How frequent storms affect wetland vegetation: a preview of climate-change impacts

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Predicting how vegetation may change in response to an increasingly variable climate is difficult, but the analysis of observed responses to past climatic oscillations can inform the forecasting process. The consequences of multiple extreme events were recorded (1978–1998) for a California salt marsh. Ultimately, after less-extreme decadal weather patterns were preceded by more-extreme ones resulting from the Pacific Decadal Oscillation, six types of climate-change-related effects on vegetation became apparent. Among the identified effect types in this system, "sequential" (or event-order-dependent) effects were the most severe with regard to abrupt biodiversity losses. Similar outcomes could be applied to other ecosystems subjected to variable conditions. Managers and restoration ecologists need to anticipate the many ways in which extreme events can affect vegetation and use this knowledge to build resilience into restoration targets and plantings. A national program of adaptive restoration could first be applied in downstream wetlands, where the cumulative effects of flooding and sedimentation will cause vegetation to respond rapidly, and where adaptive approaches (eg futuristic assemblages) could be tested in large field experiments.

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As the inevitability of human-induced climate change is increasingly acknowledged by policy makers, natural resource agencies are seeking ways to preserve biodiversity (eg Wisconsin Initiative on Climate Change 2008). At the same time, restoration ecologists are being asked to identify plant assemblages with built-in resilience – that is, species that could persist despite a changing climate. Practitioners in the temperate zones of the Northern Hemisphere may be able to select plant assemblages that can tolerate gradually increasing temperatures and rainfall by choosing species or genotypes with more southerly distributions, but they will have greater difficulty choosing species on the basis of resilience to extremes that cannot be predicted.

In anticipation of novel environmental conditions, several ecologists recommend looking beyond recent and current vegetation states as targets for ecological restoration (Ewel and Putz 2004; Harris *et al.* 2006; Hobbs *et al.* 2006; Jackson and Hobbs 2009). Yet the conditions that vegetation will need to be able to adapt to are unknown. For even a single factor, such as increased rainfall, it is necessary to anticipate timing, severity, and duration, as well as other conditions that might precede, co-occur with, or follow rainfall events. In fact, the sequence of events (eg flood then drought versus drought then flood) will likely make a critical difference to plant responses (Miao *et al.* 2009). Important gaps in our knowledge about the effects of increased storminess include both empirical examples of vegetation change and incomplete theory of ecosystem behavior (Cadenasso *et al.* 2006).

For restoration ecologists to move beyond speculation and provide evidence-based recommendations for sustaining biodiversity (Sutherland *et al.* 2004), forecasts could rely on long-term monitoring and an understanding of why some species persist while others do not. Useful datasets include climate oscillations during decades with less versus more frequent extreme events. Such examples are rare, but one long-term study meets these criteria. The salt marsh of Tijuana Estuary in southern California experienced decades of "benign" conditions followed by decades with frequent extreme events (Zedler and West 2008). The interpretation of how extreme events altered this salt marsh has led me to identify six types of effects and a series of adaptive actions that ecosystem managers can take to help sustain biodiversity.

In a nutshell:

- Past oscillations between less and more extreme weather (due to the Pacific Decadal Oscillation) offer a preview of how vegetation might respond to increased variability as a result of climate change
- The diverse effects of extreme weather events are readily studied in wetland vegetation
- Biodiversity decreased abruptly as a result of "sequential" effects (those dependent on event order)
- Anticipating the effects of frequent extreme weather events can inform efforts to sustain biodiversity under a changing climate

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Salt-marsh diversity loss

Under average conditions, southern California's climate is warm and mild, with ~25 cm of annual rainfall, most of which falls periodically during the cool season (November–March). Tijuana Estuary typically has saline to hypersaline water and salt-marsh soil as a result of twice-daily tidal inundation, low rainfall levels, and limited riverine influence. When I first sampled the salt marsh in 1974, no one predicted that the estuary would suddenly experience multiple years of catastrophic storms and floods. Much later, Bromirski *et al.* (2003) recognized that the shift from less to more stormy conditions occurs at the scale of two to three decades, under the influence of the Pacific Decadal Oscillation (PDO). Their analysis of tidal data from 1858 onward found decadal-scale variability in sea level, which in turn causes "intense storminess…that directs storm tracks toward the California coast". Superimposed on these weather conditions is the El Niño Southern Oscillation (ENSO), which operates at a shorter time scale and temporarily raises sea level and adds to storminess (Flick and Cayan 1984; see http://faculty.washington.edu/kessler/ENSO/soi-1950-98.gif for data from 1950 onward).

