**Temporal effectiveness of biodiversity surrogates in coral reefs in the British Virgin Islands**

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**Abstract**

Biodiversity is declining around the world, necessitating rapid identification of species distribution contractions and population declines to identify conservation priorities. Surrogates are increasingly being used to meet this challenge. A good surrogate is expected to be easier to monitor than the target component of biodiversity and meets the assumption that the target-surrogate relationship is constant over space and time. Our objective was to evaluate the spatio-temporal stability of surrogates in coral reef systems around using data from an ongoing 26-year monitoring program in the British Virgin Islands that has quantified the abundance of fish, coral, and sponge species at 8 sites. Of these taxa, corals are the most widely monitored and measures of coral cover are often assumed to be good surrogates for diversity of reef-associated taxa. We thus hypothesize that coral cover and rugosity will be good surrogates for fish, coral, and sponge species richness. We also investigated how the inclusion of recognizable taxonomic units (RTU’s) compares to species-level studies. We sought correlated relationships between the proposed surrogates and fish, coral, and sponge species richness. Our results provide insight on the use of surrogates in a coral reef ecosystem and on the inclusion of RTU’s in biodiversity studies. The identification of surrogates that maintain stable relationships with target components of biodiversity over time can inform decisions regarding existing data from monitoring studies and the allocation of limited resources for collection of future data.

**Introduction**

Biodiversity changes and declines associated with increasing levels of anthropogenic stress disrupt community dynamics and are of great concern because biodiversity contributes to ecosystem function (Emmett Duffy, 2009; Staudinger et al., 2013; Stork, 2010). There are many aspects of biodiversity: landscape, ecosystem, taxonomic, and genetic (Duelli & Obrist, 2003; Noss, 1990). Taxonomic diversity of an area, particularly the diversity of species, is fundamental to understanding interspecific interactions, environmental conditions at the site given physiological requirements of the species present, and geographic proximity of species distributions of taxonomically related species. *Consequently,* species richness, a simple measure of the count of species in an area, is the most commonly measured component of biodiversity in ecological and conservation-related field studies because it offers an intuitive metric to compare similar environments (Hamilton, 2005).

Unfortunately, a complete inventory of species present in an area is unattainable in many ecosystems and, for taxonomic groups that can be inventoried in principle, monitoring strategies that could detect all species in a given habitat are often prohibitively expensive and time-consuming (Kati et al., 2004). In practice, surrogates are often used instead of direct measures of biodiversity because they are simple indicators that provide an estimate of a target component of biodiversity (Magierowski & Johnson, 2006). Surrogates may be functional (e.g., structural complexity), taxonomic (e.g., species diversity), or landscape features (e.g., percent canopy cover; (Paillet et al., 2018; Wessels, Freitag, & van Jaarsveld, 1999). An effective surrogate takes less time, money, and experience to measure than the target and maintains a consistently strong correlation with the target over time and space (Magierowski & Johnson, 2006).

It is not surprising that most surrogate studies to date have been concerned with the effectiveness of surrogates across spatial scales (Kati et al., 2004) because ecological dynamics commonly change across spatial scales (Wiens, 1989). The prevalence of studies considering surrogates across spatial scales may also be due to the widespread use of surrogates to identify priority conservation areas; this task requires an understanding of how the size and dispersion of the areas being conserved will affect the dynamics between the surrogate and target (Margules, Pressey, & Williams, 2002; Padoa-Schioppa, Baietto, Massa, & Bottoni, 2006; Ward, Vanderklift, Nicholls, & Kenchington, 1999). However, few studies have explicitly investigated surrogate effectiveness across temporal scales, and those that have are typically quite short (e.g., 13 months and 1 year; (Magierowski & Johnson, 2006; Rubal, Veiga, Vieira, & Sousa-Pinto, 2011). An effective surrogate must maintain a stable relationship with the target over time because environmental conditions vary and a species’ ability to respond to this variation across time changes. One of the few longer studies (>10 years) concluded that their main surrogate of interest, percent canopy cover, was a reliable predictor of bird species richness at 3 of their 4 study areas (Pierson, Mortelliti, Barton, Lane, & Lindenmayer, 2016). Another ten year study identified a group of 35 surrogates that successfully predicted changes in the target assemblage of 98 benthic macroinvertebrate species in a temperate brackish system (Bevilacqua, Mistri, Terlizzi, & Munari, 2018). The need for more studies that investigate the effectiveness of surrogates over time is evident.

