Received: 25 February 2022 | Revised: 5 August 2022 | Accepted: 21 August 2022

DOI: 10.1111/jeb.14091

JOURNAL OF Evolutionary Biology eseb European Society for Evolutionary Biology

RESEARCH ARTICLE

Hunger for sex: Abundant, heterogeneous resources select for sexual reproduction in the field

Pedro Aurélio Costa Lima Pequeno[1] | **Elizabeth Franklin**[2] | **Roy A. Norton**[3]

[1]Natural Resources Program, Federal University of Roraima, Boa Vista, Brazil

[2]Biodiversity Coordination, National Institute for Amazonia Research, Manaus, Brazil

[3]College of Environmental Science and Forestry, State University of New York, Syracuse, New York, USA

Correspondence
Pedro Aurélio Costa Lima Pequeno, Natural Resources Program, Federal University of Roraima, Av. Cap. Ene Garcês, 2413, Aeroporto, Boa Vista - RR, CEP: 69310-000, Brazil.
Email: pacolipe@gmail.com

Abstract

Major hypotheses on sex evolution predict that resource abundance and heterogeneity should either select for or against sexual reproduction. However, seldom have these predictions been explicitly tested in the field. Here, we investigated this question using soil oribatid mites, a diverse and abundant group of soil arthropods whose local communities can be dominated by either sexual or asexual species. First, we refined theoretical predictions by addressing how the effects of resource abundance, heterogeneity and abiotic conditions could modify each other. Then, we estimated the strength of selection for sexual species in local communities while controlling for phylogeny and neutral processes (ecological drift and dispersal), and tested its relation to resource and abiotic gradients. We show that sexual species tended to be favoured with increasing litter amount, a measure of basal resource abundance. Further, there was some evidence that this response occurred mainly under higher tree species richness, a measure of basal resource heterogeneity. This response to resources is unlikely to reflect niche partitioning between reproductive modes, as sexual and asexual species overlapped in trophic niche according to a comparative analysis using literature data on stable isotope ratios. Rather, these findings are consistent with the hypothesis that sex facilitates adaptation by breaking unfavourable genetic associations, an advantage that should increase with effective population size when many loci are under selection and, thus, with resource abundance.

KEYWORDS
competition, linkage disequilibrium, mutation load, niche overlap, parthenogenesis, selection interference

1 | INTRODUCTION

Asexual clones could quickly dominate populations by dispensing with male production and mating (Bell, 1982). And yet, most known species engage in sexual reproduction, at least sporadically, which has led to many hypotheses on the spread and maintenance of sex (Hartfield & Keightley, 2012). Recent studies have helped to restrict the range of plausible mechanisms selecting for sex given variation in reproductive mode (Archetti, 2022; Brandeis, 2018; Sharp & Otto, 2016), but there remains significant uncertainty about the selective agents operating on reproductive mode under natural conditions (Neiman et al., 2018; Tilquin & Kokko, 2016). Natural selection is ultimately caused by ecological or environmental factors (MacColl, 2011), so accounting for such factors is crucial for any comprehensive theory of sexual reproduction.

Yet, the relative fitness of sex under certain environmental conditions depends on its genetic mechanisms. Currently, the most supported mechanisms are (reviewed by Archetti, 2022; Hartfield & Keightley, 2012; Neiman et al., 2018; Sharp & Otto, 2016; Song et al., 2011; Table 1): (1) combining beneficial mutations arising in different genomes through mating and (2) accelerating their fixation by separating them from deleterious mutations through

TABLE 1 Major genetic mechanisms proposed to mediate selection for sexual reproduction, their predicted fitness advantage and its expected response to larger effective population size

Sex genetic mechanism	Fitness advantage	Response to larger effective population size
1. Joins new, good alleles	Higher variance	Higher advantage
2. Eases fixing good alleles	Higher variance	Higher advantage
3. Eases purging bad alleles	Higher variance	Higher advantage
4. Keeps heterozygosity	Higher mean	Lower advantage
5. Creates offspring different from parents	Higher mean	Constant advantage

segregation and recombination (e.g. Fisher-Muller hypothesis); (3) facilitating the elimination of deleterious mutations by separating them from beneficial ones through segregation and recombination (e.g. Muller's ratchet hypothesis); (4) silencing recessive deleterious mutations by keeping heterozygosity through meiosis (e.g. Loss of Complementation hypothesis) and (5) creating new genotypes through segregation and recombination whose fitness is higher than that of their parents (e.g. Red Queen, Tangled Bank, Structured Resource and Spatial Heterogeneity hypotheses). Mechanisms 1, 2 and 3 are similar in that they reduce selection interference among linked loci, thereby increasing fitness variance and facilitating adaptation (collectively known as Hill-Robertson hypothesis), whereas mechanisms 4 and 5 directly increase the mean fitness of offspring (Sharp & Otto, 2016).

The fitness advantage provided by these mechanisms may depend on effective population size (Table 1) and, thus, on population limitation by resources (White, 2008). As effective population size increases, so does the total supply of mutations, possibly increasing the advantage of sex in joining beneficial mutations (mechanism 1; Colegrave, 2002; Gossmann et al., 2012). Likewise, when many loci are under selection (e.g. complex traits), the proportion of unrealized genetic combinations increases with effective population size, and sex can be favoured by breaking linked loci and releasing genetic variance (mechanisms 2 and 3; da Silva & Galbraith, 2017; Iles et al., 2003). In parallel, heterozygosity loss is faster in effectively smaller populations due to stronger inbreeding and drift (Palstra & Ruzzante, 2008), and thus sex may be more advantageous in these populations by maintaining heterozygosity (mechanism 4). By contrast, direct increases in offspring relative to parental fitness (mechanism 5) may not depend on effective population size (Becks & Agrawal, 2010; Song et al., 2011).

