Processes driving understory community dynamics in Ulleungdo Island broadleaved forest, South Korea

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Abstract
The development stage of forest trees has considerable impact on the understory plant species; however, little research has been dedicated to in-depth investigation of the changes in the ecological processes (deterministic and stochastic) over a mid-term observational period (≥10 years). We analyzed the forest floor environment, including bare mineral soil, tree communities (density and biomass), understory plant species composition, diversity, cover, and changes in co-occurring species in the Albongbunji Basin on Ulleungdo Island over an 11-year period (2009–2019). The forest floor environment exhibited a broad spectrum of changes, beginning in the middle of the observation period and after heavy rainfall, and heavy sediment deposition events were observed. The overstory tree density showed patterns of a general increase and subsequent decline, and the overstory tree biomass increased and then remained steady. The heavy rainfall and sediment deposition as disturbance events also coincided with changes in species composition and the turnover rate of the understory plant communities, causing changes in major ecological processes. The general pattern of species co-occurrence (zeta diversity) was fitted to an exponential model, indicating the dominance of stochastic processes. The results show a shift in relative importance from deterministic to stochastic processes in the successional stages of understory plant community assembly over a mid-term observational period.

KEYWORDS
disturbance, Fagus engleriana, plant community, stochasticity, understory dynamics

1 | INTRODUCTION

In forest ecosystems, understory vegetation displays heterogeneous species composition, structure, and spatial distribution patterns, according to the overstory plant species composition, thereby enhancing forest biodiversity and forming a large variety of habitats (Antos, 2009; Gilliam, 2007). The understory vegetation also influences the energy flow and nutrient cycling as major factors in the succession of the overstory vegetation by rapidly responding to disturbances (Liu et al., 2018; Nelson et al., 2007). Many studies on vegetation dynamics in temperate forests have
emphasized the importance of the understory vegetation dynamics and related ecological processes (Dovčiak & Halpern, 2010; Hart & Chen, 2006; Roberts, 2004).

Efforts have been made to understand the importance of key assembly processes that determine small-scale community structure and composition, depending on the post-disturbance succession, namely, the traditional deterministic and stochastic models, and more recently, the neutral model (Liu et al., 2018; Måren et al., 2018). These three viewpoints make their respective predictions for successional patterns of community composition and species co-occurrence. If the deterministic processes driven by plant traits (such as shade tolerance and climbing) are dominant during succession (Clements model; Clements, 1916), we can expect predictable species turnover, given that the system will proceed through successional stages composed of characteristic species emerging at different points in time. From this, it inevitably follows that the changes in community composition within the same system are repeatable at different successional stages. Further, given that species with similar ecological requirements will respond to the successional gradients in mostly similar ways, a relatively stable composition of co-occurring species can be expected (McCook, 1994). The Gleason model emphasizes the random aspect of community assembly, which is difficult to predict (Eliot, 2007). If stochastic disturbances such as flood-induced sedimentation and forest gaps caused by strong winds are dominant over succession, we can observe a consistently high species turnover rate within the time range of succession, depending on the priority effects of colonizing species and fulfillment of niche requirements in different successional stages. However, species may enter or be excluded from the community at different points in time, depending on the individual species reactions and the interaction between niche requirements and chance events such as dispersal. Therefore, constant changes in species composition are expected between successional systems and during succession. The most rapid change in both composition and co-occurrence is expected in early successional stages provided that the community has not reached a saturated state whereby species can neither enter nor leave the system. Once the community is saturated, progressive or repetitive species co-occurrence patterns can become dominant over randomness (Måren et al., 2018). The randomness of community assembly processes emphasized by Gleason (1926) links with the biodiversity neutral model proposed by Hubbell (2001). The neutral model (Hubbellian model), which assumes species equivalence determined by the dynamics and interactions of colonization and extinction rather than by the differences in niche requirements, supports non-random species composition during succession (Ulrich et al., 2016). However, we can expect low repeatability (predictability) in the characteristic community composition and species co-occurrence patterns throughout the successional time and repetitive successional stages.

