Quantifying scales of spatial variability in algal turf assemblages on coral reefs

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ABSTRACT: Quantifying variability over multiple spatial scales is a fundamental goal in ecology, providing insight into which scale-dependent processes most strongly influence community structure. On coral reefs, the ubiquitous turf algae are the primary food source for herbivores and competitors for space with corals. Turf algae will likely increase in the future, because they thrive under conditions that reduce coral cover. Turfs are typically treated as a single homogeneous functional group, but analyzing them as a variable assemblage is more informative. We used a hierarchical sampling design to quantify 4 scales of variability in turf assemblages from centimeters (within single dead coral heads) to kilometers (across islands) on the rarely studied Lhaviyani Atoll, Maldives. We used 4 metrics, each reflecting different ecological processes: percent cover, canopy height, richness, and assemblage composition. For most of these metrics, variability was significant at multiple spatial scales. However, for all metrics, the smallest scale (centimeters) explained the greatest proportion of overall variability. The least variability in cover, canopy height, and richness occurred among sites (100s meters), suggesting that processes such as competition, predation, and vegetative growth are heterogeneous at small scales. In contrast, assemblage composition was least variable at the largest scale (kilometers), suggesting that oceanographic processes or a well-mixed propagule supply reduce variability. With declining coral and increasing cover of turf on reefs worldwide, it will become increasingly important to understand the dynamics of coral–turf competitive interactions. However, because turf assemblages are highly variable at small spatial scales, these interactions require more detailed consideration.

KEY WORDS: Epilithic algal matrix · Spatial variability · Algal assemblage · Patchiness · Hierarchical analysis

INTRODUCTION

Spatial heterogeneity is an intrinsic feature of ecological communities, and quantifying the hierarchical scales of this variability is a fundamental goal of ecology (Levin 1992). Numerous ecological and environmental factors, acting on different spatial scales, affect the variable abundance and distribution of species across a landscape (Menge & Olson 1990). Heterogeneity in community or assemblage structure is driven by succession (Odum 1969), which in turn is driven by disturbance (Connell 1978). Mechanisms behind the relationship between disturbance, suc-

cession, and community structure include life history strategies, nutrient uptake, reproductive potential, and interspecific competition (Connell & Slatyer 1977). Therefore, identifying scales of the greatest heterogeneity can elucidate which scale-dependent processes exert the most influence on community structure.

In many ecosystems, the smallest scales are characterized by stochastic events or processes, while at larger scales these random processes and patchy distributions even out and become more generalizable as biogeographic patterns (Levin 1992, Coleman 2002, Fraschetti et al. 2005). However, small-scale

patchiness is not simply random, ecological noise (Coleman 2002). In terrestrial, aquatic, and marine systems, small-scale heterogeneity and community diversity is driven by dispersal ability (Levin 1992, Marhaver et al. 2013), micro-patchiness in the physical habitat or substrate, and both facilitative and inhibitive biological interactions (Pacala & Levin 1997). At larger scales (e.g. >100 km), biogeographic factors, such as habitat and long-distance dispersal, appear to be more important (Underwood & Chapman 1996, Fraschetti et al. 2005). This spatial variability can be either compounded or counteracted by temporal variation, particularly in systems where small-scale spatial heterogeneity is the largest source of variation (Underwood 1991). However, interactions between spatial and temporal scales of variation require explicit examination of nested scales in both dimensions, which was beyond the scope of this study. Therefore, here we examine only the spatial aspects of variability as a foundation for future investigation into temporal variability.

Marine benthic community structure is typically, but not always, most spatially variable at small scales (Fraschetti et al. 2005). Grazing and competition (Steneck & Dethier 1994) are two of the most dominant processes that drive succession and thus heterogeneity in community structure. However, the effects of grazing are widely variable at scales ranging from meters (Iveša et al. 2010, Poray & Carpenter 2014) to local (Fletcher 1987) and regional scales (Foster 1990). Disturbance has long been known to play a major role in driving variability among communities separated by several meters in the rocky intertidal and subtidal habitats (Sousa 1979, Smale et al. 2010), and large-scale disturbances such as storms, fires, or El Niño events can create heterogeneity over a scale of 10s or 100s of meters (Kennelly 1987, Collins 1992, Dayton et al. 1992). Propagule dispersal and recruitment contribute to community heterogeneity at both small (meters) (Andrew & Viejo 1998) and very large (100s of kilometers) spatial scales (Deysher & Norton 1981), depending on the type of reproduction (Bellgrove et al. 2004).

Many of these processes contribute to heterogeneity in marine algal assemblages, which can be most variable at scales ranging from centimeters (Rowan & Knowlton 1995) to kilometers (Tribollet et al. 2010). Importantly, though, marine algal assemblages appear to not be consistently structured at a global scale. One of the most widely applicable trends in global diversity patterns, the latitudinal diversity gradient, is a broad pattern of high species diversity at the equator and decreasing diversity as latitude increases (Pianka 1966). While the latitudinal diversity gradient is observed in almost every group of organisms in marine, terrestrial, and aquatic environments (Witman & Roy 2009), it, notably, does not apply to marine macroalgae (Santelices et al. 2009). Therefore, smaller-scale processes may be more important in driving variability in algal communities. Specifically, heterogeneous recruitment and recovery from disturbance appear to be the most influential in structuring temperate algal turfing assemblages, which are most heterogeneous at smaller scales (Chapman & Underwood 1998).

Turf algae comprise a multi-species assemblage of taxonomically diverse algae and cyanobacteria. The definition of algal turf varies among temperate and tropical systems (Hatcher & Larkum 1983, Connell et al. 2014), sometimes including associated invertebrates (Huff 2006) and organic matter (Wilson et al. 2003). Here, tropical turf refers to only the algal component of the community with a canopy height of less than 1 cm. On coral reefs, turf algae are typically found growing on the calcium carbonate substrata of dead corals and rubble.

Turf assemblages are ecologically important, abundant, and significantly understudied components of the coral reef ecosystem. Turf algae are the main source of primary production on reefs (Wanders 1976), the primary food source for most coral reef herbivores (Carpenter 1986, Ledlie et al. 2007), can reduce the abundance of both adult and juvenile corals directly (i.e. overgrowth, allelochemicals) and indirectly (i.e. pre-emption of space, overgrowth of crustose coralline algae) (Birrell et al. 2005, 2008, Vermeij et al. 2010), and are rapid colonizers of open space after physical disturbances (Fong & Paul 2011), coral bleaching and disease (Diaz-Pulido & McCook 2002), and corallivory (Bonaldo & Bellwood 2009). Turf algae are more abundant than both coral and macroalgae on many coral reefs (Wismer et al. 2009), and are likely to become more abundant in the future, because they thrive under conditions that threaten coral health, such as overfishing of herbivores, nutrient pollution (Smith et al. 2010), ocean acidification (Falkenberg et al. 2013), and sedimentation (Birrell et al. 2005). As anthropogenic impacts become more frequent and more extreme, turf algae will likely play an increasingly central role in the coral reef communities of the future. Therefore, a more comprehensive understanding of the structure and variability of turf assemblages is needed to better understand the overall ecology of reef ecosystems.

Most ecological studies treat turf algae as a single homogeneous functional group. However, there is

mounting evidence that different turf assemblages may play variable ecological roles. Turf assemblages at different successional stages vary in canopy height, density, and heterogeneity, causing variable effects on coral larval settlement (Birrell et al. 2005). Canopy height in particular may be an important physical trait of turf algae, as taller turf assemblages trap more sediment, making them less susceptible to herbivory and possibly triggering a positive feedback loop leading to a persistent state of ungrazed, sediment-laden turf that is inhospitable to coral settlement (Bellwood & Fulton 2008). In addition to canopy height, morphologically distinct species within a turf assemblage have predictable differences in productivity, longevity, and susceptibility to herbivory (Steneck & Dethier 1994, Padilla & Allen 2000). For example, turf assemblages dominated by simple, filamentous algae would likely respond more quickly to nutrient enrichment but be more susceptible to herbivory compared to more complex corticated or calcified species. Individual turf algae species that are superior competitors to corals (Jompa & McCook 2003) might be more likely to overgrow existing corals or prevent coral recovery following a disturbance event, while presence of taxa that are preferred by herbivores would indicate low levels of herbivory. A closer examination of both the physical traits and taxonomic composition of turf assemblages is needed.

