

# Direct and indirect effects of interspecific competition in a highly partitioned guild of reef fishes

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**Abstract.** Competitive interactions and resource partitioning facilitate species coexistence in complex ecosystems. However, while pairwise interactions between ecologically similar species have been well studied, multi-species competitive networks have received less attention. When interference competition between two species results in partitioning of resources, this may have indirect consequences for other species distributed along the same resource gradient. Here, we tested whether interference competition between two territorial damselfish influenced the fine-scale species distributions of five other territorial damselfish in Kimbe Bay, Papua New Guinea. These species partition habitat across three reef zones—the flat, crest, and slope, with distinct patterns of distribution within these zones. We predicted the two species with similar distributions and microhabitat use, *Pomacentrus adelus* and *Pomacentrus bankanensis*, would display the greatest level of aggression toward one another. This was tested through an intruder experiment where stimulus fish were introduced into a resident's territory, which confirmed disproportionately high levels of interspecific aggression between these two species. We also predicted that the fine-scale differences in the distribution of each species were maintained through multi-species interference competition among neighboring species, with further indirect effects on species that did not directly interact. To test this, we conducted a large-scale (22 × 10 m) experimental removal of the most abundant species, *Po. adelus*, and quantified the abundance and distribution of all territorial damselfish species for 6 months to a 25 cm resolution. The main direct competitor, *Po. bankanensis*, exhibited a marked increase in abundance and expanded its distribution (+1.33 m) to acquire the space previously occupied by *Po. adelus*. This competitive release triggered indirect effects on the distribution of other neighboring species further back on the reef flat, with *Chrysiptera unimaculata* moving into the zone formerly occupied by *Po. bankanensis*. This study indicates that the distinct distribution patterns among the reef crest species are linked to levels of interspecific agonistic behavior. We argue that the competitive release following the removal of a superior competitor resulted in both direct and indirect effects, with the immediate neighbor shifting into the newly available space, followed by successive shifts in species responding to the change in the distributions of their immediate neighbors.

**Key words:** aggression; agonistic behavior; coral reef; damselfish; distribution gradient; species loss; intruder experiment; multi-species; niche; Papua New Guinea; removal experiment; resource partitioning.

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## INTRODUCTION

Competitive interactions among ecologically similar species are fundamental in shaping many ecological communities (Connell 1978, Schoener

1983). In structurally complex ecosystems (e.g., tropical forests and coral reefs), each species occupies an ecological niche in which it is the most effective competitor (Whittaker et al. 1973). Traditionally, interspecific competition for finite

resources was viewed in terms of a winner and a loser with the dominating species either partitioning or eliminating the subordinate from the habitat (Case and Gilpin 1974, Colwell and Fuentes 1975, Diamond 1978). Ecological theory has progressed from a focus on pairwise interactions to a multifactorial perspective of the processes and mechanisms that govern competition within a community (Jones 1991, Hixon et al. 2002, Wiens et al. 2010, Cipresso Pereira et al. 2015). However, experimental studies on interspecific competition are still dominated by studies testing the effects pairs of species have on one another (Bonin et al. 2015). Hence, our empirical understanding of competitive networks has been limited by the absence of detailed information on the extent of resource partitioning and competition at a community scale, and the effects of interactions among species that do not come into direct contact (Amarasekare 2003, Salomon et al. 2010, Siepielski and McPeck 2010, Hixon 2011).

When resources are limited, theory holds that species may coexist by partitioning resources via *exploitative competition* (depletion of a common resource) or *interference competition* (aggressive interactions that prevent access to a resource; Case and Gilpin 1974, Schoener 1983). While competition theory is largely based on exploitative competition among sympatric species (Amarasekare 2002), interference competition is the main mechanism leading to interspecific differences in patterns of distribution or use of resources. There is ample empirical evidence that interference competition influences the abundance or distribution of subordinate species for insects (Kunte 2008), birds (Pimm et al. 1985), mammals (Brown 1971), and fishes (Robertson and Gaines 1986, Munday et al. 2001, McCormick and Weaver 2012). In nature, interference competition is linked to interspecific territoriality and aggressive interactions among species that regularly come into contact, with the most aggressive species gaining priority access to resources (Grether et al. 2013). Experimental removals of dominant species invariably result in niche expansion of inferior competitors (Paine 1966, 1974, Robertson 1996, Kunte 2008). Species in the community that do not openly share a resource or compete may be indirectly linked by species that lie between them on a resource axis. Hence, when interference competition between two

species results in a partitioning of resources, this may have indirect consequences for other species distributed along the same resource gradient.

In community ecology, indirect or knock-on effects are most often observed as cascading effects between trophic levels, as a result of predator–prey, plant–herbivore interactions. Indirect effects, generally defined as how one species alters the effect that another species has on a third, can include a multitude of phenomena where the presence or density of a species influences the community (reviewed by Strauss 1991). The most well-known aquatic examples include the removal or extinction of keystone predators, triggering subsequent competitive exclusion (Paine 1966, 1974) or an ecosystem shift (Hughes 1994, Dayton et al. 1998). Changes to important trophic links between two species can indirectly alter the distribution and abundance of species between trophic levels. However, they can also have indirect effects on interactions among species within the same trophic levels (Pace et al. 1999, Shurin et al. 2002). Similar knock-on effects of subordinate competitors within trophic levels may be present after the collapse of a primary competitor and have received much less attention (Navarrete et al. 2000, Gosnell and Gaines 2012).

Coral reefs are composed of a complex network of hard corals that support rich communities of fish. Historically, the role of interspecific competition and niche partitioning in explaining the coexistence of many ecologically similar coral reef fishes was controversial. While early ecologists emphasized niche partitioning (Smith and Tyler 1972, Robertson and Lassig 1980), Sale (1977, 1978, 1980) provided evidence that competition for space was more of a lottery, with stochastic recruitment preventing any one species from excluding others. The underlying assumption of intense competition for space was later challenged, and for many years, the idea that reef fish communities were limited by recruitment prevailed in the literature (Doherty 1983, Doherty and Fowler 1994). Nevertheless, researchers have continued to address basic ecological interactions such as competition and predation (see reviews by Hixon 1991, Jones 1991, Hixon and Webster 2002, Jones and McCormick 2002, Forrester 2015, Hixon 2015). Several decades of research have generated a substantial amount of evidence that limited available habitat can result in competitive

interactions, which in turn influences the structure of reef fish communities (Robertson 1996, Holbrook and Schmitt 2002, Forrester et al. 2006, Boström-Einarsson et al. 2014). Further, interactions among interspecific competitors play an important role in reef fish spatial distributions (Robertson and Gaines 1986, McCormick and Weaver 2012). However, the majority of evidence for mobile reef fish species has involved measuring pairwise interactions experimentally and not expanded competitive networks within a community (see reviews by Forrester 2015, Bonin et al. 2015). Few studies have documented competitive interaction networks between species with similar resource requirements.

