records attest to a similar number of large and abrupt climate oscillations during the last glacial termination. We argue that, in general, Atlantic cold events (for example, the Younger Dryas occurred during dry intervals in western North America (for example, D_3); also, warm events in the Atlantic region (for example the Bølling) occurred during wet intervals in western North America (for example, W_{2a}). The last wet phase (W_4) occurred during the last Greenland warm peak.

With the advent of the Holocene, linkage of the climate regimes of the North Atlantic and western North America weakened and perhaps disappeared. Before the Holocene, relatively dry conditions occurred in western North America when the North Atlantic region was relatively cold. During the Early and Middle Holocene this relationship was reversed; that is, western North America was relatively dry and the North Atlantic region was relatively warm.

The duration, timing and similar number of climate oscillations in western North America and the North Atlantic region, indicated by this and other studies[20], suggests a climate-change link during the last glacial termination throughout at least part of the Northern Hemisphere. Errors inherent in our age model do not allow us to completely rule out an oceanic linkage; however, recent climate simulations more strongly support the concept of atmospheric forcing[11,12]. In agreement with these studies, we suggest that oscillations in wetness and temperature in western North America were linked to oscillations in the strength and pattern of the North Atlantic thermohaline circulation through its effect on sea surface temperature and atmospheric water content. Rapid climate oscillations in the North Atlantic regions have been attributed to sudden changes in the rate and location of thermohaline overturn[30–33]. We propose that cooling of the North Atlantic, resulting from a decrease in thermohaline circulation, caused a downstream cooling of the North Pacific[11], which in turn decreased the temperature and moisture content of air passing over the middle latitudes of western North America[12]. □

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Landscape ecology of algal symbionts creates variation in episodes of coral bleaching

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Reef-building corals are obligate, mutualistic symbioses of heterotrophic animals and phototrophic dinoflagellates (*Symbiodinium* spp.)[1]. Contrary to the earlier, widely accepted belief that corals harbour only one symbiont, we found that the ecologically dominant Caribbean corals *Montastraea annularis* and *M. faveolata* can act as hosts to dynamic, multi-species communities of *Symbiodinium*. Composition of these communities follows gradients of environmental irradiance, implying that physiological acclimatization[2–4] is not the only mechanism by which corals cope with environmental heterogeneity. The importance of this diversity was underlined by analysis of a natural episode of coral bleaching. Patterns of bleaching could be explained by the preferential elimination of a symbiont associated with low irradiance from the brightest parts of its distribution. Comparative analyses of symbionts before and after bleaching from the same corals supported this interpretation, and suggested that some corals were protected from bleaching by hosting an additional symbiont that is more tolerant of high irradiance and temperature. This 'natural experiment' suggests that temporal and spatial variability can favour the coexistence of diverse symbionts within a host, despite the potential for destabilizing competition among them[5,6].

The corals *Montastraea annularis* and *M. faveolata* each host three distantly related taxa[7] of the dinoflagellate genus *Symbiodinium*, denoted *A*, *B* and *C*, that are identified by restriction-fragment length polymorphisms (RFLPs) in genes encoding small ribosomal RNA (srRNA)[7]. *A* and *B* are common in shallow-water corals (high-irradiance habitats), whereas *C* predominates in deeper corals (low-irradiance habitats). Mixed samples $A + C$ and $B + C$, common at

intermediate locations[7], suggest that symbionts may actually exist as complex communities that track differences in irradiance within a colony[2].

To test this hypothesis we sampled four locations in each of 46 colonies (Fig. 1). All *M. faveolata*, and all but one colony of *M. annularis*, yielded two or three types of symbionts. As predicted, *Symbiodinium A* and *B* dominated locations with higher, downwelling irradiance (communities 1 and 2, unshaded colony tops), and *C* dominated locations of lower irradiance (communities 3 and 4, colony sides and shaded colony tops) ($P < 0.001$; χ^2 test). These patterns of intra-colony zonation largely disappear at slightly greater depths (8–11 m in *M. annularis*, and 6–12 m in *M. faveolata*), where *Symbiodinium C* is predominant overall[7]. As before[7], *Symbiodinium A* was more common in *M. faveolata* than in *M. annularis*.

