
4 Task 4.8: Evaluation of methods and designs to link biodiversity to broad scale habitat assessments

Introduction

It is generally accepted that protection of marine biodiversity requires the introduction of landscape-level planning and policies to prioritise marine conservation areas (Beger et al. 2003, Bellwood and Hughes 2001). However, the establishment of these areas is frequently hampered by lack of comprehensive biodiversity data and the resources and expertise necessary to gain this information (Williams et al., 2002, Margules and Pressey 2000). As a result habitat maps delineated from available climatic, geological, geomorphological and ecological information have been employed as biodiversity surrogates (Ward et al., 1999, Day 2000). Unfortunately, these habitat maps are generally produced in an ad-hoc manner often with little validation (Mumby & Harborne 1999), or quantitative ecological basis, so their effectiveness is unknown (Gray 2001). An alternative and cost effective biodiversity surrogate could be remotely sensed data (e.g. satellite imagery, aerial photography, multibeam and side scan sonar, Edwards 2001). However, the challenge remains in linking habitat assessment data and methods with species biodiversity patterns and drivers in an ecologically meaningful way.

In a condensed form (Table 1), this document summarises i) current ecological theories which are thought to drive patterns of biodiversity at different spatial scales, ii) the common statistical methods that have been applied to these theories, and iii) whether each theory has been applied in a practical sense as a biodiversity surrogate.

Background

Studies of biodiversity incorporate a range of spatial and temporal scales, from evolutionary and adaptive changes that are measured over thousands of years with genetics and morphometric analysis, to studies of change that occur over a matter of days in single celled organisms (Morin 1999). It is obvious that processes affecting

biodiversity occur at a number of scales, and that these processes may interact and be intrinsically linked with one another. However, there is considerable uncertainty as to the nature (both temporal and spatial) of these links and interactions in both terrestrial and marine systems (Gaston 2003).

For example, in order to understand coral biodiversity, it is necessary to identify and understand the interactions of macro-, mid- or regional scale and micro-scale ecological patterns over both time and space (Pandolfi 2001). The magnitude of differences in life spans and life histories of different coral species vary from decades (Babcock 1991) to centuries (Potts et al. 1985). Yet major drivers of community patterns may occur over brief periods of hours or days, for example, during coral spawning, dispersal and recruitment (Harrison and Wallace 1990; Baird et al. 2003), or dramatic disturbance events (Done and Potts 1992; Connell 1997). Similarly, over large spatial scales, many coral species are widely distributed (Veron 2000; Bellwood and Hughes 2001; Bellwood et al. 2005; Wallace and Muir 2005), and yet important ecological processes such as habitat selection (Baird et al. 2003) or competitive exclusion (Baird and Hughes 2000) may occur over very small scales.

It is therefore of no surprise that there is a bewildering number of theoretical, manipulative and observational studies which put forward a range of explanations for these patterns. For example, local scale niche based competitive and other biotic interactions (Robertson 1996; Carpenter 1997; Miller and Hay 1998; Baird and Hughes 2000; Baird et al. 2003), broad scale dispersal and regional enrichment (Connell and Karlson 1996; Hubbell 1997; Hughes 2002; Hughes et al. 2002; Miller and Mundy 2003) and disturbance (Done and Potts 1992; Hughes 1994; Connell 1997) are just a few of the processes that have been introduced to try and explain marine biodiversity patterns. An outline of the major current theories which have been suggested as explanations for current patterns of marine biodiversity are summarised in Table 4-1 below.

Table 4-1. Summary of macro, regional and local scale theoretical drivers of patterns of marine species richness and whether they have been applied as a biodiversity surrogate

NAME	SPATIAL SCALE OF INFLUENCE	DEFINITION APPLICATION AND ISSUES	STATISTICAL METHOD USED FOR MEASUREMENT	APPLIED AS A MARINE BIODIVERSITY SURROGATE
Latitude	Macro-scale	Based on early work of the 1950-60, two well debated and central paradigms to marine biodiversity are that as latitude decreases, biodiversity increases (Saunders 1968). It has been suggested that this pattern exists from surface water to a depth of 2000 meters (Thorson 1957; Stehli et al. 1967; Saunders 1968). A wide range of explanations for latitudinal trends have been suggested including habitat area, habitat heterogeneity, energy inputs and productivity, species community interactions and environmental and geomorphologic stability (Gray 1997; Gaston and Blackburn 2000; Gray 2001; Gray 2001).	General Linear Model (GLM)	No
Species-energy / productivity	Macro-scale	The species-energy relationship suggests that as energy levels increase in an environment then it has the capacity to support an increasing number of species. The form and cause of these energy relationships used are widely debated and encompasses direct variables such (as heterotrophy and autotrophy) and indirect variables (such as temperature and precipitation) that may be nested and cyclically linked (Morin 1999).	GLM	No
Biodiversity hotspots	Macro-scale	It is commonly found that in aquatic systems biodiversity peaks around tropical latitudes and low altitude, warm biomes. From this trend biodiversity gradients could be explained as a result of convergence of species richness from different taxa in these areas to form biodiversity hot spots. This overlap in biodiversity has been demonstrated in some species; for example, convergence of high coral and reef fish biodiversity in areas of Indo-Australian Archipelago, including Indonesia and Thailand (Bellwood et al. 2005).	GLM	No

