ARTICLE

Vegetation thresholds for the occurrence of millipedes (Diplopoda) in different tropical forest types in Andasibe, Madagascar

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ABSTRACT

Forest clearance, especially in the tropics, leads to habitat loss for many organisms including litter-dwelling arthropods. Among other invertebrates, millipedes (Diplopoda) provide important ecosystem services like decomposition and nutrient cycling in forest ecosystems. Despite their importance, little is known about litter invertebrates' response to tropical forest degradation and their role in reforestation. The present article should rather be regarded as a review of millipedes' occurrence in tropical forests with a pilot study from Madagascar, because the sample size is small and results need to be confirmed. This pilot study investigated the relationship between millipedes and vegetation characteristics in the eastern rainforests of Madagascar, in the region of Andasibe, parts of which are undergoing reforestation. Vegetation characteristics were measured in ten different forests encompassing different types: remnant rainforest, secondary forest, old *Eucalyptus* plantations, recently enriched with indigenous tree species, and degraded sites. Millipede species were searched by hand, identified and their occurrence in relation to the environmental characteristics was described.

Vegetation characteristics differed between forest types. Old *Eucalyptus* plantations, secondary forest, and primary rainforest were associated with higher litter depth and more native millipede species than degraded sites and forests afforested with native tree species since 2007. Non-native millipedes occurred in all vegetation formations except the primary rainforest site and did not show any relationship with vegetation characteristics. In contrast, native millipedes' occurrence was related to conditions associated with mature forest, such as high litter depth and high foliage cover. Logistic regression revealed a threshold of litter depth above which native millipedes are likely to occur. The results indicate that native millipedes are affected by forest degradation and are incompletely restored even when the afforested forest might approach the original state. Special care should be taken during reforestation efforts, as non-native soil arthropods can be introduced, completely replacing the indigenous biota.

RÉSUMÉ

Les conséquences de la déforestation globale sont multiples. Pour la plupart des organismes, la déforestation est la cause principale de la destruction des habitats. Les arthropodes qui vivent sur le sol forestier ou dans le feuillage sont ainsi menacés, surtout dans les forêts tropicales. Ces organismes sont pourtant indispensables au maintien de la résilience de la forêt. Dans l'écosystème forestier, les millepattes et autres arthropodes sont très importants pour la mise à disposition de différents services écosystémiques, par exemple pour leur rôle dans le cycle des éléments nutritifs, la formation des sols et la décomposition. Malgré leur importance, peu d'informations sont disponibles sur la réaction des invertébrés suite à la dégradation des forêts et leur rôle dans la reforestation.
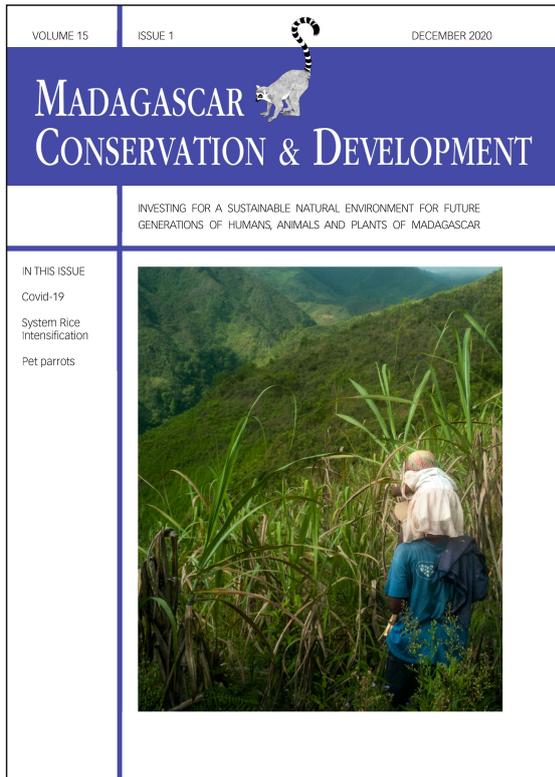
Cette étude tient surtout lieu de révision de l'occurrence des millepattes dans les forêts tropicales avec une étude pilote menée à Madagascar, dans la mesure où l'échantillonnage est réduit et que les résultats restent partiels. Cette étude pilote analyse les relations entre les millepattes et les caractéristiques végétales dans les forêts de l'Est de Madagascar, dans la région d'Andasibe. Ces forêts sont très diverses et dix types de forêt ont été considérés, à savoir une forêt récemment dégradée et une forêt dégradée, une forêt dégradée et reboisée avec des espèces arborées indigènes en 2007, 2012 ou 2015, des plantations d'Eucalyptus abandonnées depuis 1930 ou 1909, deux forêts secondaires, une forêt primaire. Dans ces différents types de forêt, les caractéristiques de la végétation ont été enregistrées et des millepattes ont été récoltés à la main. Les espèces de millepattes ont été identifiées et leur occur-

