Stability and dynamic properties of octocoral communities in the Tropical Eastern Pacific

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ABSTRACT: Octocorals are the main foundation species in rocky-wall marine communities in the Tropical Eastern Pacific; however, we have only a poor understanding of how stable these communities are. This study is the first attempt to quantify complex stability properties, such as turnover and recovery time for octocoral species. We use a Markov Chain model with transition probabilities estimated from the field and compare 2 oceanographically distinct gulfs within the same latitude in Pacific Panama: the Gulf of Panama (GP) and the Gulf of Chiriqui (GC). The model was parameterized by monitoring 4 fixed plots (1 m^2) at 8 sites from June 2014 to January 2016. The state (occupation) of each point (location) occupied by the holdfast of an octocoral colony was recorded during each survey. Thirteen octocoral species were monitored over 989 points. Octocoral dynamics in GC, where communities were more species-rich, were 3 times more stable than communities in GP, with an estimated turnover time of 4.8 yr in GC and 1.5 yr in GP. However, communities in the GC took 1.6 times longer to recover after disturbance, with an estimated species-specific recurrence time of 34 yr in GC and 21 yr in GP, possibly due to strong competition for space with other sessile organisms. In modeled communities, the effect of diversity loss was low at the gulf and study region, but increased significantly at the reef scale, especially in species-poor sites. Additional studies on environmental factors driving stability are needed to fully understand the mechanisms behind our results.

KEY WORDS: Markov chain model · Octocoral · Tropical eastern Pacific · Community stability · Species removal · Spatial scale

INTRODUCTION

Octocoral communities are ecologically important because their complex morphology makes them the main habitat-forming species that live on rocky walls (Bayer 1953). Octocoral communities form 'animal forests' (Rossi 2013, Sánchez 2016), creating complex habitat and feeding substrates for many other taxa (Cantera et al. 1987, Sánchez 2016). As suspension-feeder communities, octocorals play a key role in plankton–benthos energy flow and CO_2 storage (Bramanti et al. 2009), as they transfer energy from a less stable planktonic system to a more stable benthic one (Gili & Coma 1998). Octocoral species around the world are affected by a variety of stressors, including

an increase in the frequency and strength of tropical storms (Woodley et al. 1981, Yoshioka & Yoshioka 1987) and disease outbreaks that are the result of increases in seawater temperature (Sánchez et al. 2011, 2014, Ward et al. 2007). Some octocorals, however, have been found to be more resistant to bleaching (if zooxanthellae species) and ocean acidification than scleractinian corals (Gómez et al. 2015, Enochs et al. 2016, Sánchez 2016).

Despite the ecological importance of octocoral communities in rocky walls in the Tropical Eastern Pacific (TEP), their stability, measured as the frequency of changes and the time to recover, is poorly understood. An initiative to study the biology and ecology of these foundation species began early this

century after extensive taxonomic reviews were published (Breedy & Guzman 2002, 2007, 2011, 2016). These studies were followed by a description of the population dynamics of common species (Gomez et al. 2014), the effects of a 25% decline in population abundance on community structure (Gomez et al. 2015), their reproductive timing and output (Gomez 2017), and the relationships between recruitment, adult densities, and space limitation (Gomez 2017). To further our understanding of the dynamics of these understudied communities, we developed a Markov chain model to study the stability properties of octocoral communities along the Pacific Coast of Panama. This region has been described as a hotspot of octocoral diversity (Guzman et al. 2004, 2008) and a natural laboratory for the study of marine communities (Cortés et al. 2017).

The stability of a community can be defined and measured in different ways (Ives & Carpenter 2007), many of which are relevant for octocoral communities. These include (1) how many alternative stable states a community can have and how hard it is to change between them, such as coral reefs changing to an algae-dominated state (Fung et al. 2011), (2) the rate at which a community returns to equilibrium following perturbation, (3) how resistant a community is to change in response to disturbance, (4) the susceptibility of a community to species invasions, and (5) the impacts of species extinction and the compensatory changes in species abundance that occur following an extinction event (Gonzalez & Loreau 2009, Ives & Carpenter 2007). Additionally, the stability of a system has been linked to its diversity (Loreau et al. 2002); however, this has been a topic of debate, mainly because the strength and direction of this relationship depends on the definition of stability and the type of disturbance (Ives & Carpenter 2007). To improve our understanding of this relationship, Ives & Carpenter (2007) recommended models based on empirical data which link the dynamics of the focal system to the relevant aspect of stability. Ultimately, the aim is to identify stabilizing mechanisms and understand how they are impacted by human-caused environmental changes, such as in the case of the heavily exploited Mediterranean red coral *Corallium rubrum*, which is now threatened by climate change (Bramanti et al. 2009, Santangelo et al. 2007, 2015).

Octocoral communities are exposed to pulse disturbances, such as hurricanes, or ongoing press disturbances, such as global warming and ocean acidification (Ives & Carpenter 2007). To date no alternative stable states have been reported for octocoral communities in the TEP; however, this may be due to the lack of studies in the area. Recent population declines (Gomez et al. 2015) emphasize the need to study community stability, rates of recovery after disturbance, and the potential for compensatory changes after species extinctions.

Markov chain models have been used in ecology to understand succession and stability in a variety of natural systems, from forests (Waggoner & Stephens 1970) and plants (Isagi & Nakagoshi 1990) to marine communities such as subtropical, intertidal (Wootton 2001a,b), and subtidal (Hill et al. 2004) sessile communities and Australian coral reefs (Tanner et al. 1994). Markov chains are simple multispecies models that use transition probabilities, which are relatively easy to quantify in the field, to estimate more complex measurements of stability (Wootton 2001a) such as entropy (predictability), turnover, and recurrence times. It is a powerful tool for comparative analysis in community ecology (Hill et. al. 2004). In addition, the Markov chain model can also be used as a tool to predict the effect of species loss and identify the key species (Hill et al. 2004, Tanner et al. 1994) that, if removed, will cause disproportionate changes to the community (MacArthur 1972), without the need for experimental manipulation.

Our goal is to develop a first Markov chain model for octocoral communities in the TEP to, firstly, quantify the transition probabilities within studied species and secondly, infer the stability properties for multiple communities across 2 gulfs off the Pacific coast of Panama. In the present study, stability is defined as the community resistance based on the turnover, which measures how often a space that was occupied by the holdfast of an octocoral colony shifts to a different occupancy (i.e. another octocoral species, algae, crustose coralline algae [CCA], sponge); and by the recurrence time, which estimates how long it would take for a space to return to its original state after a disturbance (Hill et al. 2004). Additionally, this study evaluates the effect of local species extinction (removal of a species from a community) and interprets the stability of octocoral communities by the compensatory changes in species abundance after local extinction (sensu Hill et al. 2004, Wootton 2004).

