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Importance of biotic niches versus drift in a plant-inhabiting arthropod community depends on rarity and trophic group

Christopher Bosc, Cang Hui, Francois Roets and Anton Pauw

C. Bosc (https://orcid.org/0000-0003-3098-762X) ✉ (christopherbosc@gmail.com) and A. Pauw (https://orcid.org/0000-0002-4012-648X), Dept of Botany and Zoology, Stellenbosch Univ., Matieland, South Africa. – C. Hui, Centre for Invasion Biology, Dept of Mathematical Sciences, Stellenbosch Univ., and African Inst. for Mathematical Sciences, Matieland, South Africa. – F. Roets, Dept of Conservation Ecology and Entomology, Stellenbosch Univ., Matieland, South Africa.

Communities are mostly composed of rare species; yet, the factors that determine their patterns of occurrence remain obscure. Theory predicts that, in contrast with common species, the occurrence of rare species will be poorly correlated with environmental variables (niches) and more affected by stochasticity (ecological drift), but how this pattern varies across different trophic groups is still poorly understood. Here, we compared the ability of environmental variables (bottom–up biotic niches) to predict the occurrence of plant-dwelling arthropods across different abundance classes in the Cape Floristic Region of South Africa. We compared three trophic groups, including 104 herbivorous hemipteran, 171 parasitoid wasp and 84 spider species, totalling 4511 individuals in 48 quadrats. To quantify bottom–up biotic niches, we studied the influences of species composition of plants on hemipterans, and of plants and hemipterans on spiders and wasps. We compared the observed strength of the correlation between rare species and their niches with expectations that were generated by repeatedly rarefying abundant species. A large proportion of arthropod species were very rare, i.e. with only one or two individuals (49–55%). Although rarefying abundant species greatly decreased the correlation with bottom–up biotic niches, bottom–up biotic niches generally better predicted the occurrence of rarefied abundant species than very rare ones, suggesting a greater influence of drift on very rare arthropods. That is, (very) rare arthropods are distributed more randomly than rarefied abundant species. Nevertheless, trophic groups differed in the details of their response to bottom–up biotic niches. Plant species composition was a better predictor of rarefied abundant than truly rare hemipterans. In contrast, the importance of bottom–up biotic niches among abundance classes varied less visibly in spiders and wasps. Our study thus suggests that the importance of niches in structuring arthropod communities depends on species rarity and trophic group.

Keywords: arthropods, bottom–up effects, drift, niche, plants, variation partitioning

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Introduction

A recurrent feature of natural communities is that they are composed of few abundant species and many rare species (i.e. those with relatively few individuals) (Preston 1948, Kunin and Gaston 1993, Magurran and Henderson 2003). Despite the large number of rare species in communities, the ecology of rare species remains poorly understood. Theory predicts that, in contrast with abundant species, the occurrence of rare species will be poorly correlated with environmental factors (niches) because small populations are subjected to greater stochasticity (ecological drift) (Hubbell 2001, Zhang et al. 2016, Mo et al. 2018). A growing body of evidence supports this idea (Kunin and Gaston 1993, Magurran and Henderson 2003, Lennon et al. 2011, Siqueira et al. 2012, Zhang et al. 2016, Hu et al. 2018, Mo et al. 2018). Greater stochasticity would also be expected if rare species are transient species (that is 'tourists' from outside of their optimal habitat) or species temporarily rare from fluctuating environmental conditions (Magurran and Henderson 2003, Sgarbi and Melo 2018, Snell Taylor et al. 2018). This pattern, however, could also arise from a mere statistical artefact: rare species simply provide too little information to detect correlations with their niches, even if strong niche affinities exist (Lennon et al. 2003, Siqueira et al. 2012).

Niche affinity is also expected to vary among trophic groups. Among plant-dwelling arthropods, the occurrence of herbivorous insects and parasitoid wasps should be strongly correlated with the occurrence of their hosts, due to the strong bottom–up control from biotic niches to these host specialists (Wright and Samways 1999, Novotný et al. 2007, McCormick et al. 2012, Murphy et al. 2014, Forister et al. 2015, Kemp et al. 2017, Volf et al. 2017, Vidal and Murphy 2018). On the other hand, generalist predators such as spiders can exploit a large array of prey, potentially weakening the affinity with specific bottom–up biotic niches (Lanta et al. 2018); nonetheless, it is still known that plants can affect their abundance and distribution, either directly via plant structure (Gunnarsson 1990, Visser et al. 1999, Borges and Brown 2001, Romero and Vasconcellos-Neto 2005) or indirectly via prey abundance (Wimp et al. 2010, Lanta et al. 2018). However, such inferences on niche affinity for specialists versus generalists are mostly based on the most abundant species within a single trophic group, whereas samplings of arthropods typically include many very rare species, notably singletons and doubletons (i.e. species with only one or two collected individuals) (Preston 1948, Novotný and Basset 2000), and several trophic groups. Hence, there is still a need to explore whether rare arthropods are less associated with their niches than the other more abundant species, and whether this pattern varies across different trophic groups.

