades occur within only a few nodes of a food web, so that changes in predator abundance affect one or only a few species of plant (Polis 1999, Polis et al. 2000). In contrast, predators in a community-level cascade significantly affect the composition and distribution of plant biomass throughout an entire ecosystem (Polis 1999, Polis et al. 2000). This distinction has been now largely accepted in the scientific community (Schmitz et al. 2000, Shurin et al. 2006).

The vast majority of early trophic cascades identified and studied were in streams, lakes and intertidal zones, leading some to argue that true community-level trophic cascades were restricted to aquatic ecosystems (Strong 1992, Chase 2000, Polis et al. 2000, Shurin et al. 2002, Shurin et al. 2006). Several reasons have been offered to explain this pattern, including that terrestrial ecosystems tend to be more diverse, and so indirect effects are buffered through multiple nodes in a trophic web (Strong 1992, Chase 2000, Shurin et al. 2006). While many authors have since described terrestrial trophic cascades (Schmitz et al. 2000, Norrdahl et al. 2002, Krebs et al. 2003, Gruner 2004, Pringle et al. 2006) most of these have been criticized as being species-level trophic cascades, and hence, “trophic trickles,” (Strong,1992).

Studies to date have been largely biased towards top-down effects, focusing on the impact of predator loss on communities, without as much interest in bottom-up effects rising to higher trophic levels (Kagata and Ohgushi 2006). Despite the relative dearth of studies specifically looking at bottom-up effects, most trophic cascade researchers seem to agree that bottom-up forces should be the null hypothesis of food webs and likely determine the maximum productivity of an ecosystem (Strong 1992, Gruner 2004, Kagata and Ohgushi 2006). Top-down effects balance these bottom-up effects and the relative strengths of the two forces will determine the dynamics of the community. The critical difference between these two forces though, is that top-down effects “switch sign” between adjacent trophic levels, meaning that positive effects on one level will result in negative effects on the level immediately below. In contrast, bottom-up cascades share signs through all the levels, meaning that an increase in the base trophic level will result in similar increases in all trophic levels above (Herendeen 1995). Because bottom-up cascading effects can raise or lower all other trophic levels in an ecosystem, they can have profound effects on the function and dynamics of that community. This study describes a strong, bottom-up interaction that we argue is among the very few examples of terrestrial, community-level trophic cascades.

Anthropogenic Glades

Nomadic pastoralists have used the savannas of East Africa for several thousand years and traditionally corral their livestock overnight in pens, called bomas (Western and Dunne 1979, Young et al. 1995, Augustine 2004, Porensky 2011). These bomas are ringed with thorny *Acacia* trees removed from their interior and protect their occupants from predators and stock raiders while preventing livestock from wandering during the night (Western and Dunne 1979, Stelfox 1986, Porensky 2011). Bomas are most frequently occupied by cattle, though goats, sheep, and sometimes donkeys or camels were also sometimes penned in smaller enclosures within a boma (Western and Dunne 1979).

Because livestock forage in surrounding areas during the day but then deposit dung over night inside a boma, urine and dung tend to accumulate, fertilizing these small patches (Western and Dunne 1979, Blackmore et al. 1990, Young et al. 1995, Augustine 2004, Muchiru et al. 2009, Porensky 2011). Eventually, when after several months, nearby vegetation becomes depleted, the boma is relocated to a new area (Western and Dunne 1979, Porensky 2011). Following boma abandonment, grasses capitalizing on the abundant nutrients colonized these areas creating high productivity hotspots called “glades” (Stelfox 1986, Young et al. 1995, Augustine 2003, Muchiru et al. 2009).

Traditional Maasai (or more correctly in our study region, the Laikipiak and the Purko-Kisongo (Young et al. 1995)) pastoralists’ presence in this area has significantly decreased in the last 200 years due in part to rinderpest outbreaks, intercine warfare and treaties that allowed European settlers to claim much of the land for large private ranches (Young et al. 1995)). Despite the change in occupants, by and large, European settlers continued using these traditional ranching methods, penning cattle in bomas and relocating them every several months. Today, ranches still employ many of these same techniques, though lightweight, re-usable metal fences are in some places replacing the toilsome *Acacia* walls (Mike Littlewood, Mpala Conservancy Manager, personal communication). Due to the wide use of this management technique, and the fact that these nutrient-rich patches persist for decades or even a century, glades are an important landscape feature of savanna habitats throughout the Laikipia valley of Kenya (Stelfox 1986, Young et al. 1995, Turner 1998, Augustine 2003, Veblen and Young 2010, Porensky 2011).

Glades vary in size but most are between 40 and 120 m in diameter with a total area between .15 and 1.3 ha (Western and Dunne 1979, Young et al. 1995). Glade vegetation is dramatically distinct in structure and color from the surrounding savanna and tends to have sharply demarcated borders, making glades readily apparent. They are characterized by a complete absence of trees or shrubs, and are instead covered by dense, and frequently lush, grasses (Young et al. 1995).

Young and colleagues (1995) demonstrated that glades are greener and lusher than the surrounding landscape because of the high soil nutrient concentrations stemming from the livestock manure. Soil nitrogen, potassium, carbon, calcium, and sodium concentrations are highest inside glades, and progressively decrease with distance from a glade edge (Young et al. 1995). Interestingly, phosphorous, magnesium and manganese are not elevated in glades but are instead significantly lower than in surrounding areas (Young et al. 1995). Nonetheless, due to the lush growth, glades are thought to be important productivity hotspots in the East African savanna.

Glades in this ecosystem are dominated by two species of grass, *Cynodon plectostachyus* and *Pennisetum stramineum* (Young et al. 1995, Augustine 2003, Veblen and Young 2010, Porensky 2011). *C. plectostachyus* dominates in young glades is graduatlly replaced by *P. stramineum*, a late-dominant species (Veblen 2008, Veblen and Young 2010). This succession is mediated by the herbivores grazing in these bomas. Preferential grazing by large native ungulates reinforced the early-glade species *C. plectostachyus* by suppressing the invading grass species *P. stramineum* maintaining glades in their early-successional stage (Veblen and Young 2010). On the other hand, cattle and megaherbivores, particularly elephants (*Loxodonta africana*) preferentially graze on *C. plectostachyus,* thus hastening the succession from early to late stage glade vegetation (Veblen and Young 2010).

These previous studies therefore suggest that anthropogenic glades are both hotspots of primary productivity and important features in the savanna landscape. Our research extends these results by investigating how this nutrient influx can have cascading effects on higher trophic levels. Specifically, we hypothesize that the presence of abandoned bomas, will affect secondary consumers, particularly insect herbivores, as well as their predators, insectivorous geckos. We also predict that these effects will be strongest near glades and will become attenuated with increasing distance from a glade's edge.

