Dung beetle community dynamics in undisturbed tropical forests: implications for ecological evaluations of land-use change

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ABSTRACT

1. The impacts of human activities on tropical forests are widespread and increasing. Hence, a good knowledge-base about ecological processes in undisturbed tropical forest is crucial to provide a baseline for evaluating anthropogenic change.

2. Our five-year study focused on understanding the background spatial and inter-annual variation in dung beetle communities at 12 sites of undisturbed lowland tropical rainforest in the Brazilian Amazon. We then assessed how this variation may affect ecological evaluations of anthropogenic influence by comparing community metrics with comparable dung beetle data collected from 15 sites of *Eucalyptus* plantation in the same region.

3. Of all measured environmental variables, soil texture best explained spatial variation in dung beetle communities in undisturbed forests. Furthermore, soil texture was important for community assembly as it was associated with dung beetle nesting behaviours. While the relative abundance of dung beetle functional groups was stable over time, there were important inter-annual temporal dynamics, with a five-fold variation in abundance and body

mass, and with species richness ranging from 52-74. These temporal oscillations were probably caused by variation in dry season rainfall.

4. This inter-annual variation influenced the comparison between undisturbed forests and plantations, which could lead to inconsistencies in evaluation of anthropogenic change. We therefore highlight the importance of understanding natural variation in studies evaluating the consequences of land-use change and other forest disturbances on forest biodiversity.

Keywords: Scarabaeinae, pristine forest, response traits, environmental conditions, tropical forest, community assembly, drought

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INTRODUCTION

The negative influence of human beings in natural habitats has reached an unprecedented level (Ceballos *et al.,* 2015; Lewis & Maslin, 2015). Tropical rainforests are threatened by the advance of monoculture and pasture, and the exploitation of timber and non-timber resources in the remaining forests. The effects of these changes on biodiversity have been evaluated in a variety of taxa and summarised in pan-tropical and global meta-analyses (Cullen *et al*., 2000; Koh & Wilcove, 2008; Gibson *et al*., 2011; Newbold *et al*., 2015; Panday *et al*., 2015).

Most studies have highlighted the negative impacts of large changes in vegetation structure. However, the natural spatio-temporal fluctuations of many populations from 'control' or 'undisturbed' areas might lead to misinterpretations of the real effects of anthropogenic changes (Magurran *et al*., 2010). Conservation efforts could therefore benefit greatly from detailed information on spatio-temporal distribution ('Prestonian shortfall') of species and their sensitivity to habitat changes ('Hutchinsonian shortfall'; Hortal *et al*., 2015). Such information is especially important for organisms used as bioindicators of change, such as dung beetles (Cardoso *et al*., 2011; Davis *et al*., 2001).

Dung beetles are often used as focal organisms to evaluate anthropogenic impacts and habitat recovery from disturbance (e.g. Audino *et al*., 2014; Braga *et al*., 2013; Korasaki *et al*., 2013), with recent advances relating dung beetle sensitivity to disturbance to functional traits such as species body mass or size, nesting behaviour, diet preference, and activity period (Barragán *et al*., 2011; Nichols *et al*., 2013; Silva & Hernández, 2014). However, dung beetles also show high spatial variation due to their association with soil texture, which can cause changes in community composition over short distances (Hanski & Cambefort, 1991), even though some species show relatively high dispersal ability (Almeida *et al*., 2011; Gardner *et al*., 2008; Silva & Hernández, 2014, 2015). Furthermore, establishing baseline conditions is complicated by temporal change, as many dung beetle species show seasonality, and their abundances and distributions can vary inter-annually (Andrade *et al*., 2011).

To the best of our knowledge, there is no large-scale study that evaluates variation in dung beetle communities over multiple years in undisturbed tropical forests. We therefore assessed natural temporal and spatial variation in dung beetle communities over a five year period, focussing on undisturbed lowland tropical rainforest in the Brazilian Amazonia to explore the possible drivers and consequences of this variation. We tested the following hypotheses: (1) dung beetle community parameters (abundance, richness, body mass, composition, structure and abundance of functional groups - activity period, nesting behaviour and diet preference) will display high local variation. We relate any observed changes to local variation in soil texture (Osberg *et al.*, 1993; Sowig, 1995), canopy openness (Andrade *et al.*, 2011), rainfall prior to the sampling period, and geographic distance between sites; (2) inter-annual variation will be low for the community parameters listed above, as the structure of undisturbed forest buffers against external changes in the climate and offers a stable environment; and (3) natural temporal variation will influence the dissimilarity between communities in undisturbed forests and a local prevalent anthropogenic habitat, *Eucalyptus* plantations.

MATERIAL AND METHODS

Study site

The study was conducted within a cellulose company area of 1.7 Mha situated in the Jari River basin on the border between the States of Pará and Amapá in north-eastern Brazilian Amazonia (00°27′00″ - 01°30′00″ S, 51°40′00″ - 53°20′00″ W). The climate is classified as tropical monsoon (Amw - Köppen classification), with an average annual rainfall of 2115 mm (Coutinho & Pires, 1997), a marked wet season from January to June, and a distinct dry season from September to November (Parry *et al.*, 2007). The mean annual temperature is 26.9 °C (± 0.6 °C), and is constant throughout the year, with monthly maxima and minima of 31.4 °C (± 1.1 °C) and 22.5 °C (± 0.2 °C), respectively (Climate-Data.org, 2016).

The original continuous pristine forest was managed for Brazil nuts and subsistence livelihoods prior to 1967 (Coutinho & Pires, 1997). Since then, the area has been modified and is now a matrix of native forest with large patches of E*ucalyptus* plantations (c. 130,000 ha), disrupted by wide primary forest corridors (*c*. 200 m wide). There are a few human activities for subsistence within the native forest; mainly collection of Brazil nuts and other non-timber forest products, and some hunting (Parry *et al.*, 2009).

Dung beetle data

We sampled the dung beetle community during the wet season (from January to June) in each year from 2009 to 2013 at the same sampling points. We selected 12 sites of undisturbed forest, separated by 0.2 to 56 Km (average distance c. 27 km) to evaluate the shifts within this land cover, and 15 sites of *Eucalyptus* plantation, separated by 1.6 to 59.6 Km, to assess the influence of temporal variation on evaluation of human-induced impacts. In each site we installed five pitfall traps in a 600 m linear array, with traps aligned 150 m apart and 500 m from the forest/plantation edge. Pitfall traps consisted of plastic containers (19 cm diameter and 11 cm deep), which were part-filled with water, salt and detergent, and baited with 30 g of human and pig dung mixture, in the same proportion (Marsh *et al.*, 2013). Each trap was protected from rain with a plastic lid suspended 20 cm above the surface. In every year, collections took place over a period of 48 hours at each sampling site.

Dung beetle specimens were transported in 90% alcohol from the field to the laboratory, then sorted, dried and stored in paper envelopes. Voucher specimens were deposited at Coleção de Referência de Escarabeíneos Neotropicais at the Universidade Federal de Lavras (CREN – UFLA) in Minas Gerais State, Brazil. We identified the dung beetles using a key to the genera and subgenera of the subfamily Scarabaeinae of the New World (Vaz-De-Mello *et al.*, 2011), a field guide for dung beetles of the Jari River basin (Louzada, J., *unpublished*), and the reference collection at CREN – UFLA..

We grouped the species into functional groups to describe groups of species that share the same traits, forming groupings based on nesting behaviour, diet preference and activity period. We inferred dung beetle nesting behaviour based on genus, grouped as (1) rollers, which roll portions of dung away from the dung pile in small balls; (2) tunnelers, which take a small portion of the dung and bury it directly below or around the dung pile; and (3) dwellers, which nest inside the dung (Halffter & Matthew, 1966).

To determine dung beetle diet preference (coprophagous or necrophagous) and activity period, we conducted two independent surveys in January-February 2012 and November-December 2013. We set up 14 traps, spaced 100m apart, in two paired transects. We alternated the baits between 30 g of the human-pig dung mixture and 30g of rotten bovine spleen (to represent carrion) to avoid having the same bait in adjacent traps. If more than 75% of individuals were sampled in dung bait or carcass we classified them as coprophagous or necrophagous, respectively; for those species with lower percentages we classified them as generalists. For species with less than five individuals we sought the advice of neotropical dung beetle specialist Dr. Fernando Z. Vaz-de-Mello. We assessed activity period (diurnal vs. nocturnal) by setting up five pitfall traps 100 m apart. All traps were baited with 30 g human-pig dung mixture. Traps were opened and baited at 7:00 and 19:00 and exposed for 11 hours during the day or night.

We considered total abundance as the sum of individuals of all species, and richness as the number of different species at each site. We oven-dried 15 individuals (or the maximum number available) of each species at 40 ºC for 48 h, and obtained the mean dry mass. For species with low numbers of specimens, we weighed individuals from collections held at CREN - UFLA. We obtained the total body mass by multiplying each species mean weight by their abundance and summing across sites. For community-level weighted mean (CWM) body mass we replaced the abundance of each species by their relative abundance. Extrapolated richness was obtained from individual-based extrapolation for the maximum number of individuals found (591 individuals; Colwell *et al.,* 2012). We determined community composition as the occurrence (presence or absence of species) and structure considering the abundance of species. We also plotted a species accumulation curve with 95% confidence intervals for each year using the *specaccum* function in the *vegan* package

(Oksanen *et al*., 2014). All analyses were performed using R version 3.2.1 (R Core Team, 2014).

Environmental variables

We measured canopy openness at pitfall trap locations, using semi-hemispheric photography at 1.5 m above ground level. All pictures were analysed in GLA - Gap light analyser software (Frazer *et al*., 1999). As rainfall events may change community composition, due to temporal turnover in species within a season, we obtained the rainfall from three days before sampling from meteorological stations (Ramirez, 2014). To determine soil texture, we took soil cores at 0-10 cm depths in 2013 and measured the content (g/kg) of fine sand, coarse sand, silt and clay. For analysis, we selected fine sand content because it was not correlated with any other content (r_s < 0.238 and ≥ -0.392), and coarse sand content, as it was negatively correlated with silt and clay content (r_s = -0.937, r_s = -0.916, respectively). All environmental variables were standardized to a mean of zero and standard deviation of one before the analysis (Schielzeth, 2010).

Data analyses

Spatial variation of dung beetle communities

To assess the effects of environmental variables on the spatial variation of dung beetle communities we built models for each year with environmental metrics as explanatory variables. For total and functional group abundance (number of individuals with same trait), richness, and extrapolated richness we ran generalized linear models (GLM) using a negative binomial error distribution for total and functional group abundance, and quasi-Poisson for the richness metrics. We fitted total body mass and CWM body mass using linear models with Gaussian distribution. The significance of each environmental variable was determined by z tests for abundances and t tests for the other variables.

We built Bray-Curtis and Jaccard's dissimilarity matrices for community structure and composition, respectively, and for each year separately, using the function *vegdist*. We then compared each dissimilarity matrix with a matrix of geographic distances among sites, determined with Quantum GIS 2.4.0-Chugiak (Quantum GIS Development Team, 2015), using Mantel tests to evaluate the influence of spatial distribution on community structure and composition. To relate environmental variables to spatial variation in community structure and composition for each year, we used DistLM models with environmental variables as explanatory variables, using the function *adonis* with 999 permutations. All analyses were carried out using the R package *vegan* (Oksanen *et al*., 2014).

