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Critical Information Gaps Impeding Understanding of the Role of Larval Connectivity Among Coral Reef Islands in an Era of Global Change

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Populations of marine organisms on coral reef islands (CRI) are connected in space and time by seawater that transports propagules of plants, animals, and algae. Yet, despite this reality, it is often assumed that routine replenishment of populations of marine organisms on CRI is supported by locally-sourced propagules (hereafter, larvae). Following large disturbances, however, distantly-sourced larvae from less disturbed CRI within a regional meta-population are likely to be important for local population recovery, but evaluating the roles of locally- vs. distantly-sourced larvae remains difficult. While larval sources are relatively well-known for some fishes, they remain virtually unknown for most taxa, particularly those associated with the benthos, as exemplified by scleractinian corals. This review focuses on reef recovery and larval connectivity. Using corals as examples, we argue that CRI can serve as natural laboratories in which studies of these issues can enhance understanding of coral reef community dynamics under future disturbance regimes. Rather than focusing on synthesizing empirical data, we focus on the capacity for CRI to realize their potential in this research area, concluding that progress is impeded by the limited breadth, detail, and spatio-temporal concordance

of existing research. Using long-term observational programs of coral reefs in Mo'orea (French Polynesia), Okinawa (Japan), and St. John (US Virgin Islands) as examples of the data currently available, we make the case that new modes of multidisciplinary and collaborative research will be required to exploit the value of CRI in understanding the role of connectivity in mediating ecosystem resilience in a future affected by anthropogenic disturbances.

Keywords: marine larvae, coral reef, scleractinia, connectivity, resilience, ecology

MARINE CONNECTIVITY

Most generally, connectivity (**Box 1**) refers to the transport of fluid media (e.g., air, water), chemicals (e.g., nutrients, dissolved organic matter), and biota (e.g., adult organisms, reproductive propagules, microbes) among spatially distinct population patches (Hanski, 1999, 2002). Interest in demographic connectivity focuses mainly on the passage among populations of individuals and the genetic information they contain (Doherty et al., 1995; Planes and Fauvelot, 2002), thereby modulating the dynamics of local populations as well as the larger networks of populations to which they belong (Cowen et al., 2006; Holstein et al., 2014). Population connectivity is integrally related to metapopulation theory (Paris-Limouzy, 2011; Burgess et al., 2014), because it represents the capacity for exchanges among sub-populations to mediate ecosystem resilience (i.e., the ability to recover following disturbance) by supplying distantly-sourced recruits to augment locally-sourced recruits (**Box 1**). Given that local population dynamics can be strongly influenced by connectivity, this topic has featured prominently in ecological research for decades (Limouzy-Paris et al., 1997; Hanski, 2002; Cowen et al., 2003), and often has been presented as a dichotomy between connected vs. separated populations (Cowen et al., 2000). Recent work suggests connectivity is better considered as a continuum, along which populations can be intermittently connected by the periodic confluence of temporally constrained events (Kough and Paris, 2015).

Box 1 | Definition of terms used in this paper.

CRI	Coral reef island is defined as any island in tropical seas surrounded by coral reefs
Connectivity	Describes the passage of propagules among populations in a larger metapopulation structure, and here is operationally defined by the importance of locally-sources vs. distantly-sourced recruits in supporting population growth
Local	Operationally defined as the focal CRI of study
Distant	Operationally defined as any non-local CRI capable of supplying recruits to the focal CRI
Population	Operationally defined as conspecifics on a single CRI

Box 2 | Relationship between connectivity and sources of recruits.

$$Connectivity = R_{Distant}/(R_{Local} + R_{Distant})$$

Conceptual relationship between connectivity and sources of recruits in benthic marine populations, defined as originating from the focal CRI R_{Local}, or another CRI $R_{Distant}$. For a given site, the connectivity index would be expected to vary from ~ 0 (representing entirely local recruitment) to 1 (representing recruitment sourced entirely from distant sources). As conceived here, this simple ratio is independent of the magnitude or rate of overall recruitment.

Population connectivity is particularly relevant in the oceans, because water provides a dense fluid with buoyant and drag forces (Paris et al., 2013a) supporting the transport of organisms over large distances (Burgess et al., 2014) while differential advection and turbulence increase dispersion. Moreover, the majority of marine taxa has multi-stage life cycles and produce propagules capable of extensive transport by moving seawater (Wood et al., 2014). For many common benthic animals, the production of pelagic larvae supports dispersal among sessile adult populations (Paris-Limouzy, 2011; Burgess et al., 2014), for example, those found on the shores of coral reef islands (CRI). Connected by slow-moving seawater, CRI can create spatially segregated populations, among which the transport of pelagic larvae can mediate ecosystem resilience (Gunderson, 2000), although some oceanic currents can act as barriers to larval migration (Baums et al., 2006; Suzuki et al., 2016; Wood et al., 2016). Adults of highly motile taxa have the potential to move among CRI, although for many typical reef-resident taxa such as reef fishes, lobsters, and sea urchins, such dispersal appears to be infrequent (Saenz-Agudelo et al., 2011), and probably plays a modest role in connectivity relative to that facilitated by pelagic larvae (Botsford et al., 2009). Larval connectivity among CRI can be quantified as the proportional relationship at the population level of distantly-sourced larvae relative to the sum of locally- and distantly-sourced larvae recruiting at a site (**Box 2**). This ratio varies with time (e.g., seasonally) as a function of the integration time over which larval recruitment is measured.

CRI provide natural laboratories for studying population connectivity in a changing world (Kendall et al., 2013; **Figure 1**), which is an objective with broad utility in understanding the conditions favoring a return of community structure to an initial condition following a disturbance (i.e., ecosystem resilience; Gunderson, 2000). While CRI represent unique coral reef habitats that are tractable for the investigations of connectivity in mediating community recovery following disturbance, the principles they represent are applicable to a diversity of coral reef situations, for example, cohesive areas of reef that are being split into segregated communities through mortality, and fragmented

