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Land-use change differentially affects endemic, forest and open-land butterflies in Madagascar

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Abstract

1. The conversion of tropical forests into agriculture reduces biodiversity dramatically. However, species might differ in their responses, depending on their habitat specialisation and geographic origin. In this study, we assess how butterfly assemblages differ between old-growth forests, forest fragments, forest-derived vanilla agroforests, fallow-derived vanilla agroforests, woody fallows, herbaceous fallows, and rice paddies in Madagascar.
2. We recorded 88 butterfly species, of which 65 species are endemic to Madagascar. Land-use types with woody vegetation sustained many endemic (mean: 6.8 species) and forest butterfly species (mean: 4.8 species). Rice paddies and herbaceous fallows were richer in open-land species (mean: 7.6 species) and poorer in forest species (mean: 1.7 species) compared to other land-use types. Compared to herbaceous fallows, fallow-derived vanilla agroforests hosted more endemic (+164%) and forest (+239%) species. Richness of open-land species in forest-derived vanilla agroforests was six times higher than in forest fragments.

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3. Overall, 27% of species occurred exclusively in one land-use type and 19% of all species when old-growth forests were excluded. We found the highest number of exclusive species in forest-derived vanilla agroforests.
4. We conclude that all studied land-use types contribute to butterfly conservation in our study region. Especially the woody vegetation in forest fragments, vanilla agroforests, and woody fallows supports a high butterfly diversity and is pivotal for maintaining a broad diversity of forest butterflies in the agricultural matrix. Our study highlights the importance of preserving the diversity of small-scale land-use types, including agroforestry, forests and fallow land in this tropical biodiversity hotspot.

KEYWORDS
endemism, habitat dependency, habitat specialisation, lepidoptera, shifting cultivation, smallholder agricultural landscape, species origin, traits, vanilla agroforestry

INTRODUCTION

Tropical forests host a large proportion of global biodiversity and are vital for ecosystem functioning (FAO & UNEP, 2020; Mitchard, 2018). However, tropical forests face the highest deforestation and degradation pressures globally, with land-use change towards agriculture being a major threat (Curtis et al., 2018). Land-use change affects species differently (Barlow et al., 2007). Particularly endemic species and forest-dependent species are vulnerable to land-use change (Brooks et al., 2002; Steffan-Dewenter et al., 2007). In addition to forest conversion, decreasing habitat quality of remaining forests is threatening the survival of species (Watson et al., 2004). While the effects of deforestation on vertebrate taxa are well documented (Tracewski et al., 2016), the response of many insects remains widely unknown (Dunn, 2005), despite their diversity, high degrees of endemism, and importance in providing ecosystem services (Noriega et al., 2018; Stewart et al., 2007).

Butterflies are sensitive to habitat changes due to their complex holometabolic life cycle, feeding and host plant specialisation, thermoregulation, and symbiotic associations (Bonebrake et al., 2010). Due to their diversity in habitat specificity, mobility, and feeding traits, butterfly species may respond differently to habitat changes (Koh & Sodhi, 2004). For example, butterfly species with high habitat specialisation are more prone to extinction through land-use change than butterfly species with low habitat specialisation (Koh et al., 2004). This high diversity of traits and responses makes butterflies an interesting model taxon to investigate the effects of land-use change on biodiversity.

Among insects, butterflies are a relatively well-studied group, but data remain scarce for tropical butterflies even though they account for around 90% of all butterfly species (Bonebrake et al., 2010). Tropical forest conversion typically reduces butterfly diversity (Ghazoul, 2002; Norfolk et al., 2017; Sharma et al., 2020). However, not all tropical butterfly species are confined to the forest (categorised as ‘forest butterflies’; Koh et al., 2004), but many occur in human-modified open or semi-open areas such as grasslands, cropland, or secondary formations such as fallows (categorised as ‘open-land butterflies’). Forest butterflies are more sensitive to land-use change, as they occupy narrow ecological niches and show high host-plant specificity (Koh & Sodhi, 2004; Schulze et al., 2010). Many endemic species in forest biomes are habitat specialists and prefer old-growth forests (Cleary & Mooers, 2006; Lewis et al., 1998). In contrast, open-land butterflies in the human-modified landscape are more likely to be oligo- or polyphagous and thus adapted to a wider range of ecological niches (Koh & Sodhi, 2004). However, the habitat dependency of endemic, forest and open-land species in human-modified landscapes remains largely undetermined in tropical ecosystems.

High numbers of endemic species, accompanied by high rates of habitat loss, qualify Madagascar as biodiversity hotspot (Goodman & Benstead, 2005; Myers et al., 2000). Here, the expansion of cash crops and shifting cultivation increasingly replaces the large continuous forest areas resulting in a heterogeneous mosaic landscape (Curtis et al., 2018; Llopis et al., 2019; Zaehringer et al., 2015). In such heterogeneous and highly fragmented landscapes, agroforestry is promoted as a profitable and yet biodiversity-friendly land-use option (Schroth et al., 2004). Structurally diverse agroforests can harbour forest butterfly species (Francesconi et al., 2013; Norfolk et al., 2017; Schmitt et al., 2020) as well as widespread (non-endemic) butterfly species (Waltert et al., 2011). However, land-use history affects the biodiversity value of agroforests depending on their establishment on fallow or forested land (Martin et al., 2020). Thus, establishing agroforests at the expense of natural forests drives biodiversity declines (Vasconcelos et al., 2015). Another prominent land use in many tropical countries (Heinimann et al., 2017) as well as in north-eastern Madagascar is shifting cultivation, an agricultural practise for which vegetation is first cleared manually and consecutively burned before the land is used for crop cultivation and thereafter left fallow (Styger et al., 2007).

Insect diversity in Madagascar is high, but poorly described, and knowledge gaps remain across the country (Hanski et al., 2007; Paulian & Viette, 2003). Assessments and classifications of the Malagasy butterfly diversity are incomplete (Lees et al., 2003). Butterfly

