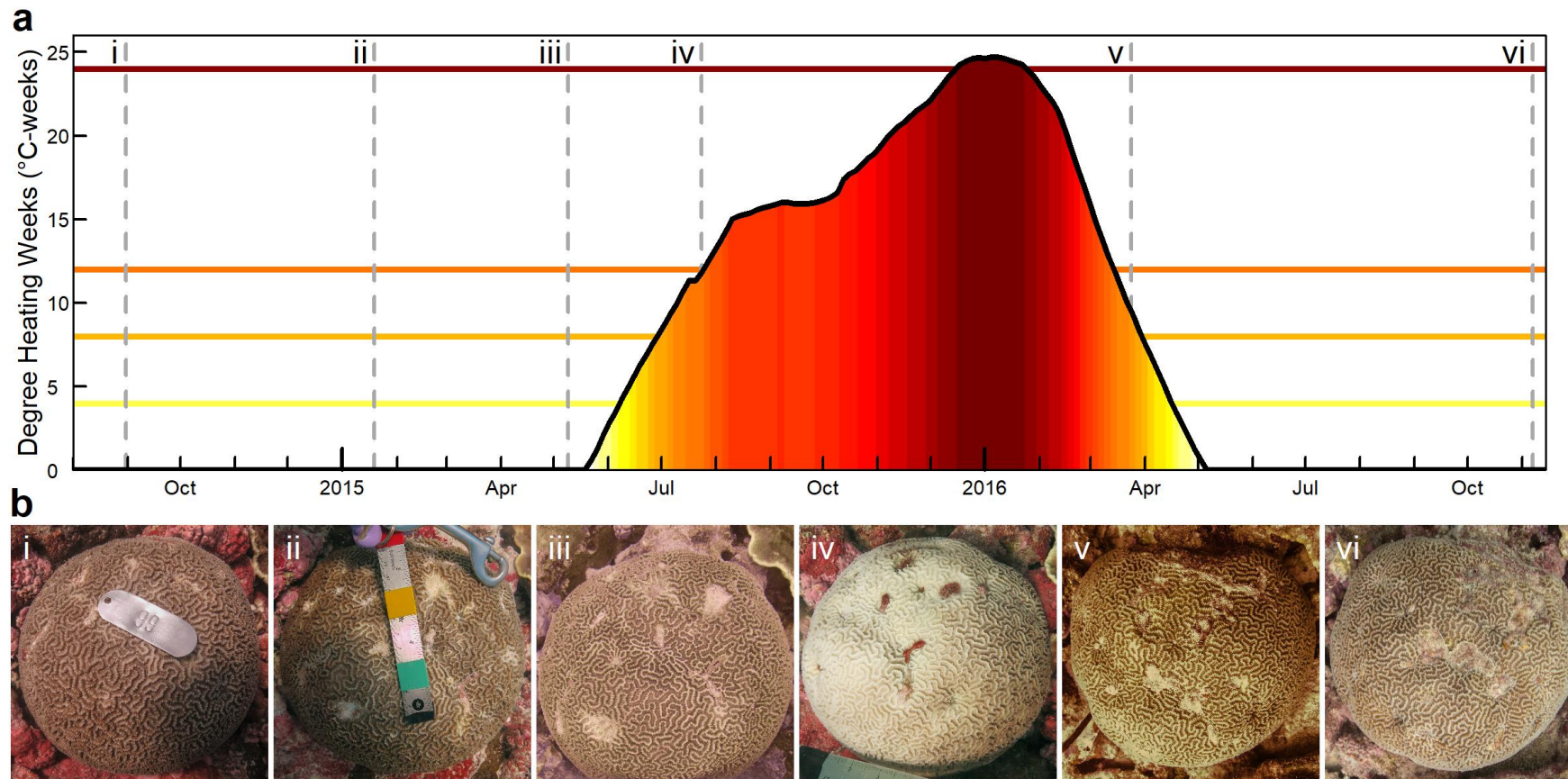


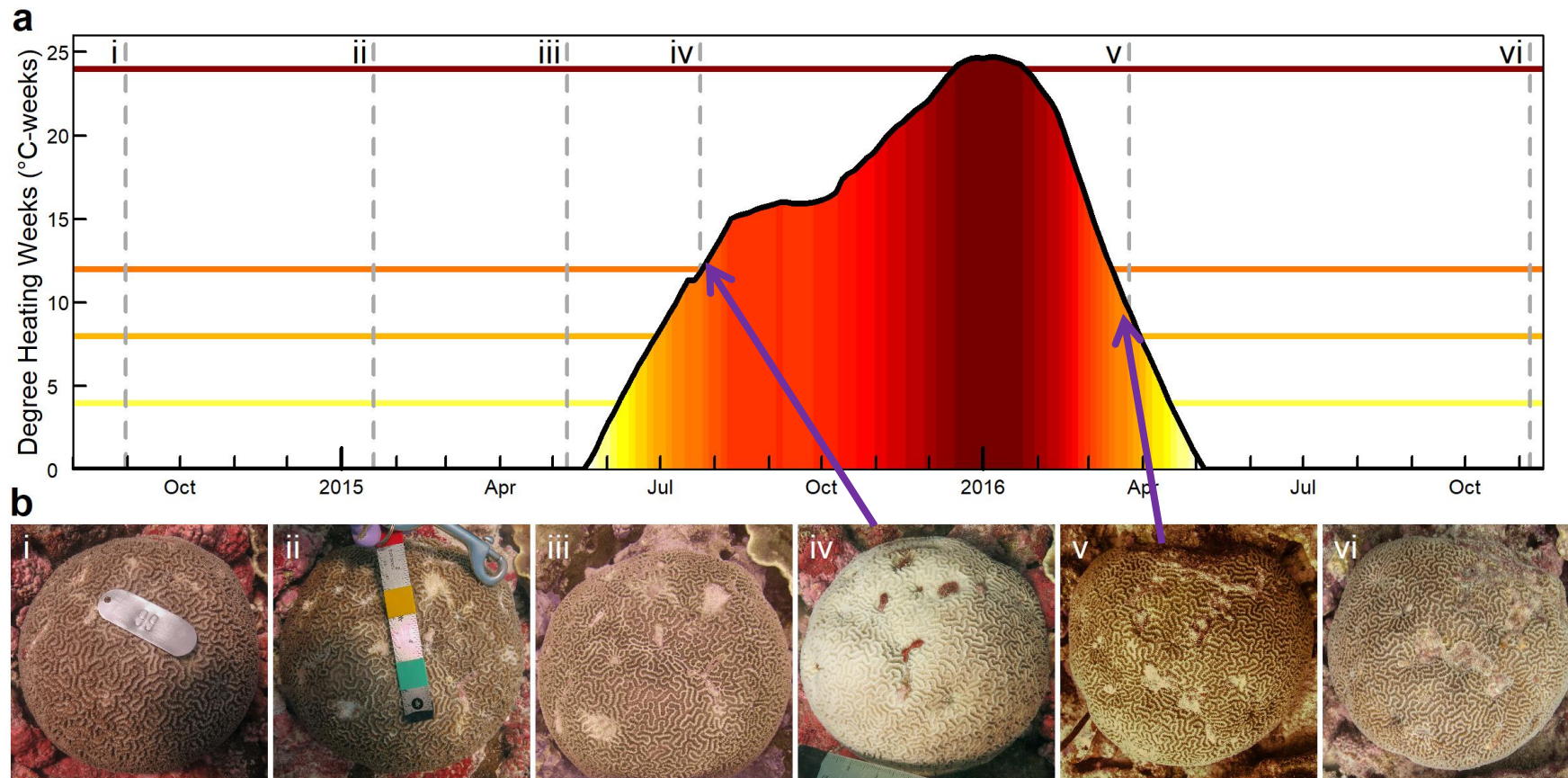
# What we did:

