

SHORT COMMUNICATION

Rapid collapse of a population of *Dieffenbachia* spp., plants used for tadpole-rearing by a poison-dart frog (*Oophaga pumilio*) in a Costa Rican rain forest

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Abstract: Amphibian populations have been declining worldwide, with multiple potential causes. At La Selva field station in north-eastern Costa Rica, previous work has shown that populations of many amphibians have decreased significantly since the 1970s, especially in primary forest. Starting in 1998, we investigated one of the most common frog species at La Selva, the poison-dart frog *Oophaga pumilio* (= *Dendrobates pumilio*). In a survey of 50 plots of 100 m² in 1998, adult frogs were 4.6 times more abundant in secondary forest than in primary forest. Tadpoles were found only in secondary-forest plots. Almost all (89%) of the tadpoles were found in leaf axils of *Dieffenbachia* spp., which were much more abundant in secondary-forest than in primary-forest plots. The greater abundance of *Dieffenbachia* spp. in secondary forest was confirmed in a broad survey of ~11 km of trails within La Selva in 2002. When the same trails were resampled in 2012, *Dieffenbachia* spp. had been extirpated from 72% of the 50-m segments where plants were present in 2002; abundance was greatly reduced in the few trail segments where any *Dieffenbachia* spp. remained in 2012. The loss of *Dieffenbachia* spp., especially in secondary forest, removed the species most often used by *O. pumilio* for tadpole rearing. Based on counts of calling frogs in 2010, there was no difference in *O. pumilio* abundance in primary versus secondary forest, in striking contrast to multiple earlier surveys that found much greater frog abundance in secondary forest. We propose that the reason for the rapid decline in *Dieffenbachia* spp. is herbivory by the collared peccary (*Pecari tajacu*), which has increased in abundance at La Selva in recent years. A likely consequence is continued reduction in *O. pumilio* populations.

Key Words: amphibian decline, collared peccary, *Dieffenbachia nitidipetiolata*, mammalian herbivory, *Oophaga pumilio*, *Pecari tajacu*, plant population, poison-dart frog, rain-forest understorey

Populations of many amphibians are declining, and nearly a third of amphibian species are threatened

with extinction worldwide (Hof *et al.* 2011, Wake & Vredenburg 2008). At La Selva Biological Station in north-eastern Costa Rica, overall populations of leaf-litter amphibians have decreased greatly since the 1970s (Whitfield *et al.* 2007). However, the population changes documented by Whitfield *et al.* (2007) differed between habitats. Primary forests experienced consistent population losses, while secondary forests in abandoned plantations of *Theobroma cacao* L. sometimes had significant increases. Populations of our study species, the poison-dart frog *Oophaga pumilio* (Schmidt, 1857), have declined by an average of 1.18% y⁻¹ since the 1970s in primary forest, but increased by 8.75% y⁻¹ in abandoned plantations (Whitfield *et al.* 2007).

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There are a number of potential reasons for the difference between *O. pumilio* populations in primary versus secondary forests at La Selva. *Oophaga* species raise their young in small pools of water that occur in the axils of leaves (Brown *et al.* 2010), and the availability of these pools may become a limiting resource for reproduction. Donnelly (1989a, b) found that *O. pumilio* populations increased in response to the experimental addition of tadpole-rearing sites at our study site in Costa Rica. Thus we hypothesized that tadpole-rearing sites are limiting to *O. pumilio* populations and could explain habitat-specific population changes.

We have been investigating the distribution of *O. pumilio* and its potential tadpole-rearing sites at La Selva Biological Station in north-eastern Costa Rica since 1998. Our goals were to (1) determine what plants *O. pumilio* uses for tadpole rearing at La Selva; (2) document the distribution of tadpole-rearing resources in primary versus secondary forest; and (3) describe the changes in population of *Dieffenbachia* spp. (Araceae), the plant taxon most heavily used by *O. pumilio* for tadpole rearing at La Selva.