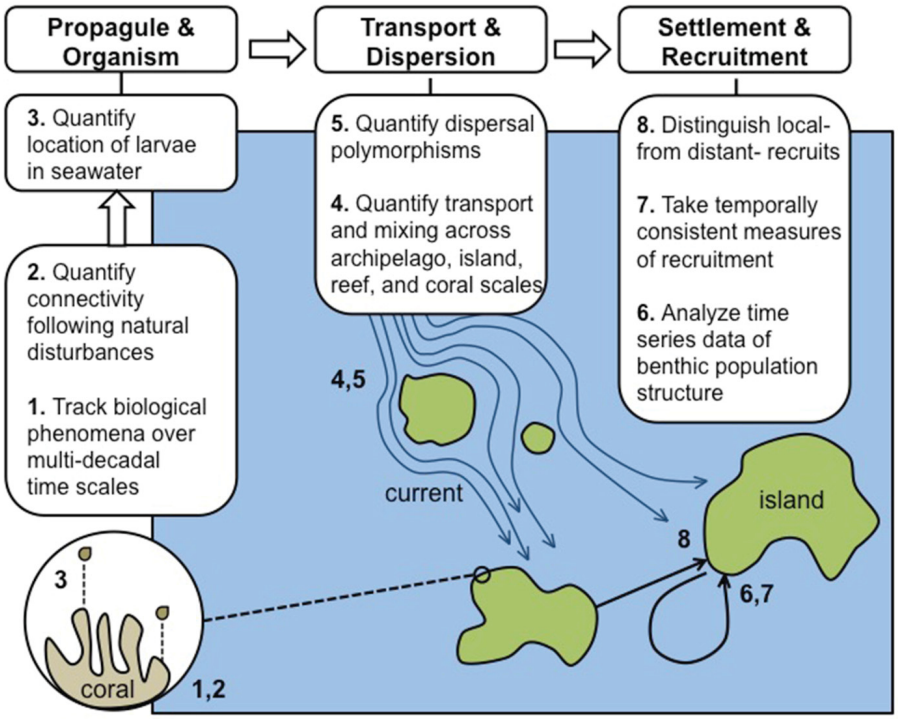

FIGURE 1 | Schematic of eight domains (described in the text with corresponding 1–8) requiring integration, concurrent research, and further quantitative data to allow CRI to achieve their full potential in advancing understanding of the role of connectivity in coral reef resilience. The needs for integration and additional data are divided into three categories underscoring the chronology of biological events beginning with reproduction and ending with recruitment, as exemplified by scleractinian corals: responses at propagule and organism levels, pelagic larval transport processes, and analysis of post-settlement and recruitment patterns.

habitats in multiple tropical ecosystems including mangroves, seagrasses, and soft sediments.

Previous studies have described the concepts associated with population connectivity in the marine realm (Cowen et al., 2006; Cowen and Sponaugle, 2009; Selkoe and Toonen, 2011), but many of these concepts require nuance in order to translate their meaning to CRI that have unique features associated with their physical oceanography, as well as the biological consequences of small and isolated populations (Paris et al., 2002; Kendall et al., 2013; Vaz et al., 2013). Many of these features differ from those affecting geographically large areas of coral reefs (e.g., continental barrier reefs; Lindo-Atichati et al., 2016), for example, because of the complex ways in which seawater flows among CRI having irregular shapes and deep underwater topography (Wolanski and Hamner, 1988; Paris et al., 2002; Baums et al., 2006). Submerged in the physical seascape surrounding CRI, near-shore reefs contain a diversity of organisms with contrasting life-history strategies that create multiple pathways for connectivity to mediate recruitment by locally- and distantly-sourced larvae (**Figure 1**). These features are likely to affect the resilience of coral reefs around CRI, and play an important role in determining whether populations of foundation species recover from landscape-scale disturbances, or remain in a depleted state (Munday et al., 2009). Clearly, the factors determining the dynamics of coral reefs around CRI are complex, and will not be fully explained by a single program focused on a single aspect of their ecology (e.g., connectivity). However, complexity does not imply intractability, and we suggest that a cohesive program focused on connectivity around CRI will greatly advance understanding of these issues. Ultimately, such a program will need to be augmented by studies of other processes, such as post-settlement success, the role of disturbances, and the factors controlling adult mortality, to realize its full potential.

CONTRASTING POPULATION DYNAMICS AMONG CORAL REEF ISLANDS

Using a framework created by the theoretical and empirical understanding of connectivity in the marine environment (Hanski, 2002; Hastings and Botsford, 2006; Burgess et al., 2014; Thompson et al., 2018), we consider how time-series analyses of the community structure of coral reefs around CRI can be interpreted within a connectivity framework. While such a framework is relevant to understanding the dynamics of a wide variety of organisms having pelagic propagules, including many fishes, algae, and invertebrates, we constrain our review to considering the utility of measures of connectivity among populations of scleractinian corals in order to enhance understanding of coral reef community dynamics. Addressing this topic constitutes a significant research challenge, but

providing definitive answers to outstanding questions is beyond the scope of what can be achieved with the available data.

Our objective is to highlight the needs for integration among studies, specifically addressing different disciplines such as physical oceanography, ecology, and genetics, and for specific types of data with the potential to deliver these answers. We underscore the importance of matched sets of complementary data that are collected on commensurate scales and can be used to support synthetic analyses within and among groups of CRI. We focus on scleractinians because they are the ecosystem engineers of coral reefs (Jones et al., 1994), and because they offer the advantage (compared to other taxa such as fishes and algae) that their settlement, recruitment, and growth provide an enduring calcified structure suitable for retrospective analyses of population dynamics. While adopting a restricted taxonomic approach, we recognize that other organisms (e.g., microbes, fish, echinoids, and algae) also support genetic exchange among CRI, and that research addressing connectivity for these groups is underway (e.g., Saenz-Agudelo et al., 2011; D'Aloia et al., 2015).

We illustrate our contribution using the shallow reefs of Mo'orea (French Polynesia), Okinawa (Japan), and St. John (US Virgin Islands), because: (a) they have decadal-scale records of coral reef community dynamics, (b) the records have been collected as part of larger programs co-located with observations of oceanographic conditions, recruitment, and population genetics, and (c) the projects are managed, or conducted, by the authors of the present contribution. Mo'orea, Okinawa, and St. John are surrounded by nearby CRI (i.e., within 10's—100's of kilometers), thereby creating the potential for locally- and distantly-sourced larvae to replenish populations following disturbances. The ecology of the coral reefs around each of these islands operates within different seascapes capturing dissimilar physical oceanography, regional-scale variation in patterns of organism diversity, disturbance histories, and local-scale anthropogenic effects created by human populations. While Mo'orea, Okinawa, and St. John provide examples of CRI within local-scale networks of other CRI, their seascape contexts suggest each CRI might interpret interactions with neighboring CRI in different ways. The coral reefs around these locations illustrate a range of fates similar to those affecting coral reefs around the world (e.g., Bruno and Selig, 2007; Jackson et al., 2014). Some reefs around St. John have undergone a phase transition to macroalgae (Rogers and Miller, 2006; Edmunds, 2015), while the resilient outer reefs of Mo'orea represent a case of rapid recovery from major coral mortality caused by a crown-of-thorns (COTs) outbreak and a cyclone between 2007 and 2010 (Bramanti and Edmunds, 2016; Holbrook et al., 2018). Okinawa represents a resilient coral community supported by exceptionally high recruitment despite frequent major typhoons and historical, yet recurrent, COTs outbreaks (Goto et al., 2011; Edmunds et al., 2015).