Inter-annual variation in dung beetle communities

To evaluate temporal variation in community metrics, we ran generalized linear mixed-effects models (GLMM) for both total and functional group abundance and richness, using a negative binomial and Poisson distribution, respectively. For total body mass, CWM body mass, and log-transformed extrapolated richness we ran linear mixed-effect models with a Gaussian distribution. We considered year as fixed and sampling site as random effects. Likelihood ratio Chi-square tests were used to compare each model against a null model to evaluate if year had an influence on community metrics. We also ran pairwise comparisons amongst years for all metrics, followed by a Holm-Bonferroni correction, using the *testInteractions* function in *phia* package (Rosario-Martinez, 2015; SAS Institute Inc., 1999). We explored if the temporal variation had any effects on functional group proportions by plotting the relative abundance of functional groups by year. We ran PERMANOVA analysis using the *adonis* function, to evaluate changes in community structure and composition over years. First, we used the respective Bray-Curtis and Jaccard matrices of dissimilarity as response variables and year as an explanatory variable. Then, we ran multiple pairwise comparisons among years, using Holm-Bonferroni corrected *p*-values.

Evaluating the effects of natural inter-annual variation in dung beetle communities on anthropogenic changes

To evaluate the effect of temporal shifts on dissimilarities between undisturbed forests and *Eucalyptus* plantations we standardized abundance, total richness, and total body mass (chosen as these metrics represent the most commonly used community metrics of dung beetle biodiversity) for both land cover classes in each year to have a mean of 0 and standard deviation of 1. Then, we plotted standardized means and their standard error for each metric to evaluate how they varied from the expected if there was no variation over years (zero-value) within land covers. We also calculated Hedge's *g*-value effect size between undisturbed forest and *Eucalyptus* plantation for the same metrics and years, using *mes* function in *compute.es* package, where zero values means no change, while positive and negative values represent a decrease and increase in means from undisturbed forest to *Eucalyptus* plantation, respectively (Del Re, 2013). The effect size was calculated in two ways: 1) comparing the value between undisturbed forest and *Eucalyptus* plantation in each year separately, and 2) using each year in undisturbed forest compared to the mean value of all five years in *Eucalyptus* plantation to isolate the effect of temporal variation in the undisturbed forests.

RESULTS

A total of 10,482 dung beetle individuals belonging to 90 species and morphospecies were sampled in undisturbed forest over the five years, wherein 48 species were identified to species level and 42 as morphospecies. We obtained data on diet and nesting behaviour for 70 species (78% of the total species collected across all years and 98% of all individuals; Table S1), and data on activity period for 61 species (68% of species and 93% of individuals; Table S1).

We sampled the highest number of individuals in 2009 (3,560), and the lowest in 2010 (623). Similarly, the highest number of species was collected in 2009 (74 spp.), and the lowest in 2010 (52 spp.). Species accumulation curves came very close to reaching their asymptote in all years, indicating that our sites provided a good representation of the overall dung beetle community in a given year (Figure S1).

Spatial variation of dung beetle communities

Rain from 3-days before sampling and canopy openness had no influence on total abundance, richness, total body mass, or CWM body mass ($p > 0.05$ in all cases). Coarse sand showed a positive relationship with abundance and total body mass (Figure 1, Table S2), whereas fine sand had a negative influence on abundance and richness (Figure 1, Table S2), and positive effect on CWM body mass (Figure 1, Table S2). Extrapolated richness was not related to any of the environmental variables ($p > 0.05$, Table S2).

For functional group abundance, fine sand content had a negative effect on all functional groups, except for necrophagous beetles, which were not affected (Figure 2). Coarse sand content had negative effects on necrophagous beetles in 2013, while the effects were positive on coprophagous and generalists species (Figure 2). There were also negative effects of canopy openness on coprophagous beetles, but positive effects on necrophagous species, while generalists were negatively related to canopy openness in 2009 and positively in 2011 (Figure 2). Coarse sand was also negatively related to rollers, but positively to tunnelers, while dwellers showed both positive and negative relationships (Figure 2). Canopy openness had no effect on dwellers, while rollers and tunnelers showed positive and negative responses, respectively (Figure 2). Both nocturnal and diurnal beetles were positively affected by coarse sand content (Figure 2). However, while diurnal beetles were negatively associated with canopy openness, nocturnal beetles were positively associated (Figure 2). Rain from 3-days before sampling was negatively related to necrophagous species ($z = -2.575$, $p = 0.010$), and positively with generalist species ($z = 2.257$, $p = 0.024$) only in 2009 and 2013, respectively.

Geographical distance significantly predicted overall spatial variation in community structure ($r_s = 0.267$, $p = 0.023$) and composition ($r_s = 0.256$, $p = 0.041$) only in 2009. On the other hand, both coarse and fine sand content influenced community composition and structure in almost every sampled year (Table S3).

Inter-annual variation in dung beetle communities

All measured community metrics varied significantly among years (Figure 3, Table 2 and S3). There was a marked decline in abundance, species richness and total body mass between 2009 and 2010 (Figure 3), but the values increased again during 2011 and 2012, so that the final measurements in 2013 were similar to the values in 2009 (Figure 3, Table S4). We observed a severe dry season in 2009 (Figure 3). Extrapolated richness was significantly lower in 2010 compared to 2009 and 2013, and in 2012 compared to 2013 (Figure 3). CWM body mass was also higher in 2010 compared to 2011, 2012 and 2013, but similar to 2009 (Figure 3).

Although there was significant variation in the absolute abundance of all functional groups across sampling years that matched inter-annual variation in overall community abundance (Figure 4, Table S5), the relative abundance of functional groups was remarkably stable across years (Figure S2).

There was strong evidence of variation in community structure and composition over years (Table S4). Ordinations revealed similar community structure and composition in 2009 and 2013, which differed from 2010 and 2011 (Figure 5).

Evaluating the effects of natural variation in dung beetle communities on anthropogenic changes

Although both undisturbed forest and *Eucalyptus* plantation presented a similar pattern of inter-annual variation of dung beetle communities metrics within each land cover, undisturbed forest presented higher variation from the expected if there was no variation (zero-value for standardized metrics) in abundance, richness, and total body mass when compared to values in *Eucalyptus* plantations (Figure 6). We observed the negative effect of conversion of undisturbed forest to *Eucalyptus* plantation on abundance, richness, and total body mass (Figure 7A). For all metrics the effect size was higher in 2009 and 2011, followed by 2010; 2012 and 2013 were almost similar (Figure 7A). Specifically, for abundance, the last two years showed very little difference between undisturbed forest and *Eucalyptus* plantation (values of effect size close to zero; Figure 7A). When we isolated the variation of undisturbed forest there were much higher dissimilarities among years, with abundance and total body mass showing no effects of land-use (values close to zero), or even, showing a gain in abundance in 2010 (value lower than zero; Figure 7B).

DISCUSSION

This five-year study of dung beetle communities in Amazonian forests revealed support for two of our three hypotheses. First, we confirmed our expectation that dung beetle communities would vary in space, and this was driven predominantly by their responses to soil texture. Second, in contrast to our expectation, we found that all evaluated metrics of dung beetles community also differed markedly among years, although there was no evidence of shifts in functional group proportion. Finally, we show for the first time how inter-annual variation affects dung beetles in undisturbed forest, and that this can add noise to evaluations of human-induced changes on tropical biota. We discuss our results examining each hypothesis in turn.

Soil texture is the main environmental variable affecting spatial variation in dung beetle communities

Our results indicated a strong relationship between soil texture and spatial variation in dung beetle communities, which even overwhelmed any effect of geographic distance between sites. It is very likely that the role of soil acts via beetle nesting behaviour (Figure 1 and 2). For example, the negative effects of coarse sand on rollers could be associated with the lower retention of moisture in sandy soils, because they usually dig shallower nests than tunnelers (Davis *et al.*, 2010; Hanski & Cambefort, 1991; Osberg *et al.*, 1993). As dwellers live in or right under the dung patch, it is not surprising that their response was less related to soil properties (only in 2009 and weakly in 2012 and 2013). Moreover, any weak relationship could be potentially explained by the indirect effects of competition with rollers or tunnellers), although it is also a possibility that soil properties influence dung humidity and other characteristics directly.

Competition could also explain the lower abundance of beetles in areas with fine sand, as large dung beetles require looser soil to dig their nests giving them a competitive advantage over smaller species, and thus reducing the richness and abundance of the entire community (Carpaneto *et al.*, 2010; Doube, 1990; Hanski & Cambefort, 1991; Figure 1). This was supported by the positive effect of fine sand content on CWM body mass in 2009 and 2011 (Figure 1), which would be consistent with a loss of small individuals or increases in larger ones. The strong influence of soil texture on dung beetle communities suggests that this environmental attribute should be measured in further studies focussing on anthropogenic-induced changes on dung beetles. However, depending on the context, it will be important to recognise that other microhabitat conditions also may influence dung beetle sampling (Mehrabi *et al.*, 2014).

Inter-annual dynamics in dung beetle communities

Dung beetle communities showed highly non-random variation over time (Figure 3, 4 and 5). The variation of all metrics from 2009 to 2010 was most likely related to a severe dry season in 2009 (Figure 3). Even though most adults and immature dung beetles can shelter from desiccation below ground or inside dung pats during the dry season, a severe drought can expose the beetles to high temperatures and low humidity, which increases larval mortality and affects the size of the population in the next year (Hanski & Cambefort, 1991; Scholtz *et al.*, 2009; Sowig, 1995; Vessby, 2001).

The low inter-annual variation in extrapolated richness shows that the severe dry season effects on species loss is related to the size of populations or frequency of capture in each site and not the richness *per se* (Figure 3). Additionally, dung beetle body mass is unlikely to be related to the decrease in species number, as we did not find high variation in CWM body mass (Figure 3), suggesting that the species were equally affected by drought, and that the slight elevation in CWM body mass was probably due the high numbers of small species (Table S1).

It is expected that dung beetles in different functional groups will show different responses to changes in habitat, as discussed in previous studies (e.g. Barragán *et al*., 2011; Nichols *et al*., 2013). However, our study suggests that the changes in community metrics within undisturbed forest are not related to specific responses of functional groups, as there was no conspicuous inter-annual variation in the relative abundance of functional groups (Figure 4 and S6) despite the change in community composition and structure (Figure 5 and Table S4). This indicates a turnover or loss of species within each functional group, but not a loss of the community's functional groups structure. However, the results might be influenced by the coarse-scale to which we have assigned the functional groups, based on categorical traits; temporal changes may be influencing functional groups classified at a finer-scale, and further research is important to fully understand how functional groups shift in space and time (e.g. continuous traits, intra-specific variation).

The recovery of biodiversity after disturbance can be linked to the scale and intensity of the initial disturbance. So while previous studies have shown that dung beetle communities recover from severe disturbances such as habitat loss and fragmentation (Quintero & Roslin, 2005), or the restoration of degraded pasture (Audino *et al.* 2014) on decadal time scales, we showed a relatively quick recovery in just one to three years after severe dry seasons in forest unaffected by other forms of disturbance (Figure 3 and 4). However, although this resilience to climatic variation is positive, there are two important caveats to this conclusion. First, the expected reduction in wet season length and prolonged dry seasons with predicted climate change in Amazonian forests might disrupt the ability of communities to recover before the next disturbance event (Li *et al*., 2006; Malhi *et al*., 2008; Nimmo *et al*., 2015). Second, at the time of the study the native forest areas of our study site were protected from additional anthropogenic disturbances, such as logging, further fragmentation, or wildfires – the combination of which are known to reduce the biodiversity value of Amazonian forests (Barlow *et al.*, 2016). Dung beetle communities could be far less resilient to climatic variation if affected by other forms of disturbance at the same time. The synergistic effects of climate change (e.g. extension and severity of dry season) and direct human-induced changes (e.g. habitat degradation, fragmentation) are known to affect trophic networks and ecosystem services in other taxa (Balvanera *et al*., 2006; Lewis *et al*., 2011; Silveira *et al.,* 2015), and could affect how dung beetles alter plant communities via their role in seedling establishment and soil properties (Lawson *et al*., 2012; Nichols *et al*., 2008; Pérez-Ramos *et al*., 2013; Slade *et al*., 2015).

