

Topography as a driver of local terrestrial vascular plant diversity patterns

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At landscape and regional scales topography is recognized as one of the most important determinants of vascular plant diversity, primarily due to the influence of mountains. As temperature changes markedly over the elevation ranges in mountain areas, topography offers a wide variety of different habitats as well as buffering against climate change. However, for local vegetation, notably in lowland areas, the general importance of topography is less well recognized and the mechanisms by which it exerts influence on local vascular plant diversity are not comprehensively understood. In this review, we provide an overview of the evidence for the different mechanisms involved in topography's control of local patterns in potential vegetation drivers, namely incident solar energy, wind exposure, hydrology, geochemistry, and biotic conditions. Furthermore, we review the processes through which these factors shape local terrestrial vascular plant diversity patterns and provide directions for future studies on this topic. We find that topography is an important factor for local vascular plant diversity patterns in a broad range of habitats throughout the world, even in relatively flat lowlands. However, the mechanisms involved are varied and complex. Local patterns in soil moisture seem to be affected by topography through more mechanisms than other topographically controlled factors and have a strong and consistent influence on local plant diversity. Hence, local hydrology is probably the main mechanistic factor through which topography influences local terrestrial vascular plant diversity patterns. Future research should focus on employing high-coverage fine-resolution topographic data to comprehensively explore the role of topography in controlling local dynamics over large areas. Moreover, we recommend including several different habitats, particularly those in which the role of topography is poorly understood. Finally, we propose to integrate relevant functional topographic variables such as topographic wetness indices instead of simple topographic measures into future investigations.

Primarily as a consequence of the tight relationship between temperature and elevation, topography is known as an important factor for vegetation patterns at the landscape and regional scales, where mountain formations are often the dominant terrain features (Grytnes 2003, Sanders and Rahbek 2012). However, at smaller spatial scales where the elevation per se does not fluctuate enough to cause variation in temperature, the impact of topography is rather poorly understood. The influence of microtopography (small-scale terrain features, see section about microtopography) on local vegetation patterns through its effects on the local abiotic environment has been recognized at least since the 1890s (Warming 1895), but the interest in the underlying mechanisms has been limited. Ayyad and Dix (1964) and Dix and Smeins (1967) were among the first to study the relationship between local plant species diversity and elevation in herbaceous communities (Grace et al. 2000) while also examining underlying mechanisms. That microtopography is important for local terrestrial plant diversity patterns has been reported for a large number

of both wet and dry habitats such as swamp forest (Økland et al. 2008), salt marshes and mangroves (Hernández et al. 2011, Moeslund et al. 2011), tropical rainforests (Svenning 1999, 2001), mountains (Kavgaci et al. 2010), grasslands (Zalathnai and Körmöcz 2004), tundras (Biasi et al. 2005), and dry savannahs and deserts (Cox and Gakahu 1985, Boudell et al. 2002). However, to our knowledge there are no recent reviews addressing its effects on local terrestrial vascular plant diversity and hence no peer-reviewed literature providing an overview of this topic. This is probably a consequence of the dearth of data in meter-scale resolution for large areas which is needed in order to address topography's general and specific roles across habitat types and in different ecosystems. Advances in the field of remote sensing and new large-scale nature monitoring programmes are now opening new opportunities for elucidating the role of topography locally. To analyse the mechanisms behind the influence of small-scale topography is a challenge since vegetation–topography relationships vary geographically (Pennings et al. 2005, Fig. 1),

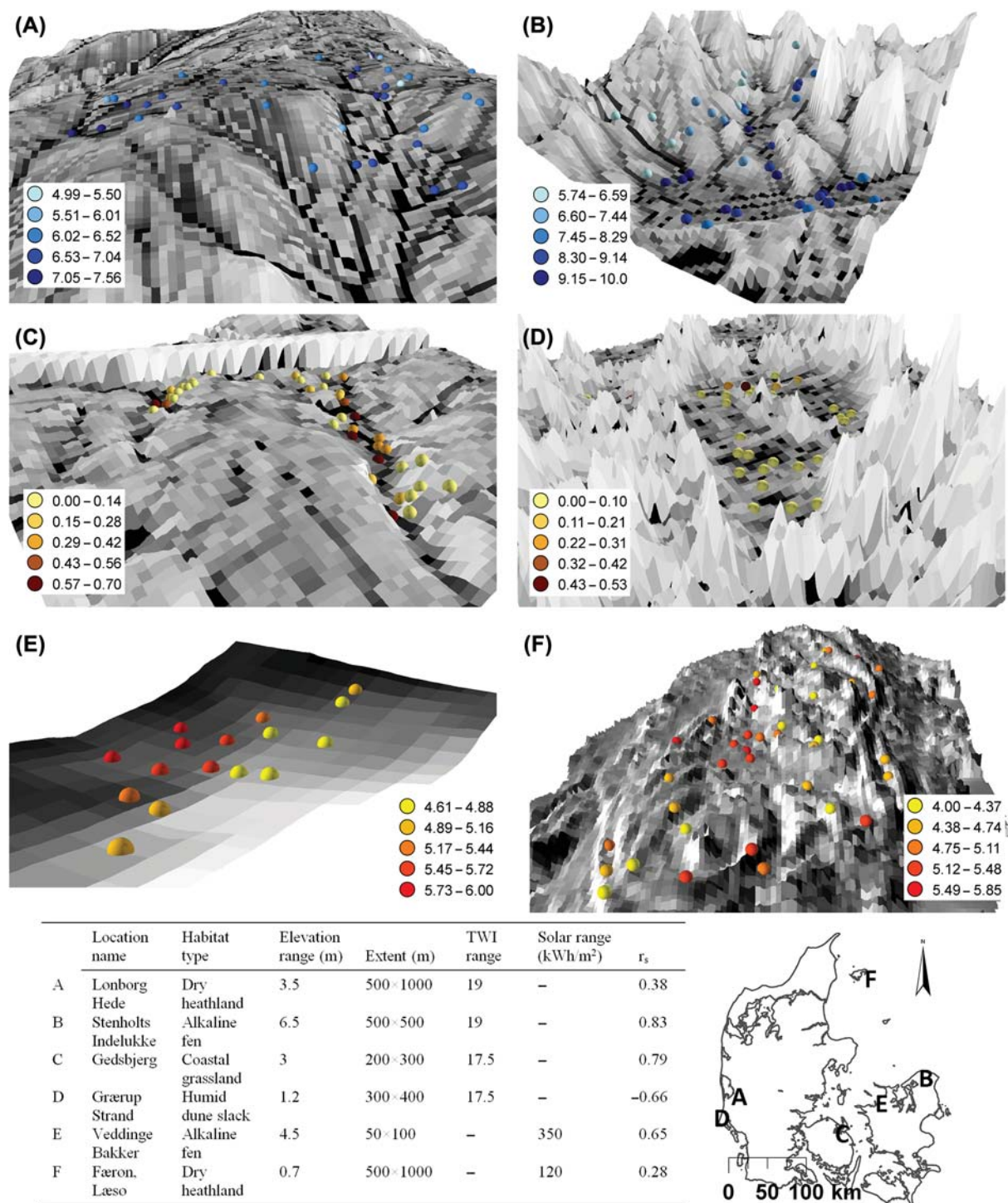


Figure 1. Relationships between topography and plant functional composition – examples from six semi-natural areas in Denmark. Functional composition is represented by coloured dots indicating the plot (size: 0.25 m²) average Ellenberg Indicator Values (EIVs, Ellenberg et al. 2001, updated following Hill et al. 1999; see details in the following) for the plant species present at the location of the dot. A topographic wetness index (Wilson and Galant 2000, panels A–D) or a layer representing potential solar radiation (calculated in ArcGis 10, panels E–F) are superimposed upon a digital terrain model, all in 10 m horizontal resolution. These two topographic measures are shown as greyscales (white is low, black is high, see figure table for ranges). Spearman's rho (r) for correlations between the functional composition measure and topographic variable in each panel are shown in the figure table. (A)–(B) visualize relationships between a topographic wetness index (TWI, Wilson and Galant 2000) and average EIV for soil moisture. (C)–(D) are relationships between TWI and average EIV for soil salinity. (E)–(F) represent relations between potential solar radiation and average EIV for temperature. The minute elevation changes are visualized by exaggerating elevation values (the real elevation ranges are given in the figure table).

among habitats (Fig. 1), and even within the same habitat type over relatively short distances (Tsuyuzaki 2006, Moeslund et al. 2011). Additionally, topography is dynamic and may sometimes change rapidly (Sterling et al. 1984, Cammeraat and Imeson 1999).