Previously, analyses of coral communities from 1992 to 2013 around Mo'orea, Okinawa, and St. John have been used to highlight among-site differences in the benthic community dynamics (Edmunds et al., 2015), particularly in terms of their responses to disturbances and their condition (e.g., coral cover) as of 2013, the most recent sampling included in the previous analysis. In evaluating why these locations have responded differently to disturbances (Edmunds et al., 2015), contrasts in key biological processes among locations emerged, including the delivery of larvae to benthic surfaces (i.e., coral recruitment on terracotta tiles) and the density of juvenile corals (colonies $\leq$ 5-cm diameter) on natural reef surfaces. For example, coral recruitment varied three orders of magnitude among islands (Okinawa > Mo'orea > St. John), the density of juvenile corals differed an order of magnitude among islands (generally Mo'orea and Okinawa > St. John), and recruitment and density of juvenile corals showed strong variation among years (Edmunds et al., 2015). A proxy for recruitment success—the ratio of the density of juvenile corals to the smaller coral recruits—differed four orders of magnitude among locations (Mo'orea > St. John > Okinawa), suggesting that the "post-settlement gauntlet" (sensu Arnold et al., 2010) was an important factor driving differential resilience of coral reefs around these CRI. This earlier analysis underscored the role of post-settlement mortality and juvenile coral success in mediating differential coral community dynamics among locations. Here we focus on the role of pre-settlement events leading to propagule delivery in determining reef resilience and recovery following disturbances. Survival during propagule delivery and settlement is among the earliest links in the chain of events comprising recruitment success and subsequent reef resilience.

With evidence of dissimilar community dynamics at three CRI, the present study began as an analysis of the role of connectivity in driving temporal differences in coral reef community structure in these locations. We reasoned that factors determining connectivity would differ among locations in ways that could inform our understanding of community dynamics. A fundamental hypothesis has been developed and can be addressed by our review: *Connectivity patterns provide insight into how future CRI community dynamics will be influenced by increasing rates of disturbance associated with climate change (Emanuel, 2005; Madin and Connolly, 2006).*

Initial inspection of the data suggested this hypothesis might be true. For example, the nearest neighboring CRI, and their sizes, differ among the locations, with St. John as close as ∼1 km to CRI ∼500 m long, and 2–3 km from CRI ∼15 km long. In contrast, Mo'orea is ∼16 km from Tahiti which is 60 km long, and Okinawa is as close as ∼0.5 km from CRI ∼ 3 km long, and within 30 km there are numerous small CRI. Consistent with these observations, the areas of coral reef from which larvae can be sourced vary among locations. For example, a 100 km radius around each CRI encompasses different areas of reef, ranging from 159 km^2 for Mo'orea, to 221 km^2 for St. John, and 407 km^2 for Okinawa (data: http://data.unep-wcmc.org/datasets/1). Likewise, the speeds of net prevailing surface currents also differ among locations, ranging from 11 to 25 cm s^{-1} for St. John, to 9–12 cm s^{-1} for Mo'orea, and 16–33 cm s^{-1} for Okinawa (data: http://bulletin.mercator-ocean.fr). Combining flow speed and distances to available source communities for coral larvae, yields estimates of the areas of reef within multiple days of seawater transport that differ among these CRI. While our observations and estimated potential larval source areas suggest that connectivity among nearby islands is a likely hypothesis

to account for differential resilience among our focal CRI due to climate change, specifically quantifying these effects proved beyond the scope the data currently available.

IMPLICATIONS OF CONNECTIVITY FOR THE RESPONSE OF CORAL REEFS AROUND CRI TO DISTURBANCES

Coral reefs are subject to numerous disturbances causing coral mortality (Nyström et al., 2000; Bellwood et al., 2004; Osborne et al., 2011), and large perturbations to ecosystem structure and function (Hughes et al., 2007; Mumby et al., 2007). Many of these disturbances also modify the genetic structure within populations (Foster et al., 2012), and connectivity to nearby populations (**Box 1**). Therefore, not only can disturbances reduce local coral cover, they can also impede the capacity for population replenishment through the delivery of larvae from other locations. For example, most corals and their photosynthetic symbionts are negatively affected by temperature elevated beyond normal summer-time values (Hoegh-Guldberg, 1999), with persistence of these conditions causing death through bleaching (Hoegh-Guldberg, 1999; Hughes et al., 2017). Even exposure to sub-lethal temperatures, or warmer-than-normal seasonal low temperatures, can have lingering effects that can depress fecundity for at least a year (Szmant and Gassman, 1990). Elevated seawater temperature also increases larval mortality (Randall and Szmant, 2009), as well as accelerates the development of coral larvae, subsequently reducing their pelagic larval duration (PLD), and the maximum distances over which they are likely to be transported by currents (O'Connor et al., 2007). The multi-faceted effects of seawater temperature on corals therefore have the potential to affect connectivity among CRI, with the implications dependent on whether specific CRI are sources or sinks for coral larvae, and the spatial extent of disturbance to which they are exposed.

Disturbances with serious implications for coral reefs are associated with rising concentrations in atmospheric pCO_2, which are driving: (1) elevated seawater temperature (Doney et al., 2012), (2) increasing intensity and frequency of severe tropical storms (Emanuel, 2005; Webster et al., 2005), and (3) declining seawater pH (i.e., ocean acidification; Doney et al., 2009). All three modes of disturbance have implications for connectivity among CRI (e.g., by mediating larval production, survival during dispersal, and settlement success), and the capacity for specific CRI to serve as larval sources or sinks (i.e., through regimes of widespread coral mortality or change in oceanic currents).

While insight into some aspects of the effects of global climate change on coral reefs is provided by decades of research on the thermal biology of corals (e.g., Coles and Jokiel, 1977; Fitt et al., 2001; Brown and Cossins, 2011), many studies lack mechanistic understanding and ecological relevance to the suite of conditions affecting corals *in situ*. Therefore, current knowledge provides an incomplete basis to evaluate the effects of rising temperature on reef corals around CRI and throughout tropical seas. Even less is known about the possible effects of ocean acidification for coral connectivity. Although some studies demonstrate adverse effects of elevated pCO_2 on the development of coral larvae (Nakamura et al., 2011; Fabricius et al., 2017), and their growth and calcification when settled and metamorphosed (Albright et al., 2008; Albright and Langdon, 2011), it is not yet clear whether, but appears likely that, these effects have ecological relevance for connectivity.

