# Climate change drives increased directional movement of landscape ecotones

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# ABSTRACT

## Context

Ecotones are boundary zones formed where overlap between neighboring ecosystems creates an intermediate ecosystem with unique ecological characteristics. Dynamic ecotones change position along a boundary over time and can be further categorized as either shifting, where the adjacent ecosystems alternatively drive movement of the ecotone but maintain the same relative location over time, or directional, where one system encroaches into the other and the ecotone moves laterally.

## Objectives

The purpose of this work was to examine how climate change alters movement dynamics of both directional and shifting ecotones.

## Methods

In three ecosystem case studies, we examine the effects of climate change on landscape-scale ecotone movement across the marine, terrestrial, and interfacing environments.

## Results

Shifts in local and global climate drive changes in ecotone patterns, increasing directional ecotone movement at both shifting and directional ecotones. Specifically, unidirectional changes in climate patterns disrupt dynamic equilibria at shifting ecosystem boundaries, thereby facilitating unidirectional movement at the previously shifting boundaries. Climate changes additionally accelerate pre-existing directional migration of ecotones through changes to abiotic gradients.

## Conclusion

Directional climate change increases directional movement in multiple types of ecotone. Future work should consider the rate and feedback mechanisms of ecotone movement and function at additional ecotones.

**Keywords**

Ecosystem boundary, ecotone function, desertification, marsh migration, deep chlorophyll maximum, climate change

## DECLARATIONS

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## INTRODUCTION

Ecotones, confined transitional boundaries between two distinct ecosystems whose overlap results in a unique ecological community, are relatively dynamic and unstable zones compared to their neighboring ecosystems and are frequently characterized by a change in abiotic stressors (Longhurst 2006; Wasson et al. 2013; Wang et al. 2019). Relatively high stress at the ecotone reduces the competitive dominance of species from the less-stressed adjacent ecosystem and forces the establishment of a community comprised of species from both adjacent ecosystems as well as unique species that are competitively dominant under increased stress (Lloyd et al. 2000) or facilitated by novel species interaction (Maher et al. 2005). The littoral zone of a lake serves as a model ecotone (van der Maarel 1990). The boundary between dry and submerged benthos at the littoral zone changes seasonally: high water levels in winter months inundate the area, and low water levels in summer months expose the area to both oxygen and heat. These seasonal changes create drastically different environmental conditions in the intertidal than in either of the adjacent ecosystems, leading to the establishment of a unique biological community and a distinct ecosystem. Although ecotones exist at a variety of spatial scales, from biomes to soil-plant interactions (Gosz 1993), here we focus on ecotones at the landscape scale (~1-100m) because of the climatic factors that drive landscape dynamics.

Like its biological community, an ecotone's structure and function are derived from the adjacent systems but remain unique from either ecosystem. The unique combination of habitat features may create a larger diversity of niches and, consequently, higher species richness than in the adjacent ecosystems (Horváth et al. 2001; Ribalet et al. 2010); however, this is not universal (Delcourt and Delcourt 1992; Risser 1995; Senft 2009) and may be limited to large ecotones (Smith et al. 1997). Similarly, ecosystem functions may be enhanced within some ecotones, as seen with the increased sedimentation and organic matter preservation in wetlands (Kolasa and Zalewski 1995). Conversely, ecotones may limit the movement of species, materials, or drivers (e.g., wind) from crossing to an adjacent ecosystem (Naiman et al. 1989; Johnston 1991; Forman and Moore 1992). The movement, or lack thereof, of species or material across the ecotone may contribute to feedback loops that either shift or maintain the position of the ecotone and adjacent ecosystems (Kolasa and Zalewski 1995), leading to dynamism and variation in ecosystem function across the ecotone transition.

Ecotones can be classified based on their long-term stability and direction of movement as stationary, shifting, or directional (Peters et al. 2006). Stationary ecotones occur where abiotic controls over an ecotone's location are inherent, reinforced by strong biotic feedbacks, and, consequently, stable over time, as seen in ecosystem transitions at abrupt elevation or geomorphological gradients (Körner 1998; Peters et al. 2006; Figure 1a). Shifting ecotones are more dynamic and, while they maintain a relatively constant location over time, they exist in an unstable equilibrium and periodically move laterally into adjacent ecosystems (Figure 1b). Shifting ecotones occur where varying environmental conditions allow for dominance by either ecosystem to shift at the boundary. For example, at the grassland-shrubland ecotone, increased drought or winter precipitation may cause the ecotone boundary to shift farther into grassland (i.e., grassland converts to shrubland), whereas, during a rainy period, movement of the ecotone may reverse direction and migrate into adjacent shrubland (Peters 2002; Shiponeni et al. 2011; Moreno-de las Heras et al. 2016). Short-term assessments of ecotone position may indicate that the ecotone is moving unidirectionally; however, the net movement of a shifting ecotone's position over many years is minimal because of the periodic reversals in movement and overall bidirectionality of ecotone movement. Conversely, directional ecotones move unidirectionally over time (Figure 1c). Typically, positive feedbacks on the leading end of the directional ecotone stabilize the encroaching ecotone and spur advancement into the adjacent ecosystem (in Figure 1c, ecosystem II). The trailing edge of the ecotone is then converted into the adjacent encroaching ecosystem (in Figure 1c, ecosystem I), leading to net movement of the ecotone over time. This is seen at the boundary between salt marsh and forest, where sea-level rise causes forest dieback and marsh encroachment, and the marsh-upland ecotone moves inland (Smith 2013; Wasson et al. 2013; Schieder et al. 2018).

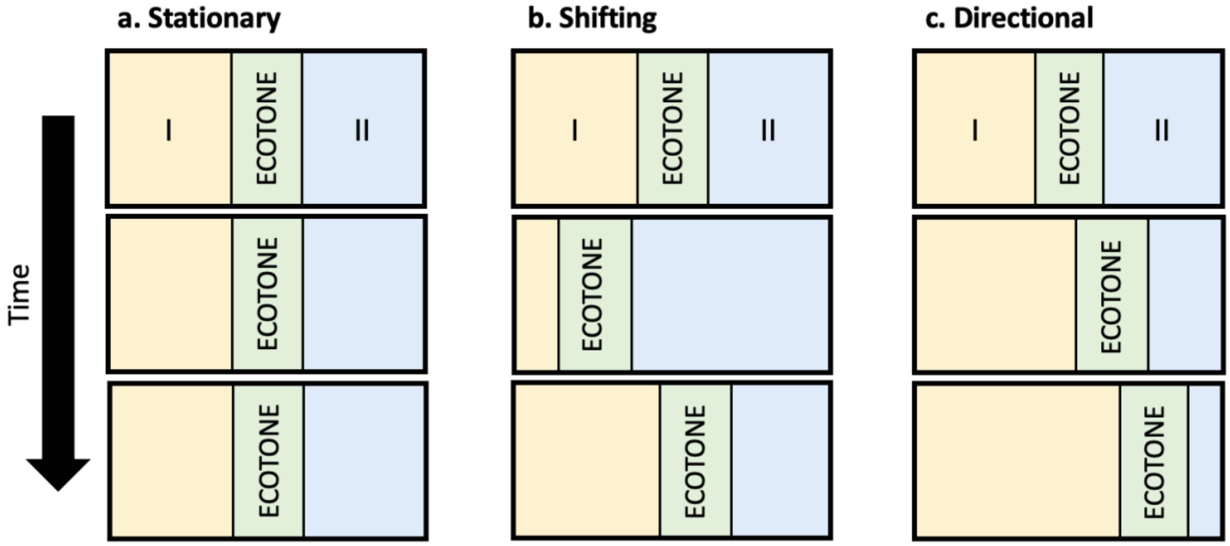

**Fig. 1** Schematic of (a) stationary, (b) shifting, and (c) directional ecotone movement over time where I and II are the ecosystems adjacent to the ecotone

