What drives the dynamics of a soil mite population under seasonal flooding? A null model analysis

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Abstract Floods can inflict high mortality on terrestrial organisms, but may also promote adaptive evolution. In seasonal floodplains, several taxa show flood-related traits that may be important for their long-term persistence, but the available evidence is conflicting. Here, we used a simulation approach to investigate the interplay between seasonal floods and submersion resistance in driving the population dynamics of the parthenogenetic soil mite *Rostrozetes ovulum* in an Amazonian blackwater floodplain. First, we gathered data from two flood cycles to estimate field survival rate. Next, we used further data from a submersion survival laboratory experiment and a historical flood record to build a null model for *R. ovulum*'s survival rate under seasonal flooding, and then tested it against field survival estimates. Floods caused marked density declines, but the two estimates of field survival rate were statistically equivalent, suggesting relatively constant survival across years. Submersion survival time varied tenfold among individuals, but its variability was within the range known for life history traits of other asexual invertebrates. Both field survival rates were consistent with the null model, supporting seasonal flooding as the main mortality factor. Surprisingly, though, average flood duration was actually larger than the average mite could survive, suggesting that population persistence relies on relatively rare, super-resistant phenotypes. Overall, the studied *R. ovulum* population appears to have a mainly density-independent dynamics across years, with its viability depending on mechanisms that buffer flood survival rate against temporal oscillations.

Keywords Abundance · Asexual reproduction · Disturbance · Haplozetidae · Monte Carlo simulation · Truncation selection

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Introduction

Organisms are subject to a range of natural disturbances, i.e. extrinsic, discrete events that inflict mortality such as fires, storms and droughts. Depending on their pattern of occurrence, disturbances can either drive population decline and extinction or foster adaptive evolution, particularly when they recur within an organism's life cycle (Souza 1984; Lytle 2001; Schowalter 2012). Thus, in ecosystems characterized by a marked disturbance regime, one may expect the dynamics of populations to reflect both disturbances themselves and their evolutionary signature on individuals.

In the central Amazon floodplain, the environment has been shaped by a monomodal flood pulse during the last 1 million years, which raises the water table over 10 m and submerges floodplains for up to 7 months (Junk 1997). Accordingly, the soil biota is characterized by an array of flood-related traits (Adis and Junk 2002), and laboratory studies have provided mechanistic insight into some of them (Adis 1986; Messner et al. 1992; Messner and Adis 2000; Zerm and Adis 2000, 2001, 2003; Zerm et al. 2004a, b, c). While such traits may arguably mediate long-term species persistence under seasonal flooding, their link to population dynamics remains elusive.

The parthenogenetic oribatid mite *Rostrozetes ovulum* Berlese (Oribatida: Haplozetidae) (synonym of *R. foveolatus* according to Norton and Kethley 1989) is among the commonest species of the soil fauna in Amazonian forests, including flooded ones (Beck 1969, 1972; Franklin et al. 2006). Adults from floodplains have higher submersion resistance than those from non-flooded forests, and may survive submersion up to remarkable 684 days in laboratory (Franklin et al. 2001). Supposing that the oribatid mode of parthenogenesis produces effectively clonal progeny (Heethoff et al. 2009), one can expect this trait to be heritable. If so, the seasonal flood regime could eliminate low-resistance genotypes, thus increasing average submersion resistance and decreasing its variance. Nonetheless, submersion resistance is actually more variable in floodplain populations (Franklin et al. 2001), and field data suggest that as little as 10 % of the adults experiencing seasonal flood actually survive (Beck 1972). While some mite species escape floods by migrating (Franklin et al. 1997a), this is unlikely for *R. ovulum*: its mobility is rather low, and individuals do not float when submerged (P. Pequeno, personal observation). Thus, there is an apparent decoupling between the performances of individuals and populations.