The effects of hurricanes and cyclones on coral reefs are well-documented (e.g., Woodley et al., 1981; Massel and Done, 1993; Harmelin-Vivien, 1994), but their projected increased severity in the coming century (Emanuel, 2005; Mann and Emanuel, 2006) is likely to increase the extent, and the rate of formation, of vacant space that is available for coral recruitment. While increased frequency of major storm impacts could increase coral recruitment by creating open space, more frequent scouring of benthic surfaces and high sedimentation associated with coastal run off and physical disturbance of reef sediments could be expected to impede recruitment and frequently reset CRI communities to early post-disturbance states (Grigg, 1983). Large storms can increase ocean mixing (e.g., Bernardo et al., 2017) and result in net decreases in water column temperatures, and some corals may synchronize their reproduction to occur in the period just before wet seasons that are frequently associated with latitudinal shifts in intertropical convergence zones (ITCZ) and storms (Mendes and Woodley, 2002). Thus, coral populations around CRI might receive increased input of larvae associated with connectivity from nearby CRI under future climate scenarios of increased storm frequency and disturbance. However, the combination of physical connectivity among CRI with increasing disturbance frequency, may not favor ecological resilience of coral communities as the spatial scale of reef damage expands.

Storms reflect local weather that is mediated by climatic phenomena, including El Niño, La Niña, Pacific Decadal Oscillation (PDO), the Atlantic Multi-decadal Oscillation (AMO), and latitudinal shifts in the Intertropical Convergence Zones (ITCZ), which may also change in intensity as global temperature rises (Cai et al., 2014). These phenomena bring large-scale changes in local conditions including seawater temperature and oceanic circulation (Cai et al., 2014) that have the potential to alter the transport of pelagic larvae among CRI (Treml et al., 2015; Wood et al., 2016). The effects of these disturbances are likely to be intensified by rising sea level resulting from the melting of polar ice caps and steric thermal expansion of seawater (Stammer et al., 2013), which in turn, will affect physical connectivity among CRI (Veron, 1995). Coral reefs that fringe submarine volcanoes in deep water—for example, Mo'orea and Oahu—are unlikely to experience major changes in absolute reef area, or the ways in which seawater circulates among them, as sea level rises. In contrast, a rise in sea level of only a few decimeters will inundate shallow island platforms in locations such as the Maldives and the Bahamas (Khan et al., 2002; Dasgupta et al., 2009), thereby increasing the area of benthic surfaces for reef growth, and perhaps increasing the net transport of seawater among islands (Veron, 1995). On a smaller scale, increases in sea level of only a few centimeters could enhance the passage of seawater over reef crests separating outer-

and back-reef communities (Monismith et al., 2013; Taebi and Pattiaratchi, 2014), and if the corals and algae at the crest are unable to accrete vertically to restrict the flow, this change could enhance connectivity between outer- and back-reef habitats and mediating their ecological resilience.

Finally, major disturbances, as well as numerous more minor and chronic mechanisms, are likely to alter species assemblages on CRI. The near-extirpation of *Acropora* spp. throughout the Caribbean by white band disease (Aronson and Precht, 2001) provides one example of this possibility. This loss increased the likelihood of local-recruitment for the coral community remaining, because with the rarity of spawning *Acropora* spp. (Aronson and Precht, 2001; Alvarez-Filip et al., 2009), many shallow Caribbean reefs now have high relative abundances of *Porites astreoides* (Green et al., 2008; Burman et al., 2012). Although spawning corals generally disperse greater distances than brooding corals (Connolly and Baird, 2010; Figueiredo et al., 2013), which favors strong connectivity among CRI, regional declines in population sizes of these corals are likely to reduce their total larval production. As species assemblages of reef corals and other taxa are modified through ecosystem degradation (Adjeroud et al., 2009; Done et al., 2015), the abundance of taxa producing larvae that can be transported large distances is likely to decrease, and probably will alter both connectivity among CRI and ecosystem resilience.

ACHIEVING THE POTENTIAL FOR CRI TO ADVANCE STUDIES OF CORAL REEF RECOVERY

The previous section highlights the complex processes that must be understood to evaluate the ecological implications of connectivity among CRI; achieving this understanding presents significant research challenges. There are compelling reasons to address these challenges because CRI can be used to answer long-standing questions regarding the dynamics of coral reef communities, both in CRI and more generally, throughout tropical regions (**Table 1**). Initially we reasoned that CRI for which time-series analyses of coral communities are well developed would provide opportunities to answer at least some of these questions. Yet despite the large quantities of data provided by the time series for our three focal sites, the data remained incomplete or spatio-temporally incompatible for one or more response variables (**Table 2**). Where data were more complete, often the sampling frequencies were inconsistent among variables, making it challenging to integrate data streams to achieve emergent properties of value in understanding of connectivity (**Figure 2**).

Although the biological and physical data available for Mo'orea, Okinawa, and St. John, are extensive by comparison to most CRI (**Table 2**), substantial limitations were encountered when we attempted to use them to quantify the role of connectivity in mediating coral community dynamics. Quantitative information from eight domains was required for this effort (described below), but in all cases the data available were limited. The temporal mismatch among data from CRI

TABLE 1 | Select questions addressing fundamental mechanisms mediating coral reef community dynamics in an age of strong anthropogenic disturbances that could be addressed using revised programs of integrated time-series analyses at CRI that address Domains 1–8 (in the text).

Question	Data types
1. Under what circumstances is hydrodynamic connectivity (and larval transport therein) strong vs. weak among adjacent CRI?	1,3–8
2. Where are the sources and sinks for larvae among adjacent CRI, and how are those related to their degree of resilience?	3–5,7,8
3. How will patterns of hydrodynamic connectivity among CRI be altered as a result of Global Climate Change, and will these effects differ spatially across tropical oceans?	3, 4,5
4. How much stochasticity in larval recruitment is created by inter-annual temporal variation in the hydrodynamic regime?	3–5,7,8
5. To what extent is there self-recruitment vs. external recruitment within CRI?	5,7,8
6. How does spatio-temporal variation in hydrodynamic regime interact with biological attributes of larvae (e.g., arising from brooding vs. broadcasting reproduction) to modulate patterns of connectivity?	1–5,7,8

Data types identify the domains from which data will need to be drawn to answer the questions.

