

Conceptual and applied approaches to marine invasions

by

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Abstract

The accelerating rise in global trade and travel means that our world is more interconnected than ever before. This trend could severely impact species and ecosystems globally, as it increases opportunities for species to invade regions beyond their natural range. In this thesis, I combine ecological theory and data synthesis with empirical field-studies to tackle the questions of what makes some communities more easily invaded than others, and how can both natural and anthropogenic control interventions affect the persistence and impacts of invasive species. I first evaluate the relationship between native species diversity and invasibility, or the vulnerability of a community to invasion. Using a meta-analytic approach, I show that the conflicting patterns between diversity and invasibility that are often observed in the literature are likely due to not only differences in spatial scales between studies but also to differences in the metrics researchers use to measure invader success. I then use the invasion of Caribbean coral reefs by the predatory Indo-Pacific lionfish as a model system to test natural and anthropogenic means of controlling the invader. Using a combination of fisheries-derived sampling of native grouper predators and a field experiment conducted across a gradient of grouper abundance, I examine the ability of native grouper predators to mitigate the negative effects of lionfish predation in the Bahamas. I reveal little evidence for direct predation by groupers on lionfish, but show that fear of native groupers alone by lionfish is sufficient to evoke behavioural changes in lionfish that could potentially reduce their impact on native prey. Finally, I use a long-term field experiment to investigate the ecological effectiveness of infrequent culling (i.e., the physical removal of lionfish from reefs by divers). I demonstrate that infrequent culling can reduce lionfish abundance, but is insufficient to halt the decline in native prey fish biomass. Moreover, I show that large-scale natural disturbances, like hurricanes, and density-dependent movement by lionfish from neighbouring reefs can undermine culling efforts. Overall, my thesis reveals that the development of standardized metrics is key to generate a holistic understanding of invasion dynamics, and that both natural and anthropogenic control over invaders is unlikely to stymy biological invasions at the scale currently observed for Indo-Pacific lionfish in the Caribbean.

Keywords: diversity-invasibility relationship; invasion paradox; meta-analysis; biotic resistance; lionfish; invasive species control

To my mom, Portia Maria Smith (1951-1998),

and to my dad, James Herbert Smith

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Chapter 1.

Introduction

The world's biological diversity is under attack. Major threats include overexploitation, habitat loss and fragmentation, climate change, pollution, and invasive species (Groom et al. 2005). More than half of known local to global marine extinctions are due to overexploitation while 65% of IUCN Red List birds are impacted by invasive species (Dulvy et al. 2003; Kappel 2005). The Earth is now in its sixth mass extinction, as species are being lost at an unprecedented rate (Ceballos et al. 2017).

What are the implications of biodiversity loss for the planet? A philosophical perspective highlights the intrinsic value of species and our moral imperative to conserve them (Pearson 2016). A utilitarian view, in contrast, emphasizes the goods and services that biodiversity supports, and the human societies that depend on them (Pearson 2016). The latter standpoint is the focus of much ecological research (e.g., Nelson et al. 2009; Zavaleta et al. 2010; Outeiro et al. 2019). From food provisioning and crop pollination to carbon sequestration and resistance to invasions, high-diversity environments (e.g., genetic, species, functional, phylogenetic) are better at sustaining ecosystem services and functions than low-diversity ones (Zavaleta et al. 2010; Oliver et al. 2015a, 2015b). Moreover, species-rich assemblages are required to maintain multiple ecosystem functions simultaneously (Zavaleta et al. 2010). But at what scale(s) does diversity act? Because of tradeoffs between ecosystem functions, high diversity both at the plot level and across landscapes may be required to sustain multiple ecosystem functions (Zavaleta et al. 2010). However for some functions, like resistance to invasive species, diversity might be more important at only local scales, where biotic interactions are strongest (Stachowicz 1999; Kennedy et al. 2002; Lockwood et al. 2013).

One of the potential benefits of biodiversity is that it can confer biotic resistance to ecological communities. Biotic resistance is the ability of a community to prevent or limit the establishment or success of non-native species (Elton 1958; Levine et al. 2004; Von Holle 2005). This concept has gained increased significance as the number of successful invasions each year has grown at an accelerating pace (Cohen and Carlton 1998; Pimentel et al. 2000; Ricciardi & Atkinson 2004). Invasion hotspots, like the

eastern Mediterranean Sea, are now dominated by non-indigenous species (Edelist et al. 2013). Resistance can emerge from a number of biotic interactions, including competition (Green et al. 2004), infection with parasites or pathogens (Beckstead & Parker 2003; Reinhart et al. 2003), and predation (Nyström 2005; Britton 2012; Yamanishi et al. 2012; Yorisue et al. 2019). Predation is of particular interest because this potentially important process of biotic resistance is being eroded by the disappearance of top predators from many of the world's ecosystems (Johnson et al. 2007; Heithaus et al. 2008; Ritchie and Johnson 2009). But how do predators help ecological communities to resist invasions? Direct consumption of non-native prey is one mechanism (e.g., Britton 2012; Yamanishi et al. 2012), but the mere presence of predators is known to trigger a range of behavioural responses in their prey (e.g., Lima 1998; Dill et al. 2003; Stallings 2008; Suraci et al. 2016). Is there also a role for non-consumptive or fear effects of predators in biotic resistance? The answer is currently unclear.

Invasive species management comes to the forefront when biotic resistance fails. Management entails the prevention, early detection, eradication, and control of invasive species (Lookwood et al. 2007). Invasions are costly to the environment and to the economy. Native species extinctions, extirpations, declines in abundances, and disruptions to local food webs and ecosystem functions have all been linked to invasive species (Savidge 1987; Vitousek 1990; Wilcove et al. 1998; Sala et al. 2000; Crooks 2002; Blackburn 2005). At the same time, the damages and control efforts associated with invasive species cost billions of US dollars per year globally (Pimentel et al. 2000; 2005). There is therefore a critical need to effectively manage biological invasions within the constraints of the many competing demands on a nation and/or region's limited resources, particularly those in the Global South. Given the above, how do we limit the growth and spread of invasive species more efficiently? Are there biotic and/or abiotic factors that could potentially undermine control efforts? The answers can be gained by doing long-term manipulative experiments in natural ecosystems that are guided by real-life economic constraints, but such experiments have seldom been carried out.

In this thesis, I address a number of gaps in current knowledge related to (1) the role of species diversity in an ecological community's susceptibility to invasions, (2) the mechanisms by which native predators can act as a form of biotic resistance, and (3) the circumstances under which local control efforts of an invasive species are challenged,

with the added realism of limited time and financial resources. Specifically, in Chapter 2, I examine the invasion paradox: the conflicting patterns between diversity and community vulnerability to invasions (i.e., invasibility) (Fridley et al. 2007; Clark and Johnston 2011). By quantitatively investigating the roles of spatial scale and of the metrics used to measure invasion success, I partly resolve the paradox and show that both scale and invasibility metrics can influence the magnitude and direction of diversity-invasibility relationships. In Chapter 3, I directly address an ongoing debate in the scientific literature regarding whether native Caribbean predators can provide some biotic resistance against invasive, Indo-Pacific lionfish in coral reef systems (Mumby et al. 2011; Valdivia et al. 2014). In this case study, I explore the potential for both consumptive and non-consumptive (or fear) effects by native groupers to limit lionfish population growth and impacts on native prey fishes. I find little evidence of direct predation of lionfish by groupers. However, I show that fear of native groupers changes lionfish behaviour in ways that may reduce lionfish foraging success. Finally in Chapter 4, I investigate the ecological effectiveness of the most common method for controlling invasive lionfish populations in the Caribbean. Culling, or the physical removal of lionfish by divers, is used throughout the Caribbean to reduce lionfish populations and halt the decline of native prey fishes (Green et al. 2014). I demonstrate that when removals are done on time scales that are in keeping with the reality of severe resource constraints in small island developing states, culling can reduce lionfish abundance but it does not mitigate their negative effects on native prey. Moreover, density-dependent movement of lionfish among neighbouring reefs and large-scale natural disturbances, like hurricanes, can undermine local control efforts. Taken together, the answers I provide to key questions relating to the roles of species diversity and native predators in biotic resistance, as well as the ecological effectiveness of local lionfish control efforts help to advance both the theory and practice of biological invasions.

Chapter 2.

Multiple drivers of contrasting diversity-invasibility relationships at fine spatial grains¹

Abstract

The diversity–invasibility hypothesis and ecological theory predict that high-diversity communities should be less easily invaded than species-poor communities, but empirical evidence does not consistently support this prediction. While fine-scale experiments tend to yield the predicted negative association between diversity and invasibility, broad-scale observational surveys generally report a positive correlation. This conflicting pattern between experiments and observational studies is referred to as the invasion paradox, and is thought to arise because different processes control species composition at different spatial scales. Here, we test empirically the extent to which the strength and direction of published diversity–invasibility relationships depend on spatial scale and on the metrics used to measure invasibility. Using a meta-analytic framework, we explicitly separate the two components of spatial scale: grain and extent, by focusing on fine-grain studies that vary in extent. We find evidence of multiple drivers of the paradox. When we consider only fine-grain studies, we still observe conflicting patterns between experiments and observational studies. In contrast, when we examine studies that are conducted at both a fine grain and fine extent, there is broad overlap in effect sizes between experiments and observation, suggesting that comparing studies with similar extents resolves the paradox at local scales. However, we uncover systematic differences in the metrics used to measure invasibility between experiments, which use predominantly invader performance, and observational studies, which use mainly invader richness. When we consider studies with the same metric (i.e., invader performance), the contrasting associations between study types also disappears. It is not possible, at present, to fully disentangle the effect of spatial extent and metric on the paradox because both variables are systematically associated in different directions with study type. There is therefore an urgent need to conduct experiments and observational

¹ A version of this chapter appears as Smith NS, Côté IM. 2019. Multiple drivers of contrasting diversity-invasibility relationships at fine spatial grains. *Ecology*. 100(2):e02573

studies that incorporate the full range of variability in spatial extent and invasibility metric.

Introduction

A long-standing debate in ecology is the nature of the relationship between diversity and a community's susceptibility to invasion, i.e., invasibility (Levine and D'Antonio 1999, Shea and Chesson 2002, Herben et al. 2004, Fridley et al. 2007, Lockwood et al. 2013). Elton's (1958) diversity–invasibility hypothesis and classic ecological theory predict that high-diversity communities should be less easily invaded than low-diversity communities (Case 1990, Shea and Chesson 2002, Tilman et al. 2014), but empirical evidence does not consistently support this prediction. While fine-scale experiments tend to yield the predicted negative association between diversity and invasibility (e.g., Hodgson et al. 2002; Kennedy et al. 2002; Stachowicz et al. 2002; van Elsas et al. 2012), broad-scale observational surveys generally report a positive association (Lonsdale 1999, Stohlgren et al. 1999, 2003, Herben et al. 2004, Davies et al. 2005). This conflicting pattern between experiments and observational studies is referred to as the invasion paradox (Clark and Johnston 2011).

The invasion paradox is generally thought to arise because different processes control species composition at different spatial scales (Levine 2000, Shea and Chesson 2002, Byers and Noonburg 2003, Davies et al. 2005, Knight and Reich 2005, Fridley et al. 2007). Experiments are typically conducted at fine spatial scales where competition-driven biotic interactions, such as niche complementarity or sampling effects, are thought to determine community membership (Stachowicz 1999, Wardle 2001, Kennedy et al. 2002b, Stachowicz et al. 2002, Lockwood et al. 2013). Niche complementarity occurs when species differ in their use of resources, making species-rich communities more resistant to invasion because resident species use limiting resources more completely and efficiently, leaving little available niche space for newly arriving species (Stachowicz 1999, Shea and Chesson 2002, Stachowicz et al. 2002). Species-rich communities might also be more difficult to invade because it is more likely that a competitively superior species (or species combination) that excludes invaders is present as the number of species increases (i.e., a sampling effect) (Huston 1997, Wardle 2001). Observational studies, on the other hand, tend to occur at broad spatial scales where extrinsic factors that covary with diversity are considered to be the

dominant forces shaping species composition (Levine 2000, Naeem et al. 2000, Brown and Peet 2003, Davies et al. 2005, Fridley et al. 2007, Lockwood et al. 2013). Spatial environmental heterogeneity, for example, can lead to a positive diversity–invasibility relationship at large spatial scales because of its positive effect on beta diversity in both native and exotic species (Shea and Chesson 2002, Byers and Noonburg 2003, Davies et al. 2005). Similarly, dispersal processes can drive a positive diversity–invasibility relationship (Levine 2000, Knight and Reich 2005, Holle and Simberloff 2005). Levine (2000), for example, showed that at broad spatial scales high propagule supply of both native and exotic species in a riparian plant system swamped the otherwise negative effect of native diversity on invasion susceptibility.

While many agree that the effect of spatial scale is important to understanding variability in diversity–invasibility patterns, how to assess spatial scale is less obvious. Spatial scale can be defined in at least two different ways: grain or extent. Spatial grain refers to the size of a sampling plot while spatial extent reflects how far apart sampling plots are spaced (Rahbek 2005; Adler et al. 2011; Anderson 2018). Thus, studies that manipulate spatial grain over a limited spatial extent might be more likely to generate negative diversity–invasibility relationships than studies of small spatial grain that range over broad extents because the former are unlikely to capture the large-scale environmental heterogeneity of the latter. Surprisingly, many invasion studies are vague on which aspect of scale they manipulate, despite the demonstrated importance of this distinction in other areas (Rahbek 2005).

Variability in the diversity–invasibility relationship has also been ascribed to other factors than scale (Davies et al. 2007, Fridley et al. 2007). For example, at a given spatial scale, the strength and/or direction of the diversity–invasibility relationship can change when environmental conditions are altered. This shift has been documented, for instance, with changes in productivity (Jiang and Morin 2004, Davies et al. 2007), environmental stress (Holle 2013) and disturbance regimes (Suding and Gross 2006, Belote et al. 2008, Hill and Fischer 2014a). Another potentially important but relatively unexplored influence on the invasion paradox is the metric used to measure invasion vulnerability (but see Jeschke et al. 2012; 2018). While many experiments tend to quantify invasibility using some metric of performance of a single invader (e.g., abundance or survival), most observational studies quantify invasibility using measures of exotic diversity (typically species richness). Yet different invasibility metrics can lead to different, or even

conflicting, conclusions about the nature of the diversity–invasibility relationship even within the same community (Cleland et al. 2004, Tabacchi and Planty-Tabacchi 2005, Guo and Symstad 2008, Hill and Fischer 2014a, Guo et al. 2015).

These multiple confounding variables hinder our understanding of what factors drive the invasion paradox. Here, focusing only on studies conducted at fine spatial grain, we partially disentangle the effects of two factors, i.e., spatial extent and invasibility metric, to deepen our understanding of contrasting diversity–invasibility patterns between experiments and observational studies. We do so by quantifying both the strength and direction of published diversity–invasibility relationships using a meta-analytic framework in which we isolate pertinent factors by examining subgroups of our full data set in mixed-effects models.

Methods

Study selection, data extraction and coding

We conducted a systematic search of the peer-reviewed literature for studies that measured the relationship between diversity and invasibility, following the protocol outlined in the PRISMA (Preferred Reporting Items for Systematic Reviews and Meta-analyses) statement (Moher et al. 2009). We identified relevant studies on 13 March 2017 using the search term ‘diversity–invasibility’ and three academic databases for all available years through the end of 2016: the Aquatic Sciences and Fisheries Abstracts Database Guide (ASFA), Google Scholar and ISI Web of Science (Fig. A.1). Additionally, we searched the references list of publications included in our meta-analysis as well as other major reviews to identify any other relevant studies.

Papers had to meet five criteria to be included in our analyses. First, and critically, the study had to be conducted at a fine spatial grain. Since the definition of fine spatial grain varies among taxa, we only included publications in which the author(s) indicated that the study was conducted at a scale in which biotic interactions within a plot should be important, i.e., ‘all or most individuals within an area directly interact with one another’ (Fridley et al. 2007). Some studies reported findings at multiple spatial grains, all of which can be considered fine. In this instance, we included studies conducted at the most common grain for a particular taxon in our dataset (e.g., 1 m² for terrestrial plants).

Second, native diversity was restricted to measurements of species richness. Third, we included only experimental and observational studies (thus excluded mathematical models and simulations). Fourth, we restricted studies to those containing linear univariate models that measured the relationship between diversity and invasibility using regression, Pearson's correlation, or non-parametric Spearman's rank correlation. Linear multivariate models (e.g., multiple linear regression) were excluded from analyses because unless the explanatory variables are completely uncorrelated, which is unlikely in ecology, the effect size estimate for the factor of interest depends on the other predictors included in the model (Quinn and Keough 2002, Nakagawa and Cuthill 2007). A final criterion was that the study must be available in English.

We recorded the following data from each study: (1) the correlation coefficient and sample size, (2) study type, i.e., experiment or observational, (3) the spatial grain of the study, (4) the spatial extent of the study, and (5) the invasibility metric, i.e., invader performance or species richness. To determine spatial extent, we divided studies into three groups: (1) small (i.e., the study comprised a single site), (2) medium (i.e., the study contained multiple sites within an island, state, or country), and (3) large spatial extent (i.e., the study included multiple islands, states, or countries), as has been done elsewhere (Adler et al. 2011). We excluded studies from spatial extent analyses if the number of sites was not explicitly stated, the study community comprised soil microbes, or the study included a block design. When invader performance was used as a metric of invasibility, we grouped studies into measures related to either survival (e.g., proportion or % surviving) or abundance (e.g., number of individuals, % cover, total biomass; Table A.1). If multiple performance measures were provided for the same individual (or colony), we randomly selected one measure to avoid issues arising from non-independence (Gurevitch and Hedges 1999, Noble et al. 2017). Likewise, if more than one invasibility metric was presented for focal taxa within the same plot (e.g., a performance metric for a single invasive species and total invasive species richness), we randomly selected one measure of invasibility. We included multiple effect sizes from the same study only if separate effect sizes were reported for taxa in separate plots (Table A.1 and Fig A.2). When the diversity–invasibility relationship was reported at several time points throughout a study, we included only the final time point in our analyses. Lastly, if a study examined the diversity–invasibility relationship before and after a disturbance (e.g., fire), we included only the pre-disturbance findings because

disturbance can alter the diversity–invasibility relationship (Belote et al. 2008; Clark and Johnston 2011).

Statistical analysis

Effect size

We used correlation coefficients (Pearson’s and Spearman’s) as a standardized effect size. Using both parametric and nonparametric statistics increased our sample size by allowing for studies that did not meet the assumption of bivariate normality to be included in our analyses - although the two metrics are calculated differently (i.e., Pearson’s correlation coefficient is based on the numerical values of two variables while Spearman’s correlation coefficient relies on rank data). We chose the correlation coefficient because it is a common measure of the diversity–invasibility relationship in both experiments and observational studies. Furthermore, it is dimensionless and thus, comparable across studies (Nakagawa and Cuthill 2007, Borenstein et al. 2009, Nakagawa et al. 2017). When studies used linear regression to describe the diversity–invasibility relationship, we converted the coefficient of determination (R^2) to the correlation coefficient by taking the square root of R^2 . Because the variance of the correlation coefficient depends on the strength of the correlation (Borenstein et al. 2009), we converted all correlation coefficients to Fisher’s z-transformed correlation coefficient (Zr) prior to analyses using the equation below:

$$Zr = \frac{1}{2} \ln \left(\frac{1+r}{1-r} \right)$$

where r is the correlation coefficient (Sokal and Rohlf 1995). An approximation of the asymptotic variance of Fisher’s z-transformed correlation coefficient (V_z) was subsequently calculated as:

$$V_z = \frac{1}{n - 3}$$

where n is the sample size (Sokal and Rohlf 1995). Zr ranges from $-\infty$ to $+\infty$, where negative values represent a negative association, positive values represent a positive association, and zero represents no association (Rosenberg et al. 2000).

We weighted each effect size (Z_r) by the inverse of the sampling variance so that more precise studies (e.g., those with larger sample sizes) were given more weight than less precise studies when calculating the mean effect size (Fig. S2; Adams et al. 1997; Gurevitch and Hedges 1999; Gates 2002; Harrison 2011). We also generated 95% confidence intervals of the mean. A mean effect size is considered to be significantly different from zero if the confidence interval does not span zero (Fig. A.2; Rosenberg et al. 2000; Harrison 2011). Following all analyses, we back-transformed Z_r so that results are reported as the correlation coefficient, which is easier to interpret and has benchmarks for what is considered to be a ‘small’, ‘medium’ or ‘large’ effect (i.e., $r = 0.1$, 0.3, and 0.5, respectively; Cohen 1988; Nakagawa and Cuthill 2007).

Models

We fitted five random-effects models to examine the overall relationship between diversity and invasibility at fine spatial grains across all studies and across various subgroups of the full data set (Table 2.1). Random-effects models were appropriate because they allow effect size estimates to vary due to study-specific sampling error as well as due to underlying ecological differences in true effect size among studies arising from factors such as differing taxa, which is treated as purely random (Borenstein et al. 2009, Viechtbauer 2010, Nakagawa et al. 2017, Noble et al. 2017). However, one limitation of a random-effects model in meta-analysis is that it assumes that each study contributes only one effect size to the dataset, which is not the case for most meta-analyses in ecology and evolution (Nakagawa and Santos 2012, Noble et al. 2017), or here. Omitting multiple effect sizes from a study reduces statistical power and could result in a loss of information (Nakagawa and Santos 2012). We therefore also conducted alternative meta-analyses, as has been done elsewhere (Gurevitch et al. 2001, Gates 2002, Côté et al. 2005, Noble et al. 2017), to assess how sensitive our estimates of overall effect sizes based on random-effects models were to inclusion of multiple effect sizes from a single study, i.e., inclusion of non-independent effect sizes (Fig. A.3; see *Assessing publication bias and other sensitivity analyses* subsection for details).

Table 2.1 Mixed-effects models with corresponding hypotheses and predictions used in our meta-analysis by subsetting the data for studies conducted at fine spatial grains.

Model number	Hypothesis	Extent subset	Metric subset	Study type subset	Explanatory variable	Prediction
1	Study types show conflicting diversity-invasibility patterns at fine spatial grains	All extents	All metrics	All study types	Study type	Exp. will have a negative effect size while Obs. will have a positive effect size
2	Increasing spatial extent leads to a positive diversity-invasibility association	All extents	Richness only	Obs. only	Spatial extent	Negative effect size at fine extents will weaken and become positive with increasing extent
3	Differences in diversity-invasibility patterns between study types disappear when considering studies of similar extent and grain	Fine only	All metrics	All study types	Study type	Both Exp. and Obs. will have a negative effect size at fine extents
4	Invasibility metric is the primary driver of contrasting diversity-invasibility correlations	All extents	All metrics	Obs. only	Metric	Obs. that use performance will show an effect size that is opposite in direction from Obs. that use richness
5	Differences in diversity-invasibility associations between study types should disappear when considering studies with the same metric	All extents	Performance only	All study types	Study type	Exp. and Obs. will display effect sizes with similar directions

In all models, study was treated as a random effect, while the explanatory variable was treated as a fixed effect. Spatial extents: small, medium, large; invasibility metrics: performance, richness; study types: experimental (exp.), observational (obs.).

To test our hypotheses on the roles of spatial extent and invasibility metric on the invasion paradox at fine grains, we constructed five separate mixed-effects models in which each *a priori* explanatory variable was treated as a fixed effect while study was treated as a random effect to account for instances in which multiple effect sizes originated from a single study (Table 2.1). In other words, we used ‘multilevel meta-regressions’ (Nakagawa and Santos 2012; Noble et al. 2017). However, to examine the effect of invasibility metric on the paradox at fine grains, we also conducted a chi-squared (χ^2) contingency test to assess whether there was bias in how invasibility was

quantified (i.e., using performance metrics or species richness) between study types. Because few experiments used species richness as a measure of invasion vulnerability (see Results), we restricted our fourth mixed-effects model to only observational studies (Table 2.1). We ascertained that we could justifiably combine various performance metrics (Fig. A.4). In all instances, we used omnibus tests and confidence intervals to assess the significance of parameter estimates (Viechtbauer 2010).

Assessing heterogeneity

We measured residual heterogeneity among effect sizes (i.e., between-study variance, τ^2) using restricted maximum-likelihood estimation (Viechtbauer 2005). Cochran's Q test (Hedges and Olkin 1985) was used to test the significance of τ^2 for both random-effects and mixed-effects models (Viechtbauer 2010). The inclusion of explanatory variables (whether categorical or continuous) in mixed-effects models is appropriate when the total heterogeneity of the sample, i.e., Q_{total} (also referred to as Cochran's Q or Q_T), in a random-effects model is significant, which suggests that other factors might explain this additional variation (Rosenberg et al. 2000, Borenstein et al. 2009, Nakagawa and Santos 2012, Nakagawa et al. 2017). When explanatory variables were included in mixed-effects models, we used the Q_M statistic to determine whether these variables accounted for some of the heterogeneity among studies.

Assessing publication bias and other sensitivity analyses

Publication bias is the largest potential source of Type I error in meta-analysis (Harrison 2011). We tested for publication bias in our overall dataset using standard graphical and statistical methods. Funnel plot asymmetry can be indicative of bias, i.e. when studies with results that are non-significant or in the opposite direction from what is expected are less likely to be published (Viechtbauer 2010, Harrison 2011, Nakagawa and Santos 2012, Nakagawa et al. 2017). We checked for asymmetry in a funnel plot of effect sizes (Z_r) versus standard errors both visually (Fig. A.5) and statistically with Egger's regression test (Egger et al. 1997, Sterne and Egger 2005). Additionally, we evaluated the robustness of our findings by calculating the Rosenberg fail-safe number (Rosenberg 2005), which reveals the number of unpublished, non-significant studies that would overturn a significant finding (Gurevitch and Hedges 1999, Rosenberg 2005, Harrison 2011). A large fail-safe number relative to the number of studies included in the meta-

analysis suggests that an observed mean effect size is a robust estimate of the true effect (Gurevitch and Hedges 1999, Rosenberg 2005, Harrison 2011).

Finally, we assessed the effects of non-independence and potentially influential studies and effect sizes on our general conclusions. To evaluate the consequences of using non-independent effect sizes in random-effects models, we conducted alternative meta-analyses in which we randomly selected one effect size per study that reported multiple effect sizes. We then compared results from meta-analytic models with and without non-independent effect sizes (e.g., Côté et al. 2005, Nakagawa and Santos 2012; Fig. A.3). Also, we assessed whether a single study or effect size substantially influenced estimates of overall effect size in random-effects models via ‘leave-one-out’ cross validation in which we systematically removed each study and effect size from our dataset (with replacement) and then re-fitted the model. Nevertheless, we acknowledge that there are other potential sources of non-independence that we have not quantitatively assessed such as instances in which multiple studies are conducted by the same group of researchers.

We conducted all analyses using the metafor package (Viechtbauer 2010) and visualizations using the ggplot2 package (Wickham 2009) in R (v. 3.2.3; R Development Core Team 2014).

Results

Overview

A total of 58 diversity–invasibility relationships from 34 studies published from 1999 through 2015 were included in our analyses (Figs A.1 and A.2; Table A.1). The number of correlations (i.e., effect sizes) reported per study ranged from one to eight, with a mean of 1.71 (± 1.6 SD) and a median of one (Fig. A.2; Table A.1). Diversity–invasibility associations were derived from 18 experiments and 40 observational studies (Table A.1). Egger’s regression test for asymmetry in a funnel plot of effect size (Z_r) versus standard error revealed no evidence of publication bias ($z = -0.75$, $P = 0.45$). Furthermore, the Rosenberg fail-safe number was large (10,927), suggesting that our conclusions are robust to publication bias.

There was little difference in overall effect size estimates between random-effects models that included all effect sizes and those that included only one randomly selected effect size per study (Fig. A.3). Likewise, leave-one-out cross validations showed that no single effect size or study overly influenced our general conclusions. We therefore present the results from random-effects models that included all effect sizes here (Table 2.2). All models revealed significant total heterogeneity among studies (Q_T in Table 2.2), and therefore justified the inclusion of other factors that might explain this variation in mixed-effects models (Table 2.2).

Table 2.2 Heterogeneity statistics for the various meta-analytic models presented in Table 2.1.

Model number	Statistical model	df	τ^2 (se)	Q	P	df	Q_M	P
1	Random-effects	57	0.46 (0.09)	5023.62	< 0.0001	NA	NA	NA
	Mixed-effects	56	0.38 (0.08)	4513.72	< 0.0001	2	11.58	0.003
2	Random-effects	33	0.33 (0.09)	4110.06	< 0.0001	NA	NA	NA
	Mixed-effects	31	0.32 (0.09)	2034.42	< 0.0001	3	7.94	0.047
3	Random-effects	24	0.17 (0.07)	192.06	< 0.0001	NA	NA	NA
	Mixed-effects	23	0.17 (0.06)	150.14	< 0.0001	2	2.54	0.28
4	Random-effects	39	0.33 (0.08)	4186.91	< 0.0001	NA	NA	NA
	Mixed-effects	38	0.32 (0.08)	4171.18	< 0.0001	2	6.24	0.04
5	Random-effects	21	0.47 (0.16)	810.80	< 0.0001	NA	NA	NA
	Mixed-effects	20	0.49(0.17)	378.79	< 0.0001	2	6.51	0.04

Df indicates degrees of freedom; τ^2 is a measure of between-study variance, (with standard error, se); Q is a heterogeneity statistic (i.e., Q_T in random-effects models and Q_E in mixed-effects models); Q_M is between-group heterogeneity in mixed-effects models. Random-effects models were used to estimate the overall relationship between diversity and invasibility at fine spatial grains across various subgroupings. Mixed-effects models were used to evaluate the effects of *a priori* explanatory variables on diversity-invasibility associations, with study as a random factor.

Evidence of the paradox among fine-grain studies

Study type (i.e., experiment vs. observational) was a significant predictor of the strength and direction of diversity–invasibility relationships carried out at fine spatial grains (Q_M in model 1 of Table 2.2; Fig. 2.1b). Moreover, experiments and observational studies still showed the conflicting pattern that defines the invasion paradox. On average, experiments yielded a moderate to large, negative association between diversity and invasion vulnerability while observational studies reported a weak, positive correlation

(Fig. 2.1b). This effect was significant for experiments (Fig. 2.1b) but marginally not significant for observational studies ($P = 0.08$; Fig. 2.1b). There was still significant residual heterogeneity (Q_E statistic in mixed-effects model results, Table 2.1), suggesting that other factors might be important.

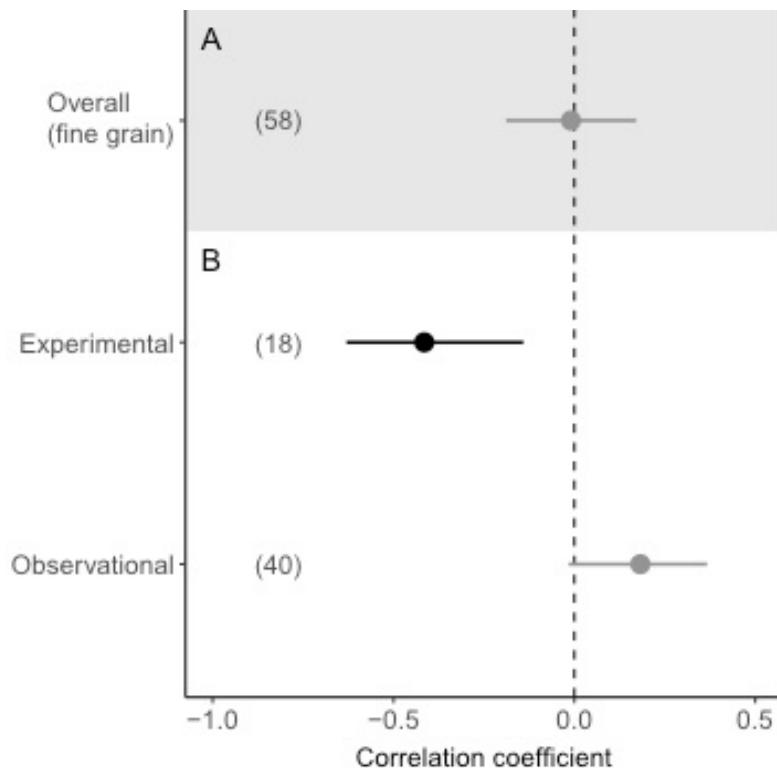


Figure 2.1 Strength and direction of the diversity–invasibility relationship in experiments and observational studies at fine spatial grain.

(A) Overall effect size, estimated from a random-effects model, and (B) effect sizes for experiments and observational studies, estimated from a mixed-effects model. Mean effect sizes (r , correlation coefficients) are shown, bounded by 95% confidence intervals. Significant effect sizes are shown in black while non-significant results are shown in grey. Sample sizes are indicated in parentheses to the left of each mean.

Effect of spatial extent

Spatial extent was a significant predictor of among-study variation (Q_M statistic in mixed-effects model 2 of Table 2.2). Furthermore, the strength of the positive correlation between diversity and invasion vulnerability increased with increasing extent, but the association between diversity and invasibility was only significant for studies conducted at the largest extent (Fig. 2.2b).

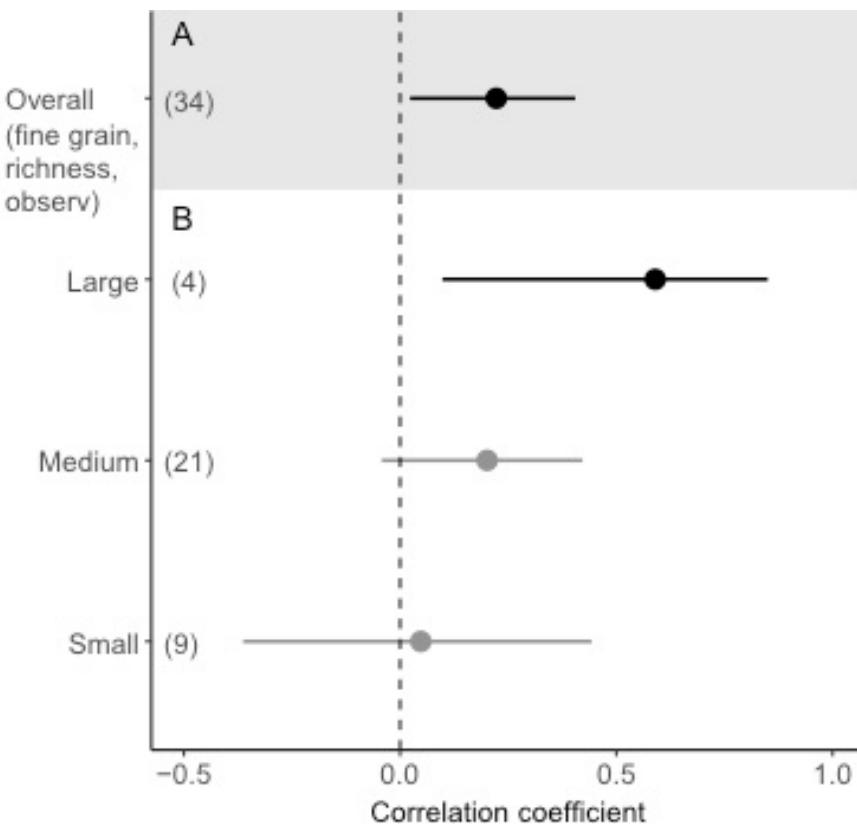


Figure 2.2 Effect of sampling extent on the strength and direction of the diversity-invasibility relationship when study type and invasibility metric are the same (i.e., observational studies, richness).

(A) Overall effect size, estimated from a random-effects model, and (B) effect sizes for three levels of spatial extent, estimated from a mixed-effects model. Mean effect sizes (r , correlation coefficients) are shown, bounded by 95% confidence intervals. Significant effect sizes are shown in black while non-significant results are shown in grey. Sample sizes are indicated in parentheses to the left of each mean.

When we considered only studies conducted at a fine spatial grain and extent, the correlation between native diversity and invasibility was not different from zero for both study types (Fig. 2.3b). Moreover, study type was no longer a significant predictor of variability in diversity–invasibility patterns ($P=0.28$; mixed-effects model 3 of Table 2.2). However, there was still significant, unexplained heterogeneity among studies (Q_E in the mixed-effects model 3 of Table 2.2).

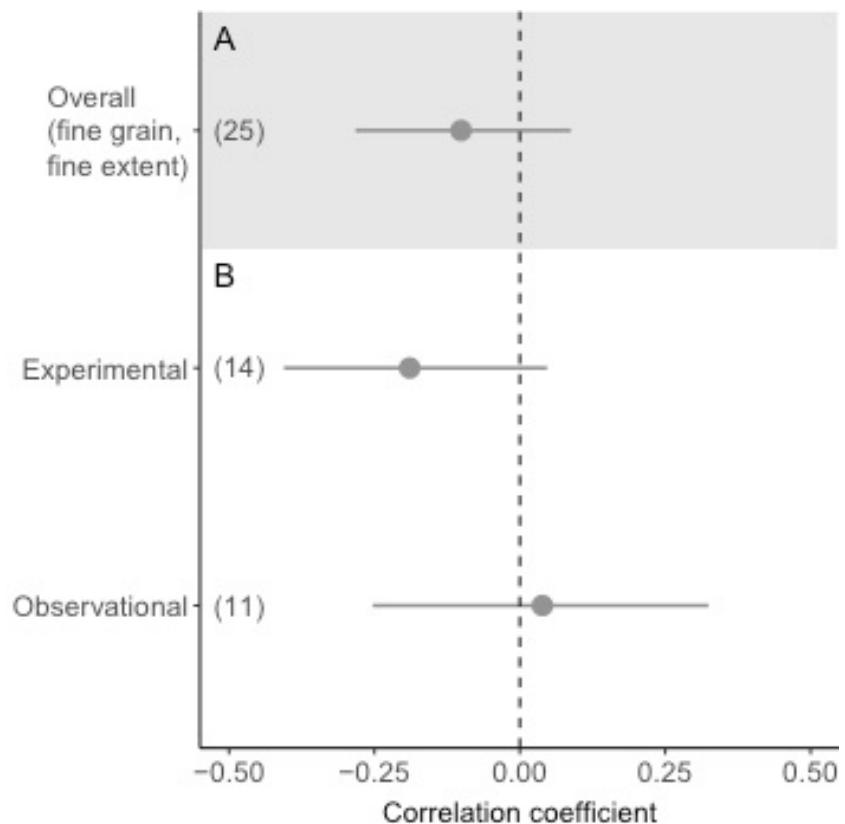


Figure 2.3 The effect of study type on the diversity-invasibility relationship when studies are conducted at a fine grain and fine extent.

(A) Overall effect size, estimated from a random-effects model, and (B) effect sizes for experiments versus observational studies, estimated from a mixed-effects model. Mean effect sizes (r , correlation coefficients) are shown, bounded by 95% confidence intervals. All results were non-significant (shown in grey). Sample sizes are indicated in parentheses to the left of each mean.

Effect of invasibility metric

There was a significant bias in how invasion susceptibility was measured in experiments versus observational studies (χ^2 contingency test: $\chi^2 = 32.01$, df = 1, P = 0.0005; Fig. 2.4). While experiments most often quantified invasibility in terms of invader performance, observational studies typically used exotic species richness (Fig. 2.4). Different invader performance metrics (i.e., abundance versus survival) yielded similar diversity–invasibility relationships (Fig. A.4), and were therefore pooled for further analysis.

