Morphological traits reflect dung beetle response to land use changes in tropical karst ecosystems of Vietnam

Van Bac Bui[a,b], Thomas Ziegler[c], Michael Bonkowski[a,*]

[a] *Department of Biology, Institute of Zoology, Terrestrial Ecology, University of Cologne, Zülpicher Strasse 47b, D-50674 Cologne, Germany*
[b] *Department of Plant Protection, Faculty of Forest Resources and Environmental Management, Vietnam National University of Forestry, Xuan Mai, Chuong My, Hanoi, Viet Nam*
[c] *AG Zoologischer Garten Köln, Riehler Strasse 173, D-50735 Cologne, Germany*

ARTICLE INFO

ABSTRACT

Dung beetles (Coleoptera, Scarabaeidae) are known to respond sensitive to habitat changes, but difficulties in the delineation of species together with their high local diversity have hindered the generalization of results. Morphological traits instead may better reflect species' adaptations to habitat changes. We investigated changes in morphological traits of 41 tunnelling dung beetle species in a sequence of land use change from primary forests, to secondary forests and meadows in a tropical karst mountain ecosystem in Vietnam (South East Asia). Tunnellers were by far the dominant functional group of dung beetles in these ecosystems. In addition, we measured dung removal rate as a key ecosystem service of these beetles. By combining RLQ and fourth-corner methods to characterize shifts in morphological species traits, we identified three distinct morphological trait clusters of dung beetles, reflecting distinct community adaptations to land use changes. Meadows, despite harbouring highest dung beetle abundance and species richness were severely impoverished in large-bodied dung beetles. The large-bodied dung beetles however, turned out to play crucial roles for dung removal. These data indicate that land use change led to significant changes of species traits in dung beetle communities which in turn fed back on critical ecosystem services. Our data demonstrate that trait-based approaches are well suited to describe the functional implications of environmental changes on species-rich arthropod communities and may better allow generalizations of adaptive responses between ecosystems.

1. Introduction

Dung beetles (DB) (Coleoptera, Scarabaeidae) are highly sensitive to changes in the physical structure of terrestrial habitats, and have been widely used as indicators in the assessment of habitat disturbances (Audino et al., 2014; Beiroz et al., 2017; Davis et al., 2001; Nichols et al., 2007). Because DB typically utilize vertebrate droppings and carcasses as essential food and nesting resources, they may further reflect changes in the composition and structure of vertebrate communities (Andresen and Laurance, 2007; Enari et al., 2013; Estrada et al., 1999; Harvey et al., 2006; Vulinec, 2000). Land use change (LUC) may thus directly feed back on vital ecosystem functions that DB provide through their feeding and nesting processes, such as dung removal, nutrient cycling, secondary seed dispersal and biological control of vertebrate parasites (Doube, 2018; Hanski and Krikken, 1991; Nichols et al., 2008; Vulinec, 2002).

Research on the influence of LUC on DB communities has been conducted worldwide, from Europe (Frank et al., 2017; Hutton and Giller, 2003) to South America (Audino et al., 2014; Beiroz et al., 2017) and Southeast Asia (Boonrotpong et al., 2004; Davis et al., 2001; Hayes et al., 2009; Shahabuddin et al., 2005). These studies were traditionally based on taxonomic information of the community composition. However, the intricate taxonomy and high diversity of DB pose problems because many taxa have similar external morphological characters, separated only by minute morphological differences, such as in *Onthophagus* species. In addition, morphological boundaries are sometimes poorly defined in DB taxonomy (Hanski and Krikken, 1991; Philips, 2016). Therefore, it is not clear if inconsistent responses of DB communities to LUC, can be partly attributed to taxonomic resolution, to different phylogenetic trajectories in DB evolution between continents, or to differences in functional responses. For example, Quintero and Roslin (2005) and Vulinec (2002) were unable to detect differences in species richness between primary forests (1stForests) and secondary forests (2ndForests) DB communities in South America, whereas,

Gardner et al. (2007) reported severely impoverished DB communities in 2ndForests compared to 1stForests. Similarly, changes within individual functional groups, such as dung rollers, were inconsistent across biogeographical regions in responses to LUC (Favila and Halffter, 1997; Hayes et al., 2009; Vulinec, 2002).

Trait analyses provide a reliable means to investigate functional changes, as traits directly reflect adaptations to the environment and have consequences for performance and fitness, such as foraging and nesting success, fecundity and survival (McGill et al., 2006). These fitness traits in turn can influence demographic characteristics of populations, such as the timing of dung-beetle immigration to or and emigration from dung (Gittings and Giller, 1998; Finn and Giller, 2000; Arnold, 1983; Violle et al., 2007). Thus, traits hold information about community structure and functioning, and the niche space occupied by species traits may better predict community responses to anthropogenic disturbances than species diversity (Gagic et al., 2015). Recently, Raine et al. (2018) confirmed intraspecific variation in morphological traits between 12 dung-beetle species across tropical land use types in Sabah (Malaysian Borneo), and suggested the use of morphological traits as predictors of behaviour functional traits. Dung beetles exhibit a large variety of morphological traits strictly associated with their ecosystem functions and adaptations to environmental conditions. For example, the rollers possess elongated hind legs for moving dung balls away from manure patches, and they are restricted to litter free areas because obstacles on the soil surface hinder the rolling process (Nichols et al., 2013; Scholtz et al., 2009). The tunnellers bear relatively short and thick forelegs for digging; hence their distribution is stronger dependent on soil texture (Hanski and Cambefort, 2014). Body size of DB has been related to habitat disturbance, indicating that large-bodied DB are more vulnerable to habitat change (Larsen et al., 2005; Senior et al., 2013). Especially large-bodied DB have been shown to play important roles for dung removal in various ecosystems (Nervo et al., 2014; Tixier et al., 2015; Frank et al., 2017). Therefore, approaches focusing DB traits, such as shifts in body size, body mass and wing loading, have gained increasing attention (Frank et al., 2017; Gardner et al., 2007; Larsen et al., 2008; Nichols et al., 2013; Tixier et al., 2015, Raine et al.,2018). Such studies hold promise to show more consistent shifts in trait patterns of DB communities in responses to disturbance than taxonomic identity. As different functional groups typically show contrasting responses to habitat change, it is important to separately analyze the responses of individual functional groups (Hayes et al., 2009). Yet, there is still a lack of understanding of whether and how specific morphological traits of specific functional groups of DB differ across gradients of LUC.

Dung beetles have been commonly classified into three functional groups according their feeding and nesting behaviour, as tunnellers, rollers and dwellers. The tunneller group in SE Asia is species-rich and abundant, and predominantly responsible for dung removal in these tropical ecosystems, representing around 90% of the captured DB species in this region (Boonrotpong et al., 2004; Davis et al., 2001; Hayes et al., 2009). Focusing on the dominant tunnellers, our aim was to evaluate the influence of LUC on the diversity and functional traits of DB in SE Asian tropical ecosystems on limestone. We hypothesised that morphological traits of DB, associated with the dispersal capacity and foraging behaviour would reflect community level shifts to LUC. By applying RLQ and fourth-corner methods on DB traits, we expected to identify clusters of DB with specific morphological adaptations. A further aim was to better assess the value of 2ndForests for DB conservation in the study region.

