

1 **Effects of invasive Pacific red lionfish *Pterois***
2 ***volitans* vs. a native predator on Bahamian**
3 **coral-reef fish communities**

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10 **Abstract** The recent irruption of Pacific red lionfish (*Pterois volitans*) on Caribbean and Atlantic
11 coral reefs could prove to be one of the most damaging marine invasions to date. Invasive lionfish
12 are reaching densities much higher than those reported from their native range, and they have a
13 strong negative effect on the recruitment and abundance of a broad diversity of native coral-reef
14 fishes. Otherwise, little is known about how lionfish affect native coral-reef communities,
15 especially compared to ecologically similar native predators. A controlled field experiment
16 conducted on small patch-reefs in the Bahamas over an 8 wk period demonstrated that (1) lionfish
17 caused a reduction in the abundance of small native coral-reef fishes that was 2.5 ± 0.5 times
18 (mean \pm SEM) greater than that caused by a similarly sized native piscivore, the coney grouper
19 *Cephalopholis fulva* (93.7% vs. 36.3% reductions); (2) lionfish caused a reduction in the species
20 richness of small coral-reef fishes (loss of 4.6 ± 1.6 species), whereas the native piscivore did not
21 have a significant effect on prey richness; (3) the greatest effects on the reef-fish community, in
22 terms of both abundance and richness, occurred when both native and invasive predators were
23 present; and (4) lionfish grew significantly faster (> 6 times) than the native predator under the
24 same field conditions. These results suggest that invasive lionfish have stronger ecological effects
25 than similarly sized native piscivores, and may pose a substantial threat to native coral-reef fish
26 communities.

27
28 **Keywords:** *invasive species, coral reefs, predation, community structure,*
29 *piscivory, marine fishes*

30

1 **Introduction**

2 Some of the most damaging biological invasions, in terms of loss of native species
3 and disruption of ecosystems, have resulted from the introduction of non-native
4 predatory freshwater fishes (e.g., Ogutu-Ohwayo 1990, Thomas 1993, Jackson
5 2002, Pyke 2008). Introductions of non-native predatory diadromous fishes have
6 also resulted in invasions that have negatively affected native communities and
7 ecosystems (e.g., Christie 1974, Simon and Townsend 2003).

8 In contrast, while some strictly marine fishes have been introduced into
9 new ecosystems by humans, both intentionally and unintentionally, relatively few
10 of these introductions have resulted in the establishment of self-sustaining,
11 reproductive populations (Baltz 1991, Randall 1987). Examples of marine fishes
12 which have become established after introduction include the peacock grouper
13 (*Cephalopholis argus*) and the bluelined snapper (*Lutjanus kasmira*), both of
14 which were introduced intentionally to the Hawaiian archipelago in the 1950s in
15 an attempt to augment nearshore fisheries (Randall 1987). *C. argus* now
16 constitutes more than 80% of the large piscivore biomass on some reefs in the
17 main Hawaiian Islands (Dierking et al. 2009), and *L. kasmira* has become one of
18 the most numerous reef fishes across a large part of the Hawaiian archipelago
19 (Randall 1987, Friedlander et al. 2002).

20 Very few studies have examined the effects of introduced marine fishes on
21 native communities (Helfman 2007). Most such studies were conducted decades
22 after the introductions occurred and were restricted to observational rather than
23 experimental approaches. Thus, while some evidence exists that introduced
24 marine fishes, when successful, may cause deleterious changes in native
25 ecosystems (Friedlander et al. 2002, Bariche et al. 2004, Goren and Galil 2005,
26 Schumacher & Parrish 2005, Dierking et al. 2009), unequivocal causal linkages
27 between these introductions and observed changes in native systems are lacking
28 (*but see* Albins & Hixon 2008).

29 Few marine fish introductions have resulted in range expansions as rapid
30 or extensive as that recently demonstrated by lionfish (*Pterois volitans*) in the
31 Western Atlantic and Caribbean. Lionfish were initially introduced, likely via the
32 aquarium trade, to coastal waters of southeast Florida in the mid-to-late 1980s

1 (Semmens et al. 2004). Since the early 2000s, their range has expanded rapidly
2 throughout the tropical and sub-tropical Western Atlantic Ocean and Caribbean
3 Sea (Schofield 2009, 2010). In addition to their rapid range expansion, invasive
4 lionfish are of particular concern for several reasons. Lionfish in the Atlantic
5 demonstrate high individual growth and reproductive rates (Morris & Whitfield
6 2009) and high population growth rates (Albins & Hixon 2011). They are
7 reaching higher densities (nearly 5 times greater) in the invaded range (Green &
8 Côté 2009) than have been reported from their native Pacific range (Kulbicki et al.
9 2012). Invasive lionfish also appear to reach larger maximum sizes in the invaded
10 range (Whitfield et al. 2007) than have been reported from their native Pacific
11 (Randall et al. 1990).

12 Novel traits of introduced predators and naïveté of native prey to such
13 traits are generally thought to contribute to predator invasion success and may
14 result in strong relative effects of invasive predators on native prey (Sih et al.
15 2010). Invasive mammalian and avian predators across a variety of systems have
16 been shown to have stronger effects on native prey than do native predators (Salo
17 et al. 2007). However, at least one study of an invasive predatory freshwater fish
18 has found the opposite (Baber & Babbitt 2003), indicating that in some situations,
19 non-native predators may be relatively poorly adapted to capture and consume
20 certain native prey. Lionfish demonstrate a suite of predatory characteristics and
21 behaviors that is novel in the invaded system, and which may confer a high degree
22 of predatory efficiency relative to native piscivores (Albins & Hixon 2011, Albins
23 & Lyons 2012). A combination of slow stalking movements, cryptic coloration,
24 elongated fin rays, and numerous spine-like and fleshy projections on the head
25 and face, may provide crypsis, or cause lionfish to appear like a harmless plant or
26 invertebrate, resulting in reduced prey vigilance (Albins & Hixon 2011). When
27 hunting, lionfish slowly approach prey with their large fan-like pectoral fins flared
28 and held perpendicular to their body (Allen & Eschmeyer 1973). Prey are often
29 herded into a corner and consumed with a rapid strike (Albins & Hixon 2011).
30 When approaching prey, lionfish occasionally direct jets of water at the prey fish.
31 This recently documented predatory behavior of *P. volitans* appears to be unique
32 among piscivores, may confuse the lateral-line sensory system of prey and/or may
33 increase the incidence of head-first capture (Albins & Lyons 2012). Prey species
34 that have coexisted with predator species over long periods are likely to evolve

1 traits that reduce the risk of predation. In contrast, prey encountering a newly
2 introduced alien predator with novel characteristics, such as lionfish with their
3 unique morphology and predatory behaviors, may not recognize the invader as a
4 threat, and may lack morphological or behavioral traits to reduce risk.

5 Lionfish consume a broad diversity of native Atlantic coral-reef fishes
6 (Albins & Hixon 2008, Morris & Akins 2009) and appear to have strong effects
7 on native prey. A previous field experiment demonstrated that single lionfish are
8 capable of reducing overall recruitment of native coral-reef fishes to small patch-
9 reefs by nearly 80% over short time periods (Albins & Hixon 2008) and an
10 observational study has documented 65% reductions in the biomass of fish prey
11 on invaded reefs (Green et al. 2012). Such large reductions in populations of
12 small fishes could have detrimental effects on native coral-reef communities in a
13 variety of ways (Albins & Hixon 2011). First, if lionfish reduce the number of
14 juveniles substantially, then they could have a negative effect on realized adult
15 abundances of a wide range of species. Second, lionfish could have substantial
16 indirect negative effects on native piscivores by reducing prey availability. While
17 native piscivore populations are already severely reduced across a majority of the
18 Caribbean due to overfishing, relatively healthy populations still exist in remote
19 locations with low human populations and inside some marine reserves (Stallings
20 2009). Invasive lionfish have reached some of the most remote reefs and readily
21 enter reserves. Therefore, potential competitive interactions between lionfish and
22 native piscivores could inhibit conservation and stock rebuilding efforts for these
23 species. Third, if lionfish cause reductions in the survival of juvenile herbivorous
24 fish, then the invasion could have far reaching, destabilizing effects on entire
25 coral-reef ecosystems by reducing herbivory, thereby allowing seaweeds to
26 outcompete or otherwise inhibit reef-building corals (Mumby et al. 2006).
27 Additionally, lionfish could have broad effects on coral-reef ecosystems by
28 consuming other ecologically important species, such as cleaners, the loss of
29 which could result in reduced reef fish abundance and diversity (Losey et al. 1999,
30 Côté 2000).

31 This potential for lionfish to cause indirect destabilizing effects on native
32 coral reefs is of particular concern because these ecosystems have already been
33 substantially degraded by a suite of disturbances, including overfishing, pollution,
34 and climate change (Mora 2008). In short, what is currently known of the ecology

1 of lionfish suggests that this predator could manifest one of the most damaging
2 marine-fish invasions to date (Sutherland et al. 2010, Albins & Hixon 2011).