Analyses at a finer scale (~1 cm) confirmed that symbionts occupy distinct but overlapping habitats (Fig. 2). Unshaded columns of *M. annularis* create a localized gradient of low (on the side, no downwelling) to high (on the top, full downwelling) irradiance, which we sampled along transects. At intermediate depths (3–7 m) this gradient coincides with the transition from *Symbiodinium C* to *B*, *B* + *C*, or *A* (Fig. 2a–d). Analyses of shallower (1–2 m) and deeper (9–12 m) corals (Fig. 2d) show that depth[7] and intracolony zonation of the symbionts occur in parallel. These consistent patterns strongly argue that zonation is controlled by ambient irradiance. Furthermore, experimentally toppled columns, which experienced immediate and severe changes in irradiance gradients, largely re-established expected patterns of symbiont zonation during a six-month period (Fig. 2e,f). This response shows that the patterns are maintained dynamically.

Symbioses between corals and dinoflagellates are stable mutualisms, with the notable exception of coral bleaching, which involves the loss of symbionts and/or photosynthetic pigments[3,8]. Bleaching is an ecologically important but poorly understood response to environmental stress[3,8,9]. Many bleaching events exhibit intraspecific variation distributed within and among habitats in ways

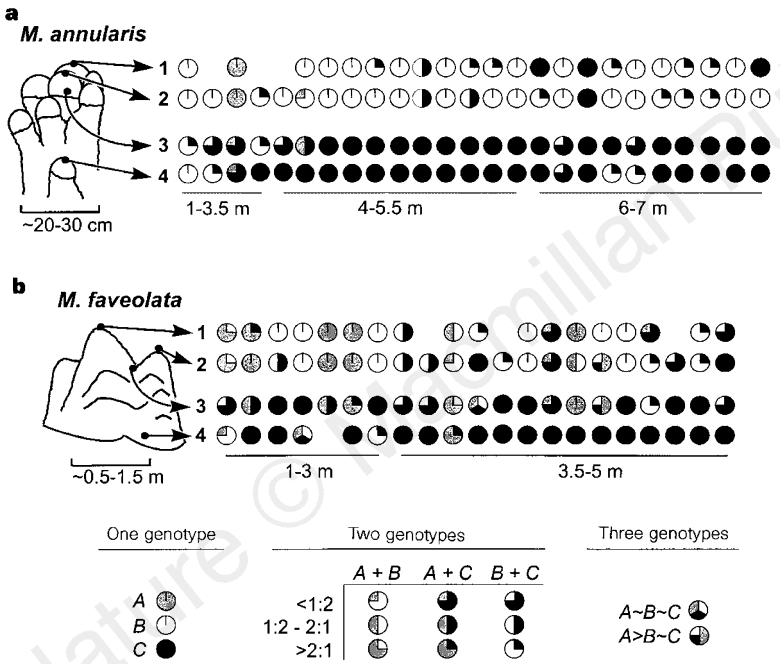

Figure 1 Symbiont communities in *M. annularis* (**a**) and *M. faveolata* (**b**). Each symbol represents one core sample that contained *Symbiodinium A*, *B*, *C* or mixtures of taxa summarized according to the code shown below. Columns in the data matrices represent individual coral colonies (depth increases from left to right), and rows represent locations of higher (rows 1 and 2) and lower (rows 3 and 4) irradiance, as defined in the diagrams to the left. Samples were collected in January 1995.

