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LARGE-SCALE EVOLUTIONARY PATTERNS IN THE REEF-CORAL MONTASTRAEA: THE ROLE OF PHENOTYPIC PLASTICITY

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ABSTRACT

Multivariate statistical analyses were used to reconstruct evolutionary patterns in Caribbean Montastraea over the past 25 Ma. The material consisted of 225 fossil colonies from four time intervals, roughly 5 Ma in length, and 72 colonies from four populations of the two modern species. Sixteen characters were measured on 8-10 corallites per colony. Cluster analyses were performed on each interval using Mahalanobis' distances between colonies. The clusters were modified using canonical discriminant analysis. The resulting species were linked into lineages using Mahalanobis' distances. The shape of the clade suggests that speciation and extinction rates were generally low, maximum species durations high, and phyletic evolution minimal. Amounts of overall phenotypic plasticity in each species were estimated using intracolony variances in principal components within species. Species were found to differ in plasticity. Plasticity was not related to extinction in the clade. Low plasticity was associated with increased speciation. Plasticity decreased both within and between species in the clade through time.

INTRODUCTION

Phenotypic plasticity is generally regarded as a characteristic of weedy, tolerant species that allows individuals to alter their morphology without genetic change in response to change in environment (Bradshaw 1965). The amount of plasticity and the characters involved are species-or even population- specific (Foster 1979, Willis 1985). As explained by Schlichting (1986), phenotypic plasticity occurs as a result of change in 'typical' developmental sequence and is favored under specific selection regimes, such as disruptive selection. It has been argued that unstable genotypes are typically more plastic and that, in fact, phenotypic plasticity should inhibit character evolution (Stearns 1982). These relationships suggest that phenotypic plasticity would be higher earlier during the longterm evolution of a clade (Meyer 1987) and that plastic lineages would commonly experience stasis. Moreover, plastic lineages would be expected to have longer durations and survive extinction episodes. Lewontin (1957), however, has postulated that phylogenetically advanced groups would tend to evolve phenotypic plasticity as genetic variation decreased. The universality of any relationships has been seriously questioned, since characters and their plasticity evolve independently (Schlichting 1986).

The purpose of this paper is to examine the evolution of phenotypic plasticity in the common Caribbean reef-coral Montastraea through the past 25 Ma. Three questions are addressed: (1) Has phenotypic plasticity decreased in the clade through time (both within and between lineages)? (2) Do more plastic lineages evolve less? (3) Do more plastic lineages have longer durations and do they more frequently survive extinction episodes? To answer these questions, this paper also demonstrates: (1) how scleractinian lineages can be reconstructed quantitatively using data from the fossil record and (2) how the lineages can be used to test questions such as those above.

MATERIAL AND MEASUREMENTS

Montastraea has been selected for study for several reasons: (1) previous transplantation experiments have shown that living species of the genus are highly phenotypically plastic (Foster 1979), (2) it has an abundant fossil record in the Caribbean ranging from late Oligocene to Recent time, (3) Caribbean members of the genus are believed to constitute a monophyletic clade, (4) colonies are massive, and corallites discrete and non-polymorphic; therefore, corallite variation within colonies can be used to estimate phenotypic plasticity, and (5) colonies grow by accretion at a constant rate (4-10 mm/yr), and astogenetic variation is minimal. The genus currently contains two Caribbean and seven Indo-Pacific living species, and extends back to early Cretaceous time. Montastraea became a dominant reef-coral in the Caribbean during the early Miocene after an extinction episode during the late Oligocene. Despite its low diversity, it continues to dominate Caribbean reefs today.

Colonies of fossil Montastraea have been selected for analysis from various Caribbean localities (Table 1). These include collections at the US National Museum of Natural History (USNM), the University of Illinois (UI), the Natural History Museum in Basel, Switzerland (NMB), and the University of Iowa (SUI). Age

Table 1. Localities and number of colonies measured in each of five time intervals.

