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RESEARCH ARTICLE

Animal Functional Traits

Interactions between protea plants and their animal mutualists and antagonists are structured more by energetic than morphological trait matching

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Abstract

1. Traits mediate mutualistic and antagonistic interactions between plants and animals, and should thus be useful for predicting trophic species interactions. Studies to date have examined the importance of morphological trait matching for plant–animal interactions, but have rarely explored the extent to which these interactions are shaped by matching between energetic provisions of plants and energetic demands of animals.
2. We tested whether energetic and/or morphological trait matching shapes interactions between *Protea* plant species and their interacting animal mutualists and antagonists in the Cape Floristic Region, South Africa.
3. We recorded interactions between 22 *Protea* species, pollinating insects and vertebrates as well as seed predators (endophagous insect larvae in protea cones) at 21 study sites. To relate species interactions to matching trait pairs, we measured key morphological traits (shape and size of flower heads and seed cones, and mouth part length as well as body length) and quantified the animals' energetic demands (metabolic rate) together with the plants' energetic provisions (nectar sugar amount, seed-to-cone mass ratio). We calculated log ratios of both energetic and morphological traits between animals and plants as predictor variables for the number of observed interactions between *Protea* species and their animal interaction partners.
4. For both mutualistic and antagonistic interactions, we found significant effects of morphological and energetic trait ratios on the interactions between plants and animals. Trait ratios accounted for 11% to 22% of variation in species interactions. Consistent with energetic trait matching, we found a hump-shaped relationship between interaction frequency and log ratios of energetic traits of animals and plants, indicating that interactions were most frequent at intermediate log ratios between energetic demand and provision. Effects of morphological

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trait ratios on interactions were statistically supported in most cases, but were variable in the magnitude and shape of the predicted relationships.

5. Across animal taxa and interaction types, energetic traits had more consistent effects on interactions between plants and animals than morphological traits. This suggests that energy can function as an important interaction currency and facilitate the understanding and prediction of trophic species interactions.

KEYWORDS
cape floristic region, energy, functional traits, interaction networks, morphology, pollination, *Protea*, seed predation

1 | INTRODUCTION

Interacting species in ecological networks can either be linked through mutualistic interactions, such as pollination, or by antagonistic interactions, such as seed predation and herbivory (Bascompte, 2010). While many studies have examined how the structure of mutualistic and antagonistic networks varies in space and time (Poisot et al., 2015; Trøjelsgaard & Olesen, 2016), less is known about the determinants of the individual interactions composing these networks (but see Bartomeus et al., 2016; Eklöf et al., 2013).

Functional traits, that is, the measurable characteristics of a species that influence its performance and interactions with other species (Cadotte et al., 2011; Dehling & Stouffer, 2018), can inform a mechanistic understanding of species interactions (Bartomeus et al., 2016; Eklöf et al., 2013). One approach to understand the formation of individual interactions is to relate interaction data to functional traits of potential interaction partners (Dehling & Stouffer, 2018). For example, Stang et al. (2006) found that visitor numbers of insects to plants were related to the matching of plant and insect traits. Other work has shown that trait matching between plant and animal species is a general phenomenon across avian seed-dispersal networks (Bender et al., 2018). However, studies that identify functional traits applicable to both mutualistic and antagonistic interactions are rare.

Morphological traits related to the size and shape of organisms have been identified as key determinants of interaction preferences of species in different types of networks (Bartomeus et al., 2016). For example, morphological traits of resource and consumer species were the most important type of matching traits in a study across different types of ecological networks (Eklöf et al., 2013). As such, morphological trait matching between species can be used to identify interaction rules (Morales-Castilla et al., 2015; Stang et al., 2009) and predict species interactions (Gravel et al., 2013). In addition to species' morphology, energy-related traits, given by the energetic provisions of resource species and the metabolic demands of consumers, influence the occurrence and frequency of trophic interactions (Gravel et al., 2016). Energy-based traits can outperform morphological traits in predicting the composition of consumer communities (Geerts et al., 2020). Combined analyses of morphological and energy-related traits could therefore help to build a general framework on how functional traits and interactions are related in ecological networks.

General insights into ecological networks may be derived through the integration of metabolic theory by matching energetic demands and provisions of consumer and resource species in trophic interactions (Moore & de Ruiter, 2012). Previous studies of food webs have shown a displacement of smaller-sized species with lower metabolic rates to resources with lower energetic provisions (Loeuille & Loreau, 2005), consistent with the niche model of food web structure (Williams & Martinez, 2000). This is because individuals with a high metabolic rate usually display a higher competitive ability compared to individuals with a lower metabolic rate (Biro & Stamps, 2010; Pettersen et al., 2020). Competitive interactions, that is, the utilization of shared, but limited resources, can therefore lead to competitive hierarchies where large-bodied species with high metabolic demand dominate energy-rich resources, whereas subordinate smaller-bodied species with lower metabolic demands are displaced to less energetic resources (Ford & Paton, 1982; Mac Nally & Timewell, 2005). In combination, these processes are expected to lead to energetic trait matching between consumer and resource species in trophic interactions.

We studied *Protea* species (Family Proteaceae) and their animal mutualists (pollinators) and antagonists (endophagous insect larvae in protea cones) in the Cape Floristic Region (CFR), South Africa. Proteas are ideally suited to test for the effects of morphological and energetic traits on species interactions because proteas often dominate plant communities in the CFR (Campbell, 1986; van Wilgen, 1982), exhibit large morphological variation in their reproductive traits (Rebelo, 2001), produce large amounts of nectar and are a key resource for numerous animals, in particular birds, insects and rodents (Hargreaves et al., 2004; Nottebrock, Schmid, Mayer, et al., 2017). Furthermore, they accumulate considerable amounts of nutrients in their canopy-stored seed banks (Bond, 1985; Esler et al., 1989), providing a key energy source for endophagous larvae of several insect species (Coetzee & Gilomee, 1987; Roets et al., 2006; Wright, 1994). Studying protea communities, therefore, provides an unprecedented opportunity to identify functional traits associated with mutualistic and antagonistic interactions between plants and animals.

We tested for both energetic and morphological trait matching between plants and animals in protea communities by calculating log trait ratios between the energetic and morphological traits of consumer and resource species. Hump-shaped relationships between interaction frequencies and these trait ratios would indicate energetic and morphological trait matching so that consumer species interact with resource species within a preferred range of matching trait values (Rohr et al., 2010). Specifically, we tested the following hypotheses. (1) Energetic trait matching between plants and animals leads to a hump-shaped relationship between interaction frequencies and the energy ratios of consumer and resource species (Bartomeus et al., 2016; Rohr et al., 2010), (2) Morphological plant–animal trait matching causes a hump-shaped relationship between interaction frequencies and morphological trait ratios (Eklöf et al., 2013).

