Ecology and Evolution

Mind the gap: treefalls as drivers of parental trade-offs

Bibiana Rojas[1,2]

[1]Department of Biological and Environmental Science, Centre of Excellence in Biological Interactions, University of Jyvaskyla, PO Box 35, Jyväskylä, 40014, Finland
[2]Centre for Integrative Ecology, School of Life and Environmental Sciences, Deakin University at Waurn Ponds, Pigdons Road, Geelong, Vic. 3217, Australia

Abstract

Tree-fall gaps are small-scale disturbances whose formation, colonization, and role in forest dynamics are well documented, but whose effects on animal ecology are still greatly overlooked, except for studies comparing species richness of gaps 6+ months old to that in the closed canopy. Other factors associated with the invasion of fresh tree-fall gaps such as animal breeding adaptations have been largely neglected. I studied the immediate (within hours and days) arrival of the poison frog *Dendrobates tinctorius* in new tree-fall gaps to examine the dynamics of their invasion in relation to tadpole rearing. I found that rearing sites are occupied sooner and tadpoles deposited at higher rates in fresh gaps than in the closed forest, but that the rate of cannibalism is also much greater in the former. This suggests that invading new tree-fall gaps can be the best parental decision when parents arrive early because they get access to fresh, high-quality resources, but it could be to the detriment of the offspring if parents arrive late, because of overcrowding and cannibalism. These results highlight the importance of studying the earliest stages of invasions in order to have a better understanding of the composition of communities in disturbed ecosystems at later successional stages.

Introduction

Apart from human-mediated phenomena, several natural disturbances such as fires, floods, landslides, and windstorms can occur at large scales. However, disturbances may also occur at smaller scales but still have a great impact on ecosystems (Sousa 1984; White and Jentsch 2001). Such is the case of the gaps formed in forests when a treefalls or its largest branches snap (van der Meer and Bongers 1996; Chao et al. 2009; Schliemann and Bockheim 2011).

As small-scale disturbances, treefalls can nevertheless have a great impact on ecosystems (Sousa 1984; White and Jentsch 2001). Numerous studies have focused on the differences in species richness and composition in established gaps compared to closed forest (Schemske and Brokaw 1981; Shelly 1988; Greenberg 2001; Greenberg and Lanham 2001; Hill et al. 2001; Gorham et al. 2002; Strojny and Hunter 2010), others have demonstrated how some species have evolved adaptations to invading disturbed or early successional habitats (Hill et al. 2001; White and Jentsch 2001), and tree-fall gaps in particular. The new light environment favors the germination of buried seeds and the colonisation by pioneer plant species (Connell 1989; Schupp et al. 1989), and the coarse debris offers a whole new range of food items, shelter, perches for display, and other kinds of resources previously unavailable to multiple animal species (Blake and Hoppes 1986; Bouget and Duelli 2004). However, like any other disturbance, treefalls can induce survival and reproductive challenges that may trigger adaptations in the life histories of the organisms affected (White and Jentsch 2001).

Despite the broad documentation of natural tree-fall gaps' formation and colonization as an important phenomenon in forest dynamics (Hartshorn 1980; Sousa 1984; van der Meer and Bongers 1996, 2001), little is known about their direct effects on animal assemblages

(Sousa 1984; Shelly 1988). This is presumably due to the unpredictability of their occurrence and to the difficulty of quantifying their effects on mobile versus sessile organisms (Sousa 1984). Moreover, no information on the immediate (within hours and days) or short-term (within weeks) effects of treefalls is available. With only a few exceptions, studies on 'young' tree-fall gaps to date have been carried out in gaps between 6 months and 3 years old (Blake and Hoppes 1986; Popma and Bongers 1988; Feener and Schupp 1998; Peñaloza and Farji-Brener 2003; Champlin et al. 2009; Fukui et al. 2011), thereby overlooking the initial interactions that may set the dynamics of gap communities at later successional stages.