Age	Locality	# colonies	Repository
1. late Oligocene	Anahuac Fm, Texas	9	SUI
	Juana Diaz Fm, Puerto Rico	12	SUI
	Browns Town Fm, Jamaica	5	SUI
2. early Miocene	Tampa Fm, Florida	8	USNM
	Chattahoochee Fm, Georgia	11	USNM
	Lares Fm, Puerto Rico	7	SUI
	Santa Ana, Rio Lajas Fms, Chiapas	24	UI
3. middle Miocene	Anguilla Fm, Anguilla	23	USNM
	La Boca Fm, Panama	27	USNM
	Baitoa Fm, Dominican Republic	9	NMB
4. late Miocene/ early Pliocene	Cercado, Gurabo, Mao Fms, Dominican Republic	90	NMB
5. Recent	Discovery Bay, Jamaica	72	SUI

dates for these localities are based primarily on Bold (1972) and Saunders et al. (1978). The collections have been subdivided into five time intervals, approximately 5 Ma in length (Table 1). As many well-preserved, large colonies as possible were selected from each locality, and 2-3 transverse thinsections were prepared from locations across the colony surface. Montastraea was distinguished from genera with similar morphologies (e.g. Agathiphyllia, Favia) by its porous costate coenosteum, its septothecate wall structure, its trabecular columella (lacking true pali), and the prevalence of extratentacular budding. No a priori judgements were made concerning species identifications.

Sixteen measurements or counts (Table 2) were made on 8-10 mature corallites in each colony. The measurements describe the size and porosity of various corallite architectural features as well as the size and spacing of the corallites themselves (see Foster 1983 for details). These characters have commonly been used to distinguish species in Montastraea. Corallite maturity was judged by the development of the highest septal cycle. Distributions of most characters within colonies were normal. Identical measurements made previously on 32 living colonies of M. cavernosa and 40 living colonies of M. annularis (Foster 1985) were also used in the statistical analyses. These colonies were collected from four contrasting reef habitats near Discovery Bay, Jamaica.

DISCRIMINATION OF SPECIES

Species are notoriously difficult to distinguish morphologically in scleractinian corals, both because of their widespread variability and because of the overlap between morphologically similar species. In the current study, species have been distinguished following a procedure similar to that of Foster (1983), consisting of three steps: (1) Mahalanobis' distances were calculated between colonies within each of the four fossil time intervals, (2) these distances were used to group colonies from each interval into clusters by average linkage cluster analysis (UPGMA), (3) a series of canonical discriminant analyses were run on the clusters, and on combinations and modifications thereof, until the clusters were distinct at $p<.0001$. Running separate analyses on each time interval prevents artificially inducing stasis, which may result from a single all-inclusive discriminant analysis. The use of Mahalanobis' distances in cluster analysis (step 1) most heavily weights those characters which best distinguish between colonies. Canonical discriminant analysis (step 2) further refines the clusters and thereby alleviates some of the ambiguities associated with choice of clustering level. The analyses have been run on the University of Iowa IBM4381 computer using SAS and SPSS-X.

The final canonical discriminant results are shown in Fig.1. In all cases, Mahalanobis' distances show that 100% of colonies were assigned correctly to groups. In the late Oligocene, three discrete "species" were found. The first canonical variable (CV1) explains 60.0% of the variation and the second (CV2) 40.0%. CD and -SLS are most heavily weighted on CV1; SLS, CLW, and -CD on CV2. In the early Miocene, five discrete "species" were found. CV1 describes 66.6% of the variation and CV2 26.2%. CD and -SLP are most heavily weighted on CV1; CNP, SLT, and -CD on CV2. In the middle Miocene, four discrete "species" were found. CV1 describes 74.6% of the variation and CV2 19.5%. CD and -SLP are most heavily weighted on CV1; -CD and -NND on CV2. In the late Miocene/early Pliocene, seven "species" were found, some of which are partially overlapping. CV1 describes 87.4% of the variation and CV2 4.8%. CD is most heavily weighted on CV1 and SLP on CV2. Thus, similar loadings were found on the first two canonical variables in all four analyses (especially CD on the CV1).

Table 2. List of characters.

Character	Abbreviation
1. corallite diameter	CD
2. total number of septa	NS
3. corallite spacing	NND
4. coenosteum diameter	CND
5. coenosteum density	CNNV
6. coenosteum density	CNP
7. columella width	CLW
8. columella density	CLNV
9. theca thickness	TT
10. septum length (1st cycle)	SLP
11. septum length (2nd cycle)	SLS
12. septum length (highest cycle)	SLT
13. septum thickness (1st cycle)	STP
14. septum thickness (2nd cycle)	STS
15. septum thickness (highest cycle)	STT
16. costa thickness (1st cycle)	CST

RECONSTRUCTION OF LINEAGES

The 19 fossil "species" found above and the two modern species were then linked into "lineages" representing single species lines using Mahalanobis' distances among all 21 species (Table 3). In this procedure, distances between species in successive time intervals were compared with distances between species within time intervals. Species in successive time intervals were linked if the distance between them was less than the minimum distance between species within each of the two intervals. Three exceptions were made: (1) the linkage of species 2/3 and 5/1, (2) the nonlinkage of species 1/1 and 2/3, and (3) the linkage of species 4/6 and 5/2. In the first case, two nonsuccessive species were linked because of their exceptionally low F-value. In the second case, two species with a low F-value were not linked, because their distance increased dramatically after the linkage in the first case. In the third case, the lowest distance on table 3 was not linked, because of the extremely low distance obtained when comparing time intervals 4 and 5 alone.

