



Drivers of taxonomic, functional and phylogenetic diversities in dominant ground-dwelling arthropods of coastal heathlands

Axel Hacala^{1,2} · Denis Lafage^{1,3} · Andreas Prinzing¹ · Jérôme Sawtschuk² · Julien Pétilion¹

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Abstract

Although functional and phylogenetic diversities are increasingly used in ecology for a variety of purposes, their relationship remains unclear, and this relationship likely differs among taxa, yet most recent studies focused on plants. We hypothesize that communities may be diverse in functional traits due to presence of: many phylogenetic lineages, trait divergence within lineages, many species and random functional variation among species, weak filtering of traits in favorable environments, or strong trait divergence in unfavorable environments. We tested these predictions for taxa showing higher (ants), or lower (spiders, ground beetles) degrees of competition and niche construction, both of which might decouple functional traits from phylogenetic position or from the environment. Studying > 11,000 individuals and 216 species from coastal heathlands, we estimated functional as minimum spanning trees using traits related to the morphology, feeding habits and dispersal, respectively. Relationships between functional and phylogenetic diversities were overall positive and strong. In ants, this relationship disappeared after accounting for taxonomic diversities and environments, whereas in beetles and spiders taxonomic diversity is related to functional diversity only via increasing phylogenetic diversity. Environmental constraints reduced functional diversity in ants, but affected functional diversity only indirectly via phylogenetic diversity (ground beetles) and taxonomic and then phylogenetic diversity (spiders and ground beetles). Results are consistent with phylogenetic conservatism in traits in spiders and ground beetles. In ants, in contrast, traits appear more phylogenetically neutral with any new species potentially representing a new trait state, tentatively suggesting that competition or niche construction might decouple phylogenetics from trait diversity.

Keywords Neutral theory · Phylogenetic conservatism · Functional trait · Spiders · Carabids · Ants · Maritime clifftops · Habitat filtering

Introduction

Species communities are considered particularly valuable if they are biologically diverse. Biological diversity has for long been quantified in terms of richness of species, i.e. “taxonomic diversity” (TD). However, a community that is diverse taxonomically is not necessarily diverse in terms of phylogenetic lineages or functional traits represented by the community, quantified as minimum spanning tree connecting all species across a phylogeny or in a trait-space: the phylogenetic or functional diversities (PD, FD), sensu Faith (1992). Growing in popularity during the last twenty years (Webb et al. 2002; Campbell et al. 2010), FD and PD have been very useful in a large variety of contexts. In applied ecology for instance, phylogenetic diversity (PD) was successfully used to establish conservation prioritization (Rodrigues et al. 2005; Magura 2016; Tucker et al. 2018; Wong

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Axel Hacala and Denis Lafage contributed equally to the work.

✉ Axel Hacala
axel.hacala@gmail.com

¹ UMR CNRS 6553 Ecobio, Université de Rennes, 263 Avenue du Gal Leclerc, CS 74205, 35042 Rennes Cedex, France

² EA Géoarchitecture: Territoires, Urbanisation, Biodiversité, Environnement, Université de Bretagne Occidentale, CS 93837, 29238 Brest Cedex 3, France

³ Department of Environmental and Life Sciences/Biology, Karlstad University, Karlstad, Sweden

et al. 2019). PD was also proven relevant for understanding community assembly rules and underlying interactions (Cavender-Bares et al. 2009). The same is true for functional diversity (FD), with cases where functional diversity led to a better understanding of ecological processes that classical taxonomic diversity alone did not properly assess (Leroy et al. 2014; Campbell et al. 2010; Wong et al. 2019).

A positive relationship between different aspects of diversities has often been taken for granted, for instance when using PD as a proxy for FD (Webb et al. 2002). However, existing theory on ecological communities makes different hypotheses and predictions on relationships between diversities. Specifically, we may hypothesize that communities may be diverse in functional traits due to the presence of many phylogenetic lineages and trait conservatism within lineages (sensu Wiens et al. 2010). Phylogenetic conservatism is often considered to be strong (Darwin 1859 in Webb et al. 2002; Wiens 2010), but has rarely been demonstrated locally (Pavoine et al. 2010) and hence the links between local PD and FD are not fully elucidated (Gerhold et al. 2015; Cadotte et al. 2019). Only if local phylogenetic conservatism is perfect, does an increase in PD inevitably increase FD (Webb et al. 2002). However, locally, phylogenetic conservatism may not be perfect or even be absent (Eterovick et al. 2010; Haak et al. 2014; Grundler et al. 2018; Baulechner et al. 2020). In that case, we may hypothesize that community assembly is driven by the most simple, neutral processes (Hubbell 2001): traits are unimportant so that any species arriving or going extinct carries a random chance of representing a unique trait state within a given community (Purves and Turnbull 2010; Novack-Gottshall 2016). FD would hence increase with taxonomic diversity (TD), not with PD. Alternatively, we may hypothesize that under low PD, character displacement occurs: the many related species outcompete each other if too similar, leading to a negative relationship between PD and FD (Prinzing et al. 2008) or at least a disappearance of positive relationship. Finally, FD may be driven by the environment rather than PD or TD of the community. We may hypothesize that severe environmental constraints select against certain functional trait states and hence reduce FD (Webb et al. 2002), or that such constraints impose character displacement among species and reduce niche packing (Safi et al. 2011; Prinzing 2016) and thereby increase FD. FD would hence decrease or increase, respectively, with environmental constraints. Different hypotheses might apply to different taxa. Taxa where competition is important are least likely to show a positive relationship between PD and FD and most likely to show a negative. Also, in taxa capable of niche construction (i.e. enduringly manipulating their selective environment: Odling-Smee et al. 2013), traits might become emancipated from the environment, resulting in species diversity being little constrained by environmental filters.

Despite this diversity of theoretically possible relationships between PD and FD, several authors argued that PD is a proxy of FD, and that the more traits are used to calculate FD the more it will resemble PD (Flynn et al. 2011; Khalil et al. 2018; Tucker et al. 2018). As recently highlighted by Cadotte et al. (2019), most studies showed a positive correlation between phylogenetic and functional diversity (PFC). Yet the spectrum of correlation strength is wide, with a few studies even reporting negative correlations (Prinzing et al. 2008; Bernard-Verdier et al. 2013). This gray area led to debate about the relationships between PD and FD (Pavoine et al. 2013; Tucker et al. 2018), and highlights the need for more empirical studies. Yet, most of previous work was done on plant communities (Cavender-Bares et al. 2009; Campbell et al. 2010), this redundancy of study models being recurrent in ecology, and easily fixed by multiplying model taxa (Coelho et al. 2009; Gerlach et al. 2013; Wong et al. 2019).