In December 1998, we quantified the abundance of *O. pumilio* and potential tadpole-rearing sites in 50 plots of 100 m². Most previous work on *O. pumilio* at La Selva took place in abandoned *T. cacao* plantations (as reviewed by Whitfield *et al.* 2007). However, we also sampled old-growth primary forest as well as other types of secondary forest, including successional forest of varying ages and selectively logged forest. Plots were located along the following named trails: CES, STR, SOR, SHO, SSO and LOC; see McDade *et al.* (1994) for trail maps and classification of forest types. To choose plot locations, we used the permanent trail markers that are placed every 50 m along La Selva's trails. Forty square 10 × 10-m plots were located 50 paces perpendicular to the trail from the markers. An additional 10 rectangular 5 × 20-m plots were placed directly adjacent to trails.

Five observers walked systematically through each plot to search for *O. pumilio* adults. All frogs were temporarily captured and sexed by means of throat colouration (Donnelly 1989a). We also searched for pools of water accessible to us (< 2 m in height). Any standing pool of water above the forest floor of ≥ 1 ml (smallest volume in which tadpoles were found) was considered a potential tadpole-rearing site. The water in each pool was extracted by suction with a calibrated pipette in order to search for tadpoles and to measure pool volume.

We also counted the number of shoots of *Dieffenbachia* spp. and bromeliads (Bromeliaceae) in each plot, regardless of whether the plants had any leaf-axil pools. Most of the bromeliads we encountered were fallen epiphytes persisting on the forest floor. *Dieffenbachia* species are perennial clonal herbs that can form dense stands in the understorey of wet tropical forests (Croat

1983), including La Selva (Young 1986). *Dieffenbachia* plants at La Selva often have been referred to as *Dieffenbachia longispatha* (McDade *et al.* 1994), but this species does not occur in Costa Rica (Croat 2004). Based on field characters, the plants we observed were almost all *Dieffenbachia nitidipetiolata* Croat & Grayum. Because we could not always be sure of species identification during field surveys, we refer to our plants as *Dieffenbachia* spp.

In 1998 there were adult frogs in 43 out of 50 plots (Figure 1), with an average abundance of 4.0 ± 0.53 (mean ± SE) frogs per plot of 100 m². Of 166 sexed adults, 65.7% were female. Frogs were more common in secondary forest (6.26 ± 0.72 frogs per plot) versus primary forest (1.35 ± 0.25 per plot; Mann–Whitney test, $U = 563$, $P < 0.001$). The number of adult frogs per plot was highly correlated with the number of shoots of *Dieffenbachia* spp. in the plot (Spearman rank correlation, $r_s = 0.69$, $P < 0.001$; Figure 1). The correlation between number of adult frogs and number of bromeliad plants was not significant ($r_s = 0.27$, $P = 0.065$).

We found 19 tadpoles in 11 of the 50 plots. Seventeen of the 19 tadpoles were in leaf axils of shoots of *Dieffenbachia* spp., one was in a bromeliad and one was in a tree hole. The average volume of water in pools with tadpoles was 3.0 ± 0.4 ml (range = 1.0–7.0 ml). All plots with tadpoles were in secondary forest, so there was a highly significant difference in tadpole distribution between primary and secondary forest (Fisher's exact test, $df = 1$, $P < 0.001$). Plots with tadpoles had about eight times more shoots of *Dieffenbachia* spp. (16.4 ± 2.9 plants per plot) than plots without tadpoles (2.0 ± 0.9 plants per plot; Mann–Whitney test, $U = 43$, $P < 0.001$; Figure 1). Of 307 pools found with water volume ≥ 1 ml, 69.1% were in leaf axils of *Dieffenbachia* spp., 29.6% in leaf axils of bromeliads and 1.3% in tree holes.

In 1998, shoots of *Dieffenbachia* spp. were found much more frequently in secondary forest (73.1% of 26 plots) compared with primary forest (13.0% of 23 plots; Fisher's exact test, $df = 1$, $P < 0.0001$). Bromeliads also were more common in secondary (53.8% of plots) versus primary forest (26.1% of plots; Fisher's exact test, $df = 1$, $P = 0.033$).