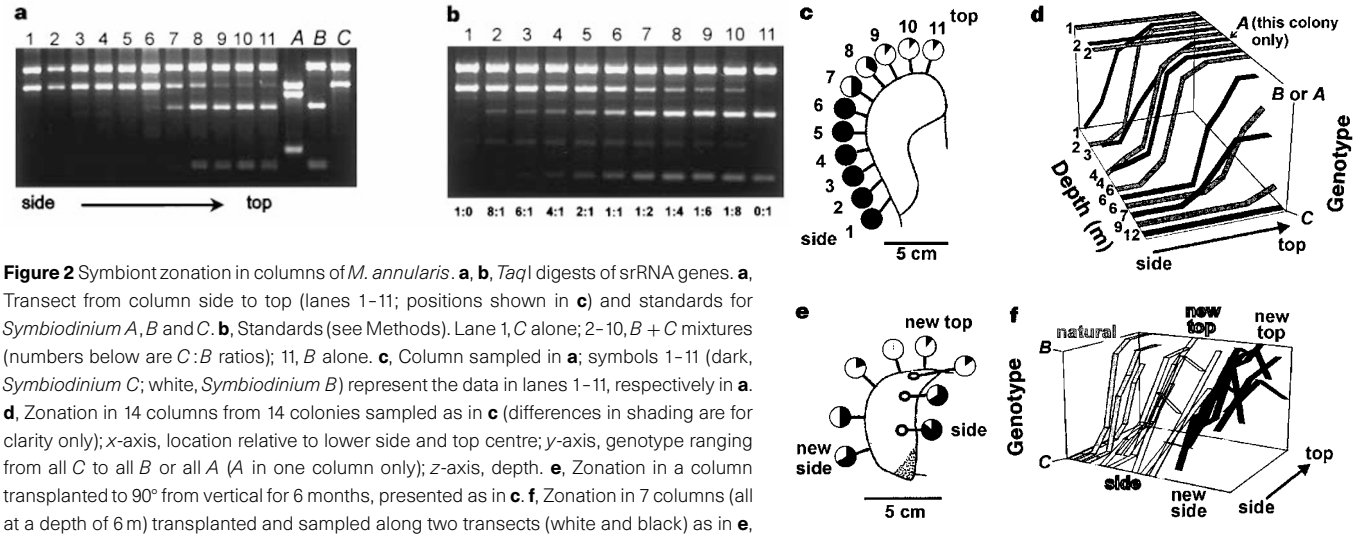

Figure 2 Symbiont zonation in columns of *M. annularis*. **a**, **b**, *Taq*I digests of srRNA genes. **a**, Transect from column side to top (lanes 1–11; positions shown in **c**) and standards for *Symbiodinium A*, *B* and *C*. **b**, Standards (see Methods). Lane 1, *C* alone; 2–10, *B* + *C* mixtures (numbers below are *C* : *B* ratios); 11, *B* alone. **c**, Column sampled in **a**; symbols 1–11 (dark, *Symbiodinium C*; white, *Symbiodinium B*) represent the data in lanes 1–11, respectively in **a**. **d**, Zonation in 14 columns from 14 colonies sampled as in **c** (differences in shading are for clarity only); *x*-axis, location relative to lower side and top centre; *y*-axis, genotype ranging from all *C* to all *B* or all *A* (*A* in one column only); *z*-axis, depth. **e**, Zonation in a column transplanted to 90° from vertical for 6 months, presented as in **c**. **f**, Zonation in 7 columns (all at a depth of 6 m) transplanted and sampled along two transects (white and black) as in **e**, presented as in **d**; zonation in natural columns at a depth of 6 m (from **d**) are plotted for comparison (grey).

that are difficult to explain[9–12]. Because irradiance and temperature act synergistically to induce bleaching[12–14], and the symbionts of *M. annularis* and *M. faveolata* exhibit different associations with irradiance (Figs 1 and 2), we hypothesized that symbiont polymorphism underlies this variation.

We observed 'paling' in several colonies of *M. annularis* and *M. faveolata* on 18 September 1995, and bleaching was extensive by the second week in October, both in Panama and elsewhere[15]. At our study site, this event was 'typical': like a similar event there in 1983 (ref. 16), it followed a prolonged excursion above the mean summer maximum of temperature (Fig. 3e); it also coincided with atypically high water clarity (data in ref. 17), which implies increased irradiance at depth[2]. We also observed complex[9,10,18] bleaching patterns in both *M. annularis* and *M. faveolata*. Bleaching was rare or slight at both shallow (<2 m) and deep (>15 m) sites; in between, however, both species displayed a curious pattern, with shallower colonies bleached preferentially in shaded places (Fig. 3a,b) and deeper colonies bleached preferentially in unshaded places (Fig. 3c,d). Among *M. annularis* partitioned as in Fig. 1a (communities 1 and 2 versus 3 and 4) and by depth (above 8 m versus below 8 m), this difference was significant ($n = 76$ colonies, 64 bleached; $P < 0.05$, χ^2 test). Some colonies exhibited a 'ring' of bleaching at the boundary between column top and side (Fig. 3a). *M. faveolata* colonies are not easily partitioned into two distinct irradiance microhabitats, but they clearly showed the same reciprocal pattern (Fig. 3b,d), with a shallower (~6 m) centre. Such observations have previously been hard to explain[12] because the environment is isothermal, and the associations with irradiance and colony morphology are inconsistent.

