Received: 6 June 2020 | Accepted: 28 August 2020

DOI: 10.1111/1365-2664.13766

RESEARCH ARTICLE

Journal of Applied Ecology BRITISH ECOLOGICAL SOCIETY

Decreasing predation rates and shifting predator compositions along a land-use gradient in Madagascar's vanilla landscapes

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Funding information
Volkswagen Foundation, Grant/Award Number: 11-76251-99-35/13 (ZN3119)

Handling Editor: Ricardo Solar

Abstract

1. Land-use change is the main driver of deforestation and land degradation resulting in the loss of biodiversity and ecosystem functioning in north-eastern Madagascar. Vanilla, the region's main cash crop, is grown in agroforestry systems and may provide an opportunity for the conservation of biodiversity and ecosystem functioning.
2. We used dummy caterpillars to assess predation rates and predator communities along a land-use gradient including unburned old-growth and forest fragments, herbaceous and woody fallows after shifting cultivation with fire usage, as well as rice paddies. The studied vanilla agroforests were either forest-derived or fallow-derived. Besides land-use type, we considered the effects of land-use history (unburned/burned), plot-level parameters and the landscape composition to conclude on management recommendations.
3. Old-growth forest and forest fragments exhibited highest predation rates, which decreased with land-use intensity. Overall, predation was higher in unburned land-use types than in more open, previously burned habitats and rice paddies. High stem and vegetation densities were positively related to predation rates, but decreased with land-use intensity. High forest cover in the surrounding landscape led to higher predation rates, while local structural parameters remained more important.
4. The predator community was arthropod-dominated across all land-use types with ants responsible for between 33% and 69% of all predation events. Overall predator composition in old-growth and forest fragments differed from all other land-use types. Predation by Gryllacrididae (Orthoptera) was lower in all land-use

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types, including forest-derived vanilla, than in old-growth forest and forest fragments, where they were important contributors to total predation. Vertebrate predation was low throughout.

5. *Synthesis and applications*. Forested habitats feature higher predation rates and different predator compositions than other land-use systems. Maintaining or restoring tree- and understorey-rich vanilla agroforestry represents a viable tool in landscape conservation programmes as it has the potential to contribute to the conservation of predation as an important ecosystem function in both forest- and fallow-derived agroforests. However, vanilla agroforestry has limited value in conserving forest-specialized predator communities. While the establishment of tree-rich agroforests on former fallow land is favourable for conservation ecosystem functioning, further forest transformation should be avoided.

KEYWORDS

conservation, dummy caterpillars, ecosystem functioning, land-use history, Madagascar, predation, shifting cultivation, vanilla agroforestry

1 | INTRODUCTION

Resulting from long-term isolation and a diverse landscape composition, a plethora of different ecosystems and species has evolved in Madagascar (Ganzhorn et al., 2014). Most of Madagascar's species depend on forests and the island's most biodiverse areas are found in the humid rainforest zones along its eastern coast and mountain range (Allnutt et al., 2013). Like many other tropical rainforests, these forests are threatened by selective logging and, in contrast to the global trend of agro-industrial development, by the expansion of increasingly unsustainable shifting cultivation through smallholder farmers (Styger et al., 2007; Zaehringer et al., 2016). As a result, Madagascar has lost 44% of its forest cover since 1953 with the largest remaining continuous tracts located in the island's north-east (Vieilledent et al., 2018).

Vanilla *Vanilla planifolia* is the main cash crop in north-eastern Madagascar and contributes to the livelihoods of more than 80% of local smallholders (Haenke et al., 2018). A recent price boom in processed vanilla has led to economic growth and the expansion of vanilla cultivation in the region (Llopis et al., 2019). The vanilla orchids are grown in agroforestry systems that are either established in forests or on fallow lands (Martin et al., 2020) underlining the crop's ambiguous role in the region's landscape; the vanilla boom may incentivize further encroachment of plantations into forests, but vanilla agroforests that are established on formerly fallow land may rehabilitate tree cover in the landscape matrix and put a halt to shifting cultivation.

Overall, agroforests are considered a ‘biodiversity-friendly’ farming option since typical forests structures persist in these systems, and with them some forest specialist species (Bhagwat et al., 2008) as well as associated ecosystem functions and services, such as natural biocontrol (Jose, 2009; Pumariño et al., 2015). Furthermore, natural biocontrol is often directly linked to crop yields in tropical agricultural systems (Karp et al., 2013; Maas et al., 2013), where yield losses to pests are generally more severe than in temperate systems (Oerke, 2006). These considerations also make agroforestry a popular tool in landscape restoration projects across the tropics (Food and Agriculture Organization of the United Nations, 2017). However, the potential to conserve this ecosystem function in agroforests depends on many contributing factors such as landscape composition (Maas et al., 2015; Tscharntke et al., 2011) and onsite farming activities, like shade tree removal or the weeding of undergrowth vegetation (Nurdiansyah, Clough, et al., 2016; Tscharntke et al., 2011).

Generally, deforestation affects biotic interactions like biological control, as a result of landscape-wide structural simplification (Morante-Filho et al., 2016). Many predators respond quickly to environmental change as they are often larger bodied and less abundant than their prey. Accordingly, skewed trophic structures and shifting predator compositions are early manifestations of the loss of biodiversity and ecosystem functioning (Duffy, 2002). Several studies have suggested that analysing process rates, including predation, in altered systems enables to track changes of ecosystem functioning compared to primary habitat (Barnes et al., 2014; Duffy, 2002; Hooper et al., 2005).