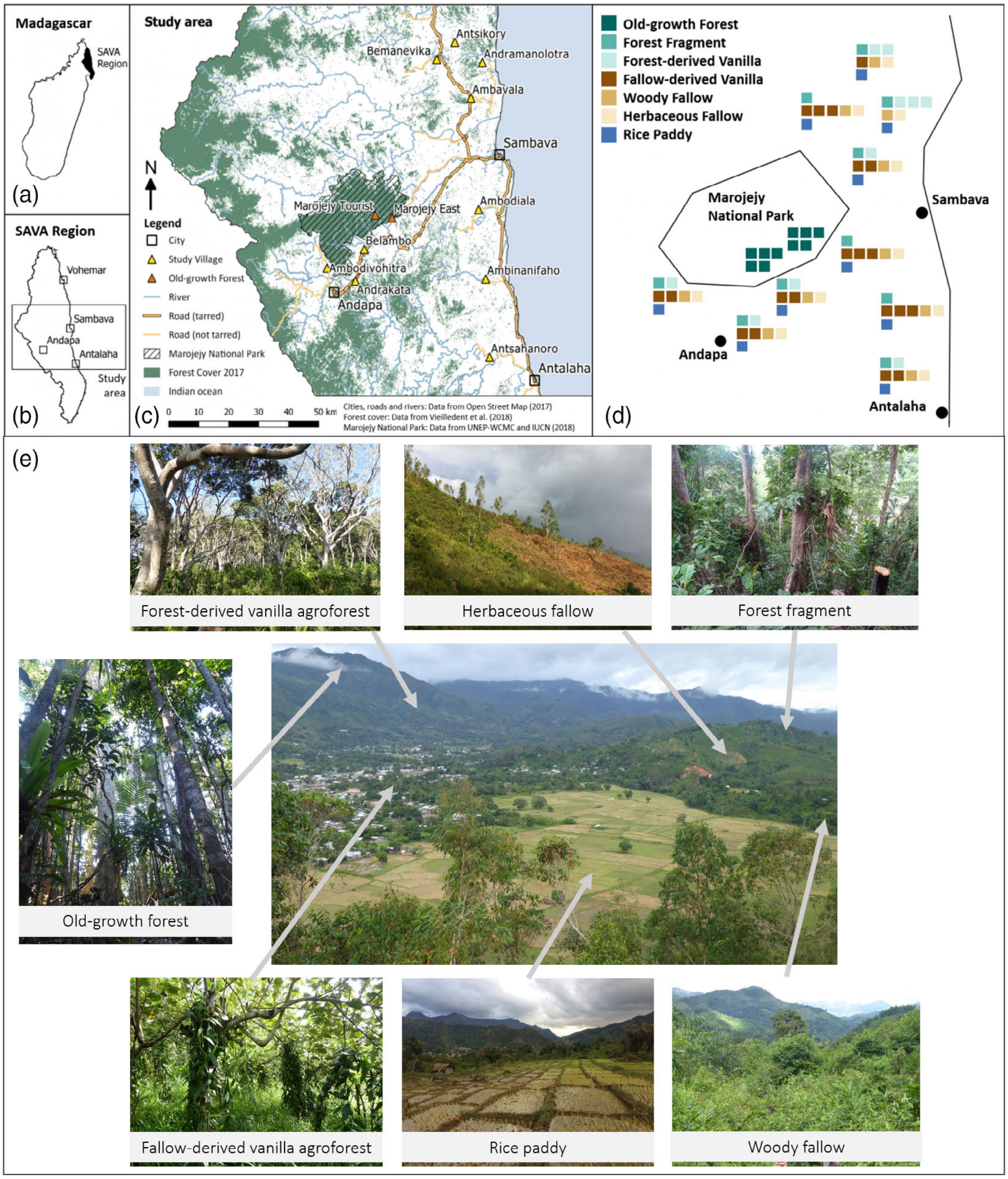

FIGURE 1 Study design overview. (a) The island of Madagascar with the SAVA region highlighted. (b) the SAVA region. (c) Study area with forest cover in 2017 (Vieilledent et al., 2018), roads, rivers, and the 10 study villages and two sampling sites within Marojejy National Park. (d) Land-use type distribution across 10 villages and Marojejy NP. (e) Prevalent land-use types in north-eastern Madagascar with a typical landscape in the centre. Example locations are indicated with arrows

species data largely depend on historical museum specimens and field inventories conducted in Ranomafana and Masoala National Parks (Kremen, 1992; Kremen et al., 1999) or have been compiled from a combination of museum records and field recordings (Allnutt et al., 2008; Kremen et al., 2008). In addition, detailed butterfly data are not widely available for different land uses and largely stems from forest inventories (Kremen, 1992; Kremen et al., 2008). At present, Madagascar counts 321 described butterfly species (de Jong & Coutsis, 2017; Lees, 2016; Lees et al., 2003; Libert, 2014) with species-level endemism of at least 72% (Lees et al., 2003).

Using butterflies as a model group, our study assesses how different land-use types are related to butterfly diversity within a small-scale agricultural landscape in north-eastern Madagascar, an area that has historically been covered by almost continuous forest cover. Our research objectives were to assess how (1) overall, endemic, forest-, and open-land butterfly species richness and (2) species composition differs between land-use types in the agricultural matrix compared to old-growth forest. In addition, we investigated (3) which land-use types were most important for butterflies in terms of supporting high numbers of individuals per species.

MATERIALS AND METHODS

Study region

We carried out the study in the SAVA region in north-eastern Madagascar (Figure 1). A warm and humid climate with an annual rainfall of 2223 mm and a mean annual temperature of 24 °C characterises the region (Karger et al., 2017), which encompass various protected areas with lowland and mountainous rainforest, including Marojejy National Park (CPGU, 2012). The region is part of a global and also national biodiversity hotspot with high rates of endemism (Barthlott et al., 2005; Brown et al., 2016). North-eastern Madagascar today represents a heterogeneous landscape mosaic comprising forests, rice paddies, shifting cultivation (fallows, hill rice), pastures, and vanilla agroforestry (Llopis et al., 2019). Currently, vanilla is the prevalent and expanding cash crop in the SAVA region, making Madagascar the main vanilla producer globally (FAO, 2020; Hänke et al., 2018; Llopis et al., 2019). In our study region, the majority of vanilla agroforests are fallow derived (~70%) and the minority (~30%) are forest derived (Hänke et al., 2018). Other cash crops such as cloves, coffee and beans are cultivated; however, vanilla and paddy rice remain most important (Hänke et al., 2018). Deforestation rates are high, mainly due to shifting cultivation for hill rice production (Vieilledent et al., 2018; Zaehringer et al., 2015).

Study design

We collected data in 10 study villages covering seven different land-use types, representing the common land-uses in north-eastern Madagascar, and two old-growth forest sites as reference (Figure 1). The characteristics of each land-use type are described in Table 1. For each village, we selected one plot each in a forest fragment, woody fallow, herbaceous fallow, and rice paddy, as well as three in vanilla agroforests. We categorised the vanilla agroforests based on land-use history into fallow-derived or forest-derived vanilla agroforests (Martin et al., 2020). Forest-derived vanilla agroforests were established without the use of fire inside forests and fallow-derived vanilla agroforests were established on land that was formerly cleared by fire. We did not find both fallow- and forest-derived vanilla agroforests in all villages, thus resulting in an imbalanced distribution of vanilla agroforests between villages. Overall, we sampled 70 plots across 10 villages and 10 plots across two old-growth forest sites, totalling 80 plots. The average minimum distance between plots was 719 m (SD ± 438 m) with an average elevation of 192 m.a.s.l (SD ± 207 m.a.s.l).

Based on inventories of trees (Osen et al., 2021) and herbaceous plants (Raveloaritiana et al., 2021) on the same plots, we characterised our land-use types into either woody land-use types or open-land-use types. We defined all tree-containing land-use types (forest fragments, forest- and fallow-derived vanilla agroforests, and woody fallows) as woody land-use types and all land-use types with no trees and predominantly herbaceous vegetation (herbaceous fallows and rice paddies) as open land-use types. Furthermore, we hereafter refer to old-growth forest as a land-use type to allow a joint terminology.