Symbiont zonation provides a simple hypothesis to explain these bleaching patterns. Bleaching was disproportionately common in what seems to be the upper limit of *Symbiodinium C*'s 'adaptive zone': low-irradiance parts of corals in shallower water, and high-irradiance parts of corals in deeper water. Slight increases in temperature and irradiance might push these symbioses, but not others, beyond some physiological limit, resulting in bleaching. This hypothesis accounts for our bleaching observations, including areas of slight bleaching[9,15,19] (see Fig. 3a, b), if *Symbiodinium C* were expelled selectively from mixed symbiont communities.

An analysis of symbionts collected in late October supported this interpretation of events. Post-bleaching samples were obtained <1 cm from many sites sampled the previous January (Fig. 1). All available samples from communities that had previously contained mixtures of *Symbiodinium C* plus either *A* or *B* (or both) were identified (Fig. 1) and analysed. We reasoned *a priori* (Fig. 2) that these sites accurately defined the limit of *Symbiodinium C* in corals under non-bleaching conditions. Such mixtures also allow the fates of different symbionts to be compared directly. We also tested archived samples taken at the same time as, and <1 cm away from, the original (pre-bleaching event) samples. In every case, *Symbiodinium* srRNA RFLPs in these replicate, pre-bleaching pairs were equivalent (data not shown), indicating that the small distance between pre- and post-bleaching samples was unlikely to be significant.

As predicted, *Symbiodinium C* had decreased in relative abundance in all 18 communities tested (see Fig. 4a–c). Absolute responses of different symbionts within a mixed community were compared by using estimates of relative abundances (from RFLP data; see Fig. 4a–c) to partition direct counts of symbionts into each genotype (Fig. 4d). Losses of *Symbiodinium C* were typically close to 100%, whereas *B* underwent a median decrease of 14%, and *A* more than doubled in 3 of 5 instances. The single sample that contained all three symbionts exhibited these same trends (Fig. 4c, d). Changes in colony chlorophyll contents and subjective assessments of bleaching paralleled changes in symbiont numbers (Fig. 4e). From these data we can tentatively rank the 'fitness' of the different *Symbiodinium* taxa as symbionts under 'bleaching conditions'. The ranking obtained in this manner is: $A > B \gg C$.

Our study provides a fuller understanding of *M. annularis* and *M. faveolata*, which are dominant members of western Atlantic reefs[20]

