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Native and introduced land snail species as ecological indicators in different land use types in Java

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ABSTRACT

We investigated the effects of different land use types and environmental parameters on the number and abundance of native and introduced land snail species in East Java. 2919 specimens were sampled and assigned to 55 species of which 8 are introduced. Whereas species richness was highest in primary forest, the highest number of introduced species was found in agroforest. The snail assemblages in different habitat types differ much clearer in composition than in total species richness. Plantations and agroforest are dominated by introduced pulmonates with regard to number of individuals, while primary forest is dominated by native prosobranchs. The habitat requirements of the introduced pulmonates differ from those of the native species. In the study area, the abundance of native as well as introduced pulmonate species increased with increasing human impact. However, the abundance of introduced pulmonate species decreased with increasing density of the canopy cover, whereas the abundance of native pulmonate species increased with increasing canopy cover. The abundance of native prosobranch land snails also tends to increase with increasing canopy cover and with the availability of deadwood, but decreased with increasing human impact. Improving the canopy cover and retaining deadwood in plantations and agroforests might help to control the populations of introduced species or even prevent their establishment in these habitats. Land snails are good indicators for the long-term stability of natural habitats, because several species are restricted to undisturbed natural habitats and because of their low dispersal abilities. However, complete inventories of land snail species are costly. Therefore we propose two indices that can be scored with much less effort, namely the percentage of prosobranch individuals and the percentage of individuals of introduced species. Both indices are significantly correlated with the number of native species. Dense plantations and agroforests bordering primary forests may protect the latter from introduced species and help to conserve the native fauna by reducing desiccation and buffering the human impact on the primary forests.

1. Introduction

Human-mediated dispersal increasingly homogenized biotas worldwide. The influence of biogeographic barriers and long distances on the distribution of organisms is decreasing so that the ranges of human distributed species are primarily explained by the prevailing climate (Capinha et al., 2015). For a better understanding of the invasion risks and for conceiving measures to control introduced species and to conserve the native fauna, it is necessary to investigate the factors that determine the success of introduced species. Introduced species are not homogeneously distributed in the regions where they are introduced. An investigation of the success of introduced species in different land use systems can improve our understanding of the factors that facilitate the establishment and the expansion of introduced species.

Modified habitats that potentially facilitate the establishment and expansion of introduced species increasingly dominate tropical landscapes characterized originally by a rich native fauna and flora. Land snails are sensitive to habitat changes and they are characterized by a low active mobility, so that the composition of land snail assemblages reflects changes in environmental variables even if they vary across short distances. Thus, we studied land snails in Java, the most populous island in the world. Only about 6% of Java is still covered by primary forest (Margono et al., 2014). Java (and its adjacent satellite islands) has a rich land snail fauna including 205 land snail species, of which 12 species are introduced and

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63 are endemic (van Benthem Jutting, 1948, 1950, 1952; Loosjes, 1953; Butot, 1955; de Winter, 1983; Dharma, 1992, 2007, 2015; Whitten et al., 1997; de Winter and Vermeulen, 1998; Vermeulen and Whitten, 1998; Gomes and Thomé, 2004; Heryanto, 2011).

We studied native and introduced land snail species in three land use types: teak plantations, small-scale agricultural systems (hereafter 'agroforests'), and primary forest in East Java. We focused on the following questions. (i) How do the snail assemblages from these habitats differ? (ii) How many introduced land snail species occur in plantations, agroforests and primary forest? (iii) Which environmental variables affect the abundance of native and introduced snail species and the assemblage composition? (iv) Which indices might be used as simple indicators for disturbance versus long-term habitat stability? (v) Which measures might impede the establishment and expansion of introduced species?

2. Material and methods

2.1. Study area

The study area (8°20′S–8°24′S 112°26′E–112°31′E) is situated in the Kendeng Mountains in Malang regency, East Java, Indonesia (Fig. 1). The Kendeng Mountains are limestone hills with an altitudinal range from 0 to 650 m a.s.l. The climate of Malang is governed by the Asia-Australian monsoon. The west monsoon occurs during the Asian winter (December–February) and brings rain with a peak (350–400 mm) in January, while the east monsoon, which occurs during the Australian winter (June–August) results in a dry season with less than 100 mm monthly rainfall between June and October (mean annual rainfall about 2300 mm). Mean annual temperature is about 25 °C.

We investigated primary lowland rainforest and teak plantation bordered by primary forest in the Kondang Merak area, and agroforest and teak plantation bordered by agroforest near Kedungsalam village. The most distant plots were less than 12 km apart. Javanese agroforest (Tumpangsari) is a kind of home garden where the farmers usually cultivate maize or cassava or other low vegetation under growing trees such as teak or Cajeput tree (Scales and Marsden, 2008).

2.2. Sampling and determination

Sampling was conducted in May and November 2014. We selected 40 plots of 10 m × 10 m, 10 plots each from primary forest, teak plantation bordered by primary forest, teak plantation bordered by agroforest and agroforest. The plots were placed randomly within the different land use areas. A combination of visual searching and sorting a standardized volume of litter and soil is the most efficient method for land snail inventories if repeated visits are not possible (Emberton et al., 1996; Cameron and Pokryszko, 2005; Schilthuizen, 2011). Thus, all living slugs and snails as well as their empty shells were collected by two researchers for one hour at each plot. In addition, 5L of leaf litter and surface soil were sampled at each plot. Later, the litter samples were dried, fractioned by sieving and sorted. Several environmental variables were recorded at each plot, i.e. habitat type, altitude, percentage of canopy cover, density of herbaceous layer, presence of deadwood, stones and bare rock, amount of leaf litter, and degree of human impact (cultivation or removal of plants, presence of livestock, human trails, information from locals) (Supplementary Table S1).

All specimens were identified to species level using van Benthem Jutting (1948, 1950, 1952) and Vermeulen and Whitten (1998). The specimens are kept in the Museum Zoologicum Bogoriense (Indonesia) and the Zoological Museum of the University of Hamburg (Germany).