2 | MATERIALS AND METHODS

2.1 | Study system and study sites

We worked at 21 study sites (see Table S1) in the fire-prone CFR (Goldblatt, 1978). Study sites were selected so that they represented a range of *Protea* diversity (2–9 species), protea density (79–127,000 individuals per site) and post-fire age (2.2–25 years). Each site covered an area of 120 m × 120 m. The minimum distance between sites was 150 m; the mean distance was 8530 m. We worked on the same study sites in 2017 and 2018 ($n = 21$ sites), but one study site burned in late 2017 and could only be sampled in 2017. We conducted the field work during the austral winter (April to September). At that time of the year, most *Protea* species flower and protea nectar is the main resource for most nectarivorous birds and insects in the CFR (Rebelo, 2001). The abundance and richness of antagonists in protea cones also peaks in the austral winter (Roets et al., 2006). We visited each study site on 2 days per year to cover the flowering peaks of most of the *Protea* species (Rebelo, 2001). The field work was conducted under CapeNature permits 0028-AAA008-00262 and 0056-AAA008-00070.

2.2 | Mutualist observations

We conducted the monitoring on sunny and calm days only. On each observation day, we first selected 12 focal plants of all currently flowering *Protea* species being a representative subset of the flowering individuals and bearing ideally two adjacent flower heads (i.e. max. 24 focal flower heads on 12 focal plants per site and day). Before starting insect observations, we set up 12 time-lapse cameras focused on both flower heads of each of the 12 focal protea plants (PlotWatcher Pro by Day 6 Outdoors, see supplemental files for two exemplary videos of a pollinating bird and rodent) to monitor the interactions of vertebrate mutualists (observation time between 8:00 am and 4:00 pm). We analysed a standardized time of four observation hours for each plant. Overall, we analysed video material for 1605 flower heads and 6420 observation hours across the 21 study sites.

After setting up the time-lapse cameras, two observers started the insect observation on the same two focal flower heads per focal plant simultaneously for 15 min, observing all 12 focal plants one after the other (observation time between 10:00 am and 4:30 pm). All insects seen probing the florets or moving into a flower head were recorded. We caught representatives of all visiting insect morphospecies with an insect aspirator for morphological measurements, and stored them in a reference collection covering both study years. All specimens were identified to species level whenever possible, otherwise to the next highest taxonomic level. Pollinating insect observations resulted in a dataset comprising 401 observation hours across 21 study sites.

We performed separate analyses for insect and vertebrate mutualists, given the different observation times for both groups. All analyses were restricted to legitimate flower visits showing a contact between the animal and the reproductive plant parts or moving into the florets. Potential links between plants and animals were defined by the co-occurrence of an animal species and a flowering *Protea* species on a particular observation day and site. We aggregated interaction data at site level and summed the interaction frequencies between pairs of co-occurring *Protea* and mutualist species across observation days.

2.3 | Antagonist sampling

We sampled antagonists by collecting cones from ideally five focal plants per species on 20 study sites in 2017 or 2018 (one site was too young and plants had not yet developed cones). We worked on serotinous *Protea* species only, as these species retain their seeds inside closed cones for a number of years (Bond, 1985). On every focal plant, we chose cones from up to the last three cohorts, each representing a different flowering season and ranging back 3 years in time. For each cohort, we aimed to collect one open cone (seeds released due to damage or predation) and one closed cone (seeds retained, i.e. an externally intact cone). Overall, we collected 1915 open and closed cones of 20 *Protea* species across the 20 study sites.

We cut the closed cones open and stored all antagonist insects and their larval cases in a reference collection for later trait measurements. Each antagonist species leaves characteristic frass and feeding marks which we assigned to the encountered specimen. Based on these findings, we were able to assign most traces found in closed and open cones to specific antagonist species. Potential links between plants and animals were defined by the spatiotemporal co-occurrence of *Protea* species and animal antagonists. For the analyses, we aggregated data at site level and counted the number of realized interactions (presences) and of unrealized interactions (absences) between each co-occurring species pair.

2.4 | Plant and animal functional traits

We selected potentially matching energetic and morphological traits of plants and animals. For mutualistic interactions, energetic traits were sugar amount per flower head for plants and metabolic rate for animals. Morphological traits were flower head closedness for plants and mouth part length for animals. For antagonistic interactions, energetic traits were cone-to-seed-mass ratio for plants and metabolic rate for animals, while morphological traits were bract thickness for plants and borer head width for animals. Plant traits were measured in the field on several protea individuals for each site by species combination (see Nottebrock, Schmid, Mayer, et al., 2017; Table S7). Animal traits were measured on several individuals per species (see Tables S8 and S9 for details). Insects traits were measured on the sampled individuals, vertebrate traits were measured in museum collections (Iziko South African Museum in Cape Town, South Africa; Senckenberg Naturmuseum Frankfurt, Germany) and derived from literature. We calculated species-level mean trait values for all traits, except for cone dry mass, seed dry mass and bract thickness. For these traits, we used site-level means for each *Protea* species because these traits showed high intraspecific variability among sites. In the following, we provide a short description of the specific trait measurements for plants and animals.

For plants, we complemented existing nectar data from the same study sites and species (Nottebrock, Schmid, Mayer, et al., 2017), by extracting nectar by centrifugation of open flower heads (Armstrong & Paton, 1990) and measurement of nectar sugar concentration (w/w). We then calculated potential sugar amount (mg) per flower head as the product of nectar sugar concentration (transformed into weight per volume) and nectar volume. The flower head morphology influences the access of animal pollinators to proteas (Bruce et al., 2014). Open protea flower heads have a bowl-like shape (e.g. *P. cynaroides*, *P. nitida*), while closed flower heads have a tube-like shape and usually bear elongated bearded perianths that constrain animal access (e.g. *P. coronata*, *P. speciosa*; Rebelo et al., 1984). To describe this range between open (easily accessible) and closed (difficult to access) flower heads, we calculated the mean flower head closedness as the ratio between the diameter at the flower head base to the diameter at the top of the involucral bracts (data from Nottebrock, Schmid, Treurnicht, et al., 2017).

Protea seeds represent an abundant source of system-scarce nutrients such as N and P (Esler et al., 1989). Seed-predating antagonist species occur more frequently in *Protea* species with a high seed set (Wright, 1994) and low cone mass (Wright & Samways, 1999). To determine the number of fertile seeds per cone, cones were cut open through the middle of the seeds, and fertile seeds (plump and bright contrary to small and dull infertile seeds) were counted by visual inspection. Afterwards, these cones were oven dried at 70°C and weighed using precision scales (accurate to 0.001 g) to calculate mean cone dry mass. Seed mass was not calculated from these cones, as all fertile seeds were destroyed by the heat. Fertile seed mass was instead measured from additional cones from each site. Fertile, dried seeds were weighed using precision scales. The total fertile seed mass per cone (defined as the product of the potential fertile seed crop and fertile seed mass; see Nottebrock, Schmid, Treurnicht, et al., 2017) was divided by mean cone mass to obtain a measure of seed-to-cone mass. We further recorded the bract thickness as a key defence structure against antagonists (Wright & Samways, 1999), especially against species boring through the bracts as larvae or imago (Coetzee & Gilomee, 1987). To this end, we measured bract thickness just above the seed level (approximately 0.5–1.0 cm above the receptacle) using digital callipers.