In reef fish ecology, removal experiments can be used to measure the effect of a species on its environment at a community scale. Studies have demonstrated that the selective removal of fishes from a habitat is followed by a redistribution of conspecific (Williams 1978, Webster and Hixon 2000, Meadows 2001) and heterospecific (Belk 1975, Sale 1978, 1979, Robertson and Gaines 1986, Robertson 1996) neighboring species. Of the studies that demonstrated heterospecific acquisition of space following the removal of a dominant competitor, few studies examined more than one competitor within the community (but see, Sale 1978, 1979, Robertson and Gaines 1986, Robertson 1996). Additionally, most studies have used field experiments to measure variation in the strength of competition spatially, but few expand on this to look at how species respond over time (Schmitt and Holbrook 2007, Forrester and Steele 2008, Hixon et al. 2012). By examining how species recover after a selective removal, we can address how and whether competitive interactions and recruitment interact.

Guilds of territorial damselfish (Pomacentridae) provide ideal model systems for understanding the outcomes of competition. Territorial damselfish play an integral role in the structure of coral reefs through their abundance and role as small-bodied consumers (Hata and Kato 2004, Ceccarelli et al. 2005a, Jones et al. 2006). For most species, ecological parameters, or the measurable niche properties whose value is a determinant of the ecosystem characteristics, can be effectively obtained due to their highly site attached habits, territorial behaviors, and lack of concern for observer presence (Ceccarelli et al. 2005b,

Ceccarelli 2007). Furthermore, patterns of distribution and partitioning of space along the natural reef profile gradient—the reef flat, reef crest, and reef slope, have been well documented (Robertson and Lassig 1980, Waldner and Robertson 1980, Meekan et al. 1995, MacDonald et al. 2018). A distinctive pattern of zonal distribution along this steep physical gradient provides an experimentally tractable system for isolating the direct and indirect effects of any one species on all others occupying the same resource gradient.

In the present study, we explore the direct and indirect effects of agonistic interactions and interference competition on distribution and abundance in a guild of seven territorial damselfish. At our study location (Kimbe Bay, Papua New Guinea), these species partition the reef flat, reef crest, and upper reef slope habitats on a fine scale (1–2 m; Ceccarelli 2007, Eurich et al. 2018a). All species are aggressive and defend discrete territories (mean 1–1.5 m<sup>2</sup> territory sizes per individual) against conspecifics, interspecific competitors, and other benthic feeding fishes (Ceccarelli 2007, Eurich et al. 2018b). Eurich et al. (2018a) found that neighboring damselfish constrain their microhabitat use to facilitate the cohabitation of reef zones, but that microhabitat selectivity alone was insufficient in explaining the distinct zonation and limited distributional overlap. Additionally, it was suggested that interspecific aggression helps maintain the distributional boundaries between neighboring species. Two abundant species, *Pomacentrus adelus* and *Pomacentrus bankanensis*, have overlapping distributions with similar microhabitat use and selectivity. The partitioning raises the question of whether the presence of *Po. adelus* alters the abundance and distribution of *Po. bankanensis* and other species within the community. However, an experimental removal of a dominant competitor is necessary to see whether interference competition is present and whether subordinate distributional shifts would occur.

Here, we employ an observational experiment and a manipulative field experiment to examine the intensity of agonistic interactions among species and the extent to which *Po. adelus* influences the distribution and abundance of neighboring and non-neighboring species in the guild. To test which species *Po. adelus* is most likely to competitively influence, we conducted

an intruder experiment to measure aggression. We hypothesized (1) *Po. adelus* and *Po. bankanensis*, the co-inhabiting species with similar microhabitat use, would display the greatest levels of aggression to each other compared to other neighboring species. We then evaluated the direct and indirect effects of a competitive release from *Po. adelus* on the distribution and abundance of other species in the guild using a long-term experimental removal of *Po. adelus*. Spatial patterns of all territorial damselfish were described down to a resolution of 25 cm prior to the experimental field manipulation and continuously thereafter for 6 months. Post-removal, we predicted (2) *Po. bankanensis* would increase in abundance and expand its distribution to acquire the previously occupied space; (3) adjacent reef flat species would also increase in

abundance and spatially shift toward the preferred habitat due to *Po. bankanensis* having the ability to occupy the reef crest; and (4) the larger reef crest occupying species, *Plectroglyphidodon lacrymatus*, and the two species associated with the reef slope, *Neoglyphidodon nigroris* and *Pomacentrus burroughi*, would be unaffected due to lack of resource overlap.

## MATERIALS AND METHODS

### Study location and species

The study was conducted on inshore platform reefs in Kimbe Bay, West New Britain, Papua New Guinea (Fig. 1; 5°30' S, 150°05' E), between July 2015 and March 2016. Kimbe Bay lies within the Indo-Australian Archipelago (Coral Triangle),