Here, we estimated the importance of bottom–up biotic niches on very rare species (singletons and doubletons), rare species (with three to seven individuals) and abundant species (≥ 8 individuals) of arthropod sampled on entire plant communities in a biodiversity hotspot (the Cape Floristic Region in South Africa), while comparing different trophic groups. To quantify bottom–up biotic niches, we investigated the effect of plant species composition on herbivorous hemipterans and their natural enemies (i.e. spiders and parasitoid wasps), as well as the importance of hemipteran species composition on the same natural enemies. We used variation partitioning to distinguish between the variance explained by bottom–up biotic niches and that derived from inherent spatial structure (autocorrelation) of samples. To estimate how niche affinities are affected by species rarity and to account for potential statistical artefacts, we also analysed subsets of the abundant species with comparable abundances to rare species ('rarefied' abundant species). We expected that, 1) in all trophic groups, after accounting for spatial structure, the occurrence of both very rare and rare species will be less correlated with bottom–up biotic niches than the occurrence of rarefied abundant species, suggesting relatively greater stochasticity (drift) regulating rare species. In addition, 2) the strength of the correlation with the bottom–up biotic niches was expected to vary across trophic groups. Because many species of hemipterans and parasitoid wasps may be host specialists, plant species composition should strongly affect hemipteran occurrence and, through hemipterans, affect parasitoid wasp occurrence. In contrast, most spider species may be generalist predators, but habitat structure (e.g. plant architecture) should also importantly influence them. Therefore, plant species composition should affect spider occurrence, while these generalist predators should be less affected by the species composition of hemipterans.

Material and methods

Study site

The study was conducted in the Jonkershoek Valley (33°57′S and 18°55′E), in the Jonkershoek Nature Reserve (Cape Floristic Region; Western Cape; South Africa) characterized by granite and sandstone derived soils. The valley comprises two different slopes and three 20 × 20 m sites were selected on each slope (Supplementary material Appendix 1 Fig. A1). The vegetation at all sites is fynbos, the dominant vegetation type in the region, characterized by sclerophyllous shrubs. Sampling was conducted in the sixth year of post-fire succession.

Sampling design

Within each site, we randomly chose eight 2.5 × 2.5 m quadrats (hence, a total of two slopes × three sites × 8 = 48 quadrats were selected). We sampled arthropods living in the entire plant communities, i.e. we sampled from all the plant species found in the quadrats. In each quadrat, covers of all plant species were estimated in m² by visual inspection with the help of a 1-m² frame, and then arthropods found on plants were sampled with a vacuum sampler (modified

leaf shredder vacuum/blower STIHL SH-86d; maximum airflow: 770 m³ h⁻¹) in a unique sampling session (between October and December 2014). All plants and arthropods were separated by morpho-species and identified to the lowest taxonomic level possible (mostly species level for plants; family level for insects; genus level for spiders) with help of identification keys (Scholtz and Holm 1985, Manning 2007) and/or professional taxonomists. In this study, we focused on arthropod species from three trophic groups, each comprising phylogenetically related and/or functionally similar species: herbivorous hemipterans (predatory heteropterans were excluded), spiders (Araneae; i.e. predators) and parasitoid wasps (i.e. Hymenopterans of the paraphyletic group Parasitica). Specific information on spider and wasp feeding diets were not available, but according to literature some of the most represented spider (Theridiidae, Araneidae and Philodromidae; Nyffeler 1999) and wasp (Encyrtidae and Aphelinidae; Scholtz and Holm 1985) families in our study are known to largely rely on hemipterans as prey or hosts. As hemipterans are the dominant herbivorous insect group in our study, we expected a significant influence of hemipteran occurrence on spiders and wasps. Additional information on the sampling method can be found in Bosc et al. (2018a). All morpho-species collected in this study are stored in 70% ethanol at the Stellenbosch Univ. Data sets, species lists and photographs of all arthropod species are provided in Dryad Digital Repository: <https://doi.org/10.5061/dryad.6k939m4> (Bosc et al. 2018b).

Analyses

Sampling completeness
To estimate sampling completeness, we estimated the extrapolated species richness in a species pool for plants, hemipterans, spiders and wasps and inspected their species accumulation curves. In particular, we used the R functions specpool and poolaccum from the package vegan (Oksanen et al. 2017, R Core Team). Four incidence-based estimates were used: Chao, first-order Jackknife, second-order Jackknife and bootstrap.

