THE ECOLOGICAL SOCIETY OF AMERICA

Frontiers in Ecology and the Environment

Issue No 2 Volume 11 March 2013

Latent impacts trigger coastal habitat loss

Road reclamation and forest ecosystem recovery

Ocean sprawl and jellyfish blooms

esa

Latent impacts: the role of historical human activity in coastal habitat loss

Tyler C Coverdale*, Nicholas C Herrmann, Andrew H Altieri, and Mark D Bertness

Understanding human impacts on ecosystems is critical for conservation, but can be complicated by interactions between multiple impacts occurring at different times. Using historical patterns of ditch construction on Cape Cod, Massachusetts, we tested the hypothesis that mosquito ditches have exacerbated salt marsh die-offs. Ditching activities occurred in the 1930s and were followed by post-World War II shoreline development, which created >90% of current shoreline infrastructure on Cape Cod. Recently, predator depletion caused by recreational fishing has allowed populations of a native herbivorous crab (*Sesarma reticulatum*) to increase dramatically, triggering herbivore-driven cordgrass (*Spartina alterniflora*) die-off at developed sites. Depression-era mosquito ditching had little effect for decades, but accelerated subsequent die-offs by expanding cordgrass habitat. Despite occurring decades apart, ditching interacted synergistically with shoreline development and recreational fishing to devastate ~55% of low marsh habitat (the narrow band of marsh grass necessary for marsh persistence and expansion). This suggests that historical human impacts can remain dormant for decades before interacting unexpectedly with modern perturbations. Such latent impacts are widespread in both marine and terrestrial habitats and may be common in other ecosystems with a history of disturbance.

Front Ecol Environ 2013; 11(2): 69–74, doi:10.1890/120130 (published online 17 Jan 2013)

Understanding how humans affect the structure and function of ecosystems and the services they provide is becoming increasingly important in the face of unprecedented human population growth. This is particularly problematic in coastal habitats, where human impacts are often concentrated (Halpern *et al.* 2008) and where more than three billion people currently live – a number that is expected to double by 2025 (MA 2005). Developing a mechanistic understanding of how ecosystems will respond to future human impacts is challenging. Even in simple, well-studied systems, multiple human impacts can result in unanticipated non-linear, synergistic, delayed effects (Mumby *et al.* 2004; Crain *et al.* 2008).

The field of historical ecology has recently emerged as a powerful tool to help elucidate the effects of human activities over time, to better understand current ecological patterns, and to forecast the consequences of future human impacts (Lotze and Worm 2009). This tool allows current states to be assessed in the context of historical conditions, including natural environmental variation and human impacts. Ecologists can investigate to what extent historical "legacies" or "after effects" of past conditions have shaped the current state of species, populations, and ecosystems (Swetnam and Betancourt 1998; Dupouey *et al.* 2002; Foster *et al.* 2003; Jackson *et al.* 2009). For example, contemporary patterns of diversity in systems as varied as arid forests, freshwater streams, and coral reefs have been shown to depend on conditions that existed decades or centuries ago (Hughes 1989; Harding *et al.* 1998; Swetnam and Betancourt 1998). These findings highlight the need for a combined historical and experimental approach to more fully understand the role of past events on current conditions and future trajectories (Hughes 1989).

Here, we use historical ecology to examine how interactions between multiple human disturbances occurring decades apart have affected the current condition of salt marshes on Cape Cod, a point of land that extends off the coast of Massachusetts. Salt marshes are an excellent model system for addressing latent impacts and impact interactions because these ecosystems have been exploited by humans for centuries (Gedan *et al.* 2009). Salt marshes are also easily studied with historical aerial images because they are relatively flat landscapes dominated by a few discretely zoned, clonal plant species (Figure 1).