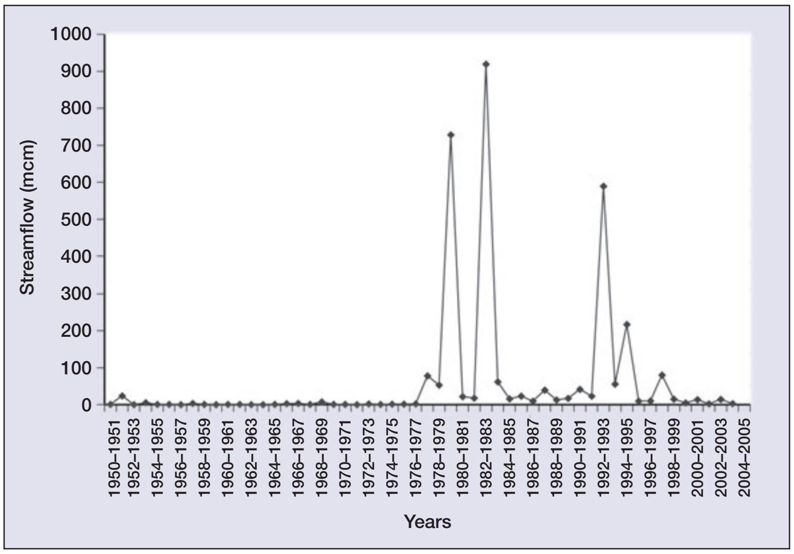

Figure 1. *Tijuana River streamflow (1950–2004) at the US–Mexico border, 8 km upstream from Tijuana Estuary. Data are million cubic meters (mcm) per rainfall year (July 1 through June 30) obtained from the International Boundary and Water Commission.*

During major rain storms, the Tijuana River collects runoff from its large watershed (73% of which is located in Mexico), resulting in catastrophic flooding, capable of destroying roads and buildings and rerouting the river (Figures 1–3). The stormy period began in 1978, after decades with minimal streamflow (Figure 1). Over the next 27 years, annual streamflow was nearly 50 times greater than that for the preceding 27 years (Table 1). A single PDO included river flooding (with associated sedimentation that elevated the marsh plain), sea storms (which caused dune washovers, channel filling, and estuary mouth closure), and drought (which was a major stressor during mouth closure). Strong winds during the ENSO event in 1983 led to sea swells from the Pacific, when water levels exceeded predicted high tides by 33 cm (Flick and Cayan 1984; Figure 4).

Vegetation monitoring before and during the stormy period documented changes in the intertidal marsh, which supports California cordgrass (*Spartina foliosa*) at the channel edges, eight common native halophytes on