Habitat heterogeneity in a homogenous landscape

Vegetation in the study area is dominated by the ant-acacia, *Acacia drepanolobium*, which accounts for more than 97 percent of the overstory cover (Young et al. 1997). The resident ant species on these ant-acacias, RRB (*Crematogaster mimosae*), BBR (*Crematogaster nigriceps*), TP (*Tetraponera penzigi*) or AB (*Crematogaster sjostedti*) are intricately intertwined with the acacia and are critical to its life history (Palmer et al. 2000, Palmer 2003, Palmer et al. 2003, Palmer 2004). In addition, only five grass species and two forbs account for more than 90 percent of relative ground cover (Young et al. 1998). This habitat's low diversity relative to other tropical terrestrial ecosystems can be attributed to the flat topography, as well as the extreme growing conditions due to the high clay content in the prevailing "black cotton" vertisol soils. This clay reduces water infiltration and causes severe shrink-swell dynamics which can shear plant roots (Darlington 2005, Pringle et al. 2010). This habitat type, called black cotton savanna, is widespread through much of East Africa, covering hundreds of thousands of square kilometers. In this extremely homogenous habitat, any spatial heterogeneity created by anthropogenic activities, especially if it penetrates to higher trophic levels is likely going to be very important for biodiversity.

Our primary research species, the Kenyan dwarf gecko (*Lygodactylus keniensis*) is the most common lizard in this area, comprising more than 90% of all individuals (Pringle et al. 2007). In some places *L. keniensis* density approaches 1000 individuals per hectare, making it the most abundant vertebrate in this habitat (Pringle et al. 2007, Pringle 2008). This gecko is small (~3 - 4 cm snout-vent length, ~1-2 g), strictly arboreal and highly territorial (Greer 1967). Adult males are easily distinguished by a chevron-shaped row of pre-anal pores and can command territories that span several trees with overlapping canopies, and which can include multiple females and subadults (Greer 1967).

L. keniensis is diurnal and feeds exclusively on tree-feeding insects (Pringle and Fox-Dobbs 2008) with the important exception of the *Acacia*-ants (Greer 1967). Small (3 – 30 mm length) arthropods comprise the majority of the geckos' diet (Greer 1967). This species has a preference for beetles (Hardy and Crnkovic 2006, Pringle et al. 2007), though its diet does include other arboreal insects ranging from small diptra to large mantids (Greer 1967). When disturbed, these geckos will flee to the grassy understory or refugia in dead galls or crevices in their tree, but if left undisturbed they will remain on individual trees for extended periods of time (Greer 1967, Pringle 2008). Their primary predators are bushbabies (*Galago senegalensis*), snakes, and birds (Pringle et al. 2007).

This study investigates a bottom-up interaction cascade driven by the presence of anthropogenic glades. We are particularly interested in the three trophic levels of this interaction cascade; primary producers and secondary and tertiary consumers with special emphasis on the gecko *L. keniensis*, the most numerically dominant vertebrate in this ecosystem. We investigated several questions relating to the different trophic levels involved. First, are the increased nutrient levels around glades associated with increases in primary productivity? Second, does herbivore biomass change with increasing distance from glades? More specifically, do grasshopper growth, diversity and abundance change inside of glades and far from glade edges? Similarly does the diversity and abundance of flying and arboreal insects change with proximity to glade edge? Third are there differences in tertiary consumer abundance, specifically the gecko *L. keniensis* as a function of distance from a glade edge? Fourth, do glades in close proximity to each other have interacting effects that alter any patterns found in primary, secondary and tertiary productivity? Finally, to what extent are these interaction effects altered by a rainfall gradient and what implications does that have on this system as climate change projections predict dryer, hotter spells in this ecosystem in the near future?

METHODS

Transects

Yo investigate the effects of glades on the trophic interactions described above, we created a total of 18, six-meter wide transects, incorporating four different experimental treatments. Three transects spanned the shortest distance between two paired glades, by definition within 150 m of each other. The length of these transects was determined by the glade edges (where trees began) and ranged from 105 meters to 135 meters. Four additional transect pairs were created on four isolated glades more than 250 meters from any other glade edge radiating from theedge of each glade in randomly chosen directions. All isolated glade transects were 100 m in length.

This experiment had two sets of controls. Four, 100 m transects created by LMP (described in Porensky 2011), were positioned in the study area in the vicinity of the other transects, but more than 250 m from any glade. They served as a baseline for the general vegetation of the area. We also used three glade controls to test the effect of large treeless gaps in this ecosystem. Three treeless patches were created, approximately 60 m in diameter by the author CR in 2006 to resemble glades without the high nutrient input of the cattle. All trees in clearing were cut and stumps were painted with undiluted Tordon (picloram) resulting in near 100% mortality without affecting grass (see CR in prep for details). Single 100 m transects were established at each of these sites in a randomly selected direction.

Finally, all selected glades were situated along a five km long rainfall gradient and within three distinct blocks; North (low rainfall), Central (intermediate rainfall), and South (high rainfall). Each block contained at least one replicate of each treatment (see Map 1).

Tree distribution, Growth and Resident Ant Species

On each transect, we tagged every tree greater than one meter in height and within three meters of the transect centerline. For each of these trees, we measured height and circumference 15 cm above the ground. We also recorded the distance from the glade edge along with distance from the transect centerline were also recorded. Distance from the edge was measured to the nearest five cm and distance from the transect centerline was estimated by CMD. Estimated measurements to the nearest 25 cm were accurate more than 95% of the time when checked on a subsample of the total trees measured. We recorded data on tree morphology, as well as colonizing ant species for a total of 1031 trees on the study transects.

Tree Growth

To quantify tree growth, we affixed, between June 08 and June 18, 2010, two, ten cm long cable ties 15 cm from the ends of two branches on each of 170 randomly selected trees growing at varying distances from glade edges and dispersed through the four glade treatments. On August 03 through August 12, 2010, these cable ties were recovered and the new distance from tie to branch tip was recorded to measure growth throughout the summer.

Grasshopper surveys

To estimate the diversity and abundance of grasshoppers we conducted surveys in the isolated glades over the course of several evenings in July 2010. Evening times (between

17:30 and 19:30) were chosen because lower temperatures reduced grasshopper activity, therefore facilitating sightings and capture. In each isolated glade we threw a one m square frame at random locations near the center of the glade, along the edge of the glade, and 100 m from the center of the glade. Within those one m squares we captured all grasshoppers by hand for further analysis. Presence of any grasshoppers not captured was recorded although this occurred only rarely. This procedure was repeated twelve times in different isolated glades over several consecutive nights. Grasshoppers were then taken back to the lab, massed and identified to morphospecies.

Grasshopper enclosures

In order to determine any possible effects of glades on grasshopper growth rates, eighteen grasshopper cages were created measuring 70 cm by 70 cm at their base by 70 cm height (Figure 5). The cages were framed with thin welded iron and covered with a single sheet of thule mesh with 2 x 2 mm holes. This mesh was attached to the cage frame with wire and carefully checked to ensure there were no potential egress points for grasshoppers.

Six cages were set up at each of three isolated glades in the north, central, and south blocks. At each glade three arbitrary sites were selected by tossing of a square towards the approximate center of the glade. Three more sites were selected by randomly throwing a quadrat into the savanna 100 m away from the glade edge along a randomly chosen transect. We secured the edges of each cage by digging a 10 cm deep trench and burying the bottom of the enclosure frame into the trench to prevent the escape of any grasshoppers. All arthropods were removed from within the cage before the start of the experiment.

