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Habitat size thresholds for predators: Why damselflies only occur in large bromeliads

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Abstract

Predators are often more sensitive to habitat size than their prey and frequently occur in only the largest habitats. Four explanations have been proposed for this pattern: (a) Small habitats do not have enough energy to support higher trophic levels; (b) small habitats are less likely to contain particular prey required by specialist predators; (c) small habitats are risky for predators with slow life histories or large body sizes; and (d) small habitats are numerically unlikely to be colonized by regionally rare species, such as predators. We critically examine these four hypotheses in relation to the predatory damselfly larva, *Mecistogaster modesta* Selys. (Pseudostigmatidae), which occurs almost exclusively in bromeliads > 100ml in capacity. We synthesize multiple years of survey data and three manipulative experiments from the Área de Conservación Guanacaste, Costa Rica, to conclude that damselflies do not occur in small bromeliads due to their higher risk of desiccation—not because of energetic limitation, trophic specialization, risk of terrestrial predation, or pure numerical effects. These results suggest that recent and predicted declines in precipitation in northwestern Costa Rica may further restrict bromeliad occupancy by damselflies, with cascading consequences for the rest of the aquatic food web.

Abstract in Spanish is available with online material.

KEYWORDS

Área de Conservación Guanacaste, cannibalism, climate change, Costa Rica, drought risk, energetic limitation, incidence function, *Mecistogaster modesta*, phytotelmata

1 | INTRODUCTION

Predators are often thought to be more sensitive to ecosystem size than their prey. Top trophic levels are typically present in only the largest habitats (McHugh, Thompson, Greig, Warburton, & McIntosh, 2014; Ostman et al., 2007; Roslin, Varkonyi, Koponen, Vikberg, & Nieminen, 2014; Schoener, 1989; Terborgh et al., 2001). Similarly, a number of studies report that reductions in habitat area result in extinctions preferentially at top trophic levels (Davies, Margules, & Lawrence, 2000; Didham, Lawton, Hammond, & Eggleton, 1998; Staddon, Lindo, Crittenden, Gilbert, & Gonzalez, 2010), although this is not always the case (Martinson & Fagan, 2014; Starzomski & Srivastava, 2007). Patch occupancy by species is also more strongly related to area for carnivores than lower trophic levels (Prugh, Hodges, Sinclair, & Brashares, 2008). A different way to see the same pattern is with species–area relationships: within food webs, top trophic levels often have steeper species–area relationships than lower trophic levels, consistent with greater sensitivity to area (Gravel, Massol, Canard, Mouillot, & Mouquet, 2011; Hoyle, 2004; With & Pavuk, 2011).

At least four explanations have been proposed to explain predators' greater sensitivity to ecosystem size. The *"energetic limitation"* hypothesis argues that ecosystem size is a proxy for the total amount of energy (Wright, 1983). If the input of resources per unit area is constant, small habitats will have lower absolute amounts of resource inputs than larger habitats. Given the inefficiencies in trophic transfer between trophic levels (Hairston & Hairston, 1993; Lindeman, 1942), in theory there must be a habitat size too small to have enough energy and nutrients to maintain a viable population of a top predator (Hurlbert & Stegen, 2014; Hutchinson, 1959; Schoener, 1989). A variant of this idea is that the diverse prey base of large habitats offers a more productive supply of prey (Holt & Hoopes, 2005). Although some ecological patterns with habitat size are consistent with energy limitation (Schoener, 1989; Terborgh et al., 2001; Vander Zanden, Shuter, Lester, & Rasmussen, 1999), it has so far not been strongly supported (Post, Pace, & Hairston, 2000; Spencer & Warren, 1996).

The *"trophic rank"* hypothesis (Holt, 2009; Holt, Lawton, Polis, & Martinez, 1999) assumes, like classic island biogeography theory, that species encounter large habitats more frequently than small habitats. However, if predators can only consume certain prey species, then predators that colonize small habitats may not be able to establish because their prey has not yet colonized the habitat (Bascompte & Sole, 1998). This compounding of area effects up the food chain can result in the ratio of predators to prey increasing with patch size (Gravel et al., 2011; Holt et al., 1999). Supporting this hypothesis, specialist—but not generalist—parasitoids have steeper species–area curves than their herbivorous prey (Cagnolo, Valladares, Salvo, Cabido, & Zak, 2009).

The *"risky habitat"* hypothesis (Amundrud & Srivastava, 2015) holds that small habitats are inherently riskier for species because they are more likely to experience catastrophic events, such as drought for a rockpool (Vanschoenwinkel et al., 2009) or storm surges for an island (Chui & Terry, 2013), or because their greater edge to area ratio allows disturbances from the matrix to penetrate more of the habitat (as shown for bushmeat hunting in reserves, Brashares, Arcese, & Sam, 2001). Predators have often been reported to be more sensitive to such disturbances than their prey (Menge & Farrell, 1989; Petes, Mouchka, Milston-Clements, Momoda, & Menge, 2008; Voigt et al., 2003). This may occur for several reasons. If predators are larger than their prey, as is typical for engulfing predators, they may not be able to access refuges from disturbance (Nash, Graham, Wilson, & Bellwood, 2013). If predators have low densities or "slow" life histories (long generation times, late age at maturity and low fecundity), their populations may not be able to recover quickly from disturbances (Newbold et al., 2013; Salguero-Gomez et al., 2016). Even if predators and prey individuals are equally susceptible to disturbance, the typically lower density of predators may result in greater likelihood of local extinction following disturbance.

Finally, the *"regional abundance"* hypothesis relates the low incidence of predators in small habitats to their lower regional abundance than prey species. Stochastic models show that species at low regional abundance can appear to be more sensitive to area (e.g., have steeper species–area relationships) than species at higher regional abundances simply through sampling effects, that is, even if individuals are randomly placed in habitat patches irrespective of trophic requirements (Holt, 2009; Srivastava, Trzcinski, Richardson, & Gilbert, 2008).

In this study, we examine whether these hypotheses can explain the distribution of a key predator in bromeliad food webs. Bromeliads are Neotropical plants that often collect water and detritus between their leaves, providing habitat for detritivorous and predatory macroinvertebrates (Richardson, 1999; Srivastava, 2006). Srivastava et al. (2008) found that predators were more sensitive to bromeliad size than detritivores, but in two field sites (Puerto Rico and Dominica) the regional abundance hypothesis accounted for such differences. The exception was Costa Rican bromeliads with high densities of damselfly larvae (*Mecistogaster modesta* Selys.) whose occurrence increased abruptly when bromeliads exceed 100 ml in capacity. Such damselflies do not occur in Puerto Rican and Dominican bromeliads. In a second analysis, Amundrud and Srivastava (2015) confirmed that *M. modesta* occurs in larger bromeliads than expected simply from its regional abundance. The proximate reason for the occurrence of *M. modesta* in large bromeliads is that adult female damselflies choose to oviposit in bromeliads greater than 100 ml in capacity, and adult males defend territories around such large bromeliads (D. S. and J. N., unpubl. results).

These observations still leave unanswered the question of why adults prefer large bromeliads. If damselflies are optimizing their fitness by choosing large bromeliads, it is likely that damselfly larvae experience lower larval survival in small bromeliads. In this study, we investigate potential reasons for the sensitivity of *M. modesta* larvae to bromeliad size. We have already concluded that the regional abundance hypothesis cannot completely account for this sensitivity, based on previous analyses (Amundrud & Srivastava, 2015; Srivastava et al., 2008). We can also discount the trophic rank hypothesis, as both feeding trials and fecal dissections indicate that *M. modesta* is a generalist predator: It consumes every macroinvertebrate species co-occurring in bromeliads (D.S. and J.W., unpubl. data, see also Srivastava, 2006). We therefore examine in detail the remaining two hypotheses, specifically the energetic limitation hypothesis (insufficient prey availability in small bromeliads) and the risky habitat hypothesis (high risk of terrestrial predation, cannibalism, or desiccation in small bromeliads). Note that although cannibalism by itself could never lead to the absence of a species, it could lead to very low abundances and the likelihood of complete loss through stochastic processes.

