

RESEARCH ARTICLE

Densities of Ecological Replacement Herbivores Required to Restore Plant Communities: A Case Study of Giant Tortoises on Pinta Island, Galápagos

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Abstract

Loss of native herbivores and introduction of livestock in many arid and semi-arid ecosystems around the world has shifted the competitive balance from herbaceous to woody plants, leading to biodiversity loss, reduced plant productivity, and soil erosion. To restore functions of these ecosystems, ecological replacements have been proposed as substitutes for extinct native herbivores. Here we predict how an ecological replacement giant tortoise population (*Chelonoidis* spp.) would interact with woody plants on Pinta Island in the Galápagos Archipelago, where a small group of replacement tortoises was introduced in 2010 to initiate restoration of the island's plant community. We developed an individual-based, spatially explicit simulation model that incorporated field-derived tortoise behavior and tortoise–plant interaction data to test whether tortoise

introductions could lead to broad-scale changes in the plant community and, if so, at what tortoise densities. Tortoises reduced vegetation density in most (81%) 50-year-long simulations if the tortoise density was at least 0.7 per hectare, a value well below typical densities. In a smaller proportion of simulations (30%), tortoises increased local vegetation patchiness. Our results suggest that even moderate-density tortoise populations can reverse woody plant encroachment. Deployment of ecological replacement giant tortoises may therefore be a viable approach for restoring other arid and semi-arid ecosystems where a native herbivore that previously had strong interactions with the plant community has gone extinct.

Key words: *Chelonoidis*, individual-based model, plant community restoration, semi-arid ecosystems, woody plant encroachment.

Introduction

Plant community composition in arid and semi-arid ecosystems has shifted throughout the world: grasses are replaced by woody shrubs to create scrublands where grasslands or savannahs once existed, a process often referred to as “woody plant encroachment” (Archer 1995; Van Auken 2000; Browning & Archer 2011). One hypothesis for the cause of woody plant encroachment is the widespread loss of native herbivores and the simultaneous introduction of non-native herbivores in the form of livestock (Holmgren 2002; Whitford & Steinberger 2010; Browning & Archer 2011). Co-evolution with native herbivores has generated plants in arid or semi-arid systems with adaptations to native herbivory that can also take advantage of herbivore seed dispersal services (Archer 1995; Weltzin et al. 1997). Loss of native herbivores, as either extinctions or severe population reductions, may shift the competitive

balance between grasses and woody shrubs in favor of shrubs (van de Koppel et al. 1997; Weltzin et al. 1997; Whitford & Steinberger 2010) due to the loss of herbivory on woody plant recruits (Weltzin et al. 1997). Introduced livestock may also shift the balance because their excessive population sizes (often subsidized by external food inputs) and herbivory are less regulated by native predators or other biotic controls (such as disease), and their feeding patterns are directed by humans in ways that reduce grass density in spatial or temporal patterns that would not be produced by native herbivores (Kerley et al. 1995; van de Koppel et al. 1997; Holmgren 2002). These effects can lead to soil erosion and a shift in water availability that favors woody plants (Walker et al. 1981). The relative contribution of the loss of native herbivores or the introduction of non-native herbivores to woody plant encroachment is rarely clear because these two processes often coincide (Kerley et al. 1995).

Degraded systems may be only partially restored through the removal or reduction of livestock, as their impacts can drastically modify soil-water regimes that have long-lasting effects (Walker et al. 1981; van de Koppel et al. 1997; Browning & Archer 2011). Restoration of many degraded semi-arid systems also likely requires the impacts of some large herbivore species at moderate population densities to maintain

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native plant community dynamics (McNaughton et al. 1988; Seabloom & Richards 2003; Whitford & Steinberger 2010). In situations where the native herbivore species is extinct, reintroductions are impossible yet it may be practical to use ecological replacement species to replace some, if not all, functions that an extinct native herbivore once provided (Donlan et al. 2006).

The use of ecological replacement species is controversial (e.g. Rubenstein et al. 2006), but deployments of ecological replacement giant tortoises have restored some functions (mainly seed dispersal) on oceanic islands (Hansen et al. 2008; Griffiths et al. 2010, 2011). Giant tortoises can be driving forces of ecosystem change, as has been witnessed on the Aldabra Atoll in the Indian Ocean, the only other island system besides the Galápagos Archipelago that still supports giant tortoises (*Aldabrachelys gigantea*) and where tortoises have reached much higher contemporary densities than in the Galápagos (Swingland & Coe 1979). Since the tortoises' resurgence on Aldabra Atoll after centuries of exploitation, tortoises have reduced woody plant density through direct herbivory and through mechanical wearing of root tissues that led to eventual mortality of adult woody trees and shrubs (Merton et al. 1976). Tortoise activities have also likely promoted grass growth (Hnatiuk et al. 1976; Gould & Swingland 1980). Although invasive goats were present on Aldabra (eradicated as of 2012), they never reached high densities, nor have tortoises been completely absent during the period of goat inhabitation (Gould & Swingland 1980); therefore, it is unclear whether tortoises would have comparable effects in ecosystems with higher livestock densities or extirpated tortoise populations.

