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RESEARCH REVIEW

Vegetation–microclimate feedbacks in woodland–grassland ecotones

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ABSTRACT

Aim Climatic conditions exert a strong control on the geographic distribution of many woodland-to-grassland transition zones (or 'tree lines'). Because woody plants have, in general, a weaker cold tolerance than herbaceous vegetation, their altitudinal or latitudinal limits are strongly controlled by cold sensitivity. While temperature controls on the dynamics of woodland–grassland ecotones are relatively well established, the ability of woody plants to modify their microclimate and to create habitat for seedling establishment and growth may involve a variety of processes that are still not completely understood. Here we investigate feedbacks between vegetation and microclimatic conditions in the proximity to woodland–grassland ecotones.

Location We concentrate on arctic and alpine tree lines, the transition between mangrove forests and salt marshes in coastal ecosystems, and the shift from shrubland to grassland along temperature gradients in arid landscapes.

Methods We review the major abiotic and biotic mechanisms underlying the ability of woody plants to alter the nocturnal microclimate by increasing the temperatures they are exposed to.

Results We find that in many arctic, alpine, desert and coastal landscapes the presence of trees or shrubs causes nocturnal warming thereby favouring the establishment and survival of woody plants.

Main conclusion Because of this feedback, trees and shrubs may establish in areas that would be otherwise unsuitable for their survival. Thus, in grassland–woodland transition zones both vegetation covers may be (alternative) stable states of the landscape, thereby affecting the way tree lines may migrate in response to regional and global climate change.

Keywords
Alternative stable states, ecosystem engineering, mangrove–marsh transition, shrub encroachment, tree line, vegetation–microclimate feedback, woodland–grassland ecotone.

INTRODUCTION

Many regions of the world exhibit a relatively abrupt transition from woody plant cover to grassland. These transitions (or 'tree lines') may be induced by a number of factors, including fires, grazing, waterlogging, soil salinity, wind abrasion and microclimate (Tranquillini, 1979; Stevens & Fox, 1991; Körner, 1998). When these transitions occur along altitudinal or latitudinal gradients, they are probably determined by the lower cold tolerance of woody plants with respect to the herbaceous life-form and will be denoted here as 'cold tree lines'. Typical examples of cold tree lines include the ecotone between boreal forest and tundra in the subarctic (e.g. Epstein *et al.*, 2004), the transition between mangrove swamps and salt marshes in subtropical inter-tidal environments (McKee & Rooth, 2008; Feller *et al.*, 2010), the margin between shrubland and grassland in freeze-prone deserts (van Auken, 2009) and the tree line between alpine forests and high-elevation meadows in mountainous landscapes

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(e.g. Grace, 1989; Körner, 1998). Because these transitions are determined by the temperature regime and the different cold tolerance of woody and herbaceous life-forms, they are particularly susceptible to change in response to regional and global climate warming (Grace, 1989; Sveinbjörnsson, 2000; Clark *et al.*, 2001; Lloyd & Fastie, 2003; Smith *et al.*, 2003). These ecotones are where climate change is expected to induce some of the most visible shifts in plant communities and associated habitats. Understanding vegetation dynamics in these transition zones is therefore crucial to the study of the long-term effect of climate change on regional plant distribution.

Trees and shrubs are limited in their altitudinal and latitudinal range by cold climate conditions, and climate warming is expected to cause an encroachment of woody plants into their adjacent (and colder) grasslands (Harte & Shaw, 1995; Lloyd & Fastie, 2003; van Auken, 2009; Hallinger *et al.*, 2010). In many ecosystems the type of vegetation cover may, in turn, affect the microclimate (e.g. Geiger, 1965; Langvall & Örlander, 2001; Bonan, 2002; D'Odorico *et al.*, 2010a). In this paper we investigate the two-way interactions between vegetation and microclimatic conditions in cold-sensitive transitional woodland–grassland zones. We focus on the ability of woody plant cover to cause a local warming effect, whereby temperatures are higher under tree canopies than in the adjacent grasslands. When this warming effect occurs, vegetation–microclimate interactions may exhibit a positive feedback, whereby the presence of woody plants modifies the surface energy balance thereby causing nocturnal warming. This warming effect reduces the exposure of cold-sensitive trees and shrubs to low temperatures and sustains their survival at the margins of their latitudinal or altitudinal range.

The existence of this feedback is evidenced by a number of field observations presented in this paper and is further confirmed by the fact that the shift from grassland to shrubland is in most cases abrupt and discontinuous. This discontinuity is often observed both in space (i.e. across the ecotone) and in time, when woody plants encroach into grasslands over relatively short time-scales (e.g. Chapman, 1975; van Auken, 2000; Epstein *et al.*, 2004; Knapp *et al.*, 2008). The presence of discontinuous switches in vegetation cover is often interpreted as a sign of the possible existence of alternative stable states in the underlying vegetation dynamics (e.g. Wilson & Agnew, 1992). In other words, both woodland and grassland would be possible stable configurations of these transitional zones. Bi-stable dynamics commonly emerge as a result of positive feedbacks between biota and environmental conditions (e.g. Wilson & Agnew, 1992; Walker & Salt, 2006). Positive feedbacks between vegetation and fires, water table, atmospheric deposition, fog precipitation or soil salinity have been associated with the emergence of alternative stable grassland/woodland states in a variety of landscapes (e.g. Dublin *et al.*, 1990; Wilson & Agnew, 1992; Ridolfi *et al.*, 2006; Runyan & D'Odorico, 2010).This paper focuses on the case of cold tree lines and discusses how, by modifying the surface energy balance, woody plants create warmer microclimatic conditions than those that would exist within grassland vegetation.

COLD TOLERANCE IN WOODY VERSUS HERBACEOUS PLANTS

A number of physiological mechanisms have been invoked to explain differences in cold sensitivity between woody plants and grasses, including cold-induced decline in photosynthesis and primary production, growth limitation, reduced regeneration capacity, frost damage, and winter frost desiccation (Tranquillini, 1979; Körner, 1998). Moreover, it has been observed that, because of their typical size, architecture, and accumulating growth habit, trees and shrubs may be at a disadvantage with respect to grasses in cold environments with scarce and spatially heterogeneous distributions of soil resources. In fact, in these environments adequate root development may become prohibitive because of cold limitations on primary productivity (Stevens & Fox, 1991).

Close to cold tree lines, the surface energy balance becomes unfavourable for trees. Because of the low temperatures and short growing seasons, carbon assimilation rates are relatively small with respect to maintaining a positive carbon budget and sustaining growth. In years with particularly short growing seasons, new plant tissues do not mature completely before the beginning of the winter and may be more sensitive to frost desiccation (Tranquillini, 1979). CO_2 uptake is further inhibited by the occurrence of frost during the previous nights, particularly if the canopy is exposed to high-sunlight conditions (see Forest–Alpine Meadow Transitions). It has been argued that in alpine tree lines, growth limitation may occur independently of the existence of an unfavourable carbon balance. According to this growth-limitation hypothesis, woody plants would require a minimum temperature for new cell production and tissue differentiation (Körner, 1998). Moreover, as an effect of cold stress, the rates of seed production and germination strongly decline in the proximity to the tree line, which limits the rate of reproduction of woody plants as well as their competitive advantage with respect to grasses (e.g. Körner, 1998).

Frost desiccation is caused by the inability of plants to take up soil water during winter when the soil is frozen. Thus, the loss of plant water via transpiration from tissues that have not developed sufficient cuticular resistance leads to the desiccation of leaves and branches emerging from the snow mantle. Frost desiccation has been reported to be a more severe disturbance than direct frost damage in woody plants located within extratropical alpine tree lines (Tranquillini, 1979). However, in tropical tree lines where soils are not seasonally frozen, direct frost damage remains a major factor determining the dominance of trees or grass along altitudinal gradients (Bader *et al.*, 2007).