In this paper, we use multiple years of survey data as well as three manipulative experiments to test the following predictions. If the energetic limitation hypothesis is important, we would expect that: (a) the amount of resources potentially available to each damselfly larva would diminish as we examined progressively smaller bromeliads until no damselflies were found, and (b) larvae transplanted into bromeliads smaller than 100 ml would fail to grow, and often die of starvation. The risky habitat hypothesis would be supported if small bromeliads had high risk of cannibalism, terrestrial predation, or desiccation. Large hunting spiders may be particularly important terrestrial predators of damselflies. If larval abundance is limited in small bromeliads by cannibalism, we would expect that (c) intraspecific encounter rates are greatest in small bromeliads. If terrestrial predators exclude damselfly larvae from small bromeliads, we would expect that (d) larvae transplanted into bromeliads with and without terrestrial predators would disappear predominately from small bromeliads with predators. Finally, if drought risk restricts damselfly larvae to large bromeliads, we would expect that (5) the likelihood of desiccation would be greatest in small bromeliads and damselfly larvae would be particularly sensitive to drought as compared to other species.

2 | METHODS

2.1 | Study site and system

We have studied, since 1997, the aquatic macroinvertebrates living in bromeliads in the premontane rain forest surrounding Estación Biológica Pitilla (Área de Conservación Guanacaste, 10°59'N, 85°26'W, 700 m a.s.l.). In this area, bromeliads that trap water between their leaves are either in the *Guzmania* genus (especially *G. scherzeriana* Mez, *G. donnellsmithii* Mez ex Donn.Sm., and *G. desautelsii* Read & L.B.Sm.) or the Vrieseeae tribe (esp *Werauhia gladioliflora* (H. Wendland) J.R. Grant, *W. sanguinolenta* (Linden ex Cogniaux & Marchal) J.R. Grant, *W. kupperiana* (Suessenguth) J.R. Grant). Water-filled bromeliads passively collect detritus through leaves and other organic matter that fall in their tanks. This detritus is an important basal energy source for the aquatic food web in the bromeliads, supplemented by algal production in open areas (Farjalla et al., 2016). The detritus is conditioned by bacteria and fungi and then consumed by a diverse suite of shredding, scraping and collecting detritivores. The microbes also fuel a community of protists (ciliates, flagellates, rotifers, amoeba), which in turn are prey to filter-feeding mosquito larvae. The detritivore and filter-feeding invertebrates are preyed upon by small-bodied predators (Ceratopogonidae, Tanypodinae, Hirudinae), and large-bodied piercing (Tabanidae) and engulfing predators (Dytiscidae, and the damselfly *Mecistogaster modesta* (Pseudostigmatidae)). Over the last 22 years, we have found > 70 species of aquatic invertebrates in bromeliads at Pitilla.

2.2 | Observational surveys: Damselflies and prey communities

We determined abundances of *M. modesta* larvae in bromeliads from the secondary forest between September and November in 1997, 2000, and 2002 (n = 20, 20 and 18 bromeliads, respectively). Prey communities in these bromeliads were also recorded in 1997 and 2002, but not 2000. Bromeliads were selected to represent a wide range of water capacity: 0.4–1530 ml in 1997, 35–4,690 ml in 2000, and 18–7,132 ml in 2002. In 1997 and 2000, both *W. sanguinolenta* and *Guzmania* spp bromeliads were included. In 2002, only *W. sanguinolenta* bromeliads were examined.

Bromeliad insect communities were censused as follows. Bromeliads were harvested from the forest and transported upright in buckets to the field station, where they were each inverted over a funnel (80 cm diameter) to collect the contained water. The water-holding capacity of the bromeliad was determined by pouring a known volume of water into all leaves of the empty bromeliad until it overflowed, and subtracting the overflow amount. Bromeliad capacity is arguably the most relevant measure of habitat size for aquatic insects and correlates better with species richness and abundance than other measures such as diameter, amount of detritus, number of leaves, or water volume on the sampling date (Srivastava et al., 2008). Each bromeliad was carefully dismantled over the funnel, leaf by leaf, and all leaf surfaces were washed into the funnel.

All collected debris and water were searched by eye for living larvae by mixing small amounts of debris with water in white trays. Individual larvae were counted and identified to species or morphospecies, and body length (excluding caudal lamellae for *M. modesta*) was measured and converted to fresh mass using empirically determined relationships (r^2 = 0.96, N = 46 for *M. modesta* and r^2 = 0.75–0.94 for prey taxa). This allowed us to estimate the total predator and prey biomass in each bromeliad. Although cannibalism occurs (based on fecal dissections and gut analyses), *M. modesta* larvae were not themselves included as prey items to avoid confounding the response and explanatory variables. Cannibalism cannot be directly measured in field surveys, but for sit-and-wait predators we might expect cannibalism to lead to a pattern of no more than one damselfly per leaf tank.

Large spiders (Trechaleidae: *Cupiennius coccineus* F.O. Pickard-Cambridge) occur in the terrestrial portion of bromeliad leaves. We visually searched for *C. coccineus* spiders in 48 bromeliads in the pastures and secondary forests surrounding the station from 29 to 31 October, 2005. We measured the maximum distance between leaf tips as an estimate of bromeliad size.

2.3 | Hydrology monitoring: Desiccation risk

To examine the effect of bromeliad size on desiccation risk, we measured water depth (± 1 mm) in three leaves (central and two peripheral) of 30 bromeliads every two days from October 2012 to October 2013. Bromeliads representing a range in capacity (12–33 ml; 6 bromeliads, 34–67 ml: 6 bromeliads, 68–100 ml: 10 bromeliads, 100 ml–580 ml: 8 bromeliads) were selected from the vicinity and transplanted to a homogeneous 1 ha of mature secondary forest. Each bromeliad was attached to the side of a vertical tree trunk using broad strips of plastic screen mesh. For each bromeliad, we calculated the sum of all drought days over the survey period, where drought was defined as all three leaf wells being completely dry (i.e., 0 mm water depth) simultaneously. We used linear regression to quantify the effect of bromeliad capacity (log-transformed) on desiccation risk (total drought days) and quantile–quantile and residual plots to check for model assumptions of linearity and homogeneous variance.

2.4 | Experiment 1: Effect of bromeliad size on damselfly survival and growth

In October 2002, we collected 29 *M. modesta* larvae (10–12 mm long, excluding caudal lamellae) and marked these insects by amputating the right middle leg, removing the last two segments (tarsus, tibia) just below the femur. Each larva was placed in a leaf axil (one larva per bromeliad), near the center of a bromeliad in the secondary forest (14 *Guzmania* spp., 15 *Werauhia* spp., 8–2,636 ml in volume). Twenty days later, we searched for marked larvae by dismantling each bromeliad leaf by leaf to search and measured bromeliad capacity. The amputated legs had only partially regrown, and the experimental damselflies could be easily recognized. To measure larval growth, we weighed larvae to the nearest 0.002 g before the experiment (but after amputation) and at the end of the experiment and calculated specific growth rate as the change in mass as a proportion of the initial mass. Recovery of larvae as a function of bromeliad capacity (log-transformed) was analyzed in a logistic generalized linear model with a logit link and binomial errors. This model was a good approximation of the data as the dispersion coefficient was approximately one.

2.5 | Experiment 2: Effect of bromeliad size on spider predation

The spider *C. coccineus* frequently lives in the terrestrial portion of bromeliads and may be an important terrestrial predator of *M. modesta* larvae. We had previously observed *C. coccineus* spiders diving underwater to capture *M. modesta* larvae in water-filled plastic cups. Twenty *Werauhia* bromeliads ranging from 68 to 700 ml in maximum capacity were collected in the vicinity of Pitilla and divided into two groups (control, experimental) with similar size ranges. Bromeliads were hung in a common garden and enclosed with netting to prevent spider and insect dispersal. Any resident spiders were removed prior to the experiment.