Resource heterogeneity (number of different resource types within a site) may also select for sex. First, linkage-based advantages of sex (mechanisms 1, 2 and 3) are predicted to increase with the number of selected loci and the strength of selection per locus (da Silva & Galbraith, 2017; Iles et al., 2003). This may pertain in complex habitats that impose multiple selective pressures (Luijckx et al., 2017) resulting from more heterogeneous resources. Second, if dispersal moves genotypes to resource patches to which they are not adapted, sexual offspring may have an immediate advantage by being different from their parents (mechanism 5). This favours sex when the habitat encompasses many patches of different resources (Spatial Heterogeneity hypothesis; Agrawal, 2009; Becks & Agrawal, 2010). Likewise, if parents deplete certain local resources, sex may create more variable offspring that better use rarer resources, increasing their fitness relative to asexual offspring (Structured Resource hypothesis; Song et al., 2011). Models based on the latter predict that sexual species should prevail where resources are scarce and/or more heterogeneous but vanish where mortality is high (e.g. harsh abiotic conditions) due to the cost of males and mating (Scheu & Drossel, 2007; Song et al., 2012). This assumes that sexual and asexual reproduction reflect mainly density-dependent and density-independent factors, respectively, with resource effects being independent of population size.

These hypotheses do not consider interactions between ecological selective agents, even though this can be expected (MacColl, 2011). For instance, resource heterogeneity may have a stronger effect in favouring sex where resource abundance is low, as using more resource types could be especially advantageous when each is scarce (e.g. Structured Resource Theory), or because resource scarcity decreases effective population size and thus heterozygosity (e.g. Loss of Complementation hypothesis). In contrast, if the main advantage of sex is breaking linkage disequilibrium (e.g. Fisher-Muller and Muller ratchet hypotheses), the increased advantage of sex under more heterogeneous resources may be even greater where resources are abundant, as this could increase effective population size. More generally, higher mortality (e.g. harsh abiotic conditions) can reduce fitness differences among species (Huston, 2014), and thus may weaken the effect of resource abundance and/or heterogeneity on selection for sex.

The above hypotheses can be investigated in the field using taxa whose species differ in reproductive mode and experience natural variation in both resource abundance across sites and within-site resource heterogeneity. This is because species sorting along environmental gradients is equivalent to selection among genotypes or alleles (Hubbell, 2001; Vellend, 2016). Oribatid mites are one such group: abundant and diverse, mostly soil-dwelling arthropods whose around 10 000 described species (Norton & Behan-Pelletier, 2009) depend largely on litter, either directly by ingesting dead plant material and using it as habitat, or indirectly by feeding on litter-dwelling fungi (Gan et al., 2014). Nearly 10% of the species are thought to be obligate parthenogens (Norton et al., 1993; Norton & Palmer, 1991), with females producing diploid, clonal progeny through automixis with terminal fusion and inverted meiosis (thelytoky), with no evidence for recombination (Bergmann et al., 2018). Yet, this mechanism maintains heterozygosity, so oribatid reproductive modes are similar in this regard (Archetti, 2022). Asexual reproduction evolved independently many times in oribatid mites, although it tends to be more common in older clades (Pachl et al., 2021). Further, the proportion of each reproductive mode varies widely among communities. Indeed, correlations between the proportion of sexual species and population density, altitude and habitat type have been interpreted as evidence for selection by resource abundance and/or abiotic conditions (Maraun et al., 2012, 2013, 2019).

However, the relationship between reproductive modes of oribatid mites and known resources such as litter has been assumed rather than shown. Also, given the higher prevalence of asexual species in older clades, patterns in the spatial distribution of reproductive modes could reflect other phylogenetically correlated traits rather than reproduction, as well as neutral processes (ecological drift or the random loss of species in smaller communities, and dispersal) that may confound the signal of selection (Swenson, 2014; Vellend, 2016). More generally, differences in the types of consumed resources could eliminate competition between sexual and asexual species and allow their coexistence regardless of fitness differences due to any genetic mechanism (Neiman et al., 2018), but the extent of trophic niche overlap between sexual and asexual oribatid species is unknown.

Here, we investigated whether resources could drive selection for sex in soil oribatid mites across a tropical rainforest landscape. First, we estimated selection strength on sexual species in local communities (48 transects of 250 m over 100 km^2), controlling for neutral processes and phylogenetic position. Then, we tested whether selection strength responded either independently or in interaction to litter mass, a basal resource for such mites; tree species richness, a major source of litter heterogeneity through physical and chemical variation; and soil water content, an important abiotic stressor for soil fauna through desiccation or hypoxia (Villani et al., 1999). Additionally, we compiled comparative data on trophic niche of tropical oribatid mites from the literature (Potapov et al., 2022) to examine whether sexual and asexual species use different resources and thus determine if their response to resource gradients could reflect niche partitioning rather than reproductive mode itself.

2 | MATERIALS AND METHODS

2.1 | Study site

Data were obtained from the Brazilian Program for Biodiversity Research (PPBio) in Reserva Ducke (2°57′47.30″S, 59°55′19.30″W), a large tropical rainforest reserve (10 × 10 km) managed by the Brazilian Institute for Amazonia Research (INPA) in Manaus, Brazilian Amazonia. Topography encompasses an alternation between sandy bottomlands subject to waterlogging and drier, clayish uplands connected by mixed-soil slopes, with altitude ranging between ca. 50 and 100 m a.s.l. Vegetation structure and species composition vary in close association with hydroedaphic gradients (Costa et al., 2022). Mean daily temperature and mean annual rainfall between 1992 and 2002 were 26.7°C and 2479 mm, respectively, with monthly rainfall below 100 mm from July to September (Coordination for Research on Climate and Hydric Resources, INPA, unpublished data).

2.2 | Oribatid community data

Oribatid mites were sampled from March 18 to May 13, 2002, across 48 sites regularly distributed over the reserve, with at least 1 km between them. On each site, one soil core (3.5 cm × 3.5 cm × 5 cm) was sampled each 12.5 m along a 250-m transect following a topographic contour line, totalling 20 cores per transect. This scheme provides a representation of the local, site-level community, as spatial autocorrelation in soil microarthropod distribution typically ranges over tenths of meters (Ettema & Wardle, 2002; Minor, 2011). Each quartet of consecutive soil cores was combined into a single plastic container to reduce the processing load and taken to the Laboratory of Systematics and Ecology of Terrestrial Arthropods at INPA's campus in Manaus. Mites were extracted with a modified Berlese-Tullgren apparatus (Franklin & Morais, 2006). Temperature was gradually increased from 28 to 45°C until soil reached a constant mass, which took from 6 to 7 days. Specimens were preserved in 4% formaldehyde solution, and adult oribatid mites were sorted into morphospecies. Whenever possible, morphospecies (hereafter species) were identified with the aid of taxonomic keys and original descriptions, by clarifying specimens with lactic acid and mounting them in temporary slides for examination under a compound microscope. Immatures were not considered but represented only 8% of extracted individuals. Voucher specimens were stored in the Entomological Collection of INPA.