New England salt marshes have been among the most heavily disturbed ecosystems in North America since colonial times (Gedan *et al.* 2009). However, recent explosive population growth on Cape Cod, beginning in the 1930s, has had particularly deleterious impacts on marshes. As a result, we chose to focus our historical reconstruction on this most recent period (1939–2005) during which the permanent human population of Cape Cod has nearly doubled every 20 years, increasing from ~30 000 in 1930 to more than 220 000 by 2000 (US Census Bureau 2002). This rapid growth resulted in many anthropogenic changes to Cape Cod's coastal wetlands. Prior to the 1930s, ditches were intentionally dug in salt marshes throughout New England to drain flooded mosquito breeding habitat, which resulted in the establishment of corridors of the low marsh cordgrass, *Spartina alterniflora*, in areas formerly dominated by high marsh

Department of Ecology and Evolutionary Biology, Brown University, Providence, RI *(*tyler_coverdale@brown.edu*)

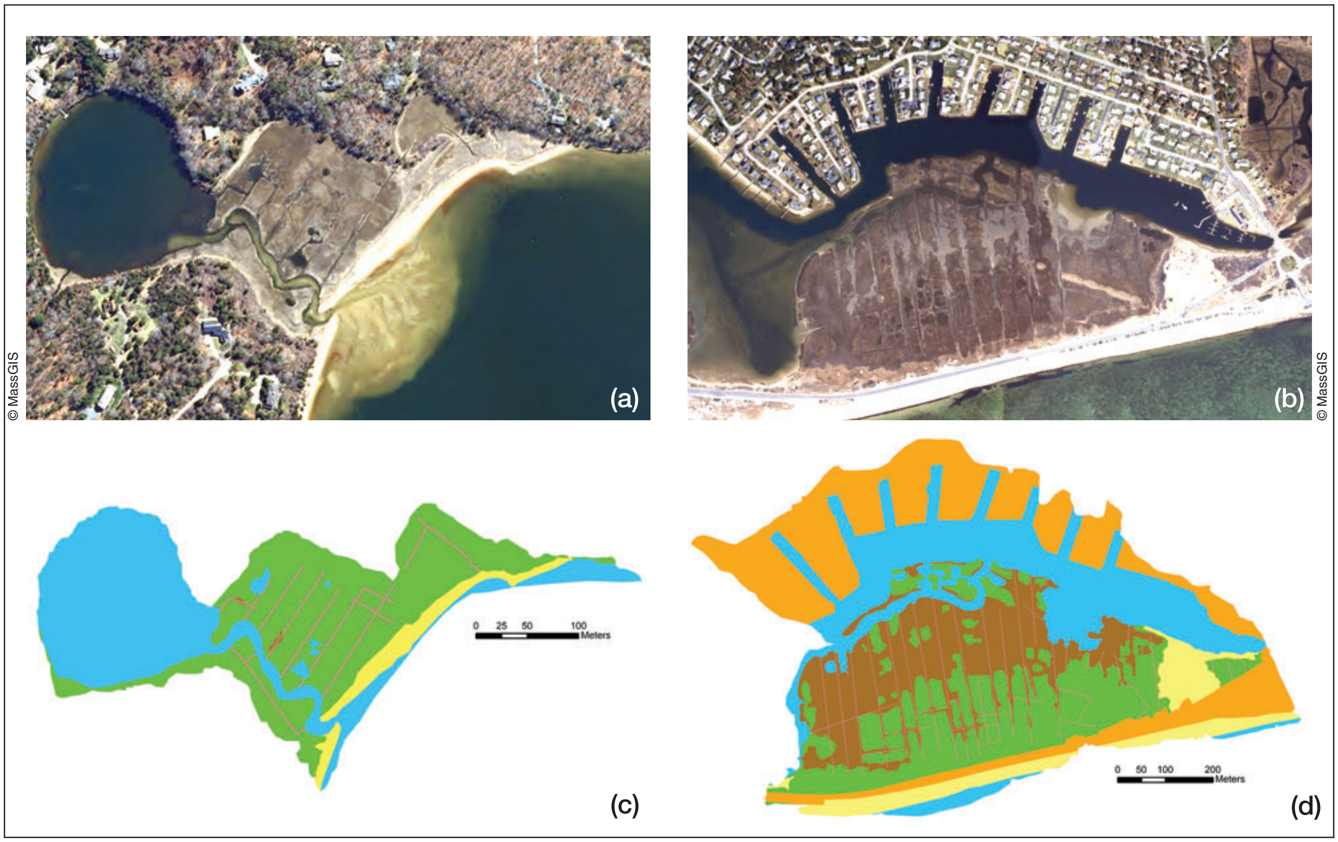
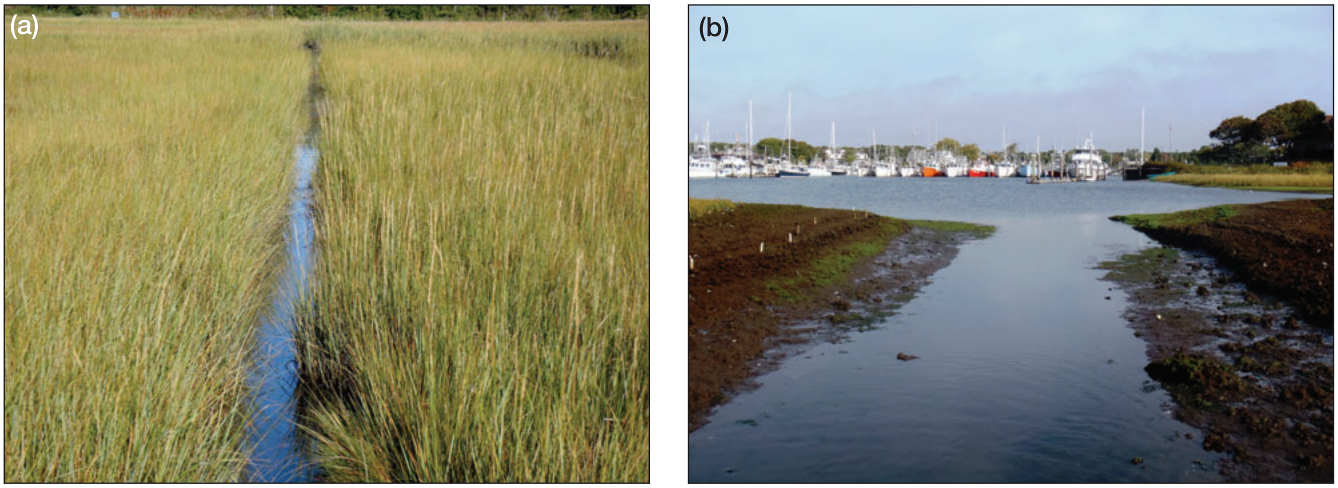


