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Tropical Cyclone Disturbances Induce Contrasting Impacts on Forest Structure, Plant Composition, and Soil Properties in Temperate Broadleaf and Coniferous Forests

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Abstract: Knowledge of forest recovery processes after severe disturbances, such as tropical cyclones, is essential for understanding the mechanisms maintaining forest diversity and ecosystem functioning. However, studies examining the impact of tropical cyclones on forest dynamics are still rare, especially in Northeast Asia. Here, we explore the complex responses of vegetation and soil chemistry to severe tropical cyclone disturbances in Hallasan National Park in South Korea. Vegetation and soil were examined five years before and five years after passages of tropical cyclones in 2012 in natural broadleaf and coniferous forests along an elevation gradient from 950 to 1770 m a.s.l., including the largest population of endemic *Abies koreana*. Tropical cyclones caused abundant tree mortality, resulting in a 46% decrease in stem basal area. Tropical cyclone disturbances triggered the spread of pioneer trees and shrubs and intense clonal propagation of graminoids, including dwarf bamboo, resulting in less diverse understory vegetation, especially in coniferous forests. In contrast, broadleaf forests at lower elevations experienced only minor disturbance. Opening of canopies after tropical cyclone disturbance led to the decrease in soil cations and doubling of available soil phosphorus stock, which likely contributed to the increased coverage of clonal graminoids, especially in coniferous forests (from 36 to 66%). Hence, increased competition of graminoids and reduction in seed fall and seedling recruitment prevented *A. koreana* regeneration. The subalpine forest dominated by *A. koreana* is forecasted to gradual loss due to the fact of temperature increases, intensified tropical cyclones and, particularly, due to the altered competition between dwarf bamboo and fir seedlings.

Keywords: typhoon; vegetation change; soil nutrients; *Abies koreana*; dwarf bamboo; graminoids; subalpine forest; South Korea

1. Introduction

The increased frequency of extreme climate events in recent decades [1,2], including catastrophic tropical cyclone disturbances [3,4] has necessitated a better understanding of the processes and mechanisms of forest recovery [5–7]. The process of forest recovery may depend on various attributes, such as the type of canopy disturbance [8], community composition before disturbance [9], the interaction of regenerating trees with understory vegetation [10], topsoil perturbation [11], leaf litter and nutrient dynamics [12], reproductive characteristics of available species [13,14], or plant life histories [15]. Hence, a better knowledge of the spatiotemporal effects of tropical cyclone disturbances on forest structure and composition requires the study of forest conditions both before and after disturbance.

Post-disturbance processes in forests are primarily driven by two main impacts caused by tropical cyclones, i.e., canopy openness and organic debris accumulation [16–18]. These impacts affect both short-term and long-term changes in environmental properties [19–22]. Tropical cyclones cause heavy precipitation and soil leaching, which can reduce soil pH, calcium and magnesium contents, and humus quality, while the tree dieback and decomposition of high amounts of accumulated woody debris can increase soil phosphorus availability [23,24]. This can have negative consequences for understory plant diversity after disturbance by supporting fast-spreading clonal graminoids over subordinate, slow-growing, nonclonal forbs [20,25]. However, little is still known about how understory herb diversity and tree regeneration respond to strong tropical cyclone disturbances, which remove much of the tree canopy.

The development of a forest community after disturbance can lead either to a return to earlier (=pioneering) communities or to an accelerated succession to mature forest communities with the predominance of non-pioneer tree species [26,27]. The result can be variable in different regions, elevations, and forest types, depending on many biotic and abiotic factors that interact with the impacts of severe storm events [5,28]. For example, population explosions of specific understory herbs can inhibit tree regeneration and thereby stop forest succession [14,29]. A low rate of tree regeneration has been documented, especially in montane forests where coniferous trees dominate due to the virtually zero ability of conifers to resprout and the absence of their seedling/sapling bank due to the rapid spread of understory herbs [30,31].

Delayed tree mortality in the canopy may also affect long-term recovery trajectories after disturbance [32]. Restoration trajectories may further rely on the spatial extent of disturbed canopies and the number and spatial pattern of surviving trees [33–35]. Understanding tree damage types, spatial patterns, and the extent of cyclone forest disturbances and forest vegetation recovery patterns, including changes in understory plant composition and soil fertility, can have important implications for nature conservation and forest management [20,31,36].

Ecological mechanisms controlling the resistance and resilience of forests to tropical cyclone disturbances can be studied by repeated field surveys of vegetation [37,38] or by indirect reconstruction of disturbance history from tree growth analysis and/or age structure [35,39,40]. The enormous variability of forest development after the disturbance has been documented mainly on tree composition and community structure [7,34]. However, the responses of herbs and shrubs to tropical cyclone disturbances are often overlooked, even though they are major components of temperate forest diversity and reflect changes in canopy openness. Turnover in their populations may also result in changed forest structure through altered regrowth/regeneration trajectories of trees [13,14].

Typhoons are a major disturbance factor in natural forests in East Asia [41,42], while other disturbances, such as fire or insect outbreaks, predominate in secondary forests and more continental regions of the mainland [43,44]. Studies on the impact of tropical cyclones on forest ecosystems have been mainly conducted in the North Atlantic Basin [45]. Relevant data covering the disturbance ecology of species-rich temperate forests in the Pacific Northwest Basin, such as Korea and Japan, are still largely lacking. In addition, documented intensification of tropical cyclones and poleward migration poses a significant threat to these unique ecosystems [3,46,47]. Hence, it is necessary to understand the complex responses of forests to tropical cyclone disturbances to mitigate the possible impacts of recent and projected shifts in tropical cyclone activity on forest ecosystems [48]. South Korea experiences strong landfall tropical cyclones, and there has been a recorded increase in the threat of tropical cyclone activity over the last decades [49,50]. For example, in September 2007 and in August and September 2012, three powerful tropical cyclones (called typhoons in the Pacific Northwest)—Nari, Bolaven, and Sanba—crossed South Korea, heavily disrupting the forest ecosystems. However, little is known about the effects of tropical cyclone disturbances on unique temperate forests in South Korea [51] in

comparison with, for example, the Caribbean or Taiwan, where relatively rich literature exists [52,53].

In this study, we examined the effects of typhoon-induced disturbances on vegetation and soil in mountain deciduous and coniferous forests in South Korea. The forests studied represent Holocene refugee communities located in Hallasan National Park [54,55], the UNESCO World Natural Heritage Site. Our aim was to (a) identify which forest type is more susceptible to typhoon disturbance in terms of forest structure, plant composition, and diversity; (b) identify the most important environmental factors controlling vegetation changes in broadleaf deciduous and coniferous forests including changes in stand structural attributes and soil chemistry.