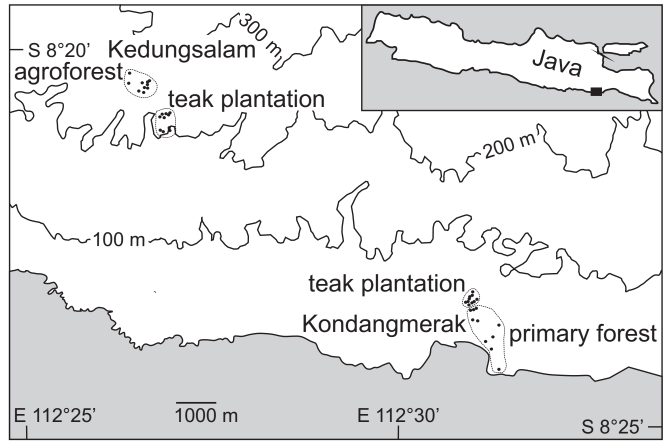

Fig. 1. Map of the study area in Malang showing the position of the 40 surveyed plots. Insert indicating the location of the study area in Java.

2.3. Comparisons of species richness and other indices between land use types

Species richness of different land use types was compared using abundance-based rarefaction (Colwell et al., 2012) as implemented in iNext online (Hsieh et al., 2013). Confidence intervals (95%) were calculated using 100 bootstrap replications. We explored the sample size dependence of the percentage of prosobranch individuals and the percentage of individuals of introduced species in different land use types using the dominance index in the species richness module of EcoSim (Gotelli and Entsminger, 2004).

2.4. Putative determinants of abundance and assemblage composition

We investigated putative determinants of abundance using multiple linear regression analyses with the statistical software R (R Core Team, 2012). We log-transformed abundances and tested the following environmental variables: density of the canopy cover (as a proxy for insolation and, as a consequence, temperature and desiccation on the forest floor) and of the herbaceous layer, presence of deadwood, stones and bare rock, amount of leaf litter and human impact (Supplementary Table S1).

Furthermore, we assessed the importance of the recorded environmental variables for determining the distribution of species and the composition of assemblages by fitting them onto an ordination plot. The ecological similarities between species and the assemblage composition were explored by a non-metric multidimensional scaling of the abundance data using quantitative Kulczyński distances (Faith et al., 1987). We used the 'vegan' package (Oksanen et al., 2013) for the statistical software R (R Core Team, 2012). Species scores were computed as implemented in the 'vegan'-function 'metaMDS' and the goodness of fit of the environmental variables was computed using the 'envfit' function in 'vegan'. Significance of the fit was tested based on 999 permutations. Finally, we assessed also the similarity of the plots based on the recorded environmental variables using categorical principal components analysis with the program SPSS Statistics version 23 (IBM).

3. Results

3.1. Land snail species richness in different land use types

In total, 2919 specimens belonging to 55 land snail species (1 neritimorph, 10 caenogastropod and 44 pulmonate species) were

Table 1
Numbers of specimens recorded in primary forest (PF), teak plantation bordered by primary forest (TP), teak plantation bordered by agroforest (TA) and agroforest (AF).