Can ecological replacement species restore ecosystems with woody plant encroachment that have suffered the loss of a native herbivore and degradation from a non-native, invasive herbivore? We addressed this question through the study of ecological replacement giant tortoises used as restoration agents in the Galápagos Archipelago. Our focus was on Pinta Island, a semi-arid ecosystem where woody plant encroachment has likely occurred due to the loss of the native species of giant tortoise and the impacts of an invasive goat population (Adersen 1989; Hamann 1993). The historical plant community on Pinta Island was likely a mosaic of woody shrubs and trees interspersed with grass-dominated areas, as evidenced by the presence of plant species on Pinta Island that require open conditions to germinate and grow, and the mosaic plant community structure on other islands in the Galápagos that have tortoise populations (Hamann 1993). The giant tortoise species native to Pinta Island (*Chelonoidis abingdonii*) was the only large-bodied herbivore on the island and has only recently become extinct, although the island has been without an ecologically effective tortoise population since overharvesting by whalers in the late 19th century (Hamann 1993). Records from U.S. whaling fleets show that 455 tortoises were removed from Pinta Island from 1831 to 1868, and there were likely many hundreds more unrecorded removals by whalers from other fleets (Reynolds & Marlow 1983), indicating a robust tortoise population once inhabited the island. Goats were introduced

to the island in 1959, and by 1975 the population numbered at least 20,000 individuals (approximately 6/ha) that rapidly devegetated the island and caused soil erosion (Hamann 1979, Campbell et al. 2004). An eradication program started in 1971 reduced the goat population to only a few hundred by 1980, which enabled the plant community to rebound immediately (Hamann 1979); the eradication was eventually completed in 2003 (Campbell et al. 2004). Botanists studying the regeneration of the plant community reported that woody plants regenerated much more rapidly and covered more area than anticipated (Hamann 1993), suggesting an enduring woody plant encroachment effect despite goat eradication.

Using an ecological replacement giant tortoise species on Pinta Island could restore functions such as disturbance and herbivory that may lead to an overall reduction in woody plant dominance and restoration of the mosaic structure of woody and non-woody vegetation. Before a full-scale introduction of replacement tortoises to Pinta Island, the Galápagos National Park undertook the release of 39 reproductively sterilized adult tortoises (14 females, 25 males) in May 2010 to assess the tortoises' ability to restore the degraded plant community (Hunter et al. 2013). Galápagos tortoises of both primary phenotypes (saddlebacked and domed) were introduced, but saddlebacked tortoises (*Chelonoidis* spp., most were hybrids) were found to better fit the ecological niche of the original Pinta tortoise species (Hunter et al. 2013). We used field observations of foraging and movement behaviors of these saddlebacked tortoises to estimate parameters of a spatially explicit, individual-based model. Our objective was to use the model to determine the minimum tortoise population density that might result in reduced vegetation density and increased spatial heterogeneity of vegetation densities on Pinta Island. We performed stochastic simulations to account for the large uncertainty in the mechanisms driving tortoise–vegetation interactions, and we used a pattern-oriented modeling approach (Grimm et al. 2005) to ensure that the model best imitated a real system in nature. These simulations enabled a scientific assessment of the ecological implications of a species replacement initiative.

Methods

Study Site

Pinta Island is the northernmost of the main islands of the Galápagos Archipelago and part of the Galápagos National Park. The island is 5,940 ha in area and reaches a maximum elevation of 667 m. Approximately two-thirds of the island is vegetated, with the lower elevations dominated by *Bursera graveolens* (Palo Santo tree), and mixed with open areas of grasses, shrubs (predominantly *Croton scouleri*), and *Opuntia galapageia* (cactus). A restricted high-elevation zone is naturally dominated by woody plants (such as *Zanthoxylum fagara* and *Chiococca alba*), but the low-elevation arid zone is experiencing woody plant encroachment.