Species abundance groups
Arthropod species were classified according to their abundance in the entire data set, i.e. the sum of their abundances in all quadrats. Species were classified in three abundance classes: very rare (VR), rare (R) and abundant (A) species. Very rare species were those with the total abundance of each species in the entire data set being either one (singletons) or two (doubletons). Abundant species were those with the total abundance of each species in the entire data set being above or equal to the 75% quartile of abundances (i.e. eight individuals). The remaining species formed the rare species class (with three to seven individuals per species). The 75% quartile threshold separating rare and abundant species was chosen following Siqueira et al. (2012).

Partitioning of the environmental and spatial variations and hypothesis testing
In all the analyses, one of the challenges was to distinguish the bottom–up effects acting on arthropods (i.e. bottom–up biotic niches) from the effect of dispersal limitation. Because environmental variables are often spatially structured, both environmental control and dispersal limitation can result in spatial autocorrelation of communities, i.e. spatial aggregation of individuals or species (Legendre et al. 2009, Smith and Lundholm 2010). To take this into account, we used a variation partitioning method (Borcard et al. 1992), with a recent implementation using Moran spectral randomisations (Wagner and Dray 2015) which accounts for spurious environment–space correlations (Clappe et al. 2018). This allowed us to distinguish the variance in the composition of arthropod species explained by bottom–up factors (i.e. plant and/or hemipteran species composition) from the spatial autocorrelation of samples that is independent of these factors (independent spatial fraction). The residual variance (independent spatial fraction + unexplained variance) could reflect the upper bound of the null effect of the absence of environmental filtering; i.e. variance explained by dispersal and drift only. It must be noted however that the residuals can also correspond to variation explained by unaccounted-for environmental variables, and so cannot unambiguously be interpreted as indicative of the effects of dispersal and drift. Hence, the variation partitioning method focuses on the interpretation of the measured environmental variables (i.e. bottom–up biotic niches).

Arthropod abundance classes (very rare, rare and abundant species) in each trophic group comprised different numbers of species, which could bias comparisons. To alleviate this bias, we compared arthropod data sets of similar dimensions. For each abundance class within each trophic group, we randomly generated 300 data sets of 10 species from the full data set. Then, separate variation partitioning procedures were performed for each data set by using redundancy analyses (RDAs). In each variation partitioning, we distinguished two explanatory datasets predicting hemipterans (including plant and spatial variables) and three explanatory datasets predicting spiders and parasitoid wasps (including plant, hemipteran and spatial variables). Because of the correlations between plants and between hemipterans, they could not be directly used as predictors in the RDAs. Instead, they were transformed separately into principal components (hereafter referred as predictor plants or hemipterans) and then used in the analyses. Quadrat spatial coordinates were transformed into MEMs (Moran's Eigenvectors Maps) and then used as spatial variables in all analyses. Further details on the spatial variables, variation partitioning method and variable selection process are provided in Supplementary material Appendix 3. Variation partitioning allowed us to obtain different fractions of the species composition of arthropods explained by the different predictors. These fractions were expressed as adjusted R-squared values (R_a^2; Peres-Neto et al. 2006, Clappe et al. 2018). The variance explained by plants and hemipterans could include independent fractions (noted

P and H respectively) and a shared fraction (noted HP). In addition, each of these fractions could include spatial and non-spatial fractions (Supplementary material Appendix 1 Fig. A2). The sum of the independent and shared fractions (P + H + HP) represented the effect of the bottom–up biotic niche.

'Rarefaction' of abundant species and hypothesis testing
The lack of information provided by rare species can reduce the ability to detect their correlations, if any, with environmental variables (niches). Differences in niche affinities for very rare, rare and abundant species could, thus, be attributable to associated statistical artefacts and not to genuine biological differences. To account for the potential statistical artefacts, we performed additional variation partitioning procedures on 'rarefied' data sets. For each of the 300 abundant species data sets, we resampled each abundant species to obtain subsamples of the size of either very rare or rare species, which could then be directly compared with the collected very rare and rare species. This was performed using the R function 'rrarefy' in the package 'vegan' on the species-by-quadrat dataset for abundant species. For each abundant species, a certain number of individuals were randomly selected, equivalent to the number of individuals of a very rare species (one or two) or a rare species (three to seven), with all the rest individuals of the species removed (thus 'rarefied'). After the rarefaction of abundant species, we obtained two types of data: data sets with species abundance distributions comparable to very rare species (i.e. one or two selected individuals; hereafter referred as Avr) and data sets with species abundance distributions comparable to rare species (i.e. three to seven selected individuals; hereafter referred as Ar). Similarly, for each of the 300 rare species data sets, rare species were 'rarefied' to obtain data sets with species abundance distributions comparable to very rare species (hereafter referred as Rvr). We thus obtained 300 replicates of Avr, Ar and Rvr data sets. Those rarefied datasets had similar dimensions (48 quadrats × 10 species) and similar amount of information

(i.e. similar abundance per species and similar total abundance) to the observed data sets of (very) rare species, allowing unbiased comparisons.