We hypothesized that broadleaf deciduous forests (at ~900–1500 m a.s.l.) are less affected by severe typhoons than coniferous forests (at >1500 m a.s.l.). Higher tree mortality in coniferous than broadleaf forests lead to more significant changes in soil and understory plant composition, with graminoids becoming more abundant due to the canopy opening. Soil leaching (loss of mobile nitrogen and basic cations) and the rise of phosphorus releasing from woody debris promote fast-growing graminoids and reduce plant diversity (especially dicot forbs) and tree seedling regeneration. Unlike coniferous forests, we expected less intense and harmful typhoon disturbance in deciduous forests, which could encourage plant diversity by reducing the dense undergrowth of dwarf bamboo and its thick layer of litter, thereby increasing tree seedling regeneration and forb abundance. Finally, stronger relationships between environmental variables and forest species composition were expected to occur before typhoon disturbance due to the fact of long-term equilibrium.

2. Materials and Methods

2.1. Site Description

The study was carried out in the Hallasan National Park covering 153 km^2 in the central part of Jeju Island (33°10′–33°34′ N, 126°10′–127° E), 90 km from the southern tip of Korean Peninsula (Figure 1). Hallasan National Park is dominated by an extinct volcano Mt. Halla, the highest peak of South Korea (1950 m a.s.l.). Its surface constitutes various volcanic landforms. Meteorological mixing between winter cold air masses from Siberia and summer monsoons and typhoons from the Pacific Ocean results in the island's highly dynamic climate regime [56]. The summer monsoon together with typhoons brings abundant moisture from the ocean and produces heavy rainfall. Precipitation rises from approximately 1500 mm in coastal areas to over 4500 mm a year in the highlands [57]. The northern coast of the island (Jeju City, 1978–2007) has a mean annual temperature of 15.7 °C, mean January temperature of 5.8 °C, and mean July temperature of 26.7 °C. Mt. Halla's mean temperature lapse rate is 6.43 °C per 1000 m (s.d. = 1.78) [56].

The vegetation of Hallasan National Park consists of sequential zones (belts) placed along an elevational gradient [58,59]. Despite the long-lasting human influence on the island, natural deciduous and coniferous forests remain in higher elevations (>900 m a.s.l.) [59]. In the middle elevations (900–1500 m), there are well developed cool-temperate deciduous forests composed mainly of *Quercus mongolica*, *Carpinus tschonoskii*, *C. laxiflora*, and *Acer pseudosieboldianum* (nomenclature follows [60]). At higher elevations (1500–1900 m), the subalpine coniferous forests of *Abies koreana* mixed with *Taxus cuspidata*, *Prunus maximowiczii*, *Sorbus commixta*, and *Betula ermanii* dominate [54,61,62]. The transition line between deciduous and coniferous forests (approximately 1500 m) is more or less distinct, and a rather abrupt increase in *Abies koreana* in forest stands occurs there [59].
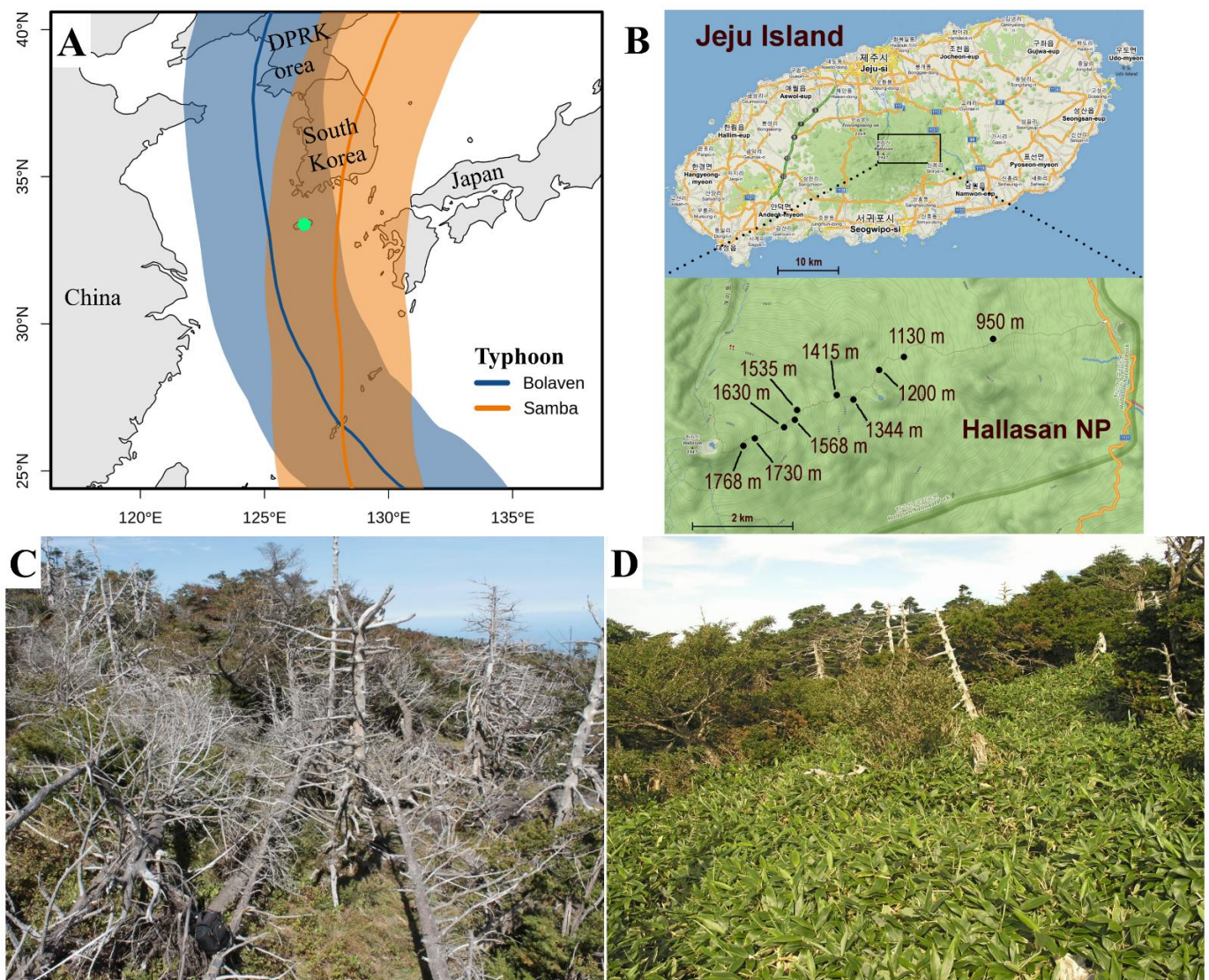
Figure 1. (**A**) Location of the study site (green dot) within East Asia with the track of two typhoons hitting and disturbing forests in Hallasan NP, Jeju Island, in late summer 2012 (for details see Section 2.1). (**B**) Detailed placement of ten permanent plots along the elevation gradient on the eastern flank of Mt. Halla (peak at 1950 m) in the Hallasan NP, Jeju Island (Map source: © Seznam.cz). Photographs of (**C**) severely disturbed coniferous *Abies koreana* stands and (**D**) an expansion of *Sasa quelpaertensis* into the disturbed coniferous *Abies koreana* stands. Photographed by Černý T. and Altman J.