Each enclosure was stocked with 12 grasshoppers, each weighed and individually marked with sharpie permanent marker. Because we were unable to capture sufficient individuals of the same species for all cages, to avoid selecting specialist grasshoppers that may bias the experimental outcome, we used a diverse sample of species captured in immediate proximity to the cages with a preference for early-instar individuals (0.25 – 0.75 g). One of the three cages in both the center and the far sites in each glade was collected after one week and the remaining four at each site were collected after two weeks had elapsed. The final wet and dry masses of all of the grasshoppers were recorded.

Flying Insect Surveys

We sampled the flying insect community by preparing and deploying sticky traps. At each of the isolated glades and each of the cleared control glades, we created a new random 90 m transect beginning at the glade edge. At 0, 30, 60 and 90 meters from the edge, four sticky traps were hung from four different trees in that immediate area. The sticky traps were made by applying Tanglefoot Insect Barrier® on to blue, yellow, green and red 7.5 by 12.5 cm index cards, with one of each color represented at each distance to prevent card color from biasing the results. The traps were allowed to hang in the open for 72 hours before being collected. Trapped insects were identified to family and counted.

Arboreal Insect Surveys

Fifty trees less than two meters in height were selected randomly at varying distances from our four isolated glades. At each tree a thin plastic drop sheet was wrapped tightly around the tree trunk and spread to cover all of the ground under the tree's canopy. Using a hand-pump knap-sack sprayer, approximately 300 to 500 ml of insecticide (alphacypermerthrin 100 g/L diluted in water at a ratio of 5ml per 10 L) was sprayed in a fine mist over the entire tree (after Kuria et al. 2010). The tree was then watched for 25 to 35 minutes and all non-ant invertebrates killed by the insecticide were collected in plastic vials.

Resident ant species, tree height, tree circumference and distance from glade edge were recorded for each tree. All insects were sorted in lab by order, counted, dried for three days and then weighed. Length and width measurements of the insect body, not including legs, were also taken for approximately the first 550 individuals collected so that, assuming the insect could be approximated as an oval, individual surface areas could also be taken into account in our analyses.

Lizard Surveys

Between June and August 2010 (June 19 – 30th, July 14 – 22nd, August 3 – 12th) we conducted three *Lygodactylus keniensis* surveys of every tree located on the study transects. Trees were exhaustively searched using ladders and long poles to probe every branch and any crevasses. Total lizard biomass for each tree was calculated by multiplying lizards counted with average gecko weights (calculated from measurements of 277 individuals (125 males, 96 females, 56 juveniles) captured between June 2006 and February 2008 by RMP).

STATISTICAL ANALYSES

Linear regression and ordinal logistic regression analyses were used to determine the relationship between distance from glade edge and a variety of parameters of interest including tree size, flying insect abundance, arboreal insect diversity and lizard abundance. Because there was a great deal of variability in lizard occupancy count data with many trees having zero, one, or two lizards and a few trees having over twelve, we created an ordinal series, reclassifying lizard abundance in each tree where average abundance of zero equals zero, between zero and one equals one, between one and two equals two, between two and three equals three and greater than three equals four. We then used ordinal logistic regression of lizard abundance, against the natural logarithm of distance from the glade (which was shown to be the best transformation) to determine if distance from glade was a strong predictor of lizard abundance. ANOVA tests were also conducted to make comparisons, for example, between transect types, or grasshopper growth. All of these analyses were conducted using JMP 8.0.2 from SAS Institute Inc.

In order to further refine our analysis we asked the question 'what parameters best predict the average total number of lizards in a given tree?' In order to answer this, we developed a list of 32 candidate models containing every combination of five explanatory variables decided upon *a priori* based on previous research (Pringle et al. 2010) and knowledge of the system. Three of the five parameters were, tree surface area (which was estimated by approximating the tree as a cylinder with base equal to the circumference of the tree trunk at 15 cm and height of the tree), distance from the nearest termite mound, and resident ant species, all of which have been shown to be significant predictors of lizard abundance. To this list we added block which was a random effect variable corresponding to transect position along the north to south rainfall gradient, and distance from glade edge. Upon examination of the shape of the relationship between the ordinal average total lizards and each response variable we amended our list of 32 candidate models to include two linear transformations: the square root of surface area and the natural logarithm of distance from the glade edge to improve fit. Using AICc we ranked the 32 models and drew conclusions based upon their relative weight following (Burnham and Anderson 2002). Finally, using our best model, we generated a series of expected lizard abundances for each tree on each glade transect. We then averaged the expected and the observed number of lizards for each 10 m subset of each transect, plotted them against each other and compared them to a 1:1 line to assess the goodness of fit of the model.

RESULTS

Primary Productivity

Glade proximity affected vegetation structure and productivity in multiple ways. *Acacia drepanolobium* trees close to glade edges had on average significantly larger surface areas than those trees far (100 m) from the glade (RSquare = 0.0233, F Ratio = 14.2836, p=0.0002, N = 602) (see figure 1). This trend was due to parallel significant trends between distance and both tree height and tree circumference (tree height: RSquare = 0.00695, F Ratio = 4.2015, p=0.0408, N = 602, tree circumference: RSquare = 0.0423, F Ratio = 26.4987, p <0.0001, N = 24).

We also found a significant negative relationship between tree growth rate (mm/day) and distance from glade edge (RSquare = 0.0520, F Ratio = 5.2682, p=0.0239, N = 98)(Figure 1b). No such trend was evident in the cleared control treatments. Finally, after weighing all standing aboveground biomass in the 70 cm plots at the conclusion of the grasshopper growth experiments, we found that there was significantly more standing biomass inside of glades than 100 m from a glade edge (FRatio = 24.499, p < 0.0001, N = 24) (see Figure 2).

Secondary Productivity

Grasshoppers

Although there were no significant differences in the number of grasshoppers caught in one-meter quadrates in the center of glades, at glade edges and far from a glade edge (ANOVA, p = 0.6058, n = 12) we found a marginally significant trend in biomass. Grasshopper biomass was highest in glade centers, intermediate in glade edges and lowest

100 m away from glades (F Ratio = 4.109, Probability>F = 0.0517, observations = 12) (see figure 3).

Grasshoppers raised in cages in the center of glades grew faster than grasshoppers raised in cages far from the glade edge when their total growth was standardized by the duration of time spent in the cage (ANOVA, F Ratio = 8.3248, Probability>F = 0.0067, observations = 37) (see figure 5). While grasshoppers in cages inside of glades gained mass on average over the study period, grasshoppers far from glade edges actually lost mass on average over the study period.

Flying Insect Surveys

We found no difference in the number of insects captured on sticky traps of different note card colors, leading us to reject the possibility that a color preference could have biased our results (ANOVA, p=0.6643). We also did not detect any difference in the total number of flying insects or total flying insect diversity between cards at the glade edge, and 30, 60 or 90 meters away from the glade edge. Furthermore we did not find a statistically significant difference in the total numbers of insects found or orders represented between the isolated glades, cleared controls, or control transects.

