EL NIÑO AND BIODIVERSITY

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GLOSSARY

bottom-up vs. top-down Description of the forces governing overall community structure: availability of nutrients is a bottom-up force and predators are a top-down force. Both may regulate, for example, the amount of standing plant biomass, or whether a lake is clear or murky.

density dependence A common ecological phenomenon whereby the effect of an entity (e.g., a species' rate of population growth) is a nonlinear function of its density. So, for instance, for the same input of energy, a species may increase in population rapidly at low and intermediate densities, but because of physical interference while foraging, more slowly at higher densities.

primary productivity The *in situ* transformation of chemical or (more commonly) solar energy into biomass, producing the primary energy source for the rest of the community.

selection regime A situation in which a particular set of evolved traits is favored. Here, the newly established population evolves in a different direction from the ancestral population.

teleconnections Atmospheric interactions between widely separated regions that have been identified through statistical correlations. For example, El Niño involves large-scale changes in climatic conditions over the Pacific that are linked to increased winter rainfall in the South West of the United States through a teleconnection.

trophic inputs Energy entering a community at higher levels in the "food chain," for example, plant matter that enters a community via drifting through in streams.

upwelling An ocean phenomenon whereby cooler, more nutrient-rich water rises up from the bottom of the ocean to the surface. This occurs where currents of contrasting temperatures meet. The extra nutrient influx allows for specific and rich "upwelling ecosystems" in these areas (e.g., off the coasts of Chile and Peru, and South-West Africa).

THE EL NIÑO-SOUTHERN OSCILLATION (ENSO) is a periodic large-scale climactic event that has varying effects on biodiversity, especially at lower latitudes. Increased sea surface temperature facilitates dispersal across the Pacific but extreme events are implicated in massive coral die-off and subsequent community collapse; rains affect succession, community structure, and trophic interactions in water-limited systems, but drought can facilitate catastrophic fires and regime shifts. Positive feedbacks associated with ENSO events (i.e., carbon input from fire) and ongoing global climate change mean that ENSO itself and its effects may self-reinforce. The ensuing impacts on biodiversity are likely to be increasingly detrimental.

I. INTRODUCTION TO EL NIÑO

The El Niño-Southern Oscillation (ENSO) is a climatic and oceanographic phenomenon centered in the Tropical Pacific. Extreme oscillations in ENSO are termed "El Niño" and "La Niña" events, depending on phase (see Figs. 1a, b), with El Niño generally being the more extreme deviation. Such ENSO events, which historically have occurred every 2–7 years on average, can have dramatic, cascading, and long-lasting effects on terrestrial and marine ecosystems spanning numerous regions worldwide.

Recent models suggest that predicted global climate change will result in more frequent and more extreme El Niño events (Tudhope *et al.*, 2001), though there are still uncertainties in the exact nature of the predicted changes. Evidence from corals, however, suggest that the amplitude of modern ENSO events appears to be significantly greater now than during any other period in the past 130,000 years (Tudhope *et al.*, 2001). The 1997/98 record-breaking El Niño followed only 15 years after the previous record El Niño event of 1982/83. The 1997/98 El Niño developed so quickly that each month set a new record for warm sea-surface temperatures (SSTs) based on records back to the middle of the nineteenth century (McPhaden, 1999).

Extreme ENSO events change weather patterns, increasing precipitation in normally dry areas and reducing precipitation in normally wetter areas, as well as increasing SSTs and reducing upwelling in the

