



Review article

The role of topographic and soil factors on woody plant encroachment in mountainous rangelands: A mini literature review

Masibonge Gxasheka^{a,b,*}, Christian Sabelo Gajana^b, Phesheya Dlamini^a^a School of Agricultural & Environmental Sciences, Department of Plant Production, Soil Science & Agricultural Engineering, University of Limpopo, Private Bag X1106, Sovenga, 0727, Limpopo, South Africa^b Department of Livestock and Pasture, Faculty of Science and Agriculture, University of Fort Hare, Alice, South Africa

ARTICLE INFO

Keywords:

Mountainous rangelands
Woody plant encroachment
Topographic factors
Soil factors
Slope aspect

ABSTRACT

Mountainous rangelands provide key ecosystem goods and services, particularly for human benefit. In spite of these benefits, mountain grasslands are undergoing extensive land-cover change as a result of woody plant encroachment. However, the influence of topographic and soil factors on woody plant encroachment is complex and has not yet been studied comprehensively. The aim of this review was to establish current knowledge on the influence of topographic and soil factors on woody plant encroachment in mountainous rangelands. To find relevant literature for our study on the impact of topographic and soil factors on woody plant encroachment in mountain rangelands, we conducted a thorough search on ScienceDirect and Google Scholar using various search terms. Initially, we found 27,745 papers. We narrowed down the search to include only 66 papers published in English that directly addressed the research area. The effect of slope aspect and slope position on woody plant encroachment is complex and dynamic, with no universal consensus on their impact. Some studies found higher woody plant encroachment on the cooler slopes, while others found increased woody plant encroachment on the warmer slopes. Slope gradient has a significant impact on woody plant encroachment, with steeper slopes tending to have more woody plant encroachment than gentle slopes. Soil texture and depth are important soil factors affecting woody plant encroachment. Coarse-textured soils promote the growth of woody plants, while fine-textured soils limit it. The effect of soil depth on woody plant encroachment remain unclear and requires further research. Soil moisture availability, soil nutrient content and soil microbial community are influenced by topography, which in turn affect the woody plant growth and distribution. In conclusion, the spread of woody plants in mountainous rangelands is a complex and dynamic process influenced by a range of factors. Further research is needed to fully understand the mechanisms behind these interactions and to develop effective strategies for managing woody plant encroachment in mountainous rangelands.

* Corresponding author. School of Agricultural & Environmental Sciences, Department of Plant Production, Soil Science & Agricultural Engineering, University of Limpopo, Private Bag X1106, Sovenga, 0727, Limpopo, South Africa.

E-mail addresses: masibonge.gxasheka@ul.ac.za, masibonge.gxasheka@gmail.com (M. Gxasheka).

<https://doi.org/10.1016/j.heliyon.2023.e20615>

Received 17 February 2023; Received in revised form 26 August 2023; Accepted 2 October 2023

Available online 12 October 2023

2405-8440/© 2023 Published by Elsevier Ltd.

This is an open access article under the CC BY-NC-ND license

(<http://creativecommons.org/licenses/by-nc-nd/4.0/>).

1. Introduction

Mountainous areas are striking landforms that rise above the surrounding terrain, characterized by their steep slopes, confined peak regions, and substantial differences in elevation [1,2]. These unique ecosystems are the result of various geological processes, and are distinct from other types of landforms such as hills, plateaus, and plains [3,4]. Mountainous areas occupy a substantial portion of the world's land surface, covering approximately 25%. This proportion includes rangelands found in mountainous areas. Mountain rangelands offer breath-taking views but also serve as habitats for an abundant array of plant species [5]. In addition to their ecological significance, mountainous rangelands offer a wealth of benefits to humans. They provide a variety of resources such as food, timber, fresh water, and serve as natural protection against hazards, storage of carbon, as well as recreation and tourism [5–7]. Furthermore, mountainous rangelands offer ample forage for livestock, with more than 360 million cattle and 600 million sheep and goats relying on their high protein and mineral content for sustenance [8,9].

Despite the numerous benefits offered by mountainous rangelands, they are increasingly threatened by the proliferation of native trees and shrubs, a process referred to as woody plant encroachment [10]; Fig. 1). The phenomenon of woody plant encroachment has undergone extensive investigation in arid, semiarid, and sub-humid ecosystems across various regions, including North America (Archer, 1994 [11]; Van Auken, 2000), Australia [12,13], and Africa [14,15]. Within these ecosystems the encroachment of woody plants alters the structure and composition of plant communities, leading to a loss of biodiversity (e.g. grass richness) and change ecosystem processes, such as nutrient cycling and water availability [16–19]. Moreover, the proliferation of woody plants exerts detrimental effects on grazing lands, as these woody plants reduce the availability of forage for livestock [20]. Consequently, this scarcity of grazing resources culminates in issues of overgrazing and soil erosion [21].

Woody plant encroachment is often caused by changes in land management practices such as increased grazing, reduced fire frequency and global factors such as climate change [10,22–24]. Increased grazing reduces the biomass and vigour of the grasses, which reduces their ability to absorb nutrients and moisture from the top soil layers [25,26]. Eventually, grasses lose their competitiveness against established tree/shrub seedlings [27,28]: [17]. Furthermore, increased grazing also results in less grass fuel, which lowers the likelihood and severity of fire incidents and promotes the development of young trees and shrubs into higher, fire-resistant stages more often [29]; Trollope 1983). Climate change also plays a significant role in the encroachment of woody plants, driven by rising temperatures and erratic rainfall patterns. For example, increasing temperatures result in decreased frost-induced tree mortality and shifts in snow melt timing, extending the growing season and promoting woody plant expansion [15,30]. Also, woody plants

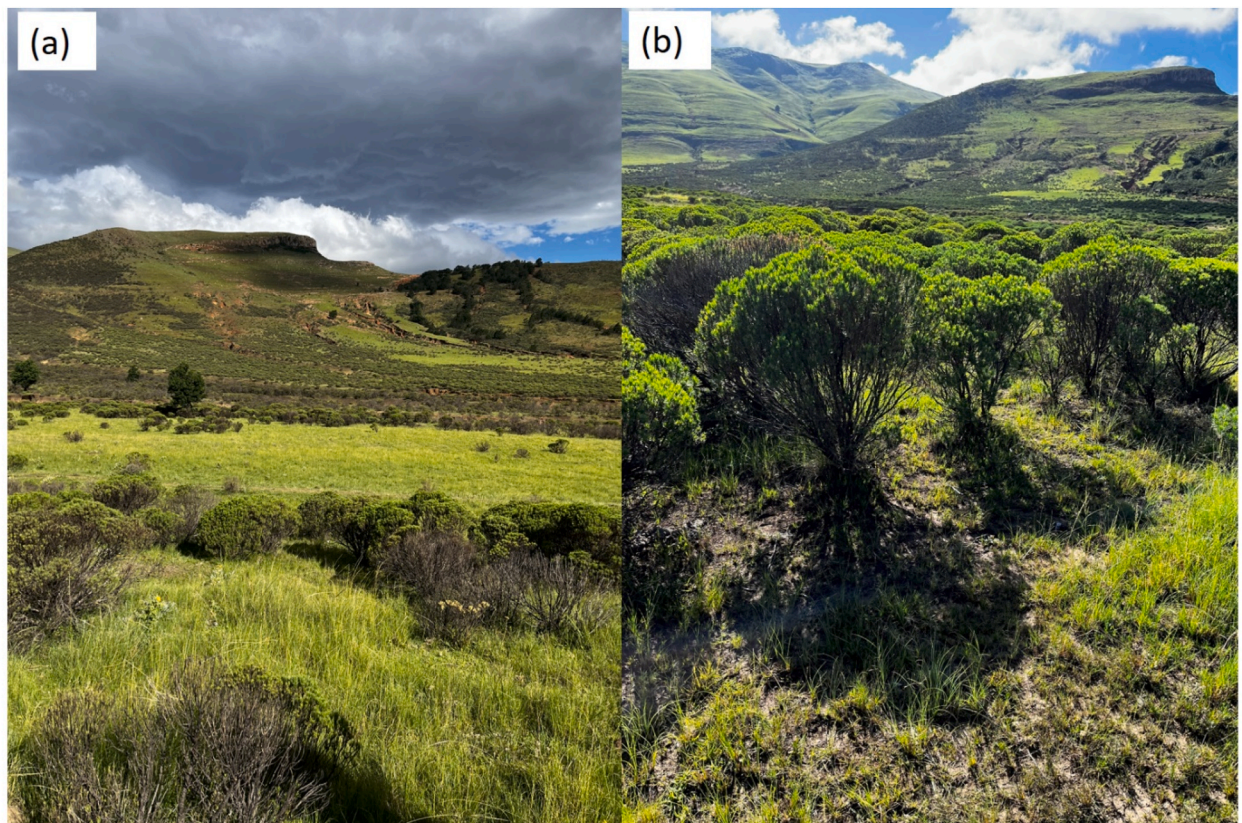


Fig. 1. Typical woody plant encroachment, (a) progression of shrub encroachment and (b) advance shrub encroachment in Mountain Ecosystems. Photo credits: M. Gxasheka.

mitigate the increased transpiration and drought stress caused by warmer temperatures by benefiting from wetter climates and increased water usage efficiency caused by rising atmospheric carbon dioxide [31]: [15]. Additionally, the increased availability of water has been linked to the proliferation of woody plants [15,32,33]. However, woody plant encroachment may also stem from the interaction of these factors with topography [34,35]. Topographic factors such as slope position, aspect, and gradient are considered key due to their influence on land shape, soil properties and microclimate distribution through alterations in precipitation, temperature, and humidity [36–38]. Consequently, topography-induced microclimate variations result in significant changes to soil properties which in turn greatly affects the development and distribution of woody plants [39,40]. The topographic factors influencing woody plant encroachment are complex [35] and have yet to be comprehensively examined. Therefore, a comprehensive understanding of the effects of topography and soil-related factors is essential for comprehending the occurrence of woody plant encroachment. This understanding is pivotal in developing sustainable and adaptable management strategies within mountain rangelands. The remainder of this paper is structured as follows: Section 2 provide an overview of the methodology used in this review. Section 3 examines the impact of topographic factors on woody plant encroachment. Section 4 explores the contribution of soil factors to the encroachment of woody plants along topographic gradients. Finally, Section 5 provides the conclusion.

2. Methodology

To investigate the role of topographic and soil factors in woody plant encroachment on mountainous rangelands, we conducted a thorough search of relevant literature in ScienceDirect and Google Scholar using various combinations of search terms, including “Topography and shrub encroachment,” “Shrub encroachment and mountain rangelands,” “Woody plant expansion and mountainous rangelands,” “Range shift and topography”, “Shrub invasion and topography”, “Range shift and montane rangelands” and “Topography and Soil factors.” The search yielded a significant number of papers, specifically 2745 papers from Science Direct and 29,400 papers from Google Scholar. We narrowed down our search to studies published in English that focused on the relevant topic and assessed the availability of full-text titles and abstracts. Then, we carefully reviewed the full papers of relevant articles and excluded articles that had inaccessible full papers or were not published in English, or did not address the role of topographic and soil factors in woody plant encroachment on mountain rangelands. As a result, we were able to identify only 66 papers that were relevant to our study.

3. Effect of topographic factors on woody plant encroachment

Our review study, which aimed to provide a comprehensive analysis of the role of topographic and soil factors in woody plant encroachment on mountain rangelands was constrained by a limited number of relevant papers, with only 66 studies included in our review. The majority of these studies were conducted in the United States (38%) and China (17%), followed by South Africa (12%) and other countries (33%) (Fig. 2). The studies focused on slope aspect, slope gradient, and elevation as they relate to soil factors that determine the conditions for woody plant growth. In the following sections, we provide a broader view of the topographic influences on woody plant encroachment. Section 3.1 reviews previous works that document the impact of slope aspect on woody plant encroachment, while sections 3.2 and 3.3 review studies on the effects of slope gradient and slope position, respectively.