Arboreal Insect Surveys

There were several statistically significant relationships between distance from a glade edge and the arboreal insects recovered from the tree fogging surveys. First, insect counts were significantly higher close to a glade edge than they were far from the edge (RSquare = 0.2158, F Ratio = 12.933, p=0.0008, n = 49) (see figure 6). Furthermore, the average total biomass and the sum total surface area of the insects captured was significantly greater close to a glade edge than farther away, (Biomass: RSquare: 0.2202, F Ratio: 13.271, p=0.0007, n = 49, Surface area: RSquare =0.1949, F Ratio = 11.3742, p=0.0015, n = 49) (see figure 6). There was significant difference in insect order diversity (RSquare = 0.2782, F Ratio = 18.119, p<0.0001, n = 49) with an average of approximately five insect orders represented on trees at the glade edge versus approximately two, 100 meters from a glade (see figure 6).

Tertiary Productivity

Geckos and Glades

Finally, there were significantly more lizards per tree and significantly more lizard biomass close to glade edges than there were 100 meters from a glade (Average Total Lizards per tree: RSquare = 0.0218, F Ratio = 13.3854, p=0.0003, n = 602. Average Total Biomass per tree: RSquare = 0.02238, F Ratio = 13.733, p=0.0002, n = 602). In trees close to the glade edge, on average over three surveys, every tree was occupied by at least one lizard. That average dropped by half 100 m from a glade.

Using ordinal logistic regression of lizard abundance, against the natural logarithm of distance from the glade we found that the distance of glade was still a strong predictor of lizard abundance especially for the higher classes of lizard abundance: two or more average lizards per tree, were particularly strongly affected by distance from glade edge (R Square (U)= 0.013, Probability>ChiSq <0.0001, n = 602) (see figure 7).

Modeling the ordinal average total number of lizards in a given tree

Using Akaike's Information Criterion (AIC) analysis (Burnham and Anderson, 2002) we found the best model of the ordinal total lizard abundance in a tree included in order of importance, tree surface area, distance from glade, distance from termite mound, followed by resident ant species. This model achieved an Akaike Weight value of 0.4786 and the only difference between the best model and the second best model was the block term, a random effect parameter, which appeared to be least important. All subsequent models after this had a ΔAIC greater than two and so had much less confidence for predicting lizard abundance. Please see Table 1 for results.

We calculated predicted values for ordinal average number of lizards according to the best model identified by AIC analysis for each tree in the dataset and then averaged the expected and observed ordinal number of lizards for each ten meter segment of transect and plotted the average observed value against the average predicted value for each segment. A 1:1 line to this scatter plot fit the data well (RSquare = 0.3676, $P < 0.0001$, Observations = 88) (see figure 9)

Comparisons between Glade Types

On average, the total number of lizards per tree was significantly higher in isolated glade transects than in cleared, control or paired transects, which were all statistically indistinguishable (F Ratio = 9.6543, Probability>F <0.0001, n = 928)(see figure 8). Average total lizard biomass followed this same trend (F Ratio = 10.9623, Probability>F <0.0001, n = 928). Furthermore, trees in isolated glades were significantly more likely to be occupied by lizards than trees in other glade types (RSquare (U) = 0.0224, Likelihood Ratio: <0.0001, Pearson <0.0001, n = 928)(see figure 13). Finally, the ordinal (as described earlier) probability of occupancy of any given tree was significantly higher in isolated glade transects than in any other transect type (RSquare (U) = 0.0219, Likelihood Ratio: <0.0001, Pearson <0.0001, n = 928).

Comparisons between blocks

The effect of block on these three trophic levels was highly variable. Trees were on average significantly taller in the north block than trees in the central block, and these in turn were significantly taller than trees in the south block (RSquare: 0.04266, F Ratio = 22.907, $p < 0.0001$, n=1031). The trend though was not as strong for tree circumference or surface area where north and central blocks were indistinguishable and the south block was slightly lower (Circumference: RSquare = 0.0568, $p < 0.0001$, Surface area: RSquare = 0.05607, $p < 0.0001$, n=1031). In contrast to tree size, average tree growth for all trees measured followed the opposite patterns being highest in the south block and no difference was detected between the north and central blocks (RSquare = 0.061, $p = 0.00064$) but tree growth in isolated glades, where tree growth should be most spurred by increased nutrient concentrations was statistically the same across all three blocks. Likewise, we found no significant effects of block on flying insect or arboreal insect abundance or diversity. Finally, on average, there were no statistically significant differences in average lizard abundance per tree between the three blocks.

DISCUSSION

Our results demonstrate how anthropogenic glades widespread through East African savannas have bottom up effects that reach across multiple trophic levels. We show that the nutrient inputs originating from such anthropogenic glades have positive effects not only on vegetation structure and productivity, but also on primary consumers, as well as their vertebrate predators (the gecko *L. keniensis*). This spatial variation in the density of primary and secondary consumers adds important heterogeneity to these populations in an otherwise homogenous landscape and is a clear example of a bottom-up community-scale trophic cascade.

Our results expand on the previous research, which demonstrates that glades are hotspots of primary productivity (Young et al. 1995, Augustine 2003, Veblen and Young 2010). We found that *Acacia drepanolobium* trees were both larger and grew significantly faster closer to glades than far away. Furthermore, we found significantly more standing above ground biomass inside of glades than 100 meters from glade edges. These results add to the existing body of evidence indicating that glades are critical hotspots of primary productivity in African drylands.

Our data also show that the effects of primary productivity of glades cascades extend up two additional trophic levels, to primary and secondary consumers (arthropods and geckos respectively). Grasshoppers penned in enclosures grew faster inside of glades than 100 m away from glades edges. While we didn't find significant differences in the diversity and abundance of flying insects using the sticky trap study, we did find significantly more arboreal insect biomass and diversity at glade edges than 100 m from glades. Additional experiments will be needed to identify the mechanism causing this pattern, though one potential answer could be differences in C:N ratios making *A. drepanolobium* leaves close to glade edges better forage than those farther away (Gruner, 2004). Gruner found that fertilizing nutrient-poor lava flows in Hawai'i significantly increased the growth rate and foliar nitrogen concentration in the dominant tree, *Metrosideros polymorpha*. He also found that this increase in tree growth and forage quality increased the abundance of arthropods feeding on these trees (Gruner 2004). It is possible that a similar mechanism might be operating in this study-site.

Finally, we found that *Lygodactylus* lizards were significantly more abundant near glade edges than they were farther away. Several, not mutually exclusive mechanisms could be contributing to this trend, including increased abundance of arboreal insects near glades, increased average tree size near glades, or differences in the proportions of the four acacia-ant species. Our AIC analysis tested these last two hypotheses and found that three factors (distance from glade, tree surface and ant identity) together were better predictors of gecko abundance per tree than any one of the factors alone, suggesting that all three mechanisms contribute to the pattern. Previous studies have demonstrated the importance of tree size, distance from termite mounds and resident ant species on *Lygodactylus* abundance in this landscape (Pringle et al. 2010) and so it is significant that to this list we can add distance from a glade edge, our parameter of interest.