Reproductive mode was inferred from published records (Cianciolo & Norton, 2006; Maraun et al., 2013; Norton et al., 1993; Norton & Palmer, 1991). In oribatid mites, thelytoky (production of diploid females from unfertilized eggs) is obligatory for the species in which it occurs; males are rare and sterile (Bergmann et al., 2018). Hence, species were conservatively assumed sexual unless asexuality was evidenced from rearing (reproduction of unmated females), sex ratios (>95% females), or the species was in a genus or family without known sexual species.

Overall, we collected 1940 adult oribatid mites from 127 (morpho)species over the 48 transects, with 832 individuals (43%) in 20 species (16%) considered asexual.

2.3 | Environmental data

Soil water content (%) was measured as one minus the ratio between the dry mass and the wet mass of the soil samples used for mite extraction, averaged for each site. Litter amount was measured for each transect by harvesting all fine litter (leaves, fruits and woody items with diameter <2 cm) in five quadrats (0.4 m × 0.6 m) with regular spacing of 50 m. Litter was dried at 65°C until it reached constant mass, to determine the average dry mass (g) per transect.

Tree species richness was determined by another team working in the same study area (Castilho et al., 2006). Trees with diameter at breast height (dbh) >30 cm were marked within a 250 × 40 m plot aligned and centralized over the transect; trees with dbh 10–30 cm were marked in an inner 250 × 20 m plot and trees with dbh 1–10 cm were marked in an innermost 250×4 plot. Trees were morphotyped and identified as possible with reference to INPA' botanical collection and the taxonomic literature.

2.4 | Comparative data on oribatid trophic niche

In a separate analysis, we used literature data to investigate the relation between species trophic niche and reproductive mode. We inferred species trophic niche using stable isotope ratios. Isotopes are alternative forms of an atom that have the same number of protons in their nuclei (i.e. same chemical element) but differ in their number of neutrons (i.e. different mass). Each element has one naturally abundant isotope and potentially many rare isotopes, but few of the latter are stable. Yet, the rare, stable isotopes of elements building organic molecules such as nitrogen (^{15}N relative to ^{14}N) and carbon (^{13}C relative to ^{12}C) tend to accumulate or be depleted in organisms depending on their diet, allowing the use of their ratios ($\delta^{15}N$ and $\delta^{13}C$) to infer trophic niche (Potapov et al., 2022). In soil organisms, $\delta^{15}N$ generally increases with trophic level, from primary decomposers (feeding on litter or roots) to secondary decomposers (feeding on fungi) to scavengers and predators (feeding on animal tissue). In parallel, $\delta^{13}C$ mainly reflects the basal carbon source of the food chain, increasing from fresh, plant-derived carbon to older, microbial carbon.

Estimates of $\delta^{15}N$ and $\delta^{13}C$ for soil oribatid mites were searched for using Google Scholar, along with the reference lists of identified studies. Because such data are not available for oribatid mites from Brazilian Amazonia, we considered tropical species in general, given that many genera have pantropical distribution and that trophic niches of oribatid species tend to be conserved within genera (Potapov et al., 2022). We searched for the terms "oribatid", "stable isotope" and "tropical". Our search included studies indexed until December 2021. We obtained the mean $\delta^{15}N$ and $\delta^{13}C$ of a given species within a given study area, subtracted from the respective values of the baseline informed by the study (typically litter) to standardize for environmental variation in isotopic signatures. We avoided data from disturbed sites to minimize anthropic influence on niche measurements. If data were presented in figures, we used WebPlotDigitizer 4.1 (Rohatgi, 2018) to extract the values. Because oribatid mites are so small (generally <1 mm long), each measurement typically represented several pooled individuals. For each species, we obtained data on reproductive mode (sexual or asexual) either from the original studies or from the literature as above. The final comparative data set included 82 species (62 sexual and 20 asexual), collected by four studies across three countries (Ecuador, Indonesia and Vietnam). Remarkably, 70% of the species collected in Reserva Ducke belonged to genera included in the comparative dataset.

2.5 | Statistical analysis

All data used in this study are available in the figshare repository (https://doi.org/10.6084/m9.figshare.20442891). We considered mites sampled from each transect as representative of the local oribatid mite community, and thus the transect was the sampling unit used in the analyses. To estimate the strength of selection on sexual species, we created a null model. Accordingly, for a given transect, a random community was created by keeping the observed number of species and the observed proportion of "lower" (basal clades) and "higher" oribatid species (Brachypylina), and randomly sampling species from the species pool (list of all observed species) with probability proportional to the number of transects in which they occurred (Swenson, 2014). Therefore, the only processes driving community composition were dispersal (sampling from the species pool based on species commonness) and drift (random variation in composition based on the number of species in the community; Hubbell, 2001; Vellend, 2016). Furthermore, the observed phylogenetic composition was kept constant, so that phylogeny did not confound the resulting composition (Figure S1). Then, the proportion of sexual species for this neutral community was computed. This procedure was repeated 9999 times, thus creating a null distribution of this proportion.

Next, we used this distribution to compute a standardized effect size (SES), by subtracting the null mean from the observed proportion and dividing this difference by the standard deviation of the null distribution (Swenson, 2014). SES is dimensionless, has no upper and lower bounds and reflects the degree to which the proportion of sexual species deviates from that expected under the null model. SES was computed for all transects and used as a measure of selection for sex: increasingly positive values represent stronger selection for sex, whereas increasingly negative values represent stronger selection against sex, akin to fitness-trait regression slopes (MacColl, 2011). We did not consider proportions of sexual individuals because species abundance distribution is highly skewed (Hubbell, 2001). Hence, a few species contribute disproportionately to total abundance, rendering individual proportions biased by singularities of such species that are difficult to discern from reproductive mode on its own.

Selection for sex was used as response variable in a multiple regression model having mean litter amount (g), tree species richness and mean soil water content (%) as predictors, including all three pairwise interactions among these predictors ($n = 48$). This represents an "eco-evolutionary landscape", informing about the putative ecological causes of selection strength (MacColl, 2011). We used the inverse of litter amount ($1/x$) to account for curvilinear, saturating relationships, as this is suggested by theoretical models (Scheu & Drossel, 2007; Song et al., 2012). Statistically non-supported interactions ($p > 0.05$) were removed to test for possible independent effects, but we also inspected the plausibility of marginally significant effects ($0.05 < p < 0.10$).