Protecting plant tissues (meristems, leaves, stems) from frost damage occurs through microhabitat selection, life-form, growth form and physiological adaptation. Perennial plants acquire physiological tolerance to freezing through a variety of gene regulation mechanisms (Ouellet, 2007). These mechanisms are initiated based on relatively gradual changes in seasonal temperatures that stimulate key metabolic processes. Most such mechanisms are designed to prevent ice crystals that can cause structural damage from forming in living cells. For example, as

temperatures decline, up-regulation occurs of genes that code for low molecular weight compounds (sugars, proline) which alter osmotic potential and lower the freezing point within plant cells throughout the extent of the cold period (Hughes & Dunn, 1996). In general, freeze tolerance mechanisms (acclimation) respond to seasonality, but acclimation is less effective under sudden and severe low winter temperatures associated with rapidly moving cold fronts.

Freezing tolerance in plants may be part of a broader suite of adaptations for general stress tolerance (e.g. heat, drought, cold; Medeiros & Pockman, 2011). Because freezing tolerance is genetically regulated, it varies among life-forms, as well as individuals within species (Ouellet, 2007). Moreover, freezing tolerance mechanisms are likely to differ between living leaf or meristematic cells maintained during winter in evergreens compared to dead xylem cells in the stems of woody plants (Davis *et al.*, 1999; Pearce, 2001). In woody species, sudden freezing under rapid and extreme cold events can induce another form of frost drought associated with xylem embolisms. These embolisms occur when dissolved gasses are forced out of solution in the xylem as ice crystals are formed. The gas bubbles enlarge creating the embolism, causing a break in the water column in the xylem tissue.

Studies on well-watered creosote bush seedlings found that freezing resistance was higher in leaves than in the xylem (Medeiros & Pockman, 2011). The same was true of individuals of *Pinus cembra* at the tree line (Buchner & Neuner, 2011). Cavender-Bares *et al.* (2005) found that the freezing tolerance of leaves varies with leaf life span: longer-lived leaves (as found on evergreens) have a higher freezing tolerance than deciduous species. Similarly, the freezing tolerance in the xylem is higher in evergreens than in deciduous species. Frost resistance in the xylem is often correlated with vessel diameter, with fatter vessels being less tolerant than thinner vessels (Cavender-Bares, 2005). Thus, there is a positive relationship between leaf and xylem freezing tolerance and greater cold acclimation in evergreen versus deciduous species. These differences are a function of xylem vessel diameter, leaf longevity and leaf mass per area (or leaf thickness). Because leaf and xylem tissues differ in their response and tolerance to freezing temperatures, they are probably operating under independent selection pressures (Cavender-Bares *et al.*, 2005). It is this combination of exposed meristems, and leaf and wood response in trees and shrubs compared to leaf tissue and underground meristems in grasses, that can partially explain differential tolerances to low temperatures between woody and herbaceous plants.

While the impact of cold microclimates on carbon budget and woody plant regeneration is controlled by diurnal temperatures, direct frost damage is induced by minimum temperatures, which typically occur at night. Frost damage appears to be a major disturbance for woody plants in tropical tree lines, desert shrub–grass ecotones, and at the limits of the latitudinal range of mangroves (Loik & Nobel, 1993; Pockman & Sperry, 1997; Bader *et al.*, 2007; Krauss *et al.*, 2008). Extreme minimum temperatures are expected to determine the geographic location of these tree lines. Conversely, it has been argued that arctic and extra-tropical alpine tree lines are more sensitive to diurnal temperatures during the growing season and to soil temperatures (Körner, 1998; Körner & Paulsen, 2004). However, as we will show in this review, there is evidence of higher rates of seedling establishment and survival in sites located under the canopies of adult trees than in open canopy areas. This effect is commonly associated with the ability of forest vegetation to reduce radiative cooling and maintain a warmer nocturnal microclimate (see Effect of Woody Plants on Microclimate). Moreover, it has been reported that alpine vegetation responds to nocturnal frost occurrence during the growing season with a reduction on CO_2 uptake (see Forest–Alpine Meadow Transitions). However, the study of vegetation sensitivity to extreme minimum temperatures and the use of climate extremes as good biogeographic indicators of tree-line location remain difficult tasks because they require long temperature records, which are seldom available world-wide. Moreover, because of the hysteresis associated with the possible existence of bi-stable tree–grass dynamics (see Mangrove Forest–Salt Marsh Transitions) there is no 1:1 dependence between temperature regime and dominant life-form. This fact is consistent with the observation that some tree lines that formed under different climates still persist today (Stevens & Fox, 1991; Körner, 1998).

THE EFFECT OF WOODY PLANTS ON MICROCLIMATE

A number of studies have documented the ability of woodland vegetation to modify its microclimate, particularly the temperature regime within the canopy (e.g. Geiger, 1965; Raynor, 1971; Lee, 1978; Chen *et al.*, 1993; Germino & Smith, 1999; Davies-Colley, 2000; Newmark, 2001; Bonan, 2002). Most of this research has focused on temperate, boreal and alpine forests, while vegetation–microclimate feedbacks in desert shrublands and mangrove forests have seldom been investigated (Kurc & Small, 2004, 2007; Krauss *et al.*, 2008; He *et al.*, 2010).

Forest canopies are found to maintain lower maximum temperatures and higher minimum temperatures than the adjacent grasslands or forest gaps (e.g. Chen *et al.*, 1993; Renaud & Rebetez, 2009; Villegas *et al.*, 2010; Royer *et al.*, 2011). Studies on diurnal temperature regimes in tropical and temperate forests found that during the day temperatures are lower in the forest than in adjacent pastureland (e.g. Young & Mitchell, 1994; Newmark, 2001). The nocturnal effect of woody plant cover on microclimate has been extensively investigated in boreal forests. In these ecosystems the warming effect associated with the presence of a forest canopy may reduce the exposure of woody plants to frost stress and provide more favourable conditions for survival and growth (e.g. Langvall & Ottosson Löfvenius, 2002). Particularly well-studied is the case of mixed stands of trembling aspen (*Populus tremuloides*) and white spruce (*Picea glauca*). In the boreal forests of western Canada these two species typically become established together after a disturbance. However, aspen grows faster and tends to reduce the light availability to spruce. At the same time, the presence of aspen trees provides protection against growing season frost, thereby favouring the growth

of white spruce (Örlander, 1993; Groot & Carlson, 1996; Langvall & Örlander, 2001; Voicu & Comeau, 2006). This 'nurse-plant' effect is important to spruce survival. In fact, despite their wintertime cold tolerance, conifers are very sensitive to freezing in the growing season and their seedlings are fatally damaged by frost (e.g. Pritchard & Comeau, 2004). The warming effect of relatively dense aspen stands has been reported to result in air temperature differences with respect to nearby forest gaps of up to 6 °C on calm, clear-sky nights, while smaller temperature differences are observed on cloudy nights (Groot & Carlson, 1996). The number of frost occurrences tends to decrease with the stand density and to increase with the size of the forest gap (Pritchard & Comeau, 2004).

A similar 'plant sheltering' effect has been observed with other species. For example, Scots pine (*Pinus silvestris* (L.)) canopies facilitate the growth of Norway spruce (*Picea abies* (L.) Karst.): during clear-sky, calm nights the minimum air temperature beneath Scots pine canopies can be up to 3 °C higher than in clearcut areas. This difference decreases on cloudy and windy nights (Langvall & Ottosson Löfvenius, 2002). Interestingly, this nurse-plant effect is commonly used in shelterwood forest regeneration, a forest logging technique that leaves a residual canopy (Man & Lieffers, 1999) to reduce the frost risk thereby enhancing forest regeneration (Barg & Edmonds, 1999; Agestam *et al.*, 2003; Pommerening & Murphy, 2004; Paquette *et al.*, 2006).

