



# Isolation promotes abundance and species richness of fishes recruiting to coral reef patches

G. P. Jones<sup>1,2</sup> · G. Barone<sup>1,3</sup> · K. Sambrook<sup>1,2</sup> · M. C. Bonin<sup>1,2,4</sup>

Received: 26 March 2020 / Accepted: 25 September 2020 / Published online: 20 October 2020  
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## Abstract

Habitat area and fragmentation are recognised as important factors that influence population size, community structure and extinction risk. Abundance and species richness universally increase with habitat area. However, the effects of different aspects of habitat fragmentation, including variation in patch size, number and isolation are often not distinguished from each other or the overall effects of habitat amount. Here we experimentally tested predictions concerning the effects of isolation on abundance, species richness and community structure of coral reef fishes colonising patch reefs by constructing clusters of patches of the same number and size, but manipulating reef spacing. Hexagonal clusters of 7 experimental patch reefs (6 edge and 1 central) with 3 levels of isolation (1 m, 5 m, and 15 m spacing) were established at Kavieng, Papua New Guinea and colonisation was recorded after 6 weeks in 2014. We also deployed video cameras to test whether isolation affected the activity of transient predatory fishes. As predicted, isolation had a positive effect on both mean abundance and species richness at both the cluster and patch scale. The cumulative abundance and species richness exhibited linear increases in relation to habitat area within clusters (from 1 to 7 patch reefs), but the slope increased with the degree of isolation. There was some evidence that transient predators remained longer and were more successful when patches were close together, which may explain the lower abundance and richness of juvenile fish assemblages on more aggregated patch reefs. This study demonstrates that while habitat amount is fundamentally important, isolation has significant effects that will need to be distinguished from other aspects of fragmentation when examining the processes structuring reef fish communities.

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Responsible Editor: K. D. Clements.

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Reviewed by undisclosed experts.

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**Electronic supplementary material** The online version of this article (<https://doi.org/10.1007/s00227-020-03772-0>) contains supplementary material, which is available to authorized users.

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✉ G. P. Jones  
geoffrey.jones@jcu.edu.au

- <sup>1</sup> College of Science and Engineering, James Cook University, Townsville, Queensland 4811, Australia
- <sup>2</sup> ARC Centre of Excellence for Coral Reef Studies, James Cook University, Townsville, QLD 4811, Australia
- <sup>3</sup> National Research Council, Institute for Biological Resources and Marine Biotechnologies, Largo Fiera della Pesca, 60125 Ancona, Italy
- <sup>4</sup> Great Barrier Reef Marine Park Authority, Townsville, QLD 4810, Australia

## Introduction

Habitat loss is considered one of the major causes of the global decline in biodiversity, with the area of many natural habitats reduced to a small fraction of their historic area (Tilman et al. 1994; Brooks et al. 2002; Hanski 2011; Watson et al. 2016). Habitat loss does not just result in a decline of the total area of habitat, it can also cause major changes in configuration, including an increase in the number of habitat fragments, a reduction in the size of habitat patches and an increase in patch isolation (Saunders et al. 1991; Fahrig 2013; Fisher and Lindenmayer 2007; Laurance 2008). The effects of habitat fragmentation, above and beyond simply the decline in area, are thought to decrease species richness and increase extinction risk (Fahrig 2013; Fattorini and Borges 2012; Hanski et al. 2013; Haddad et al. 2015), alter community composition (Davies and Margules 1998; Didham et al. 1998; Crist et al. 2006; Ewers and Didham 2006; Öckinger et al. 2010) and impair ecosystem services (Lindenmayer and Luck 2005; Cagnolo et al. 2009; Haddad et al. 2015). However, the significance of fragmentation

has become increasingly controversial. Some argue that the effects often attributed to increased fragmentation can all be explained by the overall habitat loss—the so-called “habitat amount” hypothesis (Fahrig 2013; Martin 2018; Watling et al. 2020). No general consensus has emerged for the effects of fragmentation per se, with numerous studies showing negative (e.g., Andrén 1994; Kruess and Tscharntke 1994; Davies and Margules 1998; Haddad et al. 2015, 2017; MacDonald et al. 2018), positive (e.g., Davies and Margules 1998; Scheffer et al. 2006; Fahrig 2017, 2020; Siebold et al. 2017) or little or no effect (e.g., Davies and Margules 1998; Prugh et al. 2008; De Camargo et al. 2018; Gardiner et al. 2018; Rabelo et al. 2018) on abundance and/or species richness. This has led to a heated exchange over whether fragmentation is bad or good for biodiversity (Fahrig 2017; Fletcher et al. 2018; Fahrig et al. 2019). The relative effects of habitat loss versus fragmentation appear to depend on numerous factors including the overall level of habitat loss (Andrén 1994), the spatial and temporal scale of the study (Haddad et al. 2015; Bosco et al. 2019) or whether the focus is on the centre or edge of fragmented habitats (Debinski and Holt 2000; Ries et al. 2004; Ewers and Didham 2006; Laurance 2008). Teasing apart the separate effects of overall habitat area, the number of habitat fragments, the size of habitat patches and the degree of isolation can be challenging as they almost always co-vary in some way (Fahrig 2003; Ewers and Didham 2006; MacDonald et al. 2018). The potential positive and negative effects of each are best resolved by controlled experiments in which each factor is manipulated independently (Davies and Margules 1998; McGarigal and Cushman 2002).

Of the different components of habitat loss and fragmentation, the role of patch isolation has received the least attention. According to island biogeography theory, isolated islands or patches of suitable habitat should have lower population sizes and species diversity due to lower colonization rates (MacArthur and Wilson 1967). Isolated islands commonly have lower species richness and a non-random subset of species compared to adjacent mainlands, but numerous mechanisms appear to be involved (Gilbert 2000; Simberloff 2000; Fahrig 2003). Yet high levels of endemism caution against the proposition that isolated islands should have a low conservation priority due to their lower species richness (Kier et al. 2009; Wintle et al. 2019). In the literature, studies of habitat fragments that differ in the degree of isolation have produced all possible outcomes, including decreases (e.g., Davies and Margules 1998; Steffan-Derwenter and Tscharntke 1999; Bailey et al. 2010; Haddad et al. 2015; Lindgren and Cousins 2017), increases (e.g., Quinn and Harrison 1988; Scheffer et al. 2006; Bailey et al. 2010; Fahrig 2017, 2020) and little or no effects of isolation on abundance and/or species richness (e.g., van Dorp and Opdam 1987; Andrén 1994; Prugh et al. 2008; Ord et al. 2017; De

Camargo et al. 2018; MacDonald et al. 2018). The different outcomes may be dependent on the spatial scale of the study, with increasing isolation promoting species richness at large (landscape) spatial scales, but not necessarily at small spatial scales (Fahrig 2017).

The mechanisms that might lead to either an increase or decrease in species abundance or diversity with increasing isolation are not always clear, but predator–prey dynamics may be implicated (Schneider 2001; Ryall and Fahrig 2006). Positive effects of habitat isolation on prey abundance and diversity have been linked to reduced predation pressure, perhaps because predators are more influenced by fragmentation than their prey or less likely to visit isolated habitats (Herrmann et al. 2012; Kruess and Tscharntke 1994). The effects of isolation at different spatial scales can be addressed experimentally by manipulating patch spacing while holding overall patch area, size and number constant. The mechanisms underlying isolation effects may be resolved by documenting the effects of isolation on both prey communities and predator behaviour.

Globally, coral reefs are experiencing extensive habitat loss due to a range of human impacts (Pandolfi et al. 2003; Bruno and Selig 2007; Bruno and Valdivia 2016). Overall habitat loss or the decline in the area of healthy coral cover is having a major negative effect on reef-associated fish assemblages (Jones et al. 2004; Paddock et al. 2009; Pratchett et al. 2018). This level of habitat loss is also likely to be associated with increasing fragmentation of patches of healthy coral habitat, but the relative effects of habitat area and habitat fragmentation have received little attention. Coral reefs are naturally fragmented habitats in which patch number, size and spacing are all highly variable at a range of spatial scales. Hence, while overall habitat loss may be detrimental, increasing fragmentation may have little or no effect, or may even be beneficial. For example, Bonin et al. (2011) showed experimentally that while a decline in coral cover negatively affected damselfish survival, an outcome of several small patches rather than one large one had a positive effect on diversity and abundance. Likewise, Caley et al. (2001) showed that fragmenting coral patches promoted the abundance of coral-dwelling invertebrates. In the Caribbean, Acosta and Roberston (2002) showed the cumulative diversity of fishes on many small patch reefs was higher than for the equivalent area of larger reefs and small reefs supported a greater number of rarer species.

