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Review

Forest Understorey Vegetation: Colonization and the Availability and Heterogeneity of Resources

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Abstract: Understorey vegetation comprises a major portion of plant diversity and contributes greatly to nutrient cycling and energy flow. This review examines the mechanisms involved in the response of understorey vegetation to stand development and the overstorey canopy following disturbances. The overall abundance and diversity of the understorey is enhanced with the availability and heterogeneity of light, soil nutrients, soil moisture, and substrates. Vascular plants are positively impacted by the availability and heterogeneity of light and soil nutrients, whereas non-vascular vegetation is more strongly influenced by colonization time, soil moisture, and substrates, and is decreased with a higher proportion of broadleaf overstorey. The availability of resources is a prominent driver toward the abundance and diversity of understorey vegetation, from the stand initiation to stem exclusion stage under a single-species dominated overstorey. However, resource heterogeneity dominates at the later stages of succession under a mixed overstorey. Climate and site conditions modify resource availability and heterogeneity in the understorey layer, but the extent of their influences requires more investigation. Forest management practices (clearcutting and partial harvesting) tend to increase light availability and heterogeneity, which facilitates the abundance and diversity of understorey vascular plants; however, these factors reduce the occurrence of non-vascular plants. Nevertheless, in the landscape context, anthropogenic disturbances homogenize environmental conditions and reduce beta-diversity, as well, the long-term effects of anthropogenic disturbances on understorey vegetation remain unclear, particularly compared with those in primary forests.

Keywords: overstorey canopy; resource availability; resource heterogeneity; colonization time; understorey vegetation

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1. Introduction

Understorey vegetation comprises a major component of plant diversity [1], which contributes to the structural complexity of forests, heterogeneous habitats for other biotic groups, water holding capacity, and nutrient retention [2]. Although understorey vegetation often contributes relatively a small portion to the biomass of overall forest ecosystems, it plays a critical role in nutrient cycling and energy flow due to the high turnover rates of understorey vegetation [1,3–7]. Several studies have revealed that the abundance, diversity, and composition of understorey vegetation change temporally with stand development following stand-replacing disturbances [8], and that the forest overstorey strongly mediates understorey vegetation [9]. However, the potential mechanisms involved with the responses of understorey vegetation to both stand development and overstorey are not yet fully elucidated.

Environmental or resource heterogeneity have long been recognized as promoting species coexistence and thus species diversity [10]. The availability of resources increases the abundance of organisms, and high abundance tends to be positively related to species diversity [11,12]. Understorey vegetation inhabits resource-limited environments, as the overstory asymmetrically influences the consumption of space, light, water, and nutrients [13]. Through an analysis of the published literature, Bartels and Chen [14] showed that understorey plant diversity increases with both resource heterogeneity and quantity in forests on a global scale. Nevertheless, it remains unclear how forest stand development, overstorey composition and diversity, and non-stand replacing disturbances affect understorey resource heterogeneity and quantity, and consequently influence understorey vegetation abundance and diversity. An improved understanding of the key driving factors and associated mechanisms of understorey vegetation abundance and diversity is of great significance for the conservation of biodiversity and sustainability of ecosystem service functions.

For this review, we initially introduce the primary drivers of understorey vegetation, abundance, and diversity. Subsequently, we examine the mechanisms behind understorey abundance and diversity. Then, we explore how these drivers and mechanisms may be altered due to climate and site conditions. Lastly, we compare the abundance and diversity response patterns of understorey vegetation under different forest management practices and associated mechanisms. In the first section, we focus on the patterns of understorey vegetation abundance and diversity that are impacted by stand age (colonization time), overstorey composition and diversity, and non-stand-replacing disturbances. In the second section, we examine how these three drivers modify the understorey quantity and heterogeneity of light, soil nutrients, soil moisture, and substrates, and in turn, affect understorey abundance and diversity. In the third section, we assess how local climate and site conditions modify understorey resource quantity and heterogeneity, and consequently impact understorey abundance and diversity. In the fourth section, we compare the effects of clearcutting and those of partial harvesting on the abundance and diversity of understorey vegetation, and examine the mechanisms involved that affect the patterns of these attributes in managed forests. In particular, we stress the need to understand multivariate relationships among the drivers including colonization time (i.e., stand age following stand-replacing disturbance), disturbance regimes, overstorey composition and diversity, the quantity and heterogeneity of understorey resources (e.g., light, nutrients, water, and substrates), and the abundance and diversity of understorey vegetation (Figure 1).

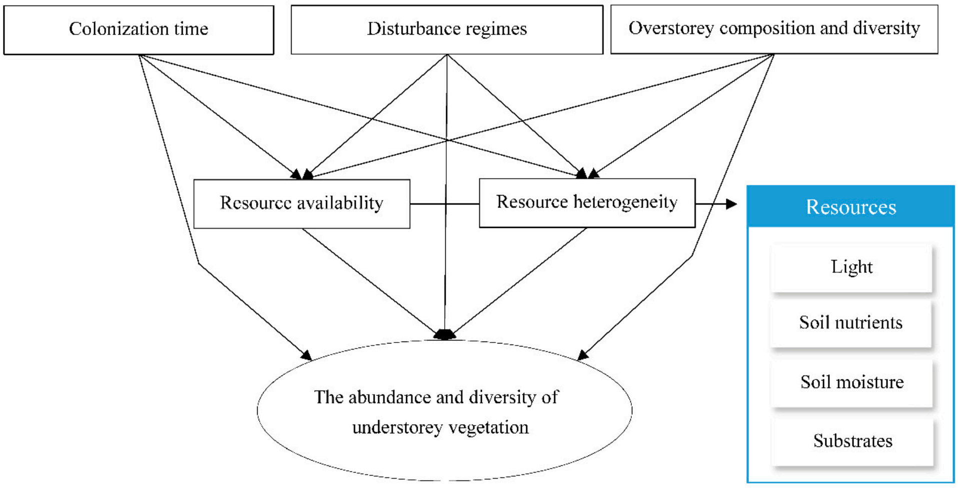

Figure 1. A conceptual model of hypothesized relationships showing how colonization time, disturbance regimes, overstorey composition and diversity, resource availability and heterogeneity influence the abundance and diversity of the understorey vegetation.

2. Driving Factors of Understorey Vegetation Abundance and Diversity

2.1. Colonization Time

Colonization time (i.e., stand age) has been emphasized as a critical driver that affects the patterns of abundance and diversity for understorey vegetation due to time-dependent colonization and the growth of understorey plants [8,15,16].

In the early stage of stand development, shade-intolerant and nutrient-demanding vascular plants colonize rapidly, due to sufficient growth space and the availability of resources (light and soil nutrients). This increases the abundance and diversity of vascular plants, while inhibiting the growth of non-vascular plants, a phenomenon that can pre-empt abundant resources [8,17]. With advancing stand age, the overstorey enters an intensely competitive stem exclusion period where competition-induced mortality, and the dramatic decline of light due to canopy closure, produces environmental filtering in the understorey layer [18,19]. This rapid reduction in the abundance and diversity of shade-intolerant vascular plants, gradually increases the abundance and diversity of shade-tolerant non-vascular plants, as non-vascular plants can tolerate lower light availability, whereas vascular plants cannot [8]. Decreased light availability may suppress the growth of all but the most shade-tolerant non-vascular plants. As the stand further matures, the increase of overstorey biomass significantly reduces the availability of resources in the understorey layer. This competition between the understorey and overstorey for soil nutrients is particularly intense; thus, it limits the growth of understorey vegetation, while decreasing the overall abundance and diversity of understorey vegetation. This reduces nutrient-demanding vascular plants to a great extent, while increasing the dominance of low nutrient-tolerant non-vascular plants [19]. When the stand develops further and transitions into the gap dynamics period, high tree mortality levels result in increased growth space, as well as abundant and heterogenous substrate resources, in the form of microtopographic tip-up mounds, and diverse classes of coarse woody debris (CWD) [20]. These changes in the understorey environment create conditions that are favorable for the growth of both vascular and non-vascular plants, and thus increases the abundance and diversity of understorey vegetation [21,22].