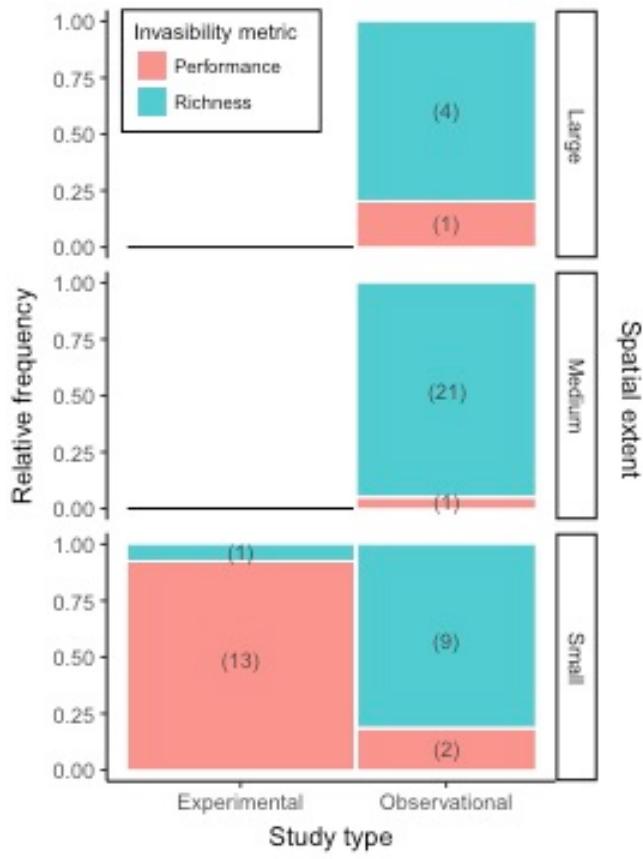


Figure 2.4 Mosaic plot illustrating the prevalence of different invasibility metrics in fine-grain experiments and fine-grain observational studies across different spatial extents.

No experiments were conducted at medium or large extents. The area of each box is proportional to the relative frequency of that combination of variables, while sample sizes are indicated in parentheses within each area.

We examined the effect of invasibility metric (performance vs. richness) on the diversity–invasibility relationship reported in observational studies—the only study type that allowed such a comparison (Fig. 2.4). Including invasibility metric as an explanatory variable in a mixed-effects model resulted in contrasting diversity-invasibility patterns: on average, studies that used invader performance reported a weakly negative association while studies that used richness showed a weakly positive association (Fig. 2.5b). The latter correlation was significant (Fig. 2.5b). Moreover, invasibility metric was a significant predictor of between-group variability ($P=0.04$; mixed-effects model 4 of Table 2.2).

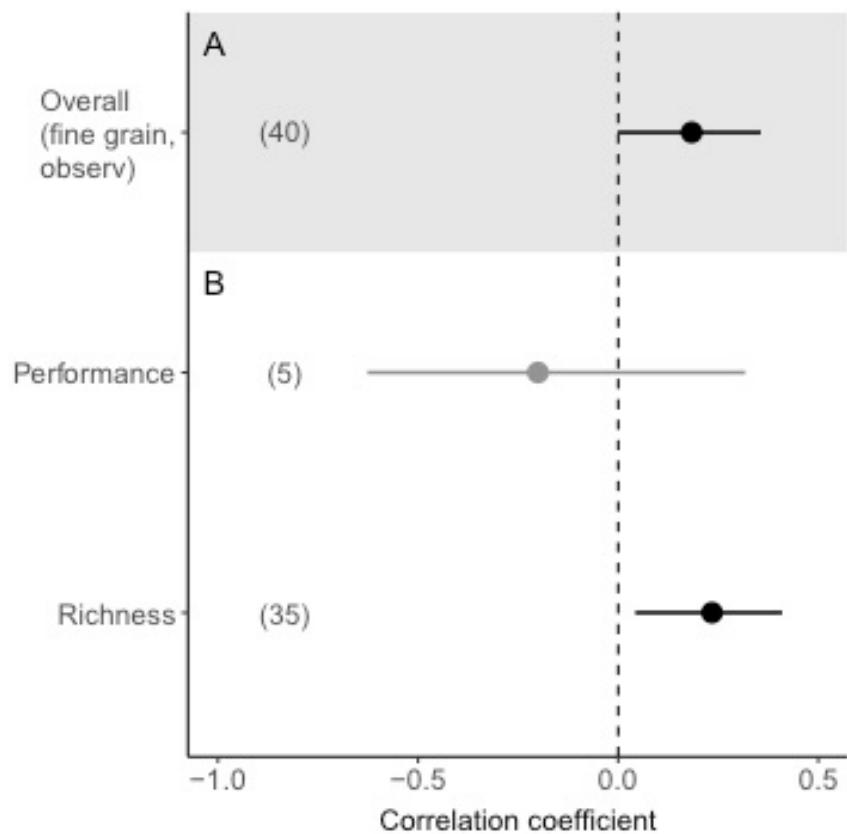


Figure 2.5 Analysis of invasibility metric. Effect of invasibility metric on the strength and direction of the diversity-invasibility relationship within fine grain, observational studies.

(A) Overall effect size, estimated from a random-effects model, and (B) effect sizes for observational studies in which invasion vulnerability is measured as invader performance or species richness, estimated from a mixed-effects model. Mean effect sizes (r , correlation coefficients) are shown, bounded by 95% confidence intervals. Significant effect sizes are shown in black while non-significant results are shown in grey. Sample sizes are indicated in parentheses to the left of each mean.

But when we considered only studies that used performance as a metric, study type was still a significant predictor of between-group variability (mixed-effects model 5 of Table 2.2). Nevertheless, both experiments and observational studies showed an overall negative association between diversity and invasibility, which is significant for the former, but not for the latter case where sample size was small ($n = 5$; Fig. 2.6b).

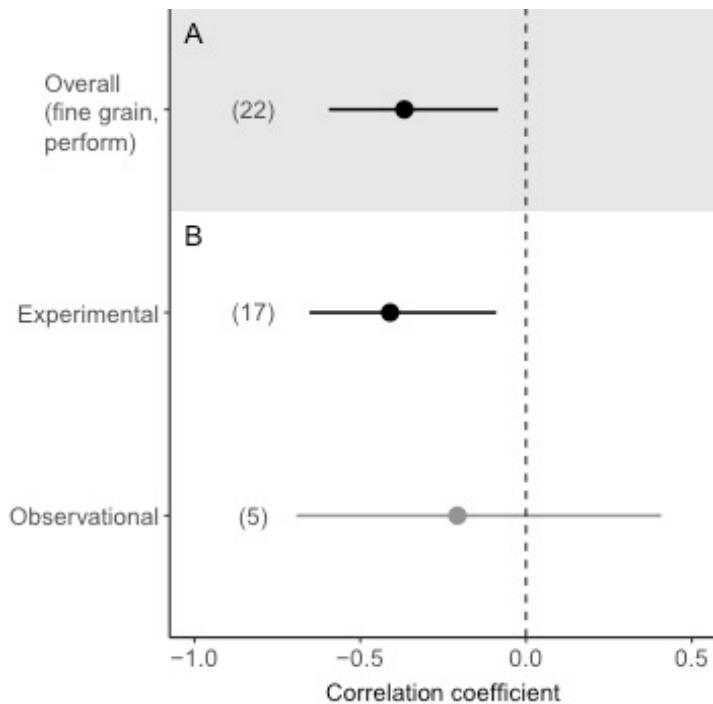


Figure 2.6 Diversity-invasibility patterns in fine grain experiments and observational studies when invasibility metric is the same (i.e., all fine grain, performance).

(A) Overall effect size, estimated from a random-effects model, and (B) effect sizes for experimental and observational studies, estimated from a mixed-effects model. Mean effect sizes (r , correlation coefficients) are shown, bounded by 95% confidence intervals. Significant effect sizes are shown in black while non-significant results are shown in grey. Sample sizes are indicated in parentheses to the left of each mean.

Discussion

We found evidence of multiple drivers of contrasting diversity–invasibility relationships. When we consider only fine-grain studies, we still observed conflicting patterns between experiments and observational studies (Fig. 2.1b). Consistent with theory, the positive association between diversity and invasion vulnerability strengthened with increasing spatial extent (Fig. 2.2b). When we examine only fine grain and fine extent studies, effect sizes for both study types did not differ from zero (Fig. 2.3). Similarly, when we consider only studies of invader performance, the conflicting pattern between study types also disappears (Fig. 2.6). It is not possible, at present, to fully disentangle the effect of spatial extent and metric on the paradox because both variables are systematically associated in different directions with study type (Figs. 2.4 and 2.5b). There is therefore an urgent need to tackle the logistical challenges of conducting experiments at large extents and observational studies using performance metrics.

Our approach to examining factors responsible for the invasion paradox at fine spatial grains differs from previous cognate reviews in three critical aspects (Levine and D'Antonio 1999, Herben et al. 2004, Fridley et al. 2007, Kimbro et al. 2013). First, we use a different set of studies. For example, previous meta-analyses of biotic resistance through native diversity used effect sizes other than the correlation coefficient (e.g., the d -statistic or log-response ratio; Levine et al. 2004, Kimbro et al. 2013). This choice likely resulted in fewer observational studies (which often report correlation coefficients) being included in previous quantitative reviews. Second, to our knowledge, our meta-analysis is the first to explore the roles of both spatial extent and invasibility metric on the invasion paradox at fine grains. Third, the conflicting diversity–invasibility relationships between experiments and observational studies have been reported within fine-scale studies (e.g., Levine and D'Antonio 1999, Fridley et al. 2007), but our study is the first to quantify this variability using a systematic literature search and test an alternative explanation for this pattern.

Differences in spatial grain may not be as important a determinant of the invasion paradox at local scales as previously thought. We expected both experiments and observational studies to show a negative association between invasibility and local diversity at the level of the sampling plot, where competition-driven biotic interactions should dominate. This expectation is consistent with well-established ecological theory (MacArthur 1970, Case 1990) and the scale-dependent explanation of the paradox (Shea and Chesson 2002, Byers and Noonburg 2003). However, we still found the conflicting pattern that defines the paradox at fine spatial grains (Fig. 2.1b), as have previous narrative reviews (e.g., Levine and D'Antonio 1999, Fridley et al. 2007), which suggests that other factors may also be important. Whether the same occurs at larger spatial grain remains unclear, as this study addressed only fine-grain studies.

Spatial extent is likely a critical driver of the paradox among fine-grain studies. The broad overlap of effect sizes between fine-grain and fine-extent experiments and observational studies suggests, at first glance, that comparing studies of similar spatial extent resolves the paradox at local scales (Fig. 2.3). However, these results are confounded by metric because invasibility in fine-extent experiments is typically assessed with performance metrics while fine-extent observational studies use richness (Fig. 2.4; see also below). Nevertheless, we can detect an independent effect of spatial extent on diversity–invasibility patterns in fine-grain observational studies that use

richness as metric (Fig. 2.2b). These studies show an increase in the strength of the positive association between native diversity and invasion susceptibility with increasing extent – although this positive association was only significant for studies at the largest extent (Fig. 2.2b). This general pattern is consistent with theory. Extrinsic factors that covary with diversity at broad scales such as spatial environmental heterogeneity (Shea and Chesson 2002, Byers and Noonburg 2003, Davies et al. 2005) and dispersal processes (Levine 2000, Knight and Reich 2005, Holle and Simberloff 2005) are expected to have a positive effect on both native and exotic species richness.

Different invasibility metrics can yield different relationships between diversity and invasion vulnerability, even within the same community (Cleland et al. 2004, Tabacchi and Planty-Tabacchi 2005, Guo and Symstad 2008, Hill and Fischer 2014, Guo et al. 2015). For example, Tabacchi and Planty-Tabacchi (2005) found a negative correlation between native and exotic cover but a positive association between native and exotic species richness within the same riparian plant communities. Moreover, this pattern was consistent at both small and large spatial scales (Tabacchi and Planty-Tabacchi 2005). Similarly, native and non-native richness in a tall-grass prairie were positively correlated while native richness was negatively associated with non-native abundance (Cleland et al. 2004). The use of both performance and diversity metrics to assess invasibility is rare within study (e.g., $n = 5$ out of 34 studies in our dataset; Fig. A.5). In fact, we found a strong bias in invasibility metrics between study types (Fig. 2.4), whereby invasibility is usually assessed in terms of invader performance in experiments but in terms of invader richness in observational studies. Furthermore, invader performance and richness produced different relationships in fine-grain observational studies (Fig. 5b), a pattern that we found frequently repeated in instances in which both metrics were reported within a single study (Fig. A.6). Others have reported similar findings, but without the use of a formal meta-analysis (see Jeschke et al. 2018). It is clear that the implicit assumption that invasibility metrics are interchangeable (i.e., show similar patterns with native diversity) in some discussions of the paradox is unfounded (e.g., ‘spatial pattern’ studies, as summarized in Levine and D’Antonio 1999; but see Fridley et al. 2007, Jeschke et al. 2018). That invasibility metric was a significant predictor of between-study variability in the mixed-effects model (Q_M for model 4 in Table 2.2) further supports our assertion that differences in how researchers quantify invasion susceptibility likely contribute to the paradox within fine-grain studies.

When we consider only fine grain studies that use performance as a metric, experiments and observational studies both showed the predicted, negative correlation between diversity and invasion vulnerability – although this effect was not significant for observational studies (Fig. 2.6b). The negative association also held, and was significant, when both study types were combined (Fig. 2.6a). It is difficult to determine whether the large uncertainty in mean effect size for observational studies is due to small sample size (i.e., $n = 5$) or to some other unmeasured variable(s). Other reasons to interpret this result with caution are: (1) study type remained a significant predictor of variability in the diversity-invasibility relationship despite examining only studies that used the same metric (mixed-effects model 5 in Table 2), and (2) spatial extent varies across observational studies but not across experiments (Fig. 2.4). Unfortunately, there are currently not enough experiments focusing on invader richness across all extents, and observational studies using performance as metric of invasibility across all extents to allow us to disentangle meaningfully the effects of spatial extent and invasibility metric on the invasion paradox. We also note that an inherent limitation of assessing diversity-invasibility patterns based on observational surveys is that they cannot determine causation. It is therefore unclear whether observed associations are due to the effect of native richness on invasibility, or to the negative impact of successful invaders on local diversity (Levine and D'Antonio 1999). Nevertheless, our results at least very tentatively support the notion that variation in metric potentially contributes to the invasion paradox within fine-grain studies.

Our meta-analysis highlights several key areas for future work. First, the invasion literature in general, and questions related to invasibility in particular, are dominated by terrestrial plant studies conducted in temperate climates. To test the robustness of generalizations about patterns and proposed mechanisms, studies conducted in other systems and latitudes are urgently needed (see also Fridley et al. 2007, Levine and D'Antonio 1999, Lockwood et al. 2013). Second, our analyses focused only on studies conducted at a fine spatial grain. It is unclear whether extent and metric will remain potential drivers of the paradox at a broad grain, but this idea should be tested. Third, and related to the previous point, although the finding that invasibility metric may contribute to the paradox is promising, our results contain considerable uncertainty and thus, warrant further exploration. We suggest that future empirical examinations of diversity–invasibility patterns at a fine grain include both performance and richness

metrics within a single study such that consistency (or lack thereof) between measures in experiments as well as observational studies can be rigorously evaluated. So far, this has been done in only a few cases at local scales (e.g., see Fig. A.6), while some ecologists have argued for an alternative metric altogether for quantifying invasibility (Guo et al. 2015). It is particularly worthwhile (and feasible) to conduct such studies in observational surveys at both fine and broad spatial scales. Finally, we suggest future investigations into other factors hypothesized to affect the strength and direction of diversity–invasibility associations, and thereby its potential role as a driver of the paradox. It is notable, for example, that the direction of the diversity–invasibility relationship can reverse through time if the factors and processes that determine invasion success change during the invasion process (Clark and Johnstom 2011, Clark et al. 2013). Even more intriguing is the observation that spatial and temporal scales are often not independent in empirical studies (Clark et al. 2013). Space and time may therefore potentially interact in complex ways to influence the invasion paradox.

Chapter 3.

Fear of native predators promotes biotic resistance on Caribbean coral reefs

Abstract

Biotic resistance is the ability of an ecological community to prevent or limit the establishment or success of non-indigenous species. Native species might typically confer resistance by outcompeting or directly consuming non-native invaders. However, the simple fear of being eaten could be sufficient to limit invader success, but non-consumptive effects have rarely been documented as a source of biotic resistance. Here we test whether native grouper predators on coral reefs can promote biotic resistance to invasive lionfish directly, through consumption, and/or indirectly, through non-consumptive effects. Stomach content analysis of more than 200 groupers, comprising five species, revealed no instances of predation on lionfish. To test for non-consumptive effects, we released tagged juvenile lionfish onto reef patches that varied in grouper densities, and monitored lionfish antipredator behaviours over five weeks. At dawn, during peak grouper and lionfish hunting times, small lionfish hid more and were less active on reefs with more groupers. In contrast, lionfish swimming distances changed with time of day and with the presence of conspecifics but not with predator density. The former behaviours are incompatible with feeding success and thus, should result in lionfish eating less prey. However, there was no evidence of cascading effects on smaller fishes at lower trophic levels: reduced lionfish predation on reefs with more groupers did not result in more lionfish prey. The seasonal peak in prey fish recruitment, which occurred during our study, might have masked the effects of lionfish predation. Fear of native predators by lionfish can therefore reduce invader foraging success, but might not fully mitigate the effects of these invaders on native prey communities. Efforts to rebuild grouper populations throughout the Caribbean may still aid in controlling the lionfish invasion despite there being little evidence of direct predation on lionfish. At broader scales, our findings highlight that the depletion of top predators across the globe can have implications beyond demographic effects on prey.

Introduction

The rise of global trade and travel has led to increases in both the magnitude and rate of biological invasions across the planet (Cohen and Carlton 1998; Pimentel et al. 2000; Ricciardi & Atkinson 2004). Invasive species are among the leading causes of biodiversity loss worldwide (Sala et al. 2000; Wilcove et al. 1998), while control efforts and damages associated with invasive species are costing regional and national economies billions of dollars annually (Pimentel et al., 2000, 2005). Not surprisingly, considerable research, management, and restoration efforts have focused on ways to increase biotic resistance in vulnerable or highly valued native communities (Kennedy et al. 2002; Levine et al. 2004; Kimbro et al. 2013). Biotic resistance is the ability of a resident community to prevent establishment or limit the success of non-indigenous species (Elton 1958; Levine et al. 2004; Von Holle 2005). Various biotic interactions can give rise to resistance, including direct consumption (Britton 2012; Yamanishi et al. 2012), competition (Green et al. 2004), and disease (Beckstead & Parker 2003; Reinhart et al. 2003). The role of non-consumptive effects of predators in biotic resistance, however, has rarely been considered (but see Nyström 2005; Yorisue et al. 2019).

Non-consumptive, or fear, effects are prevalent in nature, and refer to adaptive changes in plastic traits of prey due to the mere presence of predators (Lima 1998). Although prey that alter traits such as behaviour or morphology are less likely to be captured, detected or encountered by predators, these changes typically come at a fitness cost (Lima 1998; Creswell 2008). For example, juvenile rays in Shark Bay, Australia, rest in shallow nearshore waters when predators are abundant to reduce predation risk (Vaudo & Heithaus 2013). However, warmer temperatures associated with shallower waters mean that rays also incur metabolic costs in these refuges (Vaudo & Heithaus 2013). In terrestrial habitats, western sandpipers on northward spring migration reduce mass-dependent predation risks from similarly migrating peregrine falcons by taking a multi-stage route, which is longer and more energetically costly than a direct flight (Lank et al. 2003). Fear effects can even cascade down food webs, leading to community changes at multiple trophic levels (Werner and Peacor 2003; Schmitz et al. 2004; Preisser et al. 2005; Heithaus et al. 2008; Suraci et al. 2016). For instance, Suraci et al. (2016) found that vocalizations of large predators reduced foraging by raccoons, which led to increased abundances of crabs and other raccoon prey. Here, we ask whether fear of native

predators can also provide biotic resistance against non-native predators and initiate cascading effects on coral reefs.

Indo-Pacific lionfish (*Pterois* sp.) are mid-level predators that feed on a variety of smaller fishes and crustaceans on coral reefs (Côté and Smith 2018). Lionfish were introduced into the western Atlantic Ocean off the east coast of Florida, USA, in the mid-1980s, due to intentional and/or unintentional releases by home aquarists (Whitfield et al. 2002; Semmens et al. 2004; Schofield 2009). Since then, lionfish have spread and become established as far north as Cape Hatteras, USA, throughout the Caribbean and Gulf of Mexico, and as far south as the east coast of Venezuela (Whitfield et al. 2002, 2007; Schofield 2010). In 2014, lionfish were reported along the southeast coast of Brazil south of the Amazon-Orinoco Plume (Ferreira et al. 2015). Lionfish have had considerable, negative effects on native fauna in some parts of their invaded range (e.g., Albins 2013; Ballew et al. 2016; Ingeman 2016; Lesser & Skattery 2011; Tuttle 2017; Smith and Côté 2018). On natural reefs in The Bahamas, for example, lionfish comprise nearly 40% of total mesopredator biomass and have caused a 65% reduction in native prey fish biomass (Green et al. 2012). Regional and in some instances, local, control of lionfish populations proves elusive, as culling by divers - the most popular form of limiting lionfish spread and impacts - has had mixed results (e.g., Arias-González et al. 2011; Green et al. 2014; Alemu 2016; Dahl et al. 2016; Andradi-Brown et al. 2017; Smith et al. 2017; Usseglio et al. 2017). In some areas of the invaded range, a thriving 'lionfishery' has also emerged, but not without potential problems (Chapman et al. 2016; Carrillo-Flota & Aguilar-Perera 2017). The discovery of Caribbean grouper predation on lionfish in the wild led to early, hopeful speculation that groupers may act as a form of biotic resistance (Maljković et al. 2008). Indeed, initial correlational findings provided some support for this idea (Mumby et al. 2011), but later correlational studies have yielded conflicting results (Hackerott et al. 2013; Anton et al. 2014; Valdivia et al. 2014; Curtis et al. 2017). Unsurprisingly, a vigorous debate continues about the potential for native groupers to act as natural biocontrol agents, particularly through predation on lionfish (e.g., Mumby et al. 2013; Valdivia et al. 2014).

Here, we test whether predatory groupers can promote biotic resistance to invasive lionfish directly, through consumption, and/or indirectly, through non-consumptive effects (Fig. 3.1). Two criteria must be met for direct consumption by groupers to act as a natural form of biotic resistance. First, groupers must be abundant and widespread

throughout the invaded range of lionfish. Second, native groupers must frequently consume lionfish. Groupers are heavily fished throughout the world (Sadovy et al. 2013), and indeed, in the Caribbean (Chiappone et al. 2000; Sherman et al. 2016). It is therefore unlikely that our first criterion will be met, at least at the regional scale. However, if the frequency of occurrence of lionfish in grouper stomachs is sufficiently high, then the second criterion could be met. We tested this criterion through a fishery-dependent diet study. Native groupers could also act as a more subtle source of biotic resistance through fear effects. For example, with increasing grouper predator abundances, we might expect increases in lionfish antipredator behaviours such as hiding or inactivity, which prevent other fitness-related behaviours such as foraging (Lima 1998; Dill et al. 2003; Stallings 2008) (Fig. 3.1). The effect of grouper presence on lionfish behaviours might be most evident during peak grouper hunting times, when both lionfish predators and prey are abundant and most active (Fig. 3.1). However, the expression of antipredator behaviours by lionfish might be mitigated by competition (interspecific and intraspecific) such that lionfish might hide less or be more active with increasing competitor abundances, as the trade-off between risk of predation and missed foraging opportunities by competitors becomes too high (Fig. 3.1). Finally, fear effects have been shown to cascade down food webs in aquatic and terrestrial systems (Werner and Peacor 2003; Schmitz et al. 2004; Preisser et al. 2005; Heithaus et al. 2008; Suraci et al. 2016). We therefore look for similar evidence by considering changes in lionfish behaviour and prey abundance across reefs with variable grouper densities and manipulated lionfish numbers (Fig. 3.2).

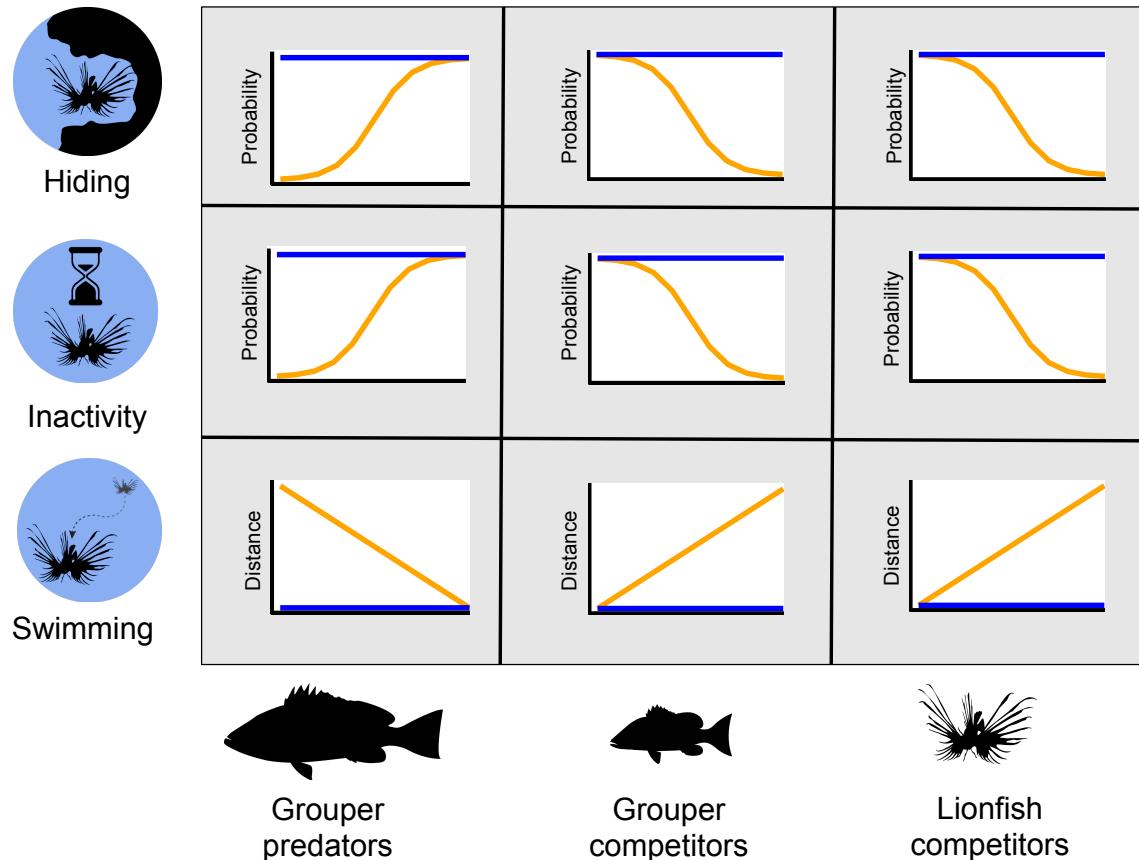


Figure 3.1 Predictions of changes in lionfish antipredator behaviours (i.e., hiding, inactivity and total swimming distance) in response to grouper predator abundance/biomass, and grouper and lionfish competitor abundance/biomass.

Colour delineates time of day: dawn (orange), and throughout the day (blue).

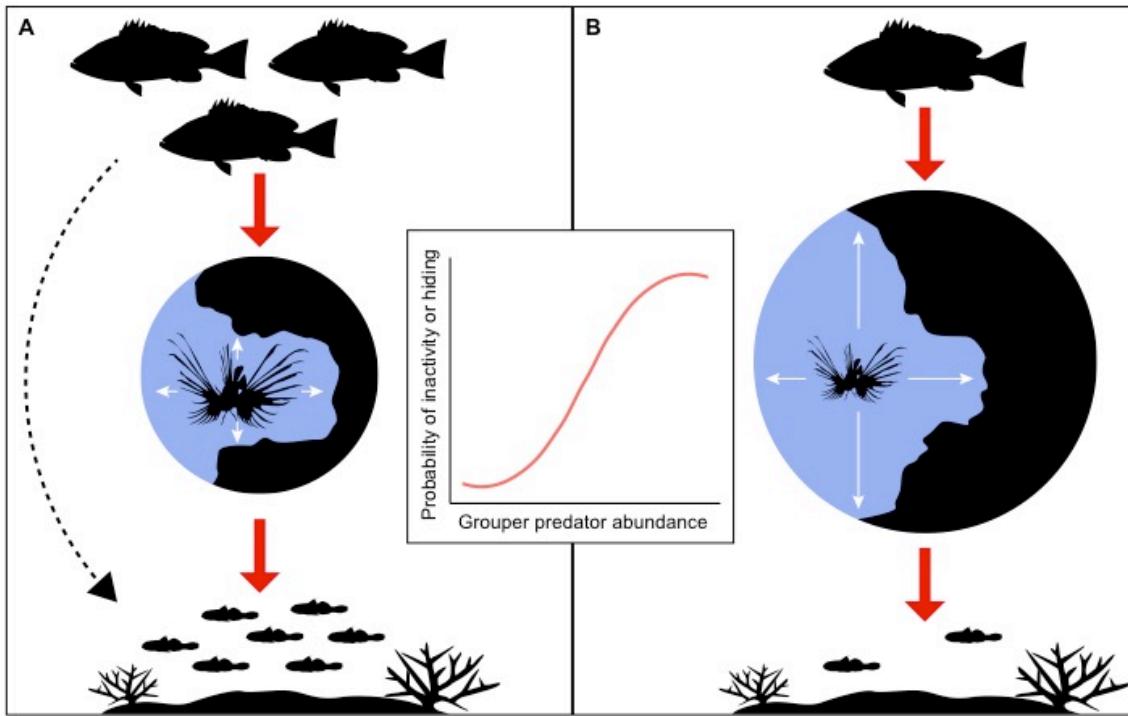


Figure 3.2 Fear of native grouper predators by invasive lionfish can cause cascading effects that impact prey abundances at lower trophic levels.

A) Presence of a fear-induced, trophic cascade. When many groupers are on a reef, lionfish hide more and are more likely to be inactive during peak grouper and lionfish hunting times. Lionfish increased antipredator behaviours result in their reduced foraging success on prey fishes at lower trophic levels. Lionfish prey increase in abundance due to reduced mortality. Grouper predators therefore have a positive, indirect effect on lionfish prey. B) Absence of a fear-induced, trophic cascade. When there are few predators on a reef, lionfish hide less and are less likely to be inactive during peak hunting periods, resulting in increased lionfish foraging success. Prey fish abundance at lower trophic levels thus decreases as their mortality rate increases.

Methods

Consumptive effects

We collected stomachs from groupers captured throughout the Bahamian archipelago by small-scale commercial, recreational, and subsistence fishers using pole spears.

Although fishers caught groupers from reefs surrounding numerous islands, specimens were brought onshore at landing sites on just two islands, New Providence and Eleuthera, where we sampled fish from May to August of 2015, and February to December of 2016, noting species and total length (TL). We considered stomachs only from groupers that were potentially large enough to consume juvenile lionfish (i.e., ≥ 30 cm TL; Anton et al. 2014; Eggleston et al. 1998; Mumby et al. 2011). We collected

stomachs on the same day that groupers were brought ashore. However, although ungutted groupers are placed on ice at landing sites, they were caught from a few hours to several days prior to being landed, which affected the condition of ingested prey. We labelled all stomachs with unique codes, and stored them in a freezer prior to visual identification of diet items. We identified stomach contents (without fixation) to the lowest possible taxonomic level, using Böhlke and Chaplin (1993), and Humann and Deloach (2002) as references.

Non-consumptive effects

Study site

To investigate the non-consumptive effects of native groupers on invasive lionfish, we conducted a field experiment on coral reef patches in Rock Sound, South Eleuthera, The Bahamas ($24^{\circ}50.000' N, 76^{\circ}14.000' W$; Fig. 3.3), from May to July 2015. Lionfish were first observed in Rock Sound in 2005, and were prevalent throughout the study area at the time of our experiment (Green et al. 2014). We selected reef patches that varied naturally in grouper densities and biomass (see Results; Fig. S1-S3; Tables S1-S8). Reefs were at similar depths (< 5 m) and of comparable size (mean \pm SD = $77 \pm 38 m^2$). Structural complexity as determined by vertical relief, i.e., the height from the sea floor to the highest point on a reef (Luckhurst & Luckhurst 1978), ranged from 0.53 m to 0.92 m and varied significantly among reefs (one-way ANOVA; $F_{10, 111} = 2.55$, $p = 0.008$). In contrast, reef rugosity, the more commonly used measure of reef structural complexity (Luckhurst & Luckhurst 1978; see Supporting information for details), ranged from 0.14 to 0.31, and was similar among sites (Kruskal-Wallis rank sum test; $\chi^2 = 8.79$, $df = 10$, $p = 0.55$). The minimum distance between two adjacent reef patches was 330 m of sand and seagrass. This distance ensured limited movement of lionfish between patches because the majority (80%) of lionfish exhibit strong site fidelity to their home patch (Tamburello and Côté 2015). We therefore considered reefs as independent samples in our analyses. In May 2015, just prior to the start of the experiment, we culled 73% \pm 37.8% (mean \pm SD) of lionfish from the study sites, as described in Smith et al. (2017) in an effort to clear the study reefs of lionfish.

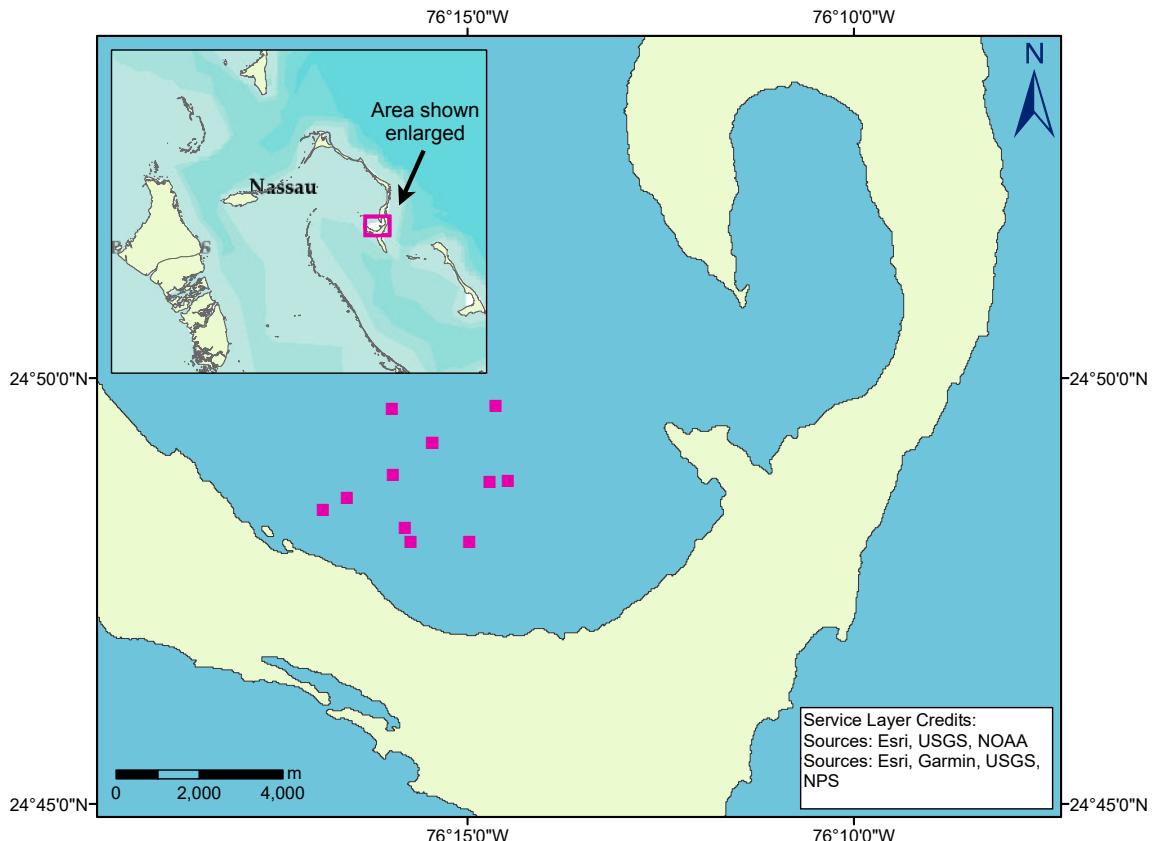


Figure 3.3 Distribution of 11 coral reef patches in Rock Sound, South Eleuthera, The Bahamas (squares).

Patches varied naturally in grouper abundance and biomass.

Lionfish capture, tagging and translocation

To increase the likelihood that lionfish were small enough to be potential prey to groupers on the study reefs, we captured the smallest lionfish available on reef patches outside the study area in May 2015, using hand nets and vinyl collection bags (Akins 2012). We housed all lionfish in a flow-through saltwater system with natural and artificial shelters for 14 days, and fed them previously frozen fish prior to their release on the study reefs in early June 2015. While in captivity, we brought each lionfish to stage II anesthesia using a saltwater bath mixed with eugenol (Iwama et al. 1989; Keene et al. 1998). Each lionfish was then weighed (± 1 g), measured (TL, ± 1 cm), and photographed. We also gave each lionfish three subcutaneous, visible implant elastomer (VIE) tags on the dorsal surface, slightly anterior to the caudal peduncle (Northwest Marine Technology Inc., 2008; see Frederick 1997) to permit individual identification. VIE tags are visible under ultra-violet (UV) light; the use of underwater UV flashlights therefore allowed us to locate and identify individual lionfish in low-light conditions during

dawn surveys (see details below). Lionfish recovered in a dark, 8 L aerated tank, in which they regained equilibrium and swam normally within roughly 5 min after tagging. Measurements for all lionfish took place on the same day.

On 2 and 3 June 2015, we randomly selected and released three to four tagged lionfish at each study reef. We observed each tagged lionfish underwater on SCUBA for 10 min following release to ensure that they were swimming normally and remained at the release site.

Fish surveys

We conducted underwater visual surveys of groupers and lionfish during the last week of May 2015 prior to the start of behavioural observations in early June 2015, and then periodically for five weeks (i.e., until the end of the experiment in July 2015). During visual surveys, a SCUBA diver swam around the perimeter of the reef patch and then over the entire reef in an S-pattern, thoroughly searching all holes and crevices with a dive light when necessary, and recorded the species and total length (TL \pm 1 cm) of all groupers and lionfish encountered (Green et al. 2013; Hackerott et al. 2013; Smith et al. 2017). Survey time ranged from 10 to 20 min per reef, with a mean and median survey time of 15 min per reef.