Figure 1. *Comparison of representative undeveloped (a and c) and developed (b and d) marshes on Cape Cod, Massachusetts. Aerial images show (a) the minimal development common at sites without die-off and (b) the dense development that characterizes sites with substantial die-off. GIS spatial maps (c and d) reveal that both of the representative sites depicted were ditched during the 1930s (red lines), but die-off (brown shading) only occurred following coastal development (orange shading) and subsequent overfishing at developed sites. Note the presence of die-off along ditch banks into the interior of the marsh at the developed site (d). This has led to substantial ditch widening and habitat loss, whereas most ditches at undeveloped sites (c) remain narrow and vegetated.*

plants (Figure 2a; Gedan *et al.* 2009). Because cordgrass is the dominant plant along natural tidal creeks, the creation of new cordgrass habitat along ditches represented an expansion of a naturally occuring habitat that had been ecologically unchanged for decades.

Recent reports of salt marsh die-offs along the east coasts of North and South America have focused attention on human impacts on salt marsh ecosystems. Salt marsh die-offs are characterized by the loss of foundation plant species to herbivores as a result of trophic dysfunction (Bertness and Silliman 2008). Salt marsh grasses, including *S alterniflora* and *Spartina patens*, form and maintain marsh habitats. Die-off was first identified on Cape Cod in 2002 and, in a series of field experiments (Altieri *et al.* 2012), it was demonstrated that die-off on Cape Cod is driven by the native herbivorous purple marsh crab (*Sesarma reticulatum*), which had denuded 50% of marsh creek banks on Cape Cod by 2008 (Holdredge *et al.* 2009). Further work showed that the increase in *S reticulatum* abundance over the past decade was caused by a potent trophic cascade triggered by recreational fishing of *S reticulatum* predators and is restricted to areas of intense coastal development (Figures 3 and 4). Recreational anglers currently make more than 377 000 fishing trips to Cape Cod annually (NMFS nd), and surveys indicate that their activity is primarily localized to areas of man-made coastal infrastructure, including docks, dredged channels, and marinas. In the absence of strong top-down control, *S reticulatum* populations have increased nearly fourfold, with cascading effects on cordgrass (*S alterniflora*) cover (Figure 4). Creek banks denuded by *S reticulatum* are subject to erosion and slumping and are a major source of marsh habitat loss.