As mentioned above, the successional dynamics of a plant community are influenced by two ecological processes, namely, deterministic and stochastic processes (Liu et al., 2018; Måren et al., 2018). The niche-based deterministic viewpoint emphasizes the opposing force of environmental filtering and competitive exclusion with regard to co-occurring species. The stochastic viewpoint emphasizes the role of dispersal limitations and stochastic demographics in determining community assembly (Liu et al., 2018). However, changes in the composition of co-occurring species are determined by disturbance events resulting in forest gaps and processes of resource-use competition or suppression between understory plants and overstory trees depending on successional processes (Franklin et al., 2002). Furthermore, given the major forest development processes (i.e., an initial increase in biomass and mid-term stagnant biomass or initial density-dependent tree mortality and subsequent density-independent tree mortality), shifts in the relative importance of the stochastic or deterministic effects may be expected.

In particular, deterministic forces, including changes in the light regime and interspecific competition, are responsible for repetitive species turnover in the understory vegetation during the decades following disturbances in a forest (Roberts & Gilliam, 2003; Royo & Ristau, 2013). Both density-dependent and density-independent processes for tree mortality are involved in early forest development, and the dominance of a single deterministic process is thus less likely (Lutz & Halpern, 2006). In this respect, emphasis is given to the shifts in the relative importance of deterministic and stochastic processes, depending on the successional sequence and the disturbance level of a successional system (Måren et al., 2018). The understory vegetation developmental process in a young tree stand at the stem exclusion stage can be generally explained, whereas little is known regarding the changes in this process over mid- or long-term observational periods (Halpern & Lutz, 2013). Efforts are underway to understand the relative importance of heterogeneous processes that change in line with the successional processes in an ecosystem (Chase & Myers, 2011; Fraterrigo et al., 2020; Liu et al., 2018; Royo & Ristau, 2013).

Despite a number of long-term observational studies investigating vegetation community assembly (Fukami & Wardle, 2005; Hobbs et al., 2007), studies on the understory vegetation changes and forest development following natural disturbances or abandonment of forest management (e.g., logging, grazing, and tilling) have been
conducted due to the complexity of the underlying landscape (i.e., disturbance intensity, environmental characteristics, and differences in the dominant mechanisms) (Liu et al., 2018; Romme et al., 2016). We observed a young forest stand in the stem exclusion stage over an 11-year period (2009–2019). In a young forest stand at the stem exclusion stage (density control stage), the understory vegetation is likely to be subjected to high uncertainty, as well as a high community turnover rate, as the filtration pressure from the overstory decreases. Following this, the turnover rate and uncertainty will change as the young forest stand develops. Based on the foregoing, we aimed to determine how community composition and diversity varied in line with the successional processes in summer-green broadleaved forest understory vegetation. In addition, we discuss the role of deterministic and stochastic ecological processes involved in structuring the understory vegetation community composition, depending on the overstory development and disturbance events.

2 | METHODS

2.1 | Study site

The study site is located in the Albongbunji Basin on the oceanic island Ulleungdo (37°14’N, 130°47’E; 37°33’N, 130°47’E; 37°14’N, 130°55’E; 37°33’N, 130°55’E) (Figure 1). Ulleungdo Island is a Quaternary volcanic island located in the northern part of the Ulleung Basin east of the Korean Peninsula. It is characterized by steep and rocky terrain with very small flatlands, except for the Nari Basin and the Albongbunji Basin (Im & Choo, 2015). The Albongbunji Basin is the cinder cone formed by a secondary eruption of lava within the Nari Basin (Korea Institute of Geoscience and Mineral Resources, 2020) and is composed of pyroclastic-flow deposits resulting from a Strombolian type of volcanic eruption (Korea National Arboretum, 2015). The Albongbunji Basin is an alluvial region with fertile volcanic ash (Park, 1997).