Some attention has been given to the effects of isolation on the structure of coral reef fish populations and assemblages. Large-scale studies have focussed on decreased species richness and high levels of endemism (Sandin et al. 2008; Hobbs et al. 2012; Luiz et al. 2015), highly nested subsets of species, including higher proportions of larger-bodied species (Bender et al. 2013, 2017; Jacquet et al. 2017), high temporal variability (Mellin et al. 2010) and high levels

of genetic differentiation and self-recruitment (Jones et al. 2009; Jones 2015) on isolated islands. At the other extreme, small-scale experimental studies tend to show the opposite pattern, with increased abundance and diversity in relation to increased isolation (Schroeder 1987; Belmaker et al. 2005, 2009; Jordan et al. 2005). These studies also emphasize a change in reef fish community structure with isolation (Jordan et al. 2005) and more variable community structure on isolated reefs (Ault and Johnson 1998). There are at least two ecological mechanisms that might promote species richness on isolated reefs. First, the “settlement redirection” hypothesis (Stier and Osenberg 2010), a mechanism which appeared to account for up to 4× higher fish settlement to isolated reefs, compared to those in close proximity. Isolated and up-current patch reefs consistently receive higher recruitment than similar-sized reefs surrounded by other reefs (Schroeder 1987; Jones 1997). Secondly, transient predators may more frequently visit closely spaced patches (Belmaker et al. 2005, 2009; Jordan et al. 2005; Overholtzer-McLeod 2006), with the large distances of sand between isolated patches a significant barrier to the fish movement

(Turgeon et al. 2010). To date, no experimental studies have separated the relative magnitude of the effects of isolation and suitable habitat area on abundance or species richness of coral reef fishes. With the notable exception of Overholtzer-McLeod (2006), few studies have examined the role of transient predators in determining the effects of isolation on prey reef fishes by manipulating reef spacing.

The aim of this study was to experimentally test the effect of isolation on the abundance, species richness and species composition of coral reef fishes colonising small patch reefs in Kavieng, New Ireland, Papua New Guinea. Hypotheses with respect to isolation were tested by constructing replicate hexagonal clusters of small coral reef patches on shallow sand flats with three levels of distance among reefs. Patch size, number and total habitat area were held constant at the landscape (cluster) scale. This design allowed us to achieve four specific hypotheses: (1) Increasing isolation promotes abundance and species richness of juvenile reef fishes, both at the cluster scale and patch scale. (2) Isolation promotes the cumulative increase in abundance and species richness in relation to habitat area within clusters. (3) The degree of isolation influences fish species composition at the cluster scale. (4) Increasing isolation reduces the visitation rates of transient fish predators by mounting surveillance cameras on the central reefs in clusters from the different isolation treatments.

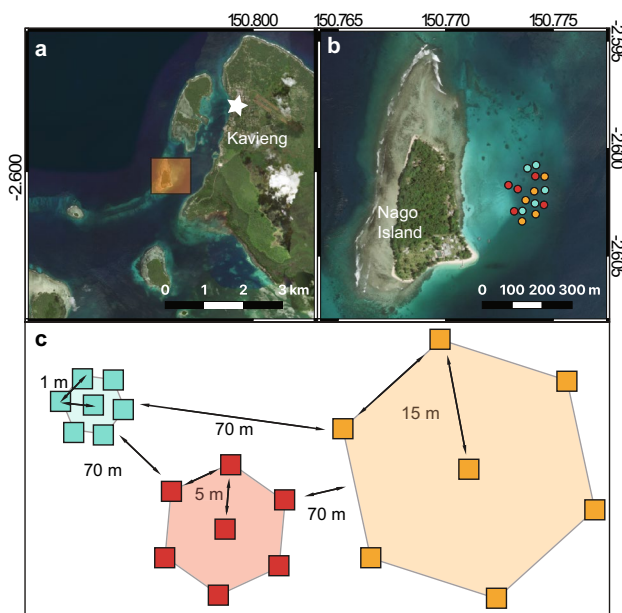
## Methods

### Study location

This study was conducted over a seven-week period between April and June 2014 in the Kavieng Lagoon, which is located at the northern end of the island of New Ireland in Papua New Guinea (2°34'S, 150°48'E; Fig. 1a). This expansive lagoon (~380 km<sup>2</sup>) is primarily composed of patches of seagrass and coral reef interspersed across a matrix of the sandy substrate. The experimental system was constructed in a large area of sand (approximately four hectares) directly adjacent to Nago Island, where Papua New Guinea's (PNG) National Fisheries Authority maintains a research and mariculture facility. The locations of the replicates of each treatment were distributed in a random array on the leeward side of the island, with a sandy slope that gradually changes in depth from 4 to 12 m (Fig. 1b).

### Experimental design

To test the effects of isolation, we constructed 15 replicate reef clusters of 7 habitat patches, with at least 70 m of open sand separating each cluster from other experimental replicates and any natural reef patches in the surrounding area.



**Fig. 1** Study area and experimental design. **(a)** Study location, Nago Island, Kavieng Lagoon, New Ireland Province, Papua New Guinea. **(b)** Experimental array near the PNG National Fisheries Authority Nago Island Mariculture & Research Facility. The experimental patch reefs were placed over the sandy bottom off the leeward side of the island. Each isolation treatment (1, 5 and 15 m) was replicated five times and allocated randomly in the area maintaining at least 70 m of open sand between clusters or between clusters and natural reef patches in the surrounding area. 1 m arrays are indicated in turquoise, 5 m arrays in red and 15 m arrays in orange. **(c)** Each of the 15 reef clusters was comprised of one central focal patch at the centre of a hexagon of six other patches to ensure equal spacing between neighbouring patches

This large spacing was considered sufficient to assume patterns of colonisation by juvenile fishes in different clusters were independent and minimise any movement between natural habitat patches and experimental clusters. Each reef cluster was arranged with a single focal patch at the centre of a hexagon of 6 other patches to facilitate equal spacing among reefs (Fig. 1c). Habitat patches within each cluster were isolated by 1, 5 or 15 m ( $n = 5$  per isolation treatment), and treatments were randomly assigned across the 15 clusters in order to minimise any influence of environmental variation across the study site on treatment effects. The three isolation distances represent a typical range in the spacing of natural patch reefs in lagoonal and sheltered coral reef environments. Similar spacings have been used in other experimental studies on the effects of isolation on reef fishes (Overholtzer-McLeod 2006; Stier and Osenberg 2010). Movement of juvenile coral reef fishes between patch reefs is possible at the 1 m spacing but would be unlikely at the 15 m spacing.

Each habitat patch was constructed to be as uniform as possible by attaching two branching coral colonies to a stacked pair of cinder blocks using cable ties. The two coral species used, *Pocillopora verrucosa* and *Porites nigricens*, are highly common branching corals on reefs in the study area and provide structurally complex recruitment habitat to a wide range of fish species. Corals were selected to minimise size variation among colonies across the habitat patches, such that the *P. verrucosa* colony was ~20 cm in diameter and the *P. nigricens* colony was ~60 cm in diameter on each patch. Each patch offered approximately 0.32 m<sup>2</sup> of live coral as recruitment habitat.

Construction of the experimental arrays occurred over one week and patches were cleared of all fish that colonised prior to the start of the experiment. Coral reef fish were subsequently allowed to recruit to the experimental system over six weeks, at which point all individuals that had recruited to each patch in each replicate reef cluster were counted and identified to species level. Recruitment of juvenile fishes in this region happens all year round (Srinivasan and Jones 2006) and the patch reefs were rapidly colonised over the 6 week period.

### Transient predator visitation

Transient predators were observed moving among the experimental reefs and surveillance video cameras were deployed to measure visitation rates and durations across isolation treatments. Five weeks after the experiment was started, GoPro video cameras were mounted on posts and positioned 1 m away from the central patch of each replicate reef cluster. Approximately 1.5 h of video of this focal patch was recorded for each replicate cluster during both the morning (6:30–8:00 h) and evening (16:30–18:00 h) when

predators were most likely to be active. For each video, data collection began 5 min after the diver left the field of view and continued until the camera ran out of battery.

Video recordings were viewed in their entirety to quantify predation pressure across experimental reefs. Predators entering the field of view were counted and identified to the highest taxonomic level possible, and their entry and exit times were also noted to quantify the duration of their visits. The frequency of predatory strikes was also recorded, and these were defined as sudden bursts of speed directed at a resident recruit. Strikes were recorded only when they were directed at fish inhabiting the central patch, although other patches were visible within the camera's field of view for the 1 and 5 m isolation treatments.

### Hypotheses and data analysis

One-way analysis of variance (ANOVA) was used to test the hypothesis that the degree of isolation (Fixed, 3 levels: 1, 5 or 15 m) would increase coral reef fish abundance and species richness at both the cluster and patch scale (H1). Counts of abundance and species obtained from individual patches were aggregated for each cluster of patches and the total count of individuals and species was used in the test ( $n = 15$ ). Patch-scale effects were tested by calculating the mean patch abundance and species richness for each cluster ( $n = 15$ ). Normality of residuals and homoscedasticity were tested prior to interpretation using the Shapiro–Wilk's normality test and Leven's test, respectively. The level of significance for all statistical tests was set at  $P < 0.05$ . Pairwise comparisons between the three isolation treatments were made using Tukey HSD tests. Raw data were illustrated as box and whiskers to visualise differences in abundance and species richness between isolation treatments. All analyses and visualisations were carried out in R.

