REVIEW

Extreme climatic events and vegetation: the role of stabilizing processes

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Abstract

Current climatic trends involve both increasing temperatures and climatic variability, with extreme events becoming more frequent. Increasing concern on extreme climatic events has triggered research on vegetation shifts. However, evidences of vegetation shifts resulting from these events are still relatively rare. Empirical evidence supports the existence of stabilizing processes minimizing and counteracting the effects of these events, reinforcing community resilience. We propose a demographic framework to understand this inertia to change based on the balance between adult mortality induced by the event and enhanced recruitment or adult survival after the event. The stabilizing processes potentially contributing to this compensation include attenuation of the adult mortality caused by the event, due to site quality variability, to tolerance, phenotypic variability, and plasticity at population level, and to facilitative interactions. Mortality compensation may also occur by increasing future survival due to beneficial effect on growth and survival of the new conditions derived from global warming and increased climatic variability, to lowered competition resulting from reduced density in affected stands, or to antagonistic release when pathogens or predators are vulnerable to the event or the ongoing climatic conditions. Finally, mortality compensation may appear by enhanced recruitment due to release of competition with established vegetation, for instance as a consequence of gap openings after event-caused mortality, or to the new conditions, which may be more favorable for seedling establishment, or to enhanced mutualistic interactions (pollination, dispersal). There are important challenges imposed by the need of long-term studies, but a research agenda focused on potentially stabilizing processes is well suited to understand the variety of responses, including lack of sudden changes and community inertia that are frequently observed in vegetation under extreme events. This understanding is crucial for the establishment of sound management strategies and actions addressed to improve ecosystem resilience under climate change scenarios.

Keywords: climate change, extreme climatic events, forest dieback, plant community resilience, vegetation dynamics

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Extreme climatic events and vegetation responses

The relevance of extreme climatic events (heat waves, cold snaps, droughts, floods) has become a hot issue in both ecological research and the global change agenda (IPCC, 2007; Jentsch, 2006; Smith, 2011). Current climatic trends and projections highlight consistent tendencies of rising temperature and increasing climatic variability (Easterling *et al.*, 2000). Accordingly, extreme events are likely to become globally more frequent and intense in the near future (IPCC, 2007), although uncertainty at small temporal and spatial scales remains (Shih-Chieh & Ganguly Auroop, 2011).

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Given the key role of climate in determining plant distribution, the current view is that extreme climatic events trigger vegetation shifts (Fig. 1A) (see Allen & Breshears, 1998; Breshears *et al.*, 2005; Miriti *et al.*, 2007) as these events can induce generalized mortality disrupting a situation in which vegetation would either remain stable or follow successional replacement in equilibrium under stable climatic conditions (Fig. 1D). Less intuitively, abrupt changes in vegetation may also occur even under baseline climatic variability, as a likely response to an accumulation of gradual environmental changes (Fig. 1C). Finally, it is also possible that no vegetation shift occurs even after extreme climatic events (Fig. 1B). We argue that this latter situation is more frequent than generally assumed and that there is much to be learnt from vegetation stability under
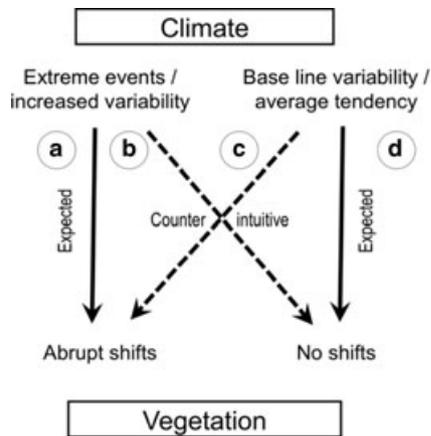
Fig. 1 Conceptual model of vegetation shift response to climate. Abrupt shifts could occur under extreme events or increased climatic variability (case A) or under gradual climatic change involving trends in mean climatic parameters and leading to a turning point (case C). Alternatively, no shifts (but gradual vegetation changes may happen on the long term) would be observed if climate change involves gradual changes in the average climatic tendency (case D), or in spite of extreme events or increased climatic variability (case B). While cases A and D are expected from classical studies of the impact of climatic changes on vegetation, cases B and C, are counterintuitive but there is both theoretical and empirical evidence supporting their importance.

extreme climatic events. Thus, in this article we analyze the existence of demographic stabilizing mechanisms that contribute to the inertia of vegetation in front of extreme climatic events, although vegetation change could eventually occur, particularly if new conditions remain pervasive.