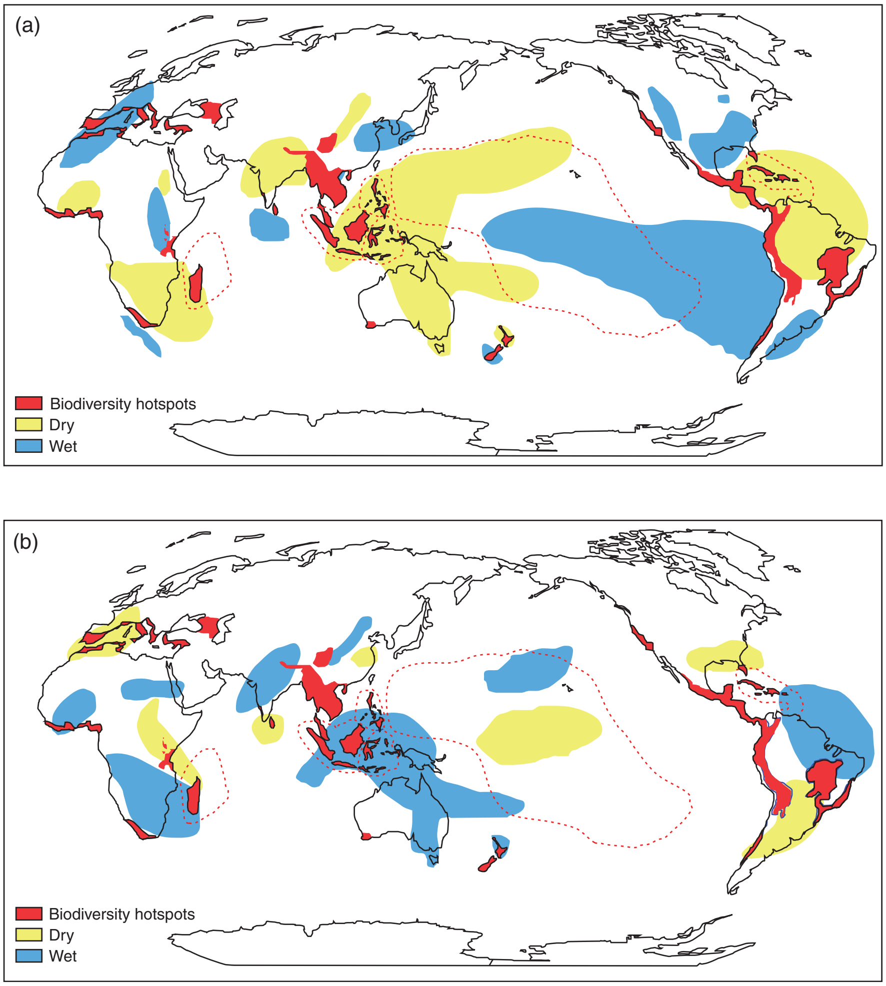

FIGURE 1 ENSO and biodiversity. A Robinson projection of the world with areas most greatly affected by the El-Niño (a) and La Niña (b), phases highlighted (data from Allan *et al.*, 1996). Yellow: areas with reduced precipitation; blue: areas with increased precipitation. Superimposed are the dark red terrestrial areas designated as world biodiversity "hotspots" (Myers *et al.*, 2000). The overlap is notable.

eastern Pacific Ocean. ENSO events have been shown to influence ecosystem functioning (Curran *et al.*, 1999); changes to ENSO therefore may affect the long-term biodiversity of large parts of the planet, especially when it is appreciated that climactic changes associated with both El Niño and La Niña occur in some of the most biodiverse areas of the planet (Holmgren *et al.*, 2006; see Figs. 1a, b). Here, we survey what we feel are some of the best-documented effects of El Niño events on biodiversity. We have chosen to organize these effects by the direct El Niño-induced change (fire and drought, increased rain, increased water temperature, and current changes) rather than the more common biome-based approach.

II. EXPECTED EFFECTS

If the climactic effects are large enough (e.g., drought-induced fire, see Section III.A), ENSO events can be characterized as cyclical disturbance events. If moderate in intensity and infrequent, such disturbances could theoretically increase local diversity over that expected under steady-state conditions (the intermediate disturbance hypothesis, Connell, 1978). So, past ENSO cycles might have encouraged increased local species richness, though retrospective studies are difficult.

Long-lived organisms (e.g., trees) may be adapted to an evolutionary history of repeated, within-lifetime disturbance. Regardless, rapid changes in ENSO intensity can increase environmental variation beyond a species' threshold, causing a die off. If disturbances occur at too high a rate relative to recruitment, successive decimations can produce severe population bottlenecks, increasing the probability of both deterministic and stochastic extinction.