While there are some significant differences in vegetation type between blocks, with trees being tallest in the northern (driest) blocks and growing fastest in the southern (wettest) blocks, the majority of the effects measured in this experiment, particularly in secondary and tertiary productivity, were indistinguishable between blocks. This is likely due to the relatively small difference in the precipitation gradient between north and south. Indeed, five km was the maximum distance available at this study site but turned out to be too small to measure the landscape scale rainfall gradient, which is most apparent one order of magnitude larger. While productivity is correlated with rainfall in many other tropical areas, this experiment would need to be replicated across more significant environmental gradients to thoroughly assess the effects of these variables on this interaction cascade and to draw any conclusions about the potential effects of climate change on these indirect effects.

Most community-level trophic cascades are found in aquatic ecosystems (Strong 1992, Chase 2000, Polis et al. 2000, Shurin et al. 2002, Shurin et al. 2006). While there are many examples of terrestrial trophic interactions with statistically significant impacts on some species within multiple trophic levels (Schmitz et al. 2000, Norrdahl et al. 2002, Krebs et al. 2003) These studies have come under fire by Strong, Polis and others as insufficiently critical to ecosystem function to warrant the term (Strong 1992, Polis et al. 2000). Polis et al. go one step further in demoting previously cited terrestrial cascades by outlining several key criteria that seem to be necessary to facilitate a true trophic cascade on land or in water. These are: (1) The system must be relatively discrete and homogenous; (2) prey populations dynamics must be fast relative to the predator dynamics; (3) the predator's prey must be common and more or less uniformly edible; and (4) the ecosystems are relatively simple and trophically stratified with strong interactions between species. Upon closer examination of these four criteria, this system qualifies as a significant terrestrial bottom-up trophic cascade.

Indeed, the black cotton savanna is highly homogenous habitat with only one species of tree, five species of grass and two forbs making up the vast majority of the plant species portfolio (Young et al. 1997, Young et al. 1998), thus clearly satisfying condition one. It is also clear that the reproductive cycle of the insects, typically on the order of months, is significantly shorter than that of the lizards. While no studies have yet to elucidate the life expectancy of these geckos, it can reasonably be assumed to be several years and therefore significantly longer than that of its prey. The arboreal insects available to this generalist and opportunistic gecko are very common and range through several insect orders, (Greer 1967, Hardy and Crnkovic 2006, Pringle et al. 2007). Finally, while this ecosystem's entire food web is complex with important dynamics mediated by the large mammalian grazers, this particular portion of the food web is very clearly stratified and is relatively simple so that positive or negative pulses in the system will have strong rippling effects across multiple trophic levels. Satisfying Polis' criteria and because we've demonstrated these anthropogenic glades have significant effects on the distribution and abundance of multiple taxa on multiple trophic levels, strengthens the argument that this interaction chain is indeed an example of a *bona fide* terrestrial trophic cascade..

Black cotton savannas are extremely widespread throughout east Africa and these traditional pastoral techniques are still being used on ranches throughout this range. Because glades persist for decades, or even as much as a century, and because they have significant effects on primary, secondary and tertiary productivity they add important spatial habitat heterogeneity to this landscape significantly affecting this landscape's community composition and ecosystem function.

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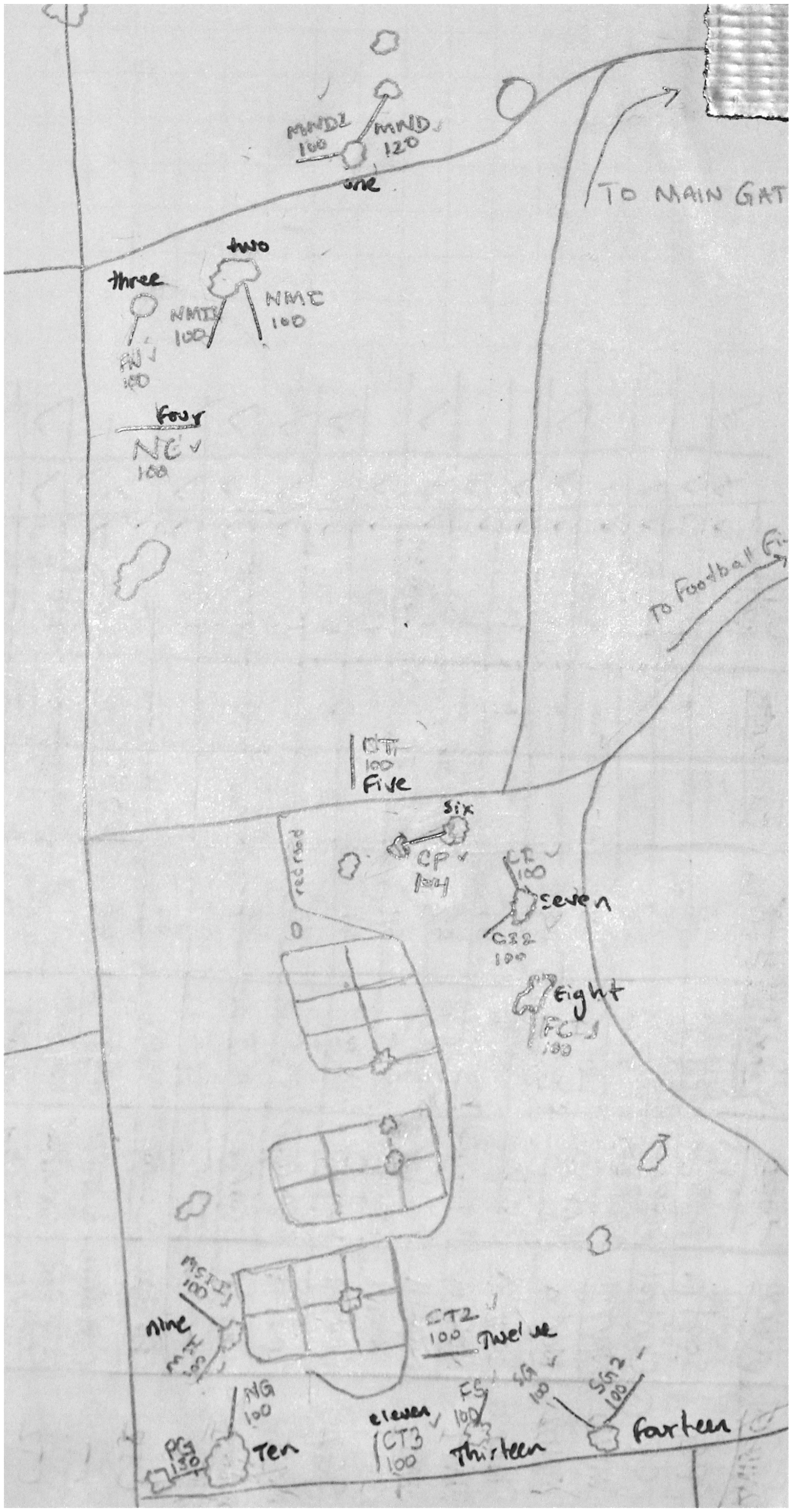


Map 1: Hand drawn map of all of the transects.