Caterpillar dummies are a cheap, simple and fast method to assess predation patterns and therefore especially suitable for field conditions (Lövei & Ferrante, 2017) but to date, few studies using this method have compared predation pressure and predator composition across different land cover types (Posa et al., 2007; Roels et al., 2018; Seifert et al., 2015; Tvardikova & Novotny, 2012). Predation pressure exerted by arthropods may suffer from habitat degradation and lowered landscape complexity, whereas bird predation may increase with simplification (Muiruri et al., 2016; Nurdiansyah, Denmead, et al., 2016; Yang et al., 2018). However, predation pressure by both birds and arthropods can increase with higher structural complexity on local and landscape levels (Langellotto & Denno, 2004; Maas et al., 2015) or decrease following forest fragmentation (Terborgh, 2001). Additionally, a global experiment revealed higher predation at lower elevations (Roslin et al., 2017).

In this study, we used dummy caterpillars in north-eastern Madagascar's seven prevalent land-use types to obtain a landscape wide overview on how land-use drives predation rates and predator composition. We took continuous old-growth forests as a baseline and hypothesized that land conversion causes significant changes in predation rates and predator composition. Specifically, we put vanilla agroforestry systems in relation to other land-use types to assess their value for the conservation of biodiversity and predation as a major part of ecosystem functioning. Furthermore, we assessed how predation patterns are affected by plot-level vegetation parameters and landscape-scale forest cover altered by land-use change, as well as by different elevations, to draw respective management conclusion. We assess if predation patterns on vanilla agroforests could potentially be influenced through respective management in order to improve their contribution to conservation and ecosystem integrity.

2 | MATERIALS AND METHODS

2.1 | Study region, land-use types and environmental indicators

Our study area was located in the central part of north-eastern Madagascar's SAVA region. We sampled in the region's seven most prevalent land-use types during the year's driest period between September and November 2018 when climate and weather are rather constant. In total, we visited 10 villages and 2 distinct sites in Marojejy National Park (Figure 1). The different land-use types in the SAVA region are created through stepwise conversions from old-growth forest (Figure 1). In most areas of the region only forest fragments remain of the once continuous forest. These fragments are usually used for the extraction of timber and fuel wood or other non-timber forest products. If the area is needed for agricultural production, old-growth or fragmented forests are cut and burned and hill rice is planted. After harvest, the hill rice plots are left fallow and recolonized by few pioneer plant species. In the first years, herbaceous plants dominate ('herbaceous fallow') until woody vegetation and trees establish ('woody fallow') and the plot is ready for another cycle of hill rice cultivation. Vanilla agroforests are either established directly in old-growth or fragmented forests or on fallow land (Martin et al., 2020). In forest-derived vanilla, the farmer thins out the understorey and mainly uses existing small trees as support trees for the vanilla vines. In fallow-derived vanilla, the support trees are secondary regrowth or planted trees, depending on the successional state of the fallow. Overall, based on their land-use history, the land-use types can therefore be classified as either burned (forests and forest-derived vanilla) or unburned land-use types (fallows and fallow-derived vanilla). The seventh land-use type, irrigated rice paddy, stands outside the described system as there is usually no conversion of rice paddies from or to other land-use types. Since

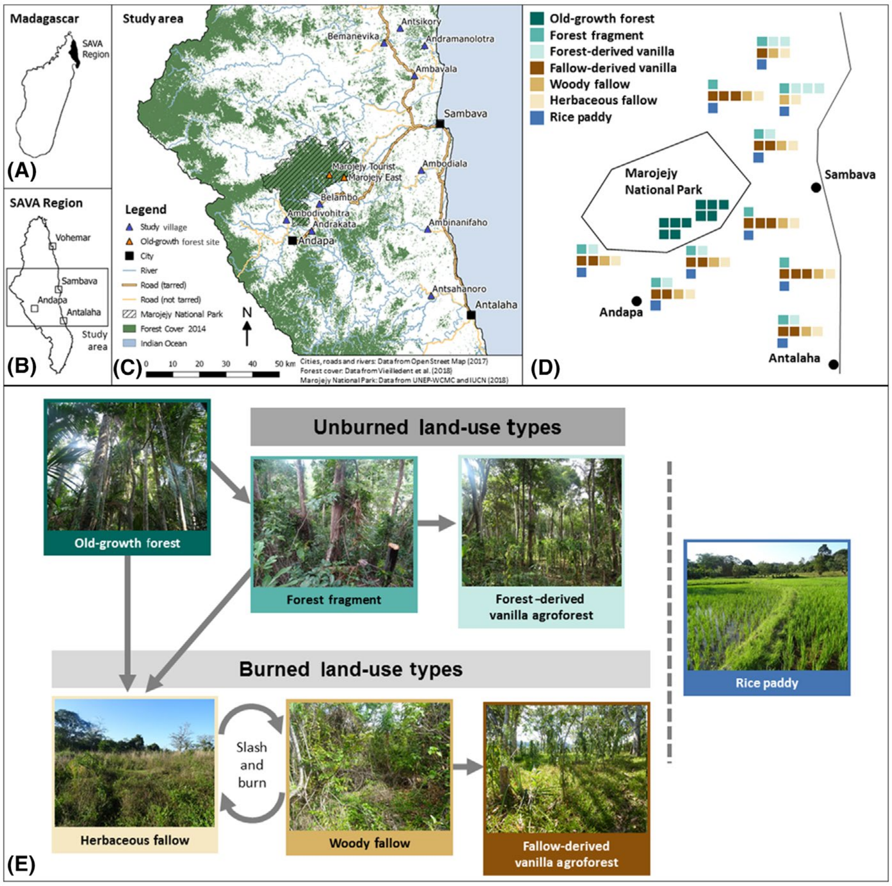

FIGURE 1 Study location and design; (A) location of SAVA in Madagascar, (B) the box marks the study area within sava, the region's main cities are indicated, (C) detailed map of study region with forest cover, all visited sites are marked with blue or orange triangles, (D) each square represents one plot of the respective land-use type sampled in the respective village, (E) prevalent land-use types in north-eastern Madagascar indicating land-use practices and their land-use history: old growth forests are converted to vanilla agroforests by manual clearing or wood extraction (forest-derived) or through the use of fire for hill rice production (fallow-derived). The arrows indicate human-induced land-use change. Conversion from or to rice paddies is extremely rare and thus stands outside the described land-use trajectory

rice paddies are also common in the region, we included them to fully cover the region's prevalent land-use types (see Table S1 in Supporting Information). Per village, we sampled one plot per land-use type and three vanilla agroforests (in total 10 forest-derived and 20 fallow-derived). Some villages were only surrounded by fallow-derived vanilla agroforest while others had access to more forest-derived agroforests. Therefore, we measured only one type or another in four villages (Figure 1). Old-growth forest was sampled inside Marojejy National Park. The mean minimum distance between the plot centres was 719 m (*SD* = 438 m) with a minimum of 260 m between two plots.