Baseline variation could influence research on anthropogenic change

It is well known that anthropogenic modifications lead to negative impacts on tropical forest communities (Arellano *et al*., 2008; Korasaki *et al*., 2013; Louzada *et al*., 2010). However, we demonstrate that dung beetle abundance, richness and body mass also show inter-annual variation in both undisturbed forest and modified habitats (*Eucalyptus* plantation; Figure 6), which is often neglected, particularly in 'space-for-time' designs or short-term studies. Although both native forests and plantations showed similar trends in inter-annual variation, we observed some inconsistency in the effect sizes of the comparisons between these systems across different years. For example, effect sizes for abundance are close to zero in 2012 and 2013, but are much larger in other years (Figure 7A), showing that studies could report very different findings depending on the year in which they were carried out.

To isolate the effect of variation from the baseline condition (primary forest communities), we repeated the analysis keeping plantation communities constant. Under this scenario, the inter-annual variation of effect size significantly increased (Figure 7B), revealing the strong importance of variation in the baseline communities. Thus, the effects of baseline variation are likely to increase when comparing areas with temporal asynchrony, in other words, areas where the disturbance has changed the communities' responses to temporal shifts. These results demonstrate the importance of understanding natural variation within ‘control areas’, and disentangling these from anthropogenic-induced changes in communities.

This study shows that a failure to appreciate inter-annual variation could lead to a failure to detect the consequences of even severe forms of land-use change, such as the conversion of native forests to exotic tree plantations, which are well known to harbour different species composition and species-poor communities (Harvey *et al.*, 2006; Vieira *et al.*, 2008; Zurita *et al.*, 2006). The influence of inter-annual variation may be even greater on more subtle forms of anthropogenic change (e.g. restoration areas: Audino *et al.*, 2014; selective logging: Bicknell *et al.*, 2014; França *et al.,* 2016; and natural gradients: Nunes *et al.,* 2016). We are aware of all logistic issues related to longer-term assessments (e.g. funding, human resources), and that short-term projects usually give faster returns. However, by demonstrating the role of temporal variation, we highlight that rapid assessment studies need to viewed with caution, and at the very least should place the survey conditions in a longer-term climatic context to highlight any abnormal conditions that could influence the findings (Chase, 2007; Slade *et al.*, 2011; Trexler *et al.*, 2005).