3.1. Slope aspect

Slope aspect is defined as the orientation of a slope in relation to cardinal points or compass directions [41]. Slope aspect is a key

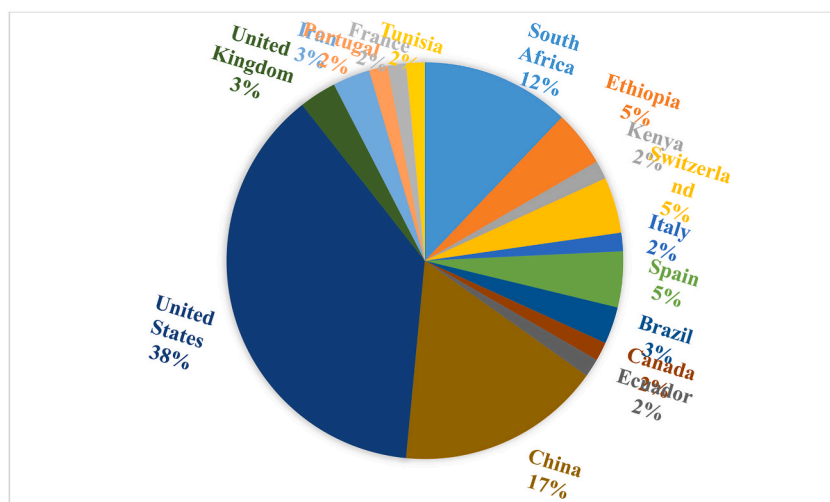


Fig. 2. Geographical distribution of papers included in the study.

topographic component affecting local site microclimate in mountain environments [42–44]. This due to the fact that slope aspect determines the amount of solar radiation received in mountain environments. In fact, solar radiation powers micrometeorological processes (such as soil heat flux and soil temperature), sensible heat flux, surface and air temperatures, wind and turbulent transport, evapotranspiration that gives a certain local microclimate, which in turn affect establishment and growth of plants [45]. In the southern hemisphere, north-facing slopes, which receive the greatest amount of solar radiation, are typically hot, dry and subject to rapid changes in seasonal and diurnal microclimate [42,46]. In contrast, south-facing slopes, which receive the least amount of insolation are cool, moist, and subject to slow changes in seasonal and daily microclimate [42,46]. This contrasts with the conditions in the Northern Hemisphere, where the situation is reversed [47]. For the purposes of this review, we will adopt the terms “warmer slope aspect” or “cooler slope aspect” to account for the differing terminology used for slope aspects in the Southern and Northern hemispheres.

The impacts of slope aspect on woody plant encroachment through changes in density/cover are highly variable and suggest that cooler slopes result in higher shrub encroachment in the mountain rangelands [17,48; Table 1]. In their study on the topographic controls of *Pteronia incana* (Blue bush) in Great fish thicket rangelands in South Africa, Kakembo et al. [49] reported higher shrub density on the cooler slopes. This was attributed to increased moisture availability, land abandonment which created an enabling environment for of *Pteronia* invasion. Similarly [50], studied the taxonomic and functional diversity of woody plant communities on the opposing slopes of inselbergs, found higher abundance of woody plants on the cooler slopes in southern Brazil, mainly as a result of high resource availability. [51] showed that woody plant expansion rates were four times greater on cooler slopes in the United States, mainly associated with plenty of moisture availability. Similarly [52], found increased woody plant encroachment on the cooler slopes in Spain, mainly as a result of the cool temperatures and sufficient moisture available. [53,54,55] also observed increased woody plant cover on the cooler slopes in Spain Switzerland, and China as a result of sufficient moisture and nitrogen deposition. In contrast, Hottman and O'Connor (1999) found 56% greater woody plant cover on the warmer slopes than cooler slopes (32%) in mountain rangelands, South Africa. The authors suggest that hotter and drier conditions favoured the specific encroaching species (such as *Acacia tortilis* and *Maytenus heterophylla*). Additionally, they indicate that the warmer slopes may have coupled with other environmental elements including altitude, overgrazing, and abandoned agricultural fields to influence the amount of woody plants present. Other few studies [56,57], reported decreasing tree density and shrub cover with increasing site exposure in the United States and South Africa, respectively, mainly as a result of less moisture availability over the landscape. Although, some authors found no effect of slope aspect. This was the case, for example of [58]; who studied the spatial and temporal patterns of recent forest encroachment in montane grasslands of the Valles Caldera, USA. They found no effect of slope aspect on the probability of tree invasion in montane grasslands. [59] also assessed landscape factors influencing the abundance and dominance of the invasive plant *potentilla recta* in rangelands of the Blue Mountains ecoregion in the USA, found no effect of slope aspect. Similarly [60,61], found no effect slope aspect on shrub abundance/invasion in Ethiopia and China, respectively.

The examined research shows that the impact of slope aspect on the encroachment of woody plants is complex and varies in different regions and studies. Therefore, extensive empirical research is necessary to better understand how slope aspect affects affect different the life forms of woody plants, including trees, tall shrubs, and dwarf shrubs in mountainous rangelands. For instance, woody plant species with greater drought tolerance and heat resistance may be favoured by warmer slope aspect, where conditions are drier and warmer leading to the observed inconclusive findings in the research. This was confirmed by other research works [64–67], who found that shrub species have tended to establish more readily on warmer slope aspect, which was attributed to the drought-tolerant nature of the shrub species. On the contrary, tree species are often more preferred by cooler slope aspects due to enhanced moisture availability and reduced heat stress [68,69]. This research approach will offer valuable insights into their ecological dynamics of encroaching woody plants in mountainous rangelands.

Table 1
Studies on the effect of slope aspect on woody plant encroachment.

Vegetation type	Climate	Rainfall (mm)	Slope aspect	Effect	Location	Reference
Alpine tundra	Alpine	1400	Cooler(NH)	↑Cover	China	[53]
Pampa	n.d.	1588	Cooler(SH)	↑Density	Brazil	[50]
Grassland and savanna	n.d.	550–730	Warmer(SH)	↑Cover	South Africa	[62]
Grassland	n.d.	430	S.A(NH)	↔Density	United States	[59]
n.d.	n.d.	488	Cooler(SH)	↑Cover	South Africa	[49]
Alpine grasslands	Alpine	1422	Warmer(NH)	↑Cover	Switzerland	[54]
Grassland	Continental	1657	Warmer(NH)	↑Cover	Spain	[52]
Grassland	Sub-arid & sub-humid	500–1000	Warmer(SH)	↓Cover	South Africa	[56]
Sagebrush grassland & Woodland	Semi-arid	300–400	Warmer(NH)	↓Density	United States	[57]
Grassland	Semi-arid & continental	576	S.A(NH)	↔Cover	United States	[58]
Woodland and Shrubland	Desert	200–350	Cooler(NH)	↑Cover	United States	[51]
Forest	n.d.	628	S.A(NH)	↔Cover	Ethiopia	[60]
Grassland and mixed-grass prairie	n.d.	600	Cooler(NH)	↑Cover	Canada	[48]
Grassland	Semi-arid	405	Cooler(NH)	↑Cover	United States	[35]
Semi-desert grassland	Semi-Arid	391	Cooler(NH)	↑Cover	United States	[63]

Note: n.d.; no data, ↑; Increase, ↓; Decrease; ↔; no effect, NH; Northern Hemisphere, SH; Southern Hemisphere.

3.2. Slope gradient

Slope gradient is one of the crucial topographic factor impacting woody plant encroachment in mountainous rangelands. It is a measure of the steepness of a slope, characterized by the maximum rate of change in altitude in relation to the horizontal plane [70, 71]. Numerous research examined the influence of slope gradients focusing on the steepness and gentleness of slopes in mountainous rangelands. The slope steepness regulates the angle between the soil surface and the direction in which rain droplets impact and irradiation occurs [72]. With an increase in slope gradient, soil moisture, soil nutrients, temperature, and infiltration decreased as a result of water runoff compared to gentle slopes [56,73].

The previous experimental studies have yielded contradictory results about the effect of slope gradient on woody plant encroachment. Some of these studies documented that steeper slopes tend to have more woody plant encroachment than gentle slope gradients (Table 2). [74] studied the influence of topography on the colonization of Subalpine grasslands by the thorny cushion dwarf *Echinospartum horridum* in Spain, and found higher woody plant encroachment on a steeper slope gradient. These authors also found high growth rates and lower death rates of the encroaching shrub on steeper slopes than gentle slopes. They suggested that encroachment resulted from less competition between *Echinospartum horridum* shrubs and grasses on steeper slopes than gentle slopes. [52] found approximately 75% of woody plant encroachment occurring on steeper slopes ranging from 15 to 40% under sparse and dense grasslands of Central Pyrenees, Spain. These authors mainly associated encroachment with less anthropogenic activities such as livestock grazing activities and cropping in steeper slope gradients. In northern Ethiopia, Haile et al. (2021) studied the ecological impacts of expansive shrubs, and found increased cover of *Tarchonanthus camphoratus* on steeper slopes, mainly as a result of the ability of the species to grow in a wide range of conditions e.g. savanna, woodland, grassland, on flats, rocky hills, mountain slopes and hillsides, riverbanks on sandy and loamy). Similarly [49], reported a greater density of *Pteronia incana* on steeper slope gradients in communal semi-arid grassland, South Africa. They suggested that deep rooted woody plants tend to outcompete grass species on thin moisture-constrained soils occurring in steeper slopes.

However, others studies [56,77,78] conducted on mountainous grasslands indicated that steeper slope gradients are characterized by shallow soils with low moisture retention compared to soils located in gentle slopes. As a result, these conditions are less favourable for woody plants growth as they slow the rate at which woody plants could encroach the environment [52,79,80]. Similarly, a study conducted by Ref. [59] that investigated landscape factors influencing the abundance and dominance of the invasive plant *potentilla recta* in rangelands of the Blue Mountains ecoregion (USA), found a decrease of *Potentilla recta* dominance as slope increased, and this attributed to less soil moisture available at the steeper slopes. The above reviewed studies showed that slope gradient affects woody plant encroachment. The effect of slope gradient could be considered as a main driver, which regulates the influence of other environmental factors (e.g., slope aspect and soil moisture) in mountainous environments [59]. As a result, the encroaching plants are able to take over the steeper slopes on cooler slope aspects than warmer slope aspects [55]. However, the interactions between the slope gradient and other topographic factors (e.g., slope aspect and elevation) of encroached landscaped are significantly less studied.

3.3. Slope position

The slope position, defined as the relative height on the hillside is another key topographic factor influencing woody plant encroachment [81,82]. It is generally divided into three categories in the current literature: upslope, midslope, and downslope [38, 40]. In mountainous rangelands, slope position regulates the microclimate and the physico-chemical characteristics of the soil, which in turn impacts the growth of woody plants [40,83]. Despite this, little is known about how slope position affects the encroachment of woody plants as some authors report that encroachment is higher on upslope position [48,52,57,58,84–87], while others report higher encroachment on the midslope position [88]; [78] as well as downslope position [53,82,89,90] or no significant changes [76,91–93].

An intensification in woody plant encroachment was observed on upslope positions under diverse environmental conditions (e.g., vegetation types, climate, and rainfall) (Table 3). In particular [86], observed that the upslope position had higher shrub cover (55%)

Table 2
Studies on the effect of slope gradient on woody plant encroachment.

