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El Niño and Biodiversity

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Glossary

Bottom-up versus 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 southwestern United States through a teleconnection.
Trophic inputs   Energy entering a community *via* pathways other than local primary production, and often at higher levels in the food chain. For example, nutrients from salmon carcasses are a periodic trophic input to the forest community adjacent to salmon 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 southwest Africa).

Introduction to El Niño-Southern Oscillation

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 Figure 1) with El Niño generally being the more extreme deviation. Such ENSO events, which have historically occurred every 2–7 years on average, can have dramatic, cascading, and long-lasting effects on terrestrial and marine ecosystems spanning numerous regions worldwide.

Some 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 suggests that the amplitude of modern ENSO events is significantly greater now than during any other period in the past 130,000 years (Tudhope *et al.*, 2001), while evidence from Galapagos diatoms indicates that the most recent 50 years have had the warmest sea-surface temperature (SST) of any 50-year period in the past 1200 years for the eastern equatorial Pacific Ocean (Conroy *et al.*, 2009). However, the complexities of modeling the interactive factors contributing to the onset, frequency, and severity of ENSO events currently preclude predictions about the magnitude and direction of future changes to this oscillation (Collins *et al.*, 2010). In recent years, the 1997/1998 record-breaking El Niño followed only 15 years after the previous record El Niño event of 1982/1983. The 1997/1998 El Niño developed so quickly that each month set a new record for warm SST based

on records dating 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 SST and reducing nutrient upwelling in the eastern Pacific Ocean. ENSO events have been shown to influence ecosystem functioning (Curran *et al.*, 1999); changes to ENSO may therefore affect the long-term biodiversity of large parts of the planet, especially when it is appreciated that climatic 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 Figure 2(a) and 2(b)). Here, we survey some of the best-documented effects of ENSO events on biodiversity. We have chosen to organize these effects by the direct ENSO-induced change (fire and drought, increased precipitation, increased SST and changes in ocean currents) rather than the more common biome-based approach.

Expected Effects

If the climatic effects are large enough (e.g., drought-induced fire, *see* Observed Effects: Fire and Drought), 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
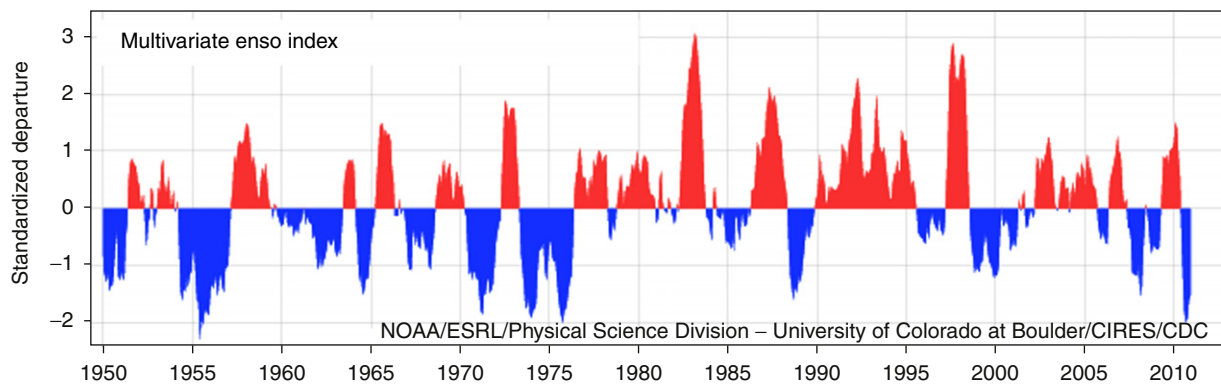
Figure 1   Time series of the Multivariate ENSO Index (MEI) from 1950–2010. The MEI is based on six observed variables over the Tropical Pacific: sea level pressure, surface zonal and meridional wind components, sea-surface temperature, surface air temperature, and cloudiness. Positive values of MEI (red) indicate warm, El Niño conditions, while negative values of MEI (blue) indicate cold, La Niña conditions. For more information about the MEI, see Wolter and Timlin (1993, 1998).