Here, we assess coral symbiosis and survival during the massive 2015/2016 El Niño event. We tagged, sampled, and photographed the same coral colonies before, during, and immediately after the El Niño event. We determined bleaching condition and survival for each coral colony, and used Illumina MiSeq ITS-2 amplicon sequencing and 97% \*de novo\* OTU clustering to evaluate changes in *Symbiodinium* community structure. To investigate mechanisms underlying the ability of these corals to not only survive a year of continuous heat stress, but to recover in the interim, we assessed the relationship between human disturbance, pre-bleaching *Symbiodinium* community structure, and coral survival, as well as the timing of *Symbiodinium* community shifts throughout this El Niño event.

**Figure 1 | Thermal stress experienced by corals, and the transition of one such coral from healthy – bleached – recovered, at the epicentre of the 2015-2016 El Niño event. a.** Degree Heating Weeks (DHW), on Kiritimati Island over the course of the 2015-2016 El Niño event. Corals are sensitive to temperatures warmer than 1°C above their normal highest summertime mean sea surface temperature (SST), known as the bleaching threshold. DHW shows how much heat stress has accumulated in an area over the past twelve weeks by summing any temperature exceeding the bleaching threshold during that period. Horizontal lines show expected bleaching severity levels: 4°C (yellow line), NOAA Coral Reef Watch (CRW) Bleaching Alert Level 1 (significant bleaching likely); 8°C (light orange line), Bleaching Alert Level 2 (widespread bleaching and mortality may occur); 12°C (dark orange line), ‘mass coral mortality’ expected to occur (Hoegh-Guldberg 2011); 24°C (dark red line) ‘not experienced by reefs yet’ (Hoegh-Guldberg 2011). Solid black line indicates *in situ* calculated DHW, and fill colors correspond to bleaching severity levels. Dashed vertical gray lines show the six sampling time points. **b.** Photographs of the same tagged *Platygyra* coral colony (#99), from the six time points (dashed grey lines), showing the initially healthy colony (i-ii) bleached after two months of heat stress (iv), ‘recovered’ to a normal brown colour after ten months of heat stress (v), and still alive six months post heat stress (vi).