While the effects of directional climate change on individual species and populations have been studied extensively (Goldblum and Rigg 2005; Caputi et al. 2013; Martínez-Soto and Johnson 2020), the effects of climate change on the directional movement of ecotones at the ecosystem scale is a developing field of research (Deaton et al. 2017; Theuerkauf and Rodriguez 2017; Smith and Kirwan 2021), despite the longstanding theory that ecotones are reactive to and indicative of climate change (Noble 1993; Wasson et al. 2013; Saintilan et al. 2014). Previous work has demonstrated that ecotones may be especially sensitive to changing conditions because species therein are nearing abiotic limits (Goldblum and Rigg 2005; Wasson et al. 2013) and that ecotones are useful study systems because they can be readily tracked over time (Kupfer and Cairns 1996). Thus, observing changes in ecotone dynamics may provide insight into climate change impacts on both ecotones and their adjacent ecosystems. Past ecotone studies have focused on the movement patterns of a single ecotone type, especially the acceleration of directional ecotone movement (Kupfer and Cairns 1996; Schieder and Kirwan 2019) and the latitudinal migration of biomes (Gonzalez et al. 2010; Coldren et al. 2018). We uniquely propose that climate-driven changes in ecotone movement may extend beyond existing directional ecotones to include changes in the movement patterns and classification of previously shifting ecotones. In this review, we present three landscape ecotone case studies in marine, terrestrial, and the interfacing environments to demonstrate how climate change is impacting historically shifting and directional ecotones. We further discuss how changes in ecotone dynamics may affect ecotone function and call for future work documenting changes in ecotone dynamics.

## LANDSCAPE ECOTONE CASE STUDIES

### <u>Shifting Ecotone</u>: deep chlorophyll layer (DCL) ecotone

Formation of the deep chlorophyll layer (DCL), the subsurface depth layer in both freshwater and marine aquatic systems that contains the maximum concentration of chlorophyll, is dependent on light attenuation depth and the nutricline (Fee 1976; Abbott et al. 1984). While light is abundant in surface waters, low nutrient availability limits the amount of primary production. Deeper in the water column, attenuation reduces the availability of light, but nutrient availability increases. These inverse environmental gradients establish the DCL at the overlapping zone between lit, nutrient-depleted surface waters and dark, nutrient-rich deep waters (Cullen 1982). While community composition of the DCL varies geographically, the DCL tends to have more flagellated planktons, pennate diatoms, and cryptophytes compared to the centric diatom-dominated surface communities (Kimor et al. 1987; Barbiero and Tuchman 2004). The DCL supports a unique community of species adapted to low-light conditions through development of accessory pigments or vertical migration to surface waters (Pollehne et al. 1993; Cullen 2015). This unique assemblage of species establishes the DCL as an ecotone.

The concentration of chlorophyll at depth has multiple important functions for the aquatic ecosystem. Because of the relatively high concentration of planktonic organisms, there is an increased presence of both mixotrophic and heterotrophic protozoans at the DCL (Bird and Kalff 1989). The rate of energy movement and grazing velocity is higher at the DCL, as is secondary organic matter export through sloppy heterotrophic feeding and sinking fecal pellets (Pollehne et al. 1993; Macías et al. 2014). Compared to adjacent ecosystems, bacteria biomass is ten times greater at the DCL, and microbial diversity is similarly found to be higher (Auer and Powell 2004; Junior et al. 2015). The DCL creates an environment with enhanced ecological functioning and biodiversity compared to the light-rich, nutrient-poor surface waters and the light-poor, nutrient-rich deep waters that border the system on either side.

*Directional movement of the DCL ecotone*

Oscillations in phytoplankton concentrations at the DCL are driven by the balance between vertical mixing and nutrient sinking (Huisman et al. 2006), where seasonal variation in nutrient availability, as controlled by the upwelling of deep, nutrient-rich waters, determines primary production throughout the year. Therefore, the location of the DCL varies based on short-term environmental conditions and weather, but its overall position remains relatively unmoved on a longer time scale, which is characteristic of a shifting ecotone (Estrada et al. 1993; Letelier et al. 2004; Figure 2a). Prior research indicates that the DCL, despite its interannual variations in depth, is relatively stable in the water column over the course of years to decades (Cullen 1982; Estrada et al. 1993). Developments in phytoplankton modeling and observation, however, challenge this notion and indicate that phytoplankton communities in DCLs can have sustained fluctuations in population density over long-term timescales (Letelier et al. 2004; Huisman et al. 2006). As global temperatures rise and surface ocean waters are heated, vertical stratification increases and, consequently, vertical mixing decreases (Bopp et al. 2001), limiting nutrient availability to phytoplankton. As a result, low phytoplankton densities at the DCL become more frequent and long lasting (Huisman et al. 2006). Sustained shifts to a warmer climate have led to increased stratification and, consequently, the depletion of the DCL and the overall directional movement of the DCL ecotone into shallower water depths in non-polar regions (Figure 2b).

DCLs in lakes similarly indicate climate-induced directional ecotone movement, but, instead of decreasing densities corresponding with warmer waters and shallower depths, DCL chlorophyll concentrations in lakes are increasing as surface temperatures increase (Barbiero and Tuchman 2004; Reinl et al. 2020). While open-ocean DCLs are limited by decreased nutrient concentrations from decreased vertical mixing, increased temperatures in lakes are associated with increased productivity and higher phytoplankton concentrations at the DCL (Reinl et al. 2020). As waters continue to warm, the DCL in lakes may also become shallower as the increased concentration of smaller phytoplankton cells increases the scattering of light and decreases light attenuation (Yvon-Durocher et al. 2011). From this, warming waters in lakes may lead to higher chlorophyll concentrations in DCLs at shallower depths, as opposed to the reduced chlorophyll concentrations seen in open-ocean DCLs (Figure 2c). Although lake and open-ocean DCLs have similar directional movements—both are shoaling—climate changes induce opposite effects on chlorophyll concentration and ecosystem function in these systems, indicating that, while climate change is driving ecotone migration, local conditions and ecosystem type can influence ecotone function (Figure 2b, 2c).