Linkage reduced the 21 species to eleven, one of which extended through all five time intervals

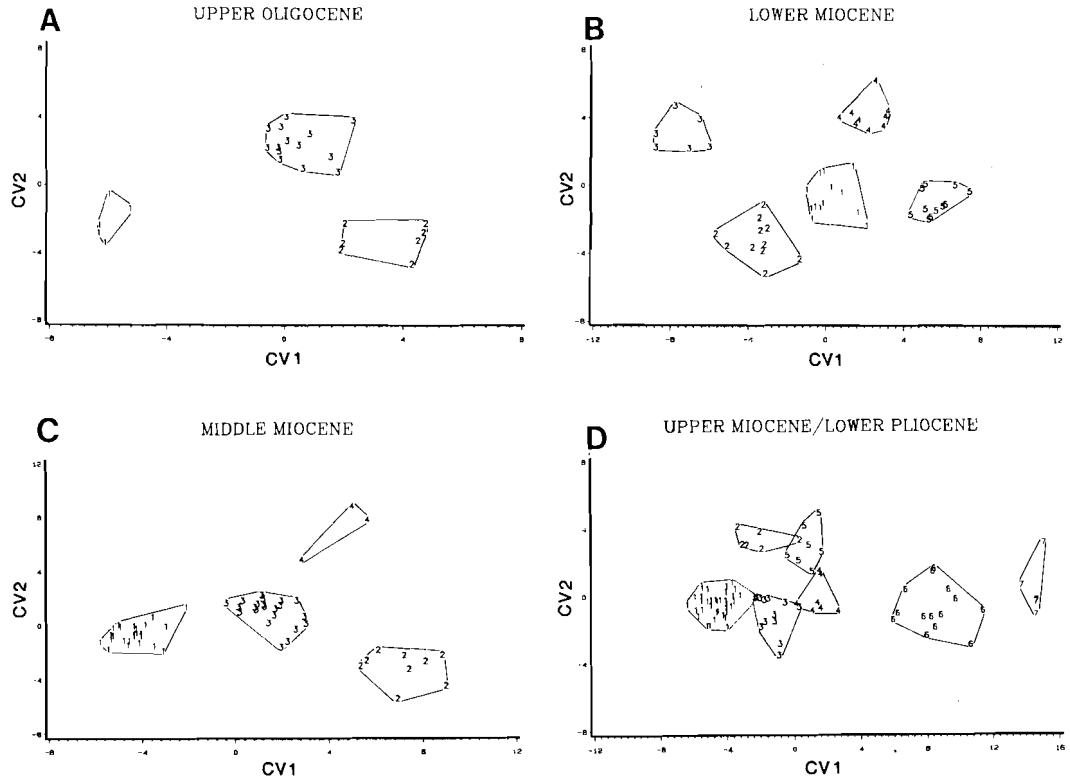

Figure 1. Final canonical discriminant analysis of material within the four fossil time intervals. Scores on the first two canonical variables (CV1, CV2) are plotted for each colony. The numbers used for each point refer to the final colony assignment to "species". Polygons outline the maximum variation within each species.

(Fig. 2). During the late Oligocene, one species became extinct. During the early Miocene, three new species arose, one of which became extinct. During the middle Miocene, one new species arose and became extinct. During the late Miocene/early Pliocene, four species arose, all of which became extinct, and two longer species lines became extinct. No new species arose after the Pliocene. Thus, rapid periods of species diversification (adaptive radiations) appear to have been rare in Montastraea, and a few species in the clade were capable of surviving extinction episodes during the late Oligocene and Plio/Pleistocene. Species generally had long durations with limited speciation and extinction within each interval. Maximum diversity occurred during the late Miocene/early Pliocene.