3 While a previous field experiment demonstrated that lionfish caused
4 reductions in the abundance of prey-sized native fishes (Albins & Hixon 2008),
5 that study did not provide an explicit frame-of-reference for evaluating the
6 magnitude of the lionfish effect. The question remains how the effect of invasive
7 lionfish compares to that of similarly sized native predators. Additionally, the
8 effects of lionfish on aspects of community composition other than overall
9 abundance (such as species richness, evenness, and diversity) have not yet been
10 examined. The current study explores the effects of lionfish on native reef-fish
11 communities relative to those of a common, similarly sized, native predator, the
12 coney grouper (*Cephalopholis fulva*). This study addresses the following
13 questions: (1) How do the effects of lionfish on native reef-fish communities
14 compare to those of a similarly sized native predator? (2) What are the combined
15 effects of invasive lionfish and the native predator on native reef-fish
16 communities? (3) Does the presence of lionfish affect the growth rates of the
17 native predator (and vice versa)? (4) How do growth rates compare between
18 invasive and native predators under identical field conditions?

19 **Materials and Methods**

20 *Study site and experimental design*

21 The study systems were communities of small (≤ 5 cm total length [TL]) native
22 fishes on coral patch-reefs near Lee Stocking Island, Bahamas. I used an existing
23 matrix of 32 live-coral patch reefs, each approximately 4 m², which were
24 translocated in the early 1990s and are now essentially natural features (Carr &
25 Hixon 1995, Hixon & Carr 1997). These experimental reefs are separated from
26 the nearest natural reefs by at least 1 km and from each other by about 200 m
27 (Fig. 1). The degree of spatial isolation among reefs, coupled with relatively
28 featureless intervening habitat (flat, sandy, seagrass beds), meant that the resident
29 reef-fish communities could be treated as independent replicates (i.e., negligible
30 juvenile and adult movement among reefs) subject to regional levels of larval
31 settlement.

1 I conducted a baseline census of all fishes on all 32 reefs at the beginning
2 of the summer of 2008. I then selected a subset of reefs ($n = 20$) and separated
3 them into five blocks of four reefs each. Blocks were based on similarity of the
4 pre-existing reef-fish communities as determined by the number of individuals in
5 major groups of strong interactors, including resident piscivores and territorial
6 damselfishes. Because this was an experimental manipulation of native and
7 invasive piscivores, I first removed all resident adult piscivores from the
8 experimental reefs (after removals, no immigrant resident piscivores were
9 observed on experimental reefs during the study). I then randomly assigned four
10 different predator treatments to the four reefs in each of the five blocks.

11 The treatments were (1) a single native grouper, (2) a single invasive
12 lionfish, (3) one grouper and one lionfish together, and (4) a predator-free control.
13 While predator-free patch reefs are naturally rare in this system, the experimental
14 control reefs provided a baseline against which to estimate, and thus compare the
15 effects of the native and invasive predators. The experimental design deliberately
16 confounded the number of resident predators with predator identity because that is
17 the nature of this invasion: a new species was added to the existing native
18 community. Before the lionfish invasion, it would have been typical to find patch
19 reefs with one or two small resident coney grouper; now it is more typical to find
20 one or two small lionfish on such reefs in addition to the original resident
21 piscivores. Therefore, the single native-predator treatment could be viewed as a
22 simplified pre-invasion food web, while the combined predator treatment
23 represented the current post-invasion situation common to reefs in the Bahamas, a
24 situation likely to become the norm across the majority of Western Atlantic and
25 Caribbean coral reefs (Morris & Whitfield 2009, Schofield 2009, 2010). The
26 lionfish-only treatment provided a comparison of effect sizes between the two
27 predator species, and could also be interpreted to represent a possible future
28 scenario where lionfish have excluded or replaced native predators.

29 Resident-predator treatments were established by transplanting onto the
30 experimental reefs from other reefs far from the study sites. Predators were
31 captured using small hand nets, held in buckets, and transplanted as quickly as
32 possible with as little handling as possible. There were no obvious indications of
33 handling effects, as post-transplant predator behaviors appeared normal.
34 However, handling effects were not examined explicitly.

1 In order to examine predator growth rates, I measured (to the nearest 0.1
2 cm TL) and wet weighed (to the nearest 0.1 g) all transplanted predators at the
3 beginning and again at the end of the experiment. All predators in each block
4 were of similar size at the outset of the experiment. The average length of
5 transplanted lionfish (\pm SEM) was 7.1 ± 0.4 cm TL, and their average mass was
6 4.0 ± 0.5 g. Transplanted grouper were, on average, 7.0 ± 0.3 cm TL, and
7 weighed, on average, 4.7 ± 0.7 g. At the end of the experiment, all native coney
8 grouper were released, and all lionfish were euthanized for further study.

9 The coney grouper was chosen as a model native predator for several
10 reasons. First, it is a common species in the region and is readily collected and
11 transplanted onto experimental reefs (e.g., Stallings 2008). Second, it is
12 comparable in size to lionfish, both in terms of maximum adult size and size of
13 individuals available in the study area. Third, its diet is similar to that of lionfish,
14 consisting primarily of small reef fishes, and secondarily of small reef
15 invertebrates (Randall 1967). Finally, and most importantly, several previous
16 experiments had demonstrated that the coney is an effective predator of small reef
17 fishes in the study system (Almany 2003, 2004a, 2004b, Stallings 2008).

18 Following predator transplants, I monitored the community of small native
19 coral-reef fishes on all experimental reefs at ca. 1 wk intervals for 8 wk during the
20 summer 2008 recruitment period (July to September). Censuses were conducted
21 by 2 divers using SCUBA, who counted and sized all fishes ≤ 5 cm TL on each
22 reef following methods described by Hixon & Beets (1989, 1993). I assumed that
23 variation in natural processes affecting reef-fish abundance and community
24 composition -- including settlement, resource availability, and predation by
25 transient predators, etc. -- would be distributed among experimental reefs with
26 negligible bias. Therefore, I attributed observed differences in reef-fish
27 abundance and community composition arising over the course of the experiment
28 to the predator treatments themselves (e.g., the mean difference in abundance of
29 small fish between lionfish-only reefs and predator-free control reefs represented
30 mortality caused by the lionfish).

31 During the summer months in this region, coral-reef fishes settle (i.e.,
32 make the transition from pelagic larvae to reef-dwelling juveniles) in relatively
33 large numbers. During the winter months, fish abundances typically decline as
34 mortality exceeds recruitment. Since this experiment ran through the summer, I

1 expected to see increasing numbers of new recruits, resulting in a positive change
2 in abundance of small native fishes, on all reefs over the course of the experiment.
3 "Recruitment" in this context is defined as an observable increase in the
4 abundance of juvenile reef fishes due to larval settlement (Jones 1991). I also
5 expected other changes in the community, such as changes in species diversity, to
6 be driven primarily by recruitment, with differences among treatments reflecting
7 the effects of different predators on small-bodied species and on post-settlement
8 juveniles of both small-bodied and large-bodied species.

9 *Statistical analyses*

10 Community response variables included change in abundance (ΔN), change in
11 species richness (ΔS), change in species evenness (ΔJ), and change in species
12 diversity ($\Delta H'$) of small (≤ 5 cm TL) native fishes. I calculated ΔN for each reef
13 census as the abundance of each species of reef fish minus the abundance of that
14 species at the baseline census for that particular reef, totaled across species:

$$15 \quad \Delta N_{it} = \sum_{j=1}^s n_{tij} - n_{0ij} \quad (1)$$

16 Where ΔN_{it} was the change in abundance for reef i at census t , and n_{tij} was the
17 abundance of species j on reef i at census t . Therefore, ΔN represented the overall
18 change in abundance for all species on each reef between the baseline census and
19 each consecutive census. The change in species richness (ΔS) was calculated for
20 each reef as the change in the number of species of small fish between the
21 baseline census and each consecutive census. Similarly, ΔJ and $\Delta H'$ were
22 calculated as the change in Pielou's J (Pielou 1966), and the change in the
23 Shannon-Wiener index H' , which combines richness and evenness (Pielou 1966),
24 between the baseline census and each consecutive census. I also examined the
25 differences in baseline abundance, richness, evenness, and diversity of small
26 native reef fishes among reefs assigned to the four predator treatments at the
27 beginning of the experiment (before establishment of predator treatments).

28 I used linear mixed-effects models (*LMM*), with two categorical
29 explanatory variables, *predator treatment* and *time step*, and a random intercept
30 for each experimental reef, to draw inferences regarding the effects of predator
31 treatments on the four community-change indices (ΔN , ΔS , ΔJ , and $\Delta H'$) over the

1 course of the experiment. I chose to include *time step* as a categorical variable,
2 rather than modeling it as a continuous variable because I did not want to assume
3 a linear relationship between the response variables and time. I used *reef*, rather
4 than *block*, as the random term in the models due to the nested nature of the data
5 (multiple observations of each reef across time steps). Likelihood Ratio Tests
6 (*LRT*) with a correction for testing-on-the-boundary (Verbeke & Molenberghs
7 2000) indicated that inclusion of the random *reef* term resulted in significantly
8 better fits for each of the response variables (Online Resource 1).

9 Initial visual examination of the standardized residuals from *LMMs* for
10 each of the response variables indicated departures from the assumptions of
11 homogeneity of variance and independence. Based on this graphical evidence, I
12 fit three alternative *LMMs* for each response variable, one incorporating
13 heteroscedasticity among treatments, one incorporating temporal autocorrelation
14 among observations within each reef (using the *AR(1)* autoregressive model), and
15 one incorporating both variance and correlation structures. I compared the
16 resulting models using Akaike's Information Criterion (*AIC*) and used the optimal
17 models for hypothesis testing (Online resource 1). Visual examination of
18 standardized residuals from the final optimal models indicated that all statistical
19 assumptions, including homogeneity, independence, and normality, were met.