MATERIALS AND METHODS

Study organisms

Octocorals are sessile marine invertebrates that inhabit rocky coral communities in very active environments, with strong currents and swell (Gomez et

al. 2014). They are considered foundation species (Sánchez 2016) with high environmental tolerance (Gómez et al. 2015, Enochs et al. 2016) and can be found in shallow and deep environments in almost all latitudes (Bayer 1981). The Pacific coast of Panama has 2 recognized hotspots of octocoral diversity and abundance located within the boundaries of the TEP: Las Perlas Archipelago in the Gulf of Panama (GP), with 38 reported species, and Coiba Island in the Gulf of Chiriqui (GC), with 36 species (Guzman et al. 2004, 2008, Breedy & Guzman 2011). Fifteen of these species inhabit both gulfs and are found in high-density patches of ~38 colonies m^{-2} (Gomez et al. 2014). The life histories of 13 of the 59 species inhabiting the Pacific coast of Panama have been studied. Gomez et al. (2014) found 2 distinct life history patterns in these species: 6 species had r-selected dynamics, with high recruitment and mortality rates, and 7 species had K-selected dynamics, with low recruitment and low mortality rates. However, the reproductive output of 2 common species within these 2 groups does not relate to their population dynamics (Gomez 2017); *Leptogorgia alba*, in the r side of the selection spectrum has high recruitment (Gomez et al. 2014) but low reproductive output (Gomez 2017), and *Muricea austera*, on the K side, has very low recruitment (Gomez et al. 2014) but high reproductive output (Gomez 2017). Contrastingly, the recruitment of these species is limited by space and positively correlated with adult density (Gomez 2017). A similar strategy, of high recruitment and low reproductive output, and vice versa, has been described for Mediterranean species (Cupido et al. 2012).

Study site

An annual wind-driven upwelling significantly reduces water temperature and increases nutrient levels during the first 4 months of each year in GP but not in GC (D'Croz & O'Dea 2007). This gulf-specific upwelling has ecological consequences for scleractinian coral reefs (Toth et al. 2017). However, in deeper environments where octocoral communities are found (>15 m), the strong differences in water temperature regimes between the two gulfs are no longer evident (Gomez 2017).

Although octocorals in both gulfs are subject to similar annual variation in water temperatures, the temporal variation in nutrient levels and its effect on octocoral species has not been studied.

Four sites within each gulf — Roca Hacha, Jicarita, Prosper and Catedrales in the Gulf of Chiriqui, and Elefante, San Telmo, Galera and Pedro Gonzalez in the Gulf of Panama (Fig. 1) — were chosen as study sites based on previous descriptions of octocoral communities on the Pacific coast of Panama and the Tropical Eastern Pacific (Guzman et al. 2004, 2008). All study sites were located in exposed areas and subject to strong currents and swells. These sites are formed by basaltic rocky formations in which octocorals share the substratum with coralline algae, small and scarce scleractinian colonies, macroalgae, tunicates, sponges, and algae turf.

Data acquisition

To parameterize the Markov chain model, four 1.68 × 0.6 m fixed plots, equivalent to 1 m^2, were installed between 15 and 20 m depth at each of the 8 study sites using SCUBA equipment. Plots at GP were located at shallower depths (~15 m) than plots in GC (~20 m) because this is where the octocoral colonies were found. In GP, sand bars surround rocky formations that generally do not extend deeper than 18 m. Plots were fixed by installing stainless steel square bars with underwater cement. Study plots were mon-
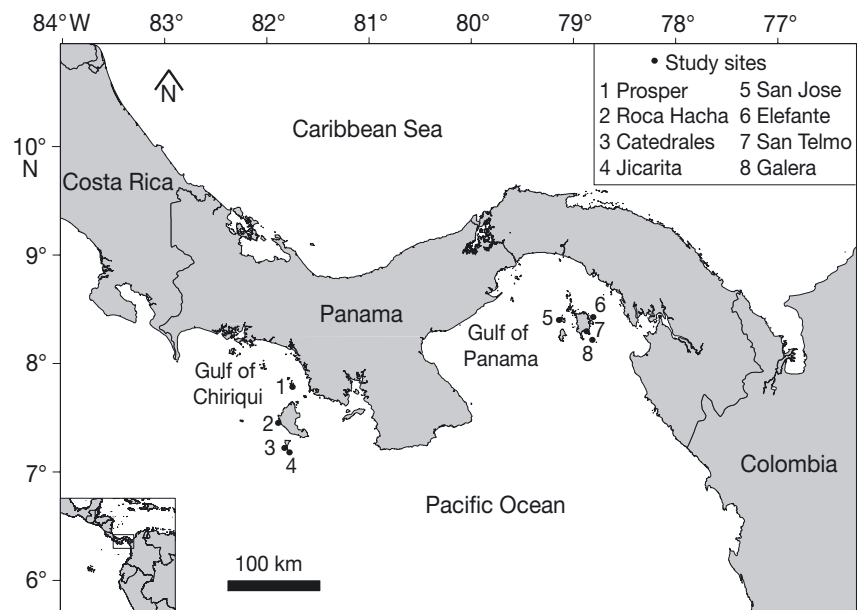

Fig. 1. Location of study sites in octocoral communities off the Pacific coast of Panama

itored on 4 occasions, every 6 mo; hereafter this is referred to as a 'sampling period', from June 2014 to January 2016. Plots were photo-monitored using a Nikon D-80 camera with a wide-angle lens inside an Ikelite underwater case and 2 external digital strobe flashes. The camera was attached to a custom-made stainless steel tripod in order to maintain a fixed object-to-lens distance (0.80 m) from the substrate. To survey each plot, an aluminum quadrat was attached to the square fixed bars, the quadrat and the bars where designed so they always fitted into each other in the same position, ensuring the monitoring of the exactly same location over time. To ensure high-resolution pictures of the substrate, the quadrat was divided into 8 equal sections (0.42 × 0.30 m); each section was photographed, resulting in a total of 8 pictures per plot. The quality of the pictures (light and exposure) was improved by using Nikon NX2 software (see Gomez et al. 2014).

Pictures taken from study plots were analyzed to obtain the data needed to set the parameters for the model. High-resolution mosaic images were created with the 8 pictures taken from each 1 m² plot. On each image, each octocoral colony was identified and located within the plot; images from consecutive surveys were visually compared. We quantified how often a point in space that was occupied by the holdfast of an octocoral colony (in any given survey) changed to a different occupation (state) — such as a new octocoral species, algae turf, CCA, sponge — or whether it stayed unchanged. A total of 989 points were monitored, equivalent to the total number of octocoral colonies attached to the substrate during the entire study period.

