

# El Niño effects on the dynamics of terrestrial ecosystems

Milena Holmgren, Marten Scheffer, Exequiel Ezcurra, Julio R. Gutiérrez and Godefridus M.J. Mohren

New studies are showing that the El Niño Southern Oscillation (ENSO) has major implications for the functioning of different ecosystems, ranging from deserts to tropical rain forests. ENSO-induced pulses of enhanced plant productivity can cascade upward through the food web invoking unforeseen feedbacks, and can cause open dryland ecosystems to shift to permanent woodlands. These insights suggest that the predicted change in extreme climatic events resulting from global warming could profoundly alter biodiversity and ecosystem functioning in many regions of the world. Our increasing ability to predict El Niño effects can be used to enhance management strategies for the restoration of degraded ecosystems.

Extensive regions around the world are influenced by the El Niño Southern Oscillation (ENSO). El Niño events occur irregularly but typically once every three to six years<sup>1</sup>. Although the effects of global warming on ENSO oscillations are difficult to predict, recent high resolution climatic models suggest that the frequency of El Niño-like conditions are expected to increase over the coming decades<sup>2</sup>. During an El Niño episode, rainfall dramatically increases in certain areas of the world, whereas severe droughts occur in other regions (Fig. 1). The rainfall during El Niño years can be four to ten times higher than average, and the phenomenon lasts approximately one year. The next phase, known as La Niña, produces roughly the opposite climate patterns to those found during an El Niño episode.

El Niño events have strong ecological<sup>3</sup> and economic consequences<sup>4</sup>. The best-studied effects on ecosystems are those in marine environments, where this climatic phenomenon is correlated with dramatic changes in the abundance and distribution of many organisms, and the collapse of fisheries<sup>5</sup>. By contrast, the effects on terrestrial ecosystems have been poorly explored. Only the spectacular greening and flowering of deserts<sup>6</sup>, and the crash of agricultural crops<sup>7</sup> in the core region of El Niño had been commonly noted. In recent years, however, results from several systematic long-term studies have become available, revealing how ENSO events can have pronounced effects on plant and animal communities in a wide range of terrestrial ecosystems. We discuss the main results, showing first the effects on plant dynamics in dry and moist habitats, then the cascading effects on animal communities and evidence for effects on the evolution of species. Finally, we discuss ways of using these insights in the management of degraded arid ecosystems.

## Effects on plant communities

### Short-term responses in arid ecosystems

The short-term response of vegetation to wet ENSO events is often spectacular. In the barren, arid islands of the Gulf of California, plant cover ranges between 0 and 4% during 'normal' years, but during rainy El Niño periods, it rises to 54–89% of the surface area available for growth. This is largely caused by a profusion of annuals and some drought-susceptible perennial species<sup>8</sup> (Fig. 2). The fast and dramatic response of annuals has been described for several ecosystems<sup>9</sup>. Landscape topographical features usually affect water availability for plants and, therefore, induce large spatial variation in the effects of rainy events. For instance, in semiarid north-central Chile, ephemeral plant cover during an El Niño year increased by over five times on a north-facing dry slope, by three times on a south-facing mesic slope, and only moderately in the relatively moist ravine<sup>10</sup>.

Although massive germination of annuals is the most spectacular effect of wet episodes in dry regions, perennial herbs, shrubs and trees also tend to show significant increases in growth, flowering and fruit production<sup>8,9</sup>. However, this usually only results in small changes in cover<sup>10</sup>. Importantly, top-down regulation by relatively inconspicuous animals such as small rodents might interact strongly with rainfall effects in regulating plant biomass in these dry areas. A large-scale field experiment conducted in northern Chile since 1989 has shown that shrub and perennial cover can increase significantly when either rodent herbivores are directly excluded, or when predators (birds of prey and foxes) are allowed to prey on herbivores<sup>9</sup>. Interestingly, the opposite is true for ephemeral herbaceous species, especially exotic annuals, which actually decrease in cover when rodents are excluded. Apparently, small rodents reduce shrub cover by browsing, and increase soil disturbance, which facilitates the colonization of disturbed patches by annuals<sup>9</sup>. A less well-studied but obviously important consequence of the pulse in primary productivity is that the seed bank in the soil can increase sharply following rainy ENSO episodes. In northern Chile, for example, the seed bank can increase almost sixfold during rainy El Niño years<sup>9,10</sup>.

