

Repeated loss of coloniality and symbiosis in scleractinian corals

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The combination of coloniality and symbiosis in Scleractinia is thought to confer competitive advantage over other benthic invertebrates, and it is likely the key factor for the dominance of corals in tropical reefs. However, the extant Scleractinia are evenly split between zooxanthellate and azooxanthellate species. Most azooxanthellate species are solitary and nearly absent from reefs, but have much wider geographic and bathymetric distributions than reef corals. Molecular phylogenetic analyses have repeatedly recovered clades formed by colonial/zooxanthellate and solitary/azooxanthellate taxa, suggesting that coloniality and symbiosis were repeatedly acquired and/or lost throughout the history of the Scleractinia. Using Bayesian ancestral state reconstruction, we found that symbiosis was lost at least three times and coloniality lost at least six times, and at least two instances in which both characters were lost. All of the azooxanthellate lineages originated from ancestors that were reconstructed as symbiotic, corroborating the onshore–offshore diversification trend recorded in marine taxa. Symbiotic sister taxa of two of these descendant lineages are extant in Caribbean reefs but disappeared from the Mediterranean before the end of the Miocene, whereas extant azooxanthellate lineages have trans-Atlantic distributions. Thus, the phyletic link between reef and nonreef communities may have played an important role in the dynamics of extinction and recovery that marks the evolutionary history of scleractinians, and some reef lineages may have escaped local extinction by diversifying into offshore environments. However, this macroevolutionary mechanism offers no hope of mitigating the effects of climate change on coral reefs in the next century.

coral reefs | Bayes Traits | zooxanthellae | ancestral state reconstruction | phylogeny

In most marine organisms, coloniality is thought to have evolved from solitary ancestors and proceeded through progressive weakening of zooidal individuality in favor of increased individualization of the colony (1). In Scleractinia, colonial species are thought to have originated from solitary ancestors, most likely via incomplete asexual budding (2). This notion is almost intuitive, since all sexually produced coral colonies start as a larva that metamorphoses into a single polyp. Colonial integration supposedly increased in evolutionary time through dissolution of skeletal barriers among polyps (2–4). This range of morphological variability is in full display in extant Scleractinia, from the exclusively solitary species within the genus *Anthemiphyllia*, to the “quasicolonial” *Anomocora carinata*, in which “the daughter corallites [break] free of the parent before a third generation bud appears” (5), to the loosely integrated colonies of *Rhizosmilia maculata* in which partial colonial mortality may yield solitary daughter polyps and finally the highly integrated colonies of *Favia fava*, in which polyp damage invariably results in a colony-wide regenerative response (6). Although most, but not all (7), authors have been careful not to present this cline as a linear evolutionary trajectory, directionality is implicit in graphical evolutionary schemes, which invariably show transitions from solitary to colonial growth forms, but rarely the reverse (3). Rosen (2) observed that such schemes are certainly didactic, but not necessarily phyletic. McShea and Venit (8) argued that there is no reason to assume that the adap-

tive pathway toward higher levels of coloniality is less complex than the opposite direction, particularly if polymorphic zooids are not present, which is the case in scleractinian corals. Indeed, Coates and Jackson (9) concluded that long-term trends in the evolution of coloniality in corals were frequently “interrupted or reversed by changes in the growth and development of reefs.”

The work by Coates and Jackson suggests that evolution of coloniality in corals is intimately linked to the geological history of reefs themselves, as coloniality is thought to be adaptive in communities strongly structured by competition for space (10). Bare, hard substratum is a limiting resource in coral reefs, and colonial animals should have a competitive edge because they occupy space through somatic growth whereas occupation by solitary organisms involves sexual recruitment (10). Even if initial recruitment is high, young solitary organisms could be easily overgrown by colonies. The trend of predominance of colonial taxa in times of reef construction over a colonial (solitary) taxa has been observed not only in the Scleractinia but also in the extinct orders Tabulata and Rugosa (9). The level of colonial integration in corals is also correlated with the presence of zooxanthellae. Highly integrated colonial corals that dominate modern reefs are always symbiotic, whereas a disproportionate majority of solitary species are azooxanthellate and found in deep (>200 m) waters (4). Mutualism with *Symbiodinium* boosts calcification rates and provides corals with orders of magnitude more energy than available to co-occurring heterotrophic organisms (11). Thus, the combination of coloniality and symbiosis is believed to be crucial to the competitive dominance of Scleractinia in modern reefs, and the predominance of zooxanthellate colonial taxa on carbonate platforms seems to date back to the very origins of the order (12–14).