In this review we describe the mechanisms through which small-scale topography impact the local diversity patterns of terrestrial vascular plants and synthesize existing evidence for these mechanisms. Used literature was procured primarily through initial searches on Web of Knowledge (<www.isiknowledge.com>) using the following search words: 'microtopography' or 'small-scale topography' in combination with 'local plant*' or 'local vegetation' or 'plant*' or 'vegetation' and/or 'diversity' (860 hits) and refined by 'wind' (58 hits), 'solar' (5 hits), 'soil moisture' (136 hits), 'hydrology' (92 hits), 'soil chemistry' (158 hits), 'abiotic' (21 hits) or 'biotic' (23 hits). At later stages the following search words were used to refine the search to pinpoint specific mechanisms: 'propagule*' (15 hits), 'soil salinity' (17 hits), 'nitrogen' (86 hits), 'nutrient*' (111 hits), 'phosphate' (9 hits), 'heat balance' (8 hits), 'light' (72 hits), 'disturbance*' (126 hits), 'litter' (78 hits), 'drainage' (35 hits), 'inundation*' (25 hits), 'fire' (44 hits) and 'competition' (52 hits). All the above refinements provided the basis for the used literature. Studies that obviously (based on their title) dealt with agriculture or other organisms than those falling within the scope of this review (non-vascular plants, fungi, animals, or those focusing on non-terrestrial vascular plants) were omitted. If in doubt, the study was checked for suitability with this review mostly based on the full version of the paper in question, although in a few cases reading the abstract was enough to decide on this. If the study was found to fit into the scope, the paper was read in detail and most often included in the review, i.e. if deemed to fit within the scope of the review. Many references in the papers brought into light by this search procedure were also used. Three papers suggested by reviewers of earlier versions of this review were also included. Because we have previously worked with projects covered by the topic of this review, roughly 30–40% of the literature was already known to us beforehand.

Being highly relevant for the whole article the term 'microtopography' is described and defined in the initial section. Subsequently, the main groups of factors mediating the influence of topography on local plant diversity are treated in separate sections. These are 'solar energy', 'wind exposure', 'hydrology', 'geochemistry' and 'biotic interactions and effects'. Finally, we conclude, emphasizing the most important mechanisms and proposing new directions for future studies to improve our understanding of the role of small scale topography in determining local vegetation patterns. Throughout this text, the term 'plant diversity' refers to terrestrial vascular plant diversity. Additionally, 'diversity' is broadly defined, encompassing not just species richness, but also composition (also functional) and distribution.

Microtopography

The term 'topography' mostly refers to the shape and characteristics of the features constituting a terrain surface (Bishop

and Shroder 2004). Topographic elements include, but are not limited to, elevation (relief), aspect and slope. To our knowledge, the term 'microtopography' has not been defined in a vegetation study context, although it has been used frequently in vegetation studies for decades. Virtually all these studies have investigated topographic effects in areas where elevation differences ranged between 2–130 cm (Ehrenfeld 1995, Vivian-Smith 1997, Boudell et al. 2002, Zalatnai and Körmöcz 2004, Bruland and Richardson 2005, Moser et al. 2007, Sadro et al. 2007, Økland et al. 2008, Pouliot et al. 2012, Rose and Malanson 2012), though in some cases up to 1.5–5.0 m (Beatty 1984, Titus 1990, Miyamoto et al. 2003). In rare cases the term has been related to greater vertical differences (Endara and Jaramillo 2011). Here, we define microtopography as the shape and characteristics of features constituting a local terrain surface covering elevation differences up to 5 m and we focus on studies satisfying this definition.

While small-scale shapes and features may arise in a multitude of different ways, there are two main processes involved: 1) geologic processes, such as sedimentation (Werner and Zedler 2002), accretion (Pedersen and Bartholdy 2007), erosion (Parsons et al. 1992, Cammeraat and Imeson 1999), ice-cap movements (Ritchie et al. 2001), and tectonics (Pal et al. 2003), and 2) biological processes such as fire events (Collins et al. 2012), tree falls (Beatty 1984), litterfall (Grell et al. 2005), cryptogamic crusts (Boudell et al. 2002), and terrain alterations caused directly by plants and animals such as animals tracks (Isselin-Nondedeu and Bédécarrats 2007), burrows (Dickman 1999), and mounds or tussocks created by ants (Vestergaard 1998), moles (Cox and Gakahu 1985) or graminoids (Gibson 1988, Vivian-Smith 1997, Bochet et al. 2000, Werner and Zedler 2002, Stribling et al. 2007).

Solar energy

Microtopography plays an important role in determining local patterns in potential incident solar radiation (Kustas et al. 2000, Bennie et al. 2008). Generally, in the Northern Hemisphere, slopes facing southwest experience a significantly warmer microclimate and a higher frequency of drought events than northeast-facing slopes (Perring 1959), and vice versa in the Southern Hemisphere (Radcliffe and Lefever 1981). These dissimilarities in heat balance between terrain aspects play an important role in controlling local plant diversity at least in some habitats (Boyko 1947, Perring 1959, Geiger 1965, Kutiel et al. 1998, Fig. 1E–F and 2D–E). However, the influence of solar irradiation on local vegetation patterns, its importance across different habitats and the underlying mechanisms are not well-understood and only scattered evidence exist. There may be several explanations for that: apart from the resolution–coverage trade-off described in the introduction, another hindrance may lie in the process of calculating proxies realistically representing potential incoming solar radiation (Pierce et al. 2005) at relevant resolutions (i.e. 1–2 m horizontal resolution) as this procedure is quite demanding in terms of computer power (Moeslund et al. unpubl.). Also, heat balance may often be assumed unimportant.

In this section, we first discuss how topography influences patterns in incident solar energy and how this factor impacts local vegetation patterns through effects on soil moisture content. Secondly, we review evidence for the direct heat balance effects, i.e. those not mediated by soil moisture. Finally, we discuss direct effects of topographically determined light patterns.

Soil moisture

Solar energy can influence local vegetation patterns in multiple ways. One of them is by causing local differences in soil moisture as a consequence of differential evaporation and evapotranspiration rates between sites (Dyer 2009). For example, Perring (1959) illustrated this in a study of how the vegetation of English chalk grasslands varied along topographic gradients. While a number of edaphic factors changed along these gradients, he observed a consistent occurrence of xeric plant species on south-facing slopes and mesophytic plants on the northwest-facing ones, mirroring the dissimilarities in soil moisture between topographic aspects caused by differences in heat load (illustrated in Fig. 2D–E). In a study of forest understorey floristic patterns in southeastern Ohio, Olivero and Hix (1998) discovered that the composition of plants < 1 m differed noticeably between southwest- and northeast-facing slopes. Furthermore, these authors noted a significantly higher number of understorey plant species on the northwest aspects than on the opposite slopes. They attributed these findings to be likely consequences of the more stressful soil moisture and nutrient conditions on the southwest slopes. Dyer (2009) recently suggested that in mesic habitats topographically controlled solar energy input is more important for soil moisture than topographic drainage (see section about drainage in this review). The above examples together with other studies (Cantlon 1953, Hutchins et al. 1976, Erdos et al. 2012) illustrate that aspect-related soil moisture differences arising from dissimilar solar energy inputs play an important role in regulating plant diversity patterns in mesic and relatively dry habitats.

