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RESEARCH ARTICLE

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The impact of livestock grazing and canopy gaps on species pool and functional diversity of ground flora in the Caspian beech forests of Iran

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Abstract

Questions: Livestock grazing is an important disturbance in many forest ecosystems. While several studies have addressed the general impact of different grazing and light intensities on temperate forest ecosystems, little is known about how the combination of these two factors can affect the species pool and functional diversity of temperate forests.

Location: Oriental beech forests of northern Iran.

Methods: Vegetation and environmental data of 104 relevés were collected. These were assigned to four groups based on their light and grazing intensities. Non-metric multidimensional scaling was used to analyze vegetation compositional relationships among groups. We used nine functional traits related to growth, reproduction, and survival for a total of 147 plant species. Redundancy analysis of community-weighted means was used to determine the response of single traits to disturbance and environmental variables. Generalized additive models were applied to examine the shape of the response pattern of community-weighted mean trait values across the grazing and light intensity gradients. Functional richness and functional divergence indices were used to analyze functional diversity–disturbance relationships.

Results: Both light and grazing intensities significantly affected species pools, single traits, and functional divergence. Suites of trait attributes including hemicryptophytes, therophytes, grass-like, hygromorphic leaves, insect-pollinated, rhizomes, and runner plants were associated with high-light sites. In closed-canopy sites the strong filtering effect of shade resulted in suites of trait attributes including taller plants, macrophanerophytes, scleromorphic leaves, simple leaves, and berry fruits. While high-light sites had a larger species pool, they exhibited less functional diversity. Cattle grazing can mediate the filtering effect of light and increase functional diversity in both low-light and high-light sites.

Conclusion: Conservation measures in this region should acknowledge that moderate traditional cattle grazing combined with individual-tree and group-tree selection in these forests may maintain or even enhance functional diversity in these valuable ecosystems.

KEYWORDS

biodiversity conservation, closed forest, close-to-nature silviculture, forest gaps, forest pastures, functional divergence, functional richness, species diversity, trait attributes, understorey vegetation

1 | INTRODUCTION

Since the mid-twentieth century, forest managers have tried to develop strategies to achieve multifunctionality and sustainability of forest ecosystems in a changing world (Ewel, 1999; Paletto et al., 2008; Schütz, 2011). Conserving biodiversity is of growing concern since it is key in many close-to-nature silvicultural systems (Bürgi, 2015; O'Hara, 2016). Some management systems attempt to mimic natural processes (e.g. addressing natural canopy gap size in single-tree and group-tree selection systems), while others try to minimize disturbances (e.g. patch or retention cut in clear-cut system; O'Hara, 2016). For both approaches, forest scientists need precise information on how disturbances drive the composition and structure of plant communities.

Each forest ecosystem is adapted to a specific disturbance regime, which involves multiple disturbance agents with different intensities across a range of spatio-temporal scales (Oliver & Larson, 1996; Nagel et al., 2010; O'Hara, 2016). Locally, disturbance may change resource availability and thus modify the environment, while the functional attributes of species are shaped over larger temporal and spatial scales (Keddy, 1992; Johnstone et al., 2016). Interactions between environmental variables and functional identities of species in response to disturbance determine ecosystem stability. Multiple disturbance interactions, novel disturbances (e.g. timber harvesting), or any changes in disturbance characteristics (e.g. intensity, frequency, and timing) may shift the environment, the species pool, or both and consequently alter ecosystem dynamics (Brando et al., 2014; McWethy et al., 2014; Johnstone et al., 2016). While the impact of single disturbances (e.g. livestock grazing or timber harvesting) on taxonomic and functional diversity is generally well documented (de Groot et al., 2016; Schulze et al., 2016; Elek et al., 2018; Schall et al., 2018; Tinya et al., 2019), their different intensities and combined effects on taxonomic and functional diversity of plants are still not completely understood (Öllerer et al., 2019).

Taxonomic diversity refers to the number of different taxa represented in a given community (Hill, 1973). Functional diversity is a measure of the traits of taxa that can affect ecosystem functioning and can be estimated using one or multiple functional traits (Tilman et al., 1997; Violle et al., 2007). Functional traits are defined as morphological, physiological, and phenological characteristics that relate to plant fitness as described by pattern of growth, reproduction, and survival, i.e., the three components of individual performance (Violle et al., 2007). Groups of species with suites of similar functional traits are assumed to show similar responses to comparable environmental changes (Simberloff & Dayan, 1991). When an environmental stressor occurs, assembly processes that shape the regional species pool (e.g. environmental filtering, competition, and facilitation) also change and may induce shifts in species diversity and functional diversity (Díaz et al., 2007; Mayfield et al., 2010). Functional diversity is ecologically important because it is a component of biodiversity that may be directly related to many ecosystem processes, such as productivity, nutrient dynamics, and ecosystem resilience to environmental change or disturbance (Tilman, 2001; Petchey et al., 2004; Cadotte et al., 2011).

Tree falls, creating canopy gaps, are predominant natural disturbances in many temperate deciduous forests and are key to revitalizing stand dynamics (Franklin et al., 2002; Nagel & Svoboda, 2008; Wagner et al., 2010). Wind can throw down either single trees or small groups of trees, creating new spaces for successional vegetation (Fischer et al., 2013). The main effect of canopy gaps is a change in the light regime in and around the gaps (Canham et al., 1990); this alteration depends on gap characteristics (e.g. gap size, age, morphology, location, and canopy height), and it is the main driver of successional plant composition and forest regeneration (Abe et al., 1995; Fischer et al., 2013). Canopy gaps may increase species richness by promoting generalist, early seral-stage species, and light-demanding plants (Sabatini et al., 2014). They can thus be a favorite foraging ground for both livestock and wild ungulates (Kuijper et al., 2009; Graham et al., 2010).

Herbivory by domestic animals is another disturbance in many forest ecosystems (Noack et al., 2010; Shakeri et al., 2012; Mazzini et al., 2018; Öllerer et al., 2019). Livestock grazing is an important part of the cultural heritage of many wood–pasture and forest–pasture ecosystems and plays an important role in local and global vegetation dynamics by promoting annuals over perennials, short plants over tall plants, and prostrate, stoloniferous, and rosette plants over erect and tussock plants (Díaz et al., 2007; Meers et al., 2008; Bergmeier et al., 2010; Varga et al., 2020). Livestock impacts on vegetation biomass, woody species regeneration, and habitat heterogeneity vary, depending on livestock type, grazing intensity, and time (Öllerer et al., 2019). From a commercial forestry point of view, livestock could change the structure and composition of forest ecosystems by selectively grazing on specific tree species, reducing their height and abundance, and can even cause regeneration failure (Ammer, 1996; Zamora et al., 2001; Didion et al., 2009; Shakeri et al., 2009).