Extreme climatic events do not always induce vegetation shifts

The idea that species and vegetation shifts are the norm under changing climatic conditions is supported by reports describing rapid distribution changes in altitude (e.g. Kelly & Goulden, 2008) in latitude (e.g. Jump *et al.*, 2009), or in ecotones (Allen & Breshears, 1998), and this paradigm is even more easily applied when sudden climatic fluctuations occur. Most efforts to analyze the effect of extreme climatic events have focused on the existence of critical thresholds and contributing factors: site quality (Lloret *et al.*, 2004; Suarez *et al.*, 2004), variations in species and individual responses (e.g. Bréda *et al.*, 2006; Koepke *et al.*, 2010), stand structure (Greenwood & Weisberg, 2008), taxonomic (Lloret *et al.*, 2007) and functional diversity (Kreyling *et al.*, 2008) and biotic interactions (Dobbertin *et al.*, 2007). A general conclusion of these studies is that the multifactorial nature of plant mortality, a prerequisite for

change, operates through different temporal scales producing a complex spatial structure of vegetation responses (e.g. Lines *et al.*, 2010).

In fact, unexpected patterns of vegetation shift are arising even in the absence of extreme climatic episodes, such as downslope range displacement in altitudinal gradients (Lenoir *et al.*, 2010), or species persistence promoted by the stability of population growth at the southern edge of the range (Doak & Morris, 2010). These findings reveal that simple associations between climate change and vegetation shift may be often unrealistic and that the number of studies strictly documenting vegetation shifts is still too low to provide a sound framework for the study of vegetation changes. In fact, plant communities dominated by long-lived species often experience a pervasive inertia to species replacement and they recover relatively easily after disturbances, a fact that recently has been proposed to be at some extent explained by higher variation of demographic traits within species than between species averages (Clark, 2010). Retrospective studies (e.g. dendrochronological approaches) or successive forest inventories may provide useful information. While some forest inventories have revealed an increase in tree mortality associated with recent climate warming or dryness (e.g. van Mantgem *et al.*, 2009), this result is far from the rule. For instance, Vilà-Cabrera *et al.* (2011) used the Spanish Forest Inventory to detect determinants of mortality rate in Scots pine (*Pinus sylvestris*) in Spain, where this species has the south-westernmost (and most arid) limit of its distribution. Although these authors found that mortality tended to be higher at drier locations, this effect was relatively small and plots with more negative anomalies of precipitation during the 10-year study period did not experience higher mortalities.

Actually, the studies specifically addressing the role of extreme climatic events on vegetation dynamics are scarce (i.e. Galiano *et al.*, 2010; Kreyling *et al.*, 2011), and in the case of an experimental manipulation of climatic extremes performed on grassland no evidences of vegetation shift have been found (Jentsch *et al.*, 2011). Obviously the study of the dynamics associated with extreme climatic events is challenged by the need for long-term and spatially representative monitoring of vegetation after the events. In a recent review of drought and heat-induced tree mortality by Allen *et al.* (2010) only approximately half of the ~100 cases reported across the world since 1970 showed stand mortality values over 30%, and approximately a third of these cases exhibited mortality rates below 20%, which may probably be too low to result in vegetation shifts. In addition, if one considers a possible publication bias in favor of studies reporting significant vegetation changes according to the prevalence of the

shifting paradigm, it seems reasonable to conclude that vegetation may often persist with little change after extreme climatic events. This is even more impacting if we consider that during the last decade we have witnessed the most extreme heat-waves and droughts on record (Ciais *et al.*, 2005).