Data analysis

Transition probabilities and dynamic properties of stationary community

A Markov chain analysis was developed using the methods proposed by Hill et al. (2004). The parameter values of this model are defined by field observations that quantify the transition probability — the frequency at which one species occupying a specific point (location) is replaced by another species. Transition probabilities can be quantified at the species level to describe the biology of each species in the context of a community (Hill et al. 2004) (see the Supplement at www.int-res.com/articles/suppl/m588p071_supp.pdf). The probabilities can also be used to create a broader description of the entire community,

which can be used to compare one community with others (Hill et al. 2004), and assess how predictable communities are (see the Supplement).

The model was defined by a transition probability matrix in which the state of a point in time $t+1$ was dependent upon the state of the point in time t. Transition matrices were averaged over time (among surveys) and estimated at 3 spatial scales by averaging octocoral transition probabilities within each reef (4 plots), per gulf (16 plots) and for the study region (32 plots) following Hill et al. (2004) (see the Supplement). However, in this case, the abiotic component was reinterpreted as the non-octocoral component and included all sessile organisms other than octocoral species, e.g. sponge, algae turf, and CCA. The following transition probabilities were calculated for each species: persistence rate (probability that the state remained unchanged in t and $t+1$), disturbance rate (octocoral state that changed to a non-octocoral state), colonization rate (non-octocoral state that changed to an octocoral state), replacement (octocoral state that changed into a different octocoral state) (Table S1 in the Supplement). Two stability metrics were also calculated at the species and community scales: turnover time (estimated time to change from an octocoral state to any other state including another octocoral species), and recurrence time (estimated time for a species-specific octocotal state to recolonize a space that was previously lost) (Table S2 in the Supplement). The normalized community entropy was calculated to estimate how predictable the transitions of each species was (Table S2). Three diversity indices were calculated; proportion of octocoral states, Shannon-Wiener index and community evenness (Table S3). Eigenvector calculations used to calculated the indices mentioned above (and detailed in the Supplement) and correlations between species abundance and transition probabilities were performed in R software version 3.2 (R Core Team 2015), using the base R package and package 'Hmisc' (Harrell & Dupont 2015) respectively.

Community convergence

For each Markov chain (one per reef and one per gulf) the rate of convergence to the stationary distribution was measured with the damping ratio (p) (sensu Tanner et al. 1994, Wootton 2001a, Hill et al. 2004), which measures the relationship between the largest and second-largest eigenvalues. The closer these 2 eigenvalues are in magnitude, the slower the convergence rate, measured as the natural logarithm

of p (Hill et al. 2004). The half-life of a perturbation was measured as ln 2 / ln p (sensu Hill et al. 2004). Damping ratios were calculated using function 'Damping.ratio' in the R software package 'Popbio' (Stubben & Milligan 2007)

Species removal

The importance of each species to the diversity of its community was quantified by calculating the proportional change in evenness between the stationary community and a modeled community in the absence of a target species (ts) (sensu Hill et al. 2004). This analysis was performed for every octocoral species at the 3 spatial scales: reef, gulf, and study region. To model the community without ts, both the column and the row of ts were set to zero in the stationary community matrix, which was then column-wise renormalized to add up to 1, and subsequently, ts row and column were removed. Community evenness was calculated for the stationary community and after each species removal following Hill et al. (2004). To calculate evenness among octocorals alone, all non-octocoral states were added as a single state and treated as the 'bare rock' state.

RESULTS

A total of 438 and 551 points in space (location of octocoral holdfast at any given time during the study period) were followed in time in GP and GC, respectively. At some point in time during the study, each of these points in space was occupied by an octocoral colony, which persisted, recruited, or was disturbed into a different state. Three points from Jicarita (GC) were removed from the analysis because they were not visible in at least one of the time-steps. The stationary community matrix from the entire study region had 17 states: 13 octocoral species (Table 1), algae turf, CCA, sponge, and pocilloporid scleractinian corals; 15 states in the GC (12 octocoral species); and 10 states in the GP

Table 1. Octocoral species (representing octocoral states in the model) in study plots off the Pacific coast of Panama (15–20 m depth). Species listed in decreasing order of abundance in the stationary community: mean ± SE temporal abundance (total number of colonies counted per species in sixteen 1 m² plots within each gulf)

| Species	Species code	Temporal abundance	
		Gulf of Chiriqui	Gulf of Panama
Leptogorgia alba	LepAlb	57.0 ± 2.7	60.3 ± 10.1
Pacifigorgia cairnsi	PacCair	77.3 ± 4.0	0.0
Leptogorgia cofrini	LepCof	6.0 ± 0.8	65.5 ± 13.7
Pacifigorgia irene	PacIre	50.3 ± 1.6	3.8 ± 0.9
Pacifigorgia rubicunda	PacRub	41.5 ± 2.6	0.0
Pacifigorgia ferruginea	PacFer	11.0 ± 1.5	9.5 ± 3.6
Pacifigorgia firma	PacFir	0.0	15.8 ± 0.5
Muricea austera	MurAus	11.0 ± 0.7	2.5 ± 0.3
Psammogorgia arbuscula	PsaArb	8.0 ± 0.7	0.0
Heterogorgia verrucosa	HetVer	6.3 ± 1.0	0.0
Carijoa riisei	CarRii	1.8 ± 1.8	2.8 ± 1.2
Pacifigorgia eximia	PacExi	3.0 ± 0.4	0.0
Leptogorgia cuspidata	LepCus	1.0 ± 0.0	0.0
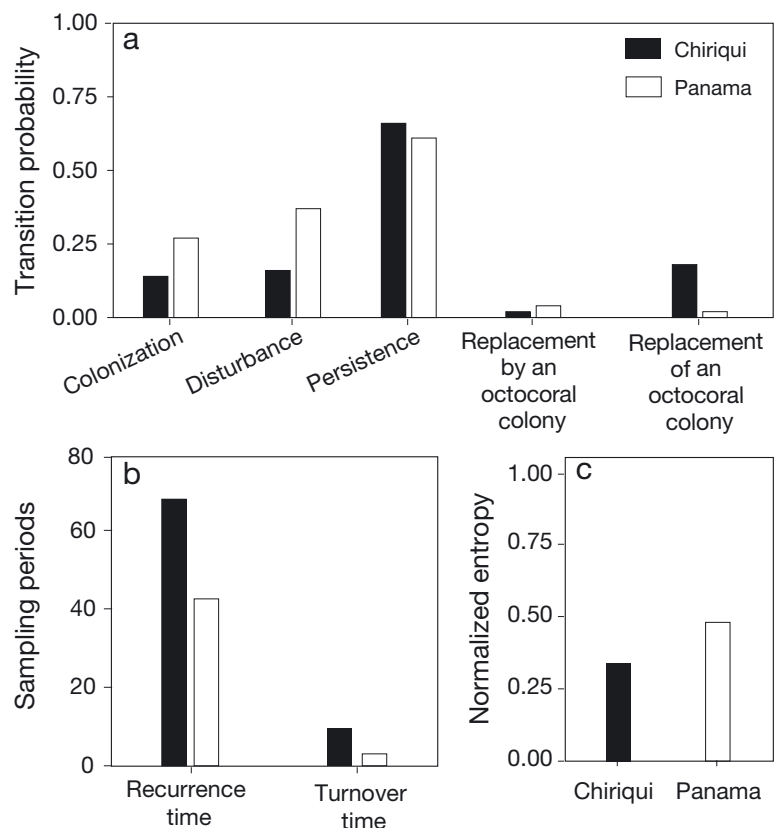
Fig. 2. (a) Transition probabilities, (b) stability properties (sampling period = 6 mo), and (c) normalized entropy or predictability of octocoral communities in the Gulf of Panama and the Gulf of Chiriqui