Table 1. Timeline of extreme events at Tijuana Estuary

1950–77	27-yr mean streamflow = ~ 2.3 million cubic meters (mcm; SD = 4.7)
1974	Salt-marsh plain richness = 4.2 spp per 0.25-m^2 plot (max = 10), with high evenness, no dominant; two short-lived species (*Salicornia bigelovii, Suaeda esteroa*) were widespread and abundant
1977–78	First flood in decades; annual flow ~ 78.3 mcm
1979–80	~ 728.1 mcm; major flooding in January and again in February 1980; cordgrass grew unusually tall and robust
1980	Second largest annual streamflow on record
1982–83	Largest annual streamflow on record (~ 919.6 mcm); rainfall and flooding continued into April, reduced soil salinity; strong El Niño; sea storms, dune washover, main channels filled, tidal prism reduced; high marsh was invaded by upland weeds
1984	Estuary mouth closed April 6 and was not reopened until December 18, after channels were dredged and sand moved back to the dune. No rain fell during the 8-month non-tidal period; channel water salinity rose to 60 ppt; the entire marsh was desiccated, and soil salinity rose to 100 ppt; the two short-lived plant species were virtually extirpated; pickleweed formed a monotype;
mean	richness = 1.84 spp per plot (max = 3).
1992–93	Third largest streamflow on record; floodwaters eroded a new river channel into the estuary, tons of sediment were mobilized and deposited on the salt marsh; accretion in cordgrass reached 8.5 cm
1994	Marsh plain averaged 8.7 cm higher than in 1984; salt-marsh plain richness = 3.7 spp per plot (max = 6), with low evenness, with pickleweed (*Salicornia* spp) and salt-marsh daisy (*Jaumea carnosa*) co-dominant and short-lived species rare
1994–95	Fourth largest flow on record (annual streamflow ~ 215.9 mcm)
1997–98	Strong El Niño conditions; cordgrass colonized mudflats
1997–99	Mudflats accreted 9.2 cm of sediment from November 1997 to August 1999
2004	Salt-marsh plain richness = 3.9 spp per plot (max = 6), with low evenness due to pickleweed and salt-marsh daisy co-dominance and rare short-lived species
1977–2004	27-yr mean streamflow = 113.9 mcm (SD = 236.0)

Notes: Streamflows are million cubic meters (mcm) per rainfall year (July through June). Detailed data are in Zedler *et al.* (1986, 1992), Ward *et al.* (2003), and Zedler and West (2008). Plot size for species richness = 0.25 m^2. ppt = parts per thousand. SD = standard deviation.

Figure 2. *In 1980, the Tijuana River flood washed out 19th Street in Imperial Beach, California; as a result of recurrent flooding this was never repaired.*

the marsh plain (the most widely distributed being pickleweed, *Sarcocornia pacifica*, formerly *Salicornia virginica*), and a high marsh with evergreen cover and a diversity of annual plants at the edges of salt pans (Zedler *et al.* 1992). Details of compositional changes are in Zedler and West (2008). Here, I describe in a conceptual manner how the vegetation responded to increased storminess (more frequent extreme events with greater extremes; Table 1). Recognizing how in-creased storminess can affect vegetation should help others forecast impacts of prolonged climate-change-related effects across a broader range of ecosystems.

Extreme events had six types of effects

Six different types of responses of the salt marsh were identified: direct, indirect, interactive, additive, unseasonal, and sequential. These cause–effect patterns are supported by experimentation and observation, but have not yet been fully tested.

Figure 3. *The Tijuana River flood in 1993 cut a new channel through the Tijuana River Valley, damaging Hollister Road, destroying an adjacent house, and moving sediment into the nearby estuary.*

Direct effects

Direct effects occur independently of other factors. The "germination window" created by heavy rainfall is a salt-marsh example; there, rainfalls exceeding 3 cm in a day are rare, but necessary to stimulate seedling recruitment (Noe and Zedler 2000, 2001). Although germination responds to both lowered soil salinity and increased soil moisture, these factors are linked in this ecosystem – when it rains heavily during low tide, soil salinity is temporarily lowered (Zedler *et al.* 1986). Sediment deposition also has a direct effect when it smothers sessile organisms. Only one halophyte (*S pacifica*) seems to thrive despite heavy sedimentation, but even this species experiences mortality when deposition exceeds 20 cm (Callaway and Zedler 2004). The survivorship of mussels (*Mytilus* spp), which cannot escape a sudden deposit of mud or sand once attached to a hard substrate, is also negatively impacted by this direct effect.