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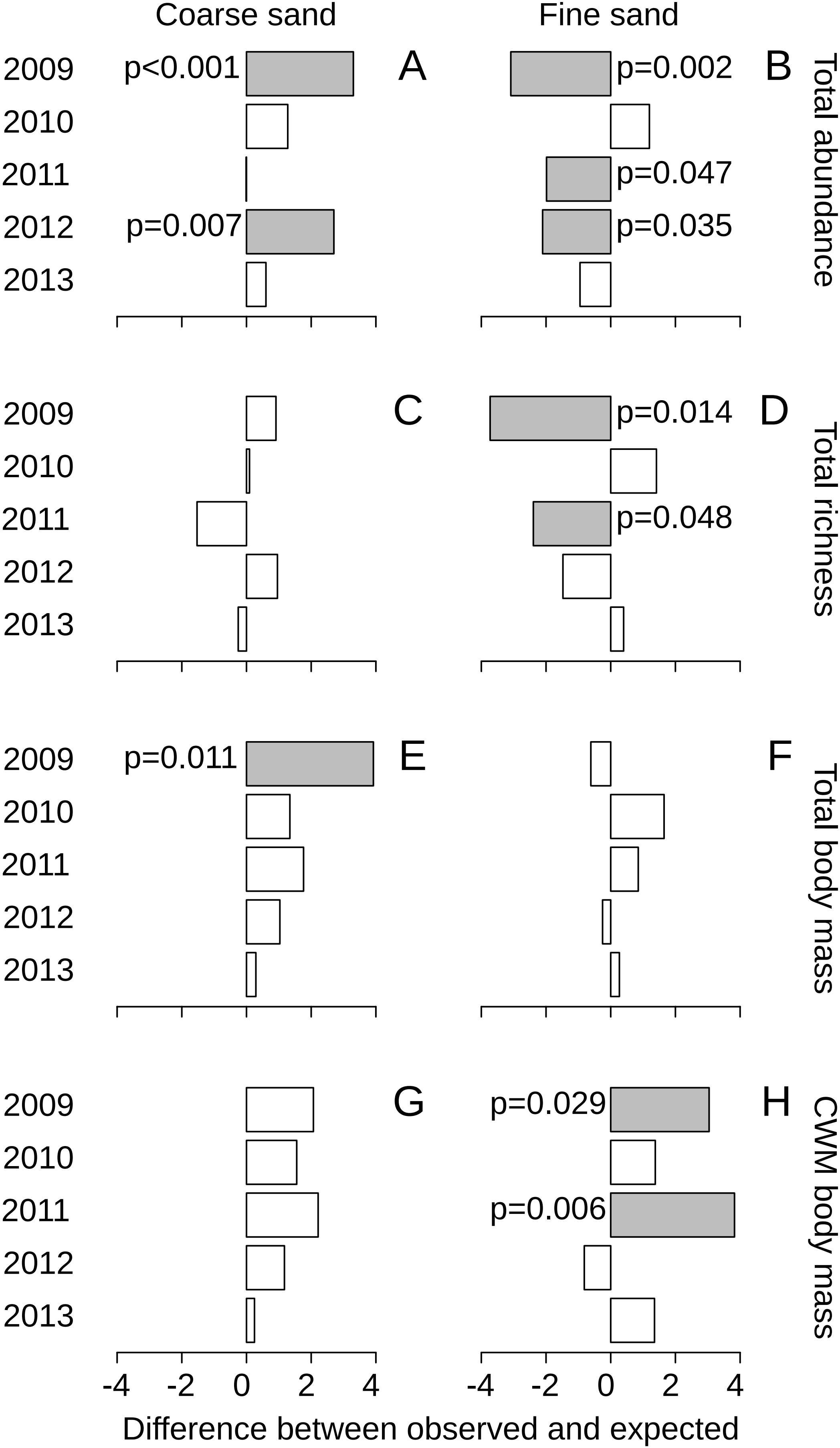
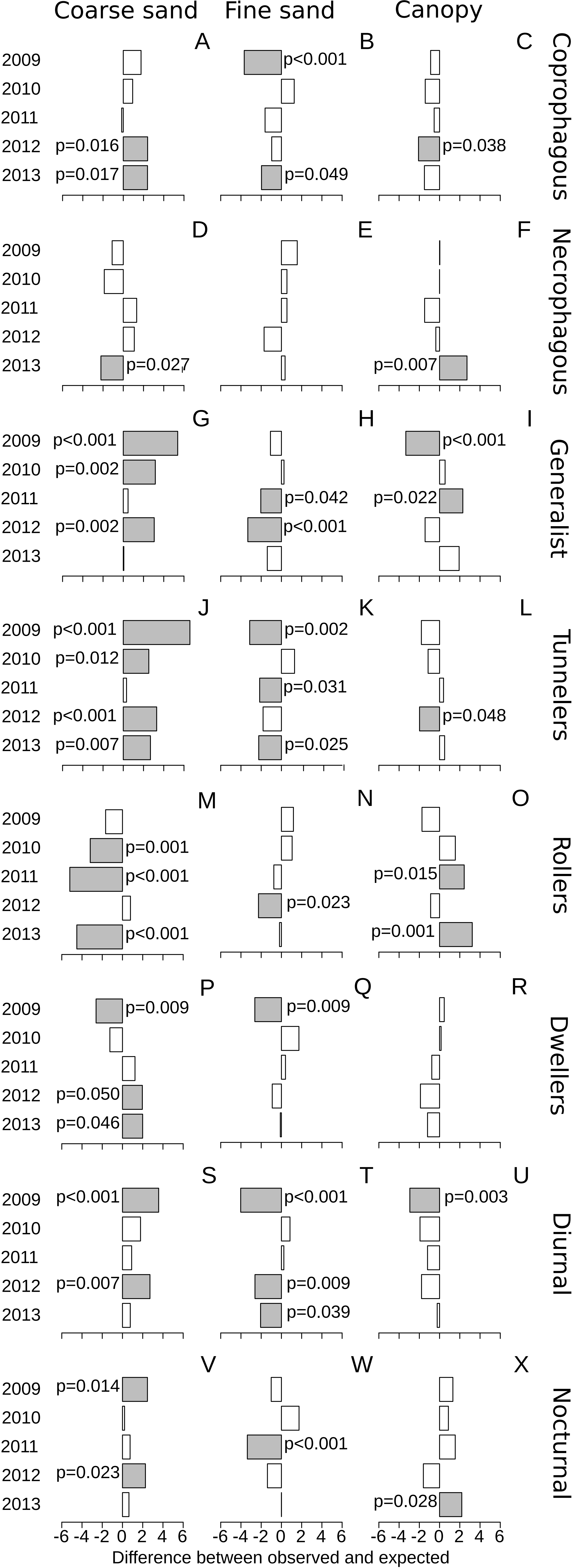
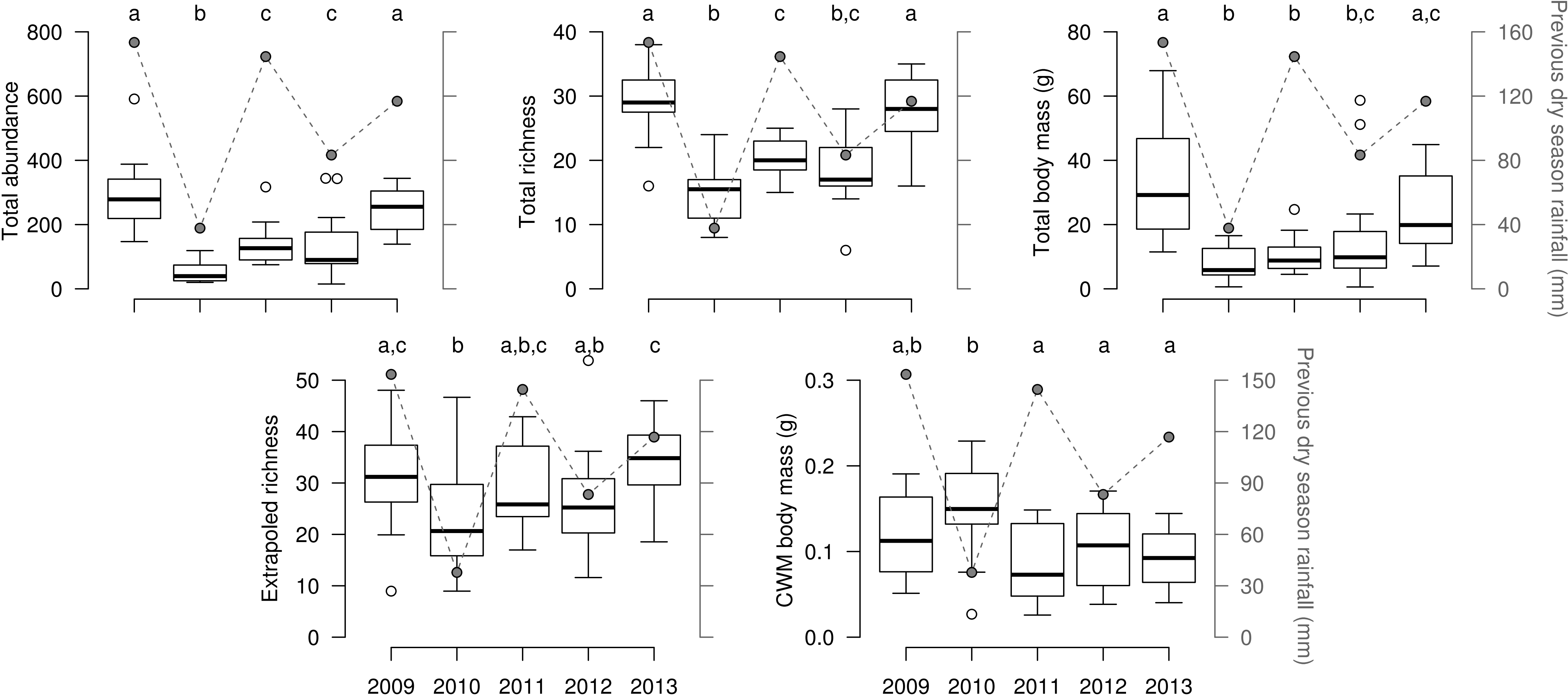
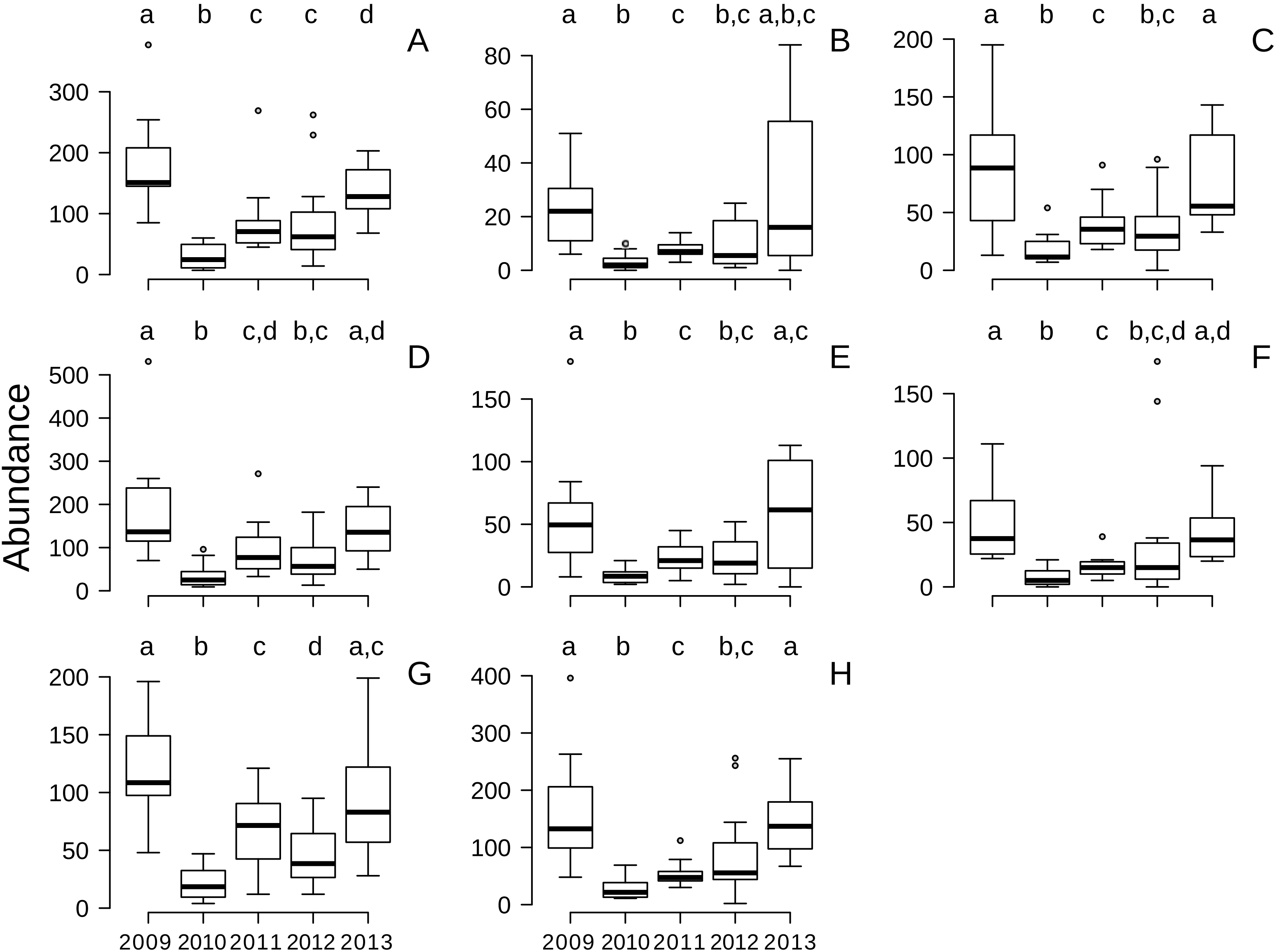
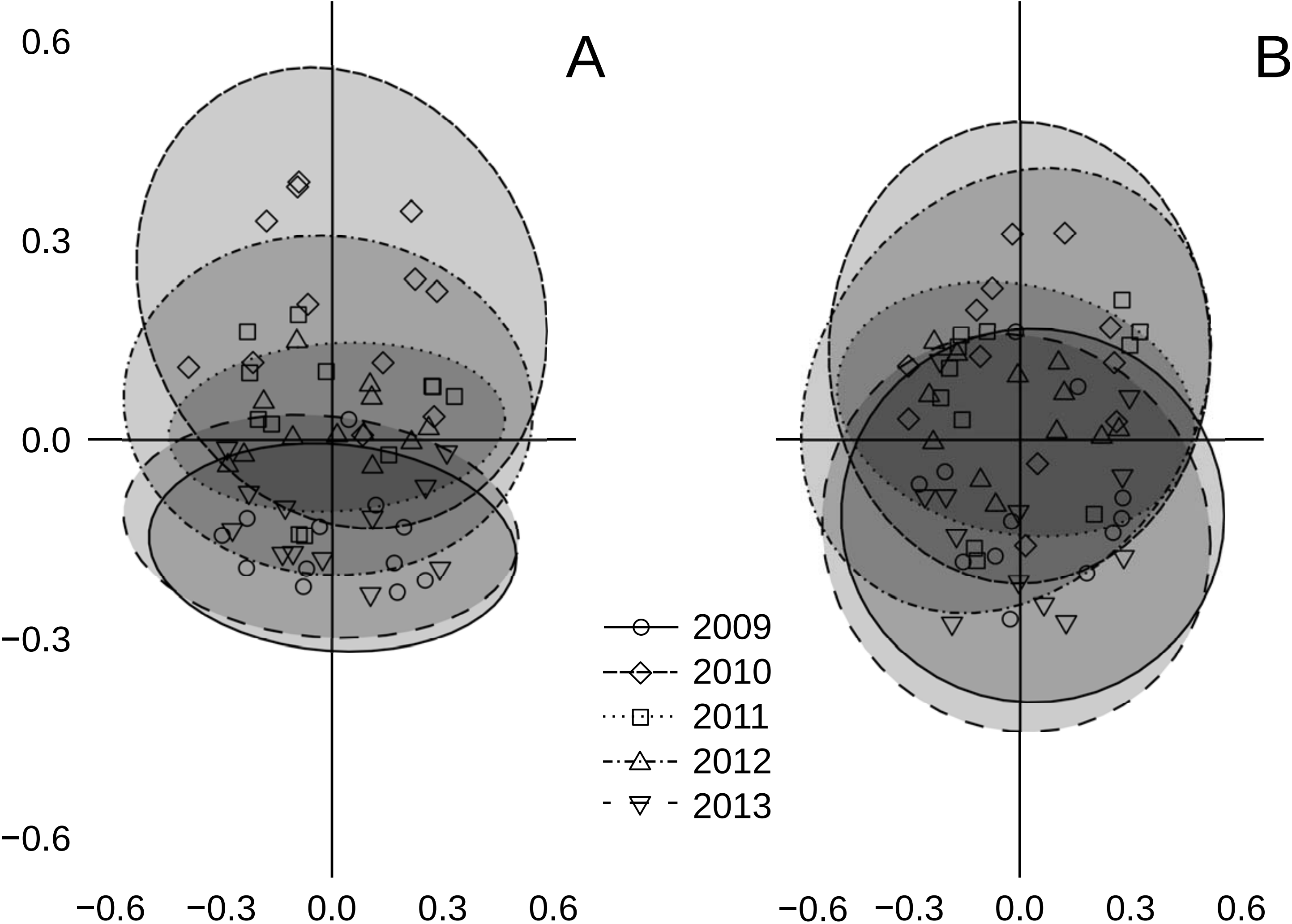
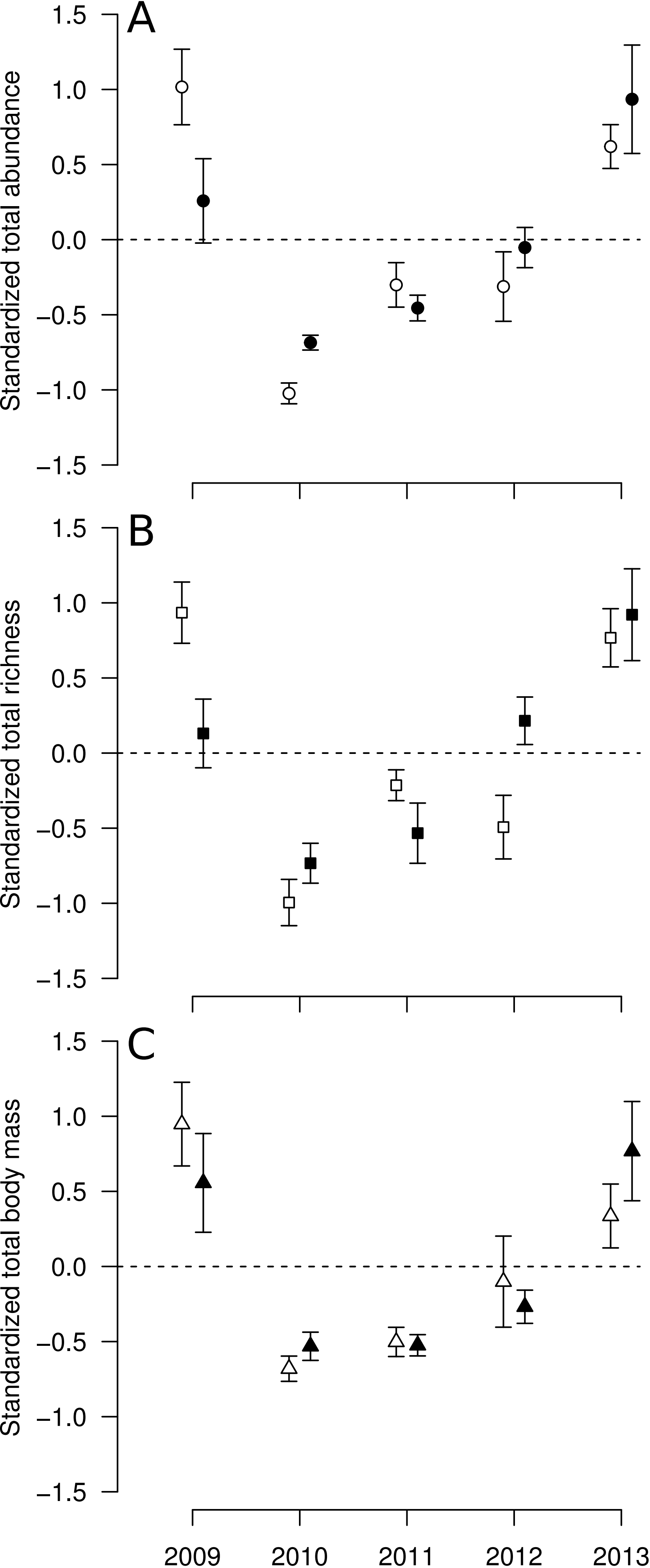