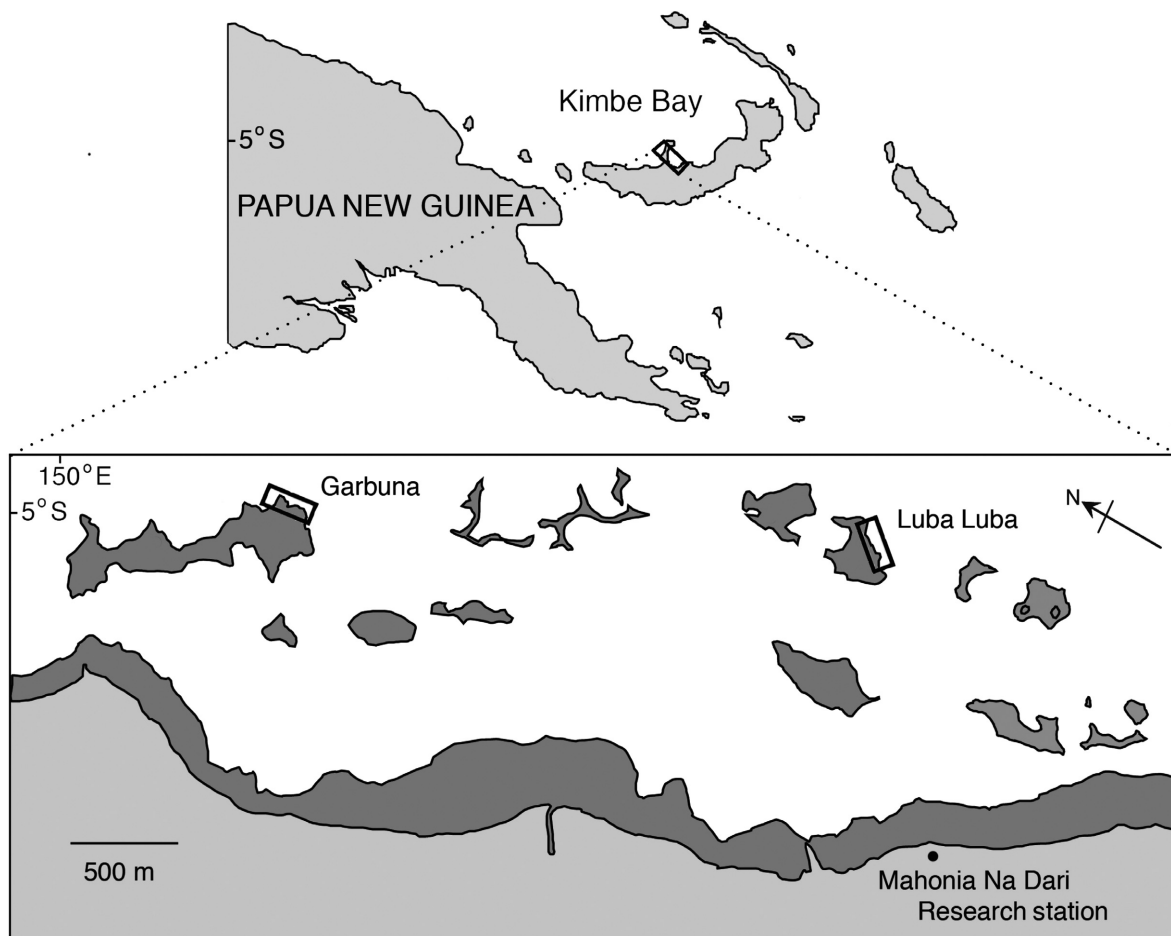


Fig. 1. Map showing the location of Kimbe Bay, West New Britain, Papua New Guinea, and study locations (Garbuna and Luba Luba) within the Tamare-Kilu reef sector.



a region recognized for exceptionally high diversity of fish and corals (Roberts et al. 2002). Extensive preliminary surveys were conducted in the Tamare-Kilu reef sector to find reefs with similar aspect and topography. All work, including quantifying the intensity of agonistic interactions and a removal experiment, was conducted on two reef locations (Garbuna and Luba Luba; Fig. 1). The observational experiment and the manipulative field experiment were executed on different areas of the reefs to assure individuals were not manipulated twice. Study sites were located on sections of reef with non-exposed reef flats, an unbroken and continuous reef crest, and steady non-vertical reef slopes to >10 m. Although sections of the reef flat break the surface, the tidal range here is relatively small (1 m) and the study locations were not exposed at low tide.

The seven species of benthic associated territorial damselfish found in Kimbe Bay are found along a gradient that extends from the reef flat to the reef crest and down the reef slope in the respective order (max size from Kimbe Bay, J. G. Eurich, unpublished data): *Pomacentrus tripunctatus* (9 cm), *Chrysiptera unimaculata* (7 cm), *Pomacentrus bankanensis* (7 cm), *Pomacentrus adelus* (7.5 cm), *Plectroglyphidodon lacrymatus* (10 cm), *Neoglyphidodon nigroris* (10 cm), and *Pomacentrus burroughi* (8 cm). The study species occupy a similar ecological niche and rely on microhabitats that mainly consist of dead coral fragments (rubble), sediment or detritus, and filamentous algae (Ceccarelli 2007, Eurich et al. 2018a).

#### Levels of interspecific aggression

Levels of aggression can be an indicator of the intensity of interference competition, with species competing for similar resources likely to be more aggressive toward one another. Eurich et al. (2018a) reported that conspecifics and neighboring species at the study site elicited significantly higher aggression, compared with heterospecific and non-adjacent species, and that levels of aggression were higher on the reef crest. Here, we employed a bottle experiment, where a stimulus individual is experimentally introduced into a resident's territory (Myrberg and Thresher 1974, Bay et al. 2001, Osório et al. 2006), to quantify levels of aggression among species to predict the competitive influence of *Po. adelus*, the most abundant species on the reef crest (Eurich et al.

2018a). The aim was to quantify levels of *Po. adelus* aggression toward potential competitors, the six damselfish, and the reciprocal levels of aggression of potential competitors toward *Po. adelus*. Stimulus fishes were captured using an anesthetic and hand nets and kept in a holding tank for 15–30 min prior to use to regain normal behavior. First, to elicit aggression, a stimulus individual was placed in a 9-L seawater-filled weighted transparent bag inside a *Po. adelus* territory (following Bay et al. 2001) and the intensity of responses by *Po. adelus* toward the stimulus was quantified. Second, bagged *Po. adelus* were introduced into the territories of the six potential competitors and the intensity of responses toward *Po. adelus* was quantified. A control treatment, in which each response fish was presented with an empty bag, was also applied. After observing the resident species for 4–5 min to establish the territorial boundaries, the stimulus bags were introduced into the center of the territory and secured to the substratum. The frequency and intensity of responses were recorded for 5 min (following the aggressive categories used in Eurich et al. 2018a; displays, charges, and bites). Each replicate was conducted using a different resident fish. To obtain aggression estimates for the different combinations of stimulus (six competing damselfish, *Po. adelus*, and an empty bag control) and resident treatments, each resident was exposed to each type of stimulus 10 times. Negligible interactions were made toward the control stimulus, so it was omitted from analyses (0.02 mean interactions per trial).