Indirect effects

Indirect effects include an intermediary, as when changes to vegetation affect an animal population or vice versa. The 1983 sea storm indirectly led to the decimation of the estuary's population of cordgrass, by filling channels with sand and causing the estuary mouth to close (Zedler *et al.* 1986; Figure 5). Cordgrass depends on tidal flushing (verified by Ibarra-Obando and Poumian-Tapia [1991] at Estero Punta Banda in Baja California, Mexico). The degraded cordgrass canopy contributed to the extirpation of the light-footed clapper rail (*Rallus longirostris levipes*, an endangered bird in the US) in 1984. This salt-marsh-dependent bird either died or emigrated when non-tidal conditions altered their habitat; without tidal flushing, the extent and vigor of their preferred nesting habitat (cordgrass) were reduced, their macroinvertebrate prey species declined, and upland predators gained access to the rails' drying home ranges.

Interactive effects

Interactions among two given stressors cause greater or more rapid changes than either factor acting alone. In the salt marsh, it is highly likely that drought and hypersalinity interacted to shift the species-diverse salt marsh toward monotypic pickleweed. Of all the perennials, pickleweed has the highest capacity to take up and sequester salt (conferring salt tolerance; Sullivan *et al.* 2007); it can also extend its roots deep in the soil, to tap the receding water table (conferring drought tolerance; Zedler and West 2008). Among beneficial interactions, short-term flooding (salinity reduction) and nutrient influxes can synergistically enhance plant growth (Zedler *et al.* 1986).

Figure 4. *Waves and wind eroded the sand dune adjacent to Tijuana Estuary during the 1983 ENSO. Small patches of sand were stabilized by a native deep-rooted perennial that was part of a dune stabilization experiment.*

Additive effects

Additive effects are those that have a cumulative impact. Here, one such effect involved the widespread accumulation of sediments that elevated the marsh plain. The effects on vegetation were related to extreme events, not gradual changes in sea level. Literature on other coastal ecosystems is focused mainly on the gradually rising sea level, with widespread impacts forecast for the Atlantic Coast (Craft *et al.* 2009). At Tijuana Estuary, however, sea-level rise (< 0.02 cm per year; Munk 2002) was dwarfed by sedimentation during the stormy period (on the mudflat, these rates were ~1 cm per year in non-ENSO 1998–99 and 8–9 cm per year during the 1997–98 ENSO; Ward *et al.* 2003). Steep slopes and erodible granitic soils within the urbanizing watershed undergo continual destabilization, with mudslides that can bury whole streets under 2 m of sediment.

Unseasonal effects

Unseasonal effects result from events that occur outside their "usual" time frame. Annual halophytes of the high marsh depend on cool-season rainfall; when rainfall exceeds 3 cm, it creates "germination windows" at a time of reduced evapotranspiration, when seedlings grow roots, shoots, and flowers before the summer drought (Noe and Zedler 2000, 2001). If heavy rain were to fall during the summer, annuals would germinate and seedlings would die as soon as their young shoots and shallow roots encountered heat, drought, and salinity stress. For annual plants to flower in summer, they would require some subsidy from perennial hosts. For example, the salt-marsh bird's beak (*Cordylanthus maritimus maritimus*, a US endangered plant) is a hemiparasite that taps into perennial host roots for water and nutrients to set seed (Fellows and Zedler 2007).

Sequential effects

Sequential effects differ with the order of events (Maio *et al.* 2009). At Tijuana Estuary, the largest effect on salt-marsh diversity occurred in 1984, when river-mouth closure was followed by drought (Figure 6). Without tidal wetting, the salt-marsh soil dried, cracked, and became extremely hypersaline (greater than three times the salinity of seawater). Two short-lived species were virtually extirpated, and one deep-rooting halophyte formed a widespread monotype. The reverse order of these effects (drought followed by mouth closure) would likely have had little effect on the vegetation because normal rainfall would have sustained the short-lived species, and a single heavy rainfall event would have impounded water, eroded the sand barrier, and reopened the mouth of the estuary.