A demographic approach to vegetation stability

Community stability and persistence implies that demographic processes of at least one dominant species, more specifically their recruitment and adult mortality rates, need to be balanced through time. Then, we can consider as stabilization mechanisms those contributing to this balance, basically by reducing mortality or increasing recruitment. While the quantification of dominant species is relatively easy in many temperate and boreal woodlands and forests, it may be difficult or even unattainable in communities with high evenness, such as tropical rainforests, grasslands and shrublands. However, the demographic approach is conceptually appropriate even in highly diverse communities. In fact, studies suggesting climate-driven vegetation shifts have usually considered changes in the relative abundance of dominant species (e.g. Olano & Palmer, 2003; Suarez & Kitzberger, 2008) in temperate forests.

Thus, a vegetation shift would occur when the relative abundance of dominant species changes abruptly over the range of natural temporal variability (Fig. 2). This would be the case if adult mortality were induced by an extreme climatic event and endogenous mechanisms are not effective enough to compensate for this mortality by recruitment. Thus, population persistence would be determined by mortality compensation through recruitment at a temporal scale that would last longer than the immediate period after the event (Fig. 2). This period can be roughly determined by the generation time of the plant species (including the persistence of the seed bank). An important issue is that the time scale of different life-history processes often varies greatly, particularly in long-lived species. For instance, while seedling dynamics often show continuous – but fluctuating – patterns of establishment and mortality through time, populations of adult overstorey trees some times experience discrete pulses of mortality due to disturbances. Note also that species abundance existing before the extreme event could stochastically influence survival and recruitment, thus favoring mortality compensation after the perturbation. In spite of the importance of mortality, most of the research effort in communities dominated by long-lived species has been devoted to recruitment, probably due to the scarcity of death events and the difficulty of recording the required long-term data.
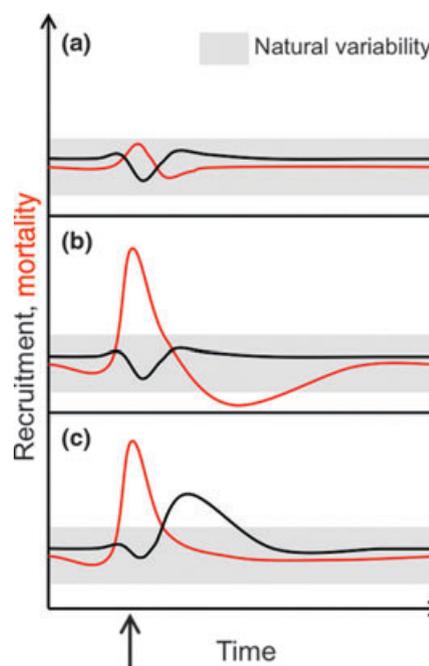

Fig. 2 Compensation model of population response to extreme events. (a) The effect of the extreme event on both recruitment and mortality falls within the natural variability of these rates. (b) The extreme event results in higher mortality rates than natural variability that are later compensated by higher survival of the remaining population. (c) The extreme event results in higher mortality rates than natural variability that are later compensated by higher recruitment; a combination of (b) and (c) is also possible, but is not drawn. The timing of extreme events is indicated by an arrow.

The demographic compensation approach described is initially established for individual species dynamics. The simplest way to scale up to the community level is by an additive balance of the different coexisting species, but demographical processes are in fact not independent from the performance of coexisting species. For instance, recruitment may be favored by resource release after the death of adult neighbors, both adult survival and recruitment are intrinsically related to the incidence of herbivores, pathogens and mycorrhiza, and the contribution of pollinators and dispersers to recruitment is in turn determined by adult performance. As we will see, this network of interactions may provide stabilizing mechanisms that reduce the likelihood of shifts after extreme climatic events.

An account of stabilizing processes

Extreme climatic events can be analyzed according to the disturbance theory. From this perspective, disturbance intensity would correspond to the climatic anomaly, severity would be determined by mortality, and

resilience could be considered equivalent to the ability to compensate for the losses experienced during the event through time. However, mortality is not exclusively caused by the environmental conditions in the event, but also by predisposing (Manion, 1991) and post-event factors. We can consider that any process minimizing severity by decreasing mortality (i.e. increasing survival) or enhancing recruitment will have a stabilizing effect in communities, particularly in those dominated by long-lived species. These stabilizing processes often operate over temporal lags after the event, and consequently any estimation of vegetation shifts should consider appropriate temporal scales. In fact, some climate manipulation experiments have found that short and long-term changes on community composition may differ or even show opposite directions (Hollister *et al.*, 2005). Then, it could be argued that some of the reported vegetation shifts are temporary changes due to uncoupled life stage dynamics of coexisting species.