In December 2010, we again measured abundance of *Dieffenbachia* spp. and bromeliads (but not frogs) in plots similar to those sampled in 1998. We surveyed 58 plots, each measuring 10 × 10 m and centred 10 m from points along the CES, STR, CEN, SSO, CCL, SOR, SUA and SHO trails; most plots were near the same trail markers sampled in 1998.

There were no *Dieffenbachia* spp. plants in any of the plots sampled in 2010, a striking reduction in abundance from 1998 when 45% of all plots had some *Dieffenbachia* spp. plants (Fisher's exact test, $df = 1$, $P < 0.0001$). Density of *Dieffenbachia* spp. in 1998 averaged 5.2 ± 1.3 plants per 100-m² plot. Bromeliad frequency did not

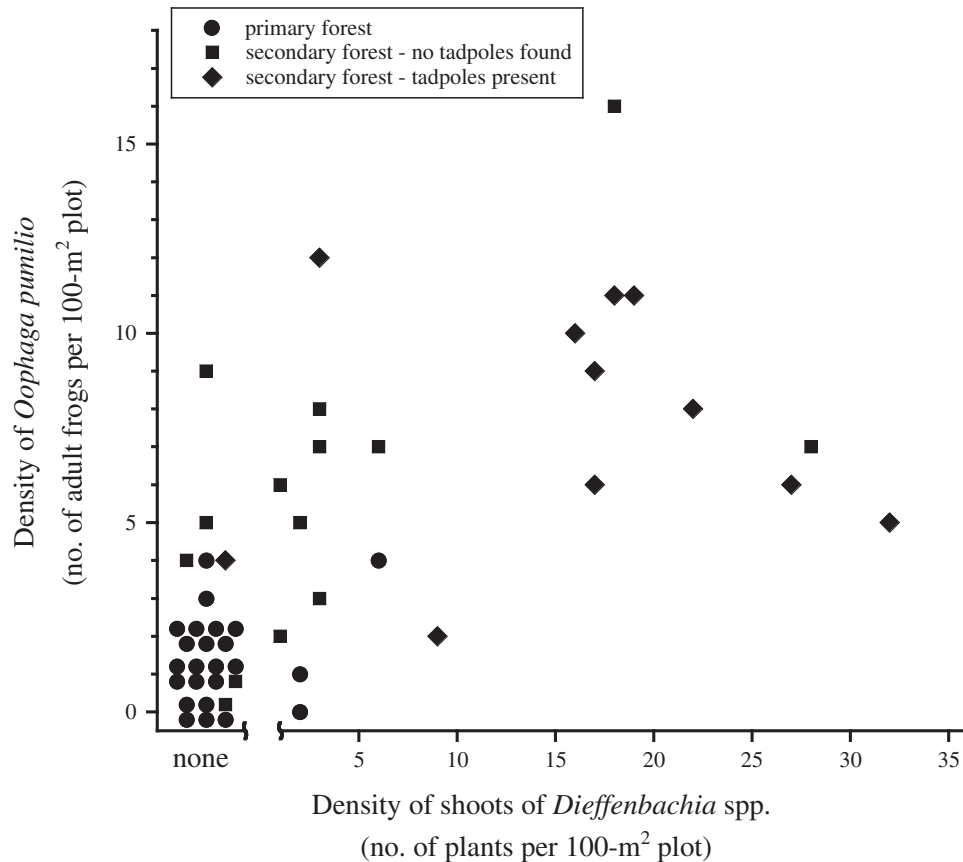


Figure 1. Density of adult frogs (*Oophaga pumilio*) among 49 plots in 1998 in relation to the density of *Dieffenbachia* spp. plants. Plots were spread across primary and secondary forest at La Selva, Costa Rica. Secondary forest included successional forest, selectively logged forest and abandoned plantations of *Theobroma cacao*. Overlapping points have been offset for visibility in the multiple plots without *Dieffenbachia* spp. Symbols indicate whether plots were in primary or secondary forest, and whether tadpoles were present in the plot. No plots with tadpoles were found in primary forest.

change significantly between 1998 (40.8% of plots with bromeliads) and 2010 (43.1% of plots with bromeliads; Fisher's exact test, $df = 1$, $P = 0.85$). Bromeliad density averaged 1.1 ± 0.3 plants per 100-m^2 plot in 1998 and 1.5 ± 0.3 in 2010.