Our study therefore proposes to compare the PFC between several dominant taxa of arthropods using a standardized sampling protocol taking advantage of a large-scale restoration design on maritime clifftops, and to assess whether taxonomic diversities and/or abiotic forces drive both functional and phylogenetic diversities in each taxa. We studied three groups of arthropods, spiders, ground beetles and ants. These arthropods are known to complement vegetation survey (Pétillon et al. 2014; Hacala et al. 2020), and thereby offer an interesting opportunity to better understand the link between PD and FD (Wong et al. 2019). Spiders, ants and ground beetles are dominant ground-active macroarthropods in several temperate habitats, and their traits and phylogeny are relatively well known (Bond et al. 2014; Pedley et al. 2014; Schirmel et al. 2016; Magura 2016; Parr et al. 2017). To our knowledge, one publication has already treated PD and FD for a single group of ground-dwelling arthropods (Arnan et al. 2015), and some have conducted simple bivariate correlations between FD to PD (Corbelli et al. 2015; Liu et al. 2016), all having observed a positive PFC (but see Ridel et al. 2021). The novelty of our study resides in the fact that we look for more than just bivariate correlation but investigate the complex driving forces behind patterns of taxonomic functional and phylogenetic diversities of spiders, carabids and ants. Moreover, we use our above framework of hypotheses to predict differences between spiders, carabids and ants in what drives FD: The three groups differ in the two characters that may influence the drivers of FD. First, competition has been frequently demonstrated among ants (Cerdeña et al. 2013) but less so in ground beetles (Niemelä 1993) and least in spiders (Wise 2006). Given our above hypotheses, we hence expect negative relationships between PD and FD to be most likely or positive relationships between PD and FD least likely in ants, and the inverse in spiders. Second, niche construction

is very strong in ants through building of formicaries and farming fungi or aphids (Odling-Smee et al. 2013), it exists to a lower degree in many spiders due to web-building, and it is probably inexistent or weak in ground beetles. Given our above hypotheses, ants might hence depend least on abiotic factors that constrain individual survival in other taxa, such as salinity or humidity (Petillon et al. 2008 for ground beetles and spiders) and ground beetles might depend most on these factors. However, we acknowledge that ants might depend more on factors that constrain the construction of formicaries such as soil depth (Schmidt et al. 2017).

Methods

Sampling and identification

Sampling took place in three coastal sites of Brittany, Western France in 2017: L'Apothicaire (47° 21' 44.0" N, 3° 15' 34.9" W), La Pointe de l'Enfer (47° 37' 18.3" N 3° 27' 46.9" W) and La Pointe de Pen-Hir, located on the mainland (48° 15' 03" N, 4° 37' 25" W). These sites were selected for they are all comparable with similar dominant vegetation (a short and dry heathland dominated by *Erica* spp. and *Ulex* spp.), and under ongoing ecological passive restoration. The degradation on each sites was subdivided into 3 degradation states. This division was defined by vegetation states, bare-ground surface and age from restoration actions. This subdivision was only used to spacialize the sampling for bare ground and was used as a proxy of degradation in our models (see full description of study sites and pictures in Hacala et al. 2020 and landscape context in Online Resource 1).

Two 400 m² plots of homogeneous vegetation were set for each degradation state, and four pitfall traps (80 mm in diameters and 100 mm deep) were set at each plot. Each plot were situated at least 100 m from the nearest differing habitats (see Online Resource 1). Traps were half-filled with a salted solution (250 g L⁻¹) with a drop of odorless soap and settled 10 m apart to avoid interference and local pseudoreplication (Topping and Sunderland 1992). This resulted in 71 traps (in one station, the sampling area was too restricted to set 4 traps spaced of 10 m apart, so 1 was removed) active between mid-March to mid-June 2017, and emptied every 2 weeks. We hence focus on the spring community as pooling with the autumn community would pool different body sizes (Lövei and Sunderland 1996) across species that de facto do not co-occur in space and time. Total plant cover was estimated in a 5 m radius circle around each trap, and all species were identified and their percentage cover estimated. Environmental variables were inferred from the vegetation communities using Ellenberg's index values (1992) extracted from Hill et al. (2004) and corrected for the British Isles, following Lafage et al. (2015, 2019) and Diekmann (2003). Anthropogenic degradation was assessed using bare ground

as a proxy of degradation intensity (Hacala et al. 2020). Pitfall samples were sorted in laboratory, arthropods transferred to ethanol 70%, and stored at the University of Rennes 1. Spiders, ground beetles and ants were identified to species level. Spiders were identified using Roberts (1985) and Nentwig et al. (2019). Ground beetles were identified using Luff (2007) and Jeannel (1941). Ants were identified to species levels using Blatrix et al. (2013).

Trait gathering

Three criteria were set to select the traits for calculating FD of all three taxa. (1) They exist under a form or can be transformed in a way to be comparable between taxa (e.g. numerical into categorical). (2) They must be reported as drivers of species assemblages for each taxon. (3) They must be available in the literature for the three taxa. The functional trait definition provided by Violle et al. (2007) and followed by Wong et al. (2019) was finally used, with the exclusion of environmental preferences as they are not strictly speaking a functional trait. Three traits were selected and their values gathered from existing literature: dispersal abilities, body size and trophic guild (Table 1), all these traits being known to be affected by environmental responses in spider, carabid and ant assemblages (Schirmel et al. 2012; Lafage et al. 2015). Dispersal trait was chosen to express dispersal at a landscape scale to account for the colonization ability of the studied species. The spider capacity to disperse by the air (ballooning) was the criterion used to discriminate dispersal ability. For ground beetles, the ability to fly based on wing development was used for dispersal ability. For the ants, the queen's way of locomotion for founding a new colony (by flight or by foot after a colony division) was used as comparable landscape level of dispersal. Body size was divided into three discreet classes to facilitate the comparison with the other variables. The division into size classes was done for each class to contain a comparable number of species. The guild trait was acquired through the feeding regime for ants and ground beetles. For spiders, the foraging strategy was used to distinguish guilds inside a predator-only taxon. We stress that traits were never inferred from phylogenetic position (see Table 1 for details and literature used).

Phylogenetic tree building

Phylogenetic trees were constructed by combining phylogenetic and taxonomic data from literature, assuming identical branch length between genus (1) and species (0.5) as real branch lengths because sequences were not available for all identified species.

The spider phylogenetic tree was adapted from Wheeler et al. (2017). Genera that were not present in Wheeler's tree were placed using Arnedo et al. (2009), Frick et al. (2010)

Table 1 Details of functional trait for each taxon. Each trait is decomposed in its modalities for each of the three taxon

Trait	Spider	Refs.	Ground beetle	Refs.	Ant	Refs.
Dispersal	Ballooning 0/1	[1, 2]	Apterous/ polymorphic/ macropterous	[5]	Colony division/ mixte/independ- ent	[9]
Size	Small: < 3 Medium: [3; 5] Large: > 5	[3]	Small: < 5 Medium: [5; 10] Large: > 10	[5]	Small: < 3 Medium: [3; 4] Large: > 4	[8–9]
Guild	Other hunters Ground hunters Sheet web weavers Space web weavers Sensing web weavers Specialists Orb web weavers Ambush hunters	[4]	Predator Omnivore Herbivore	[5–7]	Omnivor Predator Nectarivor Granivore Parasite	[8–9]

The bibliographic source from which the traits were gathered are specified (Hacala et al. 2020)

- [1] Simonneau M, Courtial C, Pétilion J (2016) Phenological and meteorological determinants of spider ballooning in an agricultural landscape. *C R Biol* 339:408–416
- [2] Bell JR, Bohan DA, Shaw EM, Weyman GS (2005) Ballooning dispersal using silk: world fauna, phylogenies, genetics and models. *Bull Entomol Res* 95:69–114
- [3] Nentwig W, Blick T, Gloor D, Hänggi A, Kropf C (2019) Version 06.2019. Online at <https://www.araneae.nmbe.chae.nmbe.ch>. Accessed 19 June 2019. <https://doi.org/10.24436/1>
- [4] Cardoso P, Pekár S, Jocqué R, Coddington JA (2011) Global patterns of guild composition and functional diversity of spiders. *PloS one* 6
- [5] Homburg K, Homburg N, Schäfer F, Schuldt A, Assmann T (2014) Carabids.org—a dynamic online database of ground beetle species traits (Coleoptera, Carabidae). *Insect Conserv Divers* 7:195–205
- [6] Ribera I, Foster GN, Downie IS, McCracken DI, Abernethy VJ (1999) A comparative study of the morphology and life traits of Scottish ground beetles (Coleoptera, Carabidae). In *Ann Zool Fenn* pp 21–37 Finnish Zoological and Botanical Publishing Board
- [7] Turin H (2000) *De Nederlandse loopkevers: verspreiding en oecologie* (Coleoptera: Carabidae) (Vol. 3). Nationaal Natuurhistorisch Museum
- [8] Arnan X, Cerdá X, Retana J (2015) Partitioning the impact of environment and spatial structure on alpha and beta components of taxonomic, functional, and phylogenetic diversity in European ants. *PeerJ* 3:e1241
- [9] Blatrix R, Galkowski C, Lebas C, Wegnez P (2013) *Guide des fourmis de France*. Delachaux et Niestlé. pp 287

and Wang et al. (2015) for Linyphiidae and Agnarsson (2004), Azevedo et al. (2018), Maddison (2015), Millidge (1978), Piacentini and Ramírez (2019) and Scharff et al. (2019) for other families. The carabid phylogenetic tree was adapted from López-López and Vogler (2017), Martínez-Navarro et al. (2005), Ober and Maddison (2008), Ruiz et al. (2009) and Sasakawa & Kubota (2007). The ant phylogenetic tree was adapted from Moreau et al. (2006).

