

# Coral species complexes through space and time: an illustration of their dynamics using *Madracis* in the Caribbean

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## Abstract

Numerous genetic studies that show close genetic relationships between morphologically-defined coral species support the concept of reticulate evolution. The ecological scenarios that lead to such genetic patterns are less well studied. The crux in such studies is to answer under which conditions gene-flow between coral morphospecies breaks down and give rise to new genetic clusters with higher gene-exchange within than between them. Coral species complexes, such as the Caribbean species of the genus *Madracis*, form an excellent opportunity to investigate the conditions under which gene-flow between its members brakes down. Two sympatric and morphologically different species, *M. decactis* and *M. pharensis*, show preference for two small-scale habitat-types, horizontal and vertical reef surfaces respectively, that occur intermingled within the species' larval dispersal envelope. The relationship between habitat composition (i.e. proportion of horizontal vs. vertical reef surface) and the relative occurrence of *Madracis* species (i.e. proportion of *M. decactis* vs. *M. pharensis*) was investigated in four locations (~100km<sup>2</sup>) throughout the Caribbean and included a total of 51 reefs (0.01km<sup>2</sup>). Though both species were present in each location, they were absent on some reefs where their preferred habitat-type was available. The pattern of underrepresentation of species was consistent within locations (i.e., functionally related to reef-scale habitat composition) but the functional relationship differed across locations. Thus, depending on small- and large-scale habitat characteristics, the potential for hybridization between the *Madracis* species varies spatially, potentially leading to different evolutionary trajectories across space.

## Introduction

The concept of reticulate evolution (Veron 1995) states that in the early stages of speciation branches of a classic Darwinian tree can fuse when populations become linked spatially and fission when constituent population are spatially divided. When considering coral evolutionary ecology, the reticulate theory is supported by experimental crosses (e.g. Szmant et al. 1997, Hatta et al. 1999) and genetic studies (e.g. Hatta et al. 1999, Van Oppen et al. 2000, 2004, Diekmann et al. 2001) showing that species boundaries are far from complete among many coral taxa. Though genetic exchange between morphologically defined species in corals is probably common (Knowlton 2000), the degree to which presumed species exchange genetic material is variable across space (Carlon & Budd 2002, Fukami et al. 2004). Although spatial differences in genetic exchange (and thus interspecific relatedness) are in agreement with the notion of reticulate evolution, insight into the processes that determine the degree of genetic exchange is scarce and could help to reconcile the field of morphology-based studies as taxonomy with modern genetic approaches.

Here we will consider the simple situation of a coral species complex consisting of two morphospecies that (1) have higher fitness in either of two existing habitat types, (2) occur sympatrically and (3) exchange genetic information to some degree. Note that the latter might take the form of hybridization between “true” species (cf. Vollmer and Palumbi 2002) or a polymorphic system where one or more loci determine morphological “options” that are present within the species’ genetic database. As long as no genetic information is available, speculation whether morphologically distinguishable coral species represent “true” species (sensu Veron 1995) or simply represent different phenotypes within the same species (what we will call “morphospecies”) is semantical and should be avoided. The degree to which both (morpho)species exchange genetic information depends on several factors that are mostly studied theoretically (e.g. Endler 1977, Roff 2002). Initially genetic exchange will depend on the local abundance of both (morpho)species, their respective fitnesses in each habitat-type and the proportion of genetic information arriving from populations elsewhere. If such factors change to reduce the potential for genetic exchange, crosses between (morpho)species can become more rare than exchange within (morpho)species, which can increase the potential of sympatric

speciation. Sympatric speciation was once believed to be rare or even impossible, but recent studies have shown that sympatric speciation has occurred in various marine taxa (Palumbi 1992, 1996, 1997, Ayre 1995, Ayre and Hughes 2000).

Sympatric speciation can occur if species show reciprocal relative fitness for locally available habitat types and furthermore depends on the relative availability of these habitat types (Roff 2002). Sympatric speciation proceeds more rapidly when the distribution of critical habitat characteristics has a spatial scale of variation that exceeds the median dispersal distance for a species or group of hybridizing species (Smith et al. 1997, Orr and Smith 1998). Over evolutionary time-scales, local recruitment will provide a feedback mechanism that will disproportionately increase the more successful (in terms of fitness and/ or abundance) morphospecies relative to the alternate morphospecies within an area of unique habitat conditions (Endler 1973).