Frogs of the Neotropical family Dendrobatidae (commonly referred to as poison frogs (Grant et al. 2006)) are diurnal rainforest dwellers with an elaborate parental care that consists of clutch attendance and the transport of newly hatched tadpoles to phytotelmata (bodies of water in plants) such as treeholes, palm bracts, or bromeliad axils where they complete their development until metamorphosis (Weygoldt 1987; Summers 1990; Crump 1996; Pröhl and Hödl 1999; Summers and Earn 1999; Summers and McKeon 2004; Brown et al. 2010). Phytotelmata have been shown to be a limited resource for poison frogs and other animals that breed in them (Donnelly 1989a,b; Fincke 1992; Poelman and Dicke 2008), and fallen trees are a potential source of new suitable phytotelmata as offspring-rearing sites. Individuals of the dyeing poison frog, *Dendrobates tinctorius*, are known anecdotally to invade the gaps formed by fallen trees in the forests of French Guiana (Born et al. 2010), in some cases moving considerable distances from their core areas (B. Rojas, pers. obs.).

I examined eight natural tree-fall gaps in a healthy, undisturbed forest, within 0.5 and 24 h of their formation and monitored six of them for at least 1 month in order to test the unexplored hypothesis that breeding adaptations may have a central role in the early invasion of tree-fall gaps. If this were the case, males would be expected to immediately invade fresh tree-fall gaps in search of new phytotelmata for tadpole deposition. To test this, I recorded the time until each body of water available was first occupied, the tadpole deposition rate, and the rates at which the number of tadpoles in a given pool grew and declined, and compared these values between artificial pools in fresh tree-fall gaps and pools in the closed forest. I predicted that (1) the time until the occupation of new bodies of water in fresh gaps should be considerably shorter than that in the closed forest; and (2) the rate at which tadpoles are deposited in water bodies within a fresh gap will be considerably higher than that in water bodies in the closed forest, because many males will try to use them. However, the sudden availability of valuable, limited resources may lead to their

overuse. Given that *D. tinctorius* tadpoles are cannibalistic (Rojas 2014); then (3) the rate of tadpole decline in treefall gaps should also be higher than that in the closed forest. Thus, the mass invasion of treefalls may entail the existence of a trade-off: On the one hand, parents readily exploit the benefits of having newly available sites suitable for their offspring development; on the other hand, parents face the cost of many males making the same decision which translates into overcrowding and potential loss of offspring to cannibalism. The consideration of this trade-off may provide new insights into our understanding of processes related to (1) the role of disturbances in the evolution of parental decision-making; (2) the colonization of disturbed or unoccupied habitats; and (3) the effect of early invaders in the future structure of newly formed communities.

Materials and Methods

Study system and study site

The dyeing poison frog, *Dendrobates tinctorius* (Fig. 1), is a diurnal, large (37–53 mm at the study site) (Rojas and Endler 2013) frog of the Neotropical family Dendrobatidae whose distribution is associated with canopy gaps in primary forests in the Eastern Guiana Shield, from sea level up to 600 m (Noonan and Gaucher 2006; Born et al. 2010). Contrary to what has been reported in captivity, where the species has been found to lay clutches of up to 14 eggs (Lötters et al. 2007), pairs in the field lay clutches of 4–5 eggs that are guarded by the male and hatch after approximately 2 weeks (pers. obs.). Tadpoles are then carried by the male, one or two at a time, to phytotelmata (Fig. 1) at variable heights (Rojas 2014) where they remain unattended until metamorphosis,

Figure 1. A male *Dendrobates tinctorius* about to deposit its tadpole in a treehole.

which occurs after 2 or 3 months (pers. obs.). This study was carried out at Camp Pararé, Les Nouragues Reserve, French Guiana (3°59′N, 52°35′W), between 2 February and 2 June 2011, during part of the breeding season of the species.