Heat balance

Temperature has numerous direct effects on plant physiology. For example, it plays important roles in processes such as photosynthesis and for the stability of various cellular membranes (Taiz and Zeiger 2002). For these reasons most plants are adapted to growth within a certain temperature range (Ellenberg et al. 2001) and thus the local temperature patterns per se are likely to be essential for shaping local patterns in plant diversity. Scherrer and Körner (2011) demonstrated topographically controlled temperature patterns to be highly important for plant functional composition patterns within a 2 km² Swiss alpine site even within a single mountain slope. Also, in a recent climate change study, Ackerly et al. (2010) presented an example showing that temperature can vary strongly (8°C) within a 1 km² area as a consequence of terrain aspect. Moreover, a new study calibrating average Ellenberg indicator values for temperature for vegetation plots to degree Celsius values found variability in these within 569 1-km² units across Scandinavia to average 2.1°C, range 0.0–6.6°C (Lenoir et al.

2013). Thermal variability within 1-km² units varied with sampling effort, topographic roughness (variability in elevation and slope), and latitude, averaging 2.0°C within the flattest (lowland) units (Lenoir et al. 2013). Topographic heterogeneity related to aspect and exposure was unimportant for thermal variability in this study.

There are a few examples from Danish habitats of the direct importance of topographically controlled solar energy for average Ellenberg indicator values for temperature (Fig. 1E–F). On the other hand, in a recent review of the influence of terrain on local climates, Dobrowski (2011) presented evidence that topography has a less marked influence on small-scale temperatures than on soil moisture: slope and aspect appeared to have only little effect on local minimum temperatures. Consequently, within small distances and in relatively flat terrain, south-facing slopes may not provide local sites of thermal shelter as seen at larger extents in mountainous areas (Randin et al. 2009), and hence in these sites there is a possibility that effects of slope and aspect on local vegetation patterns are mostly caused by differences in soil moisture. Nevertheless, a number of other studies support that topographically controlled temperature is indeed important for patterns in local plant diversity. For instance, in English grasslands *Helianthemum chamaecistus* Mill. shows clear affinities for specific slope and aspect positions, a pattern which according to the authors was probably related to insolation dynamics (Lakhani and Davis 1982), though they did not disentangle the effects of this factor from soil moisture and local temperature. Two recent vegetation studies, one in a tidal freshwater marsh at the Hudson River estuary, and one in restored wetlands in North Carolina, reported temperature differences between hummocks (highest temperatures) and hollows in the range 0.6–4.0°C, potentially playing a role for the differences in plant communities observed between these elevation positions (Bruland and Richardson 2005, Courtwright and Findlay 2011). Local patterns in temperature may also affect plant diversity indirectly by causing differences in mineralization rates (see section about soil chemistry). In Siberian alpine environments, for example, Biasi et al. (2005) recently suggested that differences in temperature between tundra hummocks and hollows could be associated with nitrogen availability. However, this effect was not observed at their study sites, most likely because it was overruled by other factors affecting mineralization rates. Finally, experimental evidence suggests that microtopographically controlled temperature patterns may cause spatial differences in the germination process for some plant species (Harper et al. 1965, Graae et al. 2008).

Light availability

Only little knowledge exists for the role of topographically controlled light in forming local vegetation patterns. According to evidence presented in a review of palm ecology (Svenning 2001), canopy gaps related to small-scale topography, particularly those associated with small creeks, can be of high relevance for the local distributions of some light-demanding palm species. Bennie et al. (2008) also mentioned topographic effects on light as potentially important for local vegetation.