To estimate abundance and size (TL \pm 1 cm) of potential lionfish prey on the study reefs, one to two divers conducted traditional belt transect surveys on the reef patches once every other week until the end of the experiment for a total of three surveys (Sale and Sharp 1983). Depending on patch size, divers placed one to three 8 m x 2 m belt transects across the reef, waited 5 min for fishes to settle, and then swam slowly over the transect line, recording species identity and size of all individuals encountered. Swim speed was approximately 10 min per transect. All surveys were conducted on SCUBA between 09:30 and 15:30, well outside crepuscular hours when most predators are likely to be hunting, sometimes off the reef (Côté et al. 2014). Divers were trained to visually estimate fish lengths underwater (\pm 1 cm) with the use of models prior to the start of the experiment. Based on the size distribution of focal lionfish (see *Results*), we considered lionfish prey to be any fish \leq 5 cm TL (Morris and Akins 2009; Muñoz et al. 2011; Smith et al. 2017).

Lionfish behavioural observations

We conducted behavioural observations on SCUBA to test several *a priori* predictions on the effects of groupers (abundance and biomass), other lionfish conspecifics (abundance and biomass), and time of day (dawn or throughout the day) on three lionfish behaviours: (1) hiding at first sighting (yes or no), (2) inactivity level (active or inactive), and (3) total swimming distance (Fig. 3.1). Observations took place both at dawn (i.e., one hour before to one hour after sunrise), and during daytime (between 11:00 and 16:30). After locating a focal lionfish, we identified the individual via its VIE tags, and used scan sampling to record, from a distance of ~1m, two lionfish behavioural states at 30-s intervals for a total of 30 min per fish per observation (Altman 1974). At first sighting, we classified each lionfish as either out in the open or hidden (i.e., within a cave or under a ledge). Every 30 seconds, we scored lionfish as either active or inactive. Active behaviours included swimming, hunting, or being in a stereotypical hunting posture (i.e., erect dorsal spines with an undulating tail and outward extending pectoral fins, while hovering with head tilted downwards toward prey). Inactive behaviours included lying on the bottom (i.e., touching a substrate with dorsal spines flat along the dorsal midline) or hovering (i.e., nearly stationary above a substrate, but not in a hunting posture) (for details see Green et al. 2011). Lastly, we estimated total swimming distance by recording and summing the distances covered by lionfish (to nearest 0.5 m) during each 30 sec interval for 30 min per fish (Green et al. 2011). During low-light conditions prior to sunrise, we used underwater UV flashlights to locate tagged individuals. We also shined a non-UV flashlight on focal lionfish every 30 s to clearly observe behaviours when light was poor. We conducted three dawn and three daytime observations on each tagged lionfish on separate days spread across the 5-week study period. However, we analyzed lionfish behaviours based on only the second and third observation periods due to missing data during the initial survey period.

Statistical analyses

Consumptive effects

We calculated the percentages of stomachs that were empty or that contained prey items by grouper species. Other diet metrics were also recorded, but were not included in this study.

Non-consumptive effects

We converted reef fish lengths estimated in the field to biomass using the allometric function:

$$B = aL^b$$

where B is biomass in g, L is TL in cm, and a and b are species-specific scaling constants derived from published literature (Froese and Pauly 2018). In cases where multiple species-specific parameters were available, we selected values from areas that were geographically closest to our study site (Froese and Pauly 2018). When species-specific parameters were not available, we used the scaling constants for closely related species with a similar body size and shape (Froese and Pauly 2018). To standardize measurements among sites, we expressed species abundance and biomass per unit area (m^2).

To determine whether there was evidence of cascading effects of lionfish fear of native predators on smaller fishes at lower trophic levels (Fig. 3.2), we examined the proportional change in prey fish biomass of lionfish (i.e., fish ≤ 5 cm TL) at the beginning (i.e., first survey period) and end (i.e., third survey period) of the experiment. The peak in recruitment of grunts (Haemulidae) coincided with the end of the experiment (see Discussion). We therefore excluded grunts from our analysis of change in prey fish biomass. For the explanatory variables, we used the abundances and biomass of groupers and lionfish estimated mid-way through the experiment (i.e., the second survey period), which is most representative of the predation levels experienced throughout the experiment.

We had two *a priori* hypotheses about which trait might be most important in determining whether a grouper acts primarily as a predator or as a competitor to lionfish. If species identity is more important, then mainly piscivorous species (i.e., Black, *Mycteroperca bonaci*, and Nassau, *Epinephelus striatus*, groupers in our study area) will act as lionfish predators, while less piscivorous species (i.e., graysby, *Cephalopholis cruentata* in our study area) are likely to act as competitors (Hackerott et al. 2013; Figs. S2a and S3a). Alternatively, if body size is the main determinant of species interactions, then all groupers larger than a minimum-size threshold (i.e., ≥ 30 cm TL in our study; Anton et al. 2014; Eggleston et al. 1998; Mumby et al. 2011), regardless of species identity, can act

as lionfish predators while groupers smaller than this threshold are more likely to be lionfish competitors (i.e., < 30 cm TL; Figs. 2, S2b and S3b). All subsequent analyses were therefore conducted twice, once with groupers classified as predators or competitors on the basis of species identity, and once with the classification based on body size.

To determine if there were differences in abundance and biomass of untagged lionfish and groupers (overall and classified by species or by size) among sites prior to the start of the study, we fitted linear mixed-effects models on each natural-log-transformed response variable, and interpreted model parameters using maximum likelihood (Figs. S1-S4; Tables S1-S8). In all cases, we treated site as a fixed effect while survey number ($n = 4$ surveys) was fitted as a random intercept.

We conducted all statistical analyses of the effect of groupers, lionfish conspecifics, and time of day on lionfish behaviour in R (v.3.5.3; R Development Core Team 2019), along with the following add-on packages, where appropriate: (1) AICcmodavg, v. 2.2-1 (Mazerolle 2019), (2) MuMin, v. 1.43.6, (Bartoń 2019), (3) car v.3.0-2 (Fox & Weisberg 2011), (4) ggplot2 v.3.1.0 (Wickham 2016), (5) lme4 v.1.1-21 (Bates et al. 2015), (6) nlme v.3.1-137 (Pinheiro et al. 2018), (7) glmmTMB v.0.2.3 (Brooks et al. 2017), (8) tidyverse v.1.2.1 (Wickham 2017), (9) TMB v.1.7.15 (Kristensen et al. 2016), (10) sjstats v.0.17.4 (Lüdecke 2019), (11) influence.ME v.0.9-9 9 (Nieuwenhuis et al. 2012) , (12) sp v.1.3-1 (Pebesma & Bivand 2005; Bivand et al. 2013), and (13) MASS v.7.3-51.1 (Venables & Ripley 2002).

Although we conducted analyses using lionfish and grouper abundances and biomass, we present only abundance findings here. Analyses of biomass were the same as abundance, are presented in the Supporting Information (Tables S1-S14). We fitted various linear models to test our primary predictions of the effects of grouper and lionfish abundances as well as time of day on lionfish behaviours (Fig. 3.1; Table 3.1).

Specifically, we predicted that (a) under increasing grouper predator abundances at dawn, the probability that lionfish hide and are inactive would increase while lionfish total swimming distance would decrease; (b) under increasing competitor abundances (i.e., both grouper, and tagged and untagged lionfish) at dawn, lionfish probability of hiding and being inactive would decrease while total swimming distance would increase; and (c) during daytime, all lionfish would hide and be inactive regardless of predator and

competitor abundances (Fig. 3.1). For each of these predictions (Fig. 3.1), we created a series of *a priori* candidate model sets based on ecological theory and our knowledge of the system (See Results). Candidate sets ranged from 12 to 28 models per major prediction (see Results). The fixed effects included various combinations of the following factors: grouper predator abundance (based on size and species identity); grouper competitor abundance based on size (i.e., < 30 cm TL); lionfish conspecific abundance; and, time of day (i.e., dawn vs. daytime). For each prediction, we compared the relative weight of support in the data for each of the candidate models using Akaike's Information Criterion corrected for small sample sizes (AICc; Burnham and Anderson 2002). Candidate model parameters were estimated using maximum likelihood. In all instances, except for the analysis of percent change in native prey fish biomass in which we used a simple general liner model, we used mixed-effects models in which we fitted lionfish identity nested within site as a random intercept. For all models, we standardized continuous explanatory variables by subtracting the mean and dividing by one standard deviation, so that effect sizes are directly comparable across factors and across studies (Schielzeth 2010). We performed the appropriate diagnostic tests for all models to ensure that model assumptions were met.

Table 3.1 Details of models used to test hypotheses on the effect of grouper abundance and other factors on lionfish behaviours and native prey fish biomass.

Model number	Response variable	Transformation of response variable prior to analysis	Form	Residuals Distribution ¹	Activity period(s)
1	Probability of hiding	None	Generalized linear mixed-effects	Binomial (logit)	Dawn
2	Total swimming distance	Natural log	Linear mixed-effects	Gaussian (identity)	Dawn, daytime
3	Probability of being inactive	None	Generalized linear mixed-effects	Negative binomial ² (log)	Dawn, daytime
4	% Change in total prey fish biomass	None	General linear model	Gaussian (identity)	Daytime

¹Accompanying link function for residual distribution in parentheses.

²We used the negative binomial parameterization in which the residual variance increases linearly with the mean (Hardin & Hilbe 2007).

As proposed by Burnham and Anderson (2002), we considered model(s) within 2 AICc units from the best-supported model to be equally supported (Symonds & Moussalli 2011). For instances in which there were more than two best-supported (i.e., ‘top’) models, we used model averaging in which we calculated the weighted average of parameter and error estimates across all top models. Specifically, we used ‘conditional’ or ‘natural’ averaging in which we averaged parameter estimates only over the models in which the parameter occurred and weighted them by the summed weights of these models (Grueber et al. 2011). We also examined the importance of a predictor relative to other explanatory variables when model averaging by comparing standardized effect sizes (Schielzeth 2010; Cade 2015; Harrison et al. 2018).

Results

Consumptive effects

We collected a total of 233 groupers at landing sites in New Providence ($n = 83$) and Eleuthera ($n = 150$). Groupers ranged in size from 30 to 140 cm TL with a mean (\pm SE) of 48.6 (± 0.92) cm TL and a median of 47 cm TL. Our dataset comprised five species: Black grouper *Mycteroperca bonaci* ($n = 36$), Nassau grouper *Epinephelus striatus* ($n = 115$), Red hind *Epinephelus guttatus* ($n = 45$), Tiger grouper *Mycteroperca tigris* ($n = 2$), and Yellowfin grouper *Mycteroperca venenosa* ($n = 35$). Overall, 41.2% (96 of 233) of stomachs were empty. We visually identified 25 items in grouper stomachs, none of which was lionfish.

Non-consumptive effects

Our study patch reefs contained Black, Nassau and Graysby groupers, which ranged in (a) size from 10 to 47 cm TL (mean \pm SD = 29 ± 9) (Fig. S1), (b) in abundance from 0.01 to 0.12 fish. m⁻² (mean \pm SD = 0.03 ± 0.02), and (c) in biomass from 0.12 to 51.45 g. m⁻² (mean \pm SD = 8.32 ± 10.84) across all survey periods. Grouper abundance and biomass differed among reef patches throughout the study period. This pattern held when all groupers were combined, as well as when we classified groupers by species (more vs. less piscivorous), or by size (larger vs. smaller than 30 cm TL) (Figs. S2-S4; Tables S1-S8). There was considerable overlap in size among grouper species in our study (Fig. 3.4).

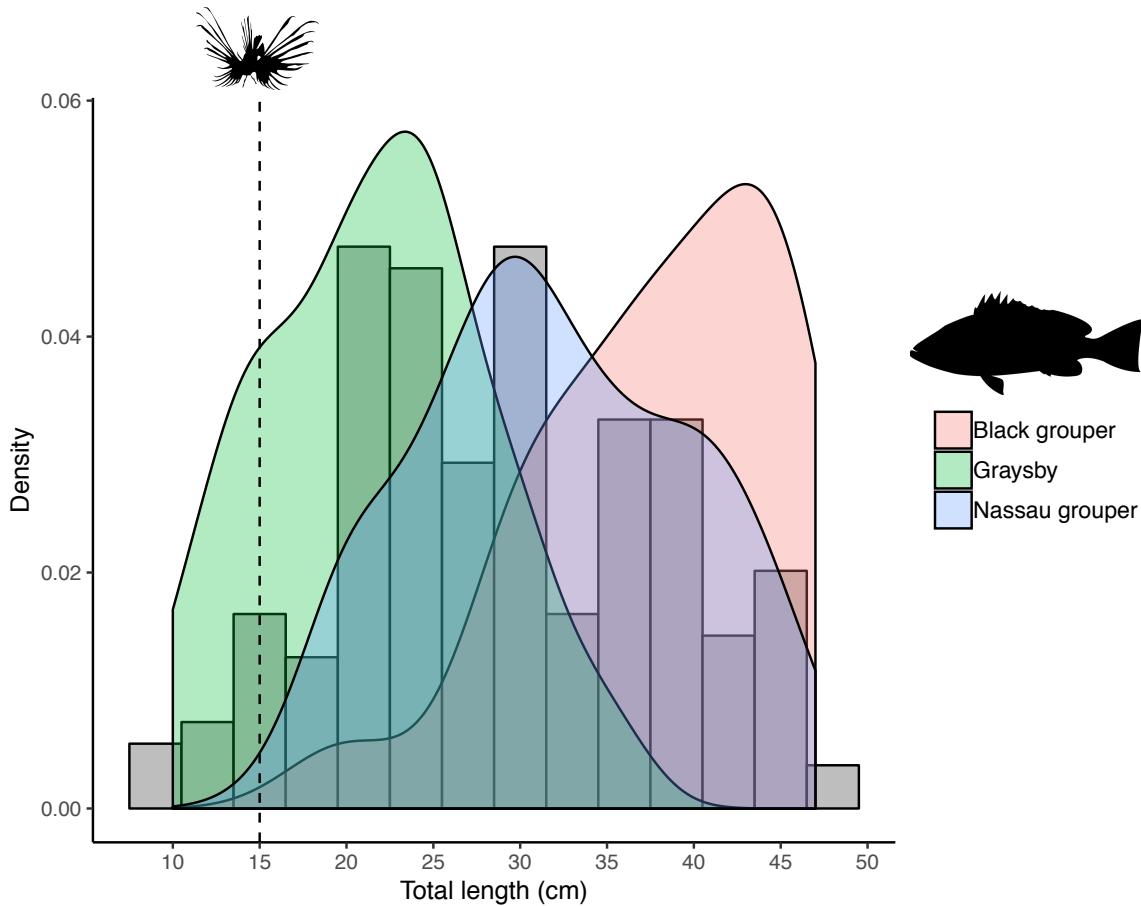


Figure 3.4 Density plot overlaid with a histogram of grouper size distribution among 11 coral reef patches over all four survey periods combined.

Dashed line indicates mean size of tagged lionfish released on coral reef patches at the start of the experiment.

Tagged lionfish ranged in size from 8 to 19 cm TL, with a median of 15.3 cm TL and a mean \pm SD of 14.9 cm \pm 2.8 cm TL (Fig. 3.5). Despite clearing all sites of most lionfish prior to the start of the experiment, lionfish naturally colonized our study sites from neighbouring patches. We monitored, but did not clear new lionfish colonists from study sites after releasing tagged lionfish. As a result, the total abundance and biomass of untagged lionfish varied naturally among sites throughout the study period (Fig. S5; Table S9-S10). Some tagged lionfish emigrated from the study sites during the experiment and were not re-sighted elsewhere. However, throughout the experiment we always observed at least one tagged individual on each study site.

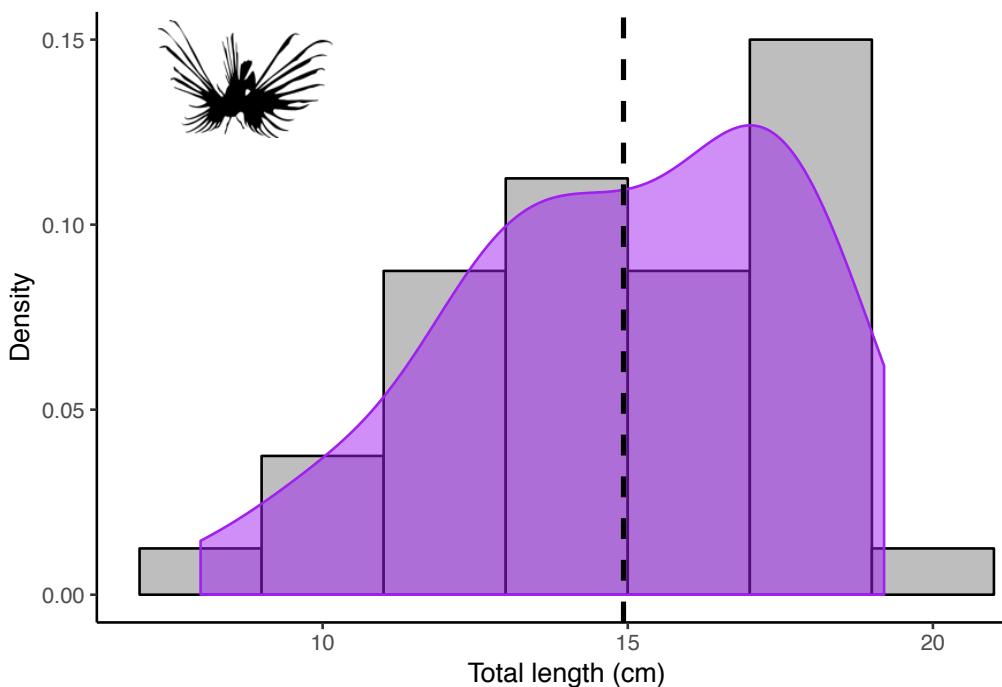


Figure 3.5 Density plot overlaid with a histogram of the size distribution for 30 tagged lionfish released on 11 coral reef patches at the start of the experiment.

Dashed line represents mean (equal to median) lionfish size.

Lionfish hiding

We examined lionfish concealment only at dawn because all lionfish remained hidden within the reef during the day. There was a single top model: the probability that lionfish were hidden at first sighting increased with increasing grouper predator abundance based on size (Table 3.2 and Fig. 3.6). There was 43% support in the data for this top model (Table 3.2). Interestingly, the first four ranked models all showed that the probability that lionfish were hidden at dawn increased with grouper predator abundance, classified either on the basis of size or species (Table 3.2). Grouper predator abundance based on size explained 55% to 60% of variation in the data for our top model, based on the delta method and the theoretical method, respectively.

Table 3.2 Results of model selection using AICc for 12 generalized linear mixed-effects models with a binomial error distribution that examine the effect of various factors on the likelihood of lionfish being hidden at first sighting during dawn surveys of patch reefs (n = 11 sites) in Eleuthera, The Bahamas.

Model	K	AICc	ΔAICc	w_i	Cumulative w_i	-Log likelihood
GPsz	4	41.98	0.00	0.43	0.43	16.12
GPsp	4	44.16	2.18	0.14	0.57	17.21
GPsz, LF	5	44.57	2.60	0.12	0.69	15.92
GPsz, GC	5	44.93	2.96	0.10	0.79	16.10
Intercept only	3	45.67	3.70	0.07	0.86	19.34
GPsp, LF	5	46.82	4.84	0.04	0.90	17.05
GPsp, GC	5	47.03	5.06	0.03	0.93	17.15
GPsz, LF, GC	6	47.80	5.83	0.02	0.95	15.90
LF	4	48.37	6.40	0.02	0.97	19.32
GC	4	48.41	6.43	0.02	0.99	19.34
GPsp, LF, GC	6	49.93	7.95	0.01	1.00	16.96
LF, GC	5	51.36	9.39	00	1.00	19.32

The best-supported model is indicated in bold. K is the number of model parameters. ΔAICc is the difference in the AICc value between model i and the best-supported candidate model. w_i is interpreted as the probability that model i is the best model of the set given the available data. We considered the model(s) within two ΔAICc of the smallest AICc value to be the best-supported model(s). GPsp grouper predator abundances based on species identity, GPsz grouper predator abundances based on size, GC grouper competitor abundances based on size, LF lionfish abundance, AP activity period (i.e., dawn or throughout the day).

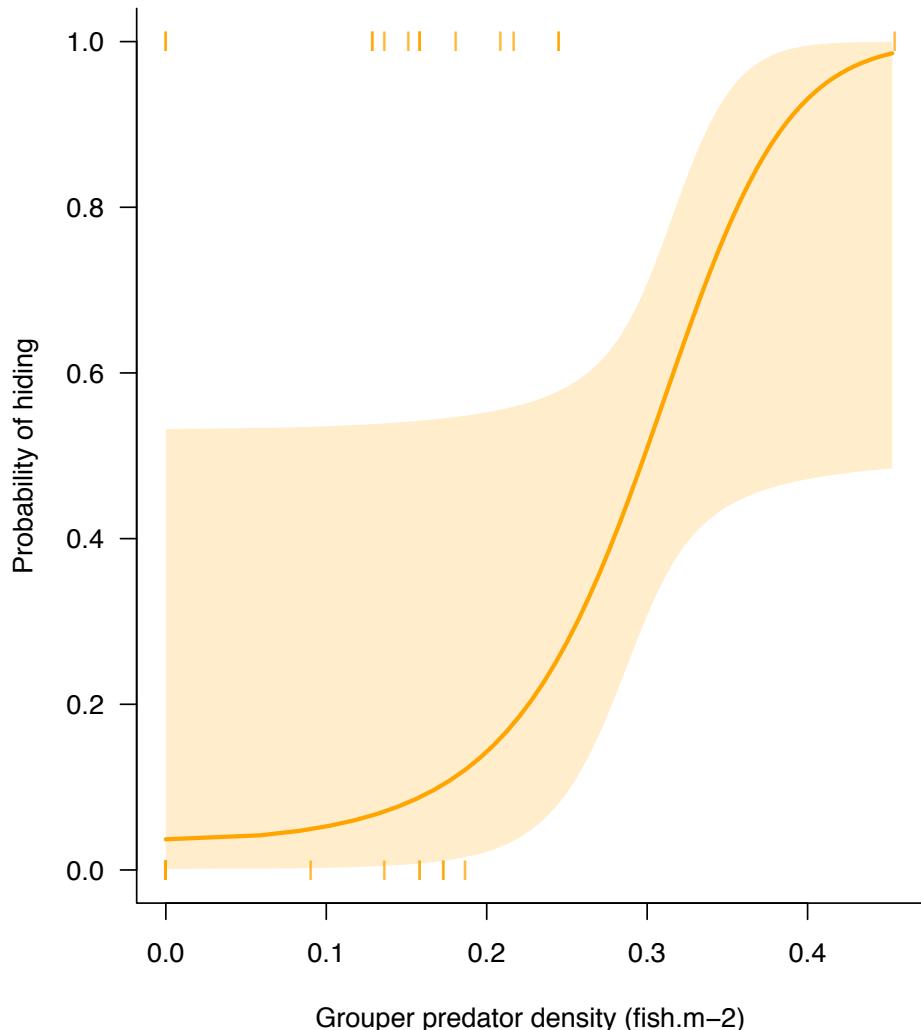


Figure 3.6 Lionfish hide more when there are more groupers on a reef at dawn. Curve is the prediction from a generalized linear mixed-effects model with a binomial distribution, and shows the probability that lionfish hide within a reef at dawn. Bands are 95% confidence intervals. Lines indicate whether an individual lionfish was observed either hiding within a reef (1), or out in the open (0), at first sighting. Darkness of lines is proportional to the number of lionfish represented by that point, with darker lines signifying more lionfish. Grouper predators were defined as Black, Nassau, and Graysby groupers that were at least 30 cm TL in size or larger.

Lionfish inactivity

There were three models within two ΔAICc units of the top model (Table 3.3). All four models contained time of day as an explanatory variable (Table 3.3). By comparing standardized effect sizes of our conditional model average output (Fig. 3.7; Table S15), we found that time of day was the most important explanatory variable, followed by grouper predator abundance based on size, lionfish abundance, and grouper competitor abundance (Table S15). While the probability of being inactive increased with increasing

grouper predator abundance (Fig. 3.7), the opposite was true for grouper and lionfish competitors: lionfish were *less likely* to be inactive as competitor abundances increased (Fig. 3.7; Table S15).

Table 3.3 Factors affecting the likelihood that lionfish are inactive on coral reef patches in Eleuthera, The Bahamas (n = 11 sites). Model selection results are from AICc for 27 generalized linear mixed-effects models with a negative binomial error distribution.

Model	K	AICc	ΔAICc	w_i	-Log likelihood	Cumulative w_i
AP	5	560.07	0	0.24	274.51	0.24
AP, LF	6	561.29	1.22	0.13	273.9	0.36
AP, GPsz, LF	7	561.37	1.3	0.12	272.67	0.49
AP, GC	6	561.93	1.86	0.09	274.21	0.58
AP, GPsz	6	562.38	2.3	0.07	274.44	0.65
AP, GPsp	6	562.49	2.42	0.07	274.49	0.72
AP, GPsp, LF	7	562.7	2.62	0.06	273.33	0.79
AP, LF, GC	7	563.16	3.09	0.05	273.56	0.84
GPsz x AP, LF	8	563.77	3.69	0.04	272.55	0.87
AP, GPsz, GC	7	564.38	4.31	0.03	274.17	0.9
AP, GPsp, GC	7	564.47	4.39	0.03	274.21	0.93
GPsz x AP	7	564.87	4.8	0.02	274.42	0.95
GPsp x AP	7	565.02	4.94	0.02	274.49	0.97
GPsp x AP, LF	8	565.33	5.25	0.02	273.33	0.99
GPsz x AP, GC	8	566.97	6.89	0.01	274.15	0.99
GPsp x AP, GC	8	567.09	7.02	0.01	274.21	1
GPsz, LF	6	586	25.93	0	286.25	1
Intercept only	4	586.28	26.2	0	288.79	1
GPsz	5	586.8	26.73	0	287.88	1
GPsp, LF	6	587.36	27.28	0	286.93	1
GPsp	5	587.38	27.31	0	288.17	1
LF	5	588.03	27.96	0	288.49	1
GC	5	588.3	28.23	0	288.62	1
GPsz, LF, GC	7	588.37	28.3	0	286.17	1
GPsz, GC	6	589.22	29.14	0	287.86	1
GPsp, GC	6	589.82	29.75	0	288.16	1
GPsp, LF, GC	7	589.87	29.8	0	286.92	1

The best-supported models are shown in bold. K is the number of model parameters. ΔAICc is the difference in the AICc value between model i and the best-supported candidate model. w_i is interpreted as the probability that model i is the best model of the set given the available data. We considered the model(s) within two ΔAICc of the smallest AICc value to be the best-supported model(s). GPsp grouper predator abundances based on species identity, GPsz grouper predator abundances based on size, GC grouper competitor abundances based on size, LF lionfish abundance, AP activity period (i.e., dawn or throughout the day).

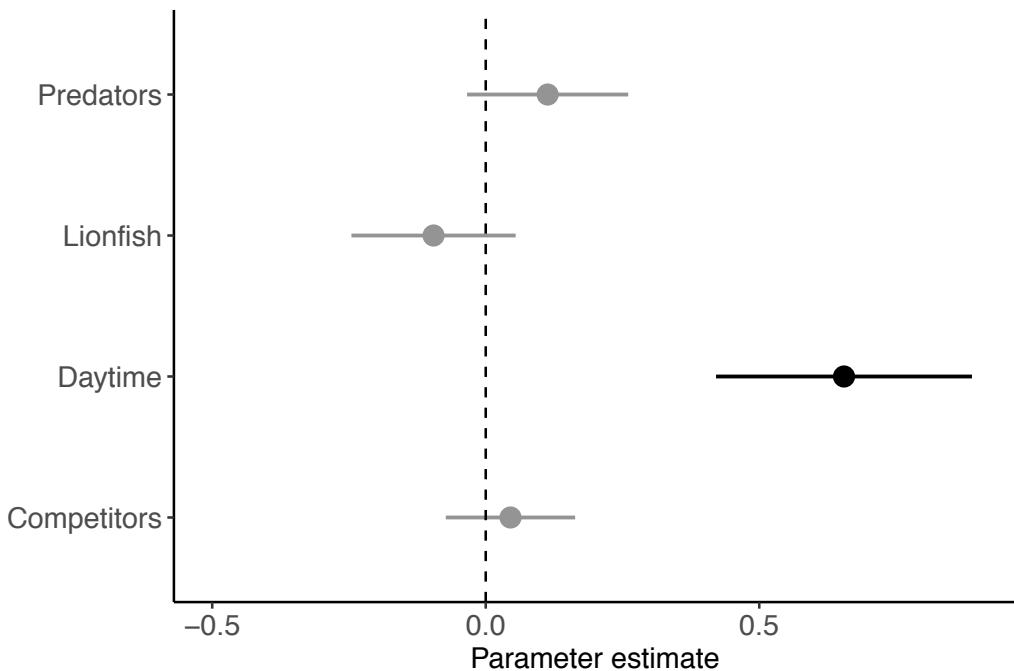


Figure 3.7 Lionfish are likely to be inactive during the daytime on reefs with many predators.

Model averaged parameter estimates of the top four generalized linear mixed-effects models (with a negative binomial distribution), explaining lionfish inactivity on a reef. Bands are 95% confidence intervals. Points to the right of the dashed line signify an increase in the odds of being inactive while points to the left of the line indicate a decrease in odds. Dark points represent substantial certainty in the direction of the parameter estimate while gray points show estimates where there is some uncertainty about the direction of the effect.

Lionfish swimming distance

The abundance of conspecifics and time of day were the primary drivers of lionfish swimming distance (Table 3.4). Lionfish swam longer distances as the number of conspecifics at a site increased (Fig. 3.8). They also swam farther at dawn than during the day (Figs. 3.8-3.9). In fact, the two best-supported models (time of day on its own, and time of day with lionfish abundance) had a > 40% probability of being the best models of the candidate set of 28 models given the available data (Table 3.4). The model with time of day and lionfish abundance explained 52% of variation in the data, while the model containing only time of day explained 51% variation in the data.

Table 3.4 AICc model selection results from 27 linear mixed-effects models that examine the effects of different factors on lionfish total swimming distance on coral reef patches in Eleuthera Island, The Bahamas (n = 11 sites).

Model	K	AICc	ΔAICc	w_i	-Log likelihood	Cumulative w_i
AP, LF	6	177.70	0.00	0.23	81.96	0.23
AP	5	178.11	0.41	0.19	83.43	0.42
AP, GPsp, LF	7	179.71	2.01	0.09	81.64	0.51
AP, GPsz	6	180.02	2.32	0.07	83.12	0.58
AP, GPsz, LF	7	180.08	2.38	0.07	81.82	0.65
AP, GPsp	6	180.25	2.55	0.07	83.23	0.72
AP, GCsz	6	180.46	2.75	0.06	83.33	0.78
GPsp x AP, LF	8	181.38	3.68	0.04	81.09	0.82
GPsz x AP, LF	8	181.50	3.80	0.03	81.15	0.85
AP, GPsz, GCsz	7	182.46	4.76	0.02	83.01	0.87
AP, GPsp, GCsz	7	182.46	4.76	0.02	83.01	0.89
GPsz x AP	7	182.48	4.78	0.02	83.02	0.91
GPsp x AP	7	182.83	5.13	0.02	83.20	0.93
Intercept only	4	183.11	5.41	0.02	87.15	0.95
LF	5	183.96	6.26	0.01	86.36	0.96
GPsz x AP, GC	8	185.02	7.32	0.01	82.91	0.96
GPsp x AP, GC	8	185.11	7.41	0.01	82.96	0.97
GPsz	5	185.34	7.63	0.01	87.04	0.98
GPsp	5	185.37	7.67	0.01	87.06	0.98
GCsz	5	185.53	7.83	0.00	87.14	0.99
GPsp, LF	6	186.05	8.34	0.00	86.13	0.99
GPsz, LF	6	186.11	8.41	0.00	86.16	0.99
LF, GCsz	6	186.46	8.76	0.00	86.34	1.00
GPsp, GCsz	6	187.85	10.15	0.00	87.03	1.00
GPsz, GCsz	6	187.86	10.16	0.00	87.04	1.00
GPsp, LF, GCsz	7	188.69	10.99	0.00	86.13	1.00
GPsz, LF, GCsz	7	188.69	10.99	0.00	86.13	1.00

Swimming distance was natural log-transformed prior to analyses to meet model assumptions. The best-supported models are shown in bold. K is the number of model parameters. ΔAICc is the difference in the AICc value between model i and the best-supported candidate model. w_i is interpreted as the probability that model i is the best model of the set given the available data. We considered the model(s) within two ΔAICc of the smallest AICc value to be the best-supported model(s). *GPsp* grouper predator abundances based on species identity, *GPsz* grouper predator abundances based on size, *GC* grouper competitor abundances based on size, *LF* lionfish abundance, *AP* activity period (i.e., dawn or throughout the day).

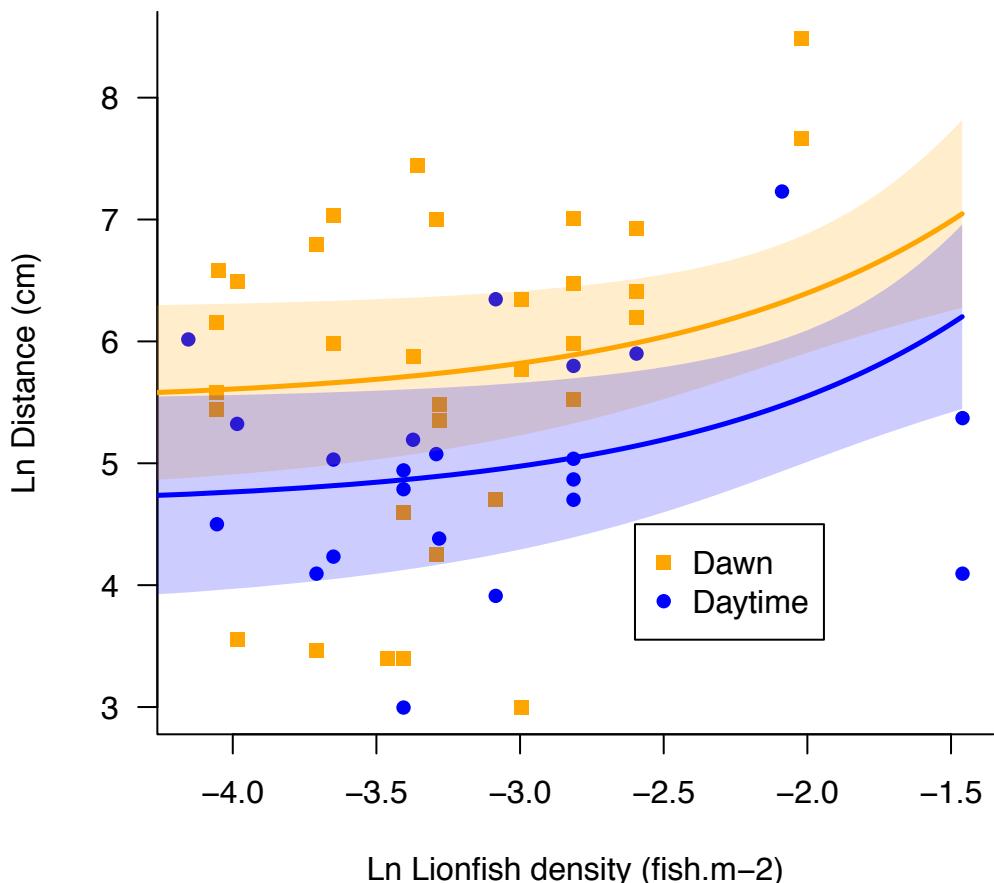


Figure 3.8 Lionfish swim greater distances at dawn on reefs that have many lionfish.

Lines are the predictions from the top linear mixed-effects model, where lionfish total swimming distance was natural log transformed prior to statistical analyses. Bands are 95% confidence intervals. Lionfish density on the x-axis is presented in natural log space for visual purposes only. Colour and shape indicates time of day: dawn (orange squares), and throughout the day (blue circles). Points represent data from individual lionfish.

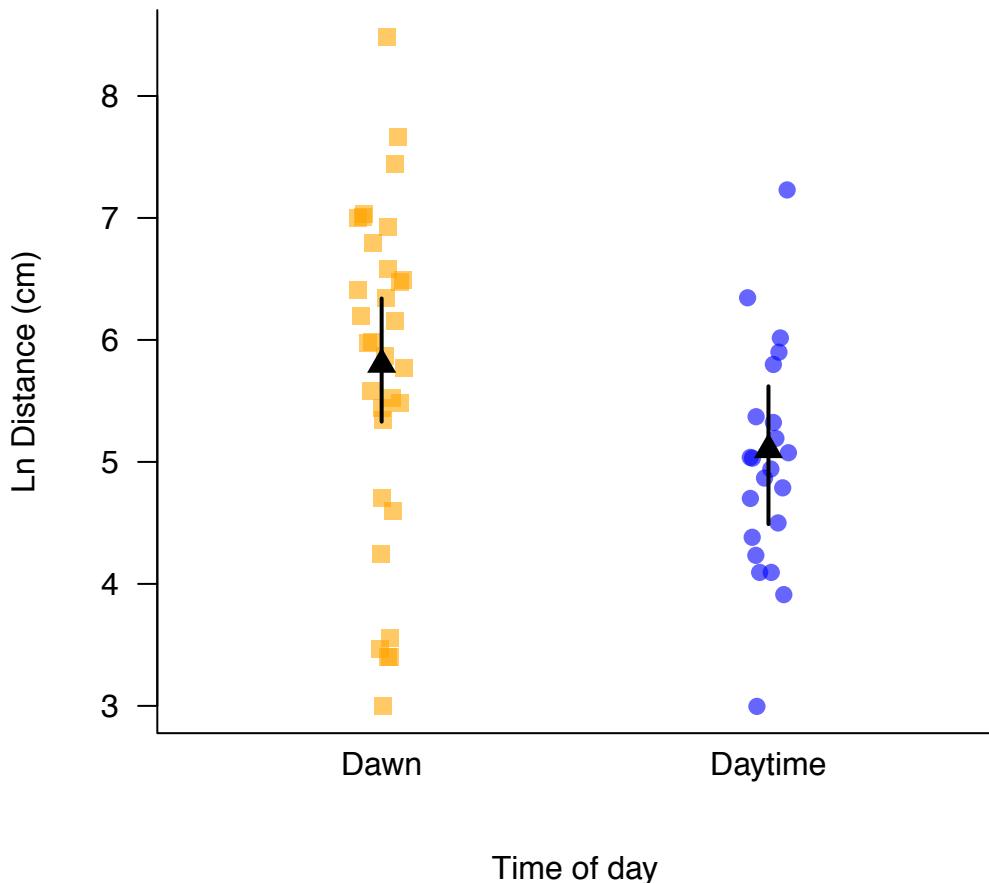


Figure 3.9 Lionfish swim greater distances at dawn than throughout the day. Parameter estimates (black triangles) from the ‘second best’ linear mixed-effects model where lionfish total swimming distance was natural log transformed prior to statistical analyses. Bands are 95% confidence intervals. Colour and shape signify total swimming distance by individual lionfish at different times: dawn (orange squares), and throughout the day (blue circles). Darkness of points is proportional to number of lionfish.

Is there evidence of cascading effects of fear of native predators?

Neither grouper predator abundance nor any of our other proposed factors (e.g., grouper or lionfish competitor abundances) influenced total percent change in lionfish prey biomass at the end of the experiment (Fig. 3.2; Table 3.5). The null model, which included only site as a random intercept, was best supported by the data (Table 3.5).