Another widespread feature of using surrogates to predict species richness is a reduction of taxonomic resolution in the case of taxonomic surrogates or the possible elimination of the need to identify species altogether in the case of functional or landscape feature surrogates (Fontaine, Devillers, Peres-Neto, & Johnson, 2015; Musco, Mikac, Tataranni, Giangrande, & Terlizzi, 2011; Olsgard & Somerfield, 2000). Monitoring species richness requires substantial taxonomic expertise (Hirst, 2008; Sebek et al., 2012). Moreover, some species that can be recognized in the lab using morphological features or genetic markers cannot be distinguished in situ during field surveys. When individuals are not phenotypically distinguishable between taxonomic groups, studies sometimes use recognizable taxonomic units (RTU’s) or morphospecies that are defined by readily identifiable characteristics in the field (Derraik et al., 2002).

Coral reefs are biodiversity hotspots that are globally threatened due to environmental and anthropogenic factors, including ocean acidification, persistent high temperatures, and overfishing (Terence P Hughes, 1994; Terry P. Hughes et al., 2017). As such, many reefs are monitored across both spatial and temporal scales. The most commonly measured features of coral reefs are hard coral cover and structural complexity (rugosity). In fact, the temporal decline of these reef features is widely documented because they are so frequently measured (Habibi, Setiasih, & Sartin, 2007; Stokes, Leichter, & Genovese, 2010). These measures make for good candidate surrogates, as they are simple and affordable to measure, yet how effective they are over long temporal scales remains unknown.

Here, I evaluate the effectiveness of hard coral cover and rugosity as surrogates for species richness of major taxonomic groups on coral reefs over time and space. Sponge cover is also included as a candidate surrogate because sponges play a dominant role in the benthic composition of the reef and contribute to the reef’s three-dimensional structure. Reef fishes, hard corals (Scleractinia), and sponges are dominant coral reef organisms that establish and maintain biodiversity by filling multiple functional roles in coral reef systems and therefore, richness of these groups will be used as the target components of biodiversity in this study (Angelini, Altieri, Silliman, & Bertness, 2018).Specifically, I use percent hard coral cover, percent sponge cover, and rugosity as landscape feature surrogates to predict species richness of corals, fishes, sponges, and combined richness (as the sum of richness across these three groups) using 27 years of monitoring data from eight sites around Guana Island in the British Virgin Islands (Forrester et al., 2015). \*\*\*\*\*\*\*\*\*\*\*\*\*\*\*\*\*\*\*\*\*\*\*\*\*\*\*\*\*\*I hypothesize that coral cover will be an effective surrogate for coral species richness because declines in coral cover have been associated with declines in coral diversity (Walton, Hayes, & Gilliam, 2018). Similarly, I hypothesize that coral cover will be an effective surrogate for predicting sponge species richness because declines in coral cover have been associated with increases in sponge cover (Ruzicka et al., 2013); this inverse relationship is most likely due to  competitive interactions between sponges and corals. Coral cover is often positively associated with fish species richness (Jones, McCormick, Srinivasan, & Eagle, 2004; Pratchett, Hoey, Wilson, Messmer, & Graham, 2011), most likely because corals provide fish with food (directly in the case of corallivores and indirectly by providing habitat for prey) and protection from predators. Therefore, I hypothesize that coral cover will be an effective surrogate for fish species richness. I hypothesize that rugosity will be an effective surrogate for fish species richness because greater rugosity should provide a wider variety of structures that may be utilized by a greater diversity of fish species (Darling et al., 2017; Graham et al., 2006; Gratwicke & Speight, 2005; Newman et al., 2015) and fish may respond primarily to the structure of the reef rather than its biological features (Wilson et al., 2009; Wilson, Graham, Pratchett, Jones, & Polunin, 2006). Finally, I hypothesize that rugosity will be an effective surrogate for coral species richness because a greater number of coral species should increase the number of coral morphological types and increase rugosity (Alvarez-Filip, Dulvy, Côteé, Watkinson, & Gill, 2011; Newman et al., 2015).

**Material and Methods**

*Field study design*

There were eight study sites around Guana Island in the British Virgin Islands (Fig. 1). All sites were similar in covering 0.6-1.0 hectares of fringing reef adjacent to the island at a depth of 10 m. Sites varied in exposure to prevailing weather; sites on the windward north side of the island are more exposed than those on the southern leeward side. Each site was surveyed annually from 1992-2018, except that sponges were not counted in 1992, 1996-1999, 2004, 1993 at Crab Cove, 2014 at Pelican Ghut, or in 2017 at Bigelow Beach and Pelican Ghut. All surveys were conducted between June and August. Each year, fish densities, coral cover, and sponge abundances were measured using 3-22 transects per site. Transects were 20-30.4 m long (mean = 29.95), and placed at selected locations within each site using a haphazard sampling approach. Data were collected as part of an ongoing professional monitoring program (Forrester et al., 2015).