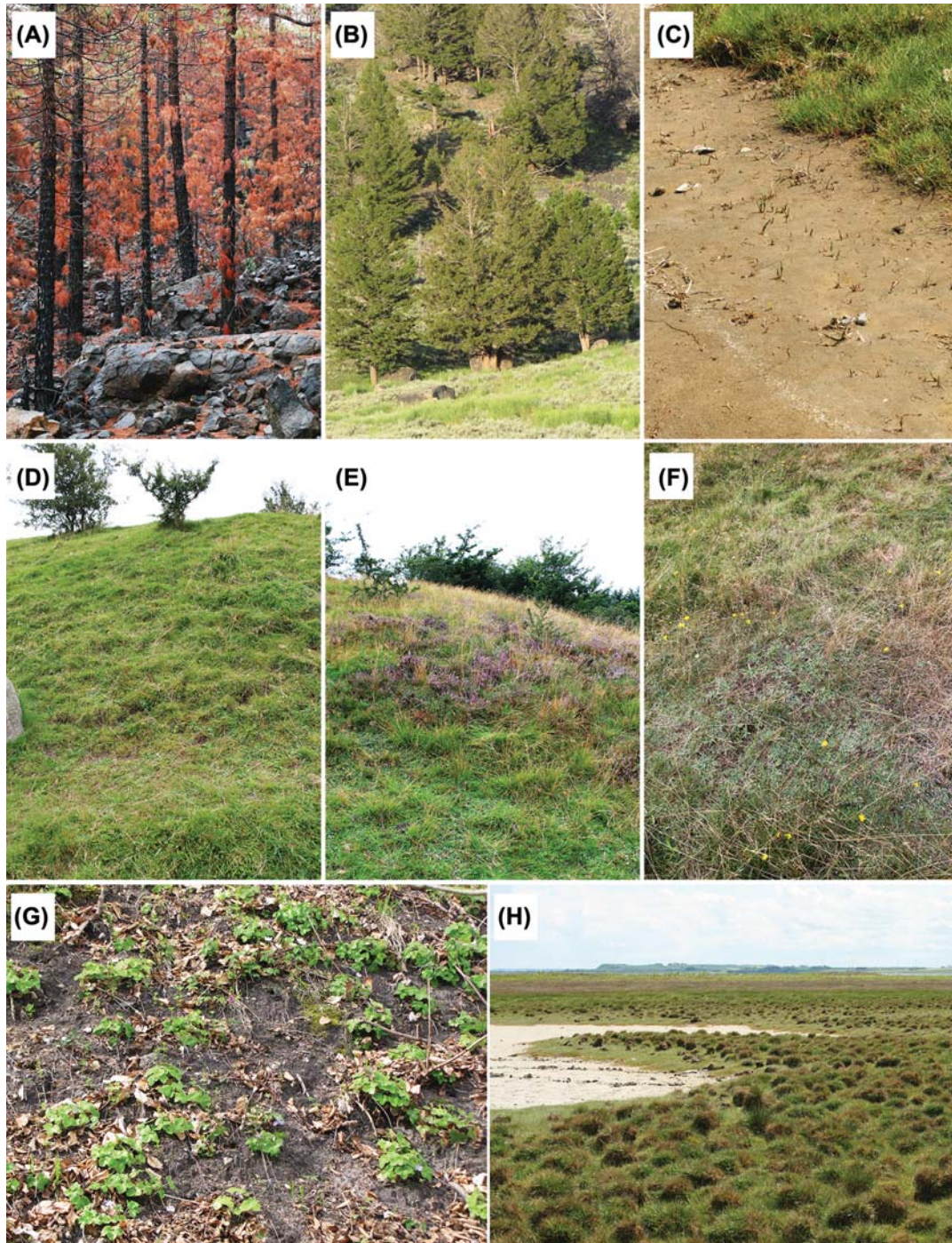


Figure 2. Examples of the influence of topography on local plant diversity in various habitat types. (A) shows a *Pinus canariensis* C. Sm. forest on Tenerife where trees emerge primarily from small depressions in the rock, probably giving shelter, maintaining a sufficient supply of water, and acting as the end station for *Pinus* seeds. (B) displays individuals of *Pseudotsuga menziesii* Mirb. (Franco) in Yellowstone National Park, Wyoming, each growing adjacent to a nurse rock which is thought to create a shady, moist microclimate beneficial to seedling survival in the dry, hot summer climate of this area. (C) shows a Danish saltmarsh. Here the elevation gradient shapes gradients in both soil moisture and salinity giving rise to distinct zones of plant species composition. On this panel the lower two zones dominated by *Salicornia europaea* L. and *Puccinellia maritima* (Huds.) Parl. respectively are present. It is also likely that the tidal water movements disturb the plants in the *Salicornia* zone. (D)–(E) are from the same Danish grassland. (D) shows a relatively moist north-facing slope and (E) a drier south-facing slope with heath plants (e.g. *Calluna vulgaris* (L.) Hull). (F) is a segment of another Danish grassland. The upper part has a slope of approximately 35° whereas the lower part only slopes 5°–10°. As seen this is clearly mirrored by the vegetation. (G) stems from a Danish deciduous forest. It shows the effect of steep slopes (approximately 45°) on the distribution of litter. *Hepatica nobilis* L. is frequent on these slopes because it often prefer to grow on more or less bare ground and do not emerge if a deep litter layer is present. (H) is from a Danish salt marsh. Here the four zones typically found on these marshes are present. The lower two zones were described above (in C). The upper two zones are normally dominated by *Juncus gerardii* Loisel. and *Festuca rubra* L. respectively. Photo credits: (A), (C), (H) by J. E. Moeslund, (B), (G) by J.-C. Svenning, (D), (E), (F) by N. S. Ebsen.

Conclusion

Topographically controlled solar radiation may influence local vegetation patterns through at least three mechanisms, namely by effects on 1) soil moisture, 2) temperature, and 3) light availability. The evidence for the first mechanism is solid although the precise local relationships between topographic solar energy and soil moisture remain to be fully understood. Particularly, it is unclear how much these relationships vary across habitats and geography and there is also uncertainties attached to the degree to which they interact with the more direct control of local hydrology by topography (see 'Hydrology'). Support for the second mechanism is also quite solid though the evidence is more scattered. Notably, there is a lack of vegetation studies that disentangle the effects of solar irradiance on soil moisture and temperature. At local scale, evidence for the third mechanism is virtually absent. Consequently, it is most likely that the primary mechanism through which topographically controlled solar energy input determines local floristic patterns is by affecting soil moisture.

Wind exposure

While local topography clearly affects wind exposure, the relationship is complex and poorly understood and consequently so is its impact on local plant diversity patterns (Ennos 1997). There are at least three different mechanisms involved, namely those underlying how wind-exposure affects soil moisture, disturbances, and propagule and litter redistribution.

Soil moisture

Some studies have suggested that wind-caused drying play a significant role in shaping local vegetation patterns. For example, in a restoration project of Texan landfills, Biederman and Whisenant (2011) showed that leeward sides of created mounds held significantly higher plant species numbers and densities compared to the windward sides. The investigators suggested these findings to be consequences of the lower evaporation and greater dew deposition on leeward sides due to shelter from wind. A similar finding emerged from a study taking place in the Kuwaitian deserts. Here, plant establishment was evidently promoted by elevated soil moisture and nutrient concentrations at the lee side of miniature dunes (Brown and Porembski 1997). In Australian dune heathland, Rayson (1957) showed that the plant species composition on the sand plains, east-, and west-facing slopes differed markedly as a consequence of interactions between microtopography and rain-bearing wind, causing east-facing slopes to be moister than west-facing sides. Microtopographically determined wind-desiccation effects have also been reported from a number of alpine environments. For instance, Lévesque (2001) found that several plant species in the polar deserts of central Ellesmere Island grew close to boulders, which provide shelter and protect the seedlings against wind-caused desiccation (Fig. 2B). In sub-arctic Finland along a treeline ecotone, birch (*Betula pubescens* var. *pumila* (L.) Govaerts) seedling establishment was impeded on flat ridge tops as a consequence of lacking seed accumulation and because wind erosion creates a relatively

dry and nutrient poor environment (Anschlag et al. 2008). Similarly, in the Colorado Front Range in the USA, Holtmeier and Broll (1992) found evidence that present-day tree islands consisting of *Picea engelmannii* Parry ex Engelm. and *Abies lasiocarpa* (Hook.) Nutt. originally developed in wind-sheltered depressions with relatively favourable conditions for germination and growth of tree seedlings.

Disturbance

At local scales wind is likely to disturb vegetation by causing erosion and transporting soil particles. In dune systems, wind-caused erosion or deposition of sand accounts for the disturbance exerted on the local flora. For example, in fore-dune habitats in Santa Catarina, Brazil, Silva et al. (2008) recently showed that plant species richness, composition and vegetation cover changed along gradients of exposure to wind and salt spray with less vegetation cover and lowest species richness on the most exposed sites. Many plants characteristic of dunes are adapted to the disturbance by sand and they tolerate sand burial and often increase their growth rates in response to increased sand deposition (Travis 1977, Boorman 1982, Lee and Ignaciuk 1985, Maun 1994). For example, mid-1900-century studies have demonstrated that dune species such as *Ammophila arenaria* (L.) Link and *A. breviligulata* Fernald are almost unaffected by 90–125 cm sand burial per year (Ranwell 1958, Woodhouse and Hanes 1966). Other plants are not adapted to sand burial of these magnitudes and are hence restricted to grow in topographic positions with less sand accretion. Similar findings are known from other habitats in which dynamic sand masses dominate such as deserts (Zhao et al. 2011). Frequently, wind also causes physical damage to plants (Thompson 1974, Wilson 1980), but the degree to which this is controlled by local topography is to our knowledge unstudied.

Propagule and litter redistribution

Topographically controlled wind exposure patterns may have a high impact on the local distribution of propagules and litter which again may influence local vegetation patterns. This is discussed further in the section on biotic interactions.

Conclusion

Wind exposure is undoubtedly linked to small-scale topography. However, the degree to which this affects local plant diversity patterns and through which mechanisms is poorly understood, with only a few ecological studies addressing this subject. One explanation may lie in the complex relationships between microtopography and wind, causing the study of their effects on vegetation to require a large effort (Ennos 1997, Siddiqui et al. 2008). Nevertheless, there is evidence for topographic wind effects through at least three pathways. Firstly, wind-exposed sites dry out faster than sheltered areas. Secondly, wind causes disturbances such as sand erosion or deposition or physical damage to individual plants. Finally, it creates spatial heterogeneity in the distribution of propagules and litter locally. There is only limited evidence for all these mechanisms, and the direct effect of wind on local vegetation patterns including its interactions with other factors remains to be elucidated. Overall, for a large number of habitats – especially those not associated

with bare soil or sand – the effect of topographically controlled wind exposure is largely unstudied, albeit likely to be of little importance.

Hydrology

Topography may potentially control local patterns in soil moisture through numerous mechanisms. Some of these mechanisms are direct topographic hydrology effects, some are more indirect. The first four subsections of this section are dedicated to review evidence for mechanisms through which topography exerts direct influence on local soil moisture. The subsequent two subsections mentions the more indirect mechanisms, while the next three subsections discuss the mechanisms through which soil moisture influences local vegetation patterns.