For animals, metabolic rates were estimated by allometric relationships with body mass for invertebrates (based on 61 insect species from seven orders and standardized to 22°C, Niven & Scharlemann, 2005) and vertebrates (Hudson et al., 2013; Niven & Scharlemann, 2005). Based on these literature data, we raised vertebrate body mass to the power of 0.71 and invertebrate body mass to the power of 0.66. For all insects (mutualists and antagonists), we measured the cumulated dry body mass of all specimens per species (accurate to 0.0001 g), divided by the number of specimens. We used literature data on body mass for birds (Dunning, 2007) and the rodent *Rhabdomys pumilio* (Wilson et al., 2017). We measured invertebrate body length to the nearest 0.01 mm from the tip of the head to the tip of the abdomen, excluding body appendages, based on the fact that pollinating insects fully enter protea flower heads. For all birds, we measured the straight-line distance from the commissural point of the upper and lower beak to the tip of the closed beak as the mouth part length, to the nearest 0.01 mm. Mouth part length of the rodent species was defined as the dorsal distance between the nasal tip and the right inner orbit to the nearest 0.01 mm. For the bract-boring antagonists, we measured the width of their head capsule to the nearest 0.01 mm as a proxy for the insect larvae's bite force. All interaction and trait data are available from the Dryad Digital Repository (Neu et al., 2022).

2.5 | Energetic and morphological trait ratios

As suggested by Rohr et al. (2010), we calculated the log ratios between matching traits of animals and plants and related the interaction frequencies between pairs of plant and animal species to these ratios. By using log ratios of species traits, this model can be applied to different types of consumer and resource traits, including those measured on different scales (Rohr et al., 2010).

Mutualistic energy matching was calculated as the log ratio of the metabolic rate divided by the sugar mass (mg) per flower head. Low log ratios represent mutualists with low energetic demands and flower heads with a high energetic provision, whereas high log ratio values represent mutualists with high energetic demands and flower heads with a low energy provision. Log ratios for energy traits of antagonists were calculated as metabolic rates divided by the seed-to-cone mass ratios. Here, low log ratios represent antagonistic insects with little energy demands and *Protea* species with high seed resource provision, whereas high log ratios represent antagonistic insects with high energy demands and *Protea* species with low seed resource provision.

Morphological matching of mutualists was calculated as the log ratio between animal body length for invertebrates, and mouth part length for vertebrates, divided by the closedness of the flower head. Low values represent short mouth parts/body lengths and closed flower heads, whereas high values represent long mouth parts/body lengths and open flower heads. Antagonistic morphological matching was defined by the bract borer's head capsule width divided by protea bract thickness. Low values correspond to a small head width (little bite force) and thick bracts (high defence), whereas high values correspond to a large head width (large bite force) and thin bracts (low defence). In the interest of comparability, all log ratios were centred and scaled to have a standard deviation of one prior to all analyses. Energetic and morphological log ratios were weakly to moderately correlated (mutualistic invertebrate interactions: $n = 422$, $r = 0.68$, $p < 0.05$; mutualistic vertebrate interactions, $n = 176$, $r = 0.22$, $p < 0.05$; all antagonistic interactions: $n = 498$, $r = 0.51$, $p < 0.05$, bract-boring antagonists only: $n = 336$, $r = 0.041$, $p = 0.45$). Despite these correlations, model estimates based on combined models (including morphological and energetic traits ratios) and individual models (including either morphological or energetic traits ratios) were qualitatively very similar (see Tables S2 and S3).

2.6 | Statistical analyses

We fitted generalized linear mixed models (GLMMs) to relate the interaction frequencies between *Protea* species and their animal partners to the log ratios of energetic and morphological traits. In the case of insect and vertebrate mutualists, we used a Poisson distribution with a log-link to model the observed interaction frequencies between plants and mutualists at each site. To control for differences in the number of observed protea individuals per species and site, we included the log number of observed protea individuals per species and site as an offset in the models. We controlled for random variation among sites, *Protea* species and animal species by including the random-intercept effects of each of these levels in all models. We fitted seven models, separately for insects and vertebrates: an unconditional null model (random effects only), three models including linear effects of energetic and morphological log trait ratios (separate and combined), and three models that included linear and quadratic terms of energy and morphological matching (separate and combined). These comparisons allow us to test for differences between models assuming no relationship between trait ratios and interactions, linear relationships between trait ratios and interactions (i.e. a general preference for specific trait values), and for hump-shaped relationships between trait ratios and interactions (i.e. energetic and/or morphological trait matching between species). The model equations in *R* followed this form, exemplified for energetic trait matching: glmer(number of interaction events ~ energy log ratio + I(energy log ratio^2) + (1|site) + (1|*Protea* species) + (1|mutualist species), family = Poisson, offset = log(protea individuals)).

For antagonist interactions, we fitted analogous GLMMs with a binomial error distribution and a logit-link. The response variable indicated the number of presences and absences of each antagonist species in the cones of each *Protea* species per site. Again, we fitted seven models to test for trait matching between plants and animals in comparison to other possible relationships between log trait ratios and interactions. We repeated this procedure twice, once for all antagonists and once for bract borers only. All models included random effects of the antagonist species on intercepts. We did not include random effects of *Protea* species and site identity in these models as they were estimated to have zero variance. The model equations in *R* followed this form, exemplified for energetic trait matching: glmer(number of presences, absences ~ energy log ratio + I(energy log ratio^2) + (1|antagonist species), family = binomial).

We fitted all models with the LME4 package (version 1.1-27; Bates et al., 2015) in R (version 4.1.0; R Core Team, 2021). We then compared the model fit among the seven candidate models according to their Akaike information criteria, corrected for small sample size (AICc), and calculated the Akaike weight for each model relative to the set of the four fitted models (Burnham & Anderson, 2002). We identified the best models according to the lowest AICc value (AICCMODAVG package version 2.3-1; Mazerolle, 2020). In addition, we computed the marginal and conditional R^2 values (MUMIN package version 1.43.17; Barton, 2022). Marginal R^2 values represent the amount of variance explained by the fixed factors only, while conditional R^2 includes the effects of both fixed and random factors (Nakagawa et al., 2017).

3 | RESULTS

3.1 | Mutualistic and antagonist interaction networks

Overall, we recorded 51 mutualist species (41 invertebrate, nine avian and one rodent species) and recorded 2429 legitimate plant–pollinator interactions across 21 *Protea* species (Figure 1; Tables S4 and S5). This resulted in two datasets with 231 potential and 125 realized links between 41 invertebrate mutualist and 21 *Protea* species, and 81 potential and 44 realized links between 10 vertebrate mutualist and 20 *Protea* species. The two most frequent insect species, the chrysomelid beetle *Chirodica chalcoptera chalcoptera* and the Cape Honeybee *Apis mellifera capensis*, represented 77.3% of the observed interactions in the mutualistic insect network (Figure 1; Table S4A). Many invertebrate mutualists were rare, for example 29 species were recorded fewer than 10 times. The two most frequent mutualists in the vertebrate interaction network were the Orange-breasted Sunbird *Anthobaphes violacea* and the Cape Sugarbird *Promerops cafer* contributing to 89.4% of all observed interactions (Figure 1; Table S4B). Five of the 10 vertebrates were species observed fewer than 10 times.