*Survey methods*

For each transect at each site, corals, sponges, and fishes were sampled once per year using well-established methods (Fig. 2). Fishes were counted within a belt transect 30 m long x 1.5 m wide, and a T-shaped bar was used to determine the transect width as the diver swam along the transect line. Fish counts were restricted to species that are amenable to visual survey, that is, day-active species that are relatively site-attached and reliably visible to divers. Nocturnal species, highly mobile groups such as mackerels (Scombridae) and jacks (Carangidae) that are transient visitors to the sites, and small cryptic groups like gobies (Gobiidae) and blennies (Blennioidei) that often hide in crevices were not surveyed. Newly recruited juvenile fishes (< 1 month on the reef) were also excluded because their abundance is strongly affected by lunar cycles, which complicates the detection of long-term trends. Because fish were the only mobile organisms of the three taxonomic groups included in this study, the fish survey was conducted first for each transect in order to reduce the bias caused by “spooking” the fish (Emslie, Cheal, MacNeil, Miller, & Sweatman, 2018). We used the linear point-intercept method to record the substrate, sponge, or coral (identified to the finest taxonomic resolution) every 0.25 m along the 30-m transect. These point observations were later converted to surface area estimates of coral percent cover and sponge percent cover (Almada-Villela, Sale, Gold-Bouchot, & Kjerfve, 2003). Sponges were surveyed using the line intercept method in which any sponge that intercepted the transect was recorded and identified to the finest taxonomic resolution.

Fish and sponge data were collected by a single respective expert observer. Coral data were collected by three observers, but new observers’ species identifications and counts were calibrated with those of another observer during a training period of at least 15 dives before their data were incorporated into the study.

Rugosity was measured as a proxy for three-dimensional structural complexity using the consecutive height difference method (McCormick, 1994), where a diver records the difference between the height of the transect tape and the substrate at 50 cm intervals along each transect. These points are used to calculate a rugosity index where a value of 0 is flat and vertical complexity increases as the value increases.

Fish, corals and sponges were identified to the most specific taxonomic group possible in the field. There were a total of 119 species of fishes, 27 recognizable taxonomic units of hard corals, and 58 recognizable taxonomic units of sponges.

*Estimating Species Richness*

We used site as the sampling unit because the richness of these taxonomic groups is more relevant at the site level than at the transect level from both ecological and management perspectives. Because there were 3-22 transects in a given year at a given site, 3 transects were randomly selected for each year for each site and site-level estimates of surrogates (coral cover, sponge cover, and rugosity) were calculated by averaging these values across the 3 randomly selected transects. For the same 3 transects for each year for each site, site-level estimates of targets (coral richness, sponge richness, fish richness, and combined richness) were calculated by adding the unique number of species per transect using the following formula.

n = number of transects counted at site j in year k (n = 3)

yijk = number of species counted at site j in transect i and not counted in transects ≠ i in year k

Yjk = number of species counted at site j in year k

Yjk=i=1nyijk

Combined richness was only calculated for sites and years for which richness of all three taxonomic groups was available.

*Statistical Analysis*

Based on first principles, we used negative binomial regression using the ‘MASS’ package to model richness because it is a count variable (Venables & Ripley, 2002).

To determine which of the candidate surrogates is best at predicting each of the targets, we used simple models with only the candidate surrogates as predictors. and compared these using Akaike Information Criterion corrected for small sample sizes (AICc; (Mazerolle, 2019). The top candidate surrogate identified for each target from this comparison was used for the following models.

To determine if relationships between targets and the top candidate surrogates remain consistent over space and time, we added additional terms to the models to account for temporal variation and variation across sites. Site is a categorical predictor of the 8 locations around Guana Island and year is a temporal trend across all sites within similar areas over the 27 years. We constrained model complexity to single pairwise comparisons because, if more complex models were supported, the relationship between the candidate surrogate and the target would not be valuable for monitoring purposes. In other words, the ecological interpretation of these more complex models would be complicated enough that there would be no clear relationship between the candidate surrogate and the target. If no candidate surrogates are supported we also included models without candidate surrogates to evaluate how much the candidate surrogates were contributing to the models described above. Models for each of the dependent variables were compared using AICc and pseudo r-squared values. We also conducted a full exploratory analysis for each of the four targets that includes the models described above with the top surrogate as well as models for the other two candidate surrogates. All data management and analysis was performed in the R programming language (R Core Team, 2019).