Twenty damselfly larvae ranging from 0.034 to 0.110 g were collected from the vicinity of the field station during surveys of bromeliad insect communities. We marked damselflies by amputating the last two segments of one leg (tarsus and tibia) as before. Each damselfly was added to a bromeliad and left to acclimate for a day before one spider was added each of the ten experimental bromeliads.

Ten *C. coccineus* spiders were collected from bromeliads near the field station, and one spider was added to each of the experimental bromeliads. After 24 hr, all bromeliads were dismantled leaf by leaf to collect the experimental spiders and damselflies, and damselfly survivorship was recorded. Survivorship was analyzed in a logistic generalized linear model with a logit link and binomial errors, and with spider presence, bromeliad capacity (log-transformed) and their interaction as explanatory factors. The dispersion coefficient was approximately one, indicating that the model error structure was a good approximation of the data.

2.6 | Experiment 3: Effect of drought on damselfly survival and growth rate

To examine the effects of drought on damselfly survival and growth, we manipulated drought length (defined as 0 mm water depth) in artificial microcosms, imposing droughts of 10, 15, 20, 25, and 30 days in length. We also had an equal number of controls, which were treated identically, except that they were not subjected to drought. Each microcosm housed a single damselfly larva. Each drought length treatment or matching control was represented by two microcosms, except for the 30-day drought treatment with six microcosms. Damselflies were fed small larvae of chironomids, tipulids, or mosquitos every two days to ensure starvation did not contribute to mortality.

The microcosms were constructed to approximate the size of a single *Werauhia* bromeliad well, but to allow water levels to be manipulated without handling or disturbing the damselflies (Amundrud & Srivastava, 2015). Each microcosm consisted of a 50-ml centrifuge tube sitting in a 207-ml plastic cup. To allow water, but not damselflies, to move between the tube and cup, we first cut off horizontally the tapered bottoms of the tubes and covered the now open bottom end of the tube with Nitex screen (80 µm mesh size). To increase the flow of water even further, we also drilled three holes into the side (d = 7 mm), covering these holes with the same type of Nitex screen. In natural bromeliads, overlapping bromeliad leaves form crevices that may act as refugia from drought, similar to the crevices in tree holes (Srivastava, 2005). We created artificial crevices by aligning two pieces (2 cm × 6 cm) of green polyethylene, gluing these together along one edge and bending back one the unglued edge. We placed one artificial crevice in each microcosm.

On 6 November 2012, we filled 28 microcosm cups with filtered stream water to a volume of 15 ml inside the tubes (an approximate water depth of 2.1 cm), a typical volume per bromeliad leaf well (Amundrud & Srivastava, 2016). We added one damselfly to each microcosm and placed microcosms on an outdoor veranda with ambient conditions similar to those of the adjacent rain forest.

On 8 November 2012, we removed all water from half of the microcosms by emptying the cups to initiate drought. After completion of each drought length treatment, we added water to the cups to return to a volume of 15 ml inside the tube. In the controls (which were never subjected to drought), 50% of water was replaced every two days to prevent hypoxia. Two days after the completion of the drought, we emptied the mesocosms of that drought treatment, as well as their corresponding controls and checked for damselfly survival. We employed a logistic generalized linear model with quasibinomial errors (due to overdispersion) to determine the drought length at which damselfly mortality equaled 50%.

3 | RESULTS

3.1 | Damselfly abundances and bromeliad size (Observational surveys, Experiment 1)

In all three years of surveys, *M. modesta* abundances were strongly correlated with bromeliad capacity (Figure 1a, Poisson GLMM with year as random effect: z = 15.4, *n* = 58, *p* < .0001): Small bromeliads rarely contained *M. modesta* larvae whereas the largest bromeliads contained up to 36 larvae. This resulted in a steep incidence function (binomial GLMM: $z = 3.12$, $n = 58$, $p = .0018$) centered on 194 ml (50% likelihood of occurrence) in which damselflies switched from only a 10% likelihood of occurrence at 100 ml to a 90% likelihood of occurrence at 365 ml (Figure 1c). The two bromeliad genera occupy different size ranges, with *Guzmania* spp. at most holding 400 ml of water, and *Werauhia* spp. holding up to 6 L of water. As genus was collinear with bromeliad size, we did not attempt to separate their effects.

In order to determine whether the observed incidence function is due to larvae experiencing different conditions in small and large bromeliads, we transplanted damselflies into bromeliads of differing size. Approximately a third (10/28) of the marked *M. modesta* larvae transplanted into bromeliads were still present when the bromeliads were dismantled 20 days later (Figure 2a). Recovery of damselflies increased with bromeliad capacity ($\chi^2 = 11.8$, $df = 1$, $p = .001$), with 50% likelihood of recovery predicted from bromeliads of 118 ml (10% likelihood at 23 ml, 90% likelihood at 623 ml). We generally did not recover cadavers of the marked damselflies, suggesting that larvae were either consumed or voluntarily left the bromeliad.

3.2 | Energetic limitation (Observational surveys, Experiment 1)

Bromeliads exhibited large variation in the availability of prey per *M. modesta* larva in both 1997 and 2002, ranging from 0.02 g prey/larvae to 0.35 g prey/larvae (Figure 1b; analysis restricted to bromeliads with damselflies). Although per capita prey availability tended to be highest in small bromeliads, there was no significant association between per capita prey availability and bromeliad capacity (LMM with year as random effect: $F_{1,18} = 3.51$, $p = .077$). This contradicts Prediction 1 of the energetic hypothesis, which anticipated that predators would depress prey biomass most in small bromeliads.

If damselflies starved to death in small bromeliads (i.e., negative growth rates indicating mass loss), we would expect to find that surviving damselflies would have near-zero growth rates in just slightly larger bromeliads and positive growth rates in much larger bromeliads (Prediction 2). However, in the transplant experiment (Experiment 1), the specific growth rate of the ten surviving larvae was uncorrelated with bromeliad size. (Figure 2b, $r = -.03$, $p = .92$, $n = 10$).

3.3 | Cannibalism (observational surveys)

We typically found a maximum of one damselfly larva per leaf compartment, suggesting that either cannibalism had reduced abundances within leaf compartments to one survivor, or that larva dispersed between compartments to reduce intraspecific encounters or resource competition. Given this distribution of larvae, cannibalism rates will depend in part on the occupation