rence ont été analysées par rapport aux caractéristiques de la végétation. Les vieilles plantations d'*Eucalyptus* et les forêts secondaire et primaire étaient caractérisées par une couche plus épaisse de feuilles et davantage d'espèces de millepattes indigènes par rapport aux forêts dégradée et replantée. Les espèces allogènes étaient présentes dans tous les types de forêt à l'exception de la forêt primaire. La présence de ces espèces n'était pas liée aux caractéristiques de la végétation. En revanche, l'occurrence des espèces indigènes était associée à des conditions qui sont caractéristiques des forêts matures, par exemple une couche de feuilles épaisse et une couverture foliaire dense. L'analyse de régression logistique a révélé une valeur seuil pour la hauteur de la couche de feuilles mortes. Au-delà de ce seuil, il est probable que les millepattes indigènes soient présents. L'étude a montré que les millepattes indigènes sont impactés par la déforestation et qu'ils ne sont pas facilement restaurés même si la restauration semble permettre à la forêt de se rapprocher de son état initial.

INTRODUCTION

Deforestation is a major problem worldwide. Although the rate of deforestation rate has decreased over the last few decades, forest gain is mainly restricted to temperate forests, while forest loss continues in the tropics (Keenan et al. 2015, Sloan and Sayer 2015). In Madagascar, after 1990 the deforestation rate was declining to 42,000 ha y-1 in 2000–2005 but increased again since 2005 to 99,000 ha y-1 for the years 2010–2014 (Vieilledent et al. 2018). The ongoing forest loss is detrimental to Madagascar's flora and fauna, given that forests are home to the majority of its biodiversity (Goodman and Benstead 2005). Approximately 80% of the biodiversity depends on forests (Waeber et al. 2020). Especially Madagascar is considered as a biodiversity hotspot with high percentages of endemism being seriously endangered (Myers et al. 2000, Ganzhorn et al. 2001). In a publication of 2003, this island is estimated to host 5,800 macroinvertebrate species of which 86% are endemic (Goodman and Benstead 2005), thereunder 268 different diplopod species of which 86% are endemic (Enghoff 2003, Wesener 2009, Wesener et al. 2009). In addition to forests, forest soil and litter are also essential for a great portion of described species worldwide. Some 25% of the global biodiversity is dependent on it (Decaëns et al. 2006). The clearance of forest (and thus of its soil and litter) poses a major threat to soil biodiversity (Mathieu et al. 2005).

Soil animals (including all organisms living in habitats related to soil, e.g., litter, dead wood or rocks) are divided into microfauna (< 0.1 mm), mesofauna (0.1–2 mm), macrofauna (2–20 mm), and megafauna (> 20 mm). In addition to arachnids and insects, which account for a large part of soil animals (Decaëns et al. 2006), slugs, snails, woodlice, earthworms, centipedes and millipedes also belong to the macrofauna (Zanella et al. 2018). Millipedes are typical forest-dwelling organisms and need sufficient humidity, being meso- to hygrophile (Golovatch and Kime 2009). They are largely restricted to the leaf litter, the soil-litter interface, the uppermost layer of soil, and dead wood of principally deciduous temperate, subtropical, and humid tropical forests, where they can feed and stay concealed in a humid shelter (Alegasan 2016). In temperate and tropical environments, they represent one of the major groups of soil and litter fauna (Alegasan 2016).

Invertebrates provide several ecosystem services, such as nutrient cycling, soil formation, and micro-climate regulation (Lavelle et al. 2006). Nutrient cycling is initiated by the ecosystem process decomposition, which in turn is accelerated by the comminution of dead organic material of soil invertebrates, by increasing the surface of detritus, which can be further decomposed by microbial organisms (Coleman and Wall 2015). Soil fauna has a positive impact on decomposition (García-Palacios et al. 2013).

Considering the ongoing deforestation worldwide, but especially in the tropics, we need to know under which habitat conditions the soil fauna is maintained and their associated important ecosystem functions remain undisturbed. Powers et al. (2009) quotes a reduction of the decomposition rate by 50% after the artificial removal of the mesofauna. Another study states also the importance of a more numerous soil fauna, indicating that the decomposition process in a humid tropical environment is accelerated when millipedes and earthworms are present in the litter layer (Tian et al. 1995). In general, there is a need of more specific knowledge of soil fauna diversity and abundance and their contribution to decomposition in tropical forests (Powers et al. 2009). Regarding the habitat requirements in tropical and subtropical forests for the soil fauna community, the literature states mostly litter quality and quantity: Burghouts et al. (1992), for example, found a positive effect of litter quantity on litter invertebrate abundance in tropical rainforests in Malaysia. Another study showed also significant effects of litter quantity and quality on litter invertebrate abundances at a local scale but argues that at a regional scale precipitation and temperature explain mostly the variance in tropical forests in China (Lu et al. 2016). Yang et al. (2007) investigated tropical forests in Puerto Rico and demonstrated that higher litter quantity results in an increase of litter arthropods abundance. They could, however, not prove that litter quality affects arthropod density. Sayer et al. (2010) investigated the effect of nutrients and litter mass in a lowland tropical forest in Panama and concluded that at a local scale, arthropod abundance is related to habitat space in terms of litter quantity, while arthropod diversity is associated to the habitat quality. For New Zealand, Wardle et al. (2006) argues that the resource quality in terms of the litter species has an effect on soil faunal diversity. For millipedes in specific, there is also an effect of litter quantity and quality documented. Litter depth is a driver for millipede's morphotaxa richness in Australian tropical rainforests and for millipede abundance in New Zealand (Nakamura et al. 2003, Tomlinson 2014). Millipede biomass is highly correlated with N concentration and C/N ratio in a tropical forest in Puerto Rico (Warren and Zou 2002). Furthermore, millipede abundance and species richness tend to be higher in leave litter with higher N content in Guadeloupe (Loranger-Merciris et al. 2008).