Table 3. F-statistics (df=16,261) testing Mahalanobis' distances between species from each time interval. For each species, the first number refers to the time interval, and the second number refers to the species within the interval.

species	1/1	1/2	1/3	2/1	2/2	2/3	2/4	2/5	3/1	3/2	3/3	3/4	4/1	4/2	4/3	4/4	4/5	4/6	4/7	5/1
1/2	6.70																			
1/3	7.12	9.91																		
2/1	4.46	5.64	11.16																	
2/2	4.12	9.04	23.41	6.48																
2/3	3.26	10.30	15.66	6.84	5.52															
2/4	5.51	8.18	3.33*	6.66	15.93	8.81														
2/5	6.89	3.93*	7.24	6.15	12.93	11.99	6.13													
3/1	4.84	13.34	38.52	12.45	2.19*	5.60	25.06	24.01												
3/2	10.01	10.13	3.21	9.81	21.02	15.67	4.38*	5.35	33.63											
3/3	5.07	5.34	11.51	4.31	8.78	8.06	7.25	2.94*	20.76	9.57										
3/4	8.01	6.39	9.27	7.10	9.64	9.64	7.27	4.24	13.56	6.66	5.75									
4/1	7.79	29.53	61.88	26.26	7.51	6.57	36.67	40.98	12.00	48.24	42.44	18.30								
4/2	4.21	12.55	18.24	7.41	2.95	4.54	13.69	12.91	4.71*	17.58	8.33	10.32	5.14							
4/3	3.56	19.60	29.86	11.54	5.89	5.13	17.81	21.69	9.76	26.91	18.48	12.36	5.99	3.33						
4/4	3.71	11.85	12.08	6.49	4.83	5.96	8.06	9.05	9.79	11.45	6.90*	8.93	10.08	2.97	5.24					
4/5	4.47	12.85	14.64	7.14	5.50	7.78	11.09	9.79	10.93	12.78	7.73	7.76	10.92	4.81	5.89	3.70				
4/6	6.38	16.32	9.08	9.32	17.41	12.89	6.62	8.16	33.11	5.96*	10.92	7.48	40.98	11.19	15.91	5.47	7.01			
4/7	11.22	17.40	10.62	15.58	22.25	19.49	10.75	11.11	32.58	7.77	15.39	9.28	37.84	17.23	21.05	12.50	13.11	5.86		
5/1	10.22	29.80	58.92	29.55	17.05	3.74*	33.59	44.31	24.23	46.87	45.31	20.80	21.14	10.26	17.42	16.54	18.68	49.81	40.00	
5/2	13.80	24.15	17.20	29.34	36.37	18.37	10.32	22.49	73.19	15.05	27.90	16.70	102.74	21.35	44.74	14.19	20.28	22.60*	20.87	90.14

* species linked in the final analysis

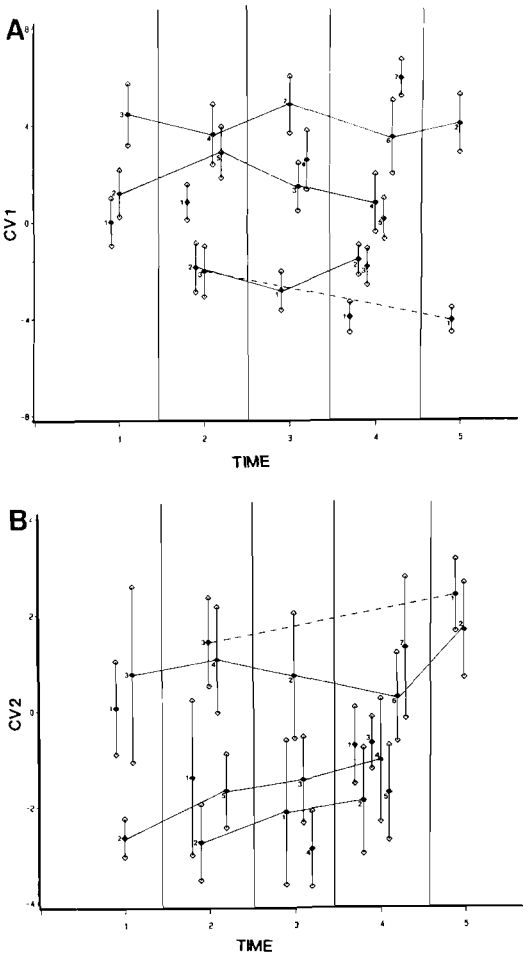

Figure 2. Variation through time in the first two canonical variables distinguishing the eleven linked species. The five time intervals are blocked off along the horizontal axis. Each bar shows the mean ± 1 s.d. for each species. Numbers for each bar refer to the species number within that interval (Fig. 1). Solid lines between bars indicate linkages. The dashed line indicates a possible linkages.