Tree-fall gaps

I studied six naturally occurring tree-fall gaps during the study period. Treefalls were easily identified as fresh because they occurred over or next to a 1.5 km longitudinal transect that was surveyed daily. Treeholes in new fallen trees are very difficult to find because of the entangled branches and the dense foliage; they become apparent only at later stages, when the leaves have shed completely. For that reason, following a treefall, I inspected it within the first 24 h and placed either two (in four treefalls) or three (in the remaining two treefalls) plastic bowls with 350 ml of water ($N = 14$ in total) on the fallen tree trunk or limbs, or tangled in branches. This is a conservative number because a single fallen tree may have up to 13 visible water-filled treeholes (pers. obs.). Bowls were at approximately 3–4 m from each other, facing up, and contained rain water, crushed leaf litter and dead leaves, as other poison frog species has proven to prefer for deposition containers with detritus as opposed to containers holding water only (Poelman et al. 2013). The number of bowls (two or three) placed in each treefall was assigned according to the treefall's size. I compared the tadpole deposition activity in tree-fall gaps with places far from treefalls by setting 15 bowls in the closed forest in places similar to those bearing the sites that frogs actually used for tadpole deposition. The bowls were checked at least five times a week from the moment they were placed and for the duration of the study period (between 3 weeks and 1.5 months) for the presence/absence and number of *D. tinctorius* tadpoles. These surveys accounted for both tadpole deposition and tadpole disappearance. Seventeen natural phytotelmata containing at least one tadpole of *D. tinctorius* (15 treeholes and two palm bracts in the closed forest; hereafter referred altogether to as natural treeholes), were also monitored for tadpole deposition as a reference to validate tadpole deposition activity in bowls far from fresh gaps. "Time to occupancy" was defined as the number of days from the day when bowls were placed in the forest until the day when the first tadpole was deposited. "Tadpole deposition rate (TDR)" was defined as the number of tadpoles deposited per bowl, per day.

Data analysis

The validity of the locations for bowls in the closed canopy was tested by comparing their patterns of tadpole deposition (TDR, and maximum and average number of tadpoles) with those of natural treeholes. I then tested for differences in TDR, maximum (MNT) and average (ANT) number of tadpoles, and latency to occupancy between bowls placed in fresh treefall gaps and bowls placed in the closed forest. Comparisons were made by means of GLMMS, using location as a predictor variable and treefall as a random factor, to correct for the nonindependence of the bowls within each treefall. Latency to occupancy was analyzed via a Cox hazard regression.

Because not all of the treefalls occurred at the same time, the total number of monitoring days for each of them was different. To account for these differences and their effect on the maximum number of tadpoles recorded for each bowl, I re-expressed these numbers as values between 0 (no tadpoles) and 1 (the maximum number of tadpoles recorded in each bowl), and calculated the time it took for each bowl to reach the maximum number of tadpoles. I also calculated the time from when the maximum number of tadpoles was reached until the moment when the minimum number of tadpoles was recorded for a given bowl. These two groups give tadpole number growth (how quickly the maximum number of tadpoles was reached) and decline (how quickly the number of tadpoles declined to its minimum) rates, respectively. For each group of data per bowl, I ran a growth regression ($Ln(Y) = a + bX$) and used the unstandardized slope coefficient b as an estimate of growth rate or decline rate in tadpole numbers. These values of growth and decline were compared between bowls in the closed forest and bowls in fresh gaps by means of GLMMs with treefall as random factor, as described above. All statistical analyses were performed with the software RStudio v. 0.99.441 (RStudio, Inc., Boston, MA) and the packages MASS and Coxme.

