Research

# Competition and species diversity: removal of dominant species increases diversity in Costa Rican butterfly communities

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Biological communities are usually dominated by a few species and show characteristically skewed species abundance distributions. Although niche apportionment and resource competition are sometimes implicated in such patterns, few experimental studies have shown direct links between resource limitation, competition with dominant species and their impacts on the overall diversity and composition of large natural communities. Here I report the results of an experiment in which I first studied species diversity and composition in two Costa Rican nectar-feeding butterfly communities numerically dominated by two species of *Anartia* butterflies. Then I removed *Anartia* from these communities to study changes in resource availability, species abundance relationships, community diversity and composition as an outcome of the removal of the dominant competitors. In the face of competition with *Anartia*, nectar was scarce, species abundance distributions were highly skewed, and species diversity was low in both communities. Within two weeks after the removal of *Anartia*, there were parallel changes in both communities: competition for nectar reduced and the nectar quantity increased substantially, which facilitated increase in community diversity and resulted in significantly less skewed species abundance distributions. Higher nectar quantity also enabled the distribution of body size and proboscis length of constituent species in the communities to expand at both ends. This study thus experimentally showed that resource competition with the dominant species was excluding many species from the communities, lowering their diversity and skewing relative species abundance relationships. These findings are of fundamental importance for competition theory and community ecology because they indicate ways in which diverse communities may be affected by and recover from competition with dominant species.

Most biological communities show skewed species abundance distributions, with a few numerically dominant species and many rare species (Fisher et al. 1943, Magurran 2004). One of the frequently suggested causes for this pattern of species abundance is the extent and nature of niche apportionment and competitive dominance in communities (MacArthur 1957, Hutchinson 1959, Tokeshi 1999). Many classic studies, e.g. on warblers in North America (MacArthur 1958), have shown that niche apportionment and competitive interactions indeed play very important roles in shaping community characteristics such as diversity and composition. Examples of the effect of competition on these community characteristics often involve herbivore-, predator- and parasite-mediated competitive interactions (Addicott 1974, Bonsall and Hassell 1997, Hudson and Greenman 1998, Rand 2003). For example, predatory *Pisaster* sea stars maintain a higher diversity in intertidal invertebrate communities by checking competitive exclusion: removal of *Pisaster* results in dominance of a few species and subsequent competitive exclusion of some benthic invertebrates and algae (Paine 1980). The effects of dominance and competition on species abundance relationships, however, have been less

frequently studied within a trophic level. Recently, studies of invasive species dynamics have enabled biologists to directly link dominance in large communities to resource competition, competitive exclusion and species diversity of communities. For example, after their introduction in the United States, two invasive ants, *Solenopsis invicta* and *Linepithema humile*, have dominated local insect communities and changed species abundance distributions, extensively decimating populations of native ant species and causing local extinctions (Porter and Savignano 1990, Human and Gordon 1997).

Statistical descriptions of species abundance distributions, however, are still routinely presented and niche apportionment models are often fitted to empirical data without studying the underlying competitive interactions and other community processes (Harte et al. 1999, Fesl 2002, Mouillot et al. 2003, Sugihara et al. 2003). This is unfortunate because, in view of alternative explanations such as community assembly and maintenance through neutral processes (Hubbell 2001, Volkov et al. 2003), patterns of species abundance relationships cannot be attributed to competition without studying species interactions, and thus any inferences drawn only from observed

patterns remain inconclusive (Nekola and Brown 2007). On the other hand, experimental studies usually focus on competing species pairs or very small, often artificial communities, and their results may not be extended to larger sets of species and the ways in which competition and other ecological interactions shape species abundance distributions in diverse natural communities.

