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Global dung webs: high trophic generalism of dung beetles along the latitudinal diversity gradient

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Authorship

K.F. and N.B. conceived the initial idea, conducted the design and formal analyses of the study and drafted the manuscript; K.F., T.S., F.T.K., P.W., E.M.S., E.R., C.S.V. and L.Y.C. carried out the field and dung sampling, identified species and/or provided unpublished datasets; T.S., F.T.K., P.W., E.S. and E.R. commented on the manuscript; N.B. acquired funding, designed and coordinated the overall study. All authors declare no conflict of interest and gave final approval for publication.

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Abstract

At the global scale, species diversity is known to strongly increase towards the equator for most taxa. According to theory, a higher resource specificity of consumers facilitates the coexistence of a larger number of species and has been suggested as an explanation for the latitudinal diversity gradient. However, only few studies support the predicted increase in specialization or even showed opposite results. Surprisingly, analyses for detritivores are still missing. Therefore, we performed an analysis on the degree of trophic specialization of dung beetles. We summarized 45 studies, covering the resource preferences of a total of 994503 individuals, to calculate the dung-specificity in each study region. Our results highlighted a significant (4.3-fold) increase in the diversity of beetles attracted to vertebrate dung towards the equator. However, their resource specificity was low, unrelated to diversity and revealed a highly generalistic use of dung resources that remained similar along the latitudinal gradient.

Introduction

The latitudinal gradient, particularly the pronounced increase in plant and animal diversity towards the equator, has fascinated biologists for a long time (Darwin 1859; Wallace 1878) and is still a popular research topic (Hillebrand 2004; LaManna *et al.* 2017; Roslin *et al.* 2017). A predicted *increase* in specialization towards the tropics has been suggested as an explanation of the high diversity found there (MacArthur 1972). Consequently, for a given resource spectrum, a higher resource partitioning in the tropics could contribute to reduce interspecific competition, and a larger resource spectrum in the tropics may additionally increase such a trend. Yet, only a few analyses of trophic or mutualistic interactions have revealed such a trend (Olesen & Jordano 2002; Dyer *et al.* 2007; Peguero *et al.* 2017). On the contrary, specialization of pollinators and frugivores (Schleuning *et al.* 2012), and bark beetles (Beaver 1979) on their host plants decreases towards the equator, and the high specialization level of herbivores and host-parasitoid networks remains similar along the latitudinal gradient (Novotny *et al.* 2006; Morris *et al.* 2014; Forister *et al.* 2015).

At the base of every food web, decomposers process organic material and provide a nutritional basis for higher trophic levels. Whereas plant litter is abundant, but comparably poor in nutrient quality for consumers, animal carcasses or dung – although representing already processed food – represent high quality resources, with high levels of all essential nutrients such as amino acids, fatty acids, and sterols (Enser *et al.* 1996; Carter *et al.* 2007; Frank *et al.* 2017a). Consequently, competition among detritivores for carcasses and dung can be pronounced, an important prerequisite for niche differentiation among competing species. Yet, there are no assessments of global specialization patterns for detritivores on their resources.

Dung beetles (Scarabaeoidea) are known to use a wide range of dung types among a few other resources such as carcasses, humus, and fungi. However, most species feed on vertebrate dung as their main resource (Hanski & Cambefort 1991). These beetles are almost ubiquitous in all climatic zones, including hot spots with over 80 sympatric species in tropical forests and savannahs (Hanski & Cambefort 1991; Davis 2000; Feer & Hingrat 2005; Barragan *et al.* 2011). Hence, we focused on this cosmopolitan superfamily of insects, which evolved a detritivorous life-style over a hundred million years ago (Krell 2006; Philips 2011), to conduct a meta-analyses of their resource-specificity. We compiled datasets from across the globe on the distribution of dung beetles occurring on two or more vertebrate dung types to quantify the extent of dung partitioning across beetle species, as a potential mechanism fostering coexistence and thus diversity. We assessed trends in species diversity and dung type specialization along the latitudinal gradient and with increasing altitude. Although highly specialized tropical dung beetle species exist, often utilizing resources other than vertebrate feces and differentiated in several other niche dimensions, the global analysis for beetle communities captured with commonly available mammalian dung revealed a highly generalistic use of dung resources. This study highlights findings contrary to classical niche theory and fills a gap in current knowledge of detritivores as a basic trophic level.