Results

All of the bowls placed in fresh tree-fall gaps were occupied at least once, whereas two of 15 (13.3%) bowls placed in the closed forest were never used by the study species. In nine of the 29 bowls used bowls (31%; five in fresh tree-fall gaps and two in the closed forest) tadpoles of other poison frog species were found at some point during the study: *Allobates femoralis* (5; 17.2%), *Ameerega hahneli* (1; 3.4%), and *D. ventrimaculatus* (3; 10.3%). Among the natural treeholes used by *Dendrobates tinctorius*, 13 of 17 (76.5%) had tadpoles of *Allobates femoralis* at some point, whereas two (11.8%) had tadpoles of *Ameerega hahneli* and two had both eggs and tadpoles of *Rhinella castaneotica*. Both eggs and tadpoles of *R. castaneotica*, as well as the tadpoles of the other dendrobatid

species, were readily consumed by the carnivorous tadpoles of *D. tinctorius* (pers. obs.). Odonate naiads and mosquito larvae were also observed in the bowls; both were eaten by *D. tinctorius* tadpoles.

The patterns of tadpole deposition in bowls placed in the closed canopy did not differ significantly from those in natural treeholes within the closed canopy, suggesting that the bowls were placed in locations that the frogs recognized as equally suitable (TDR: effect = 0.001 ± 0.095, $t = 0.011$; growth rate: effect < 0.001 ± 0.013, $t = 0.039$; decline rate: effect = −0.024 ± 0.047, $t = −0.515$; MNT: effect = −0.314 ± 0.383, $t = −0.821$; ANT: effect = −0.715 ± 0.812 $t = −0.881$; $P > 0.05$ in all cases). Therefore, all subsequent analyses included only comparisons between bowls in treefalls and bowls in the closed forest.

Bowls placed within fresh tree-fall gaps were occupied significantly sooner (within 3 days) than bowls in the closed forest (Cox hazard regression. Location: coef = 1.557 ± 0.606, $z = 2.57$, $P = 0.01$; Table 1; Fig. 2). Furthermore, tadpoles were deposited at a significantly higher rate in bowls located within fresh gaps than in those located in the closed forest (effect = 0.750 ± 0.256, $t = 2.932$, $P = 0.013$; Table 1; Fig. 3). Bowls within fresh gaps also reached a higher maximum (effect = 1.144 ± 0.348, $z = 3.287$, $P = 0.001$) and average (effect = 4.508 ± 1.748, $t = 2.579$, $P = 0.023$) number of tadpoles than bowls in the closed forest (Fig. 4).

Figure 2. Difference in latency to occupancy (time taken until first tadpole was deposited) between bowls placed in the closed forest and bowls placed in fresh tree-fall gaps. Boxes show the median and the 25th and 75th percentiles of data distribution. Vertical lines indicate data range, and filled and open circles denote extremes and outliers in data distribution, respectively.

There was much higher variation in the number of tadpoles over time in the bowls placed in treefalls than in those in the closed forest (Fig. 5). The estimated value of

Table 1. Descriptive statistics of parameters measured in the pools used by *Dendrobates tinctorius*.

Variable	Pool Type	Range	Mean ± SE	N
Time to occupancy (d)	CF	5–57	24.30 ± 4.90	13
	FG	1–20	3.57 ± 1.32	14
Max. number of tadpoles	TH	1–10	3.67 ± 0.65	18
	CF	0–10	3.60 ± 0.82	15
	FG	2–31	13.71 ± 2.54	14
Average number of tadpoles	TH	0.10–5.30	1.56 ± 0.40	17
	CF	0.00–5. 60	1.36 ± 0.39	15
	FG	1.20–18.20	6.46 ± 1.32	14
Tadpole deposition rate	TH	−0.22–0.67	0.03 ± 0.07	17
	CF	0.00–0.22	0.03 ± 0.02	15
	FG	0.00–2.44	0.81 ± 0.21	12
Estimated growth rate*	TH	0.00–0.11	0.03 ± 0.01	11
	CF	0.00–0.08	0.03 ± 0.01	12
	FG	0.04–0.18	0.10 ± 0.01	14
Estimated decline rate*	TH	−0.33–0.00	−0.06 ± 0.03	10
	CF	−0.09–0.00	−0.03 ± 0.01	8
	FG	−0.14 to −0.01	−0.06 ± 0.01	12