Despite the seeming advantages of coloniality and symbiosis, half of the extant corals are azooxanthellate and mostly solitary (5). These species are mostly absent from modern tropical reefs, but some achieve cosmopolitan distributions and exist at depths from 0 to more than 6,000 m (15), whereas their symbiotic relatives are restricted to the photic zone. The phylogenetic relationships among these corals and their reef counterparts were poorly understood until the advent of molecular phylogenetics, and subsequent phylogenies have recovered clades composed of closely related solitary/azooxanthellate and colonial/zooxanthellate taxa (16, 17). This suggests that coloniality and symbiosis in corals either evolved multiple times or that they were lost more than once. We used a robust molecular phylogeny including solitary and colonial taxa as well as state-of-the-art ancestral character reconstruction

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techniques (*i*) to distinguish between these scenarios, (*ii*) to address the existence of directional trends in the evolution of coloniality and symbiosis, and (*iii*) to test the existence of correlated evolution between these two characters.

Results

DNA sequence data were generated for 80 species belonging to 18 families (of 24 in the order), including all extant scleractinian suborders (18). Scleractinians are monophyletic according to the consensus topology computed from the posterior distribution of trees, and the order comprises two main clades, in concordance with previous molecular analyses (16, 17, 19) (Fig. 1).

The combination of the six independent reversible-jump Markov chain Monte Carlo (RJ-MCMC) analyses used for rate estimation yielded 5,400 samples from the posterior distribution after burn-in [although, due to the presence of temporal autocorrelation, the effective sample size (ESS) was smaller: ESS = 5,170 for coloniality and ESS = 5,219 for symbiosis]. Results show strong Bayesian belief that rates of colonial-to-solitary and asymbiotic-to-symbiotic transitions are equal to rates of the reverse state changes. The chains spent $\approx 99\%$ of the time on the single-rate model in both cases [$n = 5,340$ for coloniality, Bayes factor (BF) = 89.0; and $n = 5,371$ for symbiosis, BF = 185.2]. This result rejects the traditional scenario of directional evolution of colonial taxa

from solitary ancestors, supporting the contention that although trends may exist in some lineages, they do not characterize the entire evolutionary history of the group (8).

Despite the lability of both characters in evolutionary time, RJ-MCMC analyses strongly rejected the independent model of evolution. The distribution of BFs favoring the dependent model was mostly contained in the range of 20–30 (Fig. 2A). Of 21,001 non-trivial dependent models (details on the calculation of the prior distribution of models in *SI Appendix, SI Text*), 253 were sampled

