Large-scale assessment of ecological and anthropogenic drivers of beetle communities in Laos shows that conversion of natural forests into plantations leads to a decline in abundance

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Abstract

Rapid economic development can pose a threat to the biodiversity of tropical countries. In Laos, this is manifested by the conversion of natural forests into plantations, even though this area is one of the biodiversity hotspots of Southeast Asia. Beetle communities can be good indicators of the impact of anthropogenic pressure on natural ecosystems. In this study, we analyzed for the first time a countrywide inventory of Coleoptera to assess the ecological and anthropogenic drivers of beetle communities in Laos. We examined beetle communities (described at the family level) across the country, located in distinct habitat types, in order to understand the impact a rapid increase in human activities has on the region's biodiversity. We found that beetle abundance had declined in plantations compared to natural forests. At the same time, we observed fewer beetle families in plantations overall, but at the scale of sampling sites there was no difference in local diversity compared to natural forests, suggesting a homogenization of beetle communities in anthropogenic habitats. Although results are certainly sensitive to our coarse classification of beetle specimens into families, the negative impact of the conversion of natural tropical forests into agriculture area can still be clearly demonstrated. Our findings highlight that it is possible to make use of unstructured large-scale inventories to explore how beetle communities responds to landscape changes induced by human activities. We suggest that sampling beetle communities can be used as an ecological indicator to monitor anthropogenic impacts on tropical ecosystems.

Original research paper

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Abstract

Rapid economic development can pose a threat to the biodiversity of tropical countries. In Laos, this is manifested by the conversion of natural forests into plantations, even though this area is one of the biodiversity hotspots of Southeast Asia. Beetle communities can be good indicators of the impact of anthropogenic pressure on natural ecosystems. In this study, we analyzed for the first time a countrywide inventory of Coleoptera to assess the ecological and anthropogenic drivers of beetle communities in Laos. We examined beetle communities (described at the family level) across the country, located in distinct habitat types, in order to understand the impact a rapid increase in human activities has on the region's biodiversity. We found that beetle abundance had declined in plantations compared to natural forests. At the same time, we observed fewer beetle families in plantations overall, but at the scale of sampling sites there was no difference in local diversity compared to natural forests, suggesting a homogenization of beetle communities in anthropogenic habitats. Although results are certainly sensitive to our coarse classification of beetle specimens into families, the negative impact of the conversion of natural tropical forests into agriculture area can still be clearly demonstrated. Our findings highlight that it is possible to make use of unstructured large-scale inventories to explore how beetle communities responds to landscape changes induced by human activities. We suggest that sampling beetle communities can be used as an ecological indicator to monitor anthropogenic impacts on tropical ecosystems.

KEYWORDS

Beetles, biodiversity, landscape contexts, railway, rapid change.

1. INTRODUCTION

Laos covers a large part of the Indochinese limestone belt and is one of the most biodiversity-rich countries of Southeast Asia (Kumar et al., 2016). Its dominant land cover is tropical dense forests, of which approximately 80% are located in mountainous areas with steep to moderate slopes. It includes several National Protect Areas (NPAs) that are considered as biodiversity hotspots, such as the Hin Nam No NPA, which has officially been submitted to become the first natural World Heritage Site of Laos. Many studies report a highly diverse fauna in the region including amphibians, reptiles, birds, bats, and over 100 species of large mammals, new species being frequently discovered (MAF & STEA, Myers et al., 2000; Ceballos & Ehrlich, 2006; Biodiversity Country Report, 2003; MoNRE, 2016). However, as of yet, no single survey has attempted to describe the diversity of Coleoptera, or even insects in general, in Laos. Until fairly recently, the insect fauna of Laos remained one of the most poorly known in SE Asia (Sekerka & Geiser, 2016) and existing knowledge mostly comes from specimens collected by foreign visitors before the 1920s. Recently, though, we observed an increase in the number of entomological expeditions, permitted by the country becoming more accessible to foreigners.