### Long-term effects in arid ecosystems

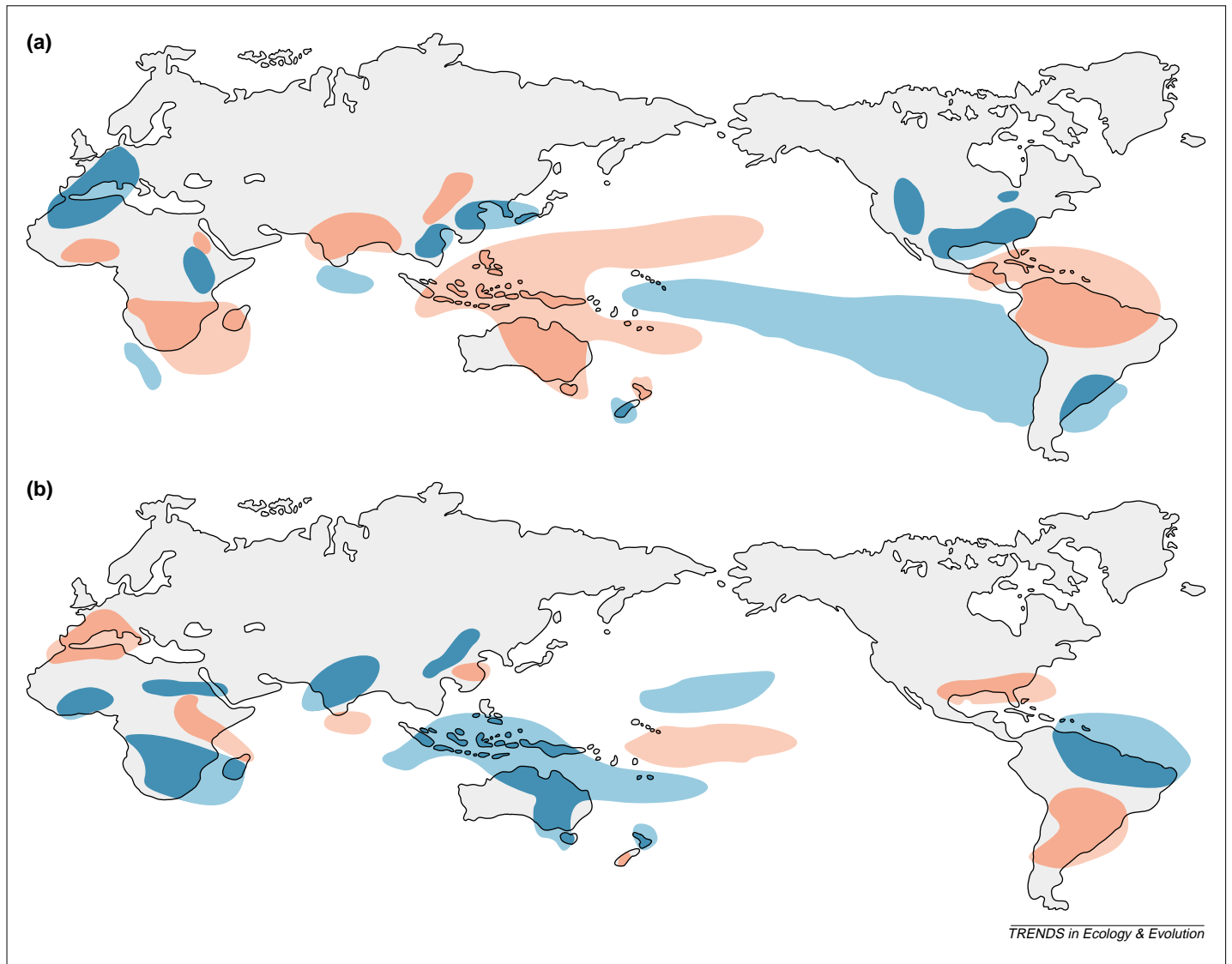
Tree ring analysis provides impressive records of ENSO effects on the growth of trees and shrubs, even

Milena Holmgren\*  
Godefridus M.J. Mohren  
Silviculture and Forest  
Ecology Group  
\*e-mail:  
Milena.Holmgren@btbo.  
bosb.wau.nl

Marten Scheffer  
Aquatic Ecology and  
Water Quality  
Management Group, Dept  
of Environmental  
Sciences, Wageningen  
University, PO Box 342,  
6700 AH Wageningen,  
The Netherlands.

Exequiel Ezcurra  
San Diego Natural History  
Museum, PO Box 121390,  
San Diego, CA 92112-  
1390, USA.

Julio R. Gutiérrez  
Departamento de  
Biología, Universidad de  
La Serena, Casilla 599,  
La Serena, Chile.