There are few studies that have explicitly addressed how tropical turf assemblages vary across spatial scales, and the results are thus far conflicting. Diversity and assemblage structure vary across ocean basins (Anderson et al. 2005), across 10s (Diaz-Pulido & McCook 2002, Stuercke & McDermid 2004) or 100s of kilometers (Chapman & Underwood 1998), with depth (Anderson et al. 2005), based on successional stage following a coral bleaching event (Diaz-Pulido & McCook 2002) and within damselfish territories (Lison de Loma & Ballesteros 2002), and in response to experimental manipulations of herbivory and nutrients (Smith et al. 2010). These results demonstrate quantifiable spatial patterns in turf assemblages and suggest that turf assemblage composition could be related to ecological function or environmental conditions. However, it remains unclear to what degree tropical turf assemblages vary at different spatial scales within a given system. A quantitative understanding of spatial variation in turf assemblages would help elucidate the spatial patterns of the biological and physical processes driving benthic reef community structure (Table 1). Once spatial patterns are understood, we can begin to examine both the processes that cause those patterns and the effects of those patterns on the community and ecosystem. Here we take the first step by quantifying the spatial patterns of a tropical turf assemblage.

Specifically, the purpose of this study was to describe a variety of turf assemblage characteristics at a greater level of detail than typically studied and to identify how these characteristics vary across spatial scales. To identify any scale-dependent processes that contribute most to the structure of tropical algal turf assemblages, we compared 4 functionally distinct metrics (total percent cover, canopy height, richness, and assemblage composition) that each reflect different dimensions of the ecological role of turf algae, identifying the spatial scale (mm, cm, m, km) that explained the majority of variation for each metric.

MATERIALS AND METHODS

Site description and sample collection

Turf algae were collected from the lagoonal reef flat of Lhaviyani Atoll (also called Faadhippolhu), Republic of the Maldives (Fig. 1). Lhaviyani is in the northern part of the Maldivian Archipelago in the Indian Ocean. The atoll is approximately 35 km in diameter and is made up of 54 islets, 5 of which are inhabited, with a total atoll population of approximately 9000 (Ministry of Planning and National

Table 1. Sampling strategy at hierarchical spatial scales and the processes that likely contribute the most to heterogeneity at each scale

Scale	Distance between replicates		n	Processes
Punch	10 cm	$(1 \times 10^{-1}$ m$)$	256	Microhabitat suitability, vegetative growth, competition, herbivory
Colony	1 m	$(1 \times 10^{0}$ m$)$	64	Vegetative growth, morphology, competition, herbivory, time since coral death
Site	100 m	$(1 \times 10^{2}$ m$)$	16	Herbivory, abiotic environment
Island	5–10 km	$(1 \times 10^{4}$ m$)$	4	Currents, propagule dispersal, herbivory, nutrient availability
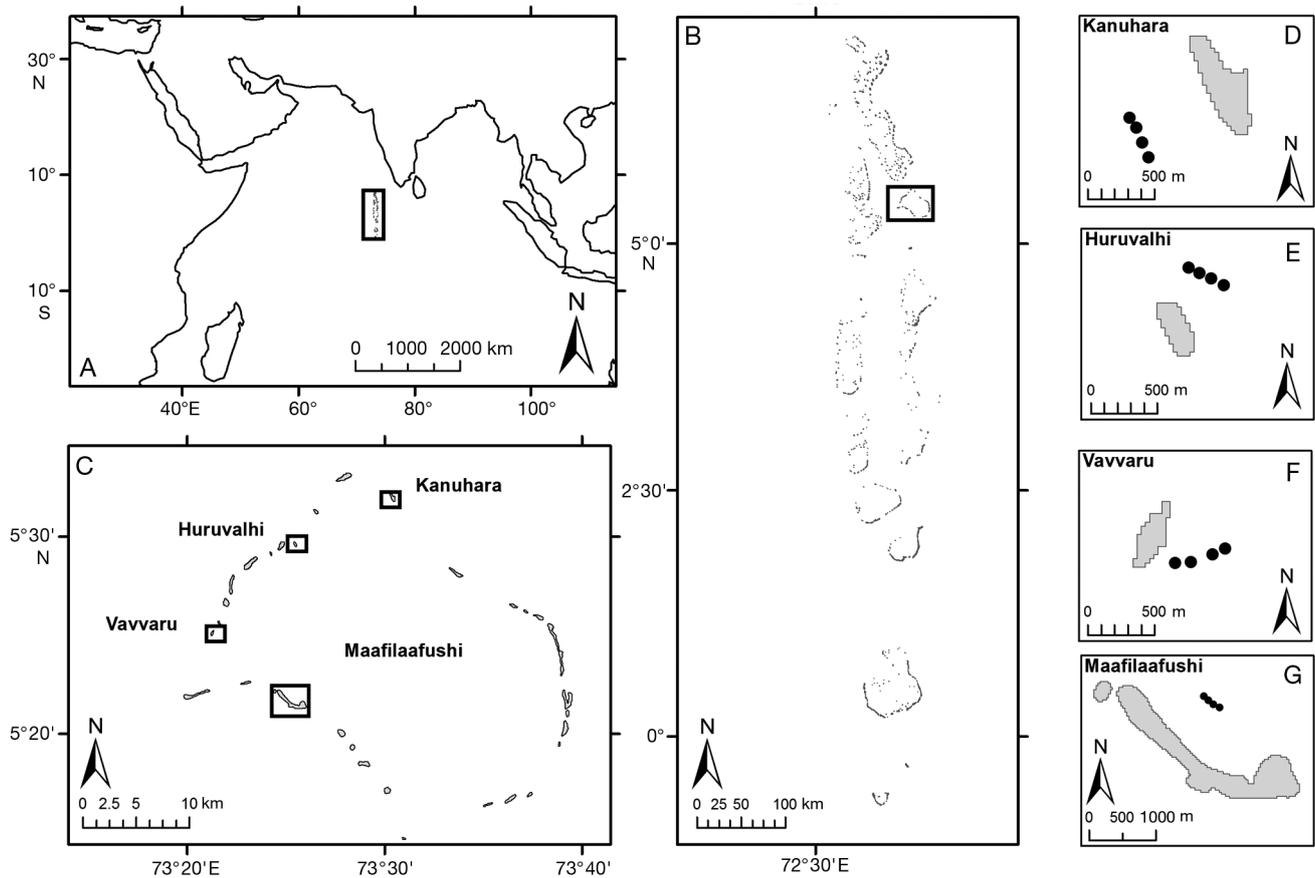
Fig. 1. Hierarchical spatial arrangement of sampling locations. Algal turf samples were collected (A) from the Republic of the Maldives in the Indian Ocean, (B) from Lhaviyani Atoll in the northern part of the Maldives archipelago, (C) at 4 islands within Lhaviyani Atoll, and (D–G) from 4 sites at each island

Development 2007). The lagoon is physically sheltered but open to ocean flushing and swell and is dominated by massive *Porites* and branching *Acropora* corals. Lagoon depths of approximately 50 m have been reported. The tropical climate is driven by seasonal monsoons, with westerly winds over the wet summer and easterly winds in the drier winter.

Reefs in Lhaviyani Atoll were recently affected by 2 major disturbance events: a massive bleaching event in 1998 and a tsunami in 2004. The bleaching event resulted in almost complete loss of branching and tabular corals in the portion of the atoll that was investigated (Loch et al. 2002, 2004). The tsunami completely washed over Lhaviyani's islands (Fritz et al. 2006, I. K. Mohamed pers. comm.), which reach a maximum elevation of 1.5 m above sea level, but it was less damaging there than in more southern parts of the Maldives. While scientific data are lacking for Lhaviyani's reefs, these 2 significant disturbances likely 'reset' much of the reef ecosystem, killing many corals and opening up space for turf coloniza-

tion. Algal turf assemblages in Lhaviyani are likely representative of algal turfs on other reefs that have experienced similar large-scale disturbances in the past few decades.

