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Human impacts decouple a fundamental ecological relationship—The positive association between host diversity and parasite diversity

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Abstract

Human impacts on ecosystems can decouple the fundamental ecological relationships that create patterns of diversity in free-living species. Despite the abundance, ubiquity, and ecological importance of parasites, it is unknown whether the same decoupling effects occur for parasitic species. We investigated the influence of fishing on the relationship between host diversity and parasite diversity for parasites of coral reef fishes on three fished and three unfished islands in the central equatorial Pacific. Fishing was associated with a shallowing of the positive host-diversity–parasite-diversity relationship. This occurred primarily through negative impacts of fishing on the presence of complex life-cycle parasites, which created a biologically impoverished parasite fauna of directly transmitted parasites resilient to changes in host biodiversity. Parasite diversity appears to be decoupled from host diversity by fishing impacts in this coral reef ecosystem, which suggests that such decoupling might also occur for parasites in other ecosystems affected by environmental change.

KEYWORDS

biodiversity, biophysical coupling, coral reefs, disease, environmental change, fishing, host–parasite interactions, parasite

1 | INTRODUCTION

The rise of “weedy” species is one of the hallmarks of the Anthropocene (Clavel, Julliard, & Devictor, 2011; Lotze et al., 2006; McGill, Dornelas, Gotelli, & Magurran, 2015). When human impacts on ecosystems systematically favor a few stress-tolerant, *r*-selected species and select against more vulnerable species (Darling, McClanahan, & Cote, 2013; McKinney & Lockwood, 1999; Olden & Rooney, 2006), ecological patterns can be simplified or erased, a phenomenon termed *biophysical decoupling* (Williams, Gove, Eynaud, Zgliczynski, & Sandin, 2015). That is, human impacts on ecosystems can erase or reverse the direction of relationships between species and their environment, rewiring the “laws of nature.” For example, anthropogenic disturbance disrupts one of the most fundamental patterns

in ecology: the species–area relationship. In a meta-analysis of data on animals in terrestrial habitat patches, only 13% of variance in the likelihood of a species occurring in a patch was accounted for by patch size (Prough, Hodges, Sinclair, & Brashares, 2008); the authors posited that disturbance had already extirpated the most vulnerable species and left behind only species insensitive to further changes in patch area. On coral reefs, fishing depresses the slope of the species–area relationship through fishing-driven reductions in species richness, species relative abundance, and patch occupancy; in the central Pacific, the slope of the species–area relationship on fished islands is ~30% shallower than it is on unfished islands (Tittensor, Micheli, Nystrom, & Worm, 2007). Similarly, on remote and unfished coral reefs of the central equatorial Pacific, hard coral cover is correlated with temperature, primary productivity, and wave action, but

on nearby, fished islands, these relationships are absent (Williams et al., 2015).

Despite extensive research into the ecology of free-living species in the Anthropocene, little information exists to suggest what this new era might hold for parasites, presenting an important research gap. Many have suggested that rates of parasitic disease are on the rise in both wildlife and humans (e.g., Harvell et al., 2004; Keesing et al., 2010). Whether such an increase is in fact occurring has yet to be established (Lafferty, Porter, & Ford, 2004; Wood, Lafferty, et al., 2014), but many recent conservation set-backs have been driven by parasites [e.g., the 1980s Caribbean urchin die-off (Lessios, 1988), 2013's sea star wasting disease epidemic on the US west coast (Hewson et al., 2014), and 2015's saiga antelope mass mortality event in central Asia (Orynbayev et al., 2016)], lending urgency to the question of whether the Anthropocene will bring more such outbreaks. On the other hand, many have suggested that the world's most imperiled wildlife might be parasitic—that the obligate dependence of parasites on their hosts renders parasitic species especially vulnerable to co-extinction, even before their hosts are at risk of extinction themselves (Colwell, Dunn, & Harris, 2012; Dunn, Harris, Colwell, Koh, & Sodhi, 2009; MacKenzie & Pert, 2018). Understanding whether parasites are on the increase or on the decline is vital for conservation, but such an understanding would also provide insight into the prospects for nonparasitic species in the Anthropocene. Parasites form a special class of consumer (Lafferty & Kuris, 2002), and are therefore analogous to other consumers, like grazers, zooplanktivores, and piscivores. Indeed, the same general mathematical modeling framework that yields predator–prey models also yields parasite–host models (Lafferty et al., 2015) and what forces govern the diversity of parasites may also govern the diversity of other consumers, particularly those with spatially close and temporally long-standing interactions with their resources (i.e., other symbionts, including mutualists and commensals). There is therefore an urgent need for a better understanding of how parasite assemblages are changing in a changing world.

Here, we investigate whether human impacts on ecosystems can erode the strength of a robust and general ecological pattern: the positive relationship between host diversity and parasite diversity. The “host-diversity-begets-parasite-diversity” hypothesis evolved from the more general “diversity-begets-diversity” paradigm, which states that increasing diversity of resource species creates new ecological niches; “begetting” species increase resource or structural complexity for “begotten” species, effectively increasing the size of the niche hyperspace or adding new axes to that space (Cazzolla Gatti, Hordijk, & Kauffman, 2017; MacArthur, 1964; Whittaker, 1972). First posited in 2005 (Hechinger & Lafferty, 2005), the host-diversity-begets-parasite-diversity hypothesis states that increasing host genetic, taxonomic, and functional diversity increases parasite diversity through mechanisms both ecological (e.g., “habitat heterogeneity” hypothesis; Hutchinson, 1959; Krasnov, Shenbrot, Khokhlova, & Degen, 2004; MacArthur, 1958; MacArthur, 1964; MacArthur & MacArthur, 1961; Rosenzweig, 1995) and evolutionary (e.g., host–parasite co-speciation; Eichler, 1942; Vas, Csorba, &

Rozsa, 2012). Although positive values of the host-diversity–parasite-diversity relationship might be expected because parasites are, by definition, dependent on their hosts, the direction of this relationship is not a foregone conclusion, nor are positive relationships merely trivial outcomes (Wood & Johnson, 2016). Negative correlations between host and parasite diversity might arise if increasing host diversity exerts sufficiently strong negative effects on parasite transmission that parasite species are driven locally extinct (i.e., an extreme dilution effect; Keesing, Holt, & Ostfeld, 2006), if pathogenic effects of parasites drive hosts locally extinct (Krasnov et al., 2004), or if forces that erode host resistance to infection (e.g., disturbance) simultaneously reduce host diversity and increase parasite diversity.

Despite the many possible relationships between host and parasite diversity, positive relationships appear to be overwhelmingly common. A recent meta-analysis revealed that, among all of the estimates of the correlation between host and parasite diversity identified in the literature, 95% (36 of 38) were positive, with a large and positive average effect size ($r = .550$, 95% CI = 0.474–0.763, $p < .001$; Kamiya, O'Dwyer, Nakagawa, & Poulin, 2014). The values included in this meta-analysis were from marine, freshwater, and terrestrial ecosystems, four phyla of parasites, and six continents, but none of the included studies consider or address whether the host-diversity–parasite-diversity relationship might be affected by human impacts on ecosystems. Here, we pose the question: How does *anthropogenic disturbance* influence the host-diversity-begets-parasite-diversity pattern?