A vegetation density index was estimated for the entire island from a multispectral satellite image (4 band, pixel size: 0.8 m) taken from the IKONOS-2 satellite on 1 March

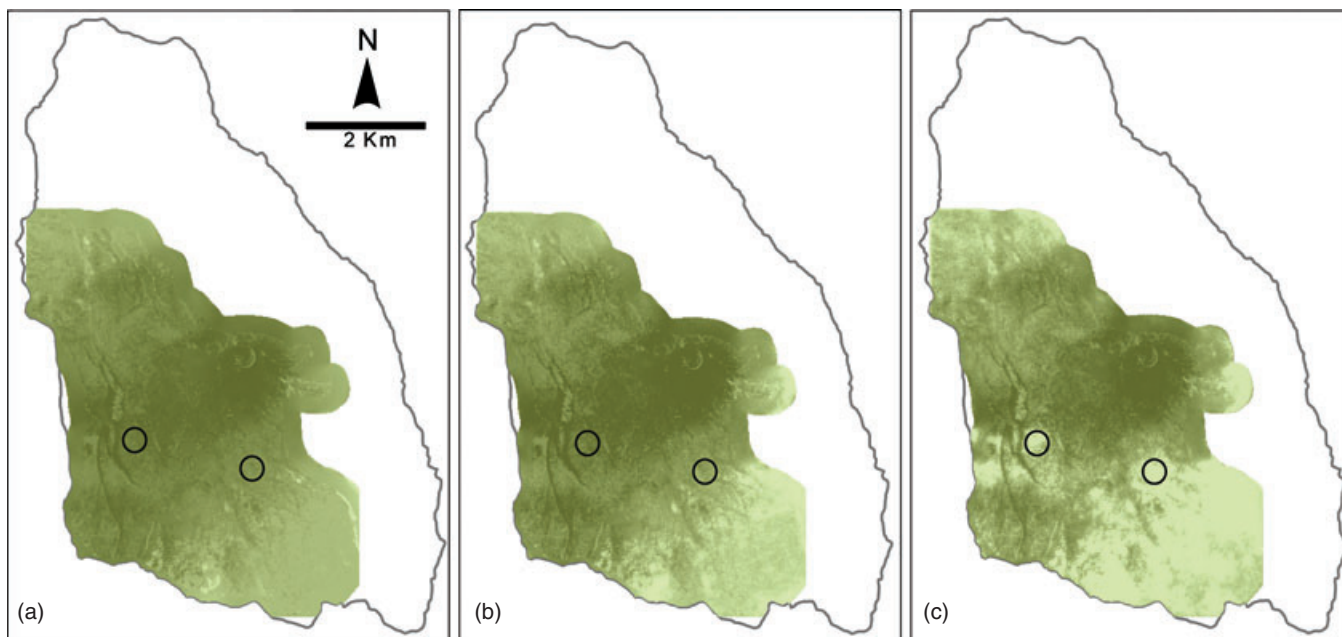


Figure 1. (a) Current vegetation density on Pinta Island, Galápagos, the focus of field and simulation studies, where white areas are unvegetated lava fields and darker shades are higher vegetation density. Two black circles indicate the introduction points for ecological replacement giant tortoises in the individual-based model (the eastern circle is the location of the actual trial introduction of tortoises in 2010). (b) Modeled vegetation density after 50 years with a maximum density of 0.3 tortoises/ha (1,000 tortoises on the island). (c) Modeled vegetation density after 50 years with a maximum density of 0.7 tortoises/ha (2,000 tortoises on the island). This figure appears in color in the online version of the article (doi: 10.1111/rec.12055).

2009. We used Iso clustered unsupervised classification (Image Classification, ArcMap 10.0; ESRI 2011) to classify the image into four vegetation density classes, ranging from no vegetation (0) to dense vegetation (3). We averaged these numerical classifications into 16-m cells to account for classification error, and we ground-truthed the classifications with field data collected in the 50-ha area surrounding the tortoise introduction point (Fig. 1a, right circle) to ensure that the vegetation density index reflected actual woody plant stem counts (Appendix S1, Supporting Information). Estimates of vegetation density and observed saddlebacked tortoise behaviors either directly provided parameter values for the individual-based model or the patterns observed were used to calibrate the model. A description of data collection on tortoise–vegetation interactions is provided in Appendix S1.

Model Summary

Here we provide an abbreviated model description; Appendix S2 provides a full description using the “Overview, Design concepts, Details” protocol of Grimm et al. (2006, 2010). The model’s purpose was to estimate changes in vegetation density due to tortoise behaviors in a landscape resembling Pinta Island, and determine whether ecological replacement tortoises could reduce vegetation density and increase vegetation heterogeneity within reasonable tortoise population density estimates. Other Galápagos giant tortoise population densities range from 0.6 tortoises/ha in the repatriated

tortoise population on Española Island (Gibbs et al. 2011) to 8 tortoises/ha in the population on Volcano Alcedo on Isabela Island (Marquez et al. 2004). On the Aldabra Atoll, giant tortoises have reached densities of 27 tortoises/ha (Swingland & Coe 1979). To determine the restoration potential of small tortoise populations, we used conservative tortoise population density estimates, ranging from 0.3 to 2.0 tortoises/ha (translating to total population sizes of approximately 1,000–6,000 tortoises in the 3,000 hectare vegetated portion of the island).