One possible explanation for this is that submersion survival time depends on the physicochemistry of the water (Schuster 1965). Soil arthropods are rapidly exposed to anoxic conditions after soil flooding (Adis and Messner 1991). For instance, the Amazonian millipede *Myrmecodesmus adisi* Hoffman (syn. *Gonographis adisi*) survived submergence for almost a year in the laboratory, but died within 48 h in anoxic water (Adis 1986). Noteworthy, the maximum submersion resistance observed for *R. ovulum* was recorded at a high oxygen saturation (61 %) relative to natural conditions (Franklin et al. 1997b), and low oxygen content had a negative effect on *R. ovulum* activity after experimental submergence (Messner et al. 1992). Thus, *R. ovulum* field populations may have a lower survival rate than that implied by laboratory measurements.

On the other hand, experiments with other floodplain arthropods suggest some degree of plasticity in submersion resistance. For instance, tiger beetle larvae (*Phaeoxantha* spp.) exposed to instantaneous flooding survived a few days to weeks, while submersion survival time was over 3 months when larvae were gradually submerged for a week (Zerm and Adis 2001). If the same applies to *R. ovulum* adults, then one would expect individuals of a given population to have higher survival times in nature than in instant submersion experiments, because seasonal flooding is not an instantaneous event.

Here, we investigated the interplay between seasonal flooding and submersion resistance in driving the dynamics of a *R. ovulum* population in an Amazonian blackwater floodplain. We gathered field data from 2 years/flood cycles to estimate survival rate, and then further data from an instant submersion experiment and a historical flood record to build a null model for *R. ovulum* survival under seasonal flooding. A null model consists of a random sampling scheme that approximates the distribution of a quantity of interest under the assumption that some specified mechanism does not operate (Gotelli and Graves 1996). By comparing an empirical estimate of this quantity with the null distribution, one can ask how likely it would be to observe such estimate if the excluded mechanism really does not operate. Statistically significant departures from the null expectation provide evidence for the neglected mechanism.

We used the null model to distinguish among three scenarios: (1) a field survival rate equal to the null expectation would imply that population dynamics in the field simply reflects the species submersion resistance, after accounting for the flood dynamics (null hypothesis); (2) a field survival rate lower than the null expectation would indicate the effect of a mortality factor other than submersion *per se*, likely low oxygen (anoxia hypothesis); (3) a field survival rate higher than the null expectation would suggest that the gradual flooding under natural conditions would enhance *R. ovulum* submersion resistance (plasticity hypothesis).

Materials and methods

Study site

All mites used in this study were collected across a site (400 × 400 m) in the blackwater floodplain of the Tarumã Mirim River, Negro River Basin, Amazonas State, Brazil (03°01′S, 60°10′W). In this area, locally known as "igapó" (Prance 1979), inundation begins in March and lasts until August/September, with a maximum water depth of 3–4 m around June. The soil consists of clay, silt and sand material. A more detailed characterization of abiotic (geomorphology, soil, climate and flood cycle) and biotic (flora and fauna) aspects is given by Adis (1981, 1984).

Data on mite counts

Two independent datasets on field counts of *R. ovulum* were used. The first dataset was originally sampled by J. Adis and collaborators and processed by E. Franklin (hereafter the 1981–82 data). Samples of the litter/soil interface (21 cm in diameter and 14 cm deep) were taken with a cylindrical soil corer early (September 21, 1981; n = 4) and late (February 17, 1982; n = 6) in the terrestrial phase across the study area. The mesofauna was extracted with a modified Kempson apparatus. The temperature was gradually increased from 27 °C to approximately 40–45 °C, and aqueous solution saturated with picric acid (3:1) was used as a preservative fluid. Samples remained in the apparatus until it was completely dry (Adis 1987). *Rostrozetes ovulum* adults were counted and preserved in alcohol 70 %. The forest was inundated a couple of weeks after the last sampling.