20 I used t-tests within this *LMM* framework, to evaluate six *a priori*
21 hypotheses regarding differences in each of the response variables among the four
22 predator treatments at the end of the experiment. I also fit similar models to those
23 described above, but with abundance, richness, evenness, and diversity (rather
24 than the *change* in each of these) as response variables in order to evaluate
25 whether these metrics differed among reefs assigned to the four predator
26 treatments at the baseline census (before establishment of predator treatments).

27 I used a generalized least squares model (*GLS*) with two categorical
28 variables, *species* (lionfish or grouper) and *treatment* (presence vs. absence of the
29 other predator), to draw inferences about differences in length growth rates. I
30 used an *LMM* with the same fixed structure, but with random intercepts for each
31 reef, to draw inferences about differences in mass growth rates. Inclusion of a
32 random term for *reef* was not found to improve the model fit based on corrected
33 *LRTs* for length growth, but inclusion of a random term for *reef* provided the best
34 fit for mass growth (Online Resource 1). Visual examination of residuals

1 indicated increasing variance with fitted values and heteroscedasticity between
2 *species* for length growth and between both *species* and *treatment* for mass
3 growth. Incorporation of heteroscedasticity in each of the models provided better
4 fits, based on *AIC*, than did equal variance models (Online Resource 1).
5 Examination of the residuals from the optimal models suggested that all
6 assumptions including homogeneity, independence, and normality, were met.
7 Once the best fitting models in terms of random effects and variance structures
8 were selected, I refit each model using Maximum Likelihood estimation, and used
9 *LRTs* to test for significance of the *species* and *treatment* terms and to reduce the
10 models in a backwards-selection procedure described in Zuur et al. (2009).

11 To further evaluate the effects of the four predator treatments on the native
12 reef-fish community, I used a combination of multivariate ordination, using non-
13 metric multidimensional scaling (NMDS, Kruskal & Wish 1978, McCune &
14 Grace 2002), and a permutation-based Multivariate Analysis of Variance
15 (perMANOVA, McArdle & Anderson 2001), with 1000 permutations constrained
16 within experimental blocks. I ran this analysis once for all experimental reefs at
17 the beginning of the experiment (before establishment of predator treatments), and
18 again for all experimental reefs at the conclusion of the experiment (week 8).
19 Before conducting the NMDS ordinations and perMANOVAs, I transformed the
20 original community matrices using a log transformation ($\log[x+1]$) to moderate
21 the influence of dominant species in relation to rarer species. I chose not to
22 relativize by species in order to avoid giving rare species an inordinate influence
23 on the outcome. I also chose not to relativize by sample units to avoid losing
24 information about differences in total abundance of native fish among the
25 experimental reefs. I used Bray-Curtis distances for both the NMDS ordinations
26 and perMANOVA hypothesis testing (Bray & Curtis 1957). NMDS ordination
27 routines followed the guidelines outlined in McCune and Grace (2002) and
28 included multiple random starts (up to 20, with up to 50 iterations each) at varying
29 levels of dimensionality (1 to 5 axes) to ensure that the global solution was
30 reached, and that the choice of dimensionality was appropriate. I also used
31 Monte-Carlo tests based on 50 runs with randomized data to ensure that the
32 ordinations were extracting stronger axes than would be expected by chance
33 (McCune & Grace 2002). For ease of interpretation, the ordination for the final

1 census data was rotated for maximum correlation between the change-in-
2 abundance (ΔN) and the first axis.

3 All statistical analyses were conducted in the *R* software environment (*R*
4 Development Core Team 2011) and used the associated packages *MASS*
5 (Venables & Ripley 2002), *nlme* (Pinheiro et al. 2011) and *vegan* (Oksanen et al.
6 2011). Evaluation of *LMMs* and selection of appropriate random structures
7 followed the guidelines and procedures described in Zuur et al. (2009). For all
8 hypothesis testing, p-values less than 0.05 were considered to represent strong
9 evidence against the null hypotheses, whereas p-values between 0.05 and 0.10
10 were considered to represent marginal evidence against the null hypotheses. A
11 comparison of univariate and multivariate responses indicated that communities of
12 small native reef-fishes at the beginning of the experiment were essentially similar
13 among experimental reefs assigned to the four treatments (see Online Resource 2
14 and Fig. 4a).

15 **Results**

16 *Native reef-fish abundance*

17 Over the course of the 8 wk experiment the abundance of small native reef fish (\leq
18 5 cm TL) increased by 66.6 ± 10.4 fish per reef (*mean* \pm SEM) on predator-free
19 control reefs (Fig. 2), increased somewhat less on native grouper reefs (42.4 ± 6.1
20 fish per reef), and remained near baseline levels on lionfish reefs (4.2 ± 5.8 fish
21 per reef) and combined predator reefs (-5.8 ± 6.8 fish per reef). Compared to
22 predator-free controls, single lionfish reduced the change-in-abundance (ΔN) by
23 62.4 ± 11.9 fish per reef ($t = 5.25$, $p < 0.001$), representing an average reduction of
24 93.7%. ΔN on native-grouper-only reefs was 24.2 ± 12.0 fish per reef lower, on
25 average, than ΔN on control reefs, an effect that was marginally significant
26 ($t = 2.01$, $p = 0.061$). The negative effect of lionfish on ΔN was 2.6 ± 0.5 times
27 stronger than the effect of the native predator ($t = 4.52$, $p < 0.001$). Compared to
28 reefs with native grouper only, net recruitment to reefs with both predators present
29 was reduced by 48.2 ± 9.2 fish per reef ($t = 5.26$, $p < 0.001$).

30 Most of the overall change in abundance on predator-free control reefs
31 (ΔN) was due to increases in the abundance of two common species, bridled goby
32 *Coryphopterus glaucofraenum* and beaugregory damselfish *Stegastes leucostictus*.

1 Fourteen other species in ten different families contributed to the increase (Table
2 1, Online Resource 3). These included three herbivores -- redband parrotfish
3 *Sparisoma aurofrenatum*, stoplight parrotfish *S. viride*, and doctorfish *Acanthurus*
4 *chirurgus* -- and one facultative cleaner -- Spanish hogfish *Bodianus rufus*. Of
5 these sixteen contributors, the average change in abundance of fifteen species
6 (including all three herbivores and *B. rufus*) was lower on both lionfish-only reefs
7 and reefs with both predators present than on control reefs. The exception was
8 goldspot goby *Gnatholepis thompsoni*, which increased slightly more on lionfish
9 reefs and combined predator reefs than on control reefs. The mean change in
10 abundance of twelve of the sixteen species, including two of the three herbivores
11 and *B. rufus*, was also lower on grouper-only reefs than on control reefs. A
12 notable exception included *S. viride*, which increased substantially more on
13 grouper-only reefs than on control reefs.

14 *Predator growth rates*

15 Lionfish growth rates were > 6 times greater, in terms of both length ($t = 9.56$,
16 $p < 0.001$) and mass ($t = 11.38$, $p < 0.001$), than growth rates of coney grouper
17 under the same field conditions. Over the course of the experiment, lionfish
18 increased in length by 0.80 ± 0.06 mm per day and in mass by 0.26 ± 0.02 g per
19 day, while grouper increased in length by 0.13 ± 0.02 mm per day and in mass by
20 0.04 ± 0.01 g per day. By the end of the 8 week experiment, lionfish were
21 therefore, on average, 11.6 cm TL and 18.6 g, whereas native grouper were 7.7 cm
22 TL and 6.9 g. Lionfish did not appear to have an affect the growth rates of native
23 grouper, and grouper had no detectable effect on lionfish growth rates (length: L-
24 ratio_{5,4} = 0.01, $p = 0.936$; mass: L-ratio_{8,7} = 0.22, $p = 0.642$).

25 *Native reef-fish richness, evenness and diversity*

26 The species richness of small reef fishes increased by 3.4 ± 1.1 species on
27 predator-free control reefs over the summer recruitment period, remained similar
28 to baseline conditions on grouper only (1.0 ± 1.1 species) and lionfish only reefs
29 (-1.2 ± 1.1 species), and dropped by 5.4 ± 1.1 species on combined grouper +
30 lionfish reefs (Fig. 3a). Compared to controls, lionfish caused a reduction in ΔS of
31 4.6 ± 1.6 species ($t = 2.84$, $p = 0.011$). The mean of ΔS was 2.4 ± 1.6 species
32 lower on grouper-only reefs than control reefs. However, this grouper effect was

1 not significant ($t = 1.48$, $p = 0.157$). The effect of lionfish on ΔS was, on average,
2 1.9 ± 0.7 times larger than the effect of native grouper, although the difference
3 between effect sizes was not significant ($t = 1.36$, $p = 0.193$). However, the effect
4 of lionfish and grouper together was 2.7 ± 0.7 times stronger than the effect of
5 grouper alone ($t = 3.95$, $p = 0.001$), resulting in a net reduction in ΔS of 6.4 ± 1.6
6 species compared to grouper-only reefs.