Tortoises were modeled as adult individuals that moved throughout the vegetated landscape of Pinta Island and, through their trampling and foraging activity, reduced vegetation density (Appendix S1). Tortoise movements were based on empirical data derived from behavioral observations of adult saddlebacked tortoises released to Pinta Island (Hunter et al. 2013). Tortoises were characterized by their behavioral state (moving, foraging, or inactive), which affected how the tortoises moved and reduced vegetation density. Tortoise behaviors and interactions with the plant community were described by two parameters: “behavior-randomness” and “vegetation-reduction.” Behavior-randomness dictated whether tortoise movements were more directed (low behavior-randomness values: tortoises moved through less dense vegetation and foraged in more dense vegetation) or more random (high behavior-randomness values: tortoises had a higher probability of making random habitat selections). Vegetation-reduction determined how much a tortoise could

Table 1. Parameters used in the individual-based model of replacement tortoise impacts on vegetation density.

Parameter	Stochastic Processes	Value/Equation	Rationale
<i>Initialization</i>			
Tortoise-density ^a	Constant	0.3, 0.7, 1.3, or 2 tortoises/ha	(Marquez et al. 2004, Gibbs et al. 2011)
<i>Move</i>			
Behavior-randomness ^a	Constant	0, 0.2, or 0.4	Uncertainty in strength of taxis to vegetation density
Step length	Gamma [shape, rate]	Moving: shape = 2.32, rate = 0.47 Foraging: shape = 1.25, rate = 1.25 Inactive: 0	Calibrated to achieve average displacement Rates (50 m/day) while matching behavior Distributions
<i>Vegetation-reduce</i>			
Vegetation-reduction ^a	Constant	0 ^b , 0.04, or 0.08	App. A; \leq minimum detectable change in vegetation plots
Maximum veg-reduce	Normal [equation, 0.01]	$(1 - 0.25 \times \text{veg-density}) \times \text{vegetation-reduction}$	App. A; nonlinear relationship between vegetation index and vegetation density
<i>State-assign</i>			
Behavior-state	Uniform [0, 1]	Moving: 0–0.2 Foraging: 0.2–0.4 Inactive: 0.4–1	(Hunter et al. 2013); From daily tortoise Activity budgets
<i>Grow</i>			
Relative growth rate	Constant	$(-0.8 \times (\text{veg-density}/\text{veg-start})^2) + 1$	Calibrated; devegetated patches grow rapidly (Hamann 1979)
Grow	Normal [equation, 0.001]	$0.00015 \times \text{Relative-growth-rate} \times \text{veg-start}$	Calibrated; slow growth rate as function of starting vegetation
ENSO growth rate	Normal [equation, 0.001]	$e^{(-1.25 \times \text{veg-start})}$	Calibrated; more ENSO precipitation for low starting vegetation
ENSO-frequency ^a	Constant	4, 7, or 10 years	Uncertainty in ENSO-frequency
<i>Introduce</i>			
Probability	Uniform [0, 1]	0.07	Approximately 50 tortoises introduced per year
<i>Reproduce</i>			
Probability	Uniform [0, 1]	0.0001	Calibrated to approximate natural population growth rate (Gibbs et al. 2011)

^aIndicates parameters that were tested for sensitivity at each of the values listed (five replicates of 50 year simulations were run at each level for these parameters). Other parameter values were drawn from the listed stochastic distributions for each daily time step for each tortoise or patch.

^bAt vegetation-reduction = 0, the maximum-vegetation-reduction equation is constrained to be positive, resulting in a true mean vegetation-reduction value of 0.008.

reduce the vegetation density within a patch in which the tortoise moved or foraged. The tortoise population had a set maximum density, and tortoises were introduced in a realistic manner and reproduced until the maximum density was reached.

The landscape that the tortoises moved through represented the vegetated area of Pinta Island and was modeled as square patches (16-m cells; Fig. 1a), with each patch assigned an initial vegetation density index (0–3 scale) derived from the satellite imagery described previously, which incorporates both herbaceous and woody plants. Vegetation density was affected by tortoise movements and the vegetation growth submodel. Vegetation periodically grew rapidly due to El Niño Southern Oscillation (ENSO)-driven precipitation regimes (Hamann 1985), with the frequency of ENSO events determined by the ENSO-frequency parameter. Parameters and mathematical relationships used in the model can be seen in Table 1.

The model was created and implemented in NetLogo 5.0 (Wilensky 1999); full model code is available in Appendix S3.

Simulation Experiments

Four parameters were tested for sensitivity: tortoise-density, vegetation-reduction, behavior-randomness, and ENSO-frequency (Table 1). Each simulation was replicated five times with two response variables reported at the end of the run: mean vegetation density and vegetation heterogeneity (using Moran's I, a measure of spatial heterogeneity where values closer to 0 are more heterogeneous and closer to 1 are more homogenous; Moran 1950), which indicated changes in local patchiness in vegetation density.