The second dataset was obtained by E. Franklin and collaborators in 1989 (hereafter the 1989 data). Eight 50 × 50 cm plots were positioned across the study area and had their litter completely harvested in February 28 (i.e. end of the terrestrial phase). Concurrently, eight galvanized metal cages (30 × 20 × 7 cm) were set on the ground across the study

area, and each of them was filled with litter collected from plots as described previously. Cages were then coated with a nylon cover (1 mm mesh size) with several lateral perforations (9–10 mm) to provide connectivity with the environment. This method allowed standardized mite sampling during the flood: cages eased litter collection underwater and, by filling the cages with a litter amount similar to that of the litter plots, the cage and plot data were also made comparable. Flooding began 8–10 days after this setup. Cages were retrieved at the end of the flood period (August 28), and mites were extracted and preserved as previously described.

Experimental determination of submersion resistance

This experiment was conducted in 1996. Litter/soil samples were collected in February and kept in plastic bags in thermally insulated containers until they were taken to the laboratory, where mites were extracted with the modified Kempson apparatus. Temperature was kept at 32 °C, and distilled water was used in place of a preservative fluid to keep the animals alive. Specimens were removed daily and identified under a stereomicroscope.

Fifty living, adult individuals of *R. ovulum* without mutilations were transferred to Petri dishes (5 cm in diameter and 1.5 cm in height) filled with a substrate of plaster of Paris 0.5 cm thick, one mite per Petri dish. Small pieces of dead leaves from the soil samples were also put on the substrate to serve as shelter. Next, experimental units were filled with distilled water to a depth of 0.5 cm and placed in a BOD chamber (12 h with light at 27 °C, and 12 h without light at 21 °C). Mites were monitored daily and fed with oat flakes and TetraMin® fish ration (Tetra Werke, Melle, Germany). Each 3 days, experimental units were cleaned from the excess of growing algae, and food and a third of the water were replaced. Mites were suspected dead if unresponsive to tactile stimuli. Such mites were further monitored for 2 weeks to confirm death.

Data analysis

To model the effect of seasonal flooding on *R. ovulum*'s abundance, we used a generalized linear model (GLM) with log link and negative binomial errors. The negative binomial distribution describes counts using two parameters, the mean μ and the dispersion k. We used mite counts as the response variable and sampling period relative to flood (i.e. a binary variable, before or after) as predictor. We fitted the GLM to each of the two count datasets, and estimated both μ and k for each sampling period. We tested for an average difference between sampling periods with randomization tests (999 permutations).

To estimate the field survival rate with the 1981–82 data, we divided the mean mite count at the beginning of the terrestrial phase (i.e. surviving the aquatic phase) by that at its end (i.e. entering the aquatic phase). Similarly, for the 1989 data, we divided the mean number of *R. ovulum* adults at the end of flood (i.e. survivor population) by that prior to the flood (i.e. submerged population). The uncertainty in the estimates was assessed with a parametric bootstrap: for each dataset, the fitted GLM was used to simulate 10,000 pairs of samples of mite counts (i.e. before and after flood), with sample sizes equal to the empirical ones in each case. At each sampling, survival rate was calculated as before, and the resulting variability was described with a 95 % confidence interval.

To build a null model for *R. ovulum*'s survival under seasonal flooding, we used statistical distributions to describe the variability in key components of the system, namely submersion survival time, flood duration and field population size. This allows one to simulate and assess the long-run variability in any quantity of interest, and then ask

whether empirical patterns are consistent with this variability (Gotelli and Graves 1996). Survival data were fit to a Weilbull distribution with shape *a* and scale *b*, a standard choice for modeling survival times (Pyke and Thompson 1986). We also calculated the coefficient of variation (CV) of survival time as a standardized description of its variability. Flood duration was modeled as a normal distribution with mean 3.9 months and standard deviation of 1.5, based on data from the study site for 95 years (see Franklin et al. 2001). Population size was described by the negative binomial GLMs as previously described.

The null model consisted of three steps: (1) simulating the survival rate given the experimentally inferred submersion resistance and the known flood regime, (2) simulating the survival rate observed in the field and then (3) comparing both rates. First, a population of size equal to that of the sample used in the submersion experiment was simulated whose submersion survival times were randomly drawn from the Weilbull distribution fitted to the laboratory data. Then, this experimental population was subject to a flood of a given duration, and the proportion of individuals whose survival times were equal or greater than the flood period was recorded. Here, flood duration was randomly drawn from a normal distribution as previously described, and then multiplied by 30 to convert months to days. Second, a field population was created that experienced a flood, so that its sizes before and after the flood were randomly drawn from the respective negative binomial distributions, as modeled by the GLM. Then, the field survival rate was calculated by dividing the population size after the flood by that before it, and this value was recorded. Lastly, the difference between the two survival rates was calculated, a measure of the discrepancy between the field survival rate and that expected based on the species submersion resistance, as experimentally determined.