Disturbances are prevalent in all natural ecosystems, and integral for the maintenance of biodiversity [23,24]; however, anthropogenic alterations of these disturbance regimes (i.e., frequency, intensity, and type of disturbance) pose global threats to biodiversity [25]. Different disturbance regimes reinitiate forest stands and trigger resource reallocation [26–31]. As such, studying the patterns of understorey vegetation following various disturbance regimes may assist with clarifying how understorey vegetation responds to particular disturbances, toward improving the conservation of biodiversity in the context of dramatic declines in biodiversity worldwide [32]. Here, for reference, we include stand-replacing fire, a common disturbance type of stand-replacing disturbances in North America as an example. Previous studies have revealed that resource conditions are liable to be affected by stand-replacing fire disturbances [8,12,33–35], which result in increased light, soil nutrients, pH, and soil temperatures, and a decrease in the organic layer depth [15]. Immediately after fire, adequate growth space and resource availability greatly favor the establishment of vascular plants, which are fast-growing, nutrient-demanding, and shade-intolerant [8]. Moreover, higher soil temperatures are beneficial for breaking seed dormancy and promoting seed germination [36], while enhancing the abundance and diversity of understorey vegetation [37]. The cover and richness of understorey vegetation tend to peak within the first 40 years following fire disturbances in boreal forests [8]. Subsequently, the abundance and diversity of nutrient-demanding shade-intolerant vascular plants gradually decrease as a consequence of canopy closure, and the immobilization of soil nutrients, while non-vascular plants (which can tolerate low levels of nutrients and light) increase in abundance and diversity [33]. The severity of a stand-replacing fire may also impact the abundance and diversity of understorey vegetation. High-intensity fire destroys the propagules of dormant seeds in the humus layer of the forest floor, which results in a reduced number of re-colonizing understorey species [38].

2.2. Disturbance Regimes

In forest ecosystems, non-stand-replacing disturbances including windthrow, insect outbreaks, and canopy dieback are also important disturbance types that cannot be ignored, which also play key roles in affecting the abundance and diversity of understorey vegetation [8,39]. A classic theory (intermediate disturbance hypothesis (IDH)), predicts that disturbances of intermediate intensity and frequency promote the co-existence of early- and late-succession species, which supports the highest species abundance and diversity [40]. As such, the abundance and diversity of understorey vegetation are closely associated with disturbance regimes (i.e., disturbance intensity and frequency) [25]. However, recent studies have revealed that species diversity experiences a greater deficit under repeatedly occurring anthropogenic disturbances, such as high-grading, and that subsequent recovery cannot attain the reference level (i.e., climax stage) until decades, or longer, following the cessation of these disturbances [41].

Previous studies indicated that the occurrence of non-stand-replacing disturbances likely increased resource heterogeneity and availability in the understorey layer, which in turn had positive effects on the abundance and diversity of understorey vegetation [8,39]. At the late-successional stage, the formation of canopy gaps is most important for providing new colonizing opportunities for late-succession species, while allowing early-succession species to remain [42]. On the other hand, although understorey abundance and diversity increase following non-stand-replacing disturbances during the late-successional stage, they are still a declining trend over the long term [8].

The sizes of canopy gaps caused by non-stand-replacing disturbances affect the abundance and diversity of vascular and non-vascular plants. Generally, large canopy gaps caused by windthrow and insect outbreaks increase light availability, soil temperatures, soil nutrients, and coarse woody debris, all of which are more favorable for the growth of vascular plants [8,31]. Conversely, small canopy gaps caused by density-dependent canopy mortality and stand self-thinning have negligible effects on the abundance and diversity of vascular plants, due to their minimal impact on resource availability in the understorey layer [43]. Increases in resource heterogeneity—such as tip-up mounds and diverse coarse woody debris classes, result in abundant growth spaces and substrate sources, which enhance the abundance and diversity of non-vascular plants [8,21,39].

2.3. Overstorey Composition and Diversity

Overstorey composition and diversity are also important factors that influence the abundance and diversity of understorey vegetation [9,16,44,45]. Overstorey diversity was found to generate positive [19], neutral [33,46,47], and negative [48] effects on overall understorey diversity. Nevertheless, differences in overstorey composition, such as the relative abundance of deciduous broadleaf vs. evergreen coniferous trees might result in distinct abundances and diversities of understorey vascular and non-vascular plants [9,11,49]. Generally, broadleaf canopies support the establishment of nutrient-demanding and shade-intolerant vascular plants, whereas coniferous trees inhibit the growth of shade-intolerant vascular plants and increase the abundance and diversity of nutrient- and shade-tolerant non-vascular plants [8,16,50]. Higher resource availability under the broadleaf canopy favors the growth of nutrient-demanding and shade-intolerant vascular plants while the high decomposition rate and high pH of broadleaf litterfall inhibit the establishment of non-vascular plants, which prefer an acidic environment and are low nutrient-tolerant [49,51,52]. Additionally, the thick litterfall layer under coniferous canopies reduces light transmission (i.e., light availability), which inhibits the colonization and growth of vascular plants [53,54]. Alternatively, the abundance of non-vascular species, such as bryophytes and lichens increase, as they can survive without the need to root into the mineral layer of the soil [1].

Mixed overstorey canopies tend to support more abundant and diverse understorey vegetation than do pure broadleaf and coniferous canopies, as a consequence of resource heterogeneity caused by overstorey diversity [10,14,49,55]. This diversity reduces interspecific competition in the understorey and enables species with different resource requirements to co-exist [19]. Alternatively, the productivity of forests with mixed overstorey's is higher than other stand types [56], which not only consume additional available resources, but form resource filtering in the understorey layer, which results in a negative effect on the abundance and diversity of understorey vegetation [19]. Therefore, the abundance and diversity of vascular plants are highest under the broadleaf overstorey and lowest under the conifer overstorey, whereas the relationship is opposite for non-vascular plant abundance and diversity. Further to the positive effect of resource heterogeneity on understorey diversity, the availability of resources is also of great importance for the abundance and diversity of understorey vegetation, thus a mixed overstorey supports these attributes [9,33,47,49].

3. The Response of Understorey Vegetation Abundance and Diversity to Resource Availability and Heterogeneity

The patterns of understorey abundance and diversity are driven by time since colonization, overstorey composition, diversity, and disturbance regimes, through resource availability and heterogeneity that are influenced by these three driving factors regulate the abundance and diversity of understorey vegetation [14,16]. In the chronosequences of stand succession following the cessation of disturbances, how the availability and heterogeneity of light, soil nutrients, soil moisture, and substrates impact the abundance and diversity of understorey vegetation is still not understood.

3.1. Light

Light is commonly considered as the major limiting resource that affects understorey vegetation establishment and growth [11,50,57–59]. During the process of understorey restoration following a disturbance, light availability in the understorey was found to be negatively correlated with stand age, and decreased as stands mature, from initiation to the stem exclusion stage [16,18,47,60]. The growth of all understory vegetation—with the exception of the most shade-tolerant non-vascular plants—are inhibited due to the decline of light availability in the understorey, with the result being the gradual replacement of shade-intolerant vascular plants by shade-tolerant non-vascular plants; thus, lowering the overall abundance and diversity of understorey vegetation [8,11,49]. In particular, at more productive moist sites on low slope positions, the pace of forest development may be more rapid. This would accelerate overstorey canopy closure, leading to a greater decrease in light availability for the understorey, translating to more dramatic declines in the cover and richness of understorey vegetation [18,61].

Further, differences in overstorey composition and diversity may alter the availability and quality of light by modifying the way that it reaches the understorey layer (that is, the amount and quality of light) [9,33,62], which can influence the abundance and diversity of understorey vegetation [14,49]. Previous investigations revealed that the proportion of evergreen coniferous trees decreased light availability to the understorey, while limiting the total and vascular plant abundance and diversity of understorey vegetation [16]. Consequently, lower light availability in conjunction with reduced understorey abundance and diversity, suggested that resource supply controls species abundance and diversity, which supports the resource quantity hypothesis [14]. On the other hand, in older stands, frequent collapses and high tree mortality create multiple canopy gaps, which are a critical source of light heterogeneity for the understorey layer, which leads to increases in the abundance and diversity of both vascular and non-vascular plants [8,16]. Furthermore, several studies have reported that high diversity in the overstorey canopy has beneficial effects for understorey abundance and diversity [60], as a consequence of the light variability in the understorey layer that is created through the complementarity and overlapping of overstorey crowns [63–65]. As such, the abundance and diversity of understorey vegetation are positively affected by light heterogeneity [47,55,66], as predicted by the resource heterogeneity hypothesis.

3.2. Soil Nutrients

Soil nutrients are also key resources that affect understorey abundance and diversity [14]. The availability of soil nutrients is intimately associated with stand age and overstorey composition and diversity [9,11,62]. Generally, broadleaf overstorey canopies have higher soil nutrient availability than do coniferous canopies, due to their nutrient-rich leaf litterfall, as higher litterfall decomposition and nutrient retention rates support enhanced vascular plant abundance and diversity [49,67–71]. On the other hand, the abundance and diversity of total understorey vegetation, particularly shade-intolerant fast-growing vascular plants, are reduced under coniferous canopies, due to the limited availability of soil nutrients [47,62].

Fire, as a dominant disturbance type, especially in North American boreal forests, can enhance the availability of soil nutrients by releasing exchangeable base cations (including Ca^{2+}, Mg^{2+}, and K^{+}) in the ash produced by fire, which results in the rapid-colonization of fast-growing vascular plants immediately following fire [8,31,33,72–74]. As the time since fire disturbance proceeds, soil nutrients are re-immobilized in organic matter, which in turn reduces the availability of soil nutrients to the understorey layer, to decrease the abundance and diversity of understorey vegetation that were initially established following fire disturbance [11,15,19]. Therefore, a reduction in the supply of soil nutrients has a negative influence on the abundance and diversity of understorey vegetation, especially nutrient-demanding vascular understorey plants, which supports the resource quantity hypothesis. Conversely, earlier studies indicated that mixed overstorey canopies with complex compositions and structures tended to develop greater variations in spatial and temporal soil nutrients of the understorey layer [14,75]. They also supported the higher abundance and diversity of understorey vegetation [60], which was consistent with the resource heterogeneity hypothesis.