Overall, we recorded 994 interactions of 10 larval antagonistic insect species across 20 *Protea* species (Figure 1; Tables S5 and S6).

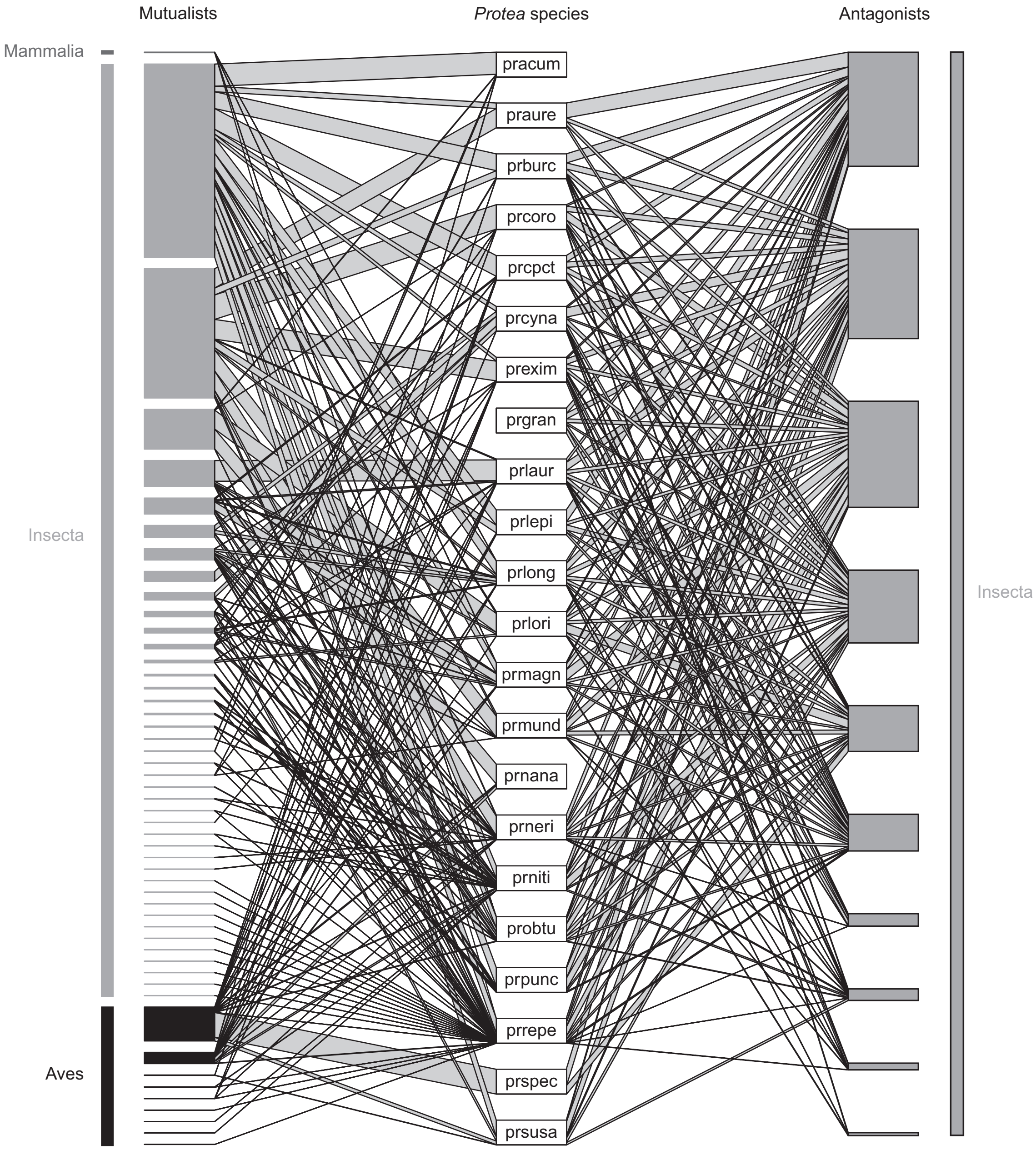

FIGURE 1 Mutualistic–antagonistic interaction network based on pollinators and endophagous insects on protea flower heads and cones from 21 study sites in the Western cape, South Africa. Left bars represent mutualists, middle bars represent *Protea* species, and right bars represent antagonists. Protea bars are standardized to represent 100% of resource use for the respective *Protea* species. The width of left and right bars indicates the relative number of observed interactions for each mutualist and antagonist species, respectively. Link width indicates the relative interaction frequency between the respective *Protea* and its animal partner species. *Protea* species names and codes are given in Table S5. We used the BIPARTITE package (Dormann et al., 2008) in R (version 4.1.0; R Core Team, 2021).

This resulted in a dataset with 177 potential and 134 realized links. The two most common species were the scarab beetle *Genuchus hottentottus* and the moth *Cryptolechia ammopleura*, contributing 45.7% of all interactions. Only one species, the butterfly *Capys alpheus*, was recorded fewer than 10 times. Most antagonists interacted with many different *Protea* species. Seven of the 10 antagonists were classified as bract borers as they tunnel through the involucral bracts of protea cones to enter and/or leave a cone (Coetzee & Gilomee, 1987).

3.2 | Energetic and morphological trait matching

For insect and vertebrate mutualists, models including linear and quadratic terms of energetic and morphological log ratios were better supported than models including only the linear terms (Table 1). Morphological and energetic log ratios explained 11% of variation in species interactions in invertebrates and 13% in vertebrates (marginal R^2 values, Table 1a,b). As expected, the relationships between interaction frequencies and log ratios of energetic traits followed a

TABLE 1 Model comparisons describing the relationships between energetic and morphological trait ratios and interaction frequencies for mutualistic interactions between protea plants and invertebrates (a) and vertebrates (b). Model comparisons include an unconditional null model, models assuming monotonous linear trends (linear terms only), and models assuming hump-shaped or parabolic relationships between log ratios and interaction frequencies (linear and quadratic terms). Given are for each generalized linear mixed model: LL, log-likelihood values; *K*, the number of estimated parameters; AICc, Akaike's information criterion adjusted for small sample sizes; ΔAICc, the differences in AICc relative to the model with the lowest AICc; ω_i, AICc weights; R^2_m, marginal R^2 values (fixed effects only), and R^2_c, conditional R^2 values (fixed and random effects). 'e' indicates linear, 'e^2' quadratic terms of energetic trait matching, 'm' indicates linear and 'm^2' quadratic morphological trait matching terms; the unconditional null model includes no fixed effects. Model summaries and sample sizes of the best models are given in Table 2