**Fig. 1.** Regions showing increased precipitation (blue) and drier conditions (orange) during El Niño (a) and La Niña (b) phases of the ENSO phenomenon. Modified, with permission, from Ref. 1.

in regions such as Israel that are usually thought to be little affected by this climatic oscillation<sup>11</sup>. Perhaps more importantly, extremely wet ENSO events might cause long-lasting effects on semiarid vegetation, as they can open rare windows of opportunity for the recruitment of trees and shrubs. For instance, the recruitment of shrubs and cacti in the Sonoran desert appears to be related to El Niño events: stands of *Larrea* shrubs usually consist of many size classes in relatively mesic places, whereas in drier areas they often contain only one cohort, suggesting that recruitment in drier areas occurs only in exceptionally favorable years<sup>12</sup>. Cactus recruitment is also restricted to rainy El Niño years in the Sonoran desert, but has an additional indirect relation to donkey grazing; nurse shrubs, under which cactus seedlings survive the drier periods, have been extirpated by these animals, resulting in a complete lack of cactus recruitment<sup>13</sup>.

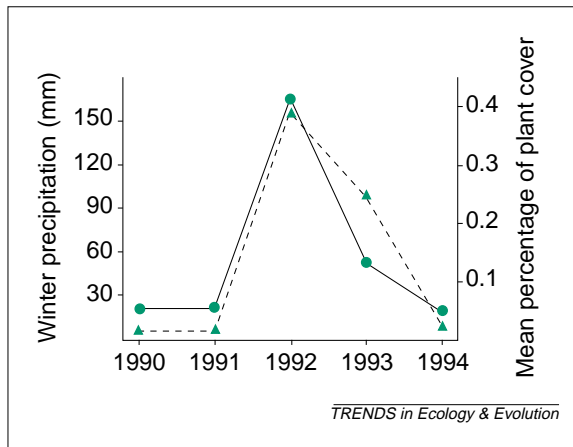
Adult trees and shrubs tend to be less vulnerable to desiccation and herbivory than are seedlings, which, once established, provide a relatively benign microclimate for subsequent seedlings.

Consequently, although initial settlement might require wet climatic conditions, woodland can be resilient and, once established, can persist for a long time<sup>14</sup>. For instance, in the shrubland–grassland transition zone of the Chihuahuan desert, large increases in shrub cover over the past decades have been related to episodes of increased winter precipitation that seem to broadly coincide with El Niño events<sup>15</sup>. Similarly, in semiarid Australia, successful seedling establishment of mulga<sup>16</sup>, as well as *Eucalyptus* and conifer woodlands<sup>17</sup>, has been linked with wetter periods during La Niña episodes. However, severe ENSO-related droughts can also induce episodes of tree mortality, as demonstrated in the open *Austrocedrus* woodlands near the forest–steppe ecotone of northern Patagonia<sup>18,19</sup>.

#### Effects on humid plant communities

Several recent studies show that El Niño effects are by no means restricted to drylands<sup>20–31</sup>. For example, El Niño events have been linked to the almost complete defoliation of mangroves<sup>20</sup>, as well as

**Fig. 2.** Winter precipitation (circles) and mean percent plant cover (triangles) on islands of the Gulf of California showing the effect of the 1992–1993 El Niño. Modified, with permission, from Ref. 8.



changes in growth and phenology of alpine forbs<sup>21</sup>, and boreal forests<sup>22</sup>. In most of the wet tropics, El Niño events are known to bring drier, warmer and sunnier conditions. In contrast to what happens during dry periods in arid ecosystems, drought in rainforests can induce enhanced seedling recruitment, population growth of understorey plant populations, such as herbs<sup>23,24</sup> and vines<sup>25</sup>, and an increase in fruit production<sup>26</sup>. The effect on the understorey is probably caused mainly by El Niño seasons being associated with high levels of mortality among canopy trees<sup>27</sup>, which causes changes in light and water availability to understorey plant populations. Interannual climate variability effects on plant and soil processes in tropical forests significantly affects the world's carbon cycle. For example, it has been suggested that, during the dry and warm El Niño years, the Amazon region acts as a

large source of carbon to the atmosphere, although in other years it acts as a carbon sink<sup>28</sup>.

ENSO droughts can also induce widespread forest fires, such as those observed in the Amazonian tropical forests<sup>29,30</sup>, or in the pine forests of North America<sup>31</sup>. These catastrophic fires have profound effects on the structure and dynamics of these ecosystems<sup>29–31</sup>.

#### Effects on animal communities

One would expect that an increase in primary productivity causes a subsequent increase in herbivores, followed by an increase in carnivores. Indeed, several long-term monitoring studies have revealed that such bottom-up effects can be seen several years after the occurrence of the El Niño event itself<sup>8,26,32–34</sup>. However, these studies also show that top-down effects can complicate the story considerably. This reinforces recent evidence that top-down trophic cascades are important in a wide variety of ecosystems<sup>35</sup>.