To quantify spatial variability in turf assemblages, replicate samples were collected using identical methods at 4 different scales: sample/punch (separated by ~10 cm), colony (separated by ~1 m), site (separated by ~100 m), and island (separated by ~10 km). Smaller scales reflect stochastic biological events and processes, such as different algal growth morphologies or individual herbivore grazing scars, while larger scales reflect broader population- or landscape-level processes including herbivore populations, propagule supply, and the abiotic environment (including thermal histories and bleaching events; Table 1).

Each scale was sampled with 4 replicates for a total of 256 turf samples. Samples were collected by SCUBA divers using a 1.3-cm diameter steel hollow punch and mallet, resulting in an area of 1.27 cm^2 per
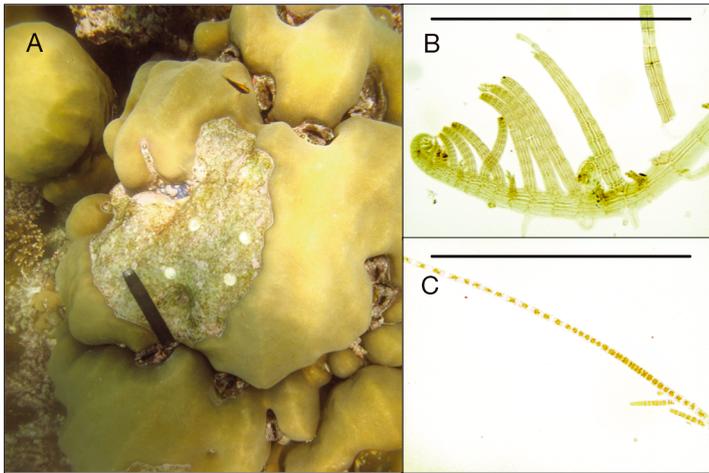
Fig. 2. Photographic examples of turf communities. (A) The typical sampling area appeared visually homogeneous (scale: black punch tool is 11.5 cm). (B) The uncorticated, terete alga *Herposiphonia* (scale bar = 1 mm) was one of the most abundant and widespread taxa. In contrast, (C) uniseriate filamentous algae in the order Ectocarpales (scale bar = 0.5 mm) were widespread but, due to their small size and growth habit, contributed a very small amount to percent cover

replicate. As the thalli of most tropical turf species are less than 1 mm in diameter, this allowed for a hypothetical assemblage of >100 densely packed filaments per punch. Importantly, this punch size was selected to allow the collection of 4 independent, non-adjacent punches from visually similar turf (Fig. 2A). To minimize variability due to light availability, exposure to herbivores, and edge effects, punches were all collected from massive *Porites* spp. coral colonies with at least 0.5 m^2 partial mortality that were overgrown with turf algae, as flat as possible, and oriented directly upward (i.e. perpendicular to incident irradiance). Sites were interior lagoonal reefs at depths of 4–5 m. Islands were individual islets comprising Lhaviyani Atoll. Samples were collected in July 2013 over the course of 11 d to minimize effects of temporal variability. Upon collection, individual samples were placed in pre-labeled Ziploc bags and held in an ambient seawater bath. Once ashore, individual samples were preserved in 10% formalin and stored for analysis.

We used 4 different metrics to analyze turf algae: total percent cover, canopy height, generic richness, and a multivariate comparison of assemblage composition. Total percent cover and canopy height are reflections of grazing pressure and algal growth rates, which can vary with nutrient availability and disturbance regimes. Differences in taxonomic richness and composition indicate an assemblage's potential ecological function or propagule dispersal. For example, dominance by heavily calcified or chemically defended taxa would characterize a turf assemblage heavily defended from grazing pressure, while dominance by fast-growing or larger taxa might suggest nutrient enrichment or signal an assemblage that would be competitively dominant over coral.

Samples were analyzed under a dissecting microscope for physical characteristics (% cover and canopy height) and taxonomic composition (to genus when possible). Total percent cover was visually estimated to the nearest 5%. Canopy height of 6 haphazardly selected algal filaments per sample was measured to the nearest 0.01 mm using digital calipers. Taxonomic composition was visually estimated to the nearest 1% (for taxa with cover ≤10%) and to the nearest 5% (for taxa with cover >10%) and recorded as a fraction of total cover, providing descriptions of relative abundance of each taxon (taxon-specific cover as a percentage of total algal cover on a given sample). Closely related algal taxa that could not be consistently identified to genus due to lack of reproductive material were grouped together as follows: CCA (several species of crustose coralline algae), cyanobacteria (separated into cyanobacterial filaments and film-like cyanobacterial mats), ectocarps (including the brown genera *Ectocarpus* spp. and *Hincksia* spp.), *Gelidium* and *Gelidiella* spp., and *Chondria* spp. and *Laurencia* spp. Following analysis, all taxa were coded as 1 of 7 functional groups following the classification scheme of Steneck & Dethier (1994).

Statistical analysis

To determine whether heterogeneity of turf algae was related to spatial scale, univariate metrics (mean canopy height, total percent cover, and total number of taxa at the genus level unless otherwise noted) were each compared using hierarchical nested ANOVA, with colony nested within site and site nested within island. All factors were treated as random. To force non-negative variance components, a restricted maximum likelihood estimation model (REML) was used to calculate variance components. Because we used a completely balanced design, REML is equivalent to a 3-way nested hierarchical ANOVA (Fletcher & Underwood 2002). To understand what proportion of total variation was due to variability at each scale, variance for the 3 metrics is presented as both absolute variance and as a percent

of total variation for each response variable separately (the 'magnitude of effect'; Graham & Edwards 2001), thus allowing us to quantify total variability attributed to each scale and to determine the proportion of total variability that occurs between specific scales, respectively (Edwards 2004). While presenting variance components as proportions prevents direct comparisons across metrics (Underwood 1997), it does allow for a clearer picture of patterns of variability across scales within a given metric. To provide an estimate of the uncertainty in the variance components, 95% confidence intervals of variance components were calculated using parametric bootstrapping. Hierarchical ANOVAs and bootstrapping were performed using the *lmer* and *confint* functions (lme4 package), respectively, in R 3.1.2 (R Development Core Team, www.r-project.org).

Multivariate approaches were used to test whether spatial variability in turf assemblage composition, at the genus level, was related to scale. A hierarchical nested PERMANOVA (permutation-based multivariate ANOVA; Anderson 2001) with 3 factors (island, site, and colony) was run on a Bray-Curtis similarity matrix of relative percent cover data using PRIMER-E (v6). As with univariate metrics, colony was nested within site and site was nested within island; all factors were treated as random. Variance components for each spatial scale were calculated from the PERMANOVA mean squares, and statistical significance was tested under a reduced model with 9999 permutations. As with the univariate metrics, PERMANOVA variance components are presented as both absolute variance (square roots of estimates of components of variation; Anderson et al. 2008) and as a proportion of total variability within each response variable separately (Underwood & Chapman 1996).

To visually represent the similarity in turf assemblage structure within and among spatial scales, nonmetric multidimensional scaling (nMDS) plots of all 256 samples were created based on ranked Bray–Curtis similarities. To visually represent the structure of turf assemblages for each island separately, individual nMDS plots were created for each of the 4 islands based on Bray–Curtis similarities of genus-level percent cover data.

We used a square-root transformation to increase the influence of less common taxa that could have unique ecological functions. We performed all analyses on both transformed and untransformed data. However, because the transformation made no material difference in the results or interpretation, we present only the untransformed data below.