To test whether gradual directional change occurred within any of the longer ranging species lines, canonical discriminant analysis was performed between the eleven linked species. The scores for the first two canonical variables were then analyzed for non-random change through time (Fig. 2). Since these two variables represent the character complexes which best distinguish species, they would most likely change if new species were formed by phyletic evolution. Characters related to corallite size (e.g. CD, SLP) are again most heavily weighted on CV1 (Table 4). In contrast, characters related to the texture of the coenosteum (e.g. CNP) are most heavily weighted on CV2. Several unrelated

Table 4. Canonical discriminant analysis between lineages. Standardized discriminant function coefficients for the first three canonical variables.

	CV1	CV2	CV3
CD	.923*+	.823*	-.074
NS	.345+	-.495	.246
NND	-.416	.175	-.114
CND	.707*	.256	-.431
CNNV	-.254	-.376	.169
CNP	-.043	.928*+	.640
CLW	.094+	.158	.230
CLNV	.297+	-.071	-.258
TT	.418	-.559	-.461
SLP	-.540+	-1.011*	.903*
SLS	.339+	.472	-.543
SLT	.005	.200	-.456
STP	.032	-.155	-.203
STS	.167	.403	.444
STT	-.463	-.055	.066
CST	-.062	-.531	-.065
% variance explained	67.64	14.46	6.34

* most heavily weighted
\+ strongly correlated

characters are heavily weighted on CV3. To analyze for non-random change in these canonical variables, Mahalanobis' distances between pairs of nearby populations of the two living Caribbean species were compared with Mahalanobis' distances between late and early time intervals for each species using the methods of Stanley and Yang (1987). Despite minor change in CV2 in the lineage extending from species 1/2 to 4/4, the results indicate that temporal change is less than or equal to environmental variation in all four lineages. Therefore, stasis prevailed.

PHENOTYPIC PLASTICITY AND ITS EVOLUTION

Since the present objective is to evaluate the overall role of phenotypic plasticity in directing evolutionary patterns, the analyses have focussed on character complexes encompassing the widest range of variation within species. The complexes have been determined by principal component analyses of all corallites within each of the 21 unlinked species. Loadings on the first three principal components were similar in these species (Table 5).

The phenotypic plasticity of these three character complexes has been estimated using natural logarithms of variances for each colony (by "jackknifing variances" of Miller 1968). These values were compared between species using Duncan's multiple range test and pairwise t-tests. The results show that species differ significantly in magnitude of overall phenotypic plasticity. Five groups of ranges were distinguished using the first and second principal components, and three using the third. These differences suggest that selection may have acted on plasticity within the clade.

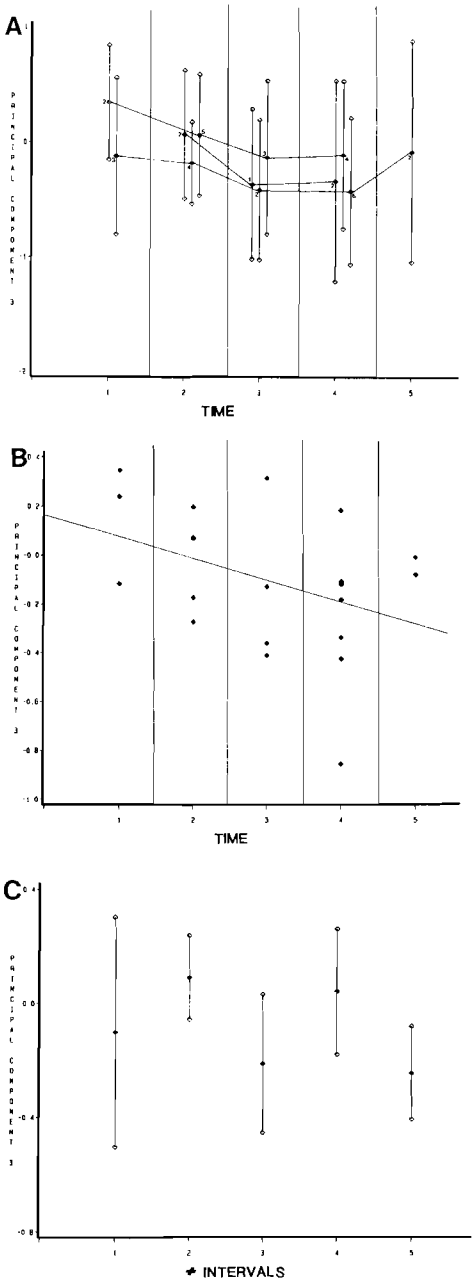

Figure 3. Trends in phenotypic plasticity through time. A, Trends of intracolony variation in the third principal component within lineages. Each bar shows the mean ± 1 s.d. for each species. B, Trends across species. The points represent species means. C, Relationship between plasticity and species duration. Each bar shows the mean (± 1 s.d.) of species surviving the corresponding number of intervals.