Table 3.5 AICc model rankings for 12 general linear models that examine factors affecting proportional changes in native prey fish biomass between the start and end of the experiment on coral reef patches in Eleuthera, The Bahamas (n = 9 sites).

Model	K	AICc	ΔAICc	w _i	-Log likelihood	Cumulative w _i
Intercept only	2	40.22	0.00	0.60	17.11	0.60
GPsz	3	42.74	2.52	0.17	15.97	0.77
GPsp	3	44.61	4.39	0.07	16.91	0.84
LF	3	44.91	4.69	0.06	17.05	0.90
GCsz	3	45.01	4.79	0.05	17.11	0.95
GPsz, LF	4	45.75	5.53	0.04	13.87	0.99
GPsz, GCsz	4	49.89	9.67	0.00	15.95	0.99
GPsp, LF	4	51.52	11.30	0.00	16.76	1.00
GPsp, GCsz	4	51.81	11.59	0.00	16.91	1.00
LF, GCsz	4	52.10	11.88	0.00	17.05	1.00
GPsz, LF, GCsz	5	57.08	16.86	0.00	13.54	1.00
GPsp, LF, GCsz	5	63.49	23.27	0.00	16.74	1.00

Native prey fish biomass surveys occurred throughout the day only. The best-supported model is indicated in bold. K is the number of model parameters. ΔAICc is the difference in the AICc value between model *i* and the best-supported candidate model. w_i is interpreted as the probability that model *i* is the best model of the set given the available data. We considered the model(s) within two ΔAICc of the smallest AICc value to be the best-supported model(s). GPsp grouper predator abundances based on species identity, GPsz grouper predator abundances based on size, GC grouper competitor abundances based on size, LF lionfish abundance.

Discussion

Multiple lines of evidence indicate that invasive lionfish modify their behaviours in ways that may make it more difficult for native predators to detect or capture them. At dawn, when prey are most abundant and groupers and lionfish are hunting (Hobson 1972; Galzin 1987; Hixon 1991; Helfman 1993; Côté et al. 2014), lionfish were more likely to hide on reefs with more groupers. Similarly, lionfish were more likely to be inactive on reefs with lots of groupers - although time of day was a stronger driver of this trait. Increasing predator abundance did not affect lionfish swimming distance. Instead, lionfish swam longer distances at dawn on reefs with many conspecifics, suggesting that competition prompts lionfish to expand their foraging range. Finally, there was no evidence of a cascading effect at lower trophic levels after five weeks. However, because lionfish anti-predator behaviours are incompatible with foraging behaviour, the behavioural changes observed might have implications for survival of lionfish prey at different times of the year or in the longer term. For example, on reefs with many groupers, reduced foraging success of lionfish is likely to having cascading effects in

winter when prey abundance of lionfish is low at our study sites, and the effect of reduced mortality is more pronounced.

In both aquatic and terrestrial systems, prey frequently trade-off the risk of being eaten with the opportunity to feed more efficiently (Lima 1998; Cresswell 2008; Salomon et al. 2010). This is because while they forage, prey generally become more vulnerable to predators (Walters and Juanes 1993; Salomon et al. 2010). On coral reefs, crepuscular periods, i.e., dawn and dusk, are prime hunting times for visual predators like native groupers and invasive lionfish, which take advantage of low light conditions to approach prey undetected (Helfman 1986; Hixon 1991; McTee and Grubich 2014). Dawn and dusk also represent times of peak prey fish abundances on coral reefs because it marks a turnover from nocturnal to diurnal species and vice versa (Hobson 1972; Galzin 1987; Helfman 1993). We found that lionfish hid more on reefs with more groupers at dawn, when lionfish should otherwise be foraging. Although we did not directly measure feeding rate in this study, increased hiding in lionfish during peak hunting periods when food is most abundant likely results in reduced lionfish foraging success. Indeed, hiding as an antipredator behaviour has been demonstrated in a number of taxa, including Caribbean reef fishes, where it is associated with diminished feeding rates (Lima 1998; Dill et al. 2003; Stallings 2008). Additionally, lionfish were more inactive on reefs with more groupers (Fig. 3.7 and Table 3.3). Inactivity is an antipredator behaviour also associated with reduced foraging (Dill et al. 2003; Stallings 2008). Despite there being some uncertainty in effect size, grouper predator abundance was the second strongest predictor of lionfish inactivity. Time of day, the strongest predictor, was expected because lionfish, like most visual coral reef predators, tend to be inactive during the day (Hixon 1991).

The observed behavioural changes in lionfish in our study could be a response to reef structural complexity, instead of predator abundance. After all, reef fish abundance is often positively correlated with reef architecture (Almany 2004; Alvarez-Filip et al. 2011), and more structurally complex reefs mean that there are also more places for lionfish to hide. However, two observations counter this argument. First, if increased lionfish hiding is a result of increasing reef complexity, we should expect that lionfish will respond similarly to all factors known to be positively correlated with reef architecture in this study (i.e., abundance of both grouper competitors and lionfish conspecifics). But this was not the case. Instead, models that included grouper competitors and/or lionfish conspecifics

had similar or less support in the data as the null hypothesis, which states that none of the measured factors affect lionfish concealment. Second, reef rugosity, the most common metric of reef complexity (Anton et al. 2014; Alvarez-Filip et al. 2009), did not vary among reefs (Kruskal-Wallis rank sum test; $\chi^2 = 8.79$, df = 10, p = 0.55), and there was no correlation between reef rugosity and grouper abundance (Spearman's rank correlation; S = 205.97, rho = 0.06, p = 0.85) or biomass (Spearman's rank correlation; S = 232, rho = 0.05, p = 0.88). It should be noted, however, that vertical relief, a less common metric of reef complexity, likely plays a small role in our findings because it varied among reefs (one-way ANOVA; $F_{10, 111} = 2.55$, p = 0.008), and grouper abundance was weakly associated with relief (Spearman's rank correlation; S = 104, rho = 0.53, p = 0.10), but not grouper biomass (Spearman's rank correlation; S = 129.79, rho = 0.41, p = 0.21).

Researchers have long questioned the relative importance of competition versus predation in structuring communities, particularly in coral reef systems (Hixon 1991). Early arguments underscored the predominance of competitive interactions (Smith & Tyler 1972; Sale 1978), while later standpoints emphasized the role of predation (Doherty and Williams 1988; Hixon 1991). In our study, we distinguished between the effects of predation versus competition in an original way. By statistically testing whether groupers based on size or species identity were more likely to act as predators or competitors, we were able to disentangle the two processes. We found that predation appeared to be more important, at least in terms of lionfish behaviour. The only signal that competition is important was for total swimming distance, as lionfish swam longer distances with increasing abundance of conspecifics (Table 3.4, Fig. 3.8). This behavioural change is likely in response to increased competition for food or space by conspecifics, as lionfish exhibit density-dependent growth (Benkwitt 2013) and movement (Tamburello and Côté 2014, Smith et al. 2017), and increased intraspecific competition can prompt lionfish to expand their foraging range (Benkwitt 2016). Indeed, our findings are similar to those of Davis et al. (2017) in the Pacific, who showed that competition affected space use in parrotfishes while predation risk influenced foraging rates. It was expected that lionfish would move more at dawn, when they are actively hunting, than throughout the day when they are most likely to be at rest (Côté et al. 2014).

There was no evidence of a fear-induced trophic cascade, as documented elsewhere (Werner and Peacor 2003; Schmitz et al. 2004; Heithaus et al. 2008; Stallings 2008; Suraci et al. 2016). Increased hiding and inactivity in lionfish on reefs with many groupers did not result in less biomass of lionfish prey fish. There are three possible explanations for this observation. First, the latter part of our experiment coincided with the seasonal peak in reef fish recruitment at our study site; the timing of our study may have therefore masked the effects of lionfish predation (Green et al. 2014). Second, the density of lionfish, particularly of large lionfish, on our reefs may not have been sufficiently high to have a measurable effect on prey fishes (Green et al. 2014; but see Benkwitt 2014). Third, fear effects in lionfish may not have been strong enough to reduce lionfish foraging success to levels necessary to detect changes in smaller fishes at lower trophic levels. At present, it is not possible to distinguish between the three mechanisms.

Top predators are on the decline worldwide, causing large-scale disruptions to ecosystem structure and function (Sala 2006; Johnson et al. 2007; Heithaus et al. 2008; Ritchie and Johnson 2009). Here, we show that current, natural densities of heavily fished, native predators can confer some resistance to invasion on coral reef patches via non-consumptive effects. Fear of native groupers caused behavioural changes in lionfish that have been associated in other studies with reduced foraging success. However, fear effects did not fully mitigate the negative impacts of these invaders on native prey fish communities at lower trophic levels. Efforts to rebuild grouper populations throughout the Caribbean may therefore still aid in limiting lionfish invasion success despite there being little evidence of direct predation on lionfish. At broader scales, our findings highlight that the depletion of top predators across the globe can have implications beyond demographic effects on prey.

Chapter 4.

Density-dependent colonization and natural disturbance limit the effectiveness of invasive lionfish culling efforts²

Abstract

Culling can be an effective management tool for reducing populations of invasive species to levels that minimize ecological effects. However, culling is labour-intensive, costly, and may have unintended ecological consequences. In the Caribbean, culling is widely used to control invasive Indo-Pacific lionfish, *Pterois volitans* and *P. miles*, but the effectiveness of infrequent culling in terms of reducing lionfish abundance and halting native prey decline is unclear. In a 21-month-long field experiment on natural reefs, we found that culling effectiveness changed after the passage of a hurricane part-way through the experiment. Before the hurricane, infrequent culling resulted in substantial reductions in lionfish density (60% to 79%, on average, albeit with large uncertainty) and slight increases in native prey species richness, but was insufficient to stem the decline in native prey biomass. Culling every three months (i.e., quarterly) and every six months (i.e., biannually) had similar effects on lionfish density and native prey fishes because of high rates of lionfish colonization among reefs. After the hurricane, lionfish densities were greater on all culled reefs compared to non-culled reefs, and prey biomass declined by 92%, and species richness by 71%, on biannually culled reefs. The two culling frequencies we examined therefore seem to offer a poor trade-off between the demonstrated conservation gains that can be achieved with frequent culling and the economy of time and money realized by infrequent culling. Moreover, stochastic events such as hurricanes can drastically limit the effectiveness of culling efforts.

² A version of this chapter appears as Smith NS, Green SJ, Akins JL, Miller S, Côté IM. 2017. Density-dependent colonization and natural disturbance limit the effectiveness of invasive lionfish culling efforts. *Biological Invasions* 19: 2385-2399.

Introduction

Culling is commonly used in conservation as a means to eradicate invasive species or to reduce their populations to levels that minimize ecological effects (Zipkin et al. 2009). In such instances, culling can be an effective management tool. For example, culling has been used to completely remove introduced goats (Campbell and Donlan 2005), cats (Nogales et al. 2004) and pigs (Cruz et al. 2005) on islands. Likewise, the removal of non-native native predators via culling or translocation increased breeding performance and population sizes of a variety of vulnerable native bird species across six continents (Smith et al. 2010). Culling is also effective in aquatic environments. In temperate lakes, repeated removals of the introduced smallmouth bass, *Micropterus dolomieu*, resulted in a decrease in overall bass biomass and subsequent increases in the abundance of several native prey fishes (Weidel et al. 2007). Similarly, culling the invasive long-spined sea urchin, *Centrostephanus rodgersii*, in discrete areas along the Tasmanian coast substantially reduced its density and the occurrence of ‘urchin barrens’ (i.e., bare areas of reef due to sea urchin overgrazing) (Tracey et al. 2015).

However, culling is also costly, labour-intensive, and sometimes has unintended ecological consequences. Both theoretical and empirical studies show that increased mortality, such as that caused by culling, can lead to greater variability in abundance and instability in the targeted population (Costantino et al. 1997; Benton et al. 2004; Cameron and Benton 2004; Abrams and Quince 2005; Zipkin et al. 2009). It can also result in overcompensation, i.e. an increase in the abundance of the targeted population with increases in mortality (Benton et al. 2004; Abrams and Quince 2005; De Roos et al. 2007; Zipkin et al. 2008, 2009). For example, Benton et al. (2004) showed that culling eggs of the soil mite *Sancassania berlesei* increased total soil mite population size in variable environments. They attributed this effect to changes in density-dependence dynamics: reducing egg number increased juvenile survival because intraspecific competition is typically intense during this early life stage (Benton et al. 2004).

Furthermore, culling can alter the behaviour of targeted species in ways that either impede the success of future culling efforts or have inadvertent impacts on native prey through behaviourally mediated indirect interactions. For example, invasive lionfish, *Pterois spp.* on regularly culled Bahamian reefs were less active and hid better than those on non-culled reefs – behaviours that can reduce their likelihood of capture during

culling events (Côté et al. 2014). Brook et al. (2012) showed that culling dingoes (*Canis lupus dingo*), an apex predator in Australia, effectively reduced their abundance, which likely reduced perceived predation risks (and increased activity levels) on feral cats, which are mesopredators that prey heavily on native species.

Culling is widely used in the Caribbean to control invasive Indo-Pacific lionfish, *Pterois volitans* and *P. miles*. These predators have colonized roughly 7.3 million km² of the western Atlantic, Caribbean Sea and Gulf of Mexico (Côté et al. 2013), and have substantially reduced native prey fish abundance and species richness on coral reefs (Albins and Hixon 2008; Green et al. 2012; Albins 2013, 2015; Benkwitt 2015; Ingeman 2016). Manual removal of individuals by spearing or netting is the most common form of lionfish culling (Akins 2012). Culling by concerned citizens or during organized tournaments currently occurs haphazardly throughout the region, but the effectiveness of these control efforts is unclear because lionfish and native prey abundances are rarely monitored (Côté et al. 2013). Empirical and theoretical studies, however, suggest that regular culling at targeted sites significantly reduces lionfish abundance and mean size (e.g., Arias-González et al. 2011; Barbour et al. 2011; Morris et al. 2011; Frazer et al. 2012; de León et al. 2013; Green et al. 2014; Johnston and Purkis 2015a), sometimes with concomitant stabilization of native fish biomass when lionfish are kept below threshold densities at which their ecological effects are predicted to be limited (Green et al. 2014).

It seems that culling lionfish must now be added to the portfolio of essential activities undertaken by Caribbean managers to maintain the native diversity and productivity of coral reef ecosystems (Morris 2012; Johnston and Purkis 2015a). Unfortunately, few small island states in the Caribbean have the resources to sustain the high culling effort required to drive and keep lionfish populations down and recover native fish populations over the long term. Theoretical models, for example, suggest that an annual exploitation rate of 35% to 65% many years in a row and at large spatial scales is needed to achieve recruitment overfishing of lionfish (Barbour et al. 2011). Such high mortality rate might be achievable with very frequent culling (e.g., at least monthly; Morris et al. 2011; Green et al. 2014; Johnston and Purkis 2015a), which is beyond the financial means of many managers. Less frequent culling is more economically realistic but might also be less ecologically effective. For instance, culling lionfish three times per year on artificial reefs in the Gulf of Mexico was insufficient to stem the decline in native prey fishes, while

lionfish densities quickly returned to pre-clearance levels on reefs that were cleared once a year (Dahl et al. 2016). The effectiveness of infrequent culling of lionfish on natural reefs is currently unclear.

Here, we assessed the effectiveness of culling lionfish at varying frequencies, some of which might be realistically in line with the financial constraints of long-term invasion management in small island states. Specifically, we compared the effectiveness of culling lionfish every three months (i.e., quarterly culls) versus every six months (i.e., biannual culls) in a 21-month-long field experiment on natural reefs. We used two criteria to evaluate whether culling lionfish was effective. First, culling should result in a decrease in lionfish density. Second, culling should also stem the decline of native prey fish biomass and species richness. We hypothesized that more frequent lionfish culls (i.e., quarterly culls) would result in larger reductions in lionfish density and larger gains in native prey fish biomass and species richness than less frequent culls (i.e., biannual culls). Beyond culling frequency, we also examined the effects of other factors that may influence lionfish abundance and native prey fishes, including: (1) culling efficiency (defined as the proportion of lionfish remaining on a reef immediately following a cull), (2) large-scale natural disturbance (i.e., the occurrence of Category 3 Hurricane Irene), and (3) seasonal changes in native fish recruitment.

Methods

Study Site

We conducted our study on 12 natural coral reef patches in Rock Sound, South Eleuthera, The Bahamas ($24^{\circ}50.000' N, 76^{\circ}14.000' W$; Fig. 4.1) over a period of 21 months, starting in December 2010. Reefs were at similar depths (i.e., 3-4 m), and of comparable size (mean \pm SD = $98.4 \pm 53.8 m^2$). The shortest distance between two adjacent reef patches was 200 m of sand and seagrass. This distance ensured limited movement of lionfish between patches because the majority (80%) of lionfish exhibit strong fidelity to their home patch (Tamburello and Côté 2014). We therefore considered reefs as independent samples in our analyses. Reefs also had similar live, hard coral cover (mean \pm SD = $9.36 \pm 4.38\%$) and structural complexity as determined by vertical relief, i.e., the height from the sea floor to the highest point on the reef (mean \pm SD = 1.3 ± 0.5 m), and by reef rugosity (mean \pm SD = 2.2 ± 0.3 ; see Supplementary Information).

Lionfish were first observed in Rock Sound in 2005, and were prevalent throughout the study area at the time of our experiment (Green et al. 2014).

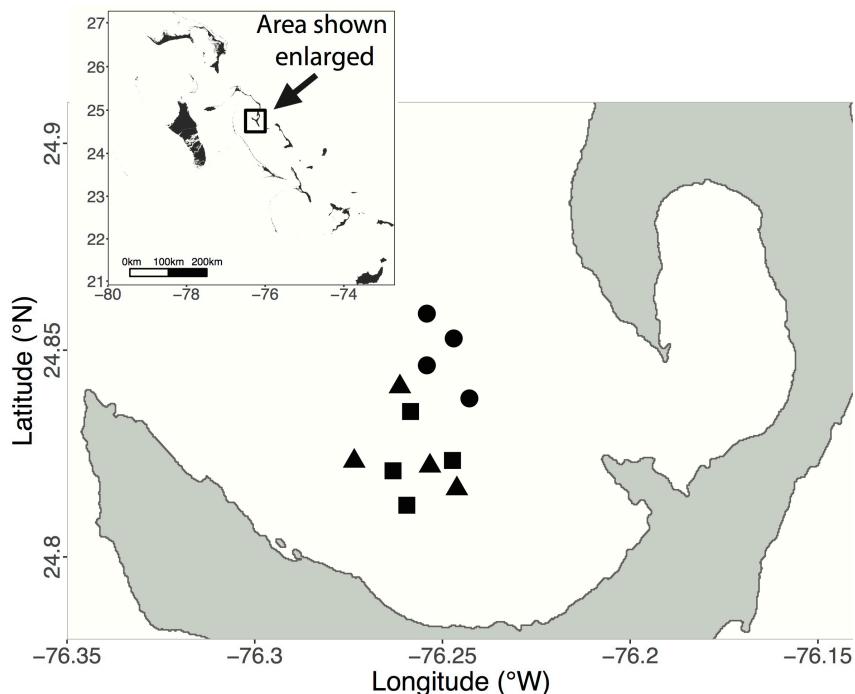


Figure 4.1 Map of study site and experimental treatments.

Distribution of 12 coral reef patches at study site in Rock Sound, South Eleuthera, The Bahamas. Each patch was randomly assigned a lionfish culling treatment: biannual culls (squares), quarterly culls (triangles) and no culls (circles).

Experimental design

We randomly assigned reefs to one of three treatments: (1) control reefs, where no culling occurred ($n = 4$ reefs); (2) biannually culled reefs, where culling occurred once every six months ($n = 4$ reefs); and (3) quarterly culled reefs, where culling occurred once every three months ($n = 4$ reefs; Fig. 4.1). In a stroke of poor luck, most of the control reefs were grouped at the north-east end of the study area (Fig. 4.1). However, while this geographic bias might influence comparisons between culled and non-culled reefs, it would not affect the more important comparisons between biannually and quarterly culled reefs. Moreover, the fact that there was no difference in lionfish density, native prey fish biomass, or native prey fish species richness among treatments at the start of the experiment (see ‘Statistical analysis’ and ‘Results’ sections for details) reassured us that geographic biases were unlikely to be severe.

We conducted surveys of lionfish and native prey fish on all 12 coral reef patches in December 2010 to provide a pre-experiment baseline, and then on a quarterly basis (i.e., every three months) until we concluded the experiment in September 2012. All surveys were conducted on SCUBA between 09:00 and 16:30, which was well outside crepuscular hours when lionfish are actively hunting, often off the reef patch (Benkwitt 2016; Cure et al. 2012; Green et al. 2011). We therefore minimized the likelihood of failing to detect lionfish that are resident on a reef patch but were foraging in the surrounding areas at the time of our survey. All divers were trained to visually estimate fish lengths underwater (\pm 1 cm) with the aid of fish models prior to the start of the experiment.

We used detailed lionfish-focused searches to estimate lionfish sizes and abundance every three months on all study reefs (Green et al. 2013). During lionfish-focused searches, two or three divers slowly swam first around the perimeter of the patch and then over the reef in an S-shaped pattern, searching all crevices and overhangs for lionfish and noting their size and location (Green et al. 2013). A dive light was used when necessary, and survey time was approximately 15 min per 100 m². We visually estimated lionfish total length (TL) to the nearest cm with the aid of a 50 cm long PVC pipe demarcated by 1 cm marks. Divers discussed the size and location of all lionfish immediately following a survey to reduce the likelihood of double counting or missing individuals.

We used traditional belt transect surveys to estimate native prey fish sizes and abundances, which we also conducted every three months on all study reefs (Sale and Sharp 1983). During native fish surveys, divers placed two to four 8 m x 2 m belt transects across the reef patch, depending on reef size. Divers waited approximately five minutes for fish to settle following the disturbance before swimming over the transect line to record the species and size (TL to the nearest cm) of every fish encountered.

We culled lionfish on treatment reefs immediately following fish surveys. During lionfish culls, a team of two or three divers manually removed as many lionfish as possible using hand nets and vinyl collection bags. Pole spears were also sometimes used for particularly large lionfish that sheltered deep within reef crevices and overhangs (Akins 2012). All divers were trained in lionfish capture and handling prior to the start of the experiment. It was not always possible to remove all lionfish from a reef because some

individuals evaded capture by retreating within the reef. Total time spent culling lionfish ranged from 14 to 110 min per reef, and we removed on average 93% (\pm SD = 13%) of all lionfish initially observed on a reef. All captured lionfish were humanely euthanized at the surface, typically by excess anesthesia in a bath of clove oil and seawater (Borski and Hodson 2003; Green et al. 2012). We weighed and measured captured lionfish in the lab. To estimate culling efficiency, two or three divers conducted lionfish-focused searches of the study reef immediately following each cull, noting the size (TL to nearest cm) and location of all remaining lionfish. Divers compared lionfish sizes, abundance and locations before and after each cull to reduce the likelihood of underestimating the number of lionfish that had evaded capture.

Statistical analysis

Although lionfish can consume prey up to half their own length in the invaded range (Morris and Akins 2009), lionfish prey are typically < 5 cm TL (Morris and Akins 2009; Muñoz et al. 2011). For example, the mean size of prey consumed by lionfish in The Bahamas varied between 1.5 and 3.0 cm TL depending on lionfish size, which ranged from 6.2 cm to 42.4 cm TL (Morris and Akins 2009). Lionfish in our study ranged from 3 to 37 cm TL, with a median size of 20 cm TL (mean \pm SD = 19.4 \pm 6.5 cm TL). Our analyses therefore focused only on native fish \leq 5 cm TL as these individuals are the main potential lionfish prey. We converted native fish size to biomass using the allometric function

$$B = aL^b$$

where B is biomass in g, L is TL in cm, and a and b are species-specific scaling constants derived from published literature (Froese and Pauly 2016). When species-specific parameters were unavailable, we used the scaling constants for closely related species with a similar body shape. To account for differences in reef sizes, we expressed lionfish abundance, native prey fish biomass and native prey fish species richness per unit area (m^2). We conducted all statistical analyses in R (v. 3.2.3; R Development Core Team 2014). We also used the following add-on packages, where appropriate: (1) nlme, v. 3.1-127 (Pinheiro et al. 2016), (2) AICcmodavg, v. 2.0-4 (Mazerolle 2016) (3) reshape, v. 0.8.5 (Wickham 2007), (4) coda, v. 0.18-1 (Plummer et

al. 2006), (5) coefplot2, v. 0.1.3.2 (Bolker and Su 2011), (6) MuMIn, v. 1.15.6, (Bartoń 2016) and (7) car, v. 2.1-1 (Fox and Weisberg 2011).

Baseline surveys

To test if there were differences among treatments at the start of the experiment in lionfish density, native prey fish biomass and native prey fish species richness, we conducted one-way analyses of variance (ANOVA) on the natural log transformed response variables. We used both visual (e.g., normal-quantile plots) and statistical methods (e.g., Levene's test for homogeneity of variance) to ensure that all assumptions of ANOVA were met (Whitlock and Schluter 2009).

Modeling hurricane effects

Large-scale natural disturbances like hurricanes and major storms are an important source of environmental stochasticity that can affect fish populations in a variety of ways (Woodley et al. 1981; Kaufman 1983; Walsh 1983; Harmelin-Vivien 1994; Johnston and Purkis 2015b). Category 3 Hurricane Irene passed over our study area in late August 2011, almost nine months after the start of the experiment. We had no *a priori* expectation regarding the duration of the effect of Hurricane Irene on fishes. We therefore used dummy coding (Quinn and Keough 2002) in linear mixed-effects models, with an Akaike Information Criterion approach corrected for small sample sizes (AICc; Burnham and Anderson 2002), to select the model(s) of hurricane effects best supported by our data. Specifically, we first used dummy coding to generate five hypotheses about how Hurricane Irene impacted fishes, ranging from a short-term effect that persisted only for several days to a longer-term effect that persisted for several months (Table 4.1). We assigned each survey period a '0' if there was no effect of Hurricane Irene and a '1' if there was an effect (Table 4.1). All survey periods before Hurricane Irene were coded as '0'. The null hypothesis that there was no effect of Hurricane Irene during any of the survey periods was represented in linear mixed-effects models that lacked hurricane as an explanatory variable.

Table 4.1 Dummy coding for various hypotheses regarding the duration of the effect of Hurricane Irene on lionfish and prey fishes.

Model	March 2011	June 2011	Sept. 2011	Dec. 2011	March 2012	June 2012	Sept. 2012
H1	0	0	1	1	1	1	1
H2	0	0	1	0	0	0	0
H3	0	0	1	1	0	0	0
H4	0	0	1	1	1	0	0
H5	0	0	1	1	1	1	0

Hurricane Irene was a Category 3 Hurricane that passed over the study area in late August 2011.

We used linear mixed-effects models to assess the duration of the effect of Hurricane Irene on lionfish density and, separately, on native prey fish biomass (Table 4.2). We included site (i.e., individual reef) as a random intercept in all models while the dummy variable hurricane was treated as a categorical, fixed effect (Table 4.2). To meet the assumption of normality of residual variance, we transformed (natural log plus a constant) both lionfish density and native prey fish biomass for these and all subsequent analyses. We examined models within each set using Maximum Likelihood estimation (ML; following Zuur et al. 2009) and then compared them using AICc, in which AICc values represented a tradeoff between model complexity and model fit (Burnham and Anderson 2002). We considered the model with the lowest AICc value to be the best model (Burnham and Anderson 2002), and used the dummy coding of the best model in all subsequent analyses that included Hurricane Irene as an explanatory variable (Tables 4.3 - 4.5). We had no reason to assume that Hurricane Irene acted differently on native prey fish biomass than on native prey fish species richness. We therefore used the best model selected based on prey biomass to examine hypotheses about prey species richness.

Modeling the effects of culling and environmental factors on lionfish density

We constructed linear mixed-effects models to examine 17 *a priori* hypotheses regarding the effect of various factors (i.e., culling frequency, culling efficiency, Hurricane Irene, and seasonal changes in native prey fish recruitment) on lionfish density (Table 4.3). We treated culling frequency as a categorical, fixed effect and hypothesized that more frequent lionfish culls would result in larger reductions in lionfish density than less frequent culls. The number of individuals removed during a cull can also affect lionfish density if leaving some lionfish behind influences colonization. We therefore accounted

for differences in culling efficiency by including the proportion of lionfish remaining on a reef immediately following a cull as a numerical, fixed effect (Table 4.3). We included the dummy variable from the best model for the impact of Hurricane Irene on lionfish density as a categorical, fixed effect (see section on ‘Modeling hurricane effect’ for details).

Lastly, coral reef fish recruitment varies seasonally in the Caribbean (e.g., Caselle and Warner 1996; Green et al. 2014), thereby leading to predictable changes in lionfish food availability that may influence lionfish density. Native fish recruitment to reef patches is lowest during June in our study area (Green et al. 2014). We therefore used dummy coding to model the effect of June lows in native fish recruitment by assigning a ‘0’ to all survey periods except June surveys, to which we assigned a ‘1’. We treated the dummy variable for seasonal changes in native fish recruitment as a categorical, fixed effect.

We performed a series of tests on our most complex model for lionfish density (Table 4.3) before arriving at the structure of our final model, as described in Zuur et al. (2009). Specifically, we first fitted our most complex model with and without site as a random intercept using restricted maximum likelihood estimation (REML) and then compared them using AICc. The model with site as a random intercept had greater support than the model without. However, visual examination of the residuals plot indicated a violation of the assumption of homogeneity of residual variance. Hence, we allowed residual variance to differ by culling frequency, which improved model fit based on AICc and met the assumption of homogeneity of residual variance. Visual examination of the autocorrelation plot indicated temporal autocorrelation between survey periods, i.e., non-independence with respect to time (Zuur et al. 2009). We therefore refitted the model with and without an auto-regressive model of order 1 (AR1) correlation structure, which is used with regularly spaced, time-series data and models the residual at time t as a function of the residual of time $t-1$ plus noise (Zuur et al. 2009). Hence, the closer two residuals are to one another in time, the higher their correlation (Zuur et al. 2009). Re-examination of the residuals from our final model, which included site as a random intercept, allowed residual variance to differ by culling frequency and included AR1 correlation structure, indicated that all assumptions of linear models were met (i.e., homoscedasticity, independence and normality of residuals).

Next, we applied the structure of our final model to our candidate set of 17 models to identify the top model(s) that best explained the effect of various factors on lionfish density. We assessed the models using ML and then compared them using AICc. We

then refitted the model with the lowest AICc value using REML to interpret parameter estimates (Zuur et al. 2009). Lastly, we performed model validation on our top model and subsequently calculated the marginal and conditional r^2 values to determine the amount of variation explained by fixed effects versus the combination of fixed and random effects, respectively (Nakagawa and Schielzeth 2013).

Modeling the effects of culling and environmental factors on native prey fishes

We generated 13 *a priori* hypotheses for the effects of culling frequency, Hurricane Irene and seasonal changes in native fish recruitment on native prey fish biomass and species richness (Tables 4.4 – 4.5). We assumed that lionfish culling efficiency would have an indirect and thus marginal effect on native prey fishes, hence we did not include it in models of native prey fishes. We followed the modelling procedure outlined above (see also Zuur et al. 2009). We used AICc to compare models of prey biomass and, separately, prey species richness, and selected our best models based on the lowest AICc value. The structure of the best model for native prey fish biomass included site as a random intercept, allowed residual variance to differ by seasonal changes in native fish recruitment and included AR1 correlation structure. In contrast, the structure of the best model for native prey fish species richness included site as a random intercept, allowed residual variance to differ by hurricane effect, and included AR1 correlation structure. Lastly, as previous described, we performed model validation on our top prey models and subsequently calculated the marginal and conditional r^2 values.

The trajectories of change in lionfish density, prey fish biomass and prey fish species richness are shown in Fig. C.1.

Results

Baseline surveys

There was no difference among treatments in lionfish density (one-way ANOVA, $F_{2,9} = 0.08$; $P = 0.92$), native prey fish biomass ($F_{2,35} = 0.48$; $P = 0.62$) or native prey fish species richness ($F_{2,35} = 0.36$; $P = 0.70$) before the experiment.

Hurricane effects on fishes

The model that best described the effect of Hurricane Irene on lionfish density was different from that for native prey fish biomass. The model that indicated a long-term effect (i.e., approximately 12 months; H1 in Table 4.1) of Hurricane Irene on lionfish density had approximately 2.3 times more support than the second-ranked model (Table 4.2a). In contrast, the model that indicated a shorter-term effect (approximately three months; H3 in Table 4.1) of Hurricane Irene on native prey fish biomass had 18.2 times more support than the second-ranked model in that set (Table 4.2b). The relevant top models were used in subsequent analyses of lionfish density and prey biomass and species richness.

Table 4.2 Results of model selection using AICc for five linear mixed-effects models that examine the effects of Hurricane Irene on (a) lionfish density (fish m⁻²) and (b) native prey fish biomass (g m⁻²) on coral reef patches around Eleuthera Island, Bahamas (n = 12 reefs).

Model	K	AICc	Δ AICc	w _i	Cumulative w _i	-Log Likelihood
(a) Lionfish density						
H1	4	203.799	0.000	0.613	0.613	97.629
H4	4	205.500	1.701	0.262	0.875	98.480
H5	4	207.343	3.544	0.104	0.979	99.401
H3	4	210.786	6.987	0.019	0.998	101.123
(b) Prey biomass						
H2	4	215.014	11.215	0.002	1.000	103.237
H3	4	814.684	0.000	0.930	0.930	403.253
H5	4	820.486	5.802	0.051	0.981	406.154
H4	4	822.502	7.818	0.019	1.000	407.162
H1	4	833.442	18.758	0.000	1.000	412.632
H2	4	834.527	19.843	0.001	1.000	413.175

Both lionfish density and prey biomass were transformed (natural log plus a constant) prior to analysis. K is the number of model parameters. Δ AICc is the difference in AICc value between model *i* and the best-supported candidate model. w_i is interpreted as the probability that model *i* is the best model of the set given the data at hand. We considered the model with the smallest AICc value to be the best-supported model.

Effects of culling and environmental factors on lionfish density

Our top model indicated that culling frequency, Hurricane Irene and the interaction between the two were important predictors of lionfish density (Table 4.3, Fig. 4.2). There was roughly 2.8 times more support in the data for our top model than for the second-

ranked model in the candidate set (Table 4.3). Based on the marginal and conditional r^2 values of our top model, fixed effects explained 24% of variation in lionfish density in our study while the combination of fixed and random effects explained 51% (Fig. 4.2).

Table 4.3 Results of model selection using AICc for 17 linear mixed-effects models that examine the effects of various factors on lionfish density (fish m⁻²) on coral reef patches around Eleuthera Island, Bahamas (n=12 reefs).

Model	K	AICc	Δ AICc	w_i	Cumulative w_i	-Log Likelihood
CF, H, CFxH	11	195.877	0.000	0.511	0.511	84.969
CF, CE, H, CFxH	12	197.924	2.046	0.184	0.694	84.598
CF, H, S, CFxH	12	198.289	2.412	0.153	0.847	84.781
CF, CE, H, S, CFxH	13	199.975	4.098	0.066	0.913	84.188
Intercept only	6	201.778	5.901	0.027	0.940	94.306
H	7	201.908	6.031	0.025	0.965	93.165
S	7	203.591	7.713	0.011	0.975	94.007
CE	7	204.070	8.192	0.008	0.984	94.246
CF, CE, H, S, CFxH, CFxS	15	204.264	8.386	0.008	0.992	83.322
CF	8	206.350	10.473	0.003	0.994	94.147
CF, H	9	206.659	10.781	0.002	0.997	93.025
CF, S	9	208.311	12.434	0.001	0.998	93.851
CF, CE	9	208.565	12.688	0.001	0.999	93.978
CF, S, CFxS	11	209.498	13.621	0.001	0.999	91.779
CF, H, S, CFxS	12	210.348	14.471	0.000	0.999	90.810
CF, CE, H, S	11	210.861	14.984	0.000	1.000	92.461
CF, H, S, CFxH	13	211.225	15.347	0.000	1.000	89.812

K is the number of model parameters. Δ AICc is the difference in AICc value between model i and the best-supported candidate model. w_i is interpreted as the probability that model i is the best model of the set given the data at hand. We considered the model with the smallest AICc value to be the best-supported model. CF: culling frequency, CE: culling efficiency (i.e., the proportion of lionfish remaining immediately after culling), H: Hurricane Irene, and S: seasonal changes in native fish recruitment.

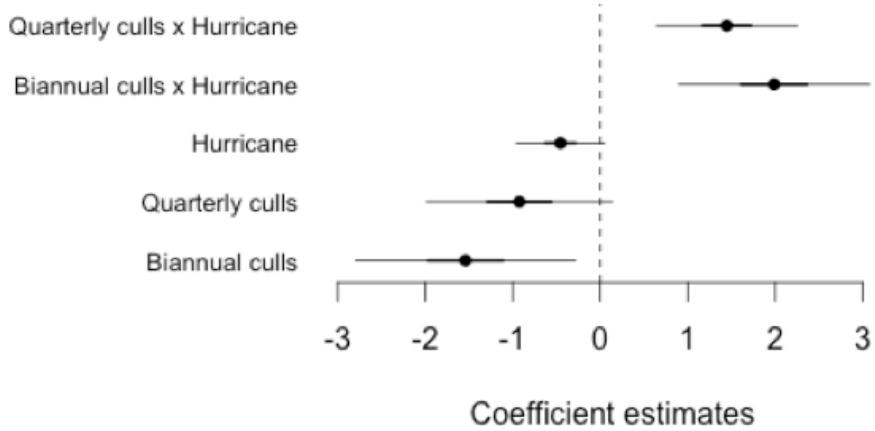


Figure 4.2 Coefficients from the top linear mixed-effects model of the effects of various factors on lionfish density (fish m^{-2}) on coral reef patches around Rock Sound, South Eleuthera, The Bahamas ($n = 12$ reefs).

Points are means bounded by 95% confidence intervals (thin bars) and standard error (thicker bars). Positive values (to the right of the dashed line) signify an increase in lionfish density while negative values (to the left of the dashed line) signify a decrease in lionfish density. Levels 'biannual culls' and 'quarterly culls' are compared against the baseline level 'no culls' (i.e., control reefs). Level 'hurricane' refers to the long-term effect of Category 3 Hurricane Irene on all survey periods following the disturbance and is compared against the baseline level 'no hurricane effect', i.e., all survey periods before the hurricane. Conditional r^2 of top model is 0.51 (i.e., proportion of variation in lionfish density among reefs explained by the combination of fixed and random effects in the model).

The effect of culling frequency on lionfish density depended on whether culling occurred before or after Hurricane Irene. Before the hurricane, culling reduced lionfish density on both biannually culled and quarterly culled reefs compared to the non-culled reefs, as evidenced by the negative effect sizes (Fig. 4.2). Specifically, lionfish density on reefs culled biannually before the hurricane was, on average, 0.22 times that on reefs where no culling occurred (Fig. 4.2). This translates to a 79% reduction in average lionfish density on biannually culled reefs compared to non-culled reefs. This reduction was significant, given that the 95% confidence interval does not overlap zero (Fig. 4.2). In contrast, lionfish density on reefs culled quarterly before the hurricane was, on average, 0.4 times that on non-culled reefs, i.e. 60% lower (Fig. 4.2). This decline was marginally non-significant. There was no difference in the effects of the two culling frequencies on lionfish density before the hurricane (Fig. C.2).

