Ecological Indicators 95 (2018) 518–526

Contents lists available at ScienceDirect

Ecological Indicators

journal homepage: www.elsevier.com/locate/ecolind

Original Articles

Spatial and temporal shifts in functional and taxonomic diversity of dung beetles in a human-modified tropical forest landscape

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ARTICLE INFO

Keywords:
Amazonia
Functional ecology
Land-use change
Scarabaeinae
Temporal dynamics

ABSTRACT

Functional diversity is commonly used to assess the conservation value of ecosystems, but we have not yet established whether functional and taxonomic approaches are interchangeable or complementary to evaluate community dynamics over time and in response to disturbances. We used a five-year dataset of dung beetles from undisturbed forest, primary forest corridors, and *Eucalyptus* plantations to compare the sensitivity of conceptually equivalent metrics to temporal variation in different anthropogenic disturbances. We compared species richness with functional richness, Pielou's evenness with functional evenness, and Simpson's diversity with Rao's quadratic entropy. We assessed the sensitivity of the metrics to anthropogenic changes. The indices showed complex patterns among habitat types, with with similar responses in some cases and not in other, and little incongruence between the pairs within the same year. The influence of disturbance on longer-term temporal variation over the five-year period revealed lower temporal variation in functional than taxonomic metrics. Both approaches showed greater variation in plantations compared to native forests. We evaluated the variation in taxonomic and functional metrics between consecutive years and among habitats. Most metrics showed similar shifts between years in all habitats, except for species and functional richness. We demonstrate that even conceptually similar indices may not provide similar information on dung beetles responses to disturbance. However, the differences between the indices can yield key insights about the drivers of change, especially over the long-term. It is important to use taxonomic and functional diversity in tandem to better understand community responses to environmental and anthropogenic changes.

1. Introduction

The past decade has seen a rapid increase in the use of functional metrics to quantify biodiversity responses to anthropogenic change (*e.g.* Elmqvist et al., 2003; Bihn et al., 2010; Barragán et al., 2011), replacing or complementing the traditional taxonomic approach, which considers each species as a unit with an equal contribution to ecosystem functioning (Mouchet et al., 2010). The functional approach is particularly important in the tropics, because the rapid rate of land-use change and the importance of biodiversity has promoted a prolific debate about the role of human-modified landscapes for ecosystem functioning and biodiversity conservation (Silver et al., 1996; Lambin et al., 2003; Gardner et al., 2008; Power, 2010; Palm et al., 2014). Additionally, the exceptionally high biological diversity of tropical environments can make it very difficult to find empirical links between biota and ecosystem functioning, which increases our reliance on functional diversity metrics (Gaston, 2000; Mouillot et al., 2013).

Many studies have estimated the conservation value of ecosystems using either taxonomic or functional diversity, and it is well established that human-induced changes affect both sets of metrics (Braga et al., 2013; Mouillot et al., 2013; Cottee-Jones et al., 2015; Bredemeier et al., 2015). Although these metrics can complement each other and provide

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https://doi.org/10.1016/j.ecolind.2018.07.062
Received 17 November 2017; Received in revised form 29 May 2018; Accepted 31 July 2018
1470-160X/

very different insights into mechanisms driving community changes, it is only recently that they have been assessed together in the same study (*e.g.* Moretti et al., 2009; Villéger et al., 2010; Baiser and Lockwood, 2011). These studies help demonstrate the importance of evaluating the sensitivity of both functional and taxonomic approaches in assessing biodiversity change, since there are valid reasons to suggest that they will show very different responses. First, most functional metrics are not related to species diversity (Villéger et al., 2008; Laliberté and Legendre, 2010), and the loss of functionally specialised species can lead to a decrease in functional diversity, even if total species richness remains high due to functionally similar species (Petchey and Gaston, 2002; Villéger et al., 2010). Second, the similarity between taxonomic and functional approaches may depend on the intensity of disturbance: low-intensity disturbance could change species composition but functional redundancy in highly diverse communities would maintain their functional structure, whereas high-intensity disturbances are likely to negatively affect both the taxonomic and functional components of biodiversity (Hidasi-Neto et al., 2012; Sterk et al., 2013; Edwards et al., 2014a).

There is currently a lack of empirical evidence to assess the sensitivity of taxonomic and functional metrics to temporal dynamics, and to determine how natural temporal variation interacts with human-induced modifications. It is important to fill this knowledge gap for two reasons: firstly, because taxonomic diversity is often a poor predictor of changes in ecosystem function (Baiser and Lockwood, 2011) and secondly, because diverse forest communities can be highly dynamic in time and the temporal variation of taxonomic or functional diversity may not show similar patterns (Villéger et al., 2010; Beiroz et al., 2017). For example, we might expect fewer changes in functional compared to taxonomic diversity over time because the traits of species within a community were selected by ecological filters (i.e. processes related to interactions among species as well as between species and the abiotic environment; Cornwell et al., 2006; Webb et al., 2010; Swenson et al., 2012), which could keep the relative frequency of traits constant even though the number of species may change. Importantly, there is little evidence of how taxonomic and functional approaches vary across time in human modified systems. We would expect the two approaches to yield more similar results as the intensity of habitat modification increases, because functional diversity declines with increasing loss of sensitive species, making it more likely that the loss of a given species will also entail a loss of function in highly disturbed areas (Leitão et al., 2016; Ricotta et al., 2016). Given the wide variation in the extent and intensity of human modifications to tropical forests, and the potential implications of disturbance for ecosystem functioning, clarifying the differences between taxonomic and functional assessments of biodiversity could provide important information for conservation and management.