FIGURE 1 Location of the study site. (a) Korean peninsula; (b) Ulleungdo Island; (c) Albongbunji Basin [Color figure can be viewed at wileyonlinelibrary.com]
From 1981 to 2010, the average annual temperature on Ulleungdo Island was 12.4 °C, and the average annual precipitation was 1,383.4 mm, which was evenly distributed throughout the year (Korea National Arboretum, 2019). Ulleungdo Island is characterized by high humidity throughout the year, and there are strong microclimatic variations caused by differences in the evaporation rate due to topographic factors (Kim et al., 2011; Lee et al., 2010). A uniform temperature distribution was observed throughout the survey period, and there were a few months with heavy rainfall that caused landslides (Korea Meteorological Administration, 2015) (Figure 2). Heavy rainfall events are indicated in Figure 2 by months with precipitation of ≥300 mm. Events with ≥300 mm precipitation occurred three times between 2009 and 2011, and events with ≥400 mm precipitation occurred three times between 2014 and 2016. Owing to its location and topographic features (high elevation mountainous terrain), Ulleungdo Island is frequently affected by landslides and rock-falls caused by heavy rainfall events (Lee et al., 2018; Seo et al., 2012). The study site, located at the inner caldera, is alluvial land consisting of sedimentary layers approximately 50–100 m thick. The thick sedimentary layers are created by mass movement during intense rainfall events (Kim & Kim, 2019). At the observation site, the average extent of soil deposition from 2009 to 2019 was 22.2 ± 26.0 cm (n = 538) aboveground (Cho et al., 2020).

Residential and agricultural activities (tilling and grazing) are concentrated in the Nari and Albong basins, which are the only flatlands on Ulleungdo Island. In the Albongbunji Basin, where the study site was established, intensive cattle grazing was previously practiced in the alluvial areas. As the livestock industry is giving way to factory breeding, with the exception of small-scale croplands, many of the fields and all pastures have been abandoned since the 1960s, and vegetation succession is in progress in this area (Park, 1997).

The survey site is a band-shaped permanent plot (20 × 100 m), which we subdivided into 20 subplots (10 × 10 m). In 2009, there were 264 trees with annual rings that could be counted at 30 cm above ground level in the 20 subplots. The mean number of annual growth rings was 38. There were 234 trees in the canopy layer, and the mean number of growth rings for these trees was 40. Taking into account the height at which the rings were counted, we calculated that it was appropriate to add 5 years to the estimated age of the trees. Therefore, the age of the forest at the study site in 2009 was 45 years. According to a widely used model, stand development can be divided into four stages: (1) stand initiation, (2) stem exclusion, (3) understory re-initiation, and (4) old-growth or structurally complex (Franklin et al., 2002; Oliver, 1980; Oliver & Larson, 1990). The survey site was assessed at the stem exclusion stage of the forest stand development stage, which is characterized by strong competition and density-dependent tree mortality, leading to a reduction in and fluctuation of the light level on the forest floor (Halpern & Lutz, 2013).

2.2 Observations of the forest plot

Observations were made over the period from June 2009 until October 2019. The permanent survey plot (20 × 100 m) was established in June 2009 in a nested

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**Figure 2** Mean temperature and rainfall in Albongbunji Basin on Ulleungdo Island, over the period 2009–2019. Red arrows indicate months with >400 mm of rainfall [Color figure can be viewed at wileyonlinelibrary.com]
design along the vertical direction, 10 m from an intermittent stream that flows only during rainfall. The plot was subdivided into 20 subplots (10 × 10 m). We also established 20 microplots (1 × 3 m), that is, one in the center of each subplot, to observe changes in the understory vegetation, and subdivided each microplot into three micro-subplots (1 × 1 m) to facilitate plant cover measurements. In the band-shaped plot, there was a greater abundance of vegetation in the understory in the area closer to the stream (20 × 50 m).