To test for trophic niche overlap between species with different reproductive modes, we used the literature data on $\delta^{15}N$ and $\delta^{13}C$ as response variables in two mixed-effects models, both having reproductive mode as predictor. We used taxonomic levels as nested random factors (i.e. genus, family, superfamily and supercohort; Norton & Behan-Pelletier, 2009) to account for phylogenetic autocorrelation (Falaschi et al., 2019), as taxonomic groupings are congruent with well-support phylogenies for the group (Schaefer & Caruso, 2019). Given the availability of data, sample sizes for δ^{15}N and δ^{13}C were 77 and 61 species, respectively. All analyses were performed in R 4.1.1 (R Core Team, 2021), with aid of the package "visreg" (Breheny & Burchett, 2017) and "MuMIn" (Barton, 2020).

3 | RESULTS

The proportion of sexual species varied from 50% to 100% across local communities. Resource variables varied three- to fourfold, between 131 and 482 g for litter amount and from 66 to 210 species for tree species richness. Variation in soil water content was moderate, from 21% to 49%.

The multiple regression model revealed that selection for sex did respond to the analysed environmental predictors (global test, $F = 2.48$, $p = 0.038$). However, of the three tested interactions between predictors (litter amount × tree richness, litter amount × soil water, and tree richness × soil water), only the first was marginally supported ($t = -1.89$, $p = 0.065$). Excluding the other non-supported interactions revealed that this marginally supported interaction remained so, whereas soil water content had no effect either in interaction or independently (Table 2). Specifically, the retained interaction suggested that selection for sex increased with mean litter amount, but this effect only occurred with increasing tree species richness (Figure 1). This model accounted for 26% of the variation in selection for sex. Excluding the marginally supported interaction revealed a single independent effect: increasing litter amount drove stronger selection for sex, accounting for 20% of its variation (Table 2; Figure 2).

Further, the comparative analysis revealed that, on average, there was no significant difference in trophic niche between sexual and asexual species when considering either δ^{15}N or δ^{13}C (Table 2; Figure 3). However, whereas most species clustered around the same mean for nitrogen, asexual species tended to cluster around higher values for carbon, forming a subset nested within the range spanned by sexual species (Figure 2).

4 | DISCUSSION

Our analysis revealed that selection for sex was generally stronger under resource abundance (litter amount), while also suggesting an interaction between the effects of resource abundance and heterogeneity (tree species richness). These results are consistent with the idea that the advantage of sex increases with effective population size (Colegrave, 2002; Gossmann et al., 2012; Iles et al., 2003) and, thus, with resource abundance (White, 2008). Under these conditions, sexual species should have higher fitness relative to asexual ones, thus dominating communities. They also hint at the idea that sexual reproduction may be favoured by resource heterogeneity (Agrawal, 2009; Becks & Agrawal, 2010). These findings seem unlikely to be confounded by resource partitioning between sexual and asexual species for two reasons. First, although asexual species clustered around higher carbon isotope ratios, suggesting predominance of fungivory over saprophagy (Potapov et al., 2022), they exploited a subset of the trophic niche of sexual species rather than a different niche (Figure 3b). Second, if increasing fungal abundance drove

TABLE 2 Final linear models on selection for sex in local communities and species trophic niche (δ^{15}N and δ^{13}C) in relation to reproductive mode in tropical oribatid mites

Response	N	R^2	Predictor	Coefficient	t	p
Selection for sex (with interaction)	48	0.26	Intercept	−5.00	–	–
			1/Litter	681.88	1.349	**0.184**
			Trees	0.04	2.096	**0.042**
			Soil water	0.95	0.568	0.573
			1/Litter × trees	−6.66	−1.893	**0.065**
Selection for sex (no interaction)	48	0.20	Intercept	−0.04	–	**–**
			1/Litter	−261.95	−3.078	**0.003**
			Trees	0.01	0.989	0.328
			Soil water	0.42	0.245	0.808
δ^{15}N	77	0.00	Intercept	2.29	–	–
			Reproduction	0.22	0.284	0.778
δ^{13}C	61	0.05	Intercept	3.85	–	–
			Reproduction	−0.95	−1.632	0.120

Note: For trophic niche, higher taxonomic groups were used as nested random factors to account for phylogenetic autocorrelation, with R^2 representing predictor effects only. Selection for sex: standardized effect size (SES) of the proportion of sexual species under a null model assuming no selection and controlling for phylogeny. 1/Litter: inverse of mean litter amount (g). Trees: tree species richness. Soil water: soil water content (%). δ^{15}N and δ^{13}C: mean stable isotope ratios of these elements. Reproduction: reproductive mode (0: asexual; 1; sexual). Bold numbers indicate statistical significance at the 0.05 level.

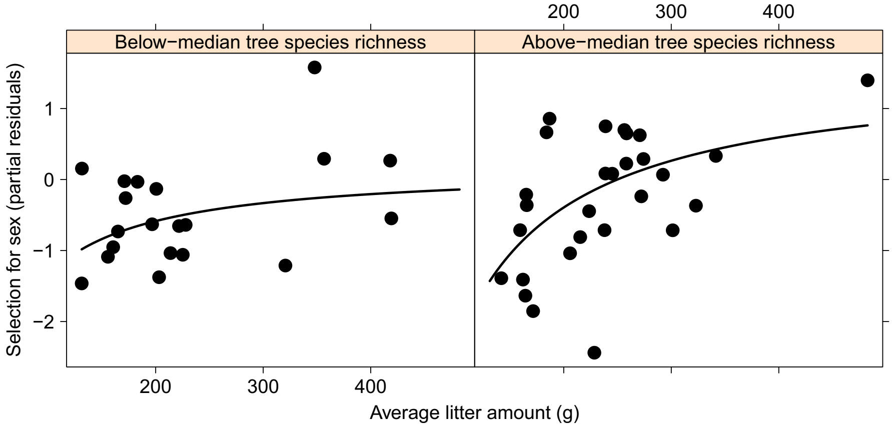

FIGURE 1 Selection for sex (standardized effect size of proportion of sexual species) in relation to the interaction between resource abundance (average litter amount) and resource heterogeneity (tree species richness) across soil oribatid mite communities in an Amazonian rainforest. Each point represents one community ($n = 48$). Partial residuals are used to control for the remaining predictor (soil water content). Solid lines indicate predicted means. Positive values represent selection for sexual species, and negative values indicate selection against them