On the basis of trends in human population growth, coastal development, and recent experimental work on the drivers of salt marsh die-off, we hypothesized that human impacts contributing to the current die-off of Cape Cod marshes occurred in three discrete periods: (1) mosquito ditching between 1900 and 1930 to drain breeding habitat and reduce disease transmission, (2) expansive coastal development between 1940 and 1970, and (3) cordgrass die-off between 1976 and the present. We also hypothesized that the extent of historical development determines the subsequent trajectory of healthy versus degraded marshes by focusing recreational fishing pressure on accessible sites. Furthermore, we hypothesized that, despite being temporally separated by several decades, Depression-era mosquito ditching exacerbated



C Harriet

Figure 2. *Representative mosquito ditches from (a) healthy and (b) die-off sites (photographed in July 2010). Ditches in both photographs were constructed during the 1930s and were initially <0.5-m wide. At healthy sites,* S alterniflora *extends all the way to the ditch bank and the ditches remain <0.5-m wide. In contrast,* S reticulatum *herbivory at die-off sites has removed large swaths of* S alterniflora *along the ditch bank. Mosquito ditches commonly expand to >10 m at die-off sites as a result of herbivory and subsequent erosion. Note the proximity to a large (>500 vessel) marina at the die-off site.*

current marsh die-off by increasing the area of marsh vulnerable to *S reticulatum* herbivory. We tested these hypotheses by reconstructing the recent history of Cape Cod marshes using archival aerial photographs.

Materials and methods

We obtained aerial photographs of 12 salt marshes from across Cape Cod that were collected during several time periods. Series of high-resolution aerial photographs covering the entire Cape Cod peninsula were available from 1939, 1976, 1994, and 2005, and were analyzed through the use of ArcGIS (Figure 1, a and b). The focal area at each site was defined as the natural extent of marsh vegetation in 1939. Marsh habitats (vegetated marsh, mosquito ditch, denuded creek bank, and coastal development) were tracked through time with the four sets of photos (ie from 1939, 1976, 1994, and 2005). Coastal development was defined as vegetated marsh habitat converted to impermeable surface, and included residential areas, docks, and marinas. Spatial maps were used to track the location and extent of each habitat through time (Figure 1, c and d). To test the hypothesis that shoreline development facilitated current patterns of cordgrass die-off, we classified sites based on a clear distinction in pre-1976 development (the period before local, state, and federal legislation restricted further coastal development in marsh habitat). Six sites experienced < 5% loss of marsh habitat (0.5 ± 0.4%) to development and were operationally defined as "undeveloped sites". The remaining six sites experienced > 5% loss (19.7 ± 3.0%) to development and were classified as "developed sites". We compared differences among sites in creek-bank habitat lost to die-off by 2005 using analysis of variance (ANOVA) to determine whether sites with greater development experienced more severe subsequent die-off. Low marsh, creek-bank habitat is the only site of marsh loss to die-off and is critical in the growth and persistence of functioning marshes as a result of sediment binding and habitat expansion. To test whether human impacts occurred in three discrete periods, we quantified the conversion of healthy marsh habitat to mosquito ditches, coastal development, and *S reticulatum*-driven cordgrass die-off throughout the 66-year study period and analyzed them with repeated measures ANOVA.

