

Tree ring studies are highly suitable for evaluating the climate sensitivity of tropical tree growth: they yield accurate measurements of diameter increment, directly reveal the lifetime growth history of trees, and allow additional measurements of stable isotope fractions. Tree ring research in temperate forests has generated important insights into tree responses to temperature, rainfall, solar radiation and other climatic variables. Using the same set of established techniques, tropical tree ring studies have shown sensitivity of tree growth to rainfall [6], air temperature [7], El Niño indices [8] and anomalies in sea surface temperature [9] (Table S1 in the supplementary material online). Such climate–growth analyses can be used to project potential tree responses under climate change scenarios [9]. Thus, tree ring data can provide a vital input for the ‘rigorous, quantitative, long-term (multi-decadal) monitoring’ that Corlett recommends.

In addition, tree ring studies can be used to evaluate whether the growth increase observed in PSPs [3] can be corroborated for longer periods. Such long-term growth increases have been observed for several Amazonian species [10], but not in Asian species [11], and are consistent with an expected positive response to increased atmospheric CO<sub>2</sub>-pressure or nutrient supply. Clarity about the (physiological) causes of growth increases can be obtained by analyzing stable isotopes of carbon ( $\delta^{13}\text{C}$ ; revealing changes in water-use-efficiency [11]) and nitrogen ( $\delta^{15}\text{N}$ ; revealing changes in nitrogen cycling [12]).

Tropical tree ring studies are a valuable addition to PSP-based approaches in evaluating tropical forest sensitivity to climatic changes. These two research techniques provide complementary information. PSPs deliver rates of recruitment, mortality and growth for all species over relatively short periods and at low temporal resolution. Tree ring analyses yield lifetime growth rates and physiological responses to environmental changes for a subset of species, over long periods and at annual resolution. Ideally, both approaches should be combined at the same or nearby sites. We conclude that tree ring research is already contributing to fulfilling the research needs formulated by Corlett – to better understand climate change effects on tropical forests – and will increasingly do so in the future.

## Acknowledgements

P.A.Z. acknowledges support by the European Research Council (ERC grant #242955); R.J.W.B. was supported by the Gordon and Betty Moore Foundation. We thank William Laurance for comments on a draft version.

## Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.tree.2011.12.007.

## References

- Corlett, R.T. (2011) Impacts of warming on tropical lowland rainforests. *Trends Ecol. Evol.* 26, 606–613
- Phillips, O.L. *et al.* (1998) Changes in the carbon balance of tropical forest: evidence from long-term plots. *Science* 282, 439–442
- Lewis, S.L. *et al.* (2009) Changing ecology of tropical forests: evidence and drivers. *Annu. Rev. Ecol. Syst.* 40, 529–549
- Worbes, M. (2002) One hundred years of tree-ring research in the tropics – a brief history and an outlook to future challenges. *Dendrochronologia* 20, 217–231
- Rozendaal, D.M.A. and Zuidema, P.A. (2011) Dendroecology in the tropics: a review. *Trees Struct. Funct.* 25, 3–16
- Brienen, R.J.W. and Zuidema, P.A. (2005) Relating tree growth to rainfall in Bolivian rain forests: a test for six species using tree ring analysis. *Oecologia* 146, 1–12
- Devall, M.S. *et al.* (1995) Dendroecological analysis of *Cordia alliodora*, *Pseudobombax septenatum* and *Annona spraguei* in central Panama. *IAWA J.* 16, 411–424
- Schöngart, J. *et al.* (2004) Teleconnection between tree growth in the Amazonian floodplains and the El Niño–Southern Oscillation effect. *Global Change Biol.* 10, 683–692
- Brienen, R.J.W. *et al.* (2010) Climate-growth analysis for a Mexican dry forest tree shows strong impact of sea surface temperatures and predicts future growth declines. *Global Change Biol.* 16, 2001–2012
- Rozendaal, D.M.A. *et al.* (2010) Tropical tree rings reveal preferential survival of fast-growing juveniles and increased juvenile growth rates over time. *New Phytol.* 185, 759–769
- Nock, C.A. *et al.* (2011) Long-term increases in intrinsic water-use efficiency do not lead to increased stem growth in a tropical monsoon forest in western Thailand. *Global Change Biol.* 17, 1049–1063
- Hietz, P. *et al.* (2011) Long-term change in the nitrogen cycle of tropical forests. *Science* 334, 664–666