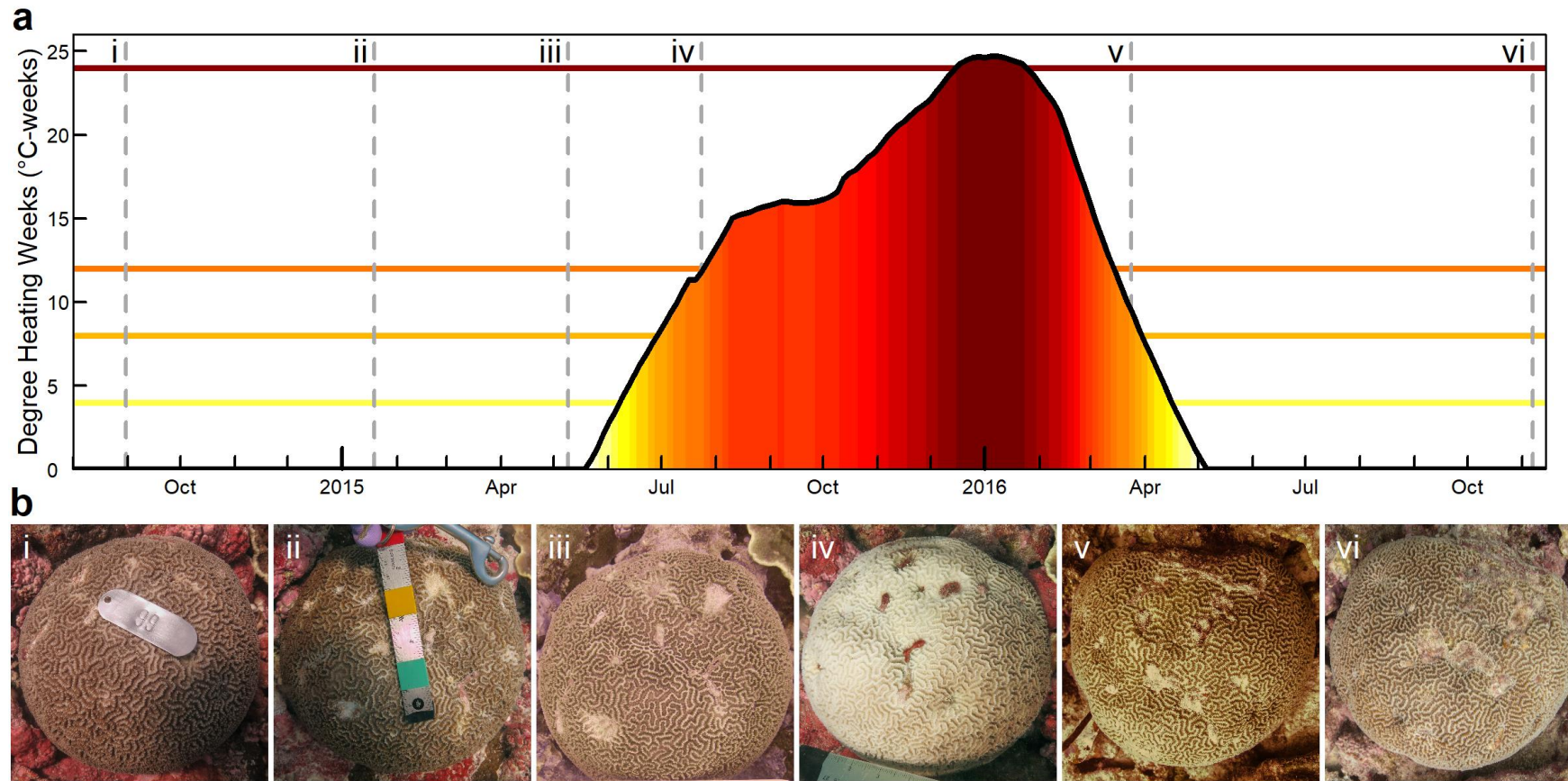


**Figure 1 | Thermal stress experienced by corals, and the transition of one such coral from healthy – bleached – recovered, at the epicentre of the 2015-2016 El Niño event. a.** Degree Heating Weeks (DHW), on Kiritimati Island over the course of the 2015-2016 El Niño event. Corals are sensitive to temperatures warmer than 1°C above their normal highest summertime mean sea surface temperature (SST), known as the bleaching threshold. DHW shows how much heat stress has accumulated in an area over the past twelve weeks by summing any temperature exceeding the bleaching threshold during that period. Horizontal lines show expected bleaching severity levels: 4°C (yellow line), NOAA Coral Reef Watch (CRW) Bleaching Alert Level 1 (significant bleaching likely); 8°C (light orange line), Bleaching Alert Level 2 (widespread bleaching and mortality may occur); 12°C (dark orange line), ‘mass coral mortality’ expected to occur (Hoegh-Guldberg 2011); 24°C (dark red line) ‘not experienced by reefs yet’ (Hoegh-Guldberg 2011). Solid black line indicates *in situ* calculated DHW, and fill colors correspond to bleaching severity levels. Dashed vertical gray lines show the six sampling time points. **b.** Photographs of the same tagged *Platygyra* coral colony (#99), from the six time points (dashed grey lines), showing the initially healthy colony (i-ii) bleached after two months of heat stress (iv), ‘recovered’ to a normal brown colour after ten months of heat stress (v), and still alive six months post heat stress (vi).