The growing demand for wood on the one hand and the discrepancy between increasing livestock and game population and forestry practices on the other led many European countries to grazing interdiction at various times in the 19th century (Bergmeier et al., 2010; Stoiculescu, 2014; Nichiforel et al., 2018). Although forest grazing by livestock was banned or restricted by law, grazing by domestic ungulates in forests persisted owing to the high dependence of local people on livestock husbandry (Humphrey et al., 1998; Varga et al., 2020). In the Caspian region, despite a long history of traditional animal husbandry within forests, commercial forestry is relatively young (Scharnweber et al., 2007; Noack et al., 2010). The first harvesting operations began in 1959 in the Iranian Caspian region within the framework of formal forestry plans. The conflict between forestry goals and cattle grazing inside the forest led to the prohibition of cattle grazing by a forest protection law in 1967; nevertheless about 2.2 million cattle still reside in 28,500 cow herds (Shamekhi, 2004). As a consequence of the inability to exclude cattle from the forest, the Iranian forest service decided to avoid classical silvicultural systems that create large openings in the forest (i.e., vast grazing areas for cattle) and has prescribed single-tree and group-tree selection since 1990 (Marvie Mohadjer, 2001). These selective harvesting methods mimic natural gap formation in the forest canopy (Fischer et al., 2013) and have been assumed to be more compatible with cattle grazing by leaving only scattered, small to medium size canopy gaps (Marvie Mohadjer, 2005).

The spatial distribution of these three disturbance agents (i.e., canopy gaps, cattle grazing, and harvesting) in Iran is patchy. The fact that at least two of them are intermingled in some areas creates a unique opportunity to study the conflicting effects of grazing and canopy gaps (i.e., through light) on the species pool, functional traits, and functional diversity of ground vegetation. We chose part of the Caspian Oriental beech (*Fagus orientalis*) forest with a well-documented history of forest management and cattle grazing to ask the following questions:

1. How do the plant species pools (i.e., species composition and beta diversity) respond to contrasting grazing intensities and light regimes?
2. How do single-trait and multivariate functional diversity of plant communities respond to different grazing intensities and different light regimes?

2 | METHODS

2.1 | Study area

We selected study sites in the Kheiroud investigation (KI) forest (Nowshahr, Mazandaran province, Iran), located in the middle of the Caspian forests (51°33′12′′–51°39′56′′ E longitude and 36°32′08′′–36°36′45′′ N latitude; Figure 1). The KI forest is about 8,000 ha in size and contains seven districts with different management histories. We chose the Patoom and Namkhaneh districts with 40 and 20 years of timber-harvesting history (single selection system), respectively, and six cowsheds (with 485 head of cattle). Additionally, Baharbon and Maniasang were selected because they are two districts with no timber harvesting but a long history of cattle grazing with nine cowsheds (with 920 head of cattle) inside the forest. Traditional animal husbandry was the most important livelihood system since the Iron Ages (i.e., 1500–550 BC.), and cattle were the most exploited livestock in the Caspian forests (Davoudi et al., 2019). Domestic cattle (*Bos taurus*) as the main mega-herbivores grazing in these forests are the closest descendants of aurochs (*Bos primigenius*) originally inhabiting Europe and Asia (Bradley et al., 1996). This traditional livestock husbandry system remained unchanged for millennia and it is in the forms of transhumance, semi-transhumance, and sedentary (Shamekhi, 2004). In the transhumance form prevalent in our study area, cattle freely graze in the forest during the day and return to their cowsheds during the night without human help. Each herd consists of 50–200 cows (on average 100 cows per herd) and the grazing territories range from 400 hectares to 600 hectares (Appendix S1). Cow herders move their herds along an elevational gradient (from −20 to 2,900 m a.s.l.) during the year to take advantage of free and fresh forage, avoid insects and parasites, and exploit appropriate weather conditions. They have specific cowsheds in three to four elevational belts, and they spend on average three to four months in each cowshed (never spending an entire year in one place; Etemad & Avatefi, 2009).

Elevation of the selected sites ranged from 500 to 2,250 m a.s.l., and mountain slopes are mostly steep with 30–60% slopes. Mean annual precipitation is 1,100–1,380 mm and mean temperature is about 12–16°C (Etemad, 2010). The prevalent soil type, which occurs mainly under beech stands, is brown soils above limestone and dolomites as the main bedrock. The overstorey contains *Fagus orientalis* (dominant species), *Acer velutinum*, *Acer cappadocicum*, *Alnus subcordata*, and *Carpinus betulus*, which form uneven-aged, old-growth stands (with diameter distribution of 5–200 cm). In syntaxonomical classification, these forests belong to the class Querco-Fagetea and contain many associations and sub-associations (Assadoallahi, 2001).

2.2 | Data collection

In beech-dominated communities, we established 104 relevés distributed among undisturbed stands (old-growth forest stands without any sign of canopy or ground disturbance due to wind, timber harvesting, or cattle grazing; control, $n = 13$), natural gaps (opening area 1,245 ± 785 m^2; Ga, $n = 11$), forest pastures with grazing (Gr, $n = 25$), gap + grazing (opening area 726 ± 556 m^2; Ga-Gr, $n = 23$), timber-harvested areas with grazing (Ha-Gr, $n = 12$), timber harvesting + gap + grazing (opening area 492 ± 138 m^2; Ha-Ga-Gr, $n = 13$), and cowshed fields (opening area 7,385 ± 7,123 m^2; CF, $n = 7$; Appendix S2). We selected gaps with an average age range of 5–15 years after wind fall or timber harvesting. Relevé sizes were obtained by the minimal-area method and ranged from 100 m^2 to 400 m^2 (Müller-Dombois & Ellenberg, 2002). Plots were sampled once between May and July 2010, and we recorded all vascular plants and measured their abundance using the Londo decimal scale (Londo, 1976). Plant specimens were collected from each relevé for determination and further trait measurements in the lab,