Vegetation type	Climate	Rainfall (mm)	Slope gradient	Effect	Location	Reference
Grassland & savanna	n.d.	550–730	Steep (n.d.)	↑Cover	South Africa	[62]
Savanna	n.d.	646	Steep (23–27°)	↑Density	Kenya	[75]
n.d.	n.d.	488	Steep(>15°)	↑Cover	South Africa	[49]
Grassland	Sub-arid & sub-humid	500–1000	Steep (n.d.)	↑Cover	South Africa	[56]
Alpine grassland	Alpine	1422	Steep(>60%)	↑Cover	Switzerland	[54]
Alpine tundra	Alpine	1400	Steep(n.d.)	↑Cover	China	[53]
Grassland	n.d.	430	Steep (>30%)	↓Density	United States	[59]
Grassland	Continental	1657	Steep (15–40°)	↑Cover	Spain	[52]
Grasslands and forests	n.d.	1500–1600	Steep (14–15°)	↑Cover	Spain	[76]
Alpine & subalpine grassland	Continental	1735	Steep (n.d.)	↑Density	Spain	[74]
Grassland	Semi-arid & continental	576	Steep (15–20°)	↑Cover	United States	[58]
Woodland and Shrubland	Desert	200–350	Gentle(<5°)	↑Cover	United States	[51]
Forest	n.d.	628	Steep (n.d.)	↑Cover	Ethiopia	[60]
Grassland and mixed-grass prairie	n.d.	600	Steep(250–260%)	↑Cover	Canada	[48]

Note: n.d.; no data, ↑; Increase, ↓; Decrease; ↔; no effect.

Table 3
Studies on the effect of slope position on woody plant encroachment.

Vegetation type	Climate	Rainfall (mm)	Slope position	Effect	Location	Reference
Grassland	Semi-arid	630	Midslope	↑ Density	South Africa	[78]
Grassland	Semi-arid	500	Downslope	↑ Density	South Africa	[82]
Grassland	n.d.	593 & 654	Downslope	↑ Density	South Africa	[90]
Grassland	Continental	1657	Upslope	↑ Cover	Spain	[52]
Sagebrush grassland & Woodlands	Semi-arid	300 & 400	Upslope	↑ Density	United States	[57]
Grassland	Semi-arid	392	S.P	↔ Cover	China	[91]
Grasslands and forests	n.d.	1500 & 1600	S.P	↔ Cover	Spain	[76]
Grassland	Semi-arid & continental	576	Upslope	↑ Cover	United States	[58]
Prairie-forest	n.d.	n.d.	Upslope	↑ Density	United States	[84]
Alpine tundra	Alpine	1400	Downslope	↑ Cover	China	[53]
Desert	n.d.	296	Midslope	↑ Cover	United States	[88]
Savanna	n.d.	579 & 618	Upslope	↑ Density	Ethiopia	[87]
Alpine Dwarf-Shrub	n.d.	1400	S.P	↔ Cover	Italy	[93]
n.d.	Semi-arid	500	S.P	↔ Density	Ethiopia	[92]
Savanna	Semi-arid	n.d.	Downslope	↑ Cover	South Africa	[89]
Bluff prairie	n.d.	590	Upslope	↑ Cover	United States	[85]
Grassland	n.d.	119	Upslope	↑ Cover	Ecuador	[86]
Woodland and Shrubland	Desert	200–350	Downslope	↑ Cover	United States	[51]
Alpine meadow grassland	n.d.	415	Downslope	↑ Density	China	[61]
Forest	n.d.	628	Downslope	↑ Cover	Ethiopia	[60]
Grassland and mixed-grass prairie	n.d.	600	Upslope	↑ Cover	Canada	[48]

Note: n.d.; no data, ↑; Increase, ↓; Decrease; ↔; no effect: S.P; Slope position.

at elevations above 3743 m in the Pa'ramo grassland in Ecuador. Similarly [58], conducted a study in semi-arid and continental grasslands and found an increase in tree invasion on the upslope position of the Jemez Mountains, Northern New Mexico. In the semi-arid Sagebrush grassland and Woodlands of the United States, Johnson and Miller (2006) equally reported greater tree density on the upslope position. They attributed differences in tree establishment and development rates to variations in moisture conditions. Other studies, [52,85]; also found an increase of woody plant encroachment on the upslope in Bluff prairie and Alpine Mountain region, respectively. They ascribed the upslope encroachment to the harsh environment that favoured the woody plants and also suggested that grasslands surrounded by woody plant habitats had a tendency to be vulnerable to woody plant encroachment. Likewise, Foster and Collins [84] studied colonization of successional grassland by *Ulmus rubra* Muhl. in relation to landscape position, found higher *Ulmus rubra* encroachment on the upslope of the successional grasslands in north-eastern Kansas, USA. The authors suggest that upslope positions had reduced litter, increased available light, and exposed bare ground that may have provided an opportunity for *Ulmus rubra* encroachment. A recent study by Ref. [87]; studied the effect of elevation on the density and species composition of encroacher woody plants, and found higher encroacher woody plant species on the upslope of Borana Rangeland in Southern Ethiopia. They suggested that the encroachment of woody plants in upslope positions may be influenced by environmental conditions, such as temperature, precipitation, and soil properties.

As a contrast, Masibonge et al. [82] found that shrub density was higher on the downslope position of semi-arid grasslands in South Africa. The authors attributed the encroachment of the shrubs in the downslope landscape position to increased soil moisture condition and accumulation of soil particles as the outcome of runoff water from the upslope positions. [53] investigated topographic influences on vegetation changes in Alpine tundra, China, and found increased woody plant encroachment on the downslope. They suggested that plants with low environmental tolerances could be less likely to invade high alpine zones with harsh environmental circumstances (characterized by frigid temperatures, strong winds, and deficient soil nutrients). In the Rand Highveld grassland of South Africa, Pule et al. [90] similarly noted greater shrub densities on the downslope sites. These authors ascribed the higher shrub density to better soil conditions brought on by surface runoff of nutrients and rainwater from upslope to downslope sites. A recent study of [60] also found higher cover of *Tarchonanthus camphoratus* at downslopes in Ethiopia, attributable to suitability of the species on downslope conditions. While, [88] studied vegetation patterns in relation to slope position, found higher shrub cover on the midslope positions in the castle cliffs area of southern Utah, United States. Similar findings were made by Ref. [78] in the semi-arid region of South Africa, who found that the midslope had higher shrub density than other slopes (i.e., the foot and valley bottom), primarily due to less soil moisture available, which favours the drought-tolerant *Seriphium plumosum*.

However, despite the evidence pointing out the influence of different slope positions on woody plant encroachment [92], and [93] found no significant effect of slope position on woody plant encroachment in Ethiopia and Italy, respectively. [76] also found no significant effect of elevation in the model predicting probability of grassland transition to shrubland or forest. Similarly [94], reported no changes in shrub cover with increasing elevation in Inner Mongolia steppe ecosystem of north China, and this attributable to function of changes in intrinsic soil properties related to texture, bulk density, soil organic carbon, and total nitrogen. Thus, more research on the influence of slope position on woody plant encroachment is needed to broaden our knowledge of woody plants as governed by slope position characteristics such as microclimate and soil factors. Thus, further research on slope position effect on woody plant encroachment is required to broaden our knowledge of woody plants as control by slope position conditions such as microclimate and soil factors.

4. Role of soil factors on woody plant encroachment in along elevational gradient

Soil factors such as texture, depth, moisture, nutrient levels and soil microbial communities are crucial determinants of the distribution and abundance of woody plant species in mountainous rangelands [17,95,96]. Elevational gradient affect these soil conditions, resulting in varying encroachment rates [17,34,97,98]. These soil factors mirror the fundamental effect of topography and define a pattern for woody plant growth and encroachment.

4.1. Soil texture

Soil texture is key soil factor characterized by various mixtures of sand, silt, and clay which makes the particle-size distribution of soils [99]. It is related to modification of infiltration rates, available nutrients and moisture, which may affect distribution of encroaching woody plants [97]. Soil texture varies across the topographic gradient from upslope to downslope. In the upslope, soils are associated with coarse texture that have more sand but low clay content and silt due to soil movement as a result of geomorphic erosion [100–104].

Several studies indicated that coarse textured soil creates a conducive environment for woody plant establishment. These soils allow woody plants access to through flow, facilitating a competitive advantage over grasses [105,106]. According to Ref. [17]; coarse textured soils enable greater water infiltration and nutrient leaching to the subsurface, which favours woody plants. Moreover, coarse-textured soils lose moisture quickly in the top layer of the soil [107], which create a barricade to the conductance and evaporation of water from deeper soil layers [108,109]. This suggests that coarse textured subsoils may benefit deeply rooted woody plants capable of exploiting soil moisture at greater depths.

According to Ref. [101]; soil particles and nutrients are transported from upslope and redeposited downslope by hillslope transport processes. The soils of the downslope are reported to be mostly fine textured with high clay and silt which results in great water retention and soil nutrients [51,78,110]. However, as much as soil texture is a key component of soil property that influences woody plant vegetation, little has been done to determine the effect of soil texture on woody plant encroachment. To date, few research studies have attempted to understand the effect of soil texture on woody plant encroachment. For instance Ref. [111], studied the topography, grazing, and soil textures control over rangelands vegetation in Iran, found that coverage of shrubs increased with increasing sand content but decreased with increasing clay content. These authors attributed to the positive relationship between sand content and elevation. Similar findings about sandy soils were also reported in other landscapes. [97,112] also found more woody plant encroachment on sandy soils than clayey soils in semi-desert grassland and mixed oak-grass savanna, respectively. These authors concluded that coarse -textured/sandy soils leach water and nutrients more rapidly thus favouring trees and shrubs with deeper root systems than fine-textured/clayey soils.

In contrast, a study of [51] found more rapid rates of woodland expansion on finer-textured soils than coarse-textured soils in central Nevada, USA. Similarly [98], reported higher woody plant cover on flat terrain on fine-textured soils compared to coarse-textured soils in the United states, mainly as a result of higher soil moisture and nutrient availability. Despite these findings, other few studies observed reduction of woody plant growth on clayey soils [110,113]. In his research on the habitat preferences of the encroacher shrub (*Seriphium plumosum*) in mountain grasslands in South Africa, Snyman (2012) documented a reduction of the shrub density from middle slope to the valley bottom with the increasing clay content. Similarly [114], found a reduction of Creosote bush cover (*Larrea tridentata*) in areas with high clay concentration compared to areas with low clay content in Mountain grasslands in southern Arizona, USA. The reduction of woody plants development in fine-textured/clayey soils may be owing to the less supply of accessible water for plant growth compared to coarse-textured soils due to greater evaporation [115,116]. Also, once they dry out the remaining small amount of moisture available tends to be more tightly bound to clay particles resulting in the low moisture available for plant growth [106,117,118]. Furthermore [119], suggest that high clay content is linked to high electric conductivity values, which may hinder nutrient absorption and prevent tree establishment and/or survival.