RESULTS

Turf assemblage composition

We identified 29 taxa (including the few higher-order taxa that were indistinguishable to finer genus level) from 11 orders across 4 algal phyla (Table 2). Red algae were both the most common, accounting for 16 of the 29 taxa, and the most abundant taxa, accounting for 56% of the total algal assemblage by cover. These patterns of red algal occurrence were driven by the abundant and diverse order Ceramiales, which accounted for 9 taxa and 40% of algae by cover. Seven of the 8 functional groups identified by Steneck & Dethier (1994) were represented, excluding only leathery macrophytes, which typically include only large macroalgae species not commonly found in turf assemblages. The most common functional group, in terms of prevalence in samples, was corticated terete algae, which included most of the taxa from the order Ceramiales.

The most abundant taxa were filamentous cyanobacteria (30 ± 22% cover, occurring on 93% of individual punches) and *Polysiphonia* spp. (29 ± 22% cover, occurring on 93% of punches; Figs. 3 & 4). The next most abundant taxa, *Gelidium/-iella* spp., *Herposiphonia* spp. (Fig. 2B), and *Dictyota* spp., each had mean cover of less than 9% (Figs. 3, 4). *Gelidium/-iella* spp. and *Herposiphonia* spp. were both abundant and widespread and were found on 62% and 68% of punches, respectively (Figs. 3, 4). In contrast, while *Dictyota* spp. were abundant, they were not widespread and were found in just 17% of punches (Figs. 3, 4). However, when present they covered a large proportion of the substrate.

Most taxa were rare: 17 taxa had less than 1% cover (Table 2), either because they were physically small filaments that, due to their growth habit, did not cover much of the substrate (e.g. *Cladophora* spp., *Sphacelaria* spp., and Ectocarpales; Fig. 2C), or because they were only found on 1 or 2 individual punches (e.g. *Griffithsia* spp., *Peyssonnelia* spp., and 2 unidentified taxa).

Turf cover, height and richness

Total cover, canopy height, and richness were all approximately normally distributed based on distributions and quantile–quantile plots, thereby satisfying the assumptions for ANOVA. Mean total algal cover across all punches was 57.5% (±1.6 SE), ranging from 10% to 100%. The remaining space was

Table 2. All algal taxa found, including percent cover (of all 256 punches) and percent occurrence (percentage of punches in which each taxon occurred). Functional groups are after Steneck & Dethier (1994): MIC: single-celled microalgae and cyanobacteria; FIL: simple uniseriate filaments; FOL: foliose (sheet of cells); CFL: complex foliose (multiple layers of cells); CRT: complex or corticated terete; ART: articulated calcified; CRU: calcified crusts; SPH: siphonous). CCA: crustose coralline algae. Abundances of the taxa shown in **bold** are presented in Fig. 4

Taxon	% Cover	% Occurrence	Order	Phylum	Functional group
Cyanobacterial filaments	30.0	93.4	–	Cyanophyta	MIC
Polysiphonia	28.9	93.0	Ceramiales	Rhodophyta	CRT
Gelidium/-iella	8.7	62.1	Gelidiales	Rhodophyta	CRT
Herposiphonia	7.9	67.6	Ceramiales	Rhodophyta	CRT
Dictyota	6.9	16.8	Dictyotales	Ochrophyta	CFL
CCA	5.0	27.7	Corallinales	Rhodophyta	CRU
Ectocarpales (multiple families)	2.8	30.1	Ectocarpales	Ochrophyta	FIL
Caulerpella	<2	41.0	Bryopsidales	Chlorophyta	SPH
Ceramium	<2	22.7	Ceramiales	Rhodophyta	CRT
Ulva	<2	16.0	Ulvales	Chlorophyta	FOL
Anotrichium	<2	12.9	Ceramiales	Rhodophyta	FIL
Gelidium – blades	<2	11.3	Gelidiales	Rhodophyta	CFL
Cladophora	<1	18.0	Cladophorales	Chlorophyta	FIL
Corallophila	<1	8.6	Ceramiales	Rhodophyta	CRT
Cyanobacterial mats	<1	5.5	–	Cyanophyta	MIC
Caulerpa	<1	4.3	Bryopsidales	Chlorophyta	SPH
Sphacelaria	<1	4.3	Sphacelariales	Ochrophyta	FIL
Bryopsis	<1	3.9	Bryopsidales	Chlorophyta	SPH
Jania	<1	3.1	Corallinales	Rhodophyta	ART
Centroceras	<1	2.3	Ceramiales	Rhodophyta	CRT
Chondria/Laurencia	<1	<2	Ceramiales	Rhodophyta	CRT
Champia	<1	<2	Rhodomeniales	Rhodophyta	CRT
Lobophora	<1	<2	Dictyotales	Ochrophyta	CFL
Rhipidosiphon	<1	<2	Bryopsidales	Chlorophyta	SPH
Condrophycus/Laurencia	<1	<1	Ceramiales	Rhodophyta	CRT
Griffithsia	<1	<1	Ceramiales	Rhodophyta	FIL
Peyssonnelia	<1	<1	Peyssonneliales	Rhodophyta	CRF
Unknown red blade	<1	<1	–	Rhodophyta	CRF
Unknown sp.	<1	<1	–	–	–

either bare limestone or microbial films. ANOVA revealed significant variation in total cover at the scales of island and colony but not among sites (Table 3).

Eight key taxa were selected to more closely investigate ecologically relevant variability across scales. These taxa included the 5 most abundant taxa (cyanobacterial filaments, *Polysiphonia* spp., *Herposiphonia* spp., *Gelidium/-iella* spp., and *Dictyota* spp.; Table 2), one 'ecologically positive' taxon known to be beneficial to reef accretion and coral settlement (CCA), and 2 'ecologically detrimental' taxa known to have harmful effects on coral (*Corallophila* spp. and *Anotrichium* spp.; Jompa & McCook 2003). Cover of all of these representative taxa was highly variable across sites, with no discernible

patterns in abundance at the colony, site, or island level (Fig. 4).