(7 octocoral species). See individual transition matrices and their temporal standard error in Table S4 in the Supplement.

Table 2. Community dynamic properties and stability measurements at 2 spatial scales calculated from transition matrices (see Table S4 in the Supplement) in octocoral communities off Pacific Panama (regional scale; thirty-two 1 m² plots) and at each gulf (gulf scale); Gulf of Chiriqui (sixteen 1 m² plots) Gulf of Panama (sixteen 1 m² plots). Rates indicate the probability of an event happening between sampling periods (every 6 mo)

| Transition probabilities and dynamic properties	Pacific Panama	Gulf of Chiriqui	Gulf of Panama
Octocoral mean disturbance rate	0.31	0.16	0.37
Octocoral mean colonization rate	0.18	0.14	0.27
Octocoral mean persistence rate	0.59	0.66	0.61
Replacement by an octocoral species	0.01	0.02	0.04
Replacement of an octocoral species	0.09	0.18	0.02
Normalized entropy (predictability)	0.39	0.34	0.48
Octocoral turnover rate	0.41	0.34	0.39
Octocoral turnover time (sampling periods)	3.70	9.58	3.04
Octocoral recurrence time (sampling periods)	66.88	67.94	42.54
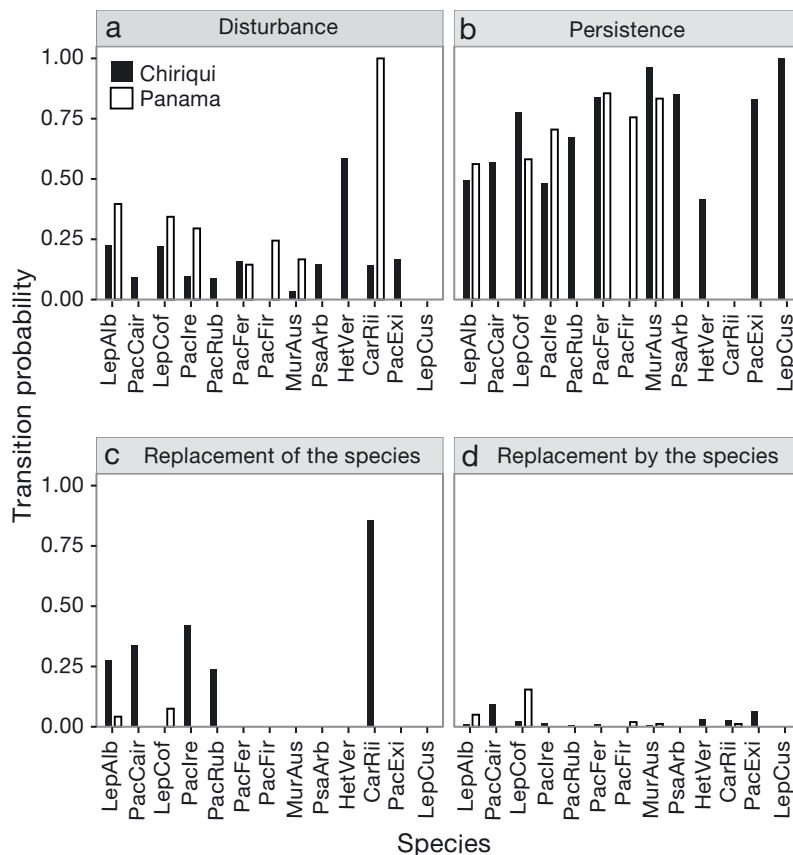
Fig. 3. Species-specific transition probabilities from the community transition matrices of octocoral communities in the Gulf of Chiriqui and the Gulf of Panama. Species are displayed in decreasing order of abundance as in Table 1. (a) Probability of disturbance; (b) probability of persistence; (c) probability that the species is replaced by another octocoral; (d) probability that the species replaces another octocoral

Community transition probabilities

At any given time, the maximum transition probability of the stationary matrix of the community at equilibrium was the persistence rate, which is when a point was occupied by the same species in *t* and in *t*+1. The persistence rate for Pacific Panama was 0.59, 0.66 for GC and 0.61 for the GP (Fig. 2a, Table 2), meaning that there was a 59–66% probability that an octocoral colony survived within a 6 mo period (sampling period). At the species level, the persistence rate ranged from 1 — species that persisted at the same point for the entire study period (*Leptogorgia cuspidata* in GC) — to 0.4 (*Heterogorgia verrucosa* in GC) (Fig. 3b). Persistence rate was not correlated with the species' mean abundance (GC: r = −0.23, p > 0.05; GP: r = −0.03, p > 0.05) (Table 3).

Next, we studied the mean disturbance rate in both communities. This was the probability that a space occupied by an octocoral colony in time *t* would change to a different occupancy (other than an octocoral), such as a sponge, CCA, or algae turf, in time *t*+1. The mean disturbance rate of the stationary community was 0.31 for Pacific Panama, 0.37 for GP and 0.16 for GC (Table 2, Fig. 2a). This means that a space occupied by an octocoral colony had 16–37% probability, depending on its location, to change to an occupation other than an octocoral in a 6 mo period. The species with the highest disturbance rate in GP was *Carijoa riisei*, as all the colonies changed to a different state. In GC, the species with the highest disturbance rate was *H. verrucosa*. *Muricea austera* had the lowest disturbance rate in GC and *P. ferruginea* had the lowest disturbance rate in GP (Fig. 3a). Disturbance rate was not correlated with the species mean abundance (GC: r = −0.16, p > 0.05; GP: r = −0.07, p > 0.05) (Table 3).