In this paper I sought to use the strengths of both these approaches to experimentally study the impacts of dominant species on resource availability, community diversity and species abundance relationships. I used two large neotropical communities of generalist nectar-feeding butterflies dominated by two species: *Anartia fatima* and *A. jatrophae*. The *Anartia* species inhabit disturbed habitats and can sometimes be very common at forest edges. First I studied species abundance relationships in presence of *Anartia* and the impacts of dominance of *Anartia* on nectar availability. Then I experimentally removed *Anartia* from the communities and quantified the ecological response to their removal. I predicted that removing *Anartia* would increase the standing nectar crop, allowing the community to enlarge by including more species. This, in turn, would change the species abundance distribution/community diversity, alter body size and proboscis length distributions, and change foraging behaviour of the constituent species in response to the competitive release. I found that exclusion of the dominant *Anartia* indeed resulted in many of these predicted changes in community diversity and species abundance relationships.

## Methods

### Study site

The Sirena Biological Station in Corcovado National Park, Costa Rica, is surrounded by coastal secondary evergreen forest with an adjoining $800 \times 40$ m airstrip. The airstrip is maintained by mowing the secondary growth, creating a habitat for the two nectar plants on which observations were taken and the two dominant *Anartia* butterfly species whose abundance was experimentally manipulated. The study lasted six weeks, from 3 July to 15 August 2003.

### Nectar plants and butterfly communities

There were two main nectar plants at the field site: *Lantana camara* (Verbenaceae) and *Wedelia* sp. (most likely *W. trilobata*, Asteraceae). *Lantana* was a large shrub with corolla tube measuring $\sim 10$ mm, *Wedelia* was a small gregarious herb with corolla tube measuring$\sim 2.5$ mm. I took observations on a large *Lantana* shrub juxtaposed with the field station at one end of the airstrip, and in an approximately 1500 m$^2$ patch of *Wedelia* at the other end of the air-strip. Both nectar plants were non-native with generalist pollination systems, and attracted a large number of nectar-feeding butterflies. Each nectar plant had a distinct butterfly assemblage, albeit with some species overlap (Appendix 1). On average, the *Lantana* assemblage had larger butterflies compared to the *Wedelia* assemblage as judged from the body size distributions (presented in the Results section), presumably because *Lantana* had larger

nectar reserves and probosces of larger butterflies were too large for the tiny *Wedelia* flowers. The *Lantana* butterfly assemblage was comprised of a greater proportion of evergreen forest species while the *Wedelia* assemblage was composed largely of species from dry forests and scrub. Two butterfly species that inhabit highly disturbed habitats, *Anartia fatima* and *A. jatrophae*, dominated both butterfly communities and comprised 60–90% of all individuals on *Lantana* and *Wedelia* at any time (Results). Their larvae feed on herbs that thrive on the airstrip, which supported unusually large populations of both species in the study area. *Anartia* started flying and foraging very early in the morning (typically around 07:30 a.m.) and, given their overwhelming abundance, they usurped the nectar resources, emptying the flowers even before most other species had started flying in the nectar patches, and keeping them drained of nectar later in the day (Results). Thus, the abundance of larval host plants of *Anartia* had led to their dominance in the nectar-feeding butterfly communities in the study area.

### *Anartia* removal experiment

In the first two weeks of the six-week study period, I took preliminary observations on the butterfly species that visited *Lantana* and *Wedelia*. In the third week I quantified the abundance, diversity and foraging behaviours of butterflies (see below) on the two nectar plants, which comprised my observations for the pre-removal treatment. In the fourth and fifth weeks I removed the entire *Anartia* populations from the study area – a total of $\sim 1200$ individuals, 60–70% of them *A. fatima* – by capturing them from the field site. Later, new individuals eclosing from pupae were removed the moment they were sighted, so that the removal of *Anartia* was largely successful: *Anartia* were represented on *Lantana* by 903 individuals in the pre-removal treatment and by 25 individuals (all *A. fatima*) in the post-removal treatment, and on *Wedelia* by 677 individuals in the pre-removal treatment and by zero individuals in the post-removal treatment. The near-complete removal of *Anartia* from the study area was possible because the *Anartia* populations were somewhat isolated from other such large populations by large tracts of forests (the nearest known populations were 3 km away), and the immigration rate was low. In the final (sixth) week, after the removal of *Anartia*, I repeated my observations on the abundance, diversity and foraging behaviours of butterflies. Note that the pre- and post-removal observations were separated only by two weeks, during which seasonal climatic changes that affect species abundance did not take place. Thus, the removal of the dominant *Anartia* butterflies largely, if not exclusively, seemed responsible for the observed changes in the diversity and composition of the butterfly communities in the two treatments.