After the hurricane, lionfish densities *increased* significantly on all culled reefs, and this effect persisted until the end of the study, roughly 12 months after the natural disturbance (Table 4.3; Fig. 4.2). Lionfish densities after the hurricane were, on average, 7.33 times (or 633%) higher on reefs culled biannually than on reefs where no culling

occurred before the hurricane (Fig. 4.2). Similarly, lionfish densities on reefs culled quarterly after the hurricane were, on average, 4.27 times (or 327%) higher than on non-culled reefs prior to the hurricane (Fig. 4.2). There was again no difference between culling frequencies in their effect on lionfish density after the hurricane, as indicated by the considerable overlap in 95% confidence intervals (Fig. 4.2).

Effects of culling and environmental factors on native prey fishes

The top model for native prey fish biomass included culling frequency, Hurricane Irene, seasonal changes in native fish recruitment and the interaction between culling frequency and Hurricane Irene (Table 4.4; Fig. 4.3). This model accounted for 69% of model support using Akaike weights and was 2.40 AICc units lower than the second top model (Table 4.4). Fixed effects explained 17.3% of variation in native prey fish biomass while the combination of fixed and random effects explained 22.3% (Fig. 4.3).

Table 4.4 Results of model selection using AICc for 13 linear mixed-effects models that examine the effects of various factors on native prey fish biomass (g m^{-2}) on coral reef patches around Eleuthera Island, Bahamas (n=12 reefs).

Model	K	AICc	ΔAICc	w_i	Cumulative w_i	-Log Likelihood
CF, H, S, CFxH	11	777.997	0.000	0.687	0.687	377.393
CF, H, S, CFxH, CFxS	13	780.394	2.397	0.207	0.894	376.354
CF, H, CFxH	10	781.988	3.991	0.093	0.988	380.491
H, S	7	787.420	9.423	0.006	0.994	386.458
CF, H, S, CFxS	11	788.432	10.435	0.004	0.998	382.611
CF, H, S	9	790.032	12.035	0.002	0.999	385.607
H	6	792.201	14.204	0.001	1.000	389.912
CF, H	8	794.706	16.709	0.000	1.000	389.027
Intercept only	5	801.186	23.189	0.000	1.000	395.459
S	6	802.508	24.511	0.000	1.000	395.065
CF	7	804.272	26.275	0.000	1.000	394.884
CF, S	8	805.703	27.706	0.000	1.000	394.526
CF, S, CFxS	10	806.063	28.067	0.000	1.000	392.529

K is the number of model parameters. ΔAICc is the difference in AICc value between model i and the best-supported candidate model. w_i is interpreted as the probability that model i is the best model of the set given the data at hand. We considered the model with the smallest AICc value to be the best-supported model. CF: culling frequency, H: Hurricane Irene, and S: seasonal changes in native fish recruitment.

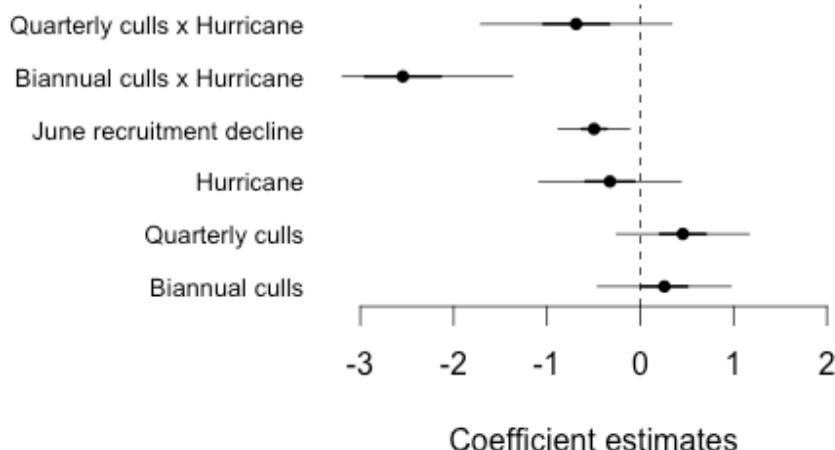


Figure 4.3 Coefficients from the top linear mixed-effects model of the effects of various factors on native prey fish biomass (g m^{-2}) on coral reef patches around Rock Sound, South Eleuthera, The Bahamas ($n = 12$ reefs).

Points are means bounded by 95% confidence intervals (thin bars) and standard error (thicker bars). Positive values (to the right of the dashed line) signify an increase in prey biomass while negative values (to the left of the dashed line) signify a decrease in prey biomass. Levels ‘biannual culls’ and ‘quarterly culls’ are compared against the baseline level ‘no culls’ (i.e., control reefs). Level ‘hurricane’ refers to the short-term effect of Category 3 Hurricane Irene on September 2011 and December 2011 surveys following the disturbance and is compared against the baseline level ‘no hurricane effect’, i.e., all other survey periods. Level ‘June recruitment decline’ refers to June lows in native fish recruitment to coral reef patches in our study area and is compared to all other survey months. Conditional r^2 of top model is 0.20 (i.e., proportion of variation in prey fish biomass among reefs explained by the combination of fixed and random effects in the model).

As expected given the low rates of native fish recruitment in June at our sites, native prey fish biomass during June surveys was, on average, 0.61 times (39% lower) than of native prey fish biomass during any other survey month (Fig. 4.3). Culling had no effect on native prey fish biomass, except on reefs culled biannually during the period in which Hurricane Irene affected prey fishes (i.e., Sept. 2011 and Dec. 2011; Fig. 4.3). In this instance, and contrary to our prediction, culling resulted in a significant 92% *decrease* in native prey fish biomass compared to non-culled reefs before the hurricane and after the effects of the disturbance had dissipated (i.e., after December 2011; Fig. 4.3).

Culling frequency, Hurricane Irene, and the interaction between the two were in the top model for native prey fish species richness (Table 4.5; Fig. 4.4). This model had 2.5 times more support than the second-ranked model (Table 4.5), and it explained 25.4% of variation in native prey richness (Fig. 4.4). Similar to prey fish biomass, the effect of culling frequency on native prey fish species richness depended on when culling

occurred in relation to the impact of Hurricane Irene. On the one hand, before the hurricane and after the impacts of the disturbance had dissipated (i.e., after Dec. 2011), culling increased native prey fish species richness relative to control reefs, as predicted (Fig. 4.4). However, the increase in native richness on biannually culled reefs was marginally non-significant, and there was no difference between biannual and quarterly culls (Fig. 4.4). Native prey fish species richness on biannually culled and quarterly culled reefs was, on average, 1.3 times (or 29% higher) to 1.4 times (or 41% higher) than that of non-culled reefs, respectively, over the same time periods (Fig. 4.4). On the other hand, during the period of hurricane impact on native prey fishes (i.e., September and December 2011), culling *decreased* prey species richness significantly, by 74%, on reefs culled biannually compared to non-culled reefs before the hurricane and after the impacts of the disturbance had dissipated, but had no effect on reefs culled quarterly (Fig. 4.4).

Table 4.5 Results of model selection using AICc for 13 linear mixed-effects models that examine the effects of various factors on native prey fish species richness(species m⁻²) on coral reef patches around Eleuthera Island, Bahamas (n=12 reefs).

Model	K	AICc	Δ AICc	w _i	Cumulative w _i	-Log Likelihood
CF, H, CFxH	10	445.051	0.000	0.667	0.667	212.023
CF, H, S, CFxH	11	446.855	1.804	0.271	0.938	211.822
CF, H, S, CFxH, CFxS	13	450.131	5.080	0.053	0.990	211.223
H	6	455.251	10.200	0.004	0.994	221.437
CF, H	8	455.913	10.861	0.003	0.997	219.630
H, S	7	457.314	12.263	0.001	0.999	221.405
CF, H, S	9	457.944	12.892	0.001	1.000	219.563
CF, H, S, CFxS	11	461.061	16.010	0.000	1.000	218.925
Intercept only	5	464.965	19.914	0.000	1.000	227.349
CF	7	465.633	20.582	0.000	1.000	225.564
S	6	465.764	20.712	0.000	1.000	226.693
CF, S	8	466.218	21.167	0.000	1.000	224.783
CF, S, CFxS	10	469.593	24.542	0.000	1.000	224.294

K is the number of model parameters. Δ AICc is the difference in AICc value between model *i* and the best-supported candidate model. w_i is interpreted as the probability that model *i* is the best model of the set given the data at hand. We considered the model with the smallest AICc value to be the best-supported model. CF: culling frequency, H: Hurricane Irene, and S: seasonal changes in native fish recruitment.

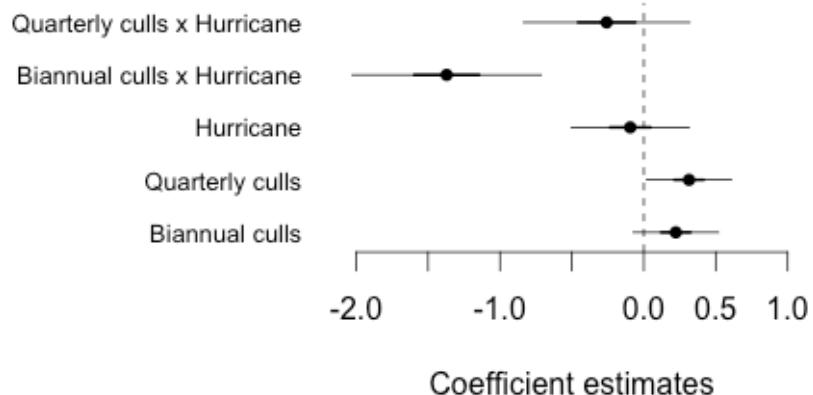


Figure 4.4 Coefficients from the top linear mixed-effects model of the effects of various factors on native prey fish species richness (species m⁻²) on coral reef patches around Rock Sound, South Eleuthera, The Bahamas (n = 12 reefs).

Points are means bounded by 95% confidence intervals (thin bars) and standard error (thicker bars). Positive values (to the right of the dashed line) signify an increase in prey species richness while negative values (to the left of the dashed line) signify a decrease in richness. Levels 'biannual culls' and 'quarterly culls' are compared against the baseline level 'no culls' (i.e., control reefs). Level 'hurricane' refers to the short-term effect of Category 3 Hurricane Irene on September 2011 and December 2011 surveys following the disturbance and is compared against the baseline level 'no hurricane effect', i.e., all other survey periods. Conditional r^2 of top model is 0.21 (i.e., proportion of variation in prey species richness among reefs explained by the combination of fixed and random effects in the model).

Discussion

Infrequent culling influenced invasive lionfish density, native prey fish biomass and native prey fish species richness on natural patch reefs. However, these effects did not vary systematically with culling frequency, and disturbance caused by the passage of a hurricane altered the effectiveness of these culling regimes as a management strategy. Before the hurricane, quarterly and biannual culling resulted in similar reductions in lionfish density and slight gains in native prey fish species richness relative to non-culled reefs. These effects, however, had large uncertainty and ranged from being statistically significant to marginally non-significant. Neither culling regime resulted in recovery of prey biomass. Importantly, after the hurricane, lionfish densities *increased* substantially on all culled reefs while both native prey fish biomass and species richness declined on reefs that were culled biannually.

In the absence of hurricanes, is culling an effective management tool for mitigating the impacts of invasive lionfish? The answer depends on how effective culling is in suppressing lionfish density and on the indicators managers use to assess the status of

native fish communities (e.g., biomass or richness). In a previous experiment conducted in the network of reef patches we studied, culling reduced lionfish density and stemmed the decline of native prey biomass, but with substantial effort (i.e., monthly culls) that are unlikely to be sustainable in the long term (Green et al. 2014). These results are supported by population and biophysical models that suggest that intensive, frequent removals are required to control lionfish populations (Morris et al. 2011; Johnston and Purkis 2015a). Our results show that much less frequent culling can reduce lionfish density and promote marginal recovery of native prey fish species richness (Figs. 4.2 and 4.4), but it had no effect on prey biomass (Fig. 4.3). The infrequent culling regimes examined here therefore did not mitigate the full range of lionfish impacts on native prey fish, compared to more labour-intensive, monthly efforts (Green et al. 2014; Johnston and Purkis 2015a; Morris et al. 2011). The limited effectiveness of our less intense culling regimes is consistent with those of Dahl et al. (2016), who found that culling lionfish three times a year on artificial reefs reduced lionfish density, but had little impact on native prey fish recovery.

We expected more frequent culls to be more effective at suppressing lionfish density than less frequent culls. However, this was not the case. There was no difference between biannual and quarterly culls in their effect on lionfish density before the hurricane (Fig. C.2). We suggest that negative density-dependent colonization of culled patches by lionfish, arriving from other patches in the network and perhaps via long-distance larval recruitment (e.g., see Andradi-Brown et al. 2017), might explain our finding. Previous work has shown that lionfish exhibit negative density dependence in movement (Tamburello and Côté 2014). Relocating lionfish preferentially move from high- to low-density patches, possibly in response to intraspecific competition for prey on high-density reefs. The likelihood of moving decreases as the difference in lionfish density between patches diminishes (Tamburello and Côté 2014). By reducing lionfish abundance, culling created low-density patches that were attractive to lionfish relocating from higher-density sites, an effect that ebbed over time as lionfish colonized culled patches and the density differences between culled and other patches in the network attenuated. Culling some patches more frequently than others temporarily ‘rejuvenated’ the attractiveness of these (quarterly culled) patches, until the density differentials disappeared once more. If lionfish exhibit negative density-dependent movement as we suggest – and as demonstrated by other invasive predators in response to culling (e.g.,

red foxes, *Vulpes vulpes*, Lieury et al. 2015; see also Doherty and Ritchie (2016) for an overview), we should expect that (1) the number of newly arriving lionfish (i.e., colonization rate) should be higher on culled than on non-culled patches, (2) that colonization rate should be higher on quarterly culled than biannually culled reefs, and (3) that, all else being equal, there should be a threshold lionfish density, determined by intraspecific interactions (e.g., competition for food), beyond which new arrivals to a patch nearly cease. In line with the first two predictions, we found that overall lionfish colonization rates were significantly higher on culled reefs than on non-culled reefs, and nearly four times as high for quarterly culled than biannually culled reefs (Fig. C.3). The third prediction is more difficult to test in the absence of more detailed records of colonization patterns but it is notable that all reefs had similar lionfish densities at the start of our experiment.

Even though there is some evidence that culling reduced lionfish density before the hurricane, especially on biannually culled reefs, it did not promote recovery of native fish biomass on reefs (Fig. 4.3). There are at least two possible explanations for this result, which are not mutually exclusive. First, there is evidence that lionfish exhibit density-dependent foraging habitat selection. At low density, they hunt mainly on coral reefs – their preferred foraging habitat (Benkwitt 2016a) – but at higher densities, they extend their foraging range to include seagrass and other microhabitats (e.g., isolated coral heads) away from their home reef – likely in response to intraspecific competition for prey (Dahl and Patterson 2014; Benkwitt 2016a, 2016b). It is therefore possible that culling lowered lionfish density enough to reduce lionfish foraging, and perhaps curb prey decline, in seagrass and other surrounding habitats, but not on reef patches – the preferred hunting ground of lionfish (Benkwitt 2016a). Second, on small reefs, just a few lionfish can overwhelm the biomass production by resident fishes and deplete prey standing biomass. Benkwitt (2015), for example, showed that a single lionfish could substantially reduce native prey biomass on small, artificial reefs in The Bahamas. Similarly, Green et al. (2014) demonstrated that monthly removals of up to 96% of lionfish on natural reef patches were required to stem the decline of native fish populations. Thus, despite relatively high culling efficiency, our interventions may not have been sufficient to recover native prey biomass.

Surprisingly, lionfish density increased on all culled reefs after the hurricane. Storms can have major short-term as well as long-lasting effects on coral reef ecosystems. They can

cause direct and indirect damage to benthic reef organisms (especially corals), change sedimentation processes, increase turbidity, lower salinity, and affect sea level (Harmelin-Vivien 1994). These changes subsequently impact reef organisms, from phytoplankton to reef-associated invertebrates and fish assemblages, in a variety of ways (Beecher 1973; Harmelin-Vivien 1994; Kaufman 1983; Walsh 1983; Woodley et al. 1981). Some species shift their distribution (e.g., by moving deeper) to seek more protected habitat (e.g. Walsh 1983), while others decline in response to habitat damage (e.g., Wantiez et al. 2006), remain unaffected (e.g., Cheal et al. 2002, Adams and Ebersole 2004) or even benefit if new habitat types are created (e.g., coral rubble fields, Kaufman 1983). In our study, there was no discernable damage to corals on patch reefs following the disturbance (SM, personal observations). Instead, the increase in lionfish abundance appears to be attributable to increased recruitment and/or movement of small lionfish, especially onto culled patches, after the hurricane. Indeed, lionfish were significantly smaller, by ~4 cm to ~10 cm on average, depending on culling treatment in December 2011 (3 months after the hurricane) than in December 2010 (pre-experiment baseline) (Fig. C.4, Fig. C.5). This size reduction is not a consequence of culling (Dahl et al. 2016; Frazer et al. 2012) since we also saw smaller lionfish on non-culled reefs (Fig. C.4, Fig. C.5). In addition, the proportion of small/young lionfish (i.e., < 10 cm TL) increased from 1 to 15% on non-culled patches and from 3-4% to 25-58% on culled patches after the hurricane (Fig. C.6), with concomitant increases in abundance (Fig. 4.1). Note that, although hurricanes are thought to have contributed to increasing both the rate of spread and population sizes of lionfish throughout the Bahamian archipelago in the early years of the invasion (Johnston and Purkis 2015b), we cannot definitively ascribe the observed pulse in lionfish recruitment to Hurricane Irene.

Two important implications for the management of lionfish in the Caribbean emerge from our study. First, in the absence of hurricanes, infrequent culling can substantially reduce lionfish density but there is much unexplained variation in response among reef patches and no difference between quarterly and biannual culling. Infrequent culling also results in modest but inconsistent gains in prey richness but has no effect on prey biomass. The two culling frequencies we examined therefore seem to offer a poor trade-off between the demonstrated conservation gains that can be achieved with frequent culling (e.g., Green et al. 2014) and the economy of time and money achieved by infrequent culling. This conclusion might only apply to networks of coral reef patches with non-negligible

rates of lionfish movement and recruitment. The effect of low culling frequencies on large, continuous expanses of coral reef remains unclear. Second, stochastic processes such as hurricanes can substantially alter the outcome of conservation management interventions like culling. In our case, lionfish density increased substantially on culled reefs after the passage of a Category 3 hurricane. If the link between the two events is causal rather than coincidental and is unaffected by culling frequency, then managers might expect lionfish culling to have more predictable effects in areas that are less likely to experience such disturbances.

Chapter 5.

General discussion

Contributions to invasion biology

Two strengths of my thesis are its broad theme and its novel approaches to tackling long-standing questions in ecology. The title of my thesis, *Conceptual and Applied Approaches to Marine Invasions*, highlights my ability to advance current thinking in both invasion theory and practice. Similarly, approaches ranging from modeling the effects of hurricanes through dummy coding to determining whether organisms are more likely to act as competitors or as predators based on size or species by competing models using information theory, demonstrate my ability to use conventional statistical approaches in somewhat non-conventional ways. In Chapter 2, I examined one of the oldest hypotheses in invasion biology, the diversity-invasibility hypothesis (Elton 1958) in relation to a relatively newer concept, the invasion paradox (Fridley et al. 2017). In Chapter 3, combining practical diet studies with the ecological theory of non-consumptive effects in predators, I addressed an ongoing debate in the literature about the relationship between native predators and invasive, Indo-Pacific lionfish in the Caribbean. Finally in Chapter 4, using a long-term field experiment that incorporated ‘real life’ environmental stochasticity (i.e., Category 3 Hurricane Irene), I directly addressed a key question in lionfish invasion management: is infrequent culling, the most widely used method of local lionfish control in the Caribbean, ecologically effective?

Where to next?

What is the next frontier in invasion research? Climate change and its effects on species invasions likely come to mind for many scientists and environmental managers. Indeed, research in this area has already begun (e.g., Hellmann et al. 2008; Rahel and Olden 2008). Some foundational texts in the field have entire chapters dedicated to the subject (e.g., Lockwood et al. 2013). A less obvious answer, however, is parasites. Despite more than half a century of research in invasion biology, when compared to other areas

(e.g., propagule pressure), relatively little is known about the roles of parasites of invasive animal or plant hosts in biological invasions. Book chapters and literature reviews exist on the matter (e.g., Prenter et al. 2004; Torchin & Lafferty 2009). However, key questions, particularly those related to mechanism, remain unanswered.

Two prominent hypotheses in invasion biology that are relevant to parasites are: (1) *the enemy-release hypothesis (ERH)*, and (2) *the evolution of increased competitive ability (EICA)*. However, when examined together under the framework of parasites and invasive hosts, they seem to produce conflicting implications for overall invader success. The ERH states that invasive species are successful at establishing and spreading in novel environments because they initially arrive with few to no native ‘enemies’ (i.e., predators, pathogens or parasites) that regulate their populations in the native range. These invasive species therefore experience demographic release in the introduced range (Torchin et al. 2003; Prenter et al. 2004; Lockwood et al. 2013). In the context of parasites, invasive species may experience increased population densities and/or increased body sizes in a novel environment because they are released from parasite-induced regulatory pressures (Dunn 2009). The closely related EICA hypothesis proposes that invasive species that escape their natural enemies in the introduced range evolve and selection favours individuals that reallocate resources from defenses to growth and reproduction, which gives them a competitive edge over native species (Blossey and Nötzold 1995). However under this scenario, although invasive species are larger and/or have higher population abundances in the newly colonized range than in their native range, they are also potentially more susceptible to novel parasites because of a loss of defenses. There therefore seems to be an inherent conflict between the initial benefits of demographic release from native parasites (as predicted by the ERH), and later increased vulnerability to new parasites in the invaded range (as predicted by the EICA). Indeed, Keogh and colleagues (2017) argue a similar point in which they highlight the “double edge to parasite escape” in invasive shore crabs.

The lionfish invasion in the western Atlantic is an excellent model system to test the predictions of the ERH and the EICA hypotheses. Observational surveys suggest that lionfish invasion success may be at least partly due to release from native parasites (i.e., the ERH). Lionfish have fewer and a lower diversity of parasites in the Atlantic than native fishes in the same environment (Sikkel et al. 2014; Loerch et al. 2015; Sellers et al. 2015; Tuttle et al. 2017). Also, lionfish grow larger, are more abundant, and have

fewer parasites in the Atlantic than in their native Indo-Pacific Oceans (Darling et al. 2011; Tuttle et al. 2017). However, what is currently missing from lionfish studies is evidence of the mechanism(s) for the above observations. For example, lionfish success in the Atlantic can be due to initial release from predators and/or from parasites from the native range. One can partly test this hypothesis by collecting lionfish from the Atlantic and separating them into two main groups: (1) lionfish that are experimentally infected with parasites native to the Pacific region, and (2) lionfish that are similarly handled, but not infected with parasites. Researchers could then monitor somatic growth rates of individuals in both groups over time. If lionfish grow larger without Pacific parasites than with them, this would provide a mechanism for release from native parasites. Of course, one can conduct more elaborate experiments that vary parasite abundance, species diversity, and/or intensity of infection over a range similar to what is observed in the native region.

In contrast to the ERH, the EICA hypothesis can be tested by comparing (1) lionfish populations in the invaded range versus populations in the native range, as well as (2) populations in the Atlantic with different invasion histories. The latter scenario is possible because of several key characteristics of the lionfish invasion, including: (1) a broad geographic extent in the invaded range (Schofield 2009; 2010), (2) the occurrence of a few populations with relatively low connectivity in the western Atlantic (Betancur-R et al. 2011), (3) quick times to sexual maturity (i.e., within the first year) (Morris 2009), and (4) a reasonably long invasion history (i.e., more than 30 years since the first introduction) (Côté and Smith 2018).

One prediction of the EICA hypothesis is that when under identical environmental conditions, individuals from a recently colonized region will have faster somatic growth than individuals from the native range (Blossey & Nötzold 1995). Researchers can use a common garden experiment to test this prediction with lionfish from both the invaded and native ranges. Specifically, one can collect lionfish from populations in the Atlantic and in the Indo-Pacific Oceans, remove all parasites from all individuals, and then hold the lionfish under identical laboratory conditions for several weeks. An outcome that is consistent with the EICA hypothesis would be that lionfish from the recently colonized, Atlantic Ocean have faster growth rates than those originating in the Pacific. To account for potential spatial variation in growth rates among lionfish populations within the same region, one could simply conduct the above experiment with lionfish from multiple

populations. In this latter instance, a result that would support the EICA hypothesis is that lionfish from the Atlantic still have overall, faster somatic growth rates than those in the Pacific Ocean, after accounting for spatial variation in growth among populations using mixed-effects models.

A second important prediction of the EICA hypothesis is that populations that have evolved to shift resources from defences to other traits that are critical in the invasion process (e.g., growth, reproduction or dispersal) will experience increased vulnerability to parasites from their native range or to generalist parasites in the newly colonized area. Similar to the above experiment, one could test this prediction by collecting lionfish from populations in both the Atlantic and the Pacific, and removing all parasites from lionfish prior to subjecting them to a common garden experiment. However, one key difference is that researchers would infect lionfish from both groups with specialist parasites native to the Pacific and/or with generalist parasites native to the Atlantic. If the EICA hypothesis is supported, after several weeks, lionfish populations that were collected from the Atlantic should show a higher prevalence of parasites and/or a greater intensity of infection than lionfish populations originating from the Pacific because the former have been investing relatively more heavily into growth than into immune function.

Even more exciting is the potential to test the predictions of the EICA hypothesis using several populations within the invaded range. The logic here is that because of spatial and temporal variation in invasion history, the evolution of parasite susceptibility may differ between lionfish populations from the range core in the western Atlantic (i.e., areas around the US eastern seaboard and The Bahamas) and populations at the invasion front or leading edge (i.e., areas along the Atlantic coasts of South America). There are two critical underlying assumptions here, among many. First, sufficient time has transpired for the evolution of parasite susceptibility to occur. This first assumption is possible because studies have shown that, at least in terms of behavioural traits under artificial selection in animals, the evolution of distinct phenotypes within populations can occur within as little as nine generations in lab mice, and three to six generations in birds (Barnard 2004). Second, we must assume that parasite selection pressure varies between the invasion front and the range core of lionfish in the western Atlantic. This second assumption is a common characteristic of ongoing invasions, where spatial

differences in pathogen pressure leads to rapid evolution in immune system function (e.g., Lee & Klasing 2004; Horrocks et al. 2011; Brown et al. 2015).

If the necessary assumptions hold true, then one prediction of the EICA hypothesis is that lionfish populations at the invasion front will display higher susceptibility to Atlantic parasites than populations at the range core. This is because as lionfish colonize new areas at the invasion front, they are likely to encounter parasites that have not yet evolved the ability to infect lionfish. Also, lionfish densities are likely to be lower at the invasion front, thereby making it more difficult for parasites and pathogens to spread within a population. Selection should therefore favour individuals that shift resources from parasite defenses to traits like somatic growth and dispersal, which are important in the spread phase of an invasion. In contrast, lionfish at the range core would have been present in the new region for substantial periods of time. This means that Atlantic parasites would have had sufficient time to evolve to infect lionfish. Furthermore, higher lionfish population densities at the range core typically allow for greater transmission of parasites and pathogens among individuals. There should therefore be strong selection pressure against individuals with reduced parasite defences.

In closing, as the rate and magnitude of biological invasions increases globally (Cohen and Carlton 1998; Ricciardi & Atkinson 2004), and their threats to biodiversity, ecosystem functions, and regional economies grow (Sala et al. 2000; Pimentel et al. 2005), it has become more urgent than ever to advance the theory of invasions and apply it to real world situations. I hope that I have accomplished the above in this thesis, and illustrated exciting new paths for future research in the field.

References

- Abrams PA, Quince C (2005) The impact of mortality on predator population size and stability in systems with stage-structured prey. *Theor Popul Biol* 68:253–266. doi: 10.1016/j.tpb.2005.05.004
- Adams DC, Gurevitch J, Rosenberg MS (1997) Resampling tests for meta-analysis of ecological data. *Ecol* 78:1277–1283.
- Adams AJ, Ebersole JP (2004) Resistance of coral reef fishes in back reef and lagoon habitats to a hurricane. *Bulletin of Marine Science* 75:101-113.
- Adler PB, Seabloom EW, Borer EL, Hillebrand H, Hautier Y, et al. (2011) Productivity is a poor predictor of plant species richness. *Science* 33:1750–1753.
- Akins JL (2012) Control strategies: tools and techniques for local control. Pp. 24-50 in Morris JA (ed.) *Invasive Lionfish: A Guide to Control and Management*. Gulf and Caribbean Fisheries Institute Special Publication Series Number 1, Marathon, Florida, USA 133pp.
- Albins MA (2013) Effects of invasive Pacific red lionfish *Pterois volitans* versus a native predator on Bahamian coral-reef fish communities. *Biol Invasions* 15:29–43.
- Albins MA (2015) Invasive Pacific lionfish *Pterois volitans* reduce abundance and species richness of native Bahamian coral-reef fishes. *Mar Ecol Prog Ser* 522:231–243. doi: 10.3354/meps11159
- Albins MA, Hixon MA (2008) Invasive Indo-Pacific lionfish *Pterois volitans* reduce recruitment of Atlantic coral-reef fishes. *Mar Ecol Prog Ser* 367:233–238.
- Alemeu JB (2016) The status and management of the lionfish, *Pterois* sp. in Trinidad and Tobago. *Marine Pollution Bulletin* 109:402-408.
- Altmann (1974) Observational study of behaviour: sampling methods. *Brill* 49:227-267.
- Alvarez-Filip L, Côté IM, Gill JA, Watkinson AR, Dulvy NK (2011) Region-wide temporal and spatial variation in Caribbean reef architecture: is coral cover the whole story? *Global Change Biology* 17:2470-2477.
- Alvarez-Filip L, Dulvy NK, Gill JA, Côté IM, Watkinson AR (2009) Flattening of Caribbean coral reefs: region-wide declines in architectural complexity. *Proc R Soc B* 276:3019-3025.
- Anderson CB (2018) Biodiversity monitoring, earth observations and the ecology of scale. *Ecology Letters*. doi:10.1111/ele.13106

- Andradi-Brown DA, Vermeij MJA, Slattery M, et al (2017) Large-scale invasion of western Atlantic mesophotic reefs by lionfish potentially undermines culling-based management. *Biol Invasions* 19:939-954.
- Anton A, Simpson MS, Vu I (2014) Environmental and biotic correlates to lionfish invasion success in Bahamian coral reefs. *PLoS One* 9:e106229. <https://doi.org/10.1371/journal.pone.0106229>.
- Arias-González JE, González-Gándara C, Cabrera JL, Christensen V (2011) Predicted impact of the invasive lionfish *Pterois volitans* on the food web of a Caribbean coral reef. *Environ Research* 111:917-925.
- Ballew NG, Bacheler NM, Kellison GT, Schueller AM (2016) Invasive lionfish reduce native fish abundance on a regional scale. *Scientific Reports* 6:32169. <https://doi.org/10.1038/srep32169>
- Barbour AB, Allen MS, Frazer TK, Sherman KD (2011) Evaluating the potential efficacy of invasive lionfish (*Pterois volitans*) removals. *PLoS One* 6(5): e19666. doi:10.1371/journal.pone.0019666
- Barnard C (2004) Animal Behaviour: mechanism, development, function and evolution. Pearson Education Limited, Essex, pp 57-63.
- Beckstead J, Parker IM (2003) Invasiveness of *Ammophila arenaria*: release from soil-borne pathogens? *Ecol* 84:2824-2831.
- Beecher H (1973) Effects of a hurricane on a shallow-water population of damselfish, *Pomacentrus variabilis*. *Copeia* 1973:613–615.
- Belote RT, Jones RH, Hood SM, Wender BW (2008) Diversity-invasibility across an experimental disturbance gradient in Appalachian Forests. *Ecol* 89:183–92.
- Benkwitt CE (2013) Density-dependent growth in invasion lionfish (*Pterois volitans*). *PLoS ONE* 8:e66995.
- Benkwitt CE (2014) Non-linear effects of invasive lionfish density on native coral-reef fish communities. *Biol. Invasions*. DOI 10.1007/s105030-014-0801-3.
- Benkwitt CE (2015) Non-linear effects of invasive lionfish density on native coral-reef fish communities. *Biol Invasions* 17:1383-1395.
- Benkwitt CE (2016a) Central-place foraging and ecological effects of an invasive predator across multiple habitats. *Ecology* 97:2729-2739.
- Benkwitt CE (2016b) Invasive lionfish increase activity and foraging movements at greater local densities. *Mar Ecol Prog Ser* 558:255-266.

- Bertness MD, Ragan C (1994) Positive interactions in communities. *Trends in Ecology and Evolution* 9:191–193.
- Betancur-R R, Hines A, Acero PA, Ortí G, Wilbur AE, et al. (2011) Reconstructing the lionfish invasion: insights into greater Caribbean biogeography. *J Biogeography* 38:1281-1293.
- Blackburn TM, Petchey OL, Cassey P, Gaston KJ (2005) Functional diversity of mammalian predators and extinction in island birds. *Ecol* 86:2916-2923.
- Blossey B, Notzold R (1995) Evolution of increased competitive ability in invasive nonindigenous plants: a hypothesis. *J Ecol* 83:887-889.
- Böhlke JE, Chaplin CC (1993) *Fishes of The Bahamas and adjacent tropical waters*. Second edition. University of Texas Press, Austin.
- Borenstein ML, Hedges LV, Higgins J, Rothstein HR (2009) *Introduction to meta-analysis*. First edition. John Wiley & Sons, Ltd, West Sussex, UK.
- Borski RJ, Hodson RG (2003) Fish research and the institutional animal care and use committee. *ILAR J* 44:286–294. doi: 10.1093/ilar.44.4.286
- Britton JR (2012) Testing strength of biotic resistance against an introduced fish: inter-specific competition or predation through facultative piscivory? *PLoS One* 7(2):e31707.doi:10.1371/journal.pone.0031707
- Brook LA, Johnson CN, Ritchie EG (2012) Effects of predator control on behaviour of an apex predator and indirect consequences for mesopredator suppression. *J Appl Ecol* 49:1278–1286. doi: 10.1111/j.1365-2664.2012.02207.x
- Brown RL, Peet RK (2003) Diversit and invasibility of southern Appalachian plant communities. *Ecol* 84:32–39.
- Brown GP, Phillips BL, Dubey S, Shine R (2015) Invader immunology: invasion history alters immune system function in cane toads (*Rhinella marina*) in tropical Australia. *Ecol Letters* 18:57-65.
- Bruno JF, Stachowicz JJ, Bertness MD (2003) Inclusion of facilitation into ecological theory. *Trends in Ecology and Evolution* 18:119–125.
- Burnham KP, Anderson DR (2002) *Model selection and multimodel inference: a practical information-theoretic approach*. Second edition. Springer, New York, USA.
- Byers JE, Noonburg EG (2003) Scale dependent effects of biotic resistance to biological invasion. *Ecol* 84:1428–1433.
- Cade BS (2015) Model averaging and muddled multimodel inferences. *Ecol* 96:2370-2382.

- Cameron TC, Benton TG (2004) Stage-structured harvesting and its effects: an empirical investigation using soil mites. *J. Animal Ecol* 73:996-1006.
- Campbell K, Donlan CJ (2005) Feral goat eradication on islands. *Conserv Biol* 19:1362–1374. doi: 10.1111/j.1523-1739.2005.00228.x
- Carrillo-Flota EDC, Aguilar-Perera A (2017) Stakeholder perceptions of red lionfish (*Pterois volitans*) as a threat to the ecosystem and its potential for human consumption in Quintana Roo, Mexico. *Ocean and Coastal Management* 136:113-119.
- Case TJ (1990) Invasion resistance arises in strongly interacting species-rich model competition communities. *Proceedings of the National Academy of Sciences of the United States of America* 87:9610–9614.
- Caselle JE, Warner RR (2013) Variability in recruitment of coral reef fishes: the importance of habitat at two spatial scales. *Ecology* 77:2488–2504.
- Ceballos G, Ehrlich PR, Dirzo R (2017) Biological annihilation via the ongoing sixth mass extinction signalled by vertebrate population losses and declines. *PNAS* e6089-e6069. <https://www.pnas.org/cgi/doi/10.1073/pnas.1704949114>.
- Chapman JK, Anderson LG, Gough CLA, Harris AR (2016) Working up an appetite for lionfish: a market-based approach to manage the invasion of *Pterois volitans* in Belize. *Marine Policy* 73:256-262.
- Cheal AJ, Coleman G, Delean S, et al (2002) Responses of coral and fish assemblages to a severe but short-lived tropical cyclone on the Great Barrier Reef, Australia. *Coral Reefs* 21:131-142.
- Chiappone M, Sluka R, Sullivan Sealey K (2000) Groupers (Pisces: Serranidae) in fished and protected areas of the Florida Keys, Bahamas and northern Caribbean. *Mar Ecol Prog Ser* 198:261-272.
- Clark GF, Johnston EL (2011) Temporal change in the diversity-invasibility relationship in the presence of a disturbance regime. *Ecology Letters* 14:52–7.
- Clark GF, Johnston EL, Leung B (2013) Intrinsic time dependence in the diversity–invasibility relationship. *Ecol* 94:25–31.
- Cleland EE, Smith MD, Andelman SJ, Bowles C, Carney KM, et al. (2004) Invasion in space and time: non-native species richness and relative abundance respond to interannual variation in productivity and diversity. *Ecology Letters* 7:947–957.
- Cohen AN, Carlton JT (1998) Accelerating invasion rate in a highly invaded estuary. *Science* 279:555-557.

Cohen J (1988) Statistical power analysis for the behavioural sciences. Second edition. Lawrence Erlbaum Associates, Hillsdale, USA.

Costantino, RF, Cushing, JM, Dennis, B and Desharnais R (1995) Experimentally-induced transitions in the dynamic behavior of insect populations. *Nature* 375:227–230.

Costantino R, Desharnais R, Cushing J, Dennis B (1997) Chaotic dynamics in an insect population. *Science* 275:389–391. doi: 10.1126/science.275.5298.389

Côté IM, Darling ES, Malpica-Cruz L, Smith NS, Green SJ, et al. (2014) What doesn't kill you makes you wary? Effect of repeated culling on the behaviour of an invasive predator. *PLoS One* 9:e94248. <https://doi.org/10.1371/journal.pone.0094248>

Côté IM, Gill JA, Gardner TA, Watkinson AR (2005) Measuring coral reef decline through meta-analysis. *Philosophical transactions of the Royal Society of London. Series B, Biological Sciences* 360:385–395.

Côté IM, Green SJ, Hixon M (2013) Predatory fish invaders: insights from Indo-Pacific lionfish in the western Atlantic and Caribbean. *Biol Conserv* 164:50–61. doi: 10.1016/j.biocon.2013.04.014

Côté IM, Smith NS (2018) The lionfish *Pterois* sp. invasion: Has the worst-case scenario come to pass? *J Fish Biol* 92:660–689.

Cresswell W (2008) Non-lethal effects of predation in birds. *Ibis* 150:3–17.