Species	Classification	native/introduced	PF	TP	TA	AF
Georissa williamsi Godwin-Austen, 1889	Neritimorpha	native	50	1	1	0
Alycaeus crenilabris Möllendorf, 1897	Caenogastropoda	native	20	6	34	0
Cyclophorus perdix (Broderip & Sowerby, 1830)	Caenogastropoda	native	9	16	0	9
Japonia ciliferum (Mousson, 1849)	Caenogastropoda	native	8	1	4	0
Japonia ciliocinctum (Martens, 1865)	Caenogastropoda	native	3	0	1	0
Japonia obliquistriatum Bullen, 1904	Caenogastropoda	native	2	0	0	0
Leptopoma perlucidum (Grateloup, 1840)	Caenogastropoda	native	6	1	1	12
Cyclotus corniculum (Mousson, 1849)	Caenogastropoda	native	11	5	0	0
Diplommatina hortulana Leschke, 1914	Caenogastropoda	native	0	0	24	0
Diplommatina nevilli (Crosse, 1879)	Caenogastropoda	native	166	31	0	1
Omphalotropis columellaris Quadras and Möllendorff, 1893	Caenogastropoda	native	229	0	1	6
Laemodonta sp.	Pulmonata	native	5	0	0	0
Succinea listeri Smith, 1888	Pulmonata	native	0	0	0	2
Succinea minuta Martens, 1867	Pulmonata	native	0	0	0	10
Elasmias sundanum (Möllendorff, 1897)	Pulmonata	native	2	0	0	0
Pupisoma dioscoricola (C. B. Adams, 1845)	Pulmonata	native	10	3	8	0
Gastrocopta pediculus (Shuttleworth, 1852)	Pulmonata	native	0	0	42	0
Gastrocopta recondita (Tapparone-Canefri, 1883)	Pulmonata	native	0	0	11	1
Gyliotrachea fruhstorferi (Möllendorff, 1897)	Pulmonata	native	11	0	1	0
Nesopupa malayana (Issel, 1874)	Pulmonata	native	12	5	17	1
Nesopupa nannodes (Quadras and Möllendorff, 1898)	Pulmonata	native	0	0	3	1
Apoecus glandula (Mousson, 1848)	Pulmonata	native	1	0	13	0
Paropeas achatinaceum (Pfeiffer, 1846)	Pulmonata	native	0	0	18	71
Discocharopa aperta (Möllendorff, 1888)	Pulmonata	native	30	0	15	25
Philalanka nannophya Rensch, 1932	Pulmonata	native	3	53	47	66
Philalanka kusana (Aldrich, 1889)	Pulmonata	native	18	0	0	0
Elaphroconcha javacensis (Férussac, 1821)	Pulmonata	native	12	20	52	29
Coneuplecta microconus (Mousson, 1865)	Pulmonata	native	45	2	54	15
Coneuplecta olivacea Vermeullen, 1996	Pulmonata	native	14	0	0	0
Liardetia angigyra (Möllendorff, 1897)	Pulmonata	native	0	1	0	2
Liardetia convexoconica (Möllendorff, 1897)	Pulmonata	native	0	0	14	17
Liardetia dolium (Pfeiffer, 1846)	Pulmonata	native	0	20	0	16
Liardetia scandens (Cox, 1872)	Pulmonata	native	27	7	17	25
Microcystina chionodiscus Vermeulen, 1996	Pulmonata	native	10	1	5	3
Microcystina gratilla van Benthem Jutting, 1950	Pulmonata	native	190	15	45	9
Microcystina sinica Möllendorf, 1885	Pulmonata	native	38	0	55	45
Microcystina subglobosa (Möllendorff, 1897)	Pulmonata	native	6	0	10	77
Queridomus fimbriosus (Quadras and Möllendorff, 1894)	Pulmonata	native	3	0	0	0
Trochomorpha bicolor Martens, 1864	Pulmonata	native	0	0	1	0
Trochomorpha strubelli Boettger, 1890	Pulmonata	native	0	0	0	2
Helicarion albellus Martens, 1867	Pulmonata	native	4	0	0	0
Sundavitrina fruhstorferi (Möllendorf, 1897)	Pulmonata	native	1	0	0	0
Macrochlamys spiralifer Vermeulen, 1996	Pulmonata	native	6	0	0	0
Amphidromus furcillatus (Mousson, 1849)	Pulmonata	native	3	1	1	8
Landouria ciliocincta (Möllendorff, 1897)	Pulmonata	native	2	0	0	0
Landouria rotatoria (von dem Busch, 1842)	Pulmonata	native	3	0	11	30
Landouria winteriana (Pfeiffer, 1841)	Pulmonata	native	9	28	14	61
Gastrocopta servilis (Gould, 1843)	Pulmonata	introduced	0	0	1	32
Rhachistia zonulata (Pfeiffer, 1846)	Pulmonata	introduced	0	0	3	0
Achatina fulica Bowdich, 1822	Pulmonata	introduced	3	66	21	37
Allopeas gracile (Hutton, 1834)	Pulmonata	introduced	18	173	93	118
Subulina octona (Bruguière, 1792)	Pulmonata	introduced	0	0	0	2
Geostilbia aperta (Swainson, 1840)	Pulmonata	introduced	2	0	1	35
Gulella bicolor (Hutton, 1834)	Pulmonata	introduced	1	13	18	23
Bradybaena similaris (Férussac, 1821)	Pulmonata	introduced	0	0	0	9

collected in the 40 studied plots (Table 1, Supplementary Table S2). In the following, we will subsume Neritimorpha and Caenogastropoda in a functional category 'prosobranch gastropods', because in both the mantle cavity is widely open, whereas it can be closed in the pulmonate species. The number of specimens per plot varied between 14 and 337. Species richness per plot ranged from 3 to 20. The most species-rich families were Euconulidae (11 species), Cyclophoridae (7 species) and Camaenidae (5 species). The most abundant families were Euconulidae (27% of all specimens) and Achatinidae (21%; including Subulinidae).

Eight of the recorded pulmonate species were introduced in Java, i.e. *Gastrocopta servilis* (Gastrocoptidae) from the Caribbean (Solem, 1989), *Rhachistia zonulata* (Cerastidae) probably from Africa (Verdcourt, 2006), *Achatina fulica* (Achatinidae) from Africa (van Benthem Jutting, 1952), *Allopeas gracile* (Achatinidae) probably from South America (Robinson, 1999), *Subulina octona* (Achatinidae) probably from South America (Robinson, 1999), *Geostilbia aperta* (Ferussaciidae) from the Caribbean (Miquel and Herrera, 2014), *Gulella bicolor* (Streptaxidae) probably from India (Naggs, 1989) and *Bradybaena similaris* (Camaenidae) from Southeast Asia (Robinson, 1999). All recorded prosobranch species were native. Four species endemic to Java were recorded in the area, i.e. *Japonia obliquistriatum* (Cyclophoridae), *Diplommatina hortulana* (Diplommatinidae), *Gyliotrachela fruhstorferi* (Gastrocoptidae), *Apoecus glandula* (Enidae) and *Microcystina subglobosa* (Euconulidae).

Land snail species richness was highest in the primary forest (39 species) followed by teak plantation bordered by agroforest (35), agroforest (33), and teak plantation bordered by primary forest (22). In contrast, the highest number of introduced species was found in agroforest (7) followed by teak plantation bordered by agroforest (6), primary forest (4), and teak plantation bordered by