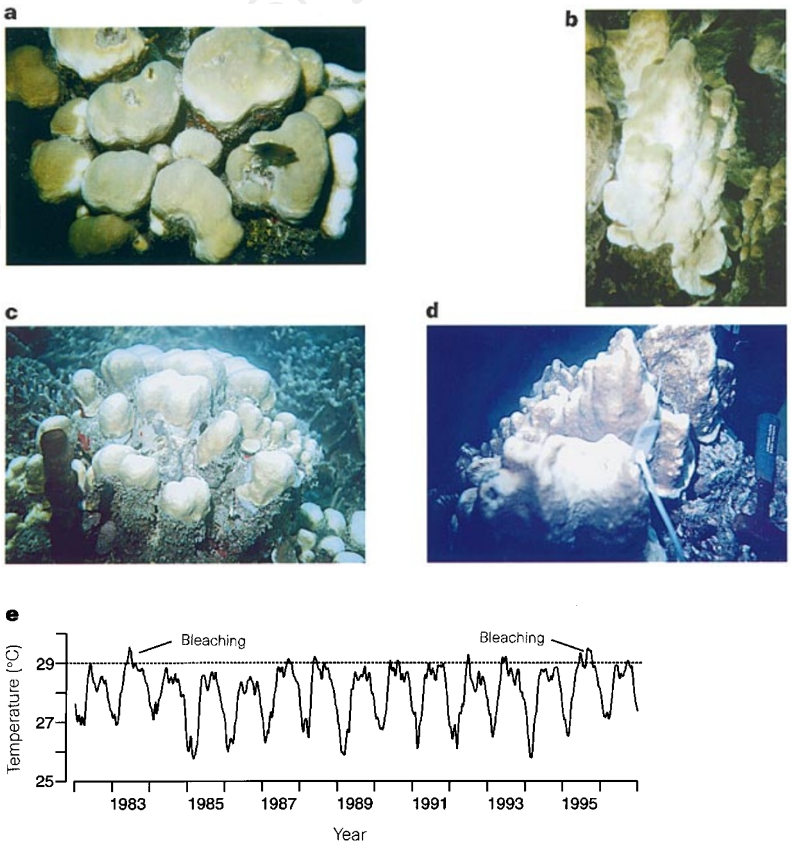

Figure 3 Bleaching in *M. annularis* (**a**, **c**) and *M. faveolata* (**b**, **d**) at the study site on 28 October 1995 showing 'shallow' (**a**, **b**) and 'deep' (**c**, **d**) patterns. **e**, Sea surface temperatures (three-week running means, from satellite data[30]) at the San Blas Islands, Panama. Temperatures above 29 °C in 1983 and 1995 were associated with coral bleaching[16] (this study). Records from our study site (at 7-m depth) since 1993 (Marine Environmental Sciences Program, Smithsonian Tropical Research Institute) corroborate satellite data.

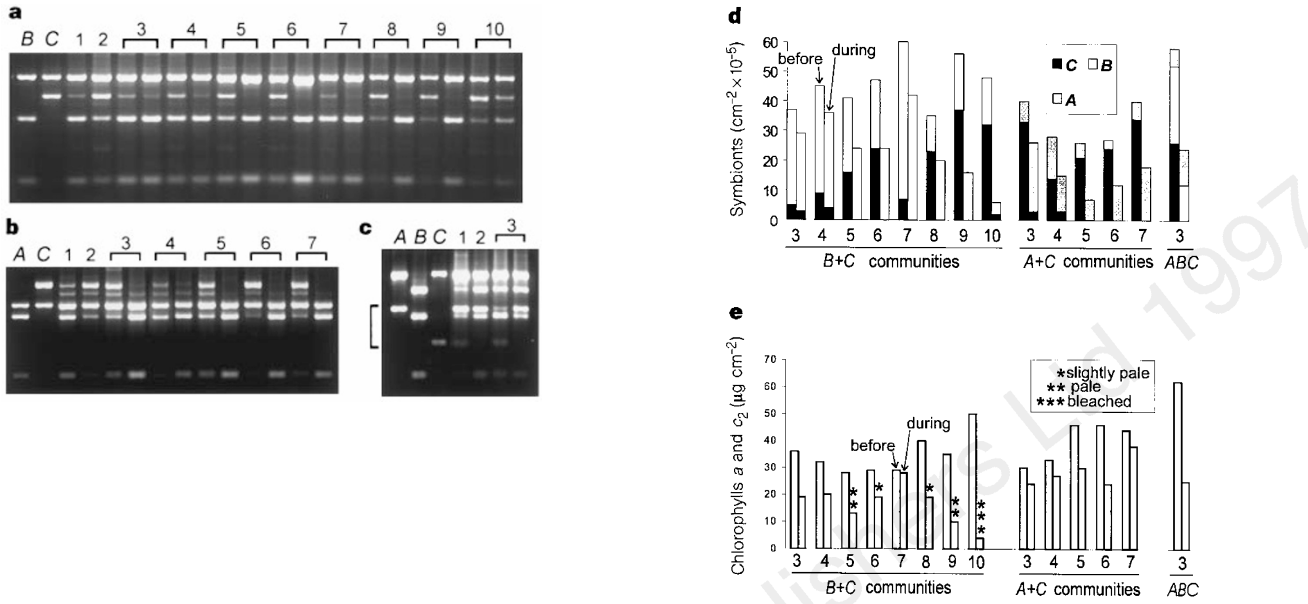

Figure 4 Symbiont communities before (January 1995) and during (October 1995) an episode of coral bleaching. **a**–**c**, Lanes contain *Taq*I (**a**, **b**) or *Dpn*II (**c**) digests of srRNA genes. **a**, Standards for *B*, *C* and *B* : *C* ratios of 8 : 1 (lane 1) and 1 : 1 (lane 2); lane pairs compare symbionts before (left) and during (right) bleaching in *M. annularis* (lanes 3–6) and *M. faveolata* (lanes 7–10). **b**, Standards for *A*, *C* and *A* : *C* ratios of 2 : 1 (lane 1) and 1 : 8 (lane 2); lane pairs 3 (*M. annularis*) and 4–7 (*M. faveolata*) compare symbionts as in **a**. **c**, Standards for *A*, *B*, *C* and equal amounts of *A*, *B* and *C* (lane 1) and *A* and *B* (lane 2); lane pair 3 compares symbionts in *M. faveolata*, as in **a** and **b**. The vertical bracket identifies bands that identify each symbiont. **d**, Densities of *A* (grey), *B* (white) and *C* (black) before and during bleaching (left and right bars of each pair, respectively) in samples reported in **a** (*B* + *C*, communities 3–10), **b** (*A* + *C*, communities 3–7) and **c** (*ABC*, community 3). **e**, Chlorophyll contents of the samples reported above, presented as in **d**. Samples were scored as 'normal' (not marked) or 'slightly pale', 'pale', or 'bleached' (marked by asterisks) when collected.