3.3. Soil Moisture

Access to soil moisture is also a non-trivial resource that impacts the abundance and diversity of understorey vegetation. The overstorey canopy can influence the availability of soil moisture through the interception of rainfall, stem flow, and water uptake from the deep soil layers [8,9,14,76]. Higher levels of soil moisture access may create conditions that are favorable for the abundance and diversity of understorey vegetation, particular for non-vascular plants such as bryophytes and lichens, which prefer moist environments [14,19,38,44,77]. Preceding studies have revealed that the biomass and diversity understorey vegetation are lower in sandy soils than clay soils, due to their rough texture, high salinity, and low available soil moisture [8,78,79]. Additionally, poorly drained lowlands possess a greater abundance and diversity of understorey vegetation than rapidly-draining uplands, which suggests that the abundance and diversity of understorey vegetation are positively influenced by the availability of soil moisture [77]. In the Northern Hemisphere, north-facing slopes typically favour higher abundance and diversity of understorey vegetation than do south-facing slopes, despite less light availability, but more soil moisture [80–82]. Moreover, access to soil moisture is intimately related with time since a stand-replacing fire disturbance. The availability of soil moisture was observed to decrease immediately following fire disturbance, due to a reduction in soil infiltration rates and organic layer depth [83]. As stands mature, soil moisture gradually increases with stand regeneration and organic layer thickening [15,83,84], while the abundance and diversity of understorey non-vascular plants also gradually increase because adequate access to soil moisture provides favorable living conditions for the colonization of understorey non-vascular plants [8]. Thus, as predicted by the resource quantity hypothesis, increased access to soil moisture supports higher understorey abundance and diversity.

3.4. Substrates

Substrates for understorey vegetation may vary, and take the form of CWD, tip-up mounds, exposed rocks and mineral soils, and plant litter [8,21,22,47,85–90]. It is known that CWD is a favorable substrate for the establishment of bryophyte and lichen species [91], while bare mineral soils and rocks provide colonizing space [85]. Thick litterfall layer directly influences the establishment and growth of understorey vegetation through the release of nutrients via decomposition, while indirectly decreasing temperature and increasing moisture at the soil surface, which alters the abundance and diversity of understorey vegetation [8,92,93].

The abundance and diversity of understorey vegetation were significantly affected by the abundance and diversity of CWD, in terms of decay status and tree species [9,14,21]. Nutrient-demanding vascular plants often colonize CWD under broadleaf canopies, while non-vascular plants are established on the CWD under coniferous canopies [94], as coniferous canopies are characterized by lower pH and nutrient content/availability than broadleaf canopies [51,95,96]. Moreover, the early stage of CWD decomposition is dominated by non-vascular plants, such as lichens and mosses. As CWD proceeds to decompose and becomes a part of the forest floor, vascular plants will gradually replace the colonized non-vascular plants in the early stage, which allows some species from prior decay classes to persist later on [21,97,98]. Forest floors with different CWD decay classes and substrate species that are provided by mixed overstorey trees, may provide niches for species with varying resource requirements, while supporting the continuous colonization of diverse species, resulting in the higher abundance and diversity of understorey vegetation [22,90,99]. Substrate heterogeneity tends to increase gradually with advancing stand age [16], which results from increasing CWD and tip-up mounds due to self-thinning at the stem exclusion stage, and longevity induced mortality at the canopy transition stage [8]. This increased substrate heterogeneity contributes to the enhanced abundance and diversity of understorey vegetation, particularly bryophyte and lichen species [21,22].

4. Effects of Climate and Site Conditions on Understorey Abundance and Diversity

The abundance and diversity of understorey vegetation are directly or indirectly impacted by time for colonization, overstorey composition and diversity, non-stand-replacing disturbances, the availability and heterogeneity of light, soil nutrients, soil moisture, and substrates [8,9,14,16,33]. However, the influences of climate and site conditions on understorey abundance and diversity, which mediate overstorey canopy, disturbances, and the availability and heterogeneity of resources in the understorey layer must also be taken into account [44,100–103].

4.1. Climate

Climate comprises one of the most critical abiotic factors for the determination of understorey vegetation richness at large spatial scales [44,104]. With rising atmospheric CO_2, resulting in global warming and gradually increasing surface soil temperatures, the climate moisture index (CMI) (which is the mean annual precipitation minus annual potential evapotranspiration) decreases. Several studies have reported that CMI is significantly positively correlated with the richness of total understorey vegetation [19,38]. In forest ecosystems, rising temperatures not only increase the frequency and severity of wildfires but accelerates the rate of litterfall decomposition. Both of these factors have a significant role in the establishment and growth of understorey vegetation, due to increasing resource availability and heterogeneity [105–107]. On the other hand, overstorey canopies, which likely serve as thermal insulators, may reduce the severity of the impacts of warming on understorey vegetation abundance and diversity by altering temperature, moisture, and wind speeds in forests at localized scales [101,102,108,109]. To predict the effects of global warming on understorey abundance and diversity, we need to better elucidate the responses of overstorey canopies to a changing climate, and how it consequently modifies the understorey microclimate and resource conditions, which regulate the abundance and diversity of understorey vegetation [14,101,102].

4.2. Site Conditions

Site conditions often play an important role in influencing the abundance and diversity of understorey vegetation through the modification of light, soil nutrients, soil moisture, and substrate diversity [15,44,47,88]. Soil texture is particularly crucial for the moisture and nutrient retention capacities of soils [110], which determine the germination and growth of tree seedlings, as well as the development of plant roots [79], while impacting the richness and cover of understorey vegetation [44,77,111]. Soils with higher available nutrients and moisture support more abundant and diverse understorey vegetation, in contrast to soils with low levers of nutrients and moisture [47]. Further, elevation, slope aspect, and slope position play a considerable role in the development of understorey vegetation communities [15,18,112,113]. In the Northern Hemisphere, northern slopes typically favor more highly abundant understorey vegetation and diversity than southern slopes, as the damp forest microclimates and fertile soils of north-facing slopes promote the generation of understorey vegetation [80–82]. In mountain landscapes, topography can affect the hydrological conditions of the area by controlling the patterns of evapotranspiration and water flow, which may significantly change the availability of resources and heterogeneity in the understorey layer (e.g., light, soil moisture, and nutrients), thereby affecting the composition and diversity of understory vegetation [114,115]. For example, topographic factors impact the depth of the organic layer by regulating the decomposition of litter and the growth of moss, which in turn influence the diversity of understorey vegetation. Sites with intermediate organic layer depth typically favor vascular plants over non-vascular plants [8,15,77].

Although climate and site conditions convey significant impacts on the abundance and diversity of understorey vegetation, few studies have quantified their simultaneous effects on the abundance and diversity of various vegetation strata. A few existing studies found that the extent of the effects of climate and site conditions on plant species diversity may vary, contingent on the differences in vegetation strata. Climate factors predominantly control overstorey diversity, while understorey diversity is regulated more by site conditions [44]. Overstorey diversity may directly or indirectly impact the abundance and diversity of understorey vegetation [9,49,116]. As such, there are complex relationships that exist between the abundance and diversity of vegetation and environmental factors, which may be attributable to interactions among plant groups and modifications to the extent of their interactions with environmental conditions [117]. There remains a considerable knowledge gap in regard to how climate and site conditions alter the overstorey canopy, to consequently affect the abundance and diversity of understorey vegetation across broad geographical scales.

5. The Effects of Forest Management Practices (Clearcutting and Partial Harvesting) on the Abundance and Diversity of Understorey Vegetation

Clearcutting and partial harvesting are two common disturbance types in forest management practices that affect the abundance and diversity of understorey vegetation [8,35,118–120]. In surveying the published literature, we found that these forest management practices influence the abundance and diversity of understorey vegetation through the mechanisms described above; colonization time, resource availability, and resource heterogeneity [39,94,118,121–123]. Elucidating how forest management practices impact the time available for plant colonization, understorey resource quantity, and variability (and thus the abundance and diversity of understorey vegetation) is critical for the conservation of biodiversity and ecosystem functionality, in the context of increasing species loss.