0169-5347/\$ – see front matter © 2012 Elsevier Ltd. All rights reserved.

doi:10.1016/j.tree.2011.12.007 Trends in Ecology and Evolution, April 2012, Vol. 27, No. 4

# Symbiotic transition of algae–coral triggered by paleoclimatic events?

Dan Tchernov<sup>1\*</sup>, Tali Mass<sup>2\*</sup> and David F. Gruber<sup>3\*</sup>

<sup>1</sup> Marine Biology Department, The Leon H. Charney School of Marine Sciences, University of Haifa, Mount Carmel, Haifa 31905, Israel

<sup>2</sup> Interuniversity Institute for Marine Science, Eilat 88103, Israel

<sup>3</sup> Department of Natural Sciences, City University of New York, Baruch College, Box A-0506, 17 Lexington Avenue, New York, NY 10010, USA

The algae–coral endosymbiosis is a canonical instance of mutualistic interaction, a textbook example of a relation-

ship between two species in which each derives benefits. The dinoflagellate algae accommodate nearly all of the respiratory demands of the coral via the excretion of readily available carbohydrates, and enhance calcification as

Corresponding author: Tchernov, D. (dtchernov@univ.haifa.ac.il).

\* All authors contributed equally.

well as nitrogen recycling. In return, the coral provides the algae with excreted nutrients and protection from predation. However, this relationship has been compromised at least three times since the Permian–Triassic (P/T) extinction event [251 million years ago (Ma)] [1]. The divorce of algae and coral has been repeatedly demonstrated to be detrimental to the host, resulting in coral bleaching events that have contributed to significant declines in reefs over the past century. Climatic factors, such as elevated water temperatures above the annual maximum average, cause the photosynthetic membrane of lipids to undergo a phase transition and ‘melt’ [2]. In many cases, the corals survive the bleaching event [3] and modify their algal community structure toward more heat-resistant clades [4]. Although acidification causes skeletal and colonial loss and may expedite bleaching, it does not break the algae–coral relationship [5], and findings suggest that, three times out of five, loss of coloniality by scleractinians (stony corals) resulted in symbiotic solitary corals [1].

Although scleractinian corals first occur in the fossil record 241 Ma, they may have first appeared far earlier in the Paleozoic, as soft-bodied, anemone-like Cnidaria [6], a theory supported by phylogenetic evidence [7]. This poses the important question: how did stony corals suddenly appear in the geological record, with numerous species present, after millions of years of vacancy? We propose that atmospheric oxygen may have had a profound impact on the algae–coral relationship, not only permitting an explosive radiation of species, but also setting the stage for the predicament that vulnerable corals presently face.

Stable fossil coral isotopes show that, since their first appearance in the fossil record during the late Anisian, 10 million years after the P/T extinction event, almost 50% of hard corals have possessed photosynthetic symbionts throughout their fossil history [8]. *Symbiodinium* spp., the main dinoflagellate algae within corals, has Form II ribulose-1,5-bisphosphate carboxylase oxygenase (RuBisCO), an ancient enzyme traced to obligatory anoxygenic bacteria that prefer low oxygen conditions. Recently, it has been demonstrated that high concentrations of oxygen within coral tissues attenuate *Symbiodinium* net photosynthesis via photorespiration, constituting an adaptive disadvantage under elevated oxygen concentrations [9].