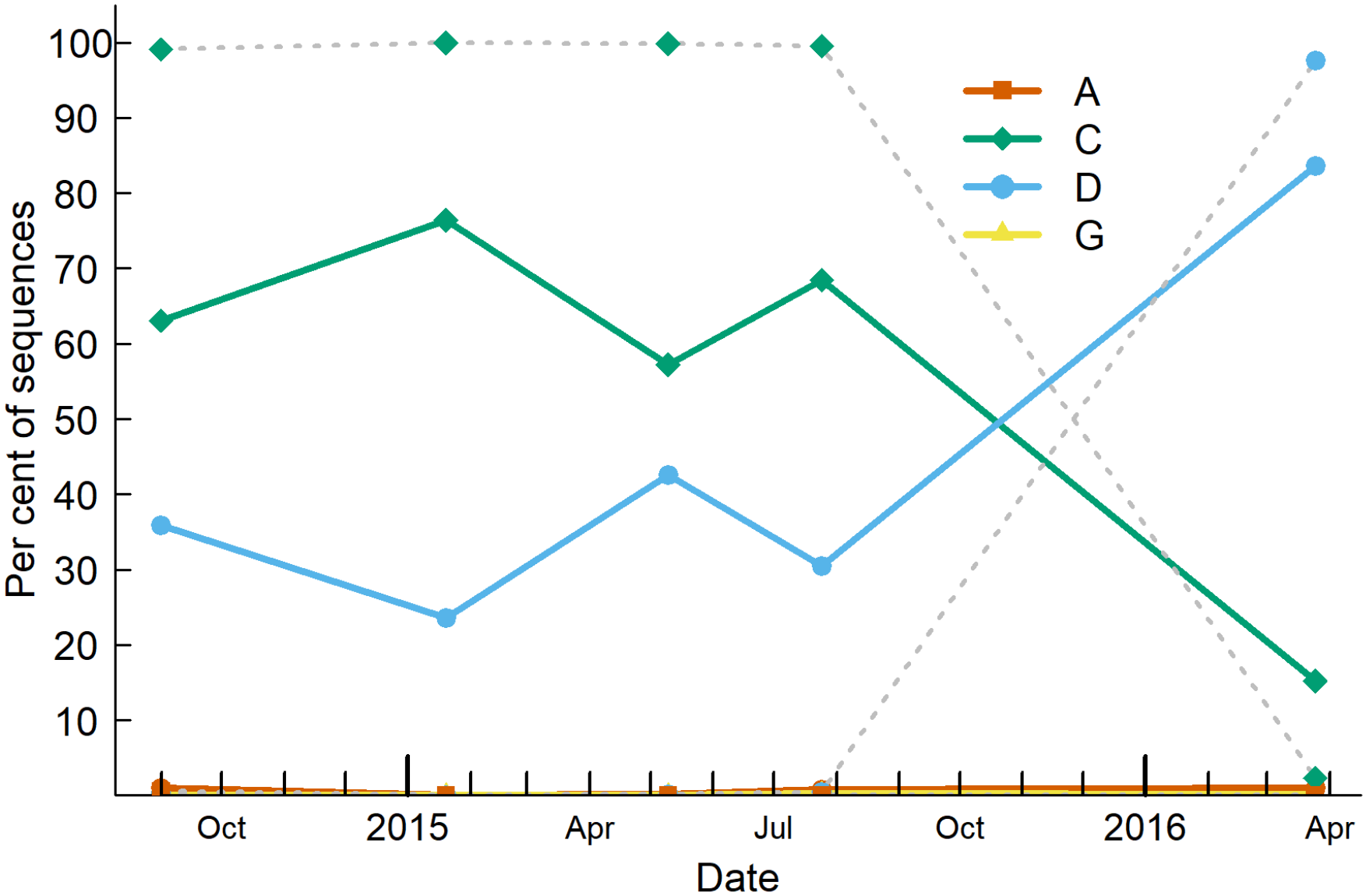


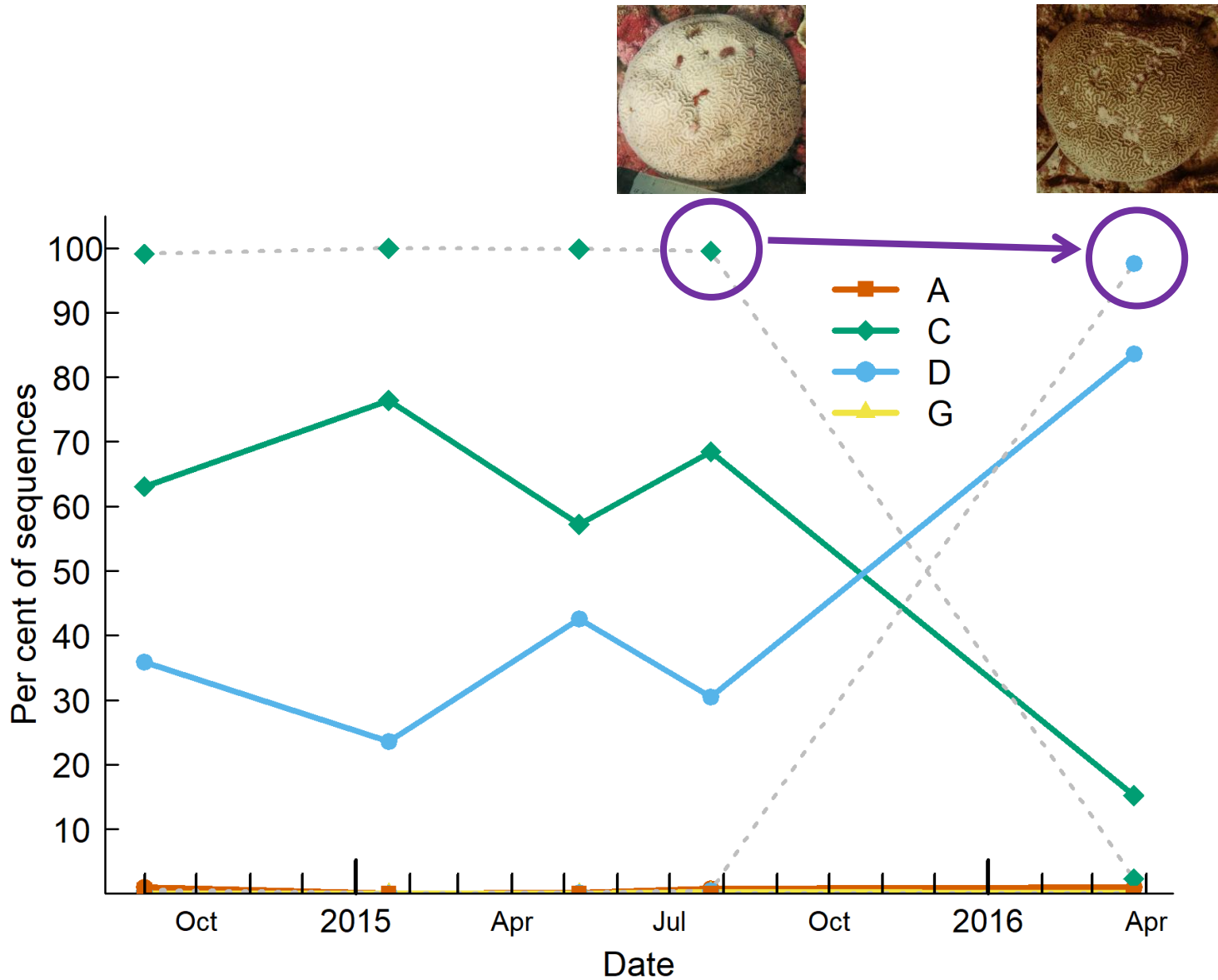


Here, we provide the first evidence that corals have the capacity to not only survive, but to regain their symbionts and visibly recover from bleaching while still under intense thermal stress (Figure 1b, 2ab). These corals (Scleractinia family Merulinidae; *Platygyra* sp. and *Favites pentagona*) were bleached within two months of the onset of warming, but had visibly recovered after 10 consecutive months of intense warming (Fig. 1).

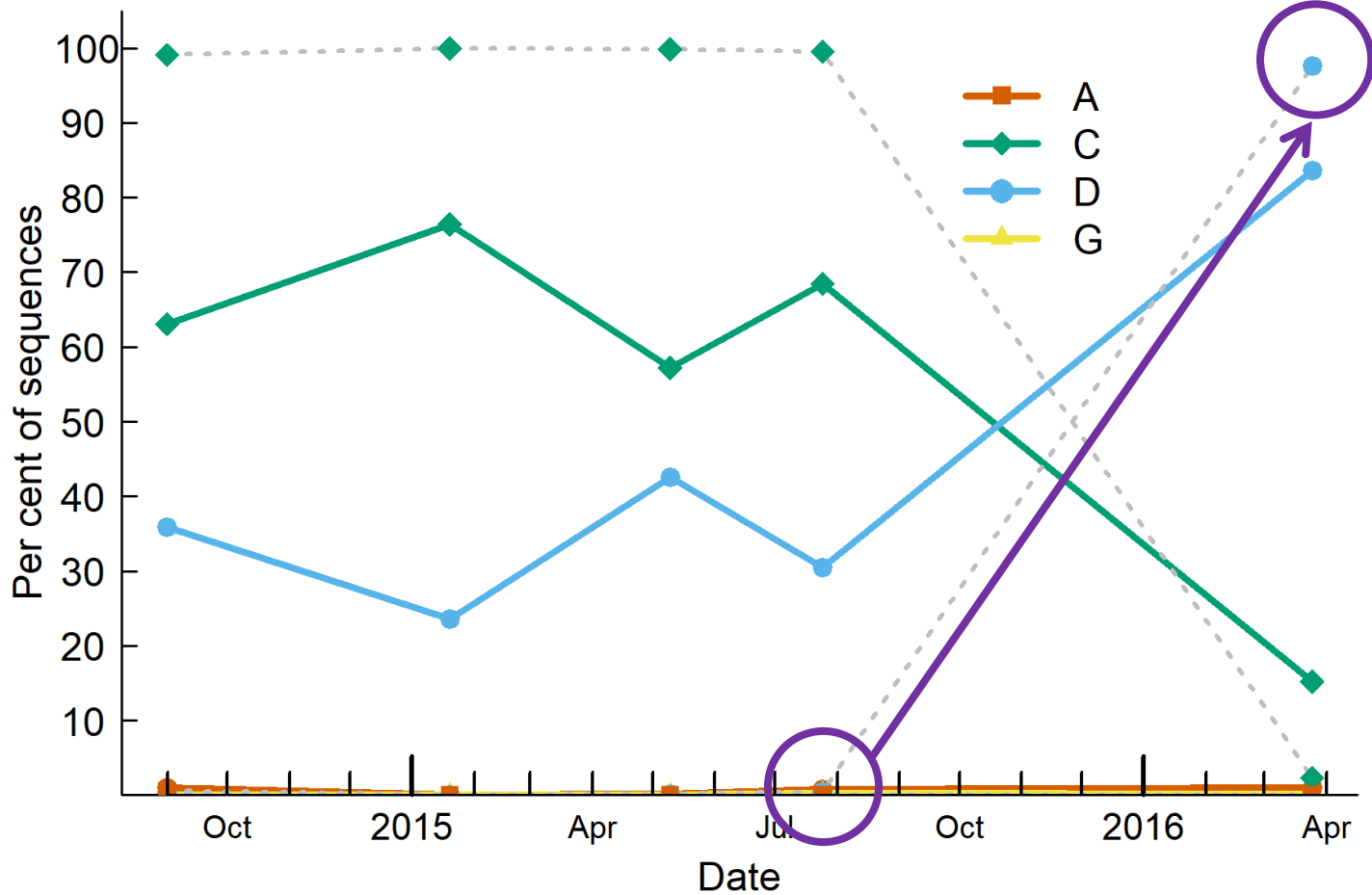
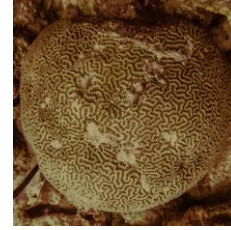


**Figure 2 | Shift in *Symbiodinium* community composition from clade C to clade D dominance over the course of the 2015-2016 El Niño.** *Symbiodinium* community composition at each of five sampled time points for **i)** the entire pool of tagged coral colonies (solid lines, n=21-67 colonies per time point), and **ii)** a single representative tagged *Platygyra* colony (dashed lines).