(**Figure 2**) is exemplified by coral recruitment, which typically is estimated by using settlement tiles. Such tiles rarely are made from the same material among studies; they are not deployed in a standardized orientation and duration; and their deployments are not matched in space or time to local measurements of physical oceanographic processes. Genetic population structure typically was measured for a small number of taxa representing a limited fraction of the local biodiversity. Sampling of biological and physical processes rarely was repeated over multiple years, and empirical data to parameterize changes in connectivity as a result of global climate change were scant. Some of these issues reflect the origins of time-series studies of coral reefs around CRI, which usually began as isolated efforts with modest research budgets, and were situated in locations of convenience such as near existing marine labs, or haphazardly with respect to the ecology and physical oceanography of a specific region. Even the longest of these times-series studies are not yet adequate for understanding climate change effects. These limitations leave investigators with an imperfect, or largely absent, set of tools for studying the role of connectivity in mediating coral reef resilience.

Nonetheless, and despite the aforementioned limitations, CRI provide a unique opportunity to study population connectivity in systems likely to change in coming decades (Kendall et al., 2013; Edmunds et al., 2014). To achieve this potential, there are important information needs for additional data that must be addressed (Botsford et al., 2009). In part, these needs can be met by adding new dependent variables to strengthen ongoing time series, applying emerging technologies (and reducing costs associated with their application), and promoting uniform methods and inter-calibration for physical and ecological observations among studies. It may also be valuable to profoundly revise of the ways that community structure on CRI is measured, notably by adding new locations

TABLE 2 | Summary of concordance and mismatches among data types originating from time-series analyses of coral reef communities around three CRI, St. John, Mo'orea, and Okinawa.

Location	Variable/feature	No. of sites	Frequency (samples/y)	Duration (y)	Taxonomic resolution
St. John	Coral recruitment	5	1	10	Family
	Coral Cover	8	1	32	Species/Genus
	Temperature	3	$\sim 10^{-5}$	28	n/a
	Larvae	n/m			
	Juvenile corals	6	1	24	Species/genus
	Flow speed	1	1	1	n/a
	Genetics	n/m			
Mo'orea	Coral recruitment	5	0.5	10	Family
	Coral Cover	6	1	12	Genus
	Temperature	>10	$\sim 10^{-5}$	12	n/a
	Larvae	n/m			
	Juvenile corals	2	1	12	Genus
	Flow speed	3	10^{-5}	12	n/a
	Genetics	17			
Okinawa	Coral recruitment	20	1	15	Family
	Coral Cover	20	1	15	
	Temperature	15	$\sim 10^{-5}$	5	
	Larvae	n/m			
	Juvenile corals	20	1	15	Genus
	Flow speed	2	$\sim 10^{-5}$	5	
	Genetics	20	<1	1	

The mismatches in space and time among these data streams motivates the identification of domains within which coordination among studies, and enhanced data delivery, is required to achieve the research potential of CRI to advance studies of connectivity and reef resilience. n/m, not measured; n/a, not applicable.

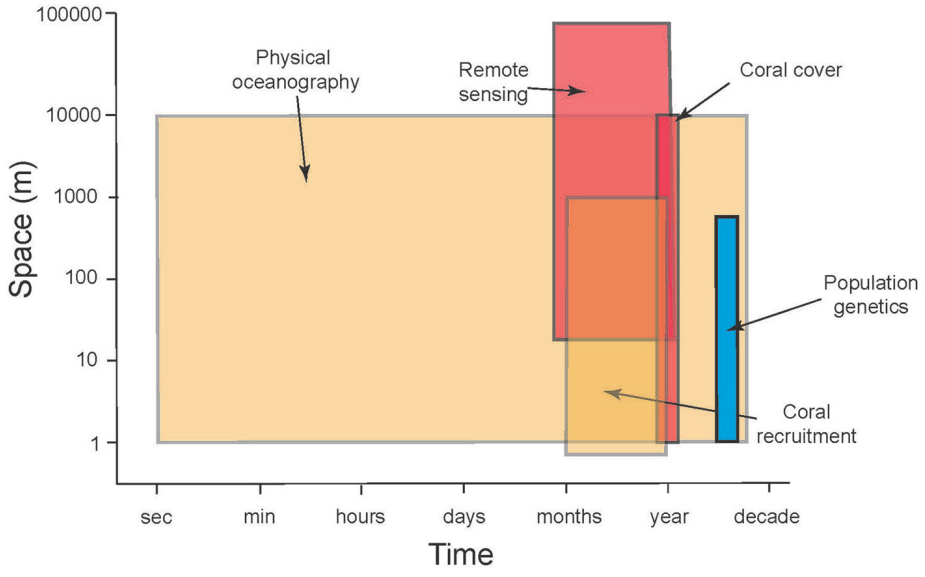

FIGURE 2 | Schematic illustrating the mismatch between scales of space (ordinate) and time (frequency of sampling, abscissa) in time-series analyses of CRI that are relevant to evaluating the roles of connectivity to reef resilience following disturbance. Shading indicates approximate longevity (number of years that sampling is sustained) of repeated sampling: blue = 1 year, brown = ≤ 20 y, red = ≤ 30 y.

that are selected in a pro-active manner to test specific hypotheses. Placement of such locations might be motivated by existing data to identify "hotspots" of larval sources (or sinks) or ecosystem resilience (Kough et al., 2013; Wood et al., 2014). Other approaches might use physical oceanographic modeling (Werner et al., 2007; White et al., 2010; Paris et al., 2013a; Treml

et al., 2015) to identify locations where community structure might be particularly sensitive to variation in larval connectivity, and differential reliance on local-recruitment vs. recruits from more distant locations (Kough et al., 2013; Snyder et al., 2014).

We propose eight domains in which time-series observations and analyses of CRI can be expanded to enhance understanding of connectivity and its role in modulating ecosystem resilience. The domains we describe are not intended to provide an exhaustive list of research needs, and largely are restricted to pre-settlement and recruitment periods. Clearly, the ecological patterns thus established are modified though post-settlement processes, and while such events are of great importance (Almany and Webster, 2006; Arnold and Steneck, 2011), they are beyond the scope of the current review. We intend here to summarize research needs with the greatest promise in rapidly advancing an understanding of the roles of connectivity in reef resilience. The eight domains are presented (**Figure 1**) to underscore research applicable to studying the focal taxon of this review (i.e., the Scleractinia), for which virtually all known larvae are pelagic and dispersive to a greater or lesser extent (Gleason and Hofmann, 2011).

PROPAGULES AND ORGANISMS

1. Multi-decadal time series are required to identify biological phenomena on CRI that operate over a wide range of time scales.

Ecological interactions often play out over long time scales, and it can be a challenge for ecologists to distinguish secular trends from noise in a time series. For this reason, long time series can be especially valuable for identifying trends in abundance and species composition of communities and detecting state shifts. Yet despite the clear need for such data, and the establishment of programs with the potential to deliver these data, multi-decadal analyses are rarely published or effectively managed to promote their discovery, access, and use. The acute need for access to data collected over ecologically meaningful time scales justifies devoting adequate resources to their management.