What causes this effect of nocturnal warming beneath forest canopies? Why is this effect more conspicuous during clear, calm nights? At night, surface radiative cooling from the ground is more intense in the absence of a forest canopy because the long-wave radiation is rapidly lost to the relatively cold overlying atmosphere. Forest canopies absorb part of the surface-emitted long-wave radiation and re-radiate it back to the ground, thereby reducing the nocturnal cooling of the near-surface air (Chen *et al.*, 1993; Grimmond *et al.*, 2000). Nocturnal temperature differences between areas with and without forest canopies depend on factors such as the vegetation density and cloud cover (Geiger, 1965). Differences are more noticeable during clear-sky nights, when radiative cooling in open areas is stronger due to the absence of clouds that absorb long-wave radiation from the ground and emit it back to the surface (Fig. 1). Moreover, during cold and calm nights air masses tend to be more thermally stratified because the lack of wind prevents the mixing of cold near-surface air with the warmer air aloft (e.g. Geiger, 1965). Although this mechanism is documented for boreal and temperate forests, similar vegetation–microclimate interactions are expected to occur in cold-prone mangrove forests. The presence of a forest canopy reduces surface radiative cooling, thereby limiting the occurrence of nocturnal frost beneath the canopy, while in adjacent marshes frost conditions can inhibit the establishment of mangrove seedlings.

In the case of desert scrubs the situation is rather different. For example, in the northern Chihuahuan Desert there are no differences in net short-wave radiation between the grassland and the shrubland because they tend to have about the same winter albedo (He *et al.*, 2010). However, shrub canopies are relatively sparse and each shrub (or shrub clump) is bordered by bare soil areas, while the adjacent grassland exhibits a relatively uniform grass cover (Schlesinger *et al.*, 1990). Because of the larger bare soil fraction, the shrubland experiences higher soil heat fluxes during the day and reaches higher soil temperatures than the grassland (He *et al.*, 2010). At night the energy stored in the ground is released in the form of long-wave radiation. The higher nocturnal upward radiation measured in the woodland causes the warming of the air beneath and around the shrub canopies (D'Odorico *et al.*, 2010a). Thus, this warming effect is not due to the retention of nocturnal long-wave radiation by the canopy but to a more intense nocturnal upwelling radiation emanating from the bare soil beneath and around shrubs (He *et al.*, 2010).

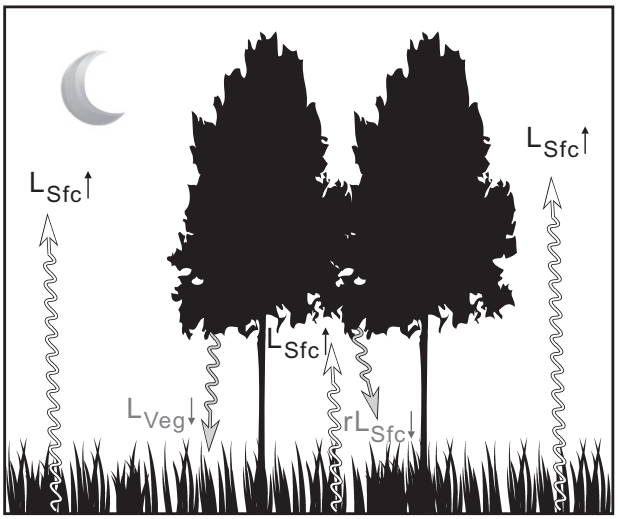

Figure 1 Schematic representation of the flows of thermal energy beneath plant canopies. The ground surface emits thermal energy (LSfc↑). Some of this energy goes to the free atmosphere and the rest is absorbed by vegetation. Because vegetation is not a black body (meaning that reflectivity, $r < 1$) it reflects some of the LSfc↑ back to the ground surface, with a magnitude of *r*LSfc↑. The vegetation has its own absolute temperature and thus emits thermal energy (LVeg↑), which can be absorbed by the ground surface. During cloudless conditions, these flows of energy (LSfc↑, LVeg↑, *r*LSfc↑) can keep the air within the vegetation canopy substantially warmer than surfaces without vegetation canopies.

In the case of arctic and alpine regions, springtime frost damages seedlings not only through its effect on bud development but also through the formation of ice crystals below the ground. These crystals grow upward towards the surface. Known as 'frost heaving', this phenomenon occurs when the near surface temperature is below freezing and there is a constant supply of water to the zone of the soil profile where ice is formed (de Chantal *et al.*, 2007). These conditions are met in cold climates when the ground surface is not covered by snow. Frost heaving can seriously damage seedling roots and even uproot them. The weaker radiative cooling typically observed under forest canopies reduces the risk of frost heaving, thereby providing more

favourable conditions for seedling establishment and survival within forest stands than in open areas (de Chantal *et al.*, 2007, 2009).

In addition to reducing radiative cooling, boreal and alpine forests modify other land surface attributes, which affect the surface energy balance, including surface roughness, albedo and emissivity. Surface roughness, which depends, for example, on vegetation height and density, alters the energy balance by affecting the turbulent coupling between the surface and the atmosphere (Geiger, 1965). Woody plants alter the surface albedo both in summer and in wintertime (Betts & Ball, 1997). In summertime, tree canopies are darker than grasses and can therefore absorb more solar irradiance (Beringer *et al.*, 2005), though it has been argued that differences in albedo among species within the tundra and boreal forest zones can be stronger than those between these two biomes (Chapin *et al.*, 2000a). In regions affected by snow, the effect on albedo is even stronger in the winter season, because tree canopies do not remain buried under the snow mantle and render the soil surface darker than the highly reflective white snow cover of grasslands and tundra (Betts & Ball, 1997; Eugster *et al.*, 2000; Chapin *et al.*, 2005; Sturm *et al.*, 2005). A similar relation between vegetation cover and albedo exists in wintertime in the case of evergreen woodlands, which maintain a darker canopy than senescent grasses. In all these cases, the lower albedo of forest vegetation is associated with a greater absorption of solar irradiance and an overall warmer microclimate than in the absence of woody plant cover (Bonan, 2002).

BOREAL FOREST–TUNDRA TRANSITIONS

The arctic tree line (Fig. 2) is typically found around the 10–12 °C maximum temperature isotherms for the warmest month of the year (July). Aspect, topography, exposure to winds, and soil thickness also contribute to the latitudinal limits of boreal forests (Sveinbjörnsson, 2000; Epstein *et al.*, 2004). The