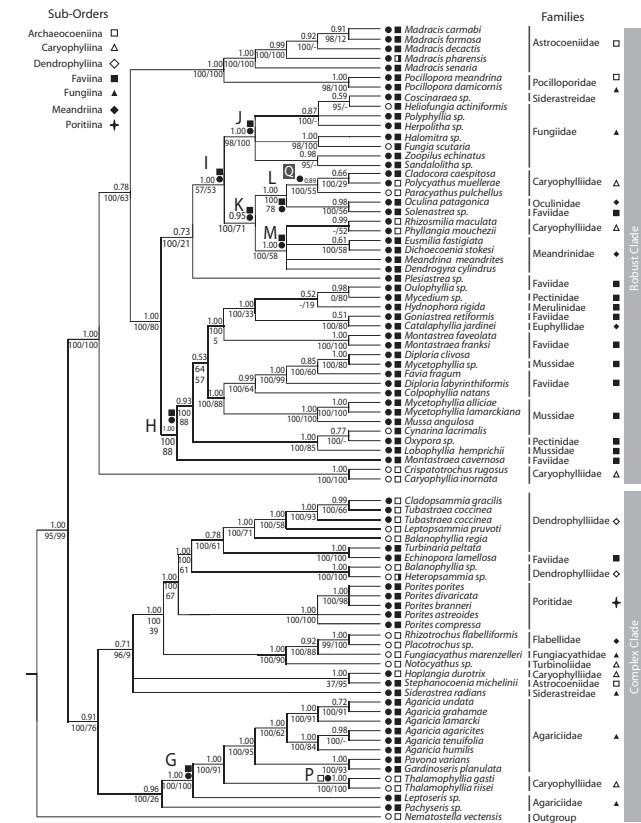


Fig. 1. Fifty-percent majority rule consensus tree computed from the thinned posterior distribution of trees ($n = 312$) obtained via MCMC. Column of symbols to the right of the list of families represent suborders (legend on graph). Numbers above nodes correspond to the Bayesian posterior probabilities and numbers below the nodes to bootstrap support obtained under maximum-likelihood and maximum-parsimony criteria, respectively. Filled circles (●) denote colonial taxa; open circles (○) denote solitary taxa. Filled squares (■) denote symbiotic taxa; open squares (□) denote asymbiotic taxa. Circles and squares above nodes indicate reconstructions supported by BFs. Node Q was reconstructed as an MRCA (*Methods*).

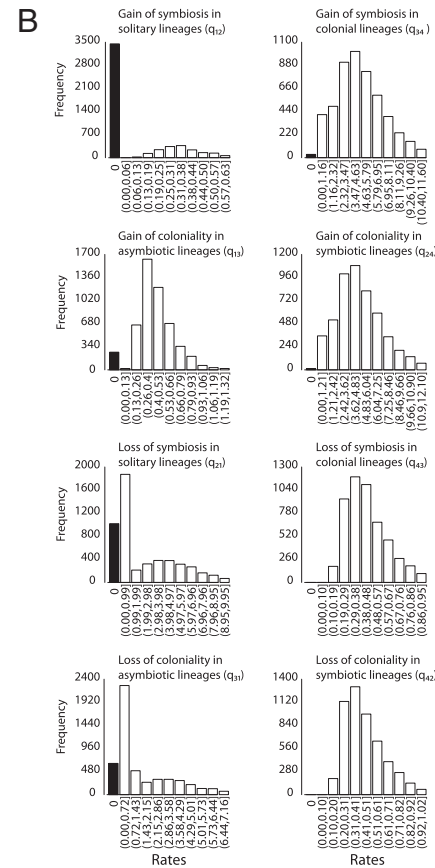
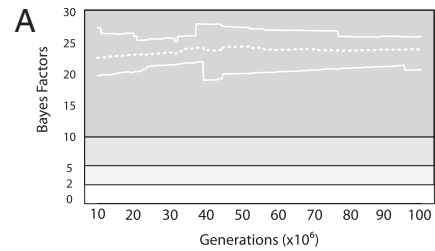


Fig. 2. (A) Plot of BFs against the number of generations. BFs were computed using the harmonic means of log-likelihood scores calculated under the dependent (correlated) and independent models of evolution. RJ-MCMC runs were replicated five times under each model and BFs were calculated for all 25 pairwise combinations. Dotted line represents median and solid lines represent maximum and minimum BF values at each sampled generation from the chain. Critical regions are denoted by progressively darker shades of gray on the background; region of nonsignificance is white. (B) Histograms of rate parameters sampled under the dependent model of evolution. Paired histograms correspond to rate distributions that are expected to be the same if characters evolved independently of each other. Dark bars indicate the number of times the rate was assigned to the zero-category. Labeling of x axis follows the conventional mathematical notation for intervals, i.e., (0.00, 0.13] is equivalent to $0.00 < x \leq 0.13$.

by the chain and 66 made up the 95% set of credible models. There is no positive evidence in favor of the preferred model when compared with the second most frequently sampled model (BF = 1.55). However, the distribution of paired rates expected to be equal under the independent model show noticeable differences between the pairs (q_{12} , q_{34}), (q_{21} , q_{43}), and (q_{31} , q_{42}), thus explaining the strong Bayesian belief in correlated evolution between coloniality and symbiosis. The main differences are due to the proportion of times that the RJ-MCMC chains set the rates q_{12} , q_{21} , and q_{31} to zero ($\approx 66\%$, 21% and 14% , respectively; Fig. 2B). The prior expectation is $\approx 20\%$, as there are 4,065 nontrivial dependent models with one rate set to zero (SI Appendix, SI Text). Therefore, models with rate q_{12} (gain of symbiosis by solitary corals; rates described in Fig. 2) set to zero were sampled thrice as frequently as expected under the prior. Evidence in favor of these models is positive for q_{12} (BF = 7.73) but not for the other rates (BF = 0.33 and BF = 0.21, respectively).