In contrast, short-lived organisms that can evolve within El Niño cycles may be constantly adapting to changing conditions. Microcosm experiments suggest that intermediate temporal variation in environments (e.g., oscillations between one benign and one "harsh" environment, such as El Niño-induced drought) may increase genetic variation, though with less of an effect than spatial heterogeneity (Kassen, 2002). However, a sharp increase in amplitude and frequency of temporal disturbance can erode genetic variation, with evolution toward either "generalist" phenotypes that do well in both regimes, or, if the harsh environment is severe enough, "specialist" phenotypes adapted to this harsh though rarer environment (e.g., adapted to El Niño drought years). El Niño events are also likely to have species-specific effects on short-term evolutionary dynamics. So, on the Galapagos islands, trait evolution of finches changed rapidly in response to the strong El Niño events of both 1976/77 and 1982/83; for instance, drought killed more females than males of one species, leading to interspecific hybridization and subsequent population genetic changes (Grant and Grant, 2002).

Through changes in current movement and increased sea temperatures (see Section III.C), regular ENSO events also increase the potential for long-range dispersal. Such migration and gene exchange often decreases geographic genetic structure. However, rarer and more extreme events may cause entirely new habitats to be colonized, especially by species with plankton. This could promote speciation by creating separated populations in novel selection regimes. As well, depending on how they affect the complexity of the new habitats, newly introduced species can either positively or negatively influence species richness in existing communities (Crooks, 2002).

III. OBSERVED EFFECTS

A. Fire and Drought

Although fires are not new to wet tropical areas, their rate of occurrence has generally been on a scale of hundreds to thousands of years so that many forests and tree species are ill-adapted to frequent large-scale fire events (Cochrane, 2003). The observed and projected increase in ENSO-induced wildfires means that forest fires are now considered to be a major threat to tropical biodiversity (Laurance, 2003).

The Brazilian Amazon and Western Indonesia, particularly eastern Borneo, are two of the areas worst affected by ENSO-induced forest fires: they also harbor among the most diverse floras and faunas in the world. El Niño-associated fires were described for East Kalimantan (Indonesian Borneo) as early as 1914, but until recently these were restricted in scale (Brown, 1998). The first recorded major burning event in East Kalimantan was during the 1982/83 ENSO event, which caused a conservative 5.5×10^9 US$ of damage, not including ecological costs (Siegert *et al.*, 2001). The 1997/98 El Niño-induced fires in East Kalimantan were even larger: an estimated 5.2 million ha of East Kalimantan were affected by fires, costing 1.4 billion US$ for smoke-related damage alone. These fires mainly occurred in recently accessed logging concessions (Siegert *et al.*, 2001).

In the Amazon, 20,000 km^2 of forest burned during the extreme 1997/98 El Niño; satellites revealed almost 45,000 individual fires, most of which were sparked by humans (Laurance, 1998). An additional 1.5 million km^2 of forest became susceptible to burning, but did not burn because of insufficient ignition sources (Nepstad *et al.*, 2001). However, frontier expansion is bringing people and thus ignition sources closer to forest tracts. Although the effects are poorly known in the Amazon, an estimated 50% of remaining forests have already been affected by fires, which have caused more deforestation than intentional clearing in recent years (Cochrane *et al.*, 1999).

Deforestation fires can smolder for up to a week (Fig. 2), and can destroy soil-stored seed, reduce the number of resprouting plants, and lead to a longer term decline in soil fertility due to combustion of organic materials. Repeated burning can deplete the seed supply and cause additional mortality to upper-canopy trees. Typical low-intensity ground fires kill nearly 40% of trees less than 10 cm dbh (diameter at breast height) and most vines and ground forbs. Mortality is highly species-specific (Slik, 2004). With multiple burns, large fire-contacted trees have no survival advantage over smaller trees (Laurance, 2003). Owing to the lack of a seed bank for climax species in the tropics, their regeneration following burn events depends on sapling survival, resprouting, and the seed rain from surviving trees. Sapling survival, however, can be very low following burning. In burned forest in East Kalimantan sapling density was only 2.5% of that found in adjacent unburned forest (Cleary *et al.*, 2006a). Resprouting is also highly species-dependent, in part due to changed light conditions (Slik, 2004); whereas a few rainforest species (e.g., *Fordia splendidissima*) are able to resprout profusely after burning, many others fail to resprout at all. Regeneration will therefore, to a large extent, depend on surviving trees and areas of unburned forest that tend to be located in low-lying topography such as forest flood plains (Slik, 2004). Multiple fire events reduce the area of remnant unburned forest because fires tend to become more probable along previously disturbed edges. Under a frequent fire regime, low-diversity stable grasslands can develop. Under a less-frequent burn regime, novel pioneer-dominated forests (e.g., dominated by "typical" pioneer genera such as *Macaranga*, *Mallotus*, or *Trema*) may replace the normal dipterocarp forests, with unknown effects on forest diversity.