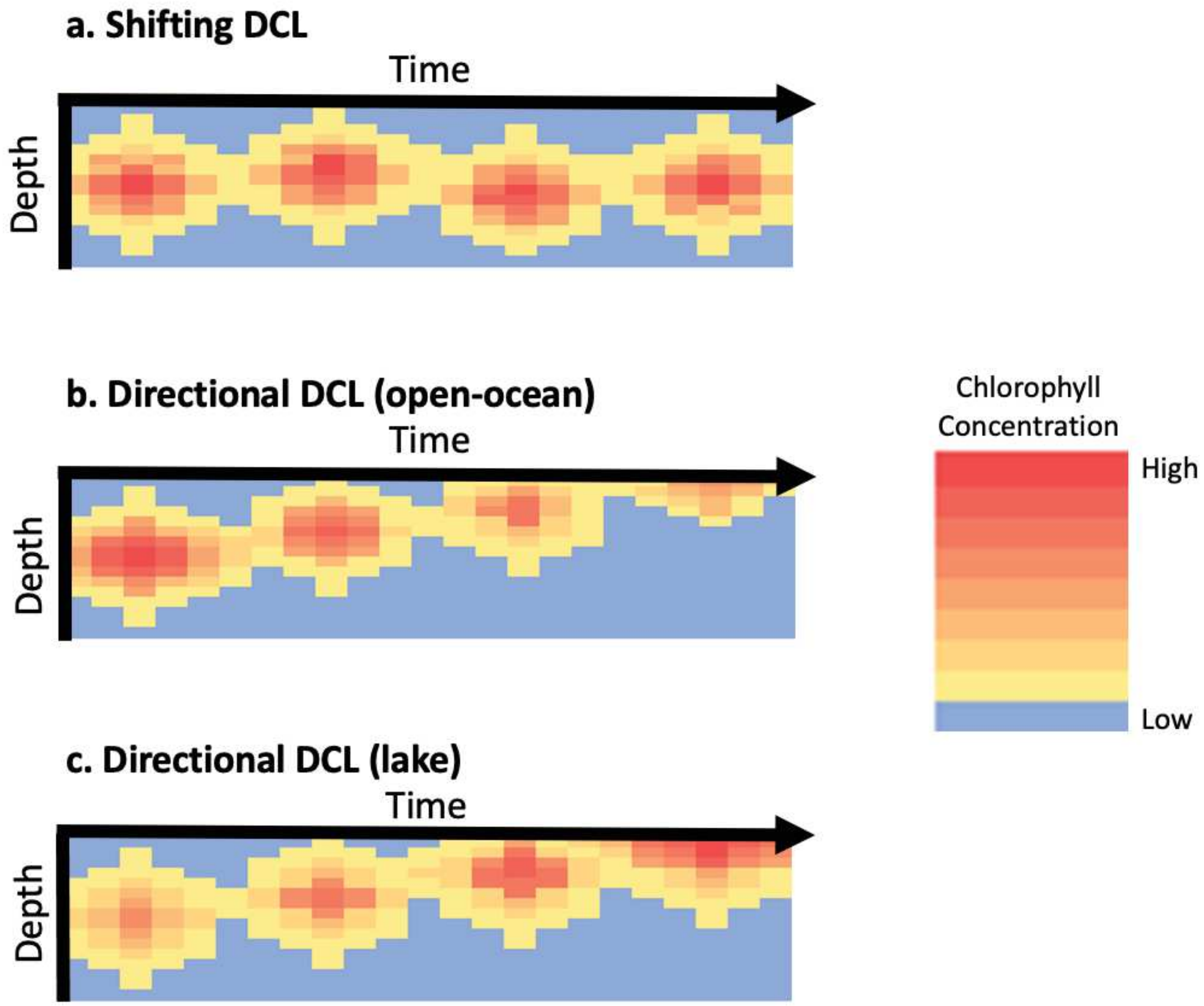

**Fig. 2** Conceptual diagram depicting (a) shifting ecotone movement of the DCL where depth is relatively maintained over time despite seasonal variation (b) directional shoaling and decreasing chlorophyll concentrations in open-ocean systems, and (c) directional shoaling and increasing chlorophyll concentrations in lake systems

<u>Shifting Ecotone</u>: grassland-shrubland ecotone

Grassland and shrubland ecosystems, located throughout the world in arid and semi-arid biomes, are characterized by frequent drought intervals, fires, and livestock grazing—

disturbances that create heterogeneous habitat patches and form the highly dynamic grassland-shrubland ecotone (Anderson 2006; Fuhlendorf et al. 2006; McGranahan et al. 2012; Connell et al. 2018). This heterogeneity in vegetation structure influences biodiversity and habitat use among ecotone residents (Connell et al. 2018). Spatial patches in the ecotone may act as habitat islands for species supported by the adjacent ecosystems (Sanchez and Parmenter 2002; Schooley et al. 2018), but the ecotone also supports species distinct from those occupying adjacent ecosystems (Jorgensen et al. 2000). The mosaic of grass and shrub patches at the ecotone thus forms a distinct ecosystem that supports a unique community.

Terrestrial ecotones are typically identified by changes in vegetation communities at the landscape scale (Risser 1995), which are determined by abiotic characteristics, disturbance, and species-environment feedback (D'Odorico et al. 2010; Porensky et al. 2016; Archer et al. 2017). Grassland and shrubland ecosystems are alternative stable states, meaning that either unique ecosystem can exist in the same area, with the same climate (Vetter 2009; Ratajczak et al. 2014). Because grassland and shrubland species coexist and compete for dominance at the ecotone, the biotic and abiotic factors that determine competitive advantage between these systems determine the position and movement of the ecotone (Peters 2002; Peters et al. 2006). Changes in environmental conditions can lead to abrupt lateral movement in the shifting ecotone and transformation of an area from one state into the alternate state (Vetter 2009).

Grass and shrub species possess competitive advantages under different precipitation patterns: grasses outcompete shrubs with frequent summer rains, and shrubs have a competitive advantage during prolonged drought and winter rain (Peters 2002; Shiponeni et al. 2011). Shrubs may act as “resource islands” that limit water accessibility to grasses and make it difficult for them to grow back after die-off (Duniway et al. 2010; Pockman and Small 2010). Additionally, shrubs may perpetuate their own survival and expansion by warming surface air temperatures in winter, preventing lethal freezes that are typically followed by grassland encroachment (D’Odorico et al. 2010), and by providing habitat for grass-grazing herbivores at the ecotone (Bestelmeyer et al. 2007). Conversely, grass species may outcompete shrubs during years with frequent summer rains or regular fire disturbance, due to their deeper root structure and regrowth (Novellie and Bezuidenhour 1994; Peters 2002; Shiponeni et al. 2011). These differences in competitive advantage contribute to their coexistence in a shifting ecotone under fluctuating and seasonal climatic conditions.

*Directional movement of the grassland-shrubland ecotone*

While grassland-shrubland boundaries are theoretically shifting ecotones, global patterns of shrub encroachment over the past century (Naito and Cairns 2011; Archer et al. 2017) indicate that the grassland-shrubland boundary has become a directional ecotone (but see Masubelele et al. 2014). This pattern of movement, also called “desertification”, is driven by a suite of interacting biotic and abiotic factors that favor shrubland over grassland, including livestock grazing (increased consumption of grasses), fire suppression (reduced shrub disturbance), and prolonged drought (decreased grass growth), the last of which is predicted to increase with future climate change (Roux 1966; Vetter 2009; Rutherford et al. 2012). Drought is the primary climactic driver of shrub encroachment (Novellie and Bezuidennour 1994; O’Connor and Roux 1995) and also amplifies the effects of secondary impacts, such as livestock grazing, on grassland to shrubland conversion (Vetter 2009). Ultimately, unidirectional changes in climate may thus disrupt the oscillating equilibrium previously held at the shifting grassland-shrubland ecotone, leading to dominance of shrubland within the ecotone and continued directional encroachment of shrubland into grassland.

<u>Directional Ecotone</u>: salt marsh-upland ecotone

In marshes, the transition between salt marsh and coastal forest forms a unique ecotone, sometimes referred to as the “ghost forest”, defined by a rapid change in species composition across an elevation and salinity gradient (Wasson et al. 2013; Santelmann et al. 2019). Vegetation composition varies across the transition from marsh to forest based on differences in inundation, soil salinity, moisture, and competition (Pennings and Callaway 1992). Germination of the upland species in the marsh-upland ecotone tends to be limited by salinity, such that the lower limit of upland vegetation zones is determined by abiotic constraints (Muñoz-Rodriguez et al. 2017). The upper limit of marsh vegetation zones, however, is determined by competition, where marsh species are outcompeted by more freshwater-reliant, terrestrial species, such as *Myrica cerifera* (wax myrtle) or *Phragmites australis* (common reed) (Veldkornet et al. 2015). This distinct zonation enables the ecotone to support high levels of vegetative complexity and biodiversity niches within a relatively small area (Traut 2005).