The extremely rapid economic growth that Laos is experiencing comes at the expense of biodiversity, which is facing a growing number of significant challenges associated with land-use changes (World Bank national accounts data, 2017). For example, during the 1990s and 2000s, the land area dedicated to rubber plantations has increased exponentially to reach an evaluated surface of 450,000 ha in 2015 (Smith et al., 2016). Such conversion of natural tropical forests into rubber plantations occurs in several tropical regions of the world where it is recognized to negatively impact biodiversity and ecosystems (Warren-Thomas et al., 2015). Moreover, the economic growth of the region is likely to continue or even accelerate in the near future, as the railway that connects Kunming, China to Bangkok, Thailand, passing through much of Laos, is completed (Chen and Haynes, 2017; Ng et al., 2020). Indeed, infrastructure development will increase the general appeal of the region and encourage foreign investment, contributing to direct and indirect threats to local ecosystems (Torres et al., 2016; Borda-de-Água et al., 2017). In this regard, insects, for which a global decline has been recently documented (Sánchez-Bayo & Wyckhuys, 2019), are among the taxa that are known to be affected by deforestation in a tropical context (Correa-Carmona et al., 2022). Generally, deforestation, agricultural intensification, and climate change, including more frequent extreme weather events, have been suggested as being the major drivers of the global insect decline (Wagner, 2020; Eggleton, 2020). However, this assessment mostly comes from population trends estimated in the Global North (Sanchez-Bayo & Wyckhuys, 2019), while

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the current state of insect diversity in tropical contexts remains poorly known. Knowledge of the influence of human impact, through an effect on landscape structure, on insect diversity in southern Asia, and in Laos in particular, is still lacking and virtually nil (Chouangthavy et al., 2020).

Beetles (Coleoptera) are the most diverse taxonomic order on Earth. Because they exhibit rich abundance, biomass, and diversity, beetles are often used as indicator species of anthropogenic impact on ecosystems, including tropical forests (Ghannem et al., 2018; Zodl & Wittmann, 2003; Parikh et al., 2021). For example, dung beetles (Scarabaeidae: Sacarabaeinae) play an important role in the functioning of tropical forest ecosystems while being also sensitive to human disturbance and environmental changes, making them ideal focal species for investigating conservation issues (Slade et al., 2011; Spector, 2006). In southern Asia and in Laos in particular, despite the fact that beetle diversity is high (Moodley et al., 2022) and human activity is growing, the approach of employing beetle community composition, richness, and abundance as surrogates for estimating the impact of agricultural intensification and anthropogenic disturbance has never been carried out. The few studies addressing the question of beetle community richness in relation to human factors were restricted to specific local contexts (Chouangthavy et al., 2020), and were insufficient to estimate more broadly the actual impact of human pressures on beetle biodiversity in Laos. There is thus a need for large-scale assessments of beetle diversity conducted in natural vs. anthropogenic landscapes, in order to estimate the effect of Laos' economic development on its rich biodiversity.

Besides human activity, there is evidence that beetle diversity is also partly structured by climate at large spatial scales (Andrew & Hughes, 2004; Hortal et al., 2011). Even at a more regional scale, beetle assemblages appear to be structured across elevation gradients following the corresponding climatic variation (Gebert et al., 2020; Dolson et al., 2021). This implies that (i) beetle species may be affected by climate change in the recent past and in the future (Harris et al., 2019), and (ii) any attempt to characterize the impact of anthropogenic factors on beetle diversity at a large geographical scale must also account for climatic gradients that may influence the richness, abundance, and composition of beetle communities. Therefore, it is likely that the beetle fauna of Laos, a country that covers a latitudinal gradient of ca. 900 km and hosts four different climate zones (Am, Aw, Cwa, Cwd, Essenwanger & Landsberg, 2001), is somewhat influenced by variation in temperature and precipitation across the country.

In order to understand how the rapid economic development of the region affects its biodiversity, we investigated beetle community composition, diversity, and abundance across a large spatial scale in Laos, focusing on two contrasting landscape contexts. Specifically, we made use of an unprecedentedly large inventory of beetles carried out across the entire country to compare beetle assemblages (characterized at the family level) in natural forests and in plantations, accounting also for climatic gradients that may be an additional driving force of the composition and diversity of beetle communities at macrogeographical scales. We hypothesize that beetle richness and abundance are higher in natural forests compared to plantations. This work provides the first assessment of the effect of landscape context and anthropization on beetle diversity that is carried out at such a large scale in this region of the world.