Primary forests are less susceptible to forest fires than logged and already burned forests because they are more humid (Brown, 1998; Cochrane, 2003) and contain less dead wood (Nepstad *et al.*, 2001). Therefore, during 1982/83 and 1997/98, logged forest suffered greater tree mortality than unlogged forests, and fire intensity was directly related to the intensity of logging (Siegert *et al.*, 2001).

Animal responses to fire are still poorly understood. Small mammals, reptiles, and amphibians, for example, were reported to increase in abundance and species richness following fires in South America while birds and insects declined (Cochrane, 2003; Barlow *et al.*, 2002; Fredericksen and Fredericksen, 2002). Animals negatively affected by forest fires in Amazonia

FIGURE 2 Burning lowland tropical Dipterocarp rainforest, Kalimantan, Indonesian Borneo, during the 1997–98 El Niño fires. Photo credit: D. F. R. Cleary.

included slow species with poor climbing ability, cavity-breeding birds, army ants, understory wasp colonies, and leaf-litter invertebrates. Affected forests were also conspicuously silent, generally lacking in the usual vocal activity of monkeys and birds. The birds most affected were uncommon species, habitat specialists, and species that avoided disturbed areas (Laurance, 2003). All of the insectivorous guilds were severely affected by fire, of which the dead-leaf-gleaners and ant-followers were worst affected.

In Borneo, butterfly species richness declined dramatically following forest fires; specialist and restricted range butterfly species recorded before the 1997/98 ENSO event were also much less likely to return to the regenerating forest than were generalist and wide-ranging species (Charrette *et al.*, 2006). In addition to this, the allelic richness of populations of one species, *Drupadia theda*, that survived the fires, was substantially lower in burned forest and a small unburned isolate than in a large unburned isolate (Cleary *et al.*, 2006b).

In general, while large frugivores and other vertebrates were adversely affected by single burn events in the Amazon, most primary forest specialists across all guilds were extirpated from twice-burnt forest (Barlow and Peres, 2006); we have found the same extreme effects of multiple fires for Bornean butterflies and dragonflies.

Even without direct burning, increasing El Niño events could affect tropical forest biodiversity. In Panama, there is a strong relationship between El Niño events, which increase fruiting in rainforest trees, and subsequent famine-induced population changes among frugivorous mammals when the following year is also dry (Wright *et al.*, 1999). ENSO-induced drought can also increase tree mortality, particularly in previously disturbed forest (Harrison, 2000; Slik, 2004). In Northern Borneo, El Niño-related drought in a small forest fragment (<6500 ha) led to mass local extinction of fig wasps thereby disrupting the important mutualism between fig wasps and their keystone fig hosts (Harrison, 2000). Also in Borneo, we found that butterfly species richness was not only substantially lower in burned forest, but also in small (<5000 ha) and large (>100,000 ha) unburned isolates surrounded by burned forest than in continuous forest or forest sampled before the 1997/98 El Niño (Cleary, 2003).

B. Increased Precipitation

1. Water as a Limiting Factor

Greater rainfall often leads to enhanced primary productivity. Normally, arid islands in the Gulf of California experienced a rise in plant cover from 0% to 4% in non-El Niño years to 54–89% during El Niño years (Polis *et al.*, 1997). While annual plants account for the majority of ground cover increase, perennial plants also respond to increased water availability by increasing their growth, and their flower and fruit production. Seed banks in arid and semiarid regions have been observed to experience a sixfold increase during El Niño-induced wet periods. The species composition of these plant communities also changes during wet years, with normally uncommon or absent species becoming dominant. Thus, the species richness of these plant communities during the common dry years is not representative of the overall diversity contained in the seed bank (Gutierrez *et al.*, 2000). El Niño therefore causes drastic changes in short-term biodiversity.