Material and Methods

We assembled datasets from the literature that included dung beetles trapped by or surveyed from two or more types of dung in the same study area. Most surveys of dung beetle diversity include only a single type of dung, hence could not be used to quantify dung resource specialization. For the comparability of the dung resource specificity, we excluded carrion and vegetable matter as resources in seven studies. We required studies that provided the total abundance of each dung beetle species on each dung type, which excluded studies that pooled species at the genus level, or where abundances were only summarized across dung types. For studies that sampled within different habitats (i.e., forests and grasslands), but with the same dung types, we conducted separate analyses for each habitat to avoid pooling habitat-specific dung beetle communities. In total, we found 34 papers published between 1966 and 2017 that fit our criteria. In addition, we also included 11 of our own unpublished datasets. All datasets including geographic coordinates, the total number beetle species, and the degree of specialization (see below) are summarized in Table S1

(Supporting Information); additional information for separate subsets of the data (habitats) is also included therein.

Data analysis

For improved comparability and to account for variation in sampling and total abundance among the studies, we calculated rarefied diversity (based on 100 permutations), as the studies showed variation in sampling effort, beetle density, and consequently the total number of individuals collected. Unlike species richness, Shannon diversity *H'* has the advantage to account for evenness in species abundance (while being closer to richness in uneven assemblages than Simpson's); its exponential form ($e^{H'}$) converts the index to an 'effective' number of species (Jost 2006). We also computed richness for comparison (Fig. S2, Supporting Information). We set a minimum value of 100 individuals for rarefaction. In seven networks (from four studies, see Table S1 in Supporting Information) the number of individuals was below this threshold and so the non-rarefied effective Shannon diversity was used for these networks.

As a measure of complementary specialization in networks, i.e., the degree of resource partitioning across dung beetle species, the standardized two-dimensional Shannon entropy H_2' (Blüthgen *et al.* 2006) was calculated for the beetle species × dung type matrix with number of individual beetles as cell entries. The minimum (H_2' = 0) is defined for the case where each of the dung beetle species is utilizing different dung types in similar proportions (e.g., cow 70%, horse 30%), whereas the maximum level (H_2' = 1) is reached if all dung types are used as exclusively as possible by different beetle species. Such minimum and maximum H_2' for each network were defined by heuristically re-distributing the beetle individuals across dung types to the highest and lowest entropy possible after fixing the marginal totals of the matrix. Hence, the total abundance of each beetle species and the total number of beetle individuals per dung type are maintained for this standardized method, facilitating comparisons across networks that vary in number of species and individuals. In a null model based on Patefield's algorithm, also based on fixed marginal totals, the individuals were randomly distributed 10^5 times, showing that in 90% of the networks, H_2' was significantly higher than random (Table S1, Supporting Information) (Blüthgen *et al.* 2006). To compare the degree of specialization on each type of dung i, we also computed the species-level Kullback-Leibler distance d_i' that is related to H_2' (Blüthgen *et al.* 2006). For each dung type i, d_i' describes the exclusiveness of the beetle species attracted, i.e., d_i' = 0 if the dung type i is used by similar proportions of each beetle species as found across all other dung types together, while d_i' = 1 if dung type i attracts only exclusive beetle species.

We also quantified the relative attractiveness of dung types, standardized for each network as $N_\mathrm{i}/N_\mathrm{max}$, where N_i is the total number of beetle individuals recorded on dung type i and N_max the maximum number of beetles found for any dung type in this network. In the same way, we quantified the relative number of species attracted as $S_\mathrm{i}/S_\mathrm{max}$, with S_i being the beetle species richness for dung type i and S_max the maximum richness for any dung type in this network. Note that there is no "standard" dung or methodology across all studies, which limits the comparability, as each dung type is evaluated in a variable context of other dung types offered in the same study. Nevertheless, this analysis should be useful for understanding the role of different dung types across the datasets. We thus tested whether these parameters change along the latitudinal gradient for five of the most attractive dung types with the largest number of sampled beetles: human, wildebeest, donkey, sheep, and pig.

We used a linear mixed effects model to test for effects on a latitudinal gradient, accounting for potential linear and quadratic effects of altitude. We thus employed altitude, altitude^2 and absolute latitude as fixed factors. To account for non-independence of data within studies providing multiple networks from the same region, we used the region(s) of each study (geographic coordinates) as random factor. We used this model structure to test the following response variables: resource specificity (H_2'), rarefied effective Shannon diversity ($e^{H'}$), specialization levels for dung types (d_i'), individual and species based attractiveness of dung (N_i/N_{max} ; S_i/S_{max}).