and are widely used as model systems in reef biology and geology[11,13,18,19,21,22]. Each coral 'species' encompasses one animal and dynamic, multi-species communities of symbiotic dinoflagellates. This strongly contradicts the 'one host, one symbiont' view of reef corals[1], in which host taxa alone are adequate units of biodiversity, environmental variability is accommodated largely by physiological acclimatization[2–4], and bleaching variability is often not understood[12]. We conclude that polymorphic symbiont communities underlie the broad distributions[20] and bleaching ecology of these corals. Directed shifts in symbiont populations following extreme environmental change (Figs 2e, f and 4) suggest that similar shifts may also occur over annual cycles of environmental variation[19]. For these corals, and for mutualisms in general, the ability to cope with environmental change through changes in symbiont community composition reflects the selective advantage of hosting several distinct symbionts, despite the potential for destabilizing competition among them[5,6].

How typical and important are the patterns documented here? *M. annularis* and *M. faveolata* in the Bahamas also host *Symbiodinium A*, *B* and *C* (data not presented), and published photographs[18] and descriptions[9,10] of bleaching elsewhere strongly resemble our own (Fig. 3a–d). With respect to Caribbean corals in general, bleaching is often predominant at intermediate depths[9]. We can attribute this pattern (and its within-colony correlate) in *M. annularis* and *M. faveolata* to symbiont polymorphism and zonation. Moreover, at least three other species of Caribbean corals host (at least) both *Symbiodinium A* and *C* (ref. 23; our unpublished data). For other species, which might host multiple but not so distantly related symbionts, refinements of *Symbiondinium* taxonomy would be essential. However, symbiont polymorphism does not exclude the significance of other attributes that are important features of coral biology, such as physiological acclimatization of hosts and symbionts[2–4] and genetic differences among hosts[11,14].

It has been hypothesized that a global warming trend, with increased frequencies of world wide coral bleaching induced by increasing temperature or ultraviolet irradiation, could have catastrophic consequences for many living coral reefs[3,8,21]. Alternatively, coral communities may adjust to climate change by recombining their existing host and symbiont genetic diversities[24–26]. Our findings supply a precedent for this idea: that one species of coral can flexibly host more than one taxon of *Symbiodinium* to produce symbioses with distinct ecological properties. For example, *M. annularis* and *M. faveolata* might adjust to a warmer Atlantic ocean by hosting more *Symbiodinium A* and less *Symbiodinium B* and *C*. However, long-term consequences of such replacements would depend on how they affect rates of coral growth and reproduction. □

Methods

Field collections and manipulations. Coral samples were collected at Aguadargana reef in San Blas, Panama[27] by coring (1.1 cm^2 surface area) and freezing immediately in liquid nitrogen (data in Figs 1 and 4). Other colonies (data in Fig. 2) were sampled by removing a defined circular area (~0.12 cm^2) of living tissue from freshly collected colonies with an airbrush. In transplant experiments (Fig. 2e, f), columns of *M. annularis* were broken off ~15 cm below the living tissue, turned on their sides, and cemented (at the non-living base) back to the colony at a comparable location; this increased (new top), decreased (new side), or did not change (side) local irradiance. All 28 transplants at a depth of 6 m seemed to be normal after 6 months. Analyses of non-transplanted (control) columns showed that natural zonation patterns were stable over this period (data not shown).