As well as such short-term changes, El Niño-associated increases in precipitation can also aid in the longer term recruitment of shrubs and trees in dry areas. Years with very wet El Niño events may act as a “window of opportunity” for establishment of seedlings, which may then help to create a less-hostile environment for future generations of seedlings (Holmgren *et al.*, 2001). In semiarid ecosystems that have alternate stable states in terms of vegetation (i.e., barren land, degraded savannah, shrubland, or dry forest), changes in precipitation can play a role in moving the ecosystem from one equilibrium to another (Holmgren *et al.*, 2006). However, accumulation of plant biomass during wet years can also lead to greater fuel loads, facilitating the ignition and spread of wildfires during contrasting dry years (Block and Richter, 2000).

The effects of increased precipitation can be even more complex. For instance, the dry ecosystems of the Gulf of California islands are influenced both by El Niño-induced influxes of primary productivity and by trophic inputs from the adjacent, highly productive marine ecosystem. Seabirds deposit guano that enhance primary productivity increases during El Niño years, and carrion from seabird feeding (i.e., remains of marine organisms) act as a food resource for scavengers more generally (Sanchez-Pinero and Polis, 2000). Omnivorous rodents on these islands obtain marine food resources during dry years, but shift to seed consumption during pulses of primary productivity. So, on these islands, this rodent guild experienced a fourfold population increase in response to one El Niño-induced pulse, and a subsequent population crash when dry conditions returned. In contrast, granivorous rodents on the same islands experienced a more moderate population increase during El Niño (1.6 times), probably mediated by interaction with the omnivorous species, but maintained a more stable population after dry conditions returned (Stapp and Polis, 2003). The importance of these direct (food resource) and indirect (nutrients via guano) spatial trophic subsidies illustrates the tight linkage between the marine and terrestrial realms in the California gulf island system. This linkage tends to weaken during El Niño events (Stapp and Polis, 2003); thus, changes in ENSO could have effects on food web dynamics and biodiversity of these islands.

In areas where water is a major limiting factor, the periodic bursts of precipitation associated with ENSO events can exert significant bottom-up effects on multiple trophic levels. The expected effect of rapidly increased primary productivity is a rise in herbivore populations, which can in turn positively affect both predator and pathogen populations. So, for instance, the 1992/93 El Niño increased precipitation in the southwestern United States, which led to increased deermouse density, allowing for a hantavirus outbreak (Holmgren *et al.*, 2006). Carnivorous bird populations respond to the variations in food resources by tracking these changes temporally (Jaksic *et al.*, 1992), and, at the community level, by forming looser guilds with divergence in diet (Jaksic *et al.*, 1993). However, top-down cascades can also be important. In the Chihuahuan Desert, Arizona, which experiences increased winter precipitation associated with El Niño events, some herbivore species that were previously abundant disappeared, some previously rare species became abundant, one novel species colonized the area, and other species experienced little change in their populations, while overall the diversity remained stable (Brown *et al.*, 1997). This indicates that the net effect on populations is dependent upon community-specific interactions within and among trophic levels. In addition, the state of the community prior to the change in precipitation is important in determining the effect of this change upon the community. For example, although Galapagos finches generally experience a population boost due to wet ENSO events, this boost can be mitigated by density-dependent effects if population levels had previously been high (Grant *et al.*, 2000).

C. Increased Sea-Surface Temperature

Increases in SSTs have both direct and indirect consequences for biological systems. ENSO-related positive SST anomalies correspond with changes in the speed and direction of ocean currents, reductions in nutrient upwelling, and changes in local environments of marine species.

1. Current Shifts

Dispersal of organisms by currents is an important process in establishing and maintaining diversity in aquatic ecosystems. For example, the Hawaiian biota comprises a subset of Polynesian biota and this similarity can be attributed to movement of organisms on currents associated with El Niño events (Richmond, in Glynn, 1990).