We recorded the species names of all trees in the subplots \((n = 20)\) and measured the diameter at breast height (DBH, at 1.2 m above ground level) with a diameter tape measure (woody plants with DBH ≥ 5 cm) except in 2010, 2014, and 2018. We recorded the species names of the woody and herbaceous plants growing to a height of ≤ 1 m in each micro-subplot and recorded the percent cover using visual assessment in all years except 2010 and 2014. We measured the following ground environmental factors: bare soil (%), woody debris (diameter > 3 cm, %), and rock (diameter > 3 cm, %) on the forest floor in all years except 2010, 2013, and 2014. As the stream overflows into the study site, all three ground environmental factors can vary according to internal and external actions (e.g., mature trees in the permanent survey plot, flood-induced sedimentation, or woody debris movement).

For the identification of the observed plants, we referred to previous Korean researchers (Kim & Kim, 2018; Lee, 1991; Lee, 2014); scientific names were taken from the plant taxa list released by the Korea Forest Service (Korea National Arboretum, 2017).

2.3 Data analysis

Based on the tree measurement data, we calculated the mean individual density and biomass of the community for each subplot \((n = 20)\). The data obtained for the micro-subplots were converted to a single dataset by calculating the mean value of the three measured values to convert the micro-subplot data to the microplot level corresponding to subplots \((n = 20)\). From the data for microplots, community-level species richness and average cover were calculated for each year. Community-level changes in the ground environmental factors (i.e., bare soil, woody debris, and rock) and overstory environmental factors (i.e., tree biomass and density) were calculated. Overstory tree biomass was estimated using allometric equations with stem DBH as the predictive variable (Table 1). Furthermore, the importance values of the understory species observed were calculated as relative cover values.

To assess the level of niche requirements (emergence of stable turnover patterns) and chance events such as species dispersal and random extinction (emergence of unstable turnover patterns) on the appearance and disappearance of species in the understory plant community, we used the turnover rates (%) of co-occurring species (Hallett et al., 2016) and zeta diversity \((\zeta)\) (Hui & McGeoch, 2014; McGeoch et al., 2017). To estimate the species ratio that varies along the time series, we calculated the turnover rate using Equation (1). For statistical assessment of deterministic processes, we analyzed the correlations with the ground, over-, and understory environmental factors by applying Pearson’s correlation coefficient (Legendre & Legendre, 2012).

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\text{Total turnover} = \frac{\text{Species gained} + \text{Species lost}}{\text{Total species observed in both timepoints}}
\]  

(1)

The number of species shared across the individual communities in the survey site was derived from the zeta diversity analysis. Zeta diversity enables the measurement of the conversion turnover for the individual combinations surveyed as \(i\) communities, that is, zeta diversity represents the mean number of shared species across \(i\) survey sites (e.g., intersection), and \(i\) is referred to as the zeta order. The unit of measurement of zeta diversity is, therefore, the “number of shared species,” with its minimum value 0 meaning “no species shared by two or more sites” and its maximum value being affected by the total species richness of the community matrix. An increase in zeta order inevitably entails a decrease in the number of shared taxonomic groups, that is, an increase in zeta order is always accompanied by a decline of zeta diversity, which is measured using a species presence/absence matrix.

We confirmed the annual change in zeta diversity and fitted a power law and exponential function to the relationship between zeta diversity and zeta order. In the null model, whereby all species have an equal chance of occurring in one place irrespective of the heterogeneity of the survey sites, this zeta diversity decline takes an exponential form (McGeoch et al., 2019). Fit analysis was performed using the overall presence/absence matrix rather than an annual analysis. The quality of the fits was determined using Akaike’s information criterion (AIC) (Akaike, 1974). This can also be used to determine the contribution of stochastic versus deterministic processes in community assembly regarding the expected rate of compositional change (McGeoch et al., 2019).