In order to preserve these crucial animals and the provision of associated ecosystem services (e.g., soil fertility and climate regulation), we have to restore their habitats but especially need to know their habitat requirements. However, the effects of restoration on ecosystem structures and native biodiversity are little studied, as are the factors controlling the recovery of litter arthropods in successional environments (Cole et al. 2016) and the response of soil macrofauna after forest clearance in the tropics (Mathieu et al. 2005). For Madagascar, the ecology of invertebrates received less attention in general and the application of vegetation thresholds remains limited.

In this context, the present pilot study investigates (i) the relationship between millipedes' occurrence and several vegetation variables, and (ii) the difference between native and introduced mil-

lipedes in their response to environmental conditions in different forest types. This pilot study complements the current literature on the links between millipede occurrence and habitat characteristics.

METHODS

STUDY AREA. The study area is located in the region of the Ankeniheny-Zahamena Corridor (CAZ), which is a 381,000 ha belt of rainforest east of the capital Antananarivo. The climate of the CAZ region is characterized as hot, humid and tropical, with an average annual rainfall of 2,500 mm and an average annual temperature of 18–24°C (Dolch 2003, Andriamananjara et al. 2016). The Andasibe region is situated at about 900 m above sea level (Vallan 2002), has a humid climate with 1–2 dry months and its soil type is mainly Ferralsols, according to FAO classification (Andriamananjara et al. 2016). The study was conducted in the Analamazaotra forest of Andasibe (Figure 1), which is managed by Madagascar National Parks. The sampling was undertaken at the Analamazaotra Forest Station situated outside the National Park; this is managed by the local Association Mitsinjo. The Analamazaotra Forest Station encompasses 700 ha of rainforest and abandoned *Eucalyptus* plantations, which are currently being restored with native tree species. In addition to the Analamazaotra forest, we investigated two types of forests which are located approximately 30 km north of Andasibe (Figure 1, with native trees in different years (R07, R12, R15), reforestation with *Eucalyptus* around 1930 (E30), reforestation with *Eucalyptus* around 1909 (E09), two secondary forests (S1, S2), and an undisturbed and accordingly primary forest (P). Until 1817, the rainforests around Andasibe were pristine (Vallan 2002). Though large deforestation started under French colonialism in the early 1900s, Analamazaotra forest was able to recover when the management was overtaken by the Ministry of Water and Forests (Ministère des Eaux et Forêts) around 1970. In 2003, the Association Mitsinjo took over the management of a portion of the secondary forest (S1). One type of reforestation forest is the monoculture of *Eucalyptus*. The fragments with monoculture of *Eucalyptus* are remains from the French colonialists, who experimented with fast growing trees for timber production. Reforestations with *Eucalyptus* took place around 1909 (E09) and 1930 (E30). Today, the old *Eucalyptus* plantations are not being exploited anymore. In contrast, the reforestation project that started in 2007 includes native tree species. We selected sites where reforestation took place in 2007 or 2008 (R07), in 2012 (R12), and in 2015 (R15). About 50 different native tree species were planted in the restoration efforts, among which are species of the genera of *Symphonia*, *Macaranga*, *Eugenia*, and *Cryptocaria*. These reforested sites have experienced different land-use management before being abandoned. Some were burned for charcoal in 1988, others experienced rice farming, manioc cultivation or tree logging (according to G. Rakotonirina, pers. comm., April 2017). Degraded sites are characterized as land laid fallow after farming, deforestation, or burning, and which has an open canopy with many gaps. After abandoning rice cultivation, herbaceous vegetation and bush fallows did establish (Vallan 2002). The older degraded (D) sites have been laid fallow since approximately 1988 and the younger sites (DY) since approximately 2008 (according to G. Rakotonirina, pers. comm., April 2017). In addition to the Analamazaotra forest, two types of forests were investigated in a different region which is located approximately 30 km north of Andasibe, and belongs to the Ankeniheny-Zahamena Corridor. These sites were selected in order to compare afforested and degraded sites with a
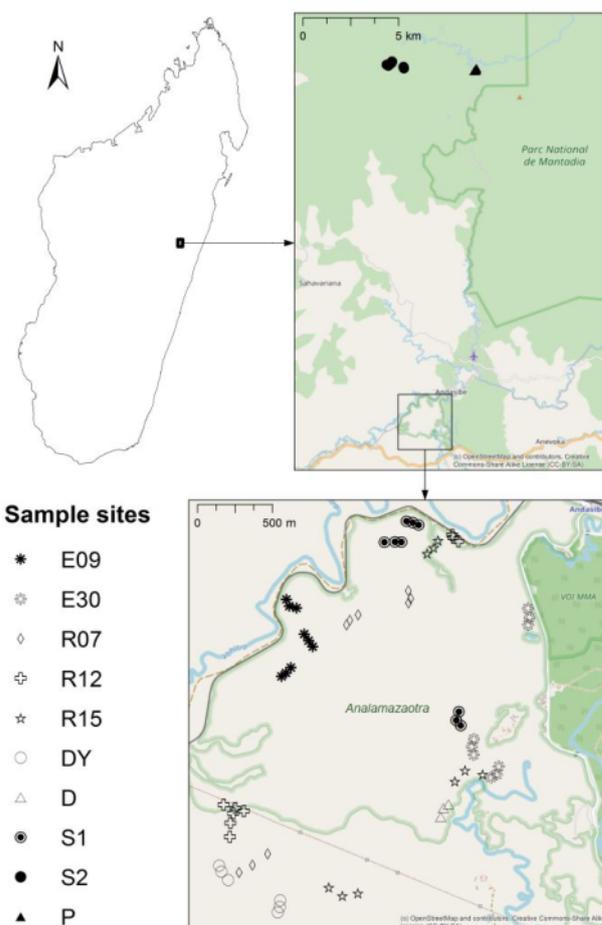