We can group stabilizing processes into several categories (Table 1). First, there are processes that mitigate the mortality directly related to the extreme event. Here we can include predisposing factors, with particular attention to site quality, tolerance, phenotypic variability and plasticity, and biological interactions, such as facilitative ones. Then, there are delayed compensatory effects counterbalancing the mortality induced by the climatic event. That may result from (i) enhanced future survival due to reduced competition from neighbor populations or to better performance under the new conditions (ii) enhanced future recruitment due to better adult reproductive performance or to improved regeneration conditions, including micro-climate shifts, competition release, or antagonistic, mutualistic, and facilitation interactions.

Processes mitigating mortality

Site quality. Variations in mortality rate associated with contrasting abiotic and biotic conditions are the norm, promoting a mosaic of severity in which surviving plants may assure the persistence of the population and eventually of the community. Suarez *et al.* (2004) have described small-scale patchiness in drought-induced mortality in Patagonian forests. This mosaic of plant survival often reflects soil properties, as reported by Lloret *et al.* (2004) in holm-oak forests with contrasting drought-impact between close sites with different bedrock permeability.

Tolerance, plasticity, and phenotypic variability. Mortality can be lower than expected due to a simple physiological mechanism: enhanced stress tolerance, that is, the capacity of an organism to attenuate the detrimental effects of stress on fitness (Valladares & Niinemets, 2008). High tolerance is observed in populations living at the edge of the species distribution range, where extreme events are expected to be more detrimental. For instance, populations of woody plants of the Northern hemisphere living at the southern edge of their distribution range are more tolerant to heat waves and severe droughts, while northern edge populations can tolerate cold snaps and freezing events better (Hampe & Petit, 2005). That is not necessarily due to local adaptation, but also to the coexistence of multiple genotypes with various levels of tolerance, the frequencies of which can vary in response to changing environmental conditions and that can attenuate the deleterious effects of extreme climatic events (Kelly *et al.*, 2003). Obviously, the specific conditions (Jentsch *et al.*, 2007) and the timing of episodic events can have profound implications for plant performance (Agrawal *et al.*, 2004).

Table 1 Stabilizing processes in response to extreme climatic events. They can be induced by changes in abiotic conditions, within-population responses and interactions, and community interactions. These processes may result in mortality mitigation or compensation by future survival or recruitment

	Abiotic	Population	Community
Mortality mitigation	Site quality	Tolerance Plasticity Phenotypic variability	Facilitation
Mortality compensation by future survival	Climate-induced survival	Lowered competition: self-thinning	Antagonism
Mortality compensation by future recruitment	Climate-induced recruitment	Competition release: self-replacement	Competition release: gap dynamics Antagonism Mutualism Facilitation Multiple species interactions

Plants have also large phenotypic plasticity, that is, the potential to modify their form and function in response to environmental changes, and particularly to changing climate (Nicotra *et al.*, 2011). Phenotypic plasticity can reduce mortality when plants are exposed to new conditions. For example, air temperatures that exceed the survival limit of plants acclimated to lower temperatures can be well within the optimum range for plants acclimated to higher temperatures. So, plant temperature tolerance is greater than predicted from trait vs. instantaneous response curves measured in non-acclimated plants. Nevertheless, acclimation is not instantaneous, and it is sensitive to several factors. For example, full acclimation to a temperature shift may take between a few days to weeks and is further affected by interactions with other factors such as drought (Valladares *et al.*, 2007). Thus, there is limited room for plasticity to attenuate mortality due to extreme events, unless they become recurrent or can be anticipated by perceiving the right cues.

A large phenotypic variability, either with or without a genetic basis, enables different individuals within a population to experience the same level of stress differently. Phenotypic differences within a population can be related to different ages. Adult trees, usually cope with severe drought better than juveniles not only because they explore deeper soil layers, but also because they have a suite of morphological and physiological traits that can attenuate the impact of unusually low soil water potential (Cavender-Bares & Bazzaz, 2000). In contrast, local adaptation to the new conditions might decrease phenotypic variability and counteract this mortality attenuation mechanism, which could be the case for rear edge populations under very stressful conditions (see Giménez-Benavides *et al.*, 2011).