Ditch banks denuded as a result of *S reticulatum* grazing were easily distinguished from vegetated areas in photographs based on color in recent images and surface texture in earlier black and white images (Figure 2). To test the hypothesis that mosquito ditching amplified the extent of the current die-off by creating corridors of vulnerable cordgrass, we measured the proportion of ditch-bank habitat and nearby unditched marsh that had succumbed to die-off by 2005. Because > 90% of marshes in New England were ditched prior to 1930, we compared die-off rates along ditch banks and in areas of marsh > 5 m from the nearest ditch at each site (Gedan *et al.* 2009). One hundred random points were identified in each habitat type at each site, and the condition of each point was scored as either die-off or healthy marsh. A two-factor ANOVA was used to test whether ditching (ditch bank versus unditched marsh) and development (developed versus undeveloped) individually and/or synergistically increased the extent of die-off.

Results

Human impacts on Cape Cod salt marshes have occurred primarily during three discrete periods (Figure 4c). Prior to 1939, one of the most conspicuous disturbances in New England marshes was mosquito ditching. Of the mosquito ditches present at the 12 sites in 2005, > 95% were created during this first period. In the second period,

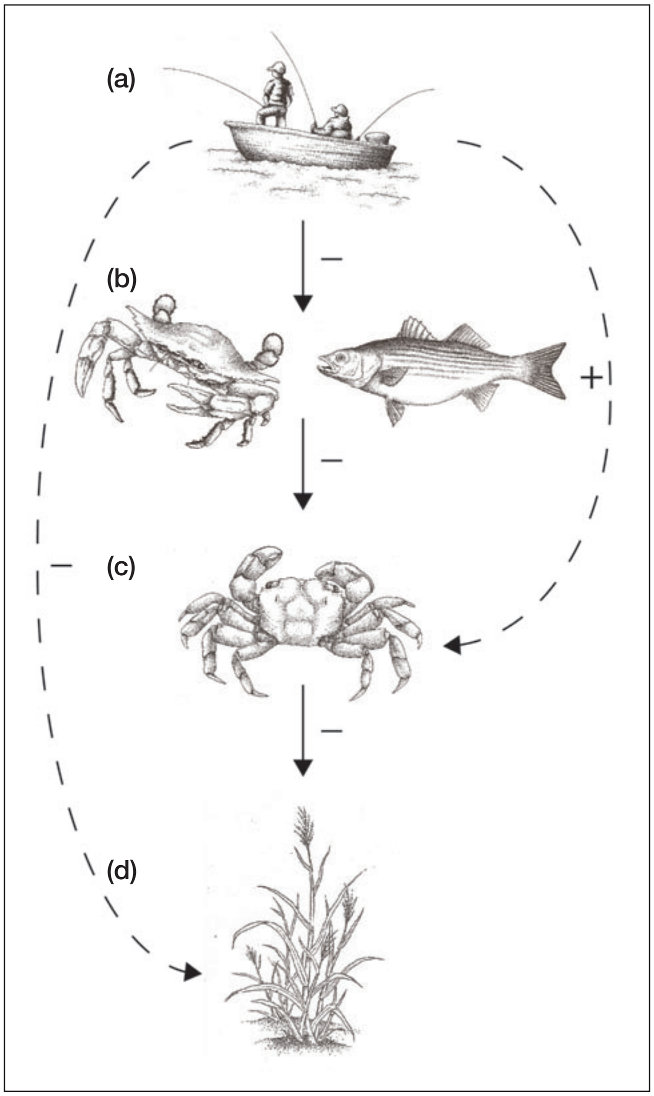


*Figure 3. At developed sites with increased accessibility and fishing pressure (a), the purple marsh crab (*S reticulatum*, [c]) is released from predatory control (eg blue crab [*Callinectes sapidus*] and striped bass [*Morone saxatilis*], [b]) and consumes cordgrass (*S alterniflora*, [d]) along creek and ditch banks. Denuded creek banks are subject to erosion and slumping and are a major source of habitat loss. Solid arrows = direct, consumptive interactions (ie predation, herbivory); dashed arrows = indirect, trophic interactions; + = positive interactions (ie predator release); – = negative interactions (ie predation, herbivory, herbivore release).*