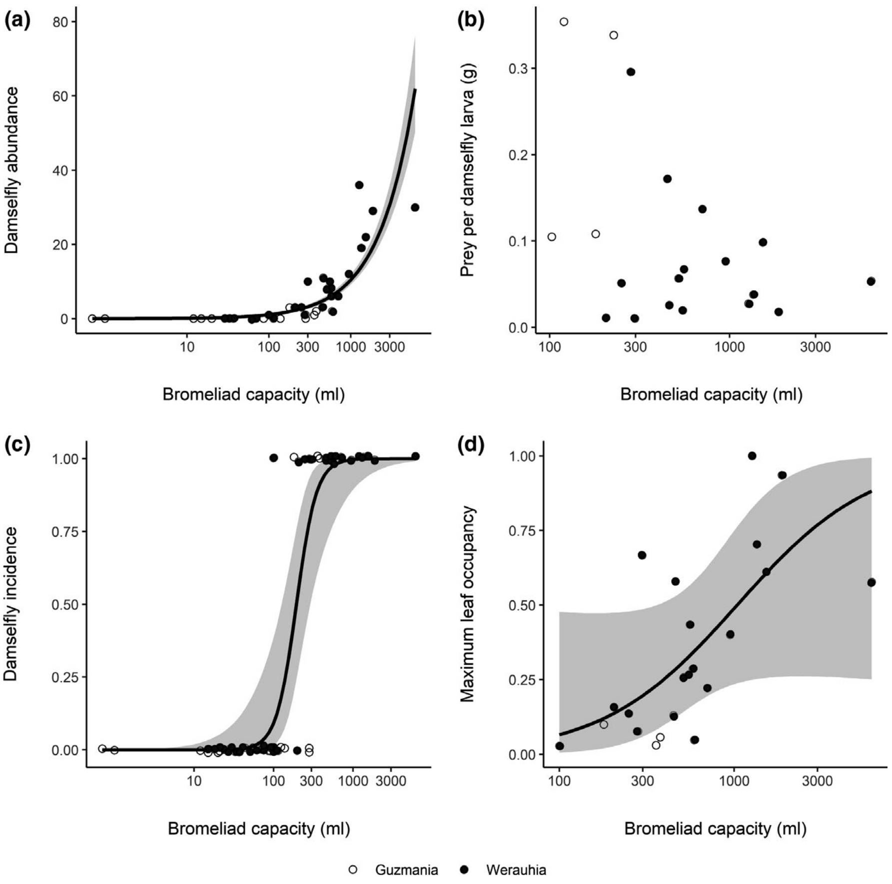


FIGURE 1 *Mecistogaster modesta* larvae were quantified in bromeliads of differing capacity (log scale in this and all figures). The (a) abundance and (c) incidence of larvae increased rapidly with bromeliad capacity. The (d) maximum occupancy of leaf compartments also increased with bromeliad capacity, assuming one damselfly per leaf. However, (b) prey availability per damselfly was unrelated to bromeliad capacity. Bromeliads were surveyed over three years at Estación Biológica Pitilla, in the Área de Conservación Guanacaste, and represented two genera, *Guzmania* and *Werauhia*. Fitted models (solid lines, with the 95% confidence band indicated by shading) are shown only when significant

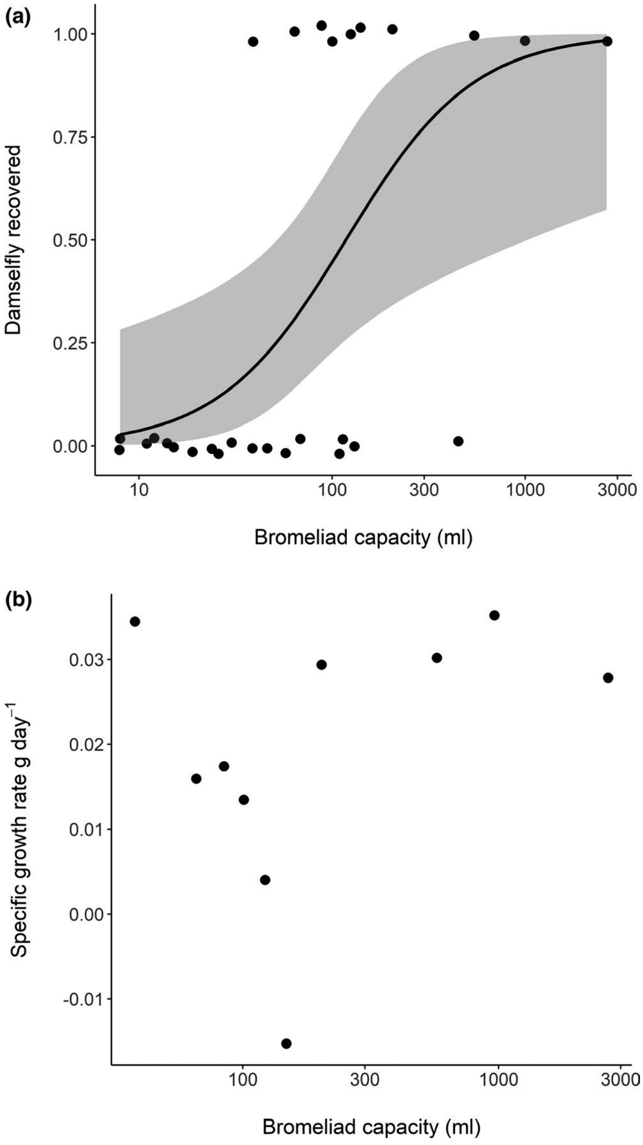


FIGURE 2 *Mecistogaster modesta* larvae that were transplanted into bromeliads of varying sizes were (a) recovered preferentially in bromeliads of > 118 ml capacity, but (b) the growth of the recovered larvae was unrelated to bromeliad capacity. Fitted models (solid lines, with the 95% confidence band indicated by shading) are shown only when significant

of leaf compartments by damselflies, as dispersing larvae will be most likely to encounter a conspecific when all leaf compartments are occupied. We calculated the proportional occupancy of compartments based on a maximum of one larva per compartment, restricting our analysis only to bromeliads with damselflies (as bromeliads without damselflies necessarily have zero occupancy). Smaller bromeliads had lower proportional occupancy of leaf compartments than larger bromeliads, where occupancy approached 100% (Figure 1d, binomial GLMM with year as a random effect: z = 2.20, *n* = 25, *p* = .027). If cannibalism limited damselflies in small bromeliads, the opposite pattern (Prediction 3) would have been expected.

3.4 | Terrestrial predation (Experiment 2, Observational survey)

In a second experiment, we transplanted *M. modesta* into bromeliads with and without the bromeliad-associated spider, *Cupiennius coccineus*. Damselfly larvae survived in only 30% of bromeliads with spiders. By contrast, damselflies survived in 80% of bromeliads without spiders—a significant difference in damselfly survival (spider effect: χ^2 = 5.30, *df* = 1, *p* = .02; Figure 3a). However, spider consumption of damselflies did not depend on bromeliad capacity (spider x log-capacity: χ^2 = 0.18, *df* = 1, *p* = .67, Figure 3b), contrary to Prediction 4 (risky habitat hypothesis: terrestrial predation), nor was there an overall effect of bromeliad capacity on damselfly survival (log-capacity: χ^2 = 0.0001, *df* = 1, *p* = .99). Even in the absence of an effect of bromeliad size on per capita rates of spider predation, *C. coccineus* spiders could still limit *M. modesta* to large bromeliads if these spiders primarily occurred in small bromeliads. Our survey shows this not to be the case, if anything, spiders are slightly more frequent in large bromeliads (*r* = 0.4, *p* = .005, *n* = 48).

3.5 | Desiccation risk (Hydrology monitoring, Experiment 3)

Desiccation risk, measured over an entire year, was greatest in small bromeliads (Figure 4). As bromeliad capacity increases, the risk of whole-plant desiccation (i.e., the number of days when all three leaf wells simultaneously had a water depth of 0 mm) decreased exponentially (R^2 = .42, $F_{1,28}$ = 20.477, *p* < .001). We also examined, for each bromeliad, the longest number of consecutive days the plant was without water. On average, bromeliads were dry for 20.4 ± 6.83 (mean ± SE) consecutive days at least once during the year.

In microcosms, drought significantly decreased damselfly survival and tended to decrease damselfly growth rate. All damselflies subjected to control treatments survived the experiment, but no damselfly survived past the 15-day drought treatment (Figure 5). Logistic regression predicted 50% damselfly mortality at a drought length of 17.51 days (± 0.03 SE, χ^2 = 16.75, *p* < .001).

4 | DISCUSSION

This study documents a non-linear increase in damselfly larval abundance with bromeliad size, crossing an apparent threshold for damselfly presence at approximately 100 ml capacity, with abundances approaching 40 larvae per bromeliad once bromeliads contain several liters of water. There are two potential explanations for the threshold for damselfly presence: (1) There are insufficient resources in small bromeliads to support even a single damselfly larva; or (2) small bromeliads are risky habitats for damselfly larva, either in terms of cannibalism, terrestrial predation, or desiccation (other explanations were discounted in the Introduction). We now examine the evidence for each of these two types of explanation.