To test the statistical significance of the differences in bottom–up biotic niche between rare species and rarefied abundant species, we used Welch t-tests (function t.test in R) and calculated Cohen's d effect sizes. We tested the alternative hypothesis that the observed distribution of R_a^2 values obtained for rare species was significantly smaller than the distribution of R_a^2 values obtained for the rarefied datasets. Very rare species were additionally compared with rarefied rare and abundant species. Observed values that are significantly lower than those obtained for rarefied datasets are consistent with a greater role of ecological drift in rarer species.

Relative importance of each plant or hemipteran species as predictor
The relative importance of particular plants or hemipteran species as predictors in the RDAs was expressed as partial R_a^2 values. Each selected principal components (PC) in the RDAs was assigned a partial R_a^2 value; that is the R_a^2 value of the RDA conducted with this PC alone. To evaluate the partial R_a^2 value of, for instance, each plant species in the corresponding RDA, for each plant PC we attributed relative weights to each species as a function of their absolute PC score, which were then multiplied by the partial R_a^2 value of the PC. Then, the partial R_a^2 value for each plant species was equal to the sum of their weighted partial R_a^2 values for all the principal components. This provided an estimation of the relative importance of each plant or hemipteran species in explaining the species composition of very rare, rare, abundant and 'rarefied' species in each trophic group.

Data deposition

Data available from the Dryad Digital Repository: <https://doi.org/10.5061/dryad.t5n8805> (Bosc et al. 2019).
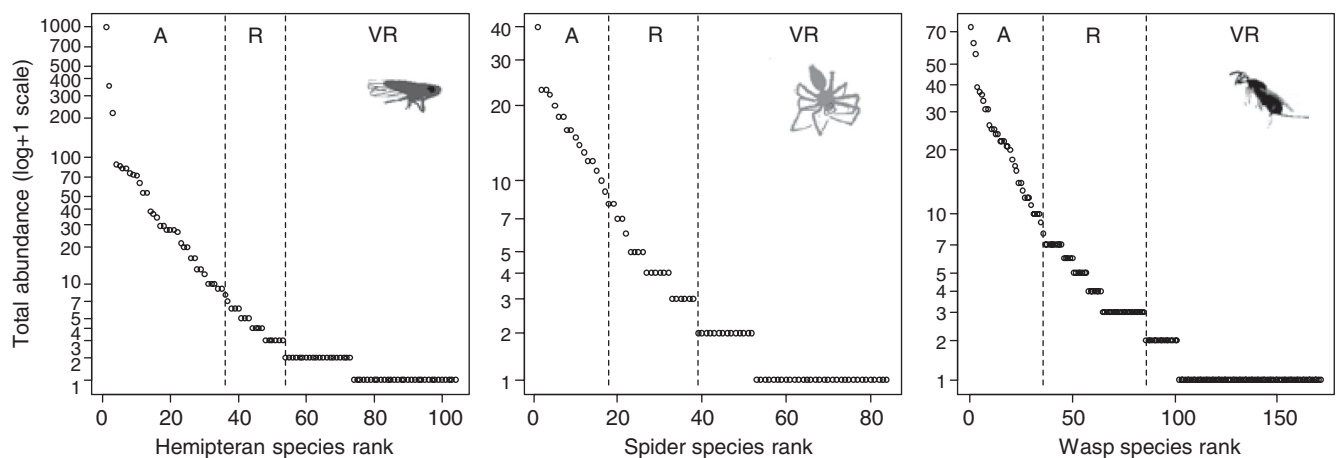

Figure 1. Rank log–abundance curves for different trophic groups of arthropods sampled in the Cape Floristic Region of South Africa.

Results

We classified the arthropods into 104 herbivorous hemipteran, 84 spider and 171 parasitoid wasp morpho-species, corresponding to 2894 hemipteran, 450 spider and 1167 wasp individuals (families presented in Supplementary material Appendix 1 Fig. A3–A5). Plant communities were represented by 109 morpho-species belonging to 37 families (Supplementary material Appendix 1 Fig. A6), of which Proteaceae and Asteraceae were the most species rich and abundant. The sampling completeness (ratio between observed and extrapolated species richness) was 66–86% for hemipterans, 59–84% for spiders, 59–85% for wasps and 79–93% for plants, depending on the estimate considered (detailed in Supplementary material Appendix 2 Table A1; accumulation curves in Supplementary material Appendix 1 Fig. A7–A10).