During the 2006–2017 investigation period, three typhoons hit Jeju Island with the potential to severely damage local forests. First, Typhoon Nari crossed Jeju Island on 16 September 2007, with a steady wind spread of 155 km/h—Category 2 on the Saffir-Simpson Hurricane Wind Scale. However, the studied montane forests remained intact—as we witnessed from our repeated visits to all permanent plots (see further) in the 2009–2011 period. Five years later, on 28 August 2012, the strong typhoon Bolaven hit Mt. Halla from the south (144 km/h, Category 1; Figure 1), causing devastating damage on Jeju Island [63]. Just three weeks later, Typhoon Sanba, one of the most powerful typhoons to hit South Korea [64], devastated forests on Mt. Halla from the north (155 km/h, Category 2; Figure 1).

2.2. Vegetation and Soil Sampling

During the first census in 2006 (September) and 2007 (June) (i.e., before the devastating damage caused by typhoons in 2012), we studied the floristic composition and species abundances by establishing 36 permanent forest plots (10 × 10 m) at nine elevation sites (four replicate plots per elevation), with 20 plots in the lower-elevation broadleaf forests (900–1500 m a.s.l.) and 16 plots in the higher-elevation coniferous forests (1500–1900 m a.s.l.; Table 1). The plots were distributed on a mild eastern flank of Mt. Halla along an elevational gradient (960–1770 m a.s.l.). This flank is built of uniform basalt bedrock [65]. We selected sites covered with typical natural old-growth forests, homogeneous in soil, vegetation, and stand characteristics and lacking indicators of past human influence. On each plot, we measured its elevation, inclination, and aspect and recorded vegetation composition by visual estimation of the coverage of all vegetation layers (i.e., trees, shrubs, and herbs) and individual plant species in each layer using the Braun–Blanquet nine-degree scale (for details see [66]; the tree layer comprised woody individuals taller than 5 m, shrub layer that with a height range 1–5 m, individuals of woody species below 1 m, and their seedlings were also recorded as juveniles; Table 2).

Table 1. Elementary information for permanent plots (4 plots per row, altogether 40 plots).

Forest Type	Altitude (m a.s.l.)	Aspect (°)	Slope (°)
Broadleaf	949–950	38	12
	1130	160–165	4
	1199–1200	130	6–10
	1344–1345	80	12–15
	1413–1415	75–80	20–23
Coniferous	1534–1535	85	7–8
	1567–1569	58–60	8–15
	1629–1631	55	10
	1730–1731	100–110	10–12
	1766–1770	110–120	23–25

Table 2. Description of the studied diversity, structural and soil variables, their abbreviations used in analyses, the mean values for both deciduous and coniferous forests before and after typhoon disturbance, and the F-test and *p*-values from repeated-measures linear mixed models (LMMs) testing the effect of forest type (FT), typhoon disturbance (TD), and their interaction (TD × FT). ns: no significant difference; * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$.

	Abbreviation	Deciduous Before	Deciduous After	Coniferous Before	Coniferous After	Repeated-Measures LMM FT	Repeated-Measures LMM TD	Repeated-Measures LMM FT × TD
Diversity and abundance variables								
Number of tree species	R_{tree}	4.9	4.95	2	2	34.1 ***	ns	ns
Number of shrub species	R_{shrub}	4.3	4.35	5.69	4.37	ns	4.1 *	4.8 *
Number of herbaceous species	R_{herb}	8.05	8.25	22.3	18.8	39.4 ***	6.8 *	8.5 **
Number of species of woody juveniles	R_{juv}	4.3	5.1	6.8	4.18	ns	ns	10.4 *
Simpson index for herbaceous species	$1/D_{herb}$	0.24	0.2	0.76	0.57	60.1 ***	55.7 ***	21.4 ***
Total cover of graminoids [a] (%)	COV_{gram}	0.25	0.85	17	25	18.1 ***	9.6 **	6.9 *
Total cover of *Sasa quelp.* (%)	COV_{Sasa}	79.3	84.9	18.1	40.9	41.9 ***	20.7 ***	6.1 *
Canopy structural variables								
Total cover of the tree layer (%)	cover3	82.45	74.4	34.25	27.5	41.9 ***	8.2 **	ns
Total cover of the shrub layer (%)	cover2	17.5	16.3	54.3	23.6	24.1 ***	29.1 ***	25.6 ***
Total stand BA [b] (m²·ha⁻¹)	BA_{tot}	53	43	48	26	5.0 *	62.1 ***	8.1 **
BA of broadleaved species (m²·ha⁻¹)	BA_{bl}	5	41	12	9	61.4 ***	9.6 **	7.7 **
BA of conifers (m²·ha⁻¹)	BA_{co}	3	2	37	16	236.1 ***	66.8 **	55.2 **
BA of *Abies koreana* (m²·ha⁻¹)	BA_{fir}	1	0	32	11	137.5 ***	63.6 ***	56.2 ***
Fraction of BA of conifers (%)	Pcon	5.8	4.5	80.6	66.7	243.2 ***	25.4 ***	14.1 ***

Table 2. *Cont.*

		Deciduous		Coniferous		Repeated-Measures LMM		
	Abbreviation	Before	After	Before	After	FT	TD	FT × TD
Soil variables								
pH (H$_2$O)	pH$_{act}$	4.4	4.3	4.5	4.3	ns	6.6 *	ns
Potential soil acidity [c]	ΔpH	0.77	0.67	0.78	0.66	ns	8.1 **	ns
Total carbon (% of dry weight)	C	20.7	16.6	23.7	20.5	10.5 **	27.8 ***	ns
Total nitrogen (% of dry weight)	N	1.38	1.15	1.53	1.41	12.9 ***	13.6 ***	ns
Carbon/nitrogen ratio	C/N	14.9	14.5	15.4	14.4	ns	13.9 ***	ns
Available P (ppm [d])	P	11.9	6.5	5.8	10.7	ns	ns	9.6 **
Mg ions (ppm)	Mg	217.6	126.6	137.1	129.7	4.9 *	27.7 ***	18.7 ***
Ca ions (ppm)	Ca	835.3	160.1	410.1	228.8	3.8 *	35.4 ***	11.8 **

[a] Fraction of the total coverage of members of the *Cyperaceae* + *Juncaceae* + *Poaceae* families, except *Sasa quelp.* (*Poaceae* family); [b] BA = basal area; [c] difference pH(H$_2$O)–pH(KCl); [d] ppm is equivalent to mg·kg^{-1}.

In these 100 m^2 plots, we measured diameters at breast height (*DBH*) for all mapped woody species—*DBH*s were used for the calculation of species-specific basal areas (*BA*s) and total broadleaved and coniferous tree stand basal areas as a surrogate for aboveground wood biomass, supplementing visual estimates of the percent tree coverages (Table 1). Furthermore, *BA* values were considered as an indirect parameter to infer relative light conditions in the understory.

During the second census in 2017 (September), we reinvestigated the vegetation composition and checked the permanent plots to evaluate the living/dead conditions of the marked trees. Data for woody species *DBH* and *BA*s were collected in 40 permanent plots, since at 1630 m four additional plots were set-up to evenly cover the entire elevation gradient.