Three lines of evidence suggest that damselflies are not limited to large bromeliads because of insufficient resources. First, the amount of prey biomass available per damselfly decreases as bromeliads increase in size, suggesting that resource competition among damselflies intensifies as bromeliads become larger. If resources limited damselfly occurrence in small bromeliads, we would expect the opposite pattern: for resource availability to increase with bromeliad size (Prediction 1). Second, larval growth rate did not differ with bromeliad size, contrary to Prediction 2. This contrasts with tree hole-dwelling odonates where larger adults emerge from larger tree holes (Fincke, 1992). However, in that case, tadpoles (restricted to the larger tree holes) probably provided substantial amounts of prey biomass to the odonates (Fincke, 1992). There were no tadpoles in the bromeliads in this study (e.g., the mid-elevation study site is outside of the range of *Oophaga* spp.), and no similar large-bodied prey item occurs exclusively in large bromeliads.

A second suite of explanations for damselfly incidence patterns involves risk associated with small habitats, whether risk of cannibalism, terrestrial predation, or desiccation. As bromeliad size increases, damselfly larvae occupy an increasing proportion of leaf compartments. If cannibalism was reducing damselfly abundances in small bromeliads, we would expect instead (Prediction 3) greatest leaf occupancy in the smallest bromeliads. Instead, cannibalism is more likely to limit abundances in large bromeliads (> 1 liter of water) where leaf occupancy approaches 80%–100%.

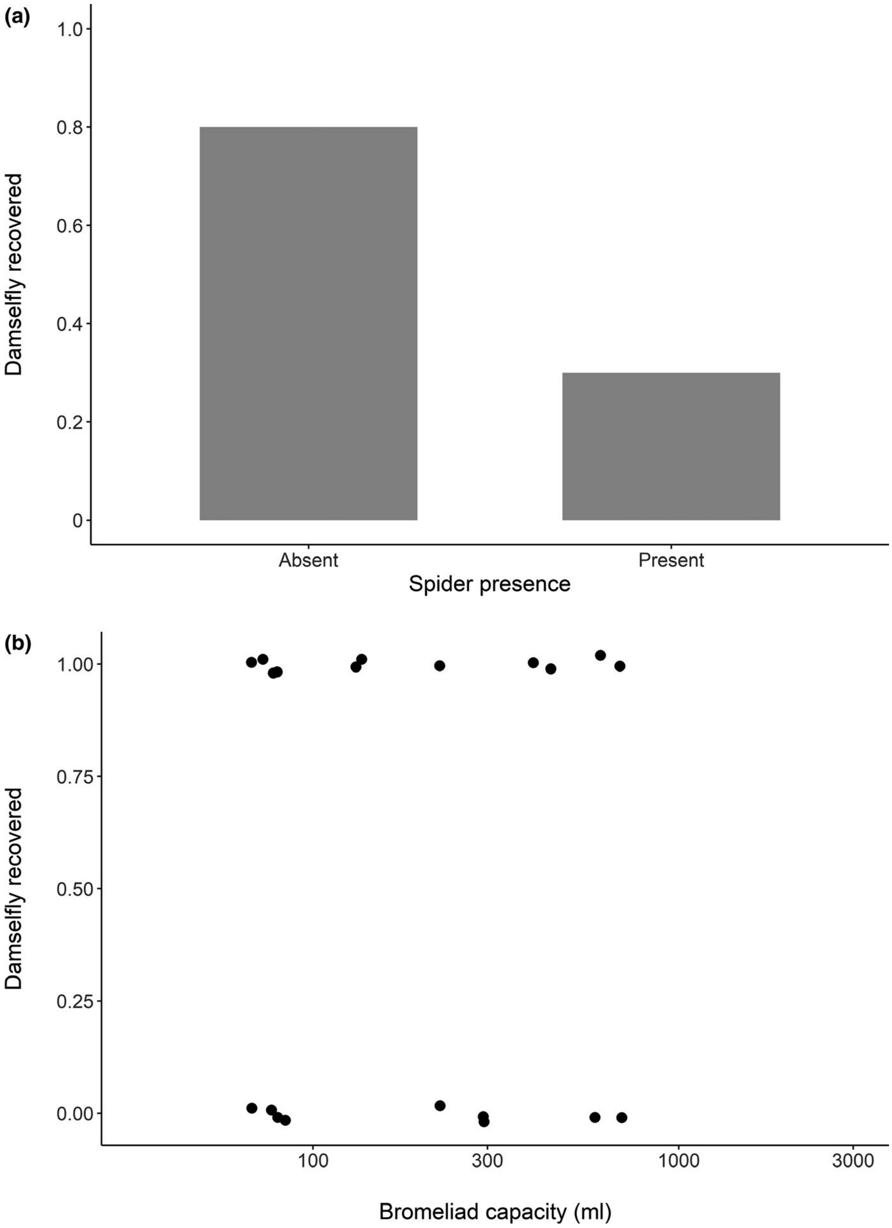
Small bromeliads could have a high risk of predation for damselfly larvae. Although there are other aquatic predators in Costa Rican bromeliads (e.g., tabanid larvae, ceratopogonid larvae), we have not found any aquatic predator able to kill a damselfly larvae in feeding trials; conversely, damselfly larvae are able to kill virtually every other species in the bromeliad as long as the damselfly is larger (D.S.S., unpubl. obs.). However, terrestrial spiders are able to prey upon damselfly larvae, as we demonstrate in Experiment 2, where 70% of damselflies disappeared in the presence of spiders. Similarly, in Brazil, the hunting spider *Corrina* gr. *rubripes* has been observed preying on damselfly larvae within bromeliads (pers. comm. GQ Romero, GC Piccoli, PM de Omena). Since spiders often capture damselfly larvae by entering the water impounded in “tanks” formed by bromeliad leaves, it is possible that small bromeliads have higher predation risk because they have shallower water in their tanks. However, this hypothesis (prediction 4) is not supported by Experiment 2, where loss of damselflies in the presence of *C. coccineus* spiders is unrelated to bromeliad size; nor do these spiders occur more often in small bromeliads. Although we only examined predation by one spider species, *Cupiennius coccineus*, it is the most common large spider associated with bromeliads at the study site. *C. coccineus* naturally occurs in large *Werauhia* spp. bromeliads and dives underwater when under threat, so this species may readily prey on damselfly larvae regardless of bromeliad size.

The final hypothesis is that small bromeliads present a high desiccation risk for larvae because their leaves contain a lower volume and depth of water (Zotz & Thomas, 1999). At the study site, there is typically a long dry season (<20 cm precipitation/month) from February to April and a shorter dry spell in September, as well as periods without rain throughout the wet season (meteorological data courtesy of Área de Conservación Guanacaste). An analysis of collection records for adult *M. modesta* suggests that, in this part of Costa Rica, their larvae may spend at least 9 months developing in the bromeliad before metamorphosis (Figure 5 in Hedstrom & Sahlen, 2001). Tree hole-dwelling odonates in the same family, Pseudostigmatidae, are estimated to require at least 5.5 to 7 months or more in the larval stage (Fincke, 1992; Fincke, Yanoviak, & Hanschu, 1997). This contrasts with the larval period of damselfly prey, typically on the order of weeks (Srivastava, 2006; Starzomski, Suen, & Srivastava, 2010). Damselflies are therefore at higher risk than other macroinvertebrates of experiencing a dry or near-dry bromeliad during their larval stage, and this difference in cumulative risk between damselflies and their prey is particularly acute in smaller bromeliads (Figure 3 in Guzman et al., 2019).

Drought could lead to damselfly mortality by exceeding physiological limits to desiccation. Our data show *M. modesta* is unable to survive with more than 17 consecutive days of drought, a threshold that was exceeded by 60% of bromeliads in our yearlong monitoring. *M. modesta* larvae may anticipate the risk of drought and leave their natal bromeliad in search of a better bromeliad; in other experiments, we have occasionally recorded larvae dispersing from the bromeliads in which they have been placed (Atwood, Hammill, Srivastava, & Richardson, 2014). However, dispersal must be a fairly risky behavior, as the nearest large bromeliad may be far away with many terrestrial predators along the route. All of the above factors are probably responsible for the loss of damselfly larvae from small bromeliads in Experiment 1.