4.2. Soil depth

Pedagogically, soil depth refers to solum depth which comprises the distance between the surface of the soil and the lower boundary of the B horizon soil [120]. Soil depth is one of the most important edaphic factors that affects the woody plant encroachment. It is important because it regulates soil texture, soil moisture and root system, which in turn affect tree growth and survival [121,122]. Soil depth varies with topography, as upslopes have shallow soils while downslopes have deep soils [51,123,124]. The shallow upslope soils are commonly underlain by fractured bedrock, which is established by systems of fractures and fissures, which create a limiting layer for root penetration of woody plants [125,126]. Consistent with the fact stated above, [114]; reported a significant decline of leguminous trees in shallow soil areas of southern Arizona. Similarly [127], in semi-arid to humid subtropical of the United States, found a decline in *P. glandulosa* trees encroachment in shallow soils, associated with inability of the trees to access more water due to the soil limiting layer. However, other studies on various ecosystems (i.e. arid and semi-arid) [128,129] suggested that woody plants can still survive on shallow soils by extending root systems through the fractured bedrock to extract soil moisture and nutrients. Additionally, shallow rooted woody plants such as dwarf shrubs can also survive in shallow soils, provided the soils have good drainage capacity [78,128,130]. This suggests that the effect of shallow soils depends on the adaptability of the woody species along the elevational gradient.

In contrast, downslope soils favour deep rooted woody plants (e.g. trees and tall shrubs) due to their ability to extend the root system into deep soil layers. A study by Ref. [121] in subtropical climate, found that deeply rooted woody plants utilized deeper (>1.5

m) stores of soil water in deep coarse-textured soils, which enhanced their distribution and survival. [78] who studied habitat preferences of the encroacher shrub (*Seriphium plumosum*) in semi-arid grasslands of South Africa, found increased shrub density along deeper soils, linked with decreased waterlogged conditions. While, observed more woody plants on deep soils in coastal prairie and coastal scrub of California coast, United States. From the existing literature, the effect of soil depth on woody plant encroachment is less studied.

4.3. Soil moisture

In arid and semi-arid ecosystems, soil moisture is one of the most critical factors that directly affect woody plant development by limiting the availability of soil nutrients [17,131]. Soil depth and texture affect soil moisture availability, which in turn affects nutrient availability [132]. In mountainous areas, topography influences soil moisture availability, resulting in higher soil moisture on the downslope than on the upslope [61,133,134]. The topographic impact on soil moisture comes as a result of slope position and slope shape, which causes water discharge from upslope and accumulation on downslopes [133–135]. However, soil depth and texture, which affect soil water retention capacity in the downslope, have a substantial impact on soil moisture availability [106,134,136,137]. Because there is a greater probability of moisture availability on the downslope, woody plant development and expansion are encouraged [138]. Although, woody plants compete with herbaceous plants (e.g., grass species) for moisture on the downslope. For example [139], discovered increased competition for water in the downslope between woody and herbaceous plants. To compete with herbaceous plants, woody plants expand their root systems to make use of below-ground moisture supplies supported by deep soils on the downslope [61,133]. Several studies have been conducted to investigate the effect of soil moisture on woody plants along the topography. According to Ref. [133]; woody plants predominate on downslope rather than upslope in water-limited environments due to their ability to absorb below groundwater. [61] discovered a favourable association between shrub abundance and soil moisture in downslope in an Alpine Meadow of Central Tibet. In contrast [78], found low shrub density on semi-arid grassland bottomlands, owing to high soil moisture. According to the findings of the reviewed studies, it is uncertain how soil moisture affects woody plants in mountainous rangelands. As a result, more thorough research is needed to explain the soil moisture dynamics as they relate to topography. This could lead to a better understanding of the impact of soil moisture on the growth and expansion of woody plants along the topography.

4.4. Soil nutrients

Soil nutrients play a key role in the success of growth and distribution of woody vegetation along elevational gradient [119,140,141]. In general, soil nutrient levels show fluctuations with elevation due to various factors such as declining temperatures, increased rainfall, and altered solar radiation [142,143]; and [144]. Some researchers looked at the effects of soil nutrient enrichment on woody plant growth and expansion in different vegetation conditions [145,146]. They discovered that soil nutrient enrichment in the soil could modify mycorrhizal association, resulting in fewer rhizomorphs, fungus structures that transport water and nutrients in exchange for carbohydrates. Similarly [147], investigated the use of ammonium sulphate in the savanna ecosystem for three decades and discovered reduced woody encroachment in terms of tree abundance. So far, little research has been done on the effects of soil nutrients on woody plant vegetation along topography. These research have revealed that soil nutrient content changes depending on topography. For instance, Hook and burke (2000) and [148] found greater C and N pools in bottomlands than uplands in Colorado and Kansas, respectively. Although, Masibonge et al. (2019) found higher organic carbon (OC), phosphorous (P), calcium, and nitrogen (N) contents in uplands than in bottomlands, and Pule et al. (2019) found no effect of slope position on any soil fertility components. Despite these findings, several research has found that woody plant encroachment is declining in nutrient-richer bottomlands. This was a case, for example, of [78]; who observed increased total N, organic C, and extractable P but low shrub density in bottomlands. Collins and Foster (2009) observed a negative relationship between C and N content and elevation, as well as low shrub density. Similarly, Masibonge et al. (2019) discovered lower shrub density but increased soil nutrients in semi-arid grasslands upland. This could imply that nutrient-poor soils sustain more encroachment of woody plants (e.g. shrubs) than nutrient-rich soils. Briefly, present studies highlight the complex relationship between soil nutrients and woody plant encroachment in mountain rangelands, with variations seen in elevation and regions. It is essential for future studies to factor in this variability to fully understand the impact of soil nutrients on woody plant encroachment.

4.5. Soil microbial communities

In mountainous areas, soil microbial communities play a crucial role in soil development and all major elemental cycles affecting plant establishment, growth and survival [96,149,150]. Shifts in soil microbial communities may lead to significant changes in carbon and nutrient cycling in plant-soil systems [151]. In general, lower elevation soils usually have higher organic and nutrients due to erosional process from higher elevation. As a results, the higher organic matter and nutrient content in lower elevation soils promote increased microbial activity [152,153]. This amplified microbial activity generally translates into faster nutrient cycling, which benefits plant growth and potential support woody plant encroachment in the area [154–157]. Despite, the importance of soil microbial communities on woody plant encroachment, the existing literature mostly focused on the influence of woody plant encroachment on soil microbial communities [156,158–160]. These studies documented that as woody plant encroachment increases, it affects the soil microbial communities through shift in the quality and quantity of leaf [161]; Wardle et al., 2004). Therefore, the altering in quality and quantity of litter inputs can shift the dominance of particular microbial groups within the soil [162];

Martínez-García et al., 2018). For example, plant litter with high carbon (C)-to-nitrogen (N) ratios often promotes fungal dominance in soils, due to differences in organismal C/N ratios and C-use efficiencies between bacteria and fungi [162–164], and may also shift bacterial community dominance to oligotrophic groups with slower growth and turnover and higher nutrient use efficiency [165,166]. In addition, the dominant encroaching woody plant could serve as direct determinants of soil microbial communities, because root-associated organisms (e.g., root pathogens and mycorrhizal fungi) are determined by the characteristics and resources of living roots [167,168]. Thus, more future research is required to increase our limited understanding of the role of the soil microbial community in woody plant encroachment along elevation.

5. Conclusion

Woody plant encroachment is a widespread problem that affects mountain rangelands across the world. Overall, our review highlights the crucial role of topography and soil attributes in shaping the encroachment patterns of woody plants, irrespective of the prevailing climatic conditions or vegetation type in mountainous rangelands. This observation stresses the complex and multifaceted nature of the topographic mechanisms linked to the encroachment of woody plants in mountainous landscapes. In particular, slope aspect appears as a prominent driver of woody plant encroachment through influencing solar radiation that changes the local microclimate. This, in turn, induces changes in the local microclimate, such as soil temperature, moisture availability, and evapotranspiration dynamics. Consequently, these changes promote increased woody plant growth and spreading, particularly on cooler slope aspects. The review also highlighted that woody plant encroachment tends to gravitate towards downslope locations, which is facilitated by the existence of favourable soil characteristics such as deep, fine-textured soils, increased moisture availability, and nutritional content. Conversely, it is essential to acknowledge that woody plant encroachment is not limited solely to the cooler slopes and downslope position, as upslope positions and warmer slopes also foster the growth and establishment of species with drought tolerance, such as shrubs. Furthermore, this review highlights the importance of soil-related variables in influencing the pattern of woody plant encroachment along elevation gradients in rangelands ecosystems. Specifically, the availability of adequate soil moisture and nutrient content emerge as primary factors governing the proliferation and spread of woody vegetation in the elevational gradient. As these factors increase at lower elevations, they become important for photosynthesis, transpiration, and contribute to the overall growth of woody plants. However, there are still several critical points that need to be addressed in future research to obtain a more comprehensive understanding of the influence of topography and soil factors on woody plant encroachment in mountainous rangelands. These points encompass various aspects. Firstly, investigating the physiological responses of the specific encroaching woody plant species (i.e. trees and shrubs) in relation to slope aspect and elevation gradient at the local sites is crucial. Secondly, it is imperative to account for the complex relationship between human-caused disturbances and Topo-Edaphic factors including, soil microbial communities. These aspects may unravel the complex mechanisms regulating woody plant encroachment in mountainous rangelands. Furthermore, the associations among all topographic and soil factors, as well as the ecological effects of climate change must be examined in mountainous grasslands.

Authors' contributions

The study was conceived and organized by MG and PD. MG and CSG performed literature search. MG wrote the first draft of the paper; the other authors offered feedback on the earlier drafts. The final manuscript has been read by and approved by all authors.

Ethical approval

Not applicable.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgements

We are grateful to the National Research Foundation (NRF-BAAP) for financing this work under project ref: BAAP200224506520 and grant number: 129426.

References

- [1] V. Kapos, J. Rhind, M. Edwards, M.F. Price, C. Ravilious, in: *Developing a map of the world's mountain forests, Forests in Sustainable Mountain Development: a State of Knowledge Report for 2000*. Task Force on Forests in Sustainable Mountain Development, Cabi Publishing, Wallingford UK, 2000, pp. 4–19. <https://doi.org/10.1079/9780851994468.0004>.
- [2] J. Wang, A. Hu, F. Meng, W. Zhao, Y. Yang, J. Soininen, J. Zhou, Embracing mountain microbiome and ecosystem functions under global change, *New Phytol.* 234 (6) (2022) 1987–2002. <https://doi.org/10.1111/nph.18051>.
- [3] A. Antonelli, W.D. Kissling, S.G. Flantua, M.A. Bermúdez, A. Mulch, A.N. Muellner-Riehl, C. Hoorn, Geological and climatic influences on mountain biodiversity, *Nat. Geosci.* 11 (10) (2018) 718–725. <https://doi.org/10.1038/s41561-018-0236-z>.