To begin exploratory investigations into the potential mechanisms underlying coral evolution, we studied two, sympatric, brooding morphospecies of the Caribbean coral genus *Madracis*, *Madracis decactis* and *M. pharensis*. The morphospecies are known to exchange genetic material on the Leeward islands of the Netherlands Antilles (Diekmann et al. 2001, Vermeij et al. 2004), have strict habitat preferences for horizontal and vertical reef surfaces respectively (Vermeij and Bak 2002, 2003) and planulae of both morphospecies start exploring the substrate immediately after release resulting in short dispersal distances (Vermeij et al. 2003). Although both morphospecies occur in vertical and horizontal habitats, the fitness of one morphospecies exceeds that of the other in its preferred habitat, i.e. *M. decactis* has higher fitness than *M. pharensis* on horizontal surfaces and vice versa for vertical surfaces (Vermeij 2002, Vermeij and Bak 2003, Vermeij et al. 2003, 2004). The collection of characteristics in the two *Madracis* morphospecies (i.e. morphospecies specific habitat preference, reversed fitness in two habitat types in which both morphospecies can occur and short dispersal distances) can drive the morphospecies-complex to fixation for one of the morphospecies under certain habitat characteristics. Theoretical studies predict that when one of the habitat types becomes rare the locally less-favored morphospecies can disappear from the population due to processes that affect the survival and rate of gene-flow between the morphospecies (May et al. 1975, Endler 1973, 1977). The potential for local genetic exchange thus

depends (at least partly) on the availability of the two habitat types that these morphospecies prefer. If the morphospecies are “true” species (Veron 1995) and do not exchange genetic information, the relationship between habitat availability and morphospecies presence should be linear as the occurrence of a morphospecies will depend solely on the presence of its preferred habitat (Endler 1973). If the morphospecies exchange genetic information, this linear relationship takes the form of a sigmoidal relationship. As one habitat type increases, Allee-effects and/or natural selection will disproportionately favor the better-adapted morphospecies resulting in an under-representation of the less well-adapted morphotype.

The effect of habitat availability on the degree to which sympatric morphospecies develop a local level of genetic isolation and structure also depends on source-sink relationships. If the population of the less abundant morphospecies is replenished through larval supply from other locations, the local effects of Allee-type dynamics, drift and/or selection weaken and fixation of either morphospecies is unlikely to occur (Endler 1977). If the relative frequency of morphospecies arriving from source populations varies across large spatial scales (e.g. through large-scale overrepresentation of one habitat-type), then the bias of external supply will be variable. In the limit when only one morphospecies arrives from external sources, drift can only cause a local extinction of the alternate morphospecies. Thus, both the degree of population isolation (increased by low population connectivity) and the large-scale relative frequencies of habitat types across locations can affect the reef-scale functional relationships between habitat availability and morphospecies abundance.

To investigate the importance of such spatial factors to the potential for *M. decactis* and *M. pharensis* to exchange genetic material we studied the distribution of both morphospecies at a large scale (i.e. “locations” of  $\sim 100\text{km}^2$ ) across a range of reefs (i.e. sites of  $\sim 0.01\text{km}^2$ ). Within each location, the reefs represent a gradient over which the proportional availability of preferred habitat-types of both morphospecies gradually changes with each habitat-type dominating the local reef topography at its outer ends. To determine whether large-scale patterns are similar between locations, we quantified the relationship between morphospecies abundance and habitat-type availability for four distant locations spread throughout the Caribbean basin ( $>1000\text{km}$ ). We tested the

hypothesis that a spatial component (i.e. the large-scale distribution of habitat-types and/or source-sink relationships) affects the potential for genetic exchange between two abundant and genetically related morphospecies of the coral genus *Madracis*.

## Material and Methods

We quantified habitat-type availability (in terms of the proportional abundance of vertical and horizontal surface, the preferred habitat-types of *M. decactis* and *M. pharensis* respectively) and the occurrence of both *Madracis* morphospecies on 22 reefs on the Leeward Netherlands Antilles (Bonaire; 12°N, 68°W and Curacao; 12°N, 69°W), 13 reefs in the Bocas Del Toro region (9°N, 82°W; Republic of Panama), 9 reefs on Navassa Island (18°N, 75°W; Haiti) and 7 reefs in the Florida Keys (25°N, 80°W; U.S.A). All reefs were chosen (1) to span a wide range of habitats, from those dominated by vertical habitats to those dominated by horizontal habitats, and (2) to cover a similarly large area in each region (approx. 100km<sup>2</sup>).

