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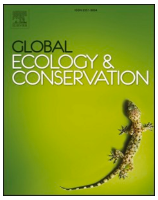

Sharing land with giants: Habitat preferences of Galapagos tortoises on farms

Kyana N. Pike[a,*,1], Stephen Blake[b,c,d], Iain J. Gordon[e,f,g,h,i,2], Freddy Cabrera[j], Ainoa Nieto-Claudin[j,k,l,3], Sharon L. Deem[j,l,4], Anne Guézou[m], Lin Schwarzkopf[a,5]

[a] College of Science and Engineering, James Cook University, Townsville, Australia
[b] Department of Biology, Saint Louis University, Saint Louis, USA
[c] Max Planck Institute for Animal Behaviour., Radolfzell, Germany
[d] Wildcare Institute, Saint Louis Zoo, Saint Louis, USA
[e] Central Queensland University, Townsville, Australia
[f] James Hutton Institute, Craigiebuckler, Aberdeen, Scotland, UK
[g] Fenner School of Environment and Society, The Australian National University, Canberra, Australia
[h] CSIRO, Townsville, Australia
[i] Lead, Protected Places Iniative, National Environmental Science Program, RRRC, Cairns, Australia
[j] Charles Darwin Research Station, Charles Darwin Foundation, Santa Cruz, Galapagos, Ecuador
[k] Complutense University of Madrid, Veterinary Faculty, Puera de Hierro Av, Madrid, Spain
[l] Saint Louis Zoo Institute for Conservation Medicine, Saint Louis, USA
[m] Galapagos Conservation Trust, Santa Cruz, Galapagos, Ecuador

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ABSTRACT

One of the most pressing dilemmas of our time is determining how to satisfy the demands of a growing human population while still conserving biodiversity. Worldwide, land modification to accommodate human resource needs has caused significant declines in wildlife populations. To help minimize biodiversity loss, we must support wildlife on human-dominated land, such as farms and urban areas, but our knowledge of how to do so is lacking. Agriculture is a major driver of land modification; but also has the potential to play a role in conserving biodiversity. To support critically endangered ecosystem engineers that use farms, such as giant Galapagos tortoises, we need to understand the characteristics encouraging or hindering them. To quantify tortoise habitat preferences, we assessed the relationship between tortoise density, habitat structure, and land-use type, by recording tortoise density on farms on Santa Cruz Island, Galapagos, over two years. Tortoise density was lowest in abandoned farmland and highest in tourist areas and was most strongly positively correlated with abundant ground cover, short vegetation, and few shrubs. The habitat features favoured by tortoises could potentially be manipulated to help support tortoise conservation on farms. Measuring wildlife preferences in human-dominated areas is an important step towards balancing biodiversity conservation and human-enterprise.

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* Corresponding author.
E-mail address: kyana.pike@my.jcu.edu.au (K.N. Pike).

[1] ORCID 0000-0001-9259-2899.

[2] ORCID 0000-0001-9704-0946.

[3] ORCID 0000-0001-5856-3779.

[4] ORCID 0000-0002-2549-3636.

[5] ORCID 0000-0002-1009-670X.

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1. Introduction

Among the most pressing issues of our time is the conflict between conserving biodiversity and meeting the water, energy, food, and space demands of a growing, and more affluent human population (Bullock et al., 2011; Gordon et al., 2016; Kremen, 2015; LeB. Hooke et al., 2012; Rosenzweig, 2003). The human population is expected to increase by 4 billion by the end of the century (United Nations, 2015), and the task of feeding this increasing population falls on our agricultural systems (Butler et al., 2007; Tilman et al., 2011). Agriculture is the leading cause of land modification, and therefore a key influence reducing biodiversity (Gordon et al., 2016; Neilly et al., 2016; Phalan et al., 2011). Many solutions have been proposed to reconcile biodiversity conservation and food production, and they typically involve land sparing (in which agriculture is intensified on existing land to avoid clearing more), or land sharing (in which agricultural land is made wildlife-friendly to share space with wildlife) (Caudill et al., 2015; Gordon, 2018; Phalan et al., 2011). No single solution can resolve all of the complex problems facing biodiversity conservation and food production around the world, but sometimes one or the other of these two possibilities is a better option (Kremen, 2015; Shackelford et al., 2015). For example, wildlife may require more space than land sparing alone can provide, and thus land sharing may be the preferred strategy to meet conservation objectives (e.g., for snow leopards *Panthera uncia* (Johansson et al., 2016). When land sharing is viable, the central issue is optimizing management practices to achieve both food production and conservation goals.