Rank	GLMM	LL	*K*	AICc	ΔAICc	ω_i	R^2_m	R^2_c
(a) Mutualistic invertebrates								
1	e + e^2 + m + m^2	−1362.40	8	2741.15	0.00	1	0.108	0.650
2	m + m^2	−1429.93	6	2872.06	130.91	0	0.061	0.612
3	e + e^2	−1502.64	6	3017.49	276.34	0	0.031	0.555
4	e	−1518.38	5	3046.91	305.76	0	0.010	0.537
5	uncond	−1519.49	4	3047.08	305.93	0	0	0.538
6	e + m	−1518.31	6	3048.83	307.68	0	0.009	0.536
7	m	−1519.35	5	3048.84	307.70	0	0.003	0.539
(b) Mutualistic vertebrates								
1	e + e^2 + m + m^2	−394.32	8	805.51	0.00	0.93	0.131	0.675
2	e + e^2	−399.18	6	810.87	5.36	0.06	0.040	0.672
3	m + m^2	−402.32	6	817.13	11.63	0	0.102	0.680
4	e + m	−407.21	6	826.91	21.41	0	0.092	0.655
5	uncond	−409.52	4	827.27	21.76	0	0	0.664
6	m	−408.68	5	827.71	22.20	0	0.035	0.651
7	e	−409.05	5	828.46	22.95	0	0.006	0.663

hump-shaped relationship for both invertebrate and vertebrate mutualists (Figure 2a,c, Figure S1A,C; Table 2), indicative of energetic trait matching. Consistently, invertebrate and vertebrate mutualists with high energy demands interacted more frequently with energy-rich flower heads, whereas mutualists with low energy demands interacted more frequently with energy-low flower heads (Figure 2a,c, Figure S1A,C). For instance, *Apis mellifera capensis* interacted with a broad range of *Protea* species, but was most frequently observed on *Protea* species bearing a medium sugar amount, whereas interaction frequencies decreased towards low and high sugar amounts. Similar hump-shaped patterns were also identified for most vertebrate mutualists (Figure 2c, Figure S1C; Table 2b, Table S2C), especially for the three sunbird species. The optimum in energetic trait matching was shifted more towards sugar-rich resources for vertebrates compared to insects (compare Figure 2a,c).

Contrary to our expectation, morphological trait matching did not follow hump-shaped relationships (Figure 2b,d, Figure S1B,D; Table 2, Table S2B,D). Interaction frequencies of insect mutualists and morphological trait ratios showed a parabolic relationship and increased either towards closed flower heads and short body lengths or towards open flower heads and long body lengths. That is, insect mutualists with long body length, such as Cape Honeybee, interacted more frequently with open flower heads (Figure 2b, Figure S1B). On the other end, insect mutualists with short body length, such as the chrysomelid beetles *Chirodica chalcoptera chalcoptera*, were more frequent on closed flower heads. In the case of vertebrate pollinators, the statistical model predicted a largely linear increase in interaction frequencies towards open flower heads and long mouth parts (Figure 2D, Figure S1D; Table 2b, Table S2D). The two most common bird species (Orange-breasted Sunbird and Cape Sugarbird), both bearing long beaks, were more likely to interact with *Protea* species with open flower heads. Nevertheless, their interaction frequencies on closed flower heads were still higher than those of all other vertebrate species (Figure 2D, Figure S1D).

Log ratios of energetic traits were also closely associated with the interaction probabilities between proteas and animal antagonists. Models including both linear and quadratic terms of log ratios generally outperformed models including only linear terms of energetic and/or morphological log ratios (Table 3). In the best model including all antagonists, interactions were only associated with energetic trait ratios, but not with morphological trait ratios (Tables 3a). Overall, energetic trait matching accounted for 22% of variation in species interactions (marginal R^2 values, Table 3a). As expected, antagonists with high energy demands were more likely to interact with *Protea* species with a high ratio of seed resource provision to cone mass (Figure 3a, Figure S2A; Table 4a). For example, the large larvae of *Capys alpheus* (Lepidoptera) were more likely to be found in cones that contained a high seed-to-cone mass ratio. On the other end of the trait spectrum, the interaction probability of the small-bodied *Resseliella proteae* (Diptera) and *Tinea* sp. (Lepidoptera) increased at low ratios of seed-to-cone mass.