The proportion of horizontal vs. vertical reef surface was determined using a profile gauge (after McCormick 1994). The absolute height difference between 800 successive points spaced 10cm apart was determined within the 15-25m isobathic region. The distance between points on the reef surface was calculated (in cm) as  $\sqrt{10^2 + (\text{height difference})^2}$ . The proportion of horizontal habitat (prop(H)) was calculated as the summed distances between successive points with <10cm height difference (i.e. forming an angle of inclination,  $\alpha$ , fitting  $|\alpha| < 45^\circ$ ) divided by the total surface distance (i.e. for all angles of inclination,  $0^\circ \leq |\alpha| < 90^\circ$ ). The proportion of vertical surface (prop(V)) is given as  $\text{prop(V)} = 1 - \text{prop(H)}$ .

All *Madracis pharensis* and *M. decactis* colonies were measured along the same isobathic range and their position on the substrate was noted (Horizontal (H) or Vertical(V), defined as substrate sloping less and more than 45° with the surface of the water, respectively). The transect was extended in some occasions to include at least 300 colonies per site in our analyses. The proportion of *M. decactis* and *M. pharensis* in their preferred habitat (H and V, respectively) was plotted against the proportional abundance of these habitat types (prop(H) and prop(V), respectively) per geographic region (Neth.

Antilles, Bocas del Toro, Navassa and the Florida Keys) and the functional form was analyzed.

Both morphospecies exchange genetic material (Diekmann et al. 2001) and the majority of planulae normally settles within 100m of the parent (Vermeij et al. 2003). These characteristics predict that local populations can become biased toward the morphospecies that matches the locally dominant habitat type, resulting in a sigmoidal morphospecies-habitat distribution across habitat frequencies (Endler 1973, 1977). When one of the habitat types becomes rare the corresponding morphospecies could disappear from the population as selection/ drift will favor the morphospecies that has higher fitness/ reproductive output in the locally dominant habitat type. The morphospecies on the rarer habitat-type will thus become underrepresented in the local population through Allee-effects, genetic drift and/or selection. Here we compare the shape of this species-habitat distributional relationship (indicative of the potential for genetic exchange along an identical habitat range) among the four regions. We realize that numerous alternative explanations can explain the patterns observed (e.g. sperm competition, gamete recognition, mutations in a “speciation-locus”, sexual vs. asexual reproduction, maternal effects). However due the complete absence of data in such fields, we want to start the exploration of causal mechanisms underlying coral evolutionary dynamics by addressing one potential mechanism, i.e. the effect of habitat-availability on the potential for genetic exchange between two coral morphospecies capable of exchanging genetic information (Diekmann et al. 2001).

## **Results and Discussion**

### Geographic differences in species-habitat relationships

Regional differences existed in the distribution of the two *Madracis* morphospecies across a similar habitat gradient in which the proportion of horizontal vs. vertical reef surface gradually increased (Figure 1; ANCOVA, region x prop(H),  $F_{4,42}=23.13$ ,  $p<0.001$ ). A sigmoidal relationship existed in the Netherlands Antilles indicating that towards the end of the habitat gradient (i.e. when either prop(H) or prop(V) approached 0.20) the population became fixed for one morphospecies whose preferred habitat-type dominated the local reef topography. Despite the presence of its preferred

habitat-type, the other morphospecies disappeared from the population either through the Allee-effect, drift and/or selection and genetic exchange between the morphospecies necessarily stops (May et al. 1975).

A similar, sigmoidal relationship was observed in Navassa, but not in Bocas del Toro and the Florida Keys (Figure 1, Table 1). In both regions, one of the morphospecies was structurally underrepresented in the population despite that its preferred habitat-type comprised over 50% of the locally available reef substrate. In Bocas del Toro, *M. decactis* was absent in all sites sampled except for two remote offshore locations (near the Zapatilla Islands) where large horizontal, limestone pavements arose from the seafloor. The absence of *M. decactis* on horizontal surfaces at all other sites in Bocas del Toro was probably caused by the large influx of fluvial sediment (Guzman and Guevara 1998) which causes stress and disturbance to benthic organisms, especially on horizontal surfaces (Airoidi 2003). Despite the fact that a morphospecies' preferred habitat was available (i.e. horizontal reef substrate), additional environmental factors (e.g. sedimentation) needed to be considered to qualify such locations as suitable habitat for colonization by the (morpho)species that prefer these habitat-types.