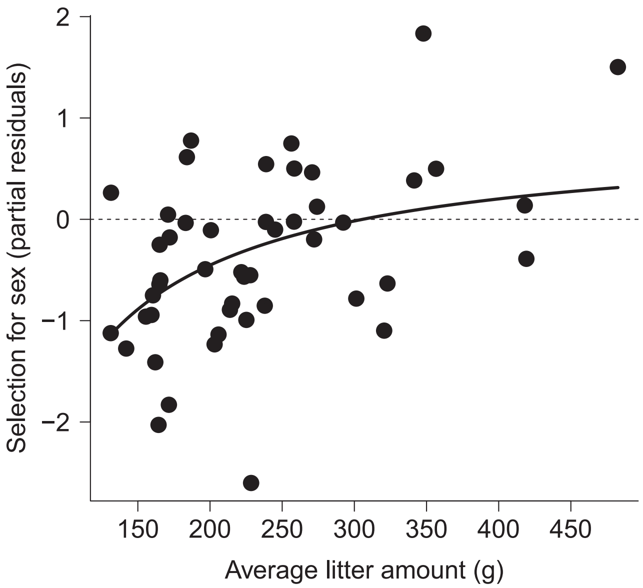

FIGURE 2 Response of selection for sex (standardized effect size of proportion of sexual species) to the independent effect of resource abundance (average litter amount) across soil oribatid mite communities in an Amazonian rainforest. Each point represents one community ($n = 48$). Partial residuals are used to control for the remaining predictors (tree species richness and soil water content). Solid lines indicate predicted means. The dashed line indicates no selection: positive values represent selection for sexual species, and negative values indicate selection against them

replacement of sexual by asexual species, one would expect the latter to increase with higher litter amount and heterogeneity, as fungal abundance and diversity tend to track these factors (Chapman & Newman, 2010; Marañón-Jiménez et al., 2021; Schmit et al., 2005). However, the opposite was found (Figures 1 and 2).

Litter supply increases oribatid mite populations in tropical forests (Ashford et al., 2013; Pequeno et al., 2020), and thus can be expected to increase the effective population size of species. Therefore, stronger selection for sex with increasing litter amount agrees with linkage-based advantages of sexual reproduction, which should increase in effectively larger populations (mechanisms 1, 2 and 3 in Table 1). These advantages should increase with population size because of the parallel increases in total supply of mutations (Colegrave, 2002; Gossmann et al., 2012) and the proportion of unrealized allelic combinations when many loci are selected, which then can be sorted and exposed to selection by sex (da Silva & Galbraith, 2017; Iles et al., 2003). The other major mechanism linking the advantage of sex to effective population size (maintenance of heterozygosity) should be more important in smaller, inbred populations (mechanism 4 in Table 1; Palstra & Ruzzante, 2008). However, asexual species of oribatid mites undergo automixis with terminal fusion and inverted meiosis, which maintains heterozygosity (Archetti, 2022; Bergmann et al., 2018) and thus renders reproductive modes similar in this regard.

Alternatively, the structured resource hypothesis assumes that sexual offspring have higher niche variability, thereby better using resources different from those depleted by their parents (mechanism 5 in Table 1; Scheu & Drossel, 2007; Song et al., 2011, 2012). Accordingly, sexual offspring would have an immediate fitness advantage over asexual offspring where resources are more heterogeneous and/or scarce (regardless of population size), and where abiotic conditions are milder. This combines features of the earlier Tangled Bank hypothesis, which considers variable selection in space, and the Red Queen hypothesis, which considers variable selection over time (Bell, 1982; Song et al., 2011). Our results, stronger selection for sex with increasing litter amount, clearly contradict this idea, as does the lack of evidence for independent effects of tree species richness (resource heterogeneity) and soil water content (abiotic condition). More generally, there is no evidence that sexual oribatid mite species tend to be ecologically more variable than asexual species, at least in terms of number of occupied habitats (Cianciolo & Norton, 2006; Norton & Palmer, 1991). Indeed, asexual oribatid mite species tend to have larger geographic ranges, although widespread species might encompass many cryptic species with smaller ranges (Maraun et al., 2022).

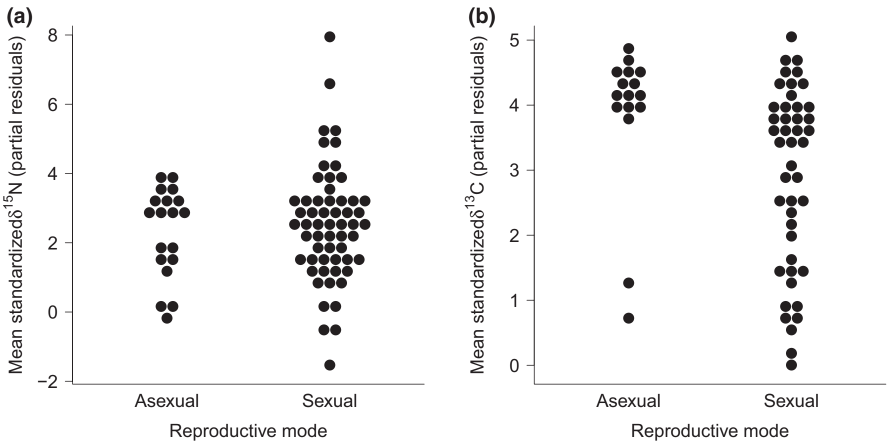

FIGURE 3 Relation between trophic niche (as measured by stable isotope ratios) and reproductive mode in tropical oribatid mites. Each point is one species ($n = 77$ for nitrogen, $n = 61$ for carbon). Partial residuals are used to control for the random factors (taxonomic groupings)

It has been suggested that an inverse relationship between the proportion of sexual species and individuals and the density of individual mites across oribatid mite communities would support the structured resource hypothesis, assuming higher mite density implies higher resource abundance (Maraun et al., 2012, 2013, 2019). However, our results and the above considerations suggest caution in this interpretation. Further, proportions of reproductive modes are themselves calculated using the number of individuals (or species, which correlates strongly with number of individuals) in communities, and thus relating these variables directly is prone to spurious self-correlations (Kenney, 1982). Community trait relationships can also be confounded by the larger sampling variability of trait composition among smaller communities (ecological drift; Swenson, 2014; Vellend, 2016). Here, we addressed these issues by estimating the strength of selection for sexual species independently of other known sources of variation in community trait composition, and by measuring its relation to environmental factors rather than to properties of communities themselves.