Analysis of covariance was used to test the hypothesis that isolation would promote the cumulative increase in the number of individuals and species of coral reef fish recruits with increasing habitat area (H2). Total abundance and species richness were the two response variables of interest, and these were modelled as a function of habitat patch isolation (categorical, 3 levels) and habitat area (continuous). Habitat area was modelled as a continuous factor by sequentially adding a patch reef at random until all seven patches in each cluster were included. Note that habitat area only includes the live coral habitat provided by the reef cluster and not the sand in between. Habitat area increased from 0.32 m<sup>2</sup> (1 patch) to 2.24 m<sup>2</sup> (7 patches).

Permutational multivariate analysis of variance (PERMANOVA; Anderson 2001) was computed in PRIMER+PERMANOVA (v7) to test the hypothesis that (H3) habitat isolation would promote changes in reef fish assemblage structure at the cluster level. PERMANOVA

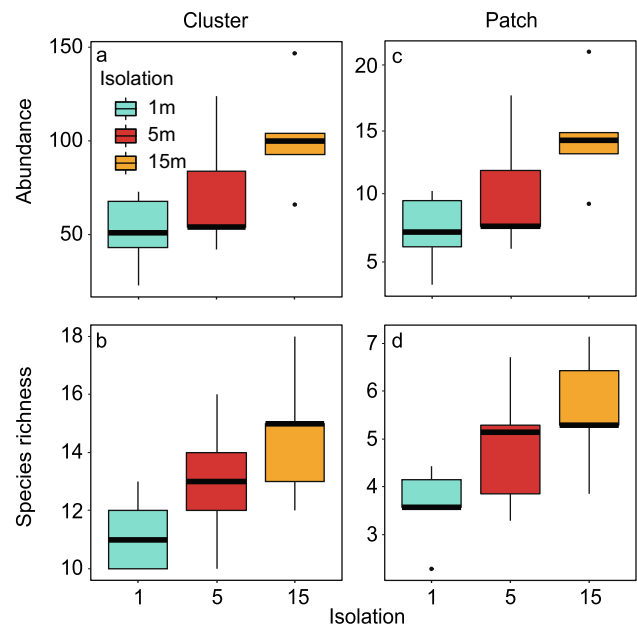


was used because it is robust to zero-inflated datasets and has significant advantages over conventional MANOVA as it makes no assumptions about underlying data distributions. One-way PERMANOVA was used to test for the effect of isolation (Fixed, 3 levels: 1, 5, 15 m) on fish assemblage composition. To reduce the influence of abundant species, the whole dataset was square-root transformed and used to calculate the resemblance matrix based on the Bray–Curtis similarity used by the model. Before analysis and transformation, counts of abundances for each fish species were aggregated for each habitat at the cluster level. This was done to acknowledge the cluster as the appropriate spatial scale for community analyses as species-accumulation curves tended to level-off, allowing valid comparisons of species richness across clusters (Gotelli and Colwell 2001). *P* values were obtained by 9999 permutations using unrestricted permutation of raw data and considered significant if *P* < 0.05. Pairwise comparisons among all pairs of levels of significant factors of interest made using the pseudo-*t* statistic obtained by doing an additional separate runs of the PERMANOVA routine (Anderson et al. 2008). Bray–Curtis similarity matrixes were then used to visually explore differences between fish assemblages by non-metric multidimensional scaling (nMDS). BEST technique was used to identify the subset of species that best explain the community-wide patterns, based on high Spearman correlations ( $\rho$ ) with the whole dataset (Clarke et al. 2014a). This result is achieved by adding and dropping species from the dataset maximising  $\rho$

**Table 1** Summary of analyses of variance (ANOVA) to test for the effects of isolation (1, 5 and 15 m spacing) on coral reef fish total abundance (a) and species richness (b) at the cluster scale, and mean abundance per patch (c) and mean species richness (d) at the patch scale. Raw data met assumptions of normality and homogeneity of variance

	<i>df</i>	SS	MS	<i>F</i> value	<i>P</i>
Mean cluster					
(a) Abundance					
Isolation	2	6441	3220.5	4.1	<b>0.0439</b>
Residuals	12	9424	785.333		
(b) Species richness					
Isolation	2	28.93	14.465	3.617	0.059
Residuals	12	48	4		
Mean patch					
(c) Abundance					
Isolation	2	131.4	65.7	4.1	<b>0.0439</b>
Residuals	12	192.3	16.025		
(d) Species richness					
Isolation	2	10.22	5.11	5.11	0.0531
Residuals	12	16.2	1.35		

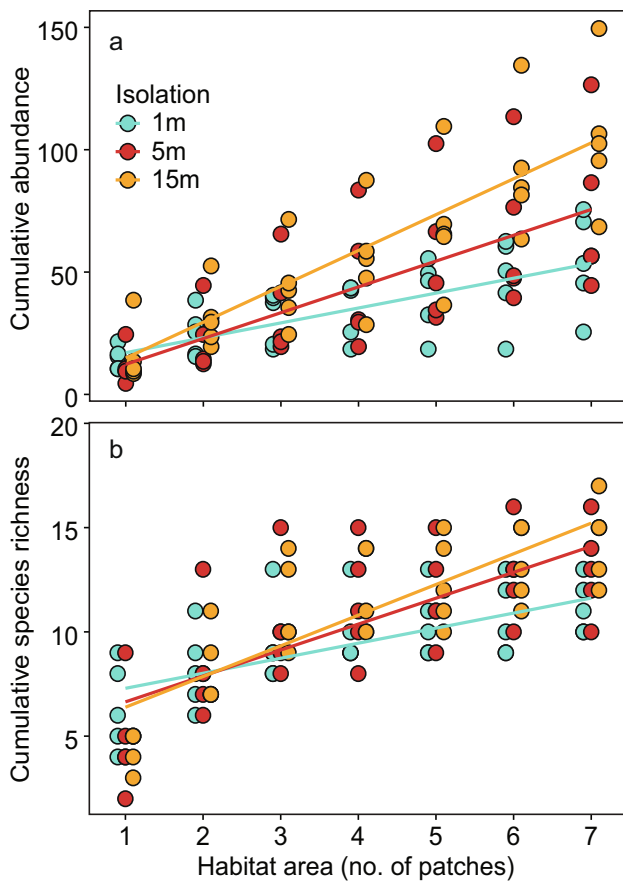
Significant *P* values in bold



**Fig. 2** Boxplot illustration of the influence of reef isolation (1, 5 and 15 m) on the abundance (top) and species richness (bottom) of coral reef fishes at the cluster (left) and patch (right) scale. Whiskers delimit the  $\pm 1.5$  interquartile range (IQR), box height denotes the IQR, heavy crossbars represent the median and dots indicate outliers

until no further improvement is possible. These species were added to the nMDS plot to visualise how taxa responded to isolation treatments. Similarity (SIMPER) analysis was used to assess the average percentage contribution of individual species to the dissimilarity between groups in a Bray–Curtis similarity matrix (Clarke 1993). Changes in abundance of the species majorly contributing to the dissimilarity between isolation treatments identified by SIMPER analysis were displayed through a shade-plot highlighting changes in abundance between groups (Clarke et al. 2014b).

One-way ANOVA was used to test the hypothesis that increasing isolation (Fixed, 3 levels: 1, 5 and 15 m) reduces predator activity (H4), which may explain effects of isolation on the abundance and species richness of juvenile fishes. Predator activity for each central patch was quantified by three predator response variables—mean number of predator visits, mean duration of predator visits, and mean frequency of strikes. Predator video data were pooled across the morning and afternoon recordings for each central patch and response variables were standardised by dividing by the total minutes of video for each replicate as no difference was observed between the two groups. The level of significance for all statistical tests was set at *P* < 0.05. For all analyses, the assumptions of normality and homogeneity of variance were checked using the Shapiro–Wilk’s normality test and Leven’s test, respectively. Data that failed to meet assumptions were square-root transformed.