7 Over the course of the experiment, species evenness dropped by $0.12 \pm$
8 0.03 on the predator-free control reefs, changed little on the grouper-only ($-0.04 \pm$
9 0.04) and lionfish-only reefs (-0.01 ± 0.04), and dropped by 0.14 ± 0.03 on the
10 combined predator reefs (Fig. 3b). Compared to controls, lionfish-alone caused an
11 increase of 0.10 ± 0.05 in ΔJ ($t = 2.27$, $p = 0.037$). On the grouper-alone reefs, ΔJ
12 was 0.08 ± 0.05 higher than on the control reefs, and the difference between the
13 two treatments was marginally significant ($t = 1.76$, $p = 0.096$). While each of the
14 predator species alone appeared to have a positive effect on ΔJ , the combined
15 native-invasive predator treatment resulted in drop in ΔJ of 0.13 ± 0.03 , similar to
16 that observed on the predator-free control reefs. Compared to the effect of
17 grouper alone, the combined predator treatment caused a reduction in ΔJ of $0.10 \pm$
18 0.05 , and this difference was marginally significant ($t = 2.07$, $p = 0.054$).

19 The Shannon-Wiener species diversity index (H') remained relatively
20 constant over the course of the experiment on predator-free control reefs ($-0.06 \pm$
21 0.13), grouper-only reefs (-0.01 ± 0.13), and lionfish-only reefs (-0.1 ± 0.13), but
22 declined by 0.73 ± 0.13 on combined grouper + lionfish reefs (Fig. 3c). Neither
23 grouper alone ($t = 0.27$, $p = 0.791$) nor lionfish alone ($t = 0.22$, $p = 0.826$) caused
24 differences in $\Delta H'$ compared to predator-free controls. However, the combined
25 native-invasive predator treatment caused a reduction in $\Delta H'$ of 0.72 ± 0.18
26 compared to the native-only treatment ($t = 4.02$, $p = 0.001$).

27 *Multivariate community response*

28 An NMDS ordination of communities at the beginning of the experiment
29 illustrated a high degree of overlap among reefs across the four treatments (final
30 stress = 18.07, linear $r^2 = 0.83$, Monte-Carlo $p = 0.02$, Fig. 4a). Results of a
31 perMANOVA suggested that no pronounced community differences existed
32 among treatment groups at the beginning of the experiment (pseudo- $F_{16,3} = 0.67$,
33 $p = 0.890$).

1 In contrast, an ordination of the small reef-fish communities at the end of
2 the experiment illustrated clear differences among the four predator treatments in
3 terms of species composition and relative abundances (final stress = 12.81, linear
4 $r^2 = 0.92$, Monte-Carlo $p = 0.02$, Fig. 4b). These differences were corroborated by
5 the results of a perMANOVA (pseudo- $F_{16,3} = 2.48$, $p = 0.006$). The four predator
6 treatment groups were distributed in a fairly clear pattern within the ordination
7 space. Predator-free control reefs did not overlap with any of the three predator-
8 addition treatments. Reefs in each of the single-predator treatments (lionfish-only
9 and grouper-only) occupied distinct areas of the plot with a small degree of
10 overlap, while reefs in the combined-predator treatment occupied a similar range
11 to lionfish-only reefs along axis-1, yet were distributed much more broadly across
12 axis-2 than any of the other treatments. Of the thirty species present on
13 experimental reefs at the end of the experiment, twelve species from six different
14 families -- including the two most commonly recruiting species (*Coryphopterus*
15 *glaucofraenum* and *Stegastes leucostictus*), two herbivores (*Sparisoma viride* and
16 *Acanthurus chirurgus*), and two facultative cleaners (bluehead wrasse *Thalassoma*
17 *bifasciatum* and *Bodianus rufus*) -- had strong positive correlations (> 0.3) with
18 the first NMDS axis, whereas only one species (barred cardinalfish *Apogon*
19 *binotatus*) had a strong negative correlation (< -0.3) with this axis (Online
20 Resource 4). Two species (*T. bifasciatum* and *Gnatholepis thompsoni*) had strong
21 positive correlations (> 0.3) with the second NMDS axis, whereas two species
22 (sharpnose puffer *Canthigaster rostrata* and flamefish *Apogon maculatus*) had
23 strong negative correlations with this axis (Online Resource 4).

24 **Discussion**

25 *Native reef-fish abundance*

26 This field experiment demonstrated that reductions in the abundance of small
27 native fishes on patch reefs caused by lionfish were substantially greater than
28 those caused by a similarly sized native predator. Native fish abundance was also
29 much lower in the combined-predator treatment than in the native-grouper
30 treatment, suggesting that large reductions in the abundance of small fishes can be
31 expected on coral reefs invaded by lionfish, at least during the summer
32 recruitment period.

1 The increase in numbers of small fish observed on predator-free control
2 reefs and on grouper-only reefs was primarily due to a large pulse of natural
3 settlement of larval fishes, which typically occurs during the summer months in
4 this region. Recruitment was dominated by two species in particular
5 (*Coryphopterus glaucofraenum* and *Stegastes leucostictus*), with a broad diversity
6 of fishes (including three herbivorous species and one cleaner) also contributing to
7 the overall increase. The presence of a single, small lionfish on a patch reef
8 effectively attenuated this local recruitment pulse to nearly zero, and this negative
9 effect was spread across a majority of the most commonly recruiting species,
10 including those in ecologically important groups.

11 Such a major reduction in the recruitment of a broad diversity of native
12 reef fishes, if widespread in the system as a whole, could have strong direct
13 demographic consequences for native fish populations. The severity of these
14 demographic consequences will, at least in part, be determined by species-specific
15 population growth sensitivities to increased rates of early post-settlement
16 mortality. Early post-settlement mortality rates in most coral-reef fishes are
17 naturally very high due to predation, represent a disproportionately large
18 component of overall mortality, and can have strong effects on adult population
19 densities as well as the structure of reef-fish communities (Carr & Hixon 1995,
20 Hixon & Jones 2005, Almany & Webster 2006). This study demonstrates that
21 lionfish are consuming large numbers of small native fish relative to a similarly
22 sized native predator. If the tremendous increases in early mortality of native
23 fishes caused by lionfish translate into reduced adult populations of ecologically
24 important species such as herbivores, then the lionfish invasion could possibly
25 have far-reaching and destabilizing consequences for coral-reef ecosystems
26 (Albins & Hixon 2011).

27 *Invasive vs. native predator growth rates*

28 In addition to the fact that lionfish consumed native reef fishes at substantially
29 higher rates than the native grouper in this study, they also grew over six times
30 faster (in both length and mass). Lionfish growth rate estimates from the current
31 study were nearly identical to those observed in a separate mark-recapture study
32 of juvenile invasive lionfish on non-experimental reefs in the same region
33 (Kindinger et al. unpublished data, Pusack et al. unpublished data). The relatively

1 rapid growth rates of lionfish documented in this study, along with evidence that
2 lionfish consume juvenile groupers (Morris & Akins 2009) suggests the
3 possibility that cohorts of lionfish may grow large enough, quickly enough, to
4 become predators of contemporaneous cohorts of native groupers.

5 Despite a clear demonstration that lionfish caused large reductions in the
6 density of reef-associated prey fish, grouper maintained equivalent growth rates in
7 the presence and absence of lionfish over the course of the experiment. It is
8 possible that, in the presence of lionfish, grouper may have compensated for
9 reduced availability of reef-associated prey fish by consuming alternative prey
10 (e.g. invertebrates or non-reef-associated fish). While such alternative prey may
11 have allowed the maintenance of normal somatic growth rates in grouper over the
12 8 wk experiment, these are likely to represent lower-quality or higher-risk food
13 sources and may not support equivalent long-term growth or reproduction.
14 Therefore, the lack of direct evidence for short-term competition between lionfish
15 and grouper in terms of individual growth rates should not be taken as evidence
16 against the likelihood of long-term competitive interactions.

17 The potential for lionfish to both compete with and consume native
18 predators is reason for concern as such simultaneous negative interactions have
19 been implicated in exacerbating the effects of other invasive predatory fishes on
20 natives (Mills et al. 2004). Native predators are severely overfished in many
21 locations across the Caribbean, especially in areas with high human population
22 densities (Stallings 2009). Although some native predators maintain relatively
23 healthy populations in remote locations and within some protected areas, lionfish
24 may represent an additional threat to these already imperiled species, a threat that
25 will neither respond to fisheries regulations nor be limited by remoteness or the
26 boundaries of marine protected areas. It will therefore be important to continue to
27 investigate the effects of lionfish on native predators, particularly those with high
28 ecological or economic importance.

29 *Native reef-fish richness, evenness, and diversity*

30 The effects of predators on prey community composition are highly context
31 dependent (see review by Hixon 1986 for fishes). In several classic examples,
32 predation has been found to disproportionately target competitively dominant prey
33 species, thereby favoring competitive subordinates and leading to increased prey

1 diversity (Paine 1966, Connell 1971). At least one introduced freshwater
2 piscivore has been found to have a similar effect, causing a decrease in the
3 abundance of common species and a concomitant increase in the abundance of
4 rare species, effectively increasing prey community evenness (He and Kitchell
5 1990). In contrast, a study of coral-reef fish found that generalist piscivores
6 disproportionately consumed rare prey species, thereby causing local reductions in
7 prey species richness (Almany & Webster 2004).

8 In this study, lionfish caused a reduction in the local richness of native
9 species, whereas native grouper did not. Additionally, lionfish and grouper
10 together (the post-invasion treatment) caused a substantial reduction in species
11 richness compared to grouper alone (the pre-invasion treatment). It is important
12 to note that species richness may have been slightly higher on the combined
13 predator treatment reefs than on the grouper-only reefs at the beginning of the
14 experiment (Online Resource 2). Despite this caveat, the experimental results
15 indicate that one of the ultimate effects of the lionfish invasion may be substantial
16 reductions in the number of native fish species on invaded reefs.