Mean canopy height across all punches was 1.3 mm (±0.03 SE), ranging from 0.4 to 3.8 mm. Mean
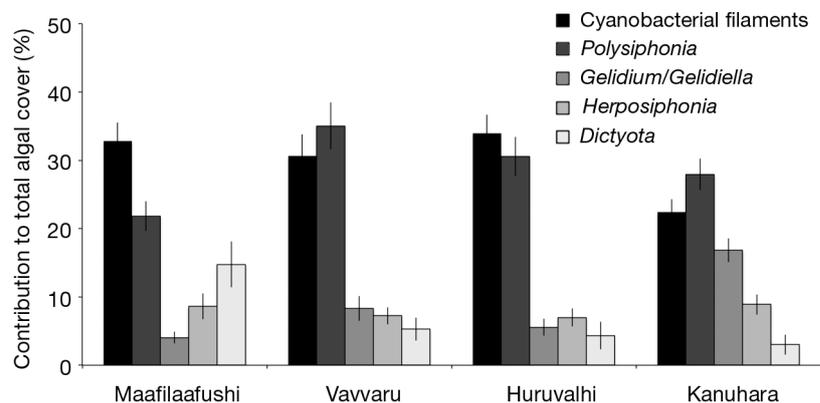
Fig. 3. Relative contribution by cover (mean ± 1 SE) of the 5 most abundant taxa on each island. Means and standard errors were calculated by treating all 64 punches on an island as individual replicates
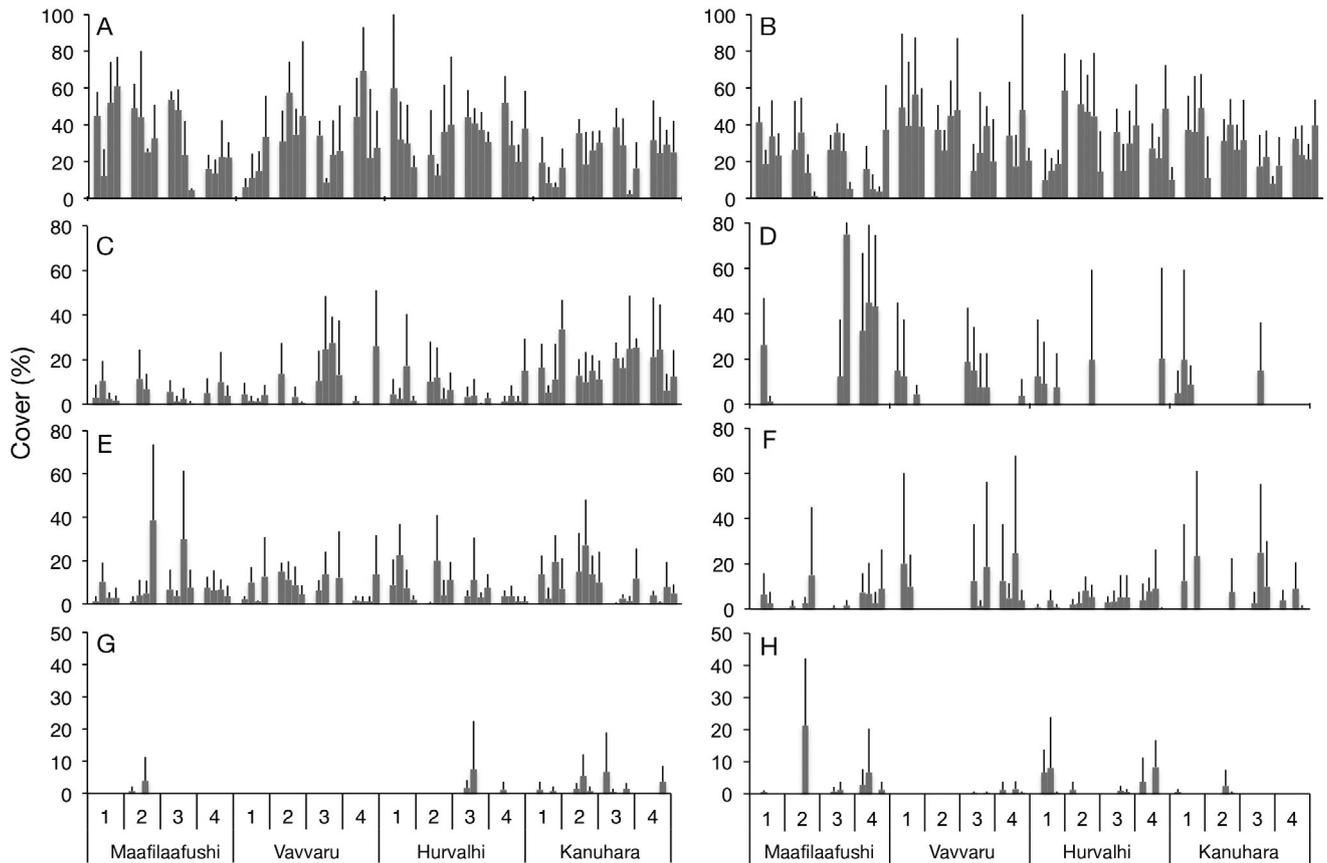
Fig. 4. Mean (±1 SD) cover of 8 key taxa by colony (n = 4 colonies per site) at each of 4 sites on each island (Maafilaafushi, Vavvaru, Hurvalhi, and Kanuhara): (A) cyanobacterial filaments, (B) *Polysiphonia* spp., (C) *Gelidium/-iella* spp., (D) *Dictyota* spp., (E) *Herposiphonia* spp., (F) crustose coralline algae (CCA), (G) *Corallophila* spp., and (H) *Anotrichium* spp. Taxa selected were the most abundant (A–E), known to have a positive effect on corals (F), or known to have a negative effect on corals (G,H)
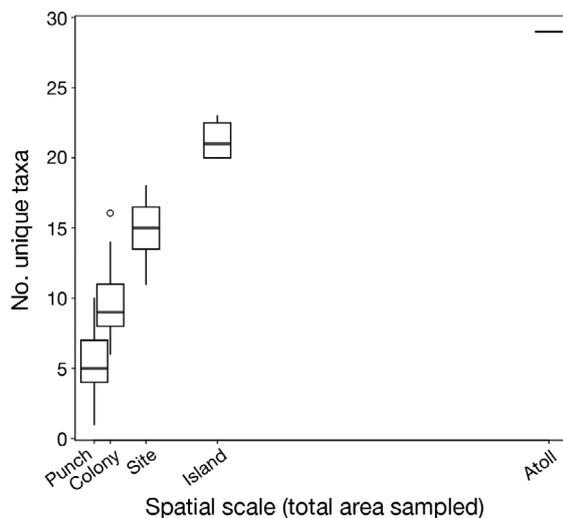
Fig. 5. Cumulative number of unique taxa at each spatial scale. Horizontal bars show medians, boxes are drawn at the first and third quartiles, whiskers display the range of the data, and outliers (open circles) are more than 1.5 times the interquartile range outside the box

canopy height varied significantly only among colonies and not at greater scales among sites or islands (Table 3).

Mean generic richness of all punches was 5.5 (±0.1 SE) taxa per punch (per 1.3 cm²). Richness ranged from 1 to 10 taxa per punch. Vavvaru had the lowest mean richness at all spatial scales, but also had the single punch with the highest richness. There was significant variation in number of taxa at the scales of island and colony, but not among sites (Table 3). The cumulative number of unique taxa increased with sampling area and appeared to approach an asymptote (n = 29 taxa) across all 256 punches (approximately 340 cm² sampled; Fig. 5).

Variance components for all 3 of these univariate measures were greatest at the smallest scale (Table 3), such that the smallest spatial scale explained the largest proportion of the total variation (Fig. 6). Estimates of residual variance were always greater than variance at any other scale and accounted for more than 50% of the total variability,

indicating that there was high variation among individual punches. Both absolute and proportional variability decreased as spatial scale increased from the punch to the site level, which always contributed the least to total variance (Table 3, Fig. 6). In fact, among-site variability contributed almost 0% to overall variability for both total cover and richness. Among-island variability always explained a greater proportion of total variation than among-site variability. Although variability was highly significant at all spatial scales, the 95% confidence intervals of variance components were overlapping among many of the larger scales. However, the confidence interval around variance at the punch level did not overlap any other confidence intervals for either percent cover or mean canopy height.

Table 3. Results of the hierarchical nested ANOVA tests, using a restricted maximum likelihood estimation model, on total algal cover, canopy height, and taxonomic richness. All factors were treated as random effects. Significance effects for $\alpha = 0.05$ are shown in **bold**. Confidence intervals were calculated by bootstrapping. The proportion of variance explained by each spatial scale is presented in Fig. 6

Source	df	MS	F	p	Variance component	95% CI
Total percent cover						
Island	3	2809	4.815	**0.020**	28.2	[0, 102.9]
Site (Island)	12	583.3	0.5279	0.89	0	[0, 45.6]
Colony (Site (Island))	48	1105	2.160	**0.0001**	122.2	[43.0, 191.1]
Residual = Punch	192	511.6			511.7	[432.8, 604.5]
Total	255					
Mean canopy height						
Island	3	0.9592	2.163	0.15	0.008	[0, 0.03]
Site (Island)	12	0.4435	1.310	0.24	0.006	[0, 0.03]
Colony (Site (Island))	48	0.3386	3.574	**<0.0001**	0.061	[0.03, 0.09]
Residual = Punch	192	0.0947			0.095	[0.08, 0.1]
Total	255					
Taxonomic richness						
Island	3	33.9	9.555	**0.0017**	0.49	[0, 1.5]
Site (Island)	12	3.553	0.9094	0.55	0	[0, 0.19]
Colony (Site (Island))	48	3.908	2.332	**0.0001**	0.54	[0.02, 0.8]
Residual = Punch	192	1.676			1.68	[0, 2.0]
.	255					

Scales of assemblage variation

Variability in taxonomic similarity among assemblages was significant at all spatial scales based on nested PERMANOVA (Table 4). As with the univariate metrics, multivariate variability was greatest at the smallest scales, and variance components decreased (assemblages became more homogeneous) as spatial scale increased (Table 4, Fig. 7D). There was approximately 32% residual variability unexplained by the scales sampled, indicating that the greatest proportion of multivariate heterogeneity was among individual punches. The variance components were significantly different from zero at all spatial scales based on 9999 permutations (Table 4) and followed the same pattern as the results obtained from the nested univariate ANOVAs.