The importance of drought in determining a bromeliad size threshold for *M. modesta* is consistent with other observations. In a study of ten species of bromeliad insects, we found that the species' physiological sensitivity to drought was a strong predictor of its preference for large bromeliads (Amundrud & Srivastava, 2015). In water-filled tree holes, which contain similar macroinvertebrate communities to bromeliads, drought has also often been reported as the main driver of community composition (Bradshaw & Holzapfel, 1988; Paradise, 2004; Srivastava, 2005). In Panama, larger tree holes contain water for a month longer than small tree holes and produce more and larger odonate larvae (Fincke, 1992). The dominant odonate species in these tree holes, *Megaloprepus coerulatus*, preferentially chooses large tree holes to oviposit (females) and defend (males), reminiscent of adult *Mecistogaster modesta* preferences for large bromeliads. Similarly, in vernal ponds, large dragonflies and fish are often at low abundance or absent in ponds that dry out periodically because of the duration of their aquatic stage or lifespan exceeds the permanence of the habitat (Schneider & Frost, 1996; Stoks & McPeek, 2003). Temporary lentic habitats, in general, are associated with macroorganisms with rapid development, such that a terrestrial or resistant stage is reached before the end of the hydroperiod. Only when these hydroperiods become so long as to be essentially permanent do such lentic habitats have large engulfing predators like odonates (Wellborn, Skelly, & Werner, 1996). The patterns we see along the bromeliad size gradient echo those seen along a lentic hydroperiod gradient, as the size of a bromeliad determines its hydroperiod.

FIGURE 3 Recovery of *M. modesta* larvae transplanted into bromeliads with and without *C. coccineus* spiders was (a) almost three times greater in the absence of spiders, but (b) unrelated to bromeliad capacity



More broadly, we expect disturbance to explain greater predator (than prey) sensitivity to habitat size under the following two conditions: (a) Disturbance is more frequent in small than large patches; and (b) predators require longer disturbance-free intervals for individual or population growth. These conditions may be met in a number of other systems, such as islands susceptible to storm surges and lakes susceptible to anoxia. For example, storm surges following hurricanes can submerge small islands in the Bahamas, causing extinction of all lizards and spiders. The longer generation time and lower dispersal ability of lizards relative to spiders (spiders are both prey and competitors of lizards: Schoener, 1989) results in slower recolonization of islands by lizards (Spiller, Schoener, & Piovia-Scott, 2018). Consequently, lizards only occur on large islands, whereas spiders can also occur on small islands (Schoener, 1989; Spiller et al., 2018). As in our transplant experiment with *M. modesta*, lizards transplanted to small islands may voluntarily abandon these islands (Schoener & Schoener, 1983). Temperate and boreal lakes may also satisfy the dual conditions of small habitats being disturbance-prone and predators being disturbance-sensitive. Shallow lakes are more prone to low oxygen levels in the winter, after the lake freezes over, and as the top predators (Northern pike, largemouth bass) are more sensitive to these conditions than their prey, these predators are restricted to the deepest lakes (Tonn & Magnuson, 1982). While the above systems are particularly well-documented examples of how disturbance restricts predators to the largest habitats, we would expect a wide range of systems to also show similar patterns. Disturbances are often more frequent or intense in small habitats due to their larger edge effects, lower thermal buffering, and fewer physical refuges. Predators may be particularly susceptible to disturbances when their longer life-cycle or larger body size prevents them from accessing refuges or dispersing.

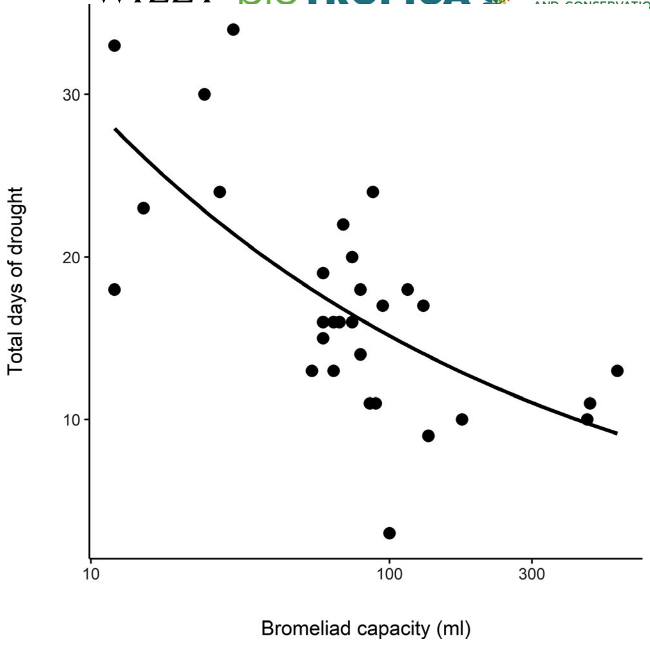


FIGURE 4 Bromeliad desiccation risk decreases with bromeliad size. Total days of drought (defined as the three tracked leaf wells being dry simultaneously) experienced by 30 bromeliads from October 2012 to October 2013 decreased rapidly with bromeliad capacity

4.1 | Implications

Mecistogaster modesta occurs primarily in tropical moist or tropical wet forest at low to mid-elevations, from Mexico to northern Venezuela (Amundrud, Videla, & Srivastava, 2018). In such forests, the largest bromeliads are found at low elevations, in well-lit environments provided by forest gaps, stream edges, and the canopy. Our results indicate that any change in either the size distribution or hydrology of bromeliads will directly impact *M. modesta* populations. Unfortunately, climate change models predict that Central America will lead the world in terms of reduced and more variable precipitation (Giorgi, 2006; Rauscher, Giorgi, Diffenbaugh, & Seth, 2008), with premontane areas of Costa Rica estimated to lose up to 40% of their annual precipitation (Karmalkar, Bradley, & Diaz, 2008). In Guanacaste, variation in precipitation has more than doubled since the year 2000, as compared to the preceding half-century, including the most severe drought on record in 2015 (Cooley et al., 2019). During the 2015 drought, the most affected area of Guanacaste was the northeast (Cooley et al., 2019), coinciding with the distribution of *M. modesta* in this province (Amundrud et al., 2018; Hedstrom & Sahlen, 2001). The global distribution of *M. modesta* is limited by low annual precipitation and high annual mean temperature (Amundrud et al., 2018), suggesting that increased drought in Guanacaste will result in a contraction of its range toward the wetter areas of the province and expansion up mountain slopes.

Any reduction in the incidence of *M. modesta* is likely to have important repercussions for the function and structure of bromeliad food webs. *M. modesta* is the only bromeliad-dwelling damselfly in its range (Mexico to northern Venezuela), and in NW Costa Rica represents up to 85% of predator biomass when it occurs. Larvae of *M. modesta* are voracious predators on detritivore larvae (Srivastava, 2006) and influence detritivore emergence more than interactions among detritivores themselves (Starzomski et al., 2010). As a result, *M. modesta* has strong top-down effects on decomposition (Srivastava, 2006), microbial communities (Srivastava & Bell, 2009), and consequently CO_2 emissions (Atwood et al., 2013). Predation of larval detritivores by *M. modesta* prevents emerging adults from exporting nutrients and thus can increase nitrogen uptake by bromeliads by an order of magnitude (Ngai & Srivastava, 2006). The sensitivity of damselflies to drought thus has the potential to transmit the effects of drought throughout the bromeliad food web (Amundrud & Srivastava, 2016). By uncovering the mechanisms behind the preference of *M. modesta* for large bromeliads, we have opened a window on understanding the sensitivity of an important freshwater ecosystem to climate change.