Diversity calculating

The two diversity metrics, PD and FD, were calculated using the BAT package (Cardoso et al. 2015). The diversities values were calculated at the trap scale with a data pooling from the season of sampling for each taxon. Distance matrices were computed with Gower distance from the FD package (Laliberté et al. 2014) for functional distances and with *as.phylo* from the *ape()* package (Paradis et al. 2019)

for phylogenetic distances. PD and FD were calculated by meaning the Jackknifes estimates from apha-estimated () function from BAT to account for sampling variability.

Statistical analysis

Correlations between PD and FD were estimated in a Bayesian framework with a Student's t distribution with the *brms* package (Bürkner 2018). We used 2000 iterations on 4 chains. Model convergence was checked by visually inspecting diagnostic plots.

To select environmental variables affecting PD and FD, models were built within a Bayesian framework using *brms* (Bürkner, 2018) with two chains and default priors. All environmental variables were standardized and centered. The models included % bare-ground, litter depth, soil depth, and vegetation height. It also included community-weighted means of nitrogen level, light, salinity, pH and humidity

based on Elenberg indicator values (modified by Hill et al. 1999). Model convergence was checked by visually inspecting diagnostic plots and using Rhat value. Parameter selection was based on “HDI+ROPE decision rule” (Kruschke and Liddell 2018) with a range value determined as $-0.1 * sd(y)$, $0.1 * sd(y)$ (Kruschke and Liddell 2018) and was performed using bayestestR (Makowski et al., 2019). We also provide we the probability of direction (pd), which is the probability that the posterior distribution of a parameter is strictly positive or negative. The thresholds beyond which the variable was considered as significant (i.e. non negligible) were $pd > 95\%$ and $ROPE < 2.5\%$.

We assessed the relative contribution of environmental variables selected by Bayesian models using structural equation modeling (SEM). The SEM approach also allowed us to assess the links between TD, PD and FD taking environment into account. A significant correlated error between the two variables would indicate the existence of an unknown parameter influencing both variables. We used the piecewiseSEM package (Lefcheck 2016) as it allows using mixed models in association with nlme package (Pinheiro et al. 2020). Our initial model included the following links: (1) PD is affected by TD and selected environmental variables, (2) FD is affected by TD, selected environmental variables and PD, (3) TD is affected by selected environmental variables and (4) there is correlated error between PD and FD. Site was used as a random factor in every link modeled using nlme (Pinheiro-Silva et al., 2020). After the specification of the initial model, we re-defined our model excluding non-significant links ($p < 0.05$) using a stepwise approach until $\Delta AICc < 2$ between two subsequent models. Finally, we assessed model fit using Fisher's C statistic.

Results

Simple correlations

Correlations between phylogenetic and functional diversities were 0.59 (95% CI 0.41–0.73), 0.65 (95% CI 0.46–0.79) and 0.72 (95% CI 0.57–0.82) for spiders, carabid beetles and ants respectively (Fig. 1), and overall increased with decreasing species richness of each taxa (153, 40 and 23, respectively).

Variable pre-selection

Humidity and salinity were the best explanatory variables for spider PD (Table 2). None of the environmental variables included in the model explained spider FD (Table 2). As for spider PD, spider TD was best explained by humidity and salinity. Percent bare-ground and salinity were the best explanatory variables for carabid beetle PD. Carabid beetle FD and TD were best explained by salinity (Table 2). Soil

depth was the best explanatory variable for ant PD, FD and TD (Table 2).

Structural equation models

When testing the relationship between diversity metrics and environmental variables, our final SEMs indicated good fit with the data both for spiders (Fisher's $C = 17.19$, $p = 0.07$; Fig. 2a) and carabid beetles (Fisher's $C = 9.77$, $p = 0.64$, Fig. 2b). The fit of the ant model could not be estimated as the best model was fully saturated (Fig. 2c).

Environmental variables (here humidity and salinity indexes) were only linked to spider TD. Direction of these links were opposite with similar sizes. Spider PD was strongly and positively related to TD while spider FD was strongly and positively linked to PD.

Similar (but weaker) relationships were found between carabid beetle α -, phylogenetic and functional diversities (Fig. 2). Environmental variables affecting carabid diversities were salinity and % bare-ground. Salinity positively influenced TD and PD. % bare-ground had a negative effect on PD.

Ant phylogenetic and functional diversities were strongly positively linked to TD. Soil depth was the only environmental variable selected by the model. It had a weak and positive effect on FD. Selected, but not significant, paths were found between functional and phylogenetic diversities ($p = 0.07$), between soil depth and TD ($p = 0.08$) and between soil depth and PD ($p = 0.22$).

Discussion

Correlations were overall positive and high between FD and PD, following general theory (Webb et al. 2002). These simple correlations between PD and FD may or may not represent mathematical artifacts from an increase of both, FD and PD with TD. We will hence focus the discussion on the results that account for TD and other variables in parallel. Accounting for TD and environments made disappear this PD/FD relationship in ants, but maintained them in spiders and ground beetles, where TD related to FD only via increasing PD. Environmental constraints reduced FD in ants, but affected FD only indirectly via PD (ground beetles) and via TD and then PD (spiders and ground beetles).

Differences of drivers between taxonomic, functional and phylogenetic diversities

The anthropogenic gradient of degradation, represented by bare ground, affected PD only in ground beetles, while this variable is known to affect TD of ground beetles in other habitats (see e.g. Pétilion et al. 2008 in salt marshes). Other