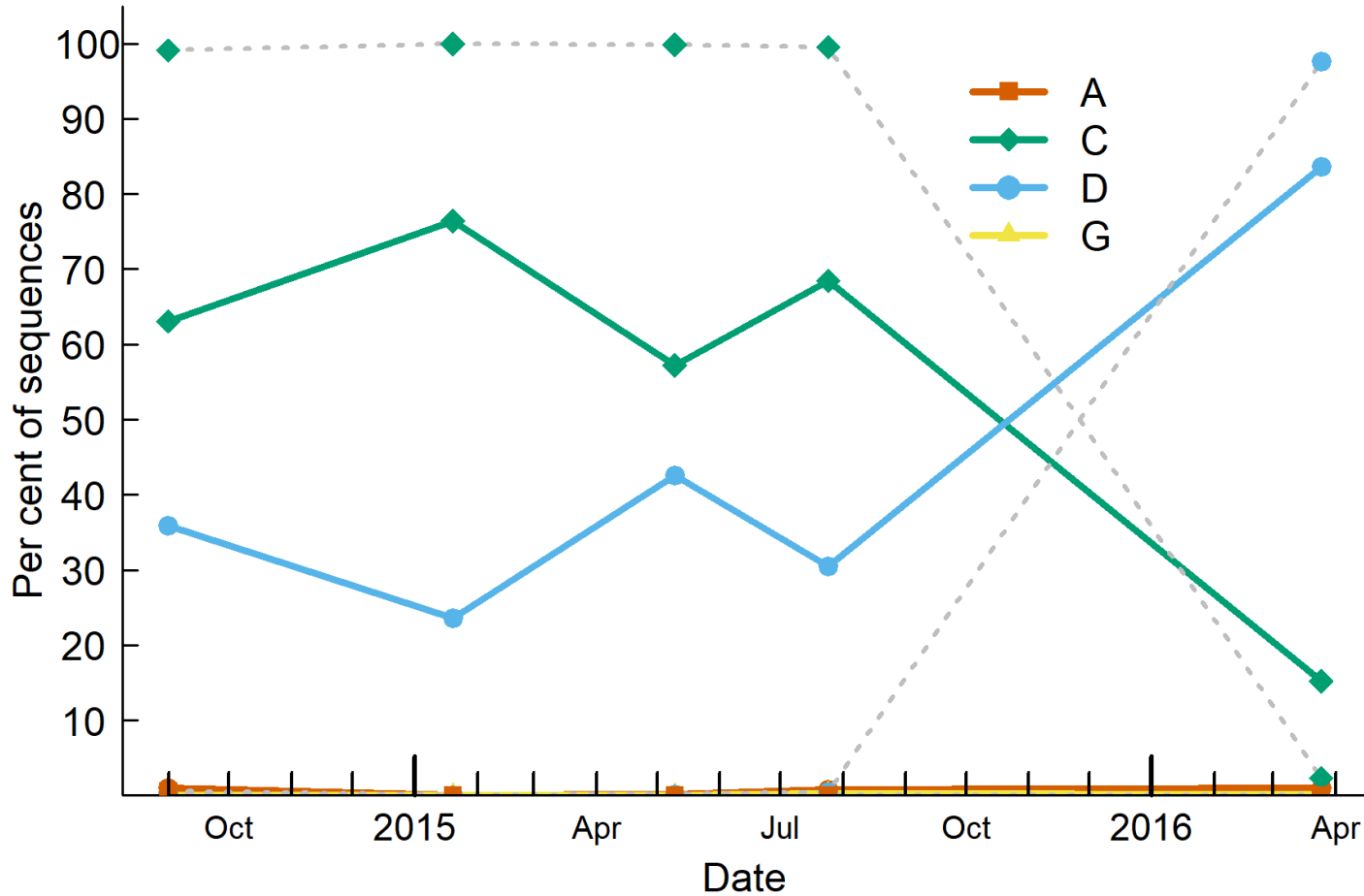
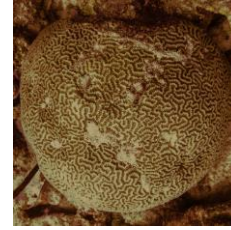




1. Bleached colony had approximately same community: Suggests non-preferential expulsion of symbionts (i.e. no preference to expel C over D)



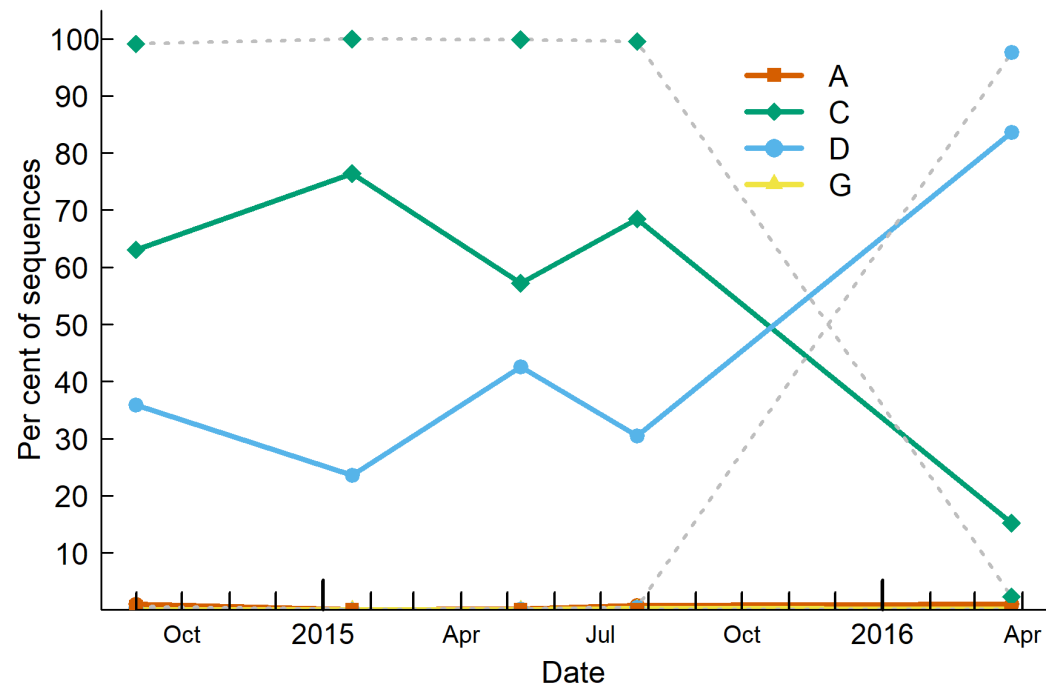
1. Bleached colony had approximately same community: Suggests non-preferential expulsion of symbionts (i.e. no preference to expel C over D)
2. *Symbiodinium* that are initially extremely rare can play a critical role in coral resilience to heat stress