Very rare species (one or two individuals) represented 49% of hemipteran, 55% of spider and 50% of wasp species (Fig. 1; singletons represented 30, 38 and 41% of species respectively). Rare species (three to seven individuals) represented 16, 23 and 29% of species respectively, and abundant species ($\geq$ 8 individuals) represented 35, 23 and 21% of species respectively.

Bottom–up biotic niche of arthropods

Figure 2 and Table 1 present the variance (R_a^2) in arthropod occurrence explained by bottom–up biotic niches; that is, the fractions of variance explained by plants (P + HP) and hemipterans (H + HP), each including a shared fraction (HP). Further details of fractions (non-spatial and spatial parts) are presented in Supplementary material Appendix 2 Table A2. The analyses generally showed that bottom–up biotic niches explained the composition of rarefied abundant species (Avr = rarefied to very rare; Ar = rarefied to rare) much less than the composition of their unrarefied counterparts (A) (a reduction of 39% on average; SE: ± 2%), but there were negligible differences in explaining the compositional variation of the rarefied rare species (Rvr) versus their unrarefied counterparts (R) (Supplementary material Appendix 2 Table A3). Hence, this indicates that a large part of the differences observed between (very) rare and abundant species can be attributed to statistical artefacts (Fig. 2). Even so, differences in the importance of bottom–up biotic niches remained noticeable according to species rarity and/or trophic group (Table 2, Supplementary material Appendix 2 Table A4, A5).

For the species composition of herbivorous hemipterans (Fig. 2; top panel), bottom–up biotic niche (plant species composition; P) explained very rare species (VR) less well than Avr (a reduction of 25 ± 5%), and explained rare species (R) much less than Ar (a reduction of 49 ± 3%). Bottom–up biotic niche explained the compositional variations of VR and Rvr equally well.
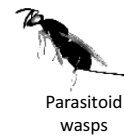
For the species composition of spiders (Fig. 2; middle panel), bottom–up biotic niche (plant and hemipteran
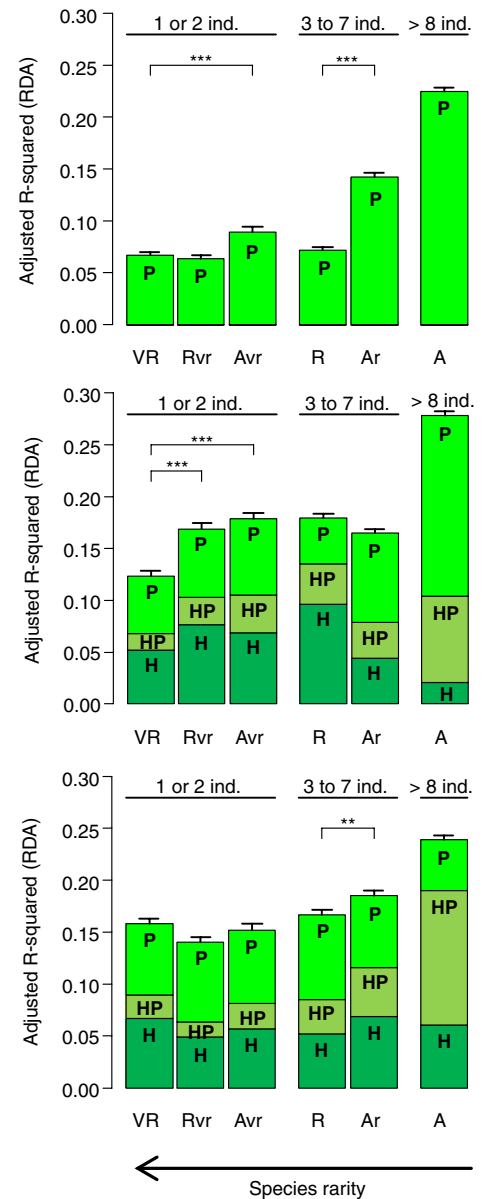

Figure 2. Variation partitioning using redundancy analyses (RDAs): plant (and hemipteran) species composition (bottom–up biotic niches) effects on arthropod species composition for very rare species (VR), rare and abundant species 'rarefied' to very rare (Rvr and Avr), rare species (R), abundant species 'rarefied' to rare (Ar) and abundant species (A). Mean fractions of variation explained by plant (and hemipteran) reported as adjusted R-squared values (R_a^2; + SE for the sum of all fractions (P + H + HP); details and spatial fractions in Supplementary material Appendix 2 Table A2). P: plant variation; H: hemipteran variation; HP: shared plant and hemipteran variation. Stars represent significance of tests that the observed R_a^2 values obtained for very rare (or rare) species was smaller than R_a^2 values obtained for the rarefied datasets (**: p < 0.01; ***: p < 0.001). Non-significant comparisons are not reported.

species compositions; P + H + HP) explained very rare species (VR) less well than Rvr and Avr (a reduction of 29 ± 4%). Overall, bottom–up biotic niche explained R and Ar equally

Table 1. Variance (mean adjusted R² values) in arthropod species composition explained by plant and/or hemipteran species composition (bottom–up biotic niches).