Crooks JA (2002) Characterizing ecosystem-level consequences of biological invasions: the role of ecosystem engineers. *Oikos* 97:153–166.

Cruz F, Josh Donlan C, Campbell K, Carrion V (2005) Conservation action in the Galapagos: Feral pig (*Sus scrofa*) eradication from Santiago Island. *Biol Conserv* 121:473–478.

Cure K, Benkwitt CE, Kindinger TL, et al (2012) Comparative behavior of red lionfish *Pterois volitans* on native Pacific versus invaded Atlantic coral reefs. *Mar Ecol Prog Ser* 467:181–192.

Curtis JS, Wall KR, Albins MA, Stallings CD (2017) Diet shifts in a native meso-predator across a range of invasive lionfish biomass. *Mar Ecol Prog Ser* 573:215–228.

Dahl KA, Patterson WF (2014) Habitat-specific density and diet of rapidly expanding invasive red lionfish, *Pterois volitans*, populations in the northern Gulf of Mexico. *PLoS ONE* 9(8): e105852. doi:10.1371/journal.pone.0105852

Dahl KA, Patterson WF, Snyder RA (2016) Experimental assessment of lionfish removals to mitigate reef fish community shifts on northern Gulf of Mexico artificial reefs. *Mar Ecol Prog Ser* 558:207–221. doi: 10.3354/meps11898

- Dahl KA, Patterson WF, Snyder RA (2016) Experimental assessment of lionfish removals to mitigate reef fish community shifts on northern Gulf of Mexico artificial reefs. *Mar Ecol Prog Ser* 558:207–221. doi: 10.3354/meps11898
- Darling ES, Green SJ, O'Leary JK, Côté IM (2011) Indo-Pacific lionfish are larger and more abundant on invaded reefs: a comparison of Kenyan and Bahamian lionfish populations. *Biol Invasions* 13:2045–2051.
- Davies KF, Chesson P, Harrison S, Inouye BD, Melbourne BA, et al. (2005) Spatial heterogeneity explains the scale dependence of the native – exotic diversity relationship. *Ecol* 86:1602–1610.
- Davies KF, Harrison S, Safford HD, Viers JH (2007) Productivity alters the scale dependence of the diversity-invasibility relationship. *Ecol* 88:1940–1947.
- Davis K, Carlson PM, Bradley D, Warner RR, Caselle JE (2017) Predation risk influences feeding rates but competition structures space use for a common Pacific parrotfish. *Oecologia* 184:139–149.
- Davis MA, Grime JP, Thompson K (2000) Fluctuating resources in plant communities: a general theory of invasibility. *J. Ecol.* 88:528–534.
- Davis MA, Pelsor M (2001) Experimental support for a mechanistic resource-based model of invasibility. *Ecology Letters* 4:421–428.
- De León R, Vane K, Bertuol P, et al (2013) Effectiveness of lionfish removal efforts in the southern Caribbean. *Endang Species Res* 22:175–182.
- De Roos AM, Schellekens T, Kooten T van, et al (2007) Food-dependent growth leads to overcompensation in stage-specific biomass when mortality increases: the influence of maturation versus reproduction regulation. *Am Nat* 170:E59–E76. doi: 10.1086/520119
- Dill LM, Heithaus MR, Walters CJ (2003) Behaviorally mediated indirect interactions in marine communities and their conservation implications. *Ecol* 84:1151–1157.
- Doherty TS, Ritchie EG (2016) Stop jumping the gun: a call for evidence-based invasive predator management. *Conservation Letters* 0:1–8.
- Dulvy NK, Sadovy Y, Reynolds JD (2003) Extinction vulnerability in marine populations. *Fish and Fisheries* 4:25–64.
- Dunn AM (2009) Parasites and biological invasions. *Advances in Parasitology* 68:161–184.
- Edelist D, Rilov G, Golani D, Carlton JT, Spanier E (2013) Restructuring the sea: profound shifts in the world's most invaded marine ecosystem. *Diversity Distrib* 19:69–77.

- Egger M, Smith GD, Schneider M, Minder C (1997) Bias in meta - analysis detected by a simple, graphical test. *British Medical Journal* 315:629–634.
- Eggleston DB, Grover JJ, Liocius RN (1998) Ontogenetic diet shifts in Nassau grouper: trophic linkages and predatory impact. *Bull Mar Sci* 63:111-126.
- Elton C (1958) The ecology of invasions by animals and plants. University of Chicago Press.
- Ferreira CEL, Luiz OJ, Floeter SR, Lucena MB, Barbosa M et al. (2015) First record of invasive lionfish (*Pterois volitans*) for the Brazilian Coast. *PLoS One* 10:e0123002.<https://doi.org/10.1371/journal.pone.0123002>
- Frazer TK, Jacoby C, Edwards M, et al (2012) Coping with the lionfish invasion: can targeted removals yield beneficial effects? *Rev Fish Sci* 20:185–191. doi: 10.1080/10641262.2012.700655
- Frederick JL (1997) Evaluation of fluorescent elastomer injection as a method for marking small fish. *Bull Mar Sci* 61, 399-408.
- Fridley JD, Stachowicz JJ, Naeem S, Sax DF, Seabloom EW et al. (2007) The invasion paradox: reconciling pattern and process in species invasions. *Ecol* 88:3–17.
- Froese R, Pauly D, (Eds) (2016) FishBase. World Wide Web electronic publication www.fishbase.org, version (10/2016)
- Froese R, Pauly D, (Eds) (2018) FishBase. World Wide Web electronic publication www.fishbase.org, version (10/2018)
- Galzin R (1987) Structure of fish communities of French Polynesian coral reefs. I. Spatial scales. *Mar Ecol Prog Ser* 41:129-136.
- Gates S (2002) Review of methodology of quantitative reviews using meta-analysis in ecology. *J. Animal Ecol.* 71:547–557.
- Green PT, Lake PS, O'Dowd DJ (2004) Resistance of island rainforest to invasion by alien plants: influence of microhabitat and herbivory on seedling performance. *Biol Invasions* 6:1-9.
- Green SJ, Akins JL, Côté IM (2011) Foraging behaviour and prey consumption in the Indo-Pacific lionfish on Bahamian coral reefs. *Mar Ecol Prog Ser* 433:159–167.
- Green SJ, Akins JL, Maljković A, Côté IM (2012) Invasive lionfish drive Atlantic coral reef fish declines. *PLoS One* 7:e32596. doi: 10.1371/journal.pone.0032596
- Green SJ, Dulvy NK, Brooks ALM, et al (2014) Linking removal targets to the ecological effects of invaders: a predictive model and field test. *Ecol Appl* 24:1311-1322.

Green SJ, Tamburello N, Miller SE, et al (2013) Habitat complexity and fish size affect the detection of Indo-Pacific lionfish on invaded coral reefs. *Coral Reefs* 32:413–421. doi: 10.1007/s00338-012-0987-8

Groom MJ, Meffe GK, Carroll CR (2005) Principles of conservation biology. Third edition. Sinauer Associates, Oxford, UK

Grueber CE, Nakagawa S, Laws RJ, Jamieson IG (2011) Multimodel inference in ecology and evolution: challenges and solutions. *J Evol Biol* 24:699–711.

Guo Q, Fei S, Dukes JS, Oswalt CM, Iannone BV, et al. (2015) A unified approach for quantifying invasibility and degree of invasion. *Ecol* 96:2613–2621.

Guo Q, Symstad A (2008) A two-part measure of degree of invasion for cross-community comparisons. *Conservation Biology* 22:666–72.

Gurevitch J, Curtis PS, Jones MH (2001) Meta-analysis in ecology. *Advances in Ecological Research* 32:199–247.

Gurevitch J, Hedges LV (1999) Statistical issues in ecological meta-analyses. *Ecol* 80:1142–1149.

Hackerott S, Valdivia A, Green SJ, Côté IM, Cox CE, Akins L, Layman CA, Precht WF, Bruno JF (2013) Native predators do not influence invasion success of Pacific lionfish on Caribbean reefs. *PLoS ONE* 8(7) e68259. doi:10.1371/journal.pone.0068259.

Harmelin-Vivien ML (1994) The effects of storms and cyclones on coral reefs: a review. *J Coastal Research* 12:211–231.

Harrison F (2011) Getting started with meta-analysis. *Methods in Ecology and Evolution* 2:1–10.

Harrison XA, Donaldson L, Correa-Cano ME, Evans J, Fisher DN, et al. (2018) A brief introduction to mixed effects modelling and multi-model inference in ecology. *PeerJ* 6:e4794 doi10.7717/peerj.4794

Hedges LV, Olkin I (1985) Statistical methods for meta-analysis. Academic Press, San Diego, USA.

Heithaus M, Frid A, Wirsing AJ, Worm B (2008) Predicting ecological consequences of marine top predator declines. *Trends in Ecology and Evolution* 23:202–210.

Halfman GS (1986) Fish behaviour by day, night and twilight. In: Pitcher T (ed) *The behaviour of teleost fishes*. Croom-Helm, London, pp 366–387.

Hellmann JJ, Byers JE, Bierwagen BG, Dukes JS (2008) Five potential consequences of climate change for invasive species. *Conservation Biol* 22:534–543.

- Herben T, Mandák B, Bímová K, Münzbergová Z (2004) Invasibility and species richness of a community: a neutral model and a survey of published data. *Ecol* 85:3223–3233.
- Hill KC, Fischer DG (2014) Native–exotic species richness relationships across spatial scales in a prairie restoration matrix. *Restoration Ecol* 22:204–213.
- Hixon MA (1991) Predation as a process structuring coral reef fish communities. In: Sale PF (ed) *The ecology of fishes on coral reefs*. Academic Press, New York, pp 475–507
- Hobson ES (1972) Activity of Hawaiian reef fishes during the evening and morning transitions between daylight and darkness. *Fish Bull* 70:715–740.
- Hodgson DJ, Rainey PB, Buckling A (2002) Mechanisms linking diversity, productivity and invasibility in experimental bacterial communities. *Philosophical Transactions of the Royal Society of London. Series B, Biological sciences* 269:2277–2283.
- Holle B Von (2013) Environmental stress alters native–nonnative relationships at the community scale. *Biol Invasions* 15:417–427.
- Holle B Von, Simberloff D (2005) Ecological resistance to biological invasion overwhelmed by propagule pressure. *Ecol* 86:3212–3218.
- Horrocks NPC, Matson KD, Tielemans BI (2011) Pathogen pressure puts immune defense into perspective. *Integr Comp Biol* 51: 563–576.
- Humann P, Deloach N (2002) *Reef fish identification: Florida, Caribbean, Bahamas*. Third edition. New World Publications, Jacksonville
- Huston MA (1997) Hidden treatments in ecological experiments: re-evaluating the ecosystem function of biodiversity. *Oecologia* 110:449–460.
- Ingeman KE (2016) Lionfish cause increased mortality rates and drive local extirpation of native prey. *Mar Ecol Progress Series* 558:235–245.
- Iwama GK, McGeer JC, Pawluk MP (1989) The effects of five fish anaesthetics on acid-base balance, hematocrit, blood gases, cortisol, and adrenaline in rainbow trout. *Can J Zool* 67:2065–2073
- Jeschke JM, Debillé S, Lortie CJ (2018) Biotic resistance and island susceptibility hypotheses. Pages 60–70 in: Jeschke, J. M., and T. Heger. (eds.). *Invasion Biology: Hypotheses and Evidence*. CABI, Wallingford, UK.
- Jeschke JM, Gómez Aparicio L, Haider S, Heger T, Lortie CJ, et al. (2012) Support for major hypotheses in invasion biology is uneven and declining. *NeoBiota* 14:1–20.

- Jiang L, Morin PJ (2004) Productivity gradients cause positive diversity-invasibility relationships in microbial communities. *Ecology Letters* 7:1047–1057.
- Johnston MW, Purkis SJ (2015a) A coordinated and sustained international strategy is required to turn the tide on the Atlantic lionfish invasion. *Mar Ecol Prog Ser* 533:219–235. doi: 10.3354/meps11399
- Johnston MW, Purkis SJ (2015b) Hurricanes accelerated the Florida-Bahamas lionfish invasion. *Glob Chang Biol* 21:2249–2260. doi: 10.1111/gcb.12874
- Kappel CV (2005) Losing pieces of the puzzle: threats to marine, estuarine, and diadromous species. *Front Ecol Environ* 3:275–282.
- Kaufman SL (1983) Coral reefs effects of Hurricane Allen on reef fish assemblages. *Coral Reefs* 2:43–47.
- Keene JL, Noakes DL, Moccia RD, Soto CG (1998) The efficacy of clove oil as an anaesthetic for rainbow trout, *Oncorhynchus mykiss* (Walbaum). *Aquaculture Research* 29:89–101.
- Kennedy TA, Naeem S, Howe KM, Knopps JMH, Tilman D et al. (2002) Biodiversity as a barrier to ecological invasion. *Nature* 417:636–638.
- Keogh CL, Miura O, Nishimura T, Byers J (2017) The double edge to parasite escape: invasive host is less infected but more infectable. *Ecol* 98:2241–2247.
- Kimbrough DL, Cheng BS, Grosholz ED (2013) Biotic resistance in marine environments. *Ecology Letters* 16:821–833.
- Knight KS, Reich PB (2005) Opposite relationships between invasibility and native species richness at patch versus landscape scales. *Oikos* 109:81–88.
- Lank DB, Butler RW, Ireland J, Ydenberg RC (2003) Effects of predation danger on migration strategies of sandpipers. *Oikos* 103:303–319.
- Lee KA, Klasing KC (2004) A role for immunology in invasion biology. *Trends Ecol Evol* 19: 523–529.
- Lesser MP, Slattery M (2011) Phase shift to algal dominated communities at mesophotic depths associated with lionfish (*Pterois volitans*) invasion on a Bahamian coral reef. *Biol Invasions* 13:1855–1868.
- Levine JM (2000) Species diversity and biological invasions: relating local process to community pattern. *Science* 288:852–854.
- Levine JM, Adler PB, Yelenik SG (2004) A meta-analysis of biotic resistance to exotic plant invasions. *Ecology Letters* 7:975–989.

- Levine JM, D'Antonio CM (1999) Elton revisited: a review of evidence linking diversity and invasibility. *Oikos* 87:15–26.
- Lieury N, Ruette S, Devillard S, et al (2015) Compensatory immigration challenges predator control: an experimental evidence-based approach improves management. *J Wildl Manag* 79:425-434.
- Lima SL (1998) Nonlethal effects in the ecology of predator-prey interactions. What are the ecological effects of anti-predator decision-making? *BioScience* 48:25-34.
- Lockwood JL, Hoopes MF, Marchetti MP (2013) Invasion ecology. Second edition. Wiley-Blackwell, Oxford, UK.
- Loerch SM, McCammon AM, Sikkel PC (2015) Low susceptibility of invasive Indo-Pacific lionfish *Pterois volitans* to ectoparasite *Neobenedenia* in the eastern Caribbean. *Environ Biol Fishes* 98:1979-1985.
- Lonsdale WM (1999) Global patterns of plant invasions and the concept of invasibility. *Ecol* 80:1522–1536.
- Luckhurst BE, Luckhurst K (1978) Analysis of the influence of substrate variables on coral reef fish communities. *Mar Biol* 49:317-323.
- Lyons KG, Schwartz MW (2001) Rare species loss alters ecosystem function - invasion resistance. *Ecology Letters* 4:358–365.
- MacArthur RH (1970) Species-packing and competitive equilibrium for many species. *Theoretical Population Biology* 1:1–11.
- Maljković A, Leeuwen TEV, Cove SN (2008) Predation on the invasive red lionfish, *Pterois volitans* (Pisces: Scorpaenidae), by native groupers in the Bahamas. *Coral Reefs* 27: 501.
- McTee SA, Grubich JR (2014) Native densities, distribution, and diurnal activity of Red Sea lionfishes (Scorpaenidae). *Mar Ecol Prog Ser* 508:223-232.
- Moe J, Stenseth NC, Smith RH (2002) Density-dependent compensation in blowfly populations give indirectly positive effects of a toxicant. *Ecology* 86:1597-1603.
- Moher D, Liberati A, Tetzlaff J, Altman DG, Altman D, et al. (2009) Preferred reporting items for systematic reviews and meta-analyses: The PRISMA statement. *PLoS Medicine* 6.
- Morris J, Akins JL (2009) Feeding ecology of invasive lionfish (*Pterois volitans*) in the Bahamian archipelago. *Environ Biol Fishes* 86:389–398. doi: 10.1007/s10641-009-9538-8

- Morris JA Jr (2009) The biology and ecology of the invasive Indo-Pacific lionfish. PhD Thesis. North Carolina State University, Raleigh, NC, USA.
- Morris JA, Shertzer KW, Rice JA (2011) A stage-based matrix population model of invasive lionfish with implications for control. *Biol Invasions* 13:7–12. doi: 10.1007/s10530-010-9786-8
- Morris, Jr J (Ed) (2012) Invasive lionfish: a guide to control and management. Gulf and Caribbean Fisheries Institute, Marathon
- Mumby PJ, Brumbaugh DR, Harbone AR, Roff G (2013) On the relationship between native grouper and invasive lionfish in the Caribbean. *PeerJ PrePrints* doi:10.7287.peerjpreprints.45v1
- Mumby PJ, Harborne AR, Brumbaugh DR (2011) Grouper as a natural biocontrol of invasive lionfish. *PLoS ONE* 6(6) e21510. doi:10.1371/journal.pone.0021510.
- Muñoz RC, Currin CA, Whitfield PE (2011) Diet of invasive lionfish on hard bottom reefs of the Southeast USA: Insights from stomach contents and stable isotopes. *Mar Ecol Prog Ser* 432:181–193. doi: 10.3354/meps09154
- Naeem S, Knops JMH, Tilman D, Howe KM, Kennedy T et al. (2000) Plant diversity increases resistance to invasion in the absence of covarying extrinsic factors. *Oikos* 91:97–108.
- Nakagawa S, Cuthill IC (2007) Effect size, confidence interval and statistical significance: A practical guide for biologists. *Biol Reviews* 82:591–605.
- Nakagawa S, Noble DWA, Senior AM, Lagisz M (2017) Meta-evaluation of meta-analysis: ten appraisal questions for biologists. *BMC Biology* 15:18.
- Nakagawa S, Santos ESA (2012) Methodological issues and advances in biological meta-analysis. *Evol Ecol* 26:1253–1274.
- Nakagawa S, Schielzeth H (2013) A general and simple method for obtaining R² from generalized linear mixed-effects models. *Methods Ecol Evol* 4:133–142. doi: 10.1111/j.2041-210x.2012.00261.x
- Nelson E, Mendoza G, Regetz J, Polasky S, Tallis H, et al. (2009) Modeling multiple ecosystem services, biodiversity conservation, commodity production, and tradeoffs at landscape scales. *Front Ecol Environ* 7:4–11.
- Noble DWA, Lagisz M, O’Dea RE, Nakagawa S (2017) Nonindependence and sensitivity analyses in ecological and evolutionary meta-analyses. *Molecular Ecol* 26:2410–2425.
- Nogales M, Martín A, Tershy BR, et al (2004) A review of feral cat eradication on islands. *Conserv Biol* 18:310–319.

- Nyström P (2005) Non-lethal predator effects on the performance of a native and an exotic crayfish species. *Freshwater Biol* 50:1938-1949.
- Oliver TH, Heard MS, Isaac NJB, Roy DB, Procter D, et al. (2015a) Biodiversity and resilience of ecosystem functions. *TREE* 30:673-684.
- Oliver TH, Isaac NJB, August TA, Woodcock BA, Roy DB, et al. (2015b) Declining resilience of ecosystem functions under biodiversity loss. *Nature Communications* doi: 10.1038/ncomms10122.
- Outeiro L, Rodrigues JG, Damásio LMA, Lopes PFM (2019) Is it just about the money? A spatial-economic approach to assess ecosystem service tradeoffs in a marine protected area in Brazil. *Ecosystem Services* 38.
<https://doi.org/10.1016/j.ecoser.2019.100959>
- Pearson RG (2016) Reasons to conserve nature. *Trend Ecol Evol* 31:366-371.
- Pimentel D, Lach L, Zuniga R, Morrison D (2000) Environmental and economic costs of nonindigenous species in the United States. *BioScience* 50:138-159.
- Pimentel D, Zuniga R, Morrison D (2005) Update on the environmental and economic costs associated with alien-invasive species in the United States. *Ecol Econ* 52:273-288.
- Preisser EL, Bolnick DI, Benard MF (2005) Scared to death? The effects of intimidation and consumption in predator-prey interactions. *Ecol* 86:501-509.
- Prenter J, MacNeil C, Dick JTA, Dunn AM (2004) Roles of parasites in animal invasions. *Trends Ecol Evol* 19: 386-390.
- Quinn GP, Keough MJ (2002) Experimental design and data analysis for biologists, First. Cambridge University Press, Cambridge
- R Development Core Team (2014) R: a language and environment for statistical computing. R Foundation for Statistical Computing. Vienna, Austria.
<http://www.R-project.org>
- Rahbek C (2005) The role of spatial scale and the perception of large-scale species-richness patterns. *Ecol Letters* 8:224–239.
- Rahel FJ, Olden JD (2008) Assessing the effects of climate change on aquatic invasive species. *Conservation Biol* 22:521-533.
- Reinhart KO, Packer A, Van der Putten WH, Clay K (2003) Plant-soil biota interactions and spatial distributions of black cherry in its native and invasive ranges. *Ecol Letters* 6:1046-1050.

- Ricciardi A, Atkinson SK (2004) Distinctiveness magnifies the impact of biological invaders in aquatic ecosystems. *Ecol Letters* 7:781-784.
- Richarson DM, Allsopp N, D'Antonio CM, Milton SJ, Rejmánek M (2007) Plant invasions - the role of mutualisms. *Biol Reviews* 75:65–93.
- Ritchie EG, Johnson CN (2009) Predator interactions, mesopredator release and biodiversity conservation. *Ecol Letters* 12:982-998.
- Rosenberg MS (2005) The file-drawer problem revisited: a general weighted method for calculating fail-safe numbers in meta-analysis. *Evol* 59:464–468.
- Rosenberg MS, Adams DC, Gurevitch J (2000) METAWIN version 2: statistical software for meta-analysis. Sinauer Associates, Boston, USA.
- Sadovy de Mitcheson Y, Craig MT, Bertoncini AA, Carpenter KE, Cheung WWL, et al. (2013) Fishing groupers towards extinction: a global assessment of threats and extinction risks in a billion dollar fishery. *Fish and Fisheries* 14:119-136.
- Sala OE, Stuart Chapin F, Armesto JJ, Berlow E, Bloomfield J et al. (2000) Global biodiversity scenarios for the year 2100. *Science* 287:1770-1774.
- Sale P (1978) Coexistence of coral reef fishes – a lottery for living space. *Environ Biol Fishes* 3:85-102.
- Sale PF, Sharp BJ (1983) Correction for bias in visual transect censuses of coral reef fishes. *Coral Reefs* 2:37–42. doi: 10.1007/BF00304730
- Sale PF, Sharp BJ (1983) Correction for bias in visual transect censuses of coral reef fishes. *Coral Reefs* 2:37–42. doi: 10.1007/BF00304730
- Salomon AK, Gaichas SK, Shears NT, Smith JE, Madin EMP, Gaines SD (2010) Key features and context-dependence of fishery-induced trophic cascades. *Conservation Biol.* 24:382-394.
- Savidge JA (1987) Extinction of an island forest avifauna by an introduced snake. *Ecol* 63:660-668.
- Schielzeth H (2010) Simple means to improve the interpretability of regression coefficients. *Methods Ecol Evol* 1:103-113.
- Schmitz OJ, Krivan V, Ovadia O (2004) Trophic cascades: the primacy of trait-mediated indirect interactions. *Ecol Letters* 7:153-163.
- Schofield P (2009) Geographic extent and chronology of the invasion of non-native lionfish (*Pterois volitans* [Linnaeus 1758] and *P. miles* [Bennett 1828]) in the western North Atlantic and Caribbean Sea. *Aquatic Invasions* 4:473-479.

- Schofield P (2010) Update on geographic spread of invasive lionfish (*Pterois volitans* [Linnaeus 1758] and *P. miles* [Bennett 1828]) in the Western North Atlantic Ocean, Caribbean Sea and Gulf of Mexico. *Aquatic Invasions* 5:S117-S122
- Sellers AJ, Ruiz GM, Leung B, Torchin ME (2015) Regional variation in parasite species richness and abundance in the introduced range of the invasive lionfish, *Pterois volitans*. *PLoS One* 10(6) e0131075. doi:10.1371/journal.pone.0131075.
- Semmens BX, Buhle ER, Salomon AK, Pattengill-Semmens CV (2004) A hotspot of non-native marine fishes: evidence for the aquarium trade as an invasion pathway. *Marine Ecol Progress Series* 266:239-244.
- Shea K, Chesson P (2002) Community ecology theory as a framework for biological invasions. *Trends in Ecology and Evolution* 17:170–176.
- Sherman KD, Dahlgren CP, Stevens JR, Tyler CR (2016) Integrating population biology into conservation management for endangered Nassau grouper *Epinephelus striatus*. *Mar Ecol Prog Ser* 554:263-280.
- Sikkel PC, Tuttle LJ, Cure K, Coil AM, Hixon MA (2014) Low susceptibility of invasive red lionfish (*Pterois volitans*) to a generalist ectoparasite in both its introduced and native ranges. *PLoS One* 9(5):e95854. doi:10.1371/journal.pone.0095854.
- Smith NS, Green SJ, Akins JL, Miller S, Côté (2017) Density-dependent colonization and natural disturbance limit the effectiveness of invasive lionfish culling efforts. *Biol. Invasions* 19:2385-2399.
- Smith RK, Pullin AS, Stewart GB, Sutherland WJ (2010) Effectiveness of predator removal for enhancing bird populations. *Conserv Biol* 24:820–829. doi: 10.1111/j.1523-1739.2009.01421.x
- Sokal RR, Rohlf FJ (1995) *Biometry: the principles and practice of statistics in biological research*. Second edition. W.H. Freeman and Company, New York, USA.
- Stachowicz JJ (1999) Species diversity and invasion resistance in a marine ecosystem. *Science* 286:1577–1579.
- Stachowicz JJ, Fried H, Osman RW, Whitlatch RB (2002) Biodiversity, invasion resistance , and marine ecosystem function: reconciling pattern and process. *Ecol* 83:2575–2590.
- Stallings CD (2008) Indirect effects of an exploited predator on recruitment of coral-reef fishes. *Ecol* 89:2090-2095.
- Sterne J, Egger M (2005) Regression methods to detect publication and other bias in meta-analyisis. Pages 99–110 in H. R. Rothstein, A. Sutton, and M. Borenstein, editors. *Publication bias in meta-analysis: prevention, assessment, and adjustments*. John Wiley & Sons, Chichester, England.

- Stohlgren TJ, Barnett DT, Kartesz JT (2003) The rich get richer: patterns of plant invasions in the United States. *Frontiers Ecol Environ* 1:11–14.
- Stohlgren TJ, Binkley D, Chong GW, Mohammed AK, Schell LD, et al. (1999) Exotic plant species invade hot spots of native plant diversity. *Ecol Monographs* 69:25–46.
- Ström L, Jansson R, Nilsson C (2014) Invasibility of boreal wetland plant communities. *J. Vegetation Science* 25:1078–1089.
- Suding KN, Gross KL (2006) Modifying native and exotic species richness correlations: the influence of fire and seed addition. *Ecol Applications* 16:1319–1326.
- Sun Y, Müller-Schärer H, Maron JL, Schaffner U (2015) Origin matters: diversity affects the performance of alien invasive species but not of native species. *The American Naturalist* 185: 725–736.
- Suraci JP, Clinchy M, Dill LM, Roberts D, Zanette LY (2016) Fear of large carnivores causes a trophic cascade. *Nature Communications* 7:10698.
- Symonds MRE, Moussalli A (2011) A brief guide to model selection, multimodel inference and model averaging in behavioural ecology using Akaike's information criterion. *Behav Ecol Sociobiology* 65:13-21
- Tabacchi E, Planty-Tabacchi AM (2005) Exotic and native plant community distributions within complex riparian landscapes: a positive correlation. *Écoscience* 12:412–423.
- Tamburrello N , Côté IM (2014) Movement ecology of Indo-Pacific lionfish on Caribbean coral reefs and its implications for invasion dynamics. *Biol Invasions* 17:1639–1653.
- Tilman D, Isbell F, Cowles JM (2014) Biodiversity and ecosystem functioning. *The Annual Review of Ecol, Evol, and Systematics* 45: 471–493.
- Torchin ME, Lafferty KD (2009) Escape from parasites In: Biological invasions in marine ecosystems: ecological, management and geographic perspectives. Rilvo G, Crooks JA (eds). Springer, Berlin, pp 203-214.
- Torchin ME, Lafferty KD, Dobson AP, McKenzie VJ, Kuris AM (2003) Introduced species and their missing parasites. *Nature* 421:628-630.
- Tracey SR, Baulch T, Hartmann K, et al (2015) Systematic culling controls a climate driven, habitat modifying invader. *Biol Invasions* 17:1885–1896. doi: 10.1007/s10530-015-0845-z

- Tuttle LJ, Sikkel PC, Cure K, Hixon MA (2017) Parasite-mediated enemy release and low biotic resistance may facilitate invasion of Atlantic coral reefs by Pacific red lionfish (*Pterois volitans*). *Biol Invasions* 19:563–575.
- Usseglio P, Selwyn JD, Downey-Wall AM, Hogan JD (2017) Effectiveness of removals of the invasion lionfish: how many dives are needed to deplete a reef? *Peer J* 5:e3043. <https://doi.org/10.7717/peerj.3043>
- Valdivia A, Bruno JF, Cox CE, Hackerott S, Green SJ (2014) Re-examining the relationship between invasive lionfish and native grouper in the Caribbean. *PeerJ* 2:e348. doi:10.7717/peerj.348.
- Van Elsas JD, Chiurazzi M, Mallon CA, Elhottová D, Kristufek V, et al. (2012) Microbial diversity determines the invasion of soil by a bacterial pathogen. *PNAS* 109:1159–1164.
- Vaudo JJ, Heithaus MR (2013) Microhabitat selection by marine mesoconsumers in a thermally heterogeneous habitat: behavioural thermoregulation or avoiding predation risk? *PLoS One* 8(4):e61907. doi:10.1371/journal.pone.0061907
- Viechtbauer W (2005) Bias and efficiency of meta-analytic variance estimators in the random-effects model. *J. Educational and Behavioral Statistics* 30:261–293.
- Viechtbauer W (2010) Conducting meta-analyses in R with the metafor package. *J Stat Software* 36:1–48.
- Vitousek PM (1990) Biological invasions and ecosystem processes: towards an integration of population biology and ecosystem studies. *Oikos* 57:7–13.
- Walsh WJ (1983) Stability of a coral reef fish community following a catastrophic storm. *Coral Reefs* 2:49–63.
- Walters CJ, Juanes F (1993) Recruitment limitation as a consequence of natural selection for use of restricted feeding habits and predation risks. *Canadian Journal of Fisheries and Aquatic Science* 50:2058–2070.
- Wantiez L, Chateau O, Le Mouellic S (2006) Initial and mid-term impacts of cyclone Erica on coral reef fish communities and habitat in the South Lagoon Marine Park of New Caledonia. *Journal of the Marine Biological Association of the United Kingdom* 86:1229–1236.
- Wardle D (2001) Experimental demonstration that plant diversity reduces invasibility - evidence of a biology mechanism or a consequence of sampling effect? *Oikos* 95:161–170.
- Weidel BC, Josephson DC, Kraft CE (2007) Littoral fish community response to smallmouth bass removal from an adirondack lake. *Trans Am Fish Soc* 136:778–789. doi: 10.1577/T06-091.1

- Werner EE, Peacor (2003) A review of trait-mediated indirect interactions in ecological communities. *Ecol* 84:1083-1100.
- White LF, Shurin JB (2007) Diversity effects on invasion vary with life history stage in marine macroalgae. *Oikos* 116:1193–1203.
- Whitfield PE, Gardiner T, Vives SP, Gilligan MR, Ray GC, et al. (2002) Biological invasion of the Indo-Pacific lionfish *Pterois volitans* along the Atlantic coast of North America. *Mar Ecol Prog Ser* 235:289-297.
- Wickham H (2009) *ggplot2: Elegant Graphics for Data Analysis*. Springer-Verlag, New York, USA.
- Wilcove DS, Rothstein D, Dubow J, Phillips A, Losos E (1998) Quantifying threats to imperilled species in the United States. *BioScience* 48:607-615.
- Woodley JD, Chornesky EA, Cliffo PA, Sid EM (1981) Hurricane Allen's impact on Jamaican coral reefs. *Science* (80) 214:749–755.
- Xu K, Ye W, Cao H, Deng X, Yang Q, et al. (2004) The role of diversity and functional traits of species in community invasibility. *Botanical Bulletin of Academia Sinica* 45: 149–157.
- Yamanishi Y, Yoshida K, Fujimori N, Yusa Y (2012) Predator-driven biotic resistance and propagule pressure regulate the invasive apple snail *Pomacea canaliculata* in Japan. *Biol Invasions* 14:1343-1352,
- Yorisue T, Ellrich JA, Momota K (2019) Mechanisms underlying predator-driven biotic resistance against introduced barnacles on the Pacific coast of Hokkaido, Japan. *Biol Invasions* 21:2345-2356.
- Zavaleta ES, Pasari JR, Hulvey KB, Tilman GD (2009) Sustaining multiple ecosystem functions in grassland communities requires higher biodiversity. *PNAS* 107:1443-1446.
- Zipkin EF, Kraft CE, Cooch EG, Sullivan PJ (2009) When can nuisance and invasive species control efforts backfire? *Ecol Appl* 19:1585–1595.
- Zipkin EF, Sullivan PJ, Cooch EG, et al (2008) Overcompensatory response of a smallmouth bass (*Micropterus dolomieu*) population to harvest: release from competition? *Can J Fish Aquat Sci* 65:2279–2292. doi: 10.1139/F08-133
- Zuur AF, Ieno EN, Walker NJ, Saveliev AA, Smith GM (2009) Mixed effects models and extensions in ecology with R. Springer, New York

Appendix A.

Supporting Information for Chapter 2

Table A.1 All studies, with corresponding summary data, included in the meta-analysis

Source	r	n	Study type	Invasibility metric	Spatial grain	Spatial extent	Invader taxon
Stachowicz et al. 1999	-0.86	20	Exp.	performance	0.01 m ²	NA	ascidian
Levine 2000	-0.46	65	Exp.	performance	0.04 m ²	small	plant
Kennedy et al. 2002	-0.69	147	Exp.	performance	9 m ²	small	plant
White & Shurin 2007	-0.40	50	Exp.	performance	0.06 m ²	NA	plant
White & Shurin 2007	-0.65	23	Obs.	richness	0.25 m ²	NA	plant
Davies et al. 2007	0.89	1,526	Obs.	richness	1 m ²	large	plant
Stachowicz et al. 2002	-0.65	120	Obs.	richness	0.06 m ²	medium	ascidian
Stachowicz et al. 2002	-0.05	15	Exp.	performance	0.01 m ²	small	ascidian
Stachowicz et al. 2002	-0.79	17	Exp.	performance	0.01 m ²	small	ascidian
Stachowicz et al. 2002	-0.65	11	Exp.	performance	0.01 m ²	small	ascidian
Stohlgren et al. 2003	0.01	340	Obs.	richness	1 m ²	large	plant
Stohlgren et al. 2003	-0.01	398	Obs.	richness	1 m ²	large	plant
Stohlgren et al. 2003	0.04	448	Obs.	richness	1 m ²	large	plant
Stohlgren et al. 2003	0.01	348	Obs.	richness	1 m ²	large	plant
Stohlgren et al. 2003	0.04	930	Obs.	richness	1 m ²	large	plant
Stohlgren et al. 2003	0.21	151	Obs.	richness	1 m ²	large	plant
Stohlgren et al. 2003	0.02	124	Obs.	richness	1 m ²	large	plant
Stohlgren et al. 2003	0.16	219	Obs.	richness	1 m ²	large	plant
Belote et al. 2008	0.01	7	Obs.	richness	1 m ²	small	plant

Source	<i>r</i>	n	Study type	Invasibility metric	Spatial grain	Spatial extent	Invader taxon
Belote et al. 2008	0.39	7	Obs.	richness	1 m ²	small	plant
Belote et al. 2008	-0.62	7	Obs.	richness	1 m ²	small	plant
Belote et al. 2008	0.25	5	Obs.	richness	1 m ²	small	plant
Eschtruth & Battles 2011	0.40	1,408	Obs.	performance	1 to 8 m ²	medium	plant
Chen et al. 2010	0.13	515	Obs.	richness	1 m ²	medium	plant
Kappes et al. 2009	0.30	27	Obs.	richness	0.5 m ²	medium	gastropod
Arndt 2006	0.48	20	Obs.	richness	0.5 m ²	large	soil macro-invertebrate
Arndt & Perner 2008	0.47	20	Obs.	richness	0.5 m ²	large	soil macro-invertebrate
Gilbert & Lechowicz 2005	0.57	67	Obs.	richness	10 m ²	NA	plant
Davies et al. 2005	-0.93	384	Obs.	richness	1 m ²	small	plant
Xu et al. 2004	-0.42	56	Exp.	performance	4.7 m ²	small	plant
Sax 2002	0.40	20	Obs.	richness	1 m ²	medium	plant
Cleland et al. 2004	0.23	90	Obs.	richness	10 m ²	medium	plant
Lyons & Schwartz 2001	-0.57	53	Exp.	performance	3.7 m ²	small	plant
Keeley et al. 2003	0.66	150	Obs.	richness	1 m ²	medium	plant
Keeley et al. 2003	0.66	200	Obs.	richness	1 m ²	medium	plant
Keeley et al. 2003	0.26	2,060	Obs.	richness	1 m ²	medium	plant
Troumbis et al. 2002	-0.47	52	Exp.	richness	4 m ²	small	plant
Capers et al. 2007	0.02	1,654	Obs.	richness	3.14 m ²	medium	plant
van Elsas et al. 2012	-0.92	44	Exp.	performance	Unavailable - microcosm	NA	soil microbe
Lilley & Vellend 2009	0.01	52	Obs.	richness	1 m ²	small	plant
Compagnoni & Halpern 2009	-0.13	24	Obs.	richness	1 m ²	small	plant
Ström et al. 2014	0.49	34	Exp.	performance	6 m ²	small	plant

Source	<i>r</i>	n	Study type	Invasibility metric	Spatial grain	Spatial extent	Invader taxon
Ström et al. 2014	0.55	10	Exp.	performance	6 m ²	small	plant
Ström et al. 2014	0.27	37	Exp.	performance	6 m ²	small	plant
Ström et al. 2014	0.45	35	Exp.	performance	6 m ²	small	plant
Ström et al. 2014	0.03	33	Exp.	performance	6 m ²	small	plant
Ström et al. 2014	0.36	35	Exp.	performance	6 m ²	small	plant
Jared et al. 2014	0.01	20	Obs.	performance	150 m ²	small	plant – adults & saplings
Jared et al. 2014	-0.08	14	Obs.	performance	150 m ²	small	plant – adults & saplings
Mallon et al. 2015	-0.96	61	Exp.	performance	1 mL	NA	soil microbe
Corenblit et al. 2014	0.82	70	Obs.	richness	4 m ²	medium	plant
Corenblit et al. 2014	0.66	65	Obs.	richness	4 m ²	medium	plant
Mineur & Johnson 2008	0.2	216	Obs.	richness	0.25 m ²	large	plant
Hill & Fischer 2014	-0.01	50	Obs.	richness	1 m ²	small	plant
Hill & Fischer 2014	0.34	50	Obs.	richness	1 m ²	small	plant
Sun et al. 2015	-0.70	19	Obs.	performance	1 m ²	large	plant
Suding & Gross 2006	0.18	115	Obs.	richness	0.25 m ²	small	plant
Perelman et al. 2007	0.90	60	Obs.	richness	0.1 m ²	medium	plant

Supplementary references

- Arndt, E. 2006. Niche occupation by invasive ground-dwelling predator species in Canarian laurel forests. *Biological Invasions* 8:893–902.
- Arndt, E., and J. Perner. 2008. Invasion patterns of ground-dwelling arthropods in Canarian laurel forests. *Acta Oecologica* 34:202–213.
- Belote, R. T., R. H. Jones, S. M. Hood, and B. W. Wender. 2008. Diversity-invasibility across an experimental disturbance gradient in Appalachian Forests. *Ecology* 89:183–92.