**Fig. 3** Influence of habitat patch isolation (1, 5 and 15 m) on the cumulative (a) abundance and (b) species richness of coral reef fishes as a function of the patch area. Patch area for each cluster is represented by the cumulative increase in the number of patches selected to represent each cluster. Subsets of patches were chosen at random from the seven available

**Table 2** Analysis of covariance for the effects of isolation (*I*) and habitat area (*A*) and the isolation-area interaction on cumulative mean total abundance and mean species richness of coral reef fishes within clusters. The analysis met the assumptions of significant linear abundance-habitat area and species richness-habitat area relationships

	df	SS	MS	F value	P
<b>(a) Abundance</b>					
Habitat area ( <i>A</i> )	1	45,698	45,698	126.8610	<b>&lt; 2.2e-16</b>
Isolation ( <i>I</i> )	2	9905	4952	13.7478	<b>5.385e-06</b>
A x I	2	5146	2573	7.1426	<b>0.001266</b>
Residual	99	35,662	360		
<b>(b) Species richness</b>					
Habitat area ( <i>A</i> )	1	550.86	550.86	119.0147	<b>&lt; 2e-16</b>
Isolation ( <i>I</i> )	2	32.93	16.47	3.5577	<b>0.03220</b>
A x I	2	41.38	20.69	4.4697	<b>0.01385</b>
Residual	99	458.22	4.63		

Significant *P* values in bold

## Results

### General patterns

A diverse assemblage of 29 species from 10 families recruited to the experimental arrays. These recruits included 8 species of damselfish (Pomacentridae), 6 species of wrasse (Labridae), 2 species of hawkfish (Cirrhitidae), 2 species of blenny (Blennidae), 2 species of pufferfish (Tetraodontidae), 1 species of butterflyfish (Chaetodontidae), 2 species of surgeonfish (Acanthuridae), 1 species of triggerfish (Balistidae), 4 species of snapper (Lutjanidae) and 1 species of sweetlips (Haemulidae). For a full list of species, see Table S1.

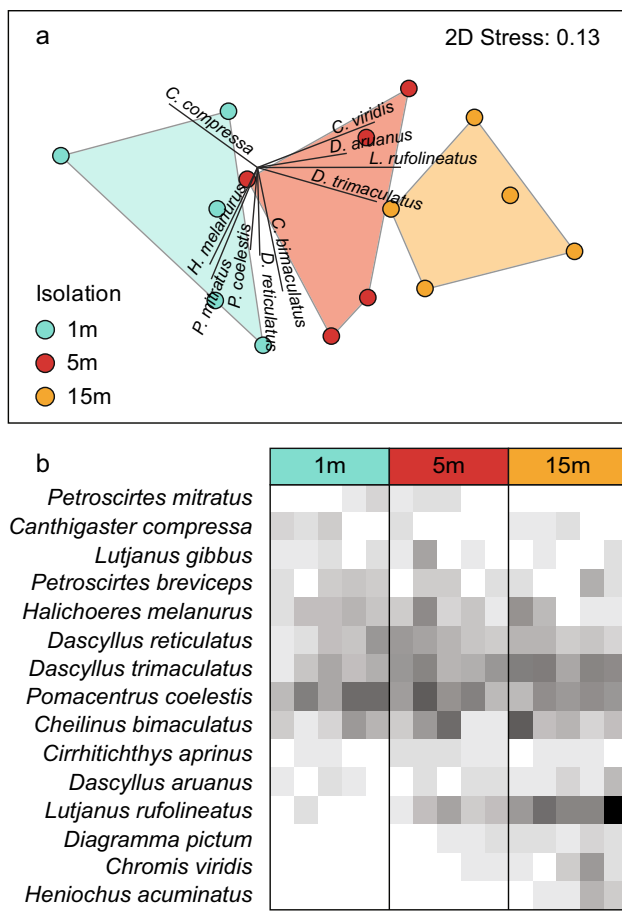
### H1: Isolation promotes abundance and species richness at cluster and patch scales

Increasing isolation had a positive effect on abundance, both for the mean total abundance at the cluster scale and for mean abundance at the patch scale (Table 1; Fig. 2a,c). On average, abundance on the most isolated reef clusters 2× higher than the most aggregated ones, both at the cluster (Tukey’s HSD, *P*=0.037) and patch scales (Tukey’s HSD, *P*=0.037). Abundance at the 15 m spacing was consistently higher than for the intermediate spacing of 5 m, which in turn, was consistently higher than for the 1 m spacing.

Species richness also showed a positive trend in its relationship with the degree of isolation, but the differences among the means were marginally non-significant at both the cluster and patch scales (Table 1, Fig. 2b,d). However, the Tukey’s HSD pairwise comparisons of the means showed that species richness for the 15 m isolation was significantly higher than for the 1 m isolation, both at the cluster (*P*=0.048) and patch (*P*=0.045) level. Species richness in the most isolated treatment tended to be ~1.5× higher than in the least isolated treatment, with species richness at the 5 m spacing tending to be intermediate.

### H2: Isolation promotes the cumulative increase in abundance and species richness in relation to habitat area within clusters

Increasing patch isolation had a positive effect on the cumulative abundance and species richness in relation to the number of patches considered within each cluster (a proxy for habitat area) (Fig. 3a, b). The slopes of the cumulative abundance-area and cumulative species richness-area linear relationships for the different isolation treatments were significantly different, as indicated by the significant interaction between the isolation and area factors in the analysis of covariance (Table 2a, b). When patches were more isolated



**Fig. 4** Representation of differences in coral reef fish assemblage structure by (a) non-metric multidimensional scaling (NMDS) based on the Bray–Curtis similarity measure of coral reef fish assemblages in the function of habitat isolation (1, 5 and 15 m). Vectors represent the correlation of the most representative species (BEST, corr: 0.953, Table S3) to the ordination. (b) Shade plot visualising changes in abundance of the species making the greatest contribution to dissimilarities among treatments (see SIMPER analysis in Table S2). The darker the shading, the more important the species

they accumulated more individuals with increasing habitat area, compared to when habitat patches were more aggregated (Fig. 3a). In addition, reefs where habitat patches were isolated by 15 m accumulated more species in relation to habitat area, compared with clusters where patches were isolated by only 1 m (Fig. 3b). Overall, habitat area explained

the greatest variation in both the number of individuals and species. However, the significant interaction terms indicate that the small positive effects of isolation incrementally get larger with the increasing total area sampled (Table 2).

**H3: Degree of isolation affects the species composition of coral reef fishes**

The composition of fish assemblages was strongly driven by the distance between individual patches (i.e., from 1 to 15 m along nMDS axis 1, Fig. 4a), and fish assemblage composition was significantly different among the isolation treatments at the cluster scale (Table 3). Pairwise tests showed that the strongest difference was observed between 1 and 15 m treatments (pseudo-*t* = 2.319, *p* = 0.009), while no significant differences were observed in the pairwise comparisons of 5 m clusters against the other two groups (pseudo-*t* < 0.040, *P* > 0.068). Dissimilarities between samples located the 5 m treatment were intermediate between the 1 m and 15 m isolation treatments (Fig. 4a,b; Table S2). Overall, habitat isolation accounted for a large component of variation ( $\sqrt{ECV} = 16.7$ ) explaining about 40% of the variability in fish assemblage structure, while the remaining 60% was due to natural variability in species-specific abundance among replicates ( $\sqrt{ECV} = 24.6$ ). Differences in assemblage composition were driven by species-specific changes in abundance within the assemblages, with some species thriving on isolated clusters and others preferring closer configurations. This pattern was best described by 10 species singled out by the BEST analysis (Fig. 4a, Table S3).

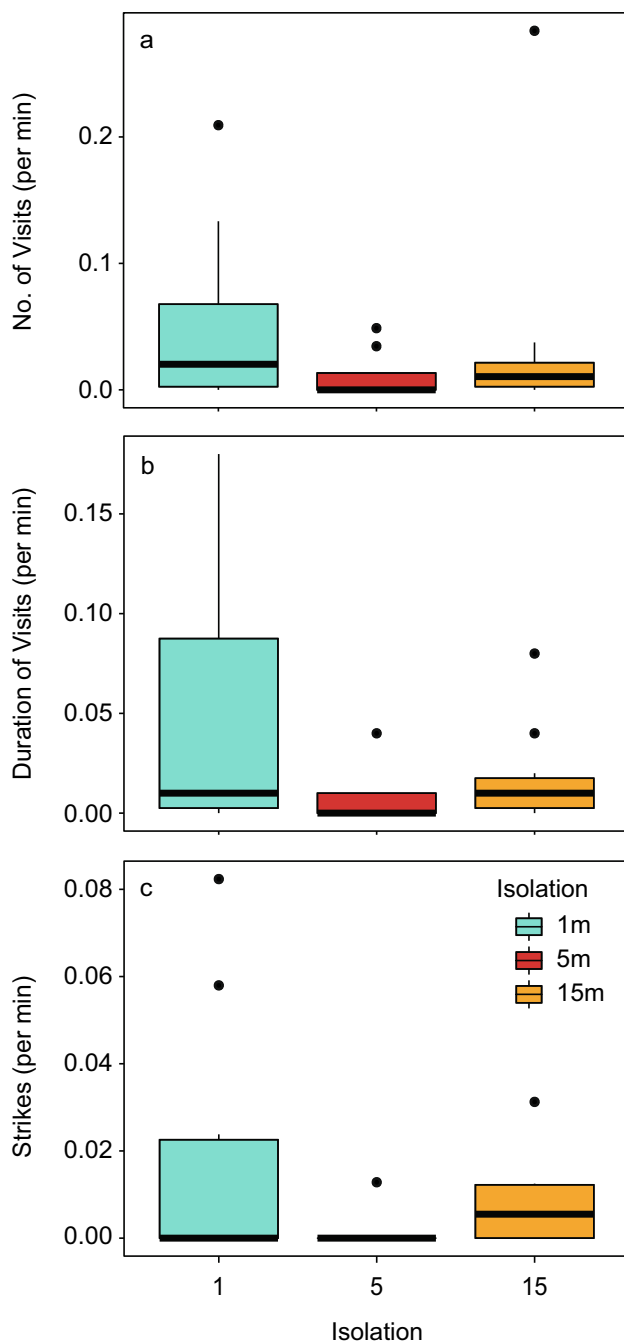
SIMPER analysis revealed that *Lutjanus rufolineatus*, *Dascyllus trimaculatus*, *Cheilinus bimaculatus*, *Chromis viridis*, *Dascyllus aruanus*, *Diagramma pictum* and *Heniochus acuminatus* were generally more abundant in clusters with 15 m spacing, while *Pomacentrus coelestis*, *Halichoeres melanurus*, *Petroscirtes breviceps* and *Canthigaster compressa* were more abundant in clusters with the 1 m spacing. *Dascyllus reticulatus*, *Cirrhitichthys aprinus*, *Lutjanus gibbus*, *Pseudobalistes flavimarginatus* and *Petroscirtes mitratus* tended to have higher abundances in the 5 m clusters (Fig. 4b, Table S2). Overall, while most of the differences between treatments were due to different quantitative responses of fishes always present, several species