We outline multiple working hypotheses to address this question, using as our study system the parasites of coral reef fishes on islands of the central equatorial Pacific. Our previous work on this system generated an important insight: fishing appears to significantly reduce parasite diversity (Wood, Sandin, Zgliczynski, Guerra, & Micheli, 2014; Wood et al., 2015; Figure 1a). Meta-analysis confirms that this pattern is general across marine ecosystems (Wood & Lafferty, 2015; Figure 1b). While our previous work has established that fishing drives declines in parasite diversity, a question that remains unanswered is: what is the mechanism by which this decline occurs? Do fishing-driven reductions in parasite diversity occur via a shift (i.e., reduction in intercept) of the host-diversity–parasite-diversity relationship or a shallowing (i.e., reduction in slope) of that relationship? Although the purpose of this paper is not to investigate the effects of fishing on fish biodiversity, we do carefully track both fishing and fish biodiversity to test whether these factors have additive, synergistic, or antagonistic effects on parasite biodiversity (Figure 2).

First, we can envision scenarios where the relationship between host and parasite diversity is preserved, and fished and unfished environments merely represent opposite ends of a biodiversity spectrum, with parasite biodiversity varying continuously as a function of host biodiversity (Figure 2a). In these scenarios, human impacts do not fundamentally alter the nature of the host-diversity–parasite-diversity relationship. Parasite biodiversity might be resilient to anthropogenic reductions in host biodiversity (Figure 2a, solid line),

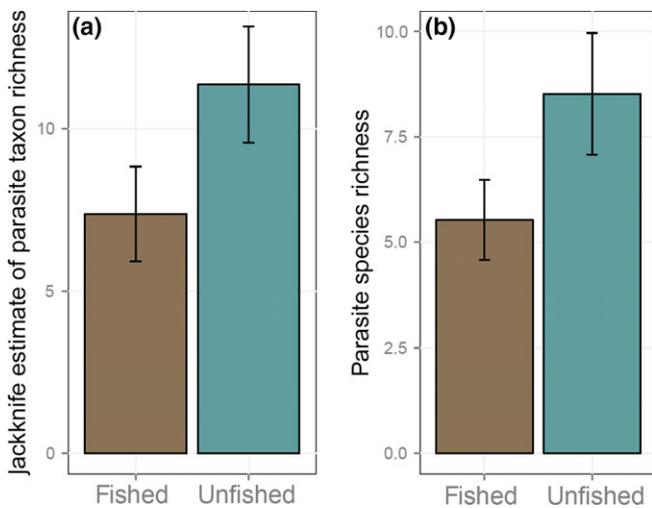


FIGURE 1 Mean and 95% CI for the effect of fishing (brown = fished, blue = unfished) on parasite diversity, (a) in coral reef fishes of the central equatorial Pacific, adapted from (Wood et al., 2015), and (b) across all published studies from marine ecosystems, adapted from (Wood & Lafferty, 2015)

particularly if parasites are generalists. In this case, we would expect the host-diversity–parasite-diversity relationship to be steeper in low-diversity than in high-diversity conditions (Figure 2a, solid line). In contrast, parasite biodiversity could be sensitive to biodiversity reductions (Figure 2a, dotted line), particularly if parasites are host-specific or have host density thresholds below which transmission becomes impossible (i.e., compensatory responses to reductions in host abundance). In this case, we would expect steeper host-diversity–parasite-diversity relationships in high-diversity relative to low-diversity conditions (Figure 2a, dotted line). Alternately, we might observe no difference in the slope of the host-diversity–parasite-diversity relationship between high-diversity and low-diversity conditions, but instead a linear reduction in parasite diversity (Figure 2a, dashed line).

We might also hypothesize scenarios in which the relationship between host and parasite diversity is decoupled, and fished and

unfished environments represent fundamentally different conditions for parasites, with parasite biodiversity varying discontinuously as a function of host biodiversity between these two environments (Figure 2b–c). Such an outcome could be related to habitat change, change in host composition (instead of mere richness), or change in unmeasured hosts (e.g., loss of zooplankton intermediate hosts in the presence of human impacts) and could produce hysteresis, where different levels of parasite biodiversity exist at the same level of host biodiversity. In these scenarios, human-driven biodiversity change fundamentally alters the nature of the host-diversity–parasite-diversity relationship. We begin by assuming that no parasites can exist where host diversity equals zero (Figure 2a–c). Human disturbance might cause a reduction in intercept (Figure 2b) if parasites of low- and high-host diversity environments are affected equally, where disturbance erodes some resource (other than host biodiversity) required across many parasite species or introduces some stressor that reduces the fitness across many parasite species. For example, some pollutants have broadly negative effects across parasite taxa (Lafferty, 1997). Human disturbance might cause a change in slope (Figure 2c) if it affects parasites of low- and high-host diversity environments unequally, eroding some resource (other than host biodiversity) required by or introducing some stressor that reduces the fitness of the species that are represented only where host diversity is high. For example, reductions in the availability of zooplankton would reduce the transmission success of specialist complex life-cycle parasites (i.e., those parasites that are obligately dependent on hosts of multiple species to complete their life cycles) but leave directly transmitted parasites unaffected (Wood et al., 2015).

We tested the influence of fishing pressure on the host-diversity–parasite-diversity relationship for metazoan parasites of coral reef fishes on three fished and three unfished islands of the central equatorial Pacific. Our data indicate that fishing drives a shallowing of the host-diversity–parasite-diversity relationship (consistent with Figure 2c), primarily through effects on complex life-cycle parasites. This work suggests that fishing decouples a fundamental ecological relationship, and is the first study to document the effects of human disturbance on the host-diversity–parasite-diversity relationship.

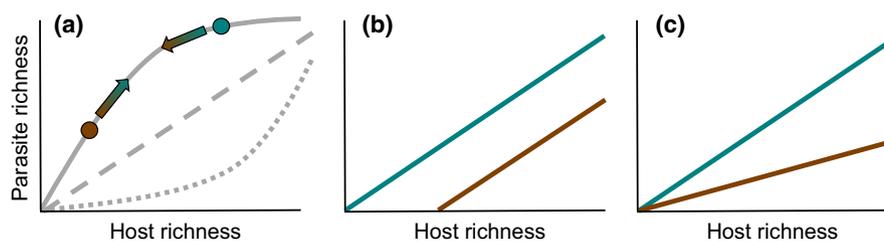


FIGURE 2 Alternative predictions for how the host-diversity–parasite-diversity relationship might change in the presence and absence of fishing. Fishing is indicated with color: blue = unfished and brown = fished. (a) Alternative scenarios under the assumption that parasite diversity changes continuously with host biodiversity, where fishing merely modulates the level of host biodiversity; blue and brown balls indicate an example scenario in which fishing reduces host biodiversity. Solid line = parasites resilient to reductions in host diversity, dotted line = parasites sensitive to reductions in host diversity, dashed line = parasite diversity changes linearly with host diversity. Additional alternative scenarios under the assumption that parasite diversity changes with host biodiversity discontinuously in fished vs. unfished environments, and where fishing drives (b) a reduction in intercept, (c) a reduction in slope