**Results**

See appendices 1-4 for AIC tables from the full exploratory analysis with all models for all candidate surrogates.

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None of the candidate surrogates seems to be related to sponge richness (Fig. 3).

**Discussion**

**Conclusions**

**Literature Cited**

Almada-Villela, P. C., Sale, P. F., Gold-Bouchot, G., & Kjerfve, B. (2003). *Manual of methods for the MBRS synoptic monitoring program: Selected methods for monitoring physical and biological parameters for use in the Mesoamerican region*. Belize City: Mesoamerican Barrier Reef Systems project (MBRS).

Angelini, C., Altieri, A. H., Silliman, B. R., & Bertness, M. D. (2018). Interactions among Foundation Species and Their Consequences ­ for Community Organization , Biodiversity , and Conservation, *61*(10). https://doi.org/10.1525/bio.2011.61.10.8

Bevilacqua, S., Mistri, M., Terlizzi, A., & Munari, C. (2018). Assessing the effectiveness of surrogates for species over time: Evidence from decadal monitoring of a Mediterranean transitional water ecosystem. *Marine Pollution Bulletin*. https://doi.org/10.1016/j.marpolbul.2018.04.047

Derraik, J. G. B., Closs, G. P., Dickinson, K. J. M., Sirvid, P., Barratt, B. I. P., & Patrick, B. H. (2002). Arthropod morphospecies versus taxonomic species: A case study with Araneae, Coleoptera, and Lepidoptera. *Conservation Biology*, *16*(4), 1015–1023. Retrieved from http://onlinelibrary.wiley.com/doi/10.1046/j.1523-1739.2002.00358.x/full

Duelli, P., & Obrist, M. K. (2003). Biodiversity indicators: The choice of values and measures. *Agriculture, Ecosystems and Environment*, *98*, 87–98. https://doi.org/10.1016/S0167-8809(03)00072-0

Emmett Duffy, J. (2009). Why biodiversity is important to the functioning of real-world ecosystems. *Frontiers in Ecology and the Environment*, *7*(8), 437–444. https://doi.org/10.1890/070195

Emslie, M. J., Cheal, A. J., MacNeil, M. A., Miller, I. R., & Sweatman, H. P. A. (2018). Reef fish communities are spooked by scuba surveys and may take hours to recover. *PeerJ*. https://doi.org/10.7717/peerj.4886

Fontaine, A., Devillers, R., Peres-Neto, P. R., & Johnson, L. E. (2015). Delineating marine ecological units: A novel approach for deciding which taxonomic group to use and which taxonomic resolution to choose. *Diversity and Distributions*, *21*, 1167–1180. https://doi.org/10.1111/ddi.12361

Forrester, G., Baily, P., Conetta, D., Forrester, L., Kintzing, E., & Jarecki, L. (2015). Comparing monitoring data collected by volunteers and professionals shows that citizen scientists can detect long-term change on coral reefs. *Journal for Nature Conservation*, *24*, 1–9. https://doi.org/10.1016/j.jnc.2015.01.002

Habibi, A., Setiasih, N., & Sartin, J. (2007). A decade of reef check monitoring: Indonesian coral reefs, condition and trends. *The Indonesian Reef Check Network*.

Hamilton, A. J. (2005). Species diversity or biodiversity? *Journal of Environmental Management*, *75*, 89–92. https://doi.org/10.1016/j.jenvman.2004.11.012

Hirst, A. J. (2008). Surrogate measures for assessing cryptic faunal biodiversity on macroalgal-dominated subtidal reefs. *Biological Conservation*, *141*, 211–220.

Hughes, Terence P. (1994). Catastrophes, phase shifts, and large-scale degradation of a Caribbean coral reef. *Science*, *265*(5178), 1547–1551.

Hughes, Terry P., Kerry, J. T., Álvarez-Noriega, M., Álvarez-Romero, J. G., Anderson, K. D., Baird, A. H., … Wilson, S. K. (2017). Global warming and recurrent mass bleaching of corals. *Nature*, *543*, 373–377. https://doi.org/10.1038/nature21707

Kati, V., Devillers, P., Dufrêne, M., Legakis, A., Vokou, D., & Lebrun, P. (2004). *Testing the value of six taxonomic groups as biodiversity indicators at a local scale*. *Conservation Biology* (Vol. 18).

Magierowski, R. H., & Johnson, C. R. (2006). Robustness of surrogates of biodiversity in marine benthic communities. *Ecological Applications*, *16*(6), 2264–2275.