CF, bowls placed in the closed forest; FG, bowls placed in fresh tree-fall gaps; and TH, natural treeholes.
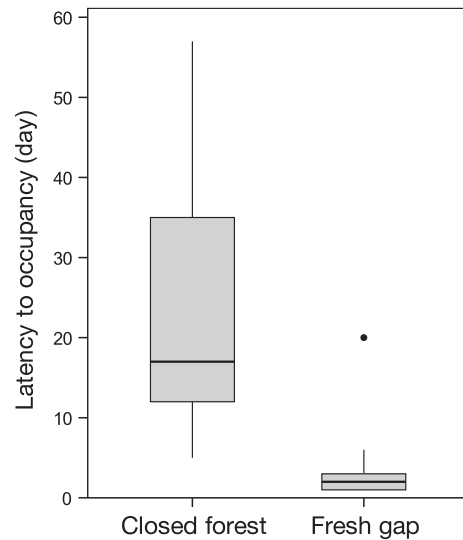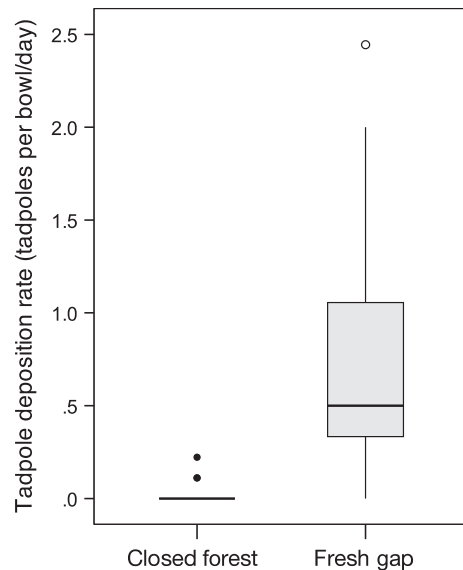*See "Materials and Methods" section for details on the calculation of these parameters.

Figure 3. Difference in tadpole deposition rate (tadpoles deposited per bowl/day) between bowls placed in the closed forest and bowls placed in fresh tree-fall gaps. Boxes show the median and the 25th and 75th percentiles of data distribution. Vertical lines indicate data range, and asterisks and circles denote extremes and outliers in data distribution, respectively.
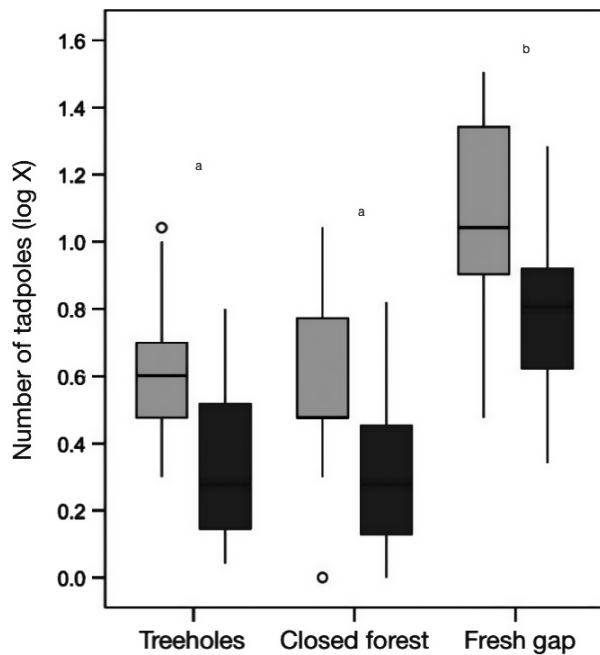
Figure 4. Average (dark boxes) and maximum (light boxes) number of tadpoles recorded during the study in bowls placed in closed forest and fresh gaps. A number of tadpoles in natural treeholes (left) are shown for reference purposes. Boxes show the median and the 25th and 75th percentiles of data distribution. Vertical lines indicate data range
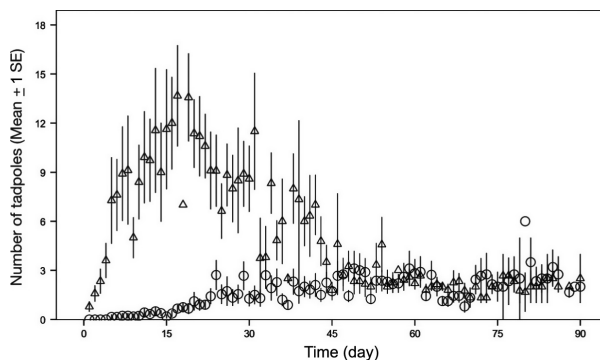