2. Materials and methods

2.1. Study sites

The study was conducted in the Pu Luong Nature Reserve (NR) (20º21′–20º34′N, 105º02′–105º20′E), Thanhhoa Province, North Central Vietnam, in Cao Son District, on the Pha He–Pha Chien mountain ridge. The NR is a forest ecosystem on limestone of the Cuc Phuong–Pu Luong range (Averyanov et al., 2003) and is influenced by a tropical monsoon climate with an average annual precipitation of 1500–1700 mm, with a dry and cool season from November to March and a mean annual temperature of 20–22 °C (Nguyen et al., 2000; Sterling et al., 2006). Like most NRs in Vietnam, much of the natural forest area within the reserve has experienced strong disturbances, primarily related to clear-cutting for shifting agriculture and/or selective logging. As a result, the NR contains a wide variety of land use types: areas of 1stForests, patches of 2ndForests, meadows, plantations or agricultural land. Although a ban on logging and shifting agriculture in natural forests has been imposed since 1991 in Vietnam (Forest Protection and Development Law No. 58-LCT/HDNN8), anthropogenic LUC, especially around settlements of ethnic minority communities is still ongoing, sometimes expansively and intensive in high mountain areas (Colfer et al., 2012; Tuyet, 2001).

Classes of LUC are including 1stForests, 2ndForests and meadows, and thus reflecting a gradient of land use intensification, were chosen as sampling sites. DB were collected along a transect spanning three land-use types at an elevational range between 780 and 900 m, with each land-use type covering a total area of 150–300 ha, and being separated by around 2 km from each other. Following the forest classification in Vietnam by Thai (1978), the 1stForests were evergreen closed forests on limestone, characterized by a complex vertical structure with five main storeys. The upper storey was dominated by trees of more than 35 m height, mostly belonging to Dipterocarpaceae and Combretaceae. The two dominant, lower storeys encompassed tree species with a height of 15–25 m, belonging to the families Lauraceae, Magnoliaceae, Meliaceae, Fagaceae, Sapindaceae, Mimosaceae, Ulmaceae and Annonaceae. The bush storey consisted of small trees and bushes below 8 m, containing species of the Rubiaceae, Acanthaceae and Apocynaceae. The ground vegetation comprised plant families of Urticaceae, Araceae and Begoniaceae. The 2ndForests were classified as swidden fallow 2ndForests, with trees re-growing on abandoned agricultural land, following forest clearing 40 years ago. The meadow sites had a fallow time of five years, and were vegetated by bushes, grasses and few small trees.

2.2. Dung beetle sampling, identification and categorization

Sampling was conducted within a 10-day period from 15th to 25th April 2016, using baited pitfall traps. We set up 15 baited pitfall traps in two parallel transects (100 m distant from each other) at each spatially independent land use type. Traps were placed at intervals of at least 150 m along a transect to minimize trap interference (da Silva and Hernández, 2015). In total, 45 traps were set up in the study. Each pitfall trap consisted of a plastic bucket (22 cm in diameter, 16 cm depth) buried to its rim in the soil, filled with 70% ethanol, and baited with 300 g of a fresh pig: buffalo dung (50: 50 ratio) mixture in order to collect a wide variety of DB species. All captured beetles were removed from the traps after 72 h of trap exposure and preserved in ethanol until examination in the laboratory.

DB species were identified according to the keys and species lists of Bui et al. (2018), Bui and Bonkowski (2018), Kabakov and Napolov (1999), and by comparison with reference collections at the French National Museum of Natural History (MNHN) (Paris, France), the National Museum Prague (NMPC) (Prague, Czech Republic), the Naturalis Biodiversity Center (RMNH) (Leiden, the Netherlands) and the private collection of Dr. Jan Krikken (Leiden, the Netherlands). Reference collections containing the species from this study are now kept in the Naturalis Biodiversity Center (RMNH) (Leiden, the Netherlands), the Zoological collection of the Institute of Zoology, the University of Cologne (UoC) (Cologne, Germany) and the Vietnam National University of Forestry (VNUF) (Hanoi, Vietnam).

The tunnellers were defined according to Hanski and Cambefort (2014), Scholtz et al. (2009) and Hayes et al. (2009). We used a

Keyence VHX-500F digital microscope for measurements of morphological traits. Only the body length of the largest species, *Synapsis tridens* Sharp 1881 was measured by a digital caliper. The following morphometric traits were measured: BoL – body length; HeadL – head length; HeadW – head width; ProL – pronotum length; ProW – pronotum width; ElyL – elytra length; ElyW – elytra width; WingL – hindwing length; WingW – hindwing width; Dist(Ely.W – Ely.apex) – distance from the elytral widest part to elytral posterior apex; ProTiL – protibia length; ProTiW – protibia width; MesoTiL – mesotibia length; MesoTiW – mesotibia width; MetaTiL – metatibia length; MetaTiW – metatibia width; MetaTaL – metatarsus length (for details see Bui et al., 2018 and Fig. S6). Dry biomass (BioM) of DB was determined after drying at 65 °C for 48 h. The BioM and morphological traits of each species were determined as mean values of 10–20 individuals of abundant species and by measuring all individuals of rare species. We used 11 response trait variables calculated from the measured morphological traits for statistical analyses, comprising body length (BoL), head length-width ratio (Head L/W), pronotal length-width ratio (Pro. L/W), elytral length-width ratio (Ely. L/W), hindwing length-width ratio (Wing. L/W), protibial length-width ratio (ProTi. L/W), mesotibial length-width ratio (MesoTi. L/W), metatibial length-width ratio (MetaTi. L/W), distance from the elytral widest part to elytral posterior apex in relation to elytra length (Dist(Ely.W – Ely.apex)/ElyL), metatarsal length-elytral length ratio (MetaTaL/ElyL) and biomass (BioM). See Table S2 and Figs. S3–S6 for trait data of beetles.

2.3. Environmental variables

Environmental data were measured and soil samples collected concurrently with dung beetle sampling. We used the quadrant-section method modified from Brower and Zar (1998) and Campos and Hernández (2013) to measure environmental variables at each research site. With the trap in the center, a cross was generated to divide each sampling site into four quadrants. In each quadrant, the nearest shrubs (DBH < 6 cm and height > 1 m) to the center point were marked, and their traits measured (crown diameter, height, distance to center point). Additionally, a small plot of 1x1 m in each quadrant was used to measure leaf litter thickness, percentage of leaf litter cover and area of ground vegetation using six ranks: 0–5%, 6–25%, 26–50%, 51–75%, 76–95% and 96–100%. Four soil samples were collected in each quadrant near the trap, mixed, and transferred to the lab to measure soil texture.

2.4. Dung removal rate

Dung removal plots were located at the trapping sites, and were set up with six plots for each land use type. In each plot, two plastic plates, each containing 300 g fresh cow dung were placed on the soil surface, one was covered with a net (mesh size of 25 × 25 mm) to prevent access of small vertebrates, the other was covered with a net (mesh size of 1.2 mm) to prevent access of DB, as control. After 72 h of dung exposure, the remaining dung of both plates was weighted to calculate the dung removal rate. The quantification of the dung removal rate was performed 15 days before DB sampling to avoid changes in the structure of DB communities related to trapping. The sampling time did not coincide with the activity period of flesh flies in the study area (which lasts from June to July according to our field observations) to ensure that dung removal was exclusively due to DB activity.

2.5. Data analysis

Statistical analyses were carried out in R software v. 3.4.0 (R Core Team, 2014). Species accumulation curves were used to assess the completeness of DB sampling across three land-use types. Non-metric multidimensional scaling (NMDS) based on Bray-Curtis dissimilarities from a species relative abundance matrix was used to characterize the

structure of DB communities inhabiting land use types. Although some of the pitfall traps were lost during the sampling period, total trapping effort for each land use type was approximately equal (14 traps in 1stForests and 13 traps each in meadows and 2ndForests), and in addition all species accumulation curves for three land-uses appear to reach asymptotes (Fig. S1). Permutational multivariate analysis of variance (PERMANOVA) was used to test for differences among DB communities. All tests and ordination plots were performed using the vegan package v. 2.4–5 (Oksanen et al., 2015), and each computed test was based on 999 permutations. To get insights into environment-community pattern relations, we fitted environmental factors onto NMDS ordinations using the envfit function in the vegan package, goodness of fit and *p*-value were permuted 999 times. In addition, species richness, evenness and abundance were fitted to NMDS ordinations to test whether these individual variables were associated with community patterns. To compare species richness and abundance on meadow and forest sites we performed generalized linear models (GLM) using Poisson distribution.