We sampled populations of *Dieffenbachia* spp. more broadly to determine overall distribution at La Selva. In December 2002 and June 2012, we surveyed most of the marked trails within 2 km of the station buildings, including the trails along which the 1998 plots were located. Specifically, we sampled trails CCL, CEN, CES, LOC, SAT, SHO, SOR, SSE, STR, SUA and SUR. We evaluated the abundance of shoots of *Dieffenbachia* spp. (> 0.3 m tall) visible from the trail on 219 50-m segments of trail, for a total of 10.95 km of trails sampled. The distance observable from the trail varied with topography and density of the understorey vegetation, but was generally between 5 and 8 m from the trail edge. The density of shoots of *Dieffenbachia* spp. per trail segment was classified as absent, low density (1–10 plants), medium

density (approximately 10–25 plants) or high density (>25 plants).

The abundance of *Dieffenbachia* spp. on trail segments declined greatly between 2002 and 2012 (Figure 2; $\chi^2 = 116$, $df = 4$, $P < 0.0001$). By 2012, *Dieffenbachia* spp. had been completely extirpated in 105 (72%) of the 145 segments that had *Dieffenbachia* spp. in 2002. *Dieffenbachia* spp. abundance in 2012 was ranked lower than in 2002 in 91% of the segments (132 out of 145). The few segments with shoots of *Dieffenbachia* spp. in 2012 had small populations; the medium- and high-abundance ranks observed in 2002 were virtually absent (Figure 2). Shoots of *Dieffenbachia* spp. were much more abundant in secondary forest than in primary forest (Figure 2), both in 2002 ($\chi^2 = 58.6$, $df = 4$, $P < 0.0001$) and 2012 ($\chi^2 = 9.29$, $df = 2$, $P < 0.01$).

The collapse of the population of a common understorey plant in such a short time is remarkable. Young (1986) reported that *Dieffenbachia* spp. were abundant at La Selva in the early 1980s, with populations in abandoned

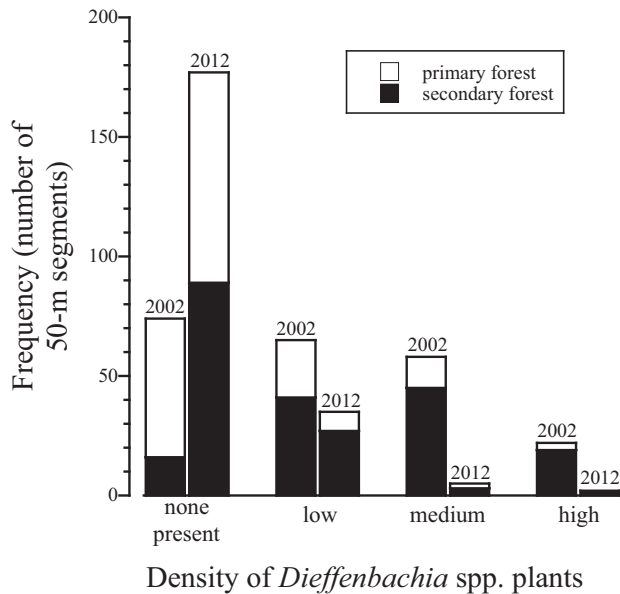


Figure 2. The density of *Dieffenbachia* spp. shoots along 50-m segments of trails in 2002 and 2012. The same 219 segments (10.95 km of trail) were counted in each year, ranging across primary and secondary forest at La Selva, Costa Rica. Plant density of each segment was classified as absent, low density (1–10 plants), medium density (approximately 10–25 plants) or high density (>25 plants). Plants were counted only if they were >0.3 m tall.

plantations (areas included in both our plot and trail samples) reaching densities of 100–200 plants per 100 m². Our *Dieffenbachia* spp. surveys show that the collapse occurred at some point between 2002 and 2010.