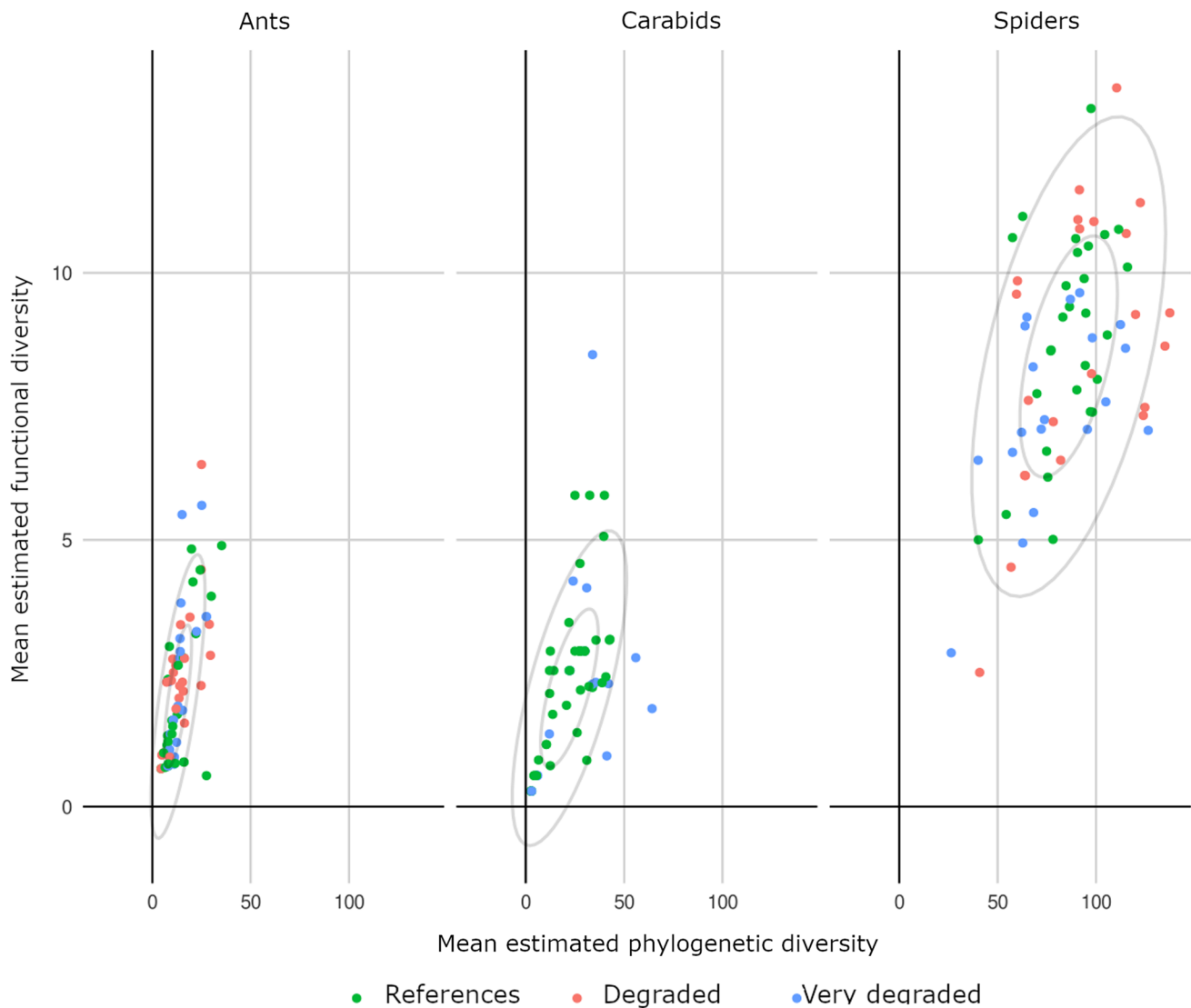


Fig. 1 Plot of mean estimated functional diversity as a function of phylogenetic diversity. Ellipses correspond to 95% and 5% normal confidence ellipses. Each dot correspond to a trap. $R^2=0.38$; 0.42,

and 0.52. See Fig. 2 for a broader picture accounting also for taxonomic diversity and the environment (Hacala et al. 2020)

environmental variables on the other hand have interacted with PD and FD in several ways, positively (humidity for spiders, salinity for ground beetles and soil depth for ants) or negatively (salinity for spiders), but most of their effects were indirect: With two exceptions (bare ground on PD of ground beetles and soil depth on FD of ants), environmental variables acted only on TD which then cascaded its effects onto PD which in turn affected FD. Both, PD and FD are estimated using minimum spanning trees, but possibly a functional minimum spanning tree contains more polytomies, and hence adding a species without adding a new trait adds little branch length (see Online Resource 2 for a simulation supporting this idea). Moreover, environments selecting for species may do so based on traits that we

did not consider in the calculus of FD, and that are highly phylogenetically convergent, leading to a major increase in PD. The fact that PD often increases with TD might reflect either the effect of an unmeasured environmental variable (e.g. weather conditions as they are known to be harsh in the studied habitat see Sawtschuck 2010) affecting both TD and PD, or a coexistence facilitated among phylogenetically distant species, which would result in a positive relationship between TD and PD. Traits involved in stress response, like drought tolerance, indeed appear to have evolved convergently (Dunn et al. 1976). Increase in the diversity of the functional traits that we did consider would only be a side effect of such selection for phylogenetically convergent tolerances or resistances. Other traits more directly related

Table 2 Results Bayesian models for variable selection to be used in the SEM models (Hacala et al. 2020)

		R^2	Variable selected	Pd (%)	Median	89% CI	% in ROPE
Spiders	PD	0.59	Humidity	99.6	16.37	[7.45; 26.31]	0
			Salinity	97.8	− 21	[− 38.68; − 4.90]	0
	FD	0.26	—				
	TD	0.66	Humidity	99.4	0.56	[0.27; 0.92]	0
Carabid beetles	PD	0.44	Salinity	99.4	− 0.98	[− 1.56; − 0.34]	0
			% Bare ground	99.2	− 6.9	[− 11.73; − 2.67]	0
	FD	0.24	Salinity	99.9	21.01	[8.11; 32.19]	0
	TD	0.44	Salinity	99.4	2.61	[0.78; 4.09]	0
Ants	PD	0.31	Soil depth	89.2	0.64	[− 0.29; 1.45]	0
	FD	0.4	Soil depth	97.5	2.84	[0.68; 5.11]	0.4
	TD	0.37	Soil depth	99.1	0.59	[0.18; 0.99]	0
	TD	0.37	Soil depth	98.1	0.36	[0.09; 0.66]	1.1

R^2 conditional R^2 , Pd probability of direction (probability that the posterior distribution of a parameter is strictly positive or negative), CI confidence interval, % in ROPE percentage of the posterior distribution in the Region of Practical Equivalence

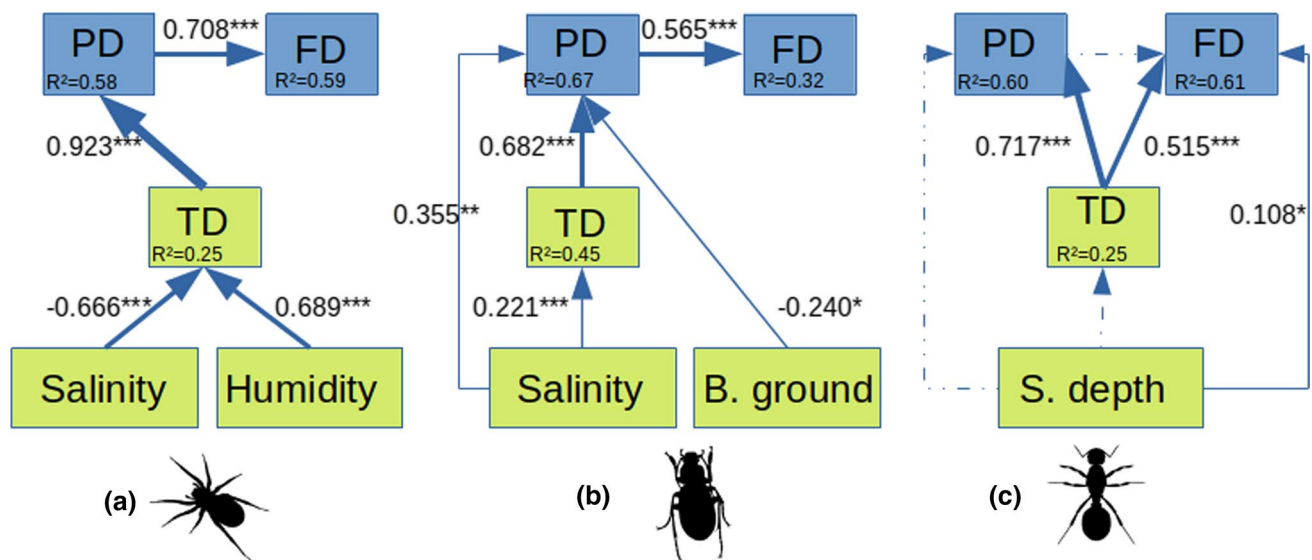


Fig. 2 Best piecewise SEMs showing links between taxonomic, phylogenetic and functional diversity and environmental variables for **a** spiders, **b** carabid beetles and **c** ants. Thickness of arrows is proportional to the standardized path coefficients (directionality and size

given within boxes). Asterisks give significance level of linkages (* < 0.05, ** < 0.01, *** < 0.001), and dashed lines correspond to paths included but not significant ($p > 0.05$). Conditional R^2 values are given within the boxes containing variables (Hacala et al. 2020)

to environmental stresses could be worthwhile to integrate in the future, as they could be available through the development of online databases (see e.g. Lowe et al. 2020 for spiders).