The stronger selection for sex with increasing litter amount in oribatid communities under higher tree species richness suggests that resource abundance and heterogeneity may have synergistic effects, although this result should be viewed with caution given its marginal statistical support. Nonetheless, plant diversity and composition can select oribatid mite species through plant resources, litter-dwelling microbial resources, litter habitat and/or soil modification by roots, as indicated by experiments (Hansen & Coleman, 1998; Nielsen et al., 2010; Sulkava & Huhta, 1998) and observational studies (Badejo et al., 2002; Krause et al., 2021; Sylvain & Buddle, 2010). In our study, oribatid species experienced plant heterogeneity both locally (e.g. neighbour tree species) and across the transect, over which they can easily disperse passively (Pequeno et al., 2021) encountering up to roughly one different species per meter. Therefore, some dispersing genotypes could be unfit to some microhabitats within transects, giving sexual offspring a direct fitness advantage as assumed by the spatial heterogeneity hypothesis (mechanism 5 in Table 1; Agrawal, 2009; Becks & Agrawal, 2010). Likewise, within-transect resource heterogeneity may drive selection on multiple linked loci, thus increasing the linkage-based advantages of sex (mechanisms 1, 2 and 3 in Table 1; Iles et al., 2003; Luijckx et al., 2017). Therefore, genetic mechanisms acting on the mean and the variance of fitness could reinforce each other. Higher litter amount also may increase resource heterogeneity on its own by creating more microhabitats for oribatid mites (Hansen & Coleman, 1998).

Our analysis did not consider temporal dynamics, but oribatid mite populations fluctuate in size in response to seasonal litterfall (Pequeno et al., 2020). Under temporal variation, selection for sex should still increase with litter amount through linkage-based mechanisms, granted that more resources support a larger (harmonic) mean effective population size over time (Charlesworth, 2009). Sex might also be favoured directly by temporal variation in resources, e.g. if different tree species shed their leaves at different times of the year. If offspring experience resource types different from those of their parents, sex could increase their fitness directly by making them different from their parents (mechanism 5 in Table 1). This is the essence of the Red Queen hypothesis, although the selective agent most often invoked in this context are parasites, whose evolution targets variable host genotypes over time (Hartfield & Keightley, 2012; Neiman et al., 2018; Sharp & Otto, 2016). Yet, even in the absence of strong host specificity, fluctuating selection creates linkage disequilibrium that can favour sex (mechanisms 1, 2, and 3 in Table 1), and this advantage should increase with effective population size when many loci are under selection (da Silva & Galbraith, 2017). Hence, further investigation of selection by temporal variation in resources is warranted.

Limitations of our study include its observational nature, and experiments will be required to confirm the proposed selective role of litter and elucidate the genetic mechanisms underlying any response to selection. That said, observational studies are important complements to experiments by helping to restrict the range of plausible selective regimes under natural conditions (Neiman et al., 2018). Second, our evidence for trophic niche overlap between reproductive modes comes from sites other than the one we sampled. This concern is lessened by the large overlap of sampled genera with those of the comparative data, since oribatid trophic niche tends to be conserved within genera (Potapov et al., 2022). Third, our findings say nothing about why the genetic and developmental mechanisms responsible for sex arose (or mutated) in the first place (Galis & van Alphen, 2020). In the case of oribatid mites, repeated evolution of asexuality in the crown group Brachypylina suggests a permissive cytogenetic system, while at the same time entirely asexual clades suggest constraints on sex evolution once asexuality has evolved.

Our analysis of Amazonian soil oribatid mites showed that sexual species were favoured by increasing resource abundance, with some evidence for a stronger effect where resources were more heterogeneous. This agrees with the idea that sexual reproduction facilitates adaptation by breaking unfavourable genetic associations, an advantage that should increase with effective population size when many loci are under selection and, thus, with resource abundance. Resource heterogeneity might enhance this effect by creating further opportunity for selection, e.g. across microhabitats connected by dispersal and/or over multiple loci. The ubiquity of variation in resource abundance and heterogeneity warrants further investigation as a common driver of selection for sex in nature.

AUTHOR CONTRIBUTIONS

PACLP and EF conceived the ideas and designed methodology; PACLP, EF and RAN collected the data; PACLP analysed the data; PACLP led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

ACKNOWLEDGEMENTS

We thank José Wellington de Morais, Rozilete Guimarães and Edilson Fagundes for their assistance in field work; Jamile de Moraes for her support with species identification and counting and Carolina Castilho for the tree data.

CONFLICT OF INTEREST

The authors declare that there is no conflict of interest.

PEER REVIEW

The peer review history for this article is available at https://publons.com/publon/10.1111/jeb.14091.

DATA AVAILABILITY STATEMENT

All data used in this study are publicly available from the figshare repository, 10.6084/m9.figshare.20442891.

ORCID

Pedro Aurélio Costa Lima Pequeno https://orcid.org/0000-0001-7350-0485

REFERENCES

Agrawal, A. F. (2009). Spatial heterogeneity and the evolution of sex in diploids. *The American Naturalist*, *174*, S54–S70.

Archetti, M. (2022). Evidence from automixis with inverted meiosis for the maintenance of sex by loss of complementation. *Journal of Evolutionary Biology*, *35*, 40–50.

Ashford, O. S., Foster, W. A., Turner, B. L., Sayer, E. J., Sutcliffe, L., & Tanner, E. V. J. (2013). Litter manipulation and the soil arthropod community in a lowland tropical rainforest. *Soil Biology and Biochemistry*, *62*, 5–12.

Badejo, M. A., Espindola, J. A. A., Guerra, J. G. M., Aquino, A. M., & Correa, M. E. F. (2002). Soil oribatid mite communities under three species of legumes in an ultisol in Brazil. *Journal of Experimental and Applied Acarology*, *27*, 283–296.