Aggression trials were analyzed separately by resident species using a generalized linear mixed-effects model. The distribution of the response variable (count of aggressive interactions: representing the summation of displays, charges, and bite attempts) was significantly different from normality (Kolmogorov–Smirnov [K-S] test,  $P < 0.05$ ) due to frequent low-intensity aggression and minimal high-intensity aggression for some species. Therefore, the parameter estimates, coefficients, and 95% likelihood profile confidence intervals for the model were fitted using a negative binomial family for overdispersion (using Pearson goodness of fit as the dispersion statistic). Location (reefs, Garbuna and Luba Luba) was considered a random factor in the mixed model. Differences in levels of aggression toward

stimulus species were tested using Tukey's honestly significant difference (HSD).

### Removal experiment

To examine whether the removal of a dominant species affected the spatial distributions of neighboring species, we conducted a controlled large-scale experimental removal of *Pomacentrus adelus*. Two plots, a removal (treatment) and control, measuring 22 m in length from the reef flat to the upper reef slope and 10 m wide (220 m<sup>2</sup> total monitoring area per plot), were established on each of the two reef locations (Garbuna and Luba Luba). The paired removal and control plots were set approximately 75 m apart, with the plot treatment type assigned randomly. The plots (removal:  $n = 2$ ; control:  $n = 2$ ) were spaced to ensure they were independent and sized so as to include the total habitat distribution limits of *Po. adelus*. Territorial damselfish are highly site attached with home ranges  $\sim 1\text{--}2\text{ m}^2$  (reviewed by Ceccarelli et al. 2001), so all fish observed on the grid were residents. To facilitate the census of fishes, individual plots were divided with permanent nylon strings and metal rods into eleven  $2 \times 10\text{ m}$  contiguous transects forming rectangles that stretched parallel to the reef crest. Additionally, each nylon string was visibly marked at 2 m intervals creating a  $2 \times 2\text{ m}$  grid throughout. All plots were established around the existing *Po. adelus* distribution with roughly 12 m of reef flat and 10 m of reef slope on either side of the central reef crest. In the present study, we refer to this lower area as the reef slope, but acknowledge it is the upper section of this habitat.

All individuals of *Po. adelus* were speared from the two removal plots and along a 5 m buffer around the plot to limit immigration into the census plots. A total of 321 and 275 individuals were removed over a 1 d period from the two removal plots. There was no immigration into the experimental plots from *Po. adelus*, but other adult species moved freely into the plot from bordering territories. Following the removal, no further *Po. adelus* were disturbed or removed and natural recruitment was permitted. Control plots were artificially disturbed with divers emulating removal techniques and swimming patterns.

The abundance and distribution of damselfish were quantified, both before and after the removal, down to a resolution of 25 cm with the

use of the spatial grids. Fish were censused over the gridded area at high tide, and each fish was identified to species, placed into a developmental category (recruit, juvenile, medium adult, and large adult), and its position was plotted on a scaled map. Individual fish positions were then entered as coordinates for analysis. Territorial damselfish were censused three times pre-removal and five times post-removal. Pre-observations were made on alternating days prior to the removal (pre 1: 5 d prior; pre 2: 3 d prior; and pre 3: the day of removal or time 0), with the final pre-removal survey occurring directly before the removal. Post-observations were conducted the following morning (post 1 d) and consecutively thereafter: post 3 d, post 1 week, post 3 months, and post 6 months.

To examine differences in abundance after the removal, species were separately tested for unequal distribution between time period (fixed continuous factor), after accounting for differences between location (random factor: Garbuna, Luba Luba) using a repeated-measures analysis of variance and a generalized linear mixed-effects model with Poisson distribution. A conservative test for compound asymmetry was used for time to address the auto-correlated nature of time series data. The three pre-removal surveys were treated as nested replicates ( $n = 3$ ) within the pre-removal time category. The pre-removal abundances were then compared to the post-removal abundances for each time periods using Tukey's post hoc pairwise comparisons of levels within significant factors to assess changes in abundance over time. Recruits (<1 cm) of all species (other than *Po. adelus*, which was analyzed separately) were omitted from the final analysis due to irregular recruitment pulses and high mortality.

Coordinate data within the spatial grids were used to determine whether other species would shift their distributions to acquire the space previously occupied by *Po. adelus*. For each survey period (pre-removal and 6 months post-removal), species' abundances were binned into 1 m increments from the reef flat to the reef slope ( $1 \times 10\text{ m}$  contiguous rectangles,  $n = 22$ ) parallel with the reef crest for presentation. A two-sample K-S test was used to determine whether the two distributions significantly differed. The mean center of each population pre-removal was calculated and compared graphically to 6 months post-

removal to quantify movement over time. Replicate pre-removal surveys were used to estimate natural spatial variability.

## RESULTS

### Levels of interspecific aggression

The intruder experiment confirmed the presence and asymmetry of aggression between *Pomacentrus adelus* and the other six territorial damselfishes. The levels of aggression *Po. adelus* displayed against *Pomacentrus bankanensis* were significantly higher than any other stimulus species (8.5 mean interactions per trial; Tukey's HSD,  $P = 0.001$ ; Fig. 2a). Reef flat species, *Pomacentrus tripunctatus* (2.3 mean interactions per trial) and *Chrysiptera unimaculata* (4.2 mean interactions per trial), received lower levels of aggression when compared to *Po. bankanensis* (Tukey's HSD,  $P = 0.008$ , and  $P = 0.026$  respectively). While *Po. adelus* displayed some aggression toward all stimulus species, less aggression was observed in trials with *Plectroglyphidodon lacrymatus* (1.9 mean interactions per trial; Tukey's HSD,  $P = 0.004$ ) and the reef slope associated species, *Neoglyphidodon nigroris* (2.3 mean interactions per trial;  $P = 0.009$ ) and *Po. burroughi* (1.8 mean interactions per trial;  $P < 0.0001$ ).

When *Po. adelus* was the intruder within the plastic bag, they elicited the greatest amount of aggression from *Po. bankanensis* compared to other resident species (Tukey's HSD,  $P < 0.0001$ ; Fig. 2b). *Pomacentrus bankanensis* displayed the highest amount of aggression toward *Po. adelus* at 11.7 mean interactions per trial followed by *Pl. lacrymatus*, which displayed 4.8 mean interactions per trial toward *Po. adelus*. Additionally, *Po. bankanensis* showed the highest rate and variability of aggressive behaviors, ranging from 3 to 49 agonistic interactions per trial. All other resident species exhibited lower aggressive interactions at  $\leq 2.4$  mean interactions per trial.