TABLE 1 Characteristics of the seven prevalent land-use types in north-eastern Madagascar

Land-use type	Description
Old-growth forest (10 plots)	Continuous and evergreen lowland forest located inside Marojejy National Park. Five old-growth forest plots located in Manantenina Valley and five in the eastern part of Marojejy National Park called Bangoabe. Sites with obvious traces of selective logging were avoided
Forest fragment (10 plots)	Fragmented evergreen forest outside of protected areas. Forest fragments were regularly used for the extraction of timber and other natural products. Forest fragments have not been burned and typically have a dense understorey vegetation and a few tall trees
Forest-derived vanilla agroforest (10 plots)	Agroforests with vanilla directly planted inside a forest (no clearance by fire). Forest understorey vegetation was partially cleared manually, whereas smaller trees served as climbing support for vanilla vines, and larger trees provided shade
Fallow-derived vanilla agroforest (20 plots)	Agroforests with vanilla plants established on an herbaceous or woody fallow used for shifting cultivation (clearance by slashing and burning the vegetation). Naturally re-growing or planted trees were used for vanilla vines as climbing support and larger trees to provide shade
Herbaceous fallow (10 plots)	Fallow land, part of the shifting cultivation system, dominated by herbaceous vegetation, which had regrown within the last 2 years since crop cultivation. Herbaceous fallows have been burned in the past
Woody fallow (10 plots)	Fallow land, part of the shifting cultivation system, dominated by woody vegetation (shrubs, small trees) which had regrown within the last 4–16 years since crop cultivation. Woody fallows have been burned in the past
Rice paddy (10 plots)	Irrigated rice field traversed by soil banks with herbaceous vegetation for passage and water retention

Sampling methods

We sampled butterflies with bait trapping and time-standardised netting between August (start of the drier season) and December 2018 (see schedule Table S1). We performed our sampling in a standardised plot circle with 25 m radius. We avoided the few rainy days. Re-sampling in the rainy season was not possible, because remote villages and the countryside were hard to reach. We caught butterflies with a bait trap hanging 1.5 m above the ground (Figure S1). We baited the traps with bananas, which we fermented for 48 h in an air-tight container before deployment. We deployed a total of eight butterfly bait traps for 24 h on each plot. We installed four bait traps each at 16.6 m and 20 m distance from the plot centre with one in each cardinal and inter-cardinal direction. Our bait traps included a white cylinder with a 20 cm diameter opening, a removable bait tray (20 cm diameter) attached to hooks below the cylinder, and a zippered side opening for removing captured butterflies. Bait trapping has the advantage of assessing butterflies in dense vegetation and habitats with difficult access as well as catching butterflies throughout the day without researcher bias (Checa et al., 2019; Freitas et al., 2014). It is mainly butterfly species of the Nymphalidae family that are attracted by the fruit bait (particularly the most diverse genus of Satyrinae in Madagascar, *Heteropsis*). Most other butterfly families (Papilionidae, Pieridae, Lycaenidae and Hesperiidae) feed on nectar-providing plants and remain largely undetected by bait traps (Checa et al., 2019) (Tables S2 and S3). We additionally performed time-standardised netting once on each plot, catching butterflies within close reach of the ground for 30 min in an imaginary 2 m wide box on either side of the sweep-net while walking at a slow and steady speed in a zigzag line (from plot edge to plot centre) to cover the plot equally. We performed time-standardised netting with a circular frame net with a nylon mesh on a 1.5 m telescopic handle (Figure S1). We did time-standardised netting during dry and low-wind conditions only, either in the morning (between 8 and 12 pm) or in the afternoon (between 1 and 5 pm). We paused the stopwatch when processing butterflies. We euthanized all captured butterflies with drops of ammonia (25% solution) in a glass jar. We preserved butterfly specimens in glassine envelopes, thereafter stored in hermetic plastic containers with silica gel to avoid mould before identification. Identifications were carried out by a taxonomic specialist (David C. Lees) at the Natural History Museum in London and cross-checked via photo identification by Szabolcs Sáfián. We stored all identified specimens at the Department of Crop Science at the University of Göttingen (export permit: No: 382 N-EA12/MG18 and No: 308 N-EA10/MG18).

Data analysis

For all analyses, we combined data collected from both sampling methods to obtain a complementary coverage of butterfly species. By this, we aim to cover as many species possible across the major families of butterflies occurring in our study region. We provide results of both sampling methods analysed separately in the supplementary information. Given the high conservation importance of endemic subspecies on islands like Madagascar (Fernández-Palacios et al., 2021), we used the minimum species endemism level. Thus, we categorised endemic butterflies as species or subspecies only occurring in the country of Madagascar following the latest publications (Aduse-Poku et al., 2016; Huang et al., 2019; Lawrence, 2016; Lees, 2016; Lees et al., 2003; Libert, 2010; Pierre & Bernaud, 1999; Pyrcz et al., 2020; Vingerhoedt et al., 2009) (Tables S4 and S5). We categorised one unidentified morphospecies (*Heteropsis* sp.) as endemic since the genus is endemic to Madagascar. In addition, we categorised butterfly species according to habitat specialisation into two types: forest and open-land species. Forest species sensu Lees et al. (2003) occur exclusively in forest ('all natural types of forest, primary or somewhat degraded'). Open-land species are all other species occurring outside of forest (grasslands, anthropogenic areas, croplands, secondary formations, i.e., fallows, forest clearings and hill rice, forest margins, beaches, marshlands) sensu Lees et al. (2003).

We performed statistical analysis in R version 3.6.3 (R Core Team, 2020). To test for significant differences in forest and open-land species richness between the seven studied land-use types, we fitted a *glmmTMB* model with a Poisson distribution (Brooks et al., 2017). In this model, we treated land-use type as an explanatory variable and village/old-growth forest site as a random effect. We performed multiple comparisons among all land-use type pairs using the *glht* function from the *multcomp* package applying a Tukey's all-pair comparisons with Bonferroni correction (Hothorn et al., 2008).

To assess the habitat dependency rank of butterflies, we identified the land-use types in which a species occurred with >50% of their relative abundance (Mendenhall et al., 2016) and referred to them in the following as 'associated to a land-use type'. By applying a 50% threshold when evaluating the relative abundance, we considered only frequently visiting or residential species. We defined a species as exclusive to a land-use type if it occurred only in one of the seven land-use types. We excluded 10 plots out of the 20 fallow-derived vanilla agroforests randomly to give each land-use type equal weight in the analysis (10 plots each). We used the package *ggplot2* to visualise habitat dependency rank across land-use types (Wickham, 2016).

To investigate differences in species composition among land-use types, we computed a permutational multivariate analysis of variance (PERMANOVA) using the *adonis* function of the *vegan* package (Oksanen et al., 2020). Also, we used the *pairwise. adonis* function of the *pairwiseAdonis* package with false discovery rate correction to assess differences between land-use types (Arbizu, 2017). Prior to PERMANOVA, we tested whether homogenous dispersion existed among land-use types by using the *betadisp* function and *permutest* function of the *vegan* package (PERMDISP test; Oksanen et al., 2020). Our results show that heterogeneous dispersion significantly affected the differences in species composition (Df $= 6$, $F = 2.76$, $p = 0.02$; Table S6), thus differences are not only explained by the location of centroids but also by the variation within each land-use type. We computed species composition by using non-metric multidimensional scaling (NMDS) with Jaccard dissimilarity distance. We calculated gamma species diversity for each land-use type by summing up all species found across 10 plots and therefore excluded 10 out of 20 fallow-derived vanilla agroforests.