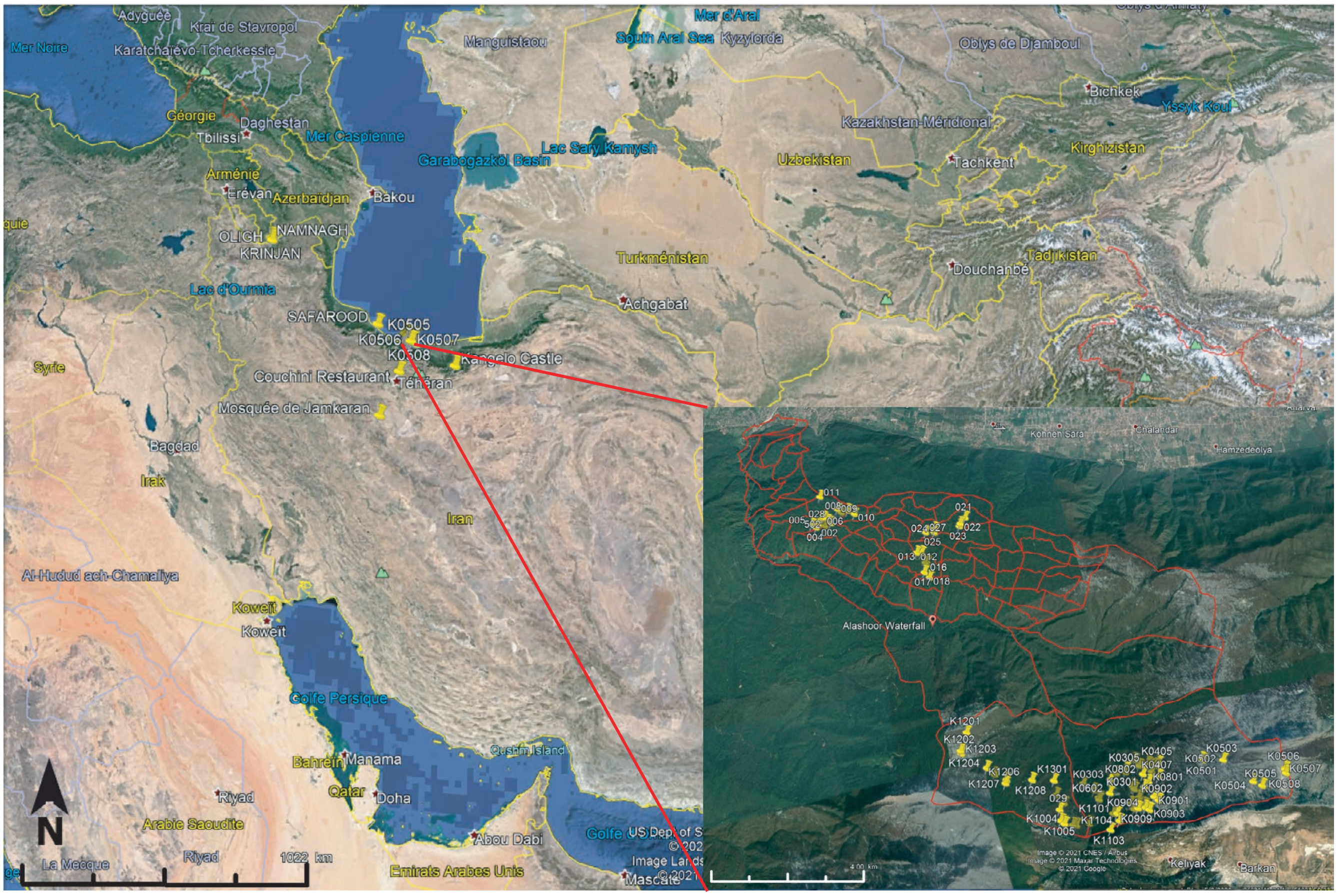


FIGURE 1 Map showing location of Kheiroud investigation forest and the study sites. Source: Google Earth, earth.google.com/web/

and vouchers were stored in the herbarium of the Department of Forestry, Faculty of Natural Resources, University of Tehran, Iran. Taxon nomenclature follows the International Plant Names Index (IPNI, 2020).

Site characteristics and environmental variables including elevation (m a.s.l.), inclination (%), aspect, litter depth (cm), soil texture, soil organic matter (%), pH, Ca, N, P, K, soil compaction (0–1 scale), and saturation moisture were measured for each sampling point (for details, see Shakeri et al., 2012). Stocking rate (per ha/year) was calculated as an estimate of grazing intensity (Thorn, 2007). For each relevé, five measurements of light intensity and a control measurement under clear sky were taken using a Lutron LX-105 light meter (Lutron Electronic Enterprise Co., Ltd, Taiwan). Measurements were made at 150 cm above ground between 10 a.m. and 3 p.m., and their averages were divided by the control values to obtain relative light intensity (0–1 scale).

2.3 | Trait selection and measurement

We confined our research to a set of traits that have been reported as good predictors of canopy disturbance (i.e., altered light) and grazing (Grace, 2002; Díaz et al., 2004; Bernhardt-Römermann et al., 2008). We selected nine traits related to different aspects of plant life: (a) growth — maximum height, life-span, and leaf form; (b) reproduction — pollination syndrome, fruit type, and vegetative reproduction; (c) survival — leaf persistence, life form, and leaf anatomy (Appendix S3; Violle et al., 2007). We validated the trait values from Flora of Iran, Flora Iranica, and direct measurements with the BiolFlor database, then we obtained the identical traits values for 72 species directly from the BiolFlor database (Kühn et al., 2004). For the remaining 75 species, we used data derived from the Flora of Iran and Flora Iranica (Rechinger, 1963; Ghahraman, 1978; Assadi et al., 1989) and additionally took some direct height measurements on-site and on herbarium vouchers.

2.4 | Diversity indices and data analysis

We categorized our relevés based on relative light and grazing intensity into four groups:

(i) *low light–low grazing* (control with an average relative light and stocking rate of 10% and 0.08 respectively);
(ii) *low light–high grazing* (pooled relevés of Gr and Ha-Gr with an average relative light and stocking rate of 9% and 0.48 respectively);
(iii) *high light–low grazing* (Ga with an average relative light and stocking rate of 60% and 0.02 respectively); and

(iv) *high light–high grazing* (pooled relevés of Ga-Gr, Ha-Ga-Gr, and CF with an average relative light and stocking rate of 59% and 0.56 respectively; Figure 2).

To understand the effect of grazing and light on whole assemblages of species, we performed a series of non-metric multidimensional scaling ordinations (NMDS) using Bray distance and three axes (*vegan* package in R; Oksanen et al., 2010). The significance of these analyses was evaluated by perMANOVAs with 999 permutations (Travis, 2003). We analyzed the low light–low grazing vs low light–high grazing and high light–low grazing vs high light–high grazing categories and we plotted the ordihull of relevés to visualize the results. We estimated the Bray–Curtis dissimilarity index in the *betapart* package as a measure of beta diversity (Baselga and Orme 2012). One-way analysis of variance and Duncan's post hoc test were used to test the differences between the beta diversities of the four groups.