- [4] M. Apollo, V. Andreychouk, in: *Mountains, humans and mountaineering adventure tourism*, Mountaineering Adventure Tourism and Local Communities, Edward Elgar Publishing, 2022, pp. 1–26. <https://doi.org/10.4337/9781802209389.00008>.
- [5] L. Joshi, R.M. Shrestha, A.W. Jasra, S. Joshi, H. Gilani, M. Ismail, *Rangeland ecosystem services in the Hindu Kush Himalayan region*, in: *High-altitude Rangelands and Their Interfaces in the Hindu Kush Himalayas*, vol. 157, 2013.
- [6] J.D. Ives, B. Messerli, R.E. Rhoades, *Agenda for Sustainable Mountain Development*. *Mountains of the World: a Global Priority*, 1997, pp. 455–466.
- [7] D.J. Gibson, *Grasses and Grassland Ecology*, Oxford University Press, 2009.
- [8] L. Huntsinger, P. Hopkinson, *Sustaining rangeland landscapes: a social and ecological process*, *Rangeland Ecol. Manag. J. Range Manag. Arch.* 49 (2) (1996) 167–173.
- [9] J.V. Henderson, T. Squires, A. Storeygard, D. Weil, *The global distribution of economic activity: nature, history, and the role of trade*, *Q. J. Econ.* 133 (1) (2018) 357–406. <https://doi.org/10.1093/qje/qjx030>.
- [10] O.W. Van Auken, *Causes and consequences of woody plant encroachment into western North American grasslands*, *J. Environ. Manag.* 90 (10) (2009) 2931–2942. <https://doi.org/10.1016/j.jenvman.2009.04.023>.
- [11] A.K. Knapp, J.M. Briggs, S.L. Collins, S.R. Archer, M.S. Bret-Harte, B.E. Ewers, M.B. Cleary, *Shrub encroachment in North American grasslands: shifts in growth form dominance rapidly alters control of ecosystem carbon inputs*, *Global Change Biol.* 14 (3) (2008) 615–623. <https://doi.org/10.1111/j.1365-2486.2007.01512.x>.
- [12] Jodi N. Price, John W. Morgan, *Woody plant encroachment reduces species richness of herb-rich woodlands in southern Australia*, *Austral Ecol.* 33 (3) (2008) 278–288. <https://doi.org/10.1111/j.1442-9993.2007.01815.x>.
- [13] D.J. Eldridge, S. Soliveres, *Are shrubs really a sign of declining ecosystem function? Disentangling the myths and truths of woody encroachment in Australia*, *Aust. J. Bot.* 62 (7) (2015) 594–608. <https://doi.org/10.1071/BT14137>.
- [14] M. Sankaran, N.P. Hanan, R.J. Scholes, J. Ratnam, D.J. Augustine, B.S. Cade, N. Zambatis, *Determinants of woody cover in African savannas*, *Nature* 438 (7069) (2005) 846–849. <https://doi.org/10.1038/nature04070>.
- [15] Z.S. Venter, M.D. Cramer, H.J. Hawkins, *Drivers of woody plant encroachment over Africa*, *Nat. Commun.* 9 (1) (2018) 2272. <https://doi.org/10.1038/s41467-018-04616-8>.
- [16] D.J. Eldridge, M.A. Bowker, F.T. Maestre, E. Roger, J.F. Reynolds, W.G. Whitford, *Impacts of shrub encroachment on ecosystem structure and functioning: towards a global synthesis*, *Ecol. Lett.* 14 (7) (2011) 709–722. <https://doi.org/10.1111/j.1461-0248.2011.01630.x>.
- [17] S.R. Archer, E.M. Andersen, K.I. Predick, S. Schwinning, R.J. Steidl, S.R. Woods, *Woody plant encroachment: causes and consequences*, *Rangeland Syst.: Process. Manag. Chall.* (2017) 25–84. https://doi.org/10.1007/978-3-319-46709-2_2.
- [18] F.T. Maestre, B.M. Benito, M. Berdugo, L. Concostrina-Zubiri, M. Delgado-Baquerizo, D.J. Eldridge, S. Soliveres, *Biogeography of global drylands*, *New Phytol.* 231 (2) (2021) 540–558. <https://doi.org/10.1111/nph.17395>.
- [19] R. Mogashoa, P. Dlamini, M. Gxasheka, *Grass species richness decreases along a woody plant encroachment gradient in a semi-arid savanna grassland, South Africa*, *Landsc. Ecol.* 36 (2021) 617–636. <https://doi.org/10.1007/s10980-020-01150-1>.
- [20] O.E. Kgosikoma, W. Mojeremane, B.A. Harvie, *Grazing management systems and their effects on Savanna ecosystem dynamics*, *Review* (2013). <https://doi.org/10.5897/JENE2013.0364>.
- [21] P.N. Macharia, W.N. Ekaya, *The impact of rangeland condition and trend to the grazing resources of a semi-arid environment in Kenya*, *J. Hum. Ecol.* 17 (2) (2005) 143–147. <https://doi.org/10.1080/09709274.2005.11905769>.
- [22] S. Archer, *Tree-grass dynamics in a Prosopis-thornscrub savanna parkland: reconstructing the past and predicting the future*, *Ecoscience* 2 (1) (1995) 83–99. <https://doi.org/10.1080/11956860.1995.11682272>.
- [23] W.J. Bond, G.F. Midgley, *Carbon dioxide and the uneasy interactions of trees and savannah grasses*, *Phil. Trans. Biol. Sci.* 367 (1588) (2012) 601–612. <https://doi.org/10.1098/rstb.2011.0182>.
- [24] W.J. Bond, *What limits trees in C4 grasslands and savannas?* *Annu. Rev. Ecol. Evol. Systemat.* 39 (2008) 641–659. <https://doi.org/10.1146/annurev.ecolsys.39.110707.173411>.
- [25] W.T. Knoop, B.H. Walker, *Interactions of woody and herbaceous vegetation in a southern African savanna*, *J. Ecol.* (1985) 235–253. <https://doi.org/10.2307/2259780>.
- [26] A. Mureva, D. Ward, *Spatial patterns of encroaching shrub species under different grazing regimes in a semi-arid savanna, eastern Karoo, South Africa*, *Afr. J. Range Forage Sci.* 33 (2) (2016) 77–89. <https://doi.org/10.2989/10220119.2016.1148775>.
- [27] C. Riginos, *Grass competition suppresses savanna tree growth across multiple demographic stages*, *Ecology* 90 (2) (2009) 335–340. <https://doi.org/10.1890/08-0462.1>.
- [28] D. Ward, K. Wiegand, S. Getzin, *Walter's two-layer hypothesis revisited: back to the roots*, *Oecologia* 172 (2013) 617–630. <https://doi.org/10.1007/s00442-012-2538-y>.
- [29] W.S.W. Trollope, *Controlling bush encroachment with fire in the savanna areas of South Africa*, *Proc. Ann. Congr. Grassland Soc. S. Afr.* 15 (1) (1980) 173–177. <https://doi.org/10.1080/00725560.1980.9648907>.
- [30] I.H. Myers-Smith, B.C. Forbes, M. Wilms, M. Hallinger, T. Lantz, D. Blok, D.S. Hik, *Shrub expansion in tundra ecosystems: dynamics, impacts and research priorities*, *Environ. Res. Lett.* 6 (4) (2011) 045509. <https://doi.org/10.1088/1748-9326/6/4/045509>.
- [31] A.P. Devine, R.A. McDonald, T. Quaife, I.M. Maclean, *Determinants of woody encroachment and cover in African savannas*, *Oecologia* 183 (2017) 939–951. <https://doi.org/10.1007/s00442-017-3807-6>.
- [32] M. Sankaran, J. Ratnam, N. Hanan, *Woody cover in African savannas: the role of resources, fire and herbivory*, *Global Ecol. Biogeogr.* 17 (2) (2008) 236–245. <https://doi.org/10.1111/j.1466-8238.2007.00360.x>.
- [33] A.C. Staver, S. Archibald, S.A. Levin, *The global extent and determinants of savanna and forest as alternative biome states*, *Science* 334 (6053) (2011) 230–232. <https://doi.org/10.1126/science.12104>.
- [34] J.R. McAuliffe, *Landscape evolution, soil formation, and ecological patterns and processes in Sonoran Desert bajadas*, *Ecol. Monogr.* 64 (2) (1994) 111–148. <https://doi.org/10.2307/2937038>.
- [35] S.A. Jones, S.R. Archer, K.A. Hartfield, S.E. Marsh, *Topoedaphic constraints on woody plant cover in a semi-arid grassland*, *Ecol. Indicat.* 151 (2023) 110226. <https://doi.org/10.1016/j.ecolind.2023.110226>.
- [36] S.H.I. Singh, P. R. A., *Understanding the role of slope aspect in shaping the vegetation attributes and soil properties in Montane ecosystems*, *Trop. Ecol.* 59 (3) (2018) 417–430.
- [37] J. Nüchel, P.K. Böcher, J.C. Svenning, *Topographic slope steepness and anthropogenic pressure interact to shape the distribution of tree cover in China*, *Appl. Geogr.* 103 (2019) 40–55. <https://doi.org/10.1016/j.apgeog.2018.12.008>.
- [38] A.A. Agbeshie, S. Abugre, *Soil properties and tree growth performance along a slope of a reclaimed land in the rain forest agroecological zone of Ghana*, *Sci. Afr.* 13 (2021) e00951. <https://doi.org/10.1016/j.sciaf.2021.e00951>.
- [39] C. Fissore, B.J. Dalzell, A.A. Berhe, M. Voegtli, M. Evans, A. Wu, *Influence of topography on soil organic carbon dynamics in a Southern California grassland*, *Catena* 149 (2017) 140–149. <https://doi.org/10.1016/j.catena.2016.09.016>.
- [40] R. Liu, Y. Pan, H. Bao, S. Liang, Y. Jiang, H. Tu, W. Huang, *Variations in soil physico-chemical properties along slope position gradient in secondary vegetation of the hilly region, Guilin, Southwest China*, *Sustainability* 12 (4) (2020) 1303. <https://doi.org/10.3390/su12041303>.
- [41] S.L. Manzello (Ed.), *Encyclopedia of Wildfires and Wildland-Urban Interface (WUI) Fires*, Springer International Publishing, Cham, 2020.
- [42] R.E. Schulze, O.S. McGee, *Climatic indices and classifications in relation to the biogeography of southern Africa*, *Biogeogr. Ecol. S. Afr.* (1978) 19–52.
- [43] S.I. Higgins, D.M. Richardson, R.M. Cowling, T.H. Trinder-Smith, *Predicting the landscape-scale distribution of alien plants and their threat to plant diversity*, *Conserv. Biol.* 13 (2) (1999) 303–313. <https://doi.org/10.1046/j.1523-1739.1999.013002303.x>.
- [44] R.E. Schulze (Ed.), *South African Atlas of Climatology and Agrohydrology*. WRC Report 1489/1/0, Water Research Commission, Pretoria, 2007.