We propose that the reason for the rapid decline of *Dieffenbachia* spp. is mammalian herbivory, in particular by the collared peccary (*Pecari tajacu* Linnaeus, 1758). This omnivorous species is abundant at La Selva, and the local population has increased greatly in recent decades (Romero *et al.* 2013). Peccary exclosures at La Selva show that these animals influence diverse ecological interactions (Michel *et al.* 2014), and can affect the populations of some amphibians and reptiles (Reider *et al.* 2013). Consumption of *Dieffenbachia* spp. by the collared peccary is well known (Timm *et al.* 1989, Wainwright 2002). The remaining plants we found in 2012 had clear evidence of mammalian herbivory, including many stems that were partially eaten. Intact shoots of *Dieffenbachia* spp. were usually found in places that were relatively inaccessible to ground-dwelling mammals, such as steep slopes or small islands in streams. Though there are several other possible hypotheses for the loss of *Dieffenbachia* spp. at La Selva (e.g. climate change, a novel pathogen, successional changes in forest composition), these do not seem sufficient to explain such a rapid loss across wide areas of secondary forest at La Selva.

There is evidence that the population of *O. pumilio* in secondary forest responded to the decline in abundance of *Dieffenbachia* spp. We used frog calls to estimate the relative abundance of *O. pumilio* males (females do not call) in December 2006 and December 2010. At sample points spaced 50 m apart, we recorded the number of distinct calling frogs over a 2-min sampling period. Counts were done in the morning when calling was much greater than later in the day (pers. obs.). In 2006, we counted calls at 24 points on two trails: STR (secondary forest) and CES (primary forest). In 2010, we counted calls at 79 sites in both primary and secondary forest, on the CES, STR, SOC, SSO, CEN and SCH trails. Each sample point was counted on two different mornings in 2006, and on five or six different mornings in 2010; number of calls per point was averaged across days for analysis.

In 2006, there were more than three times as many frogs heard per sample point in secondary forest than in primary forest (Mann–Whitney test, $U = 138$, $P < 0.001$). But in 2010, there was no difference in number of calling frogs between habitats (Mann–Whitney test, $U = 796$, $P > 0.20$). The call surveys in the different years are not directly comparable because of potential biases introduced by different observers and different weather conditions. However, the number of calling frogs in 2010 (0.39 ± 0.04 calling males per sample point in primary forest, 0.48 ± 0.06 in secondary forest) was similar to the number in primary forest in 2006 (0.67 ± 0.19) but much lower than in secondary forest in 2006 (2.12 ± 0.11). This suggests that the lack of habitat difference in 2010 was caused by a reduction in frog calls in secondary forest rather than an increase in calls in primary forest.

Our plot survey in 1998 and our calling frog survey in 2006 showed 5–6 times as many frogs in secondary versus primary forest. This is consistent with multiple other previous studies at La Selva. Based on a review of surveys in the 1970s, Whitfield *et al.* (2007) found an average of 4.5 times as many *O. pumilio* in abandoned plantations compared with primary forest. In a 1990 study, plantations abandoned 25 y previously had 3.4 times the number of *O. pumilio* as primary forest (Heinen 1992). Our 2010 calling survey is the first dataset of which we are aware that found similar densities of *O. pumilio* in primary and secondary forest at La Selva. The fact that *O. pumilio* remained relatively abundant in secondary versus primary forest in 2006 suggests that the density of *Dieffenbachia* spp. used by the frogs to rear tadpoles might have remained relatively high until that time. If so, the decline of *Dieffenbachia* spp. occurred in 4 y or less.