#### Insects and spiders on the islands of the Gulf of California

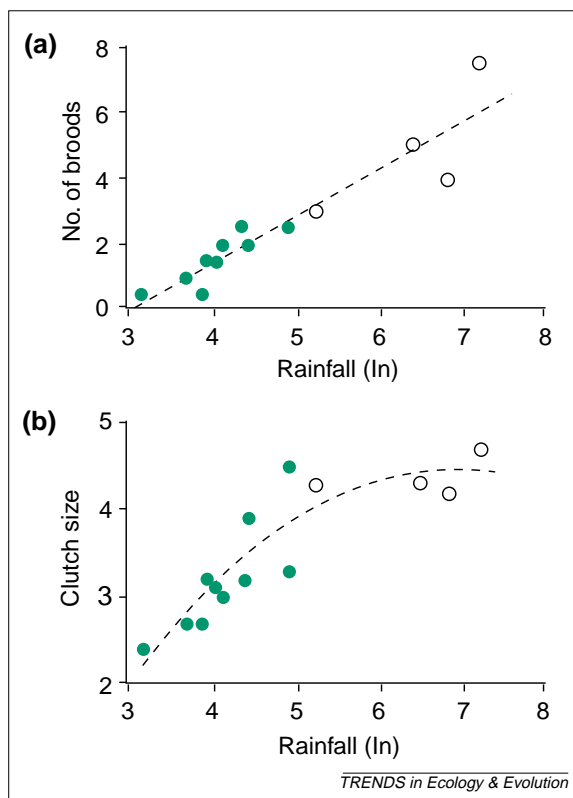
As previously described, the usually barren islands in the Gulf of California experience a tremendous explosion of plant growth, flowering and fruiting during the rainy El Niño events. Aerial insect abundance can double in response to a wet El Niño and crash to low levels in the subsequent dry period. The ENSO events also cause marked changes in the structure of the food web. During wet years, herbivores are the most important component of the insect assemblage, but in dry years, the assemblage shifts to one dominated by detritivores and scavengers, which feed on the additional detritus produced on the island during the rainy years, as well as the marine detritus deposited on the islands<sup>8</sup>.

Studies of arthropods on the California Gulf islands also confirm that ENSO effects on animal communities can involve top-down feedbacks that make the dynamics much more intricate than those of a simple bottom-up cascade. For example, after a rainy El Niño year, spider densities doubled in response to the high levels of insect prey resulting from the large changes in plant abundance and composition. However, one year later, despite continued plant and prey productivity, spider populations crashed and appeared to be suppressed by an irruption of parasitoid wasps that followed in response to the increase in the availability of nectar and pollen, the food source for adult wasps<sup>36</sup>.

#### Arthropods and birds on the Galápagos Islands

A long-term research project on the Galápagos Islands has monitored the effects on plant and animal communities since the particularly strong El Niño event of 1982. In rainy El Niño years, Darwin's finches reproduce more successfully; they have a longer breeding period, more broods and a greater

**Fig. 3.** Productivity of the finch *Geospiza fortis* on the Galápagos Islands as a function of the natural logarithm of annual rainfall (mm): (a) total number of broods per female per year, (b) largest average clutch size per female among broods in a year. Years of El Niño conditions are shown by open circles. Modified, with permission, from Ref. 33.



production of eggs and fledglings<sup>34</sup> (Fig. 3). This productivity increase seems to be explained largely by increases in food supply, such as seeds, fruits, nectar, pollen and various arthropods. Of the four El Niño events recorded, the year with most rain caused the greatest finch response. Surprisingly, however, the next wettest year had relatively low finch production. High temperature, also common during El Niño events, had an independent negative effect on breeding success and might have partly offset the positive effects of high rainfall. Also, breeding success might have been affected by density-dependent interactions. If overall density is higher, negative interactions between finches are expected to increase in terms of competition for food, territorial fights and the killing or removal of eggs and chicks. The authors conclude that starting conditions (such as initial finch density) before an El Niño event can strongly influence the observed response<sup>34</sup>.

#### *Rodents, birds and foxes in semiarid Chile*

Over the past three decades, several researchers have reported rodent outbreaks in semiarid South America, associated with the increased rainfall during ENSO events<sup>37</sup>. Since 1989, a large-scale field experiment in northern semiarid Chile has followed the ENSO effects on plant and animal populations in plots where the densities of herbivores and carnivores were manipulated. Results show that small rodents feeding on herbs and seeds can irrupt to population levels that are about 20 times higher than normal, following an ENSO event, although species responses differ in speed and magnitude<sup>38,39</sup>. In turn, top predators (hawks, owls and foxes) respond to prey abundance with a delayed increase in density that suggests a bottom-up effect<sup>33</sup>. Top-down effects also occur, although predation does not seem to affect all species densities equally.