Co-inertia (RLQ) analysis (Dolédec et al., 1996) was used to characterize the relationship between environmental variables (R), species abundance (L), and trait values for each species (Q). A cluster analysis was computed based on the species scores of the two first RLQ axes and the Calinsky-Harabasz criterion. The relationship between multiple morphological traits and multiple environmental variables was assessed using a combination of the RLQ and the fourth-corner method according to Dray et al. (2014). RLQ analysis links data on species abundance, their functional traits and environmental variables in a single ordination analysis. Dray et al. (2014) implemented the fourth-corner method as a significance test for the RLQ analysis to directly test the links between RLQ axes and trait variables or environmental variables using the fourthcorner.rlq function in the ade4 package (Dray et al., 2014). This method has been used for multi-group communities or whole invertebrate communities (Braaker et al., 2017; de Castro et al., 2018; Ding et al., 2017; Kuzmanovic et al., 2017; Luiza-Andrade et al., 2017; Mocq and Hare, 2018; Murphy et al., 2017; Ossola et al., 2015). Here we applied this method to test for relationships between community morphological traits of a single group of DB (i.e. the tunnellers group) and environmental variables.

We used Rao's index of quadratic entropy (Zoltán, 2005) to examine the effect of LUC on functional diversity, because this index is independent of species richness (Mouchet et al., 2010). Rao's index was computed from a species-by-traits matrix using the dbFD function in the "FD" package (Laliberté et al., 2014). GLM was performed using Gaussian distribution to test the effect of LUC on functional diversity.

Traits used in statistical analyses (RLQ and fourth-corner methods, Rao's index) comprised BoL, Head L/W, Pro. L/W, Ely. L/W, hindWing L/W, ProTi. L/W, MesoTi. L/W, MetaTi. L/W, Dis.(Ely.W–Ely.apex)/ElyL, MetaTaL/ElyL and BioM.

3. Results

3.1. Community structure of the tunnellers along the land use gradient

In total 1417 beetles of 41 tunnelling DB species were recorded, 30 species were found in meadows while 18 and 20 species were collected in 2ndForests and 1stForests, respectively (Table S1). The community structure of tunnellers differed significantly between LUC (PERMANOVA, F = 27.13, R^2 = 0.59, p < 0.001), clearly separating meadow communities from forest communities (Fig. 1). Although there was high overlap in Bray-Curtis diversity between the 1stForests and 2ndForests, DB communities statistically differed between these two forest types (PERMANOVA, F = 3.46, R^2 = 0.12, p = 0.006). Fitting environmental vectors to the NMDS plot demonstrated that cover of ground vegetation (GV) (R^2 = 0.78, p < 0.001) and distance to shrubs (Dst) (R^2 = 0.27, p = 0.004) significantly correlated with the community structure of tunnelling DB, while shrub height (SH) and crown diameter of shrubs (Sdia) had no influence.
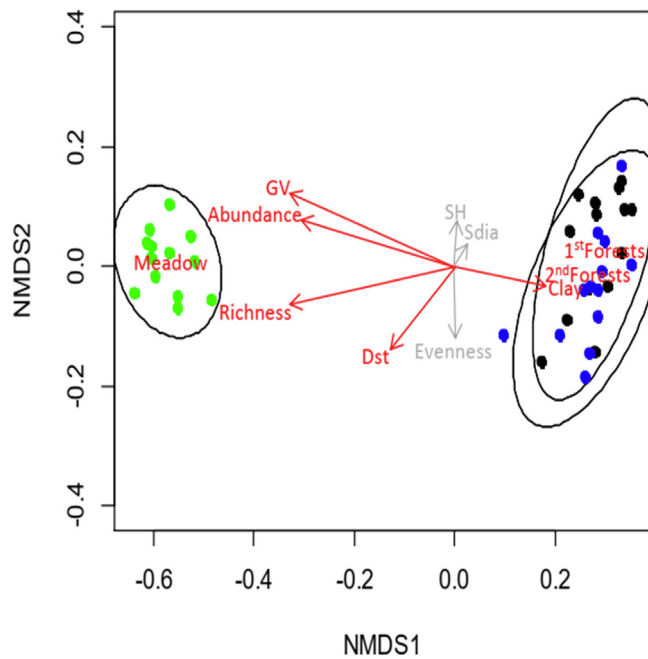
Fig. 1. NMDS ordination showing differences of the dung beetle communities between meadows and forests (stress value: 0.06). The fitted vectors of environmental variables and community attributes (species richness, evenness and abundance) are displayed for significant (p < 0.05, red arrows) and non-significant (grey arrows) variables. Meadows (green), secondary forests (blue), primary forests (black), cover of ground vegetation (GV), distance to shrubs (Dst), crown diameter of shrub (Sdia), shrub height (SH) and soil clay content (Clay).

Table 1
GLM for species richness, abundance and Rao's quadratic entropy between meadows and forests. Estimates (β), standard errors (SE), test statistics (z, t-value) and *p*-values are presented.

	β	± SE	z-value	*p*-value
Abundance	1.406	0.056	25.02	< 0.001
Species richness	0.79	0.104	7.624	< 0.001
	β	± SE	t-value	*p*-value
Functional diversity	−3.04	0.72	−4.2	< 0.001

Table 2
GLM for species richness, abundance and Rao's quadratic entropy between primary and secondary forests. Estimates (β), standard errors (SE), test statistics (z, t-value) and *p*-values are presented.

	β	± SE	z-value	*p*-value
Abundance	0.395	0.093	4.26	< 0.001
Species richness	0.085	0.149	0.57	0.567
	β	± SE	t-value	*p*-value
Functional diversity	−1.32	0.95	−1.38	0.179

Abundance and species richness of DB showed significant differences between meadows and forests (Table 1), with abundance and species richness (per trap) in meadows being more than 3.2-fold and 2-fold higher compared to forests, respectively. Similarly functional diversity (Rao's quadratic entropy) was significantly different between meadows and forests. However, there was no difference in species richness and functional diversity between 2ndForests and 1stForests, despite abundance differing between both forest types (Table 2).

3.2. Trait-Environment relationships

RLQ analysis revealed that the groups of land use types including 1stForests and 2ndForests and environmental variables including leaf litter thickness (LLT) and soil clay content (Clay) could be linked to the morphological traits representing biomass (BioM), body length (BoL) and elytral aspect ratio (i.e. elytral length-width ratio [Ely. L/W]). Meadows and cover of ground vegetation (GV) correlated with pronotal aspect ratio (i.e. pronotal length-width ratio [Pro. L/W], metatarsus relative to elytral length (i.e. metatarsal-elytral length ratio [MetaTa/ElyL]), the position of the elytral widest part (i.e. distance from the elytral widest part to elytral posterior apex-elytral length ratio [Dist (Ely.W − Ely.apex)/ElyL]), hindwing aspect ratio (i.e. hindwing length-width ratio [Wing L/W], robustness of mesotibia (i.e. mesotibial length-width ratio [MesoTi. L/W], robustness of metatibia (i.e. metatibial length-width ratio [MetaTi. L/W]) and robustness of protibia (i.e., protibial length-with ratio [ProTi. L/W]).