Multi-decadal time series on CRI are not abundant (e.g., Graham et al., 2011), but data from such diverse locations as the Caribbean (Graham et al., 2011), the Great Barrier Reef (Connell, 1997; Connell et al., 1997; Sweatman et al., 2011; Johns et al., 2014; Done et al., 2015; Tanner, 2017), northwestern Australia (Gilmour et al., 2013), Okinawa (van Woesik et al., 2011), Palau (Golbuu et al., 2007), and the Central South Pacific (Adjeroud et al., 2009; Holbrook et al., 2018) have revealed the dynamic interplay between physical and natural disturbances and the potential for subsequent community recovery. Lengthy time series provide the opportunity to capture rare events, as well as effects of repeated disturbances of different types. Sampling over long periods has revealed that after severe disturbance the return of the coral assemblage to its pre-disturbance state may take a decade or longer, depending on the life-history characteristics of the component species and the species interactions that set the pace of re-establishment of the community on the reef. For some CRI, repeated or chronic disturbances over decades have resulted in a different community state (Graham et al., 2011, 2015). The issue of shifting baselines is likely to become more critical as future climate change results in more frequent and intense disturbances to coral reefs.

Many time-series programs on coral reefs have focused primarily on assessing patterns in cover of live coral. A priority in the development of future time-series programs on CRI should be to quantify other aspects of the community, including the extent to which the coral taxonomic assemblage as well as other components of the reef community, including fishes, macroalgae, and non-coral invertebrates, re-assemble to their pre-disturbance state following perturbations (Holbrook et al., 2008; Johns et al., 2014; Done et al., 2015; Han et al., 2016; Tanner, 2017). Knowledge of the physical mechanisms and biotic interactions that influence community re-assembly and determine the similarity of pre- and post- disturbance communities is central to our understanding of community resilience in the face of climate change. It will be important to distinguish between recovery of a reef to a pre-disturbance level of coral cover as opposed to re-assembly to its pre-disturbance taxonomic structure and ecological function (i.e., "recovery without resilience" sensu Berumen and Pratchett, 2006).

2. Major natural disturbances including catastrophic storms, outbreaks of predators (e.g., Crown of Thorns Seastars), bleaching, or disease, create opportunities to quantify connectivity independent of varying historical precedence, as these disturbances typically result in large areas being reduced to an early successional state.

Despite the recurrence of large disturbance events in coral reef locations, resources rarely are mobilized in a systematic fashion to realize the potential to understand their effects on coral reefs. Patterns of initial recruitment one-to-several seasons following disturbances are likely to set population trajectories for subsequent multi-year periods (Bramanti and Edmunds, 2016). Adaptive sampling schemes to track disturbances and deploy recruitment tiles could facilitate understanding of patterns of initial recruitment among sites and regions. A large-scale, adaptive sampling approach would be able to capture such effects, but requires collaboration among researchers at multiple locations, and resource flexibility to facilitate rapid response to disturbance events. Targeting of study locations could also be aided by advanced remote sensing and prognostic models to predict, for example, storm tracks and large-scale bleaching events. Advances in remote sampling of sea surface temperature and estimation of bleaching likelihood associated with degree-heating-weeks provide one example of physical environmental observations at large spatial scales that could be used to target the location and deployment times of recruitment studies based on patterns of disturbance. While studies of the ecological effects of disturbances on coral reefs date to the beginning of modern coral reef science (Connell, 1978), such studies have largely been *ad hoc* and subject to the vagaries of disturbances occurring in regions near existing research stations and ongoing time-series programs. A more coordinated and international effort involving long-term deployment of recruitment sampling substrata and instrumentation for targeted physical sampling (e.g., of sea water

temperature, waves, and currents) to capture changes following disturbance events is likely to greatly enhance understanding of connectivity among CRI.

3 Evaluating the location of larvae in the water column during transport among CRI is of central importance in understanding how they are transported by currents among CRI.

Biological connectivity among CRI is ultimately mediated by the behavior of larvae in the water column (Paris et al., 2007; Butler et al., 2011; Treml et al., 2015), and while analyses of seawater flow (Domain 4 below) and PLD (Domain 5 below) can go a long way to evaluating the *potential* for transport, *realized* transport will depend on the temporal structuring of the physical location of larvae in the water column (Paris et al., 2007). Larvae that remain near the benthos are unlikely to be transported great distances, whereas those in wind-driven surface currents potentially can be transported over vast distances (Harii and Kayanne, 2003; Paris et al., 2007). Unfortunately, however, there is still little known about the vertical migration of most larvae of coral reefs species in the seawater column *in situ*, or how long they remain in each location during ontogeny (but see Paris and Cowen, 2004; Irisson et al., 2010; Butler et al., 2011; Suzuki et al., 2011). *In situ* experiments with newly released larvae in enclosed acrylic tubes offer potential to advance this data need (Raimondi and Morse, 2000; Tay et al., 2011), but more sophisticated free drifting devices offer the potential for analyses of movement and orientation over lengthy periods (Paris et al., 2008, 2013b; Irisson et al., 2009). The observation that full sibs of coral reef animals settled together following several weeks of larval transport points to the need to better understand the role of larval behavior during the planktonic phase (Bernardi et al., 2012).

TRANSPORT AND DISPERSION

4 High resolution, long-term measurements of physical oceanography of CRI and archipelagoes, particularly for near shore locations, are essential for understanding connectivity among CRI.

Quantifying ocean current patterns over a wide range of space and time scales is essential for understanding transport processes leading to connectivity among CRI (Thompson et al., 2018). Knowledge of these patterns can be gained from observations obtained from a variety of stationary platforms established at island research stations, and moving platforms including deployed drifters and buoys, oceanographic cruises, satellites, and ships of opportunity. Direct measurements can be used to parameterize and initialize ocean circulation models, often designed using nested, or flexible grid spacing approaches that can simulate transport processes on large scales, corresponding to archipelagoes, and small scales, corresponding to the size of corals themselves.

The most geographically extensive observations of ocean current patterns come from altimeter satellites that can be used to estimate currents at the sea surface. The observations are coarse in space ($\sim$1/4° resolution), but have been used, for example, to explore possible pathways for larval transport over long distances such as among CRI (Kendall et al., 2013). These observations are available for most CRI including Mo'orea, Okinawa, and St. John. Satellite observations have the major advantage of providing long-duration time series of ocean current patterns. The satellites resolve the "mesoscale" (i.e., 10–100 km), which includes important flow structures such as eddies, boundary currents, and large frontal features. These spatial scales are also accessible by global ocean circulation models, which can be validated by the satellite observations, while providing important insights into the dynamics of large-scale current systems. The ARGO network ($\sim$ 4000 floats) supplies additional data on large scales about water properties and large-scale flow patterns in addition to critical validation data for ocean circulation models (Werner et al., 2007).