Classifying effects is challenging where there are multiple simultaneous stressors and a range of responses, but the overall outcome was clear. Frequent extreme events reduced plant diversity, both through the rapid loss of two short-lived species in 1984 and the more gradual gain in dominance by two productive perennials (Bonin and Zedler 2008; Zedler and West 2008). Understanding how increased storminess affected salt-marsh diversity is relevant to local managers, but the implications extend to other wetlands, as well as to upland ecosystems. Below, I suggest how ecosystem managers might use the salt-marsh case study to anticipate impacts of climate change and recommend several actions for adapting restoration projects to help vegetation gain resilience to climates that feature more frequent extreme events.

■ Discussion

How ecosystem behavior changed

To link the above empirical example to ecological theory, I used the framework of Cadenasso *et al.* (2006) to suggest how a shift from benign to stormy conditions altered ecosystem behavior. These authors recommend positioning an ecosystem state along three axes representing their understanding of increasing "biocomplexity". The axes

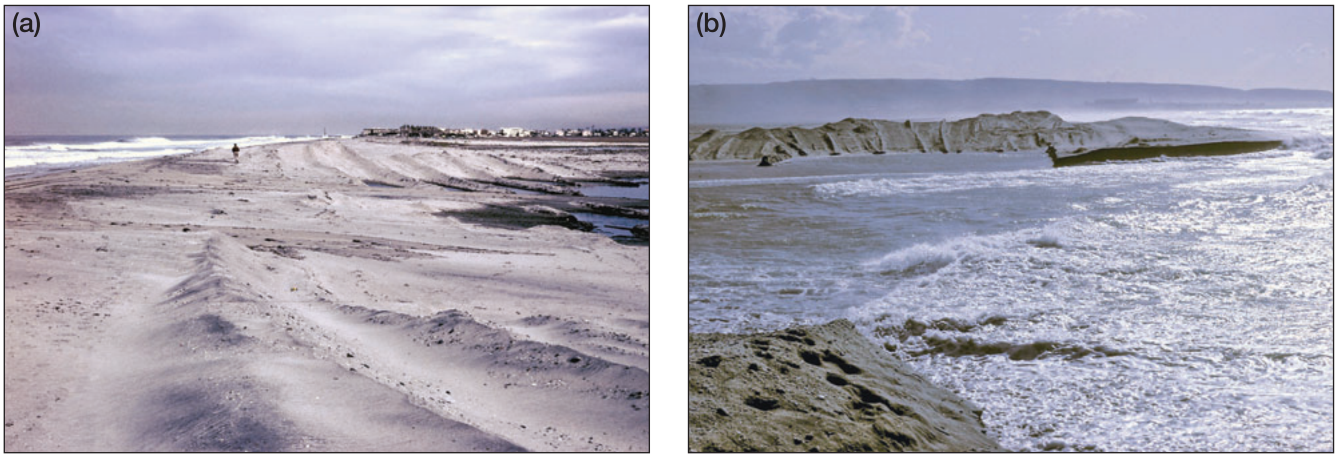

Figure 5. The mouth of the Tijuana Estuary (a) closed in April 1984 and remained closed until sand was dredged from the channels and replaced on the dunes, and bulldozers reopened it (b) in December 1984.

are organizational connectivity (simple = units with little functional connection; complex = control of the system via fluxes among units), temporal relationships (simple = direct and contemporary; complex = indirect and lag effects), and spatial heterogeneity (simple = numbers of patch types; complex = quantified changes in mosaics through time). Although the comparison of before versus during stormy periods is qualitative, the directions of change can be argued, and general behavior can be compared among ecosystems that are characterized in a similar manner.