Head aspect ratio (i.e. head length-width ratio [Head L/W]) could be related to distance to shrubs (Dst). The two environmental variables, shrub height (SH) and crown diameter of shrub (Sdia), did not correlate with morphological traits (Fig. 2).

The first axis of RLQ separated meadow and forest communities and was positively associated with cover of ground vegetation (GV), pronotal length-width ratio (Pro. L/W), metatarsal-elytral length ratio (MetaTaL/ElyL), distance from the elytral widest part to elytral posterior apex in relation to elytral length (Dist (Ely.W − Ely.apex)/ElyL), and hindwing length-width ratio (Wing L/W) (Table 3). Two environmental variables: leaf litter thickness (LLT) and soil clay content (Clay), and three morphological traits: biomass (BioM), body length (BoL) and elytral length-width ratio (Ely. L/W) together with the ecosystem function "dung removal rate (DRR)", were negatively associated with the first axis. The second axis showed no correlation with any environmental variables or traits (Table 3).

### 3.3. Cluster analysis and morphological groups

The cluster analysis identified three distinct trait clusters containing 3–31 out of the 41 species for which morphological traits were defined (Figs. 3 and 4 and S2). Trait cluster A comprised seven species of large body length and biomass (large BoL and BioM), with broad pronotum (small Pro. L/W), elongated elytra (great Ely. L/W and small Dist(Ely.W − Ely.apex)/ElyL), wide hindwing (low Wing L/W) and short metatarsi (very small MetaTaL/ElyL), being rare in meadows. Dung beetles representing trait cluster B had slender mesotibia and metatibia (i.e. great MesoTi. L/W and MetaTi.L/W), an elongated pronotum (i.e. large Pro. L/W), the elytral widest part in the front (i.e. large Dist (Ely.W − Ely.apex/ElyL), thin hindwing (high Wing L/W) and small body length and biomass, occurring mainly in meadows. Dung beetles of trait cluster C comprised 31 species of small body length and biomass, nearly semicircular elytra (i.e. small Ely. L/W and large Dist(Ely.W − Ely.apex)/ElyL), and long metatarsi (i.e. large MetaTaL/ElyL), dominating in meadows with a high cover of ground vegetation.

Among the morphological traits that correlated with the RLQ axes, BioM, BoL and Ely.L/W peaked in trait cluster A, while Dist(Ely.W − Ely.apex)/ElyL, Wing L/W and Pro. L/W peaked in trait cluster B, and MetaTaL/ElyL peaked in trait cluster C. Head aspect ratio (Head L/W) and protibial aspect ratio (ProTi. L/W) did not differ significantly among trait clusters. Head aspect ratio and protibial aspect ratio, together with MesoTi. L/W and MetaTi. L/W remained unchanged across the LUC gradient.

4. Discussion

Differences in DB communities between forests and grasslands have been previously confirmed (Braga et al., 2013; Frank et al., 2017; Negro et al., 2011; Numa et al., 2009). However, these studies did not take
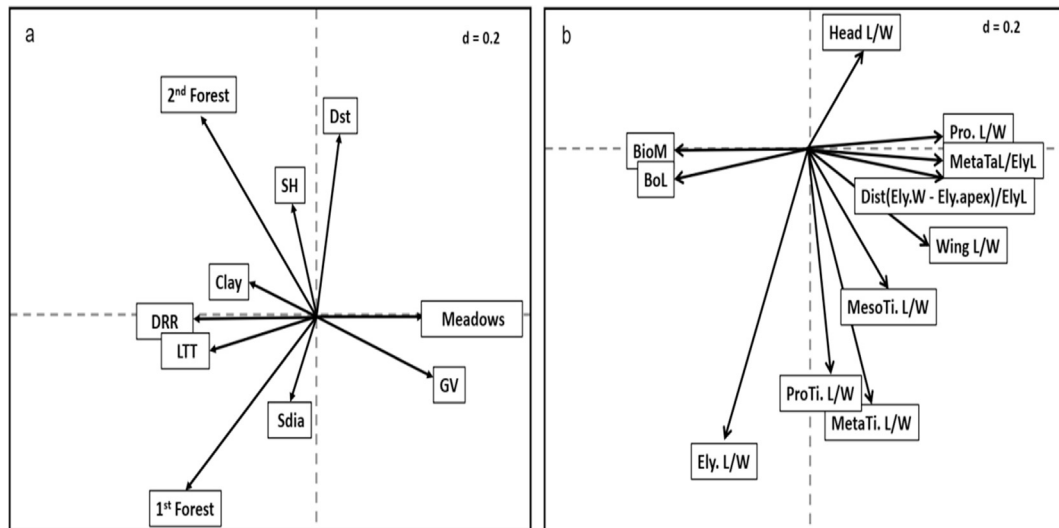
Fig. 2. Ordination of environmental variables/ ecosystem functions (a) and morphological traits (b) in RLQ. Environmental variables/ecosystem functions: primary forests (1stForests), secondary forests (2ndForests), leaf litter thickness (LLT), shrub height (SH), distance to shrubs (Dst), ground vegetation cover (GV), crown diameter of shrubs (Sdia). We further included dung removal rate (DRR) as environmental variable in order to display the relative strength and direction of this ecosystem function in the ordination. Morphological traits: biomass (BioM), body length (BoL), elytral length-width ratio (Ely. L/W), protibial length-width ratio (ProTi. L/W), metatibial length-width ratio (MetaTi. L/W), mesotibial length-width ratio (MesoTi. L/W), hindwing length-width ratio (Wing L/W), distance from the elytral widest part to elytral posterior apex in relation to elytral length (Dist(Ely.W – Ely.apex)/ElyL), metatarsal length-elytral length ratio (MetaTaL/ElyL), pronotal length-width ratio (Pro. L/W) and head length-width ratio (Head L/W).
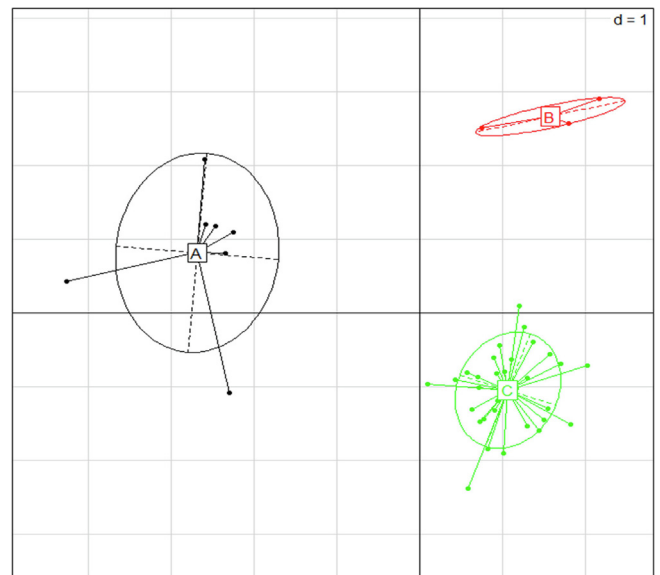
Table 3
P-values of fourth-corner analyses between the two first RLQ axes and environmental variables and traits. Bold p-values indicate significantly positive or negative (with minus) associations (see Fig. 2 for variable names).