17 Species evenness decreased on predator-free control reefs over the course
18 of the experiment, likely due to high recruitment of common species and a
19 resulting increase in the difference between the density of common and rare
20 species. Compared to controls, lionfish caused an increase in evenness on
21 experimental reefs over the course of the experiment. Increased evenness in the
22 presence of lionfish resulted from a combination of reduced abundance of
23 common species, and reduced numbers of rare species (due to extirpations).
24 While the effect of native grouper on the change in prey evenness was not
25 statistically significant, the mean effect was positive (similar to the lionfish
26 effect). However, patterns of evenness in the combined-predator treatment were
27 more similar to those in the control treatment than to either of the single-predator
28 treatments. This non-additive effect of the two predators on evenness is difficult
29 to explain. One speculative explanation is that, in combination, the two predators
30 reduced the abundance of common species so greatly that it became inefficient for
31 one or both predators to target these species, thus causing a shift to less common
32 prey species (i.e., switching behavior, Murdoch 1969). This increased predation
33 on less common species may have resulted in the observed increase in the
34 difference in abundance between common and less common species (i.e., a

1 decrease in evenness). It also appears that at least one species (*Gnatholepis*
2 *thompsoni*) may be resistant to one or both predators. This goby is one of the few
3 species for which final abundance was actually higher on combined predator reefs
4 than on control reefs (Table 1, Online Resource 3). The resulting numerical
5 dominance of this single species could have contributed to the relative drop in
6 evenness observed for this treatment.

7 Species diversity (richness and evenness combined) did not change on
8 control reefs or for either of the single-predator treatments (lionfish-only and
9 grouper-only) over the course of the experiment. Diversity remained relatively
10 constant on the control reefs because increases in species richness were offset by
11 decreased evenness. Diversity also remained relatively constant on both single-
12 predator treatments because the converse was true -- losses of species richness
13 were offset by increased evenness. However, diversity was reduced on the
14 combined predator treatment reefs compared to the other treatments because both
15 richness and evenness declined in this treatment.

16 *Multivariate community response*

17 Comparison of the ordination from the baseline census (which showed no
18 pronounced differences among experimental communities) to the ordination from
19 the final census demonstrated that the communities in the four treatments diverged
20 substantially over the course of the experiment. Linear correlations of reef-fish
21 species with axis 1 from the final ordination indicated that native grouper had a
22 moderate effect on the abundance of common species (causing a small shift
23 towards the negative end of axis 1), whereas lionfish had a stronger effect on
24 those species (causing a larger shift to the negative end of the axis). The list of
25 species that had positive correlations with this axis, and were thus negatively
26 affected by lionfish, included the most commonly recruiting species as well as two
27 herbivores and two cleaners, suggesting that the lionfish invasion may have a
28 negative effect on these ecologically important species. It is likely that the broad
29 distribution of the combined-predator reefs along the second axis was primarily
30 driven by an increasing influence of rare species as the abundances of common
31 species were drastically reduced by the combined effects of the two predators.

1 *Conclusions*

2 This study establishes a causal relationship between an invasive predator and
3 changes in the native prey community relative to an ecologically similar native
4 predator. Such studies are quite rare and are valuable, first, adding to our limited
5 knowledge regarding the mechanisms by which invasive predators affect native
6 prey communities, and second, determining the appropriate management approach
7 to a particular invasion.

8 The primary conclusion of this study is that invasive lionfish are not
9 ecologically equivalent to coney grouper, a similarly sized native piscivore.
10 Under the same field conditions, lionfish grew at substantially faster rates, and had
11 stronger effects on native coral-reef fish communities, reducing both overall
12 abundance and local species richness. Novel characteristics and behaviors of
13 lionfish and naïveté of native prey to these traits may contribute to the relative
14 strength of these effects. Large reductions in the abundance of small native coral
15 reef fishes due to lionfish predation may alter native reef-fish community
16 composition, and may have important and far-reaching consequences for coral-
17 reef ecosystems. Coral reefs and associated fishes are threatened by a wide range
18 of perturbations, including overfishing, climate change, and habitat destruction
19 (Mora 2008). Invasive species in general, and lionfish in particular, represent an
20 additional threat to these ecosystems.

21 These results indicate that managers tasked with mitigating the invasion
22 should anticipate strong direct and indirect effects between lionfish and native
23 species. However, it should be emphasized that the effects reported here were
24 caused by juvenile lionfish, and were measured over small spatial and temporal
25 scales. Given that ecological processes are often temporally and spatially scale-
26 dependent (Levin 1992), the question remains whether and how the lionfish
27 invasion will affect reef-fish communities on large contiguous reefs over longer
28 time periods. To gain a more complete understanding of the overall consequences
29 of the lionfish invasion, it will be important to assess their effects at more
30 management-relevant temporal and spatial scales.

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5

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1 **Figure Legends**

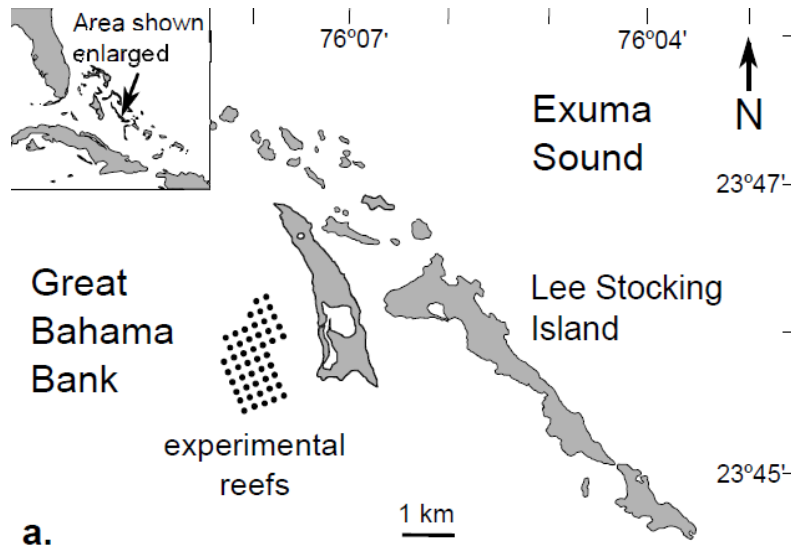
2 **Fig. 1** (a.) Matrix of patch reefs near Lee Stocking Island, Bahamas. (b.) Experimental design
3 showing treatment assignments. Grey symbols represent unused reefs. Map redrawn from
4 Almany (2003).

5 **Fig. 2** Change in abundance ΔN (mean \pm SEM) of small fish (≤ 5 cm TL) on experimental coral
6 patch-reefs under four different predator treatments: predator-free controls (solid diamonds), native
7 grouper only (open triangles), invasive lionfish only (open circles), and combined grouper +
8 lionfish (solid squares). $N = 5$ patch reefs per treatment. Values represent the change in
9 abundance between the baseline census (before establishment of predator treatments) and each
10 subsequent weekly census. Letters on the right side of the plot indicate the results of pairwise
11 comparisons among the treatments at the final census (matching letters indicate a p-value > 0.05).
12 Symbols are offset along the x-axis to facilitate viewing.

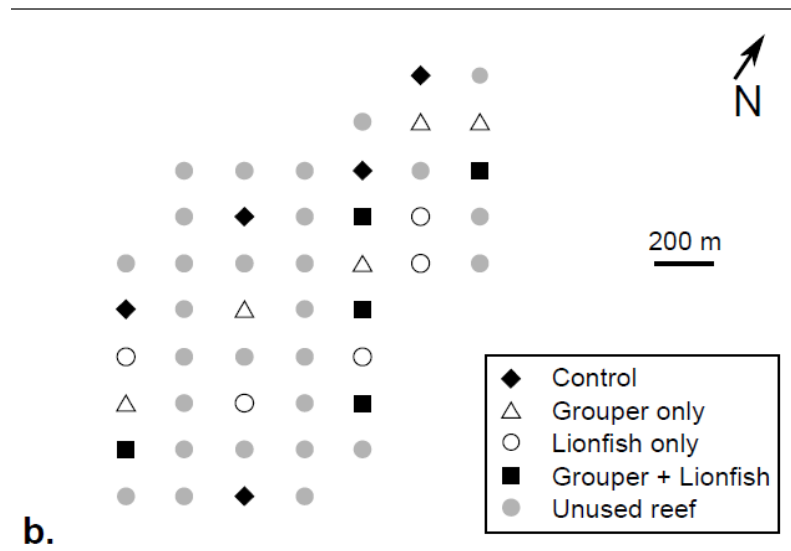
13 **Fig. 3** Changes (mean \pm SEM) in (a.) species richness ΔS , (b.) species evenness ΔJ , and (c.)
14 species diversity $\Delta H'$ of small fish (≤ 5 cm TL) on experimental coral patch-reefs under four
15 different predator treatments: predator-free controls (solid diamonds), native grouper only (open
16 triangles), invasive lionfish only (open circles), and combined grouper + lionfish (solid squares).
17 $N = 5$ patch reefs per treatment. The experiment ran for 8 weeks; values represent the change in
18 each metric between the baseline census (before establishment of predator treatments) and the final
19 census. Letters at the top of the plot indicate the results of pairwise comparisons among the
20 treatments at the final census (matching letters indicate a p-value > 0.05).