Three matrices (i.e., environmental variables, species abundances, and species traits) were used to measure functional diversity indices and to perform all further analyses including a redundancy analysis of community-weighted means (CWM-RDA). This kind of analysis has been used to link single-trait responses to environmental variables and disturbance (Kleyer et al., 2012). To this end, a site-by-trait matrix was created from the original species abundances and species trait matrices in R (R Core Team, 2019). Species abundances were used to weight the proportion of categorical traits and mean trait values for continuous traits (e.g., maximum height). The resulting CWM matrix and environmental variables matrix were subjected to a redundancy analysis (RDA), with no transformation of the response variables (i.e., trait-weighted means) and no standardization of samples, but response variables were centered and standardized in CANOCO for Windows 4.5 (Lepš & Šmilauer, 2003).

Disturbance and environmental variables were placed into four distinct groups: (1) grazing intensity (stocking rate); (2) light (relative light intensity [%]); (3) soil, (including litter depth [cm], soil organic carbon [%], pH, calcium [mg/100 g], nitrogen [%], potassium [ppm], phosphorus [ppm], clay [%], silt [%], sand [%], compaction (%, and saturation moisture [%]); and (4) topography (elevation [m a.s.l.], inclination [%], and aspect). Forward selection of environmental variables was performed to identify the most important gradients. After we selected the most important variables, RDA was repeated using relevé size as a covariate. In addition, partial RDA was performed to assess the relationship between the weighted trait data with each group of selected variables using the other environmental variables and relevé size as covariates (Kleyer et al., 2012). This analysis allowed us to determine the net effect of each group of variables and gave us a better understanding of the contribution of each variable to the variation in trait space.

To analyze the response pattern of CWM trait values across a gradient of increasing light and grazing intensity, we used generalized additive models (GAMs; Guisan et al., 2002; Hastie & Tibshirani, 1986). The GAMs were repeated with different smoothing values and the optimum degree of smoothing, given that the best *p*-value for the deviance-based test was found to be 2. Because CWM values were normally distributed, a Gaussian distribution and a logistic link function were assumed. This analysis was performed in CANOCO 4.5 (Lepš & Šmilauer, 2003).

Two FD indices — functional richness (F_{Ric}) and functional divergence (F_{Div}) — were estimated using the *FD* package in R (Laliberté & Legendre, 2010). Functional richness depends on the number of species and is a measure of functional space occupied by a species assemblage (i.e., convex hull). Functional divergence (F_{Div}) is independent of species richness and estimates the variety of trait values by measuring the distributions of species abundances toward

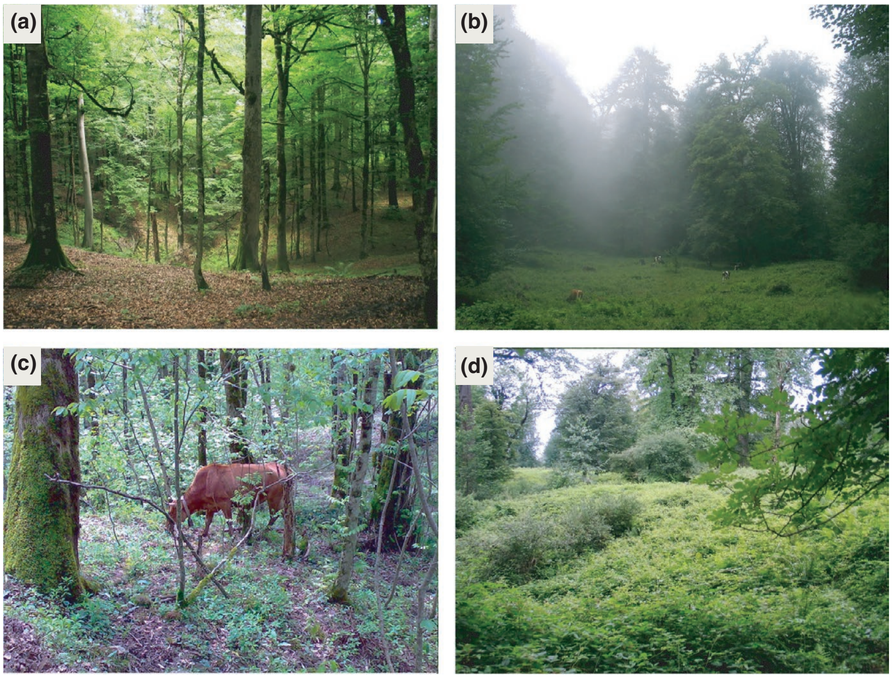


FIGURE 2 Photo of low light–low grazing (a), low light–high grazing (b), high light–high grazing (c), and high light–low grazing (d) sites (photo by ZS)

the boundaries of the convex hull (Mason et al., 2005). Because all variables were normally distributed and their variances were equal, a one-way analysis of variance (ANOVA) was conducted to compare the effect of light and grazing on F_{Ric} and F_{Div} indices. To test differences among four categories, we performed Duncan's post hoc test using the *agricolae* package in R version 3.6.3 (R Core Team, 2019).

3 | RESULTS

3.1 | Species composition and beta diversity

In total, 147 plant species belonging to 119 genera and 67 families were recorded. Altogether, high-light sites contained 129 plant species of which 71 species were shared between high light–low grazing and high light–high grazing sites, and these two categories contained eight and 50 unique species, respectively. All low-light sites collectively harbored 113 plant species, with 10 and 38 unique species in low light–low grazing and low light–high grazing sites, respectively, and 65 shared species. Although beta diversity of high-light sites significantly exceeded that of low-light sites (p-value = 0.0001), there was no difference between high light–low grazing (beta diversity: 0.535 ± 0.121, mean±se) and high light–high grazing (0.556 ± 0.090) sites or between low light–low grazing (0.359 ± 0.155) and low light–high grazing (0.387 ± 0.129) sites (Figure 3).

Non-metric multi-dimensional scaling analysis revealed significant differences between species and trait composition of low light–low grazing and low light–high grazing sites (PerMANOVA: $F_{df,df}$ =4.405, $p = 0.001$) and also between high light–high grazing and high light–low grazing sites (PerMANOVA: $F_{df,df}$ =1.859, $p = 0.026$; Figure 4).