Regardless of which types of forest management practices are adopted, the lack of sufficient time for colonization will reduce the abundance and diversity of understorey vegetation, as species with low dispersal capacities require a long time to colonize into newly available spaces and tap into resources following disturbances [16,121]. In the interim, clearcutting and partial harvesting are likely to modify the abundance and diversity of understorey vegetation by altering the understorey resource availability and heterogeneity [23,30,118,124–127]. In contrast to stand-replacing wildfire that eradicates both overstorey and understorey vegetation, and releases soil nutrients through the combustion of coarse woody debris [15,69,118,120], clearcutting, which also removes overstorey vegetation, has a lesser impact on understorey vegetation [14,33,123]. Partial harvesting is divided into uniform harvesting and patch harvesting, both of which increase light availability and heterogeneity in the understorey, particularly with patch harvesting, and decrease the availability of soil moisture [66,119,128–130].

Clearcutting and stand-replacing fire tend to have similar influences on the abundance and diversity of understorey vegetation [118,125]. Immediately following clearcutting or stand-replacing fire, the resulting increase in colonization areas, in conjunction with abundant light and soil nutrients provide suitable growth spaces for nutrient-demanding and shade-intolerant vascular plants, which results in an upsurge in the abundance and diversity of vascular plants. However, the abundance and diversity of non-vascular plants are low due to their weak colonization capacity and tolerance to low soil moisture [8,15,16,33]. As the time for colonization proceeds, overstorey canopy closure, and increasing forest biomass leads to the limited availability of understorey light and soil nutrients [16,18]. Nutrient-demanding and shade-intolerant vascular plants established at the initial successional stage are gradually replaced by low light- and nutrient-tolerant non-vascular plants, which may be attributed to the increased availability of soil moisture following the regeneration of vegetation and additional time to colonize the growth space [11,22,49,121].

The partial harvesting of overstorey trees increases understorey light availability, thereby enhancing the abundance and diversity of vascular plants [33,128,131]; however, reducing the availability of soil moisture exerts a negative influence on non-vascular plants, which have a preference for moist environments [123]. In the meantime, partial harvesting alters the quality of the substrate, particularly the CWD inputs with varying decay classes and tree species [94,132]. These substrate changes can enhance the abundance and diversity of non-vascular plants such as bryophytes [21,22,133]. The continued accumulation of fresh CWD facilitates the coexistence of species with variable soil nutrient and soil moisture requirements, thereby increasing total understorey abundance and diversity [21,94]. In comparison to natural non-stand-replacing disturbances such as windthrow, insect outbreaks, and canopy dieback [8], partial harvesting removes large logs, therefore fewer substrates are available for species with a strong preference for CWD [22,94,134]. However, the long-term effects of partial harvesting on understorey vegetation, in contrast to those of non-stand-replacing natural disturbances, remain to be examined [135].

6. Conclusions and Future Perspectives

(1) The abundance and diversity of understorey vegetations are directly affected by resource availability and heterogeneity, while stand age, various disturbance regimes, as well as overstorey composition, and diversity can also directly impact understorey vegetation. Simultaneously, the three key drivers (stand age, disturbance regimes, and overstorey composition and diversity) modify the availability and heterogeneity of understorey resources; thus, indirectly impacting the abundance and diversity of understorey vegetation. Moreover, climate and site conditions play important roles in understorey abundance and diversity by manipulating overstory composition and diversity, disturbances, and the availability and heterogeneity of resources.

(2) The abundance and diversity of understorey vegetation may be affected not only by a single resource, but also through the interactions of multiple resources, including light, soil nutrients, soil moisture, and substrates. Furthermore, the effects of resource availability and heterogeneity on understorey abundance and diversity vary with time since colonization, and overstorey composition and diversity. In general, resource availability has more influence on the abundance and diversity of understorey vegetation when the stand age lies between the initial stand development stage and the stem exclusion stage, whereas resource heterogeneity exerts a greater influence at the later stage of succession. The abundance and diversity of understorey vegetation are typically more affected by resource availability under an overstorey that is dominated by either broadleaves or conifers, due to relatively homogeneous resource conditions. However, they are more influenced by resource heterogeneity under a mixed overstorey canopy comprised of both broadleaves and conifers, due to the higher spatial and temporal variation of resources in the understorey layer.

(3) Further studies are required to investigate the relative importance and interactions of multiple resources that influence the abundance and diversity of understorey vegetation. Meanwhile, environmental factors (climate and site conditions) should also be considered in the context of global warming. Moreover, relationships between the abundance, diversity, and productivity of understorey vegetation and its contributions to overall forest ecosystems need to be better elucidated. We stress the need to improve our understanding of multivariate relationships between stand age, disturbance regimes, overstorey composition and diversity, the availability and heterogeneity of light, soil nutrients, soil moisture and substrates, climate, and site conditions, with understorey abundance and diversity.

(4) There is a growing body of studies that show when the focus is set only on species diversity within local communities—alpha diversity (number and abundance of species within local communities of interacting species)—they fail to fully evaluate the mechanisms and processes of local communities, and even overestimate its impact on ecological functionality [33,136,137]. It is important to focus on beta diversity (variation in the identities and abundance of species between local assemblages) in ecological communities, which provides insights into the mechanisms that drive changes in species diversity, and their effects on ecosystem functions [137]. In nature, both determination processes (e.g., competitive habitat filtering hierarchy among species and interspecific niche partitioning) and stochastic processes (e.g., historical contingency, ecological drift, and dispersal limitation) influence community assemblages [137–139]. Following anthropogenic disturbances such as deforestation, homogenized environmental conditions reduce the variability of species assemblages at the landscape level; that is, there is less functional distinctiveness between plant communities in these disturbed regions, and thus a reduction in beta diversity [140–143]. Crucially, there is a growing body of evidence which reveals that the decreased cover of primary forests results in a serious reduction in beta diversity [144–147]. In conclusion, it is critical to aggressively protect the remaining primary forests worldwide, in the face of the global crisis of biodiversity loss.

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References

1. Nilsson, M.C.; Wardle, D.A. Understory vegetation as a forest ecosystem driver: Evidence from the northern Swedish boreal forest. *Front. Ecol. Environ.* **2005**, *3*, 421–428. [CrossRef]
2. Whigham, D.E. Ecology of woodland herbs in temperate deciduous forests. *Annu. Rev. Ecol. Evol. Syst.* **2004**, *35*, 583–621. [CrossRef]
3. Gilliam, F.S. The ecological significance of the herbaceous layer in temperate forest ecosystems. *Bioscience* **2007**, *57*, 845–858. [CrossRef]
4. Hubau, W.; De Mil, T.; Van den Bulcke, J.; Phillips, O.L.; Angoboy Ilondea, B.; Van Acker, J.; Sullivan, M.J.P.; Nsenga, L.; Toirambe, B.; Couralet, C.; et al. The persistence of carbon in the African forest understory. *Nat. Plants* **2019**, *5*, 133–140. [CrossRef] [PubMed]
5. Powers, R.F.; Andrew Scott, D.; Sanchez, F.G.; Voldseth, R.A.; Page-Dumroese, D.; Elioff, J.D.; Stone, D.M. The North American long-term soil productivity experiment: Findings from the first decade of research. *For. Ecol. Manag.* **2005**, *220*, 31–50. [CrossRef]
6. Kumar, P.; Chen, H.Y.H.; Searle, E.B.; Shahi, C. Dynamics of understorey biomass, production and turnover associated with long-term overstorey succession in boreal forest of Canada. *For. Ecol. Manag.* **2018**, *427*, 152–161. [CrossRef]