To account for variable environmental conditions within land-use types we assessed a set of landscape and plot-level covariates. As landscape variables, we included elevation (m a.s.l.) and the surrounding forest cover in % (radius: 250 m, avoiding overlaps with other plots) in 2017 (Vieilledent et al., 2018). To obtain plot-level covariates, we conducted a tree-inventory of all trees with a diameter at breast height >8 cm, yielding tree stem density [n/ha], basal area [m^2/ha] and mean canopy closure [%] across all land-use types. Herbaceous fallows and rice paddies do not contain any trees, so we set all tree inventory-based covariates to zero on these plots. As those parameters only provide estimates on the plots' structural potential provided by trees, we also estimated the overall vegetation density to account for non-woody and shrubby vegetation, and tree re-growth in the understorey. For this estimation, we established vegetation density profiles (adapted from Van der Maarel, 1970), using six 0.5 m layers between 0 and 3 m above ground, based on three to four photographs taken in cardinal directions from the plot centre. Then we estimated a vegetation density value in % for each layer and calculated the average density of all layers on all photos as the vegetation density value [%] for each plot.

2.2 | Assessment of predation patterns

Predation events are inherently short termed and hard to investigate through direct observation (Howe et al., 2009). While predation rates can be effectively measured using sentinel prey, this method usually does not allow insights on predator compositions (Lövei & Ferrante, 2017). An established method for predation assessments that enables both predation rates and predator composition analyses is using dummy caterpillars made from plasticine (Howe et al., 2009). This inedible bait is usually not removed by attacking predators that leave characteristic bite marks on the dummy's surface, thus enabling quantification of predation rates and the identification of predators. Using caterpillars of the same colour, size, form and material triggers standardized visual and olfactory cues in potential predators across all sites and hence allows comparisons of relative predation rates (Howe et al., 2009). However, it is impossible to holistically assess total predation of the whole range of predators with this method, since only the activity of potential predators that are attracted to the given dummy caterpillars is measured; thus, for example missing out every predator that could consume the caterpillar at an earlier larval stage (Lövei & Ferrante, 2017). We used Pelikan Nakiplast® (Colour: 681/'green') and clay extruders to produce evenly shaped cylinders (35 × 5 mm) that mimic green caterpillars, indicating palatability (Howe et al., 2009). We chose this size as a rough average from previous dummy caterpillar studies in the tropics (Leles et al., 2017; Maas et al., 2015; Nurdiansyah, Clough, et al., 2016; Seifert et al., 2016).

We deployed 36 dummies for 48 hr per plot and arranged them in four subplots at 12 m from the plot centre in all four cardinal directions. Each subplot consisted of nine dummies in a 3 × 3 m grid. We used the mid veins of intact leaves on approximately 1 m height, depending on the vegetation, and applied the caterpillar dummies with insect pins on both ends. Although predation in the canopy can be higher (Loiselle & Farji-Brener, 2002), we measured predation in the understorey strata only, as crops that may benefit form biocontrol are grown there. Furthermore, this stratum was available on all land-use types allowing for standardized comparisons. In the rice paddy-plots we assessed predation by deploying dummies on vegetation along the banks closest to the respective subplot centre and noted if rice was harvested and the paddy inundated or not to account for the variable habitat conditions within this land-use type. We did not deploy on standing rice itself to account for the quick turnover in this crop and accordingly varying structural conditions. Similarly, we chose not to deploy on vanilla leaves as the pins would have damaged the farmers' plants.

To identify bite marks, which is an iterative process, we initially used images available in the literature (Low et al., 2014; Nurdiansyah, Denmead, et al., 2016) and Tvardikova's bite mark identification guide (available at https://tvardikova.weebly.com/downloads.html). We could complement our arthropod bite mark assessment though direct observations and by catching potential predators, exposing them to dummy caterpillars and using the resulting bite marks as references (Appendix S2). All bite marks that remained unidentified were noted as 'Morphobites' and grouped based on their characteristically shaped bite marks. For consistency, the identification and classification of bite marks was performed by the lead author and the same field assistant throughout the experiment. We settled on initial identifications during the retrieval and took photographs of the bite marks; however, with growing knowledge of the bite marks as well as results of direct observation and feeding experiments some bite mark identifications where reviewed and adapted post hoc.

2.3 | Statistical analysis

We calculated the predation rates [%] as the ratio of the number of predated dummies to the total number of retrieved dummies per plot. If the dummy displayed bite marks during retrieval, we counted it as predated. If we identified two distinct bite marks on a dummy, we recorded two separate predation events while we omitted missing dummies from the analysis.