In the Florida Keys, *M. decactis* dominated the local *Madracis* population due a general absence of surface complexity. The number of sites with more than 40% vertical reef surface, the habitat-type normally preferred by *M. pharensis*, was low compared to the three other localities and thus was likely to limit the regional presence of this morphospecies. Local environmental factors other than habitat-type availability (e.g. excess sedimentation in Bocas del Toro) can thus prevent the invasion by or persistence of a morphospecies of its preferred habitat-type. Environmental and geographic factors therefore affected the occurrence of both morphospecies across a gradient of their preferred habitat-types (Fig. 1).

#### *Madracis*, the Caribbean and the concept of reticulate evolution

That a spatial component partially dictates the local potential of morphospecies to exchange genetic material, is in concordance with the notion of reticulate evolution. Fukami et al. (2004) found spatial differences (i.e. Panama vs. Bahamas) in the genetic differentiation among members of the *Montastraea annularis* complex. Carlon and Budd

(2002) report similar findings at a smaller spatial scale (i.e. between sites) for *Favia fragum* in Bocas del Toro, Panama. Surprisingly, the explanation for such differences in divergence among closely related (morpho)species rarely includes discussions on the environmental setting and the habitat preferences of the (morpho)species involved (though see Carlon and Budd 2002). However, focusing upon the strong preferences for horizontal and vertical surfaces in this *Madracis* complex, we illuminated clear functional relationships between habitat and morphospecies frequencies (Fig. 1). Nevertheless, subtle differences in habitat requirements of the coral (morpho)species and the availability of such habitats in a geographic region appear to have considerable influence on the degree of genetic divergence that develops between them. Most commonly, spatial differences in genetic divergence among (morpho)species are quantified using indirect descriptors such as spatial variation in morphological characteristics, spatial differences in divergence times based on the fossil record and the use of genetic techniques. More effort should be spent to link the habitat characteristics directly to population-level differences in morphologies or morphospecies frequencies.

Evolution: patterns from genetics and processes from ecology?

Although the genetic relatedness of the two morphospecies in all four regions is largely unknown (but see Diekmann et al. 2001 for the Netherlands Antilles), a prediction can be made based on the observed morphospecies-habitat relationships. They show how morphospecies coexist in different geographical settings and in such cases could exchange genetic material. In the presence of both habitat types (i.e. on structurally complex reefs with neither type <20% of the total) on the Netherlands Antilles and Navassa, local genetic exchange will be likely (and confirmed for the Netherlands Antilles by Diekmann et al. 2001) (Fig. 1). The morphospecies will form a complex in which genetic information is maintained between the two morphospecies. In Bocas del Toro and the Florida Keys, one morphospecies dominates the local *Madracis* population (*M. pharensis* and *M. decactis* respectively) and probably represents a monophyletic (or genetically characterizable) species as its sister-species has been lost mostly through habitat-driven evolutionary dynamics. Only when each morphospecies can develop into a monophyletic species in bordering geographic areas (e.g. Bocas del Toro bay for *M.*



*pharensis* and the nearby off-shore reefs for *M. decactis*), a population structure arises, where the two species are found relatively close to one another but represent potentially genetically distinct branches in the evolutionary tree. For our four regions the predictions on the genetic relationships between the morphospecies are visualized in Figure 2.

Evidence for reticulate evolution is presently based on genetic studies that provide insight in its outcome, i.e. morphologically defined species overlap when grouped genetically (e.g. Hatta et al. 1999, Van Oppen et al. 2000, 2001, 2004, Diekmann et al. 2001). When applying a process-based approach that reveals the potential mechanisms that lead to such patterns, one important difference arises. Based on *Madracis* in the Caribbean, fusion between “true” or genetically distinguishable species can only occur if two conditions occur after substantial periods in which a local population has (nearly) approached fixation for one of the morphospecies. First, if the fitness landscape in which the species occurs is temporally variable so the fixation of one morphospecies (i.e. the formation of a genetically identifiable species) is prevented due to a changing selective landscape and second when the closed nature of the system dissipates through the influx of individuals from locations that are under a different selection regime (e.g. to changes in seawater currents). These processes prevent the divergence of closely related morphospecies towards genetically distinct species rather than reconnecting such species that had formed earlier. In addition, the rarity of the environmental conditions under which the *Madracis* species-complex becomes fixed (Figure 1) suggests that the likelihood of speciation between *M. decactis* and *M. pharensis* is probably very low.