2. MATERIALS AND METHODS

2.1 Landscape context

The study was conducted in 12 areas across Laos (Figure 1), in two contrasting landscape contexts (Table 1). Five sampling locations correspond to relatively undisturbed natural forests, which have long been recognized for their outstanding biodiversity. There, the traditional human activity consists mainly of logging, food searching, and hunting. However, natural forests have recently been facing land-use intensification pressures, due to extremely rapid economic growth leading to the development of multiple aspects of human activities, including the expansion of agricultural lands. Part of the natural forest in the study areas has been influenced by the construction of a railroad going from the north to the center of Laos, which will be part of a larger railway linking China to Thailand through Laos.

In contrast, seven sampling locations were located in plantations. This type of landscape structure had different agricultural and deforestation histories and is mostly dedicated to rubber and eucalyptus plantations,

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which have increased exponentially in the country. Part of the present study was undertaken on a large rubber plantation in northern Laos (site 4L and 4H), which covered 33,000 ha in 2016 and was occupied by various ethnic groups (Kusakabe and Chanthoumphone, 2021); more rubber plantation areas now extend to the center and to the south. Most of the deforestation happened several years before sampling, resulting in a single unfragmented rubber plantation. In addition, sampling also occurred in a eucalyptus plantation planted with a monocrop of eucalyptus trees in rows, the natural forest around plantations being used for extensive livestock and rice paddy field (site 1W, 1P, 2, and 3). Furthermore, different agricultural activities such as coffee, cabbage, strawberry farms, and grassland mixed with rice paddy fields were covered in the present study across the country (Figure 1).

2.2 Beetle sampling and taxonomic assignment

We explored beetle communities across the country in the two distinct habitat types, applying different trapping methods (pitfall traps, window traps, light trapping, and hand collection, in order to capture different aspects of community composition) throughout four consecutive years (2018-19-20-21, depending on sampling site). Pitfall traps consisted of plastic cups (300 cm^3) with a diameter of 8 cm at the top, buried in the ground so that the top rim was flush with the soil surface. The window traps were made of 1.5-liter transparent plastic drinking water bottles with one window and were suspended upside-down. The traps were hung on wooden poles at approximately 150 cm above ground level. Both trap types were filled with about 50 ml of 70% alcohol and had a cover for rain protection during the collections carried out in the rainy season. Traps were left five days in the field, then all captured insects were brought back to the laboratory, where beetles were separated from other species and debris and sorted into families under a microscope. Light trapping consisted of a 125v bulb and white clothing of 4.5 m^2 hung up between trees. All beetle specimens were directly stored in 95% alcohol in the tube after sorting. Furthermore, hand collection was done by the first author during visits to the field. All beetle specimens were assigned to the family level, like several other studies which have reported the use of higher insect taxa (family level) to investigate habitats and environmental scenarios (Parikh et al., 2021; Gonzalez et al., 2015; Baldi, 2003). We then described diversity and community composition across landscape contexts based on the identity and abundance of beetle families.

Some sites were sampled each month for several years using different trapping methods and many traps, whereas in some sampling sites collection occurred only occasionally during a few days in a single year using one or a couple of complementary trapping methods, resulting in a small number of traps. For example, four sampling sites were equipped with pitfall (2 x 30) and window (2 x 30) traps in 2020. Then, in these sites, sampling occurred each month of the year for 5 days, resulting in a particularly large sampling effort (60 traps x 5 days x 12 months). In contrast, a single sampling site was equipped with 15 window traps for nine days in 2018. Six sites were sampled by hand collection during a few days in 2019 and 2021. Finally, light trapping was used for three to five days in four sampling sites in 2019 and 2021 (Table 1).