The mean colonization rate, measured as the probability that a space that was occupied by a non-octocoral state (sponge, CCA, or algae turf) in time *t* would change to an octocoral state in time *t*+1,

was lower than the disturbance rate in both gulfs; it was 0.18 in Pacific Panama, 0.27 in GP and 0.14 in GC (Table 2, Fig. 2a). This means that a benthonic space had 14–27 % probabilities to be occupied by an octocoral colony in a 6 mo period. *P. cairnsi* and *P. eximia* had the highest probability of colonization in GC, and they were also the only species to colonize a space previously occupied by a sponge. *Leptogorgia alba* had the highest colonization rate in the GP and it was 3 times higher when colonizing a space previously occupied by algae turf. *P. firma* and *P. ferruginea* only colonized spaces previously occupied by CCA (Fig. 4). Probability of colonization was positively correlated with species mean abundance in GP (r = 0.89, p < 0.05) (Table 3).

Species replacements were rare among octocoral states (Table 2, Fig. 2a). They occurred when one octocoral colony overgrew another octocoral colony. Replacements were positively correlated with mean species abundance in GP (Table 3). The species that had the highest rate of being overgrown by another octocoral (replacement of) was *C. riisei* (0.85 in GC) (Fig. 3c). *L. cofrini* (0.15) was most prone to replace another octocoral, but only in the GP (Fig. 3d).

Community dynamics

The turnover time, which measures the frequency with which a space previously occupied by an octocoral species changed to any other benthic component but the species that was previously there (i.e. hard coral, algae, CCA, other octocorals), was 3.7 per sampling period (1.8 yr) for Pacific Panama, it was 3 times greater in GC (9.58 per sampling period, 4.79 yr) than in GP (3.04 per sampling period, 1.52 yr), and this difference was not seen in the turnover rate (Table 2, Fig. 2b). The recurrence time, which measures the time required for a specific octocoral species to re-colonize a space that was previously lost, was 66.9 sampling periods (33.45 yr) for Pacific Panama; recurrence time was 1.6 times longer in the GC (67.94 sampling periods, 33.97 yr) than in the GP (42.54 sampling periods, 21.27 yr) (Table 2, Fig. 2b). Neither of these measurements was correlated with species abundance (Table 3).

Within species, *M. austera* had the longest turnover time (27 sampling periods, 13.5 yr in GC) due to a slow turnover rate (0.04 sampling periods, or 0.02 yr), and it was followed by *P. ferruginea* (7 sampling periods in GP, 3.5 yr). *C. riisei* had the shortest turnover time in both GP and GC (1 sampling period, 0.5 yr) due to a fast turnover rate (1 sampling period, 0.5 yr) (Fig. 5a,b). *P. ferruginea* showed the slowest recurrence time of 928 sampling periods (464 yr) in the GP; this is >100 times slower than *L. alba* (8.35 sampling periods, 4.17 yr) in the GP (Fig. 5c).

Table 3. Correlation between octocoral species' dynamic properties and their mean abundance. Rates indicate the probability of an event happening between sampling periods (every 6 mo). *significant correlation (p < 0.05)

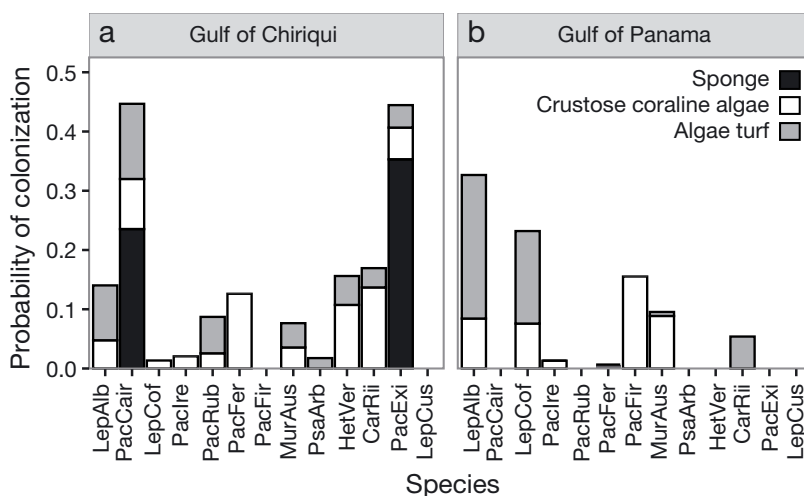| Transition probabilities and dynamic properties	Gulf of Chiriqui (n = 12 species)		Gulf of Panama (n = 7 species)	
	r	p	r	p
Disturbance rate	−0.16	0.6	−0.07	0.88
Persistence rate	−0.23	0.47	−0.03	0.9
Colonization rate	0.3	0.34	0.89	0.008*
Replacement of an octocoral colony	0.33	0.29	0.95	0.01*
Replacement by an octocoral colony	0.38	0.22	0.85	0.02*
Turnover rate	0.23	0.48	0.03	0.95
Turnover time (sampling periods)	−0.21	0.52	−0.4	0.37
Recurrence time (sampling periods)	−0.16	0.61	−0.43	0.34
Entropy (sampling periods)	0.68	0.02*	0.84	0.02*