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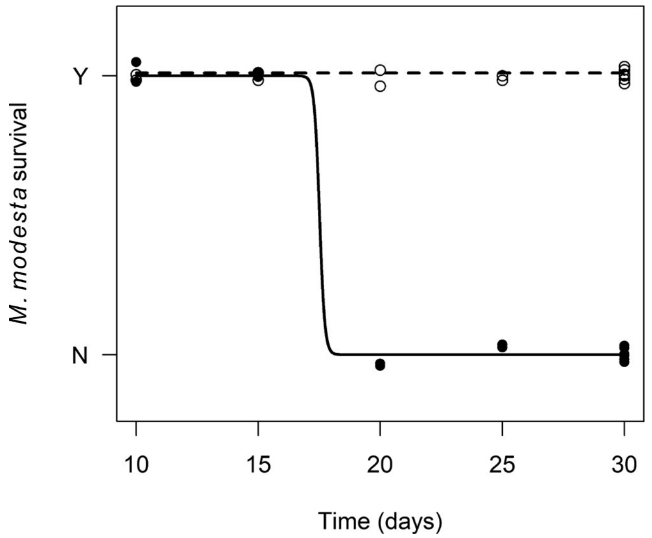

FIGURE 5 Damselfly survival decreases with drought length. Solid dots/solid line represent drought treatment, and empty dots/dashed line represent control. The continuous-water control had 100% damselfly survival, whereas 0% of damselflies survived more than 15 consecutive days of drought

Association (Worldwide Dragonfly Fund 1997), and the University of British Columbia (Martha Piper Fund 2011).

DATA AVAILABILITY STATEMENT

Data available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.4j0zpc874 (Srivastava, Ware, Ngai, Starzomski, & Amundrud, 2019).

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REFERENCES

Amundrud, S. L., & Srivastava, D. S. (2015). Drought sensitivity predicts habitat size sensitivity in an aquatic ecosystem. *Ecology*, *96*, 1957–1965.

Amundrud, S. L., & Srivastava, D. S. (2016). Trophic interactions determine the effects of drought on an aquatic ecosystem. *Ecology*, *97*, 1475–1483.

Amundrud, S. L., Videla, M., & Srivastava, D. S. (2018). Dispersal barriers and climate determine the geographic distribution of the helicopter damselfly *Mecistogaster modesta*. *Freshwater Biology*, *63*, 214–223.

Atwood, T. B., Hammill, E., Greig, H. S., Kratina, P., Shurin, J. B., Srivastava, D. S., & Richardson, J. S. (2013). Predator-induced reduction of freshwater carbon dioxide emissions. *Nature Geoscience*, *6*, 191–194.

Atwood, T. B., Hammill, E., Srivastava, D. S., & Richardson, J. S. (2014). Competitive displacement alters top-down effects on carbon dioxide concentrations in a freshwater ecosystem. *Oecologia*, *175*, 353–361.

Bascompte, J., & Sole, R. V. (1998). Effects of habitat destruction in a prey-predator metapopulation model. *Journal of Theoretical Biology*, *195*, 383–393.

Bradshaw, W. E., & Holzapfel, C. M. (1988). Drought and the organization of tree-hole mosquito communities. *Oecologia*, *74*, 507–514.

Brashares, J. S., Arcese, P., & Sam, M. K. (2001). Human demography and reserve size predict wildlife extinction in West Africa. *Proceedings of the Royal Society B-Biological Sciences*, *268*, 2473–2478.

Cagnolo, L., Valladares, G., Salvo, A., Cabido, M., & Zak, M. (2009). Habitat fragmentation and species loss across three interacting trophic levels: effects of life-history and food-web traits. *Conservation Biology*, *23*, 1167–1175.

Chui, T. F. M., & Terry, J. P. (2013). Influence of sea-level rise on freshwater lenses of different atoll island sizes and lens resilience to storm-induced salinization. *Journal of Hydrology*, *502*, 18–26.

Cooley, S. S., Williams, C. A., Fisher, J. B., Halverson, G. H., Perret, J., & Lee, C. M. (2019). Assessing regional drought impacts on vegetation and evapotranspiration: A case study in Guanacaste. *Ecological Applications*, *29*, e01834. https://doi.org/10.1002/eap.1834

Davies, K. F., Margules, C. R., & Lawrence, K. F. (2000). Which traits of species predict population declines in experimental forest fragments? *Ecology*, *81*, 1450–1461.

Didham, R. K., Lawton, J. H., Hammond, P. M., & Eggleton, P. (1998). Trophic structure stability and extinction dynamics of beetles (Coleoptera) in tropical forest fragments. *Philosophical Transactions of the Royal Society of London Series B, Biological Sciences*, *353*, 437–451.

Farjalla, V. F., Gonzalez, A. L., Cereghino, R., Dezerald, O., Marino, N. A. C., Piccoli, G. C. O., … Srivastava, D. S. (2016). Terrestrial support of aquatic food webs depends on light inputs: A geographically-replicated test using tank bromeliads. *Ecology*, *97*, 2147–2156.

Fincke, O. M. (1992). Consequences of larval ecology for territoriality and reproductive success of a Neotropical damselfly. *Ecology*, *73*, 449–462.

Fincke, O. M., Yanoviak, S. P., & Hanschu, R. D. (1997). Predation by odonates depresses mosquito abundance in water-filled tree holes in Panama. *Oecologia*, *112*, 244–253.

Giorgi, F. (2006). Climate change hot-spots. *Geophysical Research Letters*, *33*, L08707. https://doi.org/10.1029/2006GL025734

Gravel, D., Massol, F., Canard, E., Mouillot, D., & Mouquet, N. (2011). Trophic theory of island biogeography. *Ecology Letters*, *14*, 1010–1016.

Guzman, L. M., Germain, R. M., Forbes, C., Straus, S., O'Connor, M. I., Gravel, D., … Thompson, P. L. (2019). Towards a multi-trophic extension of metacommunity ecology. *Ecology Letters*, *22*, 19–33.

Hairston, N. G., & Hairston, N. G. (1993). Cause-effect relationships in energy-flow, trophic structure, and interspecific interactions. *American Naturalist*, *142*, 379–411.

Hedstrom, I., & Sahlen, G. (2001). A key to the adult Costa Rican helicopter{''} damselflies (Odonata : Pseudostigmatidae) with notes on their phenology and life zone preferences . *Revista De Biologia Tropical*, *49*, 1037–1056.

Holt, R. D. (2009). Toward a trophic island biogeography. In J. B. Losos & R. E. Ricklefs (Eds.), *The theory of island biogeography revisited* (pp. 143–185). Princeton, NJ: Princeton University Press.

Holt, R. D., & Hoopes, M. F. (2005). Food web dynamics in a metacommunity context. In M. Holyoak, M. A. Leibold & R. D. Holt (Eds.), *Metacommunities: Spatial dynamics and ecological communities* (pp. 68–94). Chicago, IL: University of Chicago Press.

Holt, R. D., Lawton, J. H., Polis, G. A., & Martinez, N. D. (1999). Trophic rank and the species-area relationship. *Ecology*, *80*, 1495–1504.

Hoyle, M. (2004). Causes of the species-area relationship by trophic level in a field-based microecosystem. *Proceedings of the Royal Society B-Biological Sciences*, *271*, 1159–1164.

Hurlbert, A. H., & Stegen, J. C. (2014). When should species richness be energy limited, and how would we know? *Ecology Letters*, *17*, 401–413.

Hutchinson, G. E. (1959). Homage to Santa-Rosalia or why are there so many kinds of animals. *American Naturalist*, *93*, 145–159.

Karmalkar, A. V., Bradley, R. S., & Diaz, H. F. (2008). Climate change scenario for Costa Rican montane forests. *Geophysical Research Letters*, *35*, L11702.

Lindeman, R. L. (1942). The trophic-dynamic aspect of ecology. *Ecology*, *23*, 399–418.