		There are also examples of mismatches of biodiversity peaks in other aquatic species (Ellingsen and Gray 2002).		
Mid-domain/ Rapoport's Rule	Macro-scale	The mid-domain effect states that over a constrained spatial domain, geographic species richness decreases in a predictable fashion from the evolutionary centre for a species group to the geographical extremes of distribution (Stevens 1989; Rapoport 1994; Roy et al. 1998; Chown and Gaston 2000). Steven's claims a wide number of species follow this rule however there is comparatively little data to support this and it has been Roy et al (1998) demonstrated it does not hold for molluscs	GLM, Ridge Regression, Spline regression	No
Evolutionary gap hypothesis	Macro-scale	This explanation for species biodiversity gradients assumes that it is mediated by the relationship between evolutionary time, speciation and extinction. It suggests that speciation rates are higher in the tropics and decrease with higher latitudes. Interpretation of these hypothesis with respect to modern patterns of speciation is problematic because if mass extinctions (over 90% of all species) that have occurred over a geological time frame (reviewed in Gray 2001).	Micro-array and Geographic/cladistic analysis	No
Random Boundary hypothesis	Macro-scale	This explanation for latitudinal gradients assumes no environmental mediation of species biodiversity but just a random association between size and midpoint of geographic range of species (Colwell and Hurtt 1994; Colwell and Lees 2000). High species biodiversity in the tropics is predicted since latitudinal species is constricted to the north and south. The restrictions may be physical factors such as geomorphic features or biological such as temperature and light. To date no studies have been done with marine data	GLM	No
Species-area	Macro-scale and regional scale	This theory suggests that with increased geographical area rates of speciation increase (through random or other drivers), and rates of species extinction decrease. Broadly speaking, this theory suggests that this mechanism explains the increased biodiversity found in tropical compared to both	GLM, General Additive Models (GAM)	Yes (Bellwood and Hughes 2002)

		temperate and polar regions (Rosenzweig and Sandlin 1997; Roy et al. 1998).		
Geomorphology	Regional and local scale	Geomorphology is associated with a suite of other prevailing abiotic processes in how it influences coral species assemblages and biodiversity (Hopley 1982). These include water temperature, currents and inter-reef larval connectivity, wave action, exposure and levels of sediment input in conjunction with wind and wave driven resuspension (Kleypas 1996; Harriott and Banks 2002).	GLM	No
Regional-enrichment	Linking regional and local scale	The regional enrichment biodiversity hypothesis suggests that local and regional richness show causal and positive interaction, where by local biodiversity is proportional subset of a regional species pool. In most systems, regional richness is thought to be responsible for approximately 50-75% of variation between species richness at local sites (Cornell and Lawton 1992; Caley and Schluter 1997; Karlson and Connell 1999; Lawton 1999). This has been demonstrated in insects, fish and primates in both present day and palaeontological studies (Hawkins and Compton 1992; Pearson and Juliano 1993; Griffiths 1997; Eeley and Lawes 1999; Karlson and Connell 1999). The dominance of the proportional relationship between local and regional richness, (particularly if difference between climate and area are considered), suggests that local species richness does not have a saturation point. In turn this suggests that local communities are not tightly organised and are open to recruitment from a regional species pool (Cornell 1999).	GLM	No
Continuous / individualistic	Local-scale (potentially linking with regional scale See Radford and Van Niel 2005 in prep)	“continuum” concept broadly states that if communities consist of weakly interacting species, then species occurrence will tend to vary independently of other species along environmental abiotic gradients (McIntosh 1967; Whittaker 1975; Austin 1985; Austin and Smith 1989; Collins et al. 1993).	GLM,GAM	Yes (see Radford and Van Niel 2005 in prep)
Discreet-niche	Local-scale	The discreet niche concept broadly states that communities consist of tightly interacting and closely associated co-	Correspondence Analysis, Non-Metric	Day et al., 2000 (Great Barrier Reef