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 ENSO 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 under both regimes, or, if the harsh environment is severe enough, specialist phenotypes adapted to the harsh, though rarer, environment (e.g., adapted to El Niño-induced drought years). ENSO events are also likely to have species-specific effects on short-term evolutionary dynamics. For example, on the Galapagos Islands trait evolution of finches changed rapidly in response to the strong El Niño evens of both 1976/1977 and 1982/1983; 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 SST (*see* Observed Effects: Increased Sea-surface Temperature), 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).

Observed Effects

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 1982/1983 ENSO event, which caused a conservative 5.5×10^9 US\$ of damage, not including ecological costs (Siegert *et al.*, 2001). The 1997/1998 El Niño-induced fires in East Kalimantan were even larger, 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 1997/1998 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 the remaining forests have already been affected by fires, which have caused more deforestation than intentional clearing in recent years (Cochrane *et al.*, 1999).

El Niño and Biodiversity hotspots
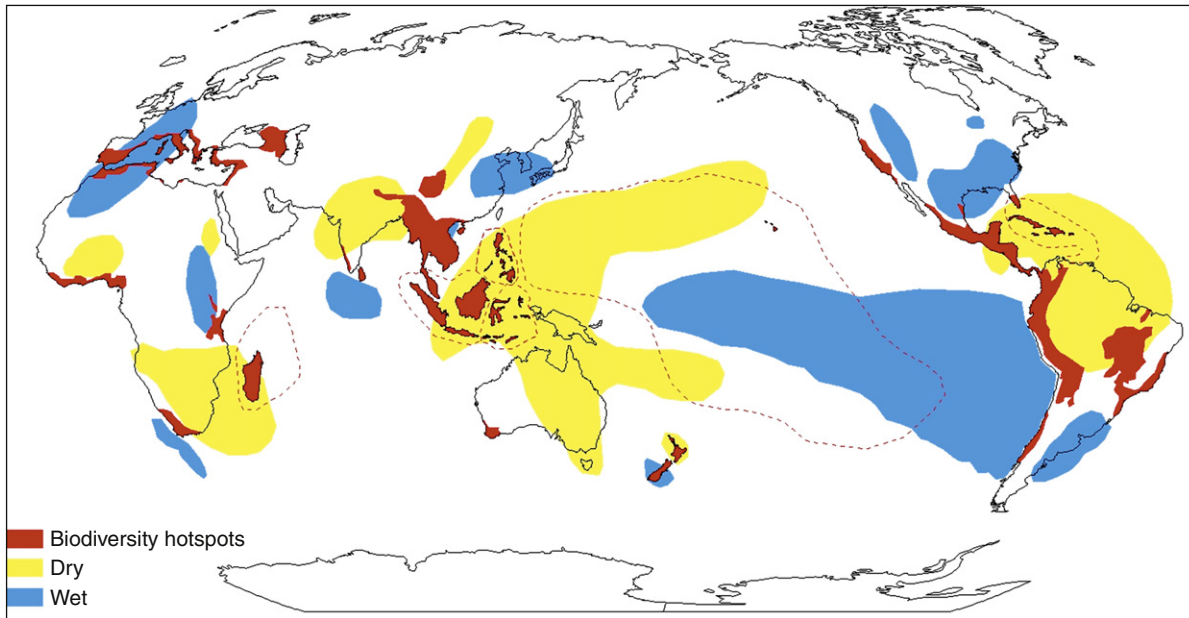
(a)