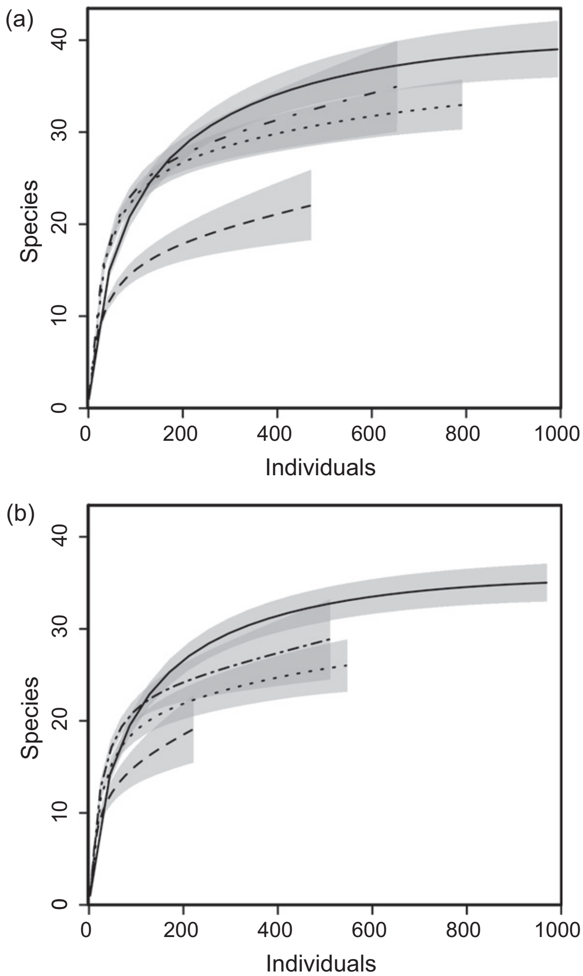

Fig. 2. Species accumulation curves for primary forest (unbroken line), teak plantation bordered by primary forest (dashed line), teak plantation bordered by agroforest (dotted-dash line) and agroforest (dotted line). (a) All species. (b) Native species. Shaded areas represent the 95% confidence intervals.

primary forest (3). The difference in species richness between primary forest and the other habitats becomes clearer if only native species were considered (Fig. 2).

3.2. Composition of land snail assemblages in different land use types and environmental variables influencing the abundance of native and introduced species

A non-metric multidimensional scaling revealed that the composition of the land snail assemblages differed most strongly between primary forest and agroforest, whereas the composition in the teak plantations was intermediate between these extremes (Fig. 3a). The comparison of the ordinations of assemblages and of the distribution of species (Fig. 3) indicates an association of introduced species with agroforest and of native prosobranch species with primary forest.

A classification of the species into native prosobranchs, native pulmonates and introduced pulmonates (Fig. 4a) shows that the number of the prosobranch species decreases from primary forest to teak plantations and agroforest, whereas the number of introduced pulmonates species increases along this gradient. The magnitude of the change in assemblage composition becomes clearer if abundances are considered (Fig. 4b). Introduced species made up only 2.4% of the specimens in primary forest, whereas 32% of the specimens in agroforest and even more than half of the individuals in the teak plantation bordered by primary forest belonged to introduced species. The strong contrast between abundance in modified habitats and abundance in primary forest is not only obvious for the whole group of introduced species, but also for each individual introduced species. Four of the eight introduced species have not been found in primary forest at all and at most 5.3% of the sampled specimens of one of the other four species occurred in primary forest. On the contrary, more than half of the individuals in the primary forest were prosobranchs (this number is unusually high because of a mass occurrence of *Omphalotropis columellaris*, but without that species still 36% of the individuals in the primary forest were prosobranchs), whereas they made up only 3.5% of the individuals in agroforest. Box plots of the abundances of introduced species and prosobranchs show that the differences between primary forest and modified habitats are consistent at the plot level (Fig. 5). Rarefaction demonstrates that the differences in

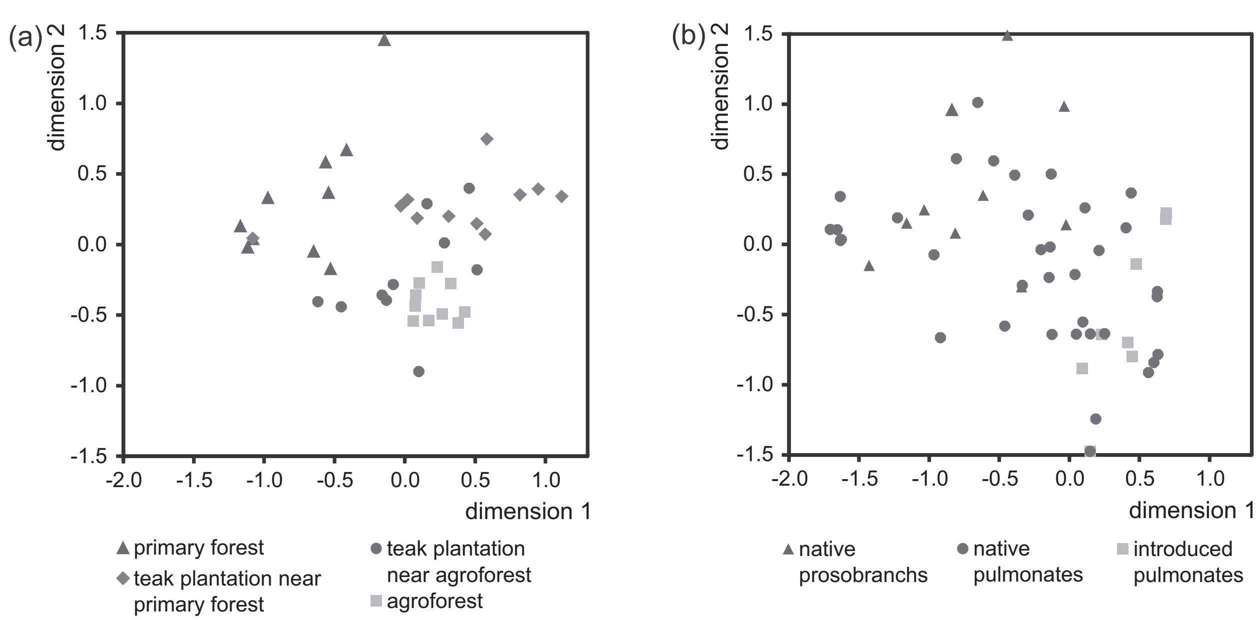

Fig. 3. Non-metric multidimensional scaling of plots (a) and species (b) based on abundance data of land snail species in the same coordinate system.