Coarse sand
Fine sand
A
B
C
D
E
F
G
H
Total abundance
Total richness
Total body mass
CWM body mass
2009
2010
2011
2012
2013
p<0.001
p=0.007
p=0.002
p=0.047
p=0.035
p=0.014
p=0.048
p=0.011
p=0.029
p=0.006
-4
-2
0
2
4
Difference between observed and expected


Coarse sand
Fine sand
Canopy
A
B
C
Coprophagous
2009
2010
2011
2012
2013
p<0.001
p=0.016
p=0.038
p=0.017
p=0.049
D
E
F
Necrophagous
2009
2010
2011
2012
2013
p=0.027
p=0.007
G
H
I
Generalist
2009
2010
2011
2012
2013
p<0.001
p<0.001
p=0.002
p=0.042
p=0.022
p=0.002
p<0.001
J
K
L
Tunnelers
2009
2010
2011
2012
2013
p<0.001
p=0.002
p=0.012
p=0.031
p<0.001
p=0.048
p=0.007
p=0.025
M
N
O
Rollers
2009
2010
2011
2012
2013
p=0.001
p<0.001
p=0.015
p=0.023
p<0.001
p=0.001
P
Q
R
Dwellers
2009
2010
2011
2012
2013
p=0.009
p=0.009
p=0.050
p=0.046
S
T
U
Diurnal
2009
2010
2011
2012
2013
p<0.001
p<0.001
p=0.003
p=0.007
p=0.009
p=0.039
V
W
X
Nocturnal
2009
2010
2011
2012
2013
p=0.014
p<0.001
p=0.023
p=0.028
-6 -4 -2 0 2 4 6
-6 -4 -2 0 2 4 6
-6 -4 -2 0 2 4 6
Difference between observed and expected


a b c c a
a b c b,c a
a b b b,c a,c
a,c b a,b,c a,b c
a,b b a a a
Total abundance
0
200
400
600
800
Total richness
0
10
20
30
40
Total body mass (g)
0
20
40
60
80
0
40
80
120
160
Previous dry season rainfall (mm)
Extrapoled richness
0
10
20
30
40
50
CWM body mass (g)
0.0
0.1
0.2
0.3
0
30
60
90
120
150
Previous dry season rainfall (mm)
2009
2010
2011
2012
2013
2009
2010
2011
2012
2013


Abundance
A
a b c c d
0
100
200
300
B
a b c b,c a,b,c
0
20
40
60
80
C
a b c b,c a
0
50
100
150
200
D
a b c,d b,c a,d
0
100
200
300
400
500
E
a b c b,c a,c
0
50
100
150
F
a b c b,c,d a,d
0
50
100
150
G
a b c d a,c
0
50
100
150
200
H
a b c b,c a
0
100
200
300
400
2009 2010 2011 2012 2013
2009 2010 2011 2012 2013


A
B
0.6
0.3
0.0
−0.3
−0.6
−0.6
−0.3
0.0
0.3
0.6
−0.6
−0.3
0.0
0.3
0.6
2009
2010
2011
2012
2013


A
Standardized total abundance
B
Standardized total richness
C
Standardized total body mass
1.5
1.0
0.5
0.0
−0.5
−1.0
−1.5
2009
2010
2011
2012
2013

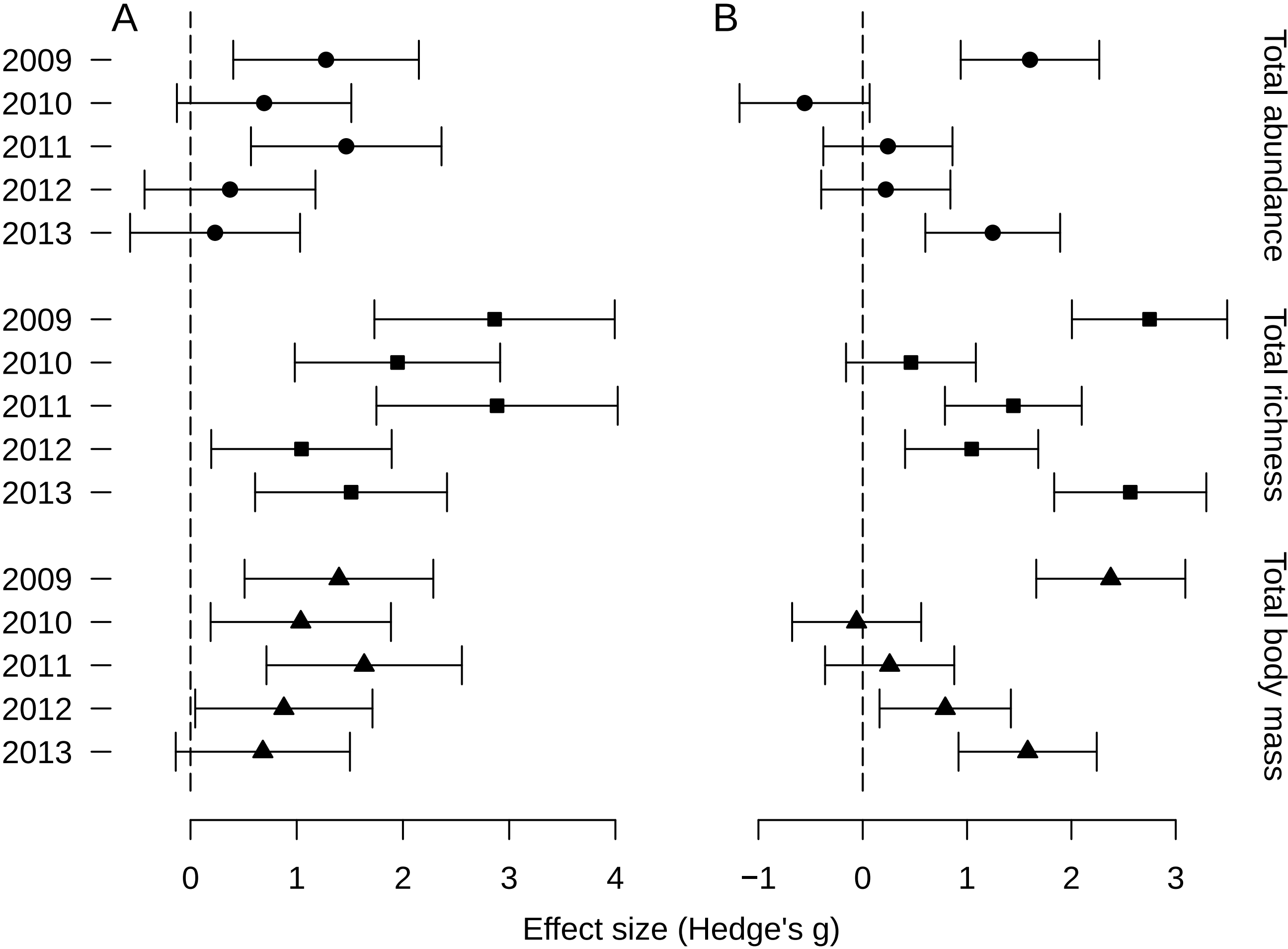

A
B
2009
2010
2011
2012
2013
2009
2010
2011
2012
2013
2009
2010
2011
2012
2013
Total abundance
Total richness
Total body mass
0
1
2
3
4
−1
0
1
2
3
Effect size (Hedge's g)

Table S3: Environmental variables found to be significantly important for changes in community structure and composition in each year.

		Structure			Composition			
		pseudo-*F*	R^2	*p*	pseudo-*F*	R^2	*p*	d.f.
2009	Coarse Sand	6.741	0.389	0.001*	5.730	0.340	0.001*	1,9
	Fine Sand	2.869	0.165	0.001*	3.492	0.207	0.001*	1,9
2010	Coarse Sand	3.286	0.309	0.003*	2.223	0.230	0.005*	1,9
2011	Coarse Sand	4.816	0.287	0.001*	5.370	0.311	0.001*	1,9
	Fine Sand	1.842	0.110	0.022*	1.379	0.080	0.180	1,9
	Rain	1.580	0.094	0.094	1.874	0.109	0.030*	1,9
2012	Coarse Sand	2.783	0.179	0.005*	3.291	0.195	0.006*	1,9
	Fine Sand	4.218	0.271	0.015*	4.989	0.296	0.019*	1,9
2013	Coarse Sand	5.547	0.380	0.003*	5.181	0.367	0.006*	1,9

Table S4: Differences for community metrics in pairwise year comparisons. All p-values are corrected by the Holm-bonferroni method. ‘E. Richness’ = extrapoled richness, ‘CWM body mass” = community weighted-level body mass, and ‘*p-F*’ = *pseudo-F*.

Years	Abundance		Richness		Total body mass		E. Richness		CWM body mass		Structure		Composition	
	X^2	p	X^2	p	X^2	p	X^2	p	X^2	p	*p-F*	p	*p-F*	p
Overall	97.670	<0.001	81.162	<0.001	43.526	<0.001	25.667	<0.001	30.307	<0.001	2.795	<0.001	1.826	<0.001
09-10	79.616	<0.001	54.888	<0.001	33.313	<0.001	12.240	<0.001	6.480	0.076	5.076	0.001	2.533	0.003
09-11	15.836	<0.001	17.667	<0.001	26.209	<0.001	0.828	0.677	5.727	0.100	3.118	0.006	1.711	0.042
09-12	16.660	0.765	28.278	<0.001	13.806	0.002	3.698	0.271	0.838	~1	2.403	0.017	1.854	0.031
09-13	0.763	<0.001	0.330	0.566	4.675	0.153	1.469	0.677	3.495	0.308	1.587	0.104	1.671	0.068
10-11	24.815	<0.001	11.515	0.003	0.425	0.514	6.758	0.065	24.389	<0.001	2.067	0.041	1.474	0.101
10-12	65.021	<0.001	5.084	0.072	4.228	0.158	2.528	0.447	11.977	0.004	1.155	0.307	0.643	0.874
10-13	65.021	0.879	47.357	<0.001	13.029	0.002	21.955	<0.001	19.493	<0.001	4.272	0.001	2.545	0.004
11-12	0.0230	0.006	1.339	0.495	1.971	0.361	1.031	0.677	2.184	0.558	1.116	0.311	1.386	0.115
11-13	9.568	0.005	13.261	0.001	8.745	0.019	4.490	0.205	0.274	~1	3.372	0.002	2.752	0.005
12-13	10.362	0.005	22.706	<0.001	2.413	0.361	9.773	0.014	0.911	~1	1.492	0.145	1.356	0.172

Table S5: Differences for functional group abundances in pairwise year comparisons. All p-values are corrected by the Holm-bonferroni method. *F* = pseudo-*F*.

