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Functional diversity and stability of litter-invertebrate communities following land-use change in Sumatra, Indonesia

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ABSTRACT

Tropical land-use intensification is rapidly increasing in regions that harbour high levels of biodiversity, thus posing a serious threat to the stability and resilience of tropical ecosystems and the important ecosystem services that they provide. We compared functional group richness and functional dispersion in litter-invertebrate communities among four different land-use systems, ranging in intensity from primary degraded lowland forest to oil-palm agriculture in two landscapes on Sumatra, Indonesia. We then investigated the consequences for functional stability and community resilience by calculating functional redundancy and response diversity of sampled communities. From primary degraded forest to intensively managed oil-palm systems, we found a 46% decrease in species richness and a 48% reduction in density, but weaker effects on functional group richness and an increase in functional dispersion. Although we detected no significant alteration of response diversity, functional redundancy of litter-invertebrate communities decreased clearly by losing 37% of functionally redundant species due to land-use change. Our results indicate that land-use change, from tropical rainforest to oil-palm agriculture, can alter both taxonomic and functional diversity of litter-invertebrate communities, resulting in the loss of functional redundancy and thus functional stability of these ecosystems. However, we also show that land-use systems of intermediate management intensity, such as jungle-rubber agroforestry, could serve as reservoirs of functional diversity and stability in monoculture-dominated production landscapes.

1. Introduction

Land-use change imposes strong impacts on biodiversity, which in turn can have important implications for the stability and resilience of natural ecosystems (Flynn et al., 2009; Foley et al., 2005; Laliberte et al., 2010). Tropical forests, which harbour particularly high levels of biodiversity, are increasingly threatened by land-use conversion and intensification to agricultural cash crop plantations (Gibson et al., 2011; Koh and Wilcove, 2007; Turner et al., 2008). In particular, oil palm (*Elaeis guineensis*) is one of the fastest expanding crops globally (Fitzherbert et al., 2008), with Indonesia and Malaysia together responsible for 90% of global palm-oil production (Sheil et al., 2009). In addition, monoculture rubber (*Hevea brasiliensis*) plantations have expanded rapidly in the region, with an increase in area of 32% over the last decade (Wilcove et al., 2013). This expansion of monoculture crops has been largely associated with the conversion of diverse tropical forests and is therefore directly linked to large-scale losses in biodiversity and ecosystem functioning (Barnes et al., 2014b; Koh and Wilcove, 2007; Wilcove et al., 2013).

Biodiversity loss resulting from monoculture expansion in tropical landscapes has been shown to span many taxonomic groups (Fitzherbert et al., 2008; Senior et al., 2012). These impacts are especially detrimental for forest-specialist species that are particularly sensitive to the loss and fragmentation of tropical rainforest landscapes (Koh and Wilcove, 2008). The high-intensity management of oil-palm dominated systems makes them an ecologically poor substitute for tropical forest ecosystems as they support relatively low species diversity (Barnes et al., 2014b; Fitzherbert et al., 2008). However, there is still very limited knowledge of the consequences of rainforest transformation to oil-palm and other tropical plantation forestry for the stability of ecosystem functioning, and how intermediate levels of land-use intensity could maintain species diversity and functional stability in these altered landscapes.

Over the last 20 years, a considerable body of research has established the importance of functional diversity in discerning the responses of biological communities to global change drivers (Cadotte

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et al., 2011; Tilman et al., 1997). Functional diversity is the diversity of functional identities of organisms in a community based on morphological, behavioural, or life-history traits, which are often directly linked to an organism's ecological performance (Gagic et al., 2015; Petchey and Gaston, 2006; Villéger et al., 2008). As such, functional diversity can be directly related to ecological attributes such as the functional stability or the resilience of communities, depending on the trait complexes measured (Laliberte et al., 2010). Various approaches for assessing functional diversity have been proposed, with a clear development of measures to deal with specific research questions. Functional group richness—the total number of species groups composed of functionally similar species—has been widely used for quantifying the functional heterogeneity of communities (Lanta and Lepš, 2007; Symstad, 2000). However, because functional group richness is a rather coarse measure of functional diversity (Petchey and Gaston, 2006), other measures such as the multivariate distance-based metric functional dispersion (Laliberte and Legendre, 2010) have been developed to detect more fine-scale patterns in functional heterogeneity.