#### *Fructivore famines on Barro Colorado Island*

During the past 49 years, famine among fructivores on Barro Colorado Island, Panama has occurred every time a mild dry season followed an El Niño event<sup>26</sup>. During such famines, monkeys, opossums, porcupines and other fructivores suffer high mortality. As mentioned previously, El Niño conditions stimulate fruit production in these wet tropical forests. The probable explanation for the subsequent famines is that the massive El Niño fruit production consumes plant-stored reserves, limiting the magnitude of their next reproductive event. Fruit production is especially reduced if the season following an El Niño year is mild and dry.

#### **Complex ecosystem responses and evolutionary consequences**

In view of our current understanding of the complex intertwined relationships that govern many ecosystems, it is not surprising that ENSO events can cause far-reaching shifts on many levels. Obviously,

in view of the complex manifold mechanisms involved, such complex shifts are also difficult to unravel. Although the evidence is necessarily more circumstantial than are results from controlled experiments or intensive studies of single species, the few studies that attempt to sketch overall ecosystem changes in response to ENSO events are particularly informative.

#### *The Galápagos Islands case*

A particularly complete study of ecosystem changes triggered by El Niño events has been carried out on the Galápagos Islands. Here, rainy conditions are thought to allow new colonizing plants to become established in the arid coastal zones. Their seeds or fruits are subsequently transported by herbivores, which are temporarily attracted by the abundant growth of coastal vegetation, back to the highlands where the constantly moist conditions allow the establishment of permanent populations. High water availability during El Niño episodes has also been shown to produce spectacular shifts in the competitive balance on these islands. The biomass of herbaceous plants and vines increases dramatically in the arid zones, and these growth forms outcompete the *Opuntia* cacti. The combination of a waterlogged root system and the heavy weight imposed by ongrowing vines kills cacti and they are unable to re-establish because of the dense grass cover<sup>32</sup>. Interestingly, animal evolution on these islands might well have been catalyzed by El Niño events. For example, food supply changes after the severe El Niño event of 1982–1983 seem to explain the high mortality among some Darwin's finches and the increased survival of their usually uncommon hybrids<sup>40</sup>. Also, the evolution of the beetle and spider fauna might be influenced by El Niño events because of an increased number of colonization events through rafting vegetation and the more favorable establishment conditions for immigrant species<sup>41</sup>.

#### *Switches in Australian ecosystem states*

The history of woodland dynamics in semiarid Australia illustrates very well how persistent ENSO effects can be, and how they interact with top-down mechanisms. Here, as in many other semiarid regions, it is the interaction between climatic fluctuations and biomass removal (managed grazing and fire) that largely drives vegetation dynamics. In the 1830s, the Pilliga scrub was an open woodland of large *Eucalyptus* and *Callitris* trees and grasses. During the next 40 years, the system was heavily invaded by shrubs owing to a management regime consisting of less frequent fires and increased grazing by cattle and sheep. The severe El Niño droughts of 1876–1877 forced grazing to stop. During the subsequent rainy year of 1878, an abundant regeneration of the original woodland trees occurred, which was so dense that grazing became impossible. A few years later, European rabbits colonized the area and made further

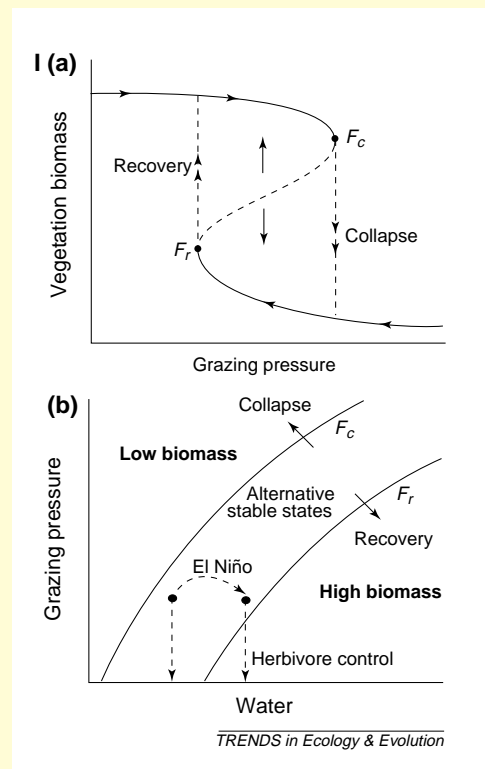


### Box 1. Potential ENSO effects in semiarid systems

Rainy El Niño events could open a window of opportunity for the restoration of degraded semiarid vegetation by means of grazer control<sup>14</sup>. A graphical model illustrates this possibility.