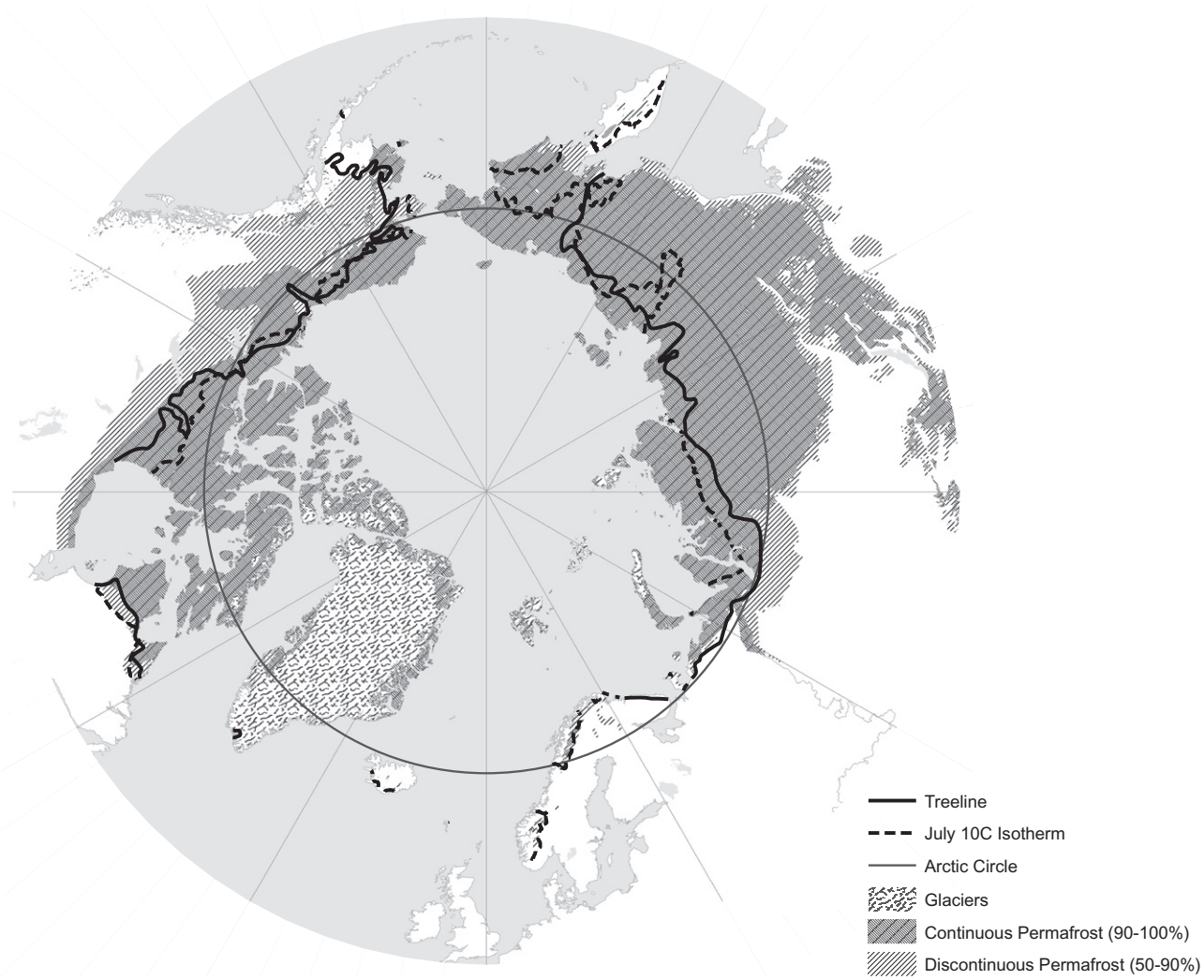

Figure 2 The arctic tree line and the July 10 °C isotherm. The tree line and permafrost data are from Brown *et al.* (1998). The July 10 °C isotherm is produced from 10′ resolution temperature field under the current (*c.* 1950–2000) condition using the WorldClim data base (http://worldclim.org/) and spatial interpolation based on Hijmans *et al.* (2005).

tree line is clearly not a 'line' but a latitudinal band stretching between the forest limit to the south and the limit point for tree survival to the north (Epstein *et al.*, 2004). Thus, the definition of 'tree line' can be somewhat ambiguous because it depends on what we consider to be a tree (only upright single stem woody plants or also shrubs?) and what we consider to be 'a forest' (Hustich, 1983; Sveinbjörnsson, 2000). Regardless, the tree line is a transitional zone from a forested landscape to an area dominated by herbaceous vegetation, sometime mixed with scattered low-stature woody plants. The strong control exerted by climate in determining the position of the Arctic tree line is confirmed by evidence that its fluctuation has been in phase with climate shifts throughout the Holocene (e.g. Elliott-Fisk, 1988; MacDonald *et al.*, 2000; Lloyd *et al.*, 2002; Epstein *et al.*, 2004).

Positive feedbacks between climate and vegetation have been documented for this ecotone more extensively than for the other woodland–grassland transitions considered in this review (e.g. Foley *et al.*, 1994; Chapin *et al.*, 2000b). The warmer microclimate typically found beneath the forest canopy with respect to the adjacent tundra is due both to the ability of the canopy to trap and back-radiate the upwelling nocturnal long-wave radiation from the ground, and to the albedo feedback. Coupled climate–land surface models have shown that the albedo feedback has important impacts on climate at the local, regional and global scales (Bonan *et al.*, 1992; Sturm *et al.*, 2005). At local scales, these feedbacks may play a crucial role in the ongoing process of woody plant encroachment in the arctic (Sturm *et al.*, 2001; Lloyd & Fastie, 2003; Tape *et al.*, 2006), similarly to the case of desert shrublands (see Shrub–Grassland Transitions in Arid Regions).

FOREST–ALPINE MEADOW TRANSITIONS

The definition of the alpine tree line is similar to that of its arctic counterpart. It is the transitional zone between alpine forests and treeless, high-elevation meadows. In this transitional zone (known as the 'kampfzone') low-stature trees and shrubs are often found. The alpine tree line occurs around the 10 °C summer isotherm (Daubenmire, 1954) – though other authors refer to a mean growing season temperature of 6–7 °C (Körner & Paulsen, 2004) – and its elevation depends on aspect, soils and latitude (Grace, 1989). It is found at about 680 m in northern Sweden (68 °N), 950 m in southern Alaska (63 °N), 1300 m in the Craigieburn Mountains of New Zealand (43 °S), 1800–2100 m in the Alps (47 °N), 2359 m in the Hida Mountains of Japan (36 °N), 3000–3500 m in the equatorial Andes (8 °N–3 °S; Bader *et al.*, 2007) and 3950 m on Mount Kilimanjaro in Tanzania (3 °S) (Körner, 1998). Even though exposure to winds and cloudiness contribute to determining the location of the alpine tree line, the major driver of tree-line dynamics is temperature (Smith *et al.*, 2003). Similarly to the case of the arctic, alpine tree lines have been fluctuating in the past 10,000 years in response to climate variability (Kullman, 1988; Grace, 1989), which indicates that this ecotone is sensitive to temperature.

Vegetation–microclimate feedbacks typical of this ecotone are similar to those reported for the arctic: tree canopies reduce radiative cooling at night. During the day trees may also increase the net incoming solar irradiance by reducing the surface albedo, particularly during the snow season. Renaud & Rebetez (2009) investigated the effect of canopy cover on microclimate in alpine forests. They reported a diurnal cooling and nocturnal warming of the near-surface air in a number of forest sites in the Swiss Alps. The same pattern was observed by Bader *et al.* (2007) in the case of tropical alpine tree lines in the Andes. Maher *et al.* (2005) reported a nocturnal warming effect for conifer seedlings (*Pinus albicaulis*) growing at the alpine tree line on the Snowy Range, Wyoming, USA. Because of their warmer nocturnal microclimate, seedlings growing within a forest stand had higher survival rates than those in open areas (Maher *et al.*, 2005; Maher & Germino, 2006). Interestingly, similar nurse-plant relations can be observed in correspondence to the inverse tree line typically found in frost hollows, treeless topographic depressions within a forest environment. Frost hollows are prone to colder nights than the surrounding forest during calm, cloudless conditions. During these conditions, strong radiative cooling at the surface causes the air over the slope to be cooler than the ambient air. The resulting downslope (katabatic) flows cause an accumulation of cold air at the bottom of the hollow. Seedling establishment close to this inverse tree line has been found to benefit from the warmer nocturnal microclimate provided by adult trees (Dy & Payette, 2007), which reduce the radiative surface cooling.

Because of the existence of temperature inversions over the valley floors, there is no gradual decrease of minimum temperatures with height (Fig. 3). The presence of a 'thermal belt' at the approximate height of the temperature inversion is widely known in agriculture and determines suitable locations for crops, plantations or vineyards (Geiger, 1965). The change in minimum temperature with height depends on many factors such as the ambient winds. If ambient winds are relatively strong, turbulent mixing suppresses the effects of radiative cooling, downslope flows do not develop and a thermal belt does not exist. Under these conditions, cooling caused by advection of cold air ('advective cooling') is more important than radiative cooling. The positive feedback between microclimate and an encroaching tree line is highly dependent on the strength of the coupling (turbulent mixing) between the canopy and the atmosphere. This coupling depends on the state of the stable boundary layer and radiation divergence (Betts, 2006).