To assess variation in predation rates along parameters, we fitted linear mixed-effect models and included village as a random effect in all models using the function 'lmer' of the package LME4 (Bates et al., 2014). For all models, we confirmed normality and homoscedasticity of our data and used the conditional R^2 to compare model performance (Nakagawa & Schielzeth, 2013). We tested for variation of predation rates against land-use type; differences were detected by using post hoc Tukey tests. Then, we fitted a linear multiple regression model with scaled environmental covariates on local and landscape levels and land-use history (burned/unburned). For two plots with missing tree-inventory data we used the average for the respective land-use types. To avoid multicollinearity we assessed variance inflation factors (VIFs) using the function 'vif' in the package CAR (Fox et al., 2020) and stem density, basal area and mean canopy closure were strongly correlated ($GVIF^{(1/(2*Df)} < \sqrt{5}$). As of those parameters only stem density is actively changed through the farmers' management operations (pruning on canopy levels does not occur) we chose to only include stem density in our model (Table S3). We simplified the model stepwise using the 'dredge'-function in the R package MuMIn (Barton, 2018). For the discussion, we considered the best models (within ΔAICc < 2) that used the least amount of covariates while still containing high information content (Symonds & Moussalli, 2011). Additionally, for exploring their relation to land-use, we plotted the respective covariates against the land-use types.

We compiled predator compositions as the amount of predation events counted for each predator per plot. Then we analysed the compositions by fitting multinomial logit models that describe the probability of predation [%] of a dummy caterpillar by a certain predator group when deployed in the respective land-use type (function 'multinom' in the R package NNET Ripley & Venables, 2016). In a further step, we visualized predator community compositions per land-use type and their relation to environmental parameters using non-metric multidimensional scaling of Bray–Curtis dissimilarities with the functions 'metaMDS' and 'envfit' with standard settings in the R package VEGAN (Oksanen, 2017). We tested for differences of predator compositions via pairwise PERMANOVA using the 'adonis' function. Since the results of tests on beta-diversity like PERMANOVA can be influenced by heterogeneity of variances within group samples (Anderson & Walsh, 2013), we also tested for between group homogeneity of multivariate dispersions using the functions 'betadisper' and conducted pairwise comparisons using 'permutest'.

When assessing predator compositions in the multinomial models, we pooled vertebrate bite marks when assessing the composition of arthropod bite marks and vice-versa. In the NMDS ordination we included all identified distinctive predator bite marks from our bite mark catalogue (Table S8). We performed all analyses in R Studio with R v.3.6.3 (R Core Team, 2020).

3 | RESULTS

Overall, we distributed 2,880 caterpillar dummies in seven different land-use types across 10 villages and at two sites inside Marojejy NP. We retrieved 2,658 from the same spot after 2 days and found 162 dummies that fell on the ground. Sixty dummy caterpillars were untraceable and omitted from further analysis. Hence, the retrieval rate in this experiment was 97.9% overall. Between land-use types the retrieval rates ranged between 100% in old-growth forest and 95.3% in rice paddies (Table S4).

3.1 | Results of predation rates

Overall, we counted 916 individual predation events resulting in a predation rate of 32.4% that declined along the land-use intensity gradient (Figure 2). Predation rates were highest in forest fragments (47.6% ± 6.0%; mean ± *SE* throughout) and old-growth forests (39.4% ± 4.2%), where they were significantly higher than in fallow-derived vanilla (23.0% ± 5.2%), herbaceous fallows (22.4% ± 6.0%)

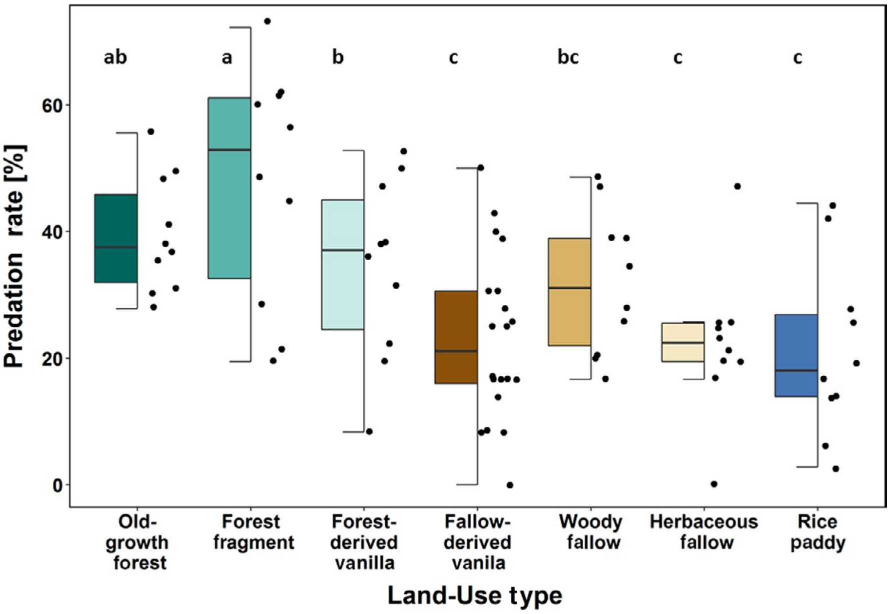

FIGURE 2 Predation rates across seven land-use types. Predation rates are based on attacked/total exposed caterpillar dummies per plot exposed for 2 days; linear mixed-effect model, $R_{LMM}(c)^2 = 0.32$. Indicated are median predation rates and 50% areas, whiskers show minimum/maximum within 1.5 IQR and dots represent sampled predation rates on plots of respective land-use types. Letters indicate significant differences in Tukey comparison (CI 95%)

and rice paddies (21.2% ± 6.0%). Forest fragments also exhibited higher predation rates than forest-derived vanilla agroforests (34.4% ± 6.0%) and woody fallows (31.9% ± 6.0%), while predation rates on forest-derived vanilla were higher than on fallow-derived agroforests, herbaceous fallows and rice paddies (Table S5). We did not measure significantly different predation rates between harvested and not harvested respectively between wet and dry rice paddies (Table S5).