La Niña
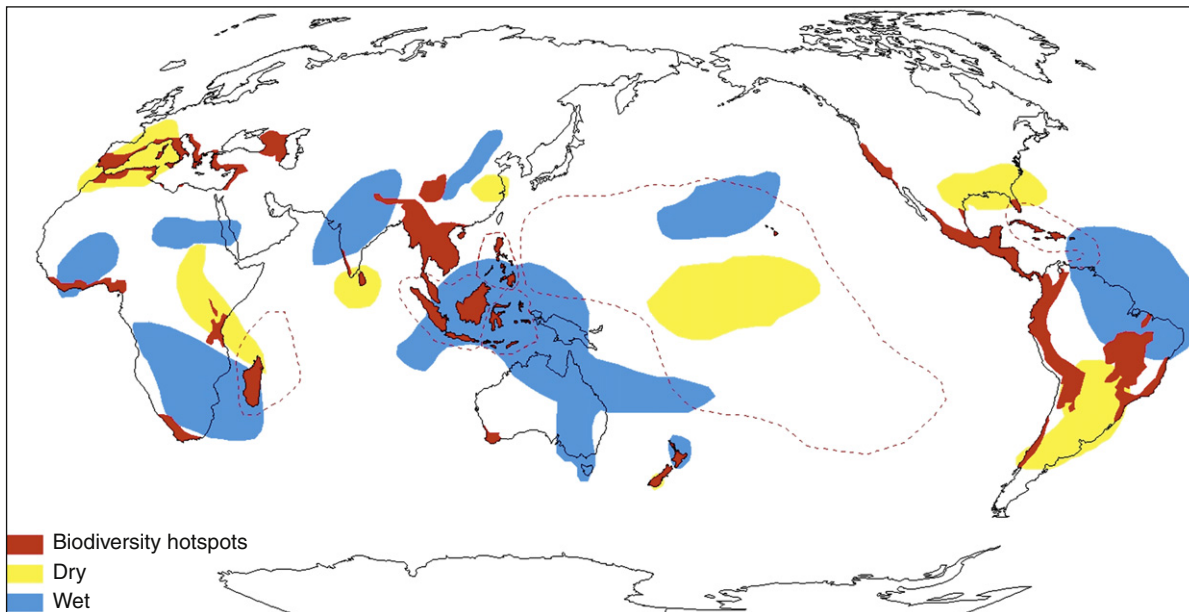
(b)

Figure 2   ENSO and biodiversity. A Robinson projection of the world with areas most greatly affected by the two phases of ENSO, El-Niño (a) and La Niña (b), highlighted (Allan *et al.*, 1996) Superimposed are the dark red terrestrial areas designated as world biodiversity ''hotspots'' (Myers *et al.*, 2000). The overlap is fairly strong, at least in part because both ENSO effects and species are concentrated in the tropics.

Deforestation fires can smolder for up to a week (**Figure 3**), 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 in diameter at breast height (dbh) 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

Figure 3 Lowland tropical Dipterocarp rainforest, Wanariset, Kalimantan, during the 1997–1998 El Niño fires.

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., 2006b). 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 biodiversity.

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 1982/1983 and 1997/1998, logged forests 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 forest 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 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 1997/1998 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., 2006a).

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 (Cleary et al., 2004).

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 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 1997/1998 El Niño (Cleary, 2003).

Increased Precipitation

Water as a Limiting Factor

ENSO-induced increases in precipitation act as resource pulses for primary producers in water-limited ecosystems. The expected effect of such pulses is an immediate increase in ephemeral plant density, with a delayed increase in perennial plant abundance, and herbivore and predator abundance. Over the short term, local biodiversity can change dramatically, as in the Flowering Desert of Copiapó, Chile. For example, normally arid islands in the Gulf of California experience an increase in plant cover from 0–4% in non-El Niño years to 54–89% during El Niño events (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 growth, and flower and fruit set production. Seed banks in arid and semiarid regions have been observed to experience a 5–10 fold increase during ENSO-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 apparent during the common, dry years is not representative of the overall diversity contained in the seed bank (Gutierrez et al., 2000).

As well as such short-term changes in plant communities, ENSO-associated increases in precipitation can also aid in the

recruitment of shrubs and trees in dry areas. Years with extreme, wet ENSO 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 of vegetation (i.e., barren land, degraded savannah, shrubland, or dry forest), pulses of precipitation can play a role in moving the ecosystem from one stable state to another (Holmgren et al., 2006). Interestingly, the process that leads to this type of phase shift may involve the periodic loss of top-down control of plant populations by herbivores. Pulses of precipitation allow plants to grow more rapidly than the numeric response of their herbivores, and this can result in a higher plant biomass equilibrium state, particularly when plants become less palatable with greater size (Scheffer et al., 2008). 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 on the islands, which enhances 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 wet years. So, on these islands, the omnivorous rodent guild experienced a fourfold population increase in response to one El Niño-induced pulse, and a subsequent crash when dry conditions returned. In contrast, granivorous rodents on the same islands experienced a more moderate population increase during the El Niño (1.6 times), probably mediated by food competition 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 in turn positively affect both predator and pathogen populations. For instance, the 1992/1993 El Niño led to increased deer mouse density in New Mexico, US, 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, and tend to follow bottom-up effects with a delay.