Laboratory analyses. Symbionts and symbiont DNA were isolated from frozen[7] and from fresh[28] samples. Nuclear srRNA genes were amplified using the 'universal' PCR primers ss5 and ss3 (all data in Fig. 1) or a combination of ss5 and the '*Symbiodinium*-biased' primer ss3Z (all data in Figs 2 and 4), and analysed with *Taq*I and *Dpn*II (data were consistent in every case)[7]. The biased primer (ss3Z) does not discriminate (within this study) against unknown, specific *Symbiodinium* genotypes (discussed in ref. 28), as confirmed by sequencing[7] and by comparing results from 'universal' and 'biased' amplifications of 30 samples that contained two genotypes (*A* + *C* or *B* + *C*) in various

proportions.

Cloned srRNA genes from *Symbiodinium A*, *B* and *C* were used as standards[7]. They were amplified singly and from defined mixtures of two (Fig. 2b) or three (Fig. 4c) types[7] to assign field samples to classes of symbiont relative abundance by visual comparison (Fig. 2a, b). To validate this procedure, approximately equal numbers of *A*, *B* and *C* cells, from three natural isolates of each type, were mixed in pairwise combinations and analysed. The results implied that *Symbiodinium B* and *C* yield (on a per-cell basis) equal signals, whereas *A* yields about twice that amount. Standard mixtures of cloned genes were adjusted accordingly.

Symbiont densities and chlorophyll contents (Fig. 4d, e) were determined from haemacytometer counts (8 replicate grids per sample) and spectrophotometrically from methanol extracts[29], respectively. These symbionts were isolated quickly (with minimal washing) from frozen samples at 4 °C under dim light. Symbiont genotypes, numbers and chlorophyll contents were obtained from subsamples of each isolate.

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A polymorphism maintained by opposite patterns of parasitism and predation

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Although polymorphism is a widespread phenomenon that has been recognized for nearly two centuries, the basic mechanisms maintaining most polymorphisms in nature are unknown[1,2]. We present evidence that a polymorphism can be maintained exclusively by balanced selection from two predatory species. For field and laboratory experiments, we used the pea aphid, *Acyrthosiphon pisum*, which occurs as 'green' and 'red' colour morphs, and two species that attack pea aphids, the parasitoid *Aphidius ervi* and the predator *Coccinella septempunctata*. We found that when parasitism rates in the field were high relative to predation rates, the proportion of red morphs increased relative to green morphs, whereas the converse was true when predation rates were high relative to parasitism rates. Detailed laboratory and field studies confirmed that green morphs suffer higher rates of parasitism than red morphs, whereas red morphs are more likely to be preyed on by predators than green morphs are. We present a mathematical model that demonstrates that biased density-dependent parasitism and/or predation on different morphs is sufficient to maintain the colour polymorphism in the population. Our findings support an important role for predation in the maintenance of genetic diversity.

Aphids occur in a range of colour morphs that can differ in growth rates, host range, defensive behaviour, and susceptibility to parasitism[3–6]. Pea aphids, *Acyrthosiphon pisum* (Harris) (Homoptera: Aphididae), in south-central Wisconsin occur as two colour morphs, green and red. The colour morphs remain distinct through the summer months because the aphids reproduce parthenogenetically. Pea aphids experience high levels of parasitism by the wasp *Aphidius ervi* Haliday (Hymenoptera: Aphidiidae) and heavy predation by several predators, including ladybird beetles, especially *Coccinella septempunctata* L. (Coleoptera: Coccinellidae). *A. ervi* is a 'parasitoid' that attacks aphids by inserting an egg through the aphid's cuticle; the developing wasp larva feeds on and eventually kills the aphid[7]. Both the parasitoid and the predator can have a major impact on pea aphid populations[8,9] and hence may be important selective agents. Although all three species are introductions to the Neartic, they have a long evolutionary history in their common Paleartic home range, where both aphid colour morphs also coexist[10–12].

In field populations, we found that the relative level of parasitism and predation had a significant effect on aphid colour morph composition. Specifically, the proportion of red morphs increased following relatively high parasitism and decreased following relatively high predation (Fig. 1), implying balancing selection by parasitism and predation. This balanced parasitism/predation hypothesis was supported by our further studies demonstrating directly that parasitism by *A. ervi* is heavier on green morphs, whereas predation by *C. septempunctata* is heavier on red morphs. The parasitism rate on green morphs in the field (53%) was significantly higher than on the red morph (42%) ($P < 0.001$). Significantly higher parasitism rates on a green morph over a red morph have also been reported for the alfalfa aphid, *Macrosiphon creelii* Davis[13]. Another study found higher parasitism on red than on green morphs of *A. pisum*[4]: the difference between this result and