High-elevation landscapes are exposed to both low nocturnal temperatures and high sunlight. This combination has been shown to inhibit photosynthetic carbon gain and reduce the survival rates of seedlings growing in these environments (Germino & Smith, 1999, 2000; Egerton *et al.*, 2000). Low-temperature photo-inhibition (LTP) is associated with the absorption of an excess of sunlight. If the plant has been exposed to low temperatures in the previous hours, its metabolic processes (e.g. carboxylation) can be slowed down and not all the absorbed light can be utilized. The excess of available light damages enzymes that are crucial to photosynthesis, thereby inhibiting assimilation (e.g. Krause, 1994). The exposure to high light and low temperatures does not need to be simultaneous,

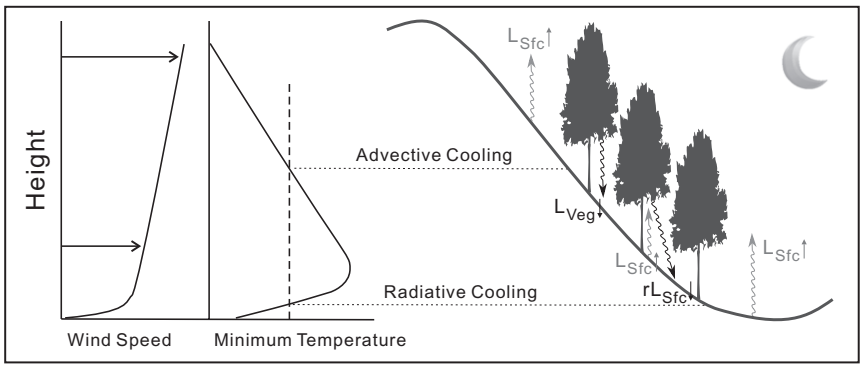

Figure 3 Idealized schematic of the relationship between ambient winds and minimum temperatures over a mountain slope, and the location of upper and lower (inverted) tree line. Minimum temperatures are established mainly by advective processes at high elevation and by radiative processes (resulting in cold air pooling) at lower elevations such as in hollows, basins and valleys. This schematic assumes an increase of wind speed with height which is generally true for the mid-latitudes, and a threshold minimum temperature below which tree seedlings cannot establish (indicated by the vertical dashed line in the temperature profile). The exposure to higher wind speeds at high elevations and other factors may influence this threshold temperature. (Terms defined in caption to Fig. 1.)

and photoinhibition occurs even if excess sunlight is preceded by exposure to low temperatures or frost in the previous night (Lundmark & Hällgren, 1987; Germino & Smith, 1999).

LTP has been reported for a number of other alpine species, including *Picea engelmannii* (Ronco, 1970) and *Eucalyptus pauciflora* trees from the Australian alpine tree lines (Ball *et al.*, 1991; Egerton *et al.*, 2000). Germino & Smith (2000) compared the LTP sensitivity of *Abies lasiocarpa* and *P. engelmannii*, two co-dominant evergreen coniferous species of the alpine ecotone in the Rocky Mountains. They found that *P. engelmannii* is more tolerant to LTP, i.e. it maintains higher light-saturated CO_2 assimilation rates under frost and sunlight exposure than *A. lasiocarpa*. Moreover *P. engelmannii* had a higher structural avoidance of LTP (e.g. lower ratios of silhouette to total leaf area) and its seedlings were found even in microsites with a relatively open canopy. Conversely, the establishment of *A. lasiocarpa* seedlings was restricted to the forest understorey, where it benefits from the nurse-plant effect of adult trees, which provide a warmer nocturnal microclimate while limiting light exposure (Germino & Smith, 2000; Germino *et al.*, 2002; Maher & Germino, 2006). This double advantage offered by understorey microsites (Fig. 4) further supports the use of shelterwood logging to enhance forest regrowth (Ball *et al.*, 1991).

SHRUB–GRASSLAND TRANSITIONS IN ARID REGIONS

Many arid and semi-arid grasslands around the world are undergoing a shift from grass to shrub dominance (Buffington & Herbel, 1965; Archer *et al.*, 1988; van Auken, 2000; Hunter *et al.*, 2001; Knapp *et al.*, 2008). Evidence of shrub encroachment can be found in all continents except Antarctica (Ravi *et al.*, 2009). In the south-western USA this process is occurring at a relatively fast pace and its causes are not completely understood. A number of mechanisms have been invoked as possible explanations of this change in plant community composition (e.g. van Auken, 2000). There is compelling evidence that fire management and overgrazing may favour shrubs over grasses in more mesic regions (Archer *et al.*, 1988; Archer, 1989; Brown & Archer, 1999; D'Odorico *et al.*, 2006). However, the boundaries between desert grasslands and shrublands are also controlled by the temperature regime, particularly by minimum temperatures and frost occurrence, which determine the geographic range of cold-intolerant shrubs (e.g. Pockman & Sperry, 1997). Therefore, global and regional warming are expected to reduce the pressure exerted by cold winters on woody plants, thereby favouring shrubland expansion. The ability of vegetation to modify its microclimate in these desert landscapes has been understood only in recent times (He *et al.*, 2010). Early evidence of a warming effect associated with loss of grass cover was reported in the Sonoran Desert: overgrazing in northern Mexico resulted in substantial temperature differences across the USA–Mexico border (Balling, 1988; Balling *et al.*, 1998). Nurse-plant effects similar to those discussed for the arctic and alpine tree lines have also been documented for desert plants. A typical example is the facilitation of the establishment of *Carnegiea gigantea* (saguaro) by adult woody plants (McAuliffe, 1984).

D'Odorico *et al.* (2010a) analysed temperature records across the shrub–grass ecotone in the northern Chihuahuan Desert and found that grass sites were exposed to lower minimum wintertime temperatures (by about 2 °C) than the shrubland. Interestingly, these temperature differences existed only at the landscape scale (i.e. between grassland and shrubland) and were not significant at the patch scale (e.g. within a range of a few metres). Thus, the positive feedback between shrub encroachment and microclimate is not a local effect. The change in microclimate is due to the increase in bare soil commonly associated with grassland-to-shrubland transitions (e.g. Kurc & Small, 2004). During the day, higher soil heat fluxes are measured in bare soil microsites than in patches with vegetation cover. The more intense soil heating is followed by higher nocturnal upwelling long-wave radiation in shrubland soils (Fig. 5),

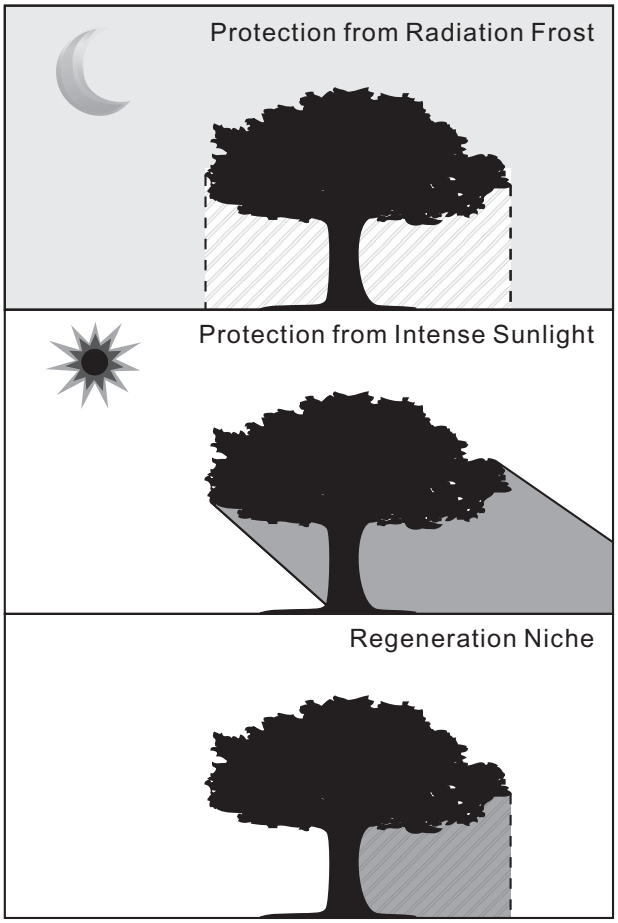

Figure 4 Combined diurnal and nocturnal effect of the canopy. The canopy reduces the radiative cooling at night and seedling exposure to intense radiation (and photoinhibition of the metabolic processes involved in the photosynthesis) during the day. The most favourable conditions for seedling establishment and growth is the zone ('regeneration niche') that benefits from both the diurnal and nocturnal effect of the canopy. Redrawn from Ball *et al.* (1991).

which reduces nocturnal cooling and limits the exposure to cold microclimate conditions (He *et al.*, 2010). This microclimate feedback has been shown to enhance the survival of shrub seedlings (D'Odorico *et al.*, 2010a).