Vertical distance to water

In habitats located within a few meters in vertical distance from a water table, microtopography to a high degree dictates local patterns in soil moisture. For instance, this is the case in many wetland habitats. In ombrotrophic peatlands, uniformly distributed structures named hummocks (hills) and hollows (depressions) arise from the differential growth and characteristics of *Sphagnum* species (Nungesser 2003). Typically, elevation differences between hollows and hummocks are a few decimetres (Tsuyuzaki 2006, Økland et al. 2008). This microtopographic structuring controls soil moisture levels: depressions are often inundated or saturated with water and consequently constitute a reducing environment while hummocks are less moist and mostly represent an oxidizing environment (Chimner and Hart 1996, Tsuyuzaki 2006, Økland et al. 2008). This has consequences for local plant species diversity (illustrated in Fig. 1B). For example, in English meadows, Silvertown et al. (1999) showed that wetland functional composition was linked to a hydrological gradient. They explained this to be a consequence of the plants' adaptations to drought and flooding tolerances. In Michigan forest peatlands, Chimner and Hart (1996) found that individuals of *Thuja occidentalis* L. regenerate almost exclusively on the hummocks because seedlings are unable to cope with the wet conditions found in the hollows. Similarly, in a Chinese wetland, the local patterns in functional distribution was also evident with *Carex* sp. and *Potamogeton perfoliatus* L. found primarily in the hollows, and *Trollius ranunculoides* Hemsl. which prefers lower soil moisture levels on the hummocks (Tsuyuzaki 2006). Habitats that are relatively dry, but still close to the groundwater table are widespread in some parts of the world. For example, this applies to areas in the South African fynbos where free-draining sand can be found quite close to the water table. The effects of topographically controlled soil moisture on local vegetation in such an area were recently illustrated by Araya et al. (2011). These authors demonstrated that vegetation from eight fynbos sites segregated along local-scale hydrological gradients in a manner similar to that of the vegetation from the 22 wetlands also included in the study. They suggested the trade-off between opening stomata for capturing CO₂ and closing them to conserve water to be main responsible for

the observed hydrological niche segregation of plants along the soil moisture gradients in these habitat types.

As mentioned, species richness also responds to topographically controlled variation in soil moisture. For example, Vivian-Smith (1997) demonstrated that the species richness was significantly higher on hummocks than in hollows in a wetland mesocosm experiment, probably because relatively few terrestrial plant species are adapted to growth in water-logged soils. Similarly and for the same reasons, Titus (1990) found that woody seedlings occurred more often on elevated sites than in the bottom sites in a hardwood floodplain swamp in Florida. The pattern of species richness being lowest in low-lying wetland sites is widespread, has been demonstrated often (Lieberman et al. 1985, Huenneke and Sharitz 1986, Stribling et al. 2006, 2007, Økland et al. 2008, Raulings et al. 2010, Courtwright and Findlay 2011, Moeslund et al. 2011), and hence seems to be rather consistent and general.

Drainage

Many habitats receive water primarily from precipitation as the distance to the water table is long. While this distance is consequently unlikely to be important here, topography is still expected to exert major impact on patterns in soil moisture. Higher lying areas are virtually always better drained as a consequence of gravity. As small soil particles sometimes tend to be transported away from highs and subsequently gather in depressions (Li et al. 2008), microtopography may also influence the soil grain size distribution which plays a major role for how fast the water drains into deeper layers of the surface soil. Water drains through sand relatively fast, but is often hindered from draining through clay as a consequence of the compact and very small particles constituting this soil type. Semi-dry and dry habitats like grasslands, forests, savannahs, deserts, and prairies are examples of habitats in which drainage may affect the local patterns in soil moisture. For example, Moeslund et al. (2013) recently demonstrated that topographically controlled hydrology was the main topographic driver of plant diversity in a study of 258 Danish grasslands. These findings are likely to be a consequence of topographic influence on local patterns in drainage as most of these grasslands are rain-fed (also see Fig. 1A where a topography-vegetation relationship in a drainage-dominated heathland is visualized). Additionally, in Great Hungarian Plain and Sierra de Guadarrama grasslands as well as in fixed dune grasslands in northwestern Wales, there is convincing evidence that different distinct plant communities are found at different microtopographic positions (Sterling et al. 1984, Gibson 1988, Zalatnai and Körmöcz 2004). All authors suggested these observations to be a consequence of topographically controlled soil moisture and chemistry (see Geochemistry). In eastern Germany a recent study of dry grassland and heath vegetation on rock outcrops demonstrated that the floristic gradient was highly related to soil moisture and nutrient availability, and suggested these factors to be controlled by microtopography (Wesche et al. 2005). In some forests, topographically related drainage is also likely to be among the most important mechanisms influencing soil moisture. For example, in Amazonian terrace forests, Normand et al. (2006) found soil moisture and

topography to be the most important environmental determinants of local palm species distributions. Additionally, in old-growth forests in British Columbia, *Thuja plicata* Donn and *Epilobium angustifolium* L. were significantly more widespread in depressions than in flat areas and mounds despite the fact that the authors found no differences in soil chemistry between these locations (Messier and Kimmins 1992). Although they did not measure soil moisture, they suggested this factor to be main responsible for the distribution of the two plant species. In Kenyan savannahs, Cox and Gakahu (1985) showed that the plant species composition of mounds created by the east African mole rat (*Tachyoryctes splendens* Rüppell) differs from that of the intermounds. This difference was partly attributed to the fact that these elevated sites offered a better drainage of the soil favouring many savannah plant species. In the Chihuahuan desert in southern New Mexico, microtopography is strongly correlated with the cover of long-lived grasses through its effects on soil water drainage (Nash et al. 2003). Similar evidence exists for coastal desert systems at the Sinai Peninsula (El-Bana et al. 2002).

Water runoff flow paths

On slopes, microtopography in some cases influences the paths followed by run-off water. Bergkamp (1998) exemplified this in a study in Spanish semiarid shrublands, reporting vegetation mounds to play a main role in the distribution of surface water flow which again through a positive feedback mechanism favoured the existence of these local vegetation knolls. Additionally, in a study of Chihuahuan desert grasses, Yao et al. (2006) found that local water redistribution by microtopography was important for plant cover for both *Sporobolus flexuosus* (Thurb. ex Vasey) Rydb. and *Pleuraphis mutica* Buckley before and after a severe drought. Evidence for the effect of microtopography on water flow paths is not rare, but the local vegetation patterns shaped by this mechanism are poorly studied (Poesen et al. 1990, Lavee and Poesen 1991, Kutiel et al. 1998, Ludwig et al. 2005).

Inundation

In habitats fringing coastlines or other water bodies, soil moisture may be partly or primarily controlled by frequent inundations, whose frequency and duration are controlled by the local topography. Salt and freshwater marshes are examples of habitats in which this is a dominant phenomenon (Vestergaard 2002, Stribling et al. 2006, 2007, Courtwright and Findlay 2011). For instance, in a recent study of local vegetation patterns in 27 Danish salt meadows, Moeslund et al. (2011) found clear links between microelevation and plant species diversity and functional composition respectively: the species richness significantly increased with elevation and the vegetation zonation markedly changed from highly salt and water-logging tolerant species to species that tolerate only small concentrations of salt and prefer less moist sites. These patterns were considered likely to arise partly from effects of flooding frequency and duration on soil moisture. Similar observations and causes have also been suggested for other tidal areas such as mangroves (Lara and Cohen 2006). Finally, topographic control of inundation dynamics is also known from non-coastal habitats. For example, in Turkish

Taurus mountain ponds, microelevation is the most important vegetation determinant because it exerts primary control of the duration of inundation from rain and melting snow (Kavgaci et al. 2010, Šilc et al. 2011).

Wind

The sub-section on soil-moisture within the section about wind examines how wind can influence patterns in local soil moisture.

Solar energy

The sub-section on soil-moisture in the section concerning solar energy discusses how incident solar energy can shape the local soil moisture patterns.

Direct effects of water availability on local plant diversity

Hydrology can form local vegetation patterns through several mechanisms (this and the next two subsections). One of them involves the direct response of plant species to different soil moisture levels. Some species are adapted to growth in waterlogged soils, some to relatively dry and well-aerated sites and most species in-between (Ellenberg et al. 2001). The local plant diversity patterns formed by soil moisture are discussed in the first subsections of this section. The physiological and morphological adaptations of the individual plant species to different soil moisture levels is beyond the scope of this review, but is a key topic in numerous books on plant physiology (Taiz and Zeiger 2002).

Geochemistry

Soil moisture has a high impact on the concentration of nitrogen and other geochemical components. In the geochemistry section the influence of topographically controlled soil moisture on geochemistry and the local vegetation patterns resulting from this are reviewed.