Model Analysis

A regression tree was used to evaluate the relationship between the response variables (vegetation density and heterogeneity) and the predictor variables (tortoise-density, vegetation-reduction, behavior-randomness, and ENSO-frequency). To avoid over-fitting, the regression tree was "pruned" using ten-fold cross-validation, in which the number of splits for each

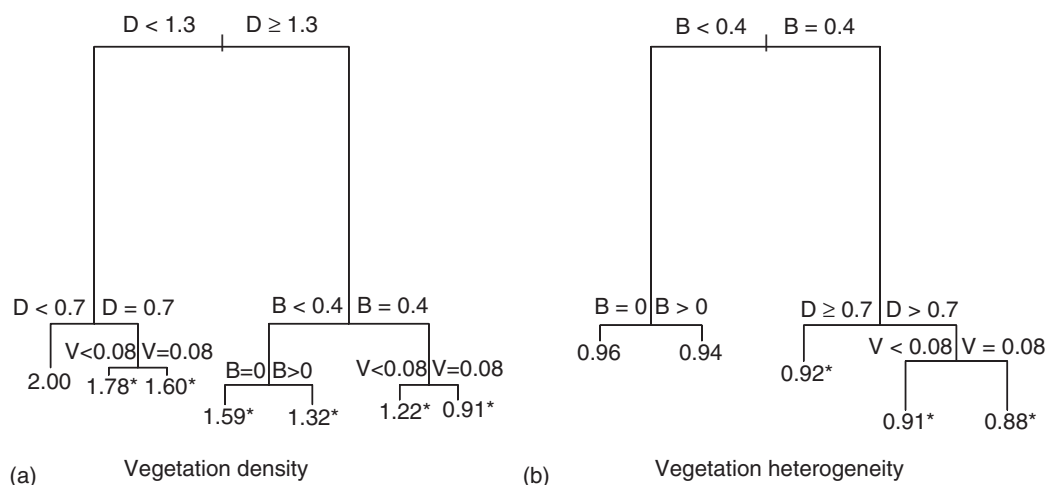


Figure 2. Regression trees of variation in vegetation density (a) and heterogeneity (b) in an individual-based model of giant tortoise effects on vegetation density. Simulations were replicated five times for each level of four predictor variables: tortoise-density (D), behavior-randomness (B), vegetation-reduction (V), and ENSO-frequency (E), for a total of 540 simulations. * indicates outcomes where vegetation density was significantly reduced from the mean starting value of 1.99 or vegetation homogeneity was reduced from a Moran's I starting value of 0.936 (one-sided t -test, $\alpha = 0.05$).

tree was selected to maximize deviance reduction (De'ath & Fabricius 2000). Tree building and cross-validation were performed using the "tree" package in program R (Ripley 2010). Each parameter value combination was compared to the starting value of the response variable using a one-sided t -test, so that the threshold conditions could be identified that would lead to reductions in vegetation density or increases in vegetation heterogeneity. To examine the relative importance of each predictor variable, a "random forest" of 500 regression trees was created for each response variable (Liaw & Wiener 2002). The percent increase in mean squared error when each variable was removed from the model was recorded, with higher increases indicating more important variables. All statistical analyses were conducted in program R 2.10.1 (R Development Core Team 2011).

Results

Vegetation density was reduced for most tested parameter value combinations (Fig. 2a). Maximum tortoise density contributed most to the final vegetation density value at the end of a 50-year simulation (Table 2), with higher tortoise densities generating larger reductions. Vegetation density was consistently reduced at tortoise densities at or above 0.7 tortoises/ha (2000 tortoises), but with only 0.3 tortoises/ha (1000 tortoises) vegetation density was not reduced (Figs. 3, 4b, & 4c). Of the 108 parameter value combinations, 81% of the simulations indicated reductions ($p < 0.05$) in vegetation density; the remaining 19% were all simulations with 0.3 tortoises/ha, had more frequent ENSO events, and lower individual vegetation-reduction rates. Tortoise behavior that was more random (higher behavior-randomness values) also led to increased reductions in vegetation density. The vegetation-reduction parameter and the ENSO-frequency parameter had minimal

Table 2. The importance of predictor variables in determining the value of the response variable in the individual-based model of giant tortoise effects on vegetation density.

Response Variable	Predictor Variable	% MSE Increase
Vegetation density	Tortoise-density	9.9
	Behavior-randomness	2.3
	Vegetation-reduction	0.8
	ENSO-frequency	<0.1
Vegetation heterogeneity	Tortoise-density	<0.1
	Behavior-randomness	0.1
	Vegetation-reduction	<0.1
	ENSO-frequency	<0.1

Values are the percent mean squared error (MSE) increase when each predictor variable is removed from prediction of the response variable in a random forest analysis. Larger values mean the predictor variable is more important in determining the value of the response variable.

influence on vegetation density (Table 2), with vegetation density reduced even with very low vegetation-reduction parameter values. Most vegetation-reductions occurred at lower elevation areas where the starting vegetation density was lower than in higher elevation areas and around the two tortoise introduction points (Figs. 1c & 4c).