2 | MATERIALS AND METHODS

2.1 | Study system

We quantified host and parasite biodiversity at three fished and three unfished coral islands of the Line Islands archipelago in the central equatorial Pacific (from north to south: Kingman Reef, Palmyra Atoll, Teraina [Washington] Island, Tabuaeran [Fanning] Island, Kiritimati [Christmas] Island, and Jarvis Island; Figure 3). The unfished islands, Jarvis, Kingman, and Palmyra, are US possessions that were incorporated into the US Pacific Remote Islands Marine National Monument in 2009 (Bush, 2009), and protected prior to that as US National Wildlife Refuges (beginning in 1974 for Jarvis and 2001 for Kingman and Palmyra; Maragos, Friedlander, et al., 2008). Both designations involve a strict ban on habitation and fishing, and all of these islands are extremely remote and were probably only sporadically visited by humans prior to formal protection (Maragos, Miller, et al., 2008). In contrast, Teraina, Tabuaeran, and Kiritimati are islands of the Republic of Kiribati, and each are inhabited by between several hundred and several thousand people who engage in subsistence fishing as a primary economic activity [see data S1 in Sandin et al. (2008)]. Fishing is primarily by hook and line, with some spearfishing, and tends to target predatory species of fish (Zgliczynski & Sandin, 2017). On Kiritimati and Tabuaeran, fishing occurs primarily from outrigger boats, targeting reef and nearshore pelagic habitats [see data S1 in Sandin et al. (2008)]. On Teraina, where there is limited boat access, nearshore spearfishing is common [see data S1 in Sandin et al. (2008)]. Previous studies have shown strong divergence in the fish communities between these three fished and three unfished islands, with higher fish biomass and abundance of top predators on unfished islands, and higher abundance of low trophic-level fishes like planktivores on fished islands, possibly due to release from predation pressure (DeMartini, Friedlander, Sandin, & Sala, 2008; Sandin et al., 2008). Island size, latitude, average sea surface temperature, and productivity are not correlated with fishing pressure among the six islands, and pooling data within the three fished and three unfished islands allows us to homogenize the influence of oceanographic factors across the archipelago (Sandin et al., 2008; Wood, Sandin, et al., 2014; Wood et al., 2015). This system is therefore a suitable natural experiment for testing the impacts of fishing-driven environmental change on a variety of ecosystem parameters, including host and parasite biodiversity.

Among our six focal islands, impacts other than fishing arise from human occupation, including inputs of waste to coral reef ecosystems [see data S1 in Sandin et al. (2008)]. Given high per capita rates of fish consumption (72–207 kg per person year⁻¹), the high rate of participation in fisheries activities (89%–96%), and high rates of subsistence reef fish catch (e.g., ~8 tons/week on Kiritimati), we surmise that fishing impacts on coral reef fish communities are large relative to human population size [see data S1 in Sandin et al. (2008)]. No industrial agriculture or manufacturing exist on the human-occupied islands, but these islands do lack

infrastructure for management of solid and human waste, and waste therefore flows directly onto reefs [see data S1 in Sandin et al. (2008)]. While we acknowledge that this nutrient input could affect reef ecosystems (including the relationship between host diversity and parasite diversity on reefs), we contextualize this by pointing out that the estimated per capita nutrient input on our human-occupied, focal islands (3.5 kg/year) is <5% of the typical per capita input of industrialized, noninsular populations (Sandin et al., 2008). We therefore expect that any ecological differences between human-occupied and unoccupied islands will arise primarily due to fishing impacts.

All sampling was conducted at between two and 10 sites within each island, as conditions permitted [see appendix C in Wood, Sandin, et al. (2014)]. By logistical necessity, host biodiversity surveys and host collections were conducted separately. Host biodiversity surveys were conducted between 2001 and 2010; collections were performed between July 2009 and July 2011, with the bulk (90.2%) of samples arising from an expedition mounted in October/November 2010. The use of data collected in different years and seasons makes it possible for temporal mismatch to confound our ability to detect relationships between host diversity (measured 2001–2010) and parasite diversity (measured 2009–2011). However, because no major disturbances (e.g., hurricanes) occurred during this time frame, and because coral reef fishes are relatively long-lived (Choat & Robertson, 2002) and many of the parasites we detected are probably long-lived in their hosts (Bailey, Margolis, & Workman, 1989; Hislop & McKenzie, 1976; Margolis & Boyce, 1969; Moller, 1976), estimates of host and parasite diversity are likely to be relatively stable over decadal scales.

2.2 | Host biodiversity surveys

At each of the multiple host-biodiversity sampling stations within each island, we assessed fish biodiversity of all fishes >3 cm in total length using standardized belt transects. We chose sampling stations randomly within the area on each island that could be safely surveyed and ensured that all stations were separated by at least 1 km. At each station, transect bearings were longshore, approximately isobathic, and confined to between 10 and 12 m depth. Surveys were conducted by paired divers, rotating among teams to distribute potential biases. Large-bodied (≥ 20 cm total length), vagile fishes were quantified in a 4-m wide strip (two 2-m wide strips separated by 1 m) on the swim out along the 25-m long transect, and small-bodied (<20 cm total length), site-attached fish were tallied in a 2-m wide strip on the return swim along the transect line. All fish were identified to species and binned into 5-cm total length classes. More details of fish survey methods are given in Friedlander, Sandin, DeMartini, and Sala (2010) and Zgliczynski and Sandin (2017).

Because differences in sampling effort can confound the comparison of diversity among replicates, we accounted for differences in number of fish encountered by calculating richness estimates. The jackknife estimator projects fish species richness at the saturation of the species accumulation curve for each sampling station (Zelmer &

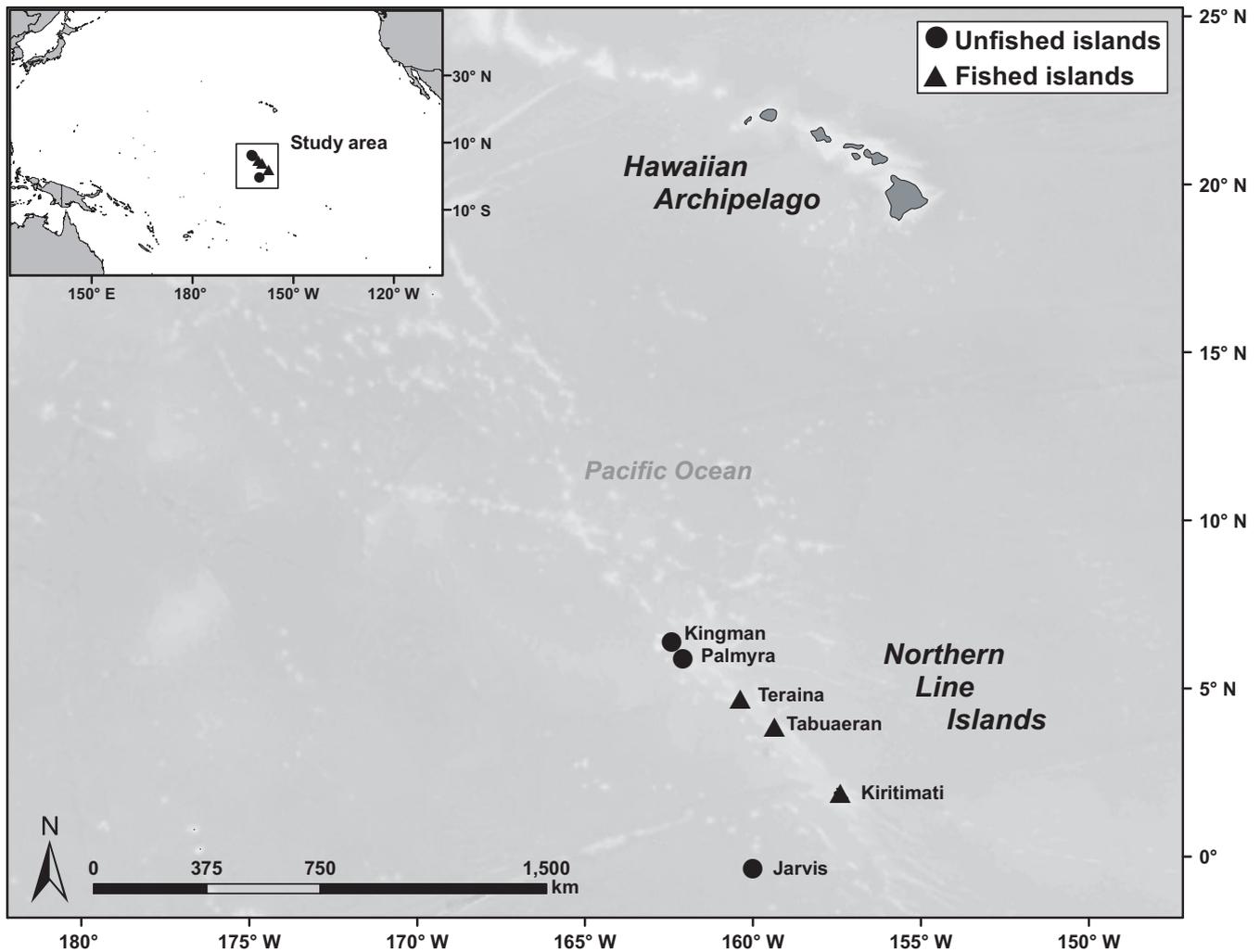


FIGURE 3 Three fished islands (Teraina, Tabuaeran, and Kiritimati) and three unfished islands (Jarvis, Kingman, Palmyra) of the Line Islands archipelago

Esch, 1999), and was calculated using the SPECIES package in R. Jackknife estimates of large- and small-bodied fish species richness were calculated separately and added together to obtain total fish species richness for each transect, and transect-level estimates of total jackknife richness were averaged to obtain island-level jackknife richness.