Differences of drivers between taxa

Diversity patterns differing between taxa was one of our expectations (Wong et al. 2019). We had expected positive relationships between PD and FD to be least likely in ants and most likely in spiders. This expectation was confirmed

for ants, albeit not for spiders. We had also expected that ants might depend least (and ground beetles most) on abiotic factors that constrain individual survival in other taxa, such as salinity or humidity, albeit ants might depend more on factors that constrain the construction of formicaries such as soil depth. This overall expectation was confirmed for ants, but not for carabid beetles. We will below discuss the relationships individually.

Spider TD responded negatively to salinity and drought. Salinity is a known environmental filter for spiders (Desender and Maelfait 1999; Pétiillon et al. 2005, 2007;

Traut 2005) hence the salinity-resisting spider species are selected, reducing the local species richness. TD directly decreased with salinity, but PD and FD were only affected through TD. Salinity resistance, a trait not included in our analysis, thus may have appeared randomly in different parts of spider phylogenetic tree (see Online Resource 1): sorting for the few salinity tolerant species does not sort for phylogenetically particularly proximate or distant species. Humidity directly impacted only TD and impacted PD and FD only indirectly through TD. This could again be explained by environmental preferences and tolerances (not considered as traits here) if randomly distributed over spider phylogeny. Spider assemblage in the studied environment most likely result from a combination of humidity tolerant and mesohygrophilous species like in other ecotones (Traut 2005), which would explain the positive effect of humidity on spider TD (see also Entling et al. 2007, Weininger & Fagan 2000 and Lafage et al. 2015; 2019). The positive effect of PD on FD in spiders suggests a phylogenetic signal of traits. This may appear contradictory with the tolerance traits considered above interpreted as being random across spider phylogeny, but these tolerance traits may not be representative of the whole spectrum of traits that characterize spiders. The majority of traits could show phylogenetic signal (Flynn et al. 2011; Khalil et al. 2018; Tucker et al. 2018). For instance, the hunting guild differs among families and hence shows strong phylogenetic signal (Cardoso et al. 2011).

TD and PD of ground beetles responded positively to salinity and negatively to bare ground. For ground beetles, contrary to spiders, salinity has a higher and positive impact on PD than on TD. This would mean that salinity resistance is not restricted to a single or few phylogenetic branches but evolved convergently across distant branches of the phylogeny (consistent with suggestions of Baulechner et al. 2020 for other traits). Again, the absence of a direct effect of salinity on FD but only through PD can be explained by the spectrum of traits used here that may not affect salinity tolerance. The increase of TD with salinity appears inconsistent with existing literature from hypersaline habitats (Desender and Maelfait 1999; Pétilon et al. 2007). The high-cliff heathlands we studied are less saline and salinity might not exclude species, but only permit the additional occurrence of haloresistant species, therefore rising TD. The negative effect of bare ground on PD but not on TD suggests that bare ground selected for one, albeit species-rich phylogenetic lineage. Bare ground is anthropogenic here, and TD of ground beetles not declining under anthropogenic perturbation was previously reported (Verschoor and Krebs 1995), and possibly reflects quick recolonization post-perturbation by eurytopic and highly-dispersive species (Varet et al. 2013) although the species richness of specialist species is often reduced by

disturbances for this taxon (see the reviews Niemla and Kotz 2009; Magura et al. 2010).

Ants were the only taxon in which FD was controlled not by PD but by environmental constraints and TD. Presence of a negative, or absence of a positive relationship between PD and FD were expected in particular in ants due to existing competition between many ant species (Cerdeira et al. 2013). Little relationships of FD to the environment was also expected given capacity of niche construction, albeit strong relationship may emerge if niche construction as such is possible only in some environments, consistent with earlier observations on responses of ant assemblages FD to environmental filters (Campbell et al. 2010; Flynn et al. 2011; Arnan et al. 2015; Fichaux et al. 2019). A positive effect of soil depth on FD is consistent with the fact that most temperate species of ants nest underground (Torossian 1997) and hence profit from deep soils. Moreover, the increase of FD with TD, but not with PD suggests that traits accounted for in FD are not phylogenetically conserved nor convergent in ants. Instead, adding a species seems to, on average, add trait values to the community independent of the selection pressure of environmental constraints. This result appears to be more consistent with a neutral model, with any new species potentially representing a new trait state (Purves and Turnbull 2010; Novack-Gottshall 2016; Stevens and Grimshaw 2020) or superposition of patterns resulting from phylogenetic conservatism and of mutual exclusion of similar related species.

Conclusions

Overall, among the models formulated in the Introduction, results are consistent with phylogenetic conservatism in traits in spiders and ground beetles: PD relates positively to FD (Webb et al. 2002), even when accounting for TD. Our results are not consistent with models of strong character displacement among close relatives that should lead to negative relationships between PD and FD (Prinzing et al. 2008), or reduced niche packing under environmental constraints (Safi et al. 2011). These models invoke strong competitive interactions, stronger than found among ground-dwelling predators (see Wise 2006 for spiders and Fichaux et al. 2019 for ants). Overall, characterizing multiple aspects of biological diversity and of the environment, and relating them through structural equation modeling, revealed major differences among ground-dwelling predators in what drives their functional diversity. In particular, the positive relationships between PD and FD found among spiders and ground beetles disappears among ants, possibly resulting from somewhat higher competition among ants. Future studies might explicitly test the relationship between competition and the loss of positive FD/PD relationships using either null

model approaches (e.g. Magura and Lövei 2019) or using our approach of structural equation modeling but applied across a larger number of taxa.