from 1939–1976, the permanent human population of Cape Cod nearly tripled, increasing from 37 000 in 1940 to >100 000 in 1976 (US Census Bureau 2002). This population boom triggered increased destruction of salt marsh habitat to facilitate coastal development and recreation, and the only significant loss of marsh to development occurred during this period (die-off sites = 614.6 ± 289.3 hectares [ha], healthy sites = 21.8 ± 17.6 ha; site type × time interaction: $F_{3,21} = 8.57$, $P < 0.001$), during which nearly 95% of the human development in Cape Cod's salt marshes occurred. Significant loss of marsh due to *S reticulatum* occurred only after 1976, at developed sites (site type × time interaction: $F_{3,30} = 3.86$, $P = 0.019$; Figure 4b). Die-off led to the destruction of more than 90% of the remaining low marsh at some of the most heavily impacted sites on Cape Cod. Despite previous reports that die-off first occurred on Cape Cod in the late 1980s (Holdredge *et al.* 2009), patches of denuded creek bank were detected in photographs from as early as 1976.

In addition to the division into temporally distinct periods, the suite of human impacts affecting Cape Cod marshes is also spatially restricted to certain sites (Figure 4, a and b). All sites were ditched prior to the 1940s, but the effects of human development and die-off are restricted to only a subset of those sites. Undeveloped sites experienced low levels (<5%) of die-off after 1976, while developed sites diverged from undeveloped sites by 1976 in terms of overall marsh loss ($F_{3,28} = 18.58$, $P < 0.0001$), and subsequently experienced higher levels of post-1976, *S reticulatum*-driven die-off (Figure 4). Sites classified as developed in this study correspond to those classified as "die-off" by Altieri *et al.* (2012), who recorded substantially greater recreational fishing pressure at die-off sites than undeveloped sites in 2010.

Finally, 1930s-era mosquito ditching and pre-1976 coastal development interacted synergistically to amplify the extent of the current die-off, which was first detected in 1976 and steadily increased to the present (site type × ditching interaction: $F_{1,20} = 22.35$, $P < 0.001$). Despite being temporally separated by more than 30 years, mosquito ditching and coastal development significantly amplified rates of contemporary salt marsh die-off by creating additional low marsh habitat suitable for *S alterniflora* and *S reticulatum* and providing the physical structures necessary for recreational anglers at developed sites, respectively (Figure 2). More than half (52%) of the total die-off experienced at developed sites can be directly attributed to the creation of low marsh habitat by mosquito ditches, whereas >90% of the die-off at undeveloped sites occurred along ditch banks, suggesting that predator populations might be concentrated in larger natural channels and are largely absent from narrower mosquito ditches, even at sites with minimal fishing pressure.

Discussion

Our results reveal that Cape Cod salt marshes have been affected by a series of human impacts that went unrealized for decades before synergistically triggering widespread, unanticipated marsh loss. Mosquito ditching during the Great Depression was a relatively benign disturbance for decades before the development of recreational fishing infrastructure and associated fishing pressure released herbivorous crabs from consumer control. As a result, marshes in our study followed one of two trajectories beginning in 1939 (Figure 4, a and b). Marshes that initially lost large amounts of area to development also lost the greatest area to subsequent herbivore-driven die-off, while marshes that experienced little human development remained intact. This spatial divergence, in conjunction with previous experimental work, suggests that the pre-1976 construction of marinas, dredged channels, and coastal residential areas provided the infrastructure for the depletion of *S reticulatum* predators and cordgrass die-off, which was detectable in photographs from 1976, 1994, and 2005 (Figure 4b). Mosquito ditches, which contributed little to habitat loss for decades and continue to have little impact at undeveloped sites, emerged as a synergistic accelerant of die-off in the presence of shoreline development. It is important to note, however, that the divergence between developed and undeveloped sites observed since 1939 likely represents only the most recent degradation of a system that has been heavily impacted for centuries (Gedan *et al.* 2009). While the discovery of latent impacts at developed sites comes too late for management intervention, these results provide a warning that similarly widespread habitat loss is possible at undeveloped sites should future conditions change. In light of the expansive ditch networks at undeveloped sites (totaling more than 14 km in some marshland areas), our results suggest that management strategies should aim to reduce further development and fishing pressure. Under effective management, latent human impacts could remain unrealized while acting as a reminder of the ecological and economic costs of interactions between multiple human perturbations.