In conclusion, we found that the population of *Dieffenbachia* spp. declined drastically across La Selva in less than a decade. The loss of a species favoured as a tadpole-rearing site by *O. pumilio* may have consequences for the population of these frogs, and it will be important

to continue monitoring frog populations of La Selva and other forests where peccaries are common. While concern has focused on large-scale drivers of amphibian declines such as climate change (Hof *et al.* 2011), our work suggests that local food web interactions may also rapidly change the distribution and abundance of amphibians.

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LITERATURE CITED

- BROWN, J. L., MORALES, V. & SUMMERS, K. 2010. A key ecological trait drove the evolution of biparental care and monogamy in an amphibian. *American Naturalist* 175:436–446.
- CROAT, T. B. 1983. *Dieffenbachia* (lotería, dumb cane). Pp. 234–236 in JANZEN, D. H. (ed.). *Costa Rican natural history*. University of Chicago Press, Chicago.
- CROAT, T. B. 2004. Revision of *Dieffenbachia* (Araceae) of Mexico, Central America, and the West Indies. *Annals of the Missouri Botanical Garden* 91:668–772.
- DONNELLY, M. A. 1989a. Demographic effects of reproductive resource supplementation in a territorial frog, *Dendrobates pumilio*. *Ecological Monographs* 59:207–221.
- DONNELLY, M. A. 1989b. Effects of reproductive resource supplementation on space-use patterns in *Dendrobates pumilio*. *Oecologia* 81:212–218.
- HEINEN, J. T. 1992. Comparisons of the leaf litter herpetofauna in abandoned cacao plantations and primary rain forest in Costa Rica: some implications for faunal restoration. *Biotropica* 24:431–439.
- HOF, C., ARAÚJO, M. B., JETZ, W. & RAHBEK, C. 2011. Additive threats from pathogens, climate and land-use change for global amphibian diversity. *Nature* 480:516–519.
- MCDADE, L. A., BAWA, K. S., HESPENHEIDE, H. A. & HARTSHORN, G. S. 1994. *La Selva: ecology and natural history of a Neotropical rain forest*. University of Chicago Press, Chicago. 486 pp.
- MICHEL, N. L., SHERRY, T. W. & CARSON, W. P. 2014. The omnivorous collared peccary negates an insectivore-generated trophic cascade in Costa Rican wet tropical forest understorey. *Journal of Tropical Ecology* 30:1–11.
- REIDER, K. E., CARSON, W. P. & DONNELLY, M. A. 2013. Effects of collared peccary (*Pecari tajacu*) exclusion on leaf litter amphibians and reptiles in a Neotropical wet forest, Costa Rica. *Biological Conservation* 163:90–98.
- ROMERO, A., O'NEILL, B. J., TIMM, R. M., GEROW, K. G. & MCCLEARN, D. 2013. Group dynamics, behavior, and current and historical abundance of peccaries in Costa Rica's Caribbean lowlands. *Journal of Mammalogy* 94:771–791.
- TIMM, R. M., WILSON, D. E., CLAUSON, B. L., LAVAL, R. K. & VAUGHAN, C. S. 1989. Mammals of the La Selva – Braulio Carrillo complex, Costa Rica. *North American Fauna* 75:1–162.
- WAINWRIGHT, M. 2002. *The natural history of Costa Rican mammals*. Zona Tropical Publications, Cornell University Press, Ithaca. 384 pp.
- WAKE, D. B. & VREDENBURG, V. T. 2008. Are we in the midst of the sixth mass extinction? A view from the world of amphibians. *Proceedings of the National Academy of Sciences USA* 105:11466–11473.
- WHITFIELD, S. M., BELL, K. E., PHILIPPI, T., SASA, M., BOLAÑOS, F., CHAVES, G., SAVAGE, J. M. & DONNELLY, M. A. 2007. Amphibian and reptile declines over 35 years at La Selva, Costa Rica. *Proceedings of the National Academy of Sciences USA* 104:8352–8356.
- YOUNG, H. J. 1986. Beetle pollination of *Dieffenbachia longispatha* (Araceae). *American Journal of Botany* 73:931–944.