Overall, the differences between probability distributions for both states become more accentuated in nodes closer to the tips of the trees (Fig. 1). Posterior probability distributions of ancestral states for the nodes with significant Bayes factors are shown in SI Appendix, Fig. S1. Ancestors *G*, *H*, *J*, *K*, *I*, *L*, and *M* were reconstructed as colonial and zooxanthellate (Fig. 1). We reconstructed the states at the hypothetical ancestor *P* to ascertain whether transitions occurred before or after the split between the two daughter lineages. Coloniality was lost at least twice in lineages leading to *Thalamophyllia* spp., but symbiosis was lost before the species split. Coloniality and symbiosis were lost at least one other time in the lineage leading to *Paracyathus pulchellus*. We also attempted to reconstruct the states at the most recent common ancestor (MRCA) of the clade formed by *Cladocora caespitosa*, *Polycyathus muelleriae*, and *P. pulchellus*. Because the ancestor's Bayesian posterior probability (BPP) does not exceed 0.95, we used the MRCA approach described by Pagel et al. (20). Bayes Traits calculates the posterior probabilities of states in all nodes across the posterior distributions of trees that are hypothetical ancestors to the taxa of interest. This "floating" ancestor was reconstructed as colonial, but symbiosis state was not reconstructed with confidence; hence, coloniality was lost at least once after *P. pulchellus* split from ancestor *J* (Fig. 1). Coloniality was lost three additional times, in lineages leading to the zooxanthellate species *Cynarina lacrimalis*, *Heliofungia actiniformis*, and *Fungia scutaria*. Symbiosis was lost at least one other time in the ancestral lineage leading to *Rhizosmilia maculata* and *Phyllangia mouchezii* (Fig. 1). Reconstructions at other nodes of interest closer to the crown groups were inconclusive and thus were not reported.

Discussion

We have provided robust phylogenetic evidence that deep water coral species arose from shallow water lineages. This is concordant with the long-standing hypothesis of diversification of marine taxa in shallow waters followed by colonization of off-shore habitats (21, 22), and with more recent analyses that suggest that reefs have historically been sources of biodiversity in the Phanerozoic, particularly in the case of corals (23). Our findings, in concert with recent phylogenetic hypotheses for the Scleractinia, change our understanding of evolution in the taxon.

Loss of Symbiosis, Diversification, and Extinction. Endosymbiosis between reef corals and zooxanthellae has long been considered critical to the ecological success of the Scleractinia. The symbiosis provides energy to the host, facilitates the recycling of nitrogen compounds that would otherwise be excreted (11), and boosts calcification rates over those of azooxanthellate species by an order of magnitude (12). However, symbiosis also limits the distribution of corals to the photic zone, whereas asymbiotic corals survive today in a variety of habitats (including aphotic depths), and some species reach cosmopolitan distributions (18). Habitat

breadth (24) and species range (25–27) appear to be more critical than abundance in determining extinction risk. Indeed, the pattern of extinction across the Cretaceous–Paleogene boundary indicates that zooxanthellate corals were affected disproportionately in comparison with their asymbiotic counterparts (28, 29).