7. Landuyt, D.; De Lombaerde, E.; Perring, M.P.; Hertzog, L.R.; Ampoorter, E.; Maes, S.L.; De Frenne, P.; Ma, S.; Proesmans, W.; Blondeel, H. The functional role of temperate forest understorey vegetation in a changing world. *Glob. Chang. Biol.* **2019**, *25*, 3625–3641. [CrossRef]
8. Hart, S.A.; Chen, H.Y.H. Understory vegetation dynamics of North American boreal forests. *Crit. Rev. Plant Sci.* **2006**, *25*, 381–397. [CrossRef]
9. Barbier, S.; Gosselin, F.; Balandier, P. Influence of tree species on understory vegetation diversity and mechanisms involved—A critical review for temperate and boreal forests. *For. Ecol. Manag.* **2008**, *254*, 1–15. [CrossRef]
10. Stein, A.; Gerstner, K.; Kreft, H. Environmental heterogeneity as a universal driver of species richness across taxa, biomes and spatial scales. *Ecol. Lett.* **2014**, *17*, 866–880. [CrossRef]
11. Reich, P.B.; Frelich, L.E.; Voldseth, R.A.; Bakken, P.; Adair, E.C. Understorey diversity in southern boreal forests is regulated by productivity and its indirect impacts on resource availability and heterogeneity. *J. Ecol.* **2012**, *100*, 539–545. [CrossRef]
12. Veldman, J.W.; Brudvig, L.A.; Damschen, E.I.; Orrock, J.L.; Mattingly, W.B.; Walker, J.L. Fire frequency, agricultural history and the multivariate control of pine savanna understorey plant diversity. *J. Veg. Sci.* **2015**, *25*, 1438–1449. [CrossRef]
13. Grime, J.P. Benefits of plant diversity to ecosystems: immediate, filter and founder effects. *J. Ecol.* **1998**, *86*, 902–910. [CrossRef]
14. Bartels, S.F.; Chen, H.Y. Is understory plant species diversity driven by resource quantity or resource heterogeneity? *Ecology* **2010**, *91*, 1931–1938. [CrossRef]
15. Liu, B.; Yang, J.; Johnstone, J.F. Understory vascular plant community assembly in relation to time-since-fire and environmental variables in a Chinese boreal forest. *J. Mt. Sci.* **2017**, *14*, 1317–1328. [CrossRef]
16. Kumar, P.; Chen, H.Y.H.; Thomas, S.C.; Shahi, C.; Gilliam, F. Linking resource availability and heterogeneity to understorey species diversity through succession in boreal forest of Canada. *J. Ecol.* **2018**, *106*, 1266–1276. [CrossRef]
17. Chipman, S.J.; Johnson, E.A. Understory vascular plant species diversity in the mixedwood boreal forest of Western Canada. *Ecol. Appl.* **2002**, *12*, 588–601. [CrossRef]
18. Halpern, C.B.; Lutz, J.A. Canopy closure exerts weak controls on understory dynamics: A 30-year study of overstory–understory interactions. *Ecol. Monogr.* **2013**, *83*, 221–237. [CrossRef]
19. Zhang, Y.; Chen, H.Y.H.; Taylor, A.R.; Ostertag, R. Positive species diversity and above-ground biomass relationships are ubiquitous across forest strata despite interference from overstorey trees. *Funct. Ecol.* **2017**, *31*, 419–426. [CrossRef]
20. Chen, H.Y.; Popadiouk, R.V. Dynamics of North American boreal mixedwoods. *Environ. Rev.* **2002**, *10*, 137–166. [CrossRef]
21. Kumar, P.; Chen, H.Y.; Thomas, S.C.; Shahi, C. Effects of coarse woody debris on plant and lichen species composition in boreal forests. *J. Veg. Sci.* **2017**, *28*, 389–400. [CrossRef]
22. Kumar, P.; Chen, H.Y.H.; Thomas, S.C.; Shahi, C. Epixylic vegetation abundance, diversity, and composition vary with coarse woody debris decay class and substrate species in boreal forest. *Can. J. For. Res.* **2018**, *48*, 399–411. [CrossRef]
23. Guitet, S.; Sabatier, D.; Brunaux, O.; Couteron, P.; Denis, T.; Freycon, V.; Gonzalez, S.; Hérault, B.; Jaouen, G.; Molino, J.F. Disturbance regimes drive the diversity of regional floristic pools across Guianan rainforest landscapes. *Sci. Rep.* **2018**, *8*, 3872. [CrossRef] [PubMed]
24. Bengtsson, J.; Nilsson, S.G.; Franc, A.; Menozzi, P. Biodiversity, disturbances, ecosystem function and management of european forests. *For. Ecol. Manag.* **2000**, *132*, 39–50. [CrossRef]
25. Newbold, T.; Hudson, L.N.; Hill, S.L.; Contu, S.; Lysenko, I.; Senior, R.A.; Börger, L.; Bennett, D.J.; Choimes, A.; Collen, B. Global effects of land use on local terrestrial biodiversity. *Nature* **2015**, *520*, 45. [CrossRef] [PubMed]
26. Alcañiz, M.; Outeiro, L.; Francos, M.; Farguell, J.; Úbeda, X. Long-term dynamics of soil chemical properties after a prescribed fire in a mediterranean forest (montgrí massif, Catalonia, Spain). *Sci. Tot. Environ.* **2016**, *572*, 1329–1335. [CrossRef]
27. Zhou, L.; Cai, L.; He, Z.; Wang, R.; Wu, P.; Ma, X. Thinning increases understory diversity and biomass, and improves soil properties without decreasing growth of Chinese fir in southern china. *Environ. Sci. Pollut. Res.* **2016**, *23*, 24135–24150. [CrossRef]

28. Döbert, T.F.; Webber, B.L.; Sugau, J.B.; Dickinson, K.J.M.; Didham, R.K. Logging increases the functional and phylogenetic dispersion of understorey plant communities in tropical lowland rainforest. *J. Ecol.* **2017**, *105*, 1235–1245. [CrossRef]
29. Fahey, R.; Puettmann, K. Ground-layer disturbance and initial conditions influence gap partitioning of understorey vegetation. *J. Ecol.* **2007**, *95*, 1098–1109. [CrossRef]
30. Barefoot, C.R.; Willson, K.G.; Hart, J.L.; Schweitzer, C.J.; Dey, D.C. Effects of thinning and prescribed fire frequency on ground flora in mixed pinus-hardwood stands. *For. Ecol. Manag.* **2019**, *432*, 729–740. [CrossRef]
31. Scharenbroch, B.C.; Nix, B.; Jacobs, K.A.; Bowles, M.L. Two decades of low-severity prescribed fire increases soil nutrient availability in a midwestern, USA oak (*quercus*) forest. *Geoderma* **2012**, *183–184*, 80–91. [CrossRef]
32. Chang, C.C.; Turner, B.L. Ecological succession in a changing world. *J. Ecol.* **2019**, *107*, 503–509. [CrossRef]
33. Hart, S.A.; Chen, H.Y. Fire, logging, and overstory affect understory abundance, diversity, and composition in boreal forest. *Ecol. Monogr.* **2008**, *78*, 123–140. [CrossRef]
34. Grossman, J.J.; Cavender-Bares, J.; Reich, P.B.; Montgomery, R.A.; Hobbie, S.E.; Shefferson, R. Neighborhood diversity simultaneously increased and decreased susceptibility to contrasting herbivores in an early stage forest diversity experiment. *J. Ecol.* **2018**, *107*, 1492–1505. [CrossRef]
35. Goodwin, M.J.; North, M.P.; Zald, H.S.; Hurteau, M.D. The 15-year post-treatment response of a mixed-conifer understory plant community to thinning and burning treatments. *For. Ecol. Manag.* **2018**, *429*, 617–624. [CrossRef]
36. Santana, V.M.; Bradstock, R.A.; Ooi, M.K.J.; Denham, A.J.; Auld, T.D.; Baeza, M.J. Effects of soil temperature regimes after fire on seed dormancy and germination in six Australian *Fabaceae* species. *Aust. J. Bot.* **2010**, *58*, 539–545. [CrossRef]
37. Hu, M.; Liu, Y.; Sun, Z.; Zhang, K.; Liu, Y.; Miao, R.; Wan, S. Fire rather than nitrogen addition affects understory plant communities in the short term in a coniferous-broadleaf mixed forest. *Ecol. Evol.* **2018**, *8*, 8135–8148. [CrossRef]
38. Yeboah, D.; Chen, H.Y.H.; Kingston, S. Tree species richness decreases while species evenness increases with disturbance frequency in a natural boreal forest landscape. *Ecol. Evol.* **2016**, *6*, 842–850. [CrossRef]
39. Grandpré, L.; Boucher, D.; Bergeron, Y.; Gagnon, D. Effects of small canopy gaps on boreal mixedwood understory vegetation dynamics. *Commun. Ecol.* **2011**, *12*, 67–77. [CrossRef]
40. Connell, J.H. Diversity in tropical rain forests and coral reefs. *Science* **1978**, *199*, 1302–1310. [CrossRef]
41. Moreno-Mateos, D.; Barbier, E.B.; Jones, P.C.; Jones, H.P.; Aronson, J.; López-López, J.A.; McCrackin, M.L.; Meli, P.; Montoya, D.; Benayas, J.M.R. Anthropogenic ecosystem disturbance and the recovery debt. *Nat. Commun.* **2017**, *8*, 14163. [CrossRef] [PubMed]
42. De Grandpre, L.; Bergeron, Y. Diversity and stability of understorey communities following disturbance in the southern boreal forest. *J. Ecol.* **1997**, *85*, 777–784. [CrossRef]
43. Guo, Y.; Zhao, P.; Yue, M. Canopy disturbance and gap partitioning promote the persistence of a pioneer tree population in a near-climax temperate forest of the Qinling mountains, China. *Ecol. Evol.* **2019**, *9*, 7677–7687. [CrossRef] [PubMed]
44. Zhang, Y.; Chen, H.Y.H.; Taylor, A. Multiple drivers of plant diversity in forest ecosystems. *Glob. Ecol. Biogeogr.* **2014**, *23*, 885–893. [CrossRef]
45. Jo, I.; Potter, K.M.; Domke, G.M.; Fei, S. Dominant forest tree mycorrhizal type mediates understory plant invasions. *Ecol. Lett.* **2018**, *21*, 217–224. [CrossRef]
46. Cook, J.E. Structural effects on understory attributes in second-growth forests of northern Wisconsin, USA. *For. Ecol. Manag.* **2015**, *347*, 188–199. [CrossRef]
47. Chen, H.Y.H.; Biswas, S.R.; Sobey, T.M.; Brassard, B.W.; Bartels, S.F.; Mori, A. Reclamation strategies for mined forest soils and overstorey drive understorey vegetation. *J. Appl. Ecol.* **2018**, *55*, 926–936. [CrossRef]
48. Ellum, D.S.; Ashton, M.S.; Siccama, T.G. Spatial pattern in herb diversity and abundance of second growth mixed deciduous-evergreen forest of Southern New England, USA. *For. Ecol. Manag.* **2010**, *259*, 1416–1426. [CrossRef]
49. Bartels, S.F.; Chen, H.Y.H. Interactions between overstorey and understorey vegetation along an overstorey compositional gradient. *J. Veg. Sci.* **2013**, *24*, 543–552. [CrossRef]
50. Liu, T.Y.; Lin, K.C.; Vadeboncoeur, M.A.; Chen, M.Z.; Huang, M.Y.; Lin, T.C. Understorey plant community and light availability in conifer plantations and natural hardwood forests in Taiwan. *Appl. Veg. Sci.* **2015**, *18*, 591–602. [CrossRef]