Barton, K. (2020). *MuMIn: Multi-model inference*. R package version 1.43.17. https://CRAN.R-project.org/package=MuMIn

Becks, L., & Agrawal, A. F. (2010). Higher rates of sex evolve in spatially heterogeneous environments. *Nature*, *468*, 89–92.

Bell, G. (1982). *The masterpiece of nature*. Croom Helm.

Bergmann, P., Laumann, M., Norton, R. A., & Heethoff, M. (2018). Cytological evidence for automictic thelytoky in parthenogenetic oribatid mites (Acari, Oribatida): Synaptonemal complexes confirm meiosis in archegozetes longisetosus. *Acarologia*, *58*, 342–356.

Brandeis, M. (2018). New-age ideas about age-old sex: Separating meiosis from mating could solve a century-old conundrum. *Biological Reviews*, *93*, 801–810.

Breheny, P. & Burchett, W. (2017). Visualization of regression models using visreg. R package 1-15.

Castilho, C. V., Magnusson, W. E., de Araújo, R. N. O., Luizão, R. C. C., Luizão, F. J., Lima, A. P., & Higuchi, N. (2006). Variation in aboveground tree live biomass in a central Amazonian Forest: Effects of soil and topography. *Forest Ecology and Management*, *234*, 85–96.

Chapman, S. K., & Newman, G. S. (2010). Biodiversity at the plant-soil interface: Microbial abundance and community structure respond to litter mixing. *Oecologia*, *162*, 763–769.

Charlesworth, B. (2009). Effective population size and patterns of molecular evolution and variation. *Nature Reviews Genetics*, *10*, 195–205.

Cianciolo, J. M., & Norton, R. A. (2006). The ecological distribution of reproductive mode in oribatid mites, as related to biological complexity. *Experimental & Applied Acarology*, *40*, 1–25.

Colegrave, N. (2002). Sex releases the speed limit on evolution. *Nature*, *420*, 660–664.

Costa, F. R. C., Schietti, J., Stark, S. C., & Smith, M. N. (2022). The other side of tropical forest drought: Do shallow water table regions of Amazonia act as large-scale hydrological refugia from drought? *New Phytologist*. https://doi.org/10.1111/nph.17914

da Silva, J., & Galbraith, J. D. (2017). Hill–Robertson interference maintained by Red Queen dynamics favours the evolution of sex. *Journal of Evolutionary Biology*, *30*, 994–1010.

Ettema, C. H., & Wardle, D. A. (2002). Spatial soil ecology. *Trends in Ecology & Evolution*, *17*, 177–183.

Falaschi, M., Manenti, R., Thuiller, W., & Ficetola, G. F. (2019). Continental-scale determinants of population trends in European amphibians and reptiles. *Global Change Biology*, *25*, 3504–3515.

Franklin, E., & Morais, J. W. (2006). Soil mesofauna in central Amazon. In F. M. S. Moreira, J. O. Siqueira, & L. Brussaard (Eds.), *Soil biodiversity in Amazonian and other Brazilian ecosystems* (pp. 142–162). CABI Publishing.

Galis, F., & van Alphen, J. J. M. (2020). Parthenogenesis and developmental constraints. *Evolution and Development*, *22*, 205–217.

Gan, H., Zak, D. R., & Hunter, M. D. (2014). Trophic stability of soil oribatid mites in the face of environmental change. *Soil Biology and Biochemistry*, *68*, 71–77.

Gossmann, T. I., Keightley, P. D., & Eyre-Walker, A. (2012). The effect of variation in the effective population size on the rate of adaptive molecular evolution in eukaryotes. *Genome Biology and Evolution*, *4*, 658–667.

Hansen, R. A., & Coleman, D. C. (1998). Litter complexity and composition are determinants of the diversity and species composition of oribatid mites (Acari: Oribatida) in litterbags. *Applied Soil Ecology*, *9*, 17–23.

Hartfield, M., & Keightley, P. D. (2012). Current hypotheses for the evolution of sex and recombination. *Integrative Zoology*, *7*, 192–209.

Hubbell, S. P. (2001). *The unified neutral theory of biodiversity and biogeography*. Princeton University Press.

Huston, M. A. (2014). Disturbance, productivity, and species diversity: empiricism vs. logic in ecological theory. *Ecology*, *95*, 2382–2396.

Iles, M. M., Walters, K., & Cannings, C. (2003). Recombination can evolve in large finite populations given selection on sufficient loci. *Genetics*, *165*, 2249–2258.

Kenney, B. C. (1982). Beware of spurious self-correlations! *Water Resources Research*, *18*, 1041–1048.

Krause, A., Sandmann, D., Potapov, A., Ermilov, S., Widyastuti, R., Haneda, N. F., Scheu, S., & Maraun, M. (2021). Variation in community-level trophic niches of soil microarthropods with conversion of tropical rainforest into plantation systems as indicated by stable isotopes (15N, 13C). *Frontiers in Ecology and Evolution*, *9*, 1–10.

Luijckx, P., Ho, E. K., Gasim, M., Chen, S., Stanic, A., Yanchus, C., Kim, Y. S., & Agrawal, A. F. (2017). Higher rates of sex evolve during adaptation to more complex environments. *Proceedings of the National Academy of Sciences*, *114*, 534–539.

MacColl, A. D. C. (2011). The ecological causes of evolution. *Trends in Ecology and Evolution*, *26*, 514–522.

Marañón-Jiménez, S., Radujković, D., Verbruggen, E., Grau, O., Cuntz, M., Peñuelas, J., Richter, A., Schrumpf, M., & Rebmann, C. (2021). Shifts in the abundances of saprotrophic and ectomycorrhizal fungi with altered leaf litter inputs. *Frontiers in Plant Science*, *12*, 1–17.

Maraun, M., Bischof, P. S. P., Klemp, F. L., Pollack, J., Raab, L., Schmerbach, J., Schaefer, I., Scheu, S., & Caruso, T. (2022). "Jack-of-all-trades" is parthenogenetic. *Ecology and Evolution*, *12*, e9036.

Maraun, M., Caruso, T., Hense, J., Lehmitz, R., Mumladze, L., Murvanidze, M., Nae, I., Schulz, J., Seniczak, A., & Scheu, S. (2019). Parthenogenetic vs. sexual reproduction in oribatid mite communities. *Ecology and Evolution*, *9*, 7324–7332.