The two equally best (ΔAICc < 2) models identified in our model selection included either only the plot-level parameter stem density [n/ha] (Estimate = 0.27, *SE* = 0.05; $SD_{\text{village}} = 0.01$, $R_{\text{LMM}}(\text{c})^2 = 0.26$) or both, stem and vegetation density [%] ($E_{\text{Stem density}} = 0.19$, $SE_{\text{Stem density}} = 0.06$, $E_{\text{Vegetation density}} = 0.15$, $SE_{\text{Vegetation density}} = 0.06$; $SD_{\text{village}} = 0.01$, $R_{\text{LMM}}(\text{c})^2 = 0.31$). Both covariates are positively correlated to predation rates (Figure 3). The following models that included a maximum of two covariates considered effects of stem and vegetation density together with the effects of surrounding forest cover or land-use history. Looking at these covariates' effects individually revealed a positive correlation between surrounding forest cover and predation rates ($E_{\text{Forest covery}} = 0.20$, $SE_{\text{Forest cover}} = 0.06$; $SD_{\text{village}} = 0.00$, $R_{\text{LMM}}(\text{c})^2 = 0.18$) and higher predation rates in unburned land-use types (0.40 ± 0.03; mean ± *SE* throughout) than in burned (0.25 ± 0.03, $p < 0.001$) or rice paddy plots (0.21 ± 0.05, $p < 0.001$). Elevation did not contain sufficient information to be considered (Table S6).

In the different land-use types, stem density decreased continuously from old-growth forest to herbaceous fallows and rice paddies while vegetation density was highest in forests and woody fallows, intermediate in both types of vanilla agroforest and herbaceous fallows and the lowest in rice paddies (Figure S7).

3.2 | Results of predator composition

We identified and consistently recognized a total of 12 different predator groups and bite mark types. Vertebrate predators consisted of birds, reptiles and mammals. Amongst the identified arthropod bite marks, we identified bite marks left by ants

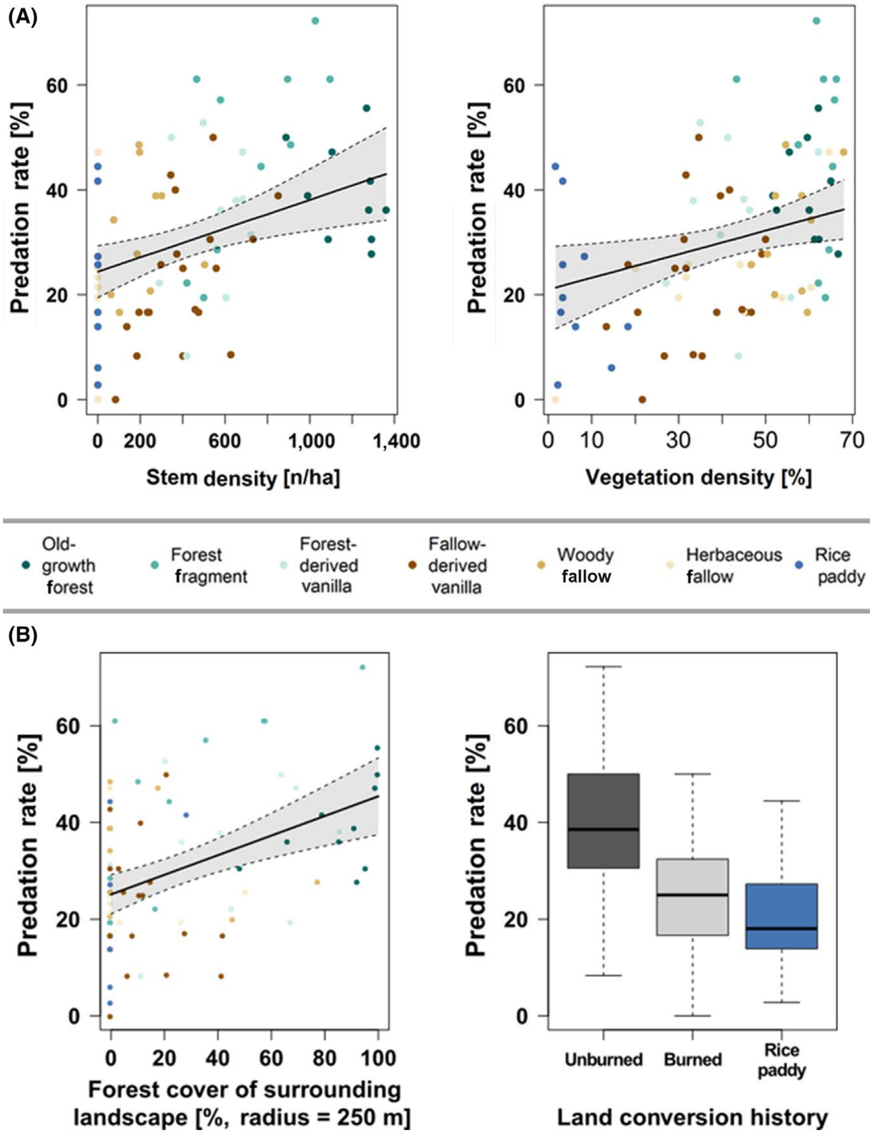

FIGURE 3 Relation of predation rates [%] with environmental covariates. Predation rates are based on attacked/total exposed caterpillar dummies per plot exposed for 2 days. The effects of (A) stem and vegetation density [0–3 m above ground] were tested in a multi-regression mixed effect model and are shown while the other variable is kept constant. These variables were the strongest predictors for changing predation rates. The effects of (B) forest cover and land-use history were tested in linear mixed effect models. Displayed is raw data, coloured by land-use type, and model prediction (solid line) with 95% confidence interval (shaded area) or median predation rates and 50% area with whiskers showing minimum/maximum within 1.5 IQ and letters indicating significant differences in Tukey comparison (CI 95%)