		<p>occurring species groups (often known as guilds). These groups will tend to increase or decrease together along influential environmental gradients. Within habitats, species composition and richness is thought to be primarily a result of strong species interactions, habitat differentiation and competition for available resources (such as food). This approach has been used to identify clusters in the way species group to utilise resources in their environment (Inger and Colwell 1977; Winemiller and Pianka 1990).</p>	<p>Multidimensional Scaling, Correspondence Analysis, Canonical Correspondence Analysis, Hierarchical Cluster analysis (Legendre and Legendre 1998)</p>	<p>Marine park bioregional zones used NMDS and expert user (known as "Delphi" approach T.Ward pers comm)</p>
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References

- Austin, M. P. (1985). "Continuum concept, ordination methods, and niche theory." Annual Review of Ecology and Systematics **16**: 39-61.
- Austin, M. P. and T. M. Smith (1989). "A new model for the continuum concept." Vegetatio **83**: 35-47.
- Babcock, R. C. (1991). "Comparative demography of three species of scleractinian corals using age- and size-dependent classifications." Ecological Monographs **61**: 225-244.
- Baird, A. H., et al. (2003). "Habitat selection by larvae influences the depth distribution of six common coral species." Marine Ecology Progress Series **252**: 289-293.
- Baird, A. H. and T. P. Hughes (2000). "Competitive dominance by tabular corals: an experimental analysis of recruitment and survival of understorey assemblages." Journal of Experimental Marine Biology and Ecology **251**: 117-132.
- Bellwood, D. R. and T. P. Hughes (2001). "Regional-scale assembly rules and biodiversity of coral reefs." Science **292**(5521): 1532-1534.
- Bellwood, D. R., et al. (2005). "Environmental and geometric constraints on Indo-Pacific coral reef biodiversity." Ecology Letters **8**(6): 643-651.
- Caley, M. J. and D. Schluter (1997). "The relationship between local and regional diversity." Ecology **78**: 70.
- Carpenter, R. C. (1997). Invertebrate predators and grazers. Life and death of coral reefs. C. Birkeland. New York, Chapman and Hall: 198-229.
- Chown, S. L. and K. J. Gaston (2000). "Areas, cradles and museums: the latitudinal gradient in species richness." Trends In Ecology & Evolution **15**: 311-315.
- Collins, S. L., et al. (1993). "The hierarchical continuum concept." Journal of Vegetation Science, **4**: 149-156.
- Colwell, R. K. and G. C. Hurtt (1994). "Nonbiological gradients in species richness and a spurious Rapoport effect." American Naturalist **144**: 570-595.
- Colwell, R. K. and D. C. Lees (2000). "The mid-domain effect: geometric constraints on the geography of species richness." Trends In Ecology & Evolution **15**: 70-76.
- Connell, H. V. and R. H. Karlson (1996). "Species richness of reef-building corals determined by local and regional processes." Journal of Animal Ecology **65**: 233-241.
- Connell, J. H. (1997). "Disturbance and recovery of coral assemblages." Coral Reefs **16**, **Supplemental**: S101-S113.
- Cornell, H. V. (1999). "Unsaturation and regional influences on species richness in ecological communities: a review of the evidence." Ecoscience **6**: 303.
- Cornell, H. V. and J. H. Lawton (1992). "Species interactions, local and regional processes, and limits to the richness of ecological communities: a theoretical perspective." J. Anim. Ecol. **61**: 1.
- Done, T. J. and D. C. Potts (1992). "Influences of habitat and natural disturbances on contributions of massive Porites coral to reef communities." Marine Biology **114**: 479-493.