Table 5. Results of principal component analyses of corallites within species. Numbers of species in which each character was heavily weighted are listed for the first three principal components.

character	PC1	PC2	PC3
CD	18	1	-
NS	-	1	3
NND	4	5	5
CND	-	7	2
CNNV	1	4	4
CNP	-	5	3
CLW	4	1	-
CLNV	2	-	-
TT	-	4	3
SLP	3	-	-
SLS	1	1	-
SLT	1	2	2
STP	1	-	-
STS	1	4	1
STT	-	-	3
CST	1	1	3

Variation in these principal components has therefore been studied across the clade through time. With a few exceptions, values within species lines appear consistently high, medium, or low in magnitude. However, variation in the first component and, to a lesser extent, the second component is strongly correlated with size (Table 4). These two components therefore show few temporal trends. Variation in the third principal component is unrelated to size and reveals three trends across the clade (Fig. 3): (1) it decreased through time both within and between species, (2) species with short durations tended to have low and variable amounts of phenotypic plasticity, and (3) high phenotypic plasticity was not associated with ability to survive extinction episodes. The slight upturn in interval 5 (Fig. 3a, 3b) indicates that plasticity increased slightly after the extinction episode during the Plio/ Pleistocene. Phenotypic plasticity was lowest in interval 4 when speciation rates were highest. Fig. 3c shows that the relationship between phenotypic plasticity and species duration is not strong. When species with the shortest durations are compared against all others, phenotypic plasticity is lower in species with short durations ($t=-2.321$, d.f. 129.3, $p=0.022$).

DISCUSSION AND CONCLUSION

This reconstruction of evolutionary patterns in Caribbean Montastraea shows that the clade has three distinctive attributes: (1) low extinction rates, (2) low speciation rates, and (3) long species durations (maximum= 25 Ma). These attributes appear even more striking when compared to those of the genus Porites in the same region. In Porites, as many as 4-5 new species arose during the Plio/Pleistocene, and no central Caribbean species survived from the Pliocene to the Recent (Foster 1986).

The results of this study suggest that phenotypic plasticity played little role in increasing the durations of species of Montastraea or in making species within the clade less susceptible to extinction. The two lineages surviving the Plio/Pleistocene extinctions have only moderate plasticities. Other life history traits (e.g. recruitment rates) must have been responsible for differential extinction within the clade. This conclusion does not rule out the possibility that large-scale differences in plasticity between clades such as Montastraea or Porites could not be responsible for their differences in extinction patterns. Phenotypic plasticity may be so high in general in Montastraea that differences between species had little effect on relative susceptibility to extinction. However, these results do suggest that low phenotypic plasticity is associated with high speciation rates (e.g. in interval 4). This relationship appears even stronger in preliminary reconstructions of the Montastraea clade in the Mediterranean Miocene (Foster and Stemann 1987). Here, one new genus (Tarbellastraea) arose as endemism increased and phenotypic plasticity decreased.

The most pervasive trend found, however, is that of decreased phenotypic plasticity through time. The slight upturn in phenotypic plasticity in the two lineages extending into the Recent may have been caused by disruption of the genetic system during the extinction episode. To understand the trend of overall decrease in plasticity, phenotypic plasticity must be described further by analyzing the components of the character complexes and how they differ between populations and species. Questions which need to be addressed experimentally include: Is the variation in these complexes related to developmental pathways? Are the complexes adaptive or do they just result from changes in growth rate?

In summary, this study has shown:
(1) Caribbean Montastraea tends to have low speciation and extinction rates and long species durations. Little tendency exists for adaptive radiation.
(2) Species within the clade differ in amounts of plasticity suggesting that plasticity may have been acted on by selection.
(3) Stasis prevails within lineages thoughout the evolution of the clade. Therefore, little relationship appears to exist between plasticity and the rate of character evolution.
(4) Differences in extinction within the clade do not appear related to amounts of phenotypic plasticity, although species with very short durations tend to have low plasticities.
(5) High speciation rates within the clade could be associated with low plasticities.
(6) Plasticity decreases within the clade, in a trend unrelated to speciation or extinction.

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