### Abundance and species data

On both nectar plants I counted the number and species of butterflies in 15 five-minute sessions before and after I removed *Anartia* from the study area. During each session I counted all butterflies feeding on the *Lantana* bush and in a

70 × 2 m transect in the *Wedelia* patch. Counts were taken between 9 a.m. and 2 p.m. only on sunny days, when butterflies were active. The list and cumulative abundance of species are given in Appendix 1.

## Morphometrics of butterflies

In order to study the community composition in terms of the body size and proboscis length distributions in the pre- and post-removal treatments, I used two morphometric measurements of the 54 species that used *Lantana* and *Wedelia* as nectar plants during the study period. It was not possible at the time to measure body mass of live butterflies, so I used body length as a surrogate for body size. I measured proboscis length from the base of the labial palps to the tip, by inserting a needle in the center of the coiled proboscis and gently straightening it. I used an additional metric – relative proboscis length – calculated as the ratio of proboscis length to body length, since relative proboscis length, rather than raw proboscis length, affects the foraging efficiency of butterflies (Kunte 2007). I used Vernier calipers for all measurements, photographed the butterflies for identification purposes, marked them with a permanent marker to avoid recapture, and then released them. Capture and handling for morphometric measurements did not seem to harm the butterflies or cause significant dispersal (cf. Singer and Wedlake 1981): many of the butterflies I measured and marked revisited the plants on which they were first captured, and some of them were recorded for several days both on *Lantana* and *Wedelia*, which were 800 m apart. The number of morphometric measurements for each species depended on its commonness and ease of capture, and ranged from 1 to 10. Morphometric measurements given in Appendix 1 are averages for the species.

## Foraging behaviours

I chose a random sample of butterfly species to study two foraging behaviours: handling time and the proportion of flowers probed in an inflorescence. The two behaviours were chosen because they were expected to be sensitive to the amount of nectar available in flowers and the profitability of spending time on an inflorescence, which were affected by the presence or absence of *Anartia*. If the amount of nectar per flower increased in the post-removal treatment, I expected the butterflies to spend more time on the flower to sip more nectar from the flower (increasing the handling time) in the post-removal treatment. Similarly, if the nectar quantity and proportion of nectarful flowers in an inflorescence increased after the removal of *Anartia*, probing more flowers from the inflorescence before moving onto another inflorescence would increase nectar uptake rate in the post-removal treatment.

I calculated handling time as the time spent on an inflorescence in actually probing flowers, divided by the number of flowers probed in that inflorescence. These observations were also made between 9 a.m. and 2 p.m. The two behaviours were studied with between 8 and 25 observations per species.

## Plant data

I measured the volume of nectar per flower in three treatments: (1) before the removal of *Anartia*, (2) after the removal of *Anartia*, and (3) in bagged inflorescences before and after the removal of *Anartia*. For the last treatment, I bagged inflorescences with mosquito netting that allowed ambient levels of humidity, ventilation and light for the plants while preventing butterflies and other significant nectar-feeders from taking nectar. The first treatment represented nectar volume available to nectar-ivores in the face of competition from dominant *Anartia*, the second treatment represented nectar volume available in less competitive environments, and the third treatment represented the total amount of nectar produced by plants when no nectar was removed by nectarivores; i.e. the maximum amount of nectar available per flower at a given time. In the pre- and post-removal treatments, I measured nectar quantities at 08 a.m., before most butterflies started foraging, and at noon, when the foraging activity peaked. I measured nectar quantity only from fresh flowers by inserting a 1 µl (λ) capillary tube into a flower and directly measuring the amount of nectar drawn into the tube.