Variable	Axis 1	Axis 2
Environmental factors		
Forest.1	0.555	0.179
Forest.2	0.471	0.403
Meadows	**0.027**	1
DRR	**−0.001**	0.983
GV	**0.001**	0.861
LLT	**−0.001**	0.952
Dst	0.06	0.426
SH	0.338	0.543
Sdia	0.544	0.764
Clay	**−0.010**	0.933
Community traits		
BioM	**−0.001**	0.942
BoL	**−0.001**	0.995
Dist(Ely.W – Ely. apex)/ElyL	**0.001**	0.960
Ely. L/W	**−0.004**	0.303
Wing L/W	**0.001**	0.867
Head L/W	0.175	0.416
ProTi. L/W	0.405	0.426
MesoTi. L/W	0.062	0.704
MetaTaL/ElyL	**0.001**	0.964
MetaTi. L/W	0.220	0.428
Pro. L/W	**0.001**	0.967

Fig. 3. Three distinct functional trait groups of dung beetles defined from cluster analysis: cluster A (seven species), cluster B (three species) and cluster C (31 species).

functional aspects of species morphological traits, at the community level, into account. Our data show that the conversion of forests to meadows has resulted in significant shifts of morphological traits of SE Asian tunnelling DB, as well as dung removal rate, being one of the most important ecosystem functions.

In contrast to Numa et al. (2009) and Braga et al. (2013), our results show an increase of tunnelling DB species in meadows as a result of an increasing number of small-bodied DB. These tunnelling DB were dominated by *Onthophagus* species, accounting nearly 50% and 70% of the total recorded individuals and species, respectively in Puluong. This shift is a typical pattern for SE Asian DB (Davis et al., 2001; Hayes et al.,

2009; Shahabuddin et al., 2005) but never observed in Europe and South America (Braga et al., 2013; Campos and Hernández, 2013; Campos and Hernández, 2015; Costa et al., 2017; Frank et al., 2017; Harvey et al., 2006). Although dwellers and rollers were included in some of these studies, tunnellers are the dominant functional group in SE Asia, accounting for 90% of the total recorded dung beetles of this area. In agreement with Frank et al. (2017), most *Onthophagus* species, together with the abundant genus *Liatongus* were exclusively found in meadows, leading to the overall high abundance and species richness of tunnelling DB in meadows compared to forests in Puluong. According to our results, it seems likely that the similarity of specific morphological traits between *Onthophagus* species and *Liatongus* species reflect convergent adaptations to the environmental conditions in meadows.
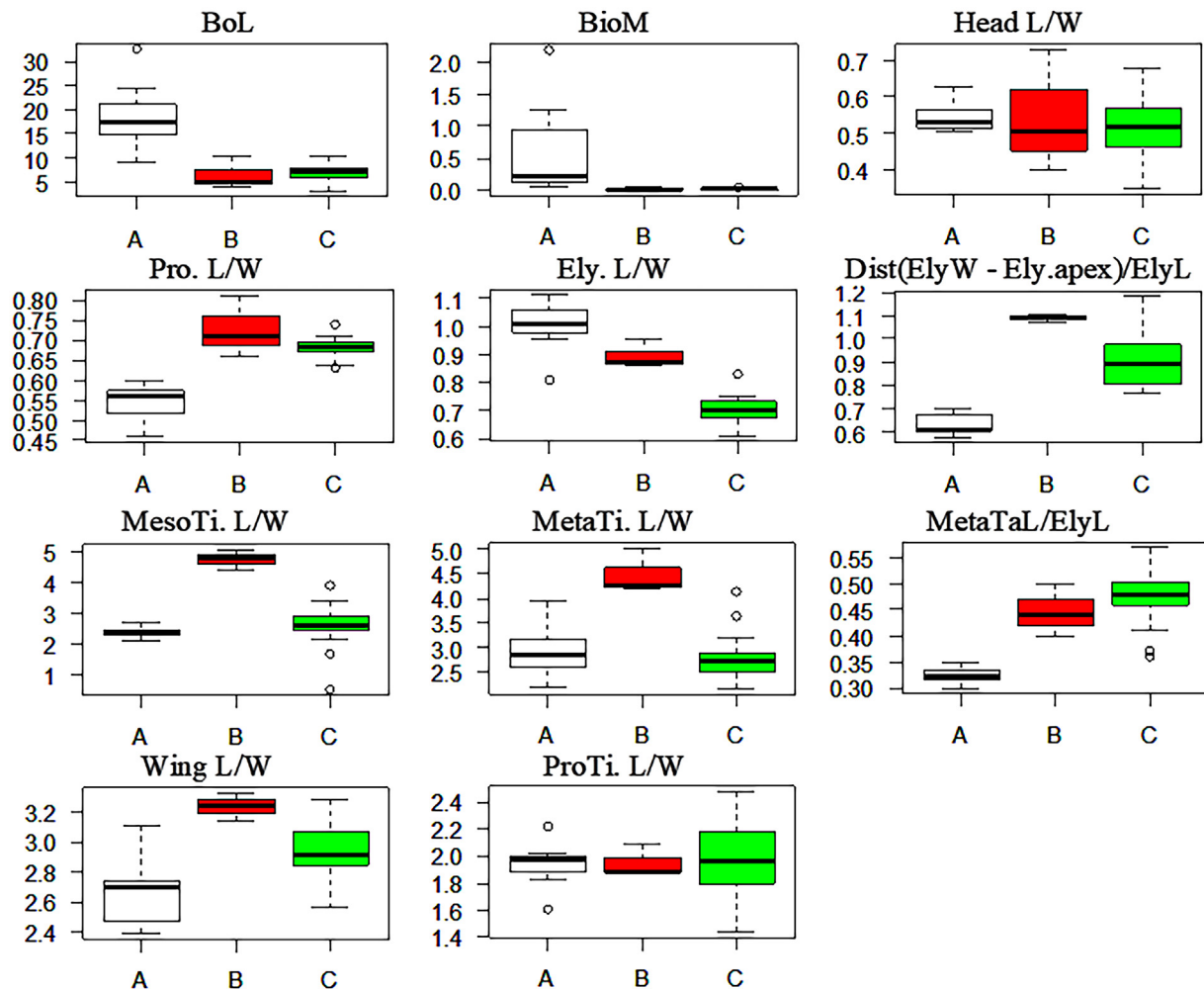
Fig. 4. Box plots showing quantitative morphological traits of three distinct trait clusters A, B and C of tunnelling dung beetles.

Given that the morphological traits of DB will influence their contribution to ecosystem functions and services (Raine et al., 2018; Slade et al., 2007), it is important to identify the specific morphological traits of DB communities associated with LUC. We found significant changes in specific traits associated with dispersal and perching capacity of DB across land use types, reflected by an increase of tunnelling DB species of small body length and biomass, nearly semicircular elytra and long metatarsi in meadows, and a severe decrease of large-bodied DB in this habitat. Morphological traits of DB in forests likely reflect adaptations to the thickness of the leaf litter layer by increased DB biomass, associated with an elongation of the body (BoL), a decreased ratio of hindwing length to width and an increase of elytral length relative to width (Ely. L/W). In particular the ecosystem function "dung removal rate" appeared to be strongly associated with pronotal aspect ratio (i.e. pronotal length-width ratio), but it was not associated with the robustness of the protibia, mesotibia and metatibia (i.e. protibial length-width ratio, mesotibial length-width ratio and metatibial length-width ratio).