The response of semiarid vegetation to increased grazing pressure might be discontinuous because of the presence of alternative stable states (Fig. 1a). In the absence of grazing vegetation biomass is relatively high. The effect of a gradual increase in grazing is small until a critical threshold ( $F_c$ ) is reached at which the vegetation biomass collapses to a low level. Recovery from this state is difficult because the low biomass state and the high biomass state (upper and the lower branches of the curve) represent alternative attractors for intermediate grazing pressures. Only when grazing pressure is reduced below another low critical level ( $F_r$ ) the high-biomass state recovers. To see how effects of grazing and water availability might interact, the position of the two bifurcation points ( $F_c$  and  $F_r$ ) is plotted as a function of water availability (Fig. 1b). Under drier conditions,

critical grazing rates for collapse ( $F_c$ ) and recovery ( $F_r$ ) of vegetation are assumed to be lower. An implication is that not only a reduction in grazing pressure, but also a rainy El Niño event could potentially trigger vegetation recovery, provided that it sufficiently enhances water availability to pass the critical level ( $F_r$ ). The dotted arrows illustrate that the exclusion of herbivores coinciding with an increase in water availability due to an El Niño event could bring the system over the critical threshold to induce vegetation recovery, even if those two factors by themselves would be insufficient to trigger the switch.



regeneration of the original trees impossible; however, because of slow sapling growth, the forest remained dense until the early 1950s. Then, a second natural experiment took place during the rainy aftermath of the 1951 ENSO when, coincidentally, rabbits were practically eliminated by the myxoma epizootic. Once again, the combined effects of rainy conditions and the absence of grazing triggered the natural regeneration of the woodland trees, which has occurred in every suitable wet year since then<sup>17</sup>.

#### Prospects

It is becoming clearer that ENSO events can have

profound and complex effects on entire ecosystems. In dry ecosystems, ENSO episodes of increased rainfall enhance plant production and this causes an increase in the abundance of many herbivores and carnivores. However, long-term studies indicate that, rather than straightforward bottom-up propagation of the productivity pulse, top-down feedbacks and other regulation mechanisms complicate the process. This could explain why the same ecosystem can sometimes respond differently to subsequent ENSO events. For instance, the response of a population to increased resource availability might be suppressed if at the onset of a rainy period there happens to be a particularly high density of grazers<sup>9,17</sup>, predators<sup>9</sup> or competitors<sup>34</sup>.

Another remarkable emerging pattern is that extreme climatic events can cause a shift in the ecosystem to a state that persists for many years<sup>17</sup>. The possibility of alternative equilibria has been well established for drylands<sup>42,43</sup>, and evidence has been accumulating during the past decade that this phenomenon might in fact be common in a wide range of ecosystems<sup>44</sup>. If alternative attractors are indeed common, this requires a distinct theoretical framework for interpreting the effects of extreme ENSO events. Such events could 'tip the balance', causing a permanent shift to a different stable state. From a management perspective, one might want to reduce or enhance the chances of such a shift by managing other factors of influence in tune with predicted ENSO events. For instance, it has been hypothesized that the chance of a rainy ENSO event triggering a permanent recovery of degraded semiarid ecosystems can be enhanced by a temporary reduction of the grazer density<sup>14</sup> (Box 1).

Forecasting ENSO episodes and their effects is starting to be used in rangeland and semiarid production systems to identify the risks of overgrazing and fire during dry years<sup>45,46</sup> and to stimulate pasture regeneration during rainy years<sup>47</sup>. Models are also being developed to predict ENSO effects on fire risks in tropical forests<sup>29</sup>, on crop productivity<sup>48,49</sup> and on rodent outbreak risks<sup>50</sup>. We are, however, still far from a comprehensive understanding of ENSO effects on most terrestrial ecosystems. In view of the predicted increase of ENSO frequency with global warming, the profound ENSO impact on ecosystems justifies a substantial future research effort. The present results suggest that particularly important insights could be obtained from further long-term field experiments and observations. The interplay of top-down and bottom-up effects seems a particularly relevant aspect to focus on, as it might explain large variations in response and suggest ways to use ENSO events as windows of opportunity for the restoration of ecosystems.

#### Acknowledgements

We thank three reviewers for their constructive criticism of this article. Julio Gutiérrez is also grateful for support by FONDECYT 1000041.