Maraun, M., Fronczek, S., Marian, F., Sandmann, D., & Scheu, S. (2013). More sex at higher altitudes: Changes in the frequency of parthenogenesis in oribatid mites in tropical montane rain forests. *Pedobiologia*, *56*, 185–190.

Maraun, M., Norton, R. A., Ehnes, R. B., Scheu, S., & Erdmann, G. (2012). Positive correlation between density and parthenogenetic reproduction in oribatid mites (Acari) supports the structured resource theory of sexual reproduction. *Evolutionary Ecology Research*, *14*, 311–323.

Minor, M. A. (2011). Spatial patterns and local diversity in soil oribatid mites (Acari: Oribatida) in three pine plantation forests. *European Journal of Soil Biology*, *47*, 122–128.

Neiman, M., Meirmans, P. G., Schwander, T., & Meirmans, S. (2018). Sex in the wild: How and why field-based studies contribute to solving the problem of sex. *Evolution*, *72*, 1194–1203.

Nielsen, U. N., Osler, G. H. R., Campbell, C. D., Neilson, R., Burslem, D. F. R. P., & van der Wal, R. (2010). The enigma of soil animal species diversity revisited: The role of small-scale heterogeneity. *PLoS One*, *5*, e11567.

Norton, R. A., & Behan-Pelletier, V. M. (2009). Suborder Oribatida. In G. W. Krantz & D. E. Walter (Eds.), *A manual of acarology* (pp. 430–564). Texas Tech University Press.

Norton, R. A., Kethley, J. B., Johnston, D. E., & OConnor, B. M. (1993). Phylogenetic perspectives on genetic systems and reproductive modes of mites. In D. L. Wrensch & M. A. Ebbert (Eds.), *Evolution and diversity of sex ratio in insects and mites* (pp. 8–99). Chapman & Hall.

Norton, R. A., & Palmer, S. C. (1991). The distribution, mechanisms and evolutionary significance of parthenogenesis in oribatid mites. In R. Schuster & P. W. Murphy (Eds.), *The Acari: Reproduction, development and life history strategies* (pp. 107–136). Springer.

Pachl, P., Uusitalo, M., Scheu, S., Schaefer, I., & Maraun, M. (2021). Repeated convergent evolution of parthenogenesis in Acariformes (Acari). *Ecology and Evolution*, *11*, 321–337.

Palstra, F. P. & Ruzzante, D. E. (2008). Genetic estimates of contemporary effective population size: What can they tell us about the importance of genetic stochasticity for wild population persistence? *Molecular Ecology*, *17*, 3428–3447. https://doi.org/10.1111/j.1365-294X.2008.03842.x

Pequeno, P. A. C. L., Franklin, E., & Norton, R. A. (2020). Determinants of intra-annual population dynamics in a tropical soil arthropod. *Biotropica*, *52*, 129–138.

Pequeno, P. A. C. L., Franklin, E., & Norton, R. A. (2021). Modelling selection, drift, dispersal and their interactions in the community assembly of Amazonian soil mites. *Oecologia*, *196*, 805–814.

Potapov, A. M., Beaulieu, F., Birkhofer, K., Bluhm, S. L., Degtyarev, M. I., Devetter, M., Goncharov, A. A., Gongalsky, K. B., Klarner, B., Korobushkin, D. I., Liebke, D. F., Maraun, M., Mc Donnell, R. J., Pollierer, M. M., Schaefer, I., Shrubovych, J., Semenyuk, I. I., Sendra, A., Tuma, J., … Scheu, S. (2022). Feeding habits and multifunctional classification of soil-associated consumers from protists to vertebrates. *Biological Reviews*, *97*, 1057–1117. https://doi.org/10.1111/brv.12832

R Core Team (2021). *R: A language and environment for statistical computing*. R Foundation for Statistical Computing. https://www.R-project.org

Rohatgi, A. (2018). *WebPlotDigitizer*. https://automeris.io/WebPlotDigitizer

Schaefer, I., & Caruso, T. (2019). Oribatid mites show that soil food web complexity and close aboveground-belowground linkages emerged in the early Paleozoic. *Communications Biology*, *2*, 1–8.

Scheu, S., & Drossel, B. (2007). Sexual reproduction prevails in a world of structured resources in short supply. *Proceedings of the Royal Society B*, *274*, 1225–1231.

Schmit, J. P., Mueller, G. M., Leacock, P. R., Mata, J. L., Wu, Q., & Huang, Y. (2005). Assessment of tree species richness as a surrogate for macrofungal species richness. *Biological Conservation*, *121*, 99–110.

Sharp, N. P., & Otto, S. P. (2016). Evolution of sex: Using experimental genomics to select among competing theories. *BioEssays*, *38*, 751–757.

Song, Y., Drossel, B., & Scheu, S. (2011). Tangled Bank dismissed too early. *Oikos*, *120*, 1601–1607.

Song, Y., Scheu, S., & Drossel, B. (2012). The ecological advantage of sexual reproduction in multicellular long-lived organisms. *Journal of Evolutionary Biology*, *25*, 556–565.

Sulkava, P., & Huhta, V. (1998). Habitat patchiness affects decomposition and faunal diversity: A microcosm experiment on forest floor. *Oecologia*, *116*, 390–396.

Swenson, N. G. (2014). *Functional and phylogenetic ecology in R*. Springer.

Sylvain, Z. A., & Buddle, C. M. (2010). Effects of forest stand type on oribatid mite (Acari: Oribatida) assemblages in a southwestern Quebec forest. *Pedobiologia*, *53*, 321–325.

Tilquin, A., & Kokko, H. (2016). What does the geography of parthenogenesis teach us about sex? *Philosophical Transactions of the Royal Society B: Biological Sciences*, *371*, 1–15.

Vellend, M. (2016). *The theory of ecological communities*. Princeton University Press.

Villani, M. G., Allee, L. L., Diaz, A., & Robbins, P. S. (1999). Adaptive strategies of edaphic arthropods. *Annual Review of Entomology*, *44*, 233–256.

White, T. C. R. (2008). The role of food, weather and climate in limiting the abundance of animals. *Biological Reviews*, *83*, 227–248.

SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

How to cite this article: Pequeno, P. A. C., Franklin, E., & Norton, R. A. (2022). Hunger for sex: Abundant, heterogeneous resources select for sexual reproduction in the field. *Journal of Evolutionary Biology*, *00*, 1–9. https://doi.org/10.1111/jeb.14091