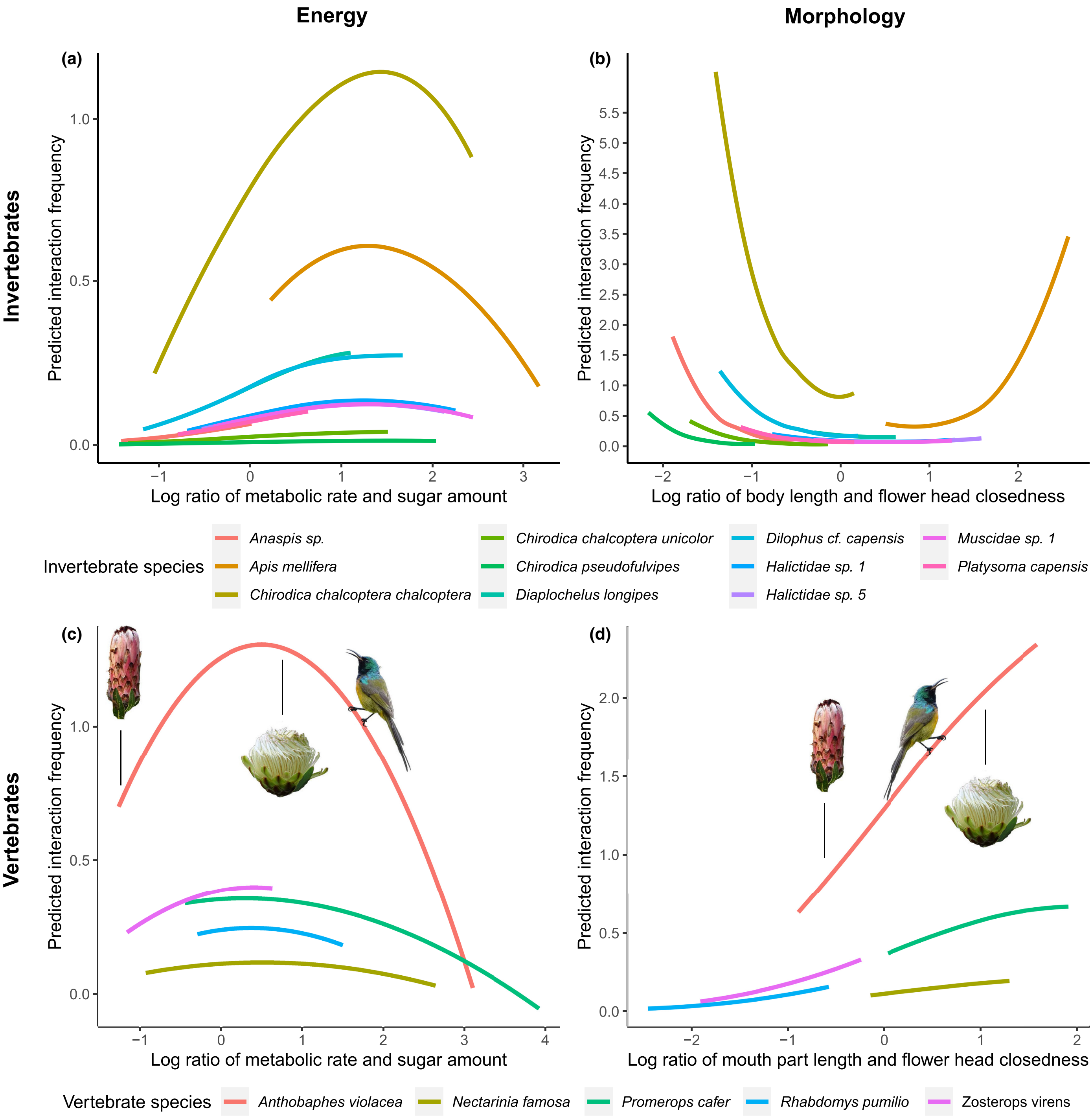

FIGURE 2 Mutualistic plant–animal trait matching for energetic (a, c) and morphological log ratios (b, d) and for invertebrate (a, b) and vertebrate mutualists (c, d). Plots show the fitted trend lines of the relationships between interaction frequencies and log ratios for invertebrate species (a, b) and vertebrate species (c, d). Smoothed trend lines for each animal species (indicated by different colours) are based on the predictions from the respective best model (see Table 2 for model summaries) and account for the linear and quadratic term of the respective fixed effect plus the random term of animal species, maintaining the effects of the other fixed and random terms constant. Trend lines are only shown for animal species with a minimum of 10 interaction events and indicate the predicted number of interaction events between a single plant individual and an animal species per 15 mins (for a, d) and 240 mins (c, d) respectively. As exemplified in (c), interaction frequencies of the Orange-breasted Sunbird *Anthobaphes violacea* are lowest for *Protea* species with little sugar amount per flower head (e.g. *P. mundii*, not shown) and highest for flower heads with medium sugar amount (e.g. *P. nitida*). In (d), interaction frequencies are lowest for *Protea* species with closed flower heads (e.g. *P. neriifolia*) and highest for open flower heads (e.g. *P. nitida*); picture copyright by the authors. Corresponding raw data are shown in Figure S1.

TABLE 2 Model summaries of the best models for mutualistic interactions between plants and invertebrates (a), as well as between plants and vertebrates (b). Results are based on generalized linear mixed models testing the association between log ratios of energetic and morphological traits and the interaction frequencies between protea plants and invertebrate (a) and vertebrate (b) mutualists. Best models included both linear and quadratic terms of energetic and morphological log ratios. Given are model estimates for the respective linear and quadratic terms along with their standard error, *z*-value and *p*-value, as well as the number of factor levels (*n*) and the variance (var) of each random effect. Number of observations: (a) $n = 422$ and (b) $n = 176$

Fixed effects	Estimate	SE	*z* value	*p*
(a) Mutualistic invertebrates				
Intercept	−3.22	0.341	−9.46	<0.001
energy	0.76	0.212	3.58	<0.001
energy^2	−0.30	0.028	−10.75	<0.001
morphology	−0.65	0.270	−2.41	0.016
morphology^2	0.60	0.041	14.81	<0.001
Random effects: Animal species (*n* = 41, var = 1.669), *Protea* species (*n* = 21, var = 0.634), site (*n* = 21, var = 0.400)				
(b) Mutualistic vertebrates				
Intercept	−2.06	0.500	−4.13	<0.001
energy	0.17	0.181	0.96	0.339
energy^2	−0.23	0.062	−3.71	<0.001
morphology	0.62	0.265	2.36	0.018
morphology^2	−0.16	0.066	−2.46	0.014
Random effects: Animal species (*n* = 10, var = 0.430), *Protea* species (*n* = 20, var = 0.232), site (n = 21, var = 1.756)				

Morphological trait matching was only found to be statistically supported if the analyses were restricted to bract borers (Table 3b). Consistent with morphological trait matching, we found a hump-shaped relationship (Table 4b, Table S3D) so that species with a small head width were more likely to interact with protea cones with thin involucral bracts (Figure 3b, Figure S2B). For instance, *Tinea* sp. (Lepidoptera) could not access cones with thick involucral bracts, whereas *Capys alpheus*, the species with the largest head width, was more likely to be found in cones of *Protea* species with thick involucral bracts.

4 | DISCUSSION

We show how energetic traits were associated with pairwise species interactions for both mutualistic and antagonistic interactions. Across interaction types, consumer species were more frequently interacting with resource species offering energetic provisions that matched their energetic demands. In comparison, the type of morphological trait matching varied contingent on the type of interaction and taxa, because morphological as well as behavioural differences in the type of floral access modulated the morphological effects on species interactions. Overall, functional traits explained a reasonable amount of variation in species interaction frequencies (11% to 22% of variation). In addition, other factors captured by the random effects in the models, for example, differences in species abundances, unmeasured traits as well as site-dependent effects, explained variability in species interactions. In the following, we discuss mechanisms of energetic and morphological trait matching and sketch how energetic trait matching could be incorporated into future trait-based studies on trophic species interactions.

4.1 | Energetic trait matching

A recurrent pattern in our analyses across taxa and interaction types was that energetic demand and provision were matching so that species with high metabolic rates were rarely found on energy-poor resources, whereas species with low metabolic rates tended to avoid energy-rich resources. This corresponds to studies from Loeuille and Loreau (2005) and Biro and Stamps (2010) who showed that smaller-sized species with lower metabolic demand can be displaced to resources with lower energetic provisions, while large species with high metabolic demand usually dominate resources with high energetic provisions.

A plausible explanation for energetic trait matching in mutualistic interactions is that pollinators aim to optimize their energy intake and energy expenditure while foraging (Zimmerman, 1981). The optimal foraging theory (MacArthur & Pianka, 1966) suggests that consumer species avoid common, but less rewarding plant species if the benefits of visiting rarer, but more rewarding plant species outweigh the travelling costs (Song & Feldman, 2014). Furthermore, it has been shown that large-bodied species with high metabolic demand (such as the Cape Sugarbird) require higher energy amounts than smaller species to occupy a site (Schmid et al., 2015b).

We further found that consumer species with low metabolic rates were rarely found on energy-rich resources. This is in line with Pettersen et al. (2020), who reported a lower competitive ability in individuals with low metabolic rates. It is likely that competitive interactions of pollinators displace these species from energy-rich resources (Ford & Paton, 1982). Similar competitive hierarchies have been shown in other nectarivorous animal communities (Mac Nally & Timewell, 2005). For example, we found that interaction frequencies of Orange-breasted Sunbirds decreased for the most rewarding *Protea* species. This is likely the consequence of the presence of dominant territorial bird species, such as the larger Cape Sugarbird, chasing sunbirds away from protea flower heads (Schmid et al., 2015a; Wooller, 1982).