*Accelerated directional movement of the marsh-upland ecotone*

Shifting environmental gradients drive the lateral movement of the marsh-upland ecotone while maintaining species composition within the ecotone (Smith 2013; Figure 3). Where sea levels are rising, the marsh-upland ecotone exhibits directional migration into upland systems (Smith 2013; Schieder et al. 2018). The chronic press of saline intrusion into forests limits forest regeneration, and acute storm pulses kill mature, salinity-resistant trees (Fagherazzi et al. 2019). Together, these processes facilitate the inland migration of marsh vegetation, a process often referred to as marsh migration. With this unidirectional ecotone movement, vegetative structure is preserved within the directional ecotone as persistent zones of marsh and ecotone habitat encroach into upland forests concurrently (Wasson et al. 2013). The ecotone itself is typically dominated by snags left over from the retreating upland forest and grass species from the encroaching salt marsh, along with ecotone-specific species (Kirwan and Gedan 2019).

Although the directional movement of the marsh-upland ecotone has been a naturally occurring process throughout the Holocene (Horton et al. 2018), anthropogenic climate change processes have intensified the drivers of ecotone movement (Donnelly and Bertness 2001). As the global rate of sea-level rise and the frequency of storms has increased, the directional movement of the marsh-upland ecotone has also accelerated, where possible (Schieder and Kirwan 2019).

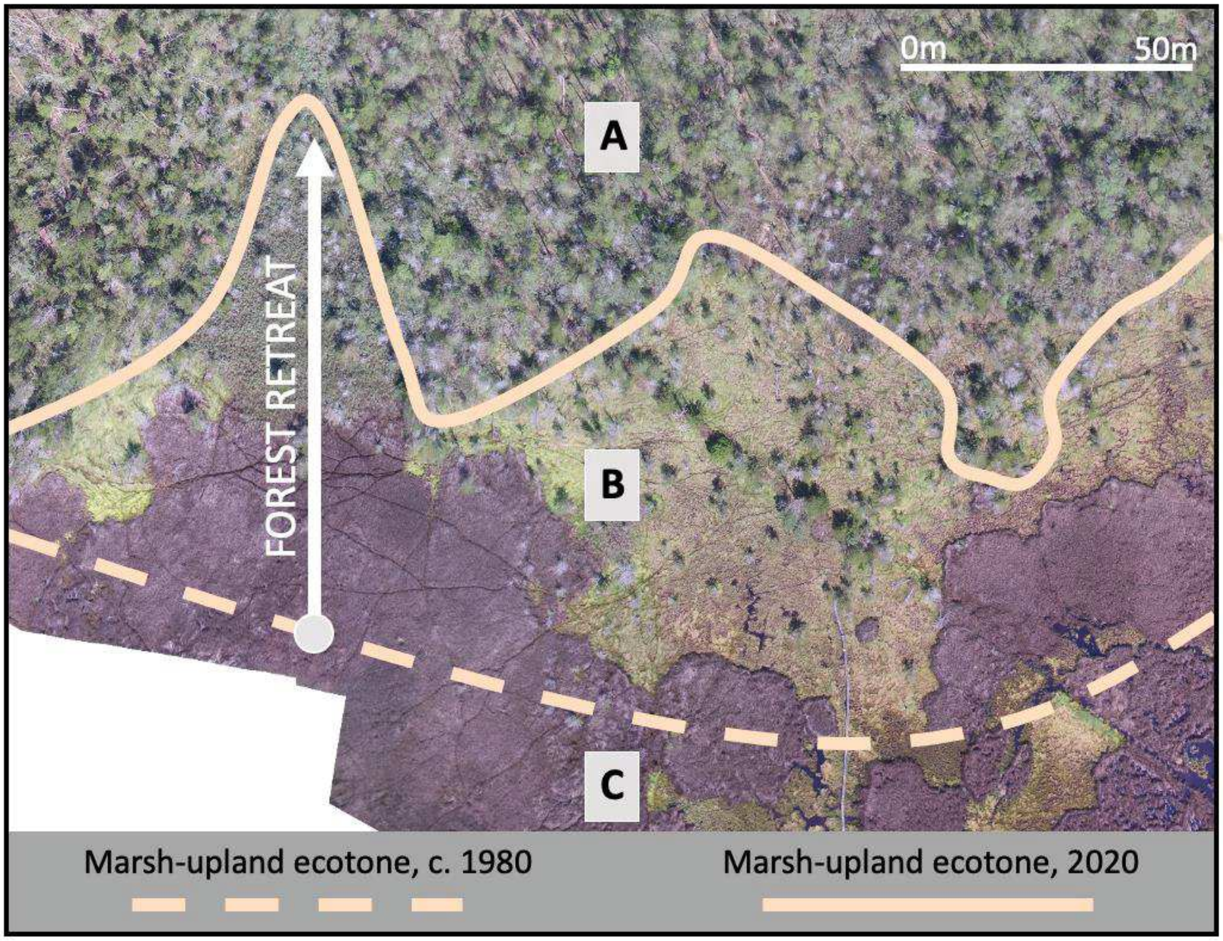

**Fig. 3** Aerial, true-color image from Brownsville Preserve (Virginia, USA) showing upland movement of the directional marsh-upland ecotone as tidal marsh migrates into space previously occupied by coastal forest. The tan lines represent the approximate locations of the marsh-upland ecotone in 1980 (dashed) and 2020 (solid), while the white line shows the direction and extent of

forest retreat between 1980 and 2020. Letters represent zones of (A) forest, (B) new marsh formed since 1980, and (C) marsh older than 40 years. Data from Smith and Kirwan (2021)

## DISCUSSION

### *Climate change and ecotone dynamics*

In the case studies reviewed, we see the manifestation of global changes in ecotone dynamics on the ecosystem level. From these examples, we find evidence that changing climates at both the local and global scales can propel directional ecotones by manipulating the abiotic conditions that determine the width and position of shifting ecotones (deep chlorophyll layer), limiting reversals in shifting ecotones (grassland-shrubland), and directly accelerating the drivers of directional ecotones (marsh-upland). Local and global climate changes have caused ecotone dynamics to change in a variety of landscapes, but we find evidence for a general shift toward directional ecotone movement as abiotic gradients are modified by changes in global climate drivers.

In the deep chlorophyll layer (DCL) case study, shifts in environmental conditions caused by global climate changes—specifically warming-induced stratification—disrupt the previously shifting ecotone. In response to warming, the DCL reaches a shallower depth and either increases or decreases its chlorophyll concentration depending on the local conditions of the system. Warming surface waters in lakes increase phytoplankton productivity, albeit at shallower depths, whereas increased ocean stratification and reduced vertical mixing diminish productivity and shrink the DCL in open-ocean ecosystems (Bopp et al. 2001; Huisman et al. 2006; Reinl et al. 2020). These differences emphasize that local conditions interact with climate to determine the effect of directional ecotone movement on ecosystem function.

The grassland-shrubland and salt marsh-upland ecotone case studies demonstrate more uniform directional movement of ecotones, driven by a changing climate in two distinct ways.