## References

- 1 Allan, R. *et al.* (1996) *El Niño Southern Oscillation and Climatic Variability*, CSIRO
- 2 Timmermann, A. *et al.* (1999) Increased El Niño frequency in a climate model forced by future greenhouse warming. *Nature* 398, 694–696
- 3 Glynn, P.W., ed. (1990) *Global Ecological Consequences of the 1982–1983 El Niño-Southern Oscillation*, Elsevier Oceanography Series 52
- 4 Bouma, M.J. *et al.* (1997) Global assessment of El Niño's disaster burden. *Lancet* 350, 1435–1438
- 5 Jordan, R.S. (1991) Impact of ENSO events on the southeastern Pacific region with special reference to the interaction of fishing and climatic variability. In *ENSO Teleconnections Linking Worldwide Climate Anomalies: Scientific Basis and Societal Impacts* (Glantz, M. *et al.*, eds), pp. 401–430, Cambridge University Press
- 6 Dillon, M.O. and Rundel, P.W. (1990) The botanical response of the Atacama and Peruvian Desert floras to the 1982–1983 El Niño event. In *Global Ecological Consequences of the 1982–1983 El Niño-Southern Oscillation* (Glynn, P.W., ed.), pp. 487–504, Elsevier Oceanography Series 52
- 7 Taylor, J.A. and Tulloch, D. (1985) Rainfall in the wet-dry tropics: extreme events at Darwin and similarities between years during the period 1870–1983 inclusive. *Aust. J. Ecol.* 10, 281–295
- 8 Polis, G.A. *et al.* (1997) El Niño effects on the dynamics and control of an island ecosystem in the Gulf of California. *Ecology* 78, 1884–1897
- 9 Gutiérrez, J.R. *et al.* (1997) Effects of small mammals and vertebrate predators on vegetation in the Chilean semiarid zone. *Oecologia* 109, 398–406
- 10 Gutiérrez, J.R. *et al.* (2000) Variation in vegetation and seed bank in a Chilean semiarid community affected by ENSO 1997. *J. Veg. Sci.* 11, 641–648
- 11 Yakir, D. *et al.* (1996) El Niño and tree growth near Jerusalem over the last 20 years. *Glob. Change Biol.* 2, 97–101
- 12 Barbour, M.G. and Diaz, D.V. (1973) Larrea plant communities on bajada and moisture gradients in the United States and Argentina. *Vegetatio* 28, 335–352
- 13 Bowers, J.E. (1997) Demographic patterns of *Ferocactus cylindraceus* in relation to substrate age and grazing history. *Plant Ecol.* 133, 37–48
- 14 Holmgren, M. and Scheffer, M. El Niño as a window of opportunity for the restoration of degraded arid ecosystems. *Ecosystems* (in press)
- 15 Brown, J.H. *et al.* (1997) Reorganization of an arid ecosystem in response to recent climate change. *Proc. Natl. Acad. Sci. U. S. A.* 94, 9729–9733
- 16 Nicholls, N. (1992) Historical El Niño/Southern Oscillation variability in the Australasian region. In *El Niño: Historical and Paleoclimatic Aspects of the Southern Oscillation* (Diaz, H.F. and Markgraf, V., eds), Cambridge University Press
- 17 Austin, M.P. and Williams, O. (1988) Influence of climate and community composition on the population demography of pasture species in semi-arid Australia. *Vegetatio* 77, 43–49
- 18 Villalba, R. and Veblen, T.T. (1997) Regional patterns of tree population age structures in northern Patagonia: climatic and disturbance influences. *J. Ecol.* 85, 113–124
- 19 Villalba, R. and Veblen, T.T. (1998) Influences of large-scale climatic variability on episodic tree mortality in northern Patagonia. *Ecology* 79, 2624–2640
- 20 McKillup, S.C. and McKillup, R.V. (1997) An outbreak of the moth *Achaea serva* (Fabr.) on the mangrove *Excoecaria agallocha* (L.). *Pan Pacific Entomol.* 73, 184–185
- 21 Walker, M.D. *et al.* (1995) Effects of interannual climate variation on phenology and growth of two alpine forbs. *Ecology* 76, 1067–1083
- 22 Black, T.A. *et al.* (2000) Increased carbon sequestration by a boreal deciduous forest in years with a warm spring. *Geophys. Res. Lett.* 27, 1271–1274
- 23 Horvitz, C.C. and Schemske, D.W. (1994) Effects of dispersers, gaps, and predators on dormancy and seedling emergence in a tropical herb. *Ecology* 75, 1949–1958
- 24 Horvitz, C.C. and Schemske, D.W. (1995) Spatiotemporal variation in demographic transitions of a tropical understory herb: projection matrix analysis. *Ecol. Monogr.* 65, 155–192
- 25 Aide, T.M. and Zimmerman, J.K. (1990) Patterns of insect herbivory, growth, and survivorship in juveniles of a neotropical liana. *Ecology* 71, 1412–1421
