Original Articles

Forest cover is more important than farmland heterogeneity and livestock intensification for the retention of dung beetle phylogenetic diversity

Fredy Alvarado[a,b,*], Edyla R. Andrade[c], Bráulio A. Santos[d], Graham Prescott[e], Gustavo Souza[f], Federico Escobar[b]

[a] Programa de Pós-graduação em Biodiversidade (PPGBIO), Centro de Ciências Agrárias, Universidade Federal da Paraíba, Rodovia PB-079, 58397-000 Areia, PB, Brazil
[b] Instituto de Ecología, A. C., Carretera Antigua a Coatepec 351, El Haya, Xalapa 91000, Veracruz, Mexico
[c] Programa de Pós-Graduação em Ecologia e Conservação da Biodiversidade (PPGECB), Laboratório de Ecologia Aplicada à Conservação, Universidade Estadual de Santa Cruz, Rodovia Jorge Amado km 16, 45662-900 Ilhéus, Bahia, Brazil
[d] Departamento de Sistemática e Ecologia, Universidade Federal da Paraíba, s/n-Castelo Branco, João Pessoa 58051-900, Paraíba, Brazil
[e] Department of Biological Sciences, National University of Singapore, 14 Science Drive 4, Singapore 117543, Singapore
[f] Departamento de Botânica, Universidade Federal de Pernambuco, Recife 50670-901, Pernambuco, Brazil

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ABSTRACT

Pasture and grazing land is one of the dominant global land-uses in the Anthropocene. There are two broad strategies for preserving phylogenetic diversity (PD) within livestock regions: land sharing, which increases farmland heterogeneity at the expense of yield and forest cover, and land sparing, which increases forest cover and yields at the expense of farmland heterogeneity. We assessed the relative merits of the two strategies in the context of preserving dung beetle PD in twenty 1-km^2 livestock landscapes in a Neotropical biodiversity hotspot. We calculated six complementary metrics of PD: phylogenetic richness ($^0D(T)$), divergence ($^2D(T)$, MPD and MNTD) and structure (NRI and NTI). Dung beetle density varied irrespective of forest cover, cattle yield and farmland heterogeneity, but phylogenetic richness and divergence decreased in more deforested landscapes, resulting in reduced phylogenetic dispersion closer to the tips (i.e. higher relatedness within genera). Similarly, increased net cattle yield resulted in reduced phylogenetic richness and divergence (except MNTD), but had a weaker effect on phylogenetic structure. While farmland heterogeneity had no significant effect on phylogenetic metrics, model selection indicated that forest cover was more important than livestock intensification in determining dung beetle PD. To avoid losing evolutionary lineages of dung beetles and increase cattle yield, we recommend implementing land sparing in the region by concentrating cattle production—i.e. producing the same yield on a smaller area of land through intensification—to set aside more land for forest conservation.

1. Introduction

The conversion of tropical forest to grazing land is the major driver of the global extinction crisis (Laurance et al., 2014), causing dramatic species loss and simplifying biological communities (Gibson et al., 2011; Edwards et al., 2017). Maintaining biodiversity and its associated ecosystem services in agricultural landscapes has therefore become a major ecological and socio-economic issue worldwide (Duflot et al., 2017). Key strategies for protecting biodiversity in the face of agricultural demand include both increasing landscape heterogeneity (Fahrig et al., 2011) and conserving areas of natural habitat (Gray et al., 2016). There may be a trade-off between these two strategies. Any given quantity of crops can either be produced on a larger area of lower-yielding farmland that supports higher biodiversity ('land sharing'), or a smaller area of intensive agriculture that supports less biodiversity within the farm but leaves more land available for natural habitats ('land sparing') (Green et al., 2005). Empirical studies using this framework have largely concluded that conserving natural habitat is the most important factor for preventing population declines and have thus supported land sparing (Green et al., 2005; Phalan et al., 2011; Gilroy et al., 2014; Williams et al., 2017). Critics of this approach however have contested the dichotomous framing of the question and countered that these findings neglect the negative externalities of intensive agriculture and the importance of heterogeneous agricultural landscapes for dispersal between patches of remaining natural habitat (Paul and Knoke 2015; Monck-Whipp et al., 2018).

Previous studies have largely focused on population density and species richness, while neglecting phylogenetic diversity (Phalan et al., 2011; Gilroy et al., 2014; Cisneros et al. 2015). As the effects of habitat conversion on species may be affected by evolutionarily constrained traits (e.g. habitat requirements, dispersal abilities, physiological constraints), approaches based only on species richness alone may provide an incomplete or misleading impression about the consequences of human activities at the landscape scale (Arroyo-Rodríguez et al., 2012; Cisneros et al., 2015; Prescott et al., 2016; Edwards et al., 2017).

Phylogenetic diversity measures the distribution of shared evolutionary history across a community, and can thereby provide insights into mechanisms of community assembly in response to change at the landscape level (Webb et al., 2002; Rolland et al., 2012; Prescott et al., 2016; Ribeiro et al., 2016 Tucker et al., 2017; Matos et al. 2017). High phylogenetic diversity is thought to underpin higher levels of ecosystem function and stability (Cadotte et al., 2012; Matos et al., 2017), and is therefore of conservation and management interest. Nevertheless, we are still lacking information on how best to enhance phylogenetic diversity across agricultural landscapes (but see Frishkoff et al., 2014; Prescott et al., 2016).