21 **Fig. 4** Non-metric multidimensional scaling ordinations of experimental reefs in species space (a.)
22 at the beginning of the experiment (baseline census) and (b.) at the end of the experiment (final
23 census) with minimum convex hull polygons for each predator treatment group: predator-free
24 controls, native grouper only, invasive lionfish only, and combined grouper + lionfish. For ease of
25 interpretation, the ordination for the final census has been rotated for maximum correlation
26 between axis one and overall change in abundance. See supplementary materials (Table 4) for a
27 list of species-specific linear correlations with each NMDS axis.

28



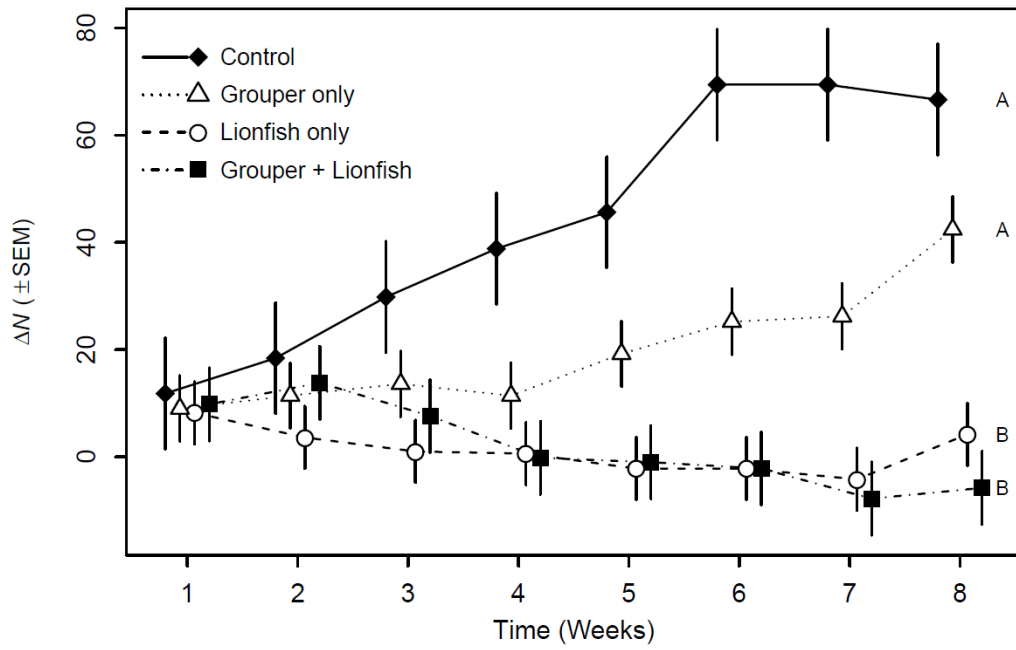
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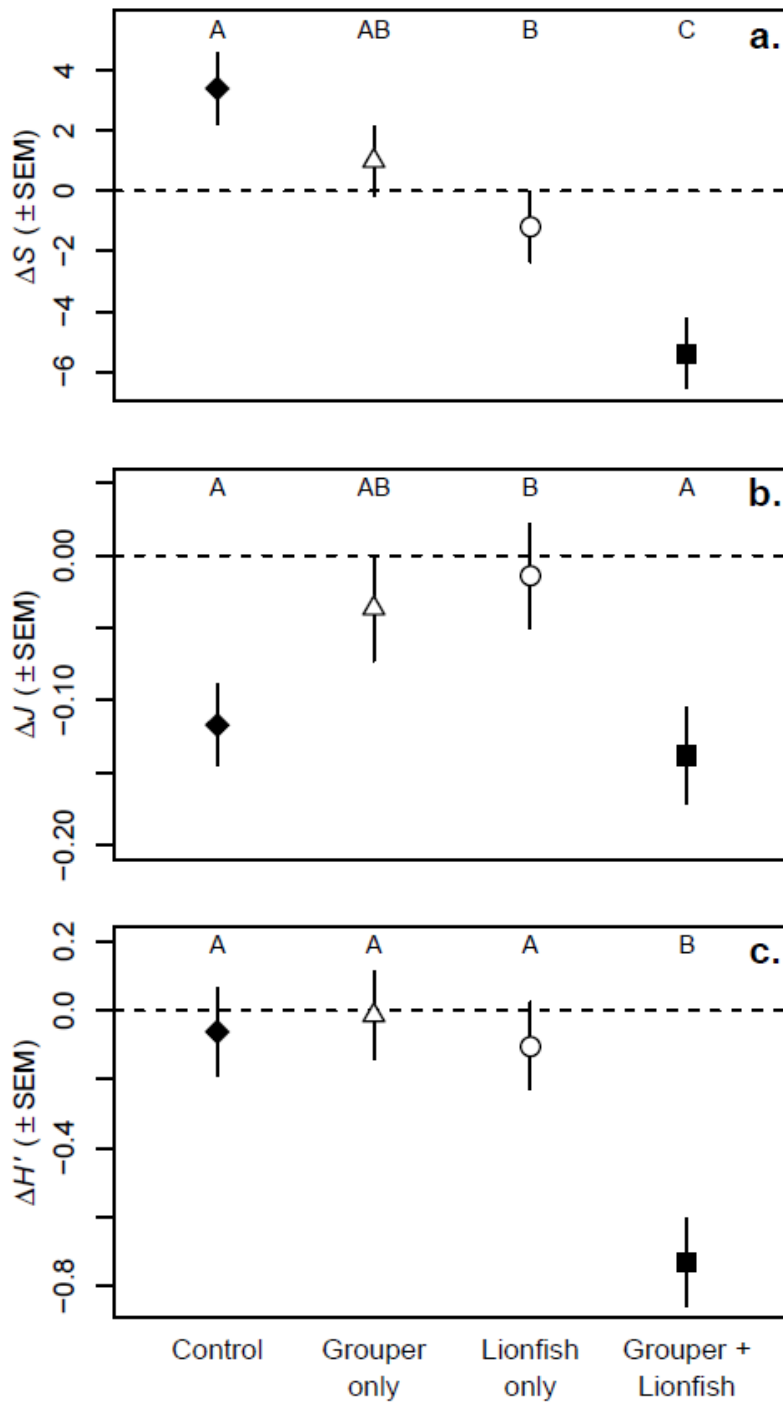
Figure 1



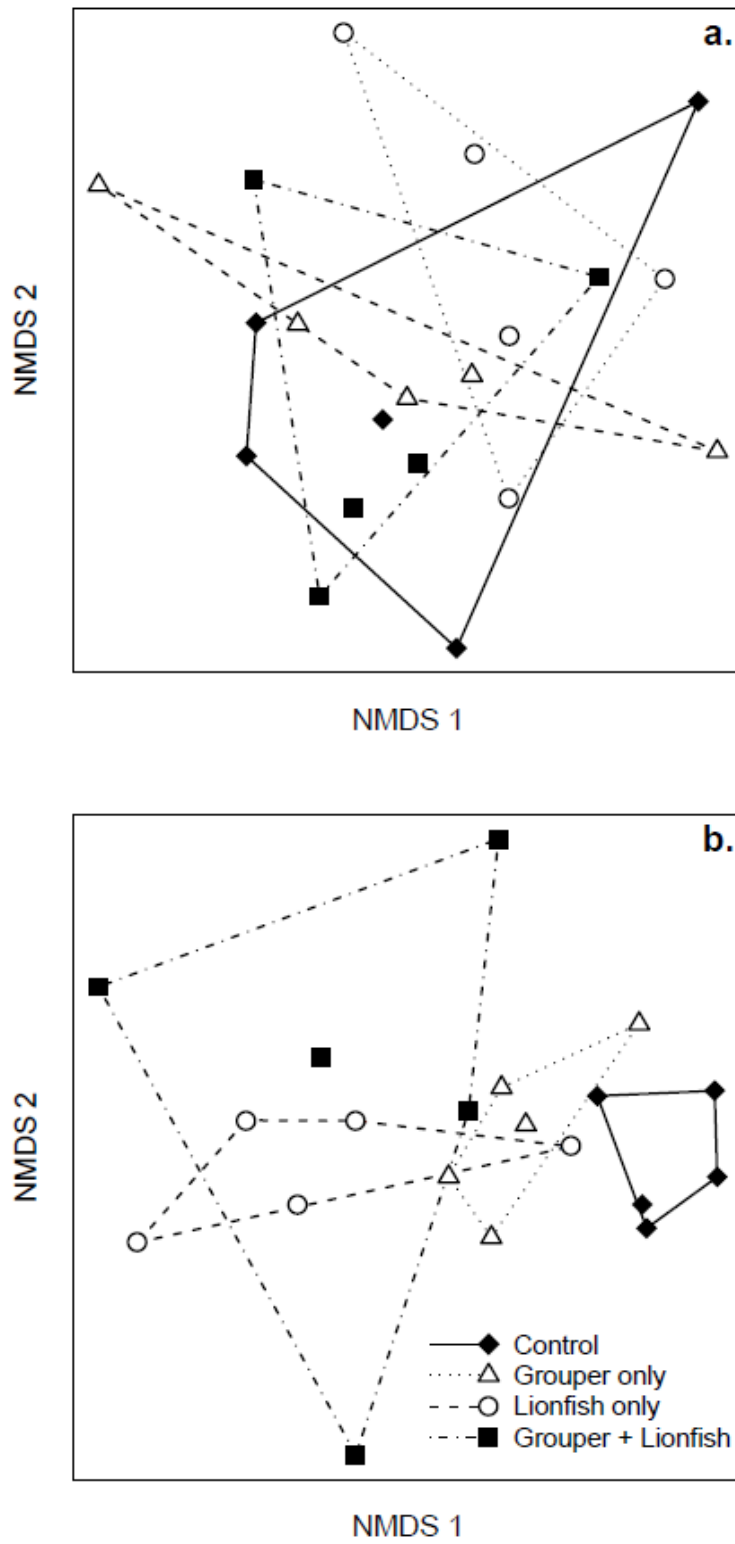
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2 Figure 3
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2 Figure 4