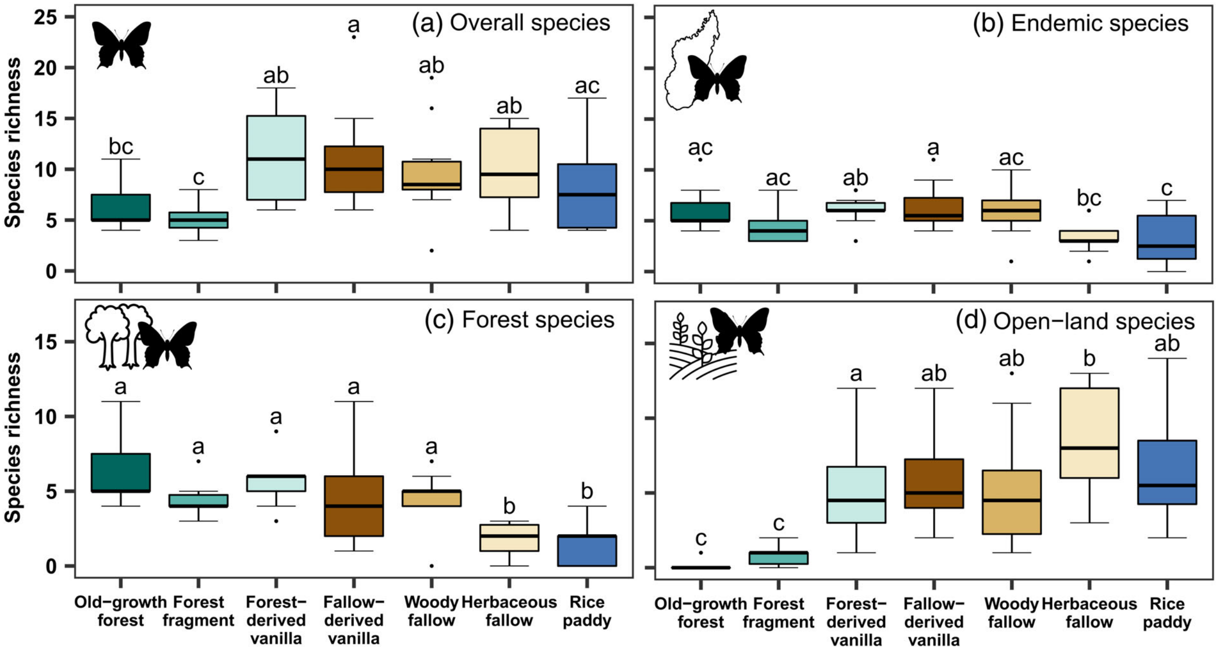

FIGURE 2 Species richness of overall (a), endemic (b), forest (c), and open-land (d) species sensu Lees et al. (2003) across land-use types in north-eastern Madagascar. Non-shared letters indicate significant differences between pairs of land-use types based on pairwise Tukey's honest significance tests ($p < 0.05$). The line inside the boxplot represents the median. The lower and upper boundaries of the boxplot show the 25th–75th percentiles of the observational data, respectively. The lower and upper whisker represents the scores outside 50% of data scores. Icons created by Made, Linseed Studio and Shashank Singh from the Noun Project

RESULTS

We recorded a total of 2643 individuals of 88 butterfly species belonging to six families (50 Nymphalidae, 14 Lycaenidae, 14 Hesperiidae, 2 Papilionidae, 6 Pieridae, and 2 Riodinidae species) and 49 genera (Tables S6 and S7; Figures S2 and S3). The majority of individuals belonged to the *Nymphalidae* family and were caught in forest- and fallow-derived vanilla agroforests (>400 individuals in each; Table S8). Overall, we identified 65 endemic, 42 open-land, and 46 forest butterfly species. Out of the 65 endemic butterflies, the majority of species were forest butterflies (43 species; Table S9). Differentiated by sampling method, we caught 18 species exclusively with bait traps, 46 exclusively with time-standardised catch and 21 species with both sampling methods (Figure S4). We detected most species in woody land-use types (64 species; 25 exclusive species; Figure S5). Sampling coverage was >81% across land-use types for overall and endemic species richness. For forest species richness, we reached a sampling coverage of >75% and for open-land species richness >85% (Table S10, Figure S6).

Across land-use types, overall species richness did not differ among land-use types, except for old-growth forests and forest fragments, which had the lowest species richness (Figure 2a; Tables S11 and S12). When looking at endemics only, herbaceous fallows (mean: 4.5 species ± SD: 2.2) and rice paddies (4.1 species ±2.8) had significantly fewer endemic species than fallow-derived vanilla agroforests, and rice paddies had significantly fewer endemic species than forest-derived vanilla agroforests (Figure 2b).

At plot-level, average forest species richness did not differ between land-use types, except for rice paddies (1.5 species ± 1.4) and herbaceous fallows (1.8 species ± 1.0), which had significantly fewer forest species than all other land-use types (Figure 2c). Average open-land species richness was significantly lower in old-growth forests (0.1 species ± 0.3) and forest fragments (0.8 species ± 0.6) than all other land-use types (Figure 2d).

Generally, differences in species richness between land-use types became less apparent when analysing bait and time-standardised catch data separately (Figures S7 and S8; Tables S13 and S14). In particular, bait data did not show differences between rice paddies and woody habitats for forest species richness as well as between rice paddies and old-growth forests for open-land species richness. In addition, time-standardised catch data did not detect any differences in endemic species richness between land-use types.

Species composition across all land-use types fell into four clusters (Figure 3, PERMANOVA: $R2 = 0.34$, $p < 0.001$, $Df = 6$): Species composition firstly differed between old-growth forests and forest fragments, secondly between forest fragments and woody land-use types, and thirdly between woody and open-land-use types (Table S15). Species composition did not differ significantly between forest- and fallow-derived vanilla agroforests and woody fallows ($p > 0.05$; Table S15). Also, species composition in rice paddies and herbaceous fallows did not differ significantly ($p > 0.05$; Table S15).

When analysing species composition separately for bait and time-standardised catch data, we confirm a unique species composition for old-growth forests and a similar species composition among woody

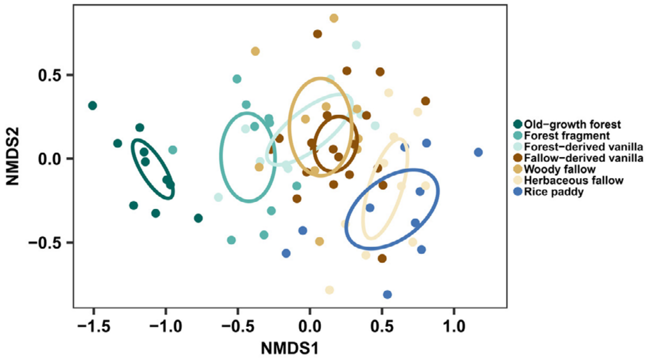

FIGURE 3 Butterfly species composition across land-use types with four compositional clusters (old-growth forest, forest fragment, woody land-use types, open land-use types from left to right). Non-metric multidimensional scaling (NMDS) illustrates butterfly species composition (bait trap and time-standardised netting data combined; $R2 = 0.839$, stress = 0.191). Each point represents one plot (jittering width = 0.1 and height = 0.1). Ellipses represent 95% confidence intervals for the estimated centre of each land-use type fitted into the ordination (see pairwise test results in table S15)

land-use types and open land-use types (Figure S9; Tables S16 and S17). However, we did not detect clear differences between woody and open land-use types.