	Tunnelers		Rollers		Dwellers	
	X^2	p	X^2	p	X^2	p
Overall	42.718	<0.001*	38.365	<0.001*	29.371	<0.001*
2009-2010	58.747	<0.001*	42.934	<0.001*	30.436	<0.001*
2009-2011	9.043	0.011*	10.650	0.007*	10.684	0.008*
2009-2012	18.386	<0.001*	10.354	0.007*	0.445	~1.000
2009-2013	1.433	0.402	0.008	~1.000	0.183	~1.000
2010-2011	21.238	<0.001*	11.542	0.005*	5.314	0.085
2010-2012	11.190	0.005*	11.315	0.005*	23.703	<0.001*
2010-2013	42.050	<0.001*	42.163	<0.001*	26.020	<0.001*
2011-2012	1.636	0.402	0.000	~1.000	6.791	0.046*
2011-2013	3.319	0.205	9.828	0.007*	8.085	0.027*
2012-2013	9.874	0.008*	9.892	0.007*	0.057	~1.000

	Coprophagous		Necrophagous		Generalists	
	X^2	p	X^2	p	X^2	p
Overall	43.170	<0.001*	39.836	<0.001*	42.508	<0.001*
2009-2010	61.858	<0.001*	39.379	<0.001*	52.726	<0.001*
2009-2011	10.254	0.008*	10.807	0.006*	13.496	0.001*
2009-2012	9.988	0.008*	10.104	0.006*	18.796	<0.001*
2009-2013	1.615	0.408	0.040	~1.000	0.169	0.975
2010-2011	22.074	<0.001*	9.991	0.006*	13.545	0.001*
2010-2012	22.466	<0.001*	10.813	0.006*	8.832	0.009*
2010-2013	43.710	<0.001*	42.511	<0.001*	46.702	<0.001*
2011-2012	0.002	0.967	0.010	~1.000	0.482	0.975

2011-2013	3.735	0.213	11.653	0.005*	10.568	0.005*
2012-2013	3.575	0.213	11.742	0.005*	15.481	0.001*

	Nocturnal		Diurnal	
	X^2	p	X^2	p
Overall	51.124	<0.001*	44.964	<0.001*
2009-2010	78.099	<0.001*	53.916	<0.001*
2009-2011	9.387	0.009*	21.676	<0.001*
2009-2012	28.645	<0.001*	6.284	0.049*
2009-2013	2.148	0.221	0.161	0.688
2010-2011	33.756	<0.001*	7.467	0.031*
2010-2012	12.693	0.002*	22.841	<0.001*
2010-2013	55.198	<0.001*	48.200	<0.001*
2011-2012	5.362	0.062	4.411	0.103
2011-2013	2.546	0.221	18.155	<0.001*
2012-2013	15.314	0.001*	4.475	0.103

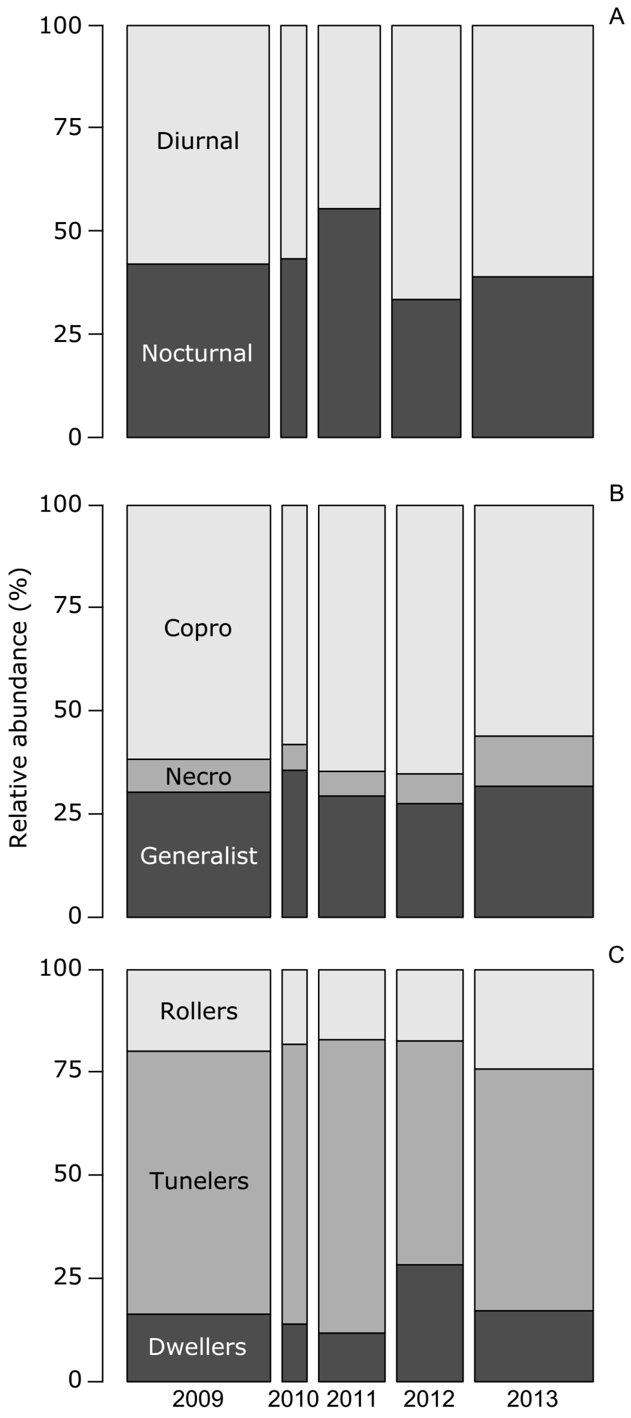


Figure S2: Relative abundance of functional groups by activity period (A), diet preference (B), and nesting behaviour (C). Bars width represents the proportion of total abundance for each year. Copro = Coprophagous and Necro = Necrophagous.

Table S1: List of species and their functional groups. ‘Noc’ = nocturnal, ‘Diu’ = diurnal, ‘Cop’ = coprophagous, ‘Nec’ =, ‘Gen’ = generalist, ‘Tun’ = tunnelers, ‘Rol’ = rollers and ‘Dwe’ = dwellers. ‘body mass’ is the average species body mass.

Morphospecies	Activity Period	Diet preference	Nesting Behaviour	Body mass (g)
Ateuchus aff. *conexus*	Noc	Cop	Tun	0.0198
Ateuchus aff. *murrayi*	Diu	Cop	Tun	0.0065
Ateuchus irinus	-	Cop	Tun	0.0177
Ateuchus pauki	Diu	Gen	Tun	0.0134
Ateuchus sp. A	Noc	Cop	Tun	0.0073
Ateuchus sp. E	-	Cop	Tun	0.0080
Ateuchus sp. F	Diu	Cop	Tun	0.0010
Canthidium aff. *deyrollei*	Diu	Cop	Tun	0.0127
Canthidium aff. *lentum*	Noc	Cop	Tun	0.0095
Canthidium sp. A	Noc	Cop	Tun	0.0214
Canthidium sp. B	Diu	Cop	Tun	0.0278
Canthidium sp. D	Noc	Nec	Tun	0.0046
Canthidium sp. F	-	Cop	Tun	0.0055
Canthidium sp. H	Diu	Cop	Tun	0.0285
Canthidium sp. K	-	Cop	Tun	0.0037
Canthidium sp. L	-	Nec	Tun	0.0065
Canthon bicolor	Noc	Cop	Rol	0.0184
Canthon bimaculatus	Diu	Cop	Rol	0.0585
Canthon lituratus	Diu	Cop	Rol	0.0684
Canthon quadriguttatus	Diu	Nec	Rol	0.0094
Canthon scrutator	Diu	Nec	Rol	0.0091
Canthon simulans	Diu	Cop	Rol	0.0055
Canthon subhyalinus	Diu	Gen	Rol	0.0628
Canthon triangularis	Diu	Gen	Rol	0.0252
Coprophanaeus dardanus	Diu	Nec	Tun	0.2523
Coprophanaeus jasius	Diu	Nec	Tun	0.4884
Coprophanaeus lancifer	Diu	Nec	Tun	2.9072
Deltochilum aff. *peruanum*	Noc	Gen	Rol	0.0430
Deltochilum aff. *submetallicum*	Noc	Nec	Rol	0.2426
Deltochilum carinatum	Noc	Nec	Rol	0.0683
Deltochilum icarus	Noc	Gen	Rol	0.4736
Deltochilum orbiculare	Noc	Cop	Rol	0.4426
Deltochilum septemstriatum	Diu	Nec	Rol	0.0285
Deltochilum sp. A	-	Nec	Rol	0.0674
Deltochilum sp. B	-	Nec	Rol	0.0891
Dichotomius aff. *lucasi*	Noc	Gen	Tun	0.0407
Dichotomius apicalis	Noc	Cop	Tun	0.1297

Dichotomius boreus	Noc	Cop	Tun	0.6393
Dichotomius carinatus	Noc	Cop	Tun	0.4479
Dichotomius imitator	Noc	Cop	Tun	0.1167
Dichotomius latilobatus	Noc	Cop	Tun	0.2568
Dichotomius mamilatus	Noc	Gen	Tun	0.4531
Dichotomius robustus	Noc	Cop	Tun	0.1460
Dichotomius subaeneus	Noc	Cop	Tun	0.1215
Dichotomius worontzowi	Noc	Cop	Tun	0.0158
Eurysternus atrosericus	Diu	Cop	Dwe	0.0505
Eurysternus balachowskyi	Diu	Cop	Dwe	0.0290
Eurysternus caribaeus	Diu	Cop	Dwe	0.0645
Eurysternus cayennensis	Diu	Cop	Dwe	0.0220
Eurysternus foedus	Diu	Cop	Dwe	0.0714
Eurysternus hamaticollis	Noc	Cop	Dwe	0.1170
Eurysternus hypocrita	Diu	Cop	Dwe	0.1733
Eurysternus vastiorum	-	Cop	Dwe	0.0100
Eurysternus ventricosus	Diu	Cop	Dwe	0.0324
Ontherus carinifrons	Noc	Cop	Tun	0.0762
Ontherus sulcator	Noc	Cop	Tun	0.0528
Onthophagus aff. *bidentatus*	Diu	Cop	Tun	0.0072
Onthophagus aff. *clypeatus*	-	Cop	Tun	0.0111
Onthophagus aff. *haemathopus*	Diu	Cop	Tun	0.0075
Oxysternon durantoni	Diu	Cop	Tun	0.1891
Oxysternon festivum	Diu	Gen	Tun	0.3266
Oxysternon silenus	Diu	Gen	Tun	0.0790
Phanaeus cambeforti	Diu	Cop	Tun	0.1060
Phanaeus chalcomelas	Diu	Cop	Tun	0.0520
Sulcophanaeus faunus	Diu	Cop	Tun	1.9300
Sylvicanthon candezei	Diu	Cop	Rol	0.1705
Trichillum pauliani	Noc	Cop	Dwe	0.0205
Uroxys sp. A	Noc	Cop	Tun	0.0074
Uroxys sp. B	Noc	Cop	Tun	0.0011
Uroxys sp. C	Noc	Cop	Tun	0.0086

Table S2: Values of regression analysis for all response variables, with z or t-value depending on the response variable. ‘d.f.’ = degrees of freedom, ‘Canopy’ = Canopy openness, ‘Coarse’ = Coarse sand content, ‘Fine’ = Fine sand content and ‘Rainfall’ = Rainfall of three days before sampling.