We collected a mixed soil sample from the *Ah* horizon on each plot with vegetation records, both before and after disturbance. Total organic nitrogen (N) and carbon (C); plant-available phosphorus (P), calcium (Ca), and magnesium (Mg); pH(H$_2$O); pH(KCl) were analyzed in the soil samples (Table 2, for details of analyses see [54]).

2.3. Statistical Analyses

We performed both multivariate and univariate statistical tests to yield the maximum information hidden in the data and to address hypothesized mechanisms. To evaluate the temporal changes in vegetation composition (i.e., difference before and after disturbance) for two basic forest types (lower-elevation broadleaf forests between 900 and 1500 m a.s.l. and higher-elevation coniferous forests between 1500 and 1900 m a.s.l.), we used canonical correspondence analysis (CCA), a constrained unimodal ordination method (the length of the first unconstrained DCA axis > 3 S.D. indicated a heterogeneous dataset on which unimodal methods should be used; [67]). To emphasize the interaction between the forest type (broadleaf versus conifer) and disturbance (before and after disturbance), partial CCA (pCCA) was performed, where the effects of disturbance were excluded, and the interaction effects of forest type and disturbance were used as the only explanatory variables. In total, we conducted four analyses to test the main effects and their interactions as follows: (CCA1) forest type (FT) × typhoon disturbance (TD) as the sole explanatory variable—the analysis accounted for all, the main effects of TD, FT, and their interactions, with (pCCA2) TD being an environmental variable and FT a covariable, and (pCCA3) FT being an environmental variable and TD a covariable. Such a design accounted just for the additive (main) effect of the respective environmental variable. Note that because FT and TD are orthogonal, the amount of explained variability (i.e., the sum of canonical axes) was not affected by the use of a covariable. (pCCA4) The interaction TD × FT is the environmental variable, and TD and plot identifiers are covariables. This accounts for the interaction between TD and FT (i.e., for the non-additivity of their effects). This corresponds to the interaction in repeated measures ANOVA. These four analyses were made separately for species in the herb layer (herbs and woody juveniles) and woody species in the shrub–tree layers to test if these two guilds differ in responses to typhoon disturbance. The significance of

these relationships was tested using the Monte Carlo permutation test (999 permutations) constructed for a split-plot design (i.e., permutations restricted within the pairs of the identical plots) using Canoco 5 software [67]. CCA ordination diagrams were amended with vectors of supplementary variables (i.e., basal areas, species richness, and proportion of graminoids) to help interpret the meaning of ordination axes.

The univariate data on species richness (numbers of species), diversity (Simpson's diversity index), and cover abundance were further analyzed by the *lmer* function for the repeated-measures linear mixed-effect model in R package "*lme4*" [68], with the main fixed effects of FT, TD, the interaction between the two, and elevation-specific plot identifiers as repeated measures, followed by Tukey's post hoc test. Changes in diversity measures were analyzed for total species numbers as well as the numbers of species in individual vegetation layers (i.e., herbs and woody juveniles, shrubs, and trees). We also analyzed changes in abundance and diversity of graminoids (i.e., order *Poales*), as they were expected to respond strongly to overstory disturbance. Quantitative changes in measured vegetation, forest structure, and soil variables in the studied plots before and after disturbance were compared separately for broadleaf and coniferous forests with paired *t*-tests for the evaluation of trends in their values, amended with boxplots as the graphical output. Finally, a series of multiple linear regressions using the pooled data per elevation (i.e., mean values) of plant diversity and abundance variables (i.e., richness, Simpson index, and cover) and key environmental variables (i.e., elevation, canopy structural parameters, and soil variables) were performed in R [69] to find robust ecological patterns in both pre-disturbance and post-disturbance vegetation. In these linear regressions, backward selection of predictors based on AIC was performed to build up the most parsimonious models, and the residuals were checked to conform with normal distribution.

3. Results

3.1. Changes in Vegetation Composition and Forest Structure

Before typhoon disturbance, plant species composition and diversity differed between broadleaf and coniferous forests (Table 3, Figure 2 and Figure S1). Before typhoon disturbance, coniferous forests had a higher richness of shrubs, herbs, and tree juveniles, higher overall plant diversity but lower understory herb cover and comparable stand tree basal area with broadleaf forests (Figure 3). Typhoon disturbance had a significant effect on the retreat of *Abies koreana* and species composition in the herb layer (analysis CCA3a in Table 3, Figure S1), with more pronounced changes in coniferous compared to broadleaf forests (Figures 2 and S1). Compared to understory herbs, typhoon disturbance had a rather negligible effect on the net change in woody species composition, i.e., trees and shrubs, except high mortality in *Abies koreana* (analysis CCA3b in Table 3). *Abies koreana* trees experienced a four-fold decrease in *BA*s of living individuals in coniferous forests (Figure 3). Higher mortality was found mainly in larger *A. koreana* trees (58%) compared to smaller trees (20% in individuals in the smallest 0–10 cm *DBH* class). Similar mortality was found across *DBH* classes in the lower-elevation broadleaf forests, but its overall rate was low, approximately 10% (Figure 4).

Plant understory composition changed after typhoon disturbances as related to the decrease in total stand *BA* (Table 2, Figure 3) and a decrease in the coverage of the shrub layer (Table 2). In broadleaf forests, stand *BA*, *BA* of both broadleaf species and conifers, and Simpson's diversity for herbs significantly declined after typhoon disturbance, while coverages of herbs and a total cover of graminoids significantly increased (Figure 3). In coniferous forests, most diversity and tree abundance variables significantly decreased, and two variables increased in their values—coverage of herbs and total cover of graminoids (Figure 3). Most prominent decreases were attained in coverage of shrubs, Simpson's diversity index for herbs, total stand *BA*, *BA* of conifers, and *BA* of *Abies koreana* (Table 3, Figure 3).

In both forest types, we observed a significant reduction in plant species diversity after typhoon disturbance. Forest understory herbs and woody juveniles underwent significant

changes in species composition, with much stronger changes recorded in coniferous forests compared to broadleaf forests (significant interaction between Typhoon disturbance and Forest type, see Analyses CCA1a, CCA1b in Table 3). Among most retreating species, we identified especially those typical for closed forest interior (e.g., *Clintonia udensis*, *Galium kamtschaticum*, *Luzula plumosa*, *Maianthemum bifolium*, and *Parasenecio adenostyloides*; Figures 2A and S1A). Species that increased their abundances in post-disturbance stands were especially light-demanding graminoids (*Calamagrostis langsdorffii* and *Carex* sp. div.) and pioneer trees and shrubs (*Fraxinus rhynchophylla*, *Quercus crispula*, *Sorbus commixta*, and *Symplocos sawafutagi*; Figures 2C and S1A). Dominant dwarf bamboo *Sasa quelpaertensis* increased its mean coverages from 79% to 85% in broadleaf forests (p = 0.02) and from 18% to 41% in coniferous forests (p = 0.003; Table 2). We detected a slight change in species composition of tree and shrub layers that occurred only in coniferous forests after disturbance, leading to species impoverishment, e.g., *Acer mono*, *Symplocos coreana* or *Weigela florida* (Figure S2).