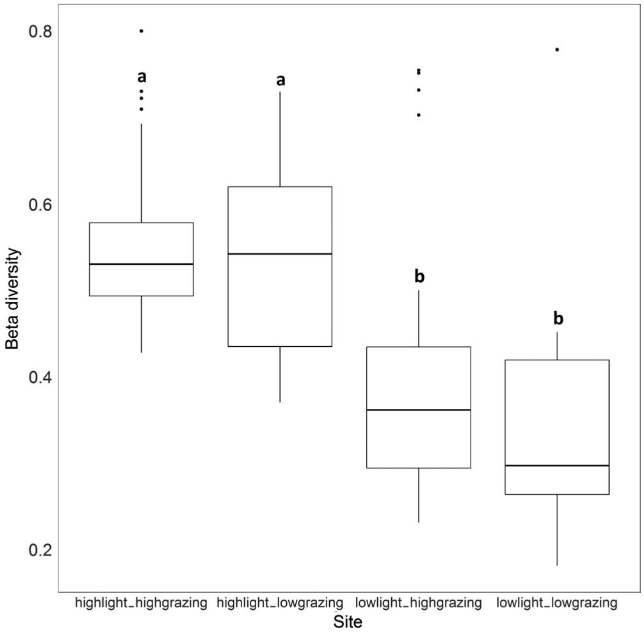


FIGURE 3 Box-plots of high-light and low-light sites based on Bray–Curtis dissimilarity index of beta diversity. Letters denote Duncan's post hoc comparison test

3.2 | Single-trait attributes and functional diversity

The result of CWM-RDA showed that all variables together explained 42.2% of the total variation in trait space. The first axis of RDA correlated with light intensity and explained 15.4% of the variation while the second axis correlated with grazing intensity and represented a weaker gradient explaining 5.6% of the total variance. Forward selection in CWM-RDA led to nine significant variables out of 25 initial variables. These variables represent the above-mentioned variable groups as follows: (a) grazing intensity (stocking rate); (b) soil (litter depth, soil potassium, calcium, and soil compaction); (c) light (relative light intensity); and (d) topography (elevation, southern, and northwestern aspects). These selected variables explained 31.7% of the variation. Partial CWM-RDA with light intensity as explanatory variable and the other selected variables as covariates explained 11.8% of variation, which indicates a substantial effect of light intensity on trait distribution. Other groups of variables including soil, topography, and grazing intensity were also significant and explained 10.5%, 8.3%, and 1.6% of the variation, respectively (Table 1).

The biplot of selected variables and traits revealed a clear relationship between disturbance and trait attributes including reproduction (R1 to R30), survival (S1 to S17), and growth (G1 to G18; Figure 5). Low light–low grazing and low light–high grazing categories (i.e., closed-canopy forest stands) were located on the left side of the figure where the depth of the litter on the forest floor was higher. In this part of the figure, a suite of trait attributes including wind-pollinated (R2), simple leaf form (G9), maximum height, and macrophanerophytes (S4) was more abundant. High light–low grazing and high light–high grazing categories (i.e., large gaps and open forest stands) were associated with southern aspects and located on the right side of the figure where soil was more compacted. In this part of the plot, a suite of trait attributes including insect-pollinated (R3), runner plants (R5), hemicryptophytes (S3), summer green (S10), and hygromorphic leaves (S16) was more abundant.

The response curves of GAMs fitted for CWM trait values against the light intensity and stocking rate index resulted in 16 trait attributes significantly and non-linearly related to light intensity and 32 trait attributes significantly and non-linearly related to stocking rate (p-value < 0.05; Figure 6). These response curves could be classified into three groups: positive (J-shape), negative (inverse J-shape), and unimodal. Six CWM trait attributes including annuals (G1), biennials (G2), perennials-hapaxanth (G3), therophytes (S8), hygromorphic leaf anatomy (S16), and pinnatifid leaf form (G12) showed a J-shape response while seven CWM trait attributes including wind pollination (R2), perennials (G4), macrophanerophyte (S4), fern roots (R16), mesomorphic leaf anatomy (S15), nut fruits (R23), and maximum height (G18) showed an inverse J-shape response to light intensity. Succulent leaf anatomy (S13), aggregate follicle fruits (R25), and legume fruits (R21) showed a unimodal response to light intensity.

Ten CWM trait attributes including self-pollination (R1), insect-pollination (R3), annual (G1), biennial (G2), perennial-hapaxanth (G3), therophyte (S8), summer green (S10), pinnatifid leaf form (G12),

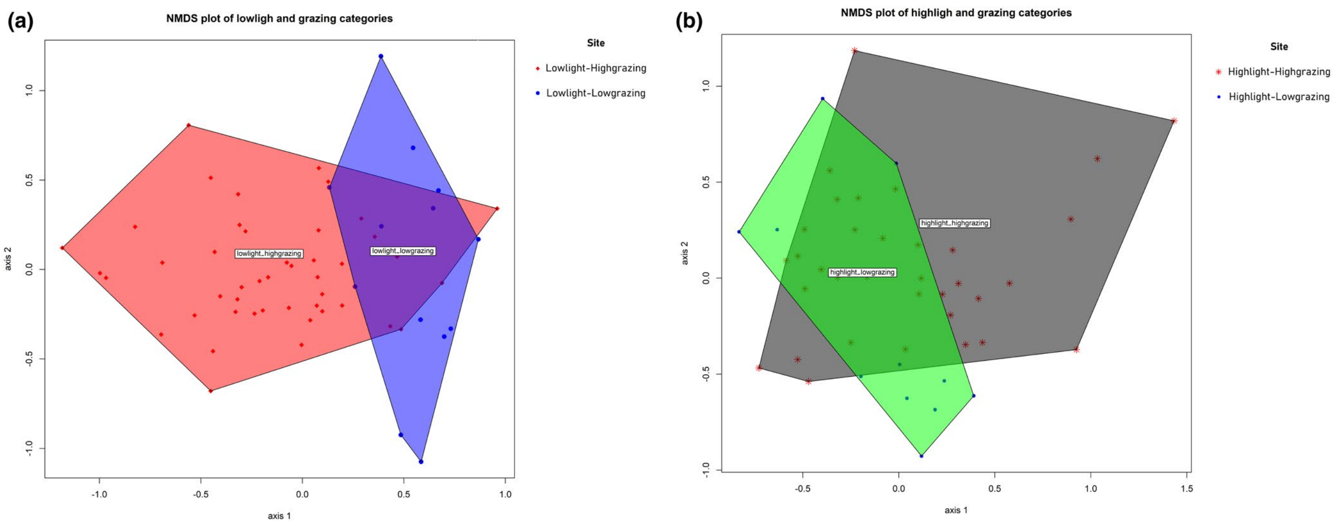


FIGURE 4 Non-metric multidimensional scaling (NMDS) hull plot based on species abundances of (a) low light°low grazing vs low light–high grazing and (b) high light–low grazing versus high light–high grazing

bipinnate leaf form (G16), and schizocarp fruit type (R29) showed a J-shape response while pseudo-phanerophyte (S6), runner stems (R5), palmate leaf form (G14), and berry fruit type (R18) showed an inverse J-shape response to stocking rate. wind pollination (R2), perennial (G4), chameophyte (S1), macrophanerophyte (S4), nanophanerophyte (S5), runner-bulbs (R6), rhizome-pleiocorm (R12), root bud (R14), persistent green leaf (S12), acicular leaf (G5), long leaf (G8), simple leaf (G9), berry fruit (R18), maximum height (G18), hemicryptophyte (S3), full leaf (G10), pinnate leaf (G15) and legume fruit (R21) showed a unimodal response to stocking rate.