Table 1. Mean change in abundance (individuals per reef) of small native coral-reef fishes on predator-free control reefs ($\Delta N_{control}$) over the course of the 8-week experiment and the effect of each predator treatment on the mean change in abundance for each reef-fish species. The treatment effects are calculated as the difference between mean change in abundance on control reefs at week 8 ($\Delta N_{control}$) and mean change in abundance on grouper only ($\Delta N_{grouper}$), lionfish only ($\Delta N_{lionfish}$), and grouper + lionfish ($\Delta N_{grouper+lionfish}$) treatment reefs at week 8 (e.g. grouper effect = $\Delta N_{grouper} - \Delta N_{control}$). Table is sorted by increasing change in abundance on control reefs. Species with zeros in all columns were counted during reef censuses, but did not change in mean abundance over the course of the experiment on any of the four treatments. Table continued on next page.

Family	Species	Control	Grouper effect	Lionfish effect	Combined effect
		($\Delta N_{control}$)	($\Delta N_{grouper} - \Delta N_{control}$)	($\Delta N_{lionfish} - \Delta N_{control}$)	($\Delta N_{grouper+lionfish} - \Delta N_{control}$)
Gobiidae	<i>Coryphopterus glaucofraenum</i>	35.2	-12.4	-30.4	-32.6
Pomacentridae	<i>Stegastes leucostictus</i>	18.2	-14.2	-19.6	-19.6
Gobiidae	<i>Gnatholepis thompsoni</i>	5.0	0.6	1.2	1.2
Labrisomidae	<i>Malacoctenus macropus</i>	4.0	-3.8	-4.4	-6.6
Scaridae	<i>Sparisoma aurofrenatum</i>	4.0	-0.6	-2.0	-1.6
Scaridae	<i>Sparisoma viride</i>	1.8	4.8	-3.4	-5.2
Labridae	<i>Halichoeres pictus</i>	1.8	-0.6	-1.8	-1.8
Acanthuridae	<i>Acanthurus chirurgus</i>	0.6	-0.6	-0.6	-0.8
Pomacentridae	<i>Stegastes partitus</i>	0.6	0.0	-0.4	-1.4
Tetraodontidae	<i>Canthigaster rostrata</i>	0.6	-0.6	-0.8	-0.4
Gobiidae	<i>Priolepis hipoliti</i>	0.2	0.0	-0.4	-0.2
Labridae	<i>Halichoeres poeyi</i>	0.2	-0.6	-0.6	-0.2
Serranidae	<i>Serranus tigrinus</i>	0.2	-0.2	-0.2	-0.2
Haemulidae	<i>Haemulon</i> sp. (juvenile)	0.2	-0.2	-0.2	-0.2
Scorpaenidae	<i>Scorpaena plumeiri</i>	0.2	-0.2	-0.2	-0.2
Labridae	<i>Bodianus rufus</i>	0.2	-0.4	-0.2	-0.2
Scaridae	<i>Cryptotomus roseus</i>	0.0	0.0	0.0	-0.4
Gobiidae	<i>Gobiosoma genie</i>	0.0	-0.2	-0.2	-0.2
Pomacanthidae	<i>Holocanthus tricolor</i>	0.0	0.0	0.0	-0.2
Holocentridae	<i>Sargocentron coruscum</i>	0.0	0.0	0.0	-0.2
Gobiidae	<i>Coryphopterus dicrus</i>	0.0	0.0	0.4	0.0
Labridae	<i>Halichoeres radiatus</i>	0.0	0.0	0.0	-0.4
Haemulidae	<i>Haemulon melanurum</i>	0.0	0.0	0.0	0.0
Apogonidae	<i>Apogon binotatus</i>	0.0	0.0	0.4	-0.2
Acanthuridae	<i>Acanthurus coeruleus</i>	0.0	0.0	0.0	0.2
Apogonidae	<i>Apogon townsendi</i>	0.0	0.2	0.2	0.0
Labrisomidae	<i>Malacoctenus triangulatus</i>	0.0	0.0	0.0	0.0
Mullidae	<i>Pseudupeneus maculatus</i>	0.0	0.0	0.0	0.0
Paralichthyidae	<i>Paralichthys albigutta</i>	0.0	0.0	0.0	0.0
Apogonidae	<i>Apogon maculatus</i>	0.0	0.0	0.0	0.2
Serranidae	<i>Epinephelus guttatus</i>	0.0	0.0	0.0	-0.2
Pomacanthidae	<i>Holocanthus ciliaris</i>	0.0	0.0	-0.2	0.0
Holocentridae	<i>Holocentrus adscensionis</i>	0.0	-0.6	0.0	-0.4

Labridae	<i>Halichoeres maculipinna</i>	-0.2	-0.2	-0.2	-1.4
Serranidae	<i>Cephalopholis cruentatus</i>	-0.2	0.2	0.2	0.2
Pomacentridae	<i>Stegastes variabilis</i>	-0.2	0.2	0.2	0.2
Labrisomidae	<i>Malacoctenus macropus</i>	-0.2	0.2	0.2	0.0
Haemulidae	<i>Haemulon plumieri</i>	-0.4	0.4	0.2	-0.2
Labridae	<i>Thalassoma bifasciatum</i>	-0.4	0.4	-2.2	0.0
Callionymidae	<i>Paradiplogrammus bairdi</i>	-0.6	0.2	0.2	0.4
Scaridae	<i>Scarus taeniopterus</i>	-0.6	1.0	0.4	-0.8
Scaridae	<i>Sparisoma atomarium</i>	-0.6	0.4	-0.2	0.0
Labridae	<i>Halichoeres garnoti</i>	-0.8	1.0	0.0	-1.0
Pomacentridae	<i>Chromis cyanea</i>	-2.2	2.0	2.2	2.2
TOTAL		66.6	-23.8	-62.4	-72.2

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Journal Name: Biological Invasions

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Online Resource 1 (supplementary table): Selection criteria for random effects, variance structure, and autocorrelation structure for candidate models for each response variable. LRT results: likelihood ratios, and p-values (corrected for testing-on-the-boundary) resulting from tests between models without random effects, and models with *reef* as a random effect. Variance structure -- equal: equal variance; treatment: separate variances for each treatment; species: separate variances for each species; species \times treatment: separate variances for each species treatment combination. Autocorrelation structure -- none: no autocorrelation; AR(1): AR(1) structure within reefs; n.a.: temporal correlation was not applicable. AIC -- Akaike's Information Criterion for each model. The best fitting models have the lowest AIC values (indicated in bold faced type).

Response variable	<i>LRT results</i>		Variance structure	Autocorrelation structure	AIC
	L Ratio	p*			
Change in abundance (ΔN)	47.3	< 0.001	equal	none	1145.6
			treatment	none	1129.1
			equal	AR(1)	1124.8
			treatment	AR(1)	1107.6
Change in richness (ΔS)	35.3	< 0.001	equal	none	678.6
			treatment	none	679.2
			equal	AR(1)	648.4
			treatment	AR(1)	652.8
Change in evenness (ΔJ)	62.4	< 0.001	equal	none	-236.9
			treatment	none	-244.3
			equal	AR(1)	-243.1
			treatment	AR(1)	-248.4
Change in diversity ($\Delta H'$)	58.8	< 0.001	equal	none	92.1
			treatment	none	98.0
			equal	AR(1)	74.8
			treatment	AR(1)	76.6
Rate of length growth	0.38	0.268	equal	n.a.	-65.4
			species	n.a.	-73.6
			treatment	n.a.	-64.6
			species \times treatment	n.a.	-71.8
Rate of mass growth	5.26	0.022	equal	n.a.	-7.6
			species	n.a.	-22.0
			treatment	n.a.	-15.9
			species \times treatment	n.a.	-26.2

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Online Resource 2 (supplementary table): Estimated baseline fitted values and contrast coefficients with associated statistics from linear mixed effects models of four community response variables on reefs assigned to the four predator treatments at the baseline census (before predator treatments were established). Standard errors (SE), t-statistics (t), and p-values (p), are included for each contrast estimate (degrees of freedom = 17 for all coefficient estimates and associated tests). Note: comparisons with significant (**) or marginally significant (*) p-values are denoted by bold face type.