Resilience of azooxanthellate taxa is corroborated in our analysis. The monophyletic clade that descends from ancestor *G* (Fig. 1) includes the solitary azooxanthellate species *Thalamophyllia gasti* and *Thalamophyllia riisei* and all of the sampled reef-dwelling, colonial, and zooxanthellate agariciids. *T. riisei* is extant in the western Atlantic, and *T. gasti* is found in the eastern Atlantic including southern Europe (18), where shallow-water reefs do not occur. In contrast, two of the reef genera in the clade, *Agaricia* and *Leptoseria*, were found both in the western Atlantic and in the Tethys Sea (the precursor of the Mediterranean) during the Miocene (30). This dichotomy is repeated in the clade that descends from ancestor *M* (Fig. 1), which contains all of the meandrinids sampled in this study plus the azooxanthellate *Rhizosmilia maculata* and *Phyllangia mouchezii* (Fig. 1). The reef-dwelling genera *Meandrina* and *Dendrogyra* were found in the Tethys Sea during the Oligocene and Miocene, respectively, and *Dichocoenia* was found on both sides of the Atlantic during the latter period (30). Whereas *R. maculata* persists in the western Atlantic and *P. mouchezii* in the eastern Atlantic and Mediterranean (18), the reef-dwelling members of the clade now occur exclusively in the western Atlantic. Virtually all of the marine life in the Tethys sea, including the aforementioned reef genera, were extinct by the time of the Messinian salinity crisis (the last stage of the Miocene, ~ 5.3 Mya), when the Tethys Sea closed. After half a million years of isolation and desiccation, the Mediterranean was flooded by the Atlantic with the opening of the Gibraltar Strait (31). By then, the circulation pattern in the North Atlantic had changed, and the eastern Atlantic was too cold to support vigorous reef accretion (30). Ancestors of *Thalamophyllia* spp. (*G*) and of the *R. maculata*–*P. mouchezii* clade (*M*) were reconstructed as zooxanthellate and colonial. Hence, they were likely shallow-water and possibly reef-dwelling species. These results suggest that some reef clades survived local extinction after tropical reefs disappeared from the eastern Atlantic through diversification into habitats that were out of bounds for their ancestors.

Correlation between the permanence of reefs and survival of Scleractinia has been debated in the literature. High-resolution studies suggest that species selection during times of extinction resulted from the interplay between changes in the physical environment and life history of coral species (32–34), whereas broader compilations suggest that diversity was similarly affected across a range of reef taxa (35) and that, in several of these episodes, extinction was a consequence of reef-building collapse (36). Biogenic reef formation is mainly a function of physical processes that affect calcareous carbonate chemistry, such as global changes in temperature, concentration of atmospheric CO₂, acid rain, and eutrophication (30, 36). Modern zooxanthellate species are restricted to depths between 0 and 70 m (15), and we have no reason to assume that this range was significantly different in the past. Hence, as reef accretion diminishes and reefs subside or erode away, reefal populations become fragmented and connectivity decreases, increasing the probability of local extinction (37). In contrast, the wide bathymetric distribution of azooxanthellate species allowed them to survive in a variety of nonreef habitats. For instance, *T. riisei* and *R. maculata* are known from depths that range from 4 to 914 m and from 0.5 to 508 m, respectively (38). Thus, diversification into nonreef habitats through repeated loss of symbiosis (and sometimes coloniality) led to expansion of habitat breadth and geographical range, which may have helped some reef clades survive the episodes of extinction that punctuate the history of Scleractinia. Further investigation with broader taxonomic, spatial, and temporal sampling is needed to confirm the generality of this mechanism. Ancestral state reconstruction requires independently derived phylogenies, and molecular data

must be collected from organic tissue. However, many extant species have a rich Cenozoic record. Hence, we believe that, in combination with fossil compilations, our approach can be very useful in clarifying the evolutionary dynamics of corals during that period.

Loss of Coloniality. Heterochrony, which is a major cause of phenotypic evolution (39), provides a simple mechanism to explain the repeated loss of coloniality among the Scleractinia (40). Reversal from colonial to a solitary growth form may have occurred on a simple developmental basis through earlier sexual maturation of the juvenile solitary polyp (ontogenetic progenesis) and suppression of asexual multiplication of astogenetic units (astogenetic neoteny or postdisplacement) (40) or via the detachment of asexually produced polyps (i.e., clonoteny) (2). Although some solitary corals do not reproduce asexually, many retain the capacity for asexual reproduction through budding. These correspond, respectively, to the solitary asexual and clonal categories of Jackson (10). It is possible to distinguish between these scenarios by measuring the age at sexual maturity and rates of astogenetic development (including detachment from the parental polyp) in extant sister species. The magnitude and direction of change could then be compared with the states observed in the MRCA, estimated using ancestral state reconstruction of continuous characters. Because of the relatively slow developmental rates of many colonial corals, this will probably be more easily accomplished by examining developmental sequences.