The clear pattern of variability decreasing as spatial scale increases is reflected in the nMDS plot of all 256 samples (Fig. 7C), which shows no clear group-

Fig. 6. Percent of total variation in 3 turf characteristics explained by each spatial scale. Percent variation explained was calculated as the 'magnitude of effect' of each scale: individual variance components divided by the sum of all variance components for each metric. Estimates of uncertainty around variance components, presented as 95% confidence intervals, are presented in Table 3
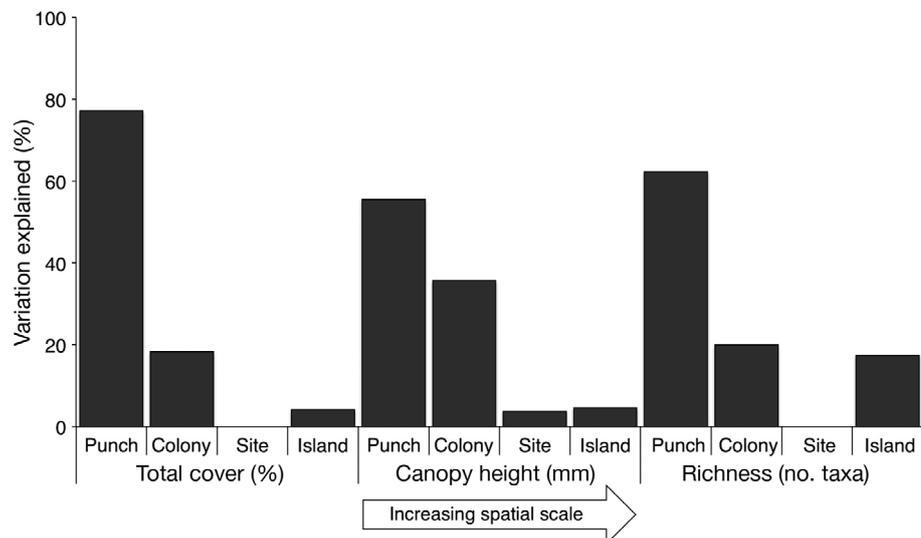
Table 4. Permutational multivariate ANOVA based on Bray−Curtis dissimilarities of relative percent cover of turf algae genera. Analysis was based on 9999 permutations. Significance effects for α = 0.05 are shown in **bold**. The proportion of variance explained by each spatial scale is presented in Fig. 7

Source	df	MS	Pseudo-F	p (perm)	Variance component
Island	3	9231.6	1.943	**0.0198**	70.02
Site (Island)	12	4750.3	1.681	**0.0037**	120.25
Colony (Site (Island))	48	2862.4	2.052	**0.0001**	362.27
Residual = Punch	192	1377.3			1377.3
Total	255				

ing among samples at the colony, site, or island level. Instead, individual punches are fairly evenly scattered such that larger-scale groups overlap completely (i.e. islands almost completely overlap all other islands).

The same inverse relationship between variability and spatial scale are visible in nMDS plots of

assemblage structure at individual islands (Fig. 8). There is no clear visual separation between sites because variability is greater within than among sites. Note, however, that with such large sample sizes (n = 64) the nMDS stress ranges from 0.16 to 0.19, and therefore these configurations should be interpreted conservatively.

DISCUSSION

All of the turf algal parameters measured here show the greatest variability at the smallest spatial scales, among assemblages separated by centimeters. While in some cases there was statistically significant variability at other spatial scales (and in fact, variance was highly significant at all spatial scales
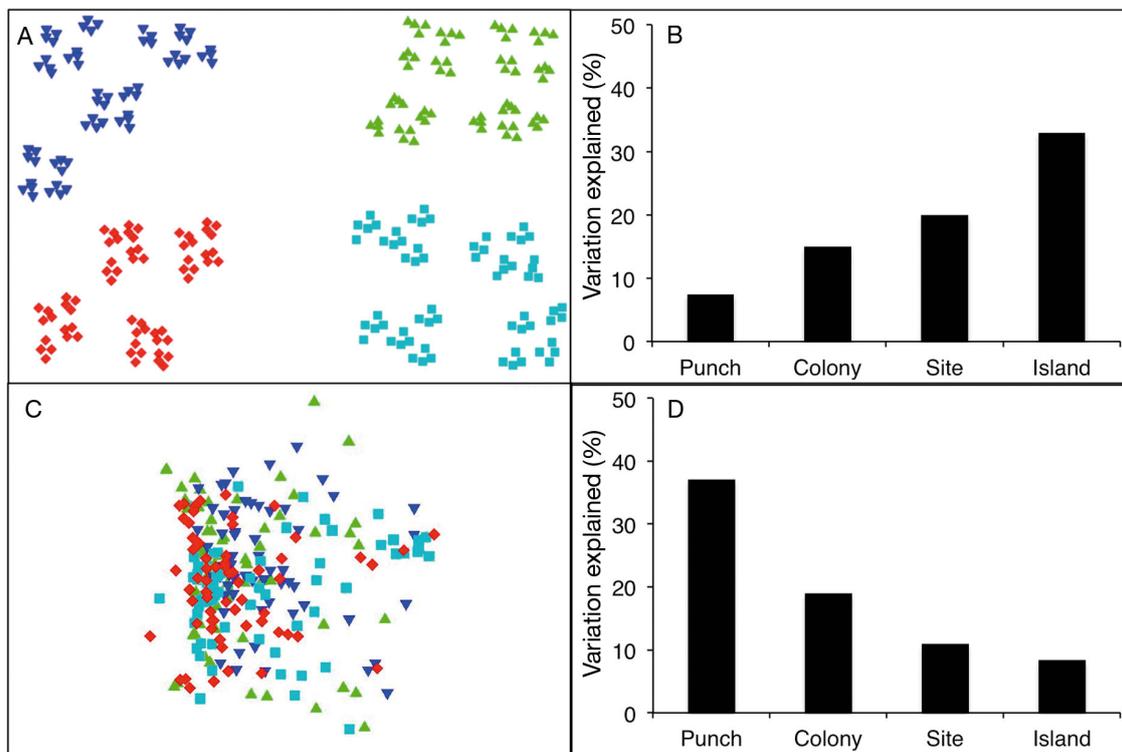
Fig. 7. Comparison of 2 possible relationships between variability and spatial scale. (A) Theoretical non-metric multidimensional scaling (nMDS) plot of similarity among samples from 4 different spatial scales in which communities are most similar at smaller scales (e.g. within a single colony) and most dissimilar at larger scales (among islands). Symbols differentiate the 4 islands: ▲, Vavvaru; ▼, Kanuhara; ■, Maafilaafushi; ◆, Huruvalhi. This clustering pattern in an MDS plot would correspond to (B) a theoretical positive relationship between spatial scale and percent of total variation in taxonomic composition, where the greatest amount of variation in community composition occurs among samples from different islands. (C) Actual nMDS plot of all samples (n = 256) based on Bray−Curtis similarities (stress = 0.2) of untransformed relative abundances. Symbols differentiate the 4 islands as in A. (D) Actual percent of total variation in turf communities explained by each spatial scale from square roots of estimates of variance components from PERMANOVA (Table 4)
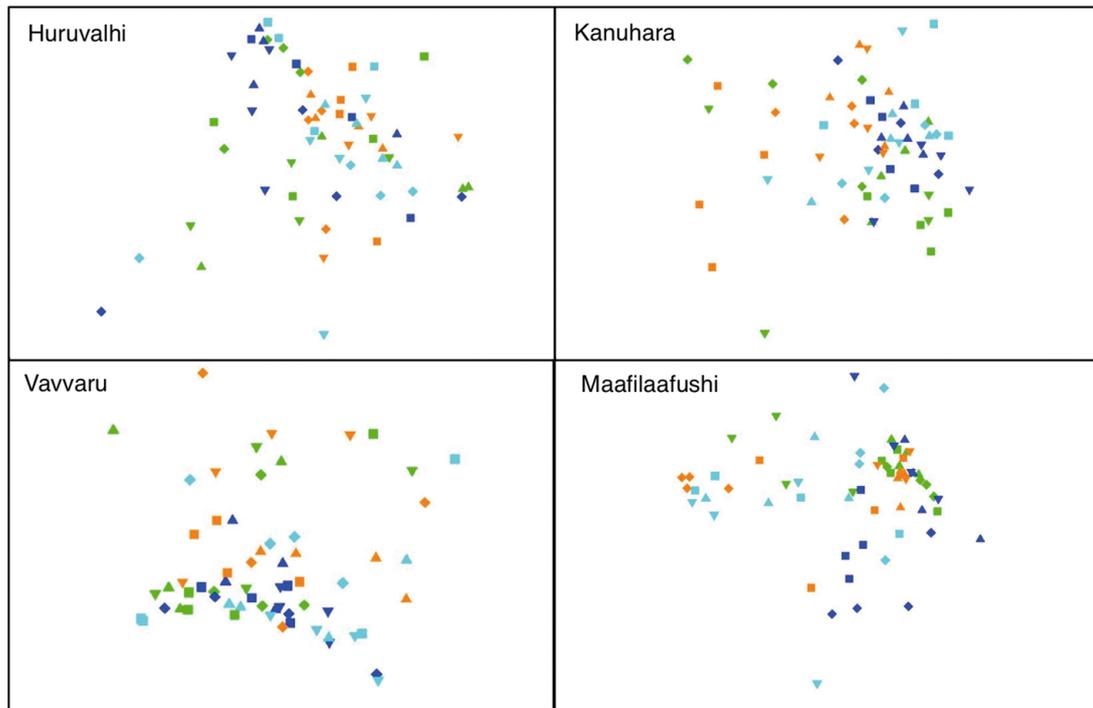
Fig. 8. Non-metric multidimensional scaling plots of untransformed relative abundance on punches (n = 64) from each island. Colors indicate site (for all islands, green = site 1, orange = site 2, dark blue = site 3, light blue = site 4) and shapes indicate colony (for all islands, square = colony 1, diamond = colony 2, triangle = colony 3, inverted triangle = colony 4). Stress values are 0.16 (Huruvalhi, Vavvaru, Maafilaafushi) and 0.19 (Kanuhara)