Facilitation. The environmental changes induced by extreme climatic events may be buffered by the presence of other individuals of the same or different species. For instance, Kreyling *et al.* (2008) observed in grassland submitted to extreme weather events that stability increased with diversity, being this effect partially explained by facilitation of two engineer species. Facilitative interactions vary throughout the different life-history stages (Miriti *et al.*, 2007), which in turn may exhibit different sensitivity to extreme climatic events. Facilitative effects can be linked to plant traits: structural traits related to temperature and water buffering are the first candidates to attenuate the mortality caused by climatic events. In conclusion, there is a complex network of facilitative interactions that constitute a strong stabilizing factor by allowing different stress-avoiding possibilities that tend to develop self-maintaining feed-backs at community level.

Compensatory processes

Beneficial effects of climate change on growth and survival. In addition to the effects of extreme climatic events, an obvious consequence of climate change is that new conditions may be beneficial, compensating the deleterious demographic effects of extreme events. In relatively seasonal cold climates, moderate climate warming can enhance baseline tree growth and survival (Scholze *et al.*, 2006), unless temperature-induced drought stress becomes disproportionately important (Wilmking *et al.*, 2004). Scots pines growing close to its European southern edge of distribution have been reported to experience die-off as a result of drought episodes (Galiano *et al.*, 2010), but in populations from the same area warm conditions also promote growth at relatively wet sites, whereas they have a large detrimental effect at dry sites (Martínez-Vilalta *et al.*, 2008). Thus, in these relatively wet localities future warmer conditions could benefit plant performance in populations that have experienced episodic climate-driven mortality.

Lowered competition. Plant density may be greatly reduced by extreme events, resulting in lower competition, at least at the intra-specific level, and lowering the vulnerability of the population to future extreme events. In forests affected by drought-induced decline, per capita soil water availability increases with mortality, and thus may promote survival after the event and especially in response to a new drought (Dale *et al.*, 2001). There is also substantial evidence that denser stands are more vulnerable to drought (e.g. Klos *et al.*, 2009; Vilà-Cabrera *et al.*, 2011) and that growth of surviving trees increases after drought events (Suarez & Kitzberger, 2010). Extreme events also involve modifications in factors not directly related to climatic fluctuation (light or nutrients). Olano & Palmer (2003) reported increased growth in small surviving trees in a temperate forest during drought events, probably due to an increase in diffuse light and sunflecks.

Nevertheless, direct evidence that a sudden reduction in density promotes future survival is limited (e.g. Vygodskaya *et al.*, 2002). An obvious reason is that this evidence requires long-term monitoring, but there are also reasons to expect that lowered competition may not necessarily promote resistance against future extreme events. There is frequently some compensation in resource use at the tree level following reductions in stand density, involving increased stomatal conductance or leaf area (cf. Sala *et al.*, 2005; McDowell *et al.*, 2006). Therefore, fast growth responses to pulses of increased resources following extreme events may lead to high vulnerability to future episodes.

Antagonistic release. The reduction in the intensity of antagonistic interactions can operate as a compensatory mechanism for the mortality of dominant plant species. Increasing temperatures and extreme climatic events have been advocated to increase the impact of phytophagous insects and diseases on forestry species (Coakley *et al.*, 1999). However, the great variation in pest species' response to meteorological conditions does not provide a clear picture (Rosenzweig *et al.*, 2001; Robinet & Roques, 2010; Jactel *et al.*, 2011). In some situations extreme climatic events that increase mortality of dominant plant species could cause a simultaneous reduction in pest and pathogen density or in herbivory (Carnicer *et al.*, 2011). For example, dry conditions are also unfavorable for sporulation of fungi (Rosenzweig *et al.*, 2001). Patterson *et al.* (1999) pointed that climate effects on insect life cycles frequently depend on pest insects thresholds induced by extreme climatic events and that in some cases these effects were more unfavorable for insects than for plants. For instance, Rabasa *et al.* (2009) described the existence of an outstanding reproductive window for Colutea hispanica during the heat wave of 2003 due to the extreme mortality suffered by *Iolana iolas* a monophagous butterfly. Similarly, Masters *et al.* (1998) observed that a combination of mild winters due to increasing temperatures and the incidence of extreme events could reduce the number of adults of insect herbivores by anticipating the egg hatch date.