Correlated Evolution of Symbiosis and Coloniality. The strong rejection of independent evolution of symbiosis and coloniality is due to the positive Bayesian evidence that acquisition of symbiosis in solitary lineages occurs less frequently than expected under the null (prior) distribution (Fig. 2). This suggests that solitary zooxanthellate species descend from zooxanthellate colonial ancestors, as evidenced by Bayesian ancestral state reconstruction. The ancestral state at the root was not reconstructed with confidence, and the posterior probability is evenly split among all possible combinations of states. If one assumes that the scleractinian ancestor was solitary and asymbiotic, results of the Bayesian analysis suggest a two-step model in which coloniality is acquired first and symbiosis is subsequently established. However, the first fossil scleractinian representatives of the Mid-Triassic show surprisingly high levels of colonial integration and are morphologically diverse at time of first appearance (41). In addition, isotopic analysis of scleractinian skeletons found in carbonate platforms of the Upper Triassic of Europe provide evidence that symbiosis was established very early in the evolution of the order (12, 14).

In contrast with acquisition, there were no significant differences between the rates of symbiosis loss between solitary and colonial lineages (*Results* and Fig. 2). Breakdown of the symbiosis with zooxanthellae should have been a relatively simple adaptive step for corals. The symbiosis is facultative in a small number of species (15), and one colonial reef species (*Montipora capitata*) is known to compensate for the loss of its zooxanthellae by increasing rates of heterotrophic feeding to meet its energetic requirements (42). However, loss of coloniality does not necessarily imply loss of symbiosis, and three out of the five instances of coloniality loss actually resulted in solitary symbiotic corals (*Heliofungia actiniformis*, *Fungia scutaria*, and *Cynarina lacrimalis*). The overwhelming majority of the models sampled from the posterior distribution (96.3%, $n = 5,202$) placed the rates q_{34} and q_{43} in the same category. These models make up only 4.08% of the prior distribution (*SI Appendix, SI Text*); thus, there is strong Bayesian belief (BF = 643.18) that coloniality loss in zooxanthellate lineages is as likely as symbiosis loss in colonial lineages (Fig. 2). Under this framework, the data indicate that transitions from colonial/zooxanthellate ancestor to solitary/azooxanthellate descendants may start either with loss of coloniality or loss of symbiosis. These results also imply that zooxanthellate corals could diversify into

aphotic habitats simply by loss of symbiosis while remaining colonial. We detected two such instances in our analysis.

Taxonomic Implications. Results of ancestral state reconstructions corroborate the long-standing hypothesis of diversification of marine taxa in shallow waters followed by colonization of offshore habitats (21, 22), and conform to paleontological observations that place the origination of Scleractinians in onshore environments (43, 44). Close phylogenetic proximity between shallow- and deep-water clades in marine organisms has been recognized for more than a century (45); however, in Scleractinia, recognition of such proximity has been obscured by traditional taxonomy. Classification of the order has been based almost entirely on skeletal characters, which are preserved in the fossil record and hence allow inference of evolutionary relationships among extinct and extant species. These characters are notorious for plasticity which occurs within single colonies, between species, at a number of taxonomic levels and across ecological and evolutionary time scales, all of which make character homologies difficult to assess (30). These issues have made the inference of higher and lower level phylogenetic relationships particularly challenging, resulting in classifications that are now recognized to contain polyphyletic taxa such as the family Caryophylliidae (16, 17). Most extant azooxanthellate species are concentrated in this family, which makes up the bulk of the suborder Caryophylliina (18). Three of the six species in which coloniality was lost are caryophylliids (Fig. 1). Our analysis points toward the high lability of coloniality during scleractinian evolution, and suggests that many more solitary/colonial clades are likely to be found with more extensive taxonomic sampling of nonreef species. This finding also has implications for current efforts to reinterpret homology of skeletal characters based on morphological characters. Given that several colonial and solitary species are closely related, characters specific to colonial growth forms (such as corallite arrangement or degree of septal confluence) cannot be informative in higher level analysis. The lack of phylogenetic information of such characters has already been reported for a clade of zooxanthellate species (46), and a similar result has been reported for features of the corallite (the skeletal counterpart of the polyp) that show considerable intraspecific phenotypic plasticity in extant species (47). We expect that transition between onshore to offshore habitats would expose lineages to greater environmental variation that could be translated into even larger skeletal plasticity, further masking the phylogenetic content of such characters. Microstructural features (the arrangement of calcification centers and fibers) (46) hold promise as phylogenetically informative characters that could be used for reverse taxonomy and phylogenetic reconstructions at higher levels. It will be interesting to see how these characters fare in recovering the relationships between deep and shallow water sister species.