- Capers, R. S., R. Selsky, G. R. Bugbee, and J. C. White. 2007. Aquatic plant community invasibility and scale-dependent patterns in native and invasive species richness. *Ecology* 88:3135–3143.
- Chen, H., H. Qian, G. Spyreas, and M. Crossland. 2010. Native-exotic species richness relationships across spatial scales and biotic homogenization in wetland plant communities of Illinois, USA. *Diversity and Distributions* 16:737–743.
- Cleland, E. E., M. D. Smith, S. J. Andelman, C. Bowles, K. M. Carney, M. Claire Horner-Devine, J. M. Drake, S. M. Emery, J. M. Gramling, and D. B. Vandermast. 2004. Invasion in space and time: non-native species richness and relative abundance respond to interannual variation in productivity and diversity. *Ecology Letters* 7:947–957.
- Compagnoni, A., and C. B. Halpern. 2009. Properties of native plant communities do not determine exotic success during early forest succession. *Ecography* 32:449–458.
- Corenblit, D., J. Steiger, E. Tabacchi, E. González, and A. M. Planty-Tabacchi. 2014. Ecosystem engineers modulate exotic invasions in riparian plant communities by modifying hydrogeomorphic connectivity. *River Research and Applications* 30:45–59.
- Davies, K. F., P. Chesson, S. Harrison, B. D. Inouye, B. a. Melbourne, and K. J. Rice. 2005. Spatial heterogeneity explains the scale dependence of the native – exotic diversity relationship. *Ecology* 86:1602–1610.
- Davies, K. F., S. Harrison, H. D. Safford, and J. H. Viers. 2007. Productivity alters the scale dependence of the diversity-invasibility relationship. *Ecology* 88:1940–1947.
- van Elsas, J. D., M. Chiurazzi, C. A. Mallon, D. Elhottová, V. Kristufek, and J. Falcão Salles. 2012. Microbial diversity determines the invasion of soil by a bacterial pathogen. *Proceedings of the National Academy of Sciences of the United States of America* 109:1159–1164.
- Eschtruth, A. K., and J. J. Battles. 2011. The importance of quantifying propagule pressure to understand invasion: an examination of riparian forest invasibility. *Ecology* 92: 1314–1322.
- Gilbert, B., and M. J. Lechowicz. 2005. Invasibility and abiotic gradients: the positive correlation between native and exotic plant diversity. *Ecology* 86:1848–1855.
- Hill, K. C., and D. G. Fischer. 2014. Native–exotic species richness relationships across spatial scales in a prairie restoration matrix. *Restoration Ecology* 22:204–213.
- Jared, C., A. Mullah, K. Klanderud, O. Totland, and D. Odee. 2014. Community invasibility and invasion by non-native *Fraxinus pennsylvanica* trees in a degraded tropical forest. *Biological Invasions* 16:2747–2755.

- Kappes, H., J. D. Delgado, M. R. Alonso, and M. Ibáñez. 2009. Native and introduced gastropods in laurel forests on Tenerife, Canary Islands. *Acta Oecologica* 35:581–589.
- Keeley, J. E., D. Lubin, and C. J. Fotheringham. 2003. Fire and grazing impacts on plant diversity and alien plant invasions in the southern Sierra Nevada. *Ecological Applications* 13:1355–1374.
- Kennedy, T. A., S. Naeem, K. M. Howe, J. M. H. Knopps, D. Tilman, and P. Reich. 2002. Biodiversity as a barrier to ecological invasion. *Nature* 417:636–638.
- Levine, J. M. 2000. Species diversity and biological invasions: relating local process to community pattern. *Science* 288:852–854.
- Lilley, P. L., and M. Vellend. 2009. Negative native-exotic diversity relationship in oak savannas explained by human influence and climate. *Oikos* 118:1373–1382.
- Lyons, K. G., and M. W. Schwartz. 2001. Rare species loss alters ecosystem function - invasion resistance. *Ecology Letters* 4:358–365.
- Mallon, C. A., F. Poly, X. Le Roux, I. Marring, J. D. van Elsas, and J. Falcão Salles. 2015. Resource pulses can alleviate the biodiversity–invasion relationship in soil microbial communities. *Ecology* 96:915–926.
- Mineur, F., M. P. Johnson, and C. A. Maggs. 2008. Non-indigenous marine macroalgae in native communities: a case study in the British Isles. *Journal of the Marine Biological Association of the United Kingdom* 88:693–698.
- Perelman, S. B., E. J. Chaneton, W. B. Batista, S. E. Burkart, and R. J. C. León. 2007. Habitat stress, species pool size and biotic resistance influence exotic plant richness in the Flooding Pampa grasslands. *Journal of Ecology* 95:662–673.
- Sax, D. F. 2002. Native and naturalized plant diversity are positively correlated in scrub communities of California and Chile. *Diversity and Distributions* 8:193–210.
- Stachowicz, J. J. 1999. Species diversity and invasion resistance in a marine ecosystem. *Science* 286:1577–1579.
- Stachowicz, J. J., H. Fried, R. W. Osman, and R. B. Whitlatch. 2002. Biodiversity, invasion resistance , and marine ecosystem function: reconciling pattern and process. *Ecology* 83:2575–2590.
- Stohlgren, T. J., D. T. Barnett, and J. T. Kartesz. 2003. The rich get richer: patterns of plant invasions in the United States. *Frontiers in Ecology and the Environment* 1:11–14.
- Ström, L., R. Jansson, and C. Nilsson. 2014. Invasibility of boreal wetland plant communities. *Journal of Vegetation Science* 25:1078–1089.

- Suding, K. N., and K. L. Gross. 2006. Modifying native and exotic species richness correlations: the influence of fire and seed addition. *Ecological Applications* 16:1319–1326.
- Sun, Y., H. Müller-Schärer, J. L. Maron, and U. Schaffner. 2015. Origin matters: diversity affects the performance of alien invasive species but not of native species. *The American Naturalist* 185: 725–736
- White, L. F., and J. B. Shurin. 2007. Diversity effects on invasion vary with life history stage in marine macroalgae. *Oikos* 116:1193–1203.
- Troumbis, A. Y., A. Galanidis, and G. D. Kokkoris. 2002. Components of short-term invasibility in experimental Mediterranean grasslands. *Oikos* 98:239–250.
- Xu, K., W. Ye, H. Cao, X. Deng, Q. Yang, and Y. Zhang. 2004. The role of diversity and functional traits of species in community invasibility. *Botanical Bulletin of Academia Sinica* 45: 149–157.

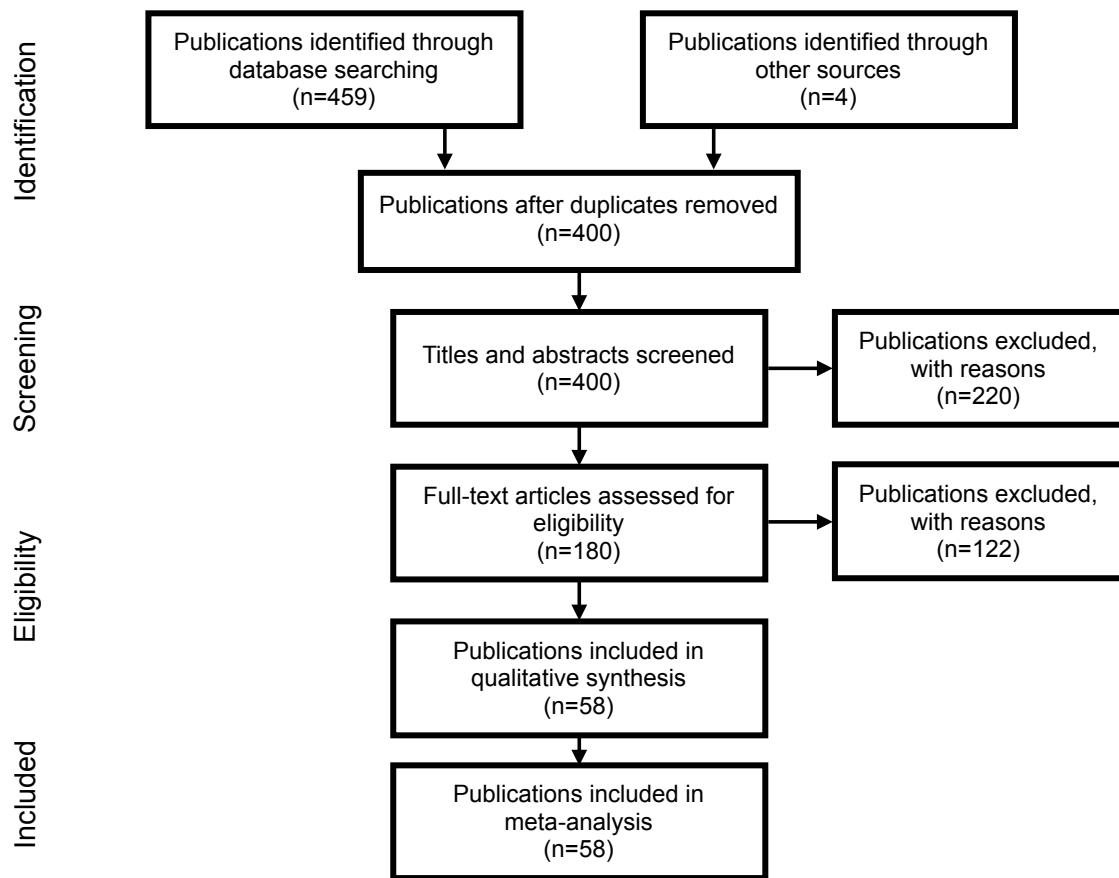


Figure A.1 PRISMA literature search flow diagram.

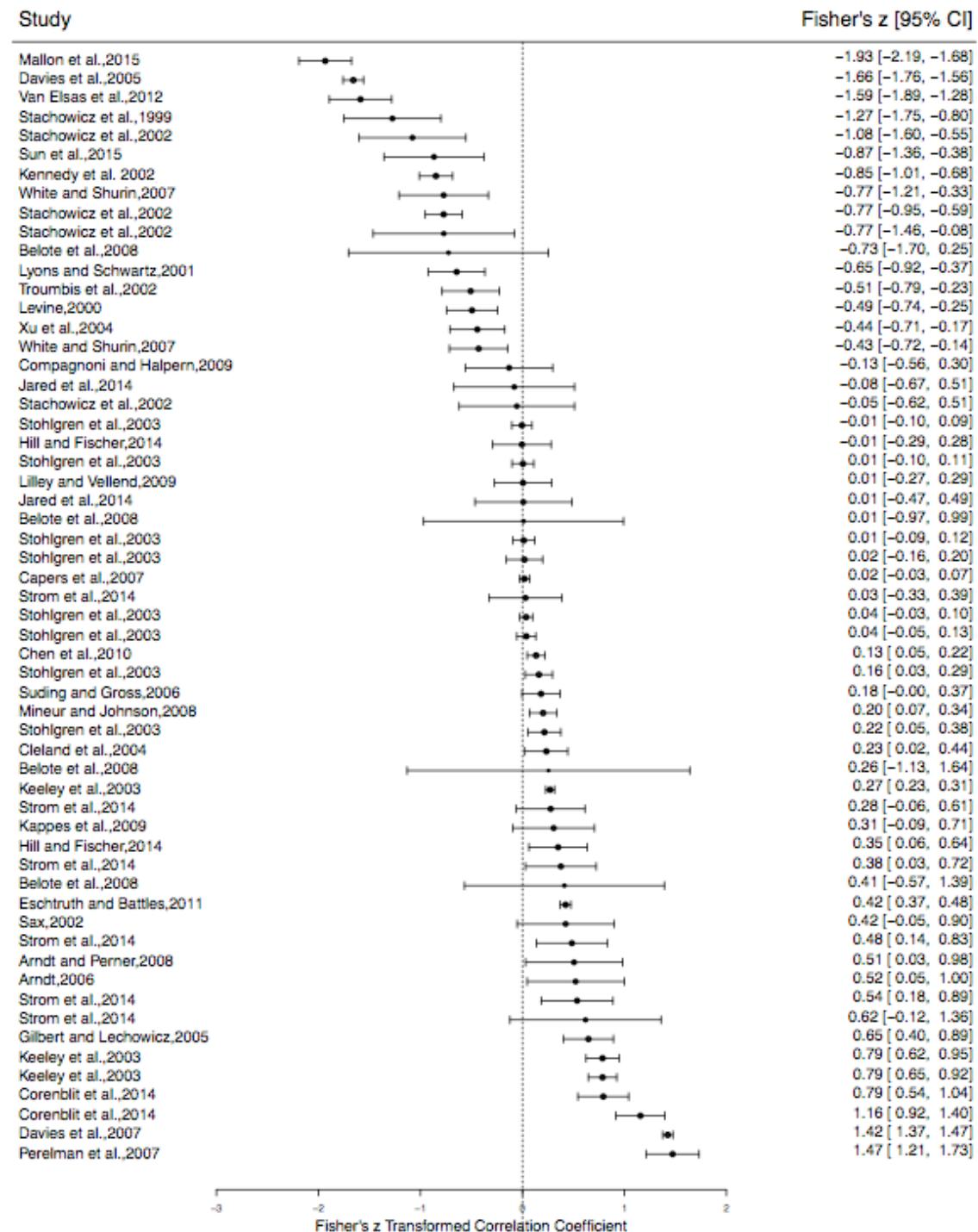


Figure A.2 Forest plot showing all 58 effect sizes (i.e., Z_r , Fisher's z-transformed correlation coefficient) with corresponding 95% confidence intervals for the relationship between diversity and invasibility, extracted from 34 studies included in the meta-analysis.

The size of each point is proportional to the precision of each effect size estimate.

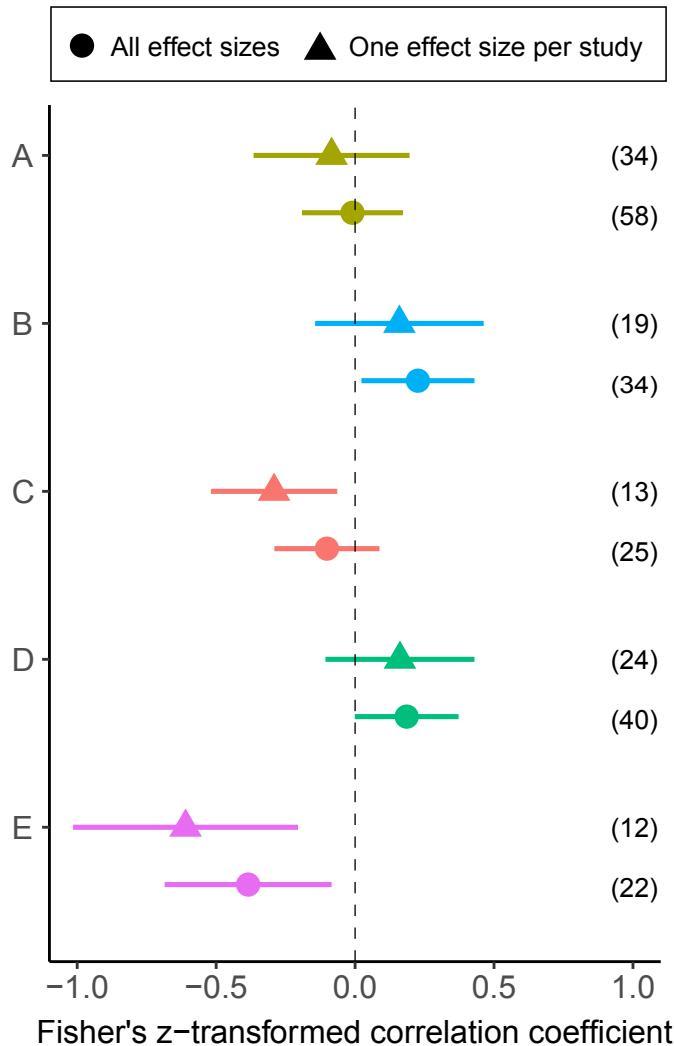


Figure A.3 Sensitivity analysis of the strength and direction of diversity–invasibility relationships, estimated by random-effects meta-analytic models using all effect sizes within a dataset versus one randomly selected effect size per study that reported multiple effect sizes.

(A) All fine spatial grain studies; (B) All fine-grain, observational studies that used richness as a metric of invasibility; (C) All fine-grain and fine-extent studies; (D) All fine-grain observational studies; and (E) All fine-grain studies that used invader performance as a metric of invasibility. Mean effect sizes (Z_r , Fisher's z-transformed correlation coefficients) are shown, bounded by 95% confidence intervals. Sample sizes are indicated in parentheses to the right of each mean.

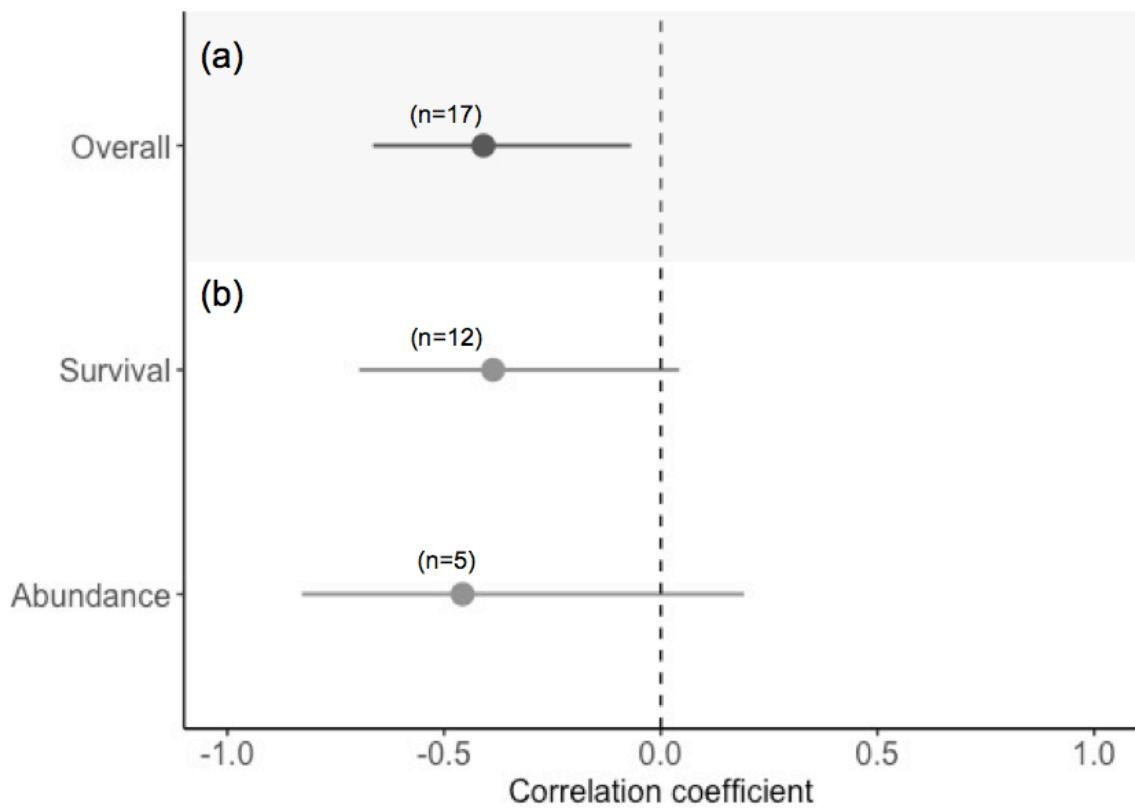


Figure A.4 Different invader performance metrics (survival or abundance) produced similar diversity–invasibility relationships in experimental studies.

(a) Overall effect size, estimated from a random-effects model, and (b) effect sizes for studies measuring invader survival or abundance, estimated from a mixed effects model where invader performance was treated as a fixed effect while study was treated as a random effect. Mean effect sizes (r , correlation coefficients) are shown, bounded by 95% confidence intervals. Significant effects are shown in black while non-significant results are shown in grey. Sample sizes are indicated in parentheses above each mean.

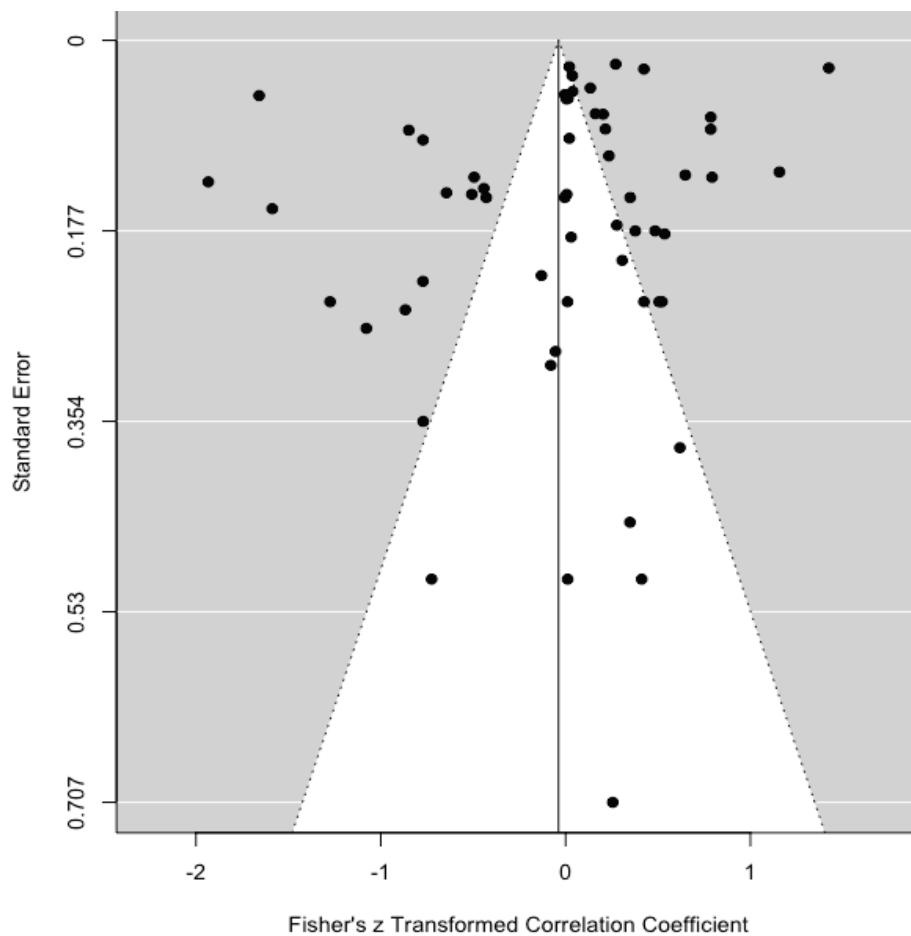


Figure A.5 Funnel plot of effect sizes (i.e., Fisher's z-transformed correlation coefficient) versus standard errors for all 58 diversity-invasibility relationships used in our meta-analysis.

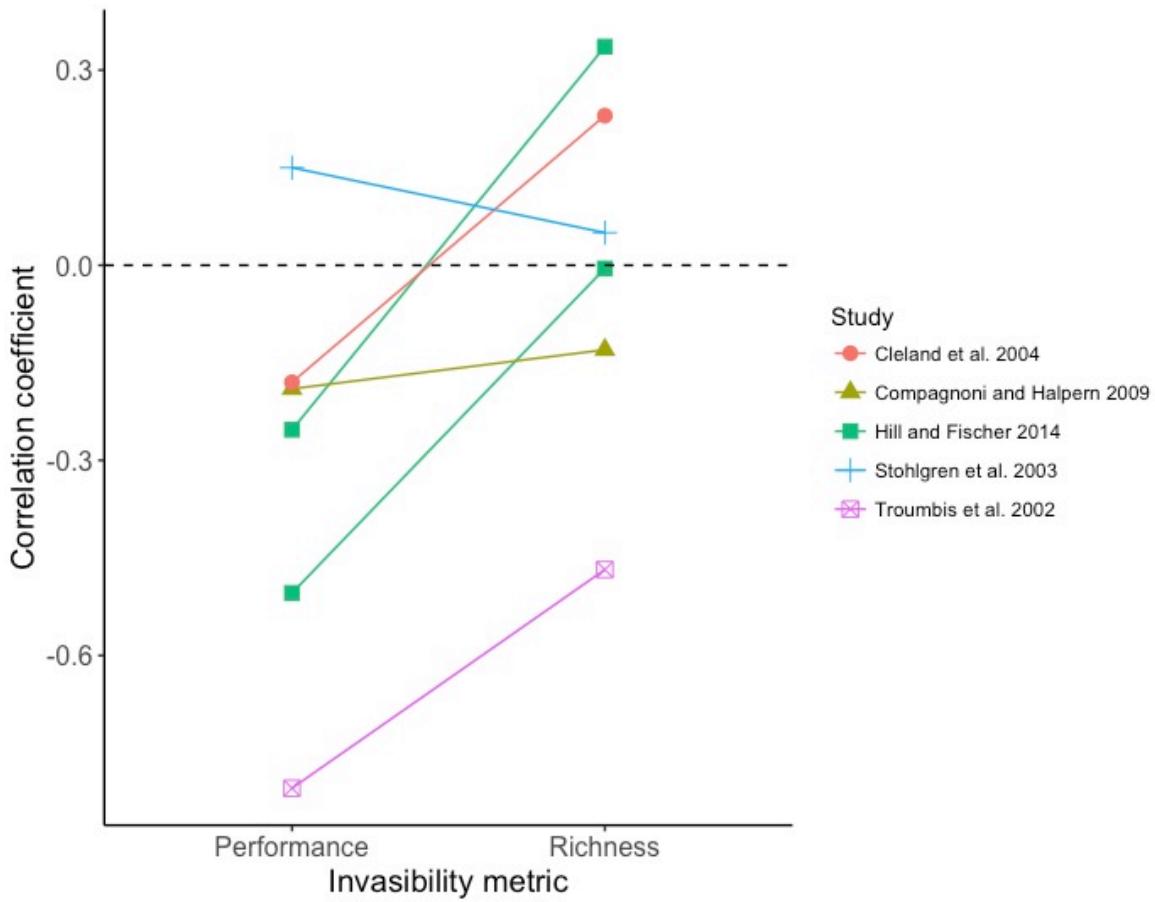


Figure A.6 Different invasibility metrics (i.e., performance or richness) yielded different relationships between native diversity and invasion vulnerability, even within the same experiment or observational study.

Three out of the six associations showed a change in the direction of the diversity-invasibility link with a change in invasibility metric while in two more instances, the relationship became less negative when invasibility was measured using richness instead of a performance metric. Each shape represents the mean effect size (r , correlation coefficient) from a different study.

Appendix B.

Supporting Information for Chapter 3

Measuring reef rugosity

We measured reef rugosity on each study reef by fitting a fine-link chain (5 m long) to the contours of the substrate along one to three 8 m transect lines at 2 m intervals. A rugosity index was then calculated as the ratio of the total chain length (i.e., actual surface distance) to the linear distance (i.e., straight-line distance along the transect), so that larger numbers reflect greater rugosity (Luckhurst and Luckhurst 1978; Wilson et al. 2007).

Supplementary references

Luckhurst BE, Luckhurst K (1978) Analysis of the influence of substrate variables on coral reef fish communities. *Mar Biol* 49:317-323.

Wilson SK, Graham NAJ, Polunin NVC (2007) Appraisal of visual assessments of habitat complexity and benthic composition on coral reefs. *Mar Biol* 151:1069-1076.

Table B.1 Overall grouper abundance differed among sites.

Parameter	Estimate	SE	T-value	P-value
Intercept	-3.75	0.21	-17.44	0.00
Site C2	0.39	0.29	1.31	0.19
Site C5	0.76	0.36	2.13	0.04
Site E2	0.77	0.29	2.69	0.01
Site NF14	-0.24	0.32	-0.75	0.45
Site NF23	-0.25	0.28	-0.90	0.37
Site NF25	-0.22	0.29	-0.73	0.47
Site NF27	-0.27	0.28	-0.96	0.34
Site NF28	0.00	0.28	0.01	0.99
Site NF3	-0.91	0.33	-2.73	0.01
Site NF5	0.96	0.29	3.25	0.00

Results from linear-mixed effects model examining overall grouper abundance among coral reef patch sites over the study period. Grouper abundance was natural log-transformed in order to meet model assumptions. Sites are compared to the baseline site A2. Significant results in bold.

Table B.2 Overall grouper biomass differed among sites.

Parameter	Estimate	SE	T-value	P-value
Intercept	1.32	0.23	5.62	0.00
Site C2	-0.05	0.33	-0.16	0.87
Site C5	1.92	0.44	4.32	0.00
Site E2	1.35	0.35	3.87	0.00
Site NF14	0.49	0.47	1.05	0.30
Site NF23	-0.24	0.31	-0.77	0.44
Site NF25	-0.88	0.32	-2.76	0.01
Site NF27	-0.62	0.31	-2.03	0.04
Site NF28	-0.32	0.31	-1.05	0.29
Site NF3	0.00	0.47	0.00	0.99
Site NF5	1.94	0.36	5.35	0.00

Results from linear-mixed effects model examining overall grouper biomass among coral reef patch sites over the study period. Grouper biomass was natural log-transformed in order to meet model assumptions. Sites are compared to the baseline site A2. Significant results in bold.

Table B.3 Grouper predator abundance classified based on species (i.e., more piscivorous) differed among sites.

Parameter	Estimate	SE	T-value	P-value
Intercept	-3.46	0.25	-13.75	0.00
Site C2	-0.08	0.38	-0.21	0.84
Site C5	0.47	0.38	1.24	0.22
Site E2	0.70	0.34	2.04	0.05
Site NF14	-0.53	0.38	-1.40	0.17
Site NF23	-0.34	0.34	-1.01	0.32
Site NF25	-0.46	0.38	-1.21	0.24
Site NF27	-0.71	0.34	-2.10	0.04
Site NF28	-0.46	0.34	-1.36	0.18
Site NF3	-1.34	0.47	-2.84	0.01
Site NF5	0.80	0.34	2.35	0.02

Results from linear-mixed effects model examining grouper predator abundance (based on species) among coral reef patch sites over the study period. Grouper predator abundance was natural log-transformed in order to meet model assumptions. Sites are compared to the baseline site A2. Significant results in bold.

Table B.4 Grouper predator abundance classified based on size (i.e., ≥ 30 cm TL) differed among sites.

Parameter	Estimate	SE	T-value	P-value
Intercept	-4.12	0.19	-21.53	0.00
Site C2	0.25	0.28	0.87	0.39
Site C5	0.96	0.30	3.18	0.00
Site E2	1.18	0.27	4.36	0.00
Site NF14	0.14	0.33	0.42	0.68
Site NF23	-0.04	0.27	-0.16	0.88
Site NF25	-0.46	0.28	-1.63	0.11
Site NF27	-0.29	0.26	-1.13	0.26
Site NF28	-0.16	0.26	-0.60	0.55
Site NF3	-0.67	0.33	-2.01	0.05
Site NF5	1.25	0.25	4.93	0.00

Results from linear-mixed effects model examining grouper predator abundance (based on size) among coral reef patch sites over the study period. Grouper predator abundance was natural log-transformed in order to meet model assumptions. Sites are compared to the baseline site A2. Significant results in bold.

Table B.5 Grouper predator biomass classified based on species (i.e., more piscivorous) differed among sites.

Parameter	Estimate	SE	T-value	P-value
Intercept	1.37	0.23	5.91	0.00
Site C2	0.71	0.33	2.15	0.03
Site C5	1.90	0.35	5.50	0.00
Site E2	1.40	0.29	4.81	0.00
Site NF14	1.02	0.43	2.37	0.02
Site NF23	0.08	0.26	0.31	0.76
Site NF25	-0.30	0.30	-1.00	0.32
Site NF27	0.07	0.28	0.25	0.80
Site NF28	0.16	0.30	0.54	0.59
Site NF3	0.57	0.58	0.98	0.33
Site NF5	1.95	0.30	6.53	0.00

Results from linear-mixed effects model examining grouper predator biomass (based on species) among coral reef patch sites over the study period. Grouper predator biomass was natural log-transformed in order to meet model assumptions. Sites are compared to the baseline site A2. Significant results in bold.

Table B.6 Grouper predator biomass classified based on size (i.e., ≥ 30 cm TL) differed among sites.

Parameter	Estimate	SE	T-value	P-value
Intercept	1.96	0.16	12.20	0.00
Site C2	0.54	0.23	2.40	0.02
Site C5	1.46	0.23	6.21	0.00
Site E2	1.07	0.20	5.36	0.00
Site NF14	0.67	0.30	2.22	0.03
Site NF23	-0.17	0.19	-0.90	0.37
Site NF25	-0.35	0.23	-1.54	0.13
Site NF27	-0.28	0.20	-1.41	0.16
Site NF28	0.20	0.22	0.94	0.35
Site NF3	-0.20	0.30	-0.65	0.51
Site NF5	1.36	0.20	6.94	0.00

Results from linear-mixed effects model examining grouper predator biomass (based on size) among coral reef patch sites over the study period. Grouper predator biomass was natural log-transformed in order to meet model assumptions. Sites are compared to the baseline site A2. Significant results in bold.

Table B.7 Grouper competitor abundance classified based on size (i.e., < 30 cm TL) weakly differed among sites.

Parameter	Estimate	SE	T-value	P-value
Intercept	-3.93	0.27	-14.82	0.00
Site C2	0.36	0.34	1.07	0.29
Site C5	0.41	0.59	0.69	0.49
Site E2	0.53	0.35	1.50	0.14
Site NF14	-0.06	0.40	-0.15	0.88
Site NF23	-0.26	0.33	-0.79	0.44
Site NF25	-0.32	0.33	-0.96	0.34
Site NF27	-0.10	0.34	-0.30	0.77
Site NF28	0.21	0.33	0.63	0.53
Site NF3	-0.51	0.46	-1.12	0.27
Site NF5	0.73	0.59	1.24	0.22

Results from linear-mixed effects model examining grouper competitor abundance (based on size) among coral reef patch sites over the study period. Grouper competitor abundance was natural log-transformed in order to meet model assumptions. Sites are compared to the baseline site A2. Significant results in bold.

Table B.8 Grouper competitor biomass classified based on size (i.e., <30 cm TL) differed among sites.

Parameter	Estimate	SE	T-value	P-value
Intercept	0.585	0.271	2.160	0.03
Site C2	-0.062	0.348	-0.180	0.86
Site C5	1.615	0.806	2.004	0.05
Site E2	1.068	0.466	2.291	0.03
Site NF14	0.431	0.514	0.838	0.41
Site NF23	-0.232	0.341	-0.679	0.50
Site NF25	-0.753	0.337	-2.238	0.03
Site NF27	-0.751	0.337	-2.225	0.03
Site NF28	-0.136	0.326	-0.419	0.68
Site NF3	0.228	0.516	0.442	0.66
Site NF5	1.818	0.806	2.255	0.03

Results from linear-mixed effects model examining grouper competitor biomass (based on size) among coral reef patch sites over the study period. Grouper competitor biomass was natural log-transformed in order to meet model assumptions. Sites are compared to the baseline site A2. Significant results in bold.

Table B.9 Lionfish abundance differed among sites.

Parameter	Estimate	SE	T-value	P-value
Intercept	-3.23	0.28	-11.64	0.00
Site C2	-0.58	0.39	-1.48	0.17
Site C5	0.41	0.39	1.06	0.31
Site E2	1.49	0.39	3.79	0.00
Site NF14	-0.41	0.39	-1.04	0.32
Site NF23	-0.48	0.39	-1.21	0.25
Site NF25	-0.13	0.39	-0.34	0.74
Site NF27	-0.62	0.39	-1.59	0.14
Site NF28	0.09	0.39	0.23	0.82
Site NF3	0.23	0.39	0.58	0.57
Site NF5	0.94	0.39	2.39	0.04

Results from linear-mixed effects model examining lionfish abundance (both tagged and untagged) among coral reef patch sites over the study period. Lionfish abundance was natural log-transformed in order to meet model assumptions. Sites are compared to the baseline site A2. Significant results in bold.

Table B.10 Lionfish biomass differed among sites.

Parameter	Estimate	SE	T-value	P-value
Intercept	4.69	0.53	8.84	0.00
Site C2	-0.63	0.97	-0.65	0.52
Site C5	-0.51	0.88	-0.58	0.56
Site E2	-1.68	0.68	-2.47	0.02
Site NF14	-0.66	0.82	-0.80	0.43
Site NF23	-1.06	0.66	-1.60	0.11
Site NF25	-0.75	0.71	-1.06	0.29
Site NF27	-2.43	0.82	-2.95	0.00
Site NF28	-1.96	0.69	-2.84	0.01
Site NF3	-0.88	0.66	-1.34	0.19
Site NF5	0.33	0.82	0.40	0.69

Results from linear-mixed effects model examining lionfish biomass (both tagged and untagged) among coral reef patch sites over the study period. Lionfish biomass was natural log-transformed in order to meet model assumptions. Sites are compared to the baseline site A2. Significant results in bold.

Table B.11 Results of model selection using AICc for 12 generalized linear mixed-effects models with a binomial error distribution that examine the effect of various factors on the likelihood of lionfish being hidden at first sighting during dawn surveys of patch reefs (n = 11 sites) in Eleuthera, The Bahamas.

Model	K	AICc	ΔAICc	w_i	Log likelihood	Cumulative w_i
GPsz	4	42.78	0.00	0.34	-16.52	0.34
GPsp	4	43.63	0.85	0.23	-16.94	0.57
GPsz, LF	5	45.59	2.80	0.08	-16.43	0.65
GPsz, GCsz	5	45.62	2.84	0.08	-16.45	0.74
Intercept only	3	45.67	2.89	0.08	-19.34	0.82
GPsp, LF	5	46.42	3.63	0.06	-16.85	0.87
GPsp, GCsz	5	46.55	3.77	0.05	-16.91	0.92
GCsz	4	48.39	5.61	0.02	-19.33	0.95
LF	4	48.41	5.63	0.02	-19.33	0.97
GPsz, LF, GCsz	6	48.70	5.92	0.02	-16.35	0.98
GPsp, LF, GCsz	6	49.62	6.84	0.01	-16.81	1.00
LF, GCsz	5	51.38	8.60	0.00	-19.33	1.00

The best-supported model is indicated in bold. K is the number of model parameters. ΔAICc is the difference in the AICc value between model i and the best-supported candidate model. w_i is interpreted as the probability that model i is the best model of the set given the available data. We considered the model(s) within two ΔAICc of the smallest AICc value to be the best-supported model(s). GPsp grouper predator biomass based on species identity, GPsz grouper predator biomass based on size, GC grouper competitor biomass based on size, LF lionfish biomass.