Overall, we found 88% of all 85 butterfly species (excluding 10/20 fallow-derived vanilla agroforests) in the agricultural matrix. In addition, we found the highest share (16%) associated with old-growth forests (>50% of abundance in old-growth forest; Figure 4a). In the agricultural landscape, the largest shares of species were associated with forest-derived vanilla agroforests (14%) and herbaceous fallows (13%). Nine out of the 20 species found in old-growth forests also occurred in the agricultural matrix and showed a higher habitat dependency rank for woody land-use types than for open land-use types (except for one species, *Melanitis leda*).

In terms of endemic species, 23% of species were associated with old-growth forests (Figure 4b). In the agricultural matrix, most endemic species were associated with fallow-derived vanilla agroforest (11%) and forest-derived vanilla agroforests (15%). Of the 44 forest species (Figure 4c), 32% were associated with old-growth forests and in the agricultural matrix most with forest-derived vanilla agroforests (16%) and woody fallows (14%). No forest species were

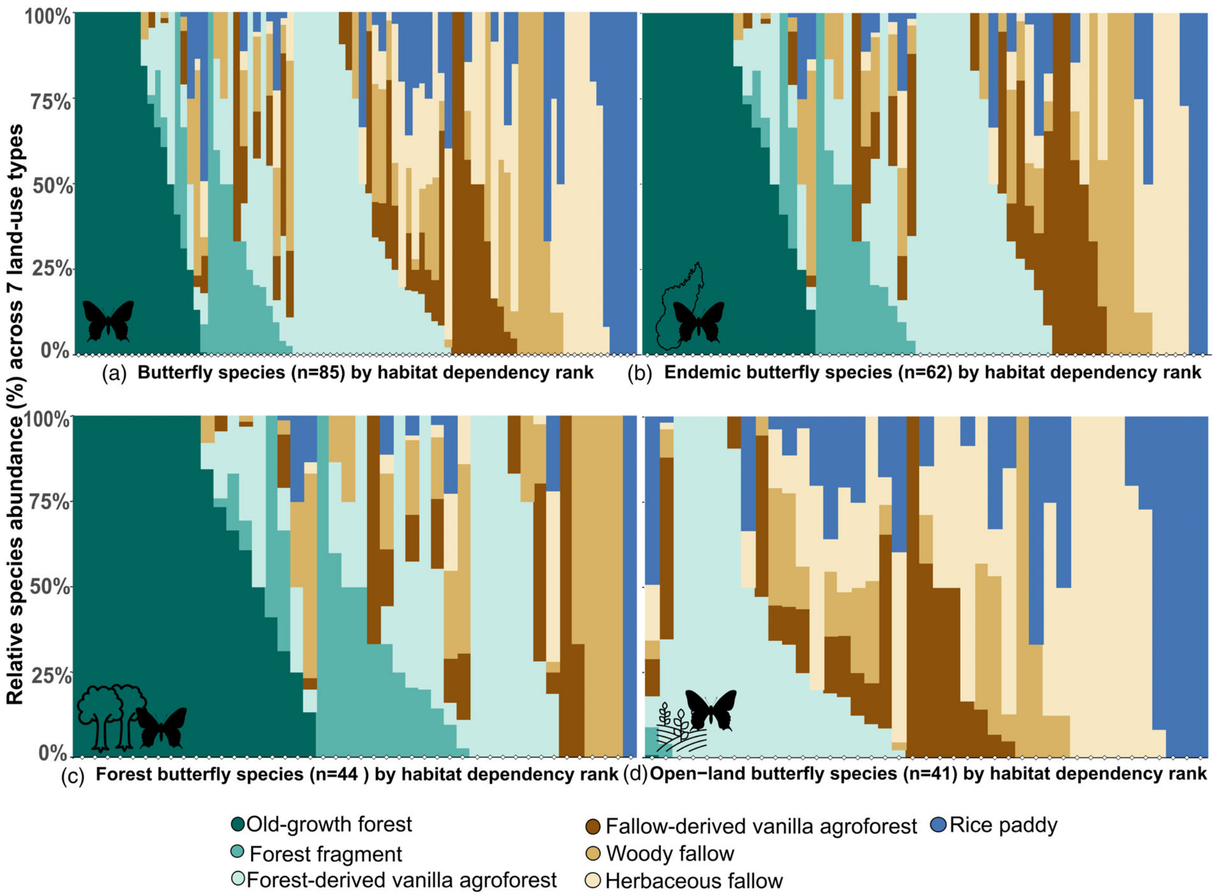

FIGURE 4 Habitat dependency rank (based on data set with 10/20 fallow-derived vanilla agroforests) for (a) 85 butterfly species and 2311 individuals, (b) 45 endemic butterfly species and 1598 individuals, (c) 44 forest butterfly species and 784 individuals, and (d) 41 open-land butterfly species and 1527 individuals. Divisions on the *x*-axis indicate one species. *Y*-axis represents relative species abundance (%) across seven land-use types. Icons created by Made, Linseed Studio and Shashank Singh from the Noun Project

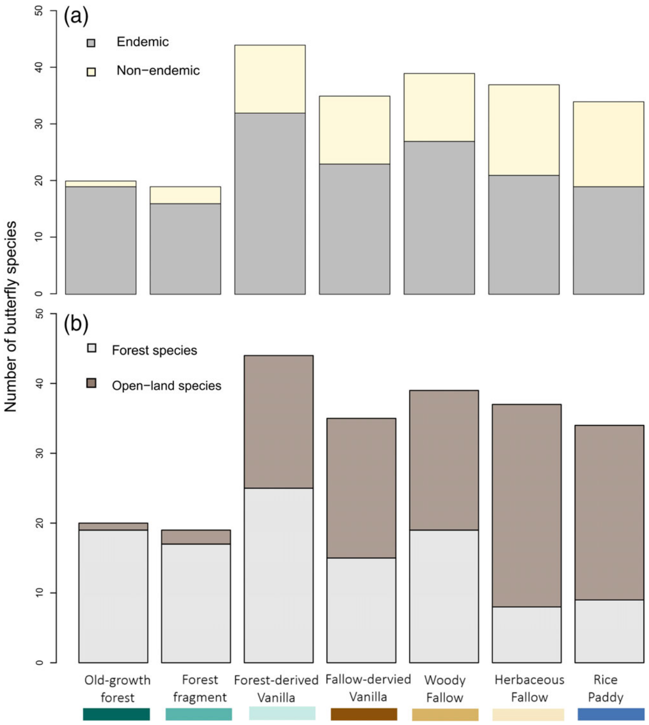

FIGURE 5 Total butterfly species richness (gamma diversity) across 70 plots and in each land-use type ($n = 10$ plots per land-use type; 10/20 fallow-derived vanilla agroforests were randomly selected, 85 species overall) with (a) the number of endemic (dark grey) and non-endemic species (yellow) and (b) number of forest (light grey) and open-land species (brown)

associated with herbaceous fallows and only 2% with rice paddies. In contrast to endemic and forest species, open-land species showed opposite patterns of habitat dependency rank (Figure 4d). Most of the 41 open-land species were associated with herbaceous fallows (27%), followed by either forest-derived vanilla agroforests, woody fallows or rice paddies (12%) and fallow-derived vanilla agroforests (10%). No open-land species were associated with old-growth forests or forest fragments.