To confirm that flower density did not change between the pre- and post-removal treatments, I measured flower density of *Lantana* in a 1 m$^2$ patch on the *Lantana* shrub and of *Wedelia* in the 70 × 2 m belt transect in which I counted butterflies.

## Diversity indices

I used Fisher's $\alpha$, Simpson's index (the reciprocal form, $E_{1/D}$) and Shannon index (H′) (Magurran 2004) for testing differences in the diversity levels in the pre- and post-removal treatments. Fisher's $\alpha$ is a parameter of the log series, which is often used as a diversity index and pertains to the number of species represented by a single individual (or "singleton") in the samples. Simpson's index (D) measures "evenness" of species abundances in a community and Shannon's index measures information (in this case, diversity) in a system. These indices thus measure different components of species diversity in different ways.

## Statistical analyses

I computed the means and standard errors of the diversity indices with 1000 bootstrap randomizations using EstimateS (Colwell 2005). For other analyses, unless otherwise noted, I tested statistical significance of differences between the pre- and post-removal treatments with non-parametric Wilcoxon two-sample test due to non-normal data (Sokal and Rohlf 1995). I performed statistical analyses using JMP 6 and online statistical calculators (Boersma 2006, Kirkman 2006).

## Results

Outcomes of the removal of *Anartia* were very similar on both nectar plants, so only results for *Lantana* are described

below. Appendix 2 gives corresponding values, Tables and Figures for *Wedelia*.

## Impact of *Anartia* removal on nectar availability

*Anartia* substantially depleted the standing nectar crop available to other species before other species started foraging; by noon, flowers were almost empty. Removal of *Anartia* significantly increased the standing nectar crop (early morning: pre-removal: $0.0033 \pm 0.01$ µl, post-removal: $0.63 \pm 0.54$ µl, W = 2048.5, DF = 118, p < 0.0001; noon: pre-removal: $0.0003 \pm 0.0017$ µl, post-removal: $0.136 \pm 0.254$ µl, W = 2444.5, DF = 118, p < 0.0001). Nectar quantities in bagged flowers (pre- and post-removal treatments pooled: $0.957 \pm 0.52$ µl) were comparable to but still significantly higher than those in the mornings of post-removal treatment (W = 3031, DF = 118, p < 0.005), indicating that the removal of *Anartia* brought the standing nectar crop close to the quantities expected under less severe level of competition for nectar, in absence of the dominant species.

There was no difference in the nectar quantities in bagged flowers between the pre- and post-removal treatments (pre-removal: $1.00 \pm 0.498$ µl, post-removal: $0.91 \pm 0.546$ µl; W = 875.5, DF = 58, p = 0.56). Similarly, the density of *Lantana* flowers had not changed between pre- and post-removal treatments (pre-removal: $7.93 \pm 2.43$ inflorescences m$^{-2}$, post-removal: $7.47 \pm 2.33$ inflorescences m$^{-2}$; W = 219, DF = 28, p = 0.59). Thus, there were no changes in nectar quantity or flower density that could have influenced species diversity in the nectar-feeding butterfly community between the *Anartia* pre- and post-removal treatments.

## Change in the intensity of competition

The average number of individuals feeding on *Lantana* decreased between the pre-removal and post-removal treatments (W = 135, DF = 28, p < 0.0001; Table 1). This was because the two *Anartia* species comprised 80% of the total number of individuals foraging at a given time on *Lantana* before their removal. Notice, however, that the number of non-*Anartia* individuals foraging on *Lantana* actually

increased (W = 120, DF = 28, p < 0.0001; Table 1). The abundance of species that were present on *Lantana* before the removal also increased in most cases after the removal of *Anartia* (Appendix 1). Thus, excluding *Anartia* increased the standing nectar crop (the net amount of resource), simultaneously reducing competition for nectar and making it profitable for a higher number of non-*Anartia* individuals to forage on *Lantana*.