51. Pereira, I.; Müller, F.; Moya, M. Influence of nothofagus bark pH on the lichen and bryophytes richness, Central Chile/influencia del ph de la corteza de nothofagus sobre la riqueza de líquenes y briófitos, Chile central. *Gayana Botanica* **2014**, *71*, 120–130. [CrossRef]
52. Botting, R.S.; Delong, C. Macrolichen and bryophyte responses to coarse woody debris characteristics in sub-boreal spruce forest. *For. Ecol. Manag.* **2009**, *258*, S85–S94. [CrossRef]
53. Koorem, K.; Moora, M. Positive association between understory species richness and a dominant shrub species (*Corylus avellana*) in a boreonemoral spruce forest. *For. Ecol. Manag.* **2010**, *260*, 1407–1413. [CrossRef]
54. Anders, M.; Jean-Pierre, H.; Thomas, P.; Sandrine, P.; Nathalie, K. The effect of deer browsing and understory light availability on stump mortality and sprout growth capacity in sessile oak. *For. Ecol. Manag.* **2018**, *430*, 134–142.
55. Evy, A.; Federico, S.; Harald, A.; Lander, B.; Sigrid, B.; Elisa, C.; Andrea, C.; Mariangela, F.; Kalliopi, R.; Nurlaila, S.N.; et al. Driving mechanisms of overstorey–understorey diversity relationships in European forests. *Perspect. Plant Ecol. Evol. Syst.* **2016**, *19*, 21–29. [CrossRef]
56. Zhang, Y.; Chen, H.Y.H.; Reich, P.B. Forest productivity increases with evenness, species richness and trait variation: A global meta-analysis. *J. Ecol.* **2012**, *100*, 742–749. [CrossRef]
57. Neufeld, H.S.; Young, D.R. Ecophysiology of the herbaceous layer in temperate deciduous forests. In *The Herbaceous Layer in Forests of Eastern North America*; Oxford University Press: New York, NY, USA, 2014.
58. Berrill, J.P.; Schneider, K.; Dagley, C.M.; Webb, L.A. Understory light predicts stump sprout growth in mixed multiaged stands in North Coastal California. *New For.* **2018**, *49*, 815–828. [CrossRef]
59. Chen, H.Y.; Klinka, K.; Kayahara, G.J. Effects of light on growth, crown architecture, and specific leaf area for naturally established *Pinus contorta* var. Latifolia and Pseudotsuga menziesii var. Glauca saplings. *Can. J. For. Res.* **1996**, *26*, 1149–1157.
60. Vockenhuber, E.A.; Scherber, C.; Langenbruch, C.; Meißner, M.; Seidel, D.; Tscharntke, T. Tree diversity and environmental context predict herb species richness and cover in Germany's largest connected deciduous forest. *Perspect. Plant Ecol. Evol. Syst.* **2011**, *13*, 111–119. [CrossRef]
61. Larson, A.J.; Lutz, J.A.; Gersonde, R.F.; Franklin, J.F.; Hietpasi, F.F. Potential site productivity influences the rate of forest structural development. *Ecol. Appl.* **2008**, *18*, 899–910. [CrossRef]
62. Chávez, V.; Macdonald, S.E. Partitioning vascular understory diversity in mixedwood boreal forests: The importance of mixed canopies for diversity conservation. *For. Ecol. Manag.* **2012**, *271*, 19–26. [CrossRef]
63. Ligot, G.; Ameztegui, A.; Courbaud, B.; Coll, L.; Kneeshaw, D. Tree light capture and spatial variability of understory light increase with species mixing and tree size heterogeneity. *Can. J. For. Res.* **2016**, *46*, 968–977. [CrossRef]
64. Vallet, P.; Pérot, T. Silver fir stand productivity is enhanced when mixed with Norway spruce: Evidence based on large-scale inventory data and a generic modelling approach. *J. Veg. Sci.* **2011**, *22*, 932–942. [CrossRef]
65. Kelty, M.J. The role of species mixtures in plantation forestry. *For. Ecol. Manag.* **2006**, *233*, 195–204. [CrossRef]
66. Tsai, H.C.; Chiang, J.M.; McEwan, R.W.; Lin, T.C. Decadal effects of thinning on understory light environments and plant community structure in a subtropical forest. *Ecosphere* **2018**, *9*, e02464. [CrossRef]
67. Leppert, K.N.; Niklaus, P.A.; Scherer-Lorenzen, M. Does species richness of subtropical tree leaf litter affect decomposition, nutrient release, transfer and subsequent uptake by plants? *Soil Biol. Biochem.* **2017**, *115*, 44–53. [CrossRef]
68. Santonja, M.; Fernandez, C.; Proffit, M.; Gers, C.; Gauquelin, T.; Reiter, I.M.; Cramer, W.; Baldy, V.; McCulley, R. Plant litter mixture partly mitigates the negative effects of extended drought on soil biota and litter decomposition in a Mediterranean oak forest. *J. Ecol.* **2017**, *105*, 801–815. [CrossRef]
69. Duan, H.; Wang, L.; Zhang, Y.; Fu, X.; Tsang, Y.; Wu, J.; Le, Y. Variable decomposition of two plant litters and their effects on the carbon sequestration ability of wetland soil in the Yangtze River estuary. *Geoderma* **2018**, *319*, 230–238. [CrossRef]
70. Cobb, R.C.; Rizzo, D.M. Litter chemistry, community shift, and non-additive effects drive litter decomposition changes following invasion by a generalist pathogen. *Ecosystems* **2016**, *19*, 1478–1490. [CrossRef]
71. Augusto, L.; De Schrijver, A.; Vesterdal, L.; Smolander, A.; Prescott, C.; Ranger, J. Influences of evergreen gymnosperm and deciduous angiosperm tree species on the functioning of temperate and boreal forests. *Biol. Rev. Camb. Philos. Soc.* **2015**, *90*, 444–466. [CrossRef]
72. Kong, J.J.; Yang, J.; Chu, H.; Xiang, X. Effects of wildfire and topography on soil nitrogen availability in a boreal larch forest of Northeastern China. *Int. J. Wildl. Fire* **2015**, *24*, 433–442. [CrossRef]