		VR	Rvr	Avr	R	Ar	A
Hemipterans	<– Plants (P)	0.067	0.063	0.089	0.072	0.142	0.225
	<– Bottom–up biotic niches (P)	0.067	0.063	0.089	0.072	0.142	0.225
Spiders	<– Plants (P + HP)	0.072	0.092	0.11	0.083	0.119	0.258
	<– Hemipterans (H + HP)	0.067	0.103	0.105	0.136	0.077	0.103
	<– Bottom–up biotic niches (P + H + HP)	0.123	0.168	0.179	0.179	0.163	0.278
Wasps	<– Plants (P + HP)	0.091	0.092	0.096	0.116	0.117	0.18
	<– Hemipterans (H + HP)	0.089	0.064	0.082	0.086	0.115	0.191
	<– Bottom–up biotic niches (P + H + HP)	0.157	0.141	0.153	0.168	0.185	0.24

well, but plant species composition (P + HP) explained R less well than Ar (a reduction of $31 \pm 3\%$) and hemipteran species composition (H + HP) explained R better than Ar (an increase of $74 \pm 6\%$).

For the species composition of parasitoid wasps (Fig. 2; bottom panel), bottom–up biotic niche (plant and hemipteran species compositions; P + H + HP) explained very rare (VR), Rvr and Avr species equally well, and explained R slightly less well than Ar species (a reduction of $10 \pm 3\%$). A large shared fraction of variance (HP) explained abundant species (A).

Relative importance of each plant or hemipteran species as predictor

When considering the plant species that explained arthropod species composition (Fig. 3, Supplementary material Appendix 1 Fig. A11), we can note differences according to species rarity and trophic group. Within trophic group, similar plant species were important, but the strength of the correlation (partial R_a^2) decreased with rarity and when abundant species were 'rarefied'. When considering hemipteran species as predictors (Fig. 4, Supplementary material Appendix 1 Fig. A12), within trophic group, we can note differences in the identity of the important hemipteran species according to rarity, especially for spiders between R and Ar species.

Discussion

The proportion of very rare species (with one or two individuals) in our study was high for a Mediterranean-type ecosystem (49–55%), but not surprising for small-scale sampling in a biodiversity hotspot. Generally, bottom–up biotic niches explained a greater part of variance in the occurrence of abundant arthropod species than for rare or very rare species. However, this pattern could be explained to a large extent by statistical artefacts affecting rare species: 'rarefaction' of abundant species greatly decreased the importance of bottom–up biotic niches, which suggests that the lack of information provided by rare species undermines species–niche correlations.

Bottom–up biotic niches better explained rarefied abundant than rare hemipterans, but less so for spiders and parasitoid wasps where different patterns emerged. For herbivorous hemipterans, plant species composition explained much less very rare and rare species than (rarefied) abundant species. These results suggest a relatively low affinity of rare hemipterans to bottom–up biotic niches which may be linked to a greater importance of drift. In contrast, the importance of plant species composition for (rarefied) abundant species could be linked to high host–plant specificity, as has previously been found in herbivorous insect communities in the region (Augustyn et al. 2013, Kemp et al. 2017). These results contradict a study by Novotný and Basset (2000) who found similar specificity of singletons and non-singleton herbivorous insect species to plants in large samples from tropical forests.

For spiders, plant and hemipteran compositions (bottom–up biotic niches) were better predictors of the occurrence of (rarefied) rare and abundant species than of very rare species, but bottom–up biotic niches did not differ between rare and (rarefied) abundant spiders. Hence,

Table 2. Differences in the importance of bottom–up biotic niches (adjusted R²) between arthropod abundance classes. VR: very rare species; Rvr: rare species rarefied to very rare; Avr: abundant species rarefied to very rare; R: rare species; Ar: abundant species rarefied to rare. Effect size d is negative when VR or R are less explained by bottom–up biotic niches than rarefied species. Standard errors are noted between parentheses. **: p < 0.01, ***: p < 0.001.