2.3 Climate data

Climate variables used in this study were based on mean annual temperature and precipitation obtained from the Worldclim web portal version 2.1 (Fick & Hijmans, 2017). The variables of Worldclim are raster surfaces derived from the interpolation of weather stations' data collected across the period 1970-2000. We imported a shapefile of Laos boundaries from the GADM database (version 3.6, https://gadm.org/), the coordinates of sampling sites and the rasters of annual precipitation and mean annual temperature from Worldclim into QGIS v.3.22.7. Then, we extracted temperature and precipitation at each sampling locations as a proxy for the climatic variation that exists across sampling sites distributed all over Laos.

2.4 Statistical analyses

We first tested the effect of four independent response variables (landscape context [i.e., natural forest vs. plantations], trapping method, temperature, and precipitation) on beetle community composition using a Permutational Multivariate Analysis of Variance (PERMANOVA) as implemented in the "vegan" R package (Oksanen et al., 2022). We then used Non-metric Multidimensional Scaling (NMDS) to represent the dissim-

ilarity of beetle communities between natural forest and plantation areas. Subsequently, we compared family richness between natural forest and plantation areas, and between trapping methods, by plotting rarefaction and extrapolation curves with the number of collected individuals as a measure of sampling intensity ('iN-EXT' package in R v.4.2.1; Hsieh et al., 2019). We used the asymptotic estimators provided by iNEXT as a measure of the total family richness (including unobserved families) in each sampling site.

The drivers of the diversity of beetle assemblages were explored with a linear model using the "*lm*" function in R (R Core Team 2022). The model included the asymptotic estimates of richness obtained in each sampling site as a dependent variable, and landscape context, trapping methods, temperature, and precipitation as independent variables. The same approach was used for Shannon and Simpson indices as estimates of the diversity of beetle communities, again using asymptotic estimators from iNEXT.

We used negative binomial regressions, fitted with the "*glm.nb*" function in the MASS R package (Venables & Ripley, 2002), to test the effect of the same variables (landscape context, trapping methods, temperature, and precipitation) on beetle abundances. Negative binomial models were used because a Poisson Generalized Linear Model (GLM) that we fitted first showed evidence of overdispersion, and the negative binomial model had a lower AIC that the Poisson GLM. Here, we had to account for the very variable sampling effort that produced the observed variation in beetle abundances; therefore, models also included as an offset the sum of the duration of sampling (the number of days) and the number of traps. The same approach was used first for the total beetle abundance, then for the most abundant beetle families separately: Carabidae, Scarabaeidae, Nitidulidae, Curculionidae, and Chrysomelidae. All statistical analyses were performed in the R platform (version 4.2.1, R development Core Team 2022).

3. RESULTS

A total of 19,053 beetle individuals were recorded across all sampling sites during the study period, which represents 64 beetle families. The rarefaction and extrapolation curves, adjusting for the number of specimens collected in natural forests and plantation areas, clearly revealed that beetle community composition in natural forests had a higher overall cumulative diversity of families compared to plantations (Figure 2). We also determined that the highest diversity was sampled at site 8, 3, and 5 in natural forests respectively (Figure S1).

Beetle community composition did not appear to be dependent on any of the variables tested, according to the PERMANOVA analysis (Table 2). However, visual examination of NMDS indicated that the beetle families collected differed between trapping methods (Figure S2), and that beetle communities were largely overlapping between natural forests and plantation areas (Figure 3).

The richness of beetle communities (in terms of the estimated number of families per site) was found to be dependent on the trapping method ($P = 0.006$) (Table 3), but was not influenced by the other three variables of interest (landscape context, temperature, and precipitation). In addition, there was also no significant effect of any variable on beetle community diversity as estimated by Shannon and Simpson indices (Table S2, S3).

There was a strongly significant effect of all tested variables, except temperature, on the variation of beetle abundance across sites (Table 4). Specifically, the abundance of beetle communities was significantly higher (ca. x3 on average) in the natural forest compared to plantations (P = 0.0014), differed between trapping methods (P = 0.0001), and was positively associated with precipitation (P = 0.0146) (Figure 4). When analyses were computed for each family separately, we highlighted a similar pattern of higher abundances in the natural forest compared to plantations; we also identified significant effects of temperature and precipitation as well as trapping methods (Table S1).