### Removal experiment

**Abundance.**—The abundance of the removed species, *Po. adelus*, was successfully reduced to 0 immediately following the removal (post 1 d; Fig. 3a). Additionally, there was no immigration from neighboring adults, as no adult *Po. adelus* were observed in the subsequent post 3 d and post 1 week census periods. Recruitment of *Po. adelus* did occur 3 d post-removal ( $3 \pm 1$ , mean

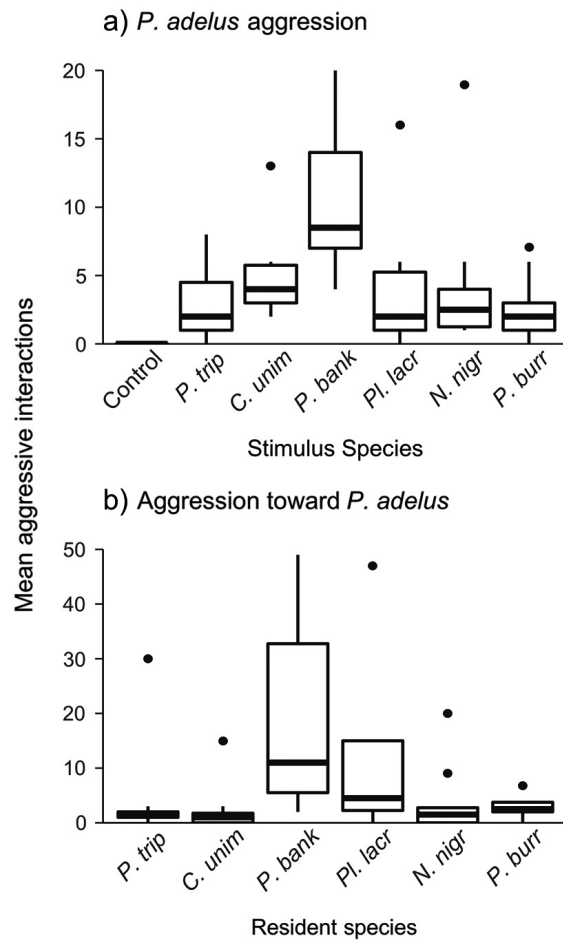


Fig. 2. Mean aggressive interactions of (a) *Pomacentrus adelus* toward conspecific stimulus species and (b) conspecific resident species toward *Po. adelus* per 4 min trial. Box and whisker plot displays lowest and highest values, with the box showing interquartile range, the median represented by the bold line, and outliers represented as black dots. Vertical axes are not comparable. Species: *Pomacentrus tripunctatus*, *Chrysiptera unimaculata*, *Pomacentrus bankanensis*, *Pomacentrus adelus*, *Plectroglyphidodon lacrymatus*, *Neoglyphidodon nigroris*, *Pomacentrus burroughi*.

individuals per  $220 \text{ m}^2 \pm$  standard error within replicates) and increased to pre-removal amounts 1 week post-removal ( $11 \pm 1$ ; Tukey's HSD,  $P = 0.984$ ; Fig. 3b). Despite regular recruitment, *Po. adelus* abundance remained significantly low 3 months ( $14 \pm 5$ ; Tukey's HSD,  $P < 0.0001$ ) and 6 months post-removal ( $39 \pm 7$ ) when compared to the pre-removal census ( $153 \pm 8$ ;  $P < 0.0001$ ).

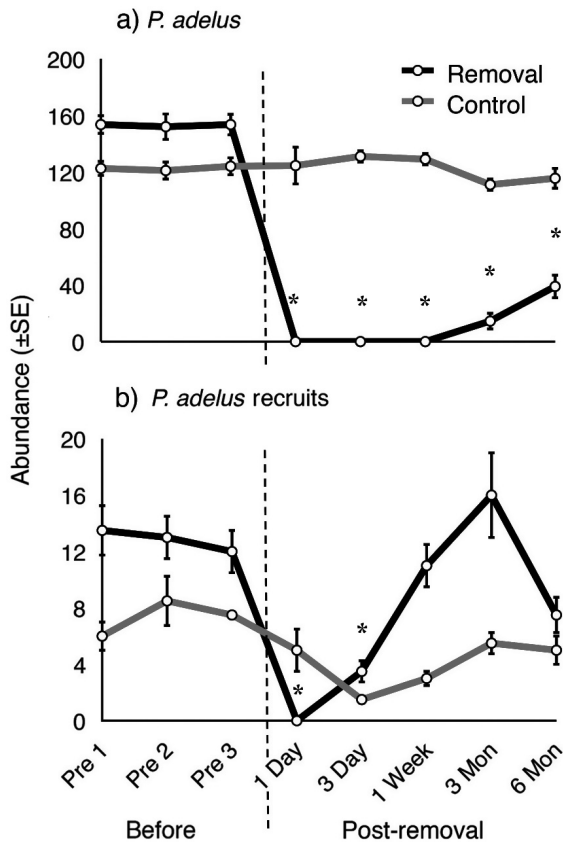


Fig. 3. Species abundances ( $\pm$  standard error) on removal (black,  $n = 2$ ) and control plots (gray,  $n = 2$ ) of (a) *Pomacentrus adelus* and (b) *Po. adelus* recruits before and consecutively after the experimental removal of *Po. adelus* denoted by the dashed line. Asterisks represent significantly different values ( $P \leq 0.05$ ) from the pre-removal abundance levels using Tukey's post hoc pairwise comparisons (Appendix S1: Table S1 for values). Vertical axes are not comparable.

However, a significant increase in abundance was observed when comparing post 3 months to post 6 months (Tukey's HSD,  $P < 0.0001$ ).