El Niño-induced changes in ocean currents may lead to long-distance dispersal of marine organisms from west to east. Genetic similarity between shallow-water populations separated by 5400 km of ocean in the eastern Pacific (known as the Eastern Pacific Barrier, EPB) indicates that gene flow occurs between these populations (Lessios *et al.*, 1998). During non-El Niño years, parcels of water carried by the North Equatorial Counter-Current take 100–155 days to cross the EPB; in El Niño years this is shortened to 50–81 days. Given the known maximum time that larvae can stay in the plankton and still successfully settle, the number of species able to successfully colonize a new region may be more than double under El Niño conditions (Richmond, in Glynn, 1990).

2. Nutrient-Level Shifts

During non-El Niño years, the eastern equatorial Pacific Ocean comprises a large upwelling ecosystem, where the relatively shallow thermocline allows nutrient-rich cool water to rise along the west coast of South America. This "tongue" of cool water extends as far west as the International Date Line and along the coast of Central and South America between ~10°N and ~20°S. During ENSO events, upwelling decreases, and the area of cool, productive water is progressively reduced to a pocket ~10% its usual size along the South American coast. ENSO-associated reductions in upwelling also occur in the near-coastal southeast Atlantic Ocean through teleconnections. As nutrient upwelling is the first-order process governing ocean primary productivity, the effects of reduced upwelling have significant impacts on both marine and terrestrial biota. These impacts can be seen along the equator in the eastern Pacific, where primary productivity can fall to as low as 6% of normal during El Niño years, while in the remaining productive region primary productivity falls to 20–50% of normal (Barber and Kogelschatz, in

Glynn, 1990). Such El Niño-induced changes heavily impact fish and species that graze zooplankton. The well-known short- and longer-term fluctuations of anchoveta and sardine in the Pacific (Chavez *et al.*, 2003) highlight how species-specific traits are important in determining response to climate fluctuations.

Declines in small fish and other food source populations have bottom-up effects on higher trophic levels. For example, Christmas Island's great frigate bird population fell from 20,000 to fewer than 100 over the course of 6 months following the extreme 1982/83 ENSO. While nest flooding and heavy rains may have caused some nestling death, adult abandonment of the island along with their young has been attributed to the disappearance of fish and squid as food resources.

In upwelling ecosystems, water temperature and availability of nutrients are tightly linked. Therefore, seabirds, fish, and marine mammals within these ecosystems have evolved behavioral adaptations that enable these species to use thermal cues as indicators of areas of abundant food. Short-term responses of species to changes in productivity may then be mediated through responses to anomalous SST during ENSO events. This results in a concentration of organisms residing in those areas where upwelling still occurs during El Niño events.

3. Coral Bleaching

Coral reefs are among the most diverse and productive ecosystems known and are one of the first to be severely affected by global climate change. The pronounced and rapid response of corals to global climate change is largely a result of the pronounced thermal sensitivity of most coral species (Graham *et al.*, 2006). Corals are successful at temperatures between 18°C and 30°C, and many reefs exist at close to their upper temperature threshold. Increases in SST and solar irradiance have been heavily implicated in the widespread bleaching (loss of symbiotic zooxanthellae) and mortality of reef-building corals during ENSO events. Excessive UV exposure, sedimentation, freshwater flooding, heavy metal pollution, cyanide poisoning, and nutrient enrichment in the form of ammonia or nitrate have also been shown to significantly affect the expulsion of symbiotic algae. When these factors come together, for example, during severe ENSO events, in reefs that have already reduced resilience due to other forms of human-induced disturbance, the effect can be dramatic (Zhu *et al.*, 2004).

Over the course of a severe episode, corals may lose 60% to $>90\%$ of their symbiotic algae, and remaining algae may lose 50–80% of their photosynthetic pigments (Glynn, 1996; Fig. 3). Depending on the