We found no significant differences between light–grazing categories for the F_{Ric} index based on ANOVA analysis (p-value = 0.177), but high light–high grazing and low light–high grazing sites had slightly higher values for functional richness. Functional divergence (F_{Div}) was significantly higher in low-light sites (i.e., low light–low grazing and low light–high grazing) than in high-light sites (i.e., high light–low grazing and high light–high grazing; p-value = 0.000; Figure 7).

4 | DISCUSSION

Disturbance has been reported as a major driver of community complexity and of functional diversity in many studies (Biswas & Mallik, 2010; Mayfield et al., 2010; Bernhardt-Römermann et al., 2011; Laliberté et al., 2013; Mouillot et al., 2013; Nathan et al., 2016; Wermelinger et al., 2017). Windfall and timber harvesting create canopy gaps and along with macro-grazers they contribute to structural and species diversity in temperate forests. Our result showed that canopy gaps and cattle grazing shape the species pool composition of plant communities in distinctive ways. Cattle grazing significantly affected vegetation composition and beta diversity of both low-light and high-light sites. The significant impact of high-intensity grazing of livestock on species composition and structure has been reported by several studies (Bovee et al., 2018; Mazzini et al., 2018; Öllerer et al., 2019; Ball & Tzanopoulos, 2020; Loto & Bravo, 2020).

In addition to creating new growing space, canopy gaps increase light intensity, humidity, and soil nutrients, thus providing more micro-sites for tree regeneration, light-demanding plants, and early-successional plants (Canham et al., 1990). Furthermore, cattle grazing may mitigate the filtering effect of environmental variables (i.e., light) by reducing abundance of dominant plants (Ammer, 1996; Didion et al., 2009), transporting diaspores (Bruun & Fritzbøger, 2002; Graetz, 2009), and altering soil nutrient availability through fecal deposition (da Silva et al., 2014; Orefice et al., 2017). Our results suggest that these impacts lead to higher numbers of unique species in high-grazing sites, and consequently sites with higher light and grazing intensity harbor a larger species pool and show greater beta diversity.

Both canopy gaps and cattle grazing affected traits related to three aspects of plant life: reproduction, growth, and survival. Both light and grazing intensity were retained as significant variables in the CWM-RDA, with relative light explaining much of the variance in the data. Among the other selected environmental variables, soil potassium, soil compaction, and litter depth also directly or indirectly depend on light and grazing intensity (Cooper, 1995; Dudley et al., 2009), and accordingly they affect plant and trait composition. Potassium is a soil nutrient that increases in open-grazed forest patches and especially in cowshed fields owing to fecal deposition by cattle (James et al., 2007). Litter depth is higher under closed-canopy and control sites and is a good predictor of soil disturbance (Biswas & Mallik, 2010). Deep litter layers may enhance the establishment of geophytes, hemicryptophytes, and perennial plants, while they may reduce establishment of therophytes and annual plants (Dudley et al., 2009; Loydi et al., 2013).

In temperate forest ecosystems, canopy gaps and light condition are good predictors of floristic composition (Bruelheide & Luginbühl, 2009). Light is an important filtering factor by promoting light-demanding and pioneer plants and eliminating shade-tolerant

TABLE 1 Results of the community-weighted mean redundancy analysis (CWM-RDA) analysis, accounting for the effects of relevé size differences

Expl. var.	Covar.	Sum of all Eigenv.	Sum of all Cano. Eigenv.	%	F	p
All	–	1	0.422	42.2	–	–
G, L, S, T	R.S.	0.978	0.313	31.7	16.15	0.001
Net effect						
Grazing intensity	L, S, T, R.S.	0.686	0.011	1.6	1.55	0.048
Light	G, S, T, R.S.	0.765	0.090	11.8	12.43	0.002
Topography	G, L, S, R.S.	0.735	0.061	8.3	5.47	0.002
Soil	G, L, T, R.S.	0.753	0.079	10.5	5.61	0.002

Note: The first row contains the full model with all variables. The second row shows the full model for significant variables only. Net effects show whether sets of variables still exerted significant effects on trait composition after effects of all other significant variables have been accounted for.

Abbreviations: %, percentage of explained variance; Covar., covariates; Eigenv., eigenvalues; Expl. var., explanatory variables; *F*, *F* ratio for the test of significance of all canonical axes (test on the trace); G, grazing intensity; L, light; *p*, corresponding probability value obtained by Monte Carlo permutation test (1,000 permutations); R.S., relevé size; S, soil; T, topography.

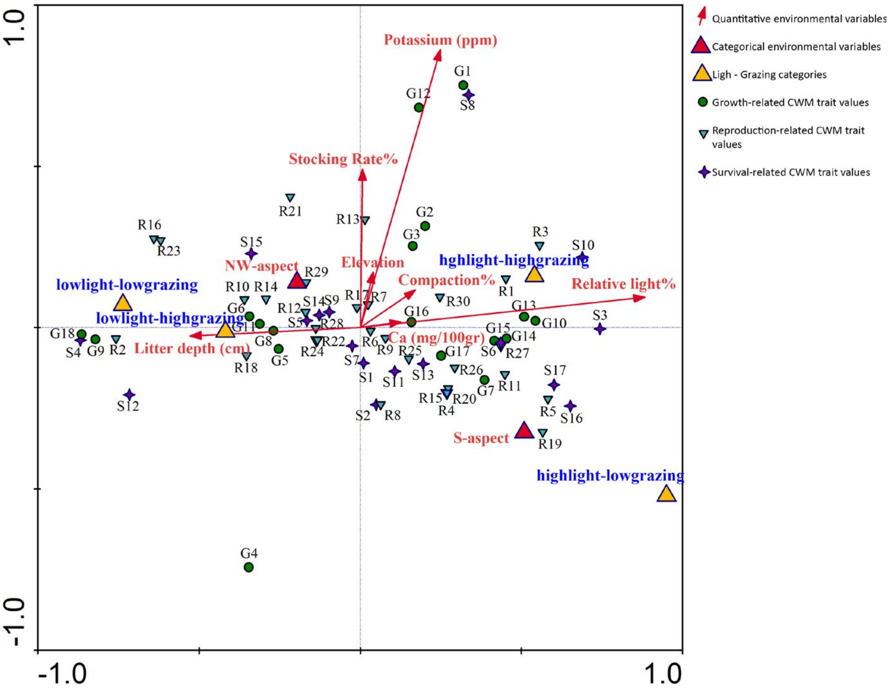


FIGURE 5 Community-weighted mean redundancy analysis (CWM-RDA) biplot of single traits and environmental variables selected in partial RDA (i.e., light intensity, stocking rate, and seven environmental variables). The eigenvalues of axis 1 and axis 2 are 0.154 and 0.056, respectively

plants (Valladares et al., 2016). Increasing light can also support more distinct plants in terms of leaf shape and leaf anatomy in forest ecosystems (Joner et al., 2012). In high-light sites, a suite of trait attributes characterized typical plants as insect-pollinated, hemicryptophytes, therophytes, grass-like, pinnatifid, and with hygromorphic leaves, drupe fruits, runners, and rhizomes as means of vegetative spread (Poorter et al., 2019). All of these trait attributes also showed a positive trend in the GAM analysis with increasing light intensity.