If sharing land with wildlife is to be a success, the habitat characteristics important for supporting wildlife must be identified. Typically, researchers assess the importance of environmental factors for wildlife by recording habitat variables that correlate positively with abundance of particular species in natural areas (Singh et al., 2009; VanDerWal et al., 2009); but some studies have quantified habitat preferences in human-modified areas such as farms (see Neilly and Schwarzkopf, 2018; Nordberg and Schwarzkopf, 2019). While knowledge of wildlife habitat preferences on agricultural land is limited, research suggests that habitat heterogeneity, farm type, and land management influence wildlife use of farms (Benton et al., 2003; Hardman et al., 2016; Neilly et al., 2016). For example, in a grazing experiment, rufous bettongs (*Aepyprymnus rufescens*), a marsupial ecosystem engineer, preferred habitats with medium- to high complexity ground cover in areas moderately grazed by livestock, over low-complexity, heavily grazed areas (Neilly and Schwarzkopf, 2018). Similarly, both coffee-plantation type (forest, shade or sun coffee) and specific habitat characteristics impact the abundance and species richness of small mammals found in coffee plantations in Costa Rica (Caudill et al., 2015). A greater understanding of the specifics of habitat preferences of wildlife using farmland is, therefore, useful for making informed decisions supporting land sharing for vulnerable wildlife.

On some islands in the Galapagos Archipelago, a hotspot for species endemism (Steinfartz, 2011), agricultural land has replaced the majority of humid highland areas, which are important habitat for many endemic species, including threatened animals and plants (Watson et al., 2010). Since the Galapagos National Park was established in 1959, regulations have been implemented that discourage land clearing and protect the National Park, making further land clearing less of a threat, and land sharing more of a priority. Species richness and abundance of many species has declined in the humid highlands, including iconic Darwin's finches (Dvorak et al., 2012). Similarly, critically endangered endemic giant tortoises (generalist grazers *sensu* Blake et al., 2020) inhabit transformed and native highland habitats, often in large numbers, as this habitat type provides high energy grass forage (Bastille-Rousseau et al., 2018; Blake et al., 2013; Pike et al., 2021; Yackulic et al., 2017). Giant tortoises have, however, been reduced to a fraction of their former numbers by past human exploitation (MacFarland et al., 1974). The remaining population is also facing health threats from various sources including invasive species (Carrion et al., 2011), pollution and exposure to antibiotics and chemicals (Nieto-Claudin et al., 2021, 2019). We do not understand the impact of agricultural land use on the ecology of the remaining tortoises (Blake et al., 2015; Pike et al., 2021).

Galapagos tortoises are ecosystem engineers, making them important for seed dispersal, nutrient input and vegetation dynamics, and a high priority for conservation (Bastille-Rousseau et al., 2017; Froyd et al., 2014; Gibbs et al., 2014). On high- elevation islands, Galapagos tortoises migrate from arid lowlands, where they breed, to the humid highlands, which are more consistently productive (Blake et al., 2013; Yackulic et al., 2017). Once tortoises are in the humid highland agricultural area, they remain for an average of 150 days, and interact with multiple landholders and farm types (Pike et al., 2021). In this study we were most interested in tortoise interactions with four land-use types: 1) livestock production (33% of farmland by area), 2) coffee production (6% of land area), 3) abandoned land (22% of farmland), and 4) land dedicated to tourism (hereafter referred to as 'touristic' land; % of land area unknown) (Laso et al., 2020). Touristic land includes agricultural land that has been repurposed to encourage wild tortoise use, as farmers generate revenue from tourists who wish to see tortoises in a semi-natural setting. Including touristic land was especially relevant, as it enabled us to evaluate the effectiveness of repurposing agricultural land to attract tortoises, and allowed us to compare tortoise use of land maintained for agricultural practices versus land maintained for tortoises. To facilitate and improve land sharing between tortoises and farmers, we sought to identify habitat features important for giant tortoises in the agricultural area.

Using a survey of tortoise density in four land-use types, and a survey of 12 habitat features, we estimated tortoise density by land-use type, and quantified how habitat influenced tortoise density across the agricultural landscape. We addressed two main questions relevant to land sharing options for conservation:

1. *Does tortoise density differ among land-use types?* We included livestock production, coffee production, abandoned land, and touristic land as land-use types. Based on the resources available in each land-use type, we predicted tortoise density would be highest on touristic land, which has more of the resources favoured by tortoises, followed by livestock production, coffee, and abandoned land.

2. *Which habitat structural features influence tortoise density most strongly?* We measured 12 variables related to the availability of food, shade, and ease of movement, to determine which had the strongest impacts on tortoise density. We predicted that tortoises would prefer habitat characteristics closely related to food availability.

2. Materials/methods

2.1. Study site

Santa Cruz Island is an extinct volcano in the centre of the Galapagos Archipelago, located approximately 1000 km from mainland Ecuador. There are three main vegetation zones in the Galapagos, the arid lowlands, the transition zone, and the humid highlands, the latter receives the most rainfall and is consistently productive (McMullen, 1999; Wiggins and Porter, 1971). Agricultural practices began in the humid highlands of Santa Cruz Island in the early 1900 s and land clearing intensified mostly in the 1960–70 s, as more Ecuadorians moved from the mainland following government incentives to settle and cultivate the island (Trueman et al., 2013). The National Park was established in 1959 and the Galapagos special law, created in 1998, now restricts further settlement from the mainland and limits who can live on Galapagos (Lu et al., 2013). Over 88% of the humid highlands have been converted to support agriculture on Santa Cruz Island (Watson et al., 2010), however, now, with the establishment of the National Park borders and a limit on migration, farming has not expanded further.