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## Table and table caption

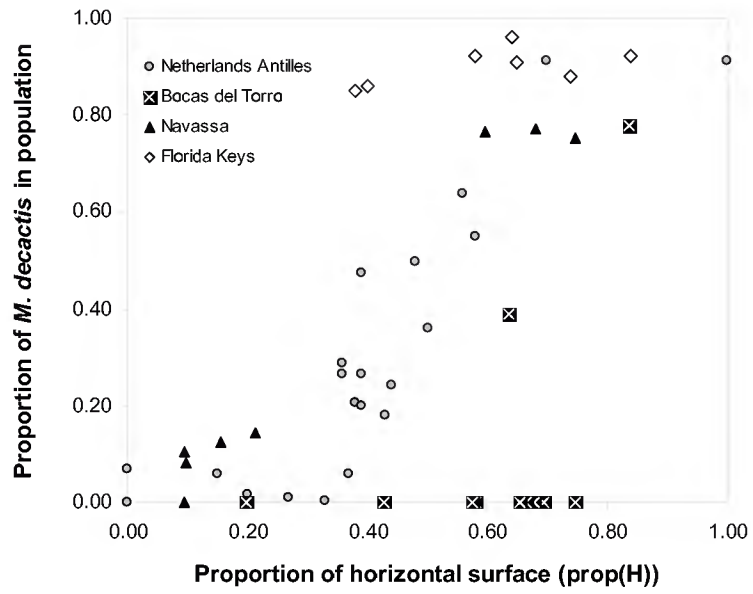
TAB. 1 – Post-hoc test results (Tukey-HSD probabilities) on differences between regions in the relationship between substrate composition and the occurrence of the two *Madracis* morphospecies.

	Navassa	Bocas del Toro	Florida Keys
Netherlands Antilles	ns	p< 0.005	p< 0.001
Navassa		p< 0.005	p< 0.001
Bocas del Toro			p< 0.001

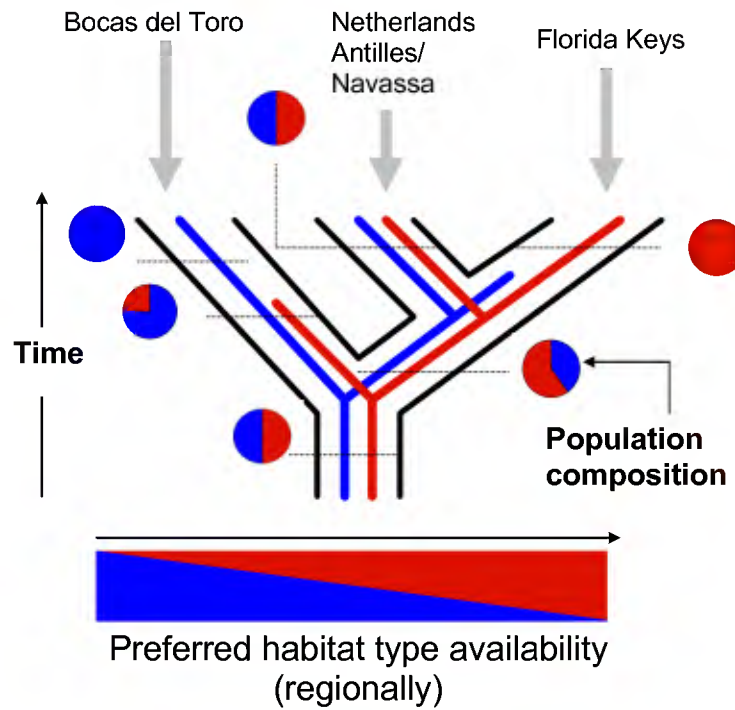
## Figure captions

FIG. 1 – The proportion of the *Madracis* population consisting of *M. decactis* for four regions in the Caribbean: Netherlands Antilles (n= 22 reefs), Bocas del Toro (n= 13 reefs), Navassa (n= 8 reefs) and the Florida Keys (n= 7 reefs) as a function of the proportional availability of horizontal surface on each reef. The pattern for *M. pharensis* is calculated as one minus the proportion of *M. decactis*. The sigmoidal curve indicates the expected distribution of morphospecies assuming some form of genetic structure between the morphospecies, exchange of genetic material and local dispersal.

FIG. 2 – Expected genetic relationships between *M. pharensis* and *M. decactis* in four regions across the Caribbean based on the relationships between population composition of *Madracis* morphospecies and habitat composition in terms of the availability of the habitat preferred by either species



-- FIGURE 1 --



-- FIGURE 2 --