In contrast to the high-light sites, in closed-canopy sites trait convergence resulted from competition for light and the high filtering effect of shade. Cattle grazing in forest ecosystems can be considered as a low-intensity disturbance compared to fire and timber harvesting (Ramírez-Marcial et al., 2001), and it contributes to the biodiversity of these ecosystems (Mazzini et al., 2018; Öllerer et al., 2019). Cattle follow a transhumance movement in the Caspian forests and they spend less than four months in each grazing region, so they do not intensively graze on vegetation especially under closed-canopy stands (Noack et al., 2010; Shakeri et al., 2012). However, even such low-level grazing in concert with the filtering effect of shade leads to a suite of trait attributes characterizing these plants as macrophanerophytes, scleromorphic, schizocarp fruits, and simple leaves. Scleromorphic plants with thickened epidermic and cuticle layer have lower palatability for cattle, while species with simple leaves are favored under conditions of understorey shade (Lin et al., 2020). Some plants with schizocarp fruits (e.g. *Acer cappadocicum*, *Acer platanoides*, and *Sanicula europaea*)

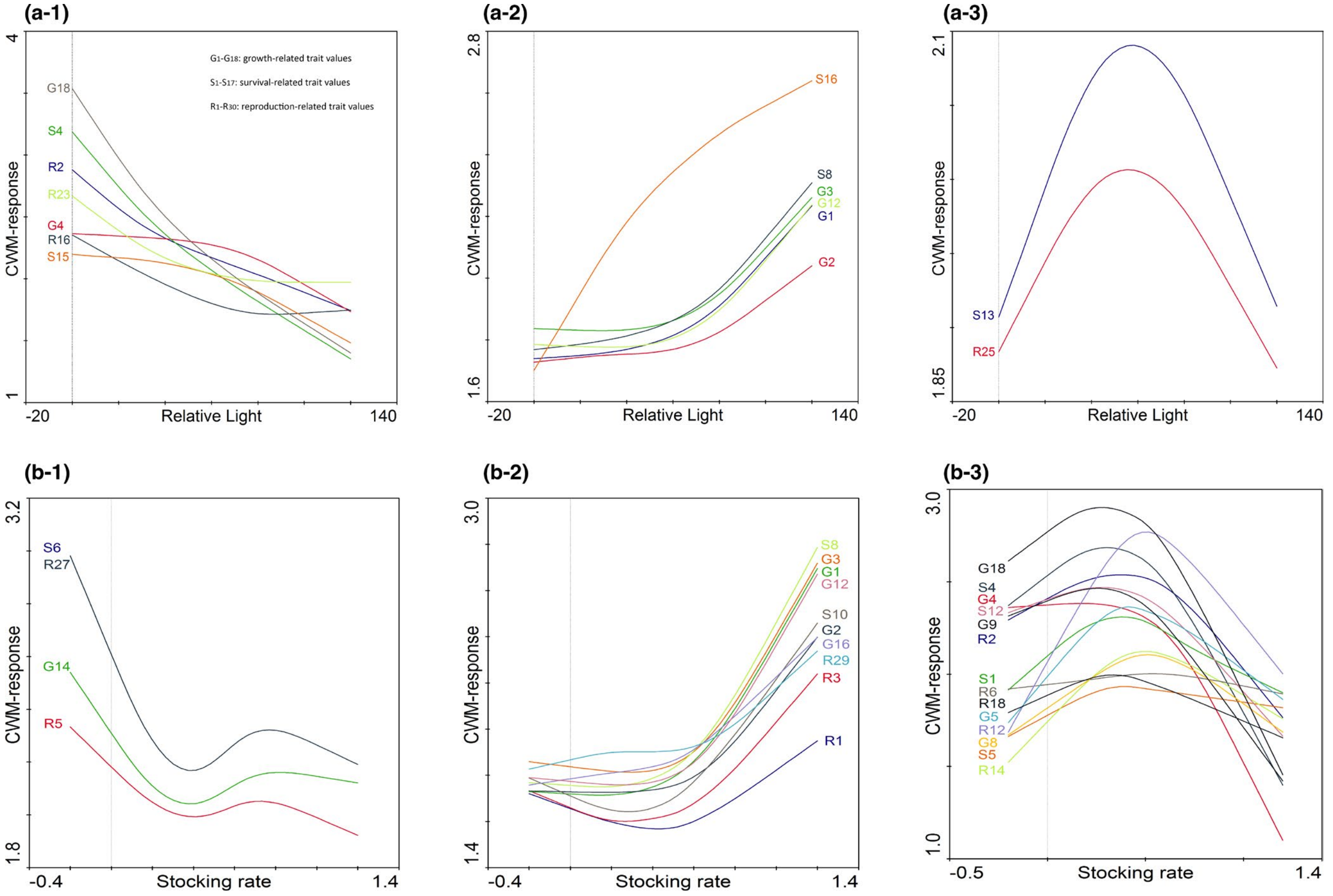
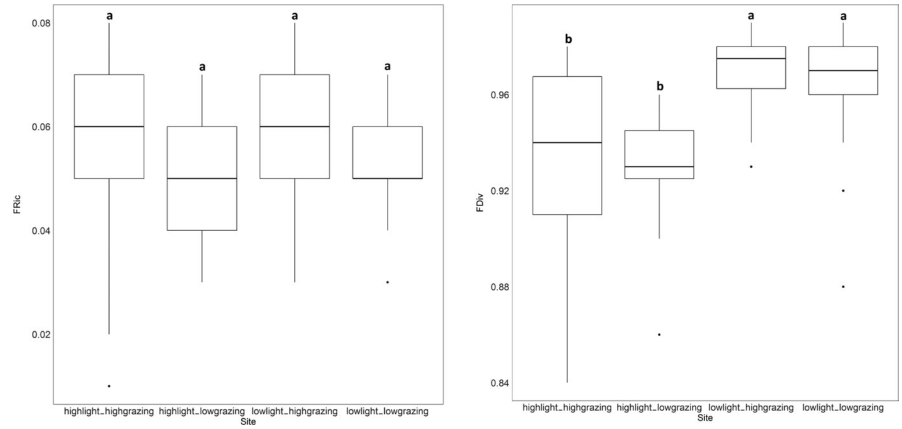