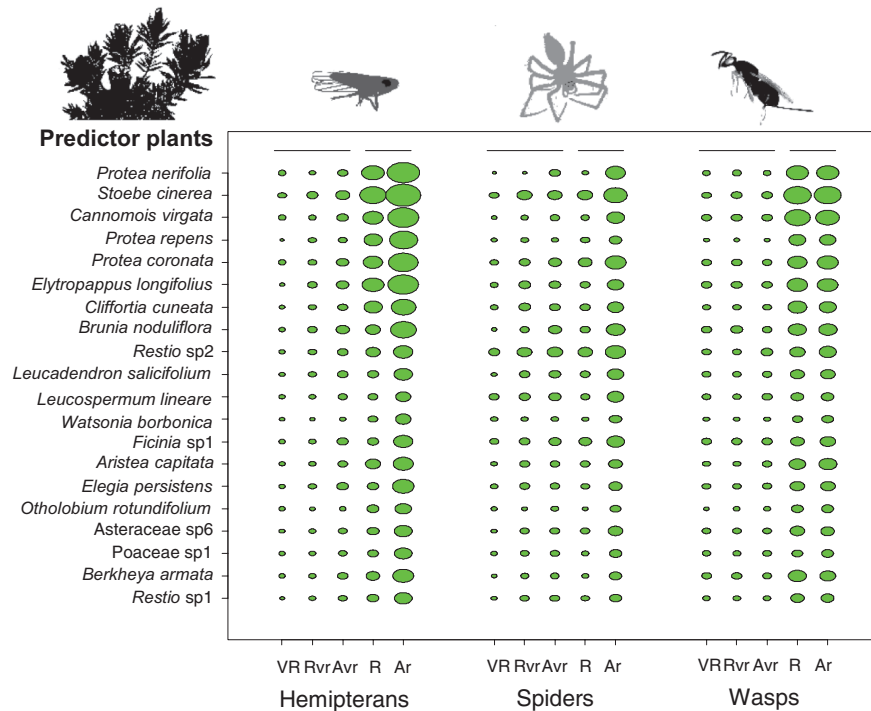|		Effect size d	Diff. adj. R²	t	p
Hemipterans	VR – Rvr	0.062 (0.082)	0.003 (0.004)	0.756	0.775
	VR – Avr	−0.363 (0.082)	−0.023 (0.004)	−4.451	< 0.001***
	R – Ar	−1.234 (0.089)	−0.07 (0.004)	−15.11	< 0.001***
Spiders	VR – Rvr	−0.485 (0.083)	−0.045 (0.006)	−5.943	< 0.001***
	VR – Avr	−0.628 (0.084)	−0.055 (0.006)	−7.696	< 0.001***
	R – Ar	0.199 (0.082)	0.015 (0.005)	2.441	0.993
Wasps	VR – Rvr	0.206 (0.082)	0.018 (0.006)	2.526	0.994
	VR – Avr	0.058 (0.082)	0.005 (0.006)	0.716	0.763
	R – Ar	−0.236 (0.082)	−0.019 (0.005)	−2.89	0.002**

Figure 3. Part of variance in arthropod species composition explained by the 20 most important plant species (full version in Supplementary material Appendix 1 Fig. A11); determined from variation partitioning using redundancy analyses (RDAs; Fig. 2) for very rare species (VR), rare and abundant species 'rarefied' to very rare (Rvr and Avr), rare species (R), abundant species 'rarefied' to rare (Ar) and abundant species (A) for different trophic groups. The size of the circles is function of the importance of each plant species, expressed as partial adjusted R^2 values.

overall, the importance of bottom–up biotic niches for spiders only weakly varied with species rarity, and therefore do not signal a noticeably larger importance of stochasticity (drift) in rare spiders. However, the results suggest that biological differences may exist between spider abundance groups. Plant species composition was especially important for (rarefied) abundant spider species, whereas hemipteran species composition was a better predictor of rare spider species. This might imply that rare spiders are more dietary specialised than abundant spiders. In contrast, abundant spider species would be mostly dietary generalists, but present strong affinities with plants. We know that plant architecture can influence the establishment of web-building spiders (Gunnarsson 1990, Visser et al. 1999, Romero and Vasconcellos-Neto 2005), and such spiders were the most represented in our communities (notably Theridiidae). This would explain the association of spiders with tall herbs or shrubs with elongated and spaced stems/leaves such as *Restio* sp. (Restionaceae) and *Leucospermum lineare* (Proteaceae), and this may be true for both rare and abundant spider species, which were affected by relatively similar plant species. Also, specific plant–spider species associations could be explained by predation pressure on spiders. High levels of bird predation on spiders were experimentally shown for the same communities (Bosc et al. 2018a). In that context, some plant species could provide spiders greater protection against their predators.

In parasitoid wasps, overall, abundance classes were equally explained by plant and hemipteran compositions (bottom–up biotic niches), which does not suggest a greater influence of drift on the rarest wasps. The results also showed an important fraction of variance in (rarefied) abundant species explained jointly by plant and hemipterans (HP). This suggests that plant–wasp species associations were, at least in part, the result of specific associations of wasps with plant–specific hemipterans. Parasitoid wasps are indeed known for their ability to exploit plant–specific insects and detect their host plant (McCormick et al. 2012, Murphy et al. 2014). The results of the present study suggest differences in the ecology of rare species between trophic groups. Rare hemipteran species would be more affected by dispersal and ecological drift (neutral processes; Hubbell 2001, Magurran and Henderson 2003) than rare spiders and parasitoid wasps.