## Changes in community diversity

The exclusion of previously dominant *Anartia* butterflies had significant impacts on the diversity of the butterfly assemblage (Table 1, Fig. 1). The total number of species recorded in 15 counts almost doubled, from 23 to 39. The average number of species recorded per count also increased (W = 182.5, p = 0.04). Values of all the diversity indices were substantially higher in the post-removal treatment compared to the pre-removal treatment, indicating that diversity – measured as the total number of species, rare species and evenness in the community – was significantly higher in the post-removal treatment. Since numerical dominance of a few species alters the performance of diversity indices and may influence the shape of species rank/abundance or "Whittaker" plots without altering the underlying species ranks of other constituent species (Magurran 2004), I excluded *Anartia* from the dataset of the pre-removal treatment to see whether diversity *relationships* changed after the removal of *Anartia*, and re-computed the diversity indices. Values of the diversity indices differed significantly even between the pre-removal dataset excluding *Anartia* and post-removal treatment (Table 1). This indicated that the predominance of *Anartia* alone was not responsible for lower diversity index values in the pre-removal treatment. Instead, it showed that the removal of *Anartia* caused a fundamental change in overall diversity of the butterfly community. Whittaker plots (Fig. 1) bolstered this conclusion: the post-removal species distribution was significantly different, and more even, than the pre-removal species distributions with or without including *Anartia* in the dataset (analysis of covariance, or ANCOVA: $F_{5,77} = 9.15$; p < 0.0001).

Table 1. Differences in the abundance and diversity of butterfly assemblages on *Lantana* before and after the removal of the dominant *Anartia* butterflies. Mean and standard deviations are presented for average number of individuals and species. Significance values for diversity indices (Fisher's α, Simpson index and Shannon index) between pre- and post-removal treatments were calculated using the student's t-test on average bootstrap values from 1000 simulations in EstimateS. Mean and standard errors from the bootstrap simulations are given for the diversity indices.

|  | Pre-removal | Pre-removal without *Anartia* included in the dataset | Post-removal |
|---|---|---|---|
| Total individuals | 1126 | 223 | 399 |
| Avg. no. individuals per count | 75±19 | 15±5.1 | 27±3.3 |
| Total species | 23 | 21 | 39 |
| Avg. no. spp. per count | 10.5±2.6 | 8.5±2.6 | 12.8±2.4 |
| Fisher's α | 3.6±0.33 | 4.87±0.63 | 6.2±0.55 |
| Simpson index (E$_{1/D}$) | 2.53±0.06 | 8.08±0.74 | 10.28±0.32 |
| Shannon index (H′) | 1.43±0.03 | 2.38±0.06 | 2.63±0.03 |

p ≪0.0001 in all pair-wise comparisons between the pre- and post-removal treatments for all the diversity indices and for average number of individuals per count. For average number of species per count, p = 0.04 (see the text).
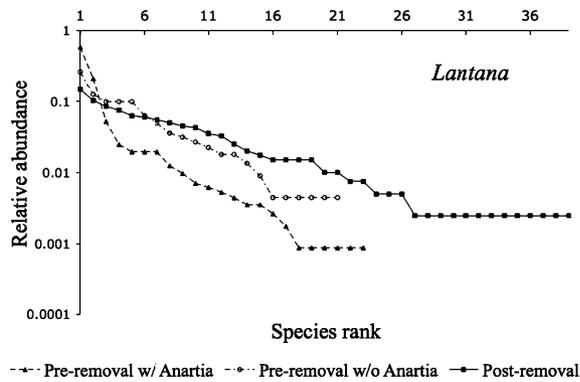
Fig. 1. Species rank/abundance or "Whittaker" plots for *Anartia* pre-removal and post-removal treatments on *Lantana*. Two plots are presented for pre-removal treatment, one including and the other excluding *Anartia* from the dataset.