- [45] L. Kumar, A.K. Skidmore, E. Knowles, Modelling topographic variation in solar radiation in a GIS environment, *Int. J. Geogr. Inf. Sci.* 11 (5) (1997) 475–497. <https://doi.org/10.1080/136588197242266>.
- [46] P.G. Holland, D.G. Steyn, Vegetational responses to latitudinal variations in slope angle and aspect, *J. Biogeogr.* (1975) 179–183.
- [47] P. Kutiel, H. Lavee, Effect of slope aspect on soil and vegetation properties along an aridity transect, *Isr. J. Plant Sci.* 47 (3) (1999) 169–178.
- [48] I. Soubry, L. Robinov, T. Chu, X. Guo, Mapping shrub cover in grasslands with an object-based approach and investigating the connection to topo-edaphic factors, *Geocarto Int.* (2022) 1–25. <https://doi.org/10.1080/10106049.2022.2120549>.
- [49] V. Kakembo, K. Rowntree, A.R. Palmer, Topographic controls on the invasion of *Pteronia incana* (Blue bush) onto hillslopes in Ngqushwa (formerly Peddie) district, Eastern Cape, South Africa, *Catena* 70 (2) (2007) 185–199. <https://doi.org/10.1016/j.catena.2006.08.005>.
- [50] M.B. Carlucci, V.A. Bastazini, G.S. Hofmann, J.H. de Macedo, G. Iob, L.D. Duarte, S.C. Müller, Taxonomic and functional diversity of woody plant communities on opposing slopes of inselbergs in southern Brazil, *Plant Ecol. Divers.* 8 (2) (2015) 187–197. <https://doi.org/10.1080/17550874.2014.955544>.
- [51] P.J. Weisberg, E. Lingua, R.B. Pillai, Spatial patterns of pinyon–juniper woodland expansion in central Nevada, *Rangel. Ecol. Manag.* 60 (2) (2007) 115–124. <https://doi.org/10.2111/05-224R2.1>.
- [52] M. Gartzia, C.L. Alados, F. Perez-Cabello, Assessment of the effects of biophysical and anthropogenic factors on woody plant encroachment in dense and sparse mountain grasslands based on remote sensing data, *Prog. Phys. Geogr.* 38 (2) (2014) 201–217. <https://doi.org/10.1177/0309133314524>.
- [53] M. Wu, H.S. He, S. Zong, X. Tan, H. Du, D. Zhao, Y. Liang, Topographic controls on vegetation changes in alpine tundra of the Changbai Mountains, *Forests* 9 (12) (2018) 756. <https://doi.org/10.3390/f9120756>.
- [54] C. Caviezel, M. Hunziker, N.J. Kuhn, Green alder encroachment in the European Alps: the need for analyzing the spread of a native-invasive species across spatial data, *Catena* 159 (2017) 149–158. <https://doi.org/10.1016/j.catena.2017.08.006>.
- [55] E. Bochet, P. García-Payos, J. Poesen, Topographic thresholds for plant colonization on semi-arid eroded slopes, *Earth Surf. Process. Landforms: J. Br. Geomorphol. Res. Group* 34 (13) (2009) 1758–1771. <https://doi.org/10.1002/esp.1860>.
- [56] S. Vetter, W.M. Goqwana, W.J. Bond, W.W. Trollope, Effects of land tenure, geology and topography on vegetation and soils of two grassland types in South Africa, *Afr. J. Range Forage Sci.* 23 (1) (2006) 13–27. <https://doi.org/10.2989/10220110609485883>.
- [57] D.D. Johnson, R.F. Miller, Structure and development of expanding western juniper woodlands as influenced by two topographic variables, *For. Ecol. Manag.* 229 (1–3) (2006) 7–15. <https://doi.org/10.1016/j.foreco.2006.03.008>.
- [58] J.D. Coop, T.J. Givnish, Spatial and temporal patterns of recent forest encroachment in montane grasslands of the Valles Caldera, New Mexico, USA, *J. Biogeogr.* 34 (5) (2007) 914–927. <https://doi.org/10.1111/j.1365-2699.2006.01660.x>.
- [59] B.A. Endress, B.J. Naylor, C.G. Parks, S.R. Radosevich, Landscape factors influencing the abundance and dominance of the invasive plant *Potentilla recta*, *Rangel. Ecol. Manag.* 60 (3) (2007) 218–224. [https://doi.org/10.2111/1551-5028\(2007\)60\[218:LFTAA\]2.0.CO;2](https://doi.org/10.2111/1551-5028(2007)60[218:LFTAA]2.0.CO;2).
- [60] M. Haile, E. Birhane, M.M. Rannestad, M.S. Adaramola, Expansive shrubs: expansion factors and ecological impacts in Northern Ethiopia, *J. Nat. Conserv.* 61 (2021), 125996. <https://doi.org/10.1016/j.jnc.2021.125996>.
- [61] T. Dorji, S.R. Moe, J.A. Klein, Ø. Totland, Plant species richness, evenness, and composition along environmental gradients in an alpine meadow grazing ecosystem in central Tibet, China, *Arctic Antarct. Alpine Res.* 46 (2) (2014) 308–326. <https://doi.org/10.1657/1938-4246-46.2.308>.
- [62] M.T. Hottman, T.G. O'Connor, Vegetation change over 40 years in the Weenen/Muden area, KwaZulu-Natal: evidence from photo-panoramas, *Afr. J. Range Forage Sci.* 16 (2–3) (1999) 71–88. <https://doi.org/10.2989/10220119909485721>.
- [63] J.M. Briggs, H. Schaafsma, D. Trenkov, Woody vegetation expansion in a desert grassland: Prehistoric human impact? *J. Arid Environ.* 69 (3) (2007) 458–472. <https://doi.org/10.1016/j.jaridenv.2006.10.012>.
- [64] E.I. Badano, L.A. Caviezes, M.A. Molina-Montenegro, C.L. Quiroz, Slope aspect influences plant association patterns in the Mediterranean matorral of central Chile, *J. Arid Environ.* 62 (1) (2005) 93–108. <https://doi.org/10.1016/j.jaridenv.2004.10.012>.
- [65] J. Bennie, M.O. Hill, R. Baxter, B. Huntley, Influence of slope and aspect on long-term vegetation change in British chalk grasslands, *J. Ecol.* 94 (2) (2006) 355–368. <https://doi.org/10.1111/j.1365-2745.2006.01104.x>.
- [66] X. Gong, H. Brueck, K.M. Giese, L. Zhang, B. Sattelmacher, S. Lin, Slope aspect has effects on productivity and species composition of hilly grassland in the Xilin River Basin, Inner Mongolia, China, *J. Arid Environ.* 72 (4) (2008) 483–493. <https://doi.org/10.1016/j.jaridenv.2007.07.001>.
- [67] M.A. Fadl, H.M. Al-Yasi, E.A. Alsharif, Impact of elevation and slope aspect on floristic composition in wadi Elkor, Sarawat Mountain, Saudi Arabia, *Sci. Rep.* 11 (1) (2021) 1–10. <https://doi.org/10.1038/s41598-021-95450-4>.
- [68] L.D. Daniels, T.T. Veblen, Spatiotemporal influences of climate on altitudinal treeline in northern Patagonia, *Ecology* 85 (5) (2004) 1284–1296. <https://doi.org/10.1890/03-0092>.
- [69] C.D. Allen, A.K. Macalady, H. Chenchouni, D. Bachelet, N. McDowell, M. Vennetier, N. Cobb, A global overview of drought and heat-induced tree mortality reveals emerging climate change risks for forests, *For. Ecol. Manag.* 259 (4) (2010) 660–684. <https://doi.org/10.1016/j.foreco.2009.09.001>.
- [70] C.D. Tomlin, *Geographic Information Systems and Cartographic Modeling*, vol. 249, Prentice Hall, Englewood Cliffs, NJ, 1990.
- [71] M. Li, H. McGrath, E. Stefanakis, Multi-resolution topographic analysis in hexagonal discrete global grid systems, *Int. J. Appl. Earth Obs. Geoinf.* 113 (2022), 102985. <https://doi.org/10.1016/j.jag.2022.102985>.
- [72] X. Zhou, T. Ke, S. Li, S. Deng, X. An, X. Ma, L. Chen, Induced biological soil crusts and soil properties varied between slope aspect, slope gradient and plant canopy in the Hobq desert of China, *Catena* 190 (2020), 104559. <https://doi.org/10.1016/j.catena.2020.104559>.
- [73] N.V. Birch, A.M. Avis, A.R. Palmer, The effect of land-use on the vegetation communities along a topo-moisture gradient in the mid-Fish River valley, South Africa, *Afr. J. Range Forage Sci.* 16 (1) (1999) 1–8. <https://doi.org/10.2989/10220119909485712>.
- [74] B. Komac, C.L. Alados, J.J. Camarero, Influence of topography on the colonization of subalpine grasslands by the thorny cushion dwarf *Echinopartum horridum*, *Arctic Antarct. Alpine Res.* 43 (4) (2011) 601–611. <https://doi.org/10.1657/1938-4246-43.4.601>.
- [75] P.M. Mutuku, D. Kenfack, Effect of local topographic heterogeneity on tree species assembly in an Acacia-dominated African savanna, *J. Trop. Ecol.* 35 (2) (2019) 46–56. <https://doi.org/10.1017/S0266467419000014>.
- [76] Y. Sanjuán, J. Arnáez, S. Beguería, N. Lana-Renault, T. Lasanta, A. Gómez-Villar, J.M. García-Ruiz, Woody plant encroachment following grazing abandonment in the subalpine belt: a case study in northern Spain, *Reg. Environ. Change* 18 (2018) 1103–1115. <https://doi.org/10.1007/s10113-017-1245-y>.
- [77] A. Gómez-Plaza, M. Martínez-Mena, J. Albaladejo, V.M. Castillo, Factors regulating spatial distribution of soil water content in small semiarid catchments, *J. Hydrol.* 253 (1–4) (2001) 211–226. [https://doi.org/10.1016/S0022-1694\(01\)00483-8](https://doi.org/10.1016/S0022-1694(01)00483-8).
- [78] H.A. Snyman, Habitat preferences of the encroacher shrub, *Seriphium plumosum*, *South Afr. J. Bot.* 81 (2012) 34–39. <https://doi.org/10.1016/j.sajb.2012.05.001>.
- [79] M. Gellrich, P. Baur, B. Koch, N.E. Zimmermann, Agricultural land abandonment and natural forest re-growth in the Swiss mountains: a spatially explicit economic analysis, *Agric. Ecosyst. Environ.* 118 (1–4) (2007) 93–108. <https://doi.org/10.1016/j.agee.2006.05.001>.
- [80] M.N. Youcefi, M.D. Bouhoun, A. Kemassi, M.D.O. El-Hadj, Relationship between topography and the distribution of matorral plant species in the Saharan Atlas: case of Djebel Amour, Algeria, *Acta Ecol. Sin.* 40 (3) (2020) 237–246. <https://doi.org/10.1016/j.chnaes.2019.05.010>.
- [81] M. Méndez-Toribio, J.A. Meave, I. Zermeño-Hernández, G. Ibarra-Manríquez, Effects of slope aspect and topographic position on environmental variables, disturbance regime and tree community attributes in a seasonal tropical dry forest, *J. Veg. Sci.* 27 (6) (2016) 1094–1103. <https://doi.org/10.1111/jvs.12455>.
- [82] G. Masibonge, S. Tefera, L. Mota, Invasion of *Euryops floribundus* in degraded South African communal grassland: unpacking the invasion relationship with elevation, soil properties, the quality and quantity of the herbaceous layer, *Afr. J. Ecol.* 58 (1) (2020) 69–79. <https://doi.org/10.1111/aje.12642>.
- [83] M. Häusser, S. Szymczak, E. Garel, S. Santoni, F. Huneau, A. Bräuning, Growth variability of two native pine species on Corsica as a function of elevation, *Dendrochronologia* 54 (2019) 49–55.
- [84] B.L. Foster, C.D. Collins, Colonization of successional grassland by *Ulmus rubra* Muhl. in relation to landscape position, habitat productivity, and proximity to seed source, *J. Torrey Bot. Soc.* 136 (3) (2009) 392–402. <https://doi.org/10.3159/08-RA-120.1>.
- [85] A.M. Pierce, P.B. Reich, The effects of eastern red cedar (*Juniperus virginiana*) invasion and removal on a dry bluff prairie ecosystem, *Biol. Invasions* 12 (2010) 241–252. <https://doi.org/10.1007/s10530-009-9446-z>.