2.3 | Collecting fish hosts for parasite biodiversity assessments

At each of these six islands, we sampled seven species of reef fishes (*Cephalopholis urodeta*, *Acanthurus nigricans*, *Ctenochaetus marginatus*, *Paracirrhites arcatus*, *Stegastes aureus*, *Chromis margaritifer*, and *Pseudanthias bartlettorum*). The seven host species span a variety of body sizes, represent important trophic and taxonomic groupings, and include only broadly distributed species present at most reefs in the region (Wood, Sandin, et al., 2014; Wood et al., 2015). To maximize our scope of inference, we selected focal host species that represent a cross-section of coral reef fish

biodiversity, allowing us to obtain an optimally representative subset of parasite species. *C. urodeta*, *A. nigricans*, *C. marginatus* are probably targeted by fishers on the focal islands (Zgliczynski & Sandin, 2017). *P. arcatus*, *S. aureus*, *C. margaritifer*, and *P. bartlettorum* are probably not exploited (Zgliczynski & Sandin, 2017). Fish were collected by scuba divers using three-pronged spears (for fish >10 cm in total length) and hand nets (for fish <10 cm). We sampled at least 25 individuals of each species from each island, and exceeded 25 individuals for most species–island combinations [see appendices A and B in Wood, Sandin, et al. (2014)]. Because habitat type and wave exposure of collection sites might influence estimates of parasite abundance, we attempted to hold these variables constant by conducting most sampling on the leeward foreereef of each island at depths between 11 and 18 m [see appendices C and D in Wood, Sandin, et al. (2014)]. We recorded several items of meta-data for each fish, including total length, standard length, fork length, and mass. Fish were frozen immediately after collection, and were kept frozen until being thawed for dissection.

2.4 | Parasite biodiversity surveys

We performed a comprehensive examination of each fish, designed to detect most metazoan parasites. We did not count mobile skin parasites or micropredators, as these are easily lost when the host is captured, and we did not search for myxozoan parasites, but all other metazoans should have been detected with our protocol. We adapted the dissection protocol to the morphology of each fish species (keeping the protocol consistent within species); both the generalized dissection protocol and departures from it are detailed elsewhere [see appendix E in Wood, Sandin, et al. (2014)]. Briefly, we examined the following organs individually under a stereomicroscope: fins, gills, eyes, heart, liver, spleen, gonad, gills, muscle, skin, and intestines [after Wood, Sandin, et al. (2014)]. Stomachs were not available for parasite analysis, but intestines were subject to a thorough parasitological examination. When an organ was missing or damaged (e.g., part of fin was missing), we recorded “n/a,” not “0,” for any parasite species typically found in that organ (e.g., fin metacercariae). Photographs of each parasite species (along with detailed images of diagnostic morphological features) and voucher specimens were archived and are available for examination by request to the corresponding author. We identified parasites to the lowest possible taxonomic level using published keys [see appendix F in Wood, Sandin, et al. (2014)].

Because differences in sampling effort can confound the comparison of diversity among replicates, we accounted for differences in number of parasites encountered by calculating richness estimates. The jackknife estimate of parasite taxon species richness (Zelmer & Esch, 1999) was calculated using the SPECIES package in R. Jackknife richness was calculated using all the parasites we detected (including rare parasite taxa) for each host species–island combination.

2.5 | Quantifying other potential drivers of parasite biodiversity

We also considered the influence of various factors as potential alternative drivers of parasite diversity.

2.5.1 | Energy

The “resource rarity hypothesis” states that species richness is constrained by partitioning of available energy among species present in a given area (Abrams, 1995; Brown, 1981; Francis & Currie, 2003; Hutchinson, 1959; Wright, Currie, & Maurer, 1993); increasing resource availability can allow more “packing” of species into niche space, increasing species diversity (MacArthur, 1970). Nearshore productivity was measured using appropriately area-scaled and masked grid cells from satellite-derived ocean color data [using MODIS maps estimating surface chlorophyll-*a* concentrations; methodological details in Gove et al. (2013)]. Briefly, long-term means of chl-*a* (mg/m³) were estimated by sampling the 8-day 0.0417° (~4-km) spatial resolution product for targeted islands over a 10-year period (2006–2016) and averaged to obtain an island-level mean.

2.5.2 | Ecosystem size

Larger areas have higher rates of speciation and lower rates of extinction, leading to higher diversity (Losos & Shluter, 2000; MacArthur & Wilson, 1963, 1967). Speciation rates may increase with ecosystem size because increasing area increases habitat diversity, the likelihood of geographic isolation, and the amount of genetic diversity and the number of individuals for natural selection to act on (Losos & Shluter, 2000). Increasing area also increases population size and habitat diversity, increasing availability of refugia and thereby decreasing extinction rates (Rosenzweig, 1995). We estimated the size of the fringing coral reef ecosystem at each island with island perimeter in km, which was measured in Google Earth.

2.5.3 | Isolation

According to the equilibrium theory of island biogeography, dispersal probability declines as island isolation increases, reducing rates of immigration and thereby reducing diversity (MacArthur & Wilson, 1963, 1967; Whittaker & Fernandez-Palacios, 2007). Isolation increases with increasing distance from propagule sources (e.g., distance from neighboring islands) and decreasing “target area” (which can modulate the likelihood of colonization by immigrants; e.g., length of shoreline, elevation range). The isolation of each island was summarized with the UNEP Island Directory’s isolation index (Dahl, 2004). The UNEP isolation index is calculated as the sum of the square root of the distances to the nearest equivalent or larger island, the nearest island group or archipelago, and the nearest continent (Dahl, 2004). UNEP did not score isolation for Kingman Reef, so we assumed that its isolation score was equivalent to that of nearby Palmyra Atoll.

2.6 | Statistical analyses

First, we assessed whether fishing changes the relationship between host and parasite diversity at the island level. We ran a generalized linear mixed model with Poisson error structure to predict variability in the jackknife estimate of parasite taxon richness. Models included an interaction between host biodiversity and fishing status (fished vs. unfished) and random effects of island and host species, to account for multiple observations within each host species (across islands) and within each island (across host species). To account for other potential drivers of parasite diversity, we also included the covariates ecosystem size (proxied by island perimeter), host body size (average host total length within host species within each island), energy (average nearshore [chl-*a*] across each island), and isolation (UNEP isolation index). Covariates were removed from the model through manual backwards elimination if they were not significant at $\alpha = 0.10$. This level of α was chosen so as to include even marginally influential covariates in the overall model, but $\alpha = 0.05$ was used as the standard for hypothesis testing. This analysis was conducted using the *glmmadmb()* function of the *glmmADMB* package in R.