Generally, for all trophic groups, dispersal is likely an important structuring factor in our communities, as significant spatial structures were found, either dependent or independent of bottom–up factors (Supplementary material Appendix 2 Table A2). Dispersal could notably be influenced by the configuration of the valley, which is composed of two deeply separated slopes (Supplementary material Appendix 1 Fig. A1). However, it must be noted that other non-neutral factors not considered in this study are also likely to influence those species. Our study focused only on bottom–up biotic factors. Other factors such as abiotic factors, competition
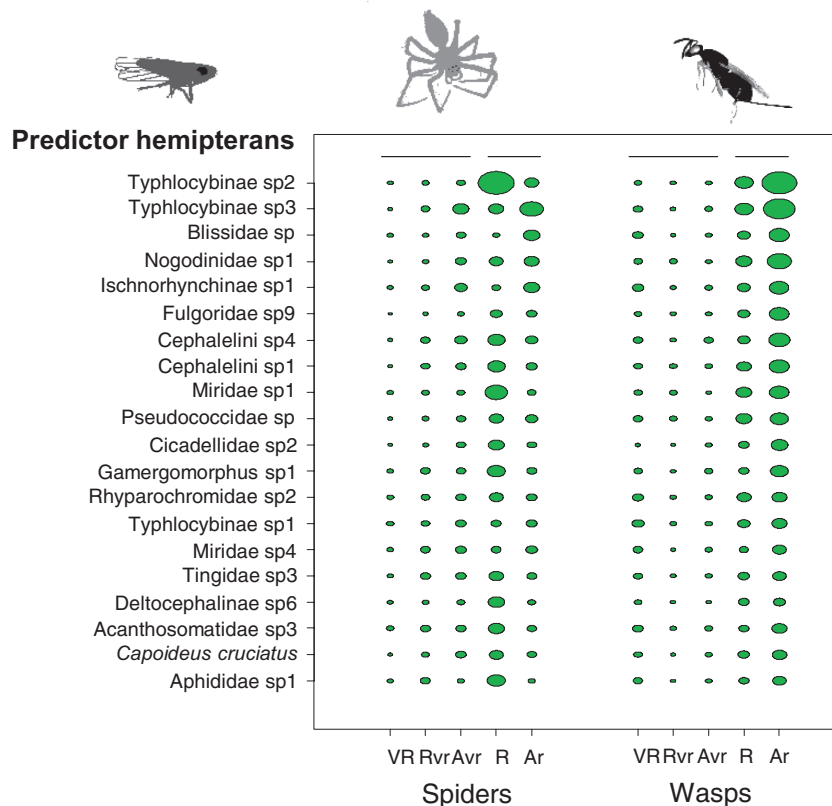
Figure 4. Part of variance in arthropod species composition explained by the 20 most important hemipteran species (full version in Supplementary material Appendix 1 Fig. A12); determined from variation partitioning using redundancy analyses (RDAs; Fig. 2) for very rare species (VR), rare and abundant species 'rarefied' to very rare (Rvr and Avr), rare species (R), abundant species 'rarefied' to rare (Ar) and abundant species (A) for different trophic groups. The size of the circles is function of the importance of each hemipteran species, expressed as partial adjusted R^2 values.

or top–down effects of predators (notably birds; Bosc et al. 2018a) could also influence them.

Also, it is possible that part of the very rare species in our study are transient species, i.e. species outside of their optimal habitat. The presence of transient rare species would be notably linked to the inflow (i.e. dispersal) of species from adjacent habitats, known as the mass or edge effect (Magurran and Henderson 2003, Sgarbi and Melo 2018). Transient species would be expected to be less affected by environmental variables compared to 'resident' species, which may account for part of the observed differences between very rare and abundant species.

In conclusion, our study showed how bottom–up biotic niches can differently affect plant-dwelling arthropods according to species rarity in different trophic groups. Especially, our results suggest a decreasing importance of bottom–up biotic niches and an increasing effect of drift with rarity in hemipterans, but not necessarily in spiders and wasps. Our study also showed how statistical artefacts can underestimate the effect of bottom–up biotic niches on rare species. Consequently, cautions should be taken when interpreting the results of ecological studies including many very rare species (singletons and doubletons). Nonetheless, not considering very rare species would not be advisable either. If carefully considered, the interpretation of very rare species could make small samples more valuable and thus avoid massive and repeated samplings, which has ethical and ecological implications, especially in a biodiversity hotspot such as the Cape Floristic Region (Myers et al. 2000).

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Supplementary material (available online as Appendix ecog-04396 at <www.ecography.org/appendix/ecog-04396>). Appendix 1–3.