Fig. 4. Species-specific transition probabilities of octocoral colonization per sampling period in spaces previously occupied by sponges, crustose coralline algae or algae turf in communities located in (a) the Gulf of Chiriqui and (b) the Gulf of Panama. Species are displayed in decreasing order of abundance as in Table 1
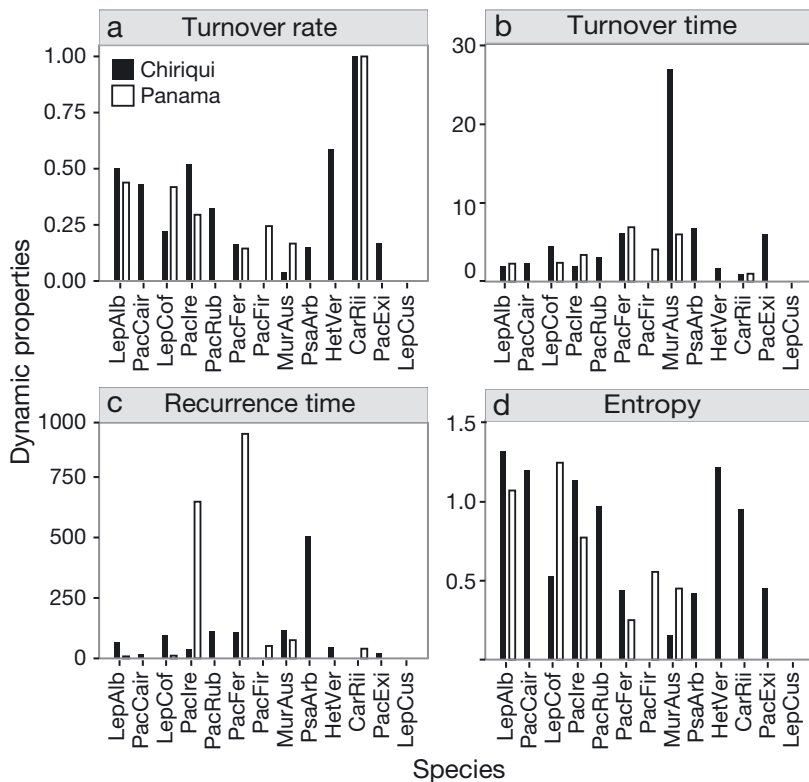
Fig. 5. Species-specific dynamic properties of per sampling period (0.5 yr) octocorals in the Gulf of Chiriqui and the Gulf of Panama. (a) Turnover rate; (b) turnover time; (c) recurrence time; (d) predictability, quantified by the entropy of the species in the transition matrix. Species are displayed in decreasing order of abundance as in Table 1

The normalized community entropy was 1.4 times greater in GP than in GC (Fig. 2c). The entropy, or predictability, of the species ranged from 1.3 (less predictable *L. alba*) to 0.15 (more predictable *M.*

austera) in GC, and 1.2 (less predictable *L. cofrini*) to 0.25 (more predictable *P. ferruginea*) in GP (Fig. 5d). Species entropy was correlated to mean abundance (r = 0.68, p < 0.05, Table 3); the maximum possible species entropy values were 2.3 in GP and 2.7 in GC.

Community convergence

The octocoral community in Pacific Panama had a damping ratio of 1.12, implying a convergence rate of 11.33 % per sampling period and a half-life of 6.12 sampling periods (3.06 yr) (Table 4). Communities in the GC had a damping ratio of 1.05, implying a convergence rate of 4.5 % per sampling period and a half-life of 15.6 sampling periods (7.8 yr). The octocoral community in the GP had a damping ratio of 1.17, implying a convergence rate of 15.7 % per sampling period and a half-life of 4.4 sampling periods (2.2 yr) (Table 4). At the reef scale, convergence rates were longer in Prosper (GC, 14 % per sampling period), Elefante (GP 19 % per sampling period), and Pedro Gonzalez (GP, 68 % per sampling period), and shorter at Galera (GP, 0.75 % per sampling period) (Table 4).

Species removal

Species evenness in the entire study region was 0.76: 0.82 in GP and 0.77 in GC (Table 5). At the study regional scale (when transition matrices from all 32 plots are averaged), the species that produced the most dramatic change in species evenness when removed was *P. cairnsi*, which lowered community evenness by 10 %. In contrast, the removal of *L. cuspidata* produced no change at the same scale. The removal of *C. riisei* produced the greatest decrease in evenness (10 %) in GC and *L. alba* in GP (15 %). However, the individual effect of species removal changed substantially when analyzed at the reef scale (Fig. 6). The removal of *P. ferruginea* in Galera produced a decrease in evenness of 80 % and the removal of *P. rubicunda* and *L. alba* in Catedrales

Table 4. Damping ratio, convergence rate and half life per sampling period (0.5 yr) in transition matrices for octocoral communities off the Pacific coast of Panama analyzed at the 3 spatial scales: regional (32 plots), gulf (16 plots) and reef (4 plots). GC: Gulf of Chiriqui; GP: Gulf of Panama

Scale	Community	Damping ratio	Convergence rate	Half-life
Regional	Pacific Panama	1.12	11.33	6.11
Gulf	Gulf of Chiriqui	1.05	4.45	15.57
Gulf	Gulf of Panama	1.17	15.71	4.41
Reef	Catedrales (GC)	1.07	6.70	10.35
Reef	Roca Hacha (GC)	1.06	5.50	12.61
Reef	Jicarita (GC)	1.04	3.81	18.18
Reef	Prosper (GC)	1.15	13.99	4.95
Reef	Elefante (GP)	1.21	18.76	3.70
Reef	San Telmo (GP)	1.08	7.89	8.78
Reef	Galera (GP)	1.01	0.75	92.69
Reef	Pedro Gonzalez (GP)	1.98	68.36	1.01

Table 5. Correlation between change in community evenness (species evenness in the stationary community) after species removal and species relative abundance in octocoral communities off the Pacific coast of Panama analyzed at 3 spatial scales: regional (32 plots), gulf (16 plots) and reef (4 plots). GC: Gulf of Chiriqui; GP: Gulf of Panama. *significant correlation ($p < 0.05$)

Scale	Community	Evenness	r	p
Regional	Pacific Panama	0.76	−0.14	0.20
Gulf	Gulf of Chiriqui	0.77	−0.03	0.80
Gulf	Gulf of Panama	0.82	−0.16	0.20
Reef	Catedrales (GC)	0.64	−1.06	0.02*
Reef	Jicarita (GC)	0.75	−0.59	0.06
Reef	Roca Hacha (GC)	0.74	−0.29	0.29
Reef	Prosper (GC)	0.19	−1.06	0.02*
Reef	Elefante (GP)	0.57	−0.59	0.34
Reef	Galera (GP)	0.30	−1.46	0.37
Reef	San Telmo (GP)	0.70	−0.75	0.11

(GC) produced decreases of 38 and 35% respectively; the removal of *L. cuspidata* and *L. alba* in Prosper (GC) resulted in decreases of 52 and 44%, respectively, rates similar to those seen after the removal of *L. cofrini* in San Telmo (GP, 51%) and Elefante (GP, 40%). The effect of species removal was correlated with species relative abundance only at Prosper (GC) and Catedrales (GC) (Table 5). The community at Pedro Gonzalez (GP) was not included in this analysis because it only had 2 octocoral species, *L. alba* and *L. cofrini* (Table S4). No octocoral keystone species were evident at regional or gulf scales.

DISCUSSION

The Markov chain model allowed us to quantify and compare measurements of community stability between octocoral communities inhabiting GP and GC off the Pacific Coast of Panama, as well to compare how octocorals differ or resemble other marine sessile communities.

Stability of octocoral communities off Pacific Panama

We found that disturbance and colonization rates varied between gulfs. Octocorals from GC had lower disturbance and colonization rates than octocorals from GP. GP had an estimated turnover time 3 times longer than GC and an estimated recurrence time 1.6 times longer than GP. Consequently, octocoral communities in GC were more stable (took longer to change) but less resilient (took longer to recover) than communities in GP.