Table B.12 Factors affecting the likelihood that lionfish are inactive on coral reef patches in Eleuthera, The Bahamas (n = 11 sites).

Model	K	AICc	ΔAICc	w_i	Log likelihood	Cumulative w_i
AP, LF	6	280.63	0.00	0.29	-133.59	0.29
AP	5	281.77	1.14	0.16	-135.37	0.45
AP, GPsz, LF	7	282.08	1.45	0.14	-133.06	0.60
AP, GPsp, LF	7	282.36	1.73	0.12	-133.20	0.72
AP, GCsz	6	282.82	2.19	0.10	-134.69	0.81
AP, GPsp	6	283.65	3.02	0.06	-135.10	0.88
AP, GPsz	6	283.72	3.09	0.06	-135.14	0.94
AP, GPsz, GCsz	7	285.12	4.49	0.03	-134.58	0.97
AP, GPsp, GCsz	7	285.23	4.60	0.03	-134.63	1.00
GPsp x AP	7	311.37	30.74	0.00	-147.70	1.00
GPsz x AP	7	311.71	31.08	0.00	-147.87	1.00
Intercept only	4	311.90	31.27	0.00	-151.62	1.00
GPsz x AP, LF	8	312.02	31.38	0.00	-146.72	1.00
GPsz	5	312.41	31.78	0.00	-150.70	1.00
GPsp	5	312.81	32.18	0.00	-150.90	1.00
GPsp x AP, LF	8	312.97	32.34	0.00	-147.20	1.00
LF	5	313.78	33.14	0.00	-151.38	1.00
GPsz, LF	6	313.83	33.20	0.00	-150.19	1.00
GCsz	5	313.94	33.31	0.00	-151.46	1.00
GPsp x AP, GCsz	8	313.98	33.35	0.00	-147.70	1.00
GPsz x AP, GCsz	8	314.30	33.67	0.00	-147.87	1.00
GPsp, LF	6	314.49	33.86	0.00	-150.52	1.00
GPsz, GCsz	6	314.65	34.02	0.00	-150.60	1.00
GPsp, GCsz	6	315.09	34.46	0.00	-150.82	1.00
LF, GCsz	6	316.03	35.40	0.00	-151.29	1.00
GPsz, LF, GCsz	7	316.30	35.67	0.00	-150.17	1.00
GPsp, LF, GCsz	7	316.97	36.34	0.00	-150.50	1.00

Model selection results are from AICc for 28 generalized linear mixed-effects models with a negative binomial error distribution. The best-supported models are shown in bold. K is the number of model parameters. ΔAICc is the difference in the AICc value between model i and the best-supported candidate model. w_i is interpreted as the probability that model i is the best model of the set given the available data. We considered the model(s) within two ΔAICc of the smallest AICc value to be the best-supported model(s). GPsp grouper predator biomass based on species identity, GPsz grouper predator biomass based on size, GC grouper competitor biomass based on size, LF lionfish biomass, AP activity period (i.e., dawn or throughout the day).

Table B.13 AICc model selection results from 28 linear mixed-effects models that examine the effects of different factors on lionfish total swimming distance on coral reef patches in Eleuthera Island, The Bahamas (n = 11 sites).

Model	K	AICc	ΔAICc	w_i	Log likelihood	Cumulative w_i
AP, GPsz, LF	7	176.80	0.00	0.19	-80.18	0.19
AP, GPsp, LF	7	177.27	0.46	0.15	-80.42	0.33
AP, LF	6	177.40	0.60	0.14	-81.81	0.47
GPsz x AP, LF	8	178.05	1.25	0.10	-79.43	0.57
AP	5	178.11	1.31	0.10	-83.43	0.67
AP, GPsz	6	178.94	2.13	0.06	-82.57	0.74
AP, GPsp	6	179.13	2.33	0.06	-82.67	0.79
GPsp x AP, LF	8	179.49	2.69	0.05	-80.15	0.84
AP, GCsz	6	180.52	3.71	0.03	-83.36	0.87
AP, GPsp, GCsz	7	181.47	4.66	0.02	-82.52	0.89
GPsz x AP	7	181.48	4.67	0.02	-82.52	0.91
AP, GPsz, GCsz	7	181.48	4.68	0.02	-82.52	0.93
GPsp x AP	7	181.77	4.96	0.02	-82.67	0.94
Intercept only	4	183.11	6.31	0.01	-87.15	0.95
GPsz, LF	6	183.35	6.55	0.01	-84.78	0.96
GPsz	5	183.77	6.96	0.01	-86.26	0.96
LF	5	183.87	7.07	0.01	-86.31	0.97
GPsz x AP, GCsz	8	184.16	7.36	0.00	-82.48	0.97
GPsp x AP, GCsz	8	184.22	7.42	0.00	-82.51	0.98
GPsp	5	184.32	7.51	0.00	-86.53	0.98
GPsp, LF	6	184.33	7.52	0.00	-85.27	0.99
GCsz	5	185.06	8.26	0.00	-86.91	0.99
GPsz, LF, GCsz	7	185.10	8.30	0.00	-84.34	0.99
GPsp, LF, GCsz	7	185.49	8.69	0.00	-84.53	0.99
LF, GCsz	6	185.54	8.74	0.00	-85.88	1.00
GPsz, GCsz	6	185.85	9.05	0.00	-86.03	1.00
GPsp, GCsz	6	186.07	9.27	0.00	-86.14	1.00

Swimming distance was natural log-transformed prior to analyses to meet model assumptions. The best-supported models are shown in bold. K is the number of model parameters. ΔAICc is the difference in the AICc value between model i and the best-supported candidate model. w_i is interpreted as the probability that model i is the best model of the set given the available data. We considered the model(s) within two ΔAICc of the smallest AICc value to be the best-supported model(s). GPsp grouper predator biomass based on species identity, GPsz grouper predator biomass based on size, GC grouper competitor biomass based on size, LF lionfish biomass, AP activity period (i.e., dawn or throughout the day).

Table B.14 AICc model rankings for 12 general linear models that examine factors affecting proportional changes in native prey fish biomass between the start and end of the experiment on coral reef patches in Eleuthera, The Bahamas (n = 9 sites).

Model	K	AICc	ΔAICc	w _i	Log likelihood	Cumulative w _i
LF	3	70.01	0.00	0.30	-31.25	0.30
Intercept only	2	70.74	0.73	0.21	-33.02	0.50
GPsp	3	72.53	2.52	0.08	-32.51	0.58
GPsp, LG	4	72.59	2.59	0.08	-30.96	0.67
GPsz	3	72.65	2.64	0.08	-32.58	0.74
GPsz, LF	4	73.09	3.08	0.06	-31.21	0.81
LF, GCsz	4	73.09	3.08	0.06	-31.21	0.87
GCsz	3	73.32	3.31	0.06	-32.91	0.93
GPsp, GCsz	4	74.84	4.83	0.03	-32.09	0.95
GPsz, GCsz	4	75.23	5.22	0.02	-32.28	0.98
GPsp, LF, GCsz	5	76.21	6.20	0.01	-30.96	0.99
GPsz, LF, GCsz	5	76.68	6.67	0.01	-31.20	1.00

Native prey fish biomass surveys occurred throughout the day only. The best-supported model is indicated in bold. K is the number of model parameters. ΔAICc is the difference in the AICc value between model *i* and the best-supported candidate model. w_i is interpreted as the probability that model *i* is the best model of the set given the available data. We considered the model(s) within two ΔAICc of the smallest AICc value to be the best-supported model(s). GPsp grouper predator biomass based on species identity, GPsz grouper predator biomass based on size, GC grouper competitor biomass based on size, LF lionfish biomass.

Table B.15 Standardized parameter estimates, measures of uncertainty, and other statistics associated with the various top models used to determine the effect of grouper abundances and/or other factors on lionfish behaviours.

Behaviour	Top model(s)	Parameter	Estimate	SE	Adjusted SE	Test statistic	P-value
Hiding	GPsz	Intercept	0.495	0.486		1.018	0.308
		GPsz	2.222	1.111		2.001	0.045
¹ Inactivity	AP, LF, GPsz, GC	Intercept	3.434	0.093	0.095	36.180	<0.001
		Daytime	0.655	0.114	0.117	5.601	<0.001
		LF	-0.095	0.074	0.075	1.271	0.204
		GPsz	0.113	0.072	0.074	1.537	0.124
		GC	0.045	0.058	0.059	0.766	0.444
² Swimming distance	AP, LF	Intercept	5.831	0.237		24.640	0.000
		Daytime	-0.846	0.276		-3.060	0.005
		LF	0.300755	0.177		1.698	0.101
		AP	5.835	0.244		23.874	0.000
		Daytime	5.051	0.275		18.362	0.000

¹The intercept resulting from model averaging is typically not interpretable (Grueber et al. 2011). Parameter estimates are relative to the dawn baseline.

²Parameter estimates are relative to the dawn baseline.

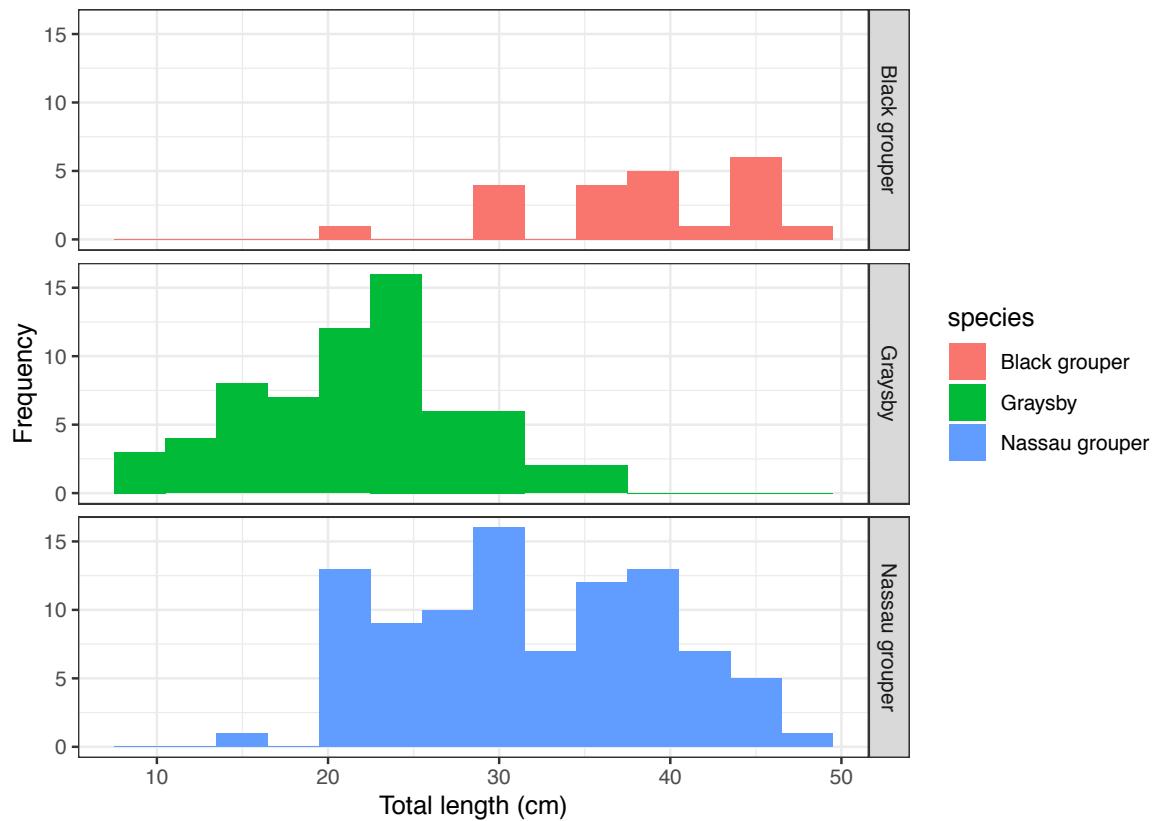


Figure B.1 Histogram of grouper size distribution for each species found at coral reef patch study sites. Grouper sizes are shown for all 4 survey periods combined.

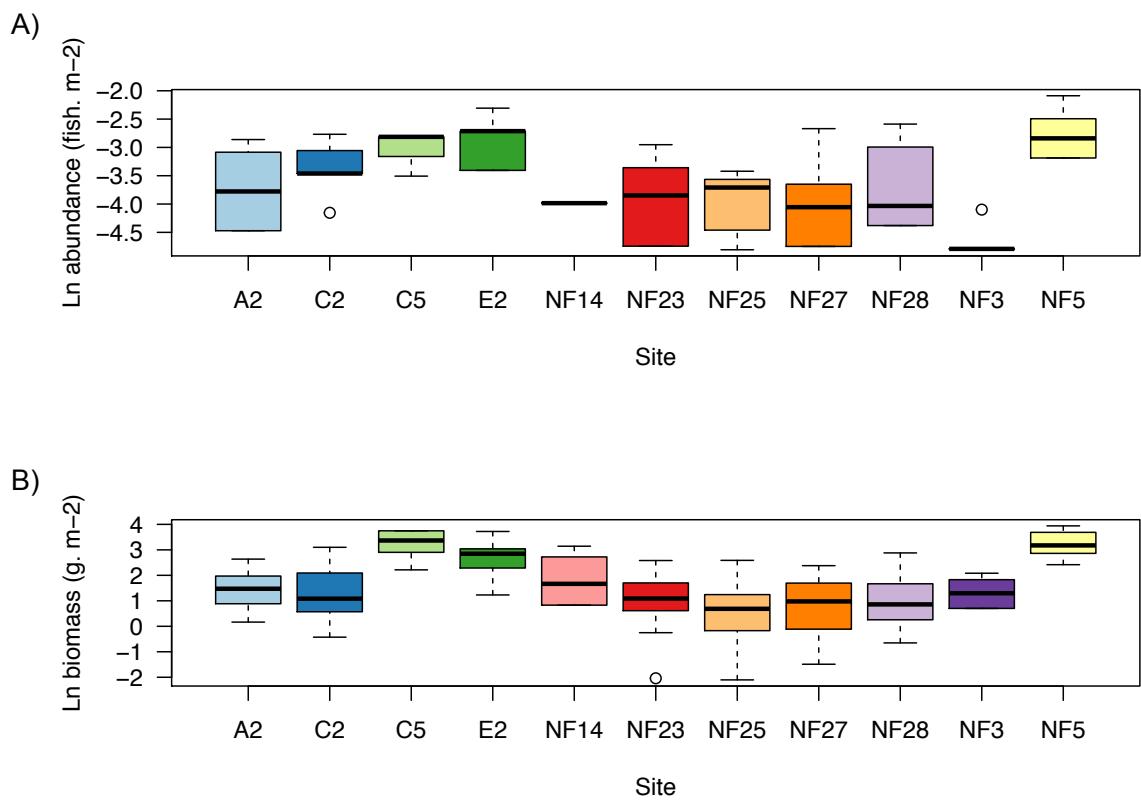


Figure B.2 Total grouper A) abundance, and B) biomass differed among coral reef patch study sites over the study period (Tables B.1-B.2).

N = 4 surveys.

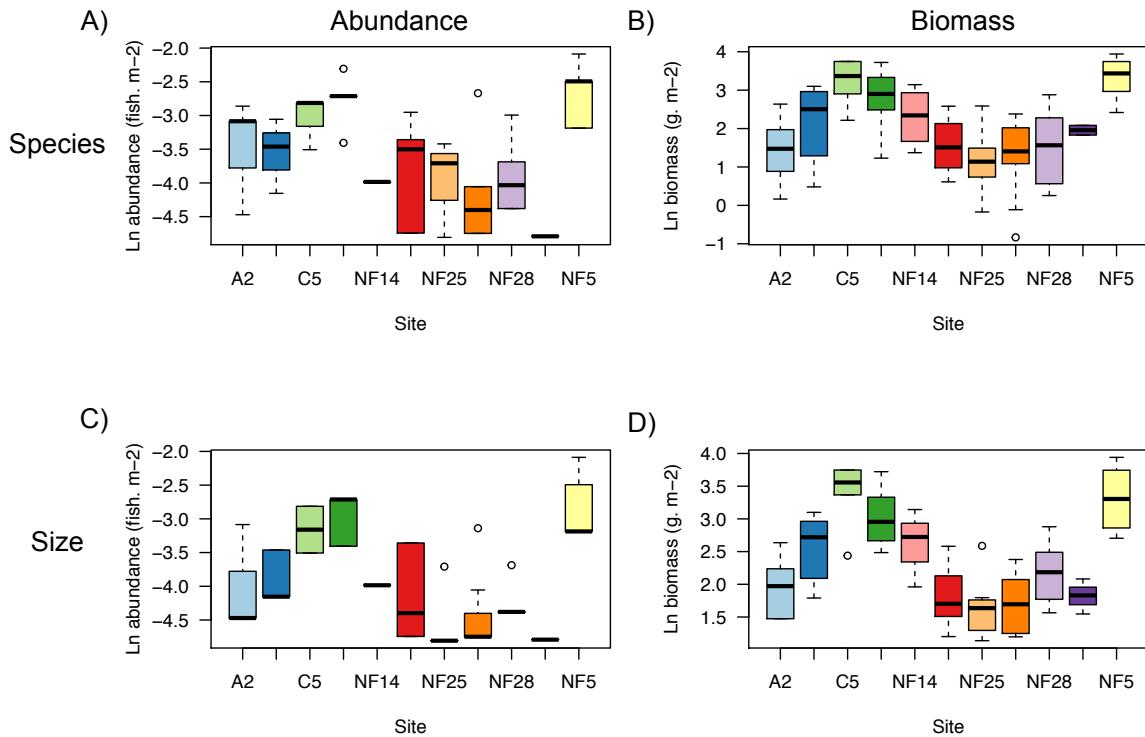


Figure B.3 Grouper predators differed among coral reef patch study sites over the study period when predators were classified based on species (i.e., more piscivorous) for A) abundance, and B) biomass.

The same was true when grouper predators were classified based on size (i.e., ≥ 30 cm TL) for C) abundance, and D) biomass. N = 4 surveys per grouping.

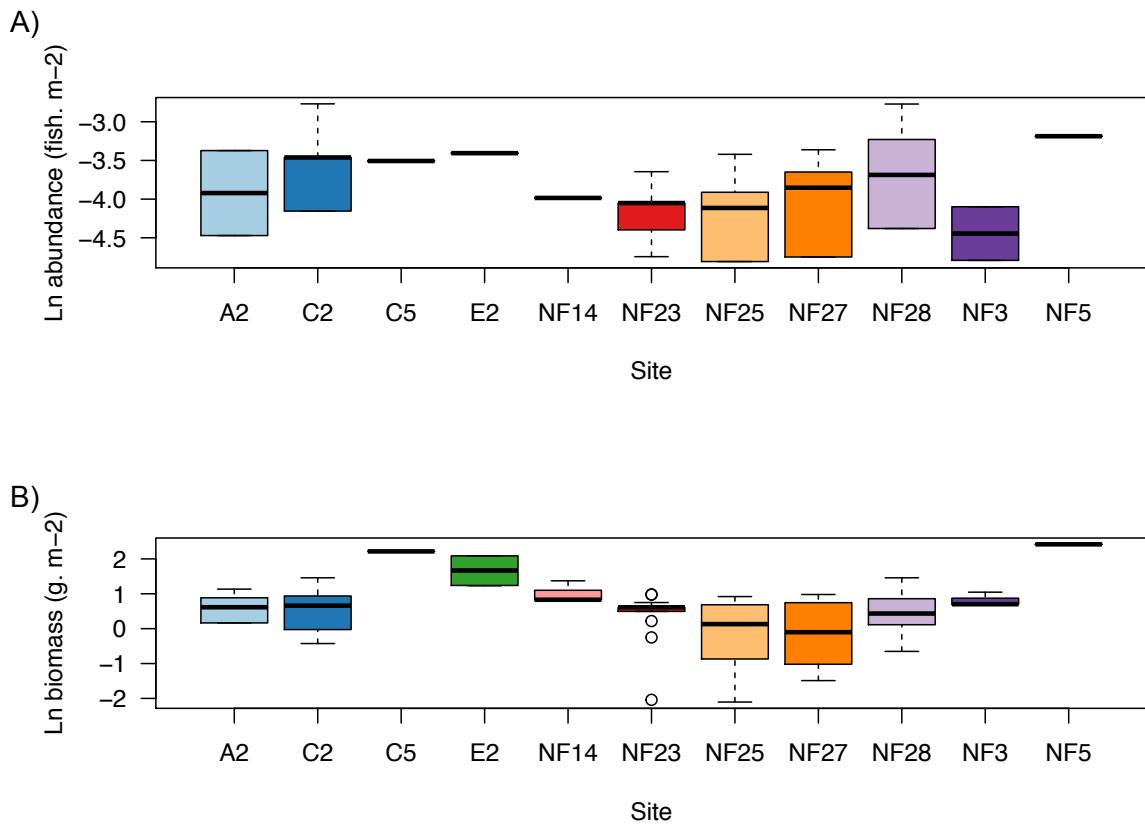


Figure B.4 Grouper competitors classified based on size (i.e., < 30 cm TL) varied among coral reef patch study sites for A) abundance, and B) biomass.

N = 4 surveys per grouping.

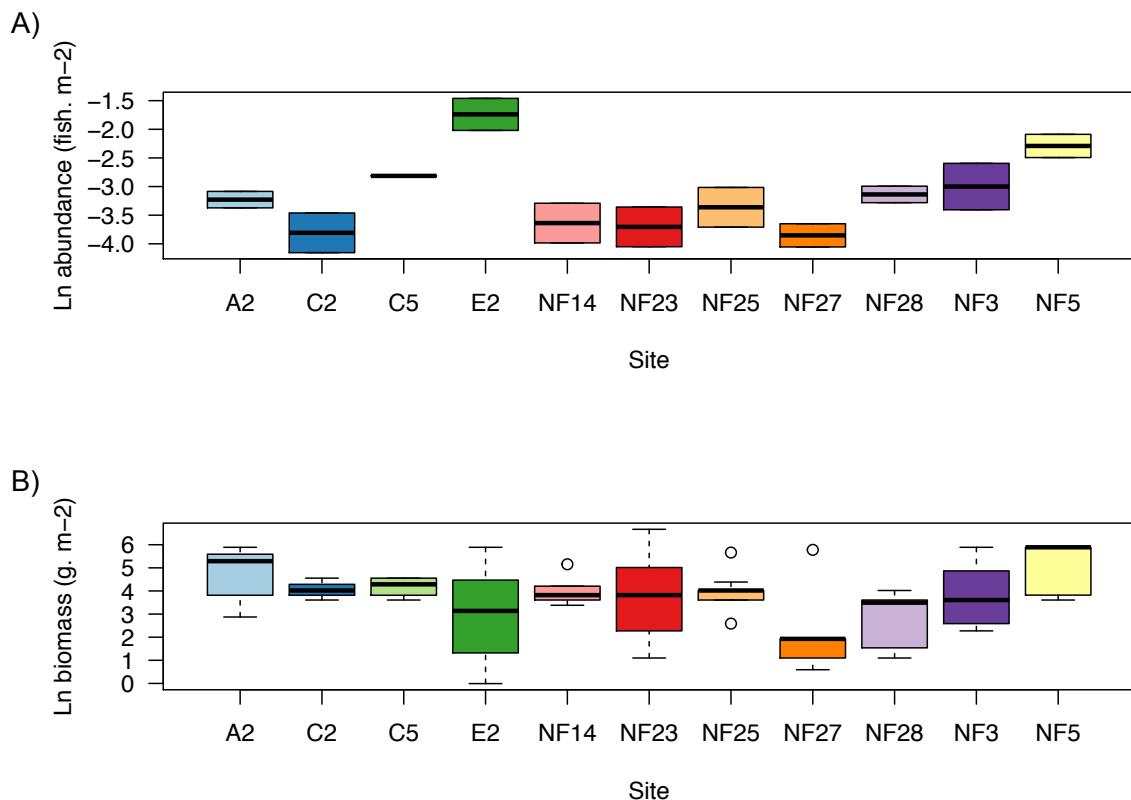


Figure B.5 Lionfish A) abundance, and B) biomass differed among coral reef patch study sites over the study period.

N = 2 surveys.

Appendix C.

Supporting Information for Chapter 4

Measuring rugosity

We measured reef rugosity on each study reef by fitting a fine-link chain (5 m long) to the contours of the substrate along two to four 8 m transect lines at 2 m intervals. A rugosity index was then calculated as the ratio of the total chain length (i.e., actual surface distance) to the linear distance (i.e., straight-line distance along the transect), so that larger numbers reflect greater rugosity (Luckhurst and Luckhurst 1978; Wilson et al. 2007).

Supplementary references

Luckhurst BE, Luckhurst K (1978) Analysis of the influence of substrate variables on coral reef fish communities. *Mar Biol* 49:317-323.

Wilson SK, Graham NAJ, Polunin NVC (2007) Appraisal of visual assessments of habitat complexity and benthic composition on coral reefs. *Mar Biol* 151:1069-1076.

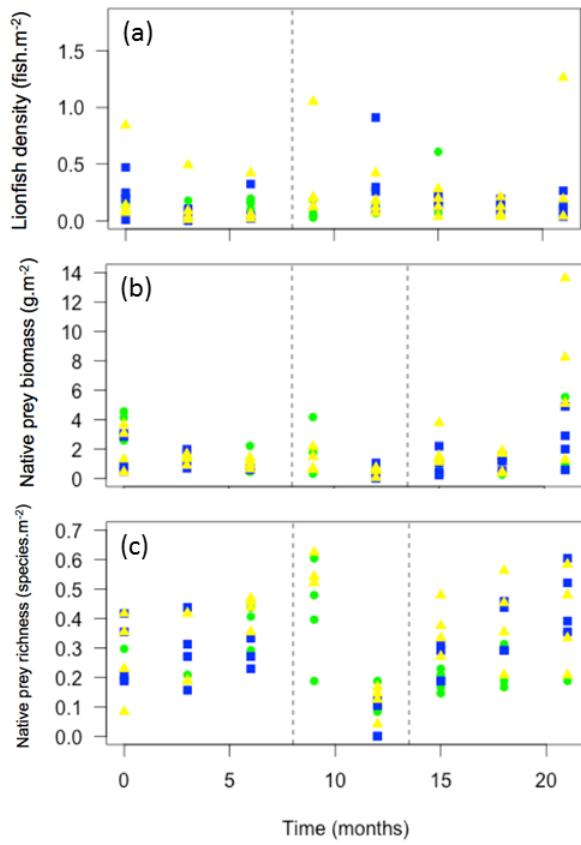


Figure C.1 Trajectories of change over the course of the study in: (a) lionfish density (fish m^{-2}); (b) native prey fish biomass (g m^{-2}); and, (c) native prey fish species richness (species m^{-2}).

The first dashed line represents the time period when Category 3 Hurricane Irene passed over the study site (i.e., August 2011), while the second dashed line represents the period after which the hurricane no longer had an effect on native prey, according to our top model. Biannually culled reefs were not surveyed during Sept. 2011, i.e., time = 9 months. Control reefs: green circles, biannually culled reefs: blue squares, and quarterly culled reefs: yellow triangles. N= 4 for all treatments.

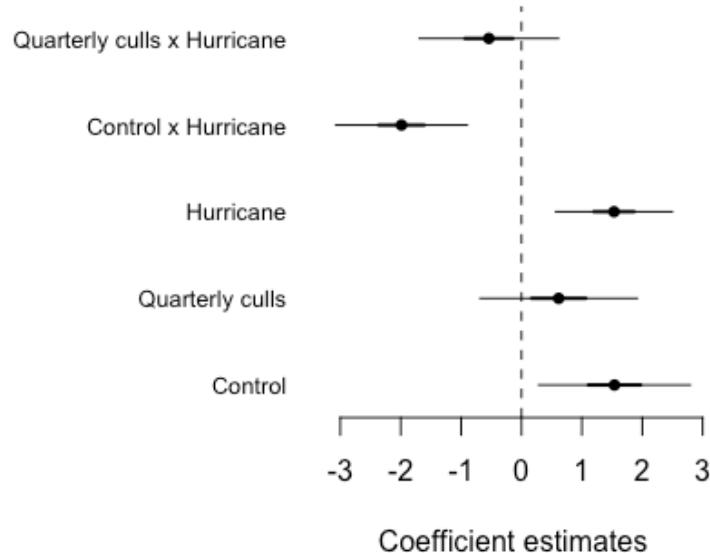


Figure C.2 Coefficients from the top linear mixed-effects model of the effects of various factors on lionfish density (fish m^{-2}) on coral reef patches around Rock Sound, South Eleuthera, The Bahamas ($n = 12$ reefs).

Points are means bounded by 95% confidence intervals (thin bars) and 50% confidence intervals (thicker bars). Positive values (to the right of the dashed line) signify an increase in lionfish density while negative values (to the left of the dashed line) signify a decrease in lionfish density. To allow a direct comparison between ‘biannual culls’ and ‘quarterly culls’, biannual culls are set as the baseline level and compared against quarterly culls and no culls (i.e., control reefs). Level ‘hurricane’ refers to the long-term effect of Category 3 Hurricane Irene on all survey periods following the disturbance and is compared against the baseline level ‘no hurricane effect’, i.e., all survey periods before the hurricane. Conditional r^2 of top model is 0.51 (i.e., proportion of variation in lionfish density among reefs explained by the combination of fixed and random effects in the model).

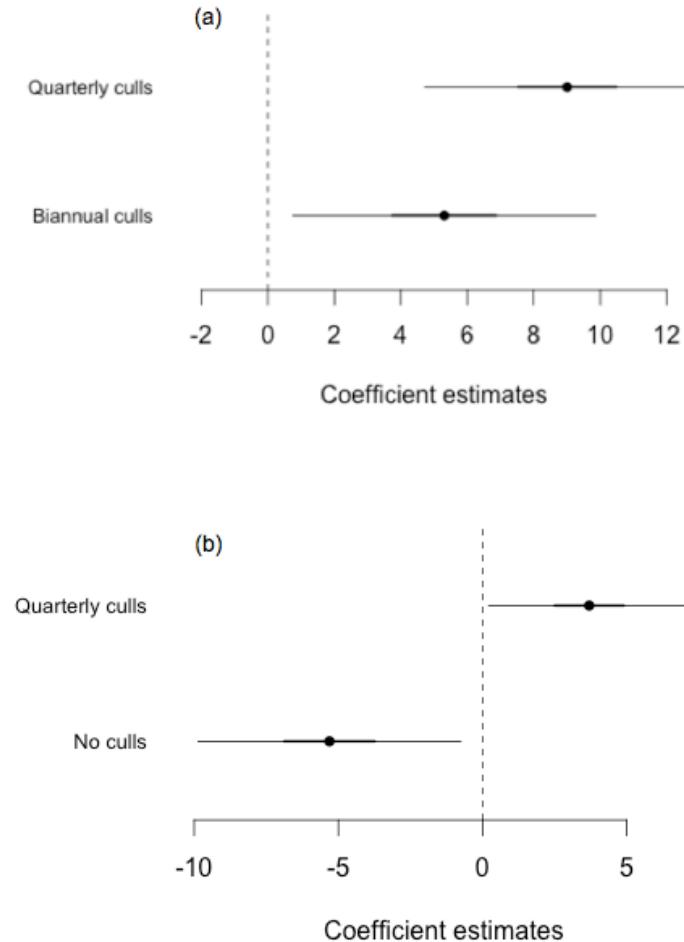


Figure C.3 Coefficients of linear mixed-effects model of the effect of lionfish culling frequency on lionfish colonization rate per reef ($n = 12$ reefs).

Lionfish colonization rate was calculated as the difference between the number of lionfish observed on a reef immediately before a cull at time t and the number of lionfish observed on a reef immediately after a cull at time $t-1$. The model was assessed using restricted maximum likelihood estimation. The model includes reef as a random intercept and culling frequency as a fixed effect, allows residual variance to differ by culling frequency, and includes an auto-regressive model of order 1 (AR1) correlation structure to account for temporal autocorrelation between surveys. Points are means bounded by 95% confidence intervals (thin bars) and 50% confidence intervals (thicker bars). Positive values (to the right of the dashed line) signify an increase in lionfish colonization rate while negative values (to the left of the dashed line) signify a decrease in lionfish colonization rate. Conditional r^2 (i.e., proportion of variation in lionfish colonization rate explained by the combination of fixed and random effects in the model) is 0.27. (a) Levels 'biannual culls' and 'quarterly culls' are compared against the baseline 'no culls'. (b) To allow a direct comparison between 'biannual culls' and 'quarterly culls', 'biannual culls' are set as the baseline level and compared to 'quarterly culls' and 'no culls' (i.e., control reefs).

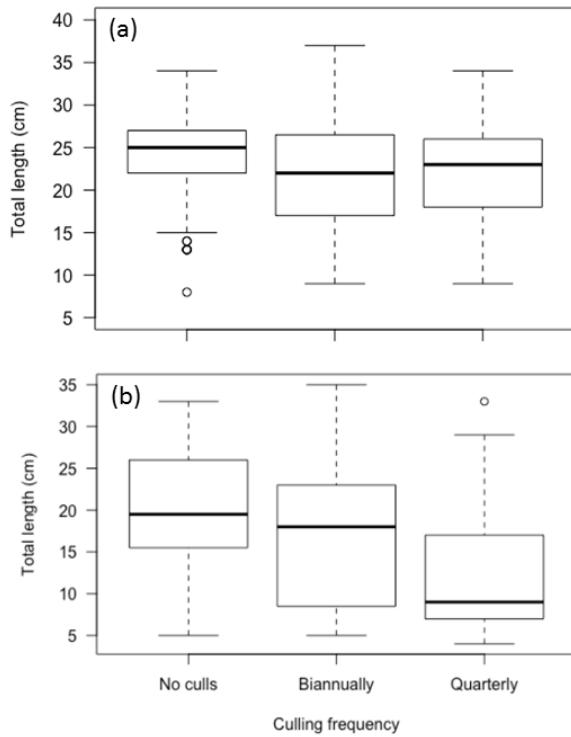


Figure C.4 Boxplots of lionfish total length on reefs experiencing different culling treatments (a) before the hurricane (i.e., December 2010 during pre-experiment baseline surveys), and (b) after the hurricane (i.e., December 2011, approximately three months after the hurricane).

Comparing lionfish sizes during the same month reduced the likelihood that observed differences might reflect seasonal changes in lionfish recruitment, although we cannot rule out the possibility of interannual variation in lionfish recruitment.

The thick horizontal lines represent the medians while the lower and upper edges of each box are the first and third quartile, respectively. Box 'whiskers' show the spread in non-extreme values in the original data, while circles represent extreme values, i.e., values > 1.5 times the interquartile range.

Mean size decreased significantly after the hurricane on both culled and non-culled reefs (biannually culled reefs: Wilcoxon rank sum test, $W = 3162.5$, $P = 0.0006$; quarterly culled reefs: Wilcoxon rank sum test, $W = 1349$, $P = 0.0000001$; non-culled reefs: Wilcoxon rank sum test, $W = 3131.5$, $P = 0.003$).

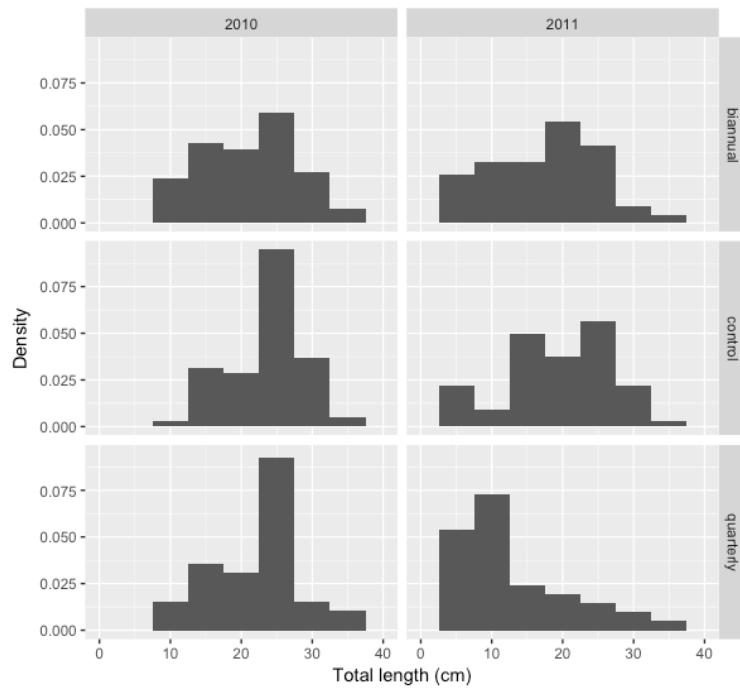


Figure C.5 Density plots showing lionfish size distribution among culling treatments before the hurricane (i.e., December 2010 during pre-experiment baseline surveys; left-hand panels) and after the hurricane (i.e., December 2011, approximately three months after the hurricane; right-hand panels).

Bars show densities, i.e., proportions of lionfish within each size class.

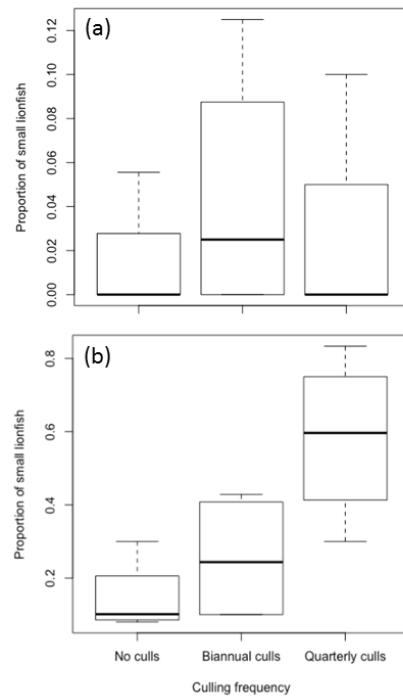


Figure C.6 Boxplot of proportion of small lionfish (i.e., < 10 cm total length) on reefs experiencing different culling treatments (a) before the hurricane (i.e., December 2010 during pre-experiment baseline surveys), and (b) after the hurricane (i.e., December 2011, approximately three months after the hurricane).

The thick horizontal lines represent the medians while the lower and upper edges of each box are the first and third quartile, respectively. Box 'whiskers' show the spread in non-extreme values in the original data, while circles represent extreme values, i.e., values > 1.5 times the interquartile range.

The proportion of small/young lionfish (i.e., < 10 cm TL) increased significantly in two of the three treatments after the hurricane. On biannually culled reefs, there was a marginally non-significant increase from 4 to 25%: Wilcoxon rank sum test, $W = 2$, $P = 0.11$; on quarterly culled reefs, a significant increase from 3 to 58% (Wilcoxon rank sum test, $W = 0$, $P = 0.03$); and on non-culled reefs, a significant increase from 1 to 15% (Wilcoxon rank sum test, $W = 0$, $P = 0.03$).