- [86] E. Matson, D. Bart, Interactions among fire legacies, grazing and topography predict shrub encroachment in post-agricultural páramo, *Landsc. Ecol.* 28 (2013) 1829–1840. <https://doi.org/10.1007/s10980-013-9926-5>.
- [87] Z. Bora, A. Angassa, Y. Wang, X. Xu, Y. You, Effect of elevation on the density and species composition of encroacher woody plants in Borana rangeland, southern Ethiopia, *Environ. Manag.* 67 (2021) 1075–1087. <https://doi.org/10.1007/s00267-021-01458-x>.
- [88] J.D. Brotherson, W.J. Masslich, Vegetation patterns in relation to slope position in the Castle Cliffs area of southern Utah, *Great Basin Nat.* (1985) 535–541.
- [89] C. Munyati, N.I. Sinthumule, Change in woody cover at representative sites in the Kruger National Park, South Africa, based on historical imagery, *SpringerPlus* 5 (2016) 1–23. <https://doi.org/10.1186/s40064-016-3036-1>.
- [90] H.T. Pule, J.T. Tjelele, M.J. Tedder, The effects of abiotic factors in South African semi-arid grassland communities on *Seriphium plumosum* L density and canopy size, *PLoS One* 13 (8) (2018), e0202809. <https://doi.org/10.1371/journal.pone.0202809>.
- [91] X.Y. Li, S.Y. Zhang, H.Y. Peng, X. Hu, Y.J. Ma, Soil water and temperature dynamics in shrub-encroached grasslands and climatic implications: results from Inner Mongolia steppe ecosystem of north China, *Agric. For. Meteorol.* 171 (2013) 20–30. <https://doi.org/10.1016/j.agrformet.2012.11.001>.
- [92] A. Angassa, Vegetation responses to site, elevation and land use in semi-arid rangeland of southern Ethiopia, *Afr. J. Agric. Res.* 11 (5) (2016) 379–391. <https://doi.org/10.5897/AJAR2014.9025>.
- [93] F. Boscutti, V. Casolo, P. Beraldo, E. Braidot, M. Zancani, C. Rixen, Shrub growth and plant diversity along an elevation gradient: evidence of indirect effects of climate on alpine ecosystems, *PLoS One* 13 (4) (2018), e0196653. <https://doi.org/10.1371/journal.pone.0196653>.
- [94] J. Li, Z. Shen, C. Li, Y. Kou, Y. Wang, B. Tu, X. Li, Stair-step pattern of soil bacterial diversity mainly driven by pH and vegetation types along the elevational gradients of Gongga Mountain, China, *Front. Microbiol.* 9 (2018) 569.
- [95] A. Nunes, M. Köbel, P. Pinho, P. Matos, E.A. Costantini, C. Soares, C. Branquinho, Local topographic and edaphic factors largely predict shrub encroachment in Mediterranean drylands, *Sci. Total Environ.* 657 (2019) 310–318. <https://doi.org/10.1016/j.scitotenv.2018.11.475>.
- [96] H. Feng, Z. Wang, P. Jia, J. Gai, B. Chen, S. Wang, Diversity and distribution of CO₂-fixing microbial community along elevation gradients in meadow soils on the Tibetan Plateau, *Sci. Rep.* 12 (1) (2022) 9621.
- [97] D.M. Browning, S.R. Archer, G.P. Asner, M.P. McClaran, C.A. Wessman, Woody plants in grasslands: post-encroachment stand dynamics, *Ecol. Appl.* 18 (4) (2008) 928–944. <https://doi.org/10.1890/07-1559.1>.
- [98] R.N. Addington, B.O. Knapp, G.G. Sorrell, M.L. Elmore, G.G. Wang, J.L. Walker, Factors affecting broadleaf woody vegetation in upland pine forests managed for longleaf pine restoration, *For. Ecol. Manag.* 354 (2015) 130–138. <https://doi.org/10.1016/j.foreco.2015.06.028>.
- [99] G.W. Gee, D. Or, 2.4 Particle-size analysis, *Methods Soil Anal.: Part 4 Phys. Methods* 5 (2002) 255–293. <https://doi.org/10.2136/sssabookser5.4.c12>.
- [100] E.T.F. Witkowski, T.G. O'connor, Topo-edaphic, floristic and physiognomic gradients of woody plants in a semi-arid African savanna woodland, *Vegetatio* 124 (1996) 9–23.
- [101] N.A. Rosenbloom, S.C. Doney, D.S. Schimel, Geomorphic evolution of soil texture and organic matter in eroding landscapes, *Global Biogeochem. Cycles* 15 (2) (2001) 365–381. <https://doi.org/10.1029/1999GB001251>.
- [102] P.B. Hook, I.C. Burke, Biogeochemistry in a shortgrass landscape: control by topography, soil texture, and microclimate, *Ecology* 81 (10) (2000) 2686–2703. [https://doi.org/10.1890/0012-9658\(2000\)081\[2686:BIASLC\]2.0.CO;2](https://doi.org/10.1890/0012-9658(2000)081[2686:BIASLC]2.0.CO;2).
- [103] X.B. Wu, S.R. Archer, Scale-dependent influence of topography-based hydrologic features on patterns of woody plant encroachment in savanna landscapes, *Landsc. Ecol.* 20 (2005) 733–742. <https://doi.org/10.1007/s10980-005-0996-x>.
- [104] C.W. Wheeler, S.R. Archer, G.P. Asner, C.R. McMurtry, Climatic/edaphic controls on soil carbon/nitrogen response to shrub encroachment in desert grassland, *Ecol. Appl.* 17 (7) (2007) 1911–1928. <https://doi.org/10.1890/06-1580.1>.
- [105] R.J. Scholes, S.R. Archer, Tree-grass interactions in savannas, *Annu. Rev. Ecol. Systemat.* 28 (1) (1997) 517–544. <https://doi.org/10.1146/annurev.ecolsys.28.1.517>.
- [106] M.S. Colgan, G.P. Asner, S.R. Levick, R.E. Martin, O.A. Chadwick, Topo-edaphic controls over woody plant biomass in South African savannas, *Biogeosciences* 9 (5) (2012) 1809–1821. <https://doi.org/10.5194/bg-9-1809-2012>.
- [107] L.M. Shown, F.A. Miller, Sagebrush conversion to grassland as affected by precipitation, soil, and cultural practices, *Rangeland Ecol. Manag. J. Range Manag. Arch.* 22 (5) (1969) 303–311.
- [108] H.U. Alizai, L.C. Hulbert, Effects of soil texture on evaporative loss and available water in semi-arid climates, *Soil Sci.* 110 (5) (1970) 328–332.
- [109] S.K. Jalota, S.S. Prihar, Effects of atmospheric evaporativity, soil type and redistribution time on evaporation from bare soil, *Soil Res.* 24 (3) (1986) 357–366. <https://doi.org/10.1071/SR9860357>.
- [110] D.R. Lane, D.P. Coffin, W.K. Lauenroth, Effects of soil texture and precipitation on above-ground net primary productivity and vegetation structure across the Central Grassland region of the United States, *J. Veg. Sci.* 9 (2) (1998) 239–250. <https://doi.org/10.2307/3237123>.
- [111] A. Sanaei, M. Li, A. Ali, Topography, grazing, and soil textures control over rangelands' vegetation quantity and quality, *Sci. Total Environ.* 697 (2019) 134153. <https://doi.org/10.1016/j.scitotenv.2019.134153>.
- [112] D.A. Robinson, I. Lebron, J.I. Querejeta, Determining soil–tree–grass relationships in a California oak savanna using eco-geophysics, *Vadose Zone J* 9 (3) (2010) 528–536. <https://doi.org/10.2136/vzj2009.0041>.
- [113] C.R. Axelsson, N.P. Hanan, Patterns in woody vegetation structure across African savannas, *Biogeosciences* 14 (13) (2017) 3239–3252. <https://doi.org/10.5194/bg-14-3239-2017>.
- [114] S.M. Munson, T.T. Sankey, G. Xian, M.L. Villarreal, C.G. Homer, Decadal shifts in grass and woody plant cover are driven by prolonged drying and modified by topo-edaphic properties, *Ecol. Appl.* 26 (8) (2016) 2480–2494. <https://doi.org/10.1002/eap.1389>.
- [115] O.E. Sala, W.J. Parton, L.A. Joyce, W.K. Lauenroth, Primary production of the central grassland region of the United States, *Ecology* 69 (1) (1988) 40–45. <https://doi.org/10.2307/1943158>.
- [116] A. Yusefi, A. Farrokhan Firouzi, M. Aminzadeh, The effects of shallow saline groundwater on evaporation, soil moisture, and temperature distribution in the presence of straw mulch, *Nord. Hydrol.* 51 (4) (2020) 720–738. <https://doi.org/10.2166/nh.2020.010>.
- [117] R.J. Fensham, R.J. Fairfax, Drought-related tree death of savanna eucalypts: species susceptibility, soil conditions and root architecture, *J. Veg. Sci.* 18 (1) (2007) 71–80. <https://doi.org/10.1111/j.1654-1103.2007.tb02517.x>.
- [118] R.J. Fensham, D.W. Butler, J. Foley, How does clay constrain woody biomass in drylands? *Global Ecol. Biogeogr.* 24 (8) (2015) 950–958. <https://doi.org/10.1111/geb.12319>.
- [119] S. Grellier, N. Florsch, J.L. Janeau, P. Podwojewski, C. Camerlynck, S. Barot, S. Lorentz, Soil clay influences Acacia encroachment in a South African grassland, *Ecohydrology* 7 (6) (2014) 1474–1484. <https://doi.org/10.1002/eco.1472>.
- [120] K.T. Osman, *Management of Soil Problems*, Springer, 2018.
- [121] A.J. Midwood, T.W. Boutton, S.R. Archer, S.E. Watts, Water use by woody plants on contrasting soils in a savanna parkland: assessment with $\delta^{2}\text{H}$ and $\delta^{18}\text{O}$, *Plant Soil* 205 (1998) 13–24.
- [122] V. Acácio, M. Holmgren, F. Moreira, G.M. Mohren, Oak persistence in Mediterranean landscapes: the combined role of management, topography, and wildfires, *Ecol. Soc.* 15 (4) (2010).
- [123] J.B. Nippert, T.W. Ocheltree, G.L. Orozco, Z. Ratajczak, B. Ling, A.M. Skibbe, Evidence of physiological decoupling from grassland ecosystem drivers by an encroaching woody shrub, *PLoS One* 8 (12) (2013), e81630. <https://doi.org/10.1371/journal.pone.0081630>.
- [124] N. Rajakaruna, R.S. Boyd, Edaphic Factor, Editor(s): Sven Erik Jørgensen, Brian D. Fath, *Encyclopedia of Ecology*, Academic Press, 2008, pp. 1201–1207.
- [125] S.A. Stothoff, D. Or, D.P. Groeneveld, S.B. Jones, The effect of vegetation on infiltration in shallow soils underlain by fissured bedrock, *J. Hydrol.* 218 (3–4) (1999) 169–190. [https://doi.org/10.1016/S0022-1694\(99\)00038-4](https://doi.org/10.1016/S0022-1694(99)00038-4).
- [126] Y. Nie, H. Chen, Y. Ding, J. Yang, K. Wang, Comparison of rooting strategies to explore rock fractures for shallow soil-adapted tree species with contrasting aboveground growth rates: a greenhouse microcosm experiment, *Front. Plant Sci.* 8 (2017) 1651. <https://doi.org/10.3389/fpls.2017.01651>.
- [127] K.D. Eggemeyer, S. Schwinning, Biogeography of woody encroachment: why is mesquite excluded from shallow soils? *Ecology: Ecosyst. Land Water Process Interact. Ecohydrogeomorphol.* 2 (1) (2009) 81–87. <https://doi.org/10.1002/eco.42>.