Year	Response variable	Explanatory variable	Slope	Standard error	*z* or *t*	*p*	d.f.
2009	Total abundance	Canopy	-0.166	0.095	-1.743	0.081	12,5
2009	Total abundance	Coarse	0.251	0.076	3.304	<0.001*	12,5
2009	Total abundance	Fine	-0.219	0.071	-3.088	0.002*	12,5
2009	Total abundance	Rainfall	0.013	0.041	0.310	0.757	12,5
2010	Total abundance	Canopy	-0.124	0.145	-0.851	0.395	12,5
2010	Total abundance	Coarse	0.317	0.248	1.276	0.202	12,5
2010	Total abundance	Fine	0.258	0.216	1.196	0.232	12,5
2010	Total abundance	Rainfall	0.622	0.486	1.279	0.201	12,5
2011	Total abundance	Canopy	0.062	0.164	0.381	0.704	12,5
2011	Total abundance	Coarse	-0.002	0.132	-0.012	0.990	12,5
2011	Total abundance	Fine	-0.228	0.115	-1.984	0.047*	12,5
2011	Total abundance	Rainfall	-0.059	0.146	-0.408	0.684	12,5
2012	Total abundance	Canopy	-0.518	0.277	-1.870	0.062	12,5
2012	Total abundance	Coarse	0.656	0.243	2.702	0.007*	12,5
2012	Total abundance	Fine	-0.352	0.167	-2.105	0.035*	12,5
2012	Total abundance	Rainfall	0.261	0.392	0.665	0.506	12,5
2013	Total abundance	Canopy	0.107	0.101	1.066	0.287	12,5
2013	Total abundance	Coarse	0.052	0.086	0.601	0.548	12,5
2013	Total abundance	Fine	-0.070	0.074	-0.949	0.342	12,5
2013	Total abundance	Rainfall	0.184	0.221	0.832	0.405	12,5
2009	Total richness	Canopy	-0.075	0.055	-1.366	0.230	12,5
2009	Total richness	Coarse	0.040	0.044	0.911	0.404	12,5
2009	Total richness	Fine	-0.177	0.048	-3.728	0.014*	12,5
2009	Total richness	Rainfall	0.003	0.023	0.142	0.893	12,5
2010	Total richness	Canopy	-0.045	0.107	-0.424	0.689	12,5
2010	Total richness	Coarse	0.017	0.178	0.093	0.929	12,5
2010	Total richness	Fine	0.201	0.142	1.414	0.216	12,5
2010	Total richness	Rainfall	0.290	0.351	0.824	0.447	12,5
2011	Total richness	Canopy	0.002	0.050	0.031	0.976	12,5
2011	Total richness	Coarse	-0.061	0.040	-1.529	0.170	12,5
2011	Total richness	Fine	-0.089	0.037	-2.392	0.048*	12,5
2011	Total richness	Rainfall	-0.012	0.045	-0.262	0.801	12,5
2012	Total richness	Canopy	-0.085	0.166	-0.510	0.626	12,5
2012	Total richness	Coarse	0.138	0.144	0.957	0.371	12,5
2012	Total richness	Fine	-0.179	0.121	-1.477	0.183	12,5
2012	Total richness	Rainfall	0.219	0.209	1.049	0.329	12,5

2013	Total richness	Canopy	0.039	0.076	0.507	0.630	12,5
2013	Total richness	Coarse	-0.017	0.067	-0.256	0.807	12,5
2013	Total richness	Fine	0.022	0.055	0.399	0.704	12,5
2013	Total richness	Rainfall	0.026	0.170	0.153	0.884	12,5
2009	Total body mass	Canopy	-1.163	4.909	-0.237	0.822	12,5
2009	Total body mass	Coarse	15.339	3.910	3.923	0.011*	12,5
2009	Total body mass	Fine	-2.181	3.553	-0.614	0.566	12,5
2009	Total body mass	Rainfall	0.798	2.109	0.378	0.721	12,5
2010	Total body mass	Canopy	-0.934	1.516	-0.616	0.565	12,5
2010	Total body mass	Coarse	3.487	2.600	1.341	0.238	12,5
2010	Total body mass	Fine	3.735	2.264	1.650	0.160	12,5
2010	Total body mass	Rainfall	6.454	5.085	1.269	0.260	12,5
2011	Total body mass	Canopy	0.856	2.298	0.373	0.720	12,5
2011	Total body mass	Coarse	3.273	1.856	1.764	0.121	12,5
2011	Total body mass	Fine	1.352	1.587	0.852	0.422	12,5
2011	Total body mass	Rainfall	-0.318	2.035	-0.156	0.880	12,5
2012	Total body mass	Canopy	-3.826	8.952	-0.427	0.682	12,5
2012	Total body mass	Coarse	8.091	7.843	1.032	0.337	12,5
2012	Total body mass	Fine	-1.322	5.256	-0.252	0.809	12,5
2012	Total body mass	Rainfall	20.936	12.759	1.641	0.145	12,5
2013	Total body mass	Canopy	6.531	6.023	1.084	0.320	12,5
2013	Total body mass	Coarse	1.487	5.126	0.290	0.781	12,5
2013	Total body mass	Fine	1.175	4.384	0.268	0.798	12,5
2013	Total body mass	Rainfall	10.505	13.159	0.798	0.455	12,5
2009	Extrapolated richness	Canopy	-0.264	0.122	-2.159	0.083	12,5
2009	Extrapolated richness	Coarse	0.229	0.104	2.195	0.080	12,5
2009	Extrapolated richness	Fine	-0.009	0.103	-0.084	0.937	12,5
2009	Extrapolated richness	Rainfall	-0.108	0.054	-2.004	0.101	12,5
2010	Extrapolated richness	Canopy	-0.201	0.145	-1.388	0.224	12,5
2010	Extrapolated richness	Coarse	0.211	0.230	0.915	0.402	12,5
2010	Extrapolated richness	Fine	0.271	0.176	1.540	0.184	12,5
2010	Extrapolated richness	Rainfall	0.007	0.460	0.014	0.989	12,5
2011	Extrapolated richness	Canopy	0.006	0.129	0.050	0.962	12,5
2011	Extrapolated richness	Coarse	-0.078	0.103	-0.758	0.473	12,5
2011	Extrapolated richness	Fine	-0.135	0.100	-1.351	0.219	12,5
2011	Extrapolated richness	Rainfall	-0.111	0.130	-0.851	0.423	12,5
2012	Extrapolated richness	Canopy	0.223	0.159	1.409	0.202	12,5
2012	Extrapolated richness	Coarse	-0.015	0.145	-0.103	0.921	12,5
2012	Extrapolated richness	Fine	-0.225	0.124	-1.817	0.112	12,5
2012	Extrapolated richness	Rainfall	-0.055	0.234	-0.235	0.821	12,5
2013	Extrapolated richness	Canopy	0.025	0.079	0.319	0.760	12,5
2013	Extrapolated richness	Coarse	-0.045	0.067	-0.666	0.530	12,5
2013	Extrapolated richness	Fine	-0.013	0.057	-0.236	0.822	12,5
2013	Extrapolated richness	Rainfall	-0.170	0.178	-0.957	0.375	12,5
2009	CWM body mass	Canopy	0.019	0.011	1.733	0.144	12,5

2009	CWM body mass	Coarse	0.018	0.009	2.069	0.093	12,5
2009	CWM body mass	Fine	0.025	0.008	3.042	0.029*	12,5
2009	CWM body mass	Rainfall	-0.003	0.005	-0.589	0.582	12,5
2010	CWM body mass	Canopy	-0.018	0.017	-1.075	0.331	12,5
2010	CWM body mass	Coarse	0.044	0.028	1.553	0.181	12,5
2010	CWM body mass	Fine	0.034	0.025	1.378	0.227	12,5
2010	CWM body mass	Rainfall	0.045	0.056	0.812	0.454	12,5
2011	CWM body mass	Canopy	-0.003	0.011	-0.272	0.793	12,5
2011	CWM body mass	Coarse	0.020	0.009	2.215	0.062	12,5
2011	CWM body mass	Fine	0.029	0.008	3.827	0.006*	12,5
2011	CWM body mass	Rainfall	0.010	0.010	1.019	0.342	12,5
2012	CWM body mass	Canopy	0.000	0.021	0.015	0.989	12,5
2012	CWM body mass	Coarse	0.021	0.018	1.173	0.279	12,5
2012	CWM body mass	Fine	-0.010	0.012	-0.817	0.441	12,5
2012	CWM body mass	Rainfall	0.038	0.029	1.283	0.240	12,5
2013	CWM body mass	Canopy	0.011	0.014	0.761	0.476	12,5
2013	CWM body mass	Coarse	0.003	0.012	0.247	0.813	12,5
2013	CWM body mass	Fine	0.014	0.010	1.354	0.225	12,5
2013	CWM body mass	Rainfall	0.017	0.031	0.559	0.596	12,5
2009	Coprophagous	Canopy	-0.092	0.104	-0.884	0.377	12,5
2009	Coprophagous	Coarse	0.145	0.082	1.758	0.079*	12,5
2009	Coprophagous	Fine	-0.286	0.078	-3.676	<0.001*	12,5
2009	Coprophagous	Rainfall	0.077	0.044	1.731	0.083	12,5
2010	Coprophagous	Canopy	-0.263	0.185	-1.417	0.156	12,5
2010	Coprophagous	Coarse	0.292	0.314	0.930	0.352	12,5
2010	Coprophagous	Fine	0.345	0.273	1.265	0.206	12,5
2010	Coprophagous	Rainfall	0.661	0.618	1.070	0.284	12,5
2011	Coprophagous	Canopy	-0.108	0.201	-0.535	0.593	12,5
2011	Coprophagous	Coarse	-0.026	0.162	-0.160	0.873	12,5
2011	Coprophagous	Fine	-0.229	0.141	-1.617	0.106	12,5
2011	Coprophagous	Rainfall	-0.014	0.179	-0.080	0.936	12,5
2012	Coprophagous	Canopy	-0.651	0.313	-2.081	0.038*	12,5
2012	Coprophagous	Coarse	0.659	0.274	2.407	0.016*	12,5
2012	Coprophagous	Fine	-0.179	0.186	-0.960	0.337	12,5
2012	Coprophagous	Rainfall	0.422	0.441	0.956	0.339	12,5
2013	Coprophagous	Canopy	-0.156	0.104	-1.498	0.134	12,5
2013	Coprophagous	Coarse	0.210	0.088	2.396	0.017	12,5
2013	Coprophagous	Fine	-0.153	0.077	-1.968	0.049*	12,5
2013	Coprophagous	Rainfall	-0.027	0.226	-0.118	0.906	12,5
2009	Necrophagous	Canopy	0.006	0.232	0.027	0.978	12,5
2009	Necrophagous	Coarse	-0.210	0.191	-1.101	0.271	12,5
2009	Necrophagous	Fine	0.261	0.167	1.566	0.117	12,5
2009	Necrophagous	Rainfall	-0.265	0.103	-2.575	0.010*	12,5
2010	Necrophagous	Canopy	0.000	0.212	-0.002	0.998	12,5
2010	Necrophagous	Coarse	-0.688	0.366	-1.878	0.060	12,5