Local heterogeneity or patchiness did not increase in the majority of the simulations as only 30% indicated decreases ($p < 0.05$) in Moran's I (Fig. 2b). Behavior-randomness was the most important variable for heterogeneity (Table 2). Random behavior (behavior-randomness = 0.4) led to increases in the amount of local patchiness (decrease in Moran's I). As with mean vegetation density, the vegetation-reduction, and ENSO-frequency parameters did little to explain the variation in vegetation heterogeneity among the simulations.

Tortoise density was not uniform across the island during the simulations (Fig. 4a). Tortoises aggregated in areas where other tortoises had been previously, especially around the

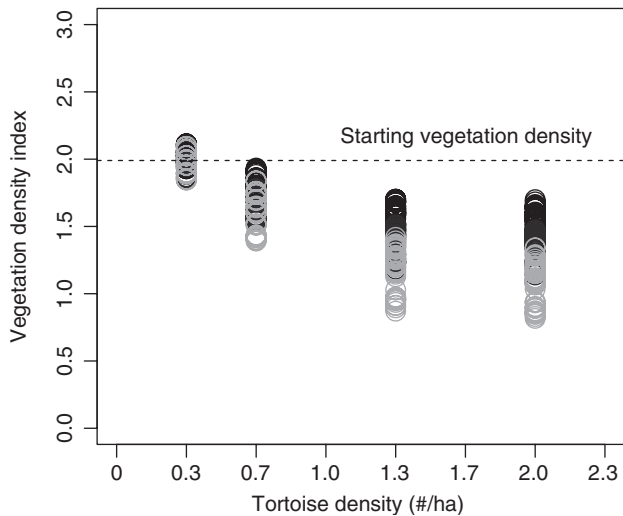


Figure 3. Relationship between vegetation density and the maximum number of simulated giant tortoises in an individual-based model of giant tortoise effects on vegetation density on Pinta Island. The dashed line is the starting vegetation density of the model and points are the vegetation density after 50 simulated years under different parameter scenarios. Black points are simulations in which tortoises have more directed behavior and gray points are simulations in which tortoises have more random behavior.

introduction sites and at lower elevations. Tortoises also tended to avoid high elevation areas (Fig. 4a). Patches that had a greater number of days when tortoises were present on the patch were generally more likely to have reductions in vegetation density (Fig. 4a–c).

Comparing simulations with ENSO precipitation events to those with only continuous vegetation growth (Fig. 5) indicated that the influx of vegetation growth with the ENSO events did not have lasting effects on overall vegetation density. The ENSO events caused vegetation growth to increase in low-elevation areas and areas where vegetation had been drastically reduced by tortoise activity, which were areas where tortoises were more often in inactive states due to low vegetation density. The ENSO plant growth caused these tortoises to become active again and reduce vegetation density more rapidly than if there had been no ENSO influx of vegetation growth (Fig. 5). This pattern of vegetation density reductions after an ENSO event occurred, however, even without the impacts of tortoises (Fig. 5).

Discussion

To our knowledge, an ecological replacement for a native herbivore has never before been implemented for woody plant encroachment remediation. The individual-based, spatially explicit model we developed and parameterized based on field studies of replacement tortoises introduced to Pinta Island to control woody vegetation revealed that replacement tortoises could reduce vegetation density, even with low densities of tortoises given sufficiently long time frames. Vegetation-reductions were predicted to occur even when individual-level

tortoise impacts (vegetation-reduction parameter) were as close to zero as possible (while still being positive), indicating that vegetation density would be reduced simply if the tortoise population is large enough. Vegetation density reductions were only produced if the tortoise population size exceeded a density threshold of 0.3 tortoises/ha, indicating that large numbers of tortoises (in this case, approximately 2,000), either introduced, or attained through internal population recruitment, would be needed for restoration.

The effects of tortoises on vegetation density heterogeneity were less clear, with tortoises increasing spatial patchiness in vegetation density only when tortoise habitat selection was more random. This outcome is intuitive because if all tortoises consistently make the same habitat selection choices (choosing to move through the least dense vegetation and forage in the most dense vegetation), effects on vegetation density will be uniform. However, habitat selection is variable both within and among individual tortoises (Gibbs et al. 2008; Blake et al. 2012), so replacement tortoises will likely increase heterogeneity and return the system to a mosaic of woody and herbaceous vegetation.