The next step down the "cascade" of processes informing connectivity among CRI are currents transporting the larvae on a spatial scale of 1–10 km, and the variability associated with these currents (D'Aloia et al., 2015). These systems are largely below the resolution limits of mesoscale circulation models and satellite observations (with the exception of along-track satellite observations), but may be observed and estimated with drifting floats, shipboard surveys, and increasingly with autonomous surface and underwater vehicles (together considered as AUVs), and oceanographic radars for measuring surface currents. Current patterns at these scales are arguably the most difficult to quantify because of the difficulty in sustaining time-series observations of sufficient duration, such as from ships, to understand the dominant processes and long-term trends. Oceanographic radars and AUVs are emerging as critical approaches for obtaining these time series.

At smaller scales (i.e., $<$1 km) are current patterns linking the inter-island scales with currents on the fore reef and on the inner-shelf closer to shore. At these scales, turbulent surface and bottom boundary layers often merge and cross-shore circulation decreases due to the island boundaries (Wolanski, 2017). To disperse from spawning areas or to reach settlement habitat, coral larvae and those of other taxa typically must cross the inner-shelf region surrounding CRI. Due to the shallower water depths, the fore reef and inner-shelf are generally more easily accessible for the placement of instrumentation to measure currents and water properties, notwithstanding the potential to lose shallow water instrumentation during large storms and swell events. Ease of instrument placement facilitates the acquisition of long time series such as have been obtained at Mo'orea and Okinawa using oceanographic moorings equipped with current meters, wave sensors, and instruments to measure various water properties. Fine-scale bathymetry data are particularly important for analyzing and modeling currents at these scales (Lindo-Atichati et al., 2016).

At the smallest scales (i.e., 1 mm−1 m) of flows around and through coral colonies, and their interactions with coral larvae and micro-scale habitats where larvae ultimately settle or where they initially disperse (Monismith, 2007; Hench and Rosman, 2013). Quantifying these flows requires instruments with high spatial resolution and rapid temporal sampling such as microstructure sensors, acoustic Doppler velocimeters,

high-resolution current profilers, and specialized high-resolution water property sensors.

5 Quantification of dispersal patterns of multiple taxa is needed to understand connectivity.

Although the relationship between dispersal distance, pelagic larval duration (PLD), and competency period is complicated by issues of scale and experimental approach (Bradbury et al., 2008; Weersing and Toonen, 2009; Selkoe and Toonen, 2011; Dawson et al., 2014), marine invertebrates, including corals, have varying capacity for dispersal, often associated with PLD and reproductive mode (Connolly and Baird, 2010). For most broadcast-spawning corals, like *Acropora* spp., PLD or time at first competency is ∼5–8 d after spawning, based upon experimental data (Nishikawa et al., 2003; Nishikawa and Sakai, 2005) and field observations (Suzuki et al., 2011). Peaks of larval settlement occur on the seventh day following spawning in *Acropora tenuis,* and on the first day post-spawning in the brooding coral, *Stylophora pistillata*. In contrast, the broadcast-spawner *Platygyra daedalea*, has a short PLD with a settlement peak ∼ 2.50–2.75 days following fertilization (Miller and Mundy, 2003). In fine-scale geographic analysis, *P. daedalea* showed higher genetic differentiation than *Goniastrea favulus*, which spawns sticky, negatively buoyant eggs (Miller and Ayre, 2008).

In addition to differences among taxa in dispersal capabilities, life history theory predicts that selection should favor dispersal polymorphisms in habitats that exhibit high temporal or spatial variability or for which competition for available space is high, such as most coral reefs (McPeek and Holt, 1992; Dingle, 1996). Such dispersal polymorphisms, in which some individuals ignore suitable habitat to disperse long distances whereas others of the same species or even among progeny of single individuals remain close to their natal site, are well-documented in terrestrial systems, but have rarely been investigated in marine taxa (Dingle, 1996; Toonen and Pawlik, 2001). A handful of examples exist among marine species (e.g., Gibson and Chia, 1989; Raimondi and Keough, 1990; Krug, 2001; Toonen and Pawlik, 2001; Marshall and Keough, 2003), but to date only a single study comparing short and long-distance dispersal within a single species has been published for corals (Torda et al., 2013).

Nevertheless, the few larvae with the greatest dispersal are the ones that maintain connectivity among reefs, and population connectivity of even brooding corals can be maintained by relatively low numbers of migrants (van Oppen et al., 2008). Even in brooding corals like some *Pocillopora damicornis sensu lato*, PLD is ∼100 days based on experimental analyses and competency model predictions (Richmond, 1987). Thus, long PLD is not exclusive to broadcast-spawning corals (Graham et al., 2008), and PLD alone is a poor predictor of mean dispersal ability (Bradbury et al., 2008; Weersing and Toonen, 2009; Selkoe and Toonen, 2011). The success of larval dispersal and recruitment in augmenting coral populations may be influenced by the fecundity of the species and by habitat characteristics (Hughes et al., 2000). Therefore, opportunities for larval dispersal and recruitment may not only vary by species but also within species (e.g., Gibson and Chia, 1989; Krug, 2001) and even among individual families (Toonen and Pawlik, 2001), especially after taking into account differences among CRI in habitat size and distance to nearest neighboring CRI. These observations underscore the importance of more synoptic analyses of dispersal potential and variability in dispersal behaviors for a wide variation of coral reef species.

SETTLEMENT AND RECRUITMENT

6 Time-series analyses of population structure of a wide diversity of taxa and functional groups of benthic organisms are needed to understand community-wide patterns of connectivity among CRI.