TABLE 1 Photo references of all identified bite marks including the number of incidences (*n*) (see Table S8 for complete list of reference marks)

Vertebrate bite mark	Predator (*n*)	Arthropod bite mark	Predator (*n*)
	Bird (53)		Ants (465)
	Reptile (4)		Gryllacrididae (140)
	Mammal (Rodent) (38)		Tettigoniidae (95)
	Mammal (Tenrec) (2)		

(Formicidae, Hymenoptera) through direct observation, as well as marks from Gryllacrididae (Orthoptera) and Tettigoniidae (Orthoptera), by using the reference dummies generated in feeding experiments (Table 1; Appendix S2). Four distinct but unknown arthropod bite marks were catalogued as 'Morphobite 1–4' (Table S8) and in one occasion we collected a dummy that was pierced, presumably by a hemipteran. In the analyses we grouped these marks as 'Unknown Arthropods'. In three occasions we encountered radula bite marks typical for slugs or snails. These were not considered true predation events and excluded from further analysis.

Arthropods were the dominant predators in all assessed systems. In particular, ants accounted for 33.1% in old-growth forest, 54.9% in forest fragments, 53.2% in forests-derived and 69.6% in fallow-derived vanilla, 47.8% in woody and 49.9% in herbaceous fallows and 39.7% in rice paddies of all predation events (Figure 4). Gryllacrididae markedly contributed to the total predation only in old-growth (31.2%) and forest fragments (24.2%). In absolute terms, ant predation was strongest in forest fragments (27.8%) and steadily decreased along the land-use gradient towards rice paddies (8.6%). Ant predation in old-growth forest (14.4%) was lower than in fragmented forest. Gryllacrididae exerted greatest predation pressure in forested habitats (old-growth: 13.6%, forest fragment: 12.2%), and displayed a drop in the presence in forest-derived vanilla agroforests (4.2%) and all other land-use types (≤3%). Tettigoniidae showed inconsistent patterns while vertebrate predation was rather low in all land-use types (<5.6%, Figure S9).

Predator compositions differed significantly across land-use types (PERMANOVA: $R^2 = 0.38$, $p < 0.01$, $df = 6$) while we found non-significant differences of sample dispersion (PERMDISP; $F = 1.42$, $p = 0.21$) between our group samples, indicating homogeneity of multivariate dispersions. Hence, old-growth forest and forest fragment harboured similar compositions, different to all other land-use types while rice paddies exhibited predator compositions that were different from all other land-use types apart from herbaceous fallows (Figure 4; Table S10). However, two direct comparisons of dispersion effects between forest-fragments with herbaceous-fallows and fallow-derived vanilla agroforests displayed significant different dispersions of variances, indicating that in these instances dispersion effects also play a role to explain differences of predator compositions (Table S10). Increasing

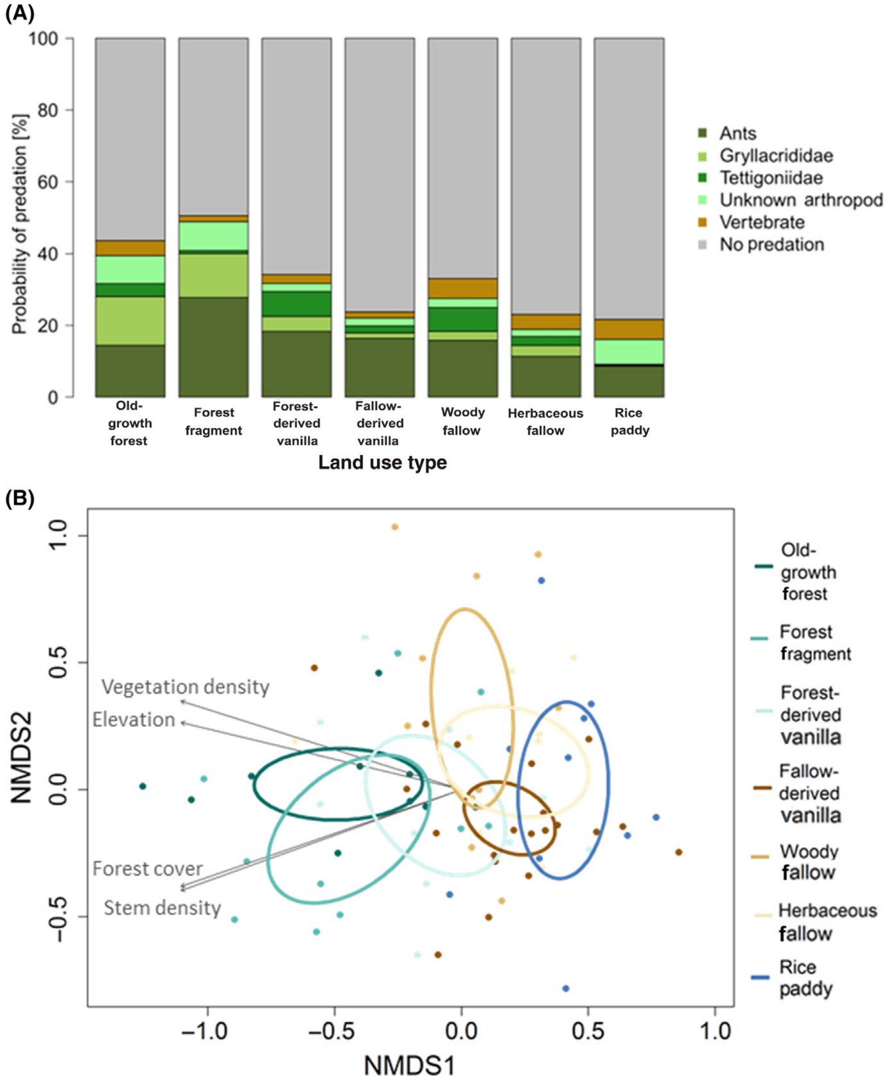

FIGURE 4 Changes in predator communities in the different land-use types; (A) Mean probabilities for predation by arthropod predators and (grouped) vertebrate predators (Multinomial model, AIC = 5,826), (B) Non-metric multidimensional scaling (Dimensions: 2, Stress: 0.1997) showing predator compositions per land-use type (SE confidence regions: 95%) and environmental covariates as driving factors, the dots represent the predator community per plot and land-use type

vegetation density, stem density, forest cover and elevation led to predator compositions more similar to those in old-growth and fragmented forests.