During an El Niño event in the Chihuahuan Desert, Arizona, some herbivore species that were previously abundant disappeared, one novel species colonized the area, and other species experienced little change in their populations, while overall diversity remained stable (Brown et al., 1997). This indicates that the net effect on populations is dependent on 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 on the community. For example, although Galapagos finches generally experience a population boost during wet ENSO events, this boost can be mitigated by density-dependent effects if population levels had previously been high (Grant et al., 2000).

Flooding

Floods cause catastrophic ecosystem change, with immediate abiotic and biotic impacts that may influence community regeneration in the long run. Erosion, changes in salinity, increased sediment in water, oxygen deprivation and habitat disruption can all have effects on biodiversity. For example, seabirds on the Galapagos lost their nests in flooding events during the 1982–1983 El Niño causing reproductive failure for the duration of this wet episode (Duffy, in Glynn, 1990).

The most important ecological effect of flooding is likely its influence on the structure of communities by providing periodic connectivity to ecosystems that are usually isolated. Floods can also maintain wetlands through periodic inundation, provide pulses of nutrients, sediment and species to areas that normally lack water connectivity, and can cause rapid habitat conversion. Rapid water flow through riverbeds can have a scouring effect, redistributing and reducing the abundance of zooplankton (de Paggi and Paggi, 2008). In some cases, resource inputs from flooding can maintain an ecosystem in a nonequilibrium state, or can speed up the process of succession (Ward et al., 2003). Though not otherwise well studied with respect to ENSO, flooding can cause differential mortality of species due to different degrees of flood resistant adaptations. For example, during the 1997/1998 El Niño event, mangrove forests in a Tanzanian wetland experienced species-specific mortality and regeneration due to extensive flooding (Erftemeijer and Hamerlynck, 2005). Whether this short-term variation in survival translates into long-term changes in biodiversity is presently unknown.

Increased Sea-surface Temperature

Increases in SST 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 the local environments of marine species.

Ocean Current Shifts

Dispersal of organisms by ocean currents is an important process in establishing and maintaining biodiversity 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 successfully settle, the number of species able to colonize a new region may more than double under El Niño conditions (Richmond, in Glynn, 1990).

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 $\sim 10°$ N and $\sim 20°$ S. During ENSO events, upwelling decreases, and the area of cool, productive water is reduced to a pocket $\sim 10\%$ of 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 Kogelshatz, in Glynn, 1990). Such El Niño-induced changes impact heavily on, for example, fish and zooplankton-grazer species. 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 six months following the extreme 1982/1983 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. Also, multi-decadal records of species diversity and abundance in the Galapagos suggest that many marine species have yet to recover from the effects of the 1982/1983 El Niño event.

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.

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 marked 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' physiological tolerance ranges between 18 °C and 30 °C, and many reefs exist at close to their upper temperature threshold. Against the baseline of rising SST associated with global climate change, the most catastrophic effects of climate change on coral reef communities are predicted to be through increasing the magnitude and frequency of extreme, periodic climate oscillations such as ENSO events (Reaser et al., 2000). 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, and these effects are compounded when reefs already have reduced resilience due to other, often human-induced disturbance (e.g., cyanide poisoning, nutrient enrichment; Zhu et al., 2004).

Over the course of a severe episode, corals may lose 60% to >90% of their symbiotic algae, and the remaining algae may lose 50–80% of their photosynthetic pigments (Glynn, 1996; Figure 4). Depending on the 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 1982/1983 ENSO (Glynn and Feingold, 1992). Also, coral mortality leads to loss of reef 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

Figure 4 Example of El Niño-induced coral bleaching. Photo of a juvenile staghorn coral (Acropora sp.) at Pulau Pari, Thousand Islands, Indonesia, taken during the 1983/1984 El Niño event. Bleaching has started at the tips and at the periphery of the coral base (see Hoeksema 1991).

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. On death, many corals are colonized by algae, which prevents coral regeneration and transforms these areas into non-reef 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. For example, in the Galapagos Islands direct or interactive El Niño effects, often mediated by coral reef deterioration, were recognized as the major threatening process for 29 of 45 species recognized as being at risk by the IUCN (Edgar et al., 2010).