Although we predicted vegetation density to be reduced for most scenarios on Pinta Island, this does not necessarily mean that tortoises will selectively reduce woody plant growth and promote grass or herbaceous plant growth. Studies on other systems with woody plant encroachment have shown potentially irreversible changes to the soil water regime that do not allow grasses to re-establish dominance within a contemporary time frame (Walker et al. 1981; van de Koppel et al. 1997). On Pinta Island, it is unlikely that this alternate stable state has been reached because of the persistence of some remnant grasslands on the island. Vegetation density was modeled as a uniform entity that can equally be affected by tortoises; however, tortoises may not be able to dislodge large trees, only reduce recruitment of smaller trees and shrubs through disturbance or herbivory (Merton et al. 1976; Gibbs et al. 2010), which means that reductions may manifest over much longer time frames than our model results indicate.

Several aspects of our model could be improved with more precise data. The vegetation growth model would benefit from field-measured data on the variability of vegetation growth rates and how these interact with climate. Feedbacks between herbivore and plant populations are complex in semi-arid systems that have variable climates and where productivity is largely determined by water availability (van de Koppel & Rietkerk 2000; Holmgren & Scheffer 2001). In the Galápagos, the effect of ENSO precipitation (or the lack of it) on vegetation dynamics is variable and not well understood (Hamann 1985). Despite the lack of data, however, the vegetation growth model assumes a baseline of positive vegetation growth through time, which is unlikely and ultimately makes vegetation-reduction by tortoises more difficult, reinforcing conclusions drawn from our results. Also, in our models ENSO events produced somewhat realistic vegetation dynamics even without tortoise activity (Fig. 5), with vegetation density slowly decreasing after an ENSO event (mimicking plant death as water resources become scarce).

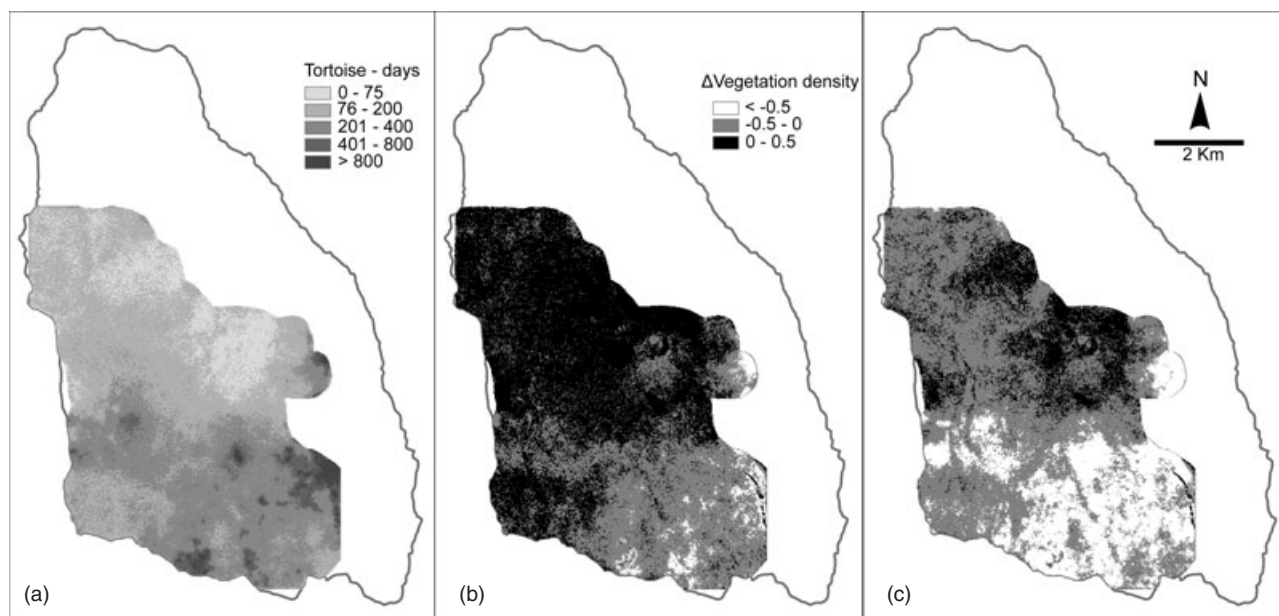


Figure 4. (a) Realized tortoise density in a simulation run with tortoise-density = 0.7 tortoises/hectare, behavior-randomness = 0.2, vegetation-reduction = 0.04, and ENSO-frequency = 7. Darker shades indicate that patches experienced more days with tortoises present. Vegetation density reductions in areas with higher tortoise activity in simulations run with tortoise-density = 0.3 (b) and 0.7 (c). Lighter shades indicate a negative change in vegetation density (greater reductions), darker shades indicate no change or a slight increase in vegetation density.