Data analyses were conducted with the statistical software R 3.3.2 (R Core Team 2016). For community analyses (species richness, Shannon diversity) we used the R package 'vegan' (Oksanen *et al.* 2007).

Results

A total of 116 dung beetle networks from 45 studies used in this analysis covered 6 continents and 28 countries, ranging from 60° N to 34° S and 151° E to 103° W (Fig. 1, Table 1) with a high density of studies in Central Europe (Fig. 1 b). As expected, the diversity of dung beetles (rarefied effective Shannon diversity $e^{H'}$) significantly increased towards the tropics (Table 2), with a 4.3-fold increase from the highest latitude (60.7°) to the equator (Fig. 2a; Fig. S2, Supporting Information). Altitude did not have a significant effect on beetle diversity across the studies used for this analysis, although some studies reported a decrease in dung beetles trapped with a single dung type with increasing altitude within a region, e.g., Escobar *et al.* (2005) and Lobo *et al.* (2007) (Table 2).

Dung beetle – resource specificity (H_2') was relatively low (0.23 ± 0.17, range). This high level of generalization remained constant with latitude as well as with altitude (Table 2). Moreover, variation in H_2' was unrelated to (rarefied) Shannon diversity ($F_{1,41} = 0.16$, $p = 0.696$ (Fig. 2b). Neither the number of dung types used in a study nor the number of feeding guilds of dung producers (carnivores, omnivores and herbivores) had a significant effect on H_2' (Fig. S3, Supporting Information). Across the different studies, human dung attracted the highest number of beetle individuals, followed by feces from several herbivorous (wildebeest, donkey, sheep, and cattle) or omnivorous large mammals (pig and wild boar). Among carnivorous mammals, lion and lynx feces had an intermediate attractiveness, whereas dung from puma, wolf, and bear were much less attractive (Fig. 3a). Most of the more attractive dung types also attracted the largest number of species (Fig. 3b). Variation in standardized attractiveness and species richness was highly significant across dung types (N_i/N_{max}: $F_{19, 286}$ =4.3, $p < 0.0001$; S_i/S_{max}: $F_{19, 286}$ =15.0, $p < 0.0001$; focusing on 20 dung types that were each represented in at least five networks). Yet, most of the focal dung types attract a largely representative spectrum of beetle species in similar proportions, resulting in relatively low specialization levels (d_i') (Fig. 3c) that were similar across dung types ($F_{19,286} = 1.1$, $p = 0.31$). Additionally, all parameters (attractiveness, richness, and d_i') remained similar along the latitudinal and altitudinal gradients for each of the four dung types used in at least 10 regions (all $p \geq 0.30$), except for an increase of N_i/N_{max} for sheep dung with latitude ($F_{1,12} = 11.6$, p = 0.005) (Figure S1, Supporting Information).

Discussion

The latitudinal gradient for species diversity and interaction-specificity is subject of ongoing research and comparative approaches (Beaver 1979; Dyer *et al.* 2007;

Schleuning *et al.* 2012; LaManna *et al.* 2017). Here, we analysed, for the first time and on a global scale, the resource specificity of dung beetles. These important detritivores, present in all climatic zones, are key biological indicators in monitoring programs (Scholtz *et al.* 2009), and are of vital importance for many ecosystem functions and services (Nichols *et al.* 2008; Beynon *et al.* 2015). Previous studies on dung beetle diet specialisation (e.g. Philips 2011; Whipple & Hoback 2012; Bogoni et al. 2014) have been regionally restricted, resulting in contradictory results, whereas our study combines a datasets across the globe based on a unified analytical approach, allowing the resource specificity of this group of detritivorous insects to be quantified and compared across larger scales.

We found dung beetle interaction networks differing widely in their degree of specialization ($0.01 \leq H_2' \leq 0.76$), but found no evidence for an increase in specialization towards the equator (Figs. 1 & 2). Dung beetles may be expected to be generalists in higher latitudes due to the low diversity of dung available to specialize on. The low specialization in the tropics may highlight the beetles' ability to opportunistically respond to available resources, as becoming a specialist can incur trade-offs.