Are the dynamics of GC linked to its greater diversity? Ives & Carpenter (2007) concluded that the strength and direction of this relationship depends on the definition of stability and the type of perturbation. In this study, the diversity–stability relationship was positive when stability was measured as the resistance to change; GC, which was more species-rich (n = 12 octocoral species), took 3 times longer to change between states (turnover time). Nevertheless, if stability was measured as the rate of return (recurrence time) this relationship was negative; in this case GP, which had fewer species (n = 7), returned 1.6 times faster to its original state. Our finding of the existence of both negative and positive diversity–stability relationships, therefore, agree with the conclusions of Ives & Carpenter (2007).

In these communities, the mechanism for the negative diversity–stability relationship is likely due to potential competition for space with other highly diverse sessile marine organisms (sponges, tunicates, CCA, algae turf). Competition for space limits octocoral recruitment in GC (Gomez 2017) and limits the ability of the community to recover after disturbance (low colonization rates and slow recurrence time). On the other hand, we suggest that the positive diversity–stability relationship we found is due to a greater variation in species-specific dynamic properties in species-rich communities (e.g. Yachi & Loreau 1999). A greater number of species means that some will persist for longer periods of time even if others are frequently disturbed. We don't know, however, how tolerant each of these species is to environmental fluctuations, but we do know that there is a wide range of interspecific variation in persistence and disturbance rates.

Species transition properties

The transition probabilities of individual species found in this study agree with previous studies in the Gulf of Chiriqui (Gomez et al. 2014, 2015), which grouped species based on their population dynamics; with the genus *Muricea* on the *K* end of the spectrum, with low recruitment and mortality rates, and the genus *Leptogorgia* on the *r* side, with high recruitment and mortality rates (Gomez et al. 2014). A persistence rate of 1 signified that all colonies of the species survived over the duration of the study, and a persistence rate of 0 signified that all colonies
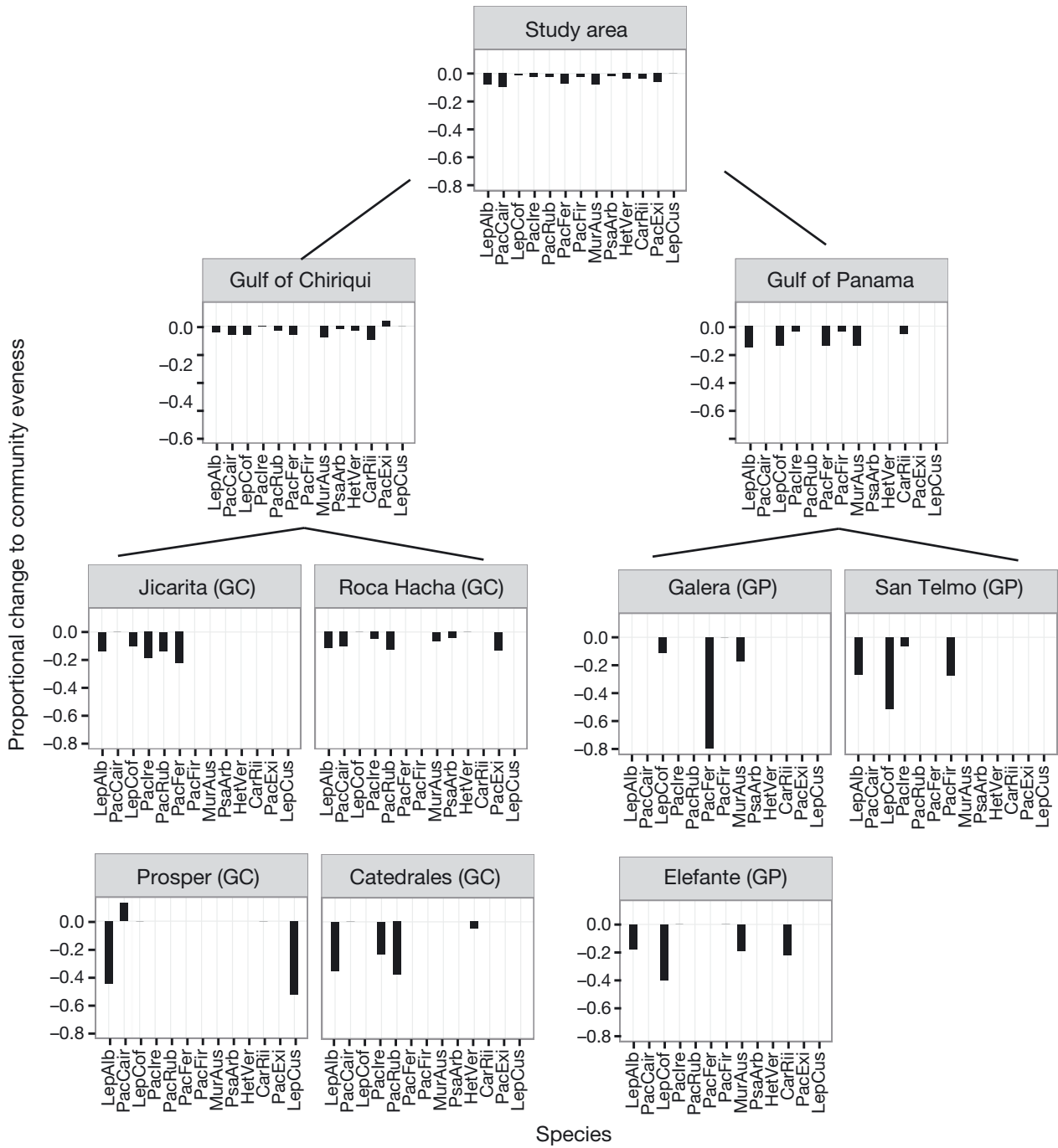
Fig. 6. Proportional change of community evenness after species removal at 3 spatial scales: study area, gulfs and individual reefs. GC: Gulf of Chiriqui; GP: Gulf of Panama. The effect of the removal of each species is displayed in decreasing order of abundance as in Table 1

of the species died during the study period, as seen for *Leptogorgia cuspidata* and *Carijoa riisei* respectively.

The snowflake *C. riisei* is known to be a good competitor for space, and can exhibit an invasive behavior (Concepcion et al. 2010). However, in this study *C. riisei* was the species most prone to being over-

grown by octocorals and other sessile organisms, and had the fastest turnover time in both gulfs. This behavior contradicts the previous descriptions made in Panama (Gomez et al. 2014, 2015) and other regions (Coles & Eldredge 2002, Calcinai et al. 2004, Kahng & Grigg 2005). The *C. riisei* population declined dur-

ing the study period, which is worth exploring in future studies.