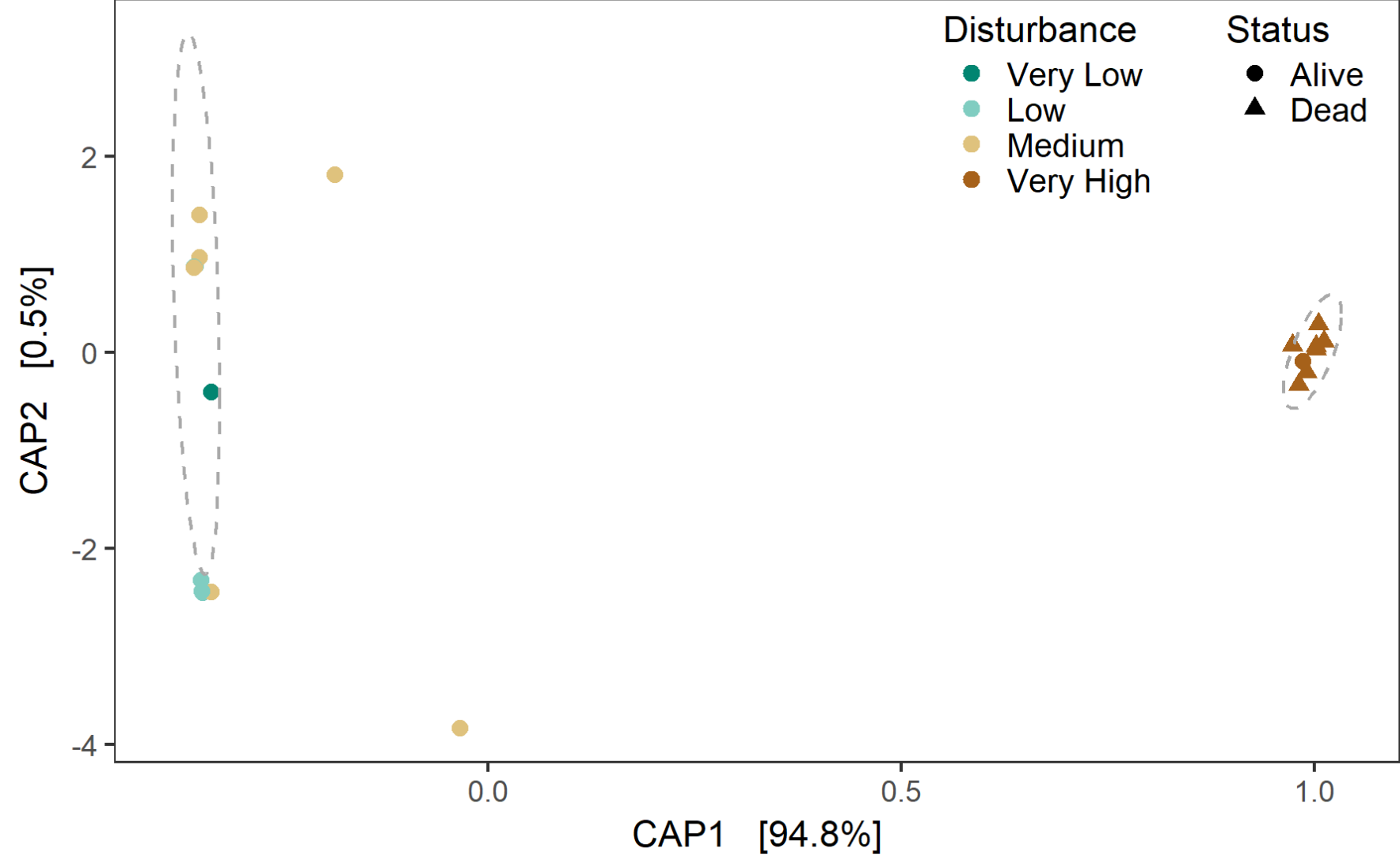
3. When you look at the overall community (as other studies do e.g. with pie charts of overall *Symbiodinium* community structure, you often can't tell if this shift is due to differential mortality (i.e. all of the colonies with C died) OR due to *Symbiodinium* shifts. Here, we show that it is due to shifts in the community (i.e. C shifted to D; while those with D died).

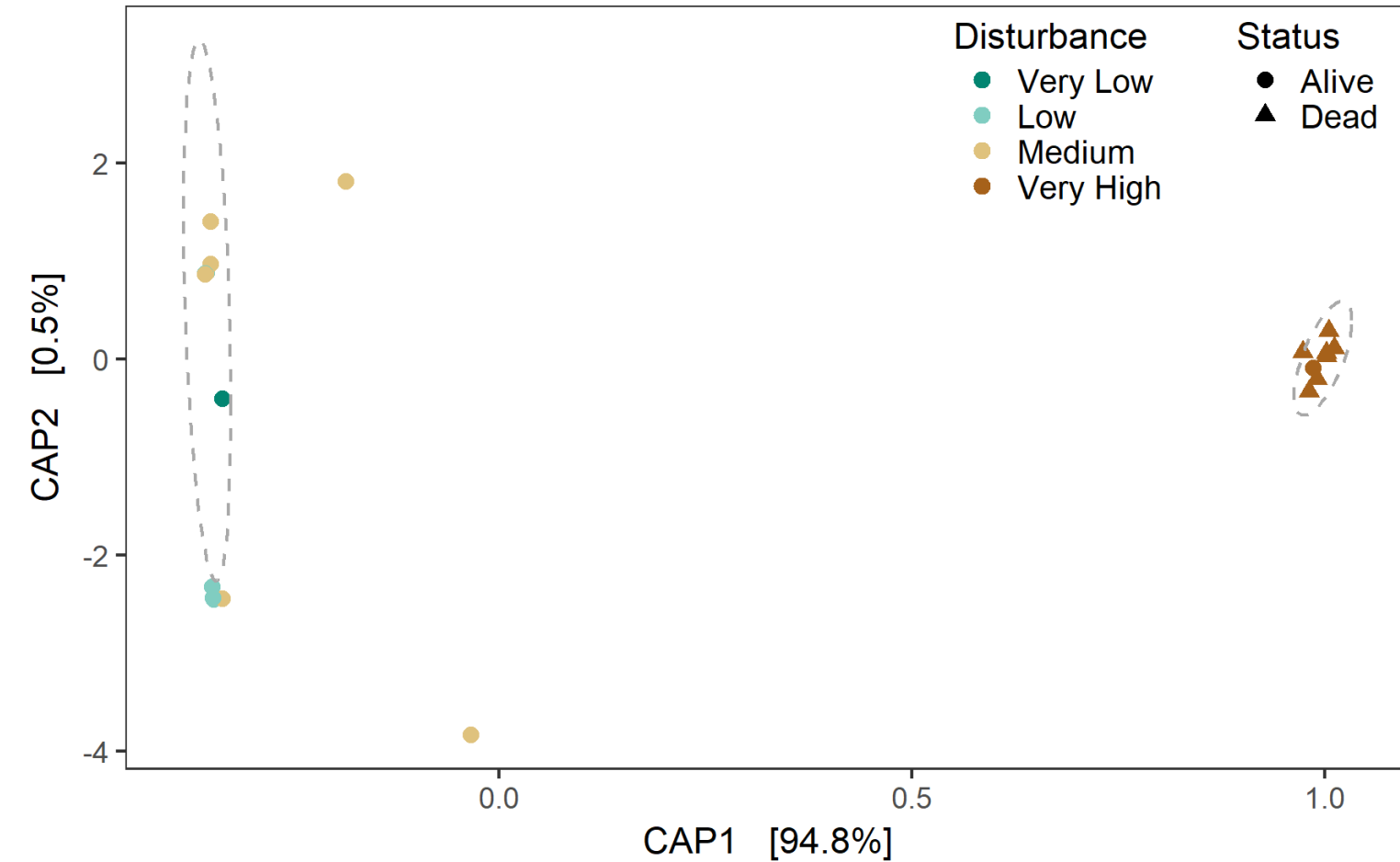


We show that after two months of heat stress, fully-bleached corals retained approximately the same *Symbiodinium* community as they had before the bleaching event (Figure 2a). This suggests that a wholesale breakdown of symbiosis occurred in bleached corals during this event, indicating a lack of preferential symbiont expulsion or exodus. Furthermore, some coral colonies changed *Symbiodinium* communities drastically upon recovery, and recovered symbiosis with *Symbiodinium* types that were present in only a negligible amount before the bleaching event (Figure 2b). This supports recent evidence suggesting that symbionts present in even very low abundances can play a critical role in coral survival and recovery