The meadow sampling sites in the current study, unlike those documented in Braga et al. (2013), are located in a protected area. Hence, the tunnelling DB communities were not affected by grassland management, such as manure or pesticide applications and mechanical disturbances like the removal of herbs and mowing, that could reduce DB numbers and diversity (Braga et al., 2013; Harvey et al., 2006; Hutton and Giller, 2003). A high cover of ground vegetation in meadows offers a wide outlook over dung resources for small DB (body length < 10 mm) that typically perch on the leaves of the ground

vegetation to locate food resources (Howden and Nealis, 1978; Larsen et al., 2008; Peck and Forsyth, 1982). Accordingly, it seems likely that the convergence of small body length and/or biomass, together with elongated metatarsi for climbing and nearly semicircular elytra reflect those morphological traits that confer a competitive advantage for DB to locate food from perches in the vegetation. Given that wingless DB in South Africa possess a more rounded body than equivalent-sized and winged species, as indicated in Chown et al. (1998), the nearly semicircular elytra of SE Asian DB could also reflect DB species of poor dispersal. Large-bodied DB in contrast cover much larger territories, because they tend to fly rather than perch to forage for food. Hence, large DB are not strictly dependent on ground vegetation. A higher sun exposure in meadows due to decreased canopy cover may be even detrimental to large-bodied DB, as their bodies could heat up within the hot weather period (i.e. from May to July) above the maximum tolerated temperature of 42 °C (Verdú et al., 2006). Additionally, large-bodied DB are constrained to utilize the dung of large herbivores due to larger food requirements for their brood masses during the breeding season (Hanski and Cambefort, 2014). However, large herbivores are relatively rare on the non-managed meadows of Puluong NR. The scarcity of mammalian dung resources, and their temporal restricted availability due to fast drying up of the sun-exposed resources many further reduce the competitiveness of large-bodied DB. Small-bodied DB species are less dependent on large mammalian dung patches by using dung resources from small animals such as lizards and rodents in meadows (Howden and Nealis, 1978). Additionally, small-bodied DB find more easily shelter from the sun heat in meadows than large DB.

The advantage of small body length and biomass in meadows may turn into a disadvantage in the shades of forests at an altitudinal range of 800–1000 m where the lower ambient temperature for flight may limit the dispersal of small-bodied DB (Verdú et al., 2006). Beiroz et al. (2017) recently identified soil texture as one of the most important environmental variables for the spatial separation of DB communities in lowland tropical rainforests in the Brazilian Amazon. Despite clay content explained a small, but significant part of DB communities, our analyses cannot ultimately confirm its relevance as soil clay content was consistently higher in meadows and therefore confounded by land use type (Fig. S7). A leaf litter layer is a typical physical barrier on the forest floor that hinders the dung removal process of DB (da Silva and Hernández, 2016; Nichols et al., 2013). A thick leaf litter layer in forests may exert a high resistance to dung burial for small-bodied DB species (da Silva and Hernández, 2015), but not for large DB who are favored in addition by the higher availability of mammalian dung resources.

Consistent with Nervo et al. (2014), Tixier et al. (2015) and Frank et al. (2017), our results confirmed positive correlations of the body length and body mass of tunnelling DB communities with dung removal rate, even though the abundance of tunnelling DB showed no correlation with dung removal rate in the current study. Thus, the size (i.e. body length, body mass) rather than the overall abundance of tunnelling DB turned out to be a key morphological trait maintaining the ecosystem service of dung removal. Dung removal rate significantly correlated with pronotal aspect ratio, hindwing aspect ratio and elytral aspect ratio, while protibial length-width ratio, mesotibial length-width ratio, metatibial length-width ratio and head aspect ratio did not correlate with this ecosystem function. These results are best explained by the fact that the tunnelling DB typically push dung balls from dung piles to their nesting sites in which the pronotal aspect ratio rather than head shape and the robustness of protibia, mesotibia and metatibia play a predominant role in the dung removal process. Tunnelling DB species possessing a broader pronotum (i.e. small pronotal L/W ratio) can collect a larger amount of dung, hence have a competitive advantage over those species with a relatively longer pronotum (i.e. large pronotal L/W ratio). In the limestone karst ecosystems where unevenly distributed and scare dung resources are common, the dispersal capacity of DB appears crucial. Our results revealed that dung beetle species with narrow hindwings dominated in meadows. In contrast, relatively wider hindwings were characteristic of the dung beetle species of forest habitats. Although beetles use their hind wings for flight, some recent studies have shown that the elytra, through their rotation angle and wing locking systems indirectly affect the ability of beetles to fly, and further influence the aerodynamic performance and the effort for the production of vertical force during flight (Sun and Bhushan, 2012; Johansson et al., 2012). In addition to pronotal aspect ratio and elytral aspect ratio, changes in other morphological traits of pronotum and elytra under LUC, such as pronotal prominences, anterior declivity and excavation, or wing loading may also affect the dung removal rate, but this requires further studies.

5. Conclusion

Anthropogenic land use change profoundly affected the community structure, taxonomic diversity, functional diversity and functional morphological traits of tunnelling dung beetle communities of tropical karst ecosystems in Vietnam. We characterized three distinct morphological trait clusters adapted to the altered environmental conditions. Tropical limestone meadows were severely impoverished by large tunnelling DB species, although this land use type contained a higher abundance and more species-rich dung beetle communities compared to forest habitats. Because body length and body mass rather than abundance determined dung removal rate, the conversion from forests to meadows may result in a reduction in the functioning of tunnelling dung beetles providing this key ecosystem service. The cover of ground vegetation in meadows appeared crucial for small-bodied dung beetles

which typically employ a leaf-perching strategy in search of food. Therefore, the maintenance of ground vegetation in meadows appears important to maintain functional diversity of dung beetles. The secondary forests, after 40 years of regrowth showed similarities in species richness and functional diversity (Rao's quadratic entropy) of tunnellers to 1[st]Forests. This gives hope for the recovery of tunnelling dung-beetle communities during forest succession.

The successful combination of RLQ and fourth-corner methods provides a new means to identify shifts in morphological species traits in response to land use change in South East Asian tropical ecosystems. In agreement with previous studies, we confirmed changes in body length and body mass of dung beetles in responses to land use changes, but in addition, we identified a number of new and potentially important functional traits, such as elytral aspect ratio, hindwing aspect ratio and the length of metatarsi in tunnelling dung beetle communities. Our results support recent calls for the increased use of trait-based approaches to assess the influence of land use change on invertebrate communities.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.ecolind.2019.105697.

References

Andresen, E., Laurance, S.G.W., 2007. Possible indirect effects of mammal hunting on dung beetle assemblages in panama. Biotropica 39, 141–146.

Arnold, S.J., 1983. Morphology, performance and fitness. Am. Zool. 23, 347–361.

Audino, L.D., Louzada, J., Comita, L., 2014. Dung beetles as indicators of tropical forest restoration success: Is it possible to recover species and functional diversity? Biol. Conserv. 169, 248–257.

Averyanov, L.V., Nguyen, T.H., Phan, K.L., Do, T.D., Regalado, J.C., 2003. Preliminary botanical survey of primary vegetation at Pu Luong Nature Reserve, Thanh Hoa province–The Pu Luong-Cuc Phuong conservation limestone landscape conservation project. Forest Protection Department, Hanoi.

Beiroz, W., Slade, E.M., Barlow, J., Silveira, J.M., Louzada, J., Sayer, E., 2017. Dung beetle community dynamics in undisturbed tropical forests: implications for ecological evaluations of land-use change. Insect Conserv. Divers. 10, 94–106.

Boonrotpong, S., Sotthibandhu, S., Pholpunthin, C., 2004. Species composition of dung beetles in the primary and secondary forests at Ton Nga Chang Wildlife Sanctuary. Sci. Asia 30, 59–65.

Braaker, S., Obrist, M.K., Ghazoul, J., Moretti, M., 2017. Habitat connectivity and local conditions shape taxonomic and functional diversity of arthropods on green roofs. J. Anim. Ecol. 86, 521–531.

Braga, R.F., Korasaki, V., Andresen, E., Louzada, J., 2013. Dung beetle community and functions along a habitat-disturbance gradient in the Amazon: a rapid assessment of ecological functions associated to biodiversity. PLoS ONE 8, e57786.