Along the connectivity axis, interactions across system units were limited and predictable during the period of benign weather conditions. Before the first major storm in 1978, river inflows were minimal, the channel water was saline, and marsh soils were hypersaline. Ocean connectivity consisted of regular and predictable tidal inundation. During stormy decades, the salt marsh experienced much stronger interactions among system units, resulting from extreme river flooding, sea storms, and dune washovers. Connectivity became more complex, as did temporal relationships. Under benign conditions, environment–vegetation links were relatively simple; that is, salinity and inundation had direct and indirect effects. During stormy conditions, these were augmented by additive, unseasonal, and sequential effects (similar to the lagged links, legacies, and slowly emerging indirect links of Cadenasso *et al.* 2006). Although connectivity and temporal relationships grew more complex, the ecosystem behaved differently along the spatial heterogeneity axis. During benign conditions, the salt-marsh vegetation was moderately complex, with vascular plant distributions related both to intertidal elevation (Zedler 1977) and microtopographic heterogeneity due to tidal creeks, small pools, and shallow depressions (Zedler *et al.* 1999). During decades of increased storminess, physical heterogeneity was reduced as recurrent sedimentation flattened the microtopography, and the vegetation patterns shifted toward fewer species and greater dominance. Thus, multiple catastrophic storms shifted ecosystem behavior along all three axes, but not necessarily in the same direction. Heterogeneity appeared to become less complex as connectivity and temporal contingencies became more complex. Additional empirical examples and theoretical advances would improve the ability to predict long-term ecosystem responses to more variable climates.

Worst-case scenarios

The "worst" cases that the future might hold could be envisioned via one of four different approaches. (1) Use historical events to envision even greater extremes. For example, the extreme sea levels experienced by the Tijuana Estuary salt marsh in 1983 and 1993 would have been exceeded if El Niño swells had coincided with maximum astronomical high tides (driven by the gravitational pull of the moon and sun) in January, and flood effects would have been more severe if higher sea levels had impounded floodwaters within the estuary to greater depths and for longer periods. (2) Postulate additional catastrophes that could coincide with each other or occur in various sequences. For example, flooding and storms can cause spills from sewage treatment plants, as well as leakage of toxic contaminants due to accidents on highways and rivers, in ports and airports, and from industrial developments. Spills during rainstorms would be especially hard to contain; toxic materials could move to downstream wetlands, where cleanup activities would damage both the vegetation and soil. (3) Envisage the effects of varied initial conditions. A permanently altered climate will not necessarily include opportunities for an ecosystem to recover lost diversity before the next extreme event; plant communities with reduced native diversity could be less resilient than those with diverse native vegetation. (4) Predict which invasive species will colonize bare soils and canopy gaps, further impeding efforts to maintain regional biodiversity. A system that has been reduced to dominance by aggressive invasive species could be quite resilient to extreme events, but the outcome most likely would not sustain native species.

Faced with a sequence of catastrophic events, native species are not likely to persist in familiar assemblages, but will instead form no-analog communities (Williams and Jackson 2007). The regional management goal could be to retain all native species somewhere in the landscape ("preserve all the parts"; Leopold 1938), rather than to sustain current plant communities or restore historical communities. Planners could then make a strong case for testing "futuristic plantings" with novel assemblages, varying species richness and genotypes, and allowing extreme events to select for tolerant combinations, thereby building resilience into subsequent restoration projects. The following actions would help restoration ecologists plan such projects.

Figure 6. *Drought during the 8-month, non-tidal period (Figure 5a) converted tidal pools and creeks into dry, salt crusts. Cordgrass died and pickleweed thrived.*

Recommended actions

Prioritize downstream wetlands

Although all ecosystems will experience the direct effects of extreme events, wetlands at the base of large watersheds are arguably poised to experience the greatest impacts of "pulsed" storm events, because downstream wetlands collect water and sediment from large areas. When the sediment reaches the downstream area, it flattens and elevates marsh topography. In freshwater wetlands, invasive species will colonize bare soil, establish and form monotypes, and further threaten native biodiversity. Higher elevations could exacerbate the effects of subsequent dry years on wetland vegetation, which is already sensitive to drought, resulting from the low water-use efficiency and shallow root systems with only limited ability to track declining water tables. Because wetlands cover a minority of the landscape (less than 9% of global land area), the subset of downstream wetlands would be an efficient starting point for assessing the effects of extreme events on vegetation, ultimately expanding efforts to a broader range of ecosystems.

Begin monitoring

Change can only be quantified where baseline data are available and where frequent sampling occurs. Monitoring was the key to identifying the six effect types on salt-marsh vegetation. If detailed data cannot be obtained at frequent intervals, managers could at least mark boundaries between native and invasive vegetation, to reveal shifts following extreme events.