The highlands supports three main livelihoods: cattle ranching, crop production, and tourism (Laso et al., 2020). The agricultural area has developed into a complex matrix of various land-use types, that includes pastoral areas for cattle and horses, annual crops (e.g., tomatoes, watermelons, corn), permanent crops (e.g., coffee, banana, pineapple), abandoned land, and tourism (Laso et al., 2020). Since the 1960 s, the tourism industry has grown steadily and now brings over 200,000 visitors each year, making tourism the backbone of the local economy in the Galapagos (Dirección del Parque Nacional Galápagos and Observatorio de Turismo de Galápagos, 2020; Epler, 2007). The rise in tourism has led some landholders to abandon productive land for more lucrative options in the tourism sector, predominantly in the township (Benitez-Capistros et al., 2019; Sampedro et al., 2018). A few other farmers have encouraged tourism in the highlands by re-purposing part of their farms, mostly for accommodation, or to attract tourists who pay to see giant tortoises roam their land in a semi-natural setting (Benitez-Capistros et al., 2016). Sections of abandoned land are now interspersed throughout the agricultural area and are mostly overgrown with invasive species that spill over into the neighbouring farms.

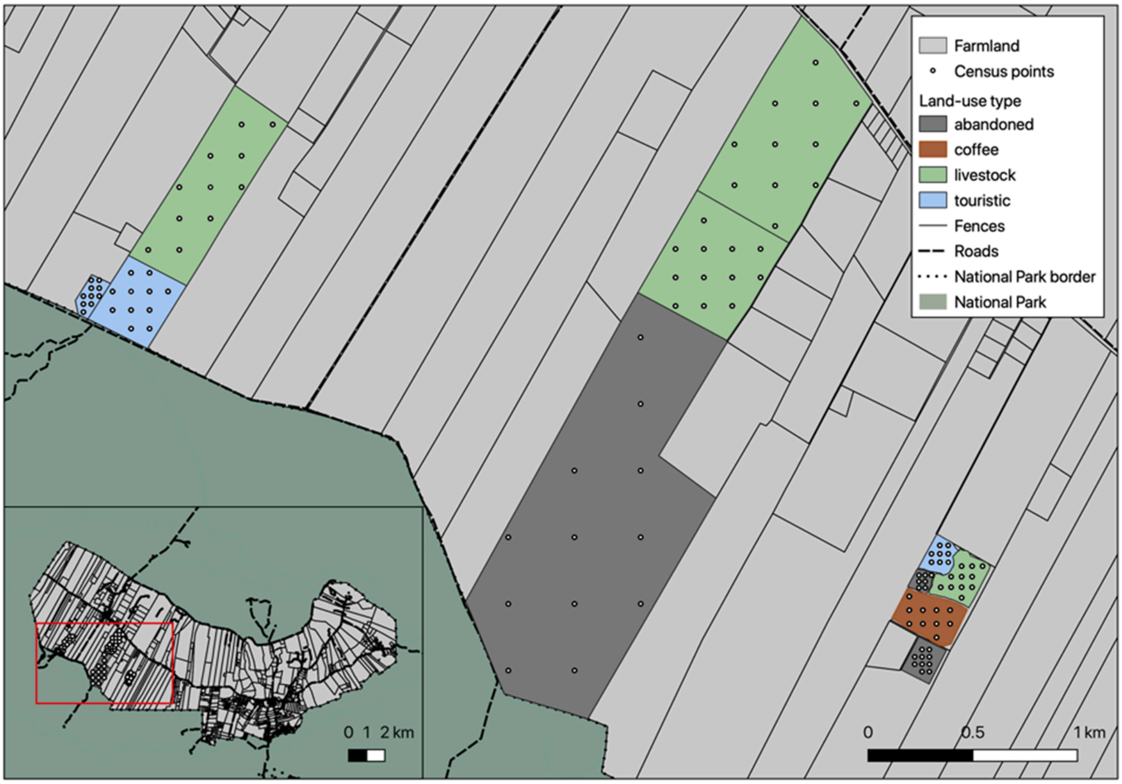

Fig. 1. View of the western agricultural area in the highlands of Santa Cruz Island, Galapagos [red rectangle on inset of entire agricultural area] where a monthly giant tortoise survey took place. Small circles depict the location of the 108 survey points and their distribution in different land-use types on three different properties.