- Eeley, H. A. C. and M. J. Lawes (1999). *Primate Communities*.
- Ellingsen, K. and J. S. Gray (2002). "Spatial patterns of benthic diversity: is there a latitudinal gradient along the Norwegian continental shelf?" *Journal of Animal Ecology* **71**(3): 373-389.
- Gaston, K. J. (2003). "Ecology the how and why of biodiversity." *Nature* **421**(6926): 900.
- Gaston, K. J. and T. M. Blackburn (2000). *Pattern and Process in Macroecology*. Oxford, Blackwell Science Ltd.
- Gray, J. S. (1997). "Marine biodiversity: patterns, threats and conservation needs." *Biodiversity and Conservation* **6**: 153-175.
- Gray, J. S. (2001). "Antarctic marine benthic biodiversity in a world-wide latitudinal context." *Polar Biology* **24**(9): 1432-2056.
- Gray, J. S. (2001). "Marine diversity: the paradigms in patterns of species richness examined." *Scientia Marina* **65**: 41-56.
- Griffiths, D. (1997). "Local and regional species richness in North American lacustrine fish." *J. Anim. Ecol.* **66**: 49.
- Harriott, V. J. and S. A. Banks (2002). "Latitudinal variation in coral communities in Eastern Australia: an integrated model of factors limiting coral reefs." *Coral Reefs* **21**(1): 82-94.
- Harrison, P. L. and C. C. Wallace (1990). Reproduction, dispersal and recruitment of the scleractinian corals. *Ecosystems of the world: Coral reefs*. Z. Dubinsky. Amsterdam, Elsevier Science Publishers B.V. **25**.
- Hawkins, B. A. and S. G. Compton (1992). "African fig wasp communities: undersaturation and latitudinal gradients in species richness." *J. Anim. Ecol.* **61**: 361.
- Hopley, D. (1982). *The geomorphology of the Great Barrier Reef: Quaternary development of coral reefs*. New York, Wiley.
- Hubbell, S. P. (1997). "A unified theory of biogeography and relative species abundance and its application to tropical rain forests and coral reefs." *Coral Reefs* **16**, Sup: S9-S21.
- Hughes, T. P. (1994). "Catastrophes, phase shifts, and large scale degradation of a Caribbean coral reef." *Science* **265**(5178): 1547-1551.
- Hughes, T. P., et al. (2002). "Detecting regional variations using meta-analysis and large-scale sampling: latitudinal patterns in recruitment." *Ecology* **83**: 436-451.
- Hughes, T. P., Bellwood, D.R., and Connolly, S.R. (2002). "Biodiversity hotspots, centres of endemism, and the conservation of coral reefs." *Ecology Letters*(5): 775-784.
- Inger, R. F. and R. K. Colwell (1977). "Organisization of contiguous communities of amphibians and reptiles in Thailand." *Ecological Monographs* **47**: 229-253.
- Karlson, R. H. and H. V. Connell (1999). "Integration of local and regional perspectives on the species richness of coral assemblages." *American Zoologist* **39**(1): 104-113.
- Kleypas, J. A. (1996). "Coral reef development under naturally turbid conditions; fringing reefs near Broad Sound, Australia." *Coral Reefs* **15**: 153-167.
- Lawton, J. H. (1999). "Are there general laws in ecology?" *Oikos* **84**: 177.
- Legendre, P. and L. Legendre (1998). *Numerical Ecology*. New York, Elsevier Health Sciences.

- McIntosh, R. P. (1967). "The continuum concept of vegetation." The Botanical Review **33**: 130-187.
- Miller, K. and C. Mundy (2003). "Rapid settlement in broadcast spawning corals: implications for larval dispersal." Coral Reefs **22**: 99-106.
- Miller, M. W. and M. E. Hay (1998). "Effects of fish predation and seaweed competition on the survival and growth of corals." Oecologia **113**: 231–238.
- Morin, P. J. (1999). Community Ecology. Massachusetts, USA, Blackwell Science.
- Pandolfi, J. M. (2001). "Coral community dynamics and multiple scales." Coral Reefs **21**: 13-23.
- Pearson, D. L. and S. A. Juliano (1993). Species Diversity in Ecological Communities.
- Potts, D. C., et al. (1985). "Dominance of a coral community by the genus *Porites* (Scleractinia)." Marine Ecology Progress Series **23**: 79-84.
- Rapoport, E. H. (1994). "Remarks on marine and continental bio-geography: and aerogeographical viewpoint." Phil. Trans. R. Soc. Lond. B **343**: 71-78.
- Robertson, D. R. (1996). "Interspecific competition controls abundance and habitat use of territorial Caribbean damselfishes." Ecology **77**: 885–899.
- Rosenzweig, M. L. and E. A. Sandlin (1997). "Species diversity and latitudes: listening to area's signal." Oikos **80**: 172.
- Roy, K., et al. (1998). "Marine latitudinal diversity gradients: tests of causal hypotheses." Proc. Natl Acad. Sci. USA **95**: 3699.
- Saunders, H. L. (1968). "Marine benthic diversity: a comparative study." American Naturalist **102**: 243-282.
- Stehli, F. G., et al. (1967). "Taxonomic diversity of recent bivalves and some implications for geology." Geological Society of America Bulletin **78**: 455-466.
- Stevens, G. C. (1989). "The latitudinal gradient in geographical range: how so many species co-exist in the tropics." American Naturalist **133**: 240.
- Thorson, G. (1957). Treatise on Marine Ecology and Palaeoecology. Memorandum of the Geological Society of America. J. W. Hedgpeth: 461-534.
- Veron, J. E. N. (2000). Corals of the World. Townsville, Australia, Australian Institute of Marine Science.
- Wallace, C. C. and P. R. Muir (2005). "Biodiversity of the Indian Ocean from the perspective of staghorn corals (*Acropora* spp)." Indian Journal Of Marine Sciences **34**(1): 42-49.
- Whittaker, R. H. (1975). Communities and Ecosystems. New York, MacMillian Press.
- Winemiller, K. O. and E. R. Pianka (1990). "Organization in natural assemblages of desert lizards and tropical fishes." Ecological Monographs **60**: 331-367.