We found that old-growth forests presented the highest number of overall forest and endemic species unique to this land-use type (10 species each, Figure 4a-c). Forest-derived vanilla agroforests harboured seven exclusive species, including six endemics. Fallow-derived vanilla agroforests had two exclusive species (both endemic). Woody fallows had four exclusive species of which three were endemic. We found four exclusive species in herbaceous fallow, including three endemics. Rice paddies harboured four exclusive species, including two endemic species. We recorded only one exclusive species (*Neptis kikideli*), which is endemic, unique to forest fragments.

We found same similar patterns of habitat dependency rank across the seven land-use types when analysing bait and time-standardised catch data separately, with the exception of bait data showing a decreased importance of fallow-derived vanilla agroforests for endemic and forest species than shown by both methods combined (Figure S10).

In terms of gamma diversity, forest-derived vanilla agroforests hosted 44 species (73% endemic, 57% forest species), more than any other land-use type (Figure 5;, Table S18). However, old-growth forests had the largest share of endemic (95%) and forest (95%) species and the lowest share of open-land species (5%). In the agricultural matrix, we found that forest fragments had the highest share of endemic (84%) and forest (89%) species, followed by forest-derived vanilla agroforests, fallow-derived vanilla agroforests (66% endemic and 43% forest species) and woody fallows (69% endemic and 49% forest species). In herbaceous fallows and rice paddies, >70% of species were open-land species and 57% and 56% endemic (lowest share across all land-use types).

We found similar patterns of endemic versus non-endemic and forest versus open-land species proportions when looking at time-standardised catch data only (Figure S11). The analysis of gamma diversity with bait data did not depict great differences in the species proportions across land-use types.

DISCUSSION

Our study indicates that the majority of endemic, forest and open-land butterfly species occur in multiple land-use types in the smallholder landscape of north-eastern Madagascar. We highlight the importance of woody land-use types, as many forest and endemic butterflies were associated with them. Herbaceous fallows and rice paddies were rich in open-land species. Moreover, we show that fallow-derived vanilla agroforests have a higher conservation value for endemic and forest species compared to herbaceous fallow, whereas forest-derived vanilla agroforests also promote open-land species while maintaining endemic and forest fauna when compared to forest fragments. Furthermore, our study shows that species composition differed between old-growth forests and forest fragments, as well as between woody land-use types and open land-use types.

Extending the current species' habitat categorisation system

Our results show that multiple species classified a priori as forest-dependent occurred outside old-growth forests and forest fragments. Forest species, which are typically highly sensitive to forest conversion and land-use change (Schulze et al., 2010), persisted particularly in woody land-use types. Here, the regenerating woody and herbaceous vegetation is likely to attract butterflies (Bobo et al., 2006; Pardonnet et al., 2013). This indicates a knowledge gap on how Malagasy butterflies use different land-use types. Thus, the forest dependency for Malagasy butterflies has been overestimated due to a lower sampling effort outside the forest with current knowledge building on a few forest inventories (Kremen, 1992; Kremen et al., 1999). Our study provides urgently needed knowledge on the occurrence of Malagasy butterflies in different land-use types and highlights the need to further investigate how butterflies use the agricultural matrix. An update and extension of the habitat categorisation system of Malagasy butterflies are needed to optimise strategies for butterfly conservation.

Species richness in a heterogeneous landscape context

We show that all land-use types contribute to sustaining a wide range of butterfly diversity encompassing forest- and open-land species. Both overall species richness and endemic species richness are comparable across land-use types. In addition, species accumulation curves confirmed the reliability of the comparison of species richness, as old-growth forests and all land-use types showed comparable sampling coverage (Figure S6; Table S10). Furthermore, our results show that many endemic butterflies also occur in open land-use types (e.g. *Strabena tamatavae* and *Fulda bernieri*; Table S19), thus a butterfly optimised landscape should ideally conserve the current mosaic of both forest and open land. Past studies have shown diverging responses of butterflies to forest conversion, with species richness either increasing (Horner-Devine et al., 2003), decreasing (Panjaitan et al., 2020; Schulze et al., 2004), or not changing (Vu, 2009). These contrasting results can be explained by the different landscape settings of these studies. Landscape variables such as distance to forest or proportion of semi-natural habitats are important to define the diversity of land-use systems in the agricultural matrix (Barlow et al., 2007; Munyuli, 2013; Norfolk et al., 2017; Vasconcelos et al., 2015). In addition, butterflies vary in their ability to move across the matrix (Scriven et al., 2017). The mobility of individual butterfly species may confound the species richness of individual land-use types because species can use multiple landscape elements (Ghazoul, 2002). In particular, strong fliers such as the forest species of genus *Charaxes* (Henning, 1989) have the ability to explore disturbed habitat (Sáfián et al., 2011), and we also found them in rice paddies and herbaceous fallows. This behaviour has also been observed for strong fliers in other human-modified landscapes (Sambhu et al., 2017). However, it remains to be understood, if the observed *Charaxes* individuals were present outside of forest habitats because they are good fliers or whether they manage to reproduce outside forest. Many species need a range of resources depending on their lifecycles and landscape heterogeneity can increase resource availability (Bonebrake et al., 2010; Tiple et al., 2011). Our study sites are located in a heterogeneous and largely extensively managed small-scale agricultural landscape with recent forest fragmentation (Vieilledent et al., 2018), which can result in high biodiversity (Marín et al., 2009; Sáfián et al., 2011). However, we need to acknowledge that the methodology used in this article is not designed to capture the full species richness particularly of old-growth forests across all vegetation strata present, which is particularly important to capture the full range of endemic species (Fermon et al., 2003). This becomes evident, comparing our species list with the greater community and higher number of endemic species found in other lowland old-growth forests of Madagascar (Kremen et al., 1999).

Land-use results in clusters of species composition

Our study highlights that species composition differs between land-use systems. Especially old-growth forests sustain a unique species composition that does not overlap with the composition in the agricultural matrix. In concordance, 10 species (all endemic) occurred exclusively in old-growth forests and the largest share of endemic and forest species was associated to old-growth forest, a finding in line with studies that highlighted the importance of mature forest for endemic butterflies (Lewis et al., 1998; Schulze et al., 2004). Thus, deforestation and landscape homogenisation would significantly reduce the species pool. According to our results, open-land species may increase when old-growth forests or forest fragments are transformed to agroforestry or shifting cultivation, accompanied with species turnover replacing forest species by species adapted to open land, supporting results by Bobo et al. (2006). Here, generalist species adapted to multiple habitats and feeding regimes are likely to benefit from forest conversion, whereas specialist species adapted to a narrow niche and with a specific food preference are likely to lose (Nilsson et al., 2008). In contrast to other studies on our study plots (Fulgence et al., 2021; Martin, Andriafanomezantsoa, et al., 2021; Osen et al., 2021), agroforest land-use history showed no relation to butterfly species composition. Instead, we find forest-, fallow-derived vanilla agroforests, and woody fallows to be similar in species composition, distinct to both herbaceous fallows and rice paddies. The similarity in species composition of woody land-use types may be related to similar light availability. This can be confirmed by leaf area index (canopy leaf area per unit ground area) measurements on our plots, which showed that canopy structure in forest- and fallow-derived vanilla agroforests and woody fallows did not differ significantly (Osen et al., 2021). In contrast, leaf area index in forest fragments was significantly higher compared to fallow-derived vanilla agroforests and woody fallows (Osen et al., 2021). The conversion of woody to open land-use types might cause compositional changes, favouring open-land species, but disadvantaging forest and endemic species. Accordingly, we found most open-land species in herbaceous fallow. Here, plant surveys on the same plots show that herbaceous plant richness is higher on herbaceous fallows than on all surveyed woody land-use types (Raveloaritiana et al., 2021), which most likely attracted many open-land species (Kitahara et al., 2008; Kremen, 1994). For example, the presence of exotic plants like *Lantana camara*, a species highly attractive for butterflies with flowers throughout the year, can result in high butterfly numbers locally, as found on fallows and smallholder farms in East Africa (Schmitt et al., 2021).