**Table 3** Summary of permutational multivariate analyses of variance (PERMANOVA) to test for the effects of isolation (1, 5 and 15 m spacing) on coral reef fish assemblage structure at the cluster level.

	<i>df</i>	SS	MS	Pseudo-F	<i>P</i> (perm)	$\sqrt{ECV}$
Isolation	2	3979.9	1989.95	3.2957	<b>0.0004</b>	16.65
Residuals	12	7245.5	603.79			24.57

Significant *P* values in bold

Analyses were based on Bray–Curtis similarity matrix calculated from square-root transformed abundance data (9999 permutations)



**Fig. 5** Transient predator activity around the central patch of each reef cluster for the different isolation treatments (1, 5 and 15 m) including (a) the mean number of visits, (b) the mean duration of each visit and (c) the mean number of predatory strikes per minute while predator present. Whiskers delimit the  $\pm 1.5$  interquartile range (IQR), box height denotes the IQR, heavy crossbars represent the median and dots indicate outliers

were exclusively present in certain isolation treatments. For example, *D. pictum*, *H. acuminatus* and *C. viridis* which clearly preferred the more isolated reefs at 15 m spacing,

in contrast to *P. mitratus*, which was commonly observed on reefs 1 m apart and never in the most isolated clusters.

#### H4: Isolation reduces predator visitation by transient predators

The hypothesis that predators visit more isolated reefs less often and are likely to have less impact on isolated reefs was not strongly supported by the data. Video recordings of the central patch revealed that the most common predators visiting the reefs were golden trevally (*Gnathanodon speciosus*), emperor (*Lethrinus nebulosus*), and flutemouth (*Fistularia commersoni*). These predators visited the reefs an average of  $2.18 \pm 0.013$  times per hour, but the number of visits by predators was not significantly different among the 3 levels of isolation (Fig. 5a,  $F_{2,25} = 0.902$ ,  $P = 0.419$ ). There was a tendency for the duration of these visits to be longer when reefs were more aggregated (Fig. 5b), however, there was no significant difference in the duration of predator visits between isolation treatments ( $F_{2,25} = 0.902$ ,  $P = 0.419$ ). Strikes by predators also tended to be more frequent when the reefs were aggregated (Fig. 5c), but again this was not significantly higher than the most isolated habitat configuration ( $F_{2,25} = 1.559$ ,  $P = 0.23$ ).

## Discussion

Overall, these findings support the conclusion that at a small scale, the abundance and diversity of coral reef fishes on patch reefs increases with isolation. In our experiment, this effect was apparent at both the scale of whole clusters and for the mean number and richness of fish on patches within clusters. The positive effect of isolation was also apparent from the linear relationships between the cumulative number of individuals and species in relation to patch reef habitat area within clusters, with the slopes increasing with the degree of isolation. The level of isolation among patches also had a major influence on the structure of fish assemblages colonising patch reefs, with some species more common on isolated reef clusters and others associated with more closely spaced reef clusters. Although there was a positive effect of isolation, suitable habitat area was clearly also a major determinant of species richness, supporting the “habitat amount” hypothesis of Fahrig (2013). However, in patch reef habitats on coral reefs, we conclude isolation is likely to be an important additional factor affecting the local structure of reef assemblages.

The increase in abundance and species richness with increasing isolation supports other studies on tropical and temperate reef fishes (Schroeder 1987; Belmaker et al. 2005, 2009; Jordan et al. 2005; Stier and Osenberg 2010; Morton and Shima 2013). Approaches to manipulating the degree



of isolation vary, in some cases testing the effects of how far reefs are from one another (Schroeder 1987; Jordan et al 2005; Stier and Osenberg 2010; Morton and Shima 2013; our study) and in others testing the effects of distance from large contiguous tracts of reef (Belmaker et al 2005; 2009). These are clearly two different things, but both support the view that reef fishes are very good at colonising and persisting on isolated reef structures. Colonisation of the most isolated reefs (15 m spacing) is most likely during the larval stage, as the small site-attached reef fishes surveyed in this experiment do not exhibit wholesale movement between reefs across open sand habitat (Frederick 1997; Turgeon et al. 2010). However, post-settlement movement is likely to have contributed to patterns seen for the tightly clustered reefs (1 m spacing). Different researchers have manipulated reef spacing at different distances and the upper limit to the effects of isolation on species richness has yet to be determined.

While this study has demonstrated some significant effects of isolation, these results also support the broader view that suitable habitat area or the “habitat-amount” hypothesis is a primary driver of diversity (Fahrig 2013; Martin 2018). At the cluster scale, there was a dramatic increase in the cumulative abundance and species richness as an area of reef increased from a single patch reef to the whole cluster. The effect of isolation was evident in terms of an effect on the slope of these linear relationships, with a higher accumulation of individuals and species in relation to patch reef area with increasing reef spacing. There is much evidence to suggest declining area of healthy coral habitat is having major detrimental effects on fish communities (Jones et al. 2004; Paddack et al. 2009; Pratchett et al. 2018). The scale of our study was obviously limited and it is of particular interest to go further and test how the isolation effect would extrapolate to larger arrays and large reef spacings. While the scale of experimentation always has constraints, there is certainly scope for implementing larger-scale tests. In addition, the effects of isolation detected here will need to be tested against other aspects of fragmentation (patch size, patch number) when assessing the overall relative importance of habitat amount and fragmentation.

Most of the previous studies on the effects of habitat fragmentation processes on coral reef fish have taken either single-species approach or relied on aggregated metrics such as total abundance and species richness. Our whole community analysis at the cluster scale clearly shows a gradual shift in species composition in response to increasing isolation. Some highly aggregated species, including juveniles of the snapper *Lutjanus rufolineatus* and the damselfish *Dascyllus trimaculatus* clearly preferred the 15 m spacing, while others such as the damselfish *Pomacentrus coelestus* and the wrasse *Halichoeres melanurus* preferred tightly clustered reefs. This diversity of responses supports the general view that the

effects of isolation may differ in magnitude and direction depending on the species (Öckinger et al. 2010; Rielly-Carroll and Freestone 2017). At this stage, the reasons for the species-specific responses to isolation are unknown, but differences in habitat selection at settlement, post-settlement relocation and behavioural interactions within and among species are likely to be implicated. Overall, our results are consistent with the idea that isolation in fragmented landscapes can affect a range of different patterns in reef fish community structure and a range of underlying processes, including habitat selection, competitive interactions and predator–prey dynamics (Overholtzer-McLeod 2006; Stier and Osenberg 2010; Morton and Shima 2013).

Our assessment of the role of transient predators in explaining lower abundance and diversity in less isolated configurations was not unequivocal. The data suggested there could be longer predator residence times and greater predator success in highly clustered reefs. The literature on coral reef fishes provides further support for the role of predators. The spatial scale of predator movement may exert differences in the patterns and processes operating within and among reefs (Frederick 1997; Turgeon et al. 2010; White et al. 2010; McCarthy and White 2016). Transient predators are more likely to move between more isolated reefs but may be less motivated to move when they have encountered a tightly clustered patch of reefs. Overholtzer-McLeod (2006) showed that transient predators were much more likely to visit aggregated reefs, inflicting much higher levels of density-dependent mortality on the resident fishes. Belmaker et al. (2005, 2009) clearly implicate predators in explaining lower abundance and diversity of patch reefs in closer proximity to large reefs supporting a greater number and diversity of predators.

More isolated reefs may also experience higher settlement rates through settlement redirection (Stier and Osenberg 2010). If the supply of arriving larvae is limited and individual larvae are well-adapted to finding isolated reefs, isolated reefs are likely to attract higher settlement. In contrast, when reefs are clustered, the same number of larvae arriving in an area may be spread among all reefs in the cluster. Both Stier and Osenberg (2010), and Morton and Shima (2013), demonstrate higher settlement rates on isolated reefs (reefs without neighbours). However, they also show increasing overall settlement to an area as a function of the total reef area, indicating habitat amount is also important. The relative importance of settlement redirection and transient predators requires further investigation but may be addressed in a larger scale experiment in which access to reefs by predators is restricted.