The experimental removal of *Po. adelus* significantly altered the abundance of all reef flat associated species. *Pomacentrus bankanensis*, the main co-inhabiting species of *Po. adelus* with similar microhabitat use, immediately increased in abundance from pre-removal levels of  $24 \pm 4$  individuals to  $32 \pm 5$  individuals 3 d post-removal as adults immigrated into the plot (Fig. 4a; Appendix S1: Table S1). Moreover, *Po. bankanensis*

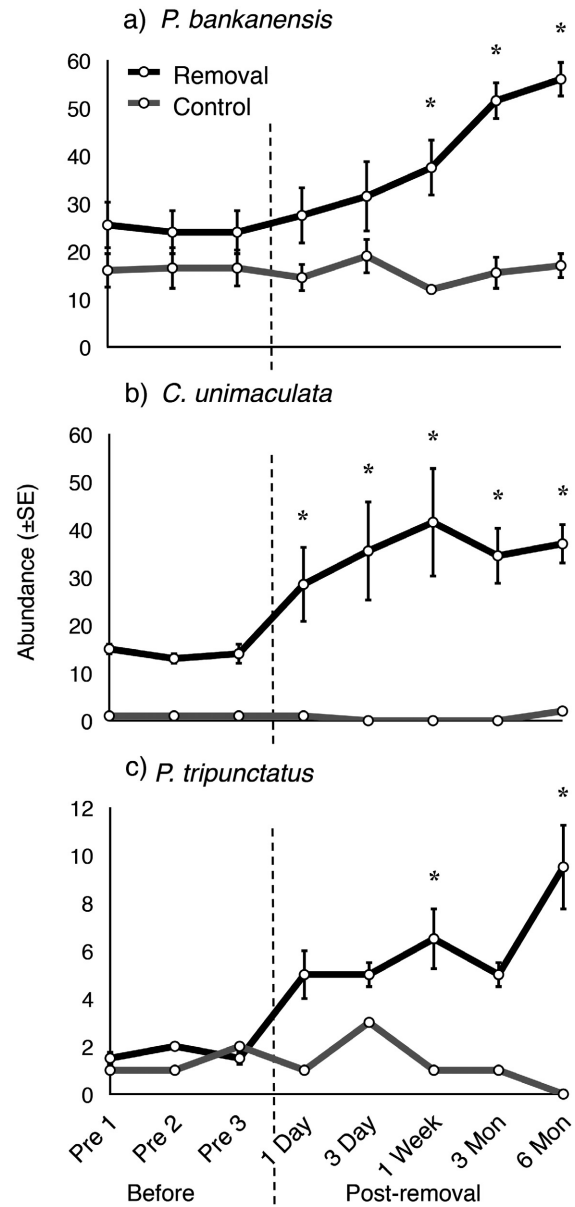


Fig. 4. Species abundances ( $\pm$  standard error when available) on removal (black,  $n = 2$ ) and control plots (gray,  $n = 2$ ) of (a) *Pomacentrus bankanensis*, (b) *Chrysiptera unimaculata*, and (c) *Pomacentrus tripunctatus* before and consecutively after the experimental removal of *Pomacentrus adelus* denoted by the dashed line. Asterisks represent significantly different values ( $P \leq 0.05$ ) from the pre-removal abundance levels using Tukey's post hoc pairwise comparisons (Appendix S1: Table S1 for values). Vertical axes are not comparable.



abundance continued to significantly increase compared to pre-removal levels 1 week ( $38 \pm 5$ ; Tukey's HSD,  $P = 0.032$ ), 3 months ( $52 \pm 4$ ;  $P < 0.0001$ ) and 6 months post-removal ( $56 \pm 3$ ;  $P < 0.0001$ ).

This pattern was also observed with *C. unimaculata*, which was distributed further onto the reef flat than *Po. bankanensis* (Fig. 4b; Appendix S1: Table S1). *Chrysiptera unimaculata* immediately increased in abundance 1 d ( $29 \pm 8$ ; Tukey's HSD,  $P < 0.0001$ ), 3 d ( $36 \pm 10$ ,  $P < 0.0001$ ), and 1 week post-removal ( $42 \pm 11$ ,  $P < 0.0001$ ) from pre-removal levels ( $14 \pm 1$ ) and remained stable 3 months ( $35 \pm 6$ ,  $P < 0.0001$ ) and 6 months thereafter ( $37 \pm 4$ ,  $P < 0.0001$ ).

*Pomacentrus tripunctatus* increased in abundance following the removal of *Po. adelus* despite not having any distributional overlap with *Po. adelus* (Fig. 4c; Appendix S1: Table S1). Abundance increased compared to pre-removal censuses from  $2 \pm 0$  individuals pre-removal to  $5 \pm 1$  (Tukey's HSD,  $P = 0.135$ ) individuals 1 d post-removal and  $5 \pm 0$  ( $P = 0.136$ ) individuals 3 d post-removal. *Pomacentrus tripunctatus* continued to increase significantly 1 week post-removal ( $7 \pm 1$ ; Tukey's HSD,  $P = 0.015$ ) and remained significantly higher than pre-removal levels 6 months thereafter ( $10 \pm 2$ ,  $P < 0.0001$ ).

As predicted, all other reef crest and reef slope associated species were unaffected by the removal of *Po. adelus* (Appendix S1: Fig. S1a–c). Despite occupying similar distributions on the reef crest, *Pl. lacrymatus* abundance remained constant throughout the experimental period (Tukey's HSD,  $P = 0.970$ ). Additionally, the abundance of *N. nigroris* and *Po. burroughi* on the reef slope was unaffected (Tukey's HSD,  $P = 0.990$  and  $P = 0.937$ , respectively). On all control plots, there were no significant changes in abundance observed for any species over the monitoring period (Appendix S1: Table S2).

**Distribution.**—The interspecific competitors that increased in abundance following the removal of *Po. adelus* also exhibited significant distributional shifts 6 months thereafter within the removal plots (Fig. 5a, b; Appendix S1: Table S3). The three populations of reef flat species began the distributional shift 1 d after the removal and retained the space 6 months later (see Appendix S1 for temporal resolution). The mean distribution of *Po. bankanensis* significantly

shifted  $1.33 \pm 0.28$  m (change in mean distribution toward reef crest  $\pm$  variance among replicate pre-removal surveys; K-S test:  $P = 0.033$ ) toward the reef crest to acquire the space previously occupied by *Po. adelus* (Fig. 5a, b; Appendix S1: Figs. S2a, b, S3). Moreover, the distributional spread, or tail of the populations, verifies population movement into the reef zone where *Po. adelus* was removed. Thirty-seven individuals relocated to the front of the reef flat/back of the reef crest where *Po. bankanensis* previously did not occupy.