We also analyzed the probability of certain species with communities of the same order to be retained (or rediscovered) in a community through measurement of the zeta ratio. As the zeta order increases, the community composition changes from low- to high-frequency species, and the zeta ratio is relative to such compositional changes. For example, a zeta ratio of \(\zeta_9\) can be interpreted as the probability that
a species will be retained in at least nine out of 10 communities (e.g., $\zeta_{10}/\zeta_{9}$).

Univariate and multivariate statistical analyses were carried out using R software. Zeta diversity was analyzed using the “zetaR” package (Latombe et al., 2018), and non-metric multidimensional scaling (NMDS) ordinations using the metaMDS function from the “vegan” package (Oksanen et al., 2020). For the correlation analysis between the NMDS ordination results and biotic factors, correlation coefficients and significance levels were calculated using the "envfit" function.

### 3 | RESULTS

#### 3.1 | Changes in the forest floor and over- and understory environments

During the observation period, while woody debris and rock cover on the forest floor of the survey site underwent repeated cycles of increase and decrease, the proportion of bare soil increased significantly from 0.0% in 2016 to 12.7% in 2019 (Figure 3). Woody debris covered the largest area from 2015 to 2016. There were fluctuations in the proportion of rock cover. The average overstory biomass continuously increased until 2016, followed by exhibiting a steady state, and the average overstory density increased until 2013, followed by a continuous slight decrease until 2019 (Figure 4).

Throughout the experimental period, a total of 64 taxa were observed in the understory vegetation. The species richness of the understory plant community showed a peak in 2013, followed by a decline until 2016 (Figure 5). The average understory cover increased from 5% in 2009 to a maximum of 13% in 2015; there was a steep decline in 2016, followed by a steady increase to 12% in 2019 (Figure 5). The turnover rate of understory vegetation species showed a multimodal pattern, whereby it was relatively low until 2013, after which it increased until 2017 and then subsequently decreased (Figure 6).

Correlation analysis revealed that most of the ground and overstory (tree density) factors were slightly negatively correlated with the understory vegetation factors (e.g., rock cover, understory vegetation abundance, and understory vegetation cover) (Figure 7). The tree biomass, which constitutes the greatest portion of the aboveground vegetation biomass, did not show any correlation with the understory vegetation factors.

#### 3.2 | Changes in species diversity and composition

##### 3.2.1 | Species diversity

The zeta diversity (Figure 8a) and ratio (Figure 8b) can be divided into two phases over time. Analysis of the zeta diversity revealed that it decreased more sharply later in the
FIGURE 3  Time-series trend (mean ± standard error) of abiotic environmental factors (bare soil, rock cover and woody debris) at Albongbunji Basin on Ulleungdo Island

FIGURE 4  Time-series trend (mean ± standard error) of biotic environmental factors (biomass and density of the overstory vegetation) at Albongbunji Basin on Ulleungdo Island

FIGURE 5  Time-series trend (mean ± standard error) of species richness and cover of the understory vegetation at Albongbunji Basin on Ulleungdo Island
observation period (2015–2019) compared to that witnessed early in the observation period (2011–2013), accompanied by an abrupt decrease in the number of co-occurring species across the survey subplots. Further, at the beginning of the observation period (2009–2013), the number of shared species across the subplots was high, with the zeta diversity reaching zero in higher zeta orders (16–19), and the number of co-occurring species reduced to zero from 2015 onwards in lower zeta orders (≤7).

In line with the changing pattern in zeta diversity, the zeta ratio showed significantly different patterns before and after 2015. The highest species retention rate was observed in an intermediate order range (12–16) before 2015, followed by a subsequent decrease (Figure 8b).