Stabilizing climate-induced recruitment. Changes in future mean climatic conditions may mitigate bottlenecks in critical life stages related to recruitment, without detrimental effects on other stages. This recruitment should compensate previous adult mortality due to extreme climatic events. This recruitment may involve interactions with other organisms, for instance when the scarcity of pollinators limits seed set, and recruitment in cold climates. Seed dispersal and the existence of safe and suitable microsites are also necessary conditions to reinforce stabilization via recruitment. Compensation by recruitment is especially effective in plant communities where dominant species have a short life cycle, or produce abundant seed banks (Aragon *et al.*, 2010). In these species the elasticity of vital rates associated with recruitment is high while in long-lived perennials the probability of recruits reaching the adult stage is more uncertain, and the life stage with the highest elasticity is the stasis of adult individuals.

Population dynamics often depend more on environmental extremes than on their means. Accordingly, sporadic recruitment in favorable years separated by significant lags is the norm in many stressful habitats.

Increased climate variability, often predicted in climatic projections, implies increasing probability of favorable conditions for recruitment during some extreme events (Knapp *et al.*, 2008; Matias *et al.*, 2011), thereby compensating for adult mortality occurring as result of extreme climatic events. This opportunistic recruitment seems to be supported by the existence of soil seed banks that exhibit a considerable inertia to between-year climatic variability, contributing to stabilizing population dynamics (Venable & Brown, 1988).

Competition release of recruitment. Extreme events can be considered disturbances promoting gap dynamics and suitable sites for recruitment under the canopy of defoliated plants, particularly for shade-intolerant seedlings or disturbance-dependent species. Then, mortality compensation would occur even several years after the event. Hiernaux *et al.* (2009) reported that woody species mortality in Sahel woodlands was compensated by recruitment under average rainfall conditions several years after the event, and they attributed that to the release of competition due to drought-induced adult mortality. Initially this recruitment was due to pioneer species previously present in the community, but several years after the drought, recruitment of previously dominant species also occurred, highlighting the resilience of the community as a whole.

Stabilizing self-replacement occurs if seedlings establish below the canopy of defoliated parents, where seeds are more likely to accumulate. Olano & Palmer (2003) documented increased recruitment related to a drought event of the dominant species of a North American temperate forest. Alternatively, self-replacement will not be favored in cases where recruitment sites are not species-specific or limited by dispersal. Similar to mortality, differential recruitment rates among species are a necessary condition to promote vegetation shifts. Thus, stabilizing recruitment implies that the different species in the community have enough viable seeds that find safe sites to compensate for their corresponding adult mortality.

Although seedling recruitment associated with gap opening in forests has been largely documented, studies on the role of gap dynamics as a stabilizing mechanism after defoliation pulses related to extreme climatic events are less abundant. For instance, Suarez & Kitzberger (2008, 2010) reported lagged seedling establishment in drought-caused gaps in Patagonian forests. However, models of dynamics based on small gap occurrence may fail to explain the response to large, infrequent, natural disturbances at larger spatial scales due to landscape effects (Turner *et al.*, 1998). Then, the effectiveness of compensation depends on the availability of seeds in permanent seed banks or dispersed from

surviving individuals or neighbor populations, as well as the action of predators.

Mutualistic effects on recruitment. At first glance, extreme events may negatively affect plant populations due to their impact on pollinators and seed dispersers. However, there is a large gap in our knowledge on the impact of extreme climatic events on mutualistic interactions and its consequences for the recruitment of dominant plant species. In some cases, the resilience of mutualistic interactions may prove to be higher than expected. Bronstein & Hossaert-McKey (1995) observed in the obligate interaction between *Ficus aureus* and *Pegoscapus jimenezi* that pollinator populations rapidly re-established within 5 months after presumed local extinction due to hurricane Andrew. In fact, extreme events may indirectly favor some mutualistic interactions. For instance, the pollinator activity of bees may be enhanced by a reduced incidence of chalkbrood disease, which is highly dependent on humid environments after an extreme drought period (Le Conte & Navajas, 2008). Also, long-term increasing average temperatures may have an overall positive effect on pollinator activity or the density of seed dispersers, particularly in temperate or cold climates, enhancing compensatory recruitment (Giménez-Benavides *et al.*, 2011).