The distributions of *C. unimaculata* and *Po. tripunctatus* subsequently expanded out of pre-removal distributions with 30 and 5 individuals relocating to space on the reef occupied by *Po. bankanensis*, respectively (Fig. 5a, b). A  $0.75 \pm 0.13$  m shift in the *C. unimaculata* population was also observed but no differences in distribution were detected at the population level because the entire distribution was not within the experimental plot (K-S test:  $P = 0.329$ ; Appendix S1: Figs. S4a, b, S5). Likewise, a significant population shift in *Po. tripunctatus* was not observed due to only the tail of the population being within the experimental plot ( $0.38 \pm 0.15$  m, K-S test:  $P = 0.518$ ; Appendix S1: Fig. S6a, b). The removed species, *Po. adelus*, recovered to its previous distribution on both removal plots 6 months after removal (Appendix S1: Fig. S7a, b). The distributions of all other species within the removal plots and all seven damselfish species within the control plots did not display any significant spatial movement over time during the experimental period (Appendix S1: Table S3).

## DISCUSSION

Our results support the conclusion that interference competition contributes to explaining the spatial structure and abundance in a multi-species guild of territorial damselfish. The distinct distribution patterns characterized by a high degree of spatial partitioning among the main reef crest species were linked to levels of agonistic behavior. Two neighboring species in particular, *Pomacentrus adelus* and *Pomacentrus bankanensis*, were highly aggressive toward one another. When *Po. adelus* was removed, *Po. bankanensis* exhibited a marked increase in

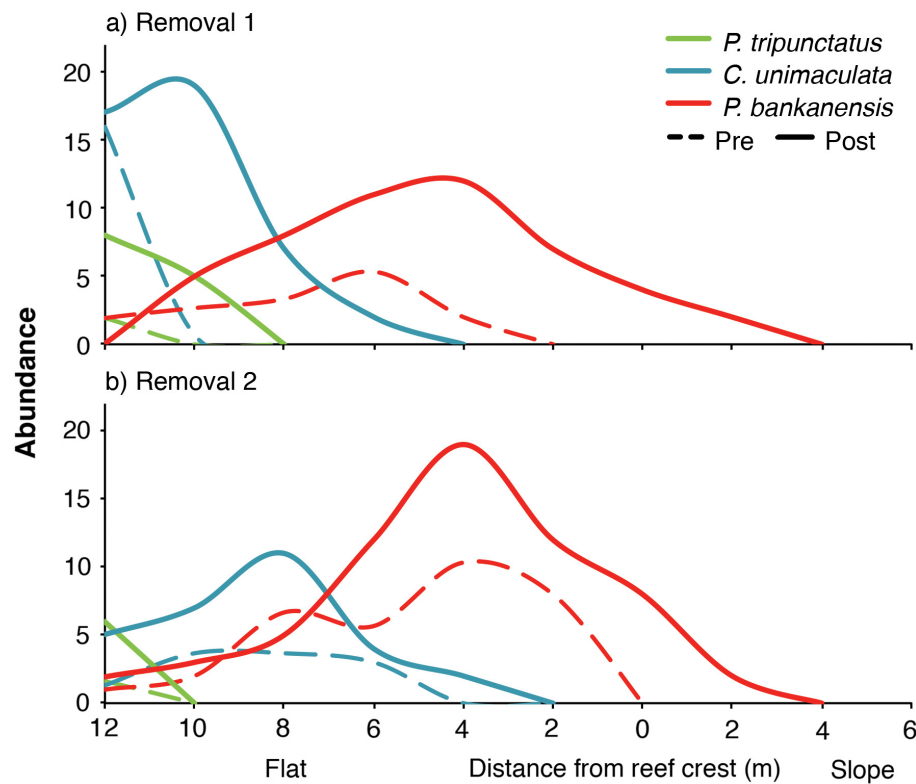


Fig. 5. Distribution frequency histogram showing the changes in reef flat species (green: *Pomacentrus tripunctatus*, blue: *Chrysiptera unimaculata*, red: *Pomacentrus bankanensis*) distributions before the removal (dotted line; averaged between pre-removal replicates:  $n = 3$ ) and 6 months after the removal of *Pomacentrus adelus* (solid line) on (a) Luba Luba and (b) Garbuna. The 0 mark on the x-axis represents the middle of the reef crest, with the distance from the crest to the flat (left) and slope (right) in meters, respectively. Note that only the upper reef slope is presented, as no fish were observed deeper. For detailed temporal resolution, see Appendix S1: Figs. S2a, b, S3, S4a, b, S5, S6a, b.

abundance and expanded its distribution to acquire the previously occupied space on the reef flat and reef crest. The competitive release triggered indirect effects, likely mediated by *Po. bankanensis*, between two other neighboring species that did not directly share resources with *Po. adelus*. Our study uniquely demonstrates that competitive networks within a community can operate directly and indirectly among ecologically similar species. Over time, a competitive release can lead to the expansion of a species realized niche as they readjust to the new competitive hierarchy.

The concept that interference competition for a limiting resource influences the abundance and distribution of animals is well established (Case and Gilpin 1974, Schoener 1983). In a community, many species interact with one another directly

by aggressively impeding access to a resource. Our research confirms the widely documented theory that interference competition plays a role in ecological segregation (Colwell and Fuentes 1975, Diamond 1978). Previous work has clearly shown that coral reef fishes compete for space and deny access to subordinate competitors when the profit of a resource is high (Robertson and Gaines 1986, McCormick and Weaver 2012, Cipresso Pereira et al. 2015). In our study system, *Po. bankanensis* distribution was regulated by the presence of *Po. adelus*. Both species exhibited intense aggression toward one another, compared to other adjacent species. The aggression is likely due to similar microhabitat use and semi-overlapping distributions (Eurich et al. 2018a). After the competitive release from *Po. adelus*, *Po. bankanensis* population increased immediately and shifted

to occupy the reef area where *Po. adelus* previously was. The quick appropriation of space (1–3 d), likely from bordering adult immigration, reflects the intensity of interference competition between the two species.