Figure 1. Sample sites. (E09: reforestation with *Eucalyptus* around 1909, E30: reforestation with *Eucalyptus* around 1930, R07: reforestation with native trees in 2007, R12: reforestation with native trees in 2012, R15: reforestation with native trees in 2015, DY: freshly degraded forest, D: degraded forest, S1: secondary forest, S2: secondary forest, P: primary forest).

primary forest fragment (P) and another secondary forest (S2). The primary forest sites are remnant rainforest patches.

COLLECTION OF ECOLOGICAL PARAMETERS. Sampling was conducted in April 2017. The sampling design was adapted to Bogyó et al. (2015) and Nakamura et al. (2003). For this, three 100 m transects (= 3 replicates) were established per site with three 2 m x 2 m plots per transect spaced 50 m apart (10 habitat types x 3 transects x 3 plots). Eight vegetation variables were measured to test their relation to millipede occurrence. After having installed the 2 m x 2 m quadrate, the four variables that needed to be recorded before the plot was disturbed, in order to collect the millipedes, were documented: (1) litter depth (cm; mean of nine measurements/plot), (2) shrub cover (%), (3) bare soil (%), and (4) absence or presence of coarse woody debris scored at four different diameters (on a scale from 0 to 3 based on maximum diameter of debris, whereby 0 = debris with a diameter of < 1 cm, 1 = 1–10 cm, 2 = 11–20 cm, 3 ≥ 21 cm).

Additional four environmental variables were recorded after the collection of the millipedes: (5) canopy height (in meters; if no canopy was present, a measurement of 0 was recorded), (6) foliage cover (%; mean of 9 measurements/plot, taken through a vertical sighting tube), (7) tree spacing measure (m; average distance from center of plot to three nearest trees), and (8) DBH (in centimeters; diameter of the tree nearest to center of plot with a minimum DBH of 10 cm).

MILLIPEDE COLLECTION AND IDENTIFICATION. Two people systematically investigated the litter for millipedes for 10 to 13 minutes, depending on the thickness of the litter layer. Litter was carefully removed and all millipedes on top of the soil or in the litter were collected by hand. The collected millipedes were stored in 70% ethanol. The hand collection method was chosen because it represents an efficient method for collecting millipedes (Snyder et al. 2006). The comparison of the methods 'pitfall trapping', 'Berlese extraction', and 'hand collection' proved that the latter yielded the greatest diversity and second highest abundance (Snyder et al. 2006).

For the identification of millipedes, we used Wesener (2009), Wesener et al. (2009), Jeekel (1999), de Saussure and Zehntner (1897, 1901, 1902), and Attems (1910, 1914, 1951). Male specimens that could not be identified with the existing literature were grouped into morphospecies, which were characterized by their differences in gonopod structure. For the order Spirobolida, Thomas Wesener also identified juvenile and female specimens. For the order of Spirostreptida, juveniles and females could not be grouped with absolute certainty to the morphospecies *Iulomorpha* sp. 1 due to the lack of reliable morphological structures. Therefore, two subgroups, *Iulomorpha* sp. 1a and *Iulomorpha* sp. 1b, are here included to highlight this uncertainty (Table 1). For the statistical analysis, the two *Iulomorpha* sp. 1 were treated as one morphospecies.