Compared to insects, vertebrates tended to exploit the more rewarding *Protea* species, as their optimum interaction frequency was shifted towards the more rewarding *Protea* species (Figure 2a,c). This suggests that invertebrates may be excluded from the most rewarding *Protea* species by competitive interactions with vertebrate pollinators (Carpenter, 1979). Another explanation is that *Protea* species differ in the type of nectar rewards, for example, by the main sugar type (Nicolson & Van Wyk, 1998) or nectar sugar concentration (Schmid et al., 2015a), to attract either vertebrate or insect pollinators. Furthermore, floral colour and scent have been shown to influence differential foraging choices of animal pollinators in the CFR (Johnson et al., 2012; Steenhuisen et al., 2012).

TABLE 3 Model comparisons describing the relationships between energetic and morphological trait ratios and interaction probabilities between protea plants and all antagonists (a) and bract borers only (b). Model comparisons include an unconditional null model, models assuming monotonous linear trends (linear terms only), and models assuming hump-shaped or parabolic relationships between log ratios and interaction frequencies (linear and quadratic terms). See Table 1 for a description of all used abbreviations. Model summaries and sample sizes of the best models are given in Table 4

Rank	GLMM	LL	K	AICc	ΔAICc	ω_i	R^2_m	R^2_c
(a) Antagonists								
1	$e+e^2$	−816.43	4	1640.94	0.00	0.83	0.220	0.585
2	$e+e^2+m+m^2$	−816.08	6	1644.34	3.40	0.15	0.188	0.567
3	uncond	−823.22	2	1650.47	9.53	0.01	0	0.574
4	e	−822.79	3	1651.64	10.70	0.00	0.004	0.553
5	m	−823.01	3	1652.07	11.13	0.00	0.005	0.560
6	em	−822.37	4	1652.82	11.88	0.00	0.027	0.539
7	$m+m^2$	−822.90	4	1653.88	12.94	0.00	0.003	0.580
(b) Antagonists, bract borers only								
1	$e+e^2+m+m^2$	−526.80	6	1065.85	0.00	0.61	0.114	0.500
2	$e+e^2$	−530.35	4	1068.82	2.98	0.14	0.078	0.490
3	e	−531.41	3	1068.89	3.04	0.13	0.039	0.491
4	$m+m^2$	−531.32	4	1070.75	4.90	0.05	0.051	0.530
5	em	−531.40	4	1070.92	5.07	0.05	0.038	0.488
6	uncond	−535.08	2	1074.20	8.35	0.01	0	0.505
7	m	−534.64	3	1075.34	9.50	0.01	0.010	0.501

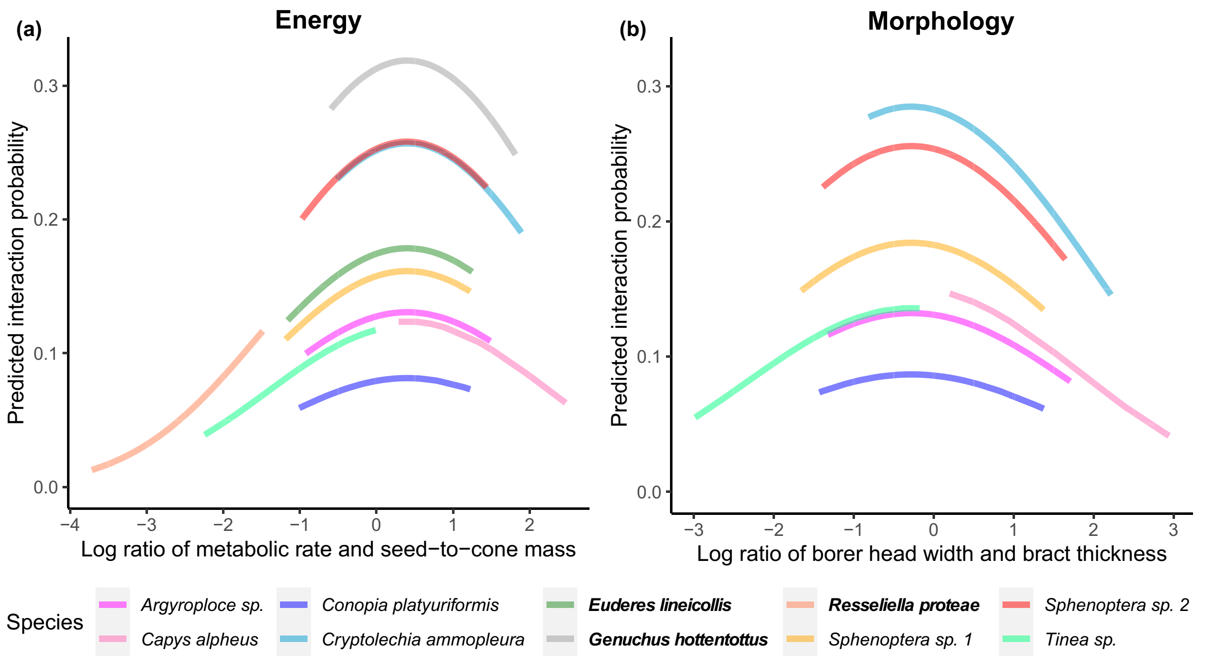

FIGURE 3 Antagonistic plant–animal trait matching for energetic (a) and morphological log ratios (b) and for all antagonists (a) and bract borers only (b). Plots show the fitted trend lines of the relationships between interaction probabilities and log ratios of energetic and morphological traits of the interacting species. Smoothed trend lines for the respective species are based on the predictions from the best model (see Table 4 for model summaries and sample sizes) and account for the linear and quadratic term of the respective fixed effect plus the random term of animal species. Trend lines indicate the predicted interaction probability between a given plant and animal species. *Euderes lineicollis*, *Genuchus hottentottus*, *Resseliella proteae* are not shown in (b), as they do not bore through the involucral bracts (bold font in legend). Corresponding raw data are shown in Figure S2.

Similar to the mutualistic networks, antagonists interacted more frequently with protea cones that provided provisions matching their energetic demands. Interactions were most likely at intermediate log ratios between energetic demand and provision, suggesting that exploitative and interference competition led to competitive exclusion and differentiation in resource choice of antagonist species (Anderson et al., 2009;

TABLE 4 Model summaries of the best models for antagonistic interactions between 20 *Protea* species and 10 antagonist species (a), as well as seven bract borers (b). Results are based on generalized linear mixed models testing the association between log ratios of energetic and morphological traits and the interaction probability (i.e. the number of presences and absences) between *Protea* species of all antagonists (a) and bract borers only (b). Best models included both linear and quadratic terms of energetic log ratios (a), or of both energetic and morphological log ratios (b). Shown are model estimates for the respective linear and quadratic terms along with their standard error, *z*-value and *p*-value, as well as the number of factors levels (*n*) and the variance (var) of the random effect. Number of observations: (a) $n = 498$, (b) $n = 336$

Fixed effects	Estimate	SE	*z* value	*p*
(a) Antagonists				
Intercept	−1.61	0.188	−8.58	<0.001
energy	0.14	0.063	2.23	0.026
energy^2	−0.17	0.050	−3.49	<0.001
Random effect animal species (*n* = 10, var = 0.279)				
(b) Antagonists, bract borers only				
Intercept	−1.63	0.226	−7.24	<0.001
energy	0.19	0.067	2.87	0.004
energy^2	−0.09	0.051	−1.68	0.093
morphology	−0.08	0.097	−0.78	0.434
morphology^2	−0.14	0.054	−2.54	0.011
Random effect animal species (*n* = 7, var = 0.257)				