Table 3. Summary of the results of the canonical correspondence analyses (CCA, pCCA) for floristic composition sampled in 36 permanent plots. Small letters indicate subsets of response variables: (a) species in the herb layer; (b) species in the tree and shrub layers. Explanatory variables (Exp. variables) used in the test: typhoon disturbance (TD); forest type (FT). The interaction of typhoon disturbance × forest type (TD × FT) is the interaction of each level of one variable with each level of the other. Covariables: plot identity (PI). Permutation (type of permutation within plots used in the Monte Carlo test) reflects the repeated measurement nature of the data (i.e., used split-plot design permutation). Here, we present permutation at the whole plot level and permutation on the split-plot level. On the split-plot level, TS means permutation restricted to times series (before–after TD) and dependent across whole plots. Explained variation (Exp. variation): % adjusted explained variation. F all, P all: values of the F-test and p-values on all ordination axes, respectively.

| CCA Analyses	Exp. Variables	Covariables	Permutation	Exp. Variation	F All	P All
Herbs and woody juveniles in the herb layer						
CCA1a	TD × FT	-	Freely, freely	18.5	6.4	**0.001**
pCCA2a	FT	TD	Freely, no	12.9	11.3	**0.001**
pCCA3a	TD	FT	No, freely	4.0	3.9	**0.04**
pCCA4a	TD × FT	TD, PI	Freely, TS	6.3	3.3	**0.001**
Woody species in the shrub and the tree layers						
CCA1b	TD × FT	-	Freely, freely	16.7	5.8	**0.001**
pCCA2b	FT	TD	Freely, no	16.3	14.7	**0.001**
pCCA3b	TD	FT	No, freely	0.6	1.4	0.75
pCCA4b	TD × FT	TD, PI	Freely, TS	6.7	3.5	**0.001**
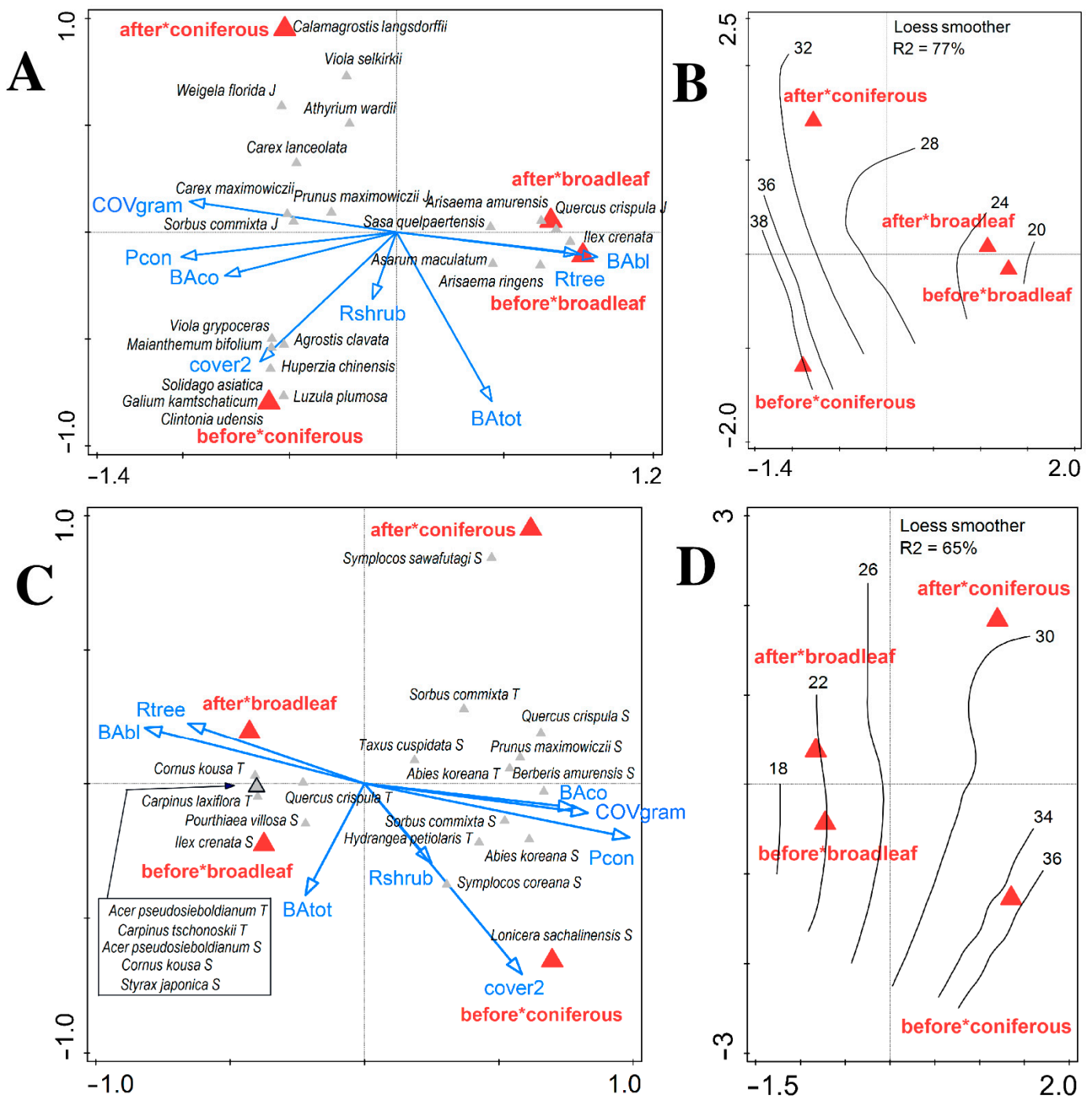