## Changes in community composition

Average body length of the constituent species increased and four very large species were added to the nectar-feeding butterfly community (including the outliers in Fig. 2a; all swallowtail butterflies, Papilionidae). The proportion of larger species increased disproportionately after the removal of *Anartia* (notice the right-skewed box-plots and longer whiskers towards higher values in the post-removal treatments in Fig. 2). These patterns, however, were not statistically significant (body length: pre-removal: $17.67 \pm 4.72$ mm, post-removal: $19.2 \pm 6.28$ mm, W $= 617.5$, DF $= 57$, p $= 0.51$; Fig. 2a). The range of proboscis length similarly became non-significantly right-skewed as a result of the removal of *Anartia* (pre-removal: $14.9 \pm 4.76$ mm, post-removal: $15 \pm 5.15$ mm, W $= 664.5$, DF $= 57$, p $= 0.94$; Fig. 2b). Changes in the range of relative proboscis length were also not significant (pre-removal: $0.86 \pm 0.23$, post-removal: $0.8 \pm 0.22$, W $= 730$, DF $= 57$, p $= 0.27$; Fig. 2c). Thus, the community composition as measured by the ranges of the three parameters changed only slightly as a result of the removal of the dominant species.

## Changes in foraging behaviour

Since the removal of *Anartia* decreased both the number of nectarivores and competition for nectar but increased the amount of available nectar, handling time and the fraction of flowers probed were expected to change between the pre- and post-removal treatments. However, there were no significant differences in the two behaviours between the two treatments (Appendix 3).

## Discussion

Few studies directly link the dominance of species and intensity of competition to resource availability and diversity in large natural communities. By experimentally manipulating dominance and competition, this study showed that the two *Anartia* species had dramatic parallel impacts on both the nectar-feeding butterfly communities studied. The experiment showed that the competitively and numerically dominant *Anartia* had suppressed resource availability, ultimately affecting diversity of the butterfly communities by competitively excluding some species. The addition of four swallowtail butterflies (three *Papilio* and a *Parides*) to the *Lantana* community after the removal of *Anartia* was particularly illuminating. Their body sizes were three times larger than the average body size in the community (Fig. 2a, Appendix 1), and their nectar requirements must similarly be much higher. In the pre-removal treatment I had only seen one *Papilio* briefly visit *Lantana* outside my butterfly counts. Apparently the extremely low nectar quantity in the pre-removal treatment was not optimal for such large butterflies, so their visits to *Lantana* were infrequent and their residency time short. In the post-removal treatment, however, their visits became very rewarding in terms of nectar intake, and they visited *Lantana* regularly and in higher numbers (Appendix 1). Similarly, some smaller species were added to the community probably because the higher standing nectar crops allowed them to extract nectar more easily from flowers that
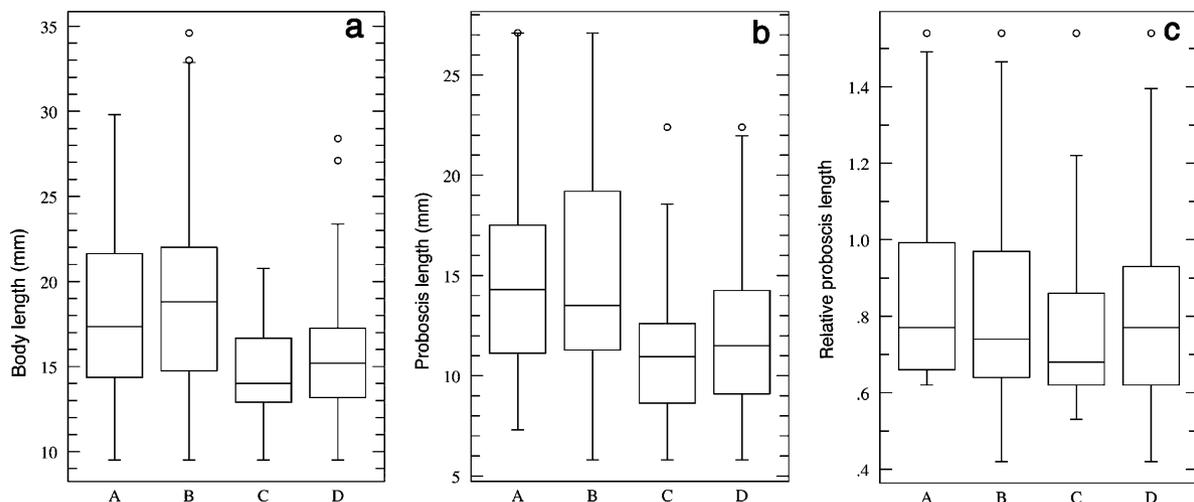