We identified parasite taxa contributing to differences in parasite community composition between fished and unfished islands using SIMPER analysis. This analysis was conducted separately for each host species, on a presence–absence matrix for each parasite species in each host individual, and was carried out using the *simper()* function in the R package *vegan*. All parasite taxa that contributed significantly to differences in composition between fished and unfished islands are reported in Table 1; their proportional contributions to overall dissimilarity are reported as percentages in that table. To assess whether these contributions were consistent with findings from previous analyses (Wood, Sandin, et al., 2014; Wood et al., 2015), we multiplied the proportional contribution to dissimilarity of each parasite taxon by the direction of the effect (+1 for parasite taxa that tended to be more common on fished islands, –1 for parasite taxa that tended to be more common on unfished islands), and used a general linear mixed model (including a random effect of host species) to test whether these contributions differed among three key groups (Wood et al., 2015): directly transmitted parasites, *Stephanostomum* spp. trematodes, and complex life-cycle parasites excluding *Stephanostomum* spp. trematodes. *Stephanostomum* spp. trematodes were set aside from the remainder of the trematodes and other complex life-cycle parasites because they have unique responses to fishing pressure, as demonstrated in previous work (Wood, Sandin, et al., 2014; Wood et al., 2015).

To identify which parasites drove the observed relationships between host diversity and parasite diversity, we ran a second SIMPER analysis that contrasted the composition of the parasite assemblage among Jarvis (high diversity), Palmyra (intermediate diversity), and Kingman (low diversity). This analysis was conducted separately for each host species, on a presence–absence matrix for each parasite species in each host individual, and was carried out using the *simper()* function in the R package *vegan*. For those species that contributed significantly to differences in composition among the three unfished islands, we plotted their likelihood of occurrence (prevalence) as a function of island-level fish diversity. This allowed us to identify parasite taxa that increased in likelihood of occurrence with increasing fish diversity, which are the taxa that create the positive host-diversity–parasite-diversity relationship.

We were especially interested in identifying those parasite taxa that were absent on either fished or unfished islands, since these taxa were especially likely to contribute to parasite richness differences between fished and unfished islands. We compiled a table of all parasite species that were entirely absent on either fished or unfished islands.

Finally, we tested whether fishing homogenized the composition of the parasite community and whether this homogenization depended upon the body size of the host species. We used a multivariate approach based on the Bray–Curtis dissimilarity index for a matrix of parasite presence/absence. Because many host species did not share any parasite species in common and were therefore infinitely different in parasite species composition, each host species was analyzed separately. Host individuals carrying no parasites were

excluded, since a fish with no parasites is undefined in parasite-species space. We calculated the homogeneity of parasite infracommunities (i.e., communities of parasites within a host individual) on fished vs. unfished islands for each host species using the *betadisper()* function of the *vegan* package in R (Okansen, 2015), with method = “w” (Koleff, Gaston, & Lennon, 2003). We subtracted the output “distances to median” (inverse of homogeneity) for fished islands from the same value for unfished islands to develop an index of fishing-driven homogenization. We then tested whether this index of homogenization differed significantly from zero to address whether fishing homogenized parasite communities. We also tested whether the homogenization index varied depending upon the body size of the host, using linear regression. We extracted body size for each host species (maximum total length in cm) from FishBase (Froese & Pauly, 2000).

3 | RESULTS

From 33 sampling stations distributed across the six islands (Wood, Sandin, et al., 2014; Figure 3), we collected 945 fish hosts that yielded 919,283 individual parasites from 75 taxa, including monogeneans, trematodes, cestodes, nematodes, acanthocephalans, and crustaceans.

The interaction between host diversity and fishing status was significant, indicating that the slope of the relationship between host and parasite diversity was more positive for unfished than for fished islands (estimate \pm SE = +0.189 \pm 0.092, $z = 2.06$, $df = 28$, $p = .039$; Figure 4). Ecosystem size was positively but nonsignificantly associated with parasite diversity (estimate \pm SE = +0.009 \pm 0.005, $z = 1.78$, $df = 28$, $p = .075$) and host body size was positively and significantly associated with parasite diversity (estimate \pm SE = +0.004 \pm 0.002, $z = 2.22$, $df = 28$, $p = .027$). All other terms (e.g., energy, isolation) were removed from the model through manual backwards elimination.

Using SIMPER, we then calculated the contribution of each parasite taxon to the compositional differences between fished and unfished islands. The taxa that significantly contributed to such differences are shown in Table 1. As in previous analyses, fished islands tended to be rich in directly transmitted parasites and trematodes in the genus *Stephanostomum*, whereas unfished islands tended to be rich in complex life-cycle parasites other than *Stephanostomum* spp. (Figure 5). This also held—with some important exceptions—when we examined parasite taxa that occurred *only* on fished or only on unfished islands (Table S1). Among the nematodes, three of four unique taxa occurred only on unfished islands and among the trematodes (excluding *Stephanostomum*), seven of nine unique taxa occurred only on unfished islands. Unexpectedly, four of five unique isopod taxa (directly transmitted parasites) occurred only on unfished islands; this was especially striking given that one isopod taxon (gnathiids in *C. marginatus*) was observed on all three unfished islands and none of the fished islands. In contrast, four of seven copepods occurred only on fished islands and two of

TABLE 1 Results of SIMPER analysis. “# obs” gives the number of fish in which each parasite was observed. Contribution % gives the percent of overall dissimilarity explained by parasite taxon. Cumulative % gives the cumulative percent, starting with the parasite taxon contributing the most to the dissimilarity. Displayed under the host species name are *p*-values indicating the significance of the difference in composition of parasite infracommunities between fished and unfished islands. [Colour table can be viewed at wileyonlinelibrary.com]

Host species	# obs	Parasite taxon	Relative abundance	Contribution %	Cumulative %
<i>Cephalopholis urodeta</i> (<i>p</i> = .001)	77	Gill metacercariae	Fished > unfished	0.1578755	0.1578755
	105	Larval nematodes (live + dead)	Unfished > fished	0.1398294	0.2977049
	131	Grandiunguid sp.	Fished > unfished	0.1296634	0.4273683
	47	<i>Hatschekia</i> sp.	Fished > unfished	0.1237275	0.5510958
	42	Visceral metacercariae	Unfished > fished	0.1195218	0.6706176
<i>Paracirrhites arcatus</i> (<i>p</i> = .001)	139	Fin metacercariae	Unfished > fished	0.0923233	0.7629409
	31	<i>Stephanostomum</i> sp. metacercariae	Fished > unfished	0.2332966	0.2332966
	29	Larval nematodes	Unfished > fished	0.1714884	0.4047850
	40	Fin metacercariae	Unfished > fished	0.1659964	0.5707814
<i>Acanthurus nigricans</i> (<i>p</i> = .043)	24	Bucephalid sp.	Unfished > fished	0.1464580	0.7172394
	83	Microscaphid sp.	Fished > unfished	0.2063013	0.2063013
	82	Gill metacercariae sp. 1	Fished > unfished	0.2021448	0.4084461
	53	Tetraphyllidean sp.	Unfished > fished	0.1904711	0.5989172
<i>Ctenochaetus marginatus</i> (<i>p</i> = .001)	29	Cucullanid nematode	Fished > unfished	0.1283453	0.7272625
	50	Grandiunguid sp. 2	Fished > unfished	0.1818326	0.1818326
	71	Grandiunguid sp. 1	Fished > unfished	0.1815747	0.3634073
	54	Gill metacercariae	Unfished > fished	0.1430694	0.5064767
	52	Tetraphyllidean sp.	Unfished > fished	0.1349762	0.6414529
<i>Chromis margaritifer</i> (<i>p</i> = .001)	116	Ancyrocephalid sp.	Fished > unfished	0.0834301	0.7248830
	24	<i>Stephanostomum</i> sp. metacercariae	Fished > unfished	0.3163030	0.3163030
<i>Pseudanthias bartlettorum</i> (<i>p</i> = .004)	22	Grandiunguid sp. 1	Unfished > fished	0.3086157	0.6249187
	6	Microscaphid sp.	Unfished > fished	0.4145455	0.4145455
	6	Grandiunguid sp. 2	Fished > unfished	0.2145454	0.6290909
<i>Stegastes aureus</i> (<i>p</i> = .001)	6	Grandiunguid sp. 1	Fished > unfished	0.2018182	0.8309091
	46	<i>Stephanostomum</i> sp. metacercariae	Fished > unfished	0.4911634	0.4911634
	64	Fin metacercariae	Unfished > fished	0.3987011	0.8898645

three *Stephanostomum* spp. occurred only on fished islands; this was especially striking for the *Stephanostomum* sp. in *A. nigricans*, which was found on all three of the fished islands and none of the unfished islands.