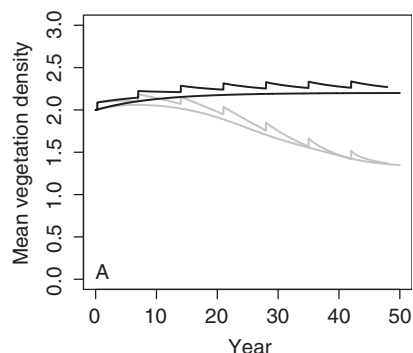


Figure 5. Changes in mean vegetation density over time for simulation runs of an individual-based model of giant tortoise effects on vegetation density. Light gray lines are example results from model runs with tortoise-density = 0.7 tortoises/hectare, behavior-randomness = 0.2, vegetation-reduction = 0.04, and ENSO-frequency = 7. Black lines are for comparison to the baseline vegetation growth model in which no tortoises are introduced. Jagged lines show ENSO event vegetation influxes, whereas smooth lines have had ENSO events removed from the vegetation growth model to highlight ENSO effects.

The model would also be improved if the tortoise movement submodel incorporated movements directed towards preferred food resources (high density adult *Opuntia* cactus stands at mid-elevations; Hunter et al. 2013); however, modeled tortoises at least avoided high elevation areas (Fig. 4), which were found to be non-preferred habitat for replacement saddlebacked tortoises (Hunter et al. 2013). Finally, the behavior model was based on introduced adult tortoises, but future tortoise introductions to Pinta Island will likely be juvenile

tortoises, which are likely to be less exploratory than adults released from captivity and will have reduced impacts on vegetation density proportional to their smaller body sizes. The introduction of pre-reproductive juveniles will also lead to a delay in the tortoise population reaching an ecologically effective size that is greater than the threshold for vegetation-reductions of 1,000 tortoises. If the model were adjusted for juvenile growth and time to reproduction, the outcomes would likely be the same but would occur over longer time periods.

Due to the time frames involved for tortoises to reduce woody plant encroachment, we suggest it is important to release more saddlebacked tortoises onto Pinta Island as soon as possible to thwart further woody plant encroachment and any possible associated plant species extinctions as it may take many decades to restore ecologically effective tortoise densities. For example, it has taken nearly 40 years and over 2,000 repatriates to reach a current population size of about 1,000 tortoises on Española Island in the Galápagos Archipelago (Gibbs et al. 2011). On Española Island, woody plants have become much more entrenched than they are on Pinta Island, threatening an endemic bird species (Anderson et al. 2002). It is possible that tortoise reintroduction occurred too late and too slowly to counteract woody plant encroachment on Española Island, and costly manual removal of woody vegetation may be necessary to provide momentum to tortoise reductions of woody vegetation (Gibbs et al. 2008, 2011). If the plant community on Pinta Island has not yet completely switched into an alternate stable state (as it seems to have done on Española Island), it is important to start enacting changes so that woody plant encroachment does not continue with the lack of herbivory

and disturbance (van de Koppel et al. 1997; Browning & Archer 2011). Climate change will likely increase the intensity and frequency of ENSO precipitation events in the Galápagos (Trueman & d'Ozouville 2010), and these conditions will favor woody plant growth (Hamann 1985). Our results show that more frequent ENSO events hinder the vegetation-reduction effects of tortoises, further underlining a need for rapid action to restore interactions between tortoises and the plant community.

Despite model uncertainties, our simulations provide evidence that replacement tortoises can begin to restore an ecosystem where the loss of a native tortoise species and the effects of an invasive goat population likely initiated woody plant encroachment. Restoration of endangered large herbivores to their native ranges should always be the priority (Rubenstein et al. 2006); where this is not possible, ecological replacement tortoises could be used as effective ecosystem restoration agents. Giant tortoises were once widespread in arid and semi-arid regions throughout the world (Auffenberg 1974), and their use as restoration agents is more controlled and less risky than for other large herbivores (Griffiths et al. 2010; Hansen et al. 2010). Although not all potential replacement species are suitable for filling an extinct species' niche (Hunter et al. 2013), ecological replacement giant tortoises clearly have potential to aid in the restoration of systems affected by woody plant encroachment.

Implications for Practice

- Low densities of ecological replacements for extinct native herbivores can alleviate woody plant encroachment in arid and semi-arid ecosystems and can be a more cost-effective, longer-term alternative than direct woody plant removal.
- During and after introductions of replacement species, careful observations of animal introduction effects on woody plants should be made to ensure that the appropriate number of individuals are introduced to achieve the desired restoration and to update models as tools for simulating future restoration scenarios. Animal enclosures and enclosures would provide useful data on animal effects on the plant community.
- Because tortoises are social and aggregate spatially, their ecosystem effects will be highest in the areas where they are directly introduced. Strategic placement of multiple nuclei for introductions may help to accelerate woody plant reduction.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Appendix S1. Empirical data used to build individual-based model.

Appendix S2. ODD description of individual-based model of tortoise–vegetation interactions.

Appendix S3. NetLogo model of tortoise–vegetation interactions on Pinta Island.