MANGROVE FOREST–SALT MARSH TRANSITIONS

Low-energy inter-tidal environments around the world are usually dominated either by salt marshes or mangrove swamps. Mangrove swamps are found in the tropics and subtropics (Tomlinson, 1986), while salt marshes are typically found at mid–high latitudes (Fig. 6). The northern and southernmost extents of cold-intolerant mangrove species are controlled by the frequency and magnitude of freezing events (Sherrod & McMillan, 1985; McMillan & Sherrod, 1986; Sherrod *et al.*, 1986; Duke *et al.*, 1998; Stuart *et al.*, 2007), and this latitudinal

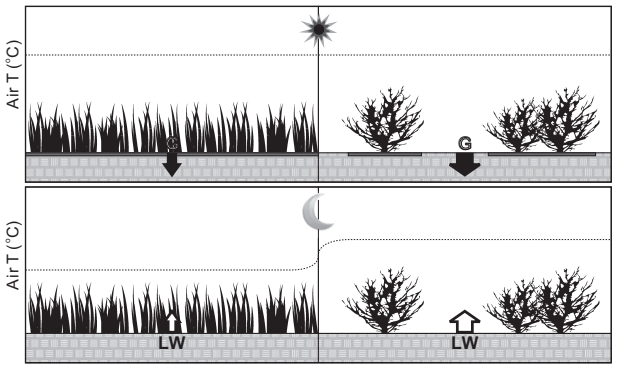

Figure 5 Schematic representation of the mechanisms causing warmer nocturnal microclimate conditions in the shrubland than in the grassland. Due to the higher bare soil fraction in the shrubland, the daytime ground heat flux (G) is stronger in the shrubland than in the grassland, thereby inducing higher soil temperatures in the shrubland. Thus, at night, more long-wave radiation (LW) is emitted from the shrubland than from the grassland, causing higher temperatures in the shrubland than in the grassland.

limit is typically located around the 20 °C winter seawater isotherm (e.g. Krauss *et al.*, 2008). In addition to temperature, the structure and productivity of mangrove communities is also strongly influenced by other aspects of their physical environment, including hydrological conditions (Proffitt & Travis, 2010), salinity (Ball, 1998; Lovelock *et al.*, 2005), available light (Smith, 1987; Sherman *et al.*, 2000; Proffitt & Devlin, 2005), sedimentation rates (Ellison & Farnsworth, 1996), nutrients (Koch, 1997; Feller *et al.*, 2003) and microclimatic conditions (e.g. Krauss *et al.*, 2006).

The Gulf of Mexico coast of the USA and the Atlantic coast of central Florida are notable examples of transitional areas between salt marshes and forests (McKee & Rooth, 2008). In this region, marsh and mangrove vegetation are found as alternative configurations (or 'states') of the ecosystem. These discontinuous switches in vegetation are often a sign of bi-stable ecosystem dynamics (e.g. Wilson & Agnew, 1992), both the marsh and mangrove vegetation being possible stable states of the system. The positive feedback mechanisms which may lead to these alternative stable states are not well understood.

Mangrove trees may alter the surface energy balance, causing local warming and reducing exposure to damaging low (e.g. close to freezing) temperatures in a manner similar to what has been observed in other types of woodland–grassland transition zones. For example, Lugo & Patterson-Zucca (1977) documented a record freeze of –2.7 °C that occurred at Seahorse Key, FL. *Avicennia germinans* seedlings growing in open areas were most affected by frost, while seedlings growing under mangrove canopies were unaffected (Krauss *et al.*, 2008). These observations indicate the existence of a nurse-plant effect in mangroves, which could be associated with microclimate warming inside mangrove canopies.

Mangrove trees are relatively short and exhibit stunted growth forms near their latitudinal limits (Saenger & Snedaker,

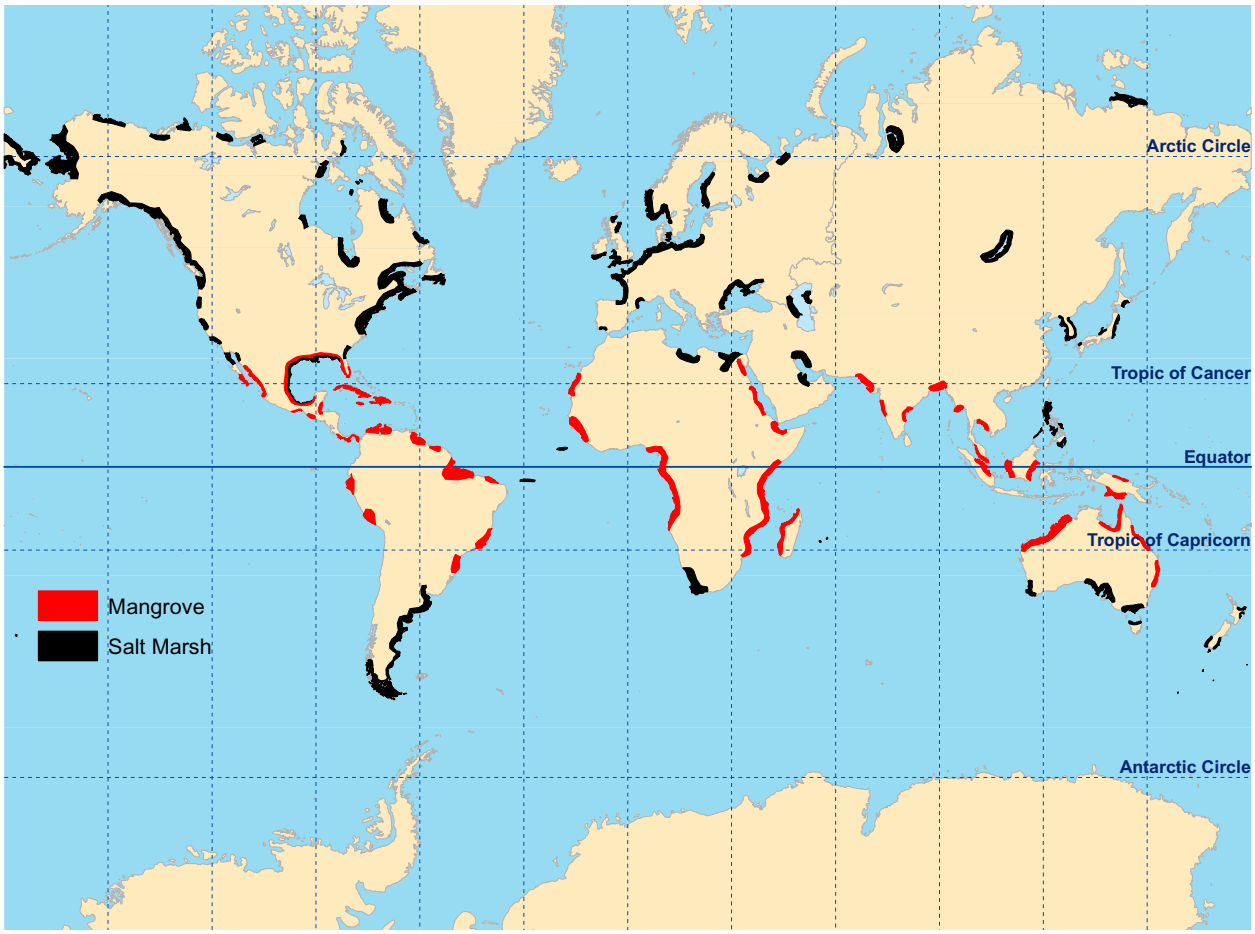

Figure 6 Global distribution of mangroves and salt marshes. Redrawn after Chapman (1975) and Mann (2000).