Figure 5. Fluctuation in the number of tadpoles of bowls placed in fresh gaps (triangles) and in the closed forest (circles) during 90 days. Values shown correspond to the mean number of tadpoles per location ±1 standard error.

tadpole number growth (effect $= 0.067 \pm 0.019$, $t = 3.611$, $P = 0.004$) was significantly higher in bowls placed in treefalls than in bowls placed in the closed forest (Table 1; Fig. 6). There was a nonsignificant trend for a higher tadpole number decline rate in tree-fall gaps than in the closed forest (effect $= -0.022 \pm 0.021$, $t = -1.044$ $P = 0.327$; Fig. 6).
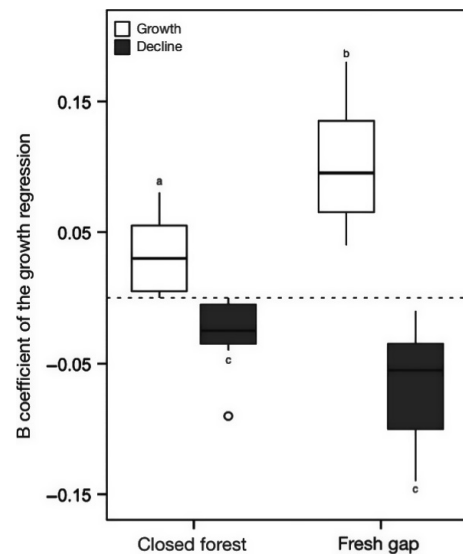

Figure 6. Differences in growth (pale boxes) and decline (dark boxes) rates of numbers of tadpoles in bowls placed in the closed forest and in fresh gaps. See "Materials and Methods" section for details on the estimation of these parameters. The dotted line indicates a value of 0 (no growth, no decline). Boxes show the median and the 25th and 75th percentiles of data distribution. Vertical lines indicate data range.

Discussion

Disturbances might be an important agent of natural selection (White and Jentsch 2001). This study shows that breeding adaptations can have a prominent role in the early invasion of disturbed ecosystems, treefalls in particular, and that disturbances can drive the evolution of parental decision-making. Using the poison frog *Dendrobates tinctorius* as a case study, I found that (1) new bodies of water placed in fresh gaps are occupied significantly sooner than those in the closed forest; (2) tadpole deposition rate within fresh gaps is considerably higher than that in water bodies in the closed forest; and (3) both the growth and decline rates of tadpole numbers in each pool are significantly higher in fresh gaps than in the closed forest, suggesting the existence of a trade-off between the benefits of finding new off-spring rearing sites and the costs associated with overcrowding and cannibalism. These results indicate that rearing sites might be a limited resource and that raising offspring in a fresh tree-fall gap can be the best parental decision when parents arrive early, but it could be to the detriment of the offspring if parents arrive late.