73. Arocena, J.; Opio, C. Prescribed fire-induced changes in properties of sub-boreal forest soils. *Geoderma* **2003**, *113*, 1–16. [CrossRef]
74. Lavoie, M.; Starr, G.; Mack, M.C.; Martin, T.A.; Gholz, H.L. Effects of a prescribed fire on understory vegetation, carbon pools, and soil nutrients in a longleaf pine-slash pine forest in Florida. *Nat. Areas J.* **2010**, *30*, 82–94. [CrossRef]
75. Macdonald, S.E.; Fenniak, T.E. Understory plant communities of boreal mixedwood forests in Western Canada: Natural patterns and response to variable-retention harvesting. *For. Ecol. Manag.* **2007**, *242*, 34–48. [CrossRef]
76. Lindh, B.C.; Gray, A.N.; Spies, T.A. Responses of herbs and shrubs to reduced root competition under canopies and in gaps: A trenching experiment in old-growth douglas-fir forests. *Can. J. For. Res.* **2003**, *33*, 2052–2057. [CrossRef]
77. Mallon, E.E.; Turetsky, M.R.; Thompson, I.D.; Fryxell, J.M.; Wiebe, P.A. Effects of disturbance on understory succession in upland and lowland boreal forests and implications for woodland caribou (*Rangifer tarandus caribou*). *For. Ecol. Manag.* **2016**, *364*, 17–26. [CrossRef]
78. Legare, S.; Bergeron, Y.; Pare, D. Influence of forest composition on understory cover in boreal mixedwood forests of Western Quebec. *Silva Fenn.* **2002**, *36*, 353–366. [CrossRef]
79. Jung, K.; Duan, M.; House, J.; Chang, S.X. Textural interfaces affected the distribution of roots, water, and nutrients in some reconstructed forest soils in the Athabasca oil sands region. *Ecol. Eng.* **2014**, *64*, 240–249. [CrossRef]
80. Sigua, G.C.; Albano, J.; Williams, M. Spatial distribution of soil phosphorus and herbage mass in beef cattle pastures: Effects of slope aspect and slope position. *Nutr. Cycl. Agroecosyst.* **2011**, *89*, 59–70. [CrossRef]
81. Sewerniak, P. Differences in early dynamics and effects of slope aspect between naturally regenerated and planted *Pinus sylvestris* woodland on inland dunes in Poland. *IForest* **2016**, *9*, 875–882. [CrossRef]
82. Thrippleton, T.; Bugmann, H.; Folini, M.; Snell, R.S. Overstorey–understorey interactions intensify after drought-induced forest die-off: Long-term effects for forest structure and composition. *Ecosystems* **2017**, *21*, 723–739. [CrossRef]
83. Bond-Lamberty, B.; Peckham, S.D.; Gower, S.T.; Ewers, B.E. Effects of fire on regional evapotranspiration in the Central Canadian boreal forest. *Glob. Chang. Biol.* **2009**, *15*, 1242–1254. [CrossRef]
84. Kasischke, E.S.; Johnstone, J.F. Variation in postfire organic layer thickness in a black spruce forest complex in interior Alaska and its effects on soil temperature and moisture. *Can. J. For. Res.* **2005**, *35*, 2164–2177. [CrossRef]
85. Brassard, B.W.; Chen, H.Y. Stand structural dynamics of North American boreal forests. *Crit. Rev. Plant Sci.* **2006**, *25*, 115–137. [CrossRef]
86. Jonsson, B.G.; Esseen, P.A. Treefall disturbance maintains high bryophyte diversity in a boreal spruce forest. *J. Ecol.* **1990**, 924–936. [CrossRef]
87. Hylander, K.; Dynesius, M.; Jonsson, B.G.; Nilsson, C. Substrate form determines the fate of bryophytes in riparian buffer strips. *Ecol. Appl.* **2005**, *15*, 674–688. [CrossRef]
88. Brassard, B.W.; Chen, H.Y.H. Effects of forest type and disturbance on diversity of coarse woody debris in boreal forest. *Ecosystems* **2008**, *11*, 1078–1090. [CrossRef]
89. Stokland, J.N.; Siitonen, J.; Jonsson, B.G. *Biodiversity in Dead Wood*; Cambridge University Press: Cambridge, UK, 2012.
90. Dittrich, S.; Jacob, M.; Bade, C.; Leuschner, C.; Hauck, M. The significance of deadwood for total bryophyte, lichen, and vascular plant diversity in an old-growth spruce forest. *Plant Ecol.* **2014**, *215*, 1123–1137. [CrossRef]
91. Bunnell, F.L.; Houde, I. Down wood and biodiversity—Implications to forest practices. *Environ. Rev.* **2010**, *18*, 397–421. [CrossRef]
92. Albrecht, M.A.; McCarthy, B.C. Seedling establishment shapes the distribution of shade-adapted forest herbs across a topographical moisture gradient. *J. Ecol.* **2009**, *97*, 1037–1049. [CrossRef]
93. Chávez, V.; Macdonald, S.E. The influence of canopy patch mosaics on understory plant community composition in boreal mixedwood forest. *For. Ecol. Manag.* **2010**, *259*, 1067–1075. [CrossRef]
94. Müller, J.; Boch, S.; Blaser, S.; Fischer, M.; Prati, D. Effects of forest management on bryophyte communities on deadwood. *Nova Hedwigia* **2015**, *100*, 423–438. [CrossRef]

95. Putna, S.; Mežaka, A. Preferences of epiphytic bryophytes for forest stand and substrate in North-East Latvia. *Folia Cryptogam. Est.* **2014**, *51*, 75–83. [CrossRef]
96. Mežaka, A.; Brūmelis, G.; Piterāns, A. Tree and stand-scale factors affecting richness and composition of epiphytic bryophytes and lichens in deciduous woodland key habitats. *Biodivers. Conserv.* **2012**, *21*, 3221–3241. [CrossRef]
97. Bartels, S.F.; Chen, H.Y.H. Dynamics of epiphytic macrolichen abundance, diversity, and composition in boreal forest. *J. Appl. Ecol.* **2015**, *52*, 181–189. [CrossRef]
98. Söderström, L. Sequence of bryophytes and lichens in relation to substrate variable of decaying coniferous wood in Northern Sweden. *Nord. J. Bot.* **2010**, *8*, 89–97. [CrossRef]
99. Chećko, E.; Jaroszewicz, B.; Olejniczak, K.; Kwiatkowska-Falińska, A.J. The importance of coarse woody debris for vascular plants in temperate mixed deciduous forests. *Can. J. For. Res.* **2015**, *45*, 1154–1163. [CrossRef]
100. Naaf, T.; Kolk, J. Initial site conditions and interactions between multiple drivers determine herb-layer changes over five decades in temperate forests. *For. Ecol. Manag.* **2016**, *366*, 153–165. [CrossRef]
101. Landuyt, D.; Perring, M.P.; Seidl, R.; Taubert, F.; Verbeeck, H.; Verheyen, K. Modelling understorey dynamics in temperate forests under global change-challenges and perspectives. *Perspect. Plant Ecol. Syst.* **2018**, *31*, 44–54. [CrossRef]
102. De Frenne, P.; Zellweger, F.; Rodriguez-Sanchez, F.; Scheffers, B.R.; Hylander, K.; Luoto, M.; Vellend, M.; Verheyen, K.; Lenoir, J. Global buffering of temperatures under forest canopies. *Nat. Ecol. Evol.* **2019**, *3*, 744–749. [CrossRef]
103. Hedwall, P.O.; Gustafsson, L.; Brunet, J.; Lindbladh, M.; Axelsson, A.L.; Strengbom, J. Half a century of multiple anthropogenic stressors has altered northern forest understory plant communities. *Ecol. Appl.* **2019**, *29*, e01874. [CrossRef] [PubMed]
104. Midgley, G.F. Ecology. Biodiversity and ecosystem function. *Science* **2012**, *335*, 174–175. [CrossRef] [PubMed]
105. Parisien, M.A.; Parks, S.A.; Krawchuk, M.A.; Flannigan, M.D.; Bowman, L.M.; Moritz, M.A. Scale-dependent controls on the area burned in the boreal forest of Canada, 1980–2005. *Ecol. Appl.* **2011**, *21*, 789–805. [CrossRef] [PubMed]
106. Bernhardt, E.L.; Hollingsworth, T.N.; Chapin, F.S., III. Fire severity mediates climate-driven shifts in understorey community composition of black spruce stands of interior Alaska. *J. Veg. Sci.* **2011**, *22*, 32–44. [CrossRef]
107. Liu, J.; Liu, S.; Li, Y.; Liu, S.; Yin, G.; Huang, J.; Xu, Y.; Zhou, G. Warming effects on the decomposition of two litter species in model subtropical forests. *Plant Soil* **2017**, *420*, 277–287. [CrossRef]
108. Barkman, J.J. Canopies and microclimate of tree species mixtures. In *The Ecology of Mixed-Species Stands of Trees*; Oxford University Press: New York, NY, USA, 1992.
109. De Frenne, P.; Rodriguez-Sanchez, F.; Coomes, D.A.; Baeten, L.; Verstraeten, G.; Vellend, M.; Bernhardt-Romermann, M.; Brown, C.D.; Brunet, J.; Cornelis, J.; et al. Microclimate moderates plant responses to macroclimate warming. *Proc. Natl. Acad. Sci. USA* **2013**, *110*, 18561–18565. [CrossRef]
110. Leatherdale, J.; Chanasyk, D.S.; Quideau, S. Soil water regimes of reclaimed upland slopes in the oil sands region of Alberta. *Can. J. Soil Sci.* **2012**, *92*, 117–129. [CrossRef]
111. Zhang, Y.; Chen, H.Y.H.; Taylor, A.R. Aboveground biomass of understorey vegetation has a negligible or negative association with overstorey tree species diversity in natural forests. *Glob. Ecol. Biogeogr.* **2016**, *25*, 141–150. [CrossRef]
112. Thrippleton, T.; Bugmann, H.; Kramer-Priewasser, K.; Snell, R.S. Herbaceous understorey: An overlooked player in forest landscape dynamics? *Ecosystems* **2016**, *19*, 1–15. [CrossRef]
113. Huo, H.; Feng, Q.; Su, Y.H. The influences of canopy species and topographic variables on understory species diversity and composition in coniferous forests. *Sci. World J.* **2014**, *2014*, 1–8. [CrossRef]
114. Griffiths, R.P.; Madritch, M.D.; Swanson, A.K. The effects of topography on forest soil characteristics in the Oregon cascade mountains (USA): Implications for the effects of climate change on soil properties. *For. Ecol. Manag.* **2009**, *257*, 1–7. [CrossRef]
115. Seibert, J.; Stendahl, J.; Sørensen, R. Topographical influences on soil properties in boreal forests. *Geoderma* **2007**, *141*, 139–148. [CrossRef]