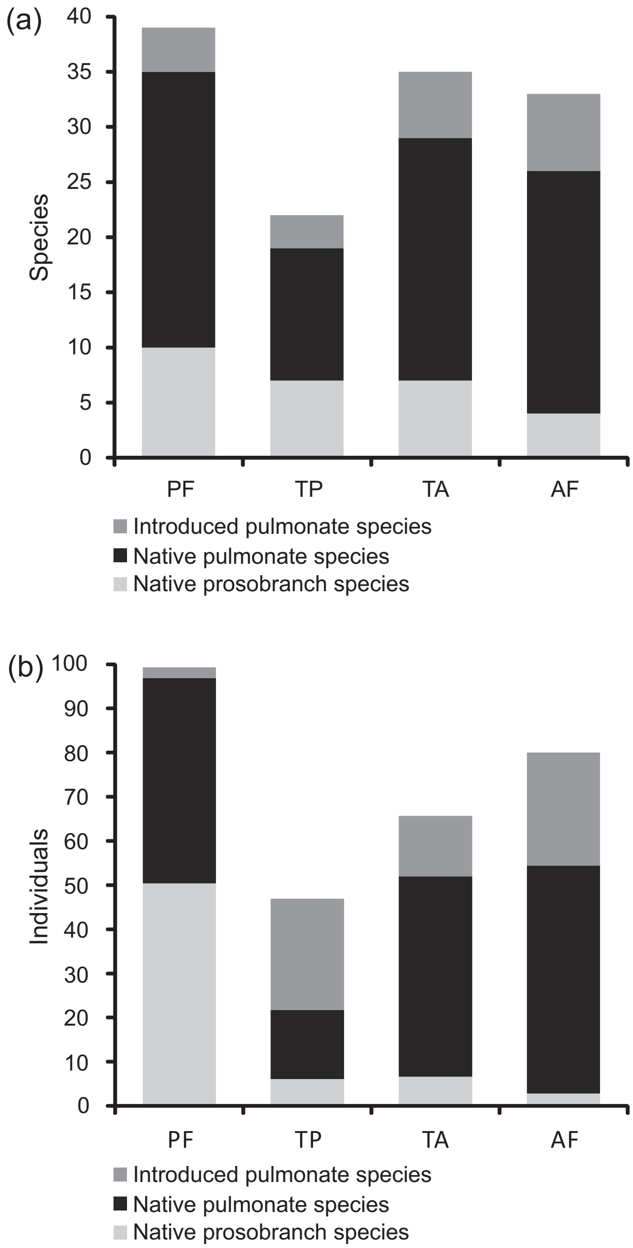

Fig. 4. Comparison of mean number and abundance of native and introduced land snail species per plot in primary forest (PF), teak plantation bordered by primary forest (TP), teak plantation bordered by agroforest (TA) and agroforest (AF). (a) Mean species richness. (b) Mean abundance.

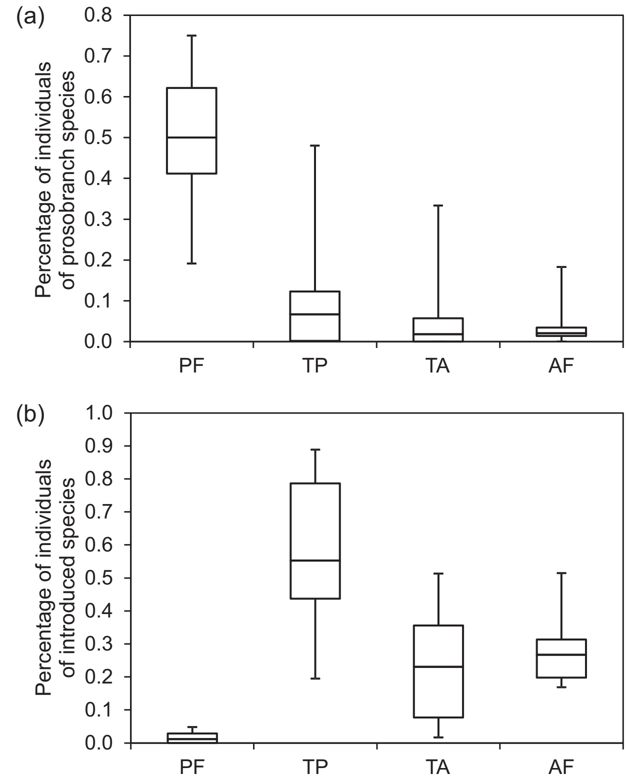

Fig. 5. Box plots of the percentages of individuals of (a) native prosobranch species and (b) introduced pulmonate species in plots in primary forest (PF), teak plantation bordered by primary forest (TP), teak plantation bordered by agroforest (TA) and agroforest (AF).

the percentage of prosobranch individuals and in the percentage of individuals of introduced species between primary forest and modified forests are obvious even with small sample sizes (Fig. 6) if samples are taken from a representative selection of spots.

To investigate the influence of a habitat on the neighbouring habitat we plotted the abundances of native prosobranchs and introduced pulmonates in plots in primary forest and in the neighbouring teak plantation against the distance from the border between the two land use types. The abundance of prosobranchs is usually high in the primary forest and does not decrease towards the teak plantation, whereas it is usually low in the teak plantation and does not increase in direction to the primary forest (Fig. 7a). Reversely, the abundance of introduced pulmonates is usually high in the teak plantation and does not decrease towards the primary forest, whereas it is usually low in the primary forest and does not increase in direction to the teak plantation (Fig. 7b).

Total abundance of all snail species together was not found to correlate with any of the recorded environmental variables (Table 2). However, if the fauna is divided into introduced pulmonate, native pulmonate and prosobranch species, correlations became apparent. The abundance of introduced pulmonate species decreased with increasing density of the canopy cover and increased with increasing human impact (Table 2). The abundance of native pulmonate species increased with increasing density of the canopy cover and increasing human impact (Table 2). By contrast to pulmonates, the abundance of prosobranch land snails significantly decreased with increasing human impact. Moreover, we found non-significant trends of prosobranch abundance to increase with the presence of deadwood and with increasing canopy cover (Table 2).