The grassland-shrubland ecotone typically acts as a shifting ecotone under stable or equally oscillating climate conditions (Peters et al. 2006; Shiponeni et al. 2011). Due to directional changes in climate, however, the shifting ecotone dynamics driven by variable abiotic and biotic conditions (e.g., precipitation patterns, grazing intensity) are suppressed, and the resulting climate conditions favor shrubland dominance (Duniway et al. 2010; Pockman and Small 2010). As grassland and shrubland ecosystems endure more prolonged droughts, conditions become more favorable for shrubland species, thereby disrupting the equilibrium of the shifting ecotone, amplifying the effects of disturbance at the transition, and promoting directional movement of the ecotone into grasslands. Here, directional movement is not directly spurred by a shifting abiotic gradient, such as salinity or light. Instead, reduced variations in climate disrupt the equilibrium inherent to a shifting ecotone and prevent the expected reversals that maintain the long-term position of the ecotone.

Conversely, rising sea levels caused by global climate changes drive the accelerating migration of salt marshes into upland ecosystems (Schieder et al. 2018). As saltwater rises and moves inland, the salinity gradient that spans from salt marsh to coastal forest also shifts inland, creating an environment favorable for migration of salt marsh species into the forest (Smith 2013; Muñoz-Rodriguez et al. 2017). As opposed to the grassland-shrubland and deep chlorophyll layer case studies, where an equilibrium is disturbed, the accelerated directional movement of the marsh-upland ecotone results from the acceleration of a preexisting pattern of movement within an existing environmental gradient.

Ecotones occur over a broad spectrum of temporal and spatial scales and are therefore subject to scale-dependent constraints and drivers. Although constraints at multiple scales are simultaneously driving ecotone dynamics (Gosz 1993), ecotone dynamics at broad spatial scales (biome and landscape ecotone) are dominated by changes in climate and topography, as compared to smaller spatial scale ecotones (population and plant-soil ecotones), which are controlled by interspecies interactions and soil chemistry. Therefore, the strongest representations of climate change's influence on ecotone dynamics will be observed at the landscape scale and above. Temporally, changes in climate—especially anthropogenic changes—manifest over the decadal to centennial scale (Magnuson 1990). Meaningful examinations of the effects of climate on ecotone movement, and ecotone dynamics more generally, therefore necessitate a broad spatial scale and a multi-decadal or centennial temporal scale. Smaller-scale observations may exhibit patterns that are not representative of the long-term impacts of climate changes on ecotone movement. For example, short-term observations of variable ecotone position may indicate shifting movement at an ecotone that is actually moving directionally when examined over the decadal time scale. From this, it is evident that spatial and temporal scales of ecotone observation must align with the questions being asked and the drivers and constraints of ecotone dynamics being examined.

### *Ecotone and adjacent ecosystem function*

In the presented case studies, changes in ecotone dynamics have the potential to reduce overall ecosystem function, though the mechanism of this reduction varies. As shifting ecotones become directional, the direction and rate of their movement, the encroaching ecosystem functionality, and the retreating ecosystem functionality will determine the change in ecosystem function at the landscape scale. The DCL case study emphasizes that, as ecotones become more variable in both ecotone area and presence, ecosystem functions—namely primary production—within these zones can diminish (Huisman et al. 2006).

The ecosystem function of a directional, migrating ecotone is likely to decrease as a mature system is replaced with a young ecosystem, which may require time for process rates to increase to those seen in mature systems (Greiner et al. 2013; Smith and Kirwan 2021). Additionally, directional ecotone movement can cause an overall reduction of functionality at the landscape scale when a low-functioning system replaces a high-functioning system, such as when seagrasses are replaced by bare sediment (Trevathan-Tackett et al. 2018). The transition from a low- to high-carbon burial system seen during directional mangrove encroachment emphasizes that net ecosystem functionality under novel landscape changes is dependent on both of the ecotones' adjacent ecosystems (Yando et al. 2016).

Because directional ecotones are constantly migrating and being displaced, the unique ecotone system must continually re-establish. The rate of migration thus determines the ability of the new ecotone to mature and reach its previous functionality. A slowly migrating ecotone is afforded time to mature, whereas rapid ecotone movement provides limited time to reach maturity before conversion to the adjacent ecosystem. Therefore, with accelerating rates of directional movement, such as those seen at the marsh-upland ecotone, mature ecotone functionality may never be reached before the ecotone is again displaced (Smith and Kirwan 2021).

Directional ecotone migration also differs based on the structure, community composition, and land use of the retreating ecosystem on which it is encroaching. Ecotones with developed boundaries on one side, such as armored shorelines in the case of the marsh-upland ecotone, tend to be truncated or absent, with minimal opportunity for ecotone migration (Wasson et al. 2013; Gehman et al. 2018). For ecotones without anthropogenic or morphological boundaries, land use in the adjacent ecosystem still affects community composition of the resulting ecotone (Anisfeld et al. 2017; Gedan and Fernandez-Pascual 2019). Because movement on the encroaching side of a directional ecotone is persistent, the upland boundary of the ecotone may influence areal extent and community composition as the ecotone migrates, possibly resulting in reductions in ecotone area or connectivity between adjacent ecosystems over time. Furthermore, invasive species, which often benefit from disturbance (Minchinton and Bertness 2003; Smith 2013), may prevent an ecotone from maintaining its structure and functionality as it migrates.

*Suggestions for future research*

As shown in the case studies explored in this paper, ecotones are unique environments that rely on controlling factors imposed by both neighboring ecosystems and global changes. Because ecotones are unique environments distinct from the surrounding, adjacent ecosystems, they warrant their own assessments and exploration of ecosystem functions, especially in dynamic ecotones where climate changes alter movement patterns. The deep chlorophyll layer and grassland-shrubland case studies exemplify the increased net ecotone movement and local changes in ecotone function that may result from climate change. Likewise, the marsh-upland case study demonstrates the potential for faster directional ecotone movement with climate change. If the demonstrated effects of climate change on ecotone movement extend beyond the included case studies to more ecotones, it will be important to consider functions within all ecosystems involved—including not only the adjacent ecosystems, but changes at the ecotone itself. Additionally, ecotone shifts due to climate changes call for future studies to consider interactive effects between traditional ecotone disturbances, local conditions, and broader controlling factors, such as global climate, as well as influences of the secondary effects of climate change (e.g., changing wind patterns, seed dispersal, and animal migration).

In response to directional climate change (e.g., sea-level rise or precipitation changes), ecotone movement patterns may change, although this response is not uniform for all ecotones (Neilson 1993; Noble 1993). When environmental conditions fall out of equilibrium and one adjacent ecosystem outcompetes the other, shifting ecotones may become directional ecotones. Further, shifts in environmental gradients may cause directional ecotones to exhibit accelerated landscape-scale migration (Allen and Breshears 1998; Wasson et al. 2013; Gedan and Fernandez-Pascual 2019; Kirwan and Gedan 2019). Observing changes in ecotone dynamics may thus provide insight into the extent of climate change impacts on both ecotones and their adjacent ecosystems.

## CONCLUSION

In the ecotone literature, studies in multiple environments—including aquatic, terrestrial, and ecosystems at the marine-terrestrial interface—show developing changes in ecotone movement at the landscape scale. Patterns of movement within the deep chlorophyll layer, grassland-shrubland, and salt marsh-upland ecotones suggest that climate change may drive changes in the movement patterns of ecotones, specifically shifting ecotone dynamics toward greater and more directional movement. This may occur through increases in climate variability (e.g., greater annual temperature variation) that change the seasonal dynamics of ecotones, unidirectional climate shifts (e.g., prolonged drought) that reduce reversals in shifting ecotone movement, or directional movement of abiotic gradients (e.g., salinity) that propagates accelerated directional ecotone movement. Future studies should consider this pattern in additional ecotones and as caused by additional climate drivers not discussed here. Future work should also examine ecosystem function in ecotones and their adjacent ecosystems, as increased directional movement may lead to changes in function, and predicted climate changes will likely accelerate ecotone displacement.