1993; Perry & Mendelssohn, 2009). Low-temperature stress regulates the height of mangrove trees because branches extending too high above the surface are subject to topkill from periodic freezing events (Lugo & Patterson-Zucca, 1977; Stevens *et al.*, 2006; Stuart *et al.*, 2007). Maintaining a low stature is a common strategy among woody species in cold environments that must reduce their exposure to damaging freezes (Wilson *et al.*, 1987; Grace *et al.*, 1989). Mangroves adopt a similar strategy, and as has been observed in woody species along tree-line regions, the short stature of mangroves in temperate climates results in an effective method for intercepting long-wave radiation emanating from the ground and water surfaces while reducing exposure to low temperature aloft (Grace *et al.*, 2002). Rising air temperatures associated with global warming may therefore lead to both an expansion in the latitudinal limits of mangroves and to increases in stand height near their current boundaries. In many of the regions where mangroves exhibit stunted growth forms due to cold stress, the distribution of these trees may also be distinctly clumped (Stevens *et al.*, 2006). Clumped trees should enable a stronger influence over local surface energy budgets (e.g. more efficient trapping of long-wave radiation) than might be achieved by solitary trees, pointing to a possible microclimatic positive feedback mechanism that may partially regulate the spatial distribution of individual trees across small spatial scales. However, several other factors may influence the density and distribution of mangrove trees where they occur, including seed dispersal patterns, nutrient availability and nutrient use efficiencies and tide regimes (Feller *et al.*, 2009).

Climate models predict a warmer future (IPCC, 2007) for the south-eastern USA, and mangrove communities are likely to expand northwards and inland as a result of the higher temperatures. Microclimate feedbacks may represent one of the mechanisms controlling the rate and extent of this mangrove expansion. This leads to the hypothesis that the geographic patterns of mangrove expansion along coastlines will depend in part on the presence and integrity of large patches that are capable of modifying microclimatic conditions to support seedling survival during periodic cold events. In wetland systems, habitat quality is often linked explicitly to the landscape heterogeneity generated by patches with trees embedded within a vegetation mosaic. Microclimate feedbacks controlling mangrove patch dynamics (and survival) thus may also be a primary factor regulating habitat quality in these systems. If microclimate influences seedling survival, there may be a minimum patch size needed to ensure the persistence of mangrove communities in transition zones near their current northern extent. Thus,

minimum patch size could be a potential measure for evaluating the quality of habitat preservation efforts.

A MODELLING FRAMEWORK FOR THE STUDY OF BI-STABLE GRASSLAND–WOODLAND ECOSYSTEMS

Positive feedback mechanisms linking microclimate regulation by trees with their survival and persistence in grasslands may have important implications for vegetation dynamics in woodland–grassland transitional zones around the world. They can induce the emergence of alternative stable states in dominant plant community types (Fig. 7) (e.g. Wilson & Agnew, 1992; Gunderson & Holling, 2002; D'Odorico *et al.*, 2010b). In this case, a disturbance to one of the alternative states (e.g. the destruction of mangrove forest by hurricanes, or insect infestation in boreal forests) could cause a largely irreversible shift to the other. In such circumstances, the lack of a tree or shrub canopy in transitional zones would prevent the maintenance of freeze-free microclimatic conditions that are crucial to seedling recruitment and establishment.

This view of tree lines as bi-stable systems induced by positive feedbacks between vegetation and microclimate can be generalized to the case of other feedbacks, including those with the fire regime (e.g. Dublin *et al.*, 1990; D'Odorico *et al.*, 2006), fog precipitation (Wilson & Agnew, 1992), water table dynamics (Ridolfi *et al.*, 2006) and salt accumulation (Runyan & D'Odorico, 2010). In all of these cases a relatively sharp transition between grassland and woodland emerges as an effect of a discontinuity in the state of the system, which is induced by the positive feedback.

To better relate the microclimate feedback to ecosystem dynamics, we developed a conceptual model of temperature-dependent woody plant growth. This model is not meant to make exact predictions of ecosystem dynamics under different climate and land-use scenarios. Rather, it is used to provide a process-based understanding of the relation between microclimate feedbacks and the emergence of nonlinearities, bifurcations, alternative stable states and abrupt state changes in ecosystem dynamics. Similar models have been developed in the past to explain woody plant encroachment as a state transition in bi-stable rangeland dynamics affected by vegetation–fire or vegetation–herbivore interactions (Noy-Meir, 1975; Walker *et al.*, 1981; Westoby *et al.*, 1989; Anderies *et al.*, 2002; D'Odorico *et al.*, 2006; Okin *et al.*, 2009). We consider the dynamics of woody plant biomass, W (mass per unit area) and assume that W changes in time according to logistic growth (e.g. Kot, 2001). Moreover W is prone to the effects of cold microclimatic conditions on reproduction, carbon budget, frost damage or winter frost desiccation. These processes reduce W at a rate proportional to the existing woody plant biomass and to a function, $f(T)$, of minimum temperature, T

$$\frac{\mathrm{d}W}{\mathrm{d}T} = \alpha W\left(1 - \frac{W}{W_c}\right) - f(T)W \tag{1}$$

where α (1/time) is the growth or reproduction rate of the logistic growth, W_c is the carrying capacity, i.e. the maximum value of W that can be sustained with the available resources. Equation (1) assumes that in the absence of cold stress the growth rate of woody plant biomass is proportional to the existing biomass, W, and to the available resources, W_c–W. Thus, in the absence of cold stress disturbance, W tends to the stable state $W^* = W_c$. The limited cold tolerance of woody plants makes them prone to mortality (or reduced regeneration and growth), which decrease the value of W at steady state to $W^* = W_c[1 - f(T)/\alpha]$. This steady-state value, W^*, is obtained by solving equation (1) for $\mathrm{d}W/\mathrm{d}t = 0$ (the other equilibrium state, $W = 0$, is unstable). The function $f(T)$ expresses the sensitivity of woody plants to low temperatures. For example, in the case of frost damage (Pockman & Sperry, 1997; Bader *et al.*, 2007) T represents the minimum temperature. For relatively high minimum temperatures (i.e. $T > T_2$, in Fig. 8) $f(T)$ is zero and no cold-induced mortality is expected to occur. For relatively low values of T (i.e. $T < T_1$, in Fig. 8) the relatively frequent and intense occurrence of cold stress prevents the stable persistence of woody plants in this microclimate (i.e. $W^* = 0$ and $f(T) = \alpha$). In

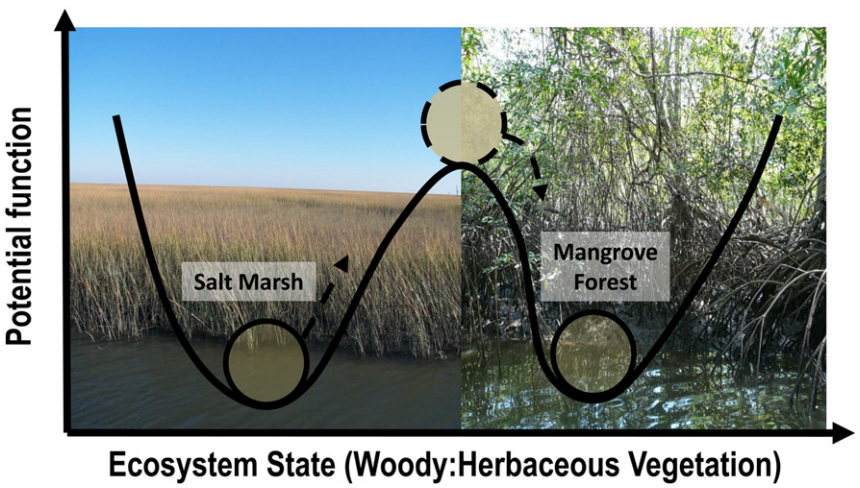

Figure 7 Salt marsh and mangrove forest as alternative ecosystem states. Mangrove stands are stable because they can maintain freeze-free conditions. Salt marshes are stable because freezing impedes mangrove establishment.