Time-series programs on CRI vary widely in time of initiation, spatial scope, taxa that are quantified, and method and frequency of sampling. Scleractinians are the foundational taxon, and they are often the major focus of study. Percent cover of live coral is the primary state variable reported, but to assess processes of disturbance and recovery, temporal patterns of population structure and colony sizes of key species, as well as overall taxonomic composition of corals, are needed. These data enable observations of recruitment to be better linked to colony survival and growth, both of which are key processes leading to the re-establishment of the coral community following disturbances. Additionally, tropical reefs support a high diversity of non-coral taxa that represent a variety of functional groups and trophic levels, and these components of the community should be incorporated into time-series analyses. Time-series programs that include measurement of population structure of fish, mobile and sessile invertebrates, and algae, matched with population genetic information, could enable comparisons of connectivity among taxa of widely differing life history strategies, trophic status, behavior, and longevity (Selkoe et al., 2016). Such knowledge will be critical for understanding the potential and realized patterns of re-assembly of a CRI community following disturbance, as well as the degree to which the community structure will change in light of future environmental and climate conditions. For example, herbivores play a critical role in suppressing the establishment of fleshy algae following landscape-scale disturbances that kill corals, thus maintaining the reef in a condition suitable for settlement and survival of corals (Adam et al., 2011, 2014; Han et al., 2016; Holbrook et al., 2016). In these cases, connectivity patterns of corals and herbivorous species are both important, and understanding them will enable more informed predictions about the potential for reefs to recover from disturbance.

7 Most measures of recruitment around CRI are inconsistent and restricted temporally to sampling events driven by logistics rather than ecological questions.

Recruitment is a critical process in the sustaining the structure and dynamics of reef communities, particularly for CRI. For example, recovery of coral populations following major disturbances depends on the level of connectivity with adjacent fecund populations, and on the growth and propagation of newly settling larval recruits (e.g., Hughes and Connell, 1999; Arnold

and Steneck, 2011; Doropoulos et al., 2015). However, given the long life span of most corals [i.e., ∼ 4 y for a recruit of < 1-mm diameter to become a mature adult colony of >5 cm (Penin et al., 2010)], understanding the implication of recruitment in coral recovery requires long-term analysis on population dynamics and demography (Adjeroud et al., 2017). Frequent sampling is necessary to resolve rapidly occurring events such as episodic recruitment, sudden-onset, lethal diseases, or transient population perturbations (Connell et al., 1997; Graham et al., 2011).

Due to the logistic difficulty of quantifying recruitment on time scales allowing cycles of community replenishment to be detected, few studies have examined the interplay among recruitment, dynamics of adult populations, and disturbances, on a relevant time-scale (> 10 y; but see Connell et al., 1997). Moreover, it is difficult to taxonomically resolve recruits, and only limited progress has been made with genetic tools for this purpose (e.g., Shearer and Coffroth, 2006; Suzuki et al., 2012). All of these limitations explain why the majority of surveys of coral recruitment have documented variability in recruitment in a restricted spatio-temporal window, and why they have not achieved their potential to link connectivity, recruitment, and critical processes such as recovery following disturbances (Graham et al., 2011; Adjeroud et al., 2017). Ongoing development of genetic tools to identify the geographic origin of coral larvae and recruits, such as DNA parentage analysis, represent an interesting way to evaluate better the relative contribution of local- vs. distant-recruitment, and to identify potential "sources" and "sinks" among networks of CRI (Adjeroud et al., 2017). In addition, subdivision of sampling intervals could be effective for estimating larval connectivity among CRI. For example, replacing the settlement tiles at 2 or 3 days intervals after a spawning event may reveal settlement peaks of local- and distantly-sourced recruits (Suzuki et al., 2011).

8 Distinguishing local- from distant-recruits for multiple taxa is central to understanding the role of connectivity around CRI, and essential for understanding connectivity of virtually all taxa on coral reefs.

Genetic studies have become an essential component for understanding recruitment and connectivity in marine systems across both ecological and evolutionary timescales (e.g., Almany et al., 2017). These studies are readily integrated into research on the relationship between connectivity among CRI and community resilience provided that sampling design is consistent with the space and time scale required by research questions relying on genetic data. For example, to determine the origin of recruits, the most reliable approach is parentage analysis, which has potential to assign recruits to specific parents at the natal site (Harrison et al., 2013; D'Aloia et al., 2015; Selkoe et al., 2016; but also see Christie et al., 2017), but could also miss some long distance connections outside of the sampling area. In contrast, to determine the relative importance of multiple environmental drivers of population structure, a probabilistic approach (sensu Paris et al., 2013b; Selkoe et al., 2016) may be sufficient to identify the origin of recruits, or to differentiate individuals according to whether they originated from local-recruitment or from more distant locations (**Box 2**).

In each genetic approach, the required sampling regimes will differ in order to address trade-offs in methodologies. For example, in parentage analysis, statistical power is increased by maximizing the proportion of the regional population sampled, whereas for probabilistic assignment of individuals to a natal site, power is increased by maximizing the number of natal sites sampled (Christie et al., 2017). Additionally, to untangle the effects of distant recruitment from the effects of post-settlement success, a different experimental design is required (e.g., Toonen and Grosberg, 2011). While distant sources of larvae may have a low proportional influence on genetic population structure on a healthy reef where settlement space is limited and competition with the preexisting populations is strong, distantly-sourced larvae may drive or modulate recovery following disturbance (Harris et al., 1984; Jennings, 2000; Armsworth, 2002; Baskett and Salomon, 2010). Alternatively, rare survivors of disturbance that are easily missed in ecological surveys may serve as sources of recruits that can drive local community recovery (Edmunds et al., 2016; Tsounis and Edmunds, 2016; Cros et al., 2017). Ultimately distinguishing among these possibilities would require comparing genetic data from adult and recruits to examine multi-generational patterns of structure and/or kinship (Toonen and Grosberg, 2011; Iacchei et al., 2013). Conducting such an analysis on recruitment pulses following disturbance on CRI (Bramanti and Edmunds, 2016), for example, would be particularly relevant.

CONCLUSIONS

CRI are abundant and unique reef formations throughout most tropical seas, and characterized by diverse and productive ecosystems on their shores. Over the last few decades, however, multiple assaults of natural and anthropogenic origin have driven coral cover downward on most CRI, and imposed multiple cycles of community destruction and recovery. Some CRI are notable in their long history of ecological and oceanographic research, but much of this effort has been insular and focused on single CRI selected for study based on happenstance or peculiar historical presence. This emphasis has overlooked the potential of CRI to serve as natural laboratories to investigate connectivity as an ecological process shaping community dynamics, and to answer critical questions addressing mechanisms of coral reef resilience (**Table 1**). Not only has this restricted intellectual advancement in the field of coral reef biology, but also it has deprived resource managers of access to the full spectrum of tools necessary to advance reef conservation. Achieving the potential of CRI to meet this need will require more than integrating the information currently available. As we describe above, there are clear needs for new data (Domains 1–8, above) and more coherence in spatio-temporal scales of sampling of biological and physical variables. Critically, there is much to be gained from the pro-active selection of new CRI for use in time-series analysis designed to address specific hypotheses.

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All authors listed have made a substantial, direct and intellectual contribution to the work, and approved it for publication.

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