This sequence was iterated 10,000 times, resulting in a distribution of differences between field and experimental survival rates that reflected the chance of observing any particular difference, given the model. This distribution thus represented the null hypothesis that *R. ovulum*' submersion resistance alone could explain the proportion of individuals surviving seasonal flooding in the field. To evaluate the robustness of the result, we ran the model using each of the datasets on mite counts.

To test the null hypothesis, we first calculated the difference between the field survival rate (i.e. estimated from mite counts) and that expected based on the laboratory experiment (i.e. the mean survival rate of the simulated experimental populations). Here, positive values would indicate higher survival in the field, while negative values would indicate the opposite. Then, a P value was determined by calculating the proportion of simulated differences equal or more extreme than the observed one. In all analyzes, parameters were estimated by maximum likelihood, and statistical significance was assumed for $P < 0.05$. All computations were performed in R 2.15.1 (R Development Core Team 2012).

Results

The mean abundance of *R. ovulum* adults was strongly reduced after the seasonal flood in the two surveyed years ($P < 0.01$) (Table 1). In 1981–82, there were 18.5 ± 5.43 adults per sample (mean ± SD) early in the emersion season and 93 ± 39.97 adults per sample (mean ± SD) just before inundation, which gives a field survival rate of $18.5 \div 93 = 0.199$ or 19.9 % (95 % CI: 0.128–0.315). In 1989, there were 215.5 ± 61.74 adults per sample (mean ± SD) prior do inundation and 52.87 ± 43.04 adults per sample (mean ± SD) by the end of the flood, thus indicating a field survival rate of

Table 1 Parameter estimates for the distributions used to model *Rostrozetes ovulum* survival to flooding

Variable	Period	N	Distribution	Parameter	Estimate
Mite counts[a]	Before flood	6	Negative binomial	μ	93
				k	5.75
	After flood	4	Negative binomial	μ	18.5
				k	31.3
Mite counts[b]	Before flood	8	Negative binomial	μ	215.5
				k	12.92
	After flood	8	Negative binomial	μ	52.87
				k	1.54
Survival times	–	50	Weibull	a	2
				b	124.93

μ mean, k dispersion, a shape, b scale

[a] Data from litter/soil cores sampled in 1981–82

[b] Data from litter plots/cages sampled in 1989

$52.87 \div 215.5 = 0.245$ or 24.5 % (95 % CI: 0.125–0.422). Survival rates were statistically equivalent between years, as indicated by the overlap between confidence intervals.

Rostrozetes ovulum's survival time in the submersion experiment averaged 110.7 days, but varied tenfold, ranging from 24 to 262 days (CV = 52 %) (Fig. 1). Under the null model, the expected (mean) experimental survival rate was 0.443 or 44.3 %. When analyzing the 1981–82 data, there was a negative difference between field and experimental survival rates ($0.199-0.443 = -0.244$), suggesting lower survival in the field. However, this value was not statistically distinct from that expected under the null model ($P = 0.42$) (Fig. 2a). When analyzing the 1989 data, there was also a negative difference between field and experimental survival rates ($0.245-0.443 = -0.198$), but again it was statistically indistinguishable from the null expectation ($P = 0.47$) (Fig. 2b).