Brower, J.E., Zar, J.H., 1998. Field and laboratory methods for general ecology. WM. C. Brown Company Publishers, Dubuque, Iowa.

Bui, V.B., Dumack, K., Bonkowski, M., 2018. Two new species and one new record for the genus *Copris* (Coleoptera: Scarabaeidae: Scarabaeinae) from Vietnam with a key to Vietnamese species. Eur. J. Entomol. 115, 167–191.

Bui, V.B., Bonkowski, M., 2018. *Synapsis puluongensis* sp. nov. and new data on the poorly known species *Synapsis horaki* (Coleoptera: Scarabaeidae) from Vietnam with a key to Vietnamese species. Acta Entomol. Musei Nationalis Pragae 58, 407–418.

Campos, R.C., Hernández, M.I.M., 2013. Dung beetle assemblages (Coleoptera, Scarabaeinae) in Atlantic forest fragments in southern Brazil. Revista Brasileira de Entomologia 57, 47–54.

Campos, R.C., Hernández, M.I.M., 2015. Changes in the dynamics of functional groups in communities of dung beetles in Atlantic forest fragments adjacent to transgenic maize crops. Ecol. Ind. 49, 216–227.

Chown, S.L., Pistorius, P., Scholtz, C.H., 1998. Morphological correlates of flightlessness in southern African Scarabaeinae (Coleoptera:Scarabaeidae): testing a condition of the water-conservation hypothesis. Can. J. Zool. 76, 1123–1133.

Colfer, C.J.P., Dahal, G.R., Capistrano, D., 2012. Lessons from forest decentralization: money, justice and the quest for good governance in Asia-Pacific. Earthscan.

Costa, C., Oliveira, V.H.F., Maciel, R., Beiroz, W., Korasaki, V., Louzada, J., 2017. Variegated tropical landscapes conserve diverse dung beetle communities. PeerJ 5, e3125.

da Silva, P.G., Hernández, M.I.M., 2015. Spatial patterns of movement of dung beetle species in a tropical forest suggest a new trap spacing for dung beetle biodiversity studies. PLoS ONE 10 (5), e0126112. https://doi.org/10.1371/journal.pone.0126112.

da Silva, P.G., Hernández, M.I.M., 2016. Spatial variation of dung beetle assemblages associated with forest structure in remnants of southern Brazilian Atlantic Forest. Revista Brasileira de Entomologia 60, 73–81.

Davis, A.J., Holloway, J.D., Huijbregts, H., Krikken, J., Kirk-Spriggs, A.H., Sutton, S.L., 2001. Dung beetles as indicators of change in the forests of northern Borneo. J. Appl. Ecol. 38, 593–616.

de Castro, D.M.P., Dolédec, S., Callisto, M., 2018. Land cover disturbance homogenizes aquatic insect functional structure in neotropical savanna streams. Ecol. Ind. 84, 573–582.

Ding, N., Yang, W., Zhou, Y., Gonzalez-Bergonzoni, I., Zhang, J., Chen, K., Vidal, N., Jeppesen, E., Liu, Z., Wang, B., 2017. Different responses of functional traits and diversity of stream macroinvertebrates to environmental and spatial factors in the Xishuangbanna watershed of the upper Mekong River Basin, China. Sci. Total Environ. 574, 288–299.

Dolédec, S., Chessel, D., ter Braak, C.J.F., Champely, S., 1996. Matching species traits to environmental variables: a new three-table ordination method. Environ. Ecol. Stat. 3, 143–166.

Doube, B.M., 2018. Ecosystem services provided by dung beetles in Australia. Basic Appl. Ecol. 26, 35–49.

Dray, S., Choler, P., Dolédec, S., Peres-Neto, P.R., Thuiller, W., Pavoine, S., ter Braak, C.J.F., 2014. Combining the fourth-corner and the RLQ methods for assessing trait responses to environmental variation. Ecology 95, 14–21.

Enari, H., Koike, S., Sakamaki, H., 2013. Influences of different large mammalian fauna on dung beetle diversity in beech forests. J. Insect. Sci. 13, 54.

Estrada, A., Anzures, D.A., Coates-Estrada, R., 1999. Tropical rain forest fragmentation, howler monkeys (Alouatta palliata), and dung beetles at Los Tuxtlas. Mexico. Am. J. Primatol. 48, 253–262.

Favila, M.E., Halffter, G., 1997. The use of indicator groups for measuring biodiversity as related to community structure and function. Acta Zoológica Mexicana (nueva serie) 1–25.

Finn, J.A., Giller, P.S., 2000. Patch size and colonisation patterns: an experimental analysis using north temperate coprophagous dung beetles. Ecography 23, 315–327.

Frank, K., Hülsmann, M., Assmann, T., Schmitt, T., Blüthgen, N., 2017. Land use affects dung beetle communities and their ecosystem service in forests and grasslands. Agric. Ecosyst. Environ. 243, 114–122.

Gagic, V., Bartomeus, I., Jonsson, T., Taylor, A., Winqvist, C., Fischer, C., Slade, E.M., Steffan-Dewenter, I., Emmerson, M., Potts, S.G., Tscharntke, T., Weisser, W., Bommarco, R., 2015. Functional identity and diversity of animals predict ecosystem functioning better than species-based indices. Proc. R. Soc. B: Biol. Sci. 282, 20142620.

Gardner, T.A., Hernández, M.I.M., Barlow, J., Peres, C.A., 2007. Understanding the biodiversity consequences of habitat change: the value of secondary and plantation forests for neotropical dung beetles. J. Appl. Ecol. 45, 883–893.

Gittings, T., Giller, P.S., 1998. Resource quality and the colonisation and succession of coprophagous dung beetles. Ecography 21, 581–592.

Hanski, I., Cambefort, Y., 2014. Dung beetle ecology. Princeton University Press.

Hanski, I., Krikken, J., 1991. Dung beetles in tropical forests in South-East Asia. In: Hanski, I., Cambefort, Y. (Eds.), Dung Beetle Ecology. Princeton University Press, New Jersey, pp. 179–197.

Harvey, C.A., Gonzalez, J., Somarriba, E., 2006. Dung Beetle and Terrestrial Mammal Diversity in Forests, Indigenous Agroforestry Systems and Plantain Monocultures in Talamanca, Costa Rica. Biodivers. Conserv. 15, 555–585.

Hayes, L., Mann, D.J., Monastyrskii, A.L., Lewis, O.T., 2009. Rapid assessments of tropical dung beetle and butterfly assemblages: contrasting trends along a forest disturbance gradient. Insect Conserv. Divers. 2, 194–203.

Howden, H., Nealis, V., 1978. Observations on height of perching in some tropical dung beetles (Scarabaeidae). Biotropica 43–46.

Hutton, S.A., Giller, P.S., 2003. The effects of the intensification of agriculture on northern temperate dung beetle communities. J. Appl. Ecol. 40, 994–1007.

Johansson, L.C., Engel, S., Baird, E., Dacke, M., Muijres, F.T., Hedenström, A., 2012. Elytra boost lift, but reduce aerodynamic efficiency in flying beetles. J. R. Soc. Interface 9, 2745–2748.

Kabakov, O.N., Napolov, A., 1999. Fauna and ecology of Lamellicornia of subfamily Scarabaeinae (Scarabaeidae, Coleoptera) of Vietnam and some parts of adjacent countries: South China, Laos and Thailand. Latvijas Entomologs 37, 58–96.

Kuzmanovic, M., Dolédec, S., de Castro-Catala, N., Ginebreda, A., Sabater, S., Muñoz, I., Barceló, D., 2017. Environmental stressors as a driver of the trait composition of benthic macroinvertebrate assemblages in polluted Iberian rivers. Environ. Res. 156, 485–493.