Figure 2. Ordination analyses (CCA1a, b, Table 2) showing temporal shifts in species composition among herbs (**A**,**B**) and shrubs and trees (**C**,**D**) in broadleaf and coniferous forests (36 permanent plots) before and after typhoons for the best fitting species together with the loess smoothed species richness isolines and selected stand variables (used as supplementary variables and represented by blue arrows; for abbreviations, see Table 1). Pgramin = graminoid fraction; T = tree layer; S = shrub layer; J = woody juveniles in the herb layer; no index = herbs.
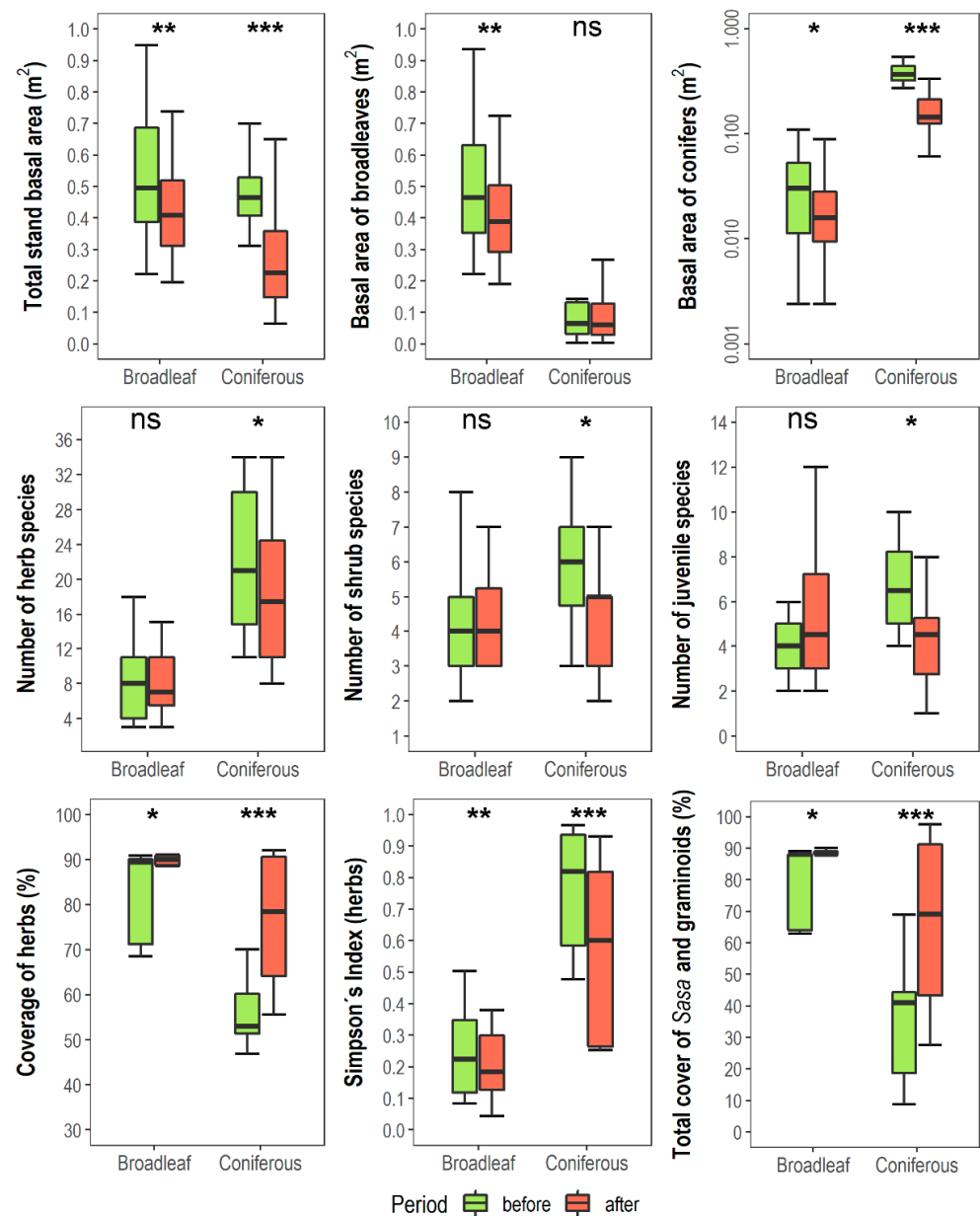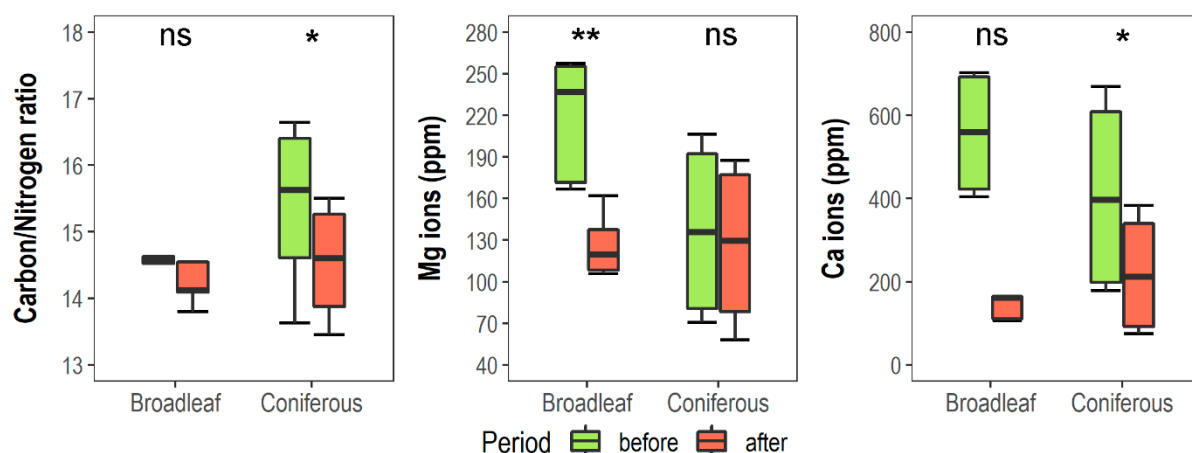
Figure 3. Differences in stand structure and vegetation diversity variables between pre-disturbance (before typhoon) and post-disturbance (after typhoon) broadleaf and coniferous forests. Data for BA values were sampled in 40 permanent plots, other data in 36 permanent plots (all but 1629–1631 m plots). The level of significance is indicated above the boxes: ns: non-significant; * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$. Boxes represent 25%–75% of values, black strips medians, whiskers 1.5 interquartile ranges. Note the logarithmic transformation of *y*-axis in the case of plotting the basal area of conifers due to the too low values of this variables in broadleaf forests.
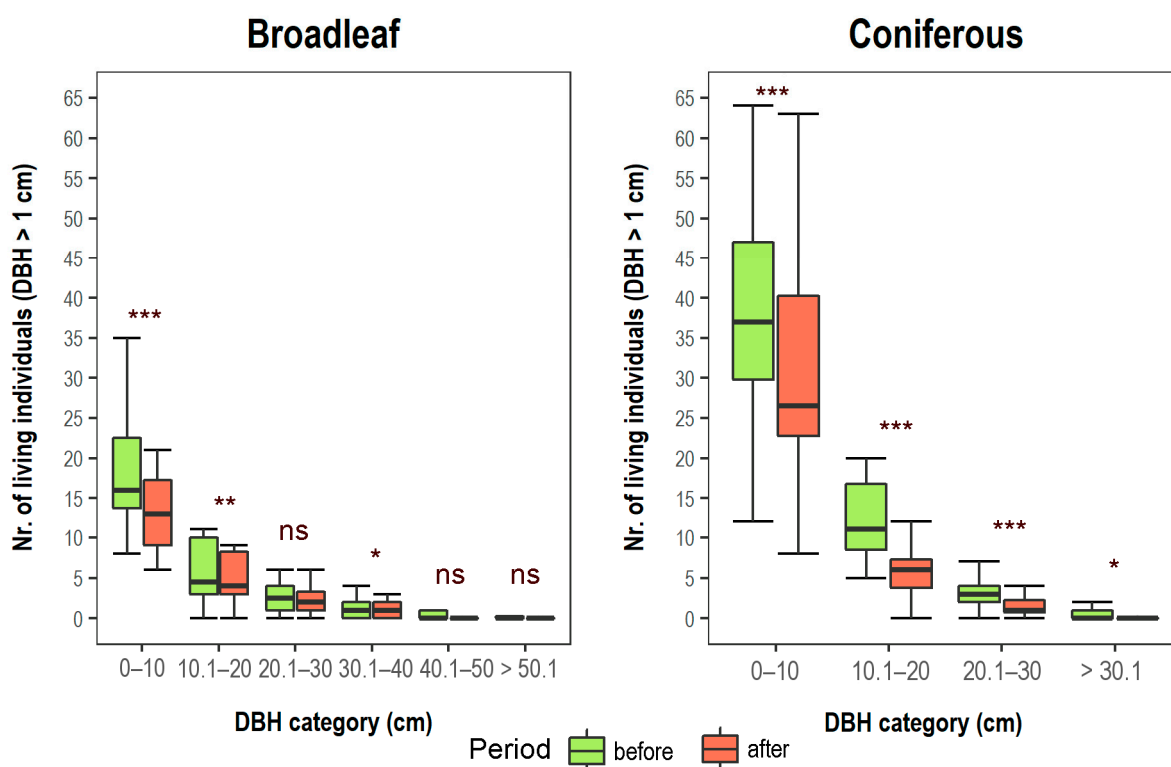
Figure 4. Differences in DBH distribution of living trees, shrubs, and saplings (DBH ≥ 1 cm) between pre-disturbance (before typhoon) and post-disturbance (after typhoon) broadleaf (**left panel**) and coniferous (**right panel**) forests (40 permanent plots). The level of significance is indicated above the boxes: ns: non-significant; * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$.