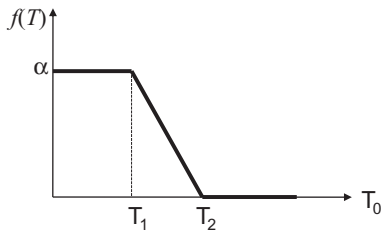

Figure 8 Schematic representation of the temperature-dependent mortality rate in equation (1).

the transitional zones investigated in this paper intermediate microclimatic conditions are expected to occur. We use a linear function to model this intermediate regime, as shown in Fig. 8, where T_1 and T_2 are two species-dependent reference temperatures expressing the cold sensitivity of woody plants. Thus, $f(T)$ is expressed as

$$f(T)=\begin{cases}\alpha; & \text{for } T<T_1\\ \alpha\dfrac{T_2-T}{T_2-T_1}; & \text{for } T_1\le T\le T_2.\\ 0; & \text{for } T>T_2\end{cases} \tag{2}$$

Due to the presence of woody vegetation, the near-surface air temperature locally increases by ΔT. To account for this feedback of microclimate we consider ΔT as a linear function of W

$$\Delta T=\Delta T_{\max}\frac{W}{W_c}, \tag{3}$$

and express in equations (1) and (2) the variable T as $T = T_0 + \Delta T$ with T_0 being the temperature that would exist with no woody plants (i.e. $W = 0$). In equation (3) $\Delta T_{\max}$ is the maximum increase in minimum T that would occur with a full woody plant canopy (i.e. with $W = W_c$). To analyse the effect of the warming feedback we can consider the case of a site where T_0 is slightly smaller than T_1. In this case, in the absence of woody plants ($W = 0$) the microclimate is unsuitable for woody plant establishment. Thus, the system is stable with $W = 0$. However, if some trees or shrubs become established, they could increase the temperature at this site, thereby favouring their own survival. Thus, the system could exhibit two (alternative) stable states corresponding to bare soil and a stable vegetation cover. These states are shown in Fig. 9 as a function of the parameter T_0, based on data from the northern Chihuahuan Desert (D'Odorico *et al.*, 2010a).

It is found that: (1) within a range of microclimatic conditions (i.e. of the parameter T_0) the system exhibits two alternative stable states. Thus, changes in vegetation cover may cause a shift to the alternative state. Because of the stability of this state, the shift could be highly irreversible; (2) gradual changes in the parameter values may lead to rather abrupt and sometimes quite unexpected changes in the state of the system. For example, global or regional warming (i.e. increase in T_0) may lead to no visible change in the grassland state (i.e. $W = 0$) up to the temperature T_b. At this point, a further increase in T_0 causes a destabilization of the grassland state and the abrupt transition to woodland. This type of 'threshold effect' could explain the relatively rapid and discontinuous (both in time and space) transition from grassland to shrubland observed in many arid landscapes around the world.

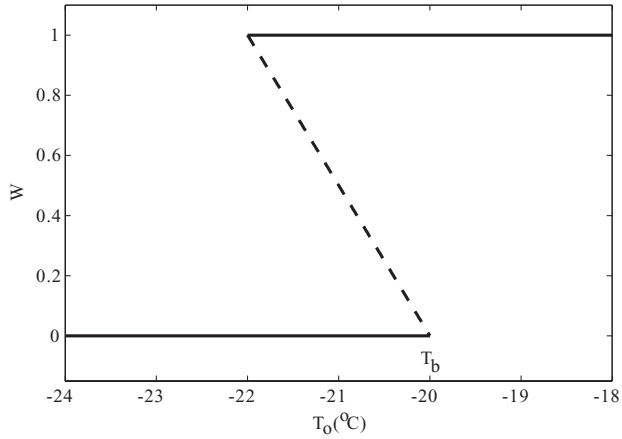

Figure 9 Stable (solid) and unstable (dashed) states of the system determined as solutions of equations (1)–(3) for $dW/dt = 0$: $W^* = W_c[1 - f_1(T_0, W^*)]$, with $f_1(T) = f(T)/\alpha$ (which is independent of α). We used parameters based on the northern Chiuhuahuan Desert, where the warming effect is around 2–3 °C (i.e. $\Delta T_{\max}$ = 2–3 °C), the survival rate decreases from 100% to zero at temperatures around –20 to –19 °C (see D'Odorico *et al.*, 2010a). Thus we assumed $r = 3$, $T_1 = -20$ °C and $T_2 = -19$ °C. W is woody plant biomass per unit area and T_0 is the temperature that would exist with no woody plants.

CONCLUSIONS

Positive feedbacks between the encroachment of woody plants and land surface–atmosphere interactions in former grasslands occur as a function of changes in albedo, surface roughness and heat storage which accompany shifts in canopy architecture. The density and height of stems, leaf morphology, total leaf area and the vertical leaf area distributions are examples of architectural properties of the canopy that are likely to influence the degree of coupling between the canopy air mass and the overlying or surrounding atmosphere (Geiger, 1965; Bonan, 2002). In most cases (e.g. arctic and alpine tree lines) the warming effect is due to the ability of the canopy to reduce nocturnal radiative cooling. However, in the case of arid grassland–shrubland transition zones the feedback mechanism is not controlled by canopy architecture but by the ability of some desert shrubs to eliminate grass cover from their surroundings (Báez & Collins, 2008), thereby increasing the bare soil fraction in shrub-dominated areas. The different thermal properties of grass and bare soil surfaces determines a difference in soil heat fluxes between the two land covers, which explains the higher nocturnal temperature in the shrubland. Several environmental factors also regulate the strength of microclimate feedbacks in

woodland–grassland transition zones, including solar angles and the land surface aspect, wind speed, cloudiness, photosynthetically active radiation, air humidity and topography.

In this review we have shown that these feedbacks have been documented across a wide range of arid, coastal, alpine and arctic grassland–woodland transitional communities. Recent studies have shown that, when integrated spatially, the microclimatic alterations caused by woody plant encroachment may have implications for larger-scale climates (e.g. Bonan *et al.*, 1992; Beltrán-Przekurat *et al.*, 2008), and global carbon cycles (Archer *et al.*, 2001; Chmura *et al.*, 2003; Chapin *et al.*, 2005).

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BIOSKETCH

This research team concentrates on the study of positive feedbacks in grassland, woodland and savanna ecosystems. Previous work by these authors focused on the ecological, hydrological, geomorphic and microclimatic significance of these feedbacks and on their impact on ecosystem stability and resilience. P.D. led the writing; Y.H. contributed to the writing, performed calculations and contributed to figure drawing; S.C. contributed to the writing; S.F.J.D.W. contributed to the writing; V.E. contributed to the writing; J.D.F. contributed to the writing.

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