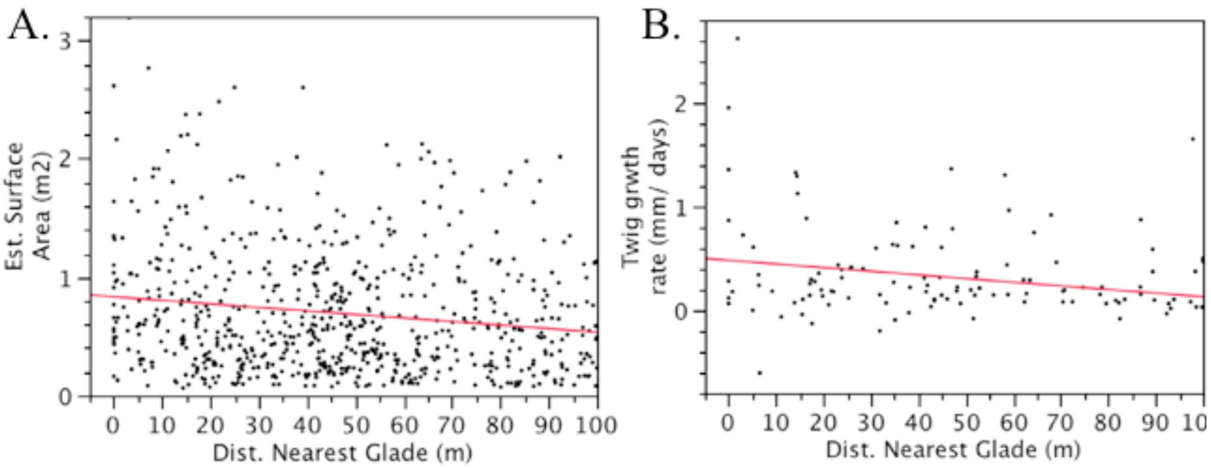


Figure 1: (A) Relationship between estimated tree surface area and distance to the nearest glade. Tree surface area was calculated by approximating a cylinder using tree base circumference and height. Distance from nearest glade only accounts for trees in isolated and paired glade transects. There was a significant negative trend (RSquare = 0.0233, F Ratio = 14.2836, p=0.0002, observations = 602). (B) Relationship between estimated twig growth rate as a function of distance from the Nearest Glade. There was a significant linear relationship (RSquare = 0.0520, F Ratio = 5.2682, p=0.0239, observations = 98).

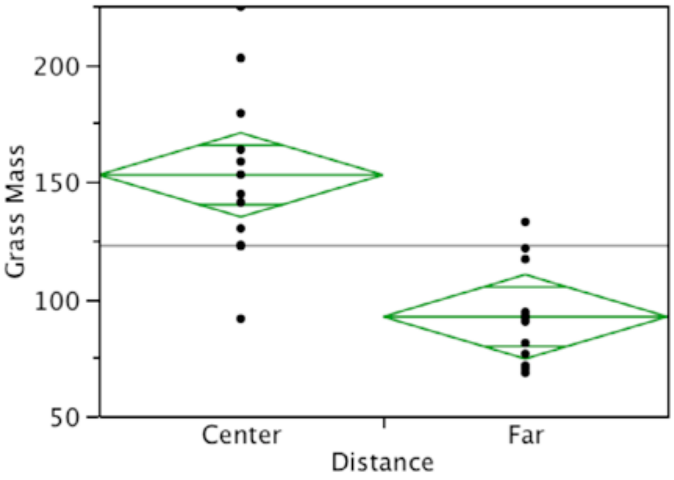


Figure 2: Analysis of variance in standing aboveground biomass between 80cm plots in the center of a glade and 100 m from a glade edge. There was significantly more standing biomass inside glades than far away (F Ratio = 24.499, Probability>F <0.0001, observations = 24).

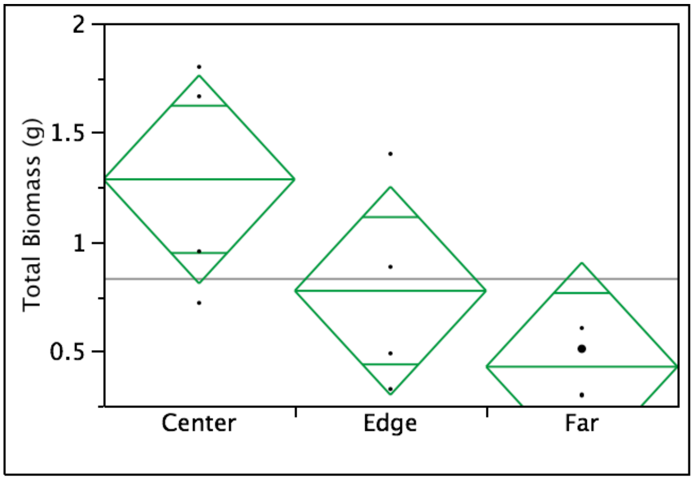


Figure 4: Analysis of variance of total grasshopper biomass captured in the center of glades, at glade edges and far from a glade. The trend is only marginally statistically significant given, likely, the low sample size (F Ratio = 4.109, Probability>F = 0.0517, observations = 12).

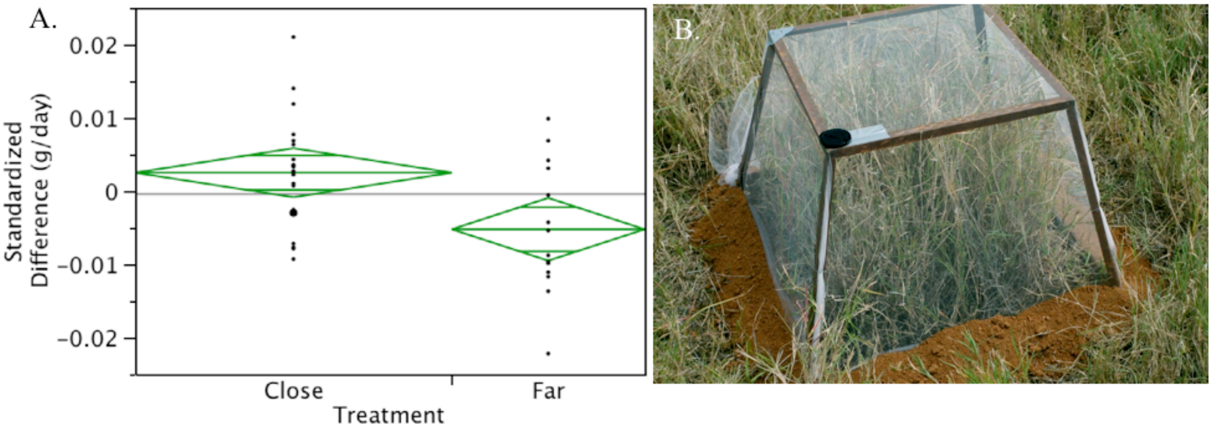


Figure 5: (A) Analysis of variance in grasshopper growth, standardized by length of time in cages, in the center of a glade and 100 m from a glade edge. Grasshoppers raised in the center of the glade generally grew faster than grasshoppers far from a glade edge (F Ratio = 8.3248, Probability>F = 0.0067, observations = 37). (B) Picture of grasshopper enclosure with 35mm lens cap for scale.