Parasite diversity did not vary with fish host diversity on fished islands, but the two factors were positively correlated on unfished islands (Figure 4). To identify the parasite species and groups that contributed to the positive host-diversity–parasite-diversity on unfished islands, we plotted the likelihood of occurrence for all of the parasite taxa that significantly contributed to parasite community composition differences among the unfished islands. That is, we took those parasite species that contributed significantly to compositional differences among the three unfished islands in a second SIMPER analysis that included only the unfished islands (in contrast

to the SIMPER analysis reported in the previous paragraph, which included all islands), and plotted the prevalence of those species as a function of island-level species richness (Figure 6). The plot suggests that the taxa contributing to the positive host-diversity–parasite-diversity relationship are primarily trematodes and cestodes.

Fished islands were not significantly more homogeneous in their parasite composition than unfished islands ($t_6 = -0.884$, $p = .411$), but whether the compositional homogeneity of the parasite community was greater on fished islands or unfished islands depended on the body size of the host ($F_{1,5} = 5.273$, $p = .070$). Parasite communities of larger fish tended to be homogenized on fished islands, but fishing actually increased the heterogeneity of parasite communities of smaller fish (Figure 7).

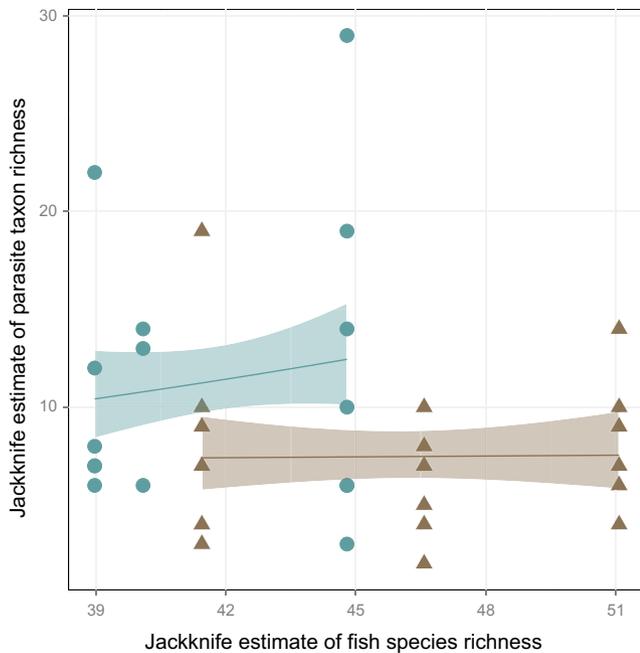


FIGURE 4 Relationships between host diversity (jackknife estimate of fish species richness) and parasite diversity (jackknife estimate of parasite taxon richness) on fished (brown) and unfished (blue) islands. Each point represents the jackknife estimate of parasite taxon richness within one host species at one island. Shaded areas indicate confidence intervals. The slope of the host-diversity–parasite-diversity relationship is significantly greater on unfished islands than on fished islands. Kingman fish species richness = 39.0, Palmyra = 40.1, Teraina = 41.4, Jarvis = 44.8, Tabuaeran = 46.6, Kiritimati = 51.1

4 | DISCUSSION

Human impacts can decouple ecological relationships (Tittensor et al., 2007; Williams et al., 2015). Here, we demonstrate for the first time that this also occurs for a fundamental parasitological relationship: that between host and parasite diversity. Our data suggest that the host-diversity–parasite-diversity relationship is positive in the absence of fishing and absent in the presence of fishing, although much variance in parasite biodiversity remains unexplained (Figure 4). Differences in overall parasite diversity between fished and unfished islands are primarily driven by the positive effect of fishing on directly transmitted parasites and *Stephanostomum* sp. trematodes and negative effects on complex life-cycle parasites (Figure 5). On the other hand, the positive host-diversity–parasite-diversity relationship on unfished islands is driven by an overlapping but slightly different suite of parasites, primarily cestodes and trematodes (Figure 6).

The positive relationship between host and parasite diversity is a nearly universal pattern, documented across ecosystems, world regions, host taxa, and parasite taxa (Kamiya et al., 2014). Among literature estimates of the correlation between host and parasite diversity identified in a comprehensive meta-analysis, 95% were positive (Kamiya et al., 2014). Our data indicate that this fundamental ecological relationship is decoupled in the presence of fishing (Figure 4). This

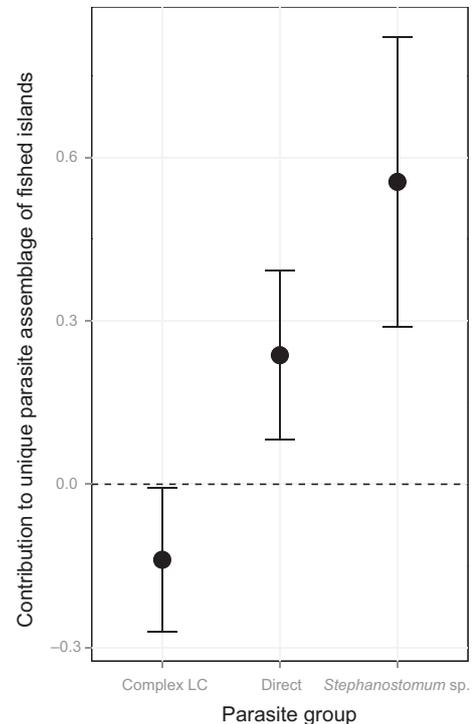


FIGURE 5 Mean and 95% CI for the contribution of each of three parasite groups (complex life cycle parasites [excluding *Stephanostomum* spp. trematodes], directly transmitted parasites, and *Stephanostomum* spp. trematodes) to the divergence in parasite assemblages between fished and unfished islands, where positive values indicate greater likelihood of occurrence on fished islands, and negative values indicate greater likelihood of occurrence on unfished islands

does not appear to be exclusively due to fishing-driven shifts in fish host diversity (as predicted in Figure 2a), because the host-diversity–parasite-diversity curves are discontinuous between fished and unfished islands (Figure 4). Instead, the data are most consistent with the prediction in Figure 2c, where parasite diversity changes with host diversity discontinuously in fished vs. unfished environments and the curves differ in slope. This suggests that, while the response of parasite diversity to fishing may constitute a response to shifts in fish host diversity in part (as in Figure 2a), other fishing-related factors also influence parasite diversity. For example, fishing may remove nonfish hosts of complex life-cycle parasites (which would not be counted in our “fish host diversity” metric); since complex life-cycle parasites tend to be represented only in high host diversity environments, this would have the effect of shallowing the host-diversity–parasite-diversity relationship on fished islands. Put simply, fishing might decouple the relationship between host and parasite diversity by taking away some other resource on which parasites depend, making it moot whether the appropriate host is present (high host diversity) or not (low host diversity), and thereby erasing what otherwise would be a positive relationship between host and parasite diversity.