under the PERMANOVA model with 9999 permutations; Table 4), by far the largest proportion of total variability always occurred at the smallest scale. This inverse relationship between spatial scale and variability suggests that at least some processes operating at small scales, such as grazing by herbivores, competition, propagule settlement, and vegetative growth, are important in structuring turf algal assemblages on these Maldivian coral reefs. Alternately, turf algae assemblages may vary over time and although we controlled for it here, temporal variability can actually conflate spatial variability on very small scales (Underwood 1991). However, the relative strengths of temporal and spatial variation are inconsistent (e.g. see opposite results in Hughes et al. 1999, Kelaher & Levinton 2003). Therefore, here we limit our interpretation to processes that drive spatial patterns.

Other studies that have examined structure of marine algal and benthic invertebrate assemblages at hierarchical spatial scales have documented similar inverse relationships between variability and spatial scale (reviewed in Fraschetti et al. 2005; see also Wiens 1989, Underwood & Chapman 1996, Smale et al. 2010, O'Leary & Potts 2011). Most heterogeneity in benthic marine taxa occurs at small, but not always

the smallest, scales (10s of centimeters to several meters) (Fraschetti et al. 2005). For example, temperate turf algal assemblages display the greatest variation at the centimeter scale (Coleman 2002), and in tropical marine environments specifically, coral reef fish assemblages are heterogeneous among individual patch reefs and become more homogeneous at larger scales (Wiens 1989). In contrast, however, coral cover varies widely among reefs separated by several kilometers, though this effect depends on reproductive strategy (brooders versus spawners; Hughes et al. 1999).

Such spatial patterns in benthic organisms can be driven by recruitment variability. There is experimental evidence that variable recruitment drives small-scale heterogeneity at the scale of 10s of centimeters in temperate macroalgae (Bellgrove et al. 2004, Smale et al. 2010) and invertebrates living in temperate turf algae (Kelaher 2005). As a general rule, marine animals with limited dispersal are most variable at the centimeter to meter scale (Underwood & Chapman 1996). Organisms with planktonic larvae vary at larger scales than do organisms with direct development (Fraschetti et al. 2005). Turf algae, specifically, have been show to vary at the centimeter scale due to recruitment patterns (Coleman 2002).

However, since algal dispersal can be hyper-local (<1 km) or more regional (up to 100 km) (Shanks et al. 2003), and algal recruitment varies temporally in species-specific ways (Bellgrove et al. 2004), we can expect recruitment to drive species-specific spatial patterns among algae that would sum to the heterogeneous assemblages measured here.

In addition to recruitment, disturbance events influence spatial patterns because space is one of the most limiting resources in benthic communities. We can expect benthic communities to be variable at small scales where isolated chance events or biological interactions dominate a landscape, and at larger spatial scales where the physical disturbances such as bleaching events, wave energy, storms, or tsunamis are the main driving forces. For example, following a large-scale bleaching event in Australia, turf succession varied among locations depending upon both the bleaching severity and the local site environment (Diaz-Pulido & McCook 2002). Recolonization after a space-clearing disturbance drives small-scale variability in temperate intertidal turfs (Benedetti-Cecchi & Cinelli 1994) and their infaunal invertebrate assemblages (Olabarria 2002). However, physical disturbances are less important than interspecific competition in structuring temperate turf assemblages (Maggi et al. 2012), and anthropogenic disturbances seem to structure turf variability on larger scales (kilometers) (Benedetti-Cecchi et al. 2001). As the largest variability we measured in tropical turf algal assemblages was at the scale of centimeters, we propose that smaller-scale disturbances are more important in structuring tropical turf communities.

Herbivorous grazing is one such spatial disturbance that structures benthic reef communities (Steneck & Dethier 1994, Poray & Carpenter 2014) and, due to its mechanics, is likely to drive small-scale patchiness of algal turf assemblages. Grazing bites can be considered centimeter-scale 'disturbances' that completely reset turf succession by cropping or entirely scraping the algae down to the underlying carbonate substrate (Bonaldo & Bellwood 2009), but this effect depends on the type of grazer (Ceccarelli et al. 2011). The effect of grazing is pronounced for turf algae, because turf algae are the preferred food source for most reef herbivores (Carpenter 1986, Ledlie et al. 2007) and, consequently, on unfished reefs, each square centimeter of turf is bitten up to 6 times per day (Hamilton et al. 2014). Since such intense grazing and its effects on algae are spatially variable due to behavioral and ecological variation among types of grazers (Carpenter 1986, Bonaldo &

Bellwood 2011, Sandin & McNamara 2012), one might expect grazing to contribute to a patchy mosaic of turf assemblages at different points in succession, as has been observed in temperate intertidal algae (Benedetti-Cecchi & Cinelli 1993). If herbivore assemblages are consistent across reefs, this pattern would be repeated at the site and island scales, such that variability decreases as spatial scale increases. As the scale of greatest variability measured here, centimeters, is approximately the bite size of dominant reef grazers (herbivorous fishes and urchins), one plausible explanation for the observed scales of spatial variability in turf algae is that turf assemblages are patchy in response to the distribution of herbivores across the landscape.