We used a five-year study of Amazonian dung beetle communities to investigate the spatial and temporal patterns of taxonomic and functional diversity, contrasting the response of conceptually similar taxonomic and functional diversity metrics between undisturbed forest (used as a baseline for comparison) and two modified habitat types: primary forest corridors, which comprise a reduction in forest extent with increased edge and isolation effects; and *Eucalyptus* plantations, which represent a highly disturbed habitat where native vegetation has been replaced by exotic trees. Dung beetles were chosen as a focal group for this study because they are sensitive to changes in vegetation structure (Gardner et al., 2008; Almeida et al., 2011; Korasaki et al., 2013), their response traits are well studied (Nichols et al., 2013), and they mediate important ecosystem functions, such as seed dispersal and incorporation of nutrients into the soil (Slade et al., 2007; Nichols et al., 2008; Slade and Roslin, 2016). Specifically, we addressed the following key research questions:

1. Which approach to measuring diversity, taxonomic or functional, shows higher sensitivity to human-induced changes?
   As functional diversity declines with increasing loss of sensitive species, we hypothesized that functional metrics will be more sensitive to intense anthropogenic disturbance. However, as the influence of species losses varies for different taxonomic and functional metrics, the two approaches will provide complementary information.
2. Is the five-year temporal variation of taxonomic and functional diversity similar?
   As functional redundancy in species-rich dung beetle communities is likely to buffer changes among years, we hypothesized that temporal variation will be greater in taxonomic diversity compared to functional diversity at low levels of human-induced change, but temporal variation will become more similar between the two approaches as disturbance intensifies.
3. Does anthropogenic modification affect inter-annual variation between consecutive years?
   Previous studies have shown that inter-annual variation of dung beetle communities in undisturbed forest is mainly driven by climate (Beiroz et al., 2017), and anthropogenic disturbance often alters forest habitat structure and micro-climate (*e.g.* Liechty et al., 1992; Popradit et al., 2015); we therefore hypothesised that the magnitude of differences between consecutive years will be affected by the intensity of forest modification.

2. Material and methods

2.1. Study site

We conducted the study in the Jari River basin, located at north-eastern Brazilian Amazonia (00°27′ – 01°30′ S, 51°40′ – 53°20′ W; Fig. 1), an area of more than 15,000 km^2, which was partially converted from pristine forest to plantations of exotic trees *ca.* 50 years ago (Coutinho and Pires, 1997). Currently, the landscape comprises exotic tree plantations (450 km^2), and regenerating secondary forest (1000 km^2) interwoven with large primary forest corridors (*ca.* 200 m wide), and surrounded by *Terra Firme* primary forest (> 5,000 km^2; Fig. 1; Coutinho and Pires, 1997; Parry et al., 2007).

The region has a marked wet season from January to June, and a distinct dry season from September to November, with a tropical monsoon climate (Amw – Köppen classification), and an average annual rainfall of 2115 mm (Coutinho and Pires, 1997; Parry et al., 2007). The mean annual temperature is 26.7 ± 0.6 °C with monthly maxima and minima of 31.4 ± 1.1 °C and 22.5 ± 0.2 °C, respectively (Climate–Data.org., 2016).

We sampled in 12 undisturbed primary forest sites, eight primary forest corridors, and 15 *Eucalyptus* plantations separated by 0.2–60 km (Fig. 1). The undisturbed forest was used as a baseline, whereas primary forest corridors (100–300 m wide) were considered a low-intensity modification, with strong edge and isolation effects. *Eucalyptus* plantations represent a highly disturbed site, as the native forest has been completely replaced by exotic trees. Both modified habitat types have a distinct dung beetle species composition and community structure, mainly by species replacement (turnover component of β-diversity in Fig. S1). However, communities in *Eucalyptus* plantations are the most dissimilar to those in undisturbed forest (Fig. S1; Barlow et al., 2010). It is also important to highlight that the *Eucalyptus* trees are harvested each 4–5 years. Thus, most of our plantations sites were harvested during the study, we are aware that this activity can strongly affect the dung beetles community but this is one of the main disturbance in fast-growing crops and was represented in this study.

2.2. Dung beetle sampling

We followed the protocol for dung beetle sampling in previous studies at same site (Barlow et al., 2007; Gardner et al., 2008; Barlow et al., 2010). Thus, we sampled dung beetles using pitfall traps baited