The loss of reef habitat and breakdown of the scleractinian–*Symbiodinium* symbiosis has been the subject of intense discussion in the scientific literature as concerns about current global climate change have grown (48). The comprehensive phylogenetic history of the Scleractinia reported here suggests how modern corals may fare under scenarios of climate change that may result in habitat loss. It is likely that azooxanthellate lineages can survive modern reef collapse. However, half of the species richness of extant Scleractinians is made up by symbiotic corals most of which are found in megadiverse tropical reef ecosystems. Thus, modern reef demise is an ecological catastrophe with no precedent in the history of mankind. Diversification into nonreef habitats evidenced in our analysis occurred over geological time scales. This cannot be construed as acceptable “remediation” for the potential loss of colonial scleractinian reef lineages over the next century. Furthermore, a recent study suggests that reefs have historically been cradles of diversification throughout the Phanerozoic (23). Hence, the potential disappearance of tropical reefs in the next century

could have evolutionary consequences for Scleractinia and other taxa that may span eons to come.

Methods

Taxon Sampling. We maximized taxonomic and morphological coverage by incorporating data from 90 individuals belonging to 80 species, 18 families, and all extant Scleractinian suborders recognized by Veron (49). Six individuals belonging to four species within four genera and three of four extant corallimorpharian families were included in the analyses, as was the sea anemone *Nematostella* sp. The final dataset included 96 individuals, 85 species, and 64 genera.

Character Coding. Morphological information was obtained from Vaughan and Wells (50) and Veron (49). All species were scored as either solitary or colonial. Species that were considered solitary in this study may give rise to other coralla via asexual reproduction, but the newly formed bud invariably detaches from the parental corallum in time. Species in which assemblages of asexually formed coralla remain connected by the skeleton were scored as colonial, even if the intervening tissue among corallites is destroyed (e.g., by predators or encrusting organisms). In the first case, the separation among polyps is programmed in the reproductive physiology of the species, whereas in the second case, the formation of solitary polyps results from the action of factors extrinsic to the organism.

Taxa were scored as azooxanthellate or zooxanthellate according to Cairns (18). Aposymbiotic taxa (i.e., taxa that may or may not exhibit symbiosis) were scored as polymorphic.

Phylogenetic Analyses. Phylogenetic reconstructions were carried out using partial sequences of the mitochondrial 12S (small-subunit) and nuclear 28S (large-subunit) ribosomal RNA genes. Secondary structures were generated for both genes. The secondary structure template used for the 28S alignment was obtained from a comprehensive sampling across eukaryotes (51). For the 12S sequences, we used the secondary structure model proposed by Pont-Kingdon et al. (52) for *Metridium senile*. Structural features of the third domain were further refined according to Hickson (53). Only structurally conserved regions were kept in the final concatenated alignment (1,428 bp). The posterior distribution of trees was obtained using the MPI version of MrBayes 3.1 (54) by combining trees yielded by four independent runs. We used the GTR +I +Γ model with the gamma distribution being approximated by four discrete categories. Base covariation in stems was taken into account by enforcing the doublet model. Parameters were unlinked across different genes (in the total evidence analysis) and across loop and stem partitions within each locus. Runs were interrupted after the average SD of split frequencies dropped to less than 0.01. Convergence of parameters was verified using Tracer v1.4 (55). We also verified convergence of topological parameters using AWTY (56). Data were partitioned by locus in maximum-likelihood (ML) analysis using RAxML-III (57) under the GTRMIX model. ML topology was inferred from 200 independent runs, and node support was assessed with 1,000 bootstrap replicates. Maximum parsimony topological support was assessed using 1,000 nonparametric bootstrap replicates conducted in TNT (58).