2.2. *Measuring tortoise density*

To describe patterns of tortoise density in agricultural areas, we performed a monthly survey on three properties in the south-western agricultural area of the highlands of Santa Cruz Island from October 2018 to December 2020. We were unable to conduct a survey in July 2019 and March, April, May and November 2020, so we conducted a total of 23 monthly surveys over the study period (15 surveys in the dry season and 8 surveys in the wet season). Each property had a mix of land-use types that included either coffee production, livestock production, tourism or abandoned land (Fig. 1). Vegetation density, and tortoise detectability, varied by land-use type, so to enable distance sampling and estimates that accounted for differences in tortoise detectability among survey points, we designed their placement using 'Distance' software (Thomas et al., 2010). For each land-use type in each farm, we allocated 7–12 survey points with equidistant spacing, ranging between 25 and 300 m apart, depending on the size of the area, for a total of 108 survey points (Table 1). In the field, each survey point was located using a GPS and marked with flagging tape. We revisited each point on foot and recorded the presence of any tortoises within the radius around that point (i.e., a radius of 15 m, 20 m or 25 m depending on size of the land-use area, Table1) so density could be calculated for a known area. Surveys were conducted by field technicians towards the end of each month in the morning between the hours of 7 am to 12 pm and typically took three days to complete each census of 108 points across the three properties. Observers would scan each point for tortoises for a few minutes and when any tortoises (either males, females, or juveniles) were present within this radius, the distance from the centre of the point to the tortoise was measured with a digital rangefinder (Nikon Forestry Pro) to use to estimate tortoise detection probability. To account for differences in tortoise abundance that may arise from variation in detectability of tortoises, we used the 'Distance' package in R Studio v. 1.3.1073 (Miller et al., 2019; RStudio Team, 2019) to calculate the probability of detecting a tortoise for each land-use type. Our detection functions were fit with either a half-normal or hazard rate distribution, depending on the land-use type and where possible the different plot sizes within each land-use type (see supplementary Table S1, and supplementary Figs. S1-S5 for details).

We examined differences in tortoise selection of habitat structure and land-use type during the dry season. As tortoises are seasonal migrants, they reach their highest density in the agricultural area during the dry season, because resources are limited in the more arid lowlands (Blake et al., 2013; Yackulic et al., 2017). Although some tortoises remain in the agricultural area during the wet season, after a surge in lowlands plant growth (Pike et al., 2021), their numbers are much lower. Because of small sample sizes, low numbers make it difficult to make precise estimates of abundance in relation to habitat and land-use type in the wet season. Broadly, however, patterns of tortoise abundance appeared similar in the dry and wet seasons, thus, we chose to focus on the dry season (supplementary Fig. S6).

2.3. *Measuring habitat structure*

Plant communities in the agricultural area typically vary by land-use type, creating a structurally diverse vegetation community (Guézou et al., 2010; Laso et al., 2020). Livestock areas often include a mix of cultivated and naturally germinated grasses and herbs, interspersed with fruit trees, often *Cirtus spp.* or guava *Psidium guajava* (Laso et al., 2020). Abandoned land typically includes invasive and naturalised species of grasses, herbs, shrubs, and trees (e.g., *P. guajava*, *Rubus niveus*, *Cedrela odorata*, *Zygsigum jambos*) that grow aggressively in a mixed forest. Coffee plantations mostly grow *Coffea arabica* or *C. canefora* (robusta) varieties as shade crops with other trees, e.g. *Cirtus spp.* or cedar *C. odorata (*Laso et al., 2020), and touristic land has well-manicured grazing lawns of grass and herbs with patches of shrubs and native and introduced trees for shade. Santa Cruz tortoises are diet generalists (Blake et al., 2021), and the structure of these plant communities is likely to impact food availability, thermal resources and tortoise movement more broadly, and the number of tortoises likely to use an area. To better understand the relationship between habitat structure and tortoise density, we collected data on habitat structural composition in the agricultural area. At each survey point, 12 vegetation structural characteristics were estimated in 10-m radius circular plots. Within each circular plot, the presence or absence of a pond, the percent cover of ground vegetation, mean height of ground cover, number of shrubs, mean shrub height, percent coverage of shrubs, number of trees in three height categories (1–4, 4–8 and >8 m), percent projected canopy cover, number of trees bearing fruit, and an estimate of the extent of fruit fall (1–10 fruits = low extent, 11–20 fruits = medium extent, and > 20 fruits = high extent).

2.4. *Analysis*

To quantify differences in tortoise density among land-use types, we used a negative binomial, zero-inflated regression model for count data via maximum likelihood from the 'countreg' package (Zeileis and Kleiber, 2020). Given that tortoise detectability varied among land use types and, thus, survey points, we standardised our results by using both survey point area, and detectability, as offsets in our models. We modelled total tortoise abundance for the dry season for each survey point as the response variable, and land-use

Table 1
An overview of the distribution of survey points by land-use type, and the total area sampled, for each land-use type of giant tortoise sampling on Santa Cruz Island, Galapagos.

Land-use type	Number of survey points	Combined maximum sample area of survey points (m^2)
Abandoned	28	33,615
Coffee	10	19,635
Livestock	43	76,655
Touristic	27	35,500

type as the explanatory variable (n = 108 survey points). As our models are based on total tortoise abundance for the dry season per *survey point*, we have also included post-hoc estimates of mean dry season density per hectare throughout the results so that these estimates are also more easily compared to other studies.