Although *Muricea austera* has abundant and constant reproductive output (Gomez 2017), it was the species with the longest turnover time estimated by the model (13.5 yr) and a relatively long recurrence time (57.5 yr) explained by low disturbance (0.03), high persistence (0.9), and low colonization (0.07) rates. On the contrary, *L. alba*, which produces few oocytes during an annual reproductive season (Gomez 2017), had short turnover (1.15 yr) and recurrence times (4.15 yr), which is explained by a high colonization rate (0.3). It is a plausible hypothesis that the high colonization rate of *L. alba*, seen in this and other studies (Gomez et al. 2014, 2015, Gomez 2017), could be due to recruits that are asexually produced by fragmentation or polyp detachment; a behavior that is well known in other octocoral species (Lasker 1988, Coffroth & Lasker 1998, Lasker & Coffroth 1999).

During the present study, octocoral colonization was frequently seen on spaces previously occupied by CCA, additionally, the recruitment of *Pacifigorgia firma* and *P. ferruginea* only occurred on CCA. Chemical cues from CAA are known to attract hard coral larvae facilitating their recruitment (Heyward & Negri 1999). It is possible that such an interaction also occurs between CCA and octocorals.

None of the species transition properties were correlated with species abundance in the Gulf of Chiriqui, but colonization, replacement, and entropy were positively correlated with species abundance in the Gulf of Panama. The lack of correlation in GC could be due to the high number of rare species and the low dominance present in this gulf (Gomez et al. 2014).

Species removal

As in many aspects of community ecology, our interpretation of an ecological process like biodiversity change is scale-dependent (Levin 1992). In this study, the effect that species removal had on community evenness depended on the spatial scale at which it was analyzed. At regional and gulf scales, the effect of species deletions was minimal, and no key species were identified. However, when analyzed at the reef scale, the effect of the deletions increased considerably.

The effect of species removal (i.e. removed from the transition matrix) was measured as the compensatory changes in the remaining species abundance in the community. The effect of species deletion on evenness was not as great in species-rich communi-

ties because the loss was compensated by the other species in the community. However, where species richness was lower, the effect of species deletion was considerably greater. This can be easily seen when comparing the effect of deletions in Roca Hacha, a species-rich community, with deletions in species-poor Galera .

It is worth noting that the high frequency of zeros within all the transition matrices (Table S4) suggests a low degree of interaction among co-occurring octocoral species (Hill et al. 2004).

How octocoral communities differ from other marine sessile communities

This analysis of our Markov Chain model allowed us to compare the dynamic features of our focal octocoral communities. The persistence rate of octocorals off Pacific Panama resembles the rate found in the subtropical subtidal rocky community studied by Hill et al. (2004) and the exposed pool of the Australian coral reef studied by Tanner et al. (1994). However, the estimated disturbance rate of octocorals was 3 times greater higher in GC compared to the disturbance rate in the rocky subtidal (Hill et al. 2004) and 8 times greater than the rocky intertidal studied by Wootton (2001b). The estimated turnover time in GC is relatively similar to that found in exposed crest of coral reefs studied by Tanner et al. (1994). The estimated recurrence time for GC, GP and for the entire Pacific Panama is similar to that from rocky subtidal communities studied by (Hill et al. 2004) and the protected crest of coral reefs studied by Tanner et al. (1994) (Table 6).

Model limitations

Our model was based on transition probabilities measured in eight 1 m^2 plots at 8 sites and assumed fix probabilities averaged in time and space. These probabilities, however, could vary due to the large spatial heterogeneity of these communities and the relatively short study period (19 mo), which could mask long-term community dynamics. The scales of space and time used in this study could especially affect our interpretation of the dynamic and stability properties of rare species (low sample size) and species with very slow dynamics (low probabilities of quantifying mortality and colonization events).

This analysis encompassed 3 definitions of stability; resistance to change, return to previous state, and

Table 6. Comparative table of dynamic properties and stability measurements in marine benthic communities: octocorals from the Tropical Eastern Pacific (Pacific Panama, Gulf of Panama [GP] and Gulf of Chiriqui [GC]); rocky subtidal (Hill et al. 2004); rocky intertidal (Wootton 2001b); exposed coral reefs (EC), exposed pool communities (EP), and protected crests (PC) (Tanner et al. 1994). Adapted from Hill et al. (2004)

| | Octocoral | | | Rocky subtidal | Rocky intertidal | Coral reef | | |
	GP	GC	Pacific Panama			EC	EP	PC
Mean disturbance rate	0.37	0.16	0.31	0.06	0.02	0.39	0.41	0.36
Mean colonization rate	0.27	0.14	0.18	0.71	0.93	0.14	0.26	0.34
Mean persistence rate	0.61	0.66	0.59	0.62	0.51	0.78	0.64	0.57
Replacement by (biotic)	0.04	0.02	0.01	0.1	0.26	0.03	0.04	0.07
Replacement of (biotic)	0.02	0.18	0.09	0.29	0.45	0.08	0.12	0.16
Normalized entropy	0.48	0.34	0.39	0.49	0.52	0.34	0.25	0.21
Biotic turnover rate	0.39	0.34	0.41	0.36	0.47	0.48	0.52	0.52
Biotic turnover time (yr)	1.52	4.79	1.85	3.4	2.9	4.8	5.2	3.3
Biotic recurrence time (yr)	21.27	33.97	33.44	37.9	14.6	121.3	87	38.1

species compensations after extinction. However, because anthropogenic disturbances affect the stability and the diversity of natural systems simultaneously, it is necessary to identify the environmental factors that drive disturbances (Ives & Carpenter 2007). These environmental factors are not well known for octocoral communities in the TEP. It is especially important to study press perturbations, which are gradual or cumulative pressures such as warming and ocean acidification, which are major ecological drivers in other coral groups (Pandolfi et al. 2011). These perturbations are likely to change the number of species, their interaction and the nature and strength of the communities, which would change the fixed probabilities we estimated for this model.

Conclusions

The Markov chain model presented in this paper provided a first insight into the stability of octocoral communities off the Pacific coast of Panama. We found these communities have long persistence times. However, stability varied with location; communities at GC are 3 times more stable than those in GP, but communities GC are also less resilient. Based on our results and a previous study (Gomez 2017), we hypothesize that this is due to strong competition for space with other sessile species, which limits octocoral recruitment and its ability to recover after disturbance. Modeled species extinctions had a greater effect in species-poor communities and at smaller spatial scales. Further studies are needed to identify environmental drivers affecting octocoral community stability.

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