A particularly important application of functional diversity is its utilization for assessing community functional stability and resilience (Laliberte et al., 2010). This approach employs functional grouping to quantify the absolute number of taxonomic species within functional effect groups (i.e., groups of species sharing similar traits important for ecosystem functioning) to assess functional redundancy, and utilizes functional dispersion within functional response groups (groups of species sharing similar traits that determine responses to environmental disturbances) to calculate response diversity. Calculated in this way, functional redundancy evaluates the risk of losing ecosystem functions resulting from the loss of all species within a functional group, providing an indication of the functional stability of an ecosystem, rather than the rate of ecosystem functioning per se. On the other hand, response diversity is a measure of the heterogeneity of responses in species assemblages within functional groups, thus giving insight into the resilience of communities regarding future disturbances. These measures clearly provide a powerful estimation of community functional stability and resilience. Although previous studies have investigated patterns in functional diversity for specific taxa within tropical agricultural landscapes (e.g., F.A. Edwards et al., 2014; Gray et al., 2014), to our knowledge there have been no studies quantifying these general measures of stability and resilience in highly diverse tropical animal communities spanning multiple higher-order taxa.

In this study, we assessed the consequences of land-use change for the stability and resilience of diverse tropical litter arthropod communities by evaluating changes in their functional trait composition following conversion of tropical rainforest to plantation agriculture. While Barnes et al. (2014b) recently demonstrated how this land-use change alters the diversity and functional efficiency of these communities, this study provides new insight into the future certainty of maintaining these ecological functions. To detect differences in functional diversity of species assemblages among land-use systems, we calculated functional group richness and functional dispersion (Laliberte and Legendre, 2010). Using these results we evaluated 1) community stability by calculating functional redundancy and 2) community resilience to future disturbances by calculating response diversity, across four tropical land-use systems of varying intensities. By comparing oil-palm and rubber monoculture systems to primary degraded forest (as defined by Margono et al. (2014)) and a less intensively managed agroforestry system, i.e., jungle rubber (Gouyon et al., 1993), we established the impacts of tropical land-use change on functional diversity, redundancy, and community resilience. Additionally, we discerned how intermediate intensities of agroforestry can serve as potential reservoirs of functional diversity and maintain community functional stability in anthropogenic landscapes.

2. Methods

2.1. Study system

Sampling took place between October and November 2012 in the Jambi Province, Sumatra, Indonesia; an area formerly known to have one of the largest tracts of rainforest in Southeast Asia. Today, the landscape is characterized by a mosaic of agroforestry plantations and primary degraded lowland rainforest. The sampling regions are at 0–400 m above sea level, with a mean annual temperature of 25 °C and an annual precipitation of 2000–3000 mm (Murdiyarso et al., 2002). The region has suffered one of the highest deforestation rates worldwide, predominantly due to conversion of land to plantation agriculture (Abood et al., 2014).

2.2. Sampling design

Macro-invertebrate communities were sampled in four land-use systems: primary degraded forest, jungle rubber, monoculture rubber (7–17 years old), and oil palm (9–16 years old), replicated four times in each of the two landscapes, Bukit Duabelas and Harapan ($n = 32$) (Fig. 1). We sieved 1 m^2 of leaf litter, using a coarse 2 cm mesh width, within each of three randomly placed 5×5 m subplots located within the 50×50 m sampling sites (Fig. 1). Macro-invertebrates were hand-collected from the litter sieves, stored in 75% ethanol and transported to the laboratory for identification and trait measurements. Macro-invertebrates were collected under Permit No. 2695/IPH.1/KS.02/XI/2012 issued by the Indonesian Institute of Sciences and the Ministry of Forestry.

2.3. Animal identification and trait measurements

All animals were identified to morphospecies based on consistent morphological characteristics. We measured four different traits for every individual: Body mass, dispersal capacity, eusociality and feeding type. These traits were defined as ‘response traits’, ‘effect traits’, or both (Table 1), where response traits determine the animal's response to environmental changes and effect traits determine the animal's effect on environmental processes (Suding et al., 2008). One important goal of this study was to assess functional diversity, redundancy and response diversity across taxonomically broad communities without bias toward any particular taxonomic groups. As such, we had to carefully choose traits that would be highly meaningful response and effect traits for all organisms that were sampled. For example, traits such as leg length would have very different functional implications for orthopterans than for diplopods, compared to the highly universal traits we used such as body size.

Metabolic demand is strongly correlated with body mass in animals (Ehnes et al., 2014), which is directly related to several biological rates and processes such as predation and decomposition (Barnes et al., 2014b). Furthermore, body mass affects species' vulnerability to disturbances and is thus related to extinction risk. For example, Barnes et al. (2014a) found that small-bodied dung beetles were most negatively affected by edge effects and matrix degradation, whereas Senior et al. (2012) found that larger-bodied carnivorous ants were most negatively affected by land-use conversion to oil-palm plantations. As such, we specified body mass as both an effect trait and a response trait. Using length-mass regressions from the literature, we calculated body mass from individual body lengths, measured to an accuracy of 0.1 mm (Barnes et al., 2014b).

Dispersal capacity gives an indication of a species' ability to escape adverse biotic and abiotic stressors. Furthermore, it delimits a species' ability to reach other resource patches in fragmented anthropogenic landscapes (Ockinger et al., 2010). We therefore used dispersal capacity as a response trait, providing information on the ability of a species to cope with land-use change. Dispersal capacity was approximated by