3.2. Changes in Soil and Shifts in Environmental Control of Vegetation Attributes

Most investigated soil variables decreased in their values after typhoon disturbance (Figure 5). A significant decrease was found in the pH, total carbon, total nitrogen, carbon/nitrogen ratio, magnesium in broadleaf forests, and calcium in coniferous forests (Table 2, Figure 5). The soil phosphorus content doubled in coniferous forests after typhoons (Table 2). Multiple regressions also revealed much stronger relationships between elevation and species richness and diversity of herbs and woody juveniles in pre-disturbance forests (Table S1). Tree richness was negatively correlated with elevation, and the strength of this relationship increased in post-disturbance plots (Table S1). From the set of canopy structural variables, only the coverage of the tree layer and proportion of conifers in pre-disturbance plots and total tree *BA* in post-disturbance plots gained significant roles in understory control (Table S1). For the influence of soil chemistry, results are quite different comparing both censuses (Table S1). Before typhoons, a strong negative relationship was revealed between herb richness/diversity parameters and available magnesium whereas, in post-disturbance stands, a weaker negative relationship was found between only a limited set of herb richness/diversity parameters and potential soil acidity (Table S1).

Figure 5. Differences in soil chemical variables between pre-disturbance (before typhoon) and post-disturbance (after typhoon) broadleaf and coniferous forests (36 permanent plots). The level of significance is indicated above the boxes: ns: non-significant; * $p < 0.05$; ** $p < 0.01$.

4. Discussion

4.1. Vegetation Changes after Typhoons

The degree of canopy damage depended on the forest type: typhoons caused mild disturbances in broadleaf oakwoods, while causing stand-replacing perturbations at high-elevation coniferous forests. Generally, there is a positive relationship between wind speed and elevation documented from the tropics to the temperate zone [31,70]. The predominant role of the elevational gradient in controlling the disturbance strength is also conditioned by the topography of Jeju Island with Mount Halla forming a solitary stratovolcano, where the friction between the cyclone air mass and the land can be neglected. The centers of the typhoons were at a minimum distance of ca. 80 km from our study plots (Figure 1A). Presumably, some trees could be preserved after the first Bolaven typhoon that reached category 1 (see also [71]). However, the combination of contrasting trajectories and the short time interval between the two typhoons led to great damage to the majority of trees at high elevations. Local topography probably has only a negligible impact on tree damages, as observed in other studies performed in slightly undulating landscapes [31,72]. Nevertheless, it is evident from our field experience that some microrefugia exist even at high elevations with more preserved treetops.

Extensive damage to *A. koreana* subalpine forests is likely related to its shallow root system on thin soil layers formed on lava substrates, making them highly vulnerable to strong typhoons [29]. Most *A. koreana* individuals were observed as uprooted than snapped in our plots (Figure S3), and uprooting was probably further intensified during the second typhoon Sanba due to the prevalence of water-saturated soils shortly after previous typhoon Bolaven [73]. Analogous results for the intensity of forest disturbance by a cyclone (category 1–2) come from the mountainous landscape in the Dominican Republic [31] and similar severity of damage was found in the Japanese warm-temperate rainforest [37]. We found a strong decline in the basal area of tree trunks in *A. koreana* mainly due to direct wind damage, while a smaller portion of *A. koreana* individuals could die from other possible causes such as snow damage, drought stress, or insect infestation. But we lack direct observations to quantify precisely these other lethal agents. The typhoons of 2012 were considered as the primary factor responsible for the death of *A. koreana* [74], which corroborates our findings.

In our surveyed plots, we found a very sparse occurrence of *A. koreana* seedlings, similar to the local studies [29,75]. Although the tree uprooting offers a sufficient supply of tip-up mounds and exposed soil, both of which are supposed to provide important regeneration niches for seedlings protected here from competitors such as dominant dwarf bamboo [10,76,77], this mechanism seems to fail on Mt. Halla. Thus, the typhoon dis-

turbances did not create a regeneration window for *A. koreana*, which is also unable to resprout or re-flush the canopy leaves like other trees. The isolated location of Halla Island also brings limited availability of propagules from source metapopulations on the Korean mainland [78,79]. In addition, *A. koreana* is sensitive to heatwaves and extended drought, which is the main reason for its threat from global warming [80–83]. Thus, wind damage of *A. koreana* trees, together with limited seedling regeneration, may contribute to future population decline or extinction of this species according to climate warming scenarios [83].

Another factor that may contribute to the decline or extinction of the local *A. koreana* population is the weak ability of its seedlings to survive within the more abundant dwarf bamboo and other graminoids after typhoons. These competitors can also effectively block germination of *A. koreana* seeds which may prevent its regeneration in subsequent stages of forest recovery [29,77]. Reduced regeneration of tree seedlings after extensive wind damage has also been reported in other montane coniferous forests [30,31,84,85]. Specifically, dwarf bamboo (*Sasa* spp.) possesses the chief competing role in the understory of Far East temperate forests, hence, largely controlling forest dynamics and structure [76,86,87].

Abies koreana is also susceptible to the browsing of Siberian roe deer (*Capreolus pygargus*) [29,75,88]. Regarding the activity of ungulates, it has been documented that the wood debris accumulation after forest blowdowns can protect seedlings from browsing herbivores [89,90], but this effect depends on the animal size [34]. Siberian roe deer is a smaller representative of the deer family, well adapted to subalpine areas on Mt. Halla, thus attaining here recently high densities [88].