**REFERENCES**:

Abbott MR, Denman KL, Powell TM, Richerson PJ, Richards RC, Goldman CR (1984) Mixing and the dynamics of the deep chlorophyll maximum in Lake Tahoe. Limnol Oceanogr 29:862-878. https://doi.org/862-878.10.4319/lo.1984.29.4.0862

Allen CD, Breshears DD (1998) Drought-induced shift of a forest–woodland ecotone: rapid landscape response to climate variation. Proc Natl Acad Sci 95:14839-14842. https://doi.org/10.1073/pnas.95.25.14839

Anderson RC (2006) Evolution and origin of the central grassland of North America: climate, fire, and mammalian grazers. J Torrey Bot Soc 133:626-647. https://doi.org/10.3159/1095-5674(2006)133[626:EAOOTC]2.0.CO;2

Anisfeld S, Cooper K, Kemp A (2017) Upslope development of a tidal marsh as a function of upland land use. Glob Chang Biol 23:755-766. https://doi.org/10.1111/gcb.13398

Archer SR, Anderson EM, Predick KI, Schwinning S, Steidl RJ, Woods SR (2017) Woody plant encroachment: causes and consequences. In: Briske D (ed) Rangeland systems, Springer, Cham, pp 25-84. https://doi.org/10.1007/978-3-319-46709-2_2

Auer MT, Powell KD (2004) Heterotrophic bacterioplankton dynamics at a site off the southern shore of Lake Superior. J Great Lakes Res 30:214-229. https://doi.org/10.1016/S0380-1330(04)70387-1

Barbiero RP, Tuchman ML (2004) The deep chlorophyll maximum in Lake Superior. J Great Lakes Res 30:256-268.

Bestelmeyer BT, Khalil NI, Peters DP (2007) Does shrub invasion indirectly limit grass establishment via seedling herbivory? A test at grassland-shrubland ecotones. J Veg Sci 18:363-371. https://doi.org/10.1111/j.1654-1103.2007.tb02548.x

Bird DF, Kalff J (1989) Phagotrophic sustenance of a metalimnetic phytoplankton peak. Limnol Oceanogr 34:155-162. https://doi.org/10.4319/lo.1989.34.1.0155

Bopp L, Monfray P, Aumont O, Dufresne JL, Le Treut H, Madec G, Terray L, Orr JC (2001) Potential impact of climate change on marine export production. Global Biogeochem Cycles 15:81-99. https://doi.org/10.1029/1999GB001256

Caputi N, De Lestang S, Frusher S, Wahle RA (2013) The impact of climate change on exploited lobster stocks. In: Phillips BF (ed) Lobsters: biology, management, aquaculture and fisheries. pp 84-112. https://doi.org/10.1002/9781118517444.ch4

Coldren GA, Langley JA, Feller IC, Chapman SK (2018) Warming accelerates mangrove expansion and surface elevation in a subtropical wetland. J Ecol 107:79-90. http://doi.org/10.1111/1365-2745.13049

Connell LC, Scasta JD, Porensky LM (2018) Prairie dogs and wildfires shape vegetation structure in a sagebrush grassland more than does rest from ungulate grazing. Ecosphere 9:e02390. https://doi.org/10.1002/ecs2.2390

Cullen JJ (1982) The deep chlorophyll maximum: comparing vertical profiles of chlorophyll a. Can J Fish Aquat Sci 39:791-803. https://doi.org/10.1139/f82-108

Cullen JJ (2015) Subsurface chlorophyll maximum layers: enduring enigma or mystery solved? Ann Rev Mar Sci 7:207-239. https://doi.org/10.1146/annurev-marine-010213-135111

D'Odorico P, Fuentes JD, Pockman WT, Collins SL, He Y, Medeiros JS, DeWekker S, Litvak ME (2010) Positive feedback between microclimate and shrub encroachment in the northern Chihuahuan desert. Ecosphere 1:1-11. https://doi.org/10.1890/ES10-00073.1

Deaton CD, Hein CJ, Kirwan ML (2017) Barrier island migration dominates ecogeomorphic feedbacks and drives salt marsh loss along the Virginia Atlantic Coast, USA. Geology 45:123-126. https://doi.org/10.1130/G38459.1

Delcourt PA, Delcourt HR (1992) Ecotone dynamics in space and time. In: Hansen AJ, di Castri F (eds) Landscape boundaries. Springer, New York, pp 19-54. https://doi.org/10.1007/978-1-4612-2804-2_2

Donnelly JP, Bertness MD (2001) Rapid shoreward encroachment of salt marsh cordgrass in response to accelerated sea-level rise. Proc Natl Acad Sci 98:14218-14223 https://doi.org/10.1073/pnas.251209298

Duniway MC, Snyder KA, Herrick JE (2010) Spatial and temporal patterns of water availability in a grass–shrub ecotone and implications for grassland recovery in arid environments. Ecohydrology 3:55-67 https://doi.org/10.1002/eco.94

Epstein PR, Diaz HF, Elias S, Grabherr G, Graham NE, Martens WJM, Mosley-Thompson E, Susskind J (1998) Biological and physical signs of climate change: focus on mosquito-borne diseases. Bull Am Meteorol Soc 79:409-418. https://doi.org/10.1175/1520-0477(1998)079<0409:BAPSOC>2.0.CO;2

Estrada M, Marrasé C, Latasa M, Berdalet E, Delgado M, Riera T (1993) Variability of deep chlorophyll maximum characteristics in the Northwestern Mediterranean. Mar Ecol Prog Ser 92:289-300. https://doi.org/ 10.3354/meps092289

Fagherazzi S, Anisfeld SC, Blum LK, Long EV, Feagin RA, Fernandes A, Kearney WS, Williams K (2019) Sea level rise and the dynamics of the marsh-upland boundary. Front Environ Sci 7:1-18. https://doi.org/10.3389/fenvs.2019.00025

Fee EJ (1976) The vertical and seasonal distribution of chlorophyll in lakes of the Experimental Lakes Area, northwestern Ontario: Implications for primary production estimates. Limnol Oceanogr 21:767-783. https://doi.org/10.4319/lo.1976.21.6.0767

Forman RT, Moore PN (1992) Theoretical foundations for understanding boundaries in landscape mosaics. In: Hansen AJ, di Castri F (eds) Landscape boundaries. (pp. 236-258). Springer, New York, pp 236-258. https://doi.org/.10.1007/978-1-4612-2804-2_11

Fuhlendorf SD, Harrell WC, Engle DM, Hamilton RG (2006) Should heterogeneity be the basis for conservation? Grassland bird response to fire and grazing. Ecol Appl 16:1706-1716. https://doi.org/10.1890/1051-0761(2006)016[1706:SHBTBF]2.0.CO;2

Gedan K, Fernández-Pascual E (2019) Salt marsh migration into salinized agricultural fields: a novel assembly of plant communities. J Veg Sci 30: 1007-1016. https://doi.org/10.1111/jvs.12774

Gehman AM, McLenaghan NA, Byers JE, Alexander CR, Pennings SC, Alber M (2018) Effects of small-scale armoring and residential development on the salt marsh-upland ecotone. Estuaries Coast 41:S54-S67. https://doi.org/10.1007/s12237-017-0300-8

Goldblum D, Rigg LS (2005). Tree growth response to climate change at the deciduous boreal forest ecotone, Ontario, Canada. Can J For Res 35:2709-2718. https://doi.org/ 10.1139/x05-185