Ancestral State Reconstruction. The program BayesTraits (59) was used for ML and Bayesian estimation of the rate parameters. It requires a posterior distribution of topologies obtained via Bayesian analysis and a matrix with character states, coded for the terminal taxa. The program has two models: "multistates," used to estimate instantaneous rates of transition among states of a character, and "discrete," used to test for correlated character evolution. In addition, two types of analyses are available: ML and MCMC. In ML mode, the program will estimate the rate (Q) matrix that maximizes the likelihood function for every tree in the posterior. In MCMC mode, the reconstruction is done in a Bayesian framework also using the topologies randomly sampled from the posterior distribution (for more details, see *SI Appendix, SI Text*).

BayesTraits requires rooted phylogenies with a positive value for the branch length leading to the outgroup. Corallimorpharians were placed outside of the Scleractinia according to the consensus topology computed with MrBayes, and their relationship to corals and anemones were unresolved. Therefore, corallimorpharians were pruned from trees in the posterior using PAUP* 4.05b

for UNIX (60) and *Nematostella* sp. was used as the outgroup. Trees were also pruned down to one individual per species, unless those individuals were not grouped in the same clade according to the 50% majority rule consensus tree. After pruning, trees retained 81 individuals, 80 species, and 59 genera. The posterior distribution of trees obtained from MrBayes was subsampled to ensure independence among trees (details on subsampling procedure in *SI Appendix, SI Text*).

BayesTraits was first used to obtain ML solutions for all trees in the posterior distribution using 25 iterations. One chain per dataset was then run for 100,000 generations in RJ-MCMC mode. It was sampled every 1,000 generations, and the resulting log-likelihood values were compared with those obtained under the ML criterion. The approach suggested by Pagel and Meade (59) was used i.e., seeding the mean of a prior exponential distribution of rate coefficients with values drawn from a uniform (hyperprior) distribution. A variety of intervals for the hyperprior distribution were tested in combination with different rate deviation ("ratedev") values until acceptance rates were within the target range (0.20–0.40) (59). Final values of ratedev were 2.00 for coloniality, 0.50 for symbiosis, 0.75 for the dependent model, and 0.10 for the independent model of evolution. Once these parameters were set, six independent chains were run for 100,000,000 generations each, sampling every 100,000 generations after a burn-in of 10,000,000 generations. The posterior distributions of likelihood scores and rate parameters were estimated separately for each character and also under the independent and dependent models of correlated evolution. Visual inspection of log-likelihood values graphed against number of generations confirmed convergence of all chains in every analysis and adequacy of the chosen burn-in value. We ran five chains under the independent and dependent models of evolution, and BFs were computed for every pairwise combination, resulting in 25 comparisons for every sampled generation (59) (hypothesis testing using BFs detailed in *SI Text*). As harmonic means are in log scale, BF values between 2 and 5 indicate positive support for the dependent over the independent model, values greater than 5 indicate strong evidence, and values >10 provide very strong evidence in favor of correlated evolution (61). Plots of running BF values of all comparisons against number of generations (*SI Appendix, Fig S2*) were used to assess convergence to stable values within these critical ranges (59).

We estimated the posterior probabilities of either ancestral state for all hypothetical ancestors of at least five terminal taxa with BPP supports of 0.95 or greater and with descendant terminal taxa exhibiting more than one character state. Because the BPP of the node caps the BPP of the state reconstruction, the probability of a type I error would always exceed 0.05 if the node BPP support was smaller than 0.95. Posterior probabilities of ancestral states for both characters were determined by using the "Addnode" option in BayesTraits, using the same settings applied to the estimation of the rate parameters and likelihoods. We replicated the estimation five times for each node, and the posterior probabilities distributions were obtained from the combination of all replicates. The significance of these probabilities for each character was assessed via BFs obtained from five RJ-MCMC chains with nodes fossilized in either state adding up to 10 separate chains of 1 billion generations (sampling every 1,000,000 generations after a 10,000,000-generation burnin) for each of the 13 selected nodes. BFs were calculated using harmonic means of log-likelihoods (59)

$$BF_{10} = 2(H_1 - H_0)$$

where the subscript number denotes the state for each character (i.e., 0 for solitary or asymbiotic and 1 for colonial or symbiotic).

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