To determine the relationship between tortoise density and habitat structure, we took a two-step approach. First, we used boosted regression trees (BRT) as a variable selection method to measure the relative influence of each of the 12 habitat variables, to determine

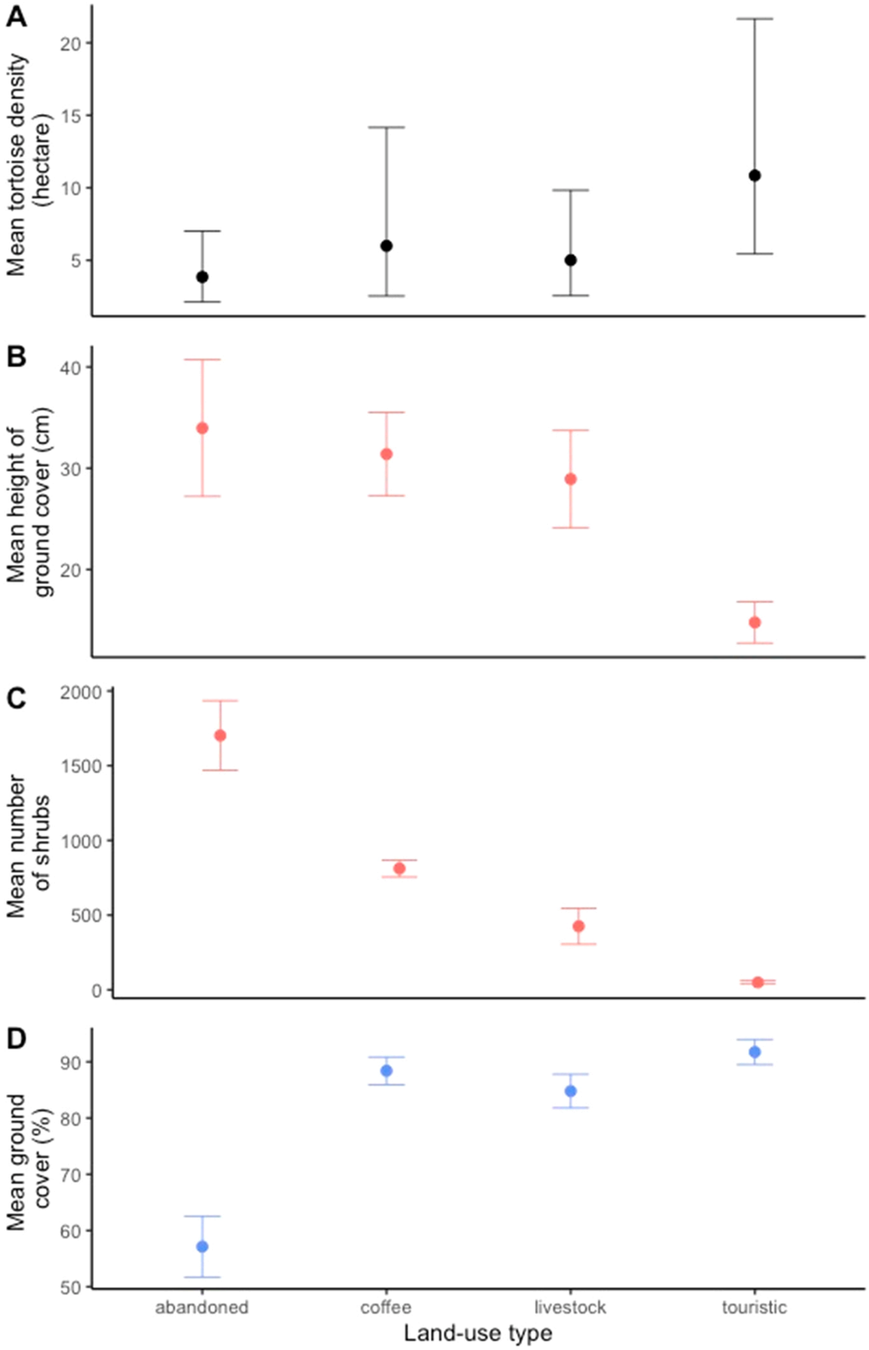

Fig. 2. A. Estimated mean dry season density per hectare (with 95% confidence intervals) for each land-use type, based on estimates from our model with land-use type and tortoise density (supplementary Table S2). The following three panels (B,C,D) show, for each land-use type, the raw mean value scaled up to a hectare (± standard errors from raw data) of the habitat structure variables identified in our habitat structure model as most important. Tortoises preferred less of the features shown in red (panels B & C) and more of the features shown in blue (D). Note that land-use types characterised by each preferred habitat variable also had higher tortoise density, and those characterised by more non-preferred variables had fewer tortoises.

which variables were appropriate candidates for further modelling. Using BRTs from the 'dismo ' package (Hijmans et al., 2020), we identified variables that consistently showed greater influence on tortoise density than expected by chance, and used only those variables in our next step, which assessed the direction and strength of their relationship with tortoise density. Our BRTs included a tree complexity of five, to allow for up to five interactions, a bagging fraction of 0.5 (i.e., 50% of the training data were discarded to avoid overfitting), and a learning rate of 0.0025 (smaller relative learning rates are preferred, to shrink the contribution of each tree as it is added sequentially to the model). We used these parameters for the BRT as this combination of learning rate and tree complexity provided enough trees (close to 1000) without overfitting (Elith et al., 2008).