4. DISCUSSION

Despite the fact that tropical areas host the majority of insect diversity, they are generally vastly undersampled compared to temperate ecosystems (Hellmann & Sanders, 2007). This knowledge gap is particularly undesirable in Southeastern Asia, which is experiencing a rapid economic growth that may imperil its rich

insect biodiversity. In this study, we report for the first time a large sampling of the whole order Coleoptera carried out across Laos, which enabled the investigation of the drivers of beetle diversity at a large spatial and taxonomical scale. This is a step towards a better understanding of insect diversity in Asian tropical forests, and of the threats they may face.

The present study first confirmed our expectation that beetle diversity is high in the country. From the ca. 20,000 collected specimens, we recorded 64 beetle families. Moreover, more than 50 beetle specimens remained impossible to assign to any known family and were thus excluded from this study. Some of them may belong to additional beetle families, suggesting that the diversity of beetle families in the region may be even larger. It is however hard to reliably estimate the actual number of families living across the various landscape contexts of the country without a meticulous approach involving standardized sampling protocols and molecular taxonomy (Garcia-Robledo et al., 2020). The data presented here reveals slightly higher number of families than that of earlier recorded data in surrounding countries such as Thailand, Vietnam, and Hong Kong (Rattanawannee et al., 2013; Thinh et al., 2004; Zhao et al., 2022). Overall, 177 Coleoptera families were recorded globally, meaning that we recorded 36% of all known beetle families (Moodley et al., 2022). However, due to practical constraints, the present study described beetle communities at the family level only. Indeed, beetle taxonomy is notoriously difficult in the absence of detailed identification keys or molecular tools (see e.g. Jin et al., 2020; Sabatelli et al., 2021). The actual diversity at the species level, i.e. species richness, is thus much more important, and may include endemic or undescribed species. It is widely accepted that Laos is a hotspot for the biodiversity of beetles, insects, and other organisms. By providing a first countrywide view of beetle family diversity of Laos, we aim to provide a basis for future studies investigating the impact of an extremely rapid economic change, associated with land use change, on beetle diversity in Laos.

According to our results, beetle abundance was reduced in plantations compared to natural forests, which is in line with global patterns which show that insects are sensitive to habitat disturbance from human activities such as agricultural expansions or settlements (New et al., 2021; Hansen et al., 2012; Sanchez-Bayo & Wyckhuys, 2019). Natural forest ecosystems play an important role in species diversity worldwide (Gibson et al., 2011), whereas intensification of agriculture is identified as a major cause of insect diversity decline and extinction (Sanchez-Bayo & Wyckhuys, 2019), but also soil carbon loss (Guo et al., 2022). A strong impact of land-use intensification has been reported for beetles and other insects in tropical forests in Asia, as well as in Africa and America (Phillips et al., 2017). Several observational and experimental studies have revealed that the conversion of natural forests into plantations is harmful to species that cannot adapt to their new environmental conditions (Uribe et al., 2021; Warren-Thomas et al., 2015); our results show that Laos is no exception. Therefore, a large number of insect communities may be, currently or in the near future, at risk from land-use intensification in Laos, even though the region is still mainly covered by mountains and forests.

A more in-depth understanding of the response of beetle diversity to current and future economic development in Laos is needed to implement practical conservation actions. In this regard, this study clearly demonstrates that the rapid and continuous land-use changes the country is experiencing may threaten beetle communities: not only their abundance declined in plantations, but across the whole survey we also sampled fewer families in plantations compared to natural forests (48 vs. 59 observed families, respectively). This finding is in line with other studies showing the impact human-modified landscapes can have on beetle biodiversity; for example, dung beetle communities are well recognized as a good indicator to estimate the influence of anthropogenic habitats in tropical forests (Gardner et al., 2008; Halffter & Arellano, 2002). In the present study, we investigated beetle communities across a large countrywide latitudinal gradient, in which the northern to center parts are facing a modernization of the road network in addition to the conversion of forests into plantations. In this regard, a recent report by Danyo et al. (2018) pointed out the potential risks of forest and biodiversity loss resulting from road improvement in Laos. We believe that our findings will therefore be useful and important in order to predict properly the conservation issues arising from the economic growth of the region.