DATA ANALYSIS. Analyses were based on the means of the vegetation characteristics per transect. For testing whether there is a threshold value that describes millipedes' occurrence, we performed logistic regression between all vegetation variables, native millipede occurrence as well as non-native millipede occurrence separately. Due to the replicated design, mixed models were conducted by including replicates as a random effect to account for the lack of independence. To assess the quality and the fit of the model a pseudo $R2$ test statistic (Nagelkerke) was calculated. We plotted the presence/absence of millipedes against the mean litter depth of each replicate. In addition, to investigate differences between native and non-native millipedes in relation to litter depth, we conducted a t-test, as both homogeneity and normality were confirmed. Normality was tested with a Shapiro-Wilk test, and Levene's test was conducted for the equality of variances. Analyses were run with R (version 3.4.2).

RESULTS

In total, 113 Diplopoda specimens from five orders (Sphaerotheriida, Siphonophorida, Polydesmida, Spirobolida, and Spirostreptida) and 12 species were recorded (Table 1). Out of the 113 individuals, 85% belonged to non-native species. The non-native species were either *Oxidus gracilis* (86 individuals) or belonged to the genus *Iulomorpha* (11 individuals). The remaining 16 individuals were species endemic to Madagascar.

The general trend for the environmental factors is the difference between the degraded (DY, D) and reforested sites with native tree species (R15, R12, R07) compared to the older sites reforested with *Eucalyptus* (E30, E09), secondary forests (S1, S2), and primary forest (P) (Table 2). The lowest amount of litter was found at the sites reforested with native tree species (R15, R12, R07) as well as at the two degraded sites (DY, D). Litter depth was highest in both secondary forests (S1, S2) as well as in the primary forest (P). Native millipede species were found in all forest types, except for the forests reforested with native trees (R15, R12, R07). Non-native millipedes (*Oxidus gracilis* and *Iulomorpha* sp.) were present in all forest types, except for the primary forest (P). The highest abundance for *Oxidus gracilis* was in R07.

Since we did not expect to find as many non-native millipedes as we did, and because single species abundances were too low for statistical analyses, with the exception of *Oxidus gracilis*, we conducted a binary categorization (native and non-native). Mixed logistic regression models did not reveal any relationship between vegetation characteristics and the occurrence of non-native species occurrence (Table 3, Figure 2). In contrast, native species were related to litter depth, foliage cover, and shrub cover (Table 3). The pseudo $R2$ value indicated the best fit of the mixed model with litter depth as the predictor variable. The threshold value for a 50%

Table 1. Millipede species with their taxonomic classification, their abundance, and their origin.

Order	Family	Genus	Species	Nbr.	Origin
Sphaerotheriida	Arthrosphaeridae	*Zoosphaerium*	*platylabum*	3	native
	Arthrosphaeridae	*Zoosphaerium*	*neptunus*	2	native
Siphonophorida	Siphonorhinidae	*Siphonorhinus*	sp.	1	native
Polydesmida	Dalodesmidae	G.	sp.	1	native
	Paradoxosomatidae	*Oxidus*	*gracilis*	86	non-native
	F.	G.	sp.	1	native
Spirobolida	Pachybolidae	G.	sp.	1	native
	Pachybolidae	*Flagellobolus*	*pauliani*	5	native
Spirostreptida	Spirostreptidae	*Charactopygus*	sp.	1	native
	Spirostreptidae	G.	sp.	1	native
	Cambalidae	*Iulomorpha*	sp. 1	6	non-native
	Cambalidae	*Iulomorpha*	sp. 1a	2	non-native
	Cambalidae	*Iulomorpha*	sp. 1b	2	non-native
	Cambalidae	*Iulomorpha*	sp. 2	1	non-native

Table 2. Average values of the environmental factors in the forest types studied and abundance of millipede species per forest type. (DY = recently degraded forest; D = degraded forest, R15 = reforested with native tree species in 2015; R12 = reforested with native tree species in 2012; R07 = reforested with native tree species in 2007 or 2008; E30 = abandoned Eucalyptus plantation from 1930; E09 = abandoned Eucalyptus plantation from 1909; S1 = secondary forest in Andasibe; S2 = secondary forest of Sahanody; P = primary forest)