4 | DISCUSSION

Our results support the hypothesis that predation is negatively affected by land use. We observed an overall decrease of predation pressure from forested to open habitat. In terms of predator composition, arthropods, especially ants, represented the main predators across all land-use types, confirming a global and well reported trend (Leles et al., 2017; Roslin et al., 2017; Tiede et al., 2017). Changing contributions to total predation by ants shape the overall predation rates in the different land-use systems, while the high predation in old-growth forest and forest fragments can be co-attributed to forest specialists like Gryllacrididae that are lost with increased land-use intensity. We identified stem density and vegetation density as the most important local characteristics that are driving predation pressure in our study region, while the plots' land-use history and the surrounding forest cover can be seen as underlying factors. Fire conversion led to reduced densities of stems, while land conversion by manual clearance in vanilla agroforests decreased the vegetation density. Accordingly, the observed change in predator composition, as well as the decreasing predation rates can be explained with the increased local habitat simplification through land-use intensification.

In our experiment, we found the highest predation rates in land-use types where typical forest structures at least partially persisted. The similar predator communities in old-growth and forest fragments indicate the potential of the region's main natural predator populations to endure disturbance and fragmentation of forests. In particular, ant activity was the dominant contributor (>50%) to total predation in forest fragments and forest-derived vanilla agroforests. While several studies have not found negative effects of gradual forest fragmentation and degradation on predation rates by ants (Leles et al., 2017; Tiede et al., 2017), experiments conducted in tree fall gaps within continuous rainforests yielded higher predation rates in the gaps, possibly due to increased understorey vegetation and habitat heterogeneity (Richards & Coley, 2007; Seifert et al., 2016).

Similarly, Luke et al. (2014) found ants well represented in logged tropical forests and intensively used adjacent oil palm plantations. Our data suggest that the disturbance in the forest fragments did not prevent predation but actually stimulated this process. However, all the above-mentioned studies identified ants as the main predators and, in our experiment, only their contribution increased after the transformation of continuous old-growth forest into forest fragments. Hence, the disturbance may only have a stimulating effect on this group but not on the others. Predation by Gryllacrididae, the second most common predators in old-growth and forest fragments, remained similar in both forest types but was much lower in forest-derived vanilla agroforests.

High densities of stems and understorey vegetation leads to increased structural connectivity that facilitates easier foraging and predation success of arboreal arthropod predators while simultaneously preventing intra-guild predation (Jimenez-Soto et al., 2019; Langellotto & Denno, 2004; Yang et al., 2018). This structural connectivity is lost in most forest-derived vanilla plots due to the repeated clearing of understorey vegetation, providing a possible explanation for the reduced predation by the arboreal Gryllacrididae. Many ant species, however, utilize both ground and understorey strata for foraging while nesting in the ground (Leles et al., 2017) and are therefore less strongly affected by the loss of connectivity. Accordingly, our NMDS ordination suggests a gradual transformation of the predator community indicated by dissimilarity of forest-derived vanilla agroforests to old growth and fragmented forests, mostly driven by changing stem and vegetation density. It shows that conversion to agroforestry, even without fire, already significantly altered the specialized forest predator community. Overall, our findings support claims that both trees and understorey vegetation are keystone elements in forests that strongly relate to changes in arthropod predator communities (Langellotto & Denno, 2004; Schuldt et al., 2019).

While overall predation rates persisted in forest-derived vanilla agroforests compared to old-growth forest, we found lower predation rates in burned land-use types. This indicates the negative impact of fire conversion on arthropod predation rates due to the total loss of structural complexity and possibly due to the recolonization of these areas by only few pioneer plants species. Posa et al. (2007) reported similar findings from degraded forests in the Philippines, while Leles et al. (2017) found that decreasing plant diversity in southern Chinese forests especially affected ant predation negatively. The temporarily flooded rice paddies seem hostile to forest predators, and even ants, whose ground nesting and foraging habits are disturbed, are being replaced by different, better adapted predators. The few studies that compared non-forested with forested habitat all reported increasing predation rates outside the forests (Posa et al., 2007; Roels et al., 2018; Seifert et al., 2015); mostly due to an increase in bird predation resulting from better prey detectability in less vegetated habitats (Muiruri et al., 2016). In our experiment, however, arthropods remained the main predators in all non-forest habitats. They did not support higher predation pressure, nor did we measure increased bird predation in these areas. Yet, we identified woody fallows as non-forest habitat that is potentially valuable for conserving predation as an ecosystem function in deforested areas. Predation rates in woody fallows reached levels similar to old-growth rainforest, likely reflecting the reestablishment of trees and a dense secondary understorey on fallow land. Nonetheless, predation by specialist species, for example, Gryllacrididae, appears to be restricted to natural forests that showed distinct compositions to all land-use types, including woody fallows despite their high vegetation density. Hence, fire conversion likely has long-lasting effects on predator composition.