Studies on dung beetles differ strongly in their sampling approach and particularly in the dung types used. Likewise, studies across the globe cover substantially different habitats and biomes, resulting in different dung beetle communities and variable resource specificities. Our analysis was confined to studies that used at least two different dung types, which is a relatively small subset of published dung beetle studies. The dung types analysed included livestock, wild animals, exotic (i.e., non-native) dung types and ranged from commonly used cow and human dung to feces of the region-specific mammalian fauna. Cow and human dung are often used as standard dung types as they are thought to attract a large part of the dung beetle fauna (Hanski & Cambefort 1991; Whipple & Hoback 2012; Marsh *et al.* 2013), which was confirmed in our analysis (Fig. 3). Including dung from non-native animals and/or livestock might bias the analysis towards relatively opportunistic, generalist species. However, the diversity of dung types used for this analysis had no effect on the degree of specialization, and native dung did not attract a more specific beetle fauna than other dung types (Fig. 3).

This study corroborates the commonly held assumption that most adult dung beetles are opportunistic and generalized, using a broad range of vertebrate dung types, yet trophic preferences of larvae of certain dung beetle species need to be examined more closely in further approaches as they can differ from adult preferences and become more specialised (Hanski & Cambefort 1991). We did not look at specialization of dung beetles beyond vertebrate dung, but we acknowledge that there are dung beetle species that are highly specialized on particular types of dung such as sloth faeces (Young 1981), marsupial dung or other food items, such as millipede carcasses (Schmitt *et al.* 2004), or, rarely, vertebrate carrion (Larsen *et al.* 2006; Scholtz *et al.* 2009). For future studies, it may also be fruitful to investigate how such specialization and carrion use vary across the beetles' phylogeny and mirror evolutionary shifts from ancestral saprophagy associated with changes in the shape of mandibles (Hanski & Cambefort 1991; Philips 2011).

Dung beetle resource-specificity did not change with altitude. All studies included in the analysis were conducted below 2000 m a.s.l. (except Martinez & Suarez 2006 at ~2600 m a.s.l.). The occurrence of dung beetles is driven firstly by the spatial distribution of dung producing mammals, and secondly by the climatic conditions which constrains all ectothermic insects (Kuhn 2010; Bogoni *et al.* 2016). Thus, the major drivers of altitudinal limitations in dung beetle occurrence are the thermal conditions and altitudinal shifts in vegetation affecting the diversity of mammals the dung beetles rely on.

Theory suggests that specialization on resources provides niche partitioning and thus potentially enhances coexistence and species diversity (McKane *et al.* 2002). However, we found dung beetle communities with high diversity but a low degree of resource specificity (Tshikae et al. 2008, 67 species, H_2' = 0.12), and communities with low diversity but with high specificity (Hewavithana et al. 2016, 22 species, H_2' = 0.41). Across the gradient in dung beetle diversity, the degree of specialization was similar (Fig 2b). This suggests that niche dimensions other than resource selectivity may be important to facilitate the coexistence of dung beetle species. These might be temporal patterns, such as variation in seasonal activity periods and day/night differentiation (Hanski & Cambefort 1991) or differences in dung discovery speed (Jacobs *et al.* 2008). Moreover, spatial partitioning into different (micro-) habitats (Hanski & Cambefort 1991; Mehrabi *et al.* 2014) may promote coexistence of species despite using similar resource types. Such niche differentiation in space, time and/or environmental conditions, e.g., vertical resource stratification due to arboreal mammals or ephemeral dung provided by migrating mammals, may increase towards the tropics and is likely to be particularly pronounced in more diverse mammal faunas. However, global trends of such niche dimensions remain to be tested. Given that dung beetle species within a community show pronounced overlap in utilization of dung resources, higher beetle diversity may improve functional complementarity and redundancy within a community (Finke & Snyder 2008), resulting in increases in the rates, stability, and resilience of ecosystem functions and services provided by dung beetles.

Conclusion

We quantified the beetles' dung-resource specificity (i.e., the degree of specialization in trophic networks characterized by the distribution of beetle species among dung types) across a large sample of all available studies using two or more dung types. Yet, many tropical regions such as the Amazonian basin are still missing in such a comparison of dung beetle resource specificity. The analysis confirms a highly generalistic use of dung by dung beetle communities, at a comparable level as reported for generalized frugivores or nectar-seeking ants (Blüthgen *et al.* 2007; Dyer *et al.* 2007), regardless of latitude or altitude. Additionally, we found no correlation between dung beetle specificity and dung beetle diversity. Although competition across beetle species for dung resources can be severe, and different life-history strategies exist to rapidly utilize and monopolize portions of dung piles, increased specialization does not provide an explanation why so many dung beetle species coexist in a given habitat. This unprecedented analysis is a first step to acquire global patterns for the most basal, trophic level, possibly stimulating global comparisons of other detritivorous systems.