116. Ampoorter, E.; Baeten, L.; Koricheva, J.; Vanhellemont, M.; Verheyen, K. Do diverse overstoreys induce diverse understoreys? Lessons learnt from an experimental–observational platform in Finland. *For. Ecol. Manag.* **2014**, *318*, 206–215. [CrossRef]
117. Speziale, K.L.; Ruggiero, A.; Ezcurra, C. Plant species richness-environment relationships across the subantarctic-patagonian transition zone. *J. Biogeogr.* **2010**, *37*, 449–464. [CrossRef]
118. Rossman, A.K.; Halpern, C.B.; Harrod, R.J.; Urgenson, L.S.; Peterson, D.W.; Bakker, J.D. Benefits of thinning and burning for understory diversity vary with spatial scale and time since treatment. *For. Ecol. Manag.* **2018**, *419*, 58–78. [CrossRef]
119. Trentini, C.P.; Campanello, P.I.; Villagra, M.; Ritter, L.; Ares, A.; Goldstein, G. Thinning of loblolly pine plantations in subtropical Argentina: Impact on microclimate and understory vegetation. *For. Ecol. Manag.* **2017**, *384*, 236–247. [CrossRef]
120. Jean, M.; Lafleur, B.; Fenton, N.J.; Paré, D.; Bergeron, Y. Influence of fire and harvest severity on understory plant communities. *For. Ecol. Manag.* **2019**, *436*, 88–104. [CrossRef]
121. Yeboah, D.; Chen, H.Y.H. Diversity–disturbance relationship in forest landscapes. *Landsc. Ecol.* **2016**, *31*, 981–987. [CrossRef]
122. Ujházy, K.; Hederová, L.; Máliš, F.; Ujházyová, M.; Bosela, M.; Čiliak, M. Overstorey dynamics controls plant diversity in age-class temperate forests. *For. Ecol. Manag.* **2017**, *391*, 96–105. [CrossRef]
123. Vanha-Majamaa, I.; Shorohova, E.; Kushnevskaya, H.; Jalonen, J. Resilience of understory vegetation after variable retention felling in boreal Norway spruce forests—A ten-year perspective. *For. Ecol. Manag.* **2017**, *393*, 12–28. [CrossRef]
124. Wang, Z.; He, Q.; Hu, B.; Pang, X.; Bao, W. Gap thinning improves soil water content, changes the vertical water distribution, and decreases the fluctuation. *Can. J. For. Res.* **2018**, *48*, 1042–1048. [CrossRef]
125. Abella, S.R.; Springer, J.D. Effects of tree cutting and fire on understory vegetation in mixed conifer forests. *For. Ecol. Manag.* **2015**, *335*, 281–299. [CrossRef]
126. Beaudet, M.; Harvey, B.D.; Messier, C.; Coates, K.D.; Poulin, J.; Kneeshaw, D.D.; Brais, S.; Bergeron, Y. Managing understory light conditions in boreal mixedwoods through variation in the intensity and spatial pattern of harvest: A modelling approach. *For. Ecol. Manag.* **2011**, *261*, 84–94. [CrossRef]
127. Man, R.; Bell, F.W. Temporal changes of understory plant community in response to pre-and post-harvesting herbicide treatments and partial cutting in aspen-dominated boreal mixedwood stands. *Eur. J. For. Res.* **2018**, *137*, 337–348. [CrossRef]
128. Cole, E.; Newton, M.; Bailey, J.D. Understory vegetation dynamics 15 years post-thinning in 50-year-old douglas-fir and douglas-fir/western hemlock stands in Western Oregon, USA. *For. Ecol. Manag.* **2017**, *384*, 358–370. [CrossRef]
129. Kitagawa, R.; Ueno, M.; Masaki, T. Initial effects of thinning and concomitant disturbance on the understory woody community in Japanese cedar plantation. *J. For. Res.* **2018**, *23*, 120–128. [CrossRef]
130. MacDonald, R.L.; Chen, H.Y.H.; Palik, B.P.; Prepas, E.E. Influence of harvesting on understory vegetation along a boreal riparian-upland gradient. *For. Ecol. Manag.* **2014**, *312*, 138–147. [CrossRef]
131. Haughian, S.R.; Frego, K.A. Short-term effects of three commercial thinning treatments on diversity of understory vascular plants in white spruce plantations of northern New Brunswick. *For. Ecol. Manag.* **2016**, *370*, 45–55. [CrossRef]
132. Duguid, M.C.; Ashton, M.S. A meta-analysis of the effect of forest management for timber on understory plant species diversity in temperate forests. *For. Ecol. Manag.* **2013**, *303*, 81–90. [CrossRef]
133. Sabovljevic, M.; Vujicic, M.; Sabovljevic, A. Diversity of saproxylic bryophytes in old-growth and managed beech forests in the Central Balkans. *Plant Biosyst.* **2010**, *144*, 234–240. [CrossRef]
134. Shorohova, E.; Kapitsa, E. Influence of the substrate and ecosystem attributes on the decomposition rates of coarse woody debris in European boreal forests. *For. Ecol. Manag.* **2014**, *315*, 173–184. [CrossRef]
135. Lilles, E.; Dhar, A.; Coates, K.D.; Haeussler, S. Retention level affects dynamics of understory plant community recovery in northern temperate hemlock-cedar forests. *For. Ecol. Manag.* **2018**, *421*, 3–15. [CrossRef]
136. Imai, N.; Seino, T.; Aiba, S.I.; Takyu, M.; Titin, J.; Kitayama, K. Effects of selective logging on tree species diversity and composition of Bornean tropical rain forests at different spatial scales. *Plant Ecol.* **2012**, *213*, 1413–1424. [CrossRef]
137. Mori, A.S.; Isbell, F.; Seidl, R. Beta-diversity, community assembly, and ecosystem functioning. *Trends Ecol. Evol.* **2018**, *33*, 549–564. [CrossRef]

138. Guo, Y.; Xiang, W.; Wang, B.; Li, D.; Mallik, A.U.; Chen, H.Y.; Huang, F.; Ding, T.; Wen, S.; Lu, S. Partitioning beta diversity in a tropical karst seasonal rainforest in Southern China. *Sci. Rep.* **2018**, *8*, 17408. [CrossRef]
139. Chai, Y.; Yue, M.; Liu, X.; Guo, Y.; Wang, M.; Xu, J.; Zhang, C.; Chen, Y.; Zhang, L.; Zhang, R. Patterns of taxonomic, phylogenetic diversity during a long-term succession of forest on the *Loess Plateau*, China: Insights into assembly process. *Sci. Rep.* **2016**, *6*, 27087. [CrossRef]
140. MacDougall, A.S.; McCann, K.S.; Gellner, G.; Turkington, R. Diversity loss with persistent human disturbance increases vulnerability to ecosystem collapse. *Nature* **2013**, *494*, 86–89. [CrossRef]
141. Beauvais, M.-P.; Pellerin, S.; Lavoie, C. Beta diversity declines while native plant species richness triples over 35 years in a suburban protected area. *Biol. Conserv.* **2016**, *195*, 73–81. [CrossRef]
142. Clavel, J.; Julliard, R.; Devictor, V. Worldwide decline of specialist species: Toward a global functional homogenization? *Front. Ecol. Environ.* **2011**, *9*, 222–228. [CrossRef]
143. Olden, J.D.; Rooney, T.P. On defining and quantifying biotic homogenization. *Glob. Ecol. Biogeogr.* **2006**, *15*, 113–120. [CrossRef]
144. Margono, B.A.; Potapov, P.V.; Turubanova, S.; Stolle, F.; Hansen, M.C. Primary forest cover loss in Indonesia over 2000–2012. *Nat. Clim. Chang.* **2014**, *4*, 730–735. [CrossRef]
145. Gibson, L.; Lee, T.M.; Koh, L.P.; Brook, B.W.; Gardner, T.A.; Barlow, J.; Peres, C.A.; Bradshaw, C.J.; Laurance, W.F.; Lovejoy, T.E. Primary forests are irreplaceable for sustaining tropical biodiversity. *Nature* **2011**, *478*, 378–381. [CrossRef] [PubMed]
146. Betts, M.G.; Wolf, C.; Ripple, W.J.; Phalan, B.; Millers, K.A.; Duarte, A.; Butchart, S.H.; Levi, T. Global forest loss disproportionately erodes biodiversity in intact landscapes. *Nature* **2017**, *547*, 441–444. [CrossRef] [PubMed]
147. Barlow, J.; Lennox, G.D.; Ferreira, J.; Berenguer, E.; Lees, A.C.; Mac Nally, R.; Thomson, J.R.; de Barros Ferraz, S.F.; Louzada, J.; Oliveira, V.H.F. Anthropogenic disturbance in tropical forests can double biodiversity loss from deforestation. *Nature* **2016**, *535*, 144–147. [CrossRef] [PubMed]