The occurrences of land snail species and the assemblage composition at the sampled plots (across all studied habitats) were related to canopy cover ($R^2 = 0.577$, $P = 0.001$), presence of bare rock ($R^2 = 0.231$, $P = 0.005$), presence of deadwood ($R^2 = 0.188$, $P = 0.003$), presence of stones ($R^2 = 0.184$, $P = 0.003$) and human impact ($R^2 = 0.177$, $P = 0.023$).

We visualized the differences of the investigated land use types with regard to the recorded environmental variables (Supplementary Table S1) in bar plots (Supplementary Fig. S1). Primary forest differs from the modified forests by a denser canopy cover, a denser herbaceous layer, more deadwood and leaf litter, but few stones and no human impact. A categorical principal components analysis of the plots based on the recorded environmental variables showed that most plots in primary forest and teak plantation bordered by primary forest form groups distinct from the plots in other habitats, whereas the plots in teak plantation bordered by agro-

Table 2
Results of multiple linear regression analyses between log-transformed abundances of the specified species groups and environmental variables ($N = 40$). β = estimated regression parameter.

	All species		Introduced pulmonate species		Native pulmonate species		Native prosobranch species	
	β	p	β	p	β	p	β	p
Canopy cover	0.004	0.146	−0.010	0.001	0.007	0.019	0.008	0.076
Herbaceous layer	0.108	0.255	0.028	0.793	0.082	0.471	0.205	0.236
Presence of deadwood	0.050	0.541	−0.154	0.101	−0.029	0.762	0.297	0.051
Presence of stones	0.094	0.443	0.000	0.998	0.149	0.311	−0.033	0.882
Presence of bare rocks	0.072	0.495	0.016	0.892	0.177	0.165	0.187	0.329
Leaf litter	−0.055	0.385	−0.038	0.595	−0.014	0.853	−0.077	0.508
Human impact	0.048	0.295	0.150	0.006	0.136	0.017	−0.177	0.037

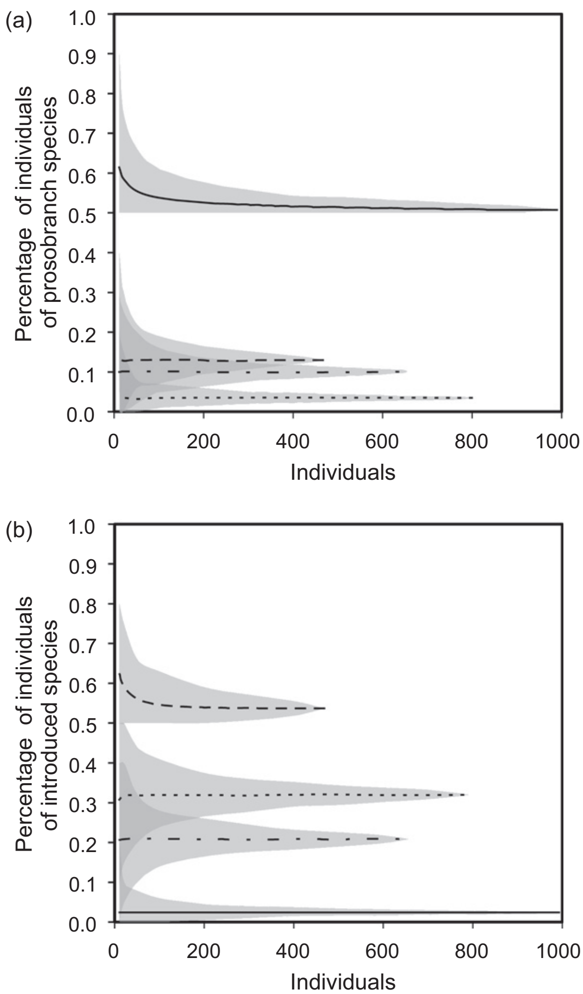

Fig. 6. Sample size dependence of (a) the percentage of prosobranch individuals and (b) the percentage of individuals of introduced species in primary forest (unbroken line), teak plantation bordered by primary forest (dashed line), teak plantation bordered by agroforest (dotted-dash line) and agroforest (dotted line). Shaded areas represent the 95% confidence intervals.

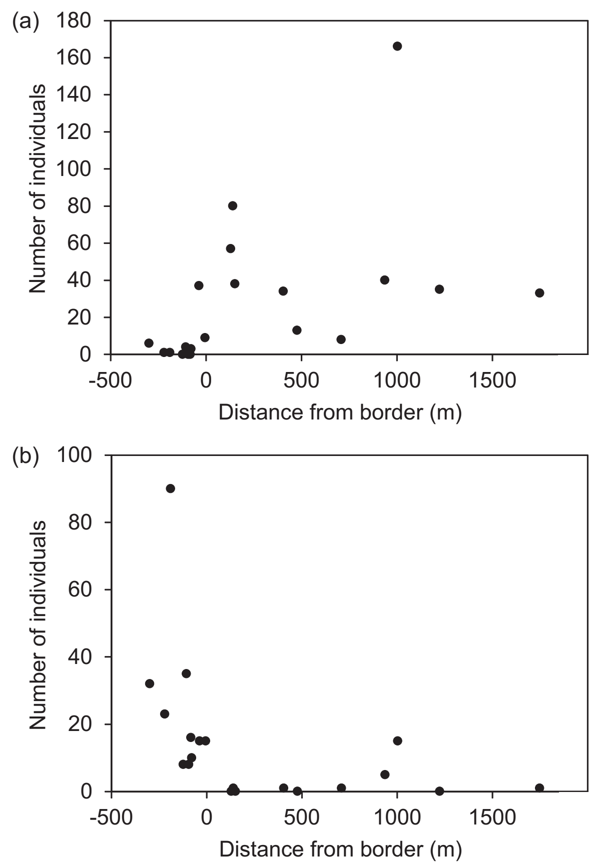

Fig. 7. Abundances of (a) native prosobranchs and (b) introduced pulmonates in plots in primary forest and the neighbouring teak plantation against the distance from the border between the two land use types (distances in primary forest positive, in teak plantation negative).

forest and agroforest cannot be separated based on the recorded environmental variables (Fig. 8).