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However, unexpectedly, the observed difference in abundance between plantations and natural forests did not correspond to differences in terms of family composition. Similarly, although fewer families were sampled in plantations at the scale of the whole country, anthropization does not seem to reduce community diversity when analyzed at the scale of each sampling site. Logically, this must be caused by a higher homogeneity of communities located in plantations, i.e. the same set of families are found in all plantations, while forest communities are more diverse from each other (despite a similar local diversity). Biotic homogenization, in which a few common species take over specialist species, is frequently observed in human-modified landscapes (McKinney & Lockwood, 1999), and has also been observed in beetles (Ramirez-Ponce et al., 2019). However, results may vary at a lower taxonomic level; it is likely that species diversity is actually reduced along human activities, in accordance with previous studies (e.g. Jung & Lee 2016; Vanbergen et al., 2005). Here, beetle individuals were assigned to the family level, since we expected that it would be sufficient to investigate the impact of rapid change caused by anthropogenic pressures associated with land use change. The beetle collection contained a huge number of specimens, and the taxonomy of many groups is challenging due to their complex diagnostic morphological characters and their small body size. An improved dataset that would distinguish individuals at the species-level may reveal a slightly picture, including perhaps an effect of agricultural development on species diversity at the local scale.

Despite the geographical scale of the study, we did not find an effect of climate on community composition. However, again, it could be because the present study has investigated families only and not species. Generally, assessments of climatic niches are considerably more precise when carried out at lower taxonomic levels (Bayliss et al., 2022; Gonzalez et al., 2011), meaning that each individual species may have vastly different responses to climatic variables that would be masked when merged into whole families. Still, the present study found more individuals in more humid areas, revealed by a positive effect of the precipitation variable on beetle abundance. This general effect may vary depending on the family composition, as evidenced by different responses of beetle abundance to temperature and precipitation depending on the family considered; the actual variation of diversity across climate gradients may thus be more complex.

5. CONCLUSIONS

The present study provides the first approach that attempts at investigating the effect of various independent variables on beetle community composition and richness along contrasted landscape types across Laos. A potential limitation of the study is that sampling did not follow a standardized protocol across the country. On the contrary, we compiled here a dataset of beetle specimens collected using different sampling efforts and methods. It was clear that both composition and abundance differed depending on the trapping method. In this case, a good sampling should probably use several complementary approaches to sample the whole diversity of beetles. For instance, while light traps are probably suitable for sampling flying insects, pitfall traps are adapted for ground-dwelling species. Still, we were able to make use of this dataset by employing various approaches to account for these unequal sampling strategies: country-scale and local family richness were estimated from accumulation curves, trapping methods were always included as covariables, and sampling effort was incorporated as an offset in statistical models. The main outcome of the present study is that the conversion of natural forests to plantations is harmful for beetle communities, at least in terms of their abundance. More studies are needed to better understand this pattern and to understand how species richness is also impacted. This may be achieved in the future by implementing long-term monitoring of beetles across Laos following a simple protocol that can be used by many volunteers, and by incorporating a better taxonomic resolution (i.e., species) in analyses.

CONFLICT OF INTEREST

The authors do not have any conflicts of interest.

DATA AVAILABILITY STATEMENT

The beetle sampling data is available in the Figshare repository. https://doi.org/10.6084/m9.figshare.21913608.v2

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FIGURE 1 Map showing the distribution of sampling areas in 2018-19-20-21 across Laos. Green and black dots indicate natural forests and plantations, respectively. Circles, upwards triangles, downwards triangles, and squares show different trapping methods (pitfall, hand, light, and window, respectively).

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FIGURE 2 Rarefaction and extrapolation curves of beetle family richness for natural forests and plantation areas.

TABLE 1 Characteristics of sampling sites, including sampling method and intensity (number of traps and sampling days), environmental variables (mean annual climate and elevation), location, and landscape context (natural forest vs. plantation).