During the 1982/1983 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 1997/1998 bleaching event was the most severe and widespread ever recorded (Nyström et al., 2000; Wilkinson, 2004). Some scientists fear that a threshold may already have 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 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 cascading effects on other taxa. Long-term

censuses of fish communities in Australia spanning bleaching events have shown species loss and distinct phase shifts in composition from pre- to postbleaching with no evidence of regeneration (Bellwood et al., 2006; Garpe et al., 2006). However, and interestingly, some evidence suggests that strong directional selection by frequent ENSO-induced thermal stress may lead to coral reef communities that experience less severe bleaching during subsequent ENSO events. While coral reef communities may become more resistant to thermal stress, the differential survivorship of corals and algal symbionts that leads to this resistance will likely also lead to large changes in species composition of coral reefs (Thompson and van Woesik, 2009).

Feedback and Conclusions

Interestingly, many of the ecological changes caused by extreme El Niño events may be self-reinforcing (see **Figure 5**).

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; Holmgren et al., 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 have increased the probability of catastrophic fires and are responsible for the catastrophic fires in 1982/1983 and 1997/1998 (Laurance, 1998; Laurance, 2003). In addition, both logging and previous fires increase the probability of future fires (Nepstad et al., 1999), which are often exacerbated by build up of fuel from dead wood. Secondary fires are, therefore, much worse than initial fires (Cochrane et al., 1999), leading to positive feedback.
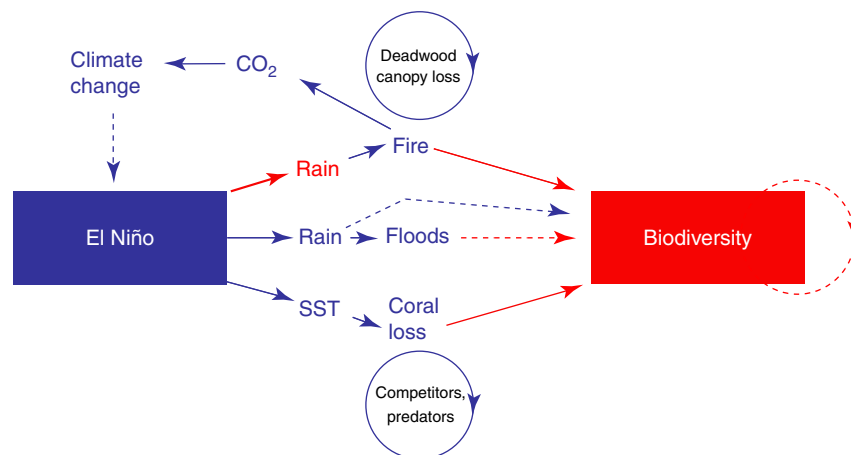

Figure 5 El-Niño feedbacks on biodiversity. Blue arrows indicate increases, and red lines indicate decreases. Solid arrows are well-established connections, and dotted arrows are more speculative. So, El Niño causes decreased rainfall, which causes fires. The fires increase the severity of future fires, 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 sea-surface temperature (SST) is implicated in coral bleaching, which decreases local biodiversity as the community shifts. Because of trophic cascades and loss of stability, losses of biodiversity may also be reinforcing.

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 1997/1998 (Cochrane, 2003). It is estimated that this, combined with other changes, has switched the tropics from a net carbon sink $(2.0$ Pg C year$^{-1})$ to a net source $(0.4$ Pg C year$^{-1})$ (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 lead the ecosystem to move 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, anthropogenic factors such as overharvesting, pollution, 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 that mediated by human activity, has strong effects on biodiversity at many spatial and temporal scales, and the evidence suggests that the bulk of these effects are undesirable.

Acknowledgments

See also: Biodiversity in Logged and Managed Forests. Climate Change and Ecology, Synergism of. Climate Change and Extinctions. Climate Change and Wild Species. Climate, Effects of. Deforestation and Land Clearing. Dispersal Biogeography. Fires, Ecological Effects of. Hotspots. Impact of Past Global Warming on Biodiversity. Mediterranean-Climate Ecosystems. Rainforest Ecosystems, Animal Diversity. Rainforest Ecosystems, Plant Diversity. Rainforest Loss and Change

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