Conservation opportunity in vanilla agroforestry

We found no significant differences in endemic or forest species richness between forest fragment, forest- and fallow-derived vanilla agroforests, and woody fallows, although previous research indicates that land-use conversions which include the use of fire negatively affect endemic species richness (Cleary & Mooers, 2006). Herbaceous fallows and rice paddies host fewer endemic species than fallow-derived vanilla agroforests and fewer forest species than all woody land-use types, comparable to the findings by Schulze et al. (2004), who find lower endemic butterfly richness in annual cultures compared to the old-growth or secondary forest in Indonesia. However, in our system in Madagascar, fallow-derived agroforests have more endemic (+164%) and forest species (+239%) and a shifted species composition compared to herbaceous fallow. This observation may indicate a reversibility of species loss on open land-use types, which corresponds with the findings of Sáfián et al. (2011), who experienced rapid recovery of West African rainforest interior butterfly assemblages in various stages of secondary forest regeneration. Higher numbers of endemic and forest species in fallow-derived vanilla agroforests compared to herbaceous fallows could be explained by the higher number of graminoids and vines associated with fallow-derived vanilla agroforest (Raveloaritiana et al., 2021). This could be because *Heteropsis*, a genus largely attracted to the fruit baits on our plots, depends on grasses and bamboos, i.e., Poaceae (Lees, 2016), as hostplants. Furthermore, increasing tree density has been related to increasing butterfly richness (Bobo et al., 2006). Trees in agroforests or woody fallows can provide fruits and foliage important for butterflies (Castro & Espinosa, 2015) or other non-food resources such as a vegetation structure for resting, sunbathing, mating, and roosting (Mahata et al., 2019). Notably, comparing fallow-derived vanilla agroforests to woody fallows, we did not see a difference in species richness of endemic, forest, or open-land species, nor did we find a difference in species composition. This similarity in species richness and composition might indicate a butterfly-neutral restoration opportunity. Forest-derived vanilla agroforests showed a high conservation value for butterfly species richness with a high number of species associated to that land-use type. Also, the gamma diversity in forest-derived vanilla agroforests for endemic and forest species was higher than the gamma diversity found in forest fragments and old-growth forests. Furthermore, the majority of butterfly species found in forest fragments (except *Heteropsis uniformis*, *Neptis kikideli*, *Borbo ratek*) were also found in forest-derived vanilla agroforest. However, species composition of forest-derived vanilla agroforests significantly changed compared to forest fragments, likely driven by the six times increase of open-land species. Noteworthy, extinction debt for endemic and forest butterflies can occur in forest-derived vanilla agroforests, as observed in Japan in forest fragments with decreasing patch size (Soga & Koike, 2013), an aspect we did not consider in our study. Larval-host-plant specificity is a major trait to predict the extinction of butterflies (Koh et al., 2004). Consequently, a high habitat quality (e.g. presence of host and food plants, suitable light conditions, and patch size) is decisive for successful larval development and butterfly survival (Shahabuddin et al., 2000). Thus, we recommend maintaining existing forest-derived vanilla agroforests and their tree structure but refraining from the conversion of further forest fragments driving compositional changes of the butterfly community.

CONCLUSION

In the agricultural matrix, land-use types with woody vegetation host surprisingly high diversities of endemic and forest butterflies, and herbaceous fallows and rice paddies are rich in open-land species. We found forest species utilising multiple land-use types outside the forest and thus we suggest updating and extending the habitat classification of Malagasy forest butterflies using the data from this study. Forest fragments deserve high conservation attention as they are home to a high share of endemic butterfly species, whereas their conversion would result in a significant shift in species composition. The establishment of vanilla agroforests on fallow land offers a conservation and habitat rehabilitation opportunity by increasing stem density and basal area (Osen et al., 2021) and also canopy cover over time (Martin, Wurz, et al., 2021), providing woody structures important for endemic and forest butterfly species. Furthermore, we suggest preserving already established forest-derived vanilla agroforests and maintaining their vegetation structure as they are home to a large share of species including endemic, open-land, and forest species. Woody fallows, forming part of the shifting cultivation system, offer habitat for endemic and forest butterflies. Old-growth forests remain irreplaceable due to its high share of endemics, its unique species composition, and its high species dependency. Our study thus highlights the importance of preserving the diversity of small-scale land-use types, including agroforestry, forests and fallow land.

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CONFLICT OF INTEREST

No potential conflict of interest was reported by the authors.

AUTHORS' CONTRIBUTIONS

Annemarie Wurz, Teja Tscharntke, Ingo Grass, Dominic Andreas Martin, Kristina Osen, Anjaharinony A. N. A. Rakotomalala conceived the idea; Annemarie Wurz, Ingo Grass, Teja Tscharntke, Szabolcs Sáfián, Jacqueline Loos designed the methodology; Annemarie Wurz, Anjaharinony A. N. A. Rakotomalala, Evrard Benasoavina, Theudy Alexis collected butterfly data; Annemarie Wurz, David C. Lees, Szabolcs Sáfián identified butterflies; David C. Lees and Anjaharinony A. N. A. Rakotomalala assisted analysis; Annemarie Wurz analysed the data and led the writing of the manuscript. All authors contributed to the writing and gave final approval for publication.

DATA AVAILABILITY STATEMENT

Data and code are available via OSF. https://osf.io/cbg4e/?view_only=196848828f024df2827fb7c2f9dccc7a

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SUPPORTING INFORMATION

Additional supporting information may be found in the online version of the article at the publisher's website.

Fig. S1 Overview methodology: Bait trap with fermented bananas hanging on shade tree in vanilla agroforest (a) - 90 cm long; https://www.wildcare.co.uk/pop-up-butterfly-trap-with-20cm-cone-opening.html. Bait trap on support stick in a rice paddy (b). Time-standardised catch along banks traversed in a rice paddy (c).

Table S1: Date of time-standardised netting and retrieval of bait traps for each plot and land-use type.

Table S2: Species numbers per family and per trapping technique (complete data set, without excluding 10 fallow-derived vanilla agroforests)

Table S3: Individual numbers per family and per trapping technique (complete data set, without excluding 10 fallow-derived vanilla agroforests)

Table S4: List of butterfly species and their endemism status at sub-species or species level (Status January 2022). Note that the genus of *Acraea* is currently under revision, and some of the *Acraea* species are now treated as *Telchinia*. Endemic =1; Non-endemic = 0.