- 26 Wright, S.J. *et al.* (1999) The El Niño Southern Oscillation, variable fruit production, and famine in a tropical forest. *Ecology* 80, 1632–1647
- 27 Condit, R. *et al.* (1996) Changes in tree species abundance in a neotropical forest over eight years: impact of climate change. *J. Trop. Ecol.* 12, 231–256
- 28 Tian, H. *et al.* (1998) Effect of interannual climate variability on carbon storage in Amazonian ecosystems. *Nature* 396, 664–667
- 29 Nepstad, D.C. *et al.* (1999) Large-scale impoverishment of Amazonian forests by logging and fire. *Nature* 398, 505–508
- 30 Cochrane, M.A. *et al.* (1999) Positive feedbacks in the fire dynamic of closed canopy tropical forests. *Science* 284, 1832–1835
- 31 Veblen, T.T. *et al.* (2000) Climatic and human influences on fire regimes in ponderosa pine forests in the Colorado Front Range. *Ecol. Appl.* 10, 1178–1195
- 32 Trillmich, F. (1991) El Niño in the Galápagos Islands: a natural experiment. In *Ecosystem Experiments* (Mooney, H.A. *et al.*, eds), SCOPE 45, John Wiley & Sons
- 33 Jaksic, F.M. *et al.* (1997) A long-term study of vertebrate predator responses to an El Niño (ENSO) disturbance in western South America. *Oikos* 78, 341–354
- 34 Grant, P.R. *et al.* (2000) Effects of El Niño events on Darwin's finch productivity. *Ecology* 81, 2442–2457
- 35 Pace, M.L. *et al.* (1999) Trophic cascades revealed in diverse ecosystems. *Trends Ecol. Evol.* 14, 483–488
- 36 Polis, G.A. *et al.* (1998) Multifactor population limitation: Variable spatial and temporal control of spiders on Gulf of California Island. *Ecology* 79, 490–502
- 37 Lima, M. and Jaksic, F.M. (1999). El Niño events, precipitation patterns and rodent outbreaks are statistically associated in semiarid Chile. *Ecography* 22, 213–218
- 38 Meserve, P.L. *et al.* (1995) Heterogeneous responses of small mammals to an El Niño Southern Oscillation event in northcentral semiarid Chile and the importance of ecological scale. *J. Mammal.* 76, 580–595
- 39 Meserve, P.L. *et al.* (1999) The interplay of biotic and abiotic factors in a semiarid Chilean mammal assemblage: results of a long-term experiment. *Oikos* 85, 364–372
- 40 Grant, B.R. and Grant, P.R. (1996) High survival of Darwin's finch hybrids: Effects of beak morphology and diets. *Ecology* 77, 500–509
- 41 Desender, K. *et al.* (1992) El Niño: events and the establishment of ground beetles in the Galápagos Archipelago. *Bull. Ins. R. Sci. Nat. Bel. Entomol.* 62, 67–74
- 42 Noy-Meir, I. (1975) Stability of grazing systems: an application of predator-prey graphs. *J. Ecol.* 63, 459–481
- 43 Rietkerk, M. and van de Koppel, J. (1997) Alternate stable states and threshold effects in semiarid grazing systems. *Oikos* 79, 69–76
- 44 Carpenter, S.R. Alternate states of ecosystems: evidence and some implications. In *Ecology: Achievement and Challenge* (Press, M.C. *et al.*, eds), Blackwell (in press)
- 45 McKeon, G.M. *et al.* (1990) Northern Australian savannas: management for pastoral production. *J. Biogeog.* 17, 355–372
- 46 Noble, J.C. and Vines, R.G. (1993) Fire studies in mallee (*Eucalyptus* spp.) communities of western New South Wales: grass fuel dynamics and associated weather patterns. *Rangel. J.* 15, 270–297
- 47 Stone, R.C. and McKeon, G.M. (1993) Tropical pasture establishment. 17. Prospects for using weather prediction to reduce pasture establishment risk. *Trop. Grassl.* 27, 206–413
- 48 Meinke, H. and Hammer, G.L. (1997) Forecasting regional crop production using SOI phases: an example for the Australian peanut industry. *Aust. J. Agric. Res.* 48, 789–793
- 49 Izaurralde, R.C. *et al.* (1999) Modelled effects of moderate and strong 'Los Niños' on crop productivity in North America. *Agric. Forest Meteorol.* 94, 259–268
- 50 Lima, M. *et al.* (1999) El Niño-Southern Oscillation-driven rainfall variability and delayed density dependence cause rodent outbreaks in western South America: linking demography and population dynamics. *Am. Nat.* 153, 476–491

## TREE subscriptions 2001

Personal subscribers – remember to renew your subscription to ensure an unbroken supply of *TREE* into 2001.

See p. IV for details of our worldwide subscription services, or contact our customer services by fax, telephone or e-mail.

Tel: +44 (0)1444 475650

Fax: +44(0)1444 445423

E-mail: ct.subs@rbi.co.uk