When comparing the different types of vanilla agroforests specifically, the predation rates in both types ranged from low, similar to herbaceous fallows, to high levels like in woody fallows or old-growth forests. As we identified local stem and vegetation density as the most influential covariates on predation, these findings show that on both types of vanilla agroforests high predation rates can be achieved, if increased stem and vegetation density is promoted by management. Forest-derived agroforests featured predator communities that appeared overall more similar to those in natural forests (Figure 4B). Yet, the predator compositions in both types of agroforest were significantly different from forest communities and shared most similarities with the compositions found in burned land-use types. Our results underline the potential of vanilla agroforestry to conserve predation as an ecosystem function, especially since this land-use type is less likely to be further converted. Nonetheless, transforming remaining natural forests into forest-derived vanilla agroforests, even without the use of fire, can already be considered unfavourable in terms of biodiversity conservation.

Many predators are highly mobile species and therefore not only exposed to local environmental conditions (Tscharntke et al., 2008). Because of this mobility, spillover effects from habitats suitable for high predation rates can enforce predation in adjacent areas that otherwise would not host high abundances and diversity of predators (Tscharntke et al., 2012). Our results suggest that spillover effects created by a higher cover of forest areas also occur in north-eastern Madagascar (Figure 3B). However, unburned systems naturally occurred more often in areas with higher forest cover while forest cover was not included among the best identified multiple linear regression models. Here the less mobile, ant dominated, arthropod predator community was more influenced by local habitat characteristics than by landscape properties, as it is the case in communities dominated by insectivorous birds (Karp et al., 2013; Maas et al., 2015). For this less mobile community, it is nonetheless likely that only a complex landscape with high forest cover and areas with increased stem and vegetation densities enables its effective dispersal (Tscharntke et al., 2008). In this context, it should also be considered that our experiment, like all dummy caterpillar experiments, only helps revealing a fraction of predator activity. The impact of landscape characteristics on local predation rates has generally been variable and depends on the studied region, land-use system and assessment method (Karp et al., 2018), while McHugh et al. (2020) also found that differing contributions of landscape factors on predation rates depend on the applied sentinel prey type. In our experiment, the captured fraction of predator activity is further limited to a certain time during the year, while seasonal variation in predation activity, including by ants, was observed for example in Ugandan forests (Molleman et al., 2016); similar variation, could also exist in Madagascar.

It is important to note that the measured predation rates cannot be directly translated into pest control services on crop fields (Chaplin-Kramer et al., 2011). Especially densely vegetated habitat does not necessarily only provide habitat for predators but also for their prey (Tscharntke et al., 2016). So far, no data from north-eastern Madagascar are available analysing how the functional composition of arthropods is changing with land-use. A study conducted in Indonesia reported a shift towards more prey and fewer predators in more intensively used areas (Klein et al., 2002), while the literature generally indicates a potentially positive relationship of pest control services with reduced land-use intensity in tropical agroforestry landscapes (Tscharntke et al., 2011). Similarly, the effect of increased predation rates on yields in vanilla agroforests has not been assessed yet and such research should be a priority in the future.

5 | CONCLUSIONS

Our experiment confirms that land-use intensity negatively affects predation patterns and shows that onsite structural features like stem and vegetation density are promoting predation rates, while the local land-use history defines the predator community composition. Unlike hill rice, the perennial vanilla agroforests can be managed less intensively, and the plots do not need to be burned to remain productive. Vanilla agroforestry can hence positively contribute to the conservation of predation as an important ecosystem function under appropriate management. To reach high predation rates, similar to those in natural forests even in fallow-derived agroforests, farmers should focus on keeping or restoring many shade trees and a dense understorey. However, this could also implicate potential trade-offs for farmers. Denser agroforests are more difficult to work in and high stem and vegetation densities might affect vanilla yields. Additionally, a denser understorey might also benefit pest species. To properly assess the relative biodiversity conservation value of vanilla agroforests they need to be put in relation to other prevalent land-use types: We did not detect significant changes of predator communities after fallow land had been converted into fallow-derived vanilla agroforestry, while predation rates may be increased if stem and vegetation density are kept high. While not causing a decrease of predation rates, establishing a vanilla agroforest in forests, however, does come at the cost of significantly altering the predator composition. Overall, establishing fallow-derived vanilla agroforests with a dense understorey and many trees can be a viable tool in landscape restoration programmes and should be the preferred option to increase the vanilla production areas, while further transformation of natural forests should be avoided.

ACKNOWLEDGEMENTS

This study has been conducted as part of the transdisciplinary research project ‘Diversity Turn in Land Use Science’ funded by the Niedersächsisches Vorab of Volkswagen Foundation (11-76251-99-35/13 (ZN3119)). Our special thanks go to Gatien Rasolofonirina who contributed crucially to the success of the field sampling. Additionally, we would like to thank the local *chefs de fokotany*, landowners and farmers, as well as Madagascar National Parks for permitting us to sample on their land and within the borders of Marojejy National Park. We collected data under research permits No 18/18/MEEF/SG/DGF/DSAP/SCB.Re and No 254/18/MEEF/SG/DGF/DSAP/SCB.Re granted by the Ministry for Water, Ecology and Forest (MEEF), Antananarivo. Furthermore, we express our gratitude to the Malagasy counterparts and all our colleagues in the Diversity Turn project.

AUTHORS' CONTRIBUTIONS

D.S., A.W., I.G. and T.T. conceived the study; D.S. collected and analysed the data with support of A.W., I.G. and T.T., and led the writing process; A.W., A.A.N.A.R., K.O., M.R.S. and D.A.M. conducted plot design and selection; K.O. and M.R.S. sampled and processed the tree-inventory data. All authors equally contributed to writing.

DATA AVAILABILITY STATEMENT

Data are available via the Dryad Digital Repository https://doi.org/10.5061/dryad.pnvx0k6k4 (Schwab et al., 2020).

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

How to cite this article: Schwab D, Wurz A, Grass I, et al. Decreasing predation rates and shifting predator compositions along a land-use gradient in Madagascar's vanilla landscapes. *J Appl Ecol*. 2021;58:360–371. https://doi.org/10.1111/1365-2664.13766