Sample efficiently

A combination of remote sensing and field sampling, including Global Positioning System satellite technology, can be used to outline the boundaries of selected species. Late senescence of the invasive reed canary grass (*Phalaris arundinacea*) facilitated the use of satellite imagery to map this invader throughout Wisconsin, where it was shown to dominate >200 000 ha of wetlands (Hatch and Bernthal 2008). New remote-sensing technology (eg Asner and Martin 2009) could improve the mapping of additional taxa that are not distinguishable by any unique phenology.

Focus on extreme events

In temperate climates (eg Wisconsin), episodes of heavy rainfall, summer flooding, and severe droughts are predicted. In addition, trends over the past 50 years indicate increasing numbers of unseasonal events, including more winter rainfall and freezing rain, shorter duration of snow/ice cover, and longer growing seasons (Kucharik *et al.* unpublished data). In agricultural landscapes, stronger rainfall pulses produce more runoff than does gentle rain, thereby releasing more sediment and mobilizing more nutrients and pesticide residues.

Restore adaptively

Wetlands that are already reduced in diversity as a result of flooding, sedimentation, and dominance by invasive plant species provide opportunities for *futuristic* restoration (ie projects designed to withstand future environmental conditions). To counter anticipated losses of native species and increases in numbers of invasive plants, others suggest increasing resilience by diversifying native species (Seastedt *et al.* 2008; Hummel *et al.* 2009). I agree, and recommend approaches that allow learning while restoring ("adaptive restoration"; Zedler and Callaway 2003). Large sites with heterogeneous microtopography and patchy resources could accommodate experimental plantings of many native species, various genotypes, assemblages that differ in species richness, and combinations that include multiple functional groups. As sites are affected by flooding and sedimentation, the persistent taxa and assemblages can be identifiable and tested further, at large spatial scales (> 1 ha). Few experiments exploit the potential afforded by large restoration sites (Wagner *et al*. 2008), perhaps because there is no mandate for integrating research and restoration.

Establish a national program that fosters adaptive restoration

The US Farm Bill already funds conservation reserves, but efforts are not organized within watersheds (Batie 2009) or required to accommodate research. If research and restoration were integrated in downstream wetlands, large experimental plantings could be evaluated for their resilience to flooding and sedimentation. Early identification of biological factors that confer resilience to extreme events, along with an understanding of cause–effect relationships, would equip land managers with the means to "keep all the parts" intact, despite stormier climates. Additional long-term studies of a broader range of ecosystems could build on those in wetlands, and demonstrate further the utility of the adaptive approach.

■ Conclusions

The example of a salt marsh's response to three decades of increased storminess led me to identify six types of effects of climate change on vegetation. Given the overall reduction in diversity, I predict that extreme events associated with longer term climate change will further reduce diversity by shifting the more tolerant species to stronger dominance (reducing evenness) and by extirpating some populations more rapidly than they can re-establish (reducing richness). This prediction probably applies beyond downstream wetlands.

In the broader context of ecosystem behavior, the Tijuana Estuary salt marsh appeared to become more complex in two dimensions (connectivity and temporal contingencies) under the stormier climate, but less complex in its physical and biological heterogeneity. Future quantification of these shifts and similar analysis of other ecosystems under changing climate will facilitate comparisons, understanding, and predictions.

Recommendations

Downstream wetlands should be prioritized, monitored, and efficiently sampled, to identify multiple effects of extreme events on vegetation. Using an adaptive framework, restoration ecologists could install large-scale experimental plantings of diverse native species, genotypes, and assemblages, all of which would be affected by extreme events under future environmental extremes. Persistent plantings could then be selected for later restoration efforts; taxa that are vulnerable would be recognized as needing further research to sustain populations, and the knowledge gained could guide subsequent adaptive approaches in a broader spectrum of ecosystems. A national program that integrates research and restoration would increase the ability to sustain diversity.

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