In conclusion, our paper contributes further evidence that small-scale isolation in patchy coral reef habitats promotes abundance and species richness. In terms of the processes contributing to the effects of isolation, both recruitment and

predation warrant further experimentation. The positive effects of isolation appear to increase as the accumulated sampling area increases. However, given that extreme isolation is known to be associated with low species diversity, the next step will be to up-scale these results to examine the relationships between species richness and habitat area changes over a larger scale of reef spacing. It will also be important to investigate the magnitude of the isolation factor compared to other components of fragmentation, including reef size and number while controlling for the overall effects of habitat area. To date, no study on coral reefs has undertaken a comprehensive assessment of all recognised components of fragmentation. The effects of habitat loss and fragmentation are likely becoming more significant as coral cover continues on a downward trajectory in most coral reef ecosystems. The positive effects of isolation are unlikely to offset the negative effects of this global phenomenon. However, they do help us understand how coral reef species exploit life in one of nature's most inherently fragmented ecosystems.

**Acknowledgements** We thank the staff at the Nago Island Mariculture and Research Facility, Kavieng, Papua New Guinea for their local knowledge and field assistance. Thanks also to Patrick Smallhorn-West for his assistance in setting up the experimental array.

**Author contributions** MCB, GPJ and GB conceived and planned the project. Fieldwork was undertaken by MCB, GB and KS. MCB, GB and KS completed all data analyses. The manuscript was written by MCB, GPJ and GB, with additional input from KS.

**Funding** This research was supported by an Australian Research Council Discovery Grant (DP140101800) to G.P. Jones.

**Data availability** Data are available at <https://knb.ecoinformatics.org/data> Mary Bonin, Geoff Jones, Giulio Barone, and Katie Sambrook. 2019. Coral reef habitat patch isolation experiment, Papua New Guinea, April to June 2014. Knowledge Network for Biocomplexity. <https://doi.org/10.5063/F13N21P2>

## Compliance with ethical standards

**Conflicts of interest** The authors declare that they have no conflict of interest.

**Ethics approval** All applicable institutional and/or national guidelines for the care and use of animals were followed. Ethics approval number A 2040, James Cook University. PNG Research Visa for G.P. Jones 10350006662 and for M.C. Bonin 10350011571.

## References

Acosta CA, Robertson DN (2002) Diversity in coral reef fish communities: the effects of habitat patchiness revisited. *Mar Ecol Prog Ser* 227:87–96. <https://doi.org/10.3354/meps227087>

- Anderson MJ (2001) A new method for non-parametric multivariate analysis of variance. *Austral Ecol* 26:32–46. <https://doi.org/10.1111/j.1442-9993.2001.01070.pp.x>
- Anderson MJ, Gorley RN, Clarke KR (2008) PERMANOVA+ for PRIMER: Guide to Software and Statistical Methods. PRIMER-E: Plymouth
- Andrén H (1994) Effects of habitat fragmentation on birds and mammals in landscapes with different proportions of suitable habitat: a review. *Oikos* 71:355–366. <https://doi.org/10.2307/3545823>
- Ault TR, Johnson CR (1998) Spatial variation in fish species richness on coral reefs: habitat fragmentation and stochastic structuring processes. *Oikos* 82:354–364. <https://doi.org/10.2307/3546976>
- Bailey D, Schmidt-Entling MH, Eberhart P, Herrmann JD, Hofer G, Kormann U, Herzog F (2010) Effects of habitat amount and isolation on biodiversity in fragmented traditional orchards. *J Applied Ecol* 47:1003–1013. <https://doi.org/10.1111/j.1365-2664.2010.01858.x>
- Belmaker J, Shashar N, Ziv Y (2005) Effects of small-scale isolation and predation on fish diversity on experimental reefs. *Mar Ecol Prog Ser* 289:273–283. <https://doi.org/10.3354/meps289273>
- Belmaker J, Ziv Y, Shashar N (2009) Habitat patchiness and predation modify the distribution of a coral-dwelling damselfish. *Mar Biol* 156:447–454. <https://doi.org/10.1007/s00227-008-1098-5>
- Bender MG, Pie MR, Rezende EL, Mouillot D, Floeter SR (2013) Biogeographic, historical and environmental influences on the taxonomic and functional structure of Atlantic reef fish assemblages. *Global Ecol Biogeogr* 22:1173–1182. <https://doi.org/10.1111/geb.12099>
- Bender MG, Leprieur F, Mouillot D, Kulbicki M, Parravicini V, Pie MR, Barneche DR, Oliveira-Santos LGR, Floeter SR (2017) Isolation drives taxonomic and functional nestedness in tropical reef fish faunas. *Ecography* 40:425–435. <https://doi.org/10.1111/ecog.02293>
- Bonin MC, Almany GR, Jones GP (2011) Contrasting effects of habitat loss and fragmentation on coral-associated reef fishes. *Ecol* 92(7):1503–1512. <https://doi.org/10.1890/10-0627.1>
- Bosco L, Wan HY, Cushman SA, Arlettaz R, Jacot A (2019) Separating the effects of habitat amount and fragmentation on invertebrate abundance using a multi-scale framework. *Landsc Ecol* 34:105–117. <https://doi.org/10.1007/s10980-018-0748-3>
- Brooks TM, Mittermeier RA, Mittermeier CG, Da Fonseca GAB, Rylands AB, Konstant WR, Flick P, Pilgrim J, Oldfield S, Magin G, Hilton-Taylor C (2002) Habitat loss and extinction in the hotspots of biodiversity. *Conserv Biol* 16:909–923. <https://doi.org/10.1046/j.1523-1739.2002.00530.x>
- Bruno JF, Selig ER (2007) Regional decline of coral cover in the Indo-Pacific: timing, extent, and subregional comparisons. *PLoS ONE* 2:e711. <https://doi.org/10.1371/journal.pone.0000711>
- Bruno JF, Valdivia A (2016) Coral reef degradation is not correlated with local human population density. *Sci Rep* 6:29778. <https://doi.org/10.1038/srep29778>
- Cagnolo L, Valladares G, Salvo A, Cabido M, Zak M (2009) Habitat fragmentation and species loss across three interacting trophic levels: effects of life-history and food-web traits. *Conserv Biol* 23:1167–1175. <https://doi.org/10.1111/j.1523-1739.2009.01214.x>
- Caley MJ, Buckley KA, Jones GP (2001) Separating ecological effects of habitat fragmentation, degradation, and loss on coral communities. *Ecol* 82:3435–3448. <https://doi.org/10.2307/2680163>
- Clarke KR (1993) Non-parametric multivariate analyses of changes in community structure. *Aust J Ecol* 18:117–143. <https://doi.org/10.1111/j.1442-9993.1993.tb00438.x>
- Clarke KR, Gorley RN, Somerfield PJ, Warwick RM (2014a) Change in marine communities: an approach to statistical analysis and interpretation, 3rd edition. PRIMER-E: Plymouth.
- Clarke KR, Tweedley JR, Valesini FJ (2014) Simple shade plots aid better long-term choices of data pre-treatment in multivariate