Table S5: Reference list for endemism status from Table S4

Table S6: Overview of the number of species and number of individuals per butterfly family (without excluding 10 fallow-derived vanilla agroforests [VFLW]).

Figure S2: Total butterfly species richness (gamma diversity) across 70 plots and in each land-use type (n = 10 plots per land-use type; 10 out of 20 fallow-derived vanilla agroforests were randomly selected) with number of species indicated per family (Nymphalidae, Lycaenidae, Hesperiidae, Papilionidae, Pieridae, Riodinidae)

Table S7: Number of species indicated per family (Nymphalidae, Lycaenidae, Hesperiidae, Papilionidae, Pieridae, Riodinidae) in each land-use type (n = 10 plots per land-use type; 10 out of 20 fallow-derived vanilla agroforests were randomly selected).

Table S8: Number of individuals indicated per family (Nymphalidae, Lycaenidae, Hesperiidae, Papilionidae, Pieridae, Riodinidae) in each land-use type (n = 10 plots per land-use type; 10 out of 20 fallow-derived vanilla agroforests were randomly selected).

Figure S3: Total number of individuals of butterfly families across 70 plots and in each land-use type (n = 10 plots per land-use type; 10 out of 20 fallow-derived vanilla agroforests were randomly selected) with number of individuals indicated per family (Nymphalidae, Lycaenidae, Hesperiidae, Papilionidae, Pieridae, Riodinidae)

Figure S4: Shared and exclusive butterfly species (88 species; complete data set, without excluding 10 Fallow-derived vanilla agroforests) trapped with either or both bait trap or time-standardised catch.

Figure S5: Shared and exclusive butterfly species (85 species) occurring across old-growth forest, woody land-use types (forest fragment, forest-, fallow-derived vanilla agroforest and woody fallow), and open land-use types (herbaceous fallow and rice paddy). N = 10 plots per land-use type; 10 out of 20 fallow-derived vanilla agroforests were randomly selected.

Table S9: Butterfly species and their habitat specialisation (forest and open-land species) sensu Lees et al. (2003) with endemism status at species and subspecies level. Endemic =1; Non-endemic = 0.

Figure S6: Gamma diversity (=species richness at regional level) across land-use types, shown by the sample coverage-based rarefaction and extrapolation curves based on a) overall, b) endemic, c) forest and d) open-land species richness (Hill number q = 0). The solid line represents the interpolation, whereas the dashed line represents the extrapolation. The shaded region represents the 95% confidence intervals. Non-overlapping of the confidence intervals represents a significant difference between two or more land-use types.

Table S10: Sampling coverage (SC) depending on taxon for each land-use type. Sampling computed with iNext function, Hill-number q = 0, datatype = incidence raw, endpoint = 20.

Table S11: Mean species richness ± SD (of overall, endemic, forest, and open-land species in 7 different land-use types.

Table S12: Tukey multiple comparisons of means for all land-use/habitat-pairs showing dissimilarities among land-use types and old-growth forest of overall, endemic, forest and open-land species richness. Pairwise comparisons were calculated with the glht-function of the package 'multcomp' (including Bonferroni correction) with all terms significant at <0.05 (highlighted in bold).

Figure S7: Species richness **(using bait data only)** of overall (a), endemic (b), forest (c), and open-land (d) species sensu Lees et al. (2003) across land-use types in north-eastern Madagascar. Non-shared letters indicate significant differences between pairs of land-use types based on pairwise Tukey's honest significance tests ($P < 0.05$). The line inside the boxplot represents the median. The lower and upper boundaries of the boxplot show the 25th-75th percentiles of the observational data, respectively. The lower and upper whisker represents the scores outside 50% of data scores.

Table S13: Tukey multiple comparisons **(using bait data only)** of means for all land-use/habitat-pairs showing dissimilarities among land-use types and old-growth forest of overall, endemic, forest and open-land species richness. Pairwise comparisons were calculated with the glht-function of the package 'multcomp' (including Bonferroni correction) with all terms significant at <0.05 (highlighted in bold).

Figure S8: Species richness **(using time-standardised catch data only)** of overall (a), endemic (b), forest (c), and open-land (d) species sensu Lees et al. (2003) across land-use types in north-eastern Madagascar. Non-shared letters indicate significant differences between pairs of land-use types based on pairwise Tukey's honest significance tests ($P < 0.05$). The line inside the boxplot represents the median. The lower and upper boundaries of the boxplot show the 25th-75th percentiles of the observational data, respectively. The lower and upper whisker represents the scores outside 50% of data scores.

Table S14: Tukey multiple comparisons **(using time-standardised catch data only)** of means for all land-use/habitat-pairs showing dissimilarities among land-use types and old-growth forest of overall, endemic, forest and open-land species richness. Pairwise comparisons were calculated with the glht-function of the package 'multcomp' (including Bonferroni correction) with all terms significant at <0.05 (highlighted in bold).

Table S15. Species composition pairwise comparisons of butterfly species composition across land-use types (with False discovery rate correction) and results of multivariate dispersion test based on Jaccard dissimilarity matrix using the *betadisp* and the *permutest* function of the vegan package.

Figure S9: Butterfly species composition across land-use types with four compositional clusters (old growth forest, forest fragment, woody land-use types, open land-use types) **comparing bait trapping data and time-standardised catch data.** Non-metric multidimensional scaling (NMDS) illustrates butterfly species composition ($R2 = 0.951$, Stress = 0.123 for time-standardized catch data; $R2 = 0.873$, Stress = 0. 168 for bait trapping data). Each point represents one plot (jittering width = 0.1 and height = 0.1). Ellipses represent 95% confidence intervals for the estimated center of each land-use type fitted into the ordination (See pairwise test results in Table S16-17).

Table S16. Species composition pairwise comparisons of butterfly species composition (**using bait trapping data only**) across land-use types (with False discovery rate correction) and results of multivariate dispersion test based on Jaccard dissimilarity matrix using the *betadisp* and the *permutest* function of the vegan package.

Table S17. Species composition pairwise comparisons of butterfly species composition (**using time-standardised catch data**) across land-use types (with False discovery rate correction) and results of multivariate dispersion test based on Jaccard dissimilarity matrix using the *betadisp* and the *permutest* function of the vegan package.

Figure S10: Habitat dependency rank (based on data set with 10 out of 20 fallow-derived vanilla agroforests) for **time-standardised catch** data (a-d) and **bait trapping** data (e-h) analysed separately. Y- Axis represents relative species abundance across 7 land-use types and each bar on the x-axis an individual species.

Figure S11: Total butterfly species richness (gamma diversity) across 70 plots and in each land-use type (n = 10 plots per land-use type for time-standardised catch (a-b) and bait data (c-d); 10 out of 20 fallow-derived vanilla agroforests were randomly selected, with a) and c) the number of endemic (grey) and non-endemic species (yellow) and b) and d) the number of forest (green) and open-land species (purple). OGF = old-growth forest; FF = forest fragment; VFST = forest-derived vanilla agroforest, VFLW = fallow-derived vanilla agroforest, WF = woody fallow; HF = herbaceous fallow; RP = rice paddy.

Table S19: List of butterfly species occurring in each land-use type (presence/absence data). Note that the genus of *Acraea* is currently under revision, and some of the *Acraea* species are now treated as *Telchinia*.

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