Margules, C. R., Pressey, R. L., & Williams, P. H. (2002). Representing biodiversity: Data and procedures for identifying priority areas for conservation. *Journal of Biosciences*, *27*(4), 309–326.

Mazerolle, M. J. (2019). AICcmodavg: Model selection and multimodel inference based on (Q)AIC(c). Retrieved from https://cran.r-project.org/package=AICcmodavg

McCormick, M. I. (1994). Comparison of field methods for measuring surface topography and their associations with a tropical reef fish assemblage. *Marine Ecology Progress Series*, *112*, 87–96. https://doi.org/10.3354/meps112087

Musco, L., Mikac, B., Tataranni, M., Giangrande, A., & Terlizzi, A. (2011). The use of coarser taxonomy in the detection of long-term changes in polychaete assemblages. *Marine Environmental Research*, *71*, 131–138. https://doi.org/10.1016/j.marenvres.2010.12.004

Noss, R. F. (1990). Indicators for monitoring biodiversity: A hierarchical approach. *Conservation Biology*, *4*(4), 355–364.

Olsgard, F., & Somerfield, P. J. (2000). Surrogates in marine benthic investigations - which taxonomic unit to target? *Journal of Aquatic Ecosystem Stress and Recovery*, *7*, 25–42.

Padoa-Schioppa, E., Baietto, M., Massa, R., & Bottoni, L. (2006). Bird communities as bioindicators: The focal species concept in agricultural landscapes. *Ecological Indicators*, *6*, 83–93. https://doi.org/10.1016/j.ecolind.2005.08.006

Paillet, Y., Archaux, F., du Puy, S., Bouget, C., Boulanger, V., Debaive, N., … Guilbert, E. (2018). The indicator side of tree microhabitats: A multi-taxon approach based on bats, birds and saproxylic beetles. *Journal of Applied Ecology*, *55*, 2147–2159. https://doi.org/10.1111/1365-2664.13181

Pierson, J. C., Mortelliti, A., Barton, P. S., Lane, P. W., & Lindenmayer, D. B. (2016). Evaluating the effectiveness of overstory cover as a surrogate for bird community diversity and population trends. *Ecological Indicators*, *61*, 790–798. https://doi.org/10.1016/j.ecolind.2015.10.031

R Core Team. (2019). R: A language and environment for statistical computing. Vienna, Austria: R Foundation for Statistical Computing. Retrieved from https://www.r-project.org/

Rubal, M., Veiga, P., Vieira, R., & Sousa-Pinto, I. (2011). Seasonal patterns of tidepool macroalgal assemblages in the North of Portugal. Consistence between species and functional group approaches. *Journal of Sea Research*, *66*, 187–194. https://doi.org/10.1016/j.seares.2011.07.003

Sebek, P., Barnouin, T., Brin, A., Brustel, H., Dufrêne, M., Gosselin, F., … Bouget, C. (2012). A test for assessment of saproxylic beetle biodiversity using subsets of “monitoring species.” *Ecological Indicators*, *20*, 304–315. https://doi.org/10.1016/j.ecolind.2012.02.033

Staudinger, M. D., Carter, S. L., Cross, M. S., Dubois, N. S., Emmett Duffy, J., Enquist, C., … Turner, W. (2013). Biodiversity in a changing climate : A synthesis of current and projected trends in the US. *Frontiers in Ecology and the Environment*, *11*(9), 465–473. https://doi.org/10.1890/120272

Stokes, M. D., Leichter, J. J., & Genovese, S. J. (2010). Long-term declines in coral cover at Bonaire, Netherlands Antilles. *Atoll Research Bulletin*.

Stork, N. E. (2010). Re-assessing current extinction rates. *Biodiversity and Conservation*, *19*, 357–371. https://doi.org/10.1007/s10531-009-9761-9

Venables, W. N., & Ripley, B. D. (2002). *Modern applied statistics with S* (Fourth). New York, New York: Springer. Retrieved from http://www.stats.ox.ac.uk/pub/MASS4

Ward, T. J., Vanderklift, M. A., Nicholls, A. O., & Kenchington, R. A. (1999). Selecting marine reserves using habitats and species assemblages as surrogates for biological diversity. *Ecological Applications*, *9*(2), 691–698.

Wessels, K. J., Freitag, S., & van Jaarsveld, A. S. (1999). The use of land facets as biodiversity surrogates during reserve selection at a local scale. *Biological Conservation*, *89*, 21–38. https://doi.org/10.1016/S0006-3207(98)00133-5

Wiens, J. A. (1989). Spatial scaling in ecology. *Functional Ecology*, *3*(4), 385–397.