Gonzalez P, Neilson RP, Lenihan JM, Drapek RJ (2010) Global patterns in the vulnerability of ecosystems to vegetation shifts due to climate change. Glob Ecol Biogeogr 19:755-768. https://doi.org/10.1111/j.1466-8238.2010.00558.x

Gosz JR (1993) Ecological hierarchies. Ecol Appl 3:369-376. https://doi.org/10.2307/1941905

Greiner JT, McGlathery KJ, Gunnell J, McKee BA (2013) Seagrass restoration enhances "blue carbon" sequestration in coastal waters. PLoS One 8:e72469. https://doi.org/10.1371/journal.pone.0072469

Horton BP, Shennan I, Bradley SL, Cahill N, Kirwan M, Kopp RE, Shaw TA (2018) Predicting marsh vulnerability to sea-level rise using Holocene relative sea-level data. Nat Commun 9:1-7. https://doi.org/10.1038/s41467-018-05080-0

Horváth A, March IJ, Wolf JH (2001) Rodent diversity and land use in Montebello, Chiapas, Mexico. Stud Neotrop Fauna Environ 36:169-176. https://doi.org/ 10.1076/snfe.36.3.169.2130

Huisman J, Pham Thi NN, Karl DM, Sommeijer B (2006) Reduced mixing generates oscillations and chaos in the oceanic deep chlorophyll maximum. Nature 439:322-325. https://doi.org/10.1038/nature04245

Johnston CA (1991) Sediment and nutrient retention by freshwater wetlands: effects on surface water quality. Crit Rev Environ Sci Technol 21:491-565. https://doi.org/10.1080/10643389109388425

Jorgensen EE, Demarais S, Monasmith T (2000) Rodent habitats in a Chihuahuan Desert/desert plains grassland ecotone. Tex J Sci 52:303-312.

Junior NA, Meirelles PM, de Oliveira Santos E, Dutilh B, Silva GG, Paranhos R, Kruger, RH (2015) Microbial community diversity and physical–chemical features of the Southwestern Atlantic Ocean. Arch Microbiol 197:165-179. https://doi.org/10.1007/s00203-014-1035-6

Kimor B, Berman T, Schneller A (1987) Phytoplankton assemblages in the deep chlorophyll maximum layers off the Mediterranean coast of Israel. J Plankton Res 9:433-443. https://doi.org/10.1093/plankt/9.3.433

Kirwan ML, Gedan KB (2019) Sea-level driven land conversion and the formation of ghost forests. Nat Clim Chang 9:450-457. https://doi.org/10.1038/s41558-019-0488-7

Kolasa J, Zalewski M (1995) Notes on ecotone attributes and functions. Hydrobiologia 303:1-7. https://doi.org/10.1007/BF00034039

Körner C (1998) A re-assessment of high elevation treeline positions and their explanation. Oecologia 115:445-459. https://doi.org/10.1007/s004420050540

Kupfer JA, Cairns DM (1996) The suitability of montane ecotones as indicators of global climatic change. Prog Phys Geogr 20:253-272. https://doi.org/10.1177/030913339602000301

Letelier RM, Karl DM, Abbott MR, Bidigare RR (2004) Light driven seasonal patterns of chlorophyll and nitrate in the lower euphotic zone of the North Pacific Subtropical Gyre. Limnol Oceanogr 49:508–519. https://doi.org/10.4319/lo.2004.49.2.0508

Lloyd KM, McQueen AA, Lee BJ, Wilson RC, Walker S, Wilson JB (2000) Evidence on ecotone concepts from switch, environmental and anthropogenic ecotones. J Veg Sci 11:903-910. https://doi.org/10.2307/3236560

Longhurst A (2006) Ecological geography of the sea, 2nd ed. Elsevier Science Publishers, New York.

Macías D, Stips A, Garcia-Gorriz E (2014) The relevance of deep chlorophyll maximum in the open Mediterranean Sea evaluated through 3D hydrodynamic-biogeochemical coupled simulations. Ecol Modell 281:26-37. https://doi.org/10.1016/j.ecolmodel.2014.03.002

Maher EL, Germino MJ, Hasselquist NJ (2005) Interactive effects of tree and herb cover on survivorship, physiology, and microclimate of conifer seedlings at the alpine tree-line ecotone. Can J For Res 35:567-574. https:/doi.org/10.1139/X04-201

Martínez-Soto KS, Johnson DS (2020) The density of the Atlantic marsh fiddler crab (Minuca pugnax, Smith, 1870)(Decapoda: Brachyura: Ocypodidae) in its expanded range in the Gulf of Maine, USA. J Crustac Biol 40:544-548. https://doi.org/10.1093/jcbiol/ruaa049

Masubelele ML, Hoffman MT, Bond WJ, Gambiza J (2014) A 50 year study shows grass cover has increased in shrublands of semi-arid South Africa. J Arid Environ 104:43-51. https://doi.org/10.1016/j.jaridenv.2014.01.011

McGranahan DA, Engle DM, Fuhlendorf SD, Winter SJ, Miller JR, Debinski DM (2012) Spatial heterogeneity across five rangelands managed with pyric-herbivory. J Appl Ecol 49:903-910. https://doi.org/10.1111/j.1365-2664.2012.02168.x

Minchinton TE, Bertness, MD (2003) Disturbance-mediated competition and the spread of Phragmites australis in a coastal marsh. Ecol Appl 13:1400-1416. https://doi.org/10.1890/02-5136

Moreno-de las Heras M, Turnbull L, Wainwright J (2016) Seed-bank structure and plant-recruitment conditions regulate the dynamics of a grassland-shrubland Chihuahuan ecotone. Ecology 97:2303-2318. https://doi.org/10.1002/ecy.1446

Muñoz-Rodríguez AF, Sanjosé I, Márquez-García B, Infante-Izquierdo MD, Polo-Ávila A, Nieva FJJ, Castillo JM (2017) Germination syndromes in response to salinity of Chenopodiaceae halophytes along the intertidal gradient. Aquat Bot 139:48-56. https://doi.org/10.1016/j.aquabot.2017.02.003

Naiman RJ, Décamps H, Pastor J, Johnston CA (1988) The potential importance of boundaries of fluvial ecosystems. J North Am Benthol Soc 7:289-306. https://doi.org/10.2307/1467295

Naito AT, Cairns DM (2011) Patterns and processes of global shrub expansion. Prog Phys Geogr 35:423-442. https://doi.org/10.1177/0309133311403538

Neilson RP (1993) Transient ecotone response to climatic change: some conceptual and modelling approaches. Ecol Appl 3:385-395. https://doi.org/ 10.2307/1941907

Noble IR (1993) A model of the responses of ecotones to climate change. Ecol Appl 3:396-403. https://doi.org/10.2307/1941908

Novellie PA, Bezuidenhout H (1994) The influence of rainfall and grazing on vegetation changes in the Mountain Zebra National Park. Afr J Wildl Res 24:60-71.

