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# This Week's Citation Classic®

**Connell J H.** Diversity in tropical rain forests and coral reefs.
*Science* 199:1302-10, 1978.
[University of California, Santa Barbara, CA]

High species diversity in tropical communities can be maintained in a nonequilibrium state by frequent disturbances, gradual changes in climate, or equivalence among species in competitive ability. If equilibrium is reached, diversity may be maintained by niche diversification or compensatory trends in recruitment, growth, or mortality. [The *SCI*® indicates that this paper has been cited in over 455 publications.]

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In 1961 I had just received tenure so I decided I could strike out in a new research direction—try something new or outrageous—without worrying about whether it might cause a hiatus in my publication record. I had been studying marine intertidal animals in temperate latitudes but had begun to wonder why so many species could coexist in tropical communities. I decided to pack up my family and head for the tropics of Australia. At the time I had a mind-set that ecological communities were all neatly regulated around some equilibrium level. I was sure that the component species had been evolutionarily selected until they were coadjusted in their niches so as to fit with each other. This was the prevailing view of most ecologists at that time.

I started work on corals on the Great Barrier Reef and also teamed up with the only two Australian ecologists then working in tropical rain forests, Len Webb and Geoff Tracey. They had the essential and rare ability to identify the many very similar tree species, without which I was helpless. They also knew a lot about the biology and ecology of the trees and forests in Queensland, as well as being all-round good company.

My working hypothesis for tropical communities was that the abundances of the different species were under frequency-dependent regulation. Whenever a species became very common, forces would begin to operate that would tend to reduce it. The reverse happened if a species became very rare. Thus, all species would be kept from becoming either extinct or very common. I held forth about all this to two Australian ecologists at teatime one day, soon after I arrived. They nodded politely and one of them, Charles Birch, said, "Fine, but also keep your eyes open for tropical weather up in Queensland—some of those cyclones might shake things up a bit." I mentally shrugged this off—I knew communities were well regulated.

I published a paper that said all of this,[1] and, having committed myself in print, was jolted from this "balanced" position by a severe hurricane that chewed its way across my coral reef and onto the coast, over one of my rain-forest plots. Birch was right, and my well-regulated communities were indeed shaken up. I decided that I had better stand back and look at the bigger picture: maybe I should entertain some alternative hypothesis about mechanisms maintaining tropical diversity instead of clinging to the one I had brought to the tropics from my temperate ivory tower.

The result was the paper that is the subject of this article. I think that it has been cited so often because it presents several different possible mechanisms that can produce or maintain high diversity in coral reefs or rain forests, and it suggests the conditions under which each could apply. Some of these have since been tested.[2,3]

The moral of this story, as James Thurber says, is that "it is better to ask some of the questions than to know all the answers."[4]

1. **Connell J H.** On the role of natural enemies in preventing competitive exclusion in some marine animals and in rain forest trees. (den Boer P J & Gradwell G R, eds.) *Dynamics of populations*. Wageningen: PUDOC, 1971. p. 298-312. (Cited 65 times.)
2. **Connell J H, Tracey J G & Webb L J.** Compensatory recruitment, growth and mortality as factors maintaining rain forest tree diversity. *Ecol. Monogr.* 54:141-64, 1984.
3. **Connell J H & Keough M.** Disturbance and patch dynamics of subtidal marine animals on hard substrates. (Pickett S T A & White P S, eds.) *The ecology of natural disturbance and patch dynamics*. New York: Academic Press, 1984. p. 125-51.
4. **Thurber J.** The scotty who knew too much. *The Thurber carnival*. New York: Penguin, 1953. p. 211.




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