In support of my first prediction, most of the bowls placed in fresh gaps were occupied within 3 days after they were placed (in some cases even on the same day). This is consistent with the fact that some males carrying tadpoles can be seen in tree-fall gaps only a few hours

after a tree has fallen. In at least four cases, males found with tadpoles on their back less than 3 h after the event were known to live (i.e. had been recaptured in the same area over at least the previous 2 months) more than 200 m away from the new treefall (pers. obs.), which makes it unlikely that they were nearby before the treefall. Also, at least four males were seen next to or going inside the bowls without tadpoles, and depositing tadpoles a few days later. Unfortunately, nothing is known about the distances that males of this species travel with their tadpoles away from their core areas before they deposit them in a treehole. How frogs are able to find fresh tree-fall gaps is also unknown, although it has been speculated without any experimental support that the vibration produced by the tree as it hits the ground may play a role (P. Gaucher, pers. comm.). This could be plausible given that frogs are able to detect seismic signals not only from conspecifics (Lewis and Narins 1985; Narins 1990; Caldwell et al. 2010a), but also from abiotic factors such as rain (Caldwell et al. 2010b).

In support of my second prediction, the number of tadpoles deposited per bowl per day (TDR) in fresh tree-fall gaps was over 20 times that of bowls in the closed forest. The same pattern was found for the estimated value of tadpole number growth. This could be interpreted in two ways: (1) the overuse of bowls in treefalls could be a by-product of adults being more concentrated around them; for instance, high rates of tadpole deposition have been found for *D. auratus* in locations of higher adult density in Panama (Summers 1990). Or (2) the presence of increased numbers of adults in treefalls could be the result of an aggregation around a relevant breeding resource, that is new tadpole deposition sites, as has been shown in other dendrobatids (Brown et al. 2009). Both scenarios would lead to a high use of bodies of water in treefalls and would help explaining the higher tadpole deposition rate in bowls placed in treefalls compared to bowls placed in the closed forest. With the exception of two palm bracts on the ground, all of the natural sites used by *D. tinctorius* for tadpole deposition were on fallen trees in older gaps, which had between one and 13 visible water-filled holes. This means that the treeholes in tree-fall gaps keep being used at later successional stages, not only when the gaps are fresh, and this might explain the patchy distribution of this species around canopy gaps throughout its geographic range (Noonan and Gaucher 2006). The current patterns of distribution of several species may reflect their abilities to colonize-specific environments, or take advantage of different types of disturbances. This patterns, however, can only be determined whether the earliest stages of such disturbances are detected and the invasion of new environments is followed up.

There are several reasons why treeholes in a fresh tree-fall gap could potentially be a valuable resource for tree-hole breeders like *D. tinctorius*. Studies comparing the growth rate and development of larval amphibians in ponds with varying canopy cover have demonstrated that primary productivity, quality of detritus and the amount of dissolved oxygen are higher in open canopy ponds, and all these factors contribute to higher growth rates of the tadpoles living in them (Skelly et al. 2002; Schiesari 2006). In contrast, a recent work demonstrated that the predacious larvae of two species of salamanders, grew larger in closed forest conditions (Earl et al. 2011). However, the authors indicate that these results are presumably due to differences in prey abundance between ponds in closed and open canopy, rather than to differences in canopy cover per se (Earl et al. 2011). It is possible that variations in canopy cover might also affect smaller aquatic ecosystems such as those in phytotelmata, rendering higher growth rates in tadpoles reared in treeholes in tree-fall gaps as opposed to treeholes in the closed forest. It is well known that gaps have warmer temperatures, more sunlight, are subject to higher wind speed, and experience reduced relative humidity in spite of the high amounts of rain (Vitt et al. 1998; Bouget and Duelli 2004). Although favorable for heliothermic organisms such as lizards (Vitt et al. 1998; Sartorius et al. 1999; Greenberg 2001), these conditions do not seem ideal for adult frogs, which may face the risk of increased water loss (Shoemaker 1992; Wells 2007). However, an increased temperature, within the limits imposed by physiology, has proven to exert positive effects on larval growth rate (Ultsch et al. 1999). This could, for example, make tadpoles reach metamorphosis and leave the unstable phytotelm environment sooner. Therefore, it may be that male *Dendrobates tinctorius* invade and deposit their tadpoles in fresh gaps because treeholes in freshly-fallen trees offer resources that are of better quality than treeholes in the closed forest. Nevertheless, establishing whether phytotelmata in fresh gaps provide better resources for tadpole development than their counterparts in the closed forest and, if so, which are the variables that make a treehole in a fresh tree-fall gap a higher-quality rearing site is a goal for future research.