The results presented here clearly indicate that parasite biodiversity tends to be higher in the absence of fishing than in its presence—there were, on average, >50% more parasite taxa on unfished than

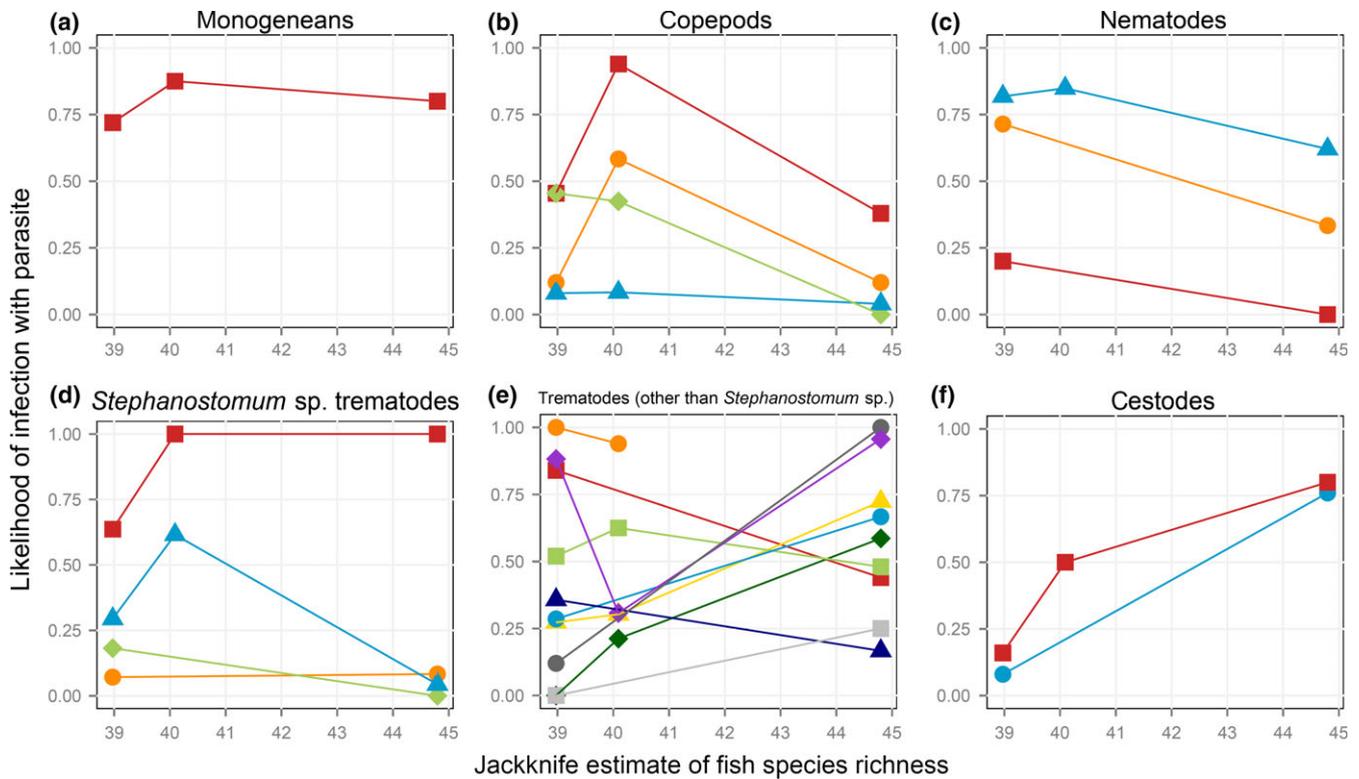


FIGURE 6 Relationships between host diversity (Jackknife estimate of fish species richness) and the likelihood of a parasite occurring in a given host individual (i.e., prevalence) on the three unfished islands (Kingman fish species richness = 53.9, Palmyra = 57.4, Jarvis = 58.8), for taxa belonging to the (a) Monogenea, (b) Copepoda, (c) Nematoda, (d) genus *Stephanostomum*, (e) Trematoda (excluding those taxa in the genus *Stephanostomum*), and (f) Cestoda. Each line indicates a single parasite taxon. The positive relationship between host diversity and parasite diversity on unfished islands (Figure 4) appears to be driven primarily by trematodes (d and e) and cestodes (f)

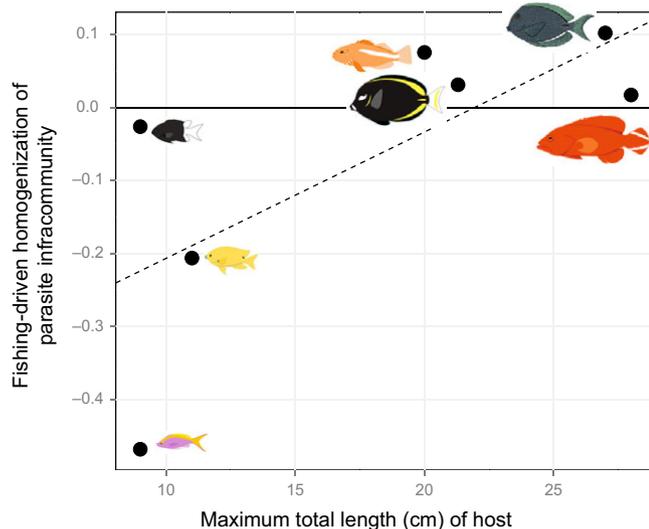


FIGURE 7 Relationship between host body size (fish maximum total length in cm) and the degree to which a host's parasite fauna is homogenized in the presence of fishing. Parasite assemblages of large-bodied hosts are homogenized in the presence of fishing, whereas parasite assemblages of small-bodied hosts actually become more heterogeneous in the presence of fishing

on fished islands (Figure 4). But which parasite taxa drive this pattern? Our analysis suggests that complex life-cycle parasites (i.e., cestodes, nematodes, trematodes other than those in the genus *Stephanostomum*) tend to be absent on fished islands, while directly transmitted parasites and trematodes in the genus *Stephanostomum* are more likely to occur on fished than on unfished islands (Figure 5). We decided to separately track the response of the genus *Stephanostomum* because it had displayed extreme responses to fishing in prior work (Wood, Sandin, et al., 2014; Wood et al., 2015). We believe that *Stephanostomum's* positive response to fishing may arise from a trophic cascade in which fish that prey on snails are lost to fishing (as in McClanahan, 1989), leading to an increase in the snail intermediate host of *Stephanostomum* (Wood, Sandin, et al., 2014). While the identities of the first intermediate hosts of the *Stephanostomum* spp. metacercariae we detected are unknown, other *Stephanostomum* spp. are known to use large, sand- and mud-dwelling whelks (superfamily Buccinoidea) and moon snails [superfamily Naticoidea; see table 4 in Barnett, Miller, and Cribb (2010)], which are prey for large, molluscivorous fishes (Palmer, 1979; Vermeij, 1977). Possessing first intermediate hosts that benefit from fishing might predispose *Stephanostomum* spp. metacercariae to respond positively to fishing pressure. It should be noted, however, that this

is merely a hypothesis, which we posit here to explain the divergent response of *Stephanostomum* spp. to fishing; this hypothesis remains to be tested. Among directly transmitted parasites, positive responses to fishing might arise from an increasing density of low-trophic level hosts released from predation pressure (Wood, Sandin, et al., 2014; Wood et al., 2015). But although a handful of directly transmitted and *Stephanostomum* sp. parasites respond positively to fishing pressure, they are swamped by the many complex life-cycle parasites that respond negatively to fishing. Complex life-cycle parasites depend on multiple host species to complete their life cycles—not just the fish quantified in our surveys, but also benthic invertebrates, zooplankton, and in some cases marine mammals, birds, and large pelagic vertebrates that sporadically visit coral reefs; as the number of obligately required hosts increases, so should the risk that one of those hosts might be lost to fishing [sensu Colwell et al. (2012)]. Additionally, many complex life-cycle parasites use apex predators as definitive hosts, which can be difficult to quantify in fish surveys (MacNeil et al., 2008; McCauley et al., 2012) and are especially sensitive to human disturbance (DeMartini et al., 2008; Sandin et al., 2008; Stevenson et al., 2007). Therefore, the diversity of complex life-cycle parasites might decline because some other resource need is unmet in fished environments—whether for unmeasured (i.e., reef-associated nonfish) hosts, appropriate habitat, or appropriate environmental conditions. In this way, overall food web simplification can drive declines in parasite diversity.