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Table 1

Number of networks (N_{webs}), total number of individulas ($N_{individuals}$), mean number of beetle species (S), mean number of dung types (N_{dung}) and mean resource specificity (H_2') per network for each reference used in the present study.

Reference	N_{webs}	$N_{individuals}$	S	N_{dung}	H_2'
Cambefort (1991)	1	52220	123	2	0.48
Barbero *et al.* (1999)	1	2244	10	4	0.19
Bogoni & Hernandez (2014)	1	426	17	4	0.06
Carpaneto *et al.* (2005)	1	1708	20	2	0.65
Carpaneto *et al.* (2010)	1	2024	25	3	0.12
Correa *et al.* (2016)	2	7089	43	3	0.11
Da Silva & Dorneles Audino (2011)	1	121	7	3	0.59
Davis (1994)	1	14648	52	3	0.33
Davis *et al.* (2010)	1	63934	47	4	0.08
Donovan (1979)	1	456357	6	5	0.01
Dormont *et al.* (2004)	3	5672	21.67	2	0.19
Dormont *et al.* (2007)	4	6353	14.25	4	0.13
Enari *et al.* (2012)	3	1771	8	4	0.31
E. Slade & E. Raine, unpubl. data	3	1141	24	8	0.15
Errouissi *et al.* (2004)	3	6684	9.67	2	0.04
Estrada *et al.* (1993)	1	1567	22	2	0.25
Foster (1993)	8	61829	18.5	2.13	0.13
Frank *et al.* (2017b) and unpubl. data	22	19348	34	7.36	0.23
Galante & Cartagena (1999)	4	955	11	2	0.63
Gardiner (1995)	3	61112	35	3	0.14
Hernandez *et al.* (2012)	1	865	21	3	0.05
Hewavithana *et al.* (2016)	1	454	22	5	0.41
Jay-Robert *et al.* (2008)	6	7485	20.67	2	0.37
Kessler *et al.* (1974)	1	2429	14	2	0.26

E. Slade, L. Yuen Chiew, C. S. Vairappan, unpubl. data	6	9123	39.34	9.34	0.2
Cambefort & Walter (1991) and unpubl. data	1	1614	73	5	0.71
Marsh *et al.* (2013)	1	1288	53	2	0.15
Martín-Piera & Lobo (1996)	1	2477	35	9	0.1
Martinez & Suarez (2006)	1	2574	6	2	0.3
Milotic *et al.* (2017)	4	7845	17	3	0.18
Morelli *et al.* (2002)	1	1846	12	2	0.14
Nibaruta (1982)	4	10123	17.5	4.5	0.27
Paetel (2002)	2	36032	76	5.5	0.18
Rainio (1966)	2	16190	22.5	3	0.26
Ricou (1981)	2	8837	13	2	0.08
Wurmitzer *et al.* (2017) (Austria) and unpubl. data	6	14604	7.34	3	0.03
Shahabuddin *et al.* (2010)	1	1429	28	2	0.04
Cambefort & Walter (1991) and unpubl. data	1	3108	72	3	0.82
Tshikae *et al.* (2008)	1	68393	67	4	0.08
Vernes *et al.* (2005)	1	541	11	5	0.33
Vinod & Sabu (2007)	1	2657	46	2	0.38
P. Walter (1978) and unpubl. data	1	18932	100	5	0.06
Whipple & Hoback (2012)	1	7395	15	11	0.03
Wurmitzer *et al.* (2017) (Argentina) and unpubl. data	4	1050	13.75	9	0.34

Table 2

Rarefied effective Shannon diversity ($e^{H'}$) increased significantly with declining latitude, while altitude had no effect. The beetles' resource specificity (H_2') showed no significant change for both, altitude and latitude.

	rarefied $e^{H'}$		H_2'	
	$F_{1,45}$	p	$F_{1,45}$	p
Altitude	0.23	0.64	2.45	0.12
Altitude^2	1.03	0.32	0.50	0.48
|Latitude|	29.44	0.0001	1.52	0.22