Fig. 2. Box plots of: (a) body length (size), (b) proboscis length, and (c) relative proboscis length, for *Anartia* pre-removal and post-removal treatments. *Lantana*: A: pre-removal, B: post-removal; *Wedelia*: C: pre-removal, and D: post-removal.

were as long as their probosces. Evidently, these species were previously competitively excluded from the community due to the predominance of and resource monopolization by *Anartia*. Thus, the removal of *Anartia*, which resulted in lower levels of competition and subsequent resource enrichment, increased the range of body size and proboscis length of constituent species in the community. Abundance of many other species also increased per count after the removal of *Anartia*. These two factors changed the species abundance relationships fundamentally, as revealed by comparisons between species abundance distributions of the pre-removal treatment without including *Anartia* in the dataset and the post-removal treatment. Thus, in this large community the dominance of species and resource competition directly influenced species abundance relationships.

Given the significant increase in nectar availability in the post-removal treatment, it was remarkable that foraging behaviour did not change. A possible explanation is that butterflies had high handling time in the pre-removal treatment in spite of the scarcity of nectar because they were trying to sip the trace amounts of nectar available in the face of intense competition from *Anartia*, whereas in the post-removal treatment they spent the same amount of time in sipping a higher quantity of nectar. The lack of response in the proportion of flowers visited was more intriguing. It is intuitive that butterflies would probe more flowers on a rewarding inflorescence than on a non-rewarding inflorescence, which would respectively correspond to inflorescences in the post- and pre-removal treatments in my experiment. Perhaps this behaviour is less plastic or needs a longer learning period. Removal of the dominant species and a subsequent increase in nectar quantity had probably altered some other behaviours, such as patch residency time, which was not studied. The lack of a significant response in the body size or proboscis length distribution was less intriguing because of a statistical constraint. The majority of species added to the butterfly communities after the removal of *Anartia* had a body size, proboscis length or relative proboscis length closer to the mean values in the pre-removal treatment. Hence, the addition of a few very large or small species did not cause a statistically significant change between the pre- and post-removal treatments, although the addition of some very large species was biologically significant, as mentioned above.

Marked seasonality in butterfly occurrence at higher latitudes is well-known, but even tropical butterflies show seasonal population fluctuations and many species occur highly seasonally (Owen 1971, DeVries et al. 1997, 1999, Kunte 1997). Care was taken to control for such seasonal effects by taking observations within two weeks of removing the dominant species. The experiment took place in the middle of the rainy season when there were no sudden climatic changes and consequent butterfly population fluctuations during the two weeks, so the changes reported here in the community properties were most likely solely due to the removal of *Anartia*. The extreme similarity in response of butterfly communities to the removal of *Anartia* on two very different kinds of nectar plants also suggests that suppression of community diversity was the predominant factor affecting these two communities. The only significant factor apart from dominance of *Anartia* that

could have affected the results is the changes in populations of other major nectarivores feeding on *Lantana* and *Wedelia*. Although this is quite possible, it is unlikely because: (a) hummingbirds and other nectarivore birds, which could affect nectar quantities and nectar-feeding butterfly communities, do not feed on either nectar plant at the field site, and (b) bees, nectar-feeding beetles, moths and other insects are known to compete with nectar-feeding butterflies (Porter et al. 1992) but these were also not reported on either nectar plant. There may be other, very small nectar-feeding arthropods feeding on these nectar plants but it is unlikely that they affected the nectar quantities as much as the larger and abundant *Anartia*. Thus, nectar availability and the changes in butterfly community diversity reported here were most likely not affected by non-butterfly members of the nectar-feeding community on the two nectar plants at the field site (cf. Dicks et al. 2002), or due to seasonal changes.