Disturbance

In tidal areas, wave action and the tide itself can influence the local plant diversity through washing away seedlings or burying them under sand or mats of plant material. For example, at Rhode Island salt marshes, *Distichlis spicata* (L.) Greene and *Salicornia europaea* L. was often found on areas recently disturbed by wrack burial (dead plant material rafted by tides onto the marsh) as these species are particularly resistant to these events (Bertness and Ellison 1987). According to the authors, the severity of these disturbances decreased with elevation above sea level and was consequently under topographic control (Fig. 2C). On the other hand, some species like the *Suaeda maritima* (L.) Dumort. are quite sensitive to such tidal disturbances: in a recent study of the factors affecting establishment success of this species, the seedlings did not tolerate burial by the sediments transported by the water and was easily washed away (Tessier et al. 2000).

Conclusion

The evidence for the effects of topographically controlled hydrology on local plant diversity is huge, but centred around the most obvious mechanisms. There is no doubt that the vertical distance to the water table is important for soil moisture and that this mechanism often plays a central

role in determining local plant diversity, notably in wetlands which per definition are close to subsurface water layers. The evidence for the remaining topography–soil-moisture mechanisms mentioned above is less massive. Although it is well-known that topography influences soil moisture by affecting the drainage and flooding duration and frequency in many habitats, the role generally played by these mechanisms in controlling vegetation patterns is not as well understood. For example, we do not know to what extent these effects vary between habitats and how they interact with other mechanisms. Examples illustrating the role of microtopography in the redistribution of surface-runoff water are scarce and the importance of this mechanism for vegetation has not been studied much. The influences of solar energy and wind on soil moisture are summed up in their respective sections elsewhere in this review.

Soil moisture may influence local plant diversity in at least three ways: firstly, it may affect vegetation directly by controlling the composition and species richness through plant preferences for varying soil moisture levels and through productivity. Secondly, it may influence the vegetation by altering the geochemistry, and thirdly by causing disturbances such as uprooting, and burial by sediments. The first mechanism is relatively well understood and the topography–soil-moisture–direct-effects pathway is probably the most studied of all in terms of how topography shapes local vegetation patterns. That inundation frequency and duration may affect local vegetation patterns, particularly in tidal settings, is relatively well-known. The role of geochemistry is summed up in the geochemistry section. It is by no means clear which of these hydrology–vegetation mechanisms are the dominant and to what extent this dominance shifts geographically and between habitats.

Although many different mechanisms are involved, this section combined with the results from a few cross-habitat studies (Araya et al. 2011, Moeslund et al. unpubl.) show that microtopographic hydrology is a fundamental and general factor in shaping and structuring local plant diversity patterns across a wide variety of habitats ranging from wet fens and bogs to dry savannahs and deserts.

Geochemistry

In this section, we present evidence for the mechanisms involved in topographic control of local patterns in soil chemistry and the plant diversity patterns formed by these relationships. The first subsection deals with effects of microtopography on local patterns in soil salinity, the second is on soil pH, and the third concerns nutrient distributions.

Soil salinity

In salt marshes and mangroves microtopography is a major determinant of soil salinity. For example, in a vegetation–topography study of 27 salt meadows in Denmark, Moeslund et al. (2011) reported that elevation was an important determinant of plant diversity and plants' preferences for soil salinity. They suggested elevation to be a major controller of the interactions between evaporation and sea water inundations giving rise to a hump-shaped or linear soil salinity pattern along elevation gradients in salt meadows (Fig. 1C,

2C, H). Also exemplifying this, Pennings et al. (2005) demonstrated that salinity was an important factor for the vegetation zonation observed in saltmarshes at Sapelo Island, southeastern USA. Importantly, these authors noted that the role played by salinity is likely to vary geographically, with the most important role at low latitudes where the creation of salt pans is a normal phenomenon due to high evaporation rates. Although salinity is not the sole determinant of vegetation patterns in salt marshes (see the section on hydrology), the elevation–soil-salinity relationship and its impact on vegetation patterns in salt marshes is strong and thought to be relatively well understood (Adams 1963, Mahall and Park 1976, Callaway et al. 1990, Amiaud et al. 1998, Vestergaard 2002, Moffett et al. 2010).

In coastal dunes, vegetation zonation is also regularly affected by topographically controlled soil salinity (Maun 1994). Already in the 1940s, the distribution of the two grasses *Uniola paniculata* L. and *Schizachyrium scoparium* (Michx.) Nash in a coastal dune system in North Carolina was demonstrated to clearly depend on soil salinity (Oosting and Billings 1942). Wind-borne salt spray was appointed responsible for adding salt to the soil, with local topography controlling where these spray particles were deposited. In Fig. 1D another example of a topography–salinity relationship in a dune environment can be found.

In a recent study in the Mexican mangroves, the salt tolerant *Avicennia germinans* (L.) L. was found to prefer elevations approximately 20 cm higher than *Rhizophora mangle* L. because the lower frequency and amplitude of tides at this position caused the salinity to be markedly higher compared to the lower-lying areas as a consequence of increased evaporation (Hernández et al. 2011). Similar mangrove zonation patterns were also observed by other authors (Lopez-Portillo and Ezcurra 1989, Ukpong 1997, Lara and Cohen 2006) who similarly suggested salt concentration to play a major role for their observations. Interestingly, there is also evidence for microtopography–soil-salinity relationships in arid habitats in which salt occasionally may accumulate. For example, in Hungarian calcareous grasslands three to four different plant communities were segregated by a microtopographic gradient of approximately 50 cm, at least partially as a consequence of changes in soil salinity along this gradient (Zalatnai and Körmöcz 2004).

Soil pH

Local microtopographic changes in pH are not widely reported, but examples do exist (Gibson 1988, Zalatnai and Körmöcz 2004). At least three pathways may be considered. The first involves changes in pH caused by topographic hydrology. For example, as a consequence of gravity and the calm waters often found in wetland depressions, soil organic matter often accumulate in these low-lying sites where subsequent decomposition causes the pH to decrease (Bruland and Richardson 2005, Courtwright and Findlay 2011). In sedgeland heaths on limestone bedrock in Tasmania, soil pH has been demonstrated to change more than 3 pH units within 20 cm of elevation, clearly affecting the local plant species composition and richness (Brown et al. 1982). The authors explained that this pattern was most likely caused by peat overgrowing alkaline soils over a period of several

hundred years, slowly lowering the pH in the resulting hillocks. A second way in which topography may affect local pH is found in areas with different geological layers close to the terrain surface. Here, microtopography can be expected to cut through these and hence create idiosyncratic spatial differences in soil reaction. For instance, in the Meerdaal forest in Belgium an ancient holloway that lies 2–3 m deeper than the surrounding terrain is significantly less acidic than the soil in the rest of the forest because it cuts through deeper niveo-eolic calcareous loess (Plue et al. 2009). This finding was manifested in the understory vegetation showing a markedly different species composition and higher species richness in the lower-lying ancient road compared to the surrounding areas. Such effects are likely to be commonplace. The third pathway has to do with active alterations of topography by animals. For instance, in Kenyan savannahs mounds created by the east African mole rat (*T. splendens*) have been found to offer a higher soil pH than intermound areas which again potentially explains vegetation differences between these two microtopographic positions (Cox and Gakahu 1985). While the authors did not explain or discuss the potential mechanisms, it seems likely that variations in soil moisture, granular macrostructure, and soil organic matter content were involved.