- assemblage studies. *J Mar Biol Ass UK* 94:1–16. <https://doi.org/10.1017/S0025315413001227>
- Crist TO, Pradhan-Devare SV, Summerville KS (2006) Spatial variation in insect community and species responses to habitat loss and plant community composition. *Oecologia* 147:510–521. <https://doi.org/10.1007/s00442-005-0275-1D>
- Davies KF, Margules CR (1998) Effects of habitat fragmentation on carabid beetles: experimental evidence. *J Anim Ecol* 67:460–471. <https://doi.org/10.1046/j.1365-2656.1998.00210.x>
- Debinski DM, Holt RD (2000) A survey and overview of habitat fragmentation experiments. *Conserv Biol* 14:342–355. <https://doi.org/10.1046/j.1523-1739.2000.98081.x>
- De Camargo RX, Boucher-Lalonde V, Currie DJ (2018) At the landscape level, birds respond strongly to habitat amount but weakly to fragmentation. *Divers Distrib* 24:629–639. <https://doi.org/10.1111/ddi.12706>
- Didham RK, Lawton JH, Hammond PM, Eggleton P (1998) Trophic structure stability and extinction dynamics of beetles (Coleoptera) in tropical forest fragments. *Philos* 353:437–451. <https://doi.org/10.1098/rstb.1998.0221>
- Ewers RM, Didham RK (2006) Confounding factors in the detection of species responses to habitat fragmentation. *Biol Rev* 81:117–142. <https://doi.org/10.1017/S1464793105006949>
- Fahrig L (2013) Rethinking patch size and isolation effects: the habitat amount hypothesis. *J Biogeogr* 40:1649–1663. <https://doi.org/10.1111/jbi.12130>
- Fahrig L (2017) Ecological responses to habitat fragmentation per se. *Annu Rev Ecol Evol Syst* 48:1–23. <https://doi.org/10.1146/annurev-ecolsys-110316-022612>
- Fahrig L (2020) Why do several small patches hold more species than few large patches? *Global Ecol Biogeogr* 29:615–628. <https://doi.org/10.1111/geb.13059>
- Fahrig L, Arroyo-Rodríguez V, Bennett JR, Boucher-Lalonde V, Cazetta E, Currie DJ, Eigenbrod F, Ford AT, Harrison SP, Jaeger JAG, Koper N, Martin AE, Martin J-L, Metzger JP, Morrison P, Rhodes JR, Saunders DA, Simberloff D, Smith AC, Tischendorf L, Vellend M, Watling JJ (2019) Is habitat fragmentation bad for biodiversity? *Biol Cons* 230:179–186. <https://doi.org/10.1016/j.biocon.2018.12.026>
- Fattorini S, Borges PAV (2012) Species-area relationships underestimate extinction rates. *Acta Oecologia* 40:27–30. <https://doi.org/10.1111/jbi.12130>
- Fisher J, Lindenmeyer DB (2007) Landscape modification and habitat fragmentation: a synthesis. *Global Ecol Biogeogr* 16:265–280
- Fletcher RJ Jr, Didham RK, Banks-Leite C, Barlow J, Ewers RM, Rosindell J, Holt RD, Gonzalez A, Pardini R, Damschen EI, Melo FPL, Ries L, Prevedello JA, Tschardt T, Laurance WJ, Lovejoy T, Haddad NM (2018) Is habitat fragmentation good for biodiversity? *Biol Cons* 226:9–15. <https://doi.org/10.1016/j.biocon.2018.07.022>
- Frederick JL (1977) Post-settlement movement of coral reef fishes and bias in survival estimates. *Mar Ecol Progr Ser* 150:65–74
- Gardiner R, Bain G, Hamer R, Jones ME, Johnson CN (2018) Habitat amount and quality, not patch size, determine persistence of a woodland-dependent mammal in an agricultural landscape. *Landsc Ecol* 33:1837–1849. <https://doi.org/10.1007/s10980-018-0722-0>
- Gilbert FS (1980) The equilibrium theory of island biogeography: fact or fiction? *J Biogeogr* 7:209–235
- Gotelli NJ, Colwell RK (2001) Quantifying biodiversity: procedures and pitfalls in the measurement and comparison of species richness. *Ecol Lett* 4:379–391. <https://doi.org/10.1046/j.1461-0248.2001.00230.x>
- Haddad NM, Brudvig LA, Clobert J, Davies KF, Gonzales A, Holt RD, Lovejoy TE, Sexton JO, Austin MP, Collins CD, Cook WM, Damschen EI, Ewers RM, Foster BL, Jenkins CN, King AJ, Laurance WF, Levey DJ, Margules CR, Melbourne BA, Nicholls AO, Orrock JL, Song D-X, Townshend JR (2015) Habitat fragmentation and its lasting impact on Earth's ecosystems. *Sci Adv* 2015:e1500052. <https://doi.org/10.1126/sciadv.1500052>
- Haddad NM, Gonzalez A, Brudvig LA, Burt MA, Levey DJ, Damschen EI (2017) Experimental evidence does not support the habitat amount hypothesis. *Ecography* 40:48–55. <https://doi.org/10.1111/ecog.02535>
- Hanski I (2011) Habitat loss, the dynamics of biodiversity, and a perspective on conservation. *Ambio* 40:248–255. <https://doi.org/10.1007/s13280-011-0147-3>
- Hanski I, Zurita GA, Bellocq MI, Rybicki J (2013) Species-fragmented area relationship. *Proc Natl Acad Sci USA* 110:12715–12720. <https://doi.org/10.1073/pnas.1311491110>
- Herrmann JD, Kormann U, Schüepp C, Stocker Y, Herzog F, Entling MH (2012) Effects of habitat isolation and predation pressure on an arboreal food-web. *Community Ecol* 13(1):82–87. <https://doi.org/10.1556/ComEc13.2012.1.10>
- Hobbs JPA, Jones GP, Munday PL, Connolly SR, Srinivasan M (2012) Biogeography and the structure of coral reef fish communities on isolated islands. *J Biogeogr* 39(1):130–139. <https://doi.org/10.1111/j.1365-2699.2011.02576.x>
- Jacquet C, Mouillot D, Kulbicki M, Gravel D (2017) Extensions of island biogeography theory predict the scaling of functional trait composition with habitat area and isolation. *Ecol Lett* 20:135–146. <https://doi.org/10.1111/ele.12716>
- Jones GP (1997) Relationships between recruitment and postrecruitment processes in lagoonal populations of two coral reef fishes. *J Exp Mar Bio Ecol* 213:231–246. [https://doi.org/10.1016/S0022-0981\(96\)02763-3](https://doi.org/10.1016/S0022-0981(96)02763-3)
- Jones GP (2015) Mission impossible: unlocking the secrets of dispersal in coral reef fishes. In: “Ecology of Fishes on Coral Reefs: The Functioning of an Ecosystem in a Changing World” (Mora C., ed). Pp 16–27. Cambridge University Press. ISBN 978-1-107-08918-1
- Jones GP, Almany GR, Russ GR, Sale PF, Steneck RS, van Oppen MJH, Willis BL (2009) Larval retention and connectivity among populations of corals and reef fishes: history, advances and challenges. *Coral Reefs* 28:307–325. <https://doi.org/10.1007/s00338-009-0469-9>
- Jones GP, McCormick MI, Srinivasan M, Eagle JV (2004) Coral decline threatens fish biodiversity in marine reserves. *Proc Natl Acad Sci* 101:8251–8253. <https://doi.org/10.1073/pnas.0401277101>
- Jordan LKB, Gilliam DS, Spieler RE (2005) Reef fish assemblage structure affected by small-scale spacing and size variations of artificial patch reefs. *J Exp Mar Bio Ecol* 326:170–186. <https://doi.org/10.1016/j.jembe.2005.05.023>
- Kier G, Kreft H, Lee T-M, Jetz W, Ibsch PL, Nowicki C, Mutke J, Barthlott W (2009) A global assessment of endemism and species richness across island and mainland regions. *Proc Nat Acad Sci* 106:9322–9327. <https://doi.org/10.1073/pnas.0810306106>
- Krauss J, Bommarco R, Guardiola M, Heikkinen RK, Helm A, Kuussaari M, Lindborg R, Ockinger E, Partel M, Pino J, Poyry J, Raatikainen KM, Sang A, Stefanescu C, Teder T, Zobel M, Steffan-Dewenter I (2010) Habitat fragmentation causes immediate and time-delayed biodiversity loss at different trophic levels. *Ecol Lett* 13:597–605. <https://doi.org/10.1111/j.1461-0248.2010.01457.x>
- Kruess A, Tschardt T (1994) Habitat fragmentation, species loss, and biological control. *Sci* 264:1581–1584. <https://doi.org/10.1126/science.264.5165.1581>
- Laurance WF (2008) Theory meets reality: how habitat fragmentation has transcended island biogeography theory. *Biol Cons* 141:1731–1744. <https://doi.org/10.1016/j.biocon.2008.05.011>
- Lindenmeyer DB, Luck G (2005) Synthesis: thresholds in conservation and management. *Biol Cons* 124:351–354. <https://doi.org/10.1016/j.biocon.2005.01.041>