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References

- Agnarsson I (2004) Morphological phylogeny of cobweb spiders and their relatives (Araneae, Araneioidea, Theridiidae). *Zool J Linn Soc* 141:447–626. <https://doi.org/10.1111/j.1096-3642.2004.00120.x>
- Arnan X, Cerdá X, Retana J (2015) Partitioning the impact of environment and spatial structure on alpha and beta components of taxonomic, functional, and phylogenetic diversity in European ants. *PeerJ* 3:e1241. <https://doi.org/10.7717/peerj.1241>
- Arnedo MA, Hormiga G, Scharff N (2009) Higher-level phylogenetics of linyphiid spiders (Araneae, Linyphiidae) based on morphological and molecular evidence. *Cladistics* 25(3):231–262. <https://doi.org/10.1111/j.1096-0031.2009.00249.x>
- Azevedo GHF, Griswold CE, Santos AJ (2018) Systematics and evolution of ground spiders revisited (Araneae, Dionycha, Gnaphosidae). *Cladistics* 34:579–626. <https://doi.org/10.1111/cla.12226>
- Baulechner D, Jauker F, Neubauer TA, Wolters V (2020) Convergent evolution of specialized generalists: implications for phylogenetic and functional diversity of carabid feeding groups. *Ecol Evol* 10:11100–11110
- Bernard-Verdier M, Flores O, Navas ML, Garnier E (2013) Partitioning phylogenetic and functional diversity into alpha and beta components along an environmental gradient in a Mediterranean rangeland. *J Veg Sci* 24:877–889
- Blatrix R, Galkowski C, Lebas C, Wegnez P (2013) Guide des fourmis de France, Delachaux et Niestlé, pp 287.
- Bond JE, Garrison NL, Hamilton CA, Godwin RL, Hedin M, Agnarsson I (2014) Phylogenomics resolves a spider backbone phylogeny and rejects a prevailing paradigm for orb web evolution. *Curr Biol* 24:1765–1771
- Bürkner P-C (2018) Advanced bayesian multilevel modeling with the R package brms. *R J* 10:395–411. <https://doi.org/10.32614/RJ-2018-017>
- Cadotte MW, Carboni M, Si X, Tatsumi S (2019) Do traits and phylogeny support congruent community diversity patterns and assembly inferences? *J Ecol* 107:2065–2077
- Campbell WB, Freeman DC, Emlen JM, Ortiz SL (2010) Correlations between plant phylogenetic and functional diversity in a high altitude cold salt desert depend on sheep grazing season: Implications for range recovery. *Ecol Indic* 10:676–686
- Cardoso P, Pekár S, Jocqué R, Coddington JA (2011) Global patterns of guild composition and functional diversity of spiders. *PLoS ONE* 6:e21710
- Cardoso P, Rigal F, Carvalho JC (2015) BAT–Biodiversity assessment tools, an R package for the measurement and estimation of alpha and beta taxon, phylogenetic and functional diversity. *Methods Ecol Evol* 6:232–236
- Cavender-Bares J, Kozak KH, Fine PV, Kembel SW (2009) The merging of community ecology and phylogenetic biology. *Ecol Lett* 12:693–715
- Cerda X, Arnan X, Retana J (2013) Is competition a significant hallmark of ant (Hymenoptera: Formicidae) ecology. *Myrmecol News* 18:131–147
- Coelho MS, Quintino AV, Fernandes GW, Santos JC, Delabie JHC (2009) Ants (Hymenoptera: Formicidae) as bioindicators of land restoration in a Brazilian Atlantic forest fragment. *Sociobiology* 54:51
- Corbelli JM, Zurita GA, Filloy J, Galvis JP, Vespa NI, Bellocq I (2015) Integrating taxonomic, functional and phylogenetic beta diversities: Interactive effects with the biome and land use across taxa. *PLoS ONE* 10:e0126854
- Darwin C (1859) On the origin of species. John Murray, London
- Desender K, Maelfait J-P (1999) Diversity and conservation of terrestrial arthropods in tidal marshes along the River Schelde: a gradient analysis. *Biol Conserv* 87:221–229
- Diekmann M (2003) Species indicator values as an important tool in applied plant ecology—a review. *Basic Appl Ecol* 4:493–506
- Dunn EL, Shropshire FM, Song LC, Mooney HA (1976) The water factor and convergent evolution in Mediterranean-type vegetation. Water and plant life. Springer, Berlin, Heidelberg, pp 492–505
- Ellenberg H, Weber HE, Düll R et al (1992) Zeigerwerte von Pflanzen in Mitteleuropa, 2nd ed. *Scr Geobot* 18:1–258
- Entling W, Schmidt MH, Bacher S, Brandl R, Nentwig W (2007) Niche properties of Central European spiders: shading, moisture and the evolution of the habitat niche. *Glob Ecol Biogeogr* 16:440–448
- Eterovick PC, Rievers CR, Kopp K, Wachlewski M, Franco BP, Dias CJ, Barata IM, Ferreira ADM, Afonso LG (2010) Lack of phylogenetic signal in the variation in anuran microhabitat use in southeastern Brazil. *Evol Ecol*. <https://doi.org/10.1007/s10682-008-9286-9>
- Faith DP (1992) Conservation evaluation and phylogenetic diversity. *Biol Conserv* 61:1–10
- Fichaux M, Béchade B, Donald J, Weyna A, Delabie JHC, Murienne J, Baraloto C, Orivel J (2019) Habitats shape taxonomic and functional composition of Neotropical ant assemblages. *Oecologia* 189:501–513