Last, but not least, I found a nonsignificant trend for higher rate of tadpole number decline in tree-fall gaps compared to that in the closed forest. The absence of significance in this relationship might be due to a low sample size rather than to a lack of biological relevance. Although tadpoles in treeholes could be preyed upon by snakes or Odonate larvae, for example, the rapid decline of tadpole numbers is most likely due to cannibalism, which has a high prevalence in this species (Rojas 2014). In fact, in 50% of the cases, cannibalism occurs within

24 h, provided a minimal difference (at least 1 mm) in size between the tadpoles involved (Rojas 2014). Cannibalism was not only observed in bowls placed in both closed forest and treefalls but also occurred spontaneously on at least 12 occasions in the natural pools used by the species. Previous work has suggested that cannibalism may be favored in situations of high competition and resource scarcity, as seems to be the case in phytotelmata (Lehtinen et al. 2004). Moreover, cannibalism has been shown to be the primary source of mortality of tadpoles of other phytotelm-breeding dendrobatids, such as *Adelphobates castaneoticus* (Caldwell and de Araujo 1998).

Parents thus seemingly face an important trade-off between the advantage of going to a tree-fall site to get more and better places for tadpoles, on the one hand, and the disadvantage of overcrowding and higher rates of cannibalism-induced mortality. If phytotelmata in fresh gaps were indeed a high-quality larval resource, it would make sense that parents always tried to take their tadpoles to such treeholes. However, this may be altered by the fact that predation, mostly via larval cannibalism, gives a survival advantage to first arrivals. Tadpoles deposited earlier will be larger than the later arrivals and will be likely to be better competitors, if not predators rather than prey. Therefore, selection should favor individuals that deposit their offspring in newly available treeholes as soon as possible after the trees fall, generating priority effects (Blaustein and Margalit 1996; Fincke 1999). There is evidence that carnivorous diets in amphibians speed up growth rates (Wildy et al. 1998; Summers 1999; Alvarez and Nicieza 2002). A tadpole that grows faster not only minimizes the risk of being cannibalised but is also able to leave the treehole sooner (Alford 1999; Harris 1999), diminishing the risks of potential pool desiccation and predation by other organisms such as odonate naiads (Fincke 1992). This is also true for other organisms which spend their early developmental stages in these aquatic environments. Further research on the actual advantages in terms of life-history traits of individuals raised in gaps as opposed to individuals raised in the closed forest would contribute to refine the proximate and ultimate causes of treefall gap invasion by several species of tree-hole breeders.

Taken together, the findings of this study suggest that the availability of new tadpole rearing sites might be a key factor explaining the invasion of tree-fall gaps by *D. tinctorius*. Rapid invasion of treeholes in treefalls seems to be favored by cannibalism, and by the pressure of intense competition from later arrivals. Parents of species that use treeholes as breeding sites, either for oviposition (such as mosquitoes or damselflies) or larval deposition (such as frogs), face tradeoffs between the benefits of a high-quality place for offspring development and the costs

of its "popularity" in terms of high predation risks and competition for food. So the degree to which animals invade gaps for breeding will depend upon the relative importance of new resources and crowded resources. Follow-up experiments are needed in order to understand the benefit of tadpoles being deposited in a gap pool, as opposed to a pool in the closed forest. Overall, these results offer intriguing insights on the role of tree-hole breeders in structuring gap communities, and insinuate the importance of studying the earliest stages of invasions in order to have a better understanding of disturbed ecosystems at later successional stages.

Acknowledgments

Conflict of Interest

None declared.

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