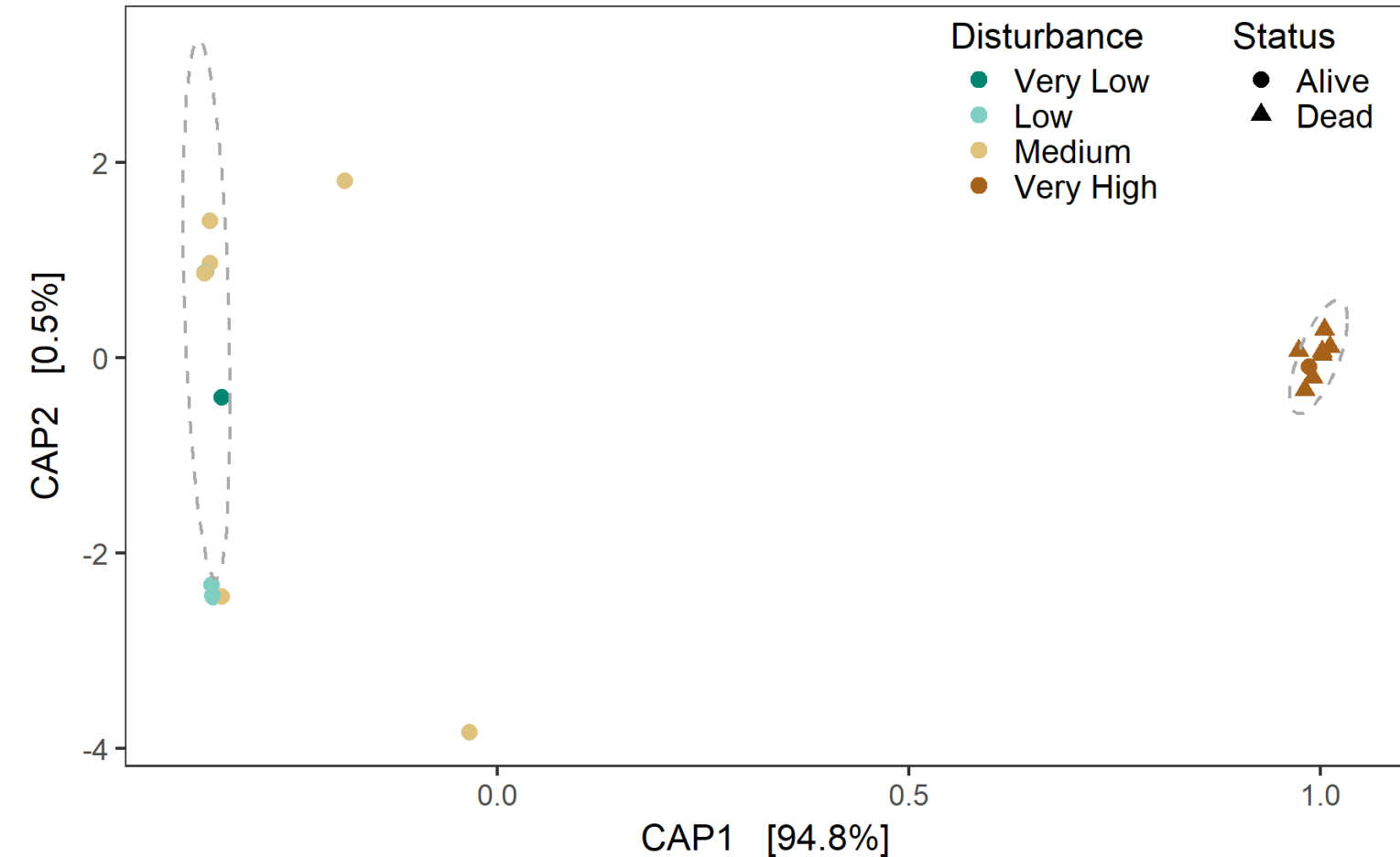


**Figure 3 | Constrained ordination plot showing groupings of *Symbiodinium* communities from individual *Platygyra* colonies, grouping into two distinct areas according to level of local disturbance.** Ellipses show separation of the corals which survived the bleaching event (“Alive”, left side of plot) and those that did not (“Dead”, right side of plot). Values in square brackets show per cent variation explained by each constrained axis.





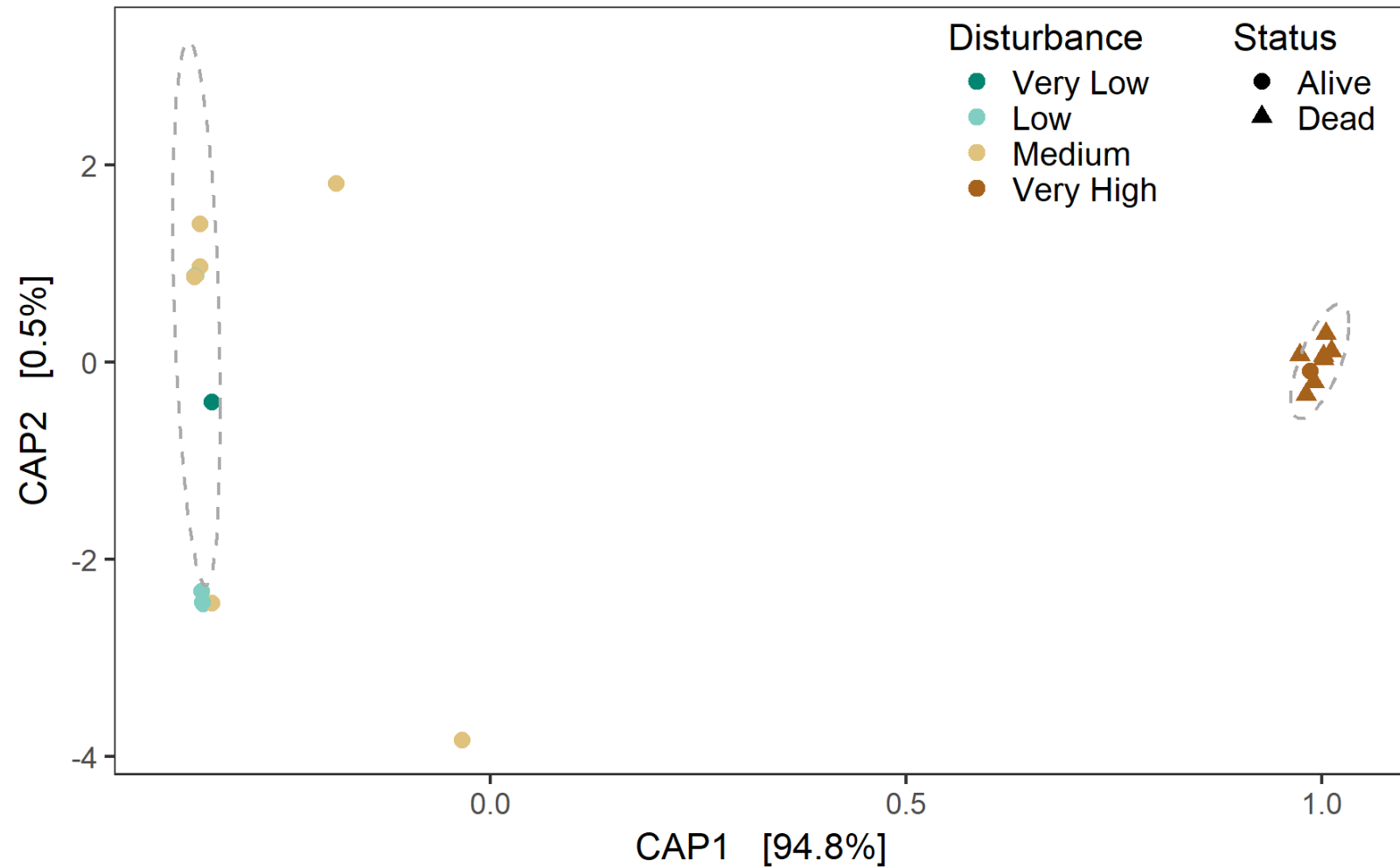
1. Significant difference between Symbiodinium communities in very high disturbance sites vs. lower impact sites.