Figure legends

Figure 1

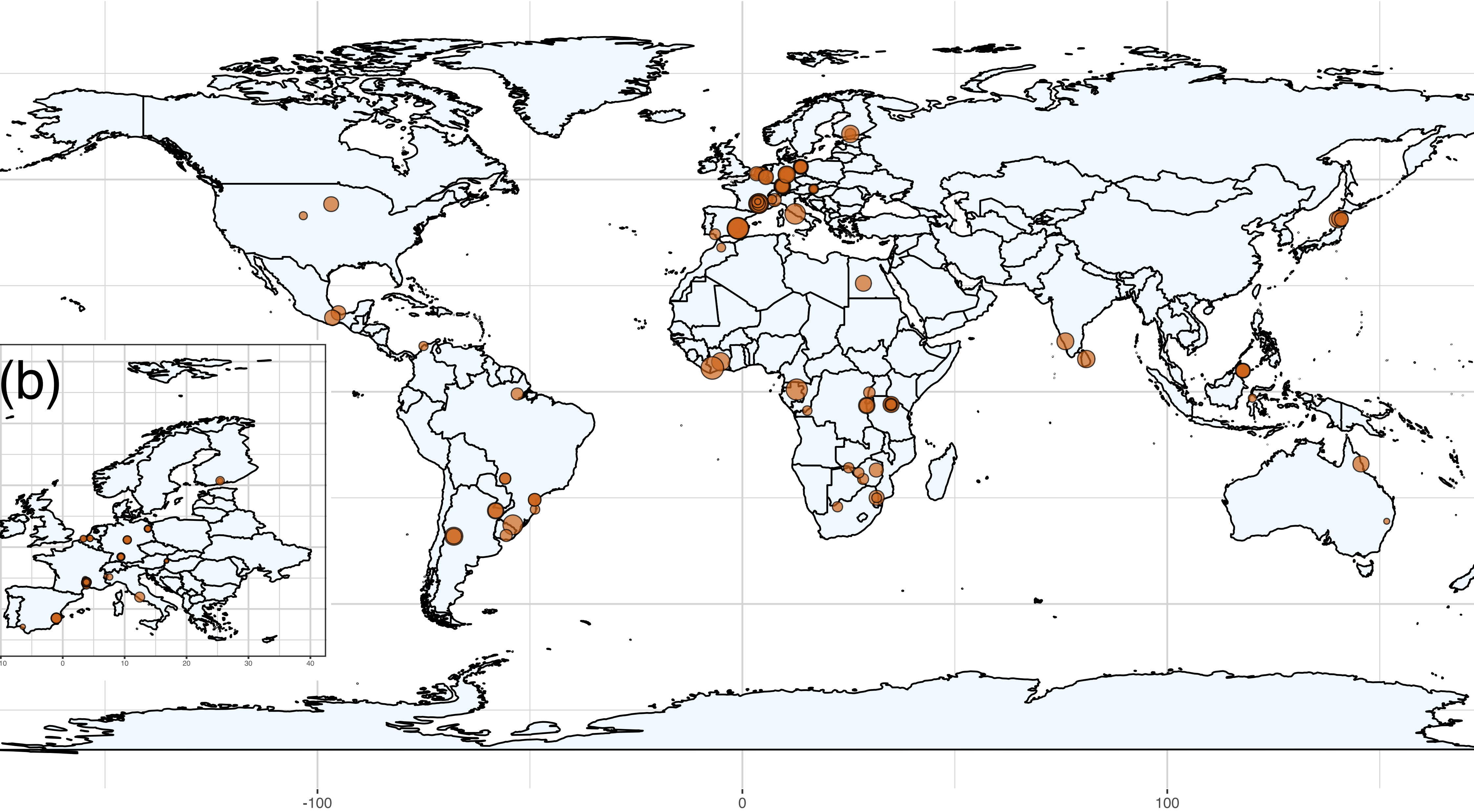
Global (a) and European (b) map for beetle – dung networks represented in this study. Dot positions represent the sampling region, their sizes increase with the degree of dung specificity H_2'.