Laliberté, E., Legendre, P., Shipley, B., 2014. FD: measuring functional diversity from multiple traits, and other tools for functional ecology. R package version 1.0-12.

Larsen, T.H., Lopera, A., Forsyth, A., 2008. Understanding trait-dependent community disassembly: dung beetles, density functions, and forest fragmentation. Conserv. Biol. 22, 1288–1298.

Larsen, T.H., Williams, N.M., Kremen, C., 2005. Extinction order and altered community structure rapidly disrupt ecosystem functioning. Ecol. Lett. 8, 538–547.

Luiza-Andrade, A., Brasil, L.S., Benone, N.L., Shimano, Y., Farias, A.P.J., Montag, L.F., Dolédec, S., Juen, L., 2017. Influence of oil palm monoculture on the taxonomic and functional composition of aquatic insect communities in eastern Brazilian Amazonia. Ecol. Ind. 82, 478–483.

McGill, B.J., Enquist, B.J., Weiher, E., Westoby, M., 2006. Rebuilding community ecology from functional traits. Trends Ecol. Evol. 21, 178–185.

Mocq, J., Hare, L., 2018. Influence of acid mine drainage, and its remediation, on Lakewater quality and benthic invertebrate communities. Water Air Soil Pollut. 229, 28.

Mouchet, M.A., Villeger, S., Mason, N.W.H., Mouillot, D., 2010. Functional diversity measures: an overview of their redundancy and their ability to discriminate community assembly rules. Funct. Ecol. 24, 867–876.

Murphy, J.F., Jones, J.I., Arnold, A., Duerdoth, C.P., Pretty, J.L., Naden, P.S., Sear, D.A., Collins, A.L., 2017. Can macroinvertebrate biological traits indicate fine-grained sediment conditions in streams? River Res. Appl. 33, 1606–1617.

Negro, M., Palestrini, C., Giraudo, M.T., Rolando, A., 2011. The effect of local environmental heterogeneity on species diversity of alpine dung beetles (Coleoptera: Scarabaeidae). Eur. J. Entomol. 108, 91.

Nervo, B., Tocco, C., Caprio, E., Palestrini, C., Rolando, A., 2014. The effects of body mass on dung removal efficiency in dung beetles. PLoS ONE 9, e107699.

Nguyen, K.V., Nguyen, T.H., Phan, K.L., Nguyen, T.H., 2000. Bioclimatic diagrams of Vietnam. Vietnam National University Publishing House, Hanoi, pp. 126.

Nichols, E., Larsen, T., Spector, S., Davis, A.L., Escobar, F., Favila, M., Vulinec, K., 2007. Global dung beetle response to tropical forest modification and fragmentation: A quantitative literature review and meta-analysis. Biol. Conserv. 137, 1–19.

Nichols, E., Spector, S., Louzada, J., Larsen, T., Amezquita, S., Favila, M.E., 2008. Ecological functions and ecosystem services provided by Scarabaeinae dung beetles. Biol. Conserv. 141, 1461–1474.

Nichols, E., Uriarte, M., Bunker, D.E., Favila, M.E., Slade, E.M., Vulinec, K., Larsen, T., Vaz-de-Mello, F.Z., Louzada, J., Naeem, S., 2013. Trait-dependent response of dung beetle populations to tropical forest conversion at local and regional scales. Ecology 94, 180–189.

Numa, C., Verdú, J.R., Sánchez, A., Galante, E., 2009. Effect of landscape structure on the spatial distribution of Mediterranean dung beetle diversity. Divers. Distrib. 15, 489–501.

Oksanen, J., Blanchet, F., Kindt, R., Legendre, P., Minchin, P., O'Hara, R., Simpson, G., Solymos, P., Stevens, M., Wagner, H., 2015. Vegan: community ecology. R package version 2.2-1. R Project for Statistical Computing, Vienna, Austria.

Ossola, A., Nash, M.A., Christie, F.J., Hahs, A.K., Livesley, S.J., 2015. Urban habitat complexity affects species richness but not environmental filtering of morphologically-diverse ants. PeerJ 3, e1356.

Peck, S.B., Forsyth, A., 1982. Composition, structure, and competitive behaviour in a guild of Ecuadorian rain forest dung beetles (Coleoptera; Scarabaeidae). Can. J. Zool. 60, 1624–1634.

Philips, T.K., 2016. Phylogeny of the Oniticellini and Onthophagini dung beetles (Scarabaeidae, Scarabaeinae) from morphological evidence. ZooKeys 9–57.

Quintero, I., Roslin, T., 2005. Rapid recovery of dung beetle communities following habitat fragmentation in Central Amazonia. Ecology 86, 3303–3311.

Raine, E.H., Gray, C.L., Mann, D.J., Slade, E.M., 2018. Tropical dung beetle morphological traits predict functional traits and show intraspecific differences across land uses. Ecol. Evol. 8, 8686–8696.

Scholtz, C.H., Davis, A.L.V., Kryger, U., 2009. Evolutionary biology and conservation of dung beetles. Pensoft Sofia-Moscow.

Senior, M.J.M., Hamer, K.C., Bottrell, S., Edwards, D.P., Fayle, T.M., Lucey, J.M., Mayhew, P.J., Newton, R., Peh, K.S.H., Sheldon, F.H., Stewart, C., Styring, A.R., Thom, M.D.F., Woodcock, P., Hill, J.K., 2013. Trait-dependent declines of species following conversion of rain forest to oil palm plantations. Biodivers. Conserv. 22, 253–268.

Shahabuddin, Schulze, C.H., Tscharntke, T., 2005. Changes of dung beetle communities from rainforests towards agroforestry systems and annual cultures in Sulawesi (Indonesia). Biodivers. Conserv. 14, 863–877.

Slade, E.M., Mann, D.J., Villanueva, J.F., Lewis, O.T., 2007. Experimental evidence for the effects of dung beetle functional group richness and composition on ecosystem function in a tropical forest. J. Anim. Ecol. 76, 1094–1104.

Sun, J., Bhushan, B., 2012. Structure and mechanical properties of beetle wings: a review. RSC Adv. 2, 12606–12623.

Sterling, E.J., Hurley, M.M., Le, D.M., 2006. The Natural History of Vietnam. Yale

University Press, New Haven, CT.

Team, R.C., 2014. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

Thai, V.T., 1978. Forest vegetation of Vietnam. Science and Technique Publishing House, Hanoi, Vietnam.

Tixier, T., Bloor, J.M., Lumaret, J.-P., 2015. Species-specific effects of dung beetle abundance on dung removal and leaf litter decomposition. Acta Oecol. 69, 31–34.

Tuyet, D., 2001. Characteristics of karst ecosystems of Vietnam and their vulnerability to human impact. Acta Geol. Sin. 75, 325–329.

Verdú, J.R., Arellano, L., Numa, C., 2006. Thermoregulation in endothermic dung beetles (Coleoptera: Scarabaeidae): Effect of body size and ecophysiological constraints in flight. J. Insect Physiol. 52, 854–860.

Violle, C., Navas, M.L., Vile, D., Kazakou, E., Fortunel, C., Hummel, I., Garnier, E., 2007. Let the concept of trait be functional!. Oikos 116, 882–892.

Vulinec, K., 2000. Dung beetles (Coleoptera: Scarabaeidae), monkeys, and conservation in Amazonia. Florida Entomol. 229–241.

Vulinec, K., 2002. Dung beetle communities and seed dispersal in primary forest and disturbed land in Amazonia. Biotropica 34, 297–309.

Zoltán, B.-D., 2005. Rao's quadratic entropy as a measure of functional diversity based on multiple traits. J. Veg. Sci. 16, 533–540.