O'Connor TG, Roux PW (1995) Vegetation changes (1949-71) in a semi-arid, grassy dwarf shrubland in the Karoo, South Africa: influence of rainfall variability and grazing by sheep. J Appl Ecol 32:612-626. https://doi.org/10.2307/2404657

Pennings S, Callaway R (1992) Salt marsh plant zonation: the relative importance of competition and physical factors. Ecology 73:681-690. https://doi.org/10.2307/1940774

Peters DPC (2002) Plant species dominance at a grassland-shrubland ecotone: an individual-based gap dynamics model of herbaceous and woody species. Ecol Modell 152:5-32. https://doi.org/10.1016/S0304-3800(01)00460-4

Peters DPC, Gosz J, Pockman WT, Small EE, Parmenter RR, Collins SL, Muldavin E (2006) Integrating patch and boundary dynamics to understand and predict biotic transitions at multiple scales. Landsc Ecol 21:19-33. https://doi.org/10.1007/s10980-005-1063-3

Pockman WT, Small EE (2010) The influence of spatial patterns of soil moisture on the grass and shrub responses to a summer rainstorm in a Chihuahuan Desert ecotone. Ecosystems 13:511-525. https://doi.org/10.1007/s10021-010-9337-2

Pollehne F, Klein B, Zeitzschel, B (1993) Low light adaptation and export production in the deep chlorophyll maximum layer in the northern Indian Ocean. Deep Sea Res 2 Top Stud Oceanogr 40:737-752. https://doi.org/10.1016/0967-0645(93)90055-R

Porensky LM, Mueller KE, Augustine DJ, Derner JD (2016) Thresholds and gradients in a semi-arid grassland: long-term grazing treatments induce slow, continuous and reversible vegetation change. J Appl Ecol 53:1013-1022. https://doi.org/10.1111/1365-2664.12630

Ratajczak Z, Nippert JB, Briggs JM, Blair JM (2014) Fire dynamics distinguish grasslands, shrublands and woodlands as alternative attractors in the Central Great Plains of North America. J Ecol 102:1374-1385. https://doi.org/10.1111/1365-2745.12311

Reinl KL, Sterner RW, Austin JA (2020) Seasonality and physical drivers of deep chlorophyll layers in Lake Superior, with implications for a rapidly warming lake. J Great Lakes Res 46:1615-1624. https://doi.org/10.1016/j.jglr.2020.09.008

Ribalet F, Marchetti A, Hubbard KA, Brown K, Durkin CA, Morales R, Robert M, Swalwell JE, Tortell PD, Armbrust EV (2010) Unveiling a phytoplankton hotspot at a narrow boundary between coastal and offshore waters. Proc Natl Acad Sci 107:16571-16576. https://doi.org/10.1073/pnas.1005638107

Risser PG (1995) The status of the science examining ecotones: a dynamic aspect of landscape is the area of steep gradients between more homogeneous vegetation associations. BioScience 45:318-325. https://doi.org/10.2307/1312492

Roux PW (1966) The effects of seasonal rainfall and grazing on mixed Karoo veld. Afr J Range Forage Sci 1:103-110.

Rutherford MC, Powrie LW, Husted LB (2012) Plant diversity consequences of a herbivore-driven biome switch from Grassland to shrub steppe in South Africa. Appl Veg Sci 15:14-25. https://doi.org/10.1111/j.1654-109X.2011.01160.x

Saintilan N, Wilson NC, Rogers K, Rajkaran A, Krauss KW (2014) Mangrove expansion and salt marsh decline at mangrove poleward limits. Glob Chang Biol 20:147-157. https://doi.org/10.1111/gcb.12341

Sanchez B, Parmenter R (2002) Patterns of shrub-dwelling arthropod diversity across a desert shrubland-grassland ecotone: a test of island biogeographic theory. J Arid Environ 50:247-265. https://doi.org/10.1006/jare.2001.0920

Santelmann MV, Boisjolie BA, Flitcroft R, Gomez M (2019) Relationships between salt marsh vegetation and surface elevation in Coos Bay Estuary, Oregon. Northwest Sci 93:137-154. https://doi.org/10.3955/046.093.0205

Schieder NW, Kirwan ML (2019) Sea-level driven acceleration in coastal forest retreat. Geology 47:1151-1155. https://doi.org/10.1130/G46607.1

Schieder NW, Walters DC, Kirwan ML (2018) Massive upland to wetland conversion compensated for historical marsh loss in Chesapeake Bay, USA. Estuaries Coast 41:940-951. https://doi.org/10.1007/s12237-017-0336-9

Schooley RL, Bestelmeyer BT, Campanella A (2018) Shrub encroachment, productivity pulses, and core-transient dynamics of Chihuahuan Desert rodents. Ecosphere 9:e02330. https://doi.org/10.1002/ecs2.2330

Senft AR (2009) Species diversity patterns at ecotones. https://doi.org/10.17615/20k5-yb32

Shiponeni N, Allsopp N, Carrick PJ, Hoffman MT (2011) Competitive interactions between grass and succulent shrubs at the ecotone between an arid grassland and succulent shrubland in the Karoo. Plant Ecol 212:795-808. https://doi.org/10.1007/s11258-010-9864-0

Smith JAM (2013) The role of Phragmites australis in mediating inland salt marsh migration in a mid-Atlantic estuary. PLoS ONE 8:e65091. https://doi.org/10.1371/journal.pone.0065091

Smith TB, Wayne RK, Girman DJ, Bruford MW (1997) A role for ecotones in generating rainforest biodiversity. Science 276:1855-1857. https://doi.org/10.1126/science.276.5320.1855

Smith AJ, Kiwan ML (2021) Sea-level driven marsh migration results in rapid net loss of carbon. Geophys Res Lett. https://doi.org/10.1029/2021GL092420

Theuerkauf EJ, Rodriguez AB (2017) Placing barrier-island transgression in a blue-carbon context. Earth's Future 5:789-810. https://doi.org/10.1002/2017EF000568

Traut B (2005) The role of coastal ecotones: a case study of the salt marsh/upland transition zone in California. J Ecol 93:279-290. https://doi.org/10.1111/j.1365-2745.2005.00969.x

Trevathan-Tackett SM, Wessel C, Cebrián J, Ralph PJ, Masqué P, & Macreadie PI (2018) Effects of small-scale, shading-induced seagrass loss on blue carbon storage: implications for management of degraded seagrass ecosystems. J Appl Ecol 55:1351-1359. https://doi.org/10.1111/1365-2664.13081

van der Maarel E (1990) Ecotones and ecoclines are different. J Veg Sci 1:135–138. https://doi.org/10.2307/3236065

Veldkornet DA, Adams JB, Potts AJ (2015) Where do you draw the line? Determining the transition thresholds between estuarine salt marshes and terrestrial vegetation. S Afr J Bot 101:153-159. https://doi.org/10.1016/j.sajb.2015.05.003

Vetter S (2009) Drought, change and resilience in South Africa's arid and semi-arid rangelands. S Afr J Sci 105:29-33. https://doi.org/10.4102/sajs.v105i1/2.35

Wang H, Cai Y, Yang Q, Gong Y, Lv G (2019) Factors that alter the relative importance of abiotic and biotic drivers on the fertile island in a desert-oasis ecotone. Sci Total Environ 697:134096. https://doi.org/ 10.1016/j.scitotenv.2019.134096

Wasson K, Woolfolk A, Fresquez C (2013) Ecotones as indicators of changing environmental conditions: rapid migration of salt marsh-upland boundaries. Estuaries Coast 36:654-664. https://doi.org/10.1007/s12237-013-9601-8

Yando ES, Osland MJ, Willis JM, Day RH, Krauss KW, Hester MW (2016) Salt marsh-mangrove ecotones: using structural gradients to investigate the effects of woody plant encroachment on plant–soil interactions and ecosystem carbon pools. J Ecol 10:1020-1031. https://doi.org/10.1111/1365-2745.12571

Yvon-Durocher G, Montoya JM, Trimmer M, Woodward G (2011) Warming alters the size spectrum and shifts the distribution of biomass in freshwater ecosystems. Glob Chang Biol 17:1681-1694. https://doi.org/10.1111/j.1365-2486.2010.02321.x