Evolutionary Ecology of the coral genus Madracis - an illustration of the nature of species in scleractinian corals
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Chapter 15

General discussion
In this thesis the evolutionary and ecological status of six *Madracis* species is addressed. Whether the observed differences can be used to reveal mechanistic species that can be used to describe the genus through evolutionary time, depends on the spatio-temporal scale on which we performed this research (Pahl-Wostl 1995). In general, temporal as well as spatial scales are characterized as a range between stability and stochasticity. Within the limited space and time of this study and based on the patterns we observed, an attempt is made to determine whether the current *Madracis* morphospecies are evolutionary meaningful units, i.e. occur at the stable end of the spatio-temporal scale. The question whether such is desirable is a second one, but at the risk that the complexity resulting from detailed descriptions of the species clouds all structural information, I will now try to describe the nature of species in scleractinian corals using *Madracis* as an example.

Based on definition, the highest systematic hierarchy at which we can describe *Madracis* is at the level of a syngameon in which spatio-temporal organization takes place. A syngameon is a group of species that...
are capable of hybridizing sensu Veron (1995). A syngameon is reproductively isolated in the present from other syngameons and therefore exists in space only. Their component species can be allopatric or sympatric separated by genetic or reproductive mechanisms or lack of hybrid fitness (Veron 1995). Our spatio-temporal scale is defined by the duration of the research (1998-2001) and the locations it was carried out (Bonaire and Curaçao; approx. 9375km²; see chapter 12 for map). Although I agree that this scale seems too limited for far reaching conclusions, I also claim that by investigating patterns observable at present, underlying processes can be characterized that are consequent through time. It is therefore necessary to adopt a process perspective describing the relations between structural and functional properties instead of a mechanistic perspective where cause and effect are often indistinguishable (Pahl-Wostl 1995).

The relational perspective results from the combination of three paradigms that are currently used in coral biology: morphometrics, genetics and ecological descriptions. All of these paradigms are informative, but limited as combinations of anthropogenic classification and interpretation and natural evolutionary organization. In summary, the organization of the genus is shown in Figure 1. The two axes indicate two of the paradigms: genetics (based on (Diekmann et al. 2001) and colony morphology. Certain species are easily distinguished based on both axes (e.g. *M. pharensis* and *M. mirabilis*). Other combinations can be separated along only one (e.g. *M. senaria* and *M. pharensis* can only be separated along the genetic axis). Most combinations can not be distinguished along both axis because of morphological and genetic overlap (e.g. *M. pharensis* and *M. decactis*). Nevertheless, we can see that the clusters representing these species differ in Figure 1. That is because we look along the third axis representing the third paradigm: ecological characteristics. Ideally, such projection of multiple species characteristics would be performed in an n-dimensional graph, where n represents the number of characteristics that were studied simultaneously. Because of logistical and analytical limitations such an approach is, unfortunately, impossible at present. I regard the three axes representative of the dominant characteristics of a species analogous to a principal component analysis.

Figure 1 indicates that *M. mirabilis* and *M. senaria* are distinct from each other and all other Madracis genetically and morphologically. Their different ecological strategies are not shown, but should be visualized by the different position of species the along the y-axis. Since *M. mirabilis* and *M. senaria* show no significant overlap with other morphospecies, they are regarded as “true” species sensu (Veron 1995). These species adapted a specialist strategy on the reef (chapter 3 and 5), which was then
followed by reproductive isolation due allo-recognition (chapter 8). Since none of the characteristics is shared with the other four species, the separation from these species likely took place 15-11 Ma ago (Budd et al. 1994, Swedberg 1994, Budd et al. 1995). At present, *M. mirabilis* and *M. senaria* provide excellent evolutionary units to study ecologically, morphologically or genetically, but they are useless to describe speciation processes in corals.

The remaining four species show interspecific overlap in morphological, genetic and ecological characteristics. Therefore they provide a much better opportunity to study organizational processes in coral evolution. I found indications of two of such organizational processes in *Madracis*: introgressive hybridization and the controlled expression of genetic polymorphisms. More precisely, the *M. pharensis/M. decactis*-complex is a genetical polymorphism organized by habitat heterogeneity at a small spatial scale (chapter 12). Secondly, introgressive hybridization between *M. formosa* and the *M. pharensis/M. decactis* complex resulting in a new species: *Madracis carmabi* (chapter 10, Diekmann et al. 2001). The participation of the *M. pharensis/M. decactis* complex in both processes clearly illustrates the evolutionary dynamics of these species. In these species, there appears to be a tendency towards speciation. Only when the environment provides conditions that allow speciation, i.e. niche diversification combined with fitness differences, the variation in species brakes down into separate new species. The scale, at which environmental variation occurs, that causes organization within species gene-pools, is surprisingly small and was found between closely located islands (chapter 12). A similar observation exists for the component species of the *Montastraea annularis* (sensu lato) complex, (Van Veghel and Bak 1993, Weil and Knowlton 1994) where divergence between the three morphs differed between islands as well, be it at a larger spatial scale. Both the *Madracis* as well as the *Montastraea* species complex indicate that the organization of gene-pools (and thus potential speciation) is determined by local, spatial factors. These conditions may vary on a temporal scale. Depending on the duration of certain environmental conditions, variation evolves into new species or dissapears when environmental factors no longer cause a disruptive gradient within the gene-pool. If reproductive isolation between newly formed morphospecies or ecotypes, has not established itself at this point, previously discrete species could fuse again. In *Madracis*, this likely to have occurred between the *M. pharensis/M. decactis* complex and *M. formosa* (Diekmann et al. 2001). Ecological data (chapter 3 and 10) and genetic data (Diekmann et al. 2001) strongly indicate that hybridization occurs between the two species, but we do not know for sure whether the
Figure 2. Impression of the relation between the Madracis morphospecies in a reticulate network. Morphospecies are defined along two axes representing paradigms. The transverse cut through the network shows the current degree of organization and indicates the presence of monophyletic species (M. mirabilis and M. senaria) as well a syngameon (M. decactis, M. formosa, M. carmabi and M. pharensis).

*M.pharensis/M. decactis* complex and *M. formosa* move apart or towards each other through evolutionary time. Separation in clusters without being genetically discrete (Diekmann et al. 2001) suggests that previously organized gene-pools (i.e. the clusters) are currently integrating due hybridization (i.e. no genetic separation). In the genus we then have an example of a group where speciation could potentially occur (*M.pharensis/M. decactis* complex), but also where existing species reintegrate due hybridization (*M.pharensis/M. decactis* complex and *M. formosa*). The concurrence of fusions and splits in *Madracis* gene-pools as they are organized through evolutionary time, supports the presence reticulate evolution in *Madracis*. This process is often visualized as a network of splitting and fusing branches, variable in width, representing the temporal organization of gene-pools. This can be visualized for *Madracis* as a horizontal cut through a network looked at from above (Figure 2). We see that when the organizational processes are known and multiple paradigms are combined simultaneously, species become visible. They can not be defined *a priori* and evolve as patterns from processes that respond to upper and lower constraints through time.
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