If traits that make species susceptible to habitat modifications are evolutionarily conserved along particular lineages, then habitat modification might reduce phylogenetic diversity (Webb et al., 2002). Mesoamerican landscapes with diversified agricultural systems (i.e. those with greater farmland heterogeneity) support higher levels of avian phylogenetic diversity than intensive monocultures (Frishkoff et al., 2014). A study that did consider this trade-off in the threatened Chocó-Andes biodiversity hotspot in south America found that land-sparing (i.e. farming intensively while offsetting large natural reserves) will save more phylogenetic diversity and evolutionarily distinct species of bird than land-sharing (i.e. a larger area of low-intensity farming), especially when farmland is isolated from contiguous forests (Edwards et al., 2015). Moreover, the extirpation of tree species at the edges or in fragments of the Brazilian Atlantic forest increased the dominance of species within a subset of clades (phylogenetic clustering), likely those adapted to disturbance (Matos et al., 2017). However, questions about how best to retain phylogenetic diversity in agricultural landscapes remain unanswered in the context of livestock production systems.

In this study, we used field data from Mesoamerican tropical dry forest of Yucatán Peninsula, Mexico, to assess the relative influence of forest cover, farmland heterogeneity and livestock intensification on dung beetle density, phylogenetic richness, divergence and structure (*sensu* Tucker et al., 2017). We use dung beetles as model communities, because they perform key ecological functions in natural ecosystems and livestock-dominated landscapes—e.g. dung removal, nutrient recycling, and fly pest control (Nichols et al., 2008)—and are a cost-effective indicator taxon (Nichols et al., 2008). We expected reduced landscape forest cover and increased cattle yield and landscape heterogeneity to correlate with the loss of entire clades and the coexistence of closely related species, reducing dung beetle phylogenetic diversity in livestock-dominated landscapes.

2. Materials and methods

2.1. Study area

We conducted our research in north-eastern Yucatán State, Mexico (20°55′55″–21°26′42″ N, 87°33′39″–88°33′31″ W; Fig. 1), an area that contains some of the largest remnants of tropical dry forest in Central America, making it a priority for global biodiversity conservation. Forest cover declined during the Classic Maya Period (100–900 CE) (Whitmore et al., 1990) but rebounded afterwards. 60% of the original forest cover however has been lost in the last 100 years, as a result of government policies promoting agriculture – particularly due to the rapid expansion of cattle ranching in the 1940s and 1950s. Mean annual precipitation is 1000–1200 mm, and mean monthly temperature is 26–28 °C. Our sites were between 4 and 34 m.a.s.l.

2.2. Study landscapes

We sampled twenty 1-km^2 (100-ha) independent study landscapes distributed along a gradient of land-use intensity (Fig. 1): four sites in a large (< 250 ha) forest fragments as a control, and 16 corresponding to four agricultural land uses with different cattle densities (mean ± SD): Traditional cattle ranches (0.8 cows ha^{-1} year^{-1} ± 0.41), silvopastoral systems (0.72 cows ha^{-1} year^{-1} ± 0.35), intensified livestock production systems (1.22 cows ha^{-1} year^{-1} ± 0.50) and maize farms (4.11 cows ha^{-1} year^{-1} ± 1.56). Traditional ranches ranged from grazed forest to large open pastures. Silvopastoral systems included a mix of pastures and banks of protein-rich legumes, such as *Leucaena leucocephala*. Intensified livestock production systems had irrigated and mechanized pastures, combined with high levels of fodder use. The maize farms in our study consisted of both cattle pasture and irrigated cropland. The spatial scope and landscape variation of our study is large enough to account for interspecific differences in dung beetle home range and daily movement patterns, and to capture variation in the alpha and beta diversity of both generalist and specialist species

2.3. Explanatory variables

Following Pasher et al., (2013), we quantified (*i*) proportion of forest cover and (*ii*) farmland heterogeneity in each study landscape as land cover diversity (Shannon of land cover type diversity of order 1; ^1D *sensu* Jost 2006). For this analysis "landscape diversity" is defined as the exponential of Shannon index (^1D), which increases with the number of landscape coverage types, thus being one of the most suitable landscape diversity measures (McGarigal and Marks, 1995). These were calculated using recent SPOT 5 satellite images (June to August 2013) and ARCMAP 10.2 (ESRI 2016), through satellite image segmentation, field validation and supervised classification considering six land cover types: forest (i.e. old-growth and secondary forests), grazed forests, crops (i.e. bean, corn, chili and papaya plantations), cattle pastures, unproductive lands (i.e. degraded lands) and human settlements. Based on field observations in 1500 points distributed throughout the region, we found that overall classification accuracy was 73% (see Supplementary material). Land cover diversity was estimated using land cover types (Fig. A1) and with iNEXT package for R (Hsieh et al., 2016).

We conducted 31 semi-structured interviews with ranch managers and owners to estimate levels of (*iii*) livestock intensification (i.e. net cattle production). This allowed us to identify the gradient of livestock intensification along which we analyzed our data. We used published estimates of protein content (http://ndb.nal.usda.gov) and a 50% fixed dressing percentage to convert reported net cattle production into estimated protein yields (i.e. kg of edible protein per hectare per year). Net cattle production calculations as a measure of livestock intensification for each management types can be complicated by external inputs of fodder and calves, but as our study landscape contains fodder-producing farms and calf-producing ranches these inputs can be ignored for this analysis without affecting the overall results (Williams et al. 2017).

2.4. Dung beetle surveys

We sampled dung beetles at each site in the rainy season of 2013 (June to August), the season in which they are most active and abundant in our study region (Alvarado et al., 2018). We distributed 25 pitfall traps evenly across each 1-km^2 landscape (100 traps per management condition, 500 traps in total). We placed traps in a grid of 833 × 833 m, with a distance between traps of 166 m to increase dung beetle dispersal capacity between traps (Silva and Hernández, 2015). Each trap consisted of a 1000-cm^3 container, buried flush with the soil