Discussion

The fit between null models and field survival rates suggests that the dynamics of the studied *R. ovulum* population largely results from the interplay between the flood regime and the species' submersion resistance (null hypothesis). This points to seasonal flooding as the main mortality factor affecting the population, suggesting a mostly density-independent dynamics across years. The striking, flood-driven declines in *R. ovulum* abundance agree with early observations (Beck 1972), although our survival rate estimates are at least twice larger than that reported by the latter author for another site in the central Amazon floodplain. However, assuming our data to be minimally representative of the region, the difference between Beck's estimate and the null expectation (i.e. $0.1-0.443 = -0.343$) also turns out to be a likely outcome ($P > 0.3$). Remarkably, though, there may still be concurrent density dependence within years (Karels and Boonstra 2000), especially during the terrestrial season (Franklin et al. 1997a).

The fit between null models and data also suggests that the experimentally inferred variability in submersion resistance reflects that occurring in the field. Intriguingly, though, while floods lasted for 3.9 months on average (ca. 117 days), submersion resistance

Fig. 1 Probability densities of submersion survival time and flood duration under the fitted distributions (i.e. Weibull and normal, respectively). Survival data were from individuals experimentally submerged in laboratory (n = 50), while flood data were from a historical yearly record (n = 95), both from the same site. The area under each curve sums to 100 %. *Vertical lines* indicate distribution averages
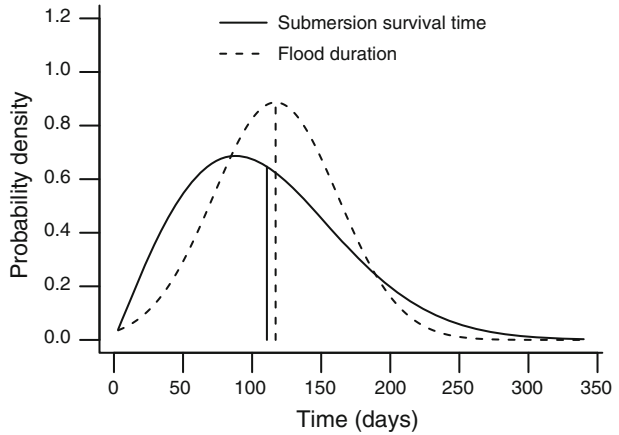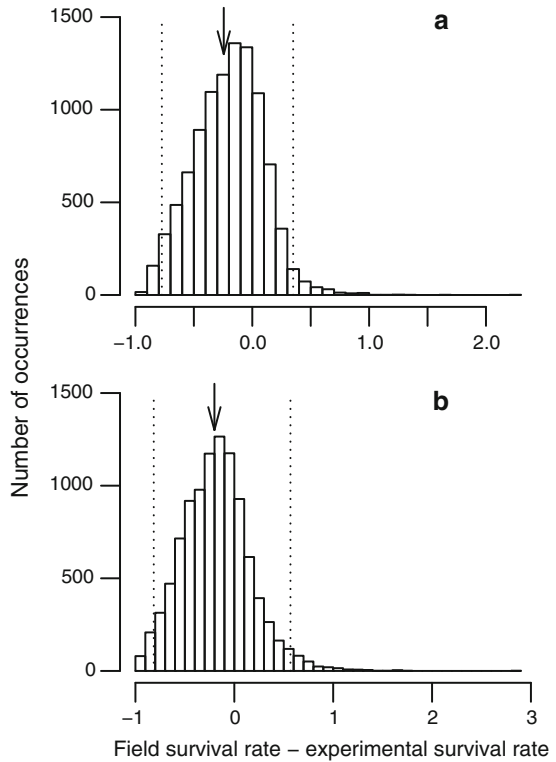
Fig. 2 Null distributions of differences between field and experimental survival rates of *Rostrozetes ovulum*. **a** Null distribution based on the 1981–82 dataset (litter/soil cores), **b** Null distribution based on the 1989 dataset (litter plots/cages). *Arrows* indicate the observed differences. *Dotted lines* indicate the limits of rejection of the null hypothesis

averaged 110.7 days. Hence, floods tended to be longer than the average mite could survive (Fig. 1), thus raising a seeming paradox: how can a positive survival rate result from such a stringent mortality regime? On the one hand, floods can be relatively short during some years, so that most individuals survive. For instance, there is a 43 % chance that a flood will actually be shorter than the average submersion survival time (Fig. 1). On the other hand, some individuals can be extraordinarily submersion-resistant. Indeed, the right tail of the survival time distribution renders extinction risk effectively negligible even

under very long floods (Fig. 1). For instance, a flood of 200 days would still allow 7.7 % of the population to survive. This underscores the importance of simultaneous extrinsic and intrinsic sources of variability in driving population viability (Fox 2005, Melbourne and Hastings 2008).