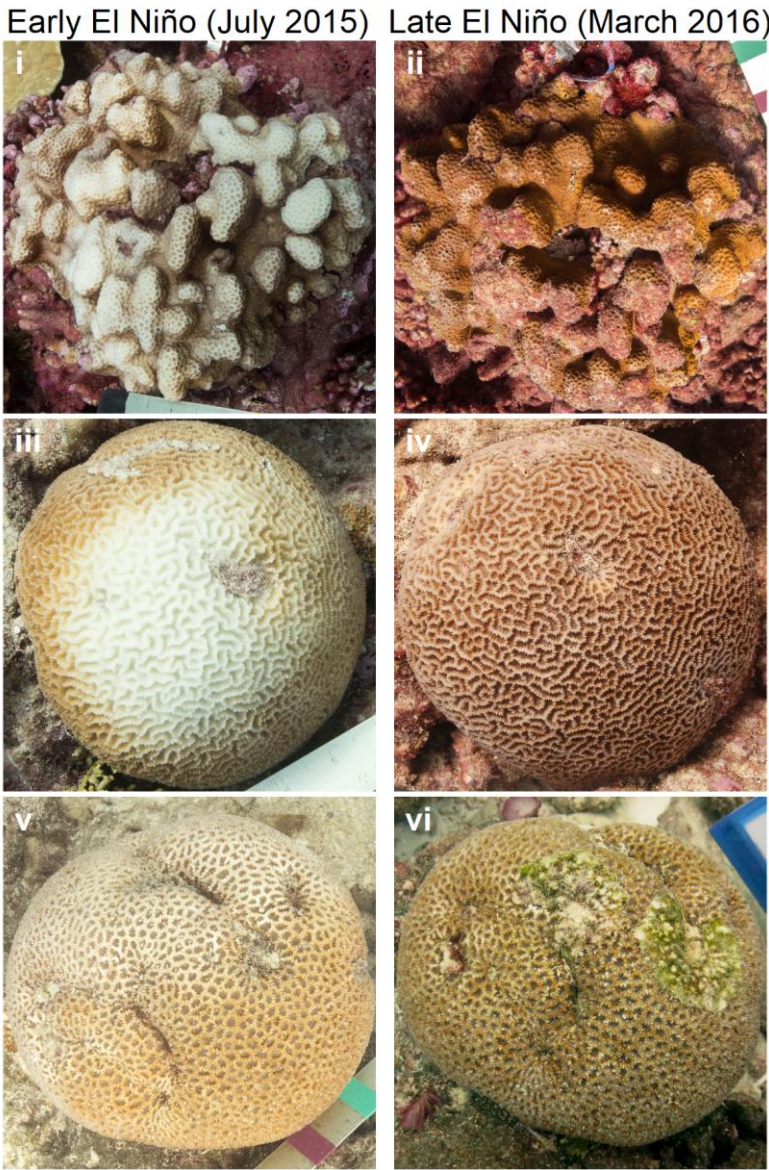
1. Significant difference between Symbiodinium communities in very high disturbance sites vs. lower impact sites.
2. All but one coral colony tagged before the event died at the very high disturbance site.



We show that corals living at different levels of local human disturbance had distinct symbiont communities that corresponded tightly to survivorship.



**Extended Data Figure 1 | Transition of individual tagged coral colonies on Kiritimati Island from bleached – recovered over the course 2015-2016 El Niño event.** Photographs of **i-ii. *Favites pentagona***, **iii-iv. *Platygyra* sp.**, **v-vi. *Favia matthaii* (*Dipsastrea matthaii*)** taken two months into the heat stress (July 2015, left column) and at the conclusion of the heat stress (March 2016, right column), demonstrating the visual recovery of several coral species before the conclusion of the heat stress event.



# Summary Paragraph (Nature Style, formatting incomplete)

Coral reefs, which already live on the edge of their thermal tolerance [Sampayo2016-vd], are under acute threat from ocean warming [Hughes2003-aj; Hoegh-Guldberg2007-fh; Baker2008-ky, newhughespapers]. The 2015/16 El Niño was the worst pulse warming event on record in terms of severity and longevity [Eakin:2016vf; Heron2016-am], yet despite massive coral mortality, some corals show resilience to this extreme event (Bauminprep). Corals live in symbiosis with a diverse genus of photosynthetic dinoflagellates (*Symbiodinium* spp.; [Muscatine1977-pn; Rowan1992-lg]), and the flexibility of this symbiosis [Baker2003-ks; Little2004-tm ... more] has contributed to novel research exploring the efficacy of assisted evolution for saving threatened reefs [Ruth and Madeline]. Warming causes the breakdown of coral symbiosis (i.e. coral "bleaching") when symbionts are expelled from the coral tissue [Brown1997-mf]. Coral bleaching can lead to mortality, although corals can recover by regaining symbionts after the stress has abated [Douglas2003-nr; Stat2009-qq]. Here, we track coral symbioses and survival at the epicenter of bleaching impact (Kiritimati, Central Pacific), and show, contrary to our current paradigm of coral bleaching and recovery dynamics, that some corals have the capacity to re-establish symbiosis before heat stress subsides. Furthermore, we demonstrate potential mechanisms for coral survival and recovery, including the lack of preferential symbiont expulsion, and the effect of local human disturbance on pre-bleaching symbiont community structure and the probability of coral survival. Together, these results show the potential for reef corals to survive extreme warming events, providing tentative hope for the survival of corals in the Anthropocene.