We then constructed models with combinations of the habitat variables identified in our BRTs as having the most influence on tortoise density and assessed which model had the greatest power in predicting variation in tortoise density, using Akaike's Information Criterion, corrected for small sample sizes (AIC$_c$; Burnham and Anderson, 2002). All models followed the same structure as modelled previously for land-use type: a negative binomial zero-inflated regression, with standardised area and detection probability as an offset. We checked for collinearity among model terms using the 'car' package (Fox and Weisberg, 2019) and inspected model residuals for model fit. We then selected the most parsimonious model with the best improvement in AIC$_c$ value, compared to our null model.

3. Results

3.1. *How did tortoise density differ among land-use types?*

Tortoise density was strongly related to land-use type. Over the sampling period, abandoned land had the lowest total tortoise density per point of 1.8 tortoises (scaled up to a mean of 3.9 tortoises per hectare per survey, 95% CI 2.1–7.0) compared to all other land-use types (Fig. 2). Compared to abandoned land, tortoise density was 1.6 times greater in coffee (scaled up to a mean of 6.0 tortoises per hectare per survey, 95% CI 2.5–14.2), 1.3 greater in livestock (scaled up to a mean of 5.0 tortoises per hectare per survey, 95% CI 2.6–9.8), and 2.8 times greater in touristic land (scaled up to a mean of 10.8 tortoises per hectare per survey, 95% CI 5.4–21.7; Fig. 2, panel A); however, only the differences between abandoned land and touristic land were statistically significant (supplementary Table S2). The zero-inflation component of our model identified livestock as having a significantly higher probability of being zero-inflated than the other land-use types (supplementary Table S2). This model also outperformed our null model by 27 AIC$_c$ values.

3.2. *Which habitat structure variables influenced tortoise density?*

The BRTs identified six habitat structure variables as having more relative influence on variation in tortoise density than expected by chance; percent ground and height of cover, number and height of shrubs, percent canopy cover, and number of trees between 1 and 4 m (supplementary Table S3). Modelling using these characteristics revealed that tortoise density was highest when there was more low ground cover, and fewer shrubs, and the best model outperformed the null model by 34 AIC$_c$ values (Fig. 2, see supplementary Table S4 for a full set of candidate models). Our model predicted total density of tortoises was 2.3 ± 0.13 SE tortoises per survey point (scaled up to a mean of 4.9 tortoises per hectare per survey, 95% CI 3.8–6.3), and tortoise density increased by 0.8% with a unit increase in percent ground cover, decreased by 1.3% with a unit increase in the height of ground cover, and decreased by 1.3% with a unit increase in shrubs (Table 2). None of these habitat structure variables impacted the probability of zero-inflation, according to the zero-inflation component (supplementary Table S5).

4. Discussion

We found strong evidence that land-use type and habitat structure impact giant tortoise density in agricultural landscapes on Santa Cruz Island, Galapagos. Abandoned land had consistently low tortoise density, and the worst combination of habitat features: less and taller ground cover, and more shrubs (Fig. 2). In contrast, touristic farms had the highest tortoise density and the best combination of features to encourage tortoises: higher coverage of shorter vegetation, and fewer shrubs (Fig. 2). Our results showed that tortoise density increased with the percent cover of ground vegetation: tortoises are generalist grazers (Blake et al., 2020; Rodhouse et al., 1975) so a higher percentage coverage of ground vegetation is probably indicative of greater food availability. We also found tortoises occurred at higher densities in areas where ground vegetation was shorter, which is typical of many large, herbivorous grazers

Table 2
Output from the best-ranking, most parsimonious model determining which habitat structure variables had a strong impact on giant tortoise density in the agricultural area of Santa Cruz Island, Galapagos. Model estimates have been back transformed and show the multiplicative impact of each habitat variable on total tortoise density per survey point in the agricultural area.

Term	Estimate	SE	z-value	P value	Low CI	High CI
Count model						
(Intercept)	2.322	0.128	6.566	0.000	1.806	2.986
Ground cover	1.008	0.006	1.275	0.202	0.996	1.021
Number of shrubs	0.987	0.006	-2.259	0.024	0.976	0.998
Height of ground cover	0.987	0.006	-2.303	0.021	0.975	0.998

(Drescher et al., 2006; Hebblewhite et al., 2008; Raynor et al., 2016). The preference for short vegetation may occur because, as ground vegetation matures, the amount of indigestible fibre increases, while protein content declines, thus nutritional value is lower relative to younger, faster growing vegetation, termed the 'forage maturation hypothesis' (Bergman et al., 2001; Fryxell, 1991). Large herbivores typically, preferentially feed on younger, more nutritious forage (Drescher et al., 2006; Hebblewhite et al., 2008).