The observed tenfold amplitude in submersion resistance seems rather large, although we are unaware of other directly comparable measurements. Part of this variability probably reflects the number of clonal lineages in the population, which is currently unknown. However, the calculated CV of 52 % is within the range known for life history traits measured in isolated individuals of the also parthenogenetic, model oribatid *Archegozetes longisetosus* Aoki in laboratory (13–80 %; calculated from Table 1 of Seniczak 2006), and for field populations of other asexual invertebrates such as brine shrimps (5.8–228 %) (Browne et al. 1984) and freshwater snails (4.68–66.35 %) (Jokela et al. 1997). Interestingly, the occurrence of extraordinarily resistant individuals that account for a small fraction of the population, as observed here, is also found in other organisms experiencing seasonally harsh environments, such as parasitic nematodes (Preisser et al. 2005) and diapausing insects (Danks 2007). We suspect that super-resistant phenotypes may be key for *R. ovulum*'s long-term persistence in the floodplain, by safeguarding the population against catastrophic floods. Still, the sources of intraspecific variation in *R. ovulum* remain to be assessed.

Noteworthy, the two estimates of field survival rate came from datasets sampled with different methods and distant almost a decade from each other and yet, were statistically equivalent. This hints at a relatively constant survival rate across flood cycles. Now, theory suggests that temporal oscillations in demographic rates (e.g. survival) increase extinction risk (Lande 1993). If so, selection should favor their buffering against temporal variation—a prediction supported by several studies, particularly with respect to those vital rates more strongly linked to population growth (Pfister 1998; Gaillard and Yoccoz 2003; Miller et al. 2011). Thus, the seasonal flood regime may have selected for mechanisms that buffer *R. ovulum*'s flood survival rate against interannual fluctuations. While this issue requires further study, we hypothesize that super-resistant phenotypes may provide one such mechanism, as discussed above.

Given the evidence for plasticity in submersion resistance in other floodplain arthropods, and the expected role of water properties in submersion survival, it is interesting that the null hypothesis could not be rejected. Nonetheless, the hypothesis tested here refers to the population level, as opposed to the individual level. For instance, while the analysis suggests that *R. ovulum*'s submersion resistance is unlikely to be a function of flooding speed, it may also be that most individuals simply do not experience flooding as a gradual process in nature, perhaps because they are instantly submerged by natural flooding rates that would be perceived as gradual by other soil arthropods (Zerm and Adis 2001, 2003). This would be expected due to the mite's rather small body size (280–450 μm long, 175–300 μm wide) (Beck 1965).

We note that our study has some caveats. First, the modest sample sizes of the mite count data, coupled to the large variability in the system we modeled, reduce our power to reject the null model. However, even a more liberal significance level (e.g. $P < 0.1$) would still support it. Second, our analyses consider adults only; assigning immatures to species in brachypiline oribatids (to which *R. ovulum* belongs) is currently impractical (Norton and Behan-Pelletier 2009). Therefore, our estimates of survival rate might be biased due to unquantified nymphs. However, this is unlikely as the abundance of immature oribatids relative to that of adults at our study site is very low (5.7 % on average; Franklin et al. 1997a).

Overall, this study suggests that the dynamics of the *R. ovulum* population is driven by the joint variability in the environment (i.e. flood duration) and the population itself (i.e. submersion resistance), with a mainly density-independent dynamics across years. Extraordinarily resistant phenotypes occur in low numbers in the population, but may be fundamental in the long-run by buffering survival rate against catastrophic floods. While the factors influencing trait variation in *R. ovulum* remain elusive, this study provides an initial link between the mite's individual performance and its population dynamics under environmental variability.

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