Damages to tree canopies by strong typhoons led to intensive insolation of understory vegetation and allogenic succession, as seen in other studies [91]. We found an increased proportion of graminoids due to their vigorous clonal growth [92] in post-disturbance open vegetation, similar to [8,84], and decrease in overall plant diversity and number of woody juveniles (i.e., lower tree regeneration). Post-disturbance tree and shrub layers experienced more intense shifts in abundance than diversity, whereas the herb layer changed mainly its overall species composition and diversity. In line with our results, previous studies have shown more rapid and ample response of the understory herb composition to tropical cyclone disturbances compared to tree species composition [8,14,25], which often leads to the inhibition of tree regeneration [92,93].

We also detected stronger links between herb layer species' composition in pre-disturbance forest vegetation and environmental predictors (elevation and soil factors). The studied stands were old-growth forests, characterized by an absence of groups of fallen logs and large gaps during the first census, and hence experiencing low disturbance activity, as also evidenced from tree-ring analyses [4,94]. Before the typhoon disturbance, the percentage of trees experiencing stand disturbance did not exceed 10% in any of the permanent plots, indicating the creation of only small gaps within canopies before our pre-typhoon sampling [94]. However, as expected, disturbances caused by typhoons in 2012 have resulted in the decoupling of tight statistical relationships between the vegetation and the environment. In other words, original vegetation-environment equilibrium was broken up and after five years of succession it still has not been re-established.

Expansion of dwarf bamboo in our plots in coniferous forest is most likely due to improved light conditions in the herb layer after the disruption of *A. koreana* canopies. Positive response of various species of dwarf bamboos (in terms of increases in culm recruitment, survival and abundance) on higher light availability was documented across East Asian forests [95]. In addition, these plants expanded local ranges and increased their abundance as a response to forest fragmentation, bearing emergence of new forest edges [96]. In fact, wind disturbances causing disruption of contiguous forest vegetation can be perceived as a source of specific forest fragmentation. We do not think that the dwarf bamboo in our plots was primarily reinforced by climate change (as documented in [97])—these processes are much slower and also *Sasa quelpaertensis* naturally ranges up to 1800 m a.s.l. on Mt. Halla, where on its upper distribution limit is still able to form relatively dense stands in subalpine scrubs [98]. However, future competitive pressure of dwarf

bamboo may be strengthened by the fact that *Sasa quelpaertensis* is well adapted to the snowy environment [99] and scenario of climate change expects increase in winter precipitation on Jeju Island [81,100]. Expansion of dwarf bamboo triggered by typhoon disturbance has the potential to direct regeneration trajectories of trees in post-disturbance succession and, hence, modify climax forest communities' composition (see further discussion).

4.2. Edaphic Conditions and Vegetation Responses

We found a two-fold increase in soil phosphorus in coniferous forests after disturbance events, which is probably due to the decomposition of a large amount of accumulated wood debris. Although this increase was non-significant, two-fold to three-fold increase in available P soil stock was reported in other post-cyclone studies [18,22,101,102]. As tree canopy serves as a physical buffer against incident raindrops, the opening of compact tree canopies by disturbance exposes forest soils to the enhanced erosion and leaching effects of rainwaters [103,104]. Storm-induced discharge events have been studied in fluvial geochemistry research [23,24], demonstrating accelerated nutrient export through leaching by heavy rains. Our data showed a decrease in parameters such as soil reaction, calcium and magnesium content, and humus quality in coniferous forests after the typhoons. As to phosphorus, its absolute values may vary for disturbed forest types due to its higher uptake by faster-growing broadleaf species compared to slow-growing conifers. The soil phosphorus content may further increase due to its continued release from slowly decomposing logs being abundant in coniferous forest [21]. Increasing phosphorus content may also support the competitiveness of nutrient-demanding species, leading to competitive elimination of weaker species and an overall decline in diversity—higher P content was found to be associated with the diversity depression in natural undisturbed forests [58].

An immediate flush of nutrients (in the scale of months after canopy damage) into the soil and groundwaters due to accumulation and decomposition of organic debris was evidenced in several studies [16,19,21,24] and such a mechanism can also add to the competitive advantage of nitrophytes (sometimes, this was connected with the spread of invasive plants after disturbances, which was not our case). The loss of basic ions from upper soil horizons together with newly accumulated woody debris in our case may result in a slowing down of the humification rate, as can indirectly indicate a decrease in the soil carbon content. Such a process may be particular to conifer-dominated forests which last for a relatively short time after a disturbance event [105]. Soil organic content can also be reduced by the enhanced decomposition associated with increased flux of carbon dioxide after disturbance [20].

4.3. Future Projection of Subalpine Coniferous Forests on Mt. Halla

Several studies predicted that oak-dominated broadleaf woodlands will replace the original subalpine *A. koreana* forests in the coming decades [29,31,91]. These studies found a negative impact of global warming on *A. koreana* growth in our study site, while the opposite was documented for oak (*Quercus mongolica*) growth [83]. In addition, our results show that *A. koreana* regeneration is suppressed by dense graminoid understory, and its subalpine forests can thus be replaced by dense bamboo vegetation, which provides only limited opportunities for forest regeneration (Figure 1D) [10,76]. Deciduous trees accompanying *A. koreana*, such as *Sorbus commixta*, *Aria alnifolia*, *Prunus maximowiczii*, and *Betula ermanii*, belong to pioneer early- to mid-successional species [77,91] with easily germinating seeds distributed by birds and wind over long distances that may better cope with dense bamboo understory filter [76,106]. In particular, members of the *Rosaceae* family (i.e., *Sorbus commixta*, *Aria alnifolia*, and *Prunus maximowiczii*) can regenerate vigorously by re-sprouting, and/or by flowering and producing seeds in larger quantities. These species also develop trunks more stable against uprooting and stem breakage [7,29]. Moreover, the prospect of *A. koreana* is critical as the typhoon tracks and intensities further in 2018, 2019 and 2020 were almost identical to those causing a severe disturbance in 2012 [107]. This suggests continued disruption to unique natural subalpine forests on Mt. Halla. Hence,

adaptive management in protected forests such as in situ assisted regeneration and ex situ expansion of endangered species populations should be implemented [75,81,82].

5. Conclusions

We investigated the impact of two severe typhoon disturbances on forest vegetation and soil properties in Hallasan National Park, using a series of permanent plots located in montane broadleaf and coniferous forests. Typhoons caused mild disturbances in lower-elevation oak (*Quercus mongolica*) forests, leading to gap-based forest dynamics. In contrast, severe disturbances in higher-elevation coniferous forests adversely influenced the largest population of endemic *A. koreana* in South Korea. Detected soil changes, together with the canopy opening after massive *A. koreana* dieback, were responsible for the observed changes in plant understory composition towards less diverse vegetation dominated by clonal graminoids. Regeneration of *A. koreana* was limited by a decrease in the seed rain and further blocked by graminoid expansion. Typhoon-triggered allogenic succession replaces subalpine *A. koreana* forests with pioneer-dominated communities, which can be eventually transformed into oak-dominated communities, a conclusion supported by other studies. Based on available literature, it seems that coniferous forests in subalpine areas within the range of tropical cyclones are particularly endangered at least in the Northern Hemisphere, with similar mechanisms of their disruption as described here. Specifically, the projected climate warming and increased frequency of strong typhoons may cause further pressure on the environment leading to the loss of *A. koreana* subalpine forests.

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