	Forest type	DY	D	R15	R12	R07	E30	E09	S1	S2	P
Vegetation characterisitcs	Replicates (n)	2	3	3	3	3	3	3	3	3	2
	Litter depth (cm)	2.75	3.43	2.85	1.94	2.93	4.99	5.32	5.6	5.52	5.74
	Woody debris (0–3)	2	2.78	1.56	1.22	1.78	2.44	1.33	1.89	2.22	2.17
	Canopy height (m)	7.46	7.55	8.43	6.84	12.43	24.42	26.45	25.64	20.72	19.13
	Foliage cover (%)	35.07	37.72	31.46	18.5	44.81	42.78	31.42	69.93	67.1	64.54
	DBH (cm)	20.48	26.27	21.21	12.61	21.33	26.82	44.87	23.23	27.24	25.6
	Shrub cover (%)	18.83	37.78	39.44	52.78	34.44	23.89	27.11	3.89	11.44	20.83
	Uncovered soil (%)	7.67	6	9.78	15.56	3.5	0.33	2.89	0	0	0
	Tree spacing measure (m)	1.27	2.1	2.58	2.34	1.67	1.74	1.57	1.02	0.91	0.92
Abundance of diplopod species	*Z. platylabum*	1	0	0	0	0	0	0	0	0	2
	Z. neptunus	0	0	0	0	0	0	0	0	0	2
	Siphonorhinus sp.	0	0	0	0	0	0	0	1	0	0
	Dalodesmidae sp.	0	0	0	0	0	0	1	0	0	0
	Oxidus gracilis	3	11	16	2	32	11	8	3	0	0
	Polydesmida sp.	0	0	0	0	0	1	0	0	0	0
	Pachybolidae sp.	0	0	0	0	0	0	0	0	1	0
	Flagellobolus pauliani	0	0	0	0	0	0	2	3	0	0
	Charactopygus sp.	0	1	0	0	0	0	0	0	0	0
	Spirostreptidae sp.	0	0	0	0	0	0	0	0	0	1
	Iulomorpha sp. 1	0	1	0	0	0	2	0	4	3	0
	Iulomorpha sp. 2	0	0	1	0	0	0	0	0	0	0

probability of occurrence of native millipede species is above a litter depth of 4.83 cm (Figure 3). Litter depth does predict native millipede presence or absence. The probability of presence exhibited a significant non-linear response to different depths of litter (Table 3, Figure 3), which indicates that native millipedes may occur above a critical minimal amount of litter.

The boxplots in Figure 4 show that native millipedes are restricted to a higher litter depth. The t-test accounts for a significant difference in litter depth between the means of the two groups (t = 2.361, df = 28, p = 0.025).

DISCUSSION

The first question of this study deals with the relation of vegetation variables with the occurrence of millipedes, the second question pertains to whether native and introduced millipedes differ in their response to environmental conditions. The majority of the collected millipede species were native species. However, non-native species occurred in much higher abundances. The most abundant species in this study, *Oxidus gracilis*, is not native to Madagascar. It occurred mainly at the reforested sites with native tree species, which is evidence of the relatively disturbed conditions in this habitat type. Other than *Oxidus gracilis*, the non-native *Iulomorpha* sp. 2 is the only other millipede species found in reforested forests, with just one specimen. The congregating behavior of *Oxidus gracilis*, inhabiting formerly unoccupied niches in high abundances, may outcompete native species (Bulpitt 2016) who could potentially return. However, Tomlinson (2014) found little evidence of non-native millipedes (including *Oxidus gracilis*) displacing native millipede fauna in small forest fragments in New Zealand. Millipedes in New Zealand might not be impacted by competition with *Oxidus gracilis*, but this says nothing about the Malagasy millipedes which are all endemic. In contrast to the reforested sites, the primary forest is associated with three native millipede species.

Regarding environmental characteristics, the *Eucalyptus* plantations, the secondary, and primary forests are similar, but different millipede species were recorded. This leads to the assumption that even though environmental variables are similar, species composition is not. Höfer et al. (2001), who investigated decomposer groups in the Amazon, as well as Mathieu et al. (2005) also found that species richness is highest in the primary forest. David and Handa (2010) question whether tropical secondary forests can provide an appropriate habitat for species that depend on old-growth forests. Although sites might meet the required habitat conditions, time is required for recolonization of arthropods (Nakamura et al. 2003). Millipedes have particularly poor dispersal abilities (Alegasan 2016). Therefore a low degree of forest patch isolation and vegetation corridors should be considered for conservation purposes, especially for invertebrates like millipedes depending on forests for dispersal (Galanes and Tomlinson 2011). An alternative explanation may be that the sampling design did not include enough sampling units to meet a species accumulation curve. For example, there is evidence of occurrence of *Zoosphaerium neptunus* in the secondary forest of Andasibe (Wesener and Schütte 2010). *Zoosphaerium neptunus* is not regarded as threatened despite the eastern rainforest's rapid declining due to fragmentation and deforestation (Vieilledent et al. 2018). It is listed as "least concern" in the IUCN RedList (Rudolf and Wesener 2017a), occurring in several protected areas and being widely distributed (Wesener and Wägele 2008).

Table 3. Results of logistic regression analysis predicting the occurrence of native and non-native millipedes.