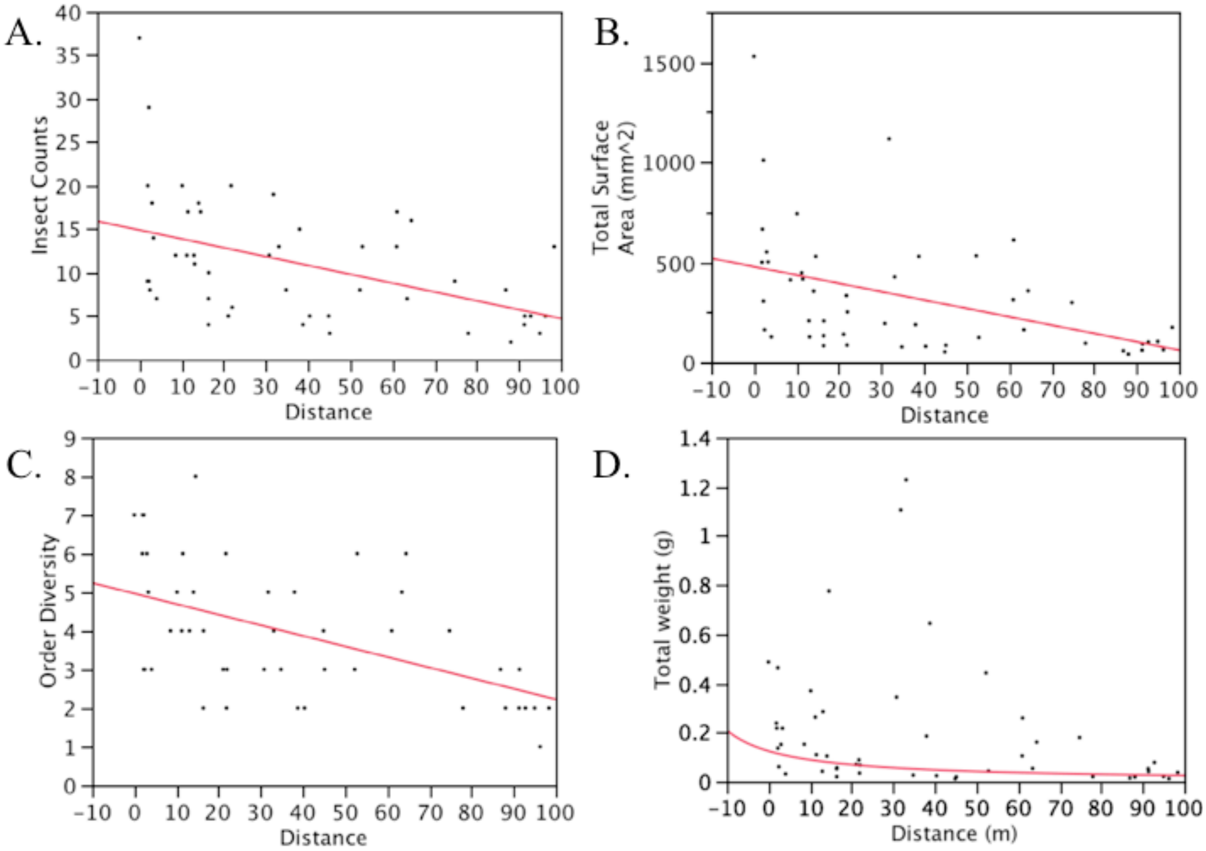


Figure 6: (A) Linear regression of total number of insects, not including ants, found after spraying trees with insecticide at various distances from a glade edge. A significant negative linear relationship was found (RSquare = 0.2158, F Ratio = 12.933, p=0.0008, observations = 49). (B) Regression of total insect surface area as a function of distance from a glade edge. Generally total surface area was much higher close to the edge, meaning there was more insect biomass close to the edge far from glades (RSquare =0.1949, F Ratio = 11.3742, p=0.0015, observations = 49). (C) Regression of insect order diversity as a function of distance from a glade edge. There was on average more than twice the order diversity at glade edges than there was far from the glade (RSquare = 0.2782, F Ratio = 18.119, p<0.0001, observations = 49). (D) Regression of total insect mass as a function of distance from a glade edge. Best fit line is the transformed fit reciprocal (1/y). There were significantly more insect biomass at glade edges than there was far from glade edges (RSquare: 0.2202, F Ratio: 13.271, p=0.0007, observations = 49).

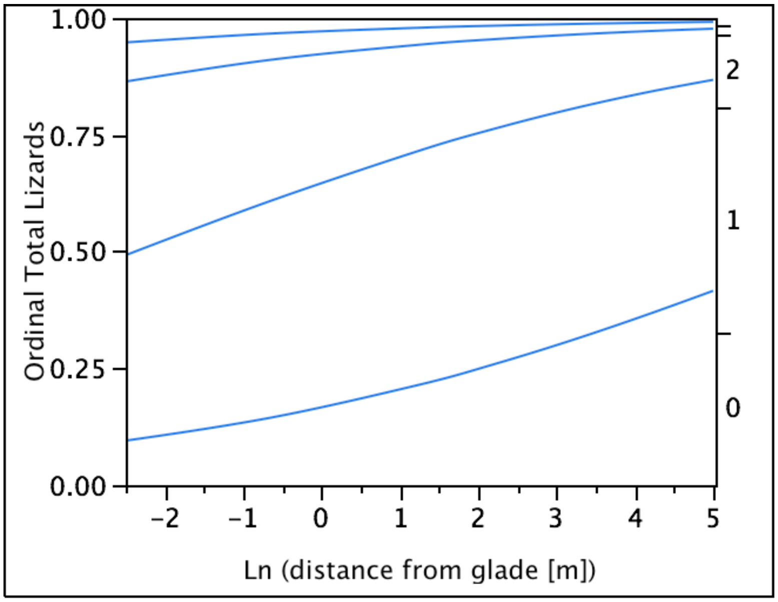


Figure 7: Ordinal logistic regression of lizard abundance category as a function of the natural logarithm of distance from the glade edge. Distance from glade edge was a particularly strong predictor of trees with 2 or more lizards on average. They were much more likely at the glade edge than far from the glade (Probability>ChiSq <0.0001, observations = 602).