4. Discussion

4.1. Composition of land snail assemblages in different land use types and environmental variables influencing the abundance of native and introduced species

Our study showed that land snail species richness was highest in the primary forest followed by teak plantation bordered by agroforest, agroforest, and teak plantation bordered by primary forest (Fig. 2a). Primary forest had also the richest native fauna (Fig. 2b). The loss of native species in the other habitats is partly compensated by the addition of introduced species. The importance of introduced species in the snail communities becomes more obvious if abundance is considered (Figs. 4 and 5b).

The number of native species recorded in plantations and agroforest in Java may result in an overestimation of the value of these modified habitats for conservation, because native species are much less abundant in modified habitats than in the primary forest (Table 1, Figs. 4 b, 7 a). Whereas only 2 of the 35 records of native species in the primary forest are based on a single specimen, 7 of the 19 records in teak plantation bordered by primary forest, 6 of the 29 records in teak plantation bordered by agroforest and 4 of the 26 records in agroforest are based on singletons. This indicates that populations of some of the species in the modified habitats may

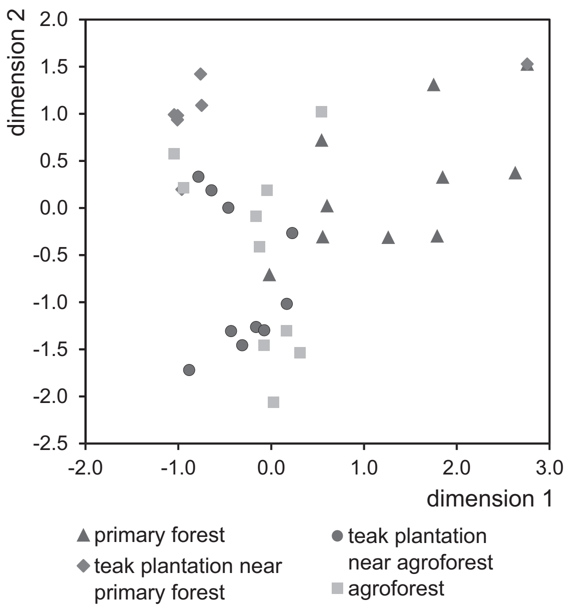

Fig. 8. Categorical principal components analysis of plots based on the recorded environmental variables.

be sink populations, i.e. populations that depend on immigration from source habitats, the primary forests, because the quality of the modified habitats is not sufficient to support self-maintaining populations of these species. Of course this is not true for all species and there are several native species that have been more abundant in one of the modified habitats than in primary forests as has also been reported for land snails in plantations in Kenya (Tattersfield et al., 2001), home gardens in Sri Lanka (Raheem et al., 2008) and plantations in Tasmania (Bonham et al., 2002).

For strategies to impede the establishment and the expansion of introduced species and conserve the native fauna it is important to identify individual environmental factors that determine the abundance of native and introduced species. Native and introduced groups of land snails have different, partly contrasting habitat requirements. In the study area, the abundance of introduced pulmonate species significantly decreased with increasing density of the canopy cover, albeit only slightly, and increases with increasing human impact (Table 2). In contrast, the abundance of the native groups increased with increasing canopy cover (albeit marginally insignificantly in prosobranchs; Table 2). Whereas the abundance of the native pulmonates was favoured by human impact just as the abundance of the introduced pulmonates, the abundance of prosobranchs declined with increasing human impact (Table 2).

The mantle cavity of prosobranch gastropods (Neritimorpha and Caenogastropoda) is widely open so that they lose more water when they are active than pulmonate gastropods, in which the mantle cavity is connected with the outside only by a narrow pneumostome that can be closed (Solem, 1974). Thus, prosobranch gastropods are more sensitive to desiccation than pulmonates. The closable pneumostome is an adaptation to drier environments that enabled diverse pulmonate gastropod species the colonization of human-made open habitats. A lower density of the canopy cover results in increasing insolation and, thus, in increasing temperature and decreasing humidity at the forest floor. Therefore, some forest snails actively avoid canopy gaps (Bloch and Stock, 2014). Our results show that the greater desiccation stress in forests with a lower density of canopy cover can result in the decrease of the abundance and finally the local extinction of species requiring the constantly high humidity of primary forests like several prosobranch gastropods as also reported by Schilthuizen et al. (2005) for limestone outcrops in Borneo. In contrast, a lower density of canopy cover favours introduced species with a higher desiccation tolerance. Furthermore, the abundance of prosobranch species was marginally positively affected by the amount of deadwood. Deadwood is an important habitat feature for many forest snails and other organisms that provides moist shelter, especially during dry periods, and bacteria as nutrition (Fog, 1979). In contrast, there was an insignificant trend of the abundance of introduced species to decrease with increasing amount of deadwood, which should be more thoroughly examined.

Because of their different habitat requirements, the different gastropod groups attain their highest abundances in different land use types as has been found for groups of other organisms (Lawton et al., 1998; Schulze et al., 2004; Barlow et al., 2007). Thus, the snail assemblages in the different land use habitat types differ much clearer in composition (Figs. 3 and 4) than in total species richness or abundance confirming earlier findings that community composition has to be considered in quantifying the biodiversity conservation value of anthropogenic habitats (Tattersfield et al., 2001; Schilthuizen et al., 2005; Barlow et al., 2007; Raheem et al., 2008; Scales and Marsden, 2008). Such differences cannot be recognized in studies that use unidentified “morphospecies” or higher taxa as indicators for biodiversity (Rahman et al., 2012).