2010	Necrophagous	Fine	0.137	0.251	0.547	0.584	12,5
2010	Necrophagous	Rainfall	-0.453	0.726	-0.624	0.532	12,5
2011	Necrophagous	Canopy	-0.229	0.155	-1.478	0.139	12,5
2011	Necrophagous	Coarse	0.161	0.121	1.326	0.185	12,5
2011	Necrophagous	Fine	0.056	0.103	0.548	0.583	12,5
2011	Necrophagous	Rainfall	-0.119	0.143	-0.833	0.405	12,5
2012	Necrophagous	Canopy	-0.150	0.404	-0.370	0.711	12,5
2012	Necrophagous	Coarse	0.391	0.358	1.090	0.276	12,5
2012	Necrophagous	Fine	-0.495	0.289	-1.714	0.087	12,5
2012	Necrophagous	Rainfall	0.013	0.570	0.023	0.981	12,5
2013	Necrophagous	Canopy	0.755	0.278	2.713	0.007*	12,5
2013	Necrophagous	Coarse	-0.535	0.242	-2.210	0.027*	12,5
2013	Necrophagous	Fine	0.073	0.202	0.362	0.717	12,5
2013	Necrophagous	Rainfall	0.085	0.621	0.137	0.891	12,5
2009	Generalists	Canopy	-0.566	0.170	-3.336	<0.001*	12,5
2009	Generalists	Coarse	0.742	0.138	5.382	<0.001*	12,5
2009	Generalists	Fine	-0.142	0.131	-1.085	0.278	12,5
2009	Generalists	Rainfall	-0.128	0.073	-1.747	0.081	12,5
2010	Generalists	Canopy	0.052	0.096	0.547	0.585	12,5
2010	Generalists	Coarse	0.536	0.169	3.168	0.002*	12,5
2010	Generalists	Fine	0.040	0.156	0.255	0.799	12,5
2010	Generalists	Rainfall	0.500	0.320	1.562	0.118	12,5
2011	Generalists	Canopy	0.360	0.157	2.300	0.022*	12,5
2011	Generalists	Coarse	0.060	0.126	0.473	0.636	12,5
2011	Generalists	Fine	-0.234	0.115	-2.039	0.042*	12,5
2011	Generalists	Rainfall	-0.200	0.148	-1.351	0.177	12,5
2012	Generalists	Canopy	-0.456	0.319	-1.430	0.153	12,5
2012	Generalists	Coarse	0.872	0.285	3.060	0.002*	12,5
2012	Generalists	Fine	-0.829	0.250	-3.321	<0.001*	12,5
2012	Generalists	Rainfall	-0.028	0.450	-0.062	0.950	12,5
2013	Generalists	Canopy	0.283	0.146	1.935	0.053	12,5
2013	Generalists	Coarse	0.007	0.126	0.056	0.956	12,5
2013	Generalists	Fine	-0.155	0.111	-1.397	0.162	12,5
2013	Generalists	Rainfall	0.727	0.322	2.257	0.024*	12,5
2009	Rollers	Canopy	-0.396	0.228	-1.738	0.082	12,5
2009	Rollers	Coarse	-0.306	0.184	-1.667	0.096	12,5
2009	Rollers	Fine	0.197	0.166	1.188	0.235	12,5
2009	Rollers	Rainfall	-0.177	0.099	-1.782	0.075	12,5
2010	Rollers	Canopy	0.195	0.125	1.557	0.120	12,5
2010	Rollers	Coarse	-0.725	0.227	-3.188	0.001*	12,5
2010	Rollers	Fine	0.167	0.158	1.059	0.290	12,5
2010	Rollers	Rainfall	0.016	0.418	0.039	0.969	12,5
2011	Rollers	Canopy	0.303	0.124	2.436	0.015*	12,5
2011	Rollers	Coarse	-0.562	0.108	-5.207	<0.001*	12,5
2011	Rollers	Fine	-0.062	0.083	-0.750	0.453	12,5

2011	Rollers	Rainfall	0.125	0.110	1.130	0.259	12,5
2012	Rollers	Canopy	-0.269	0.304	-0.883	0.377	12,5
2012	Rollers	Coarse	0.210	0.266	0.789	0.430	12,5
2012	Rollers	Fine	-0.461	0.203	-2.267	0.023*	12,5
2012	Rollers	Rainfall	0.345	0.425	0.811	0.418	12,5
2013	Rollers	Canopy	0.636	0.197	3.232	0.001*	12,5
2013	Rollers	Coarse	-0.773	0.171	-4.514	<0.001*	12,5
2013	Rollers	Fine	-0.027	0.143	-0.188	0.851	12,5
2013	Rollers	Rainfall	0.420	0.432	0.972	0.331	12,5
2009	Tunnelers	Canopy	-0.182	0.101	-1.798	0.072	12,5
2009	Tunnelers	Coarse	0.531	0.081	6.589	<0.001*	12,5
2009	Tunnelers	Fine	-0.241	0.077	-3.137	0.002*	12,5
2009	Tunnelers	Rainfall	0.021	0.043	0.484	0.628	12,5
2010	Tunnelers	Canopy	-0.166	0.146	-1.134	0.257	12,5
2010	Tunnelers	Coarse	0.632	0.250	2.525	0.012*	12,5
2010	Tunnelers	Fine	0.283	0.218	1.298	0.194	12,5
2010	Tunnelers	Rainfall	0.740	0.489	1.514	0.130	12,5
2011	Tunnelers	Canopy	0.092	0.235	0.392	0.695	12,5
2011	Tunnelers	Coarse	0.061	0.189	0.323	0.747	12,5
2011	Tunnelers	Fine	-0.357	0.166	-2.152	0.031*	12,5
2011	Tunnelers	Rainfall	-0.056	0.209	-0.266	0.790	12,5
2012	Tunnelers	Canopy	-0.490	0.247	-1.980	0.048*	12,5
2012	Tunnelers	Coarse	0.719	0.218	3.302	<0.001*	12,5
2012	Tunnelers	Fine	-0.276	0.152	-1.813	0.070	12,5
2012	Tunnelers	Rainfall	0.067	0.348	0.193	0.847	12,5
2013	Tunnelers	Canopy	0.060	0.119	0.501	0.616	12,5
2013	Tunnelers	Coarse	0.274	0.102	2.686	0.007*	12,5
2013	Tunnelers	Fine	-0.203	0.091	-2.242	0.025*	12,5
2013	Tunnelers	Rainfall	0.276	0.263	1.047	0.295	12,5
2009	Dwellers	Canopy	0.076	0.164	0.462	0.644	12,5
2009	Dwellers	Coarse	-0.339	0.130	-2.611	0.009*	12,5
2009	Dwellers	Fine	-0.324	0.123	-2.628	0.009*	12,5
2009	Dwellers	Rainfall	0.109	0.070	1.548	0.122	12,5
2010	Dwellers	Canopy	0.032	0.214	0.151	0.880	12,5
2010	Dwellers	Coarse	-0.450	0.361	-1.245	0.213	12,5
2010	Dwellers	Fine	0.502	0.290	1.731	0.084	12,5
2010	Dwellers	Rainfall	1.194	0.711	1.679	0.093	12,5
2011	Dwellers	Canopy	-0.153	0.199	-0.769	0.442	12,5
2011	Dwellers	Coarse	0.198	0.160	1.237	0.216	12,5
2011	Dwellers	Fine	0.055	0.136	0.402	0.688	12,5
2011	Dwellers	Rainfall	-0.210	0.184	-1.142	0.254	12,5
2012	Dwellers	Canopy	-1.159	0.613	-1.892	0.058	12,5
2012	Dwellers	Coarse	1.053	0.536	1.964	0.050*	12,5
2012	Dwellers	Fine	-0.335	0.369	-0.908	0.364	12,5
2012	Dwellers	Rainfall	0.707	0.861	0.821	0.412	12,5

2013	Dwellers	Canopy	-0.193	0.163	-1.190	0.234	12,5
2013	Dwellers	Coarse	0.273	0.137	1.994	0.046*	12,5
2013	Dwellers	Fine	-0.013	0.119	-0.110	0.912	12,5
2013	Dwellers	Rainfall	0.179	0.351	0.512	0.609	12,5
2009	Diurnal	Canopy	-0.342	0.116	-2.938	0.003*	12,5
2009	Diurnal	Coarse	0.332	0.093	3.577	<0.001*	12,5
2009	Diurnal	Fine	-0.365	0.091	-4.027	<0.001*	12,5
2009	Diurnal	Rainfall	0.061	0.050	1.230	0.219	12,5
2010	Diurnal	Canopy	-0.295	0.153	-1.933	0.053	12,5
2010	Diurnal	Coarse	0.459	0.258	1.783	0.075	12,5
2010	Diurnal	Fine	0.191	0.226	0.847	0.397	12,5
2010	Diurnal	Rainfall	0.599	0.507	1.181	0.238	12,5
2011	Diurnal	Canopy	-0.175	0.147	-1.190	0.234	12,5
2011	Diurnal	Coarse	0.108	0.118	0.907	0.364	12,5
2011	Diurnal	Fine	0.024	0.101	0.240	0.810	12,5
2011	Diurnal	Rainfall	-0.086	0.131	-0.653	0.514	12,5
2012	Diurnal	Canopy	-0.635	0.356	-1.783	0.075	12,5
2012	Diurnal	Coarse	0.849	0.313	2.716	0.007*	12,5
2012	Diurnal	Fine	-0.582	0.223	-2.614	0.009*	12,5
2012	Diurnal	Rainfall	0.251	0.504	0.498	0.619	12,5
2013	Diurnal	Canopy	-0.029	0.124	-0.234	0.815	12,5
2013	Diurnal	Coarse	0.081	0.105	0.770	0.442	12,5
2013	Diurnal	Fine	-0.191	0.093	-2.060	0.039	12,5
2013	Diurnal	Rainfall	0.413	0.270	1.531	0.126	12,5
2009	Nocturnal	Canopy	0.126	0.095	1.317	0.188	12,5
2009	Nocturnal	Coarse	0.187	0.076	2.468	0.014*	12,5
2009	Nocturnal	Fine	-0.070	0.070	-1.011	0.312	12,5
2009	Nocturnal	Rainfall	-0.029	0.041	-0.712	0.477	12,5
2010	Nocturnal	Canopy	0.123	0.141	0.873	0.383	12,5
2010	Nocturnal	Coarse	0.050	0.244	0.207	0.836	12,5
2010	Nocturnal	Fine	0.363	0.208	1.743	0.081	12,5
2010	Nocturnal	Rainfall	0.751	0.473	1.587	0.113	12,5
2011	Nocturnal	Canopy	0.277	0.179	1.549	0.121	12,5
2011	Nocturnal	Coarse	0.108	0.143	0.753	0.452	12,5
2011	Nocturnal	Fine	-0.452	0.134	-3.370	<0.001*	12,5
2011	Nocturnal	Rainfall	-0.133	0.163	-0.819	0.413	12,5
2012	Nocturnal	Canopy	-0.390	0.244	-1.601	0.109	12,5
2012	Nocturnal	Coarse	0.485	0.214	2.269	0.023*	12,5
2012	Nocturnal	Fine	-0.207	0.150	-1.383	0.167	12,5
2012	Nocturnal	Rainfall	0.053	0.343	0.156	0.876	12,5
2013	Nocturnal	Canopy	0.309	0.141	2.197	0.028*	12,5
2013	Nocturnal	Coarse	0.078	0.121	0.640	0.522	12,5
2013	Nocturnal	Fine	0.000	0.103	0.004	0.997	12,5
2013	Nocturnal	Rainfall	-0.087	0.316	-0.275	0.783	12,5

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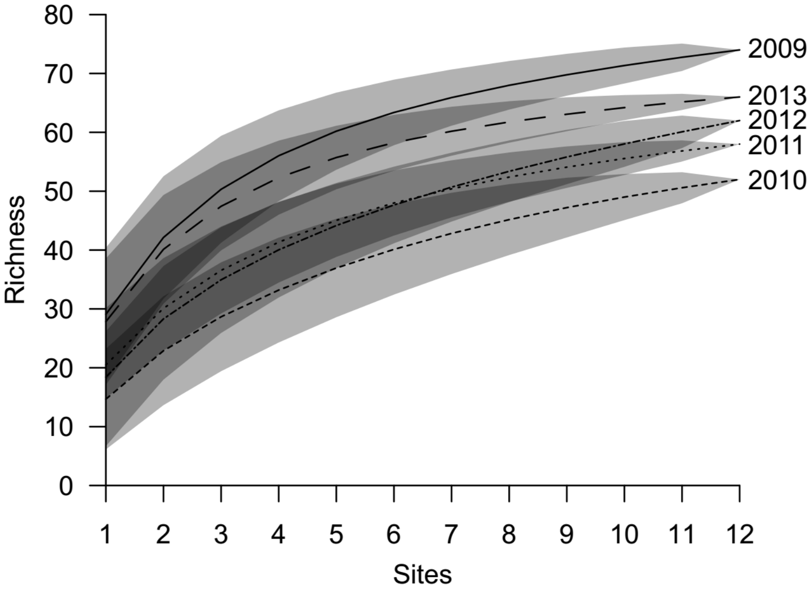

Figure S1: Species accumulation curves of the estimated richness and its 95 % confidence intervals (shaded areas).