Although herbivores influence the spatial distribution of benthic primary producers in most ecosystems, such effects tend to vary with the idiosyncratic circumstances of each system. For instance, selective herbivory on specific morphologies or life stages can act as a special type of disturbance that increases plant diversity (Hulme 1996). Grazing has been experimentally measured to be more important than physical factors in driving assemblage variability in subtropical intertidal microalgae (Christofoletti et al. 2011) and in some temperate turf systems (Benedetti-Cecchi et al. 2000). However, grazing is a negligible factor in other temperate turf systems (e.g. see Benedetti-Cecchi et al. 2012), so this comparison may not be particularly informative for predicting processes that drive spatial patterns in tropical coral reef turf algae. And while spatially patchy grazing increases heterogeneity in corals (O'Leary & Potts 2011), terrestrial vegetation (Adler et al. 2001), unicellular benthic marine algae (Sommer 2000), and intertidal coralline algae (Wai & Williams 2006), it seems to reduce spatial homogeneity of algae in a stream even at very small scales (Sarnelle et al. 1993). Therefore, while there are compelling reasons why grazing patterns might yield small-scale patchiness in turf algal assemblages, such effects are not assured.

An alternative explanation is that small-scale patchiness is simply an inherent feature of mixed-species assemblages due to the diverse growth forms represented in a typical turf algal assemblage, analogous to the way that differences in life history strategies contribute to patchiness in terrestrial plant assemblages (Shmida & Ellner 1985). For example, *Polysiphonia*, *Gelidiella/Gelidum*, and *Herposiphonia* were some of the most abundant and widespread taxa observed here. Where these red terete algae occurred, they branched out and crept across the

substrate, leaving open space for other algae. In contrast, *Dictyota* was also one of the most abundant taxa, but it was not widespread. As a foliose alga, it grows in a much different pattern than do terete filaments. In the few samples where it occurred, it grew as a thick mat, covering 100% of the substrate and leaving no room for other taxa. Smaller brown filamentous algae from the order Ectocarpales, which grow singly as simple filaments, and red calcified CCA, which grow as thick crusts, are further extreme examples of the morphological diversity within the mixed species turf assemblage. Such variable morphologies could explain the heterogeneity in existing assemblages, while random settlement processes could be responsible for starting individual turf assemblages on different trajectories. Both the 'lottery hypothesis' (Sale 1977) and the 'carousel' model (van der Maarel & Sykes 1993) rely on some amount of stochastic settlement, allowing many species with similar traits to take turns occupying the same niche space. These models explain small-scale patchiness in temperate intertidal algae (Bastow Wilson et al. 1992), and they could be equally applicable in tropical turf algae. The observed patterns of small-scale patchiness could be a straightforward result of stochastic settlement processes that are amplified as algae grow in different ways.

Comparing the richness of turfs on Maldivian reefs measured here to turf diversity reported elsewhere is not straightforward due to unknown relationships between α and β diversity of turf algae and the distribution of species at different spatial scales. Here, the smallest unit measured was 1.27 cm^2 and, with 256 samples, the total area sampled was 324 cm^2 across more than 20 km of reef. Other studies have used different areas, but it is not appropriate to simply standardize by area. Still, taxonomic richness reported here falls within the range of richness reported elsewhere for tropical turf algae (Stuercke & McDermid 2004, Anderson et al. 2005, Smith et al. 2010).

Total cover, canopy height, and taxonomic richness all displayed the same pattern: decreasing variability as spatial scale increased from punch to colony to site, and then greater variability at the island level. Therefore, these characteristics of turf assemblages were relatively homogeneous within and among sites on a given island, but there was larger variability among the 4 islands. That there was no discernible variation among sites (separated by 100−300 m) implies homogeneous environmental conditions within a given island, with dispersal barriers and/or different disturbance regimes (e.g. wave forcing or bleaching history) among islands. Therefore, we propose

that both very small-scale processes, such as vegetative growth, herbivory, and competition, and larger-scale processes, such as propagule dispersal, likely play important roles in differentiating turf assemblages on coral reefs.

Whatever processes drive the observed variation in canopy height may in part determine the ecological role of turf algae. Turf canopy height is rarely manipulated experimentally or even measured at a resolution matching the resolution presented here, but there is indirect evidence that differences of just a few millimeters in canopy height could make a difference in the ecology of turf on a coral reef. For example, an increase in turf canopy height of 3 mm (from <1 to 4 mm) increased the thickness of the benthic boundary layer (Carpenter & Williams 1993), within which there are measured changes in pH, O_2, and rates of photosynthesis and respiration (Larkum et al. 2003). Further, thicker and taller turfs trap more sediment and organic matter than thinner and shorter turfs, which has negative effects on the survival of coral larvae (reviewed in Birrell et al. 2008). Sediment within turf assemblages has strong effects on the survival of canopy-forming macroalgae in temperate systems (Alestra et al. 2014), the infaunal invertebrate community living in turf (Prathep et al. 2003), and coral settlement success (Birrell et al. 2005). Differences of millimeters in the amount of accumulated sediment within turf reduce the survival of macroalgal recruits (Chapman & Fletcher 2002), and match the scale of a proposed threshold for the creation of anoxic sediment (Clausing et al. 2014). Though it has not been experimentally tested, we expect that millimeter changes in turf canopy height could negatively affect the settlement and survival of coral larvae, which are in the micron to millimeter size range, via sediment retention, smothering, or other mechanisms. Our measured range of 0.4 to almost 4 mm matches the range in canopy height shown to cause impacts in other studies. As there was significant variation in canopy height only among colonies, any effects of variation in turf canopy height are acting on individual coral colonies. In future studies, it would be interesting to experimentally test the effect of turf canopy height on sediment retention, turf competitive ability, and coral larval settlement.

In contrast to the variability in canopy height and the other univariate measures, multivariate variability in turf assemblage decreased monotonically as spatial scale increased, with variance in assemblage at the island scale explaining the smallest proportion of the total variability. These different patterns of spatial variability for multivariate and univariate

metrics suggest that processes governing these different parameters act at separate scales. Any small-scale processes that determine assemblage structure are repeated and balanced out across larger spatial scales, while small-scale processes that determine cover, canopy, or richness increase slightly in variability from the site to the island scale.

In addition to examining whole-assemblage characteristics, spatial patterns of key taxa may be particularly informative about ecological processes. For example, 2 red algae known to be harmful to corals, *Corallophila* spp. and *Anotrichium* spp., were neither common nor abundant throughout the study (Table 2). However, closer inspection of their individual spatial patterns (Fig. 4G–H) points to a handful of individual coral colonies where one or both of these taxa were relatively abundant. Therefore, we can predict that those individual colonies either may have active coral–algal interaction zones or may, in fact, be losing space to aggressive turf assemblages laden with toxic red algae. And while among-island variability was the smallest proportion of overall assemblage variability, abundance patterns of these 2 red algae taxa point to individual islands where corals may be susceptible to turf overgrowth: turf assemblages on Kanuhara and Maafilaafushi have relatively consistent amounts of *Corallophila* spp. and *Anotrichium* spp., respectively. These taxa were low in abundance and so contributed little to variability in the total assemblage, but examining them separately from the whole assemblage provides important insight into potentially critical ecological processes underway at these 2 islands.

Taxa-specific insights, combined with the overall small-scale variability of turf algal assemblages, present a suite of implications for future analysis of coral reef communities. Knowing that turf assemblages on coral reefs can be highly variable at a scale of centimeters highlights a need for appropriate spatial sampling. Describing a 1-m quadrat by its overall turf cover may be insufficient to capture the highly variable turf assemblage. Instead, detailed samples replicated across centimeters are needed to sufficiently describe the complexity and diversity of turf assemblages, especially if different taxa within the turf assemblage have unique roles in coral–algal competition, such as producing allelochemicals that can kill corals (e.g. Jompa & McCook 2003).

With declining coral and increasing turf cover on reefs worldwide, understanding coral–turf interaction dynamics will become increasingly central to coral reef ecology and conservation. However, turf assemblages are variable at scales smaller than a single coral colony, so these interactions deserve more detailed consideration. Turf algae represent a dominant, diverse, and highly productive component of coral reef communities, so a better understanding of the processes that drive turf assemblage structure and spatial dynamics is needed.

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