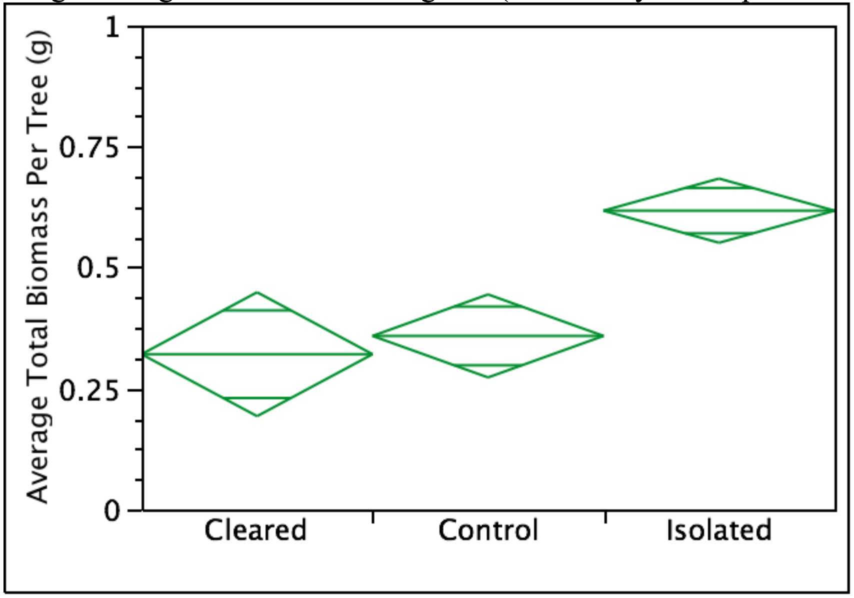
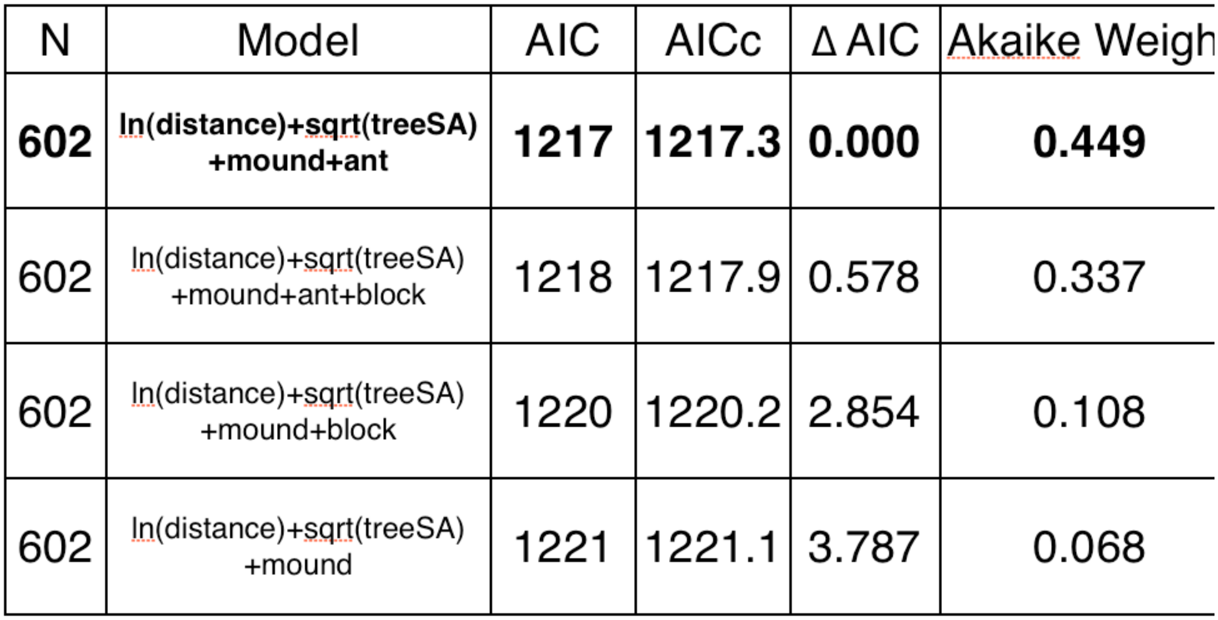


Figure 8: The average numbers of total lizards for each tree in each of the four transect types. There were significantly more lizards in trees in the isolated transects than there were in either cleared or control transects (F Ratio = 9.6543, Probability>F <0.0001, observations = 928).



N	Model	AIC	AICc	Δ AIC	Akaike Weigh
602	**ln(distance)+sqrt(treeSA) +mound+ant**	**1217**	**1217.3**	**0.000**	**0.449**
602	ln(distance)+sqrt(treeSA) +mound+ant+block	1218	1217.9	0.578	0.337
602	ln(distance)+sqrt(treeSA) +mound+block	1220	1220.2	2.854	0.108
602	ln(distance)+sqrt(treeSA) +mound	1221	1221.1	3.787	0.068

Table 1: Results of Akaike Information Criterion analysis. Presented here are the four best models with delta AIC values less than 4; the cutoff following Burnham and Anderson (2002) for models with reasonable explanatory power.

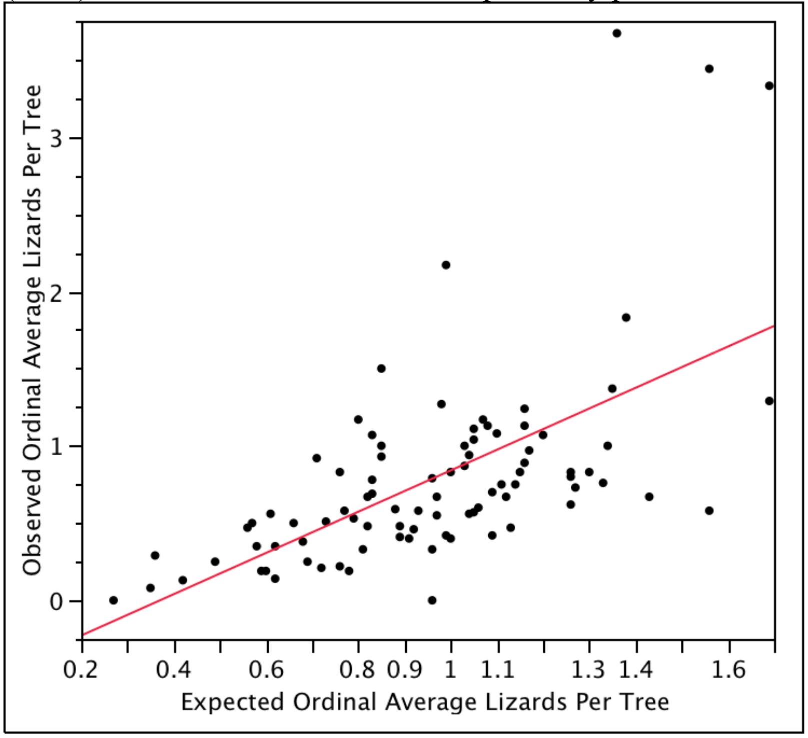


Figure 9: Plot of observed average ordinal lizards per tree against expected ordinal average lizards per tree as calculated by the best model identified by AIC analysis. Each point reflects the average expected and observed lizards at each ten meter sub-section of each isolated or paired glade. Red line is the 1:1 line and fits with RSquare = 0.3676, P < 0.0001, Observations = 88.