- [128] H.J. Schenk, Soil depth, plant rooting strategies and species' niches, *New Phytol.* 178 (2) (2008) 223–225. <https://doi.org/10.1111/j.1469-8137.2008.02427.x>.
- [129] W. Nijland, M. Van der Meijde, E.A. Addink, S.M. De Jong, Detection of soil moisture and vegetation water abstraction in a Mediterranean natural area using electrical resistivity tomography, *Catena* 81 (3) (2010) 209–216. <https://doi.org/10.1016/j.catena.2010.03.005>.
- [130] H.J. Schenk, R.B. Jackson, Rooting depths, lateral root spreads and below-ground/above-ground allometries of plants in water-limited ecosystems, *J. Ecol.* (2002) 480–494.
- [131] M.L. Britz, *The Effects of Soil Type and Management Strategy on Vegetation Structure and Function in a Semi-arid Savanna, South Africa* (Masters Dissertation, Stellenbosch University, Stellenbosch, 2004).
- [132] R.W. Wernerehl, T.J. Givnish, Relative roles of soil moisture, nutrient supply, depth, and mechanical impedance in determining composition and structure of Wisconsin prairies, *PLoS One* 10 (9) (2015), e0137963. <https://doi.org/10.1371/journal.pone.0137963>.
- [133] Y. Kim, E.A. Eltahir, Role of topography in facilitating coexistence of trees and grasses within savannas, *Water Resour. Res.* 40 (7) (2004). <https://doi.org/10.1029/2003WR002578>.
- [134] Z.Q. Yuan, C. Fang, R. Zhang, F.M. Li, M.M. Javid, I.A. Janssens, Topographic influences on soil properties and aboveground biomass in lucerne-rich vegetation in a semi-arid environment, *Geoderma* 344 (2019) 137–143. <https://doi.org/10.1016/j.geoderma.2019.03.003>.
- [135] V.J. Loeffers, P.A. Larkin-Loeffers, Slope, aspect, and slope position as factors controlling grassland communities in the coulees of the Oldman River, Alberta, *Can. J. Bot.* 65 (7) (1987) 1371–1378. <https://doi.org/10.1139/b87-189>.
- [136] L.J. Geroy, M.M. Gribb, H.P. Marshall, D.G. Chandler, S.G. Benner, J.P. McNamara, Aspect influences on soil water retention and storage, *Hydrol. Process.* 25 (25) (2011) 3836–3842. <https://doi.org/10.1002/hyp.8281>.
- [137] S.F. Dymond, J.B. Bradford, P.V. Bolstad, R.K. Kolka, S.D. Besteyten, T.M. DeSutter, Topographic, edaphic, and vegetative controls on plant-available water, *Ecology* 10 (8) (2017), e1897. <https://doi.org/10.1002/eco.1897>.
- [138] K.L. Black (Masters Dissertation), *Influence of topography and moisture and nutrient availability on green alder function on the low arctic tundra*, Wilfrid Laurier University, NT, Canada, 2017.
- [139] D.R. Rossatto, L.C.R. Silva, L.S.L. Sternberg, A.C. Franco, Do woody and herbaceous species compete for soil water across topographic gradients? Evidence for niche partitioning in a Neotropical savanna, *South Afr. J. Bot.* 91 (2014) 14–18. <https://doi.org/10.1016/j.sajb.2013.11.011>.
- [140] M.L. Britz, D. Ward, *The effects of soil conditions and grazing strategy on plant species composition in a semi-arid savanna*, *Afr. J. Range Forage Sci.* 24 (2) (2007) 51–61.
- [141] F.S. Chapin, P.A. Matson, P.M. Vitousek, F.S. Chapin, P.A. Matson, P.M. Vitousek, Nutrient cycling, *Princ. Terrestrial Ecosyst. Ecol.* (2011) 259–296.
- [142] D. Badía, A. Ruiu, A. Girona, C. Martí, J. Casanova, P. Ibarra, R. Zufiaurre, The influence of elevation on soil properties and forest litter in the siliceous Moncayo Massif, SW Europe, *J. Mt. Sci.* 13 (12) (2016). <https://doi.org/10.1007/s11629-015-3773-6>.
- [143] S. Drollinger, M. Müller, T. Kobl, N. Schwab, J. Böhner, U. Schickhoff, T. Scholten, Decreasing nutrient concentrations in soils and trees with increasing elevation across a treeline ecotone in Rolwaling Himal, Nepal, *J. Mt. Sci.* 14 (2017) 843–858. <https://doi.org/10.1007/s11629-016-4228-4>.
- [144] J. Garcia-Pausas, J. Romanya, F. Montané, A.I. Rios, M. Tauli, P. Rovira, P. Casals, Are Soil Carbon Stocks in Mountain Grasslands Compromised by Land-Use Changes? *High Mountain Conservation in a Changing World*, 2017, pp. 207–230.
- [145] H. Wallander, J.E. Nylund, Effects of excess nitrogen and phosphorus starvation on the extramatrical mycelium of ectomycorrhizas of *Pinus sylvestris* L., *New Phytol.* 120 (4) (1992) 495–503. <https://doi.org/10.1111/j.1469-8137.1992.tb01798.x>.
- [146] A. Gessler, M. Schaub, N.G. McDowell, The role of nutrients in drought-induced tree mortality and recovery, *New Phytol.* 214 (2) (2017) 513–520. <https://doi.org/10.1111/nph.14340>.
- [147] A.J. Mills, A.V. Milewski, D. Snyman, J.J. Jordaan, Effects of anabolic and catabolic nutrients on woody plant encroachment after long-term experimental fertilization in a South African savanna, *PLoS One* 12 (6) (2017), e0179848. <https://doi.org/10.1371/journal.pone.0179848>.
- [148] C.D. Collins, B.L. Foster, The role of topography and soil characteristics in the relationship between species richness and primary productivity in a Kansas grassland, *Trans. Kans. Acad. Sci.* 111 (1) (2008) 105–117. [https://doi.org/10.1660/0022-8443\(2008\)111\[105:TROTAS\]2.0.CO;2](https://doi.org/10.1660/0022-8443(2008)111[105:TROTAS]2.0.CO;2).
- [149] J. Donhauser, B. Frey, Alpine soil microbial ecology in a changing world, *FEMS Microbiol. Ecol.* 94 (9) (2018), fiy099. <https://doi.org/10.1093/femsec/fiy099>.
- [150] Mingze Tang, Lin Li, Xiaolong Wang, Jian You, Jiangnan Li, Chen Xia, Elevational is the main factor controlling the soil microbial community structure in alpine tundra of the Changbai Mountain, *Sci. Rep.* 10 (1) (2020) 12442. <https://doi.org/10.1038/s41598-020-69441-w>.
- [151] Q. Tian, Y. Jiang, Y. Tang, Y. Wu, Z. Tang, F. Liu, Soil pH and organic carbon properties drive soil bacterial communities in surface and deep layers along an elevational gradient, *Front. Microbiol.* 12 (2021) 646124. <https://doi.org/10.3389/fmicb.2021.646124>.
- [152] J. Garcia-Pausas, P. Casals, L. Camarero, C. Huguet, M.T. Sebastia, R. Thompson, J. Romanya, Soil organic carbon storage in mountain grasslands of the Pyrenees: effects of climate and topography, *Biogeochemistry* 82 (2007) 279–289. <https://doi.org/10.1007/s10533-007-9071-9>.
- [153] A. Gutiérrez-Girón, E. Díaz-Pinés, A. Rubio, R.G. Gavilán, Both altitude and vegetation affect temperature sensitivity of soil organic matter decomposition in Mediterranean high mountain soils, *Geoderma* 237 (2015) 1–8. <https://doi.org/10.1016/j.geoderma.2014.08.005>.
- [154] E.B. Hollister, C.W. Schadt, A.V. Palumbo, R.J. Ansley, T.W. Boutton, Structural and functional diversity of soil bacterial and fungal communities following woody plant encroachment in the southern Great Plains, *Soil Biol. Biochem.* 42 (10) (2010) 1816–1824. <https://doi.org/10.1016/j.soilbio.2010.06.022>.
- [155] L. Zhou, H. Li, H. Shen, Y. Xu, Y. Wang, A. Xing, J. Fang, Shrub-encroachment induced alterations in input chemistry and soil microbial community affect topsoil organic carbon in an Inner Mongolian grassland, *Biogeochemistry* 136 (2017) 311–324. <https://doi.org/10.1007/s10533-017-0396-8>.
- [156] H. Li, J. Zhang, H. Hu, L. Chen, Y. Zhu, H. Shen, J. Fang, Shift in soil microbial communities with shrub encroachment in Inner Mongolia grasslands, China, *Eur. J. Soil Biol.* 79 (2017) 40–47. <https://doi.org/10.1016/j.ejsobi.2017.02.004>.
- [157] S. Semeraro, A. Kergunteuil, S. Sánchez-Moreno, J. Puissant, T. Goodall, R. Griffiths, S. Rasmann, Relative contribution of high and low elevation soil microbes and nematodes to ecosystem functioning, *Funct. Ecol.* 36 (4) (2022) 974–986. <https://doi.org/10.1111/1365-2435.14002>.
- [158] A. Fterich, M. Mahdhi, M. Mars, Impact of grazing on soil microbial communities along a chronosequence of *Acacia tortilis* subsp. *raddiana* in arid soils in Tunisia, *Eur. J. Soil Biol.* 50 (2012) 56–63. <https://doi.org/10.1016/j.ejsobi.2011.12.002>.
- [159] O. Grau, K. Saravesi, J.M. Ninot, J. Geml, A. Markkola, S.H. Ahonen, J. Penuelas, Encroachment of shrubs into subalpine grasslands in the Pyrenees modifies the structure of soil fungal communities and soil properties, *FEMS (Fed. Eur. Microbiol. Soc.) Microbiol. Ecol.* 95 (4) (2019), fiz028. <https://doi.org/10.1093/femsec/fiz028>.
- [160] Y. Kooch, N. Noghre, The effect of shrubland and grassland vegetation types on soil fauna and flora activities in a mountainous semi-arid landscape of Iran, *Sci. Total Environ.* 703 (2020) 135497. <https://doi.org/10.1016/j.scitotenv.2019.135497>.
- [161] J.M. Cable, K. Ogle, A.P. Tyler, M.A. Pavao-Zuckerman, T.E. Huxman, Woody plant encroachment impacts on soil carbon and microbial processes: results from a hierarchical Bayesian analysis of soil incubation data, *Plant Soil* 320 (2009) 153–167. <https://doi.org/10.1007/s11104-008-9880-1>.
- [162] G.B. De Deyn, J.H. Cornelissen, R.D. Bardgett, Plant functional traits and soil carbon sequestration in contrasting biomes, *Ecol. Lett.* 11 (5) (2008) 516–531. <https://doi.org/10.1111/j.1461-0248.2008.01164.x>.
- [163] G.B. De Deyn, R.S. Shiel, N.J. Ostle, N.P. McNamara, S. Oakley, I. Young, R.D. Bardgett, Additional carbon sequestration benefits of grassland diversity restoration, *J. Appl. Ecol.* 48 (3) (2011) 600–608. <https://doi.org/10.1111/j.1365-2664.2010.01925.x>.
- [164] C.G. Collins, C.J. Carey, E.L. Aronson, C.W. Kopp, J.M. Diez, Direct and indirect effects of native range expansion on soil microbial community structure and function, *J. Ecol.* 104 (5) (2016) 1271–1283. <https://doi.org/10.1111/1365-2745.12616>.
- [165] L. Zifcakova, Factors affecting soil microbial processes, *Carbon Nitrogen Cycl. Soil* (2020) 439–461.
- [166] L. Zifcakova, Factors affecting soil microbial processes, *Carbon Nitrogen Cycl. Soil* (2020) 439–461.
- [167] A.E. Richardson, J.M. Barea, A.M. McNeill, C. Prigent-Combaret, Acquisition of Phosphorus and Nitrogen in the Rhizosphere and Plant Growth Promotion by Microorganisms, 2009. <https://doi.org/10.1007/s11104-009-9895-2>.
- [168] G. Zhang, X. Wang, X. Wu, H. Gao, S. Xiao, W. Zhang, R. Michalet, Dominant woody plants alter soil microbial community composition during succession, *Glob. Ecol. Conserv.* 31 (2021), e01852. <https://doi.org/10.1016/j.gecco.2021.e01852>.