Sites	Trapping methods	Number of traps	Number of sampling days	Mean annual temperature (°C)
Site 1W	Window	30	60	25.85
Site 1P	Pitfall	30	60	25.85
Site 2	Window	30	60	25.54
Site 3	Pitfall	30	60	25.54
Site 4L	Light	1	3	23.15
Site 4H	Hand	1	3	23.15
Site 5	Light	2	5	22.28
Site 6L	Light	1	3	24.52
Site 6H	Hand	1	3	24.52
Site 7	Window	15	9	26.05
Site 8	Light	1	2	24.32
Site 9	Hand	1	3	20.49
Site 10	Hand	1	3	20.26
Site 11	Hand	1	3	20.35
Site 12	Hand	1	3	20.35

TABLE 2 Permutational Multivariate Analysis of Variance (PERMANOVA) to test the effect of trapping method, landscape context (natural forest vs. plantation), temperature and precipitation on beetle community composition.

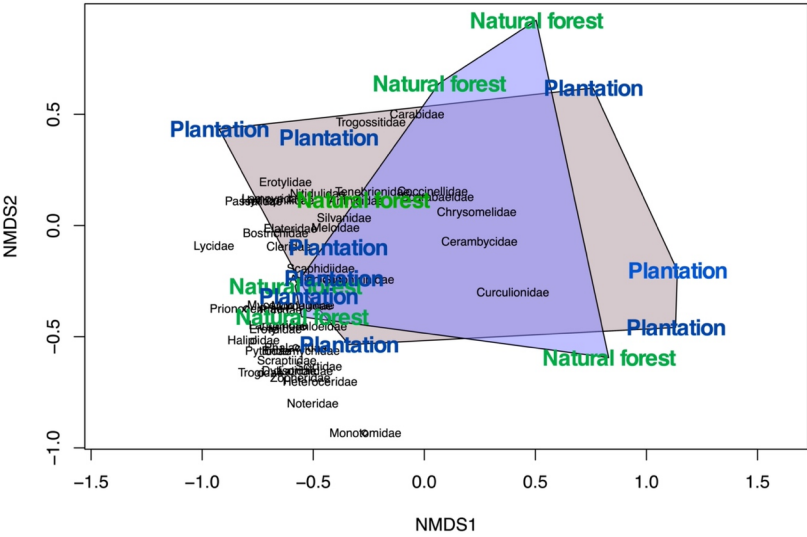| Variables	df	Sum Sq	Mean Sq	F	R^2	p-value
Trapping method	3	1.0425	0.3475	1.3217	0.2920	0.2058
Landscape context	1	0.2079	0.2079	0.7908	0.0582	0.6002
Temperature	1	0.0625	0.0625	0.2379	0.0175	0.9643
Precipitation	1	0.1535	0.1535	0.5839	0.0430	0.7448
Residuals	8	2.1034	0.2629		0.5892	
Total	14	3.5699			1.0000	

FIGURE 3 Non-metric Multidimensional Scaling (NMDS) to represent the pairwise dissimilarity of beetle communities between natural forest and plantation areas.

TABLE 3 Effect of trapping method, landscape context (natural forest vs. plantation), temperature and precipitation on beetle family richness.

Variables	df	Sum Sq	Mean Sq	F	p-value
Trapping method	3	2841.4401	947.1500	8.8233	0.0064 **
Landscape context	1	180.0810	180.0800	1.6775	0.2313
Temperature	1	3.4600	3.4600	0.0322	0.8619
Precipitation	1	462.7301	462.7301	4.3106	0.0715
Residuals	8	858.7711	107.3500		

TABLE 4 Effect of trapping method, landscape context (natural forest vs. plantation), temperature and precipitation on beetle abundance.

Variables	LR Chi²	df	p-value
Trapping method	17.9986	3	0.0001 **
Landscape context	8.6806	1	0.0014**
Temperature	0.6401	1	0.3850
Precipitation	3.7315	1	0.0146*

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FIGURE 4 Partial dependence plots showing the predicted response of beetle abundance to the four response variables tested (all effects are significant at the α=0.05 level, except temperature), modelled using a negative binomial regression.