4.2. Land snails as indicators for habitat quality

Land snails are good indicators for the long-term stability of natural habitats, because several species are restricted to undisturbed natural habitats and because of their low dispersal abilities (Douglas et al., 2013; Torre et al., 2014). If a habitat specific species became extinct in a disturbed habitat, it usually takes a long time after restoration of habitat quality until this species can colonize this habitat again because of the limited dispersal ability. However, assessing the number of (native) snail species of a habitats or monitoring of rare habitat specific snail species may be costly because large amounts of litter have to be screened to prove the presence or absence of rare species (Fig. 2; Cameron and Pokryszko, 2005).

Our findings concerning the composition of land snail communities in natural and disturbed habitats indicate that it is not obligatory to prove the presence or absence of rare species to characterize the quality of the habitats. The striking differences between the composition of snail communities in natural and disturbed forests in Java (Fig. 4) permit the use of two metrics as indicators of habitat quality that can be scored with much less effort. The first is the percentage of prosobranch individuals in a sample, which is much higher in primary forest than in disturbed forests (see also Schilthuizen et al., 2005). Prosobranchs can be easily distinguished from pulmonates by the presence of an operculum or the rounded aperture even by non-specialists. This index is especially useful in Southeast Asian forests with their rich prosobranch fauna. In other continents prosobranchs are much rarer so that this index is probably not so useful there. Actually, the high percentage of prosobranch species in Southeast Asian forests can be considered as an indicator of the long-term stability of forests in this region compared to forests in other continents.

The second metric is the percentage of individuals of introduced species. Tillier (1992) already suggested that introduced species can be considered as an index of the secondary nature of the habitat. Although this approach requires the recognition of the introduced species, this is much easier to achieve than the identification of all specimens, because there are few introduced species compared to many native species (8 versus 47 species in our study area). This indicator is applicable worldwide.

Both metrics are significantly correlated with the recorded number of native species in the studied plots. In this respect the percentage of individuals of introduced species is the better index

(Pearson correlation coefficient $R = -0.689$, two-sided $P \leq 0.001$) than percentage of prosobranch individuals (Pearson correlation coefficient $R = 0.391$, two-sided $P \leq 0.013$). There are consistent differences between plots in primary forest and in modified habitats with regard to these metrics (Fig. 5). Both metrics have the advantage that they do not require complete surveys with regard to rare species, but can be calculated based on a much smaller sample size. Rarefaction indicates that about 50 individuals taken from a representative sample are sufficient to distinguish between undisturbed and disturbed forests (Fig. 6).

An even more easily recordable indicator of disturbance in the abundance of the largest introduced snail, *Achatina fulica*, which occurred in all land use types. It is rare in primary forest (3 individuals in 10 plots), but abundant in the disturbed forests (66, 21 and 37 individuals in 10 plots each of teak plantation bordered by primary forest, teak plantation bordered by agroforest and agroforest).

4.3. Impact and control of the introduced land snail species

A direct interaction between introduced and native species has been assumed by some authors (Bonham et al., 2002; Lydeard et al., 2004). However, our study shows that introduced snail species rarely invade primary forest in Java, just as in other areas (Smith, 1981; Barker, 1982; Tillier, 1992; Cowie, 1998; Hausdorf, 2002). They generally remain restricted to modified habitats. While it is clear that habitat modification drives the increase of the number and abundance of introduced snail species, it has to be shown whether there is direct competition between the native species that persists in such habitats and the introduced species (Didham et al., 2007). Tillier (1992) suggested that non-carnivorous introduced species are probably not themselves a danger to the native fauna.

This is different at least for some carnivorous introduced land snail species which severely threaten native species. The best example is *Euglandina rosea*, which has originally deliberately introduced on Pacific islands to control the likewise introduced *Achatina fulica*, but then caused the extinction of numerous endemic species (Murray et al., 1988; Cowie, 1992; Hadfield et al., 1993; Civeyrel and Simberloff, 1996). The only carnivorous land snail species introduced into Java is *Gulella bicolor*. This species is much smaller than *Euglandina rosea* (5.8–7.4 mm versus usually 40–50 mm, but up to 74 mm shell height). Although it has been introduced in tropical regions worldwide, there are no reports on extinctions directly caused by this species. In the study area, *Gulella bicolor* is rare in all habitats and only a single individual has been found in the primary forest (among 993 recorded specimens). This is in accordance with other reports that the species does not penetrate into native vegetation (Solem, 1989). Thus, its potential impact on the native fauna is limited.

Our analysis of the habitat preferences of the introduced versus the native species implies that improving the canopy cover and perhaps retaining (or even adding) deadwood (see also Douglas et al., 2013) in plantations and agroforests might help to control the populations of introduced species or even prevent their establishment in these habitats, while it favours the native species by providing a higher humidity, shelter and nutrition.

The significant positive effect of a less dense canopy cover on the abundance of introduced snail species and its opposing effect on native species (pulmonates as well as prosobranchs) indicate that stronger insolation causing a temperature rise and desiccation of the forest floor results in an increased chance of the establishment of introduced species and a loss of native species. The effect of canopy cover becomes especially apparent in the two studied teak plantations. The much lower canopy coverage in the teak plantation near the primary forest (5–15%; Supplementary Table S1; Supplementary Fig. S1) correlates with a much higher percentage of introduced snail individuals (mean 57%), whereas the high canopy coverage in the teak plantation near the agroforest (30–90%) correlates with the low percentage of introduced snail individuals (mean 23%). This also demonstrates that the management of the forest has a high influence on the fauna even if we consider only a specific type of forest.

Desiccation because of stronger insolation also affects the margin of primary forests. Dense plantations and agroforests bordering primary forests may protect the latter from introduced species and help to conserve the native fauna by reducing desiccation and buffering the human impact on the primary forests. East Java is one of the few Indonesian provinces with a moderate reforestation of 0.07% in 2006–2009 and 0.06% in 2009–2011 (Indonesian Ministry of Environment, 2013). Based on our results, we recommend concentrating new plantations around the remaining primary forests to protect them from desiccation and human impact and, thereby, hopefully from the impact of introduced species.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.ecolind.2016.05.013.

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