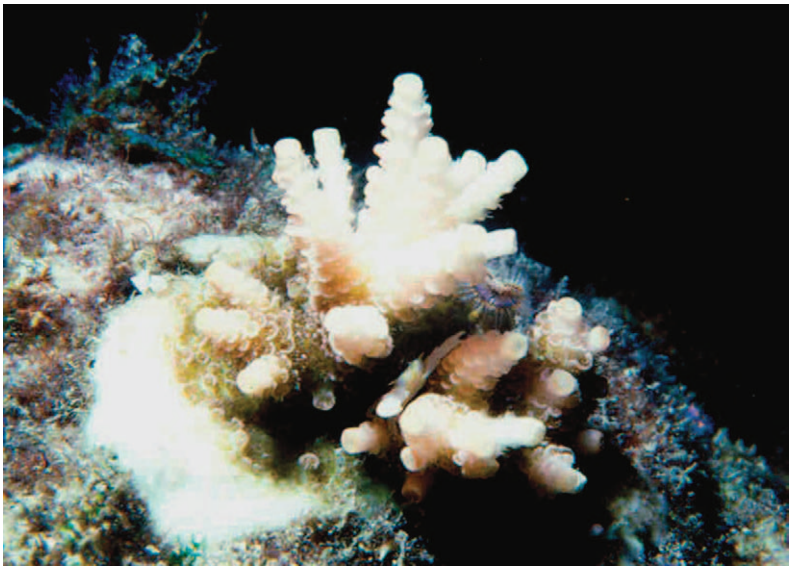

FIGURE 3 Example of El Niño-induced coral bleaching. Photo of a juvenile staghorn coral (*Acropora* sp.) at Pulau Pari, Thousand Islands, Indonesia, taken during the 1983–84 El Niño event. Bleaching has started at the tips and at the periphery of the coral base (see Hoeksema, 1991). Photo credit: Bert Hoeksema, Naturalis, The Netherlands.

severity and duration of the bleaching event, corals may regain their obligate symbionts with the return of favorable conditions. Alternatively, individuals or entire assemblages may die. Coral mortality corresponds with an often dramatic loss of coral species and reef cover of live corals. For example, two out of 12 coral species were virtually eliminated from Panama during the 1982/83 ENSO (Glynn and Feingold, 1992). As well, coral mortality leads to loss of structural complexity due to reef disintegration. In addition to the initial loss of diversity, species such as the crown-of-thorns starfish are able to exploit remaining corals more effectively, at least in part due to the corals' crustacean guards becoming less aggressive with the deterioration of their hosts (Glynn, in Glynn, 1990). Bioerosion and larval recruitment failure on damaged reefs also contribute to changes in species composition. Upon death, many corals are colonized by algae, which prevents coral regeneration and transforms these areas into nonreef-building communities (McManus and Polsenberg, 2004). As coral reefs play host to some of the world's greatest biodiversity, loss of these habitats could have profound effects on that diversity.

During the 1982/83 El Niño tropical eastern Pacific coral populations experienced up to 70–90% mortality; in the Galapagos Islands, mortality of most reefs was ~95%. Decimation of these populations has particularly profound effects in this region, where isolation from other reefs that could otherwise aid in repopulation prolongs recovery time. In coral reefs, the 1997/98 bleaching event was the most severe and widespread ever recorded (Nyström *et al*., 2000; Wilkinson, 2004). Some scientists fear that a threshold may have already been reached where reefs will not be able to cope with the increasing intensity and frequency of future bleaching events associated with ENSO-induced disturbances (Nyström *et al*., 2000). McWilliams *et al*. (2005) reported exponential increases in the extent and intensity of bleaching with increasing SST anomalies in the Caribbean; a rise of only 0.1°C resulted in 35% and 42% increases in the geographic extent and intensity of coral bleaching, respectively. Maxima of both are predicted to occur at SST anomalies of less than +1°C; this would coincide with the most conservative projection for warming in the Caribbean by the end of the twentieth century. Bleaching will, therefore, probably be a chronic stress factor for Caribbean coral reefs in the future. The loss of live corals in turn has had a number of cascade effects on other taxa. Long-term censuses of fish communities in Australia spanning bleaching events have shown species loss and highly distinct phase shifts in composition from pre-to-postbleaching with no evidence of regeneration (Bellwood *et al*., 2006; Garpe *et al*., 2006).

IV. FEEDBACK AND CONCLUSIONS

ENSO is associated with feedbacks at a global scale. Interestingly, the ecological changes caused by extreme El Niño events may also cause positive feedbacks (see Fig. 4).