Multiple interactions. Although extreme events may negatively affect pairwise interactions between species (e.g. Rosenzweig *et al.*, 2001), the ways in which changes to these interactions combine across the entire community are mostly unknown (McCann, 2007). In fact, the effects of climatic extreme events are likely to influence the levels of trophic cascades differently (Menge & Sutherland, 1987). Thus, species-specific projections are not necessarily consistent with those of whole communities (Tylianakis *et al.*, 2008). Recent studies suggest that increasing levels of interaction complexity contribute to stabilizing mechanisms in the community (Ives & Carpenter, 2007), and that they can be expected to favor plant mortality compensation. For instance, these stabilizing effects may induce simultaneous reductions of different pests and herbivores. Mazia *et al.* (2009) reported stronger control of sapling insect herbivory by birds in a year of severe El Niño/ Southern Oscillation drought. Mutualistic networks between plants and pollinators or seed dispersers have significantly nested patterns that are built upon weak and asymmetric links among species (Bascompte *et al.*, 2006). These patterns confer robustness to the loss of interactions, because a core of redundant interactions brings cohesion to the whole network (Okuyama & Holland, 2008).

Conclusions

A limitation for our understanding of the impacts of extreme events on vegetation is the contentious and frequently loose definition of extreme events, which needs refinement because climate change involves modifications in both mean and variability. The IPCC report (IPCC, 2007) could be used as a comprehensive framework as it recognizes three relevant parameters: rarity, intensity, and severity. Another limitation is the difficulty to compare study cases, particularly due to its heterogeneity in temporal and spatial scales and the disparity of response variables. Finally, we need to incorporate extreme variability into long-term experimental studies (Hollister *et al.*, 2005), by providing realistic intensities and frequencies of extreme events in relation to local conditions (Kreyling *et al.*, 2008).

However, the emerging picture is that plant response to extreme climatic events is highly variable and idiosyncratic and does not necessarily result in the replacement of the established vegetation. Long-term surveys of vegetation response to these events have not yet been completed, and trends of vegetation replacement have only been documented in some particular cases. It seems clear that dominant populations and communities present a set of ecophysiological and demographic stabilizing mechanisms, which together with a myriad of species interactions can compensate for the dieback and eventual mortality of dominant vegetation. Nevertheless, this should not underestimate the potential of these events to induce dramatic shifts, particularly if they become more frequent. Most relevant processes include mortality attenuation – based on tolerance, plasticity, and phenotypic variability – mortality compensation by increasing future survival or by enhanced future recruitment due to beneficial new conditions, resource release resulting from the death of some individuals, or enhancement of biotic interactions. Taken all together, these processes could explain why the number of described shifts after dramatic events is still low in spite of the substantial changes in climate that we have already witnessed and the wide interest in detecting and reporting their existence.

In addition to looking for thresholds that lead to vegetation shift, we propose a new focus in the study of climate effects on vegetation in which vegetation stability has a central role. Certainly, there is a lot that remains to be learnt from studies on climate-induced vegetation shifts, but we feel that by almost exclusively concentrating on these so far relatively few cases, we are taking the focus out of a general framework. Thus, we are failing to accurately represent reality and estimate the likely impact of global change on ecological systems. We propose that a research agenda analyzing the

processes and conditions that enhance the maintenance of populations exposed to extreme events would provide deep insights on vegetation responses to the new climatic conditions. Vegetation shifts would thus occur when these stabilizing processes are disrupted or do not fit with new conditions. Long-term analysis of the processes contributing to community resilience may become ultimately even more relevant than punctual records of shifting events. We argue that this approach may help to more effectively establish pro-active strategies and actions to reinforce stabilizing processes attenuating undesired effects of climate change on terrestrial ecosystems.

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