Response	Treatment	Estimate ± SE	Contrast	Estimate ± SE	t	p
Abundance (fish per reef)	control	29.6 ± 13.2	control vs. grouper	-11.8 ± 16.4	-0.72	0.481
	grouper	17.8 ± 9.7	control vs. lionfish	-5.6 ± 16.3	-0.34	0.735
	lionfish	24.0 ± 9.6	control vs. lionfish + grouper	2.2 ± 16.7	0.13	0.900
	lionfish + grouper	31.8 ± 10.2	grouper vs. lionfish	6.2 ± 13.7	0.45	0.656
			grouper vs. lionfish + grouper	14.0 ± 14.1	0.99	0.336
			lionfish vs. lionfish + grouper	7.8 ± 14.1	0.55	0.586
Richness (species per reef)	control	10.8 ± 1.4	control vs. grouper	-0.8 ± 2.0	-0.41	0.688
	grouper	10.0 ± 1.4	control vs. lionfish	-0.2 ± 2.0	-0.1	0.920
	lionfish	10.6 ± 1.4	control vs. lionfish + grouper	2.8 ± 2.0	1.43	0.171
	lionfish + grouper	13.6 ± 1.4	grouper vs. lionfish	0.6 ± 2.0	0.31	0.763
			grouper vs. lionfish + grouper	3.6 ± 2.0	1.84	*0.084
			lionfish vs. lionfish + grouper	3.0 ± 2.0	1.53	0.144
Evenness (J)	control	0.84 ± 0.02	control vs. grouper	-0.05 ± 0.04	-1.5	0.152
	grouper	0.79 ± 0.03	control vs. lionfish	-0.01 ± 0.03	-0.36	0.724
	lionfish	0.83 ± 0.03	control vs. lionfish + grouper	0.04 ± 0.03	1.31	0.209
	lionfish + grouper	0.89 ± 0.03	grouper vs. lionfish	0.04 ± 0.04	0.94	0.359
			grouper vs. lionfish + grouper	0.10 ± 0.04	2.39	**0.030
			lionfish vs. lionfish + grouper	0.06 ± 0.04	1.38	0.187
Diversity (H')	control	1.99 ± 0.12	control vs. grouper	-0.18 ± 0.17	-1.04	0.315
	grouper	1.82 ± 0.12	control vs. lionfish	-0.06 ± 0.17	-0.38	0.712
	lionfish	1.92 ± 0.12	control vs. lionfish + grouper	0.30 ± 0.17	1.77	*0.094
	lionfish + grouper	2.30 ± 0.12	grouper vs. lionfish	0.11 ± 0.17	0.66	0.510
			grouper vs. lionfish + grouper	0.48 ± 0.17	2.81	**0.012
			lionfish vs. lionfish + grouper	0.37 ± 0.17	2.15	**0.046

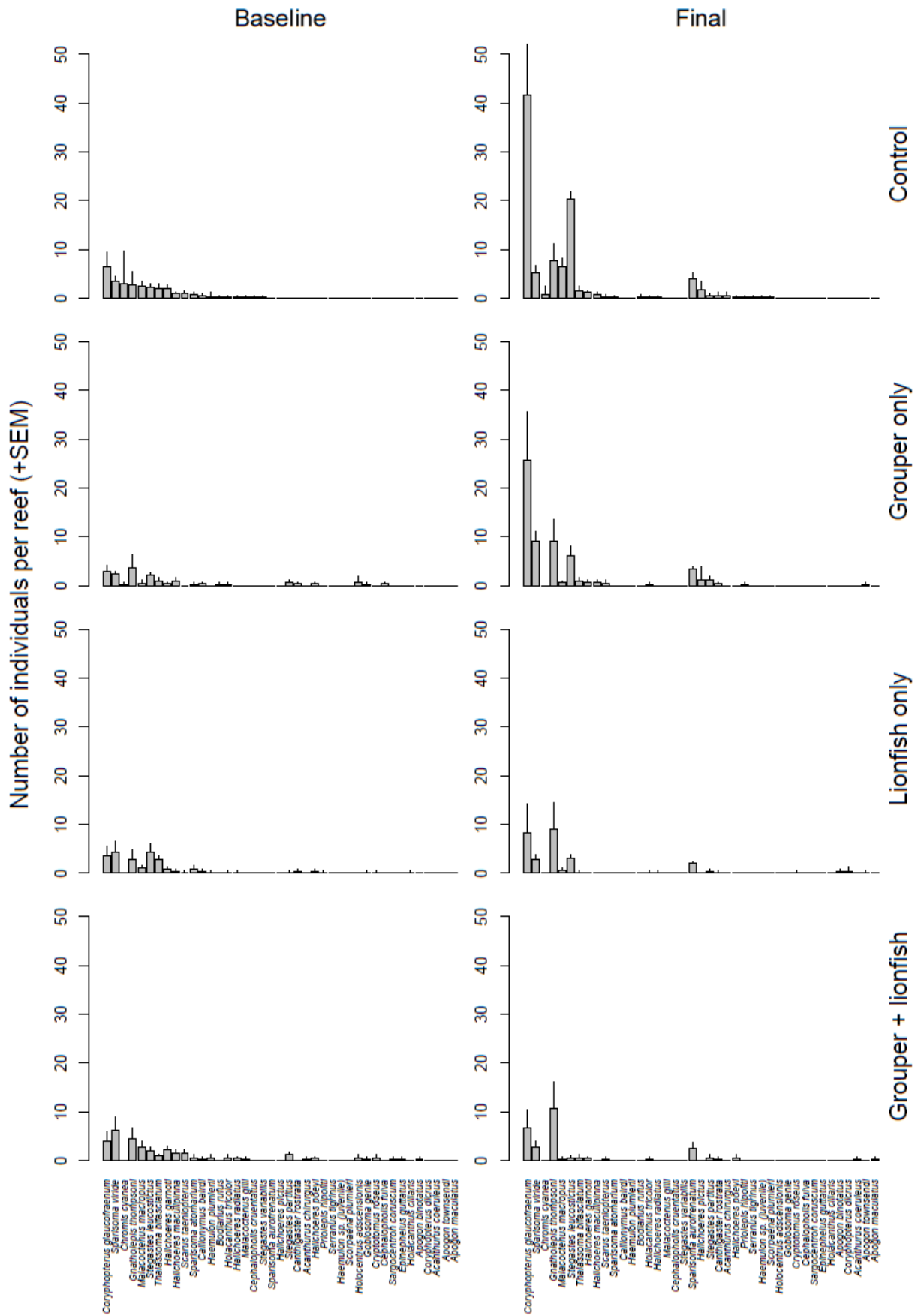
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Online Resource 3 (supplementary figure): Mean abundance of all species (individuals per reef \pm SEM) on experimental reefs at the baseline census (before predator treatments were established) and at the final census (week 8) for each of the four resident-predator treatments. N = 5 patch reefs per treatment.

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Online Resource 4 (supplementary table): List of families and species of juvenile coral reef fishes present on experimental reefs at the end of the experiment with associated linear correlations with each axis from the NMDS ordination (Fig 3). List is sorted by correlation with axis 1. Correlations with absolute values greater than 0.3 are marked with an asterisk and denoted by bold-face type.

Family	Species	Correlation	
		Axis 1	Axis 2
Gobiidae	<i>Coryphopterus glaucofraenum</i>	*0.685	0.196
Labrisomidae	<i>Malacoctenus macropus</i>	*0.605	-0.161
Pomacentridae	<i>Stegastes leucostictus</i>	*0.551	-0.278
Labridae	<i>Halichoeres garnoti</i>	*0.489	-0.172
Labridae	<i>Bodianus rufus</i>	*0.435	0.024
Labridae	<i>Halichoeres maculipinna</i>	*0.427	0.282
Labridae	<i>Halichoeres pictus</i>	*0.409	0.169
Pomacentridae	<i>Stegastes partitus</i>	*0.381	0.204
Labridae	<i>Thalassoma bifasciatum</i>	*0.378	*0.495
Scaridae	<i>Sparisoma viride</i>	*0.350	-0.077
Acanthuridae	<i>Acanthurus chirurgus</i>	*0.322	-0.250
Labridae	<i>Halichoeres radiatus</i>	*0.314	-0.121
Pomacentridae	<i>Chromis cyanea</i>	0.283	0.150
Scaridae	<i>Sparisoma aurofrenatum</i>	0.273	-0.262
Haemulidae	<i>Haemulon</i> sp. (juvenile)	0.250	-0.216
Scorpaenidae	<i>Scorpaena plumieri</i>	0.250	-0.216
Scaridae	<i>Sparisoma atomarium</i>	0.250	-0.216
Gobiidae	<i>Gnatholepis thompsoni</i>	0.244	*0.407
Gobiidae	<i>Priolepis hipoliti</i>	0.218	-0.266
Scaridae	<i>Scarus taeniopterus</i>	0.151	0.239
Serranidae	<i>Serranus tigrinus</i>	0.150	0.117
Gobiidae	<i>Coryphopterus dicrus</i>	0.117	-0.050
Tetraodontidae	<i>Canthigaster rostrata</i>	0.100	*-0.408
Apogonidae	<i>Apogon townsendi</i>	0.024	-0.097
Labridae	<i>Halichoeres poeyi</i>	0.012	-0.155
Pomacanthidae	<i>Holacanthus tricolor</i>	0.000	0.073
Acanthuridae	<i>Acanthurus coeruleus</i>	-0.050	0.083
Apogonidae	<i>Apogon maculatus</i>	-0.117	*-0.316
Scaridae	<i>Cryptotomus roseus</i>	-0.283	-0.283
Apogonidae	<i>Apogon binotatus</i>	*-0.314	-0.193

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