Following the P/T extinction event, atmospheric oxygen rapidly declined from approximately 30% to 13% and, since then, has gradually risen to the current 21% concentration. Therefore, the sharp decline in oxygen enabled an energetically beneficial photosynthetic process to occur and endowed the algae–coral holobiont with a selective advantage in the photic zone, thus accelerating coral propagation towards reef dominance. At the same time, phylum Dinoflagellata also began to emerge, as witnessed through the accumulation of dinoflagellate cysts in the geological record.

It is feasible that an early relationship between dinoflagellates and corals occurred in deeper waters, with the dinoflagellate operating in a parasitic capacity [10]. This theory is supported by studies of *Symbiodinium* living in gastrodermal cells of corals in mesophotic waters (<1%

surface irradiance intensity) that show translocation of carbon from the coral to the dinoflagellate algae [11] when light is <20% of the surface irradiance intensity. In addition, it has been suggested [12] that hydrozoa originated in deeper waters and migrated upward into the sun-drenched shallow waters.

Following the global oxygen decrease to levels where net dinoflagellate photosynthesis was enabled, the additional energy endowed to scleractinian corals became a monumental competitive advantage. When the dinoflagellate ‘parasites’ transitioned to a capacity of providing for the energetic requirements of the corals, the latter were empowered with a competitive advantage over other shallow-water organisms, enabling them to increase their calcification rates. Calcification provides corals with their own substrate, a self-made foothold that assisted their radiation to the current 1300–2500 scleractinian species.

The low oxygen event following the P/T may have contributed to the transition of the algae–coral relationship from parasitism to symbiosis and, ultimately, to the evolutionary success of corals. Now, however, many symbiont-bearing species of corals are at the boundary of their environmental threshold and are undergoing drastic declines. Thus, a symbiosis solidified by paleoclimate change is now being threatened by modern climate change, and the fate of zooxanthellae corals in the Anthropocene remains to be determined.

#### Acknowledgments

This research was supported by the Israel Science Foundation (grant #981/05 to D.T.) and US National Science Foundation (grant # 0920572 to D.F.G.).

#### References

- Barbeitos, M.S. *et al.* (2010) Repeated loss of coloniality and symbiosis in scleractinian corals. *Proc. Natl. Acad. Sci. U. S. A.* 107, 11877–11882
- Tchernov, D. *et al.* (2004) Membrane lipids of symbiotic algae are diagnostic of sensitivity to thermal bleaching in corals. *Proc. Natl. Acad. Sci. U.S.A.* 101, 13531–13535
- Tchernov, D. *et al.* (2011) Apoptosis and the selective survival of host animals following thermal bleaching in zooxanthellate corals. *Proc. Natl. Acad. Sci. U.S.A.* 108, 9905–9909
- Baker, A.C. (2001) Reef corals bleach to survive change. *Nature* 411, 765–766
- Fine, M. and Tchernov, D. (2007) Scleractinian coral species survive and recover from decalcification. *Science* 315, 1811
- Stanley, G.D. (2003) The evolution of modern corals and their early history. *Earth Sci. Rev.* 60, 195–225
- Medina, M. *et al.* (2006) Naked corals: skeleton loss in Scleractinia. *Proc. Natl. Acad. Sci. U.S.A.* 103, 9096–9100
- Stanley, G.D. and Helmle, K.P. (2010) Middle Triassic coral growth bands and their implication for photosymbiosis. *Palaaios* 25, 754–763
- Mass, T. *et al.* (2010) Flow enhances photosynthesis in marine benthic autotrophs by increasing the efflux of oxygen from the organism to the water. *Proc. Natl. Acad. Sci. U.S.A.* 107, 2527–2531
- Hovasse, R. (1924) ‘*Zooxanthella chattonii*’ (*Endodinium chattonii*). *Bull. Biol. Fr. Belg.* 58, 34–38
- Einbinder, S. *et al.* (2009) Changes in morphology and diet of the coral *Stylophora pistillata* along a depth gradient. *Mar. Ecol. Prog. Ser.* 381, 167–174
- Lindner, A. *et al.* (2008) From offshore to onshore: multiple origins of shallow-water corals from deep-sea ancestors. *PLoS ONE* 3, e2429