- Finch OD, Krummen H, Plaisier F, Schultz W (2007) Zonation of spiders (Araneae) and carabid beetles (Coleoptera: Carabidae) in island salt marshes at the North Sea coast. *Wetl Ecol Manag* 15:207–228
- Flynn DF, Mirotchnick N, Jain M, Palmer MI, Naeem S (2011) Functional and phylogenetic diversity as predictors of biodiversity–ecosystem-function relationships. *Ecology* 92:1573–1581
- Frick H, Nentwig W, Kropf C (2010) Progress in erigonine spider phylogeny—the Savignia-group is not monophyletic (Araneae: Linyphiidae). *Org Divers Evol* 10:297–310. <https://doi.org/10.1007/s13127-010-0023-1>
- Georges A, Fouillet P, Pétillon J (2011) Changes in salt-marsh carabid assemblages after an invasion by the native grass *Elymus athericus* (Link) Kerguelen. *ZooKeys* 100:407–419
- Gerhold P, Cahill JF Jr, Winter M, Bartish IV, Prinzing A (2015) Phylogenetic patterns are not proxies of community assembly mechanisms (they are far better). *Funct Ecol* 29:600–614
- Gerlach J, Samways M, Pryke J (2013) Terrestrial invertebrates as bioindicators: an overview of available taxonomic groups. *J Insect Conserv* 17:831–850. <https://doi.org/10.1007/s10841-013-9565-9>
- Götting E (2001) Development of salt marsh arthropod fauna after opening a summer polder. *Senckenberg Marit* 31:333–340
- Grundler MR, Pianka ER, Pelegrin N, Cowan MA, Rabosky DL (2018) Stable isotope ecology of a hyper-diverse community of scincid lizards from arid Australia. *PLoS ONE* 12:e0172879
- Haak DC, Ballenger BA, Moyle LC (2014) No evidence for phylogenetic constraint on natural defense evolution among wild tomatoes. *Ecology* 95:1633–1641
- Hacala A, Le Roy M, Sawtschuk J, Pétillon J (2020) Comparative responses of spiders and plants to maritime heathland restoration. *Biodivers Conserv* 29:229–249
- Harvey PR, Nellist DR, Telfer MG (2002) Provisional Atlas of British spiders (Arachnida, Araneae), volumes 1 & 2, Biological Records Centre, Huntingdon, pp 406
- Hill MO, Mountford JO, Roy DB, Bunce RGH (1999) Ellenberg's indicator values for British plants. Centre for Ecology and Hydrology, Huntingdon, Cambs, UK
- Hill MO, Preston CD, Roy DB (2004) PLANTATT-attributes of British and Irish plants: status, size, life history, geography and habitats. Centre for Ecology and Hydrology, Huntingdon
- Hubbell SP (2001) The unified neutral theory of biodiversity and biogeography. Princeton University Press, Princeton, New Jersey, USA
- Jeannel R (1941) Faune de France: Coléoptères carabiques. Fédération Française des sociétés de science naturelles, Office central de faunistique, pp 1173.
- Khalil MI, Gibson DJ, Baer SG, Willand JE (2018) Functional diversity is more sensitive to biotic filters than phylogenetic diversity during community assembly. *Ecosphere* 9:e02164. <https://doi.org/10.1002/ecs2.2164>
- Kruschke JK, Liddell TM (2018) The Bayesian New Statistics: Hypothesis testing, estimation, meta-analysis, and power analysis from a Bayesian perspective. *Psychon Bull Rev* 25:178–206
- Lafage D, Maugeness S, Bouzillé J-B, Pétillon J (2015) Disentangling the influence of local and landscape factors on alpha and beta diversities: opposite response of plants and ground-dwelling arthropods in wet meadows. *Ecol Res* 30:1025–1035
- Lafage D, Djoudi EA, Perrin G, Gallet S, Pétillon J (2019) Responses of ground-dwelling spider assemblages to changes in vegetation from wet oligotrophic habitats of Western France. *Arthropod Plant Interact* 13:653–662
- Laliberté E, Legendre P, Shipley B, Laliberté ME (2014) Package ‘FD’. Measuring functional diversity from multiple traits, and other tools for functional ecology. [Computer software]
- Lefcheck JS (2016) piecewiseSEM: piecewise structural equation modelling in r for ecology, evolution, and systematics. *Methods Ecol Evol* 7:573–579
- Leroy B, Le Viol I, Pétillon J (2014) Complementarity of rarity, specialisation and functional diversity metrics to assess community responses to environmental changes, using an example of spider communities in salt marshes. *Ecol Indic* 46:351–357
- Liu C, Guénard B, Blanchard B, Peng YQ, Economo EP (2016) Reorganization of taxonomic, functional, and phylogenetic ant biodiversity after conversion to rubber plantation. *Ecol Monogr* 86:215–227. <https://doi.org/10.1890/15-1464.1>
- López-López A, Vogler AP (2017) The mitogenome phylogeny of Adephaga (Coleoptera). *Mol Phylogenet Evol* 114:166–174. <https://doi.org/10.1016/j.ympev.2017.06.009>
- Lövei GL, Sunderland KD (1996) Ecology and behavior of ground beetles (Coleoptera: Carabidae). *Annu Rev Entomol* 41:231–256
- Lowe E, Wolff JO, Aceves-Aparicio A, Birkhofer K, Branco VV, Cardoso P, Chichorro P, Fukushima CS, Gonçalves-Souza T, Haddad CR, Isaia M, Krehenwinkel H, Lynn Audisio T, Macías-Hernández N, Malumbres-Olarte J, Mammola S, McLean DJ, Michalko R, Nentwig W, Pekár S, Pétillon J, Privet K, Scott C, Uhl G, Urbano-Tenorio F, Wong BH, Herberstein ME (2020) Towards establishment of a centralized spider traits database. *J Arachnol* 48:103–109
- Luff ML (2007) The Carabidae (ground beetles) of Britain and Ireland. RES handbooks for the identification of British Insects, vol 4 Part 2. Field Studies Council, Shrewsbury, pp 252.
- Maddison WP (2015) A phylogenetic classification of jumping spiders (Araneae: Salticidae). *J Arachnol* 43:231. <https://doi.org/10.1636/arac-43-03-231-292>
- Magura T (2016) Ignoring functional and phylogenetic features masks the edge influence on ground beetle diversity across forest-grassland gradient. *For Ecol Manage* 384:371–377. <https://doi.org/10.1016/j.foreco.2016.10.056>
- Magura T, Lövei GL (2019) Environmental filtering is the main assembly rule of ground beetles in the forest and its edge but not in the adjacent grassland. *Insect Sci* 26:154–163
- Magura T, Lövei GL, Tóthmérész B (2010) Does urbanization decrease diversity in ground beetle (Carabidae) assemblages? *Glob Ecol and Biogeogr* 19:16–26
- Makowski D, Ben-Shachar MS, Lüdtke D (2019) bayestestR: describing effects and their uncertainty, existence and significance within the Bayesian framework. *J Open Source Softw* 4:1541
- Martínez-Navarro EM, Galián J, Serrano J (2005) Phylogeny and molecular evolution of the tribe Harpalini (Coleoptera, Carabidae) inferred from mitochondrial cytochrome-oxidase I. *Mol Phylogenet Evol* 35:127–146. <https://doi.org/10.1016/j.ympev.2004.11.009>
- Millidge AF (1978) The genera Mecopisthes Simon and *Hypocephalus* n.gen. and their phylogenetic relationships Araneae: Linyphiidae. *Bull Br Arachnol Soc* 4:113–123
- Moreau CS, Bell CD, Vila R, Archibald SB, Pierce NE (2006) Phylogeny of the ants: diversification in the age of Angiosperms. *Science* 312:101–104. <https://doi.org/10.1126/science.1124891>
- Nentwig W, Blick T, Gloor D, Hänggi A, Kropf C (2019) Version 06.2019. Available at <https://www.araneae.nmbe.ch>. Accessed 19 June 2019. <https://doi.org/10.24436/1>
- Niemelä J (1993) Interspecific competition in ground-beetle assemblages (Carabidae): what have we learned? *Oikos* 66:325–335
- Niemelä J, Kotze DJ (2009) Carabid beetle assemblages along urban to rural gradients: a review. *Landsc Urban Plan* 92:65–71
- Novack-Gottshall PM (2016) General models of ecological diversification. *I Concept Synth Paleobiol* 42:185–208
- Ober KA, Maddison DR (2008) Phylogenetic relationships of tribes within Harpalinae (Coleoptera: Carabidae) as inferred from