Predicted changes in the frequency and severity of ENSO events, have the potential to greatly alter biodiversity and ecosystem functioning (Harrison, 2000; Holmgren *et al*., 2001, 2006). In particular, severe ENSO-induced droughts can cause devastating forest fires with profound effects on ecosystem dynamics (Holmgren *et al*., 2001). Although fires have always been present in Southeast Asia and in much of the world, population growth, habitat fragmentation, logging, changes in land-use, ENSO events, and the ubiquity of human ignition sources are responsible for the catastrophic fires in 1982/83 and 1997/98 (Laurance, 1998, 2003). In addition, both logging and previous fires increase the probability of future fires (Nepstad *et al*., 1999), which are often worse due to build up of fuel from dead wood. Secondary fires are, therefore, much worse than initial fires (Cochrane *et al*., 1999), leading to positive feedback.

Ironically, these fires may also be contributing to greater global warming, which may, in turn, feed back into the ENSO cycle (Fedorov and Philander, 2000). Because of their scale of occurrence, fires now have the potential to more than double carbon emission in dry years (Malhi and Grace, 2000), and fires may have released the carbon equivalent of ca. 41% of world fossil fuel use in 1997/98 (Cochrane, 2003). It is estimated that this, combined with other changes, has switched the tropics from a net carbon sink (2.0 Pg C/yr) to a net source (0.4 Pg C/yr) (Malhi and Grace, 2000). The release of large amounts of aerosols to the atmosphere can, furthermore, affect atmospheric stability and cloud formation and thereby reduce rainfall over large areas (Cochrane, 2003), thus compounding the risk of fire in these regions.

Conversely, increased precipitation in normally arid or semiarid regions can drive the restoration of degraded scrubland (Holmgren *et al*., 2006). In areas that have been subjected to overexploitation, episodes of relatively extreme moisture in conjunction with decreased grazing pressure can cause the system to move

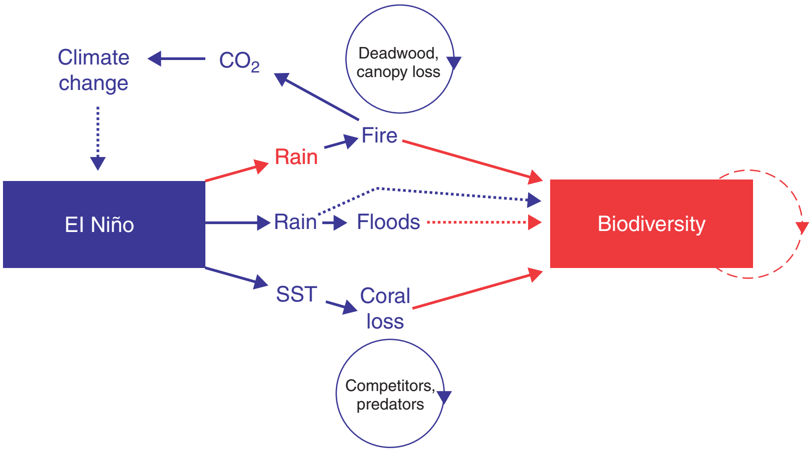

FIGURE 4 El-Niño feedbacks on biodiversity. Blue indicates increases and red indicates decreases. Solid arrows are well-established connections, and dotted arrows are more speculative. For example, El Niño causes decreased rainfall, which causes fires. The fires increase the severity of future fires, and these lead to a loss in biodiversity. Such fires also contribute CO_2 to the atmosphere, and if global climate change is linked to increased severity or frequency of ENSO-events, the feedback is positive. Likewise, increased SSTs are implicated in coral bleaching, which can reduce local biodiversity and lead to alternative stable states. Because of trophic cascades and loss of stability, losses of biodiversity may also be reinforcing.

to an alternative stable state of vegetation. In this manner, ENSO events may be partnered with land-management strategies, with a favorable outcome for biodiversity in these regions.

ENSO is one climatic cycle among many that occur over various temporal and spatial scales. It is a natural phenomenon, and has been functioning for at least the past 130,000 years (Tudhope *et al*., 2001). However, human activity may be causing ENSO events to become more frequent and extreme. As well, land-use practices leading to fragmentation and edge effects not only worsen the direct effects of ENSO but also compromise the ability of ecosystems to maintain or re-establish levels of biodiversity following disturbance. There is little doubt that ENSO-induced disturbance, at least those mediated by human activity, has strong effects on biodiversity at many spatial and temporal scales, and the evidence suggests the bulk of these effects are undesirable.

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