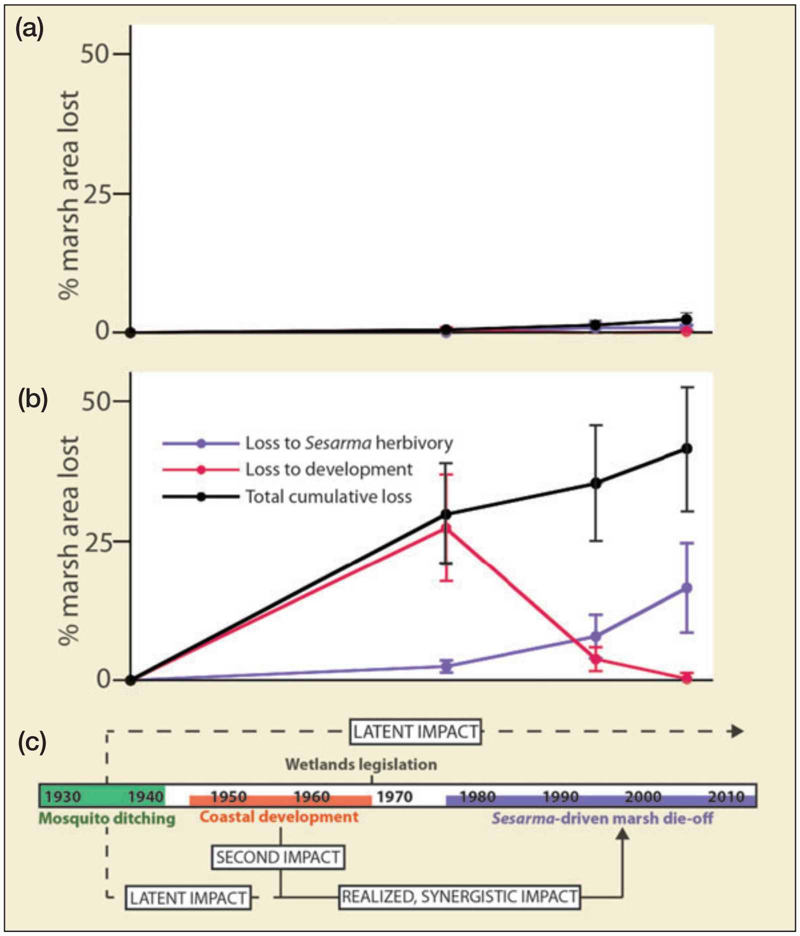


Figure 4. *Major drivers of marsh loss through time at (a) undeveloped and (b) developed sites. All sites were ditched prior to the 1930s, but subsequent coastal development (red) and herbivory by* S reticulatum *(purple) led to considerable habitat loss at developed sites. Mosquito ditches were a latent human impact for decades at developed sites but interacted synergistically with coastal development and recreational fishing (c), exacerbating the current die-off. Ditching remains a latent impact at undeveloped sites.*

Similar interactions between multiple disturbances have been reported in both marine and terrestrial systems (eg Swetnam and Betancourt 1998; Peterson *et al.* 2003; Mumby *et al.* 2004) and reveal that delays in the effects of latent human impacts and natural disturbances can cause unanticipated or novel outcomes. The possible effects of these perturbations remain wholly or partially unrealized and become apparent only following subsequent impacts or environmental changes (eg Baan 1997; Worster 2004).

The recent widespread collapse of *S alterniflora* on Cape Cod was unanticipated because ditch banks remained vegetated for more than 40 years after their construction, and because legislation protecting against coastal habitat loss by slowing shoreline development was enacted prior to the onset of die-off. That these ecosystems experienced substantial habitat loss as a result of interactions between multiple human impacts, even after broad legislative protection, indicates the importance of investigating the accumulation of latent impacts and of placing current conditions in a historical context. Human impacts on ecosystems cannot be considered in isolation, but must be understood as interactive effects of multiple disturbances. Latent natural and anthropogenic disturbances can make predicting such ecological surprises difficult in the absence of long-term datasets (Lindenmayer *et al.* 2010), but here we show that historical ecology can be a valuable tool for better understanding how multiple human disturbances occurring over several decades can produce large-scale habitat destruction and the loss of ecologically and economically valuable ecosystem services. Our findings demonstrate that the ability of ecologists to understand and predict the consequences of future development on ecosystems is dependent on an understanding of the accumulation of latent human impacts already affecting them.