FIGURE 6 Estimated response curves of community-weighted mean (CWM) trait values against relative light intensity (a-1 to a-3) and stocking rate (b-1 to b-3) resulting from generalized additive model analysis (GAM). Full trait abbreviations can be found in Appendix S3

FIGURE 7 Bar plots with standard errors of functional richness (F_{Ric}) and functional divergence (F_{Div}) indices. Letters denote Duncan's post hoc comparison test, and levels that do not significantly differ are represented by the same letter



are also shade-tolerant and sensitive to grazing; therefore, they grow under closed-canopy stands with low cattle grazing. Maximum plant height also increased significantly under control and closed-canopy grazed sites. Macrophanerophyte life form and plant height are two traits closely related to the ability of species to achieve competitive dominance (Wilson et al., 1999), leading to high competition for light among understorey species. Moderate grazing under closed-canopy forests can also reduce the palatable competitors and favor taller plants. Rapid height growth can help such plants to escape herbivores by making their leaves and shoots unavailable for browsing (Royo & Carson, 2006).The GAM analysis also indicated that these trait attributes decreased with increasing light and grazing intensity, while plants with annual, biennial, and therophyte trait attributes showed positive responses to light and grazing intensity. In general inside the high light–high grazing sites, trait attributes converged toward shorter plants, annuals, therophytes, rosettes, adhesive seeds, and insect-pollinated species (Barbero et al., 1990; McIntyre et al., 1995; Pedley & Dolman, 2014; Osem et al., 2017), while control and low-grazed sites had more geophytes, phanerophytes, and taller plants with erect-rosette form (Díaz et al., 2007; Loto & Bravo, 2020).

Functional richness does not significantly differ among the four sites, mainly because of high variation in F_{Ric} values. Positive effects of moderate grazing on F_{Ric} via competitive exclusion of dominant and subdominant plants in grasslands have been reported by other studies (Briske et al., 2003; Salick et al., 2007; Wild et al., 2008; Rahmanian et al., 2019). However, light intensity is a stronger filtering factor in forest ecosystems than in grasslands (Bruelheide & Luginbühl, 2009; Valladares et al., 2016). Therefore, the effects of light and grazing on the species pool and functional diversity of these ecosystems may differ.

Functional divergence of low-light sites significantly exceeded that of high-light sites. This result shows the potential of controlling light intensity through silvicultural practices for maintaining biodiversity in beech forests (i.e., shade-tolerant-dominated forests; Brang et al., 2014; O'Hara, 2016). In our data set, F_{Div} was highest in low light–high grazing sites (Ha + Gr and Gr). Harvesting can disturb both crown canopy and soil (by turning over and compacting the soil surface). Single-tree and group-tree selection systems have been practiced in these forests for 40 years (Marvie Mohadjer, 2001). Small and medium-sized gaps created in this system can create optimum light conditions for successful regeneration of woody plants (e.g. Oriental beech) and companion vegetation (Wagner et al., 2010). Specifically, management combining gaps with grazing could create more ecological niches and increase functional divergence in harvested and grazed sites (i.e., niche complementarity).

Positive effects of grazing on niche complementarity are more evident in low light–high grazing sites. In these situation, grazing may mediate the filtering effect of light and increase species relative abundances and functional divergence (Mouchet et al., 2010). By contrast, due to the large filtering effect of light, species with similar traits (i.e., trait redundancy) are selected, which may cause trait convergence (i.e., decreases F_{Div}) in high-light sites (de Bello et al., 2009; Valdivia et al., 2017). In general, ungulates prefer foraging in gaps rather than closed-canopy forests (Kuijper et al., 2009); cattle can have a reciprocal affect in high light–high grazing sites by mitigating the filtering effect of light (via foraging on dominant plants) and maintaining the patch matrices within these forests (via grazing on woody regeneration and preventing gap closure by tree saplings; Scharnweber et al., 2007). Without cattle grazing in high light–low grazing sites, species such as *Matteuccia struthiopteris*, *Dryopteris caucasica*, *Pteridium aquilinum*, *Rubus caesius*, *Rubus hirtus*, *Rubus hyrcanus*, and *Sambucus ebulus* will exploit extensive gaps and suppress other plants both above- and below-ground by producing closed canopies and dense rooting layers (Figure 2d). These species are “native invaders” (Simberloff & Rejmánek, 2011; Shakeri, 2012), often originating from the soil seed bank (Esmailzadeh et al., 2011), which may suppress development of some climax forest species. Additionally, these species are strong competitors limiting the establishment and invasion of non-indigenous species with similar traits that exist in disturbed habitats along roadsides (Barrett & Barrett, 2001; Badami et al., 2015).

5 | CONCLUSION

In general, sites with higher light intensity in the Caspian beech forests tend to have a larger species pool and higher beta diversity by promoting early-successional plants; however, they had lower functional diversity compare to low-light sites. While species diversity increased inside the gap, the high filtering effect of light may converge community functional space toward suites of traits adapted to these particular conditions, and consequently, decrease functional diversity. Early-successional species (e.g. *Rubus* spp., *Poa* spp., and *Carex* spp.) generally have similar life-history traits and can produce forage of high quantity and palatability for macro-grazers, hence cattle prefer grazing in such open areas inside the forest. Consequently, grazing may facilitate plants with different functional traits by reducing the abundance of dominant plants and therefore may increase functional diversity.

Single-tree and group-tree selection systems are two close-to-nature silvicultural systems that have been practiced since 1980, and livestock grazing has a long history in Iranian Caspian forests. The Iranian forest service prohibited cattle grazing in 1967 and harvesting operations in 2017 as a strict conservation measure in order to protect biodiversity in these forest ecosystems. Nevertheless, our empirical data showed that traditional cattle grazing not only allows sustainable forest management but can also maintain species diversity and increase functional diversity in the Caspian Oriental beech forests.

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AUTHOR CONTRIBUTIONS

ZS and LE conceived the ideas and designed methods; ZS collected the data; ZS, MBR, and LE analyzed the data; ZS, DS, MBR, and LE led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

DATA AVAILABILITY STATEMENT

The vegetation and trait data are available as Appendix S4.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

Appendix S1. Photo of domestic cattle and a cowshed field
Appendix S2. Description of the sites and disturbance categories
Appendix S3. Suites of traits and codes used in figures and tables
Appendix S4. Plants and trait data

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