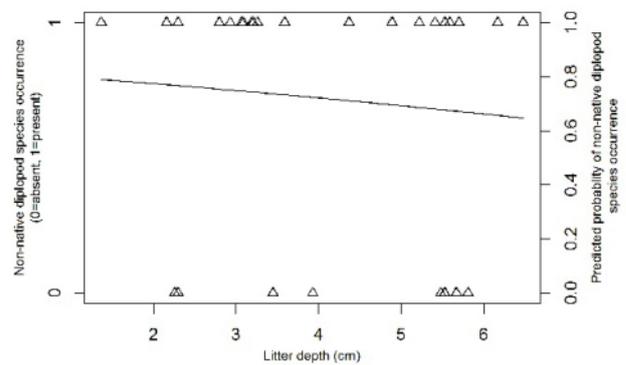|		Estimate	Standard error	z-value	p-value	Pseudo R2 Nagelkerke
Native	Litter depth	1.23	0.626	1,960	0.05	0.466
	Woody debris	0.036	0.154	0.232	0.817	0.042
	Canopy height	0.096	0.058	1,646	0.1	0.221
	Foliage cover	0.064	0.026	2,412	0.016	0.373
	DBH	0.076	0.057	1,336	0.181	0.15
	Shrub cover	-0.065	0.032	-2,012	0.044	0.252
	Uncovered soil	-0.36	0.177	-2,038	0.042	0.328
	Tree spacing measure	-1,338	0.816	-1,639	0.101	0.195
Non-native	Litter depth	-0.14	0.301	-0.466	0.642	0.012
	Woody debris	-0.246	0.2	-1,257	0.209	0.123
	Canopy height	-0.029	0.041	-0.716	0.474	0.029
	Foliage cover	0.02	0.028	0.736	0.462	0.042
	DBH	0.076	0.057	1,336	0.181	0.044
	Shrub cover	-0.0256	0.025	-1,024	0.306	0.061
	Uncovered soil	0.01	0.066	0.137	0.891	0.002
	Tree spacing measure	-0.488	0.5	-0.987	0.324	0.053

Figure 2. Occurrence of non-native diplopod species in different forests types with different litter depths (cm) and with a regression line representing the probability of occurrence based on the mixed logistic regression model in Table 3.
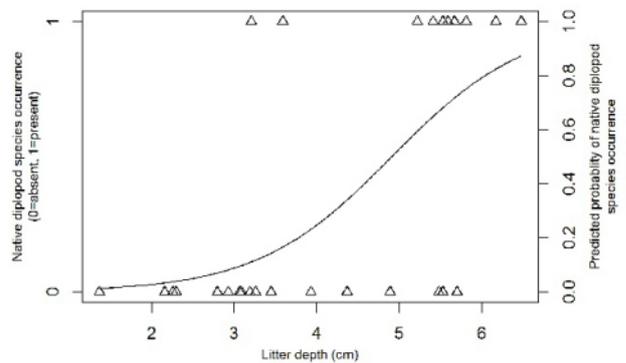

Figure 3. Occurrence of native diplopod species in different forests types with different litter depths (cm) and with a regression line representing the probability of occurrence based on the mixed logistic regression model in Table 3.
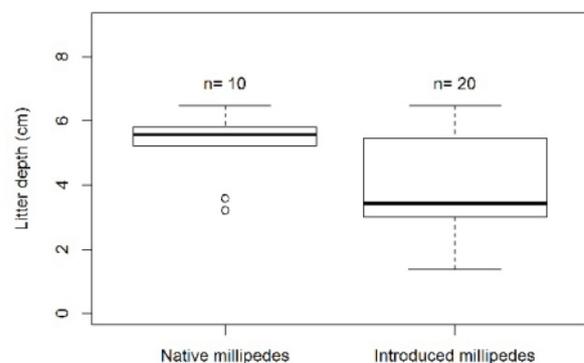

Figure 4. Comparison of the means of replicates, where native or non-native species occurred, for litter depth. (The number of samples n refers to the number of replicates where native millipedes and non-native millipedes were present, respectively)

One explanation why native millipede species were not present at the *Eucalyptus* sites may be the fact that tree species have an impact on millipede assemblages because they influence the microclimate as well as the quantity and quality of leaf litter (Stoev et al. 2010, Stašiov et al. 2012). The litter quality influences arthropod species diversity and assemblages in general (Wardle et al. 2006, Sayer et al. 2010, Lu et al. 2016), as well as millipede species richness and assemblages (Warren and Zou 2002, Loranger-Merciris et al. 2008). A possible explanation why similar native species do not inhabit the *Eucalyptus* sites could be poorer litter quality containing mainly *Eucalyptus* leaves. Furthermore, *Eucalyptus* litter has relatively low N concentrations, which is related to lower millipede biomass (Warren and Zou 2002). In addition, because tropical *Eucalyptus* plantations do not restore the original forest, in terms of diversity of tree leaf litter, macroarthropod abundance may be similar but species richness may be lower (David and Handa 2010). Concluding, saprophagous (feeding on dead/decaying organic matter) macroarthropod compositions changes according to the vegetation structure (David et al. 1999), which also influences litter quantity and quality, the main food and habitat of millipedes.