Tortoises also preferred areas with low shrub density. Tortoises may avoid shrubs for two principal reasons. Firstly, due to competition for light and nutrients, shrub density is negatively correlated with ground vegetation cover, reducing the availability of ground vegetation (Eldridge et al., 2011), and secondly, as with taller vegetation of any type, a dense understory with many shrubs can impede tortoise movement (Gibbs et al., 2014). Abandoned land is typically characterised by many invasive blackberry shrubs (*Rubus niveus*) which grow in thick, spiny masses. In such areas, tortoises were consistently absent. However, in areas with only a few shrubs, which were native (e.g. *Chiococca alba*), and have a less dense growth form, tortoises occurred at times (KP personal observation), likely seeking shade and cover from high wind and rain (Rodhouse et al., 1975).

While land-use type clearly had a strong overarching impact on tortoise density in the agricultural area, our results suggest that habitat structure could potentially be altered to modify tortoise distribution and abundance. The Galapagos highlands are already completely modified habitats and are not pristine, therefore changes to vegetation structure to better manage tortoises in these areas is less ethically questionable. Altering habitat features to encourage wildlife in agricultural areas has been used previously, for example, reducing tree density to encourage deer for game hunting, or planting wildflowers and native grains on farmland to increase wild pollinator diversity (Gallo and Pejchar, 2016; Hardman et al., 2016). Furthermore, giant tortoises are ecosystem engineers, with the capacity to modify their own environments (Ellis-Soto et al., 2017; Gibbs et al., 2014, 2010; Hunter et al., 2021). For example, the very high density of giant tortoises (*Geochelone gigantea*) on Aldraba, which are ecologically similar to Galapagos tortoises, is linked to the promotion and maintenance of 'tortoise turf', which are areas of low cropped grasses and sedges with little woody vegetation, preferred by tortoises (Hnatiuk et al., 1976). Similarly, Galapagos tortoises using livestock areas may also contribute to the maintenance of pastural areas by promoting grazing lawns (Hunter et al., 2021). It is possible, therefore, that tortoises are currently influencing habitat structure in a way that is potentially beneficial to farmers, and assisting the process by modifying vegetation structure in areas where tortoises have lower density (such as abandoned land) could promote this feedback loop. We recognise however, that the ecological services of tortoises may not always align with the needs of farmers, such as in maintaining an area for crops.

Not all land-use types are equally compatible with land sharing between resource production and wildlife conservation. Here, we found repurposed farmland designed to support tortoises for tourism is highly compatible with tortoise conservation, and is used the most by tortoises. Historical density of tortoises across the Galapagos is estimated at 2.5 tortoises per hectare of suitable habitat (Gibbs and Goldspiel, 2021), however, touristic land appears to attract roughly 11 tortoises per hectare in the dry season, and is clearly favoured by tortoises. Landowners derive significant income from tourism and facilitate tortoise use of their land, however there are currently only a few farms on Santa Cruz that have this type of operation. There may be potential for more landholders to diversify their income by repurposing sections of their farms for tourism, and, indeed, social research has shown this is desirable for many landholders in Galapagos (Benitez-Capistros et al., 2019, 2018). However, questions remain over the economic cost-to-benefit ratio of transforming productive land for tourism, how income from tortoise viewing compares to traditional farming, and how to provide the infrastructure and expertise required to make this transformation (Benitez-Capistros et al., 2019, 2018). Market saturation and local competition may also influence the viability of the tortoise viewing option for landholders, reducing its usefulness as a tortoise management option. Additionally, the impact of these areas on stress and wellbeing of tortoises is unknown and requires further research. Regardless, the success of touristic farms demonstrate that farmland can be altered to successfully support giant tortoises at higher densities, although it may be at the expense of food production in some areas, leading to more of a land-sparing and less of a land-sharing outcome.

Coffee had the second highest density of tortoises of the four land-use types, so, contrary to our predictions, the coffee plantation was regularly used by tortoises. The coffee plantation was characterised by some of the habitat features preferred by tortoises, such as a high percentage ground cover of vegetation. There were many shrubs in the coffee plantation, which normally deters tortoises, but these were mostly coffee shrubs planted in wide rows, that do not impede tortoise movement (KP personal observation), or reduce percent ground cover, unlike invasive shrubs (Fig. 2). There appears, therefore, to be important grazing resources for tortoises in coffee plantations, and this land-use type could have potential for land sharing. The compatibility of tortoises and coffee plantations has not yet been well researched, to our knowledge, and would benefit from further investigation, especially determining the costs and benefits to tortoises and coffee producers of tortoise use of these crops.