Acknowledgements

We thank L Carlson for providing guidance on GIS analysis, D Sax and H Lotze for advice on the manuscript, and L Szathmary and Q He for assistance in the lab and field. Funding was provided by Rhode Island Sea Grant, the NSF Biological Oceanography Program, and a Brown University Undergraduate Teaching and Research Award.

References

Altieri AH, Bertness MD, Coverdale TC, *et al.* 2012. A trophic cascade triggers collapse of a salt-marsh ecosystem with intensive recreational fishing. *Ecology* **93**: 1402–10.

Baan C. 1997. The economic valuation of mangroves: a manual for researchers. Ottawa, Canada: International Development Research Centre.

Bertness MD and Silliman BR. 2008. Consumer control of salt marshes driven by human disturbance. *Conserv Biol* **22**: 618–23.

Crain CM, Kroeker K, and Halpern BS. 2008. Interactive and cumulative effects of multiple human stressors in marine systems. *Ecol Lett* **11**: 1304–15.

Dupouey JL, Dambrine E, Laffite JD, and Moares C. 2002. Irreversible impact of past land use on forest soils and biodiversity. *Ecology* **83**: 2978–84.

Foster D, Swanson F, Aber J, *et al.* 2003. The importance of land-use legacies to ecology and conservation. *BioScience* **53**: 77–88.

Gedan KB, Silliman BR, and Bertness MD. 2009. Centuries of human change in salt marsh ecosystems. *Ann Rev Mar Sci* **1**: 117–41.

Halpern BS, Walbridge S, Selkoe KA, *et al.* 2008. A global map of human impact on marine ecosystems. *Science* **319**: 948–52.

Harding JS, Benfield EF, Bolstad PV, *et al.* 1998. Stream biodiversity: the ghost of land use past. *P Natl Acad Sci USA* **95**: 14843–47.

Holdredge C, Bertness MD, and Altieri AH. 2009. Role of crab herbivory in die-off of New England salt marshes. *Conserv Biol* **23**: 672–79.

Hughes TP. 1989. Community structure and diversity of coral reefs: the role of history. *Ecology* **70**: 275–79.

Jackson ST, Betancourt JL, Booth RK, and Gray ST. 2009. Ecology and the ratchet of events: climate variability, niche dimensions, and species distributions. *P Natl Acad Sci USA* **106**: 19685–92.

Lindenmayer DB, Likens GE, Krebs CJ, and Hobbs RJ. 2010. Improved probability of detection of ecological "surprises". *P Natl Acad Sci USA* **107**: 21957–62.

Lotze HK and Worm B. 2009. Historical baselines for large marine animals. *Trends Ecol Evol* **24**: 254–62.

MA (Millennium Ecosystem Assessment). 2005. Ecosystems and human well-being: current state and trends. Washington, DC: World Bank.

Mumby PJ, Dahlgren CP, Harborne AR, *et al.* 2004. Fishing, trophic cascades, and the process of grazing on coral reefs. *Science* **311**: 98–101.

NMFS (National Marine Fisheries Service). nd. Recreational fisheries statistics queries. Silver Spring, MD: NMFS. www.st.nmfs.noaa.gov/st1/recreationalnd./index.html. Viewed 7 Jan 2013.

Peterson CH, Grabowski JH, and Powers SP. 2003. Estimating enhancement of fish production resulting from restoring oyster reef habitat: quantitative valuation. *Mar Ecol-Prog Ser* **264**: 249–64.

Swetnam TW and Betancourt JL. 1998. Mesoscale disturbance and ecological response to decadal climatic variability in the American Southwest. *J Clim* **11**: 3128–47.

US Census Bureau. 2002. Population estimates 1920–2000. Washington, DC: US Census Bureau.

Worster D. 2004. Dust Bowl: the southern plains in the 1930s. Oxford, UK: Oxford University Press.