Complex life-cycle parasites drive the overall parasite diversity differences between fished and unfished islands, and they are also the species that drive the positive host-diversity–parasite-diversity relationship on unfished islands; their absence on fished islands explains why these environments do not display positive host-diversity–parasite-diversity relationships. On unfished islands, complex life-cycle parasites are the primary beneficiaries of increasing diversity (Figure 6). This is especially true for the cestodes (Figure 6f) and the trematodes (Figure 6e). The cestodes we detected use elasmobranchs as definitive hosts (Khalil, Jones, & Bray, 1994), and these fishes are exceptionally sensitive to fishing pressure (Fowler et al., 2005), which might make cestodes especially vulnerable to fishing-driven declines.

Prior analyses conducted on the same dataset investigated patterns in parasite abundance (Wood, Sandin, et al., 2014; Wood et al., 2015), whereas here we are concerned with parasite taxon richness and with investigating which parasite taxa drive patterns in richness. Consistent with previous analyses of abundance, we observed that cestodes and nematodes (i.e., complex life-cycle parasites) were significantly less likely to occur on fished than on unfished islands, and that directly transmitted parasites and *Stephanostomum* sp. trematodes were more likely to occur on fished than on unfished islands. However, one important difference between the findings presented here and those from previous efforts (Wood, Sandin, et al., 2014; Wood et al., 2015) concerns the trematodes. In prior studies, the abundance of trematodes (excluding *Stephanostomum*) did not respond to fishing pressure (Wood, Sandin, et al., 2014; Wood et al., 2015); here, the presence of trematode species was negatively related to fishing pressure (Figure 5b). We surmise that this might be due to environmental

filtering: only trematode species that are resilient to fishing impacts occur on fished islands, and they are the only species that are available for comparisons of abundance between fished and unfished islands. This finding, and its divergence from previous studies, which concluded that trematode abundance might respond equivocally to fishing pressure (Wood, Sandin, et al., 2014; Wood et al., 2015), underscores the pervasive impact of fishing on complex life-cycle parasites.

One especially surprising insight from our analysis is that fished islands support higher fish biodiversity than unfished islands. This result could arise from any of the three following mechanisms: (i) fishing might increase fish biodiversity by removing predators and thereby releasing low trophic-level fishes from regulation, increasing the diversity of many low-trophic level fishes at the expense of decreasing the diversity of a few high-trophic level fishes (e.g., Sandin et al., 2008); (ii) factors other than fishing—such as evolutionary history, island geomorphology, or oceanography—might be important determinants of fish biodiversity among the six focal islands, and these factors may be confounded with fishing status; and (iii) fishing may in fact drive declines in fish biodiversity, but these declines are insufficient to overcome the influence of other, more influential factors (as in ii). We do not have enough data to discriminate among these possibilities, but sampling of additional islands in the region should shed light on whether fishing increases, decreases, or has no effect on fish biodiversity on these coral islands.

Several covariates were removed from our statistical model because they did not predict significant variability in parasite richness, including energy (concentration of chl-*a*) and isolation (UNEP isolation index), but ecosystem size (island perimeter) and host body size (host total length) were retained in the model. There was a non-significant, positive relationship between ecosystem size and the jackknife estimate of parasite taxon richness, consistent with the prediction from island biogeography theory that larger islands should support more species (MacArthur & Wilson, 1963, 1967). The significant, positive relationship between host body size and the jackknife estimate of parasite taxon richness is probably driven by two factors: (i) larger fish are older, and older fish have had more time to accumulate long-lived parasites (e.g., Lo, Morand, & Galzin, 1998; Poulin, 2000), and (ii) larger fish have relatively higher rates of movement and consumption and greater surface area, and therefore have more opportunity for contact with parasite transmissive stages (Arneberg, 2002; Guegan & Hugueny, 1994). Energy was eliminated from the model, but because the range of productivity values across our six focal islands is narrow (0.112–0.206 mg/m³), we do not interpret this result as strong evidence for a lack influence of oceanic productivity on parasite diversity. Island isolation was also eliminated from the model, which we do not find surprising, given the strong dispersal capabilities of marine parasites (Froeschke & von der Heyden, 2014); it is likely that even remote islands are easily reached by parasite species with vagile definitive hosts (e.g., cestodes in sharks, Mackiewicz, 1988; trematodes in birds, Keeney, King, Rowe, & Poulin, 2009), long pelagic larval durations (e.g., parasitic copepods; Messmer et al., 2011), and passive dispersion of eggs (e.g., some monogeneans; Plaisance, Rousett, Morand, & Littlewood, 2008).

Our data suggest that fishing does not homogenize parasite assemblages (Figure 7), even though it does reduce their overall diversity (Figure 4). We found that the parasite assemblages of larger fishes tended to be homogenized in the presence of fishing, whereas the parasite assemblages of smaller fishes tended to become more heterogeneous (although this result was only marginally significant at $p = .07$). We expect that this might arise because larger fish are more likely to experience direct fishing pressure (reducing their density and impoverishing their dependent parasite assemblages), whereas smaller fish are more likely to experience compensatory release in response to fishing (increasing their density and enriching their dependent parasite assemblages; sensu Sandin et al., 2008). One important constraint on this study concerns the narrow spectrum of body sizes spanned by our seven focal host species. In choosing these focal hosts, we were prevented by several logistical constraints from collecting large-bodied hosts (e.g., sharks, jacks, snappers), including their transient nature, their ability to evade capture, the danger they pose to scientific collectors, their rarity at fished sites, and our concern about depleting these vulnerable populations. We have observed that the larger-bodied species among our focal hosts (i.e., *C. urodeta*, *C. marginatus*, and *A. nigricans*) are targeted by subsistence fishers on Kiritimati, Teraina, and Tabuaeran (C. L. Wood, S. A. Sandin, and B. J. Zgliczynski, personal observations). Nonetheless, we believe it would be informative to expand the range of body sizes, not only to confirm the pattern documented in Figure 7, but also to understand how host body size influences the other patterns documented here.

Biophysical decoupling has been observed before, but no study before ours has shown that anthropogenic disturbance can decouple the host-diversity–parasite-diversity relationship. Our data demonstrate that this decoupling is driven primarily by negative impacts of fishing on the presence of complex life-cycle parasites, and that these are the same highly responsive parasites primarily responsible for the positive host-diversity–parasite-diversity relationships observed in the absence of fishing. Our study suggests that fishing leaves behind a biologically impoverished parasite fauna of directly transmitted parasites resilient to changes in host biodiversity. Whether this change in the composition of the parasite assemblage results in more or less disease for host fish is an open question.

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