Livestock areas had the third highest tortoise density in our study, and supported twice the density of tortoises in the dry season than historical estimates (5 tortoises per hectare vs 2.5 tortoises). Livestock areas are designed to suit grazers, so this land-use type is generally suitable for grazing tortoises. Indeed, there is evidence to suggest giant tortoise herbivory may even improve productivity of herbaceous vegetation, especially relative to grazing by introduced herbivores, such as goats (Bastille-Rousseau et al., 2017). Socio-economic research has shown that cattle farmers are more tolerant of tortoises than are crop farmers, and perceive tortoises as less of a threat to their enterprises. Together, these factors make livestock production more compatible than cropping for land sharing with tortoises (Benitez-Capistros et al., 2018). At the tortoises' current low population level (Cayot et al., 2017), significant competition between tortoises and cattle for resources has not been a major concern, however, if circumstances change and tortoise density on farms increases, as is possible given their population is slowly increasing (Tapia et al., 2021), or resource availability decreases (e.g., via climate change), this relationship may become less salubrious for farmers. In the semi-arid grasslands of the African Sahel, high cattle density is associated with low density of the African spurred tortoise (*Centrochelys sulcata*), another large grazing tortoise (Petrozzi et al., 2018). It is unclear, however if the negative association between cattle and tortoise density is a result of direct competition, habitat loss or poaching and hunting of tortoises (Petrozzi et al., 2018), regardless, the density of tortoises and cattle in

Galapagos should be closely monitored to mitigate potential issues. Additionally, sharing land with livestock may cause other issues for tortoises, for example, exposure to potentially harmful agricultural chemicals, or development of antibiotic resistance (Nieto-Claudin et al., 2021, 2019). At present, the humid highlands remain a critical habitat for tortoises during the dry season, and future management by private landholders, and the Galapagos National Park, will need to consider land sharing with tortoises.

Abandoned land supported the fewest tortoises and is also unproductive for farmers. Currently, abandoned land makes up 22% of the agricultural area of Santa Cruz, and is a problem for both agriculturalists and the National Park, because it acts like a reservoir for highly invasive species which are difficult to manage once they spill over to farms and protected areas (Khatun, 2018; Laso et al., 2020). This issue can then become compounded when invasive species establish in the National Park and can also re-enter agricultural land. More generally, abandoned agricultural land needs to be managed to provide suitable habitat for wildlife (Benayas and Bullock, 2015; Zakkak et al., 2015). In Europe, abandoned agricultural land is characterised by fewer bird species compared to traditional rural landscapes, and is, therefore, recognised as a significant environmental threat (Zakkak et al., 2015). Clearing invasive plants from abandoned land is typically very expensive, so such areas remain unmanaged (Khatun, 2018; Laso et al., 2020). If incentives, policies, and awareness campaigns were introduced in the Galapagos to rehabilitate abandoned land to make it productive of livestock or crops, our results suggest that these areas could potentially both support more tortoises, and confer more financial benefits to landholders, in addition to reducing reservoirs of invasive species.

We have identified some of the key factors that influence tortoise density in the agricultural area of Santa Cruz Island, although there are some caveats to our conclusions. We included a variety of habitat variables that we considered most relevant to tortoises, but we omitted a few that are also likely to be important. For example, tortoises use wallows, and thus ponds are important to tortoise distribution and resource use (Ellis-Soto, 2021). Our method was too coarse to detect an impact of ponds on tortoise density, as ponds mostly fell outside our survey points. We were also limited in our ability to survey all farm types, as for instance, we had no samples in annual crops (corn, tomatoes), and only one in a permanent crop: coffee, and in only a single farm. Thus, our results may not be representative of coffee farms more generally, nor all crops. Furthermore, proximity to roads, as well as traffic levels, and types of fences, may also be important to consider in future evaluations of habitat suitability (Beaudry et al., 2008; Blake et al., 2015; Mark Peaden et al., 2017). Lastly, we prioritised an examination of the preferences of tortoises, a critically endangered keystone species, however, we acknowledge their preferences may not be a good measure of habitat suitability for other native species using farmland. Ideally, management should consider land sharing improvements based on preferences of other species (e.g., see Geladi et al., 2021 for birds in Galapagos), in conjunction with our findings for tortoises.

5. Conclusions

Understanding the drivers of wildlife distributions in agricultural lands allows us to make informed decisions on modifications to promote land sharing with vulnerable wildlife. For critically endangered Galapagos giant tortoises, we have identified several preferred habitat features, and determined how they relate to land-use type. This information may be utilised by landholders, agriculture policy makers, and the Galapagos National Park Directorate when designing strategies to make agricultural areas more tortoise-friendly, without necessarily compromising land productivity. Specifically, reducing dense shrub cover and promoting cover of shorter ground vegetation, especially in abandoned land, would likely support tortoises in farmland areas. We have highlighted here that on agricultural land, evidence-based management is still required to support tortoises, and that there is potential to benefit both food production and tortoise conservation through this process. Overall, our results have demonstrated the importance of measuring wildlife preferences within human-dominated areas as a first step towards balancing the needs of biodiversity conservation and human-enterprise.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.gecco.2022.e02171.

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