- Lindgren JP, Cousins SAO (2017) Island biogeography theory outweighs habitat amount hypothesis in predicting plant species richness in small grassland remnants. *Landsc Ecol* 32:1895–1906. <https://doi.org/10.1007/s10980-017-0544-5>
- Luiz OJ, Mendes TC, Barneche DR, Ferreira CGW, Noguchi R, Villaca RC, Rangel CA, Gasparini JL, Ferreira CEL (2015) Community structure of reef fishes on a remote oceanic island (St Peter and St Paul's Archipelago, equatorial Atlantic): the relative influence of abiotic and biotic variables. *Mar Freshwater Res* 66:739–749. <https://doi.org/10.1071/MF14150>
- MacArthur RH, Wilson EO (1967) *The theory of island biogeography*. Princeton University Press, Princeton, NJ, p 203p
- MacDonald ZG, Anderson ID, Acorn JH, Nielson SE (2018) Decoupling habitat fragmentation from habitat loss: butterfly species mobility obscures fragmentation effects in a naturally fragmented landscape of lake islands. *Oecologia* 186:11–27. <https://doi.org/10.1007/s00442-017-4005-2>
- Martin CA (2018) An early synthesis of the habitat amount hypothesis. *Landsc Ecol* 33:1831–1835. <https://doi.org/10.1007/s10980-018-0716-y>
- Mellin C, Huchery C, Caley MJ, Meekan MG, Bradshaw C (2010) Reef size and isolation determine the temporal stability of coral reef fish populations. *Ecol* 91:3138–3145. <https://doi.org/10.1890/10-0267.1>
- McCarthy EK, White JW (2016) Density-dependent prey mortality is determined by the spatial scale of predator foraging. *Oecologia* 180:305–311. <https://doi.org/10.1007/s00442-015-3374-7>
- McGarigal K, Cushman SA (2002) Comparative evaluation of experimental approaches to the study of habitat fragmentation effects. *Ecol Applic* 12:335–345. <https://doi.org/10.2307/3060945>
- Morton DN, Shima JS (2013) Habitat configuration and availability influences the settlement of temperate reef fishes (Tripterygiidae). *J Exp Mar Bio Ecol* 449:215–220. <https://doi.org/10.1016/j.jembe.2013.09.017>
- Öckinger E, Schweiger O, Crist TO, Debinski DM, Krauss J, Kuussaari M, Petersen JD, Pöyry J, Settele J, Summerville KS, Bommarco R (2010) Life-history traits predict species responses to habitat area and isolation: a cross-continental synthesis. *Ecol Lett* 13:969–979. <https://doi.org/10.1111/j.1461-0248.2010.01487.x>
- Ord TJ, Emblen J, Hagman M, Shofner R, Unruh S (2017) Manipulation of habitat isolation and area implicates deterministic factors and limited neutrality in community assembly. *Ecol and Evol* 7:5845–5860. <https://doi.org/10.1002/ece3.3126>
- Overholtzer-McLeod KL (2006) Consequences of patch reef spacing for density-dependent mortality of coral-reef fishes. *Ecol* 87:1017–1026. [https://doi.org/10.1890/0012-9658\(2006\)87\[1017:COPRSF\]2.0.CO;2](https://doi.org/10.1890/0012-9658(2006)87[1017:COPRSF]2.0.CO;2)
- Paddack MJ, Reynolds JD, Aguilar C et al (2009) Recent region-wide declines in Caribbean reef fish abundance. *Current Biol* 19:590–595. <https://doi.org/10.1016/j.cub.2009.02.041>
- Pandolfi JM, Bradbury RH, Sala E, Hughes TP, Bjorndal KA, Cooke RG, McArdle D, McClenachan L, Newman MJH, Paredes G, Warner RR, Jackson JBC (2003) Global trajectories of the long-term decline of coral reef ecosystems. *Sci* 301:955–958. <https://doi.org/10.1126/science.1085706>
- Pratchett MS, Thompson CA, Hoey AS, Cowman PF, Wilson SK (2018) Effects of coral bleaching and coral loss on the structure and function of reef fish assemblages. Pp 265–293. In: *Coral Bleaching, Ecological Studies* 233, van Oppen MJH, Lough JM (eds.), Springer International Publishing AG, part of Springer Nature. [https://doi.org/https://doi.org/10.1007/978-3-319-75393-5\\_11](https://doi.org/https://doi.org/10.1007/978-3-319-75393-5_11)
- Prugh LR, Hodges KE, Sinclair ARE, Brashares JS (2008) Effect of habitat area and isolation on fragmented animal populations. *Proc Natl Acad Sci* 105:20770–20775. <https://doi.org/10.1073/pnas.0806080105>
- Quinn JF, Harrison SP (1988) Effects of fragmentation and isolation on species richness: evidence from biogeographic patterns. *Oecologia* 75:132–140. <https://doi.org/10.1007/BF00378826>
- Rabelo RM, Aragon S, Bicca-Marques JC, Nelson BW (2019) Habitat amount hypothesis and passive sampling explain mammal species composition in Amazonian river islands. *Biotropica* 51:84–92. <https://doi.org/10.1111/btp.12615>
- Rielly-Carroll E, Freestone AL (2017) Habitat fragmentation differentially affects trophic levels and alters behavior in a multi-trophic marine system. *Oecologia* 183:899–908. <https://doi.org/10.1007/s00442-016-3791-2>
- Ries L, Fletcher RJ Jr, Battin J, Sisk TD (2004) Ecological responses to habitat edges: mechanisms, models, and variability explained. *Annu Rev Ecol Syst* 35:491–522. <https://doi.org/10.1146/annurev.ecolsys.35.112202.130148>
- Ryall KL, Fahrig L (2006) Response of predators to loss or fragmentation of prey habitat: a review of theory. *Ecol* 87:1086–1093. [https://doi.org/10.1890/0012-9658\(2006\)87\[1086:ROPTLA\]2.0.CO;2](https://doi.org/10.1890/0012-9658(2006)87[1086:ROPTLA]2.0.CO;2)
- Sandin SA, Vermeij MJA, Hurlbert AG (2008) Island biogeography of Caribbean coral reef fish. *Global Ecol Biogeogr* 17:770–777. <https://doi.org/10.1111/j.1466-8238.2008.00418.x>
- Saunders DA, Hobbs RJ, Margules CR (1991) Biological consequences of ecosystem fragmentation: a review. *Conserv Biol* 5:18–32. <https://doi.org/10.1111/j.1523-1739.1991.tb00384.x>
- Scheffer M, van Geest GJ, Zimmer K, Jeppesen E, Søndergaard M, Butler MG, Hanson MA, Declerck S, de Meester L, Persson L (2006) Small habitat size and isolation can promote species richness: second-order effects on biodiversity in shallow lakes and ponds. *Oikos* 112:227–231. <https://doi.org/10.1111/j.0030-1299.2006.14145.x>
- Schneider MF (2001) Habitat loss, fragmentation and predator impact: spatial implications for prey conservation. *J Applied Ecol* 38:720–735. <https://doi.org/10.1046/j.1365-2664.2001.00642.x>
- Schroeder RE (1987) Effects of patch reef size and isolation on coral reef fish recruitment. *Bull Mar Sci* 41:441–451
- Seibold S, Bassler C, Brandl R, Fahrig L, Förster B, Heurich M, Hothorn T, Scheipl F, Thorn S, Müller J (2017) An experimental test of the habitat-amount hypothesis for saproxylic beetles in a forested region. *Ecol* 98:1613–1622. <https://doi.org/10.1002/ecy.1819>
- Simberloff D (2000) Extinction-proneness of island species—causes and management implications. *Raffles B Zool* 48:1–9
- Srinivasan M, Jones GP (2006) Extended breeding and recruitment periods of fishes on a low latitude coral reef. *Coral Reefs* 25:673–682. <https://doi.org/10.1007/s00338-006-0153-2>
- Steffan-Dewenter I, Tschamntke T (1999) Butterfly community structure in fragmented habitats. *Ecol Lett* 3:449–456. <https://doi.org/10.1111/j.1461-0248.2000.00175.x>
- Stier AC, Osenberg CW (2010) Propagule redirection: habitat availability reduces colonization and increases recruitment in reef fishes. *Ecol* 91:2826–2832. <https://doi.org/10.1890/09-1993.1>
- Tilman D, May RM, Lehman CL, Nowak MA (1994) Habitat destruction and the extinction debt. *Nature* 371:65–66. <https://doi.org/10.1038/371065a0>
- Turgeon K, Robillard A, Grégoire J et al (2010) Functional connectivity from a reef fish perspective: behavioral tactics for moving in a fragmented landscape. *Ecol* 91:3332–3342. <https://doi.org/10.1890/09-2015.1>
- van Dorp D, Opdam PFM (1987) Effects of patch size, isolation and regional abundance on forest bird communities. *Landsc Ecol* 1:59–73. <https://doi.org/10.1007/BF02275266>
- Watling JI, Arroyo-Rodríguez V, Pfeifer M, Baeten L, Banks-Leite C, Cisneros LM, Fang R, Hamel-Leige AC, Lachat T, Leal IR, Lens L, Possingham HP, Raheem DC, Ribeiro DB, Slade EM, Urbina-Cardona JN, Wood EM, Fahrig L (2020) Support for the habitat



- amount hypothesis from a global synthesis of species density studies. *Ecol Lett* 23:674–681. <https://doi.org/10.1111/ele.13471>
- Watson JEM, Shanahan DF, Di Marco M, Allan J, Laurance WF, Sanderson EW, Mackey B, Venter O (2016) Catastrophic declines in wilderness areas undermine global environment targets. *Curr Biol* 26:2929–2934. <https://doi.org/10.1016/j.cub.2016.08.049>
- White JW, Samhuri JF, Stier AC, Wormald CL, Hamilton SL, Sandin SA (2010) Synthesizing mechanisms of density dependence in reef fishes: behaviour, habitat configuration, and observational scale. *Ecol* 91:1949–1961. <https://doi.org/10.1890/09-0298.1>
- Wintle BA, Kujala H, Whitehead A, Cameron A, Veloz S, Kukkala A, Moilanen A, Gordon A, Lentini PE, Cadenhead NCR, Bekessy SA (2019) Global synthesis of conservation studies reveals the importance of small habitat patches for biodiversity. *Proc Natl Acad Sci* 116:909–914. <https://doi.org/10.1073/pnas.1813051115>

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