Gravel et al., 2016). In the protea system, the antagonist species compete for seeds as their key energy resource at the larval stage (Roets et al., 2006). Importantly, conspecific and heterospecific co-occurrences have rarely been reported in protea cones, suggesting that antagonist species exclude and/or kill each other in the cones, since most species lay several eggs on the same cone (Coetzee, 1989). For example, *Capys alpheus* (Lepidoptera), the largest invertebrate species with the highest metabolic rate (Coetzee & Gilomee, 1987), is able to exclude interspecific competitors by its large size and early arrival to the flower heads (Sasa & Samways, 2015). On the other end of the trait spectrum, *Tinea* sp., seed-feeding moth larvae with a low metabolic rate, arrive at mature cones only (Coetzee & Gilomee, 1987) and preferentially exploit low energy resources, presumably to bypass other, more dominant antagonist species. A similarly distinct feeding strategy was found for *Resseliella proteae*, a dipteran feeding between the involucral bracts and in the outer part of the involucral receptacle (Coetzee & Gilomee, 1987).

4.2 | Morphological trait matching

Patterns of morphological trait matching were more idiosyncratic in both mutualist and antagonist networks although previous work has highlighted the generality of morphological trait matching between resource and consumer species (Bartomeus et al., 2016). For example, studies of plant–hummingbird interactions have shown that morphological traits, especially beak and flower dimensions, mediate niche partitioning in many communities (Maglianesi et al., 2014; Sonne et al., 2020) although such effects are contingent on the biogeographic and ecological context of each community (Dalsgaard et al., 2021). In systems with loose morphological associations, morphological traits may be helpful to identify preferences and barriers for relatively specialized species (e.g. Orange-breasted Sunbird), but may be less suitable for defining interaction rules of species with generalized interaction patterns (e.g. Cape Honeybee).

In contrast to our expectation, we found that invertebrate mutualists interacted more frequently with morphologically extreme *Protea* species, as indicated by a parabolic relationship of interaction frequency and morphological trait ratios (Figure 2b). Invertebrates with short body lengths were more frequently observed in closed (hard to access) flower heads. It is likely that the smallest invertebrates select the closed flower heads because of the shelter they provide, for example, *Chirodica* beetles are often the dominating visitors in such *Protea* species (Coetzee & Giliomee, 1985; Mostert et al., 1980). In contrast, medium-sized and larger-sized insects could not easily access closed flower heads, probably because the involucral bracts cover the florets and nectaries. In these species, bearded perianths on the tips of the florets prevent larger insects (e.g. Cape Honeybee) from entering the flower head. These differences in floral access between different-sized pollinators can explain why the observed patterns were inconsistent with the expected hump-shaped relationship emerging from morphological trait matching.

Vertebrate mutualists interacted more frequently with open flower heads. As the largest and dominant pollinators in the community (Ford & Paton, 1982), vertebrates choose to visit easily accessible flower heads, maybe also to reduce their own predation risk during foraging. This result is interesting because the closed or bearded *Protea* species are classified to be mainly bird pollinated (Botha, 2017; Schmid et al., 2015a), as mostly birds will make contact with the pollen presenters of these species (Rebelo et al., 1984). Indeed, bird visits to closed flower heads seem to be less frequent than those to open flower heads, especially for smaller bird species (e.g. the Orange-breasted Sunbird, see Figure 2d). Nevertheless, we observed birds to regularly visit closed flower heads so that they still can substantially contribute to pollinating these species.

In the antagonistic network, we found a signal of morphological trait matching defining the interactions between protea plants and their animal antagonists. However, we only found this effect for bract-boring insects. Other access strategies of antagonistic insects, for example, the scarab beetle *Genuchus hottentottus*, which enters and leaves the protea cone via the top, could be a strategy to circumvent plant defence. Bract borers, however, were constrained by involucral bract thickness. A previous study has reported that increasing bract thickness decreases the abundance of endophagous insect larvae (Wright & Samways, 1999). In line with this, we found that the small moth *Tinea* sp. was mostly found in protea cones with thin bracts (Figure 3b). *Tinea* sp. larvae only occur in mature cones and were apparently not able to penetrate *Protea* species with thick bracts because of their low bite force. On the other end of the trait spectrum, large antagonists, for example, *Capys alpheus* (Lepidoptera), avoided *Protea* species with thin bracts (Figure 3b) although they would be able to access these species. Avoidance of competition and direct interference with other antagonist species may explain this pattern.

4.3 | Future directions and conclusions

Our findings on energetic trait matching between resource and consumer species across taxa and interaction types are in line with seminal work that identified energy as a key currency in trophic species interactions (Brose et al., 2006; Heinrich, 1975). Since energetic demands and provisions can be measured and inferred rather easily across many different taxa (Brown et al., 2004), it will be important to test the generality of energetic trait matching across more interaction systems. Based on our findings, we argue that energetic trait matching holds particular promise for predicting trophic interactions, especially in species-rich systems where direct observations of interactions are challenging to obtain.

Nevertheless, our findings also reflect the limits of predicting species interactions from functional traits. Most importantly, we observed a high variability in species interactions across all sites that was not accounted for by energetic nor morphological trait matching. In contrast to energetic trait matching, we found that morphological trait matching depended more on the specific characteristics of species and may therefore be more limited in its potential for generalization. The identification of relevant morphological traits, therefore, requires an in-depth understanding of the study system and the measurement of specific morphological traits. It is possible that other unmeasured traits of the morphologically very diverse *Protea* genus (e.g. additional measures of flower head shape and structure) and their animal partners (e.g. animal body shape and robustness) may have yielded closer morphological linkages between plant and animal species.

In conclusion, we show that energetic and morphological traits jointly influence trophic species interactions. Notably, the energetic relationships between resource and consumer species were consistent and appear to follow general principles in both mutualist and antagonist networks. In combination with other trait data, energetic trait matching could therefore be useful to predict resource–consumer associations in diverse ecological communities.

AUTHOR CONTRIBUTIONS

Alexander Neu, Huw Cooksley, Frank M. Schurr and Matthias Schleuning conceived the ideas and designed the methodology; Alexander Neu and Huw Cooksley collected the data; Alexander Neu analysed the data with input from Matthias Schleuning; Alexander Neu wrote the first draft of the manuscript with inputs from Huw Cooksley, Karen J. Esler, Anton Pauw, Francois Roets, Frank M. Schurr and Matthias Schleuning. All authors commented on the final manuscript and gave final approval.

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CONFLICT OF INTEREST

M.S. is an Associate Editor of *Functional Ecology*, but took no part in the peer review and decision-making processes for this paper.

DATA AVAILABILITY STATEMENT

Data available from the Dryad Digital Repository https://doi.org/10.5061/dryad.nvx0k6dwm (Neu et al., 2022).

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