Martinson, H. M., & Fagan, W. F. (2014). Trophic disruption: A meta-analysis of how habitat fragmentation affects resource consumption in terrestrial arthropod systems. *Ecology Letters*, *17*, 1178–1189.

McHugh, P. A., Thompson, R. M., Greig, H. S., Warburton, H. J., & McIntosh, A. R. (2014). Habitat size influences food web structure in drying streams. *Ecography (Cop.)*, *37*, 1-13. http://doi.wiley.com/10.1111/ecog.01193

Menge, B. A., & Farrell, T. M. (1989). Community structure and interaction webs in shallow marine hard-bottom communities - tests of an environmental-stress model. *Advances in Ecological Research*, *19*, 189–262.

Nash, K. L., Graham, N. A. J., Wilson, S. K., & Bellwood, D. R. (2013). Cross-scale habitat structure drives fish body size distributions on coral reefs. *Ecosystems*, *16*, 478–490.

Newbold, T., Scharlemann, J. P. W., Butchart, S. H. M., Sekercioglu, C. H., Alkemade, R., Booth, H., & Purves, D. W. (2013). Ecological traits affect the response of tropical forest bird species to land-use intensity. *Proceedings of the Royal Society. B, Biological Sciences*, *280*, 20122131.

Ngai, J. T., & Srivastava, D. S. (2006). Predators accelerate nutrient cycling in a bromeliad ecosystem. *Science (80-.)*, *314*, 963–963. https://doi.org/10.1126/science.1132598

Ostman, O., Griffin, N. W., Strasburg, J. L., Brisson, J. A., Templeton, A. R., Knight, T. M., & Chase, J. M. (2007). Habitat area affects arthropod communities directly and indirectly through top predators. *Ecography (Cop.)*, *30*, 359–366.

Paradise, C. J. (2004). Relationship of water and leaf litter variability to insects inhabiting treeholes. *Journal of the North American Benthological Society*, *23*, 793–805.

Petes, L. E., Mouchka, M. E., Milston-Clements, R. H., Momoda, T. S., & Menge, B. A. (2008). Effects of environmental stress on intertidal mussels and their sea star predators. *Oecologia*, *156*, 671–680.

Post, D. M., Pace, M. L., & Hairston, N. G. (2000). Ecosystem size determines food-chain length in lakes. *Nature*, *405*, 1047–1049.

Prugh, L. R., Hodges, K. E., Sinclair, A. R. E., & Brashares, J. S. (2008). Effect of habitat area and isolation on fragmented animal populations. *Proceedings of the National Academy of Sciences USA*, *105*, 20770–20775.

Rauscher, S. A., Giorgi, F., Diffenbaugh, N. S., & Seth, A. (2008). Extension and Intensification of the Meso-American mid-summer drought in the twenty-first century. *Climate Dynamics*, *31*, 551–571.

Richardson, B. A. (1999). The bromeliad microcosm and the assessment of faunal diversity in a neotropical forest. *Biotropica*, *31*, 321–336.

Roslin, T., Varkonyi, G., Koponen, M., Vikberg, V., & Nieminen, M. (2014). Species-area relationships across four trophic levels - decreasing island size truncates food chains. *Ecography (Cop.)*, *37*, 443–453.

Salguero-Gomez, R., Jones, O. R., Jongejans, E., Blomberg, S. P., Hodgson, D. J., Mbeau-Ache, C., … Buckley, Y. M. (2016). Fast-slow continuum and reproductive strategies structure plant life-history variation worldwide. *Proceedings of the National Academy of Sciences*, *113*, 230–235.

Schneider, D. W., & Frost, T. M. (1996). Habitat duration and community structure in temporary ponds. *Journal of the North American Benthological Society*, *15*, 64–86.

Schoener, T. W. (1989). Food webs from the small to the large. *Ecology*, *70*, 1559–1589.

Schoener, T. W., & Schoener, A. (1983). The time to extinction of a colonizing propagule of lizards increases with island area. *Nature*, *302*, 332–334.

Spencer, M., & Warren, P. H. (1996). The effects of habitat size and productivity on food web structure in small aquatic microcosms. *Oikos*, *75*, 419–430.

Spiller, D. A., Schoener, T. W., & Piovia-Scott, J. (2018). Recovery of food webs following natural physical disturbances. *Annals of the New York Academy of Sciences*, *1429*, 100–117.

Srivastava, D. S. (2005). Do local processes scale to global patterns? The role of drought and the species pool in determining treehole insect diversity. *Oecologia*, *145*, 205–215.

Srivastava, D. S. (2006). Habitat structure, trophic structure and ecosystem function: Interactive effects in a bromeliad-insect community. *Oecologia*, *149*, 493–504.

Srivastava, D. S., & Bell, T. (2009). Reducing horizontal and vertical diversity in a foodweb triggers extinctions and impacts functions. *Ecology Letters*, *12*, 1016–1028.

Srivastava, D. S., Trzcinski, M. K., Richardson, B. A., & Gilbert, B. (2008). Why are predators more sensitive to habitat size than their prey? Insights from bromeliad insect food webs. *American Naturalist*, *172*, 761–771.

Srivastava, D. S., Ware, J. L., Ngai, J. T., Starzomski, B. M., & Amundrud, S. L. (2019). Data from: Habitat size thresholds for predators: Why damselflies only occur in large bromeliads. Dryad Digital Repository, https://doi.org/10.5061/dryad.4j0zpc874

Staddon, P., Lindo, Z., Crittenden, P. D., Gilbert, F., & Gonzalez, A. (2010). Connectivity, non-random extinction and ecosystem function in experimental metacommunities. *Ecology Letters*, *13*, 543–552.

Starzomski, B. M., & Srivastava, D. S. (2007). Landscape geometry determines community response to disturbance. *Oikos*, *116*, 690–699.

Starzomski, B. M., Suen, D., & Srivastava, D. S. (2010). Predation and facilitation determine chironomid emergence in a bromeliad-insect food web. *Ecological Entomology*, *35*, 53–60.

Stoks, R., & McPeek, M. A. (2003). Predators and life histories shape Lestes damselfly assemblages along a freshwater habitat gradient. *Ecology*, *84*, 1576–1587.

Terborgh, J., Lopez, L., Nunez, P., Rao, M., Shahabuddin, G., Orihuela, G., … Balbas, L. (2001). Ecological meltdown in predator-free forest fragments. *Science (80-)*, *294*, 1923–1926.

Tonn, W. M., & Magnuson, J. J. (1982). Patterns in the species composition and richness of fish assemblages in northern wisconsin lakes. *Ecology*, *63*, 1149–1166.

Vander Zanden, M. J., Shuter, B. J., Lester, N., & Rasmussen, J. B. (1999). Patterns of food chain length in lakes: A stable isotope study. *American Naturalist*, *154*, 406–416.

Vanschoenwinkel, B., Hulsmans, A., De Roeck, E., De Vries, C., Seaman, M., & Brendonck, L. (2009). Community structure in temporary freshwater pools: Disentangling the effects of habitat size and hydroregime. *Freshwater Biology*, *54*, 1487–1500.

Voigt, W., Perner, J., Davis, A. J., Eggers, T., Schumacher, J., Bahrmann, R., … Sander, F. W. (2003). Trophic levels are differentially sensitive to climate. *Ecology*, *84*, 2444–2453.

Wellborn, G. A., Skelly, D. K., & Werner, E. E. (1996). Mechanisms creating community structure across a freshwater habitat gradient. *Annual Review of Ecology and Systematics*, *27*, 337–363.

With, K. A., & Pavuk, D. M. (2011). Habitat area trumps fragmentation effects on arthropods in an experimental landscape system. *Landscape Ecology*, *26*, 1035–1048.

Wright, D. H. (1983). Species-energy theory - an extension of species-area theory. *Oikos*, *41*, 496–506.

Zotz, G., & Thomas, V. (1999). How much water is in the tank? Model calculations for two epiphytic bromeliads. *Annals of Botany*, *83*, 183–192.

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