Nitrogen, phosphorous and other nutrients

Soil moisture and nitrogen available for plant growth are tightly interlinked as water is required for microbial activity and controls the oxygen concentration which again affects microbial processes. The effect of soil moisture on nitrogen availability was thoroughly discussed by Araya et al. (2013) and has been the subject of many studies. For example, in restored wetlands, Bruland and Richardson (2005) found higher concentrations of both NH_4^+ and NO_3^- in hummocks compared to hollows. Here, the authors argued that the hotter and drier conditions found in the hummocks cause greater mineralization rates and hence a higher release of inorganic nitrogen in general. The opposite pattern is also observed frequently (i.e. that the NH_4^+ and NO_3^- concentrations are higher in the lower-lying zones, Simmons et al. 2011). For example, Courtwright and Findlay (2011) recently demonstrated that while the hummocks in tidal freshwater swamps mostly featured an oxidizing environment, the hollows maintained reducing conditions. This gave rise to significantly higher concentrations of water soluble phosphate and NH_4^+ in the hollows, probably because NH_4^+ becomes oxidized to NO_2^- or NO_3^- and subsequently denitrified to the gaseous N_2 or N_2O in the hummocks, and because the oxidized form of iron, Fe^{3+} , found here forms insoluble iron–phosphate complexes (Courtwright and Findlay 2011). In arctic sites, Biasi et al. (2005) explained that the unfavourable conditions for nitrogen mineralization found in the waterlogged hollows may be overruled by effects of substrate quantity and quality and that the sedges and grasses dominating the hummocks – in contrast to the hollows being dominated by bryophytes – effectively acquire both inorganic and organic nitrogen depleting these zones for nutrients. In the relatively dry fynbos habitat in South Africa, plant species was recently shown to segregate along local hydrological gradients (Araya et al. 2011). The authors

suggested that soil-moisture–nitrogen dynamics may have played an important role for these results. All in all, the relationship between plant available nitrogen and soil moisture is rather complex, but generally nitrogen availability seems to be highest under mesic conditions and lowest in waterlogged and very dry soils because nitrogen-mineralization is limited by anoxia and lack of water (Araya et al. 2011, 2013). In arid areas such as the Australian arid *Acacia* shrublands, Mott and McComb (1974) showed that elevation differences as small as ~6.5 cm cause notable differences in available nitrogen with the highest availability on the mounds. This was mirrored by the fact that plant seedlings grew faster here than in depressions under similar soil moisture conditions.

Nitrogen is not the only nutrient affected by microtopography. For instance, Miyamoto et al. (2003) reported that tree distributions in Indonesian tropical heath forests were markedly affected by microtopography, and suggested this observation to be a consequence of Na, Mn, NO_3^- and PO_4 soil concentrations being determined by local elevation variations. Grell et al. (2005) measured soil pH, conductivity, organic matter, N, P, K, Ca, Mg, S, Fe, Mn, Zn, Cu and Na along an elevation gradient of 1.5 m. Eleven of these were significantly correlated with elevation and a major part of the plant species encountered was too. These authors also found that the main floristic gradients for overstorey vegetation, herbaceous species, and seedlings were clearly related to a number of the chemical factors. All these results provide clear evidence that microtopographically controlled soil chemistry can be important for the floristic composition in forests. Microtopographic control of nutrients has also been reported from other habitats. For instance, in fixed dune grasslands in Wales, Gibson (1988) observed that the plant composition on *Arrhenatherum elatius* L. hillocks differed markedly from that of depressions and the diversity was higher here than in the lower sites. These patterns had relationships to the concentrations of PO_4 and Mn that varied consistently with microelevation. Additionally, in Sierra de Guadarrama grasslands, Sterling et al. (1984) speculated that the nutrient level together with soil moisture probably accounted for the shift in plant communities observed between old plough furrows and ridges.

Conclusion

There is much evidence that microtopography plays an important role in determining local patterns in geochemistry and thereby also local plant diversity patterns. Soil salinity, controlled by topography through its impact on inundation frequency and duration, is a strong driver of local vegetation patterns in many coastal settings and also occasionally in inland dry habitats throughout the World. The evidence for this effect is strong and consistent and wherever there is exposure to salt water, microtopography plays a major role in structuring local plant communities. Microtopography also plays a role in controlling local patterns in soil reaction although its importance is less well understood and not as widespread. Finally, microtopography clearly impacts the distribution of soil nutrients which is mirrored in local plant diversity patterns. In many cases, the control of these chemical soil components by microtopography is mediated by microtopographic soil moisture and local temperature

regimes (also see the subsection on heat balance in the solar energy section) affecting the chemical reactions. In addition, more direct microtopographic effects such as erosion processes exposing certain types of soil and bedrock are involved in some cases. While, microtopography–soil–salinity relationships are relatively well-understood, many mechanisms for microtopographic effects on local soil reaction and nutrients require further work.

Biotic interactions and effects

Biotic interactions

In the previous sections, we have reviewed evidence for the many differing, but primarily abiotic mechanisms through which microtopography affects the resources necessary for plant existence. By influencing these resources in concert, different combinations of resources are created in a local environment. Because plant species compete for these resources, as a consequence of their attempt to realize their fundamental niches (Hutchinson 1957), microtopography is also likely to influence the plants' ability to compete with one another. For instance, Kluse and Diaz (2005) recently showed that the two species *Poa pratensis* ssp. *pratensis* and *Deschampsia cespitosa* (L.) P. Beauv. with overlapping ranges in wet conditions competed for water when the soil moisture level decreased, and their individual competitive abilities were altered by this scenario, with *P. pratensis* being a much stronger competitor for water in dry environments than *D. cespitosa*. At least one study suggests microtopographically determined heat balance as playing a role in invasion resistance: in English grasslands, Bennie et al. (2006) showed that slopes receiving relatively high solar irradiation were also more resistant to invasion by competitive grasses than those receiving less solar energy. They reasoned that this finding was a consequence of the fact that the high-solar-energy slopes tend to experience a higher frequency of severe drought events to which the native species were better adapted.

Biotic effects

As already touched upon, microtopography is likely to affect spatial propagule distribution patterns (Harper et al. 1965). For example, in swamp forest habitats seeds from various species may arrive at or be trapped differently among microsites as these differs in physical structure and because the seeds may possess species-specific characteristics affecting these processes (Huenneke and Sharitz 1986, Schneider and Sharitz 1988, Titus 1990). Additionally, in a recent study of Texan landfill vegetation, Biederman and Whisenant (2011) observed that mound sides had a low establishment of pioneer species, proposing steepness of the mound sides and contingent little seed capture as the reason. Similarly, in the Belgian Meerdaal forest, Plue et al. (2009) noticed that ancient land use artefacts causing distinct microtopographic variations significantly impacted the discovered seed bank patterns. Interestingly, even at very small scales topography can have a high impact on local seed distribution patterns. For example, in the shrub-steppes of southeastern Washington, Boudell et al. (2002) reported that a large amount of seeds gathered in the crevices bordering cryptogamic crusts, and similarly Isselin-Nondedeu and Bédécarrats (2007)

observed that seed numbers were elevated in cow hoof prints in alpine environments in France. Gomes de Freitas et al. (2012) noted the possibility of animal seed dispersers having difficulties navigating steep slopes potentially explaining why certain animal dispersed plant species occur only in flat sites. These examples illustrate that microtopography frequently affect seed dispersal processes (Fig. 2A). However, this relationship is by no means simple and well-understood. For example, Li et al. (2009) noticed that the number of dune plant seeds was highest in leeward sides of semishifting dunes whereas wind-exposed sides held the highest seed numbers in fixed dunes.

The distribution of litter is also affected by microtopography as wind- or water-borne litter tends to gather in places where the kinetic energy exerted by these two factors is low. For example, in the woodlot forests south of Ottawa, Dwyer and Merriam (1981) found that topography to a high degree controlled the local distribution of litter accumulating in depressions. This phenomenon again affected local temperature, and soil moisture patterns. Where the litter layer is relatively deep (for example in depressions) it may protect seeds and seedlings from frost damage during the cold months through isolation and the elevated temperature associated with microbial activity (Uchida et al. 2005). Furthermore, topography may affect the litter cover more directly as a consequence of gravity causing less litter to congregate on steep slopes. This might have a strong impact on the emergence of certain plant species that require shallow or no litter layers to establish (Costa 2006). For example, in a recent study in central Amazonia, Rodrigues and Costa (2012) found that pteridophyte and monocot emergence was 2–4 times higher in plots with all litter removed than in plots with a relatively deep litter layer. In temperate beech forests in Denmark species such as *Hepatica nobilis* Mill. tend to favour steep slopes where the litter layer is shallow (JEM and JCS pers. obs., Fig. 2G).