Several studies confirm the positive effect of litter quantity on litter invertebrate abundance in tropical and subtropical forests (Burghouts et al. 1992, Yang et al. 2007, Sayer et al. 2010, Lu et al. 2016). Another study (Nakamura et al. 2003) identifies litter depth as a factor predicting millipede's morphotaxa richness. Suitable habitats for millipedes are characterized by a high amount of leaf litter, dead wood, closed canopy cover and a humid microclimate (Bogyó et al. 2015). Consequently, it is very likely that the more habitat space in terms of litter depth exists, the more millipede species will be present. In addition, a higher amount of litter facilitates structural habitat complexity, thus supporting more invertebrates (Lu et al. 2016). Therefore available habitat space, in this case litter depth, may be a very significant predictor of arthropod abundance (Sayer et al. 2010). Tomlinson (2014) also indicates that litter quantity is a significant variable for explaining the abundance of most native species in New Zealand, while the abundance of *Oxidus gracilis* increased significantly with decreasing fragment size and lower canopy density. For non-native millipedes, mixed logistic regression models relating the occurrence of non-native millipedes and vegetation characteristics were not significant. Accordingly, non-native millipedes occurred on plots with highly diverse vegetation characteristics.

Oxidus gracilis represents 87% of the collected specimens of non-native millipedes. The species are found in plots with a relatively high variation of litter depth, whereas, in this study, native diplopods only occur at sites with a minimum depth of 4.83 cm. There is evidence that *Oxidus gracilis* deals with a large range of habitat conditions. Its distribution is not related to specific environmental factors (Bulpitt 2016), which is probably why it occurs on each continent in greenhouses as well as in natural ecosystems, e.g., in countries like USA, Australia, China, India, Finland, Italy, Morocco, South Africa, and Madagascar (Stoev et al. 2010). How *Oxidus gracilis* was introduced remains largely unknown. The introduction of *Oxidus gracilis* in Europe, for example, is likely due to the trading of tropical plants (Stoev et al. 2010).

Native millipede species appear to be restricted to habitats with specific characteristics. Although there are no studies for millipedes, there is some indication that habitat specialists are more affected by habitat loss than habitat generalists (David and Handa

2010). In general, deforestation in the tropics could outweigh any other influence for habitat specialists (David 2009), which could pose an especially severe threat to microendemics of the genus *Zoosphaerium* in Madagascar's rainforests (Wesener 2009). However, the two pill-millipedes from this study, *Zoosphaerium neptunus* and *Zoosphaerium platylabum*, are not classified as microendemic, though they are restricted to the rainforest (Wesener 2009). Both pill-millipede species are IUCN RedListed as "least concern" (Rudolf and Wesener 2017a, 2017b). However, some studies showed the negative effects of invasive species on soil invertebrates, e.g., the abundance of many native endemic arthropod species in Hawaii decreased locally because of an invasive ant species from Argentina (*Iridomyrmex humilis*) (Cole et al. 1992) and the abundance and species richness of millipedes were impacted by non-native earthworm species *Amynthas agrestis* in the Great Smoky Mountains in the US (Snyder et al. 2011), because they compete probably for the same food resources (Snyder et al. 2013). Alien species were identified as the main drivers of millipede extinctions, particularly on the Seychelles Islands (Blackburn et al. 2019).

This pilot study identified a threshold value of around 5 cm for litter depth, indicating appropriate habitat conditions for native millipedes. Deriving conservation guidelines from habitat thresholds and predicting species responses to habitat restoration sounds promising, especially because recent empirical evidence has delivered much support and some indication for the existence and usefulness of ecological thresholds (Johnson 2013). However, conservation purposes must consider limitations of ecological thresholds and should not overestimate their relevance for management decisions (Johnson 2013). Van der Hoek et al. (2015) and Müller and Bütler (2010) even advise against applying threshold values to answer questions like "How much is enough?" and against oversimplification. While it is evident that thresholds should not be defined in absolute terms, the study illustrates that ecosystem processes are disrupted by forest degradation and are not restored easily even though the restored forest might approach the original state.

CONCLUSION

The old *Eucalyptus* sites and the primary and secondary forests are associated with more native species than the degraded sites recently reforested with native tree species. Although the reforested sites with *Eucalyptus* exhibit a similar amount of litter as the secondary and primary forests, they clearly do not provide the same litter quality characteristics. Furthermore, the study indicates that litter depth is very likely the most significant variable in explaining native millipede occurrence. It is expected that the threshold value of litter depth indicates suitable habitat conditions, because litter-dwelling millipedes are dependent on the litter layer. However, the results presented here should be interpreted with caution due to the small sample size. In future studies, changes in sample size, as well as in the sampling method should be taken into account to fully understand differences between native and non-native millipedes and to elaborate the threshold approach for millipedes in the forests of Andasibe. Of special concern is the presence of numerous introduced millipedes at sites replanted with native vegetation, in combination with the complete absence of any indigenous millipedes at these sites. As millipedes are poor dispersers, the non-native millipede species were most-likely introduced by the reforesting efforts and might outcompete the native

species. It would be useful to investigate, whether the provision of ecosystem functions like decomposition of introduced millipedes is redundant to that of endemic millipedes. Great care should thus be taken to avoid permanent damage of native forests through potential introduction of non-native soil arthropods via reforestation.

ACKNOWLEDGEMENTS

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