- 28S ribosomal DNA and the wingless gene. *J Insect Sci* 8:1–32. <https://doi.org/10.1673/031.008.6301>
- Odling-Smee FJ, Laland KN, Feldman MW (2013) Niche construction: the neglected process in evolution (MPB-37). Princeton University Press, Princeton, p 488
- Paradis E, Blomberg S, Bolker B, Brown J, Claude J, Cuong HS, Desper R (2019) Package ‘ape’. Analyses of phylogenetics and evolution version 2. [Computer software]
- Parr CL, Dunn RR, Sanders NJ, Weiser MD, Photakis M, Bishop TR, Fitzpatrick MC, Arnan X, Baccaro F, Brand Ao CRF, Chick L, Donoso DA, Fayle TM, Gomez C, Munyai BTC, Pacheco R, Retana J, Robinson A, Sagata K, Silva RR, Tista M, Vasconcelos H, Yates M, Gibb H (2017) GlobalAnts: a new database on the geography of ant traits (Hymenoptera: Formicidae). *Insect Conserv Divers* 10:5–20
- Pavoine S, Baguette M, Bonsall MB (2010) Decomposition of trait diversity among the nodes of a phylogenetic tree. *Ecol Monogr* 80:485–507
- Pavoine S, Gasc A, Bonsall MB, Mason NW (2013) Correlations between phylogenetic and functional diversity: mathematical artefacts or true ecological and evolutionary processes? *J Veg Sci* 24:781–793
- Pedley SM, Dolman PM (2014) Multi-taxa trait and functional responses to physical disturbance. *J Anim Ecol* 83:1542–1552. <https://doi.org/10.1111/1365-2656.12249>
- Pétillon J, Ysnel F, Canard A, Lefeuvre J-C (2005) Impact of an invasive plant (*Elymus athericus*) on the conservation value of tidal salt marshes in western France and implications for management: responses of spider populations. *Biol Conserv* 126:103–117
- Pétillon J, Georges A, Canard A, Ysnel F (2007) Impact of cutting and sheep grazing on ground-active spiders and carabids in intertidal salt marshes (Western France). *Anim Biodivers Conserv* 30:201–209
- Pétillon J, Georges A, Canard A, Lefeuvre J-C, Bakker JP, Ysnel F (2008) Influence of abiotic factors on spider and ground beetles communities in different salt-marsh systems. *Basic Appl Ecol* 9:743–751
- Pétillon J, Potier S, Carpentier A, Garbutt A (2014) Evaluating the success of managed realignment for the restoration of salt marshes: lessons from invertebrate communities. *Ecol Eng* 69:70–75
- Piacentini LN, Ramírez MJ (2019) Hunting the wolf: a molecular phylogeny of the wolf spiders (Araneae, Lycosidae). *Mol Phylogenet Evol* 136:227–240
- Pinheiro-Silva L, Gianuca AT, Silveira MH, Petrucio MM (2020) Grazing efficiency asymmetry drives zooplankton top-down control on phytoplankton in a subtropical lake dominated by non-toxic cyanobacteria. *Hydrobiologia* 847:3207–3220
- Prinzing A (2016) On the opportunity of using phylogenetic information to ask evolutionary questions in functional community ecology. *Fol Geobot* 51:69–74
- Prinzing A, Reiffers R, Braakhekke WG, Hennekens SM, Tackenberg O, Ozinga WA, Schaminée JHJ, Van Groenendael JM (2008) Less lineages—more trait variation: phylogenetically clustered plant communities are functionally more diverse. *Ecol Lett* 11:809–819
- Purves DW, Turnbull LA (2010) Different but equal: the implausible assumption at the heart of neutral theory. *J Anim Ecol* 79:1215–1225
- Ridel A, Lafage D, Devogel P, Lacoue-Labarthe T, Pétillon J (2021) Habitat filtering differentially modulates phylogenetic vs functional diversity relationships between dominant ground-dwelling arthropods in salt marshes. *R Soc Open Sci* 8:202093. <https://doi.org/10.1098/rsos.202093>
- Roberts MJ (1985) The spiders of Great Britain and Ireland. *J New York Entomol Soc* 93:1279–1280
- Rodrigues ASL, Brooks TM, Gaston KJ (2005) Integrating phylogenetic diversity in the selection of priority areas for conservation: does it make a difference. *Phylogeny Conserv* 8:101–119
- Ruiz C, Jordal B, Serrano J (2009) Molecular phylogeny of the tribe Sphodrini (Coleoptera: Carabidae) based on mitochondrial and nuclear markers. *Mol Phylogenet Evol* 50(1):44–58. <https://doi.org/10.1016/j.ympev.2008.09.023>
- Safi K, Cianciaruso MV, Loyola RD, Brito D, Armour-Marshall K, Diniz-Filho JAF (2011) Understanding global patterns of mammalian functional and phylogenetic diversity. *Philos Trans R Soc Lond B Biol Sci* 366:2536–2544
- Sasakawa K, Kubota K (2007) Phylogeny and genital evolution of Carabid beetles in the genus *Pterostichus* and its allied genera (Coleoptera: Carabidae) inferred from two nuclear gene sequences. *Ann Entomol Soc Am* 100(2):100–109. [https://doi.org/10.1603/0013-8746\(2007\)100\[100:PAGEOC\]2.0.CO;2](https://doi.org/10.1603/0013-8746(2007)100[100:PAGEOC]2.0.CO;2)
- Sawtschuk J (2010) Restauration écologique des pelouses et des landes des falaises littorales atlantiques: Analyse des trajectoires successionales en environnement contraint. PhD dissertation, Institut de Géoarchitecture, Université de Bretagne Occidentale, Brest, France.
- Scharff N, Coddington JA, Blackledge TA, Agnarsson I, Framenau VW, Szűts T, Hayashi CY, Dimitrov D (2019) Phylogeny of the orb-weaving spider family Araneidae (Araneae: Araneoidea). *Cladistics* 36:1–21. <https://doi.org/10.1111/cla.12382>
- Schirmel J, Blindow I, Buchholz S (2012) Life-history trait and functional diversity patterns of ground beetles and spiders along a coastal heathland successional gradient. *Basic Appl Ecol* 13:606–614. <https://doi.org/10.1016/j.baae.2012.08.015>
- Schirmel J, Thiele J, Entling MH, Buchholz S (2016) Trait composition and functional diversity of spiders and carabids in linear landscape elements. *Agric Ecosyst Environ* 235:318–328. <https://doi.org/10.1016/j.agee.2016.10.028>
- Schmidt FA, Schoereder JH, Caetano MDN (2017) Ant assemblage and morphological traits differ in response to soil compaction. *Insectes Soc* 64:219–225
- Stevens RD, Grimshaw JR (2020) Relative contributions of ecological drift and selection on bat community structure in interior Atlantic Forest of Paraguay. *Oecologia* 193:645–654
- Topping CJ, Sunderland KD (1992) Limitations to the use of pitfall traps in ecological studies exemplified by a study of spiders in a field of winter wheat. *J Appl Ecol* 29:485–491
- Torma A, Császár P, Bozsó M, Deák B, Valkó O, Kiss O, Gallé R (2019) Species and functional diversity of arthropod assemblages (Araneae, Carabidae, Heteroptera and Orthoptera) in grazed and mown salt grasslands. *Agric Ecosyst Environ* 273:70–79
- Torossian C (1977) Les fourmis rousses des bois (*Formica rufa*) indicateurs biologiques de dégradation des forêts de montagne des Pyrénées orientales. *Bull D'écologie* 8:333–348
- Traut BH (2005) The role of coastal ecotones: a case study of the salt marsh/upland transition zone in California. *J Ecol* 93:279–290. <https://doi.org/10.1111/j.1365-2745.2005.00969.x>
- Tucker CM, Davies TJ, Cadotte MW, Pearse WD (2018) On the relationship between phylogenetic diversity and trait diversity. *Ecology* 99:1473–1479
- Varet M, Burel F, Lafage D, Pétillon J (2013) Age-dependent colonization of urban habitats: a diachronic approach using carabid beetles and spiders. *Anim Biol* 63:257–269
- Verschoor BC, Krebs BPM (1995) Diversity changes in a plant and carabid community during early succession in an embanked salt-marsh area. *Pedobiologia* 39:405–416
- Violle C, Navas ML, Vile D, Kazakou E, Fortunel C, Hummel I, Garnier E (2007) Let the concept of trait be functional! *Oikos* 116:882–892
- Wang F, Ballesteros JA, Hormiga G, Chesters D, Zhan Y, Sun N, Zhu C, Chen W, Tu L (2015) Resolving the phylogeny of a speciose

- spider group, the family Linyphiidae (Araneae). *Mol Phylogenet Evol* 91:135–149. <https://doi.org/10.1016/j.ympev.2015.05.005>
- Webb CO, Ackerly DD, McPeck MA, Donoghue MJ (2002) Phylogenies and community ecology. *Annu Rev Ecol Syst* 33:475–505
- Weninger EJ, Fagan WF (2000) Effect of river flow manipulation on wolf spider assemblages at three desert riparian sites. *J Arachnol* 28:115–122
- Wheeler WC, Coddington JA, Crowley LM, Dimitrov D, Goloboff PA, Griswold CE, Hormiga G, Prendini L, Almeida-Silva L, Alvarez-Padilla F, Arnedo MA, Benavides Silva LR, Benjamin SP, Bond JE, Grismado CJ, Hasan E, Hedin M, Izquierdo MA, Labarque FM, Ledford J, Lopardo L, Maddison WP, Miller JA, Piacentini LN, Platnik NI, Polotow D, Silva-Dávila D, Scharff N, Szűts T, Ubick D, Vink CJ, Wood HM, Zhang J (2017) The spider tree of life: phylogeny of Araneae based on target-gene analyses from an extensive taxon sampling. *Cladistics* 33:574–616. <https://doi.org/10.1111/cla.12182>
- Wiens JJ, Ackerly DD, Allen AP, Anacker BL, Buckley LB, Cornell HV, Damschen EI, Davis JT, Grytnes J-A, Harrison SP, Hawkins BA, Holt RD, McCain CM, Stephens PR (2010) Niche conservatism as an emerging principle in ecology and conservation biology. *Ecol Lett* 13:1310–1324
- Wise DH (2006) Cannibalism, food limitation, intraspecific competition and the regulation of spider populations. *Annu Rev Entomol* 51:441–465
- Wong MK, Guénard B, Lewis OT (2019) Trait-based ecology of terrestrial arthropods. *Biol Rev* 94:999–1022

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