Conclusion

Much evidence suggests that local topography plays a critical role for biotic interactions and effects. As topography controls a number of vital plant resources it determines local competition conditions. Furthermore, the distributions of seeds and litter are undoubtedly influenced by topography. Together these mechanisms are likely to have a high influence on local vegetation patterns. Unfortunately, the evidence is scattered and lack holistic approaches as to examine how topography affects seed and litter distributions across habitats and to identify potential interactions between topographic litter control and seedling emergence.

Conclusion and outlook

Overall, our review shows that topography is an important factor for local plant diversity patterns across most habitats, even in relatively flat lowland areas. The mechanisms involved are varied and complex, with topography acting upon the resources needed for plant existence, shaping exogenous disturbance patterns, and/or modulating biotic interactions such as competition (Fig. 3). The main biotic and abiotic factors under local topographic influence

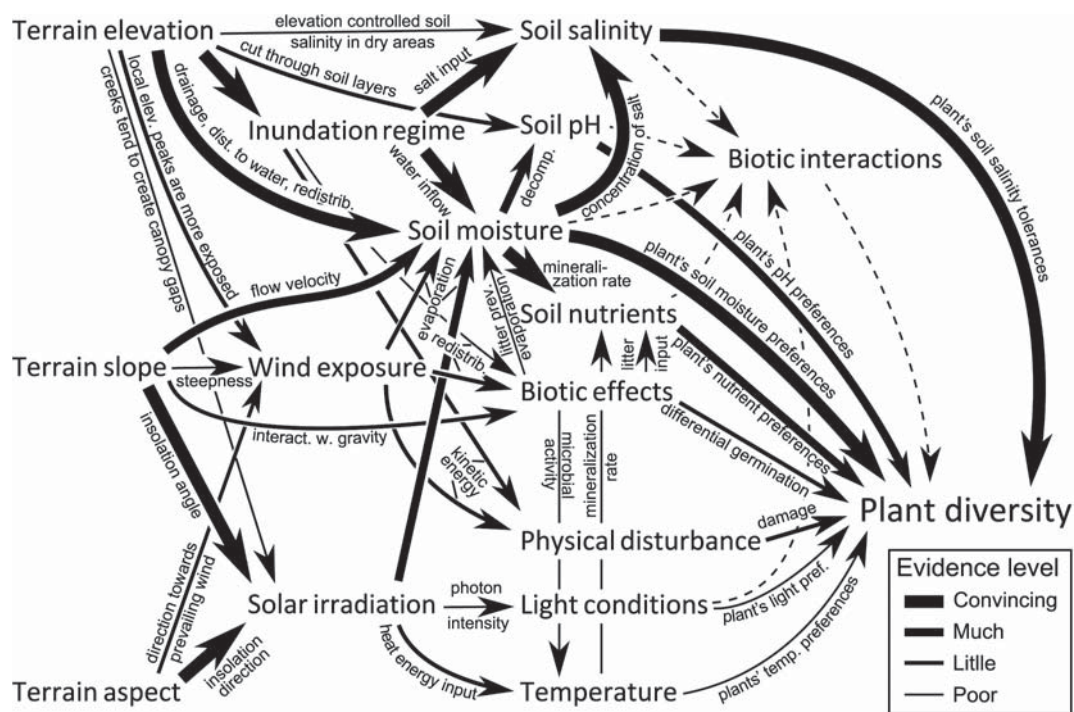


Figure 3. An overview of the mechanisms through which topography (terrain elevation, slope and aspect) influences local plant diversity. The thickness of the connectors represents the strength of the evidence for the mechanism in question based on the literature reviewed here. Dashed lines indicate relationships not reviewed thoroughly here (beyond scope of review) and hence the strength of evidence for these is not evaluated. The diagram is not exhaustive.

are hydrology, incident solar energy, wind exposure, geochemistry, and biotic conditions. As there is a lack of cross-habitat local vegetation studies covering large spatial extents, many of the underlying mechanisms are poorly understood at a general level and so are the interactions between them. From this review, though, it is clear that topographically controlled hydrology is most likely the topographic factor playing the main role in determining local vegetation patterns across a large number of different lowland habitats throughout the world. Topography affects local soil moisture through many more mechanisms than any other factor (Fig. 3) and hydrology has a strong and consistent influence on local plant diversity patterns.

In order to test this postulate and improve our understanding of many of the mechanisms involved in the interplay between topography and local vegetation patterns we believe that future research should focus on 1) comprehensively exploring the role of local topography over large areas and including many different habitats, 2) habitats in which the role of microtopography is poorly understood, 3) integrating relevant functional topographic variables instead of simple topographic measures, and 4) integrating new spatially comprehensive fine-resolution data. These four focal points are elaborated below.

Generality

A common characteristic for studies investigating the role of topography in controlling local plant diversity (including those presented here), is that they concern just one or a few local sites and hence only one habitat type. While these studies provide important insights, differences in the used data, data

collection methods, statistical methods and other factors vary much between them limiting the scope for direct comparisons and hindering the development of a more comprehensive understanding of topography's role and the mechanisms involved. The study by Araya et al. (2011) is an example where the findings from local habitats distanced by thousands of kilometres are concluded to arise by the same underlying mechanisms, consequently improving our understanding of how general a role hydrology plays in structuring local plant communities throughout the world. Studies such as that by Moeslund et al. (unpubl.) exemplify how the inclusion of many different habitats effectively reveals the main and general mechanisms underlying the effects of local topography.

Habitats

To understand the role of topography in structuring local vegetation patterns, future studies need to focus on habitats that are not traditionally recognized as zones in which topography plays a role. As evident from this review relatively little is known about the role of topography in determining local vegetation patterns in semi-dry and dry habitats because much of the evidence in our possession stems from various wetland habitats. As we have exemplified, there is a multitude of different mechanisms through which topography can act and particularly there are numerous mechanisms by which topography can determine the local hydrological patterns. Based on the reviewed literature we consider it highly likely that mechanisms differ between habitats. Notably, we know the mechanisms involved in dry habitats are markedly different from those acting within wetlands and hence especially the role played by topographically controlled incident

solar energy and wind exposure in hydrology dynamics and other factors in semi-dry and dry habitats should receive more attention.

Functional topographic variables

Many of the studies reviewed here analysed the effect of elevation, slope, and/or aspect on local plant diversity, and subsequently then the authors speculated which functional variables were potentially represented by these. However, while such an approach tells us to which degree topography is important for vegetation patterns, it does not effectively reveal the underlying mechanisms. Different approaches need to be taken to enable a comprehensive understanding of which of the functional variables controlled by topography are actually the most important for local vegetation patterns. One such approach involves translating topographic variables into functional variables directly representing topographic effects on wetness (Wilson and Galant 2000), wind (Mikita and Klimánek 2010), and potential incoming solar irradiation (Bennie et al. 2008) and heat (Parker 1988). In doing so, study results will not only tell if topography is important, but also point to which functional factors are controlled by it and reveal their relative importance.

New data types

To be able to satisfy the above research directions, researchers will not only need data in a resolution fine enough to capture relevant variations for the local vegetation; they will also need data covering relatively large areas. Data fulfilling these two criteria are still not available in many countries, but they are indeed in some and their availability is rapidly increasing. During the last ten years, Light Detection and Ranging (LiDAR) based digital terrain models covering large areas (Vierling et al. 2008) have started to appear together with massive amounts of vegetation data in fine resolutions stemming from large national monitoring programs. The amount of data from citizen science databases (Bonney et al. 2009) and biodiversity data portals (Telenius 2011) are also increasing at a high pace. Finally, algorithms enabling scientists to handle these new massive data sets are now becoming available (Danner et al. 2007, Arge et al. 2010, Møhlhave et al. 2010). By taking advantage of these novel possibilities big obstacles have been surmounted for conducting geographically comprehensive studies of the mechanisms underlying topography in structuring local vegetation patterns.

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