It is important to note that the observed changes in community diversity were most likely due to a behavioral response (i.e. increased visitation rates and residency time of butterflies on the nectar plants), and not a demographic response (increase in population sizes of non-*Anartia* species). This distinction is important. In Paine's (1974) classical experiments with intertidal invertebrate communities, for example, the major changes in community diversity and structure were a demographic response of constituent species over a longer time period. In my experiment the increase in community diversity and number of individuals that visited the nectar plants was a short-term ecological response and the species enrichment of the nectar-feeding butterfly community was from the larger species pool in the area. Higher levels of nectar-intake increase fecundity in butterflies (Mevi-Schütz and Erhardt 2005, Beck 2007), so it is conceivable that the increased access to nectar for the non-*Anartia* species in the butterfly communities studied here would produce a demographic response in the long term. Unfortunately, this could not be studied during the study period. Since there was a considerable amount of standing nectar crop in the flowers after *Anartia* were removed, it is not known whether the community size would have increased further with time with the addition of other species that were also competitively excluded from the community earlier, or whether proportions of the existing species would have increased to exploit the increased nectar quantities. A similar study with long-term monitoring of the changes in community diversity and composition would be very helpful to test whether long-term changes are qualitatively or quantitatively different from the short-term changes reported here.

In the larger community ecology context, although dominance, niche partitioning and resource competition were the initial explanations for relative species abundance distributions (MacArthur 1957, 1960), studies trying to demonstrate competition and competition-based patterns of community structure and species abundance distributions have been riddled with methodological, experimental and interpretational pitfalls (reviewed by Strong et al. 1981). Recently, alternative explanations for species abundance distributions have been gathering support. For example, numerous studies have shown that local species abundance distributions are strongly influenced by large-scale

geographic range distributions of constituent species (Brown 1984, Gaston 1996, Venier and Fahrig 1996). The unified neutral theory of biodiversity has similarly argued for non-competitive explanations for species abundance patterns (Hubbell 2001). Although competition, neutral processes and distribution-abundance relationships all seem likely explanations each with strong theoretical support, experimental support for any biological explanations for species abundance distributions still remains scarce. The distribution-abundance relationships explain a small proportion of variance in local species abundance distributions (Gaston 1996). The neutral and non-neutral explanations of biodiversity and relative species abundance patterns continue to be contentious (McGill 2003, Volkov et al. 2003). Moreover, biological significance and utility of statistical models of species abundance distributions have remained controversial (Tokeshi 1999, Magurran 2004, Nekola and Brown 2007).

In this light, my study presents one of the rare experimental examples of the role of direct competition in shaping the species abundance distributions in large natural communities. In this system, dominant species affected species abundance relationships via resource competition to such an extent that a large number of species were excluded from the community. Similar intra-guild competitive interactions and resultant species abundance relationships are probably common in many nectar- and fruit-feeding animal communities. The changes in species abundance relationships and community diversity observed in this study after the experimental suppression of dominant species may thus be instructive of the ways in which species in the same guilds compete and influence the size and species abundance relationships in other similar natural communities. Finally, many invasive species alter community characteristics in much the same way as native *Anartia* affected the butterfly communities studied here: their numerical and competitive dominance skews species abundance distributions more prominently, reduce local species diversity and may ultimately cause extinctions in the communities they invade (Silliman and Bertness 2004, Clavero and Garcia-Berthou 2005, Schutzenhofer and Valone 2006). It remains to be seen whether the current massive operations to exterminate or control invasive species, if successful, result in reversal of community structural characteristics, increased community diversity and less skewed species abundance relationships as found in the Costa Rican butterflies communities presented here.

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