Similar to the classical Connell (1961) intertidal experiments on *Balanus* and *Chthamalus*, this field experiment demonstrated *Po. bankanensis* has a fundamental niche that extends to the reef crest, but naturally occupies a smaller realized niche when in competition with *Po. adelus* (Whittaker et al. 1973). The majority of previous studies that quantify similar interactions among coral reef fishes have used laboratory experiments (Munday et al. 2001, Cipresso Pereira et al. 2015), artificial patch reefs (Sale 1978, Williams 1978, Robertson 1996, Forrester et al. 2006, McCormick and Weaver 2012, Boström-Einarsson et al. 2014), or experimental manipulations at an individual level (Belk 1975, Robertson and Gaines 1986). In the present study, interference competition was observed experimentally in the field at the population level and over a natural, larger-scale reef profile. We provide additional strong evidence that species with similar resource requirements coexist through direct competitive mechanisms.

The study of competition among coral reef fishes has typically been tested experimentally through pairwise interactions among two species, as demonstrated above with *Po. bankanensis* and *Po. adelus*. However, an ecological community, by definition, is a naturally occurring assemblage of species that potentially interact within a habitat. The ecological processes and mechanisms that maintain coexistence among similar species within highly complex systems may not always be direct (Strauss 1991, Amarasekare 2003, Siepielski and McPeck 2010). The fine-scale spatial partitioning of seven territorial damselfish presented a unique system to test the maintenance of coexistence in a multi-species competitive network (Eurich et al. 2018a). In the present study, ecological indirect effects were observed on the reef flat and reef crest following the removal of *Po. adelus*. As expected through direct interference competition, *Po. bankanensis* distribution shifted toward the reef crest following the experimental removal taking advantage of open space. Moreover, although *Pomacentrus tripunctatus* and *Chrysiptera unimaculata* did not

directly interact with *Po. adelus*, both populations also shifted toward the reef crest. The shift was likely mediated by the change in abundance and distribution of *Po. bankanensis*. It is notable that a time lag, or subsequent effects, among the three species was not observed. All three species shifted and increased in abundance within a day of the *Po. adelus* removal. Thus, it is difficult to determine which species indirectly influenced *Po. tripunctatus* and *C. unimaculata*. However, the three species increasing in abundance and shifting in order without altering composition suggests the guild is intrinsically linked through associated competitive networks. Without the removal of *Po. adelus*, the spatial partitioning remained unchanged and stable likely due to interspecific competition. The observed shift highlights the importance of indirect interactions among species in this highly diverse and partitioned ecological guild.

It is notable that increases in abundance and distributional shifts were not ubiquitous among all territorial damselfish. The contrasting results are likely due to two major differences. First, while the species on the central reef crest, *Plectroglyphidodon lacrymatus*, spatially overlaps with *Po. adelus*, the majority of the population utilized a different microhabitat, which reduced any direct competition. Eurich et al. (2018a) showed that territorial damselfish situated on the reef flat, including *Po. adelus*, exhibited a positive association with rubble and negative avoidance of algal turf, whereas *Pl. lacrymatus* was selective for algal turf. Despite this, in the present study aggressive interactions were still observed, which implies territorial interactions play a role in maintaining resources (Robertson 1996, Munday et al. 2001, Forrester et al. 2006). Second, the two species on the reef slope, *Neoglyphidodon nigroris* and *Po. burroughi*, do not often encounter *Po. adelus* as their distributions do not directly overlap (Eurich et al. 2018a). Additionally, a similar study showed that the most densely occupied zone in Kimbe Bay is the reef crest, where territorial damselfish encompass almost 100% of the substratum, compared to 40% of the substratum on the reef slope (Ceccarelli 2007). A lack of association and increased available habitat likely explains why no changes were observed on the upper reef slope. These two examples show that within complex ecosystems, the intensity and

importance of competition may vary due to resource availability and dissimilarities among sympatric species.

Given the success of *Po. bankanensis* following the intense interspecific competitive release and the indirect effects observed among reef flat species, the question arises: How will the *Po. adelus* population, the previously most abundant species, recover? As predicted, *Po. bankanensis* retained its abundance and the habitat 6 months after the removal of *Po. adelus*. Furthermore, the species on the reef flat, *Po. tripunctatus* and *C. unimaculata*, continued to persist adjacent to *Po. bankanensis*. However, 3 months post-removal only *Po. adelus* subadults were observed within this species pre-removal distribution. Srinivasan and Jones (2006) showed damselfish recruit at a low level all year round in Kimbe Bay. These individuals therefore likely recruited during the experimental monitoring period.

The pattern could indicate several mechanisms for coexistence among territorial damselfish. Firstly, it could indicate a competitive lottery for space at settlement, and an ontogenetic shift to niche partitioning among neighboring adults (Sale 1977, 1978). Cipresso Pereira et al. (2015) demonstrated the competitive mechanism between two *Gobiodon* species shifts from a lottery for space at settlement to niche partitioning among larger individuals. In our study, recruitment of *Po. adelus* was observed throughout the experimental period and only subadults were observed in the experimental plots 3 months after the removal. Six months after the removal, these individuals were classified as adults. More detailed experiments at the recruitment and settlement level are needed for a definitive conclusion on the lottery for space or immigration from nearby habitat (as per Sale 1979). Alternatively, with the quick appropriation of space by competing adult species, a dominance hierarchy is a possible explanation for the delayed *Po. adelus* recovery. Initially, adults of the subordinate species may outcompete *Po. adelus* recruits and juveniles for available habitat, but this may reverse when *Po. adelus* individuals increase in size. In any case, the lack of pre-removal abundances of *Po. adelus* adults within the experimental plots 6 months later demonstrates competitive displacement and niche partitioning. It is also possible that the *Po. adelus* population was tracking

toward a recovery, but if so, we would have expected *Po. bankanensis* abundances to trend downwards. For a full assessment of a compensatory response by a population following its release from competition, an experiment spanning multiple generations would be needed (Schmitt and Holbrook 1990, Robertson 1996).

## CONCLUSIONS

Revealing indirect relationships among ecologically similar species within a complex community remains a formidable challenge, yet it is necessary to gain generality and predictive power. We demonstrate that competitive networks within a community can operate directly, by interference competition, and indirectly through a competitive release among ecologically similar species. Evidence presented here suggests that the loss of a species through local extinction may result in ecological indirect effects that will influence other species in the assemblage. In addition, it is known that reduced habitat quality through disturbances, such as ocean acidification and coral bleaching, can alter and even reverse pairwise competitive interactions between species (McCormick 2012, McCormick et al. 2013, Boström-Einarsson et al. 2014). With growing pressures, including climate change, globalization, and migration, on the world ecosystems, we hope these effects do not extend to the progressive loss of species that cannot compete for the dwindling resources.

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