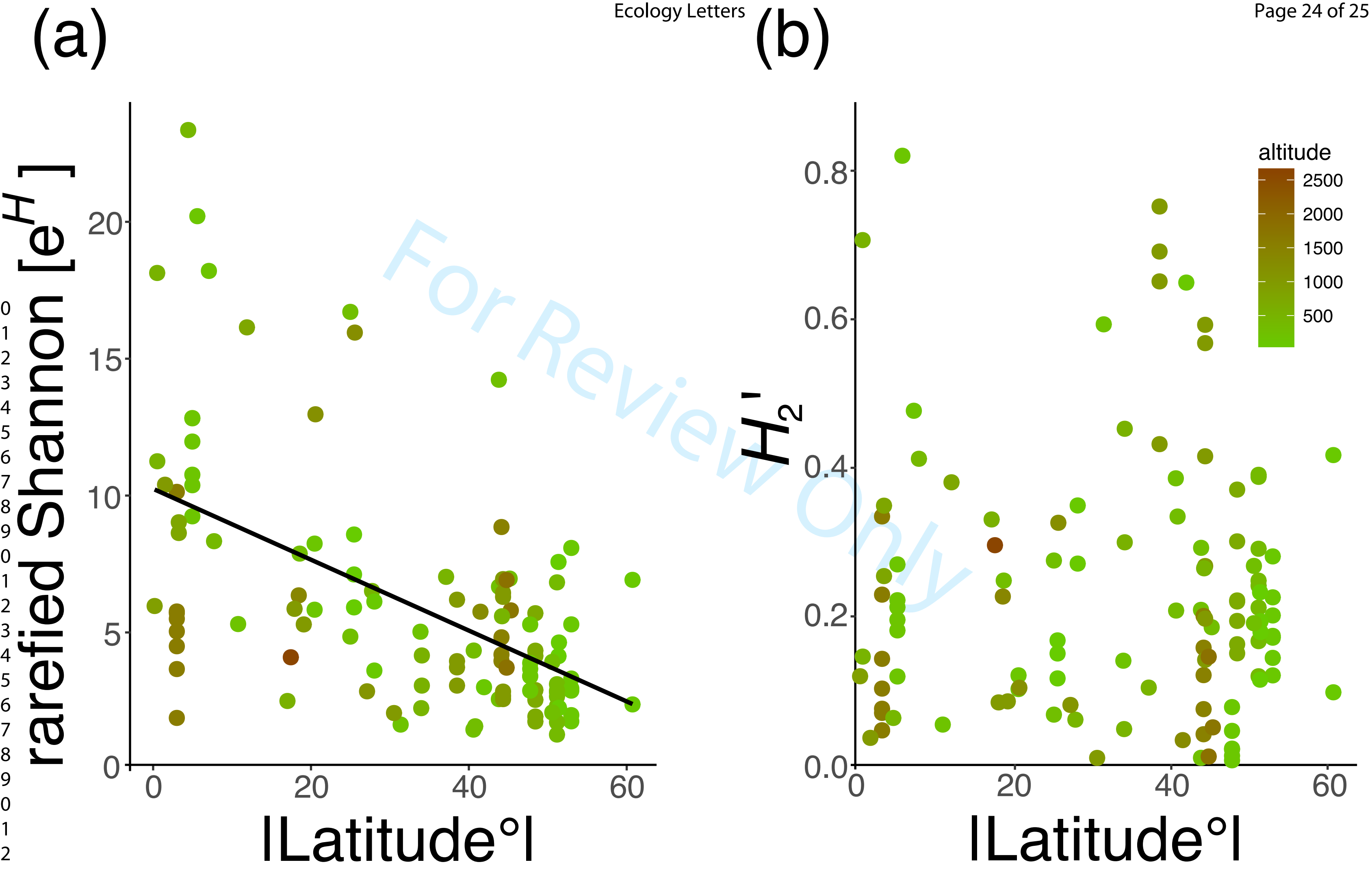
Figure 2

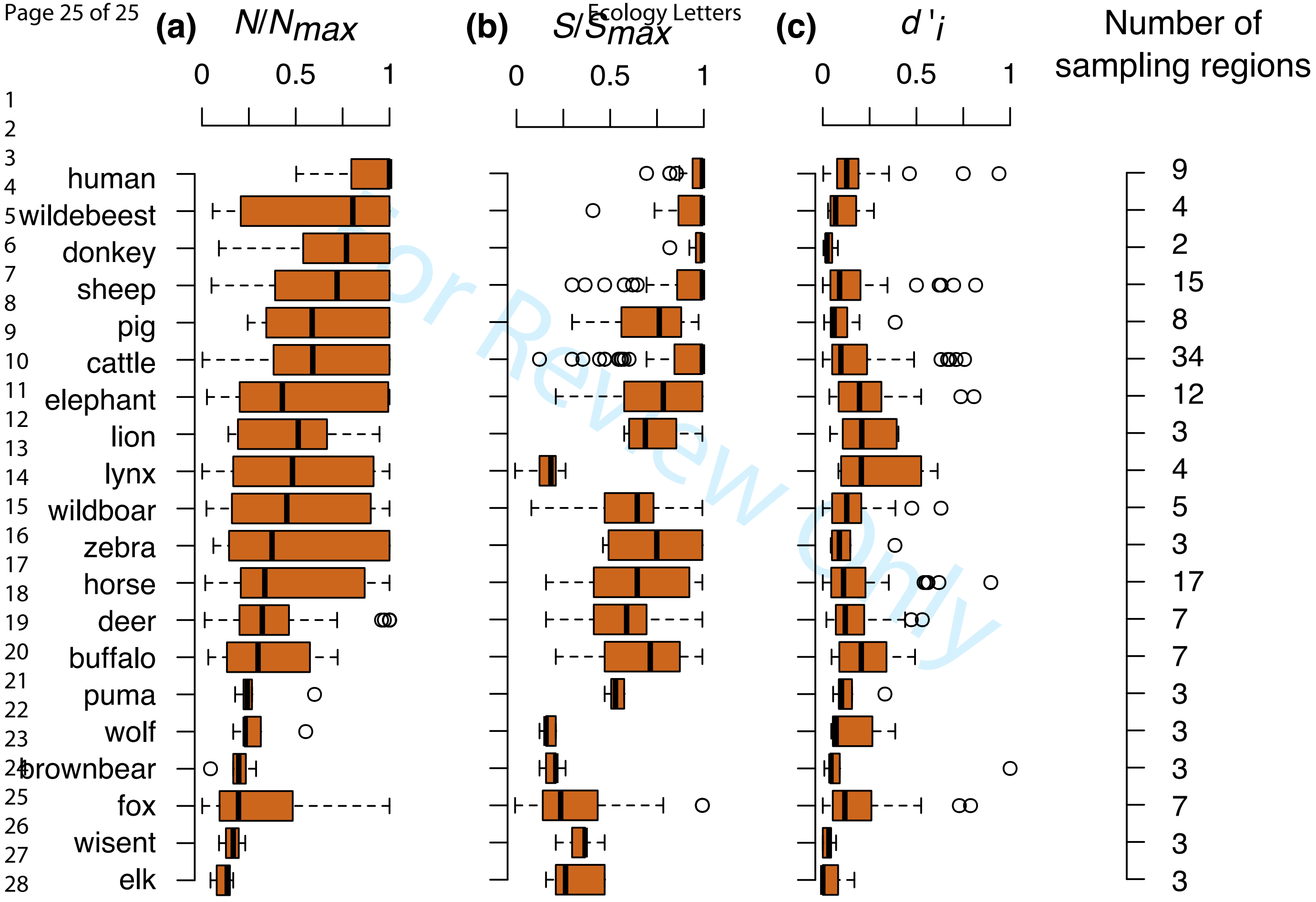
Changes in (a) effective Shannon diversity (rarefied $e^{H'}$ for 100 individuals per network) and (b) dung-type specificity H_2' along an absolute latitudinal gradient (0° = equator, northern and southern hemisphere plotted up to 60°). Colouring of dots represent the altitude of the study region.

Figure 3

Dung beetle attraction to 20 commonly used dung types (all dung types represented in at least 5 networks in our analysis). (a) The attractiveness of dung was expressed as the number of beetle individuals N_i per dung type relative to the most attractive dung type in each study (N_i/N_{max}), and (b) the number of beetle species S_i was expressed in relation to the maximum found per study accordingly (S_i/S_{max}). (c) The degree of specialisation of each dung type (d_i') quantifies the relative composition of dung beetle species in comparison to the other dung types in the study.


(b)
10
0
10
20
30
40
-100
0
100


(a)
rarefied Shannon [e^H]
0
5
10
15
20
0
20
40
60
|Latitude°|
(b)
H_2'
0.0
0.2
0.4
0.6
0.8
0
20
40
60
|Latitude°|
altitude
2500
2000
1500
1000
500


(a)
N/N_{max}
0
0.5
1
(b)
S/S_{max}
0
0.5
1
(c)
d'_i
0
0.5
1
Number of sampling regions
human
wildebeest
donkey
sheep
pig
cattle
elephant
lion
lynx
wildboar
zebra
horse
deer
buffalo
puma
wolf
brownbear
fox
wisent
elk
9
4
2
15
8
34
12
3
4
5
3
17
7
7
3
3
3
7
3
3