The changes in zeta diversity corresponded with the variation in species richness; both zeta diversity and species richness declined later in the observation period (Figure 5). Over the entire period, the form of zeta decline showed a better fit with an exponential function (ΔAIC = −31.23) (Figure 8c) than a power law function (ΔAIC = 44.16) (Figure 8d). The year-by-year observations showed the same better fit with an exponential function as that for the entire period. Except for the form of zeta decline in 2009, we can infer the tendency of change from the power law model (deterministic process) to the exponential model (stochastic process) in general (Figures S1–S3). It is difficult to explain the form of the line of the first year (2009) due to the absence of previous data;
however, overall, the shape means that compositional change is better represented by stochastic processes than by deterministic processes.

### 3.2.2 Species composition

The changes in the understory cover can be explained by the changes in the eight major understory plant species consisting of five woody species—Manchurian elm (*Ulmus laciniiata*), Engler’s beech (*Fagus engleriana*), Ulleung mountain ash (*Sorbus ulleangensis*), Korean privet (*Ligustrum foliosum*), and rocky hydrangea vine (*Schizophragma hydrangeoides*)—and three herbaceous species—scaly holly fern (*Polystichum retrosopaleaceum*), cross holly fern (*Polystichum tripteron*), and upside-down holly fern (*Arachniodes standishii*). Three types of changes were observed in the woody plant cover. These were (1) repeated increases and decreases—Manchurian elm, Korean privet, and Ulleung mountain ash; (2) increases, followed by a steady state—rocky hydrangea vine (i.e., the dominant species of the survey site); and (3) steady state, followed by an increase—Engler’s beech. The three herbaceous plants, which are all ferns, increased until the middle of the observation period,
followed by a decrease (Figure 9). Of the understory plant species, those that tended to decrease gradually were mostly forest edge species, namely, shrubs abundant in forest edges (e.g., spicate falsenettle \( \text{Boehmeria spicata} \)); herbaceous plants (e.g., riparian greenbrier \( \text{Smilax riparia} \)), East Asian sanicle \( \text{Sanicula chinensis} \), Ulleungdo jack-in-the-pulpit \( \text{Arisaema takesimense} \), East Asian wood fern \( \text{Dryopteris maximowiczii} \), Asian common ladyfern \( \text{Athyrium yokoscense} \), and climbing hydrangea \( \text{Hydrangea petiolaris} \)), and a typical late successional tree species, rigid-branch yew \( \text{Taxus cuspidata} \), which is apparently increasing (Table S1).

On the other hand, plants that were only observed later in the observation period were not shade-tolerant species but rather species that favor forest edges or disturbed habitats, such as Ulleungdo ladyfern \( \text{Athyrium acutipinnulum} \), teeth-margin crepidiastrum \( \text{Crepidiastrum denticulatum} \), island thistle \( \text{Cirsium nipponicum} \), and Sakhalin corktree \( \text{Phellodendron amurense} \).

The NMDS ordination results (stress = 0.2091, Figure 10) showed dramatic change patterns rather than a progressive change in composition along the axis. There were only small changes in species composition from 2009 to 2013. However, from 2013 onwards, species composition changed more dramatically between years, with the observed changes not always occurring in the same direction. Only the tree density on the forest floor and in the overstory showed significant correlations with NMDS 1 \( r^2 = 0.2204, p < 0.001 \).

4 | DISCUSSION

Deterministic environmental filtering triggers community assembly linked to each species functional traits (Ulrich et al., 2017). Species composition is also influenced by dispersal limitation, herbivores,
disturbances, and neutral processes related to stochastic population fluctuations within communities. These deterministic and stochastic processes are difficult to distinguish from one another, and both are ultimately controlled by the underlying environmental and spatial characteristics. It is necessary to accumulate strong evidence by conducting studies that directly verify the fundamental processes of community assembly to separate the overlapping complex effects that occur between the driving forces that cause these ecological changes in the environment. We observed the changing patterns of understory vegetation for 11 years in the summer-green broadleaved forest of Albongbunji Basin, Ulleungdo Island. In a young forest stand (<60 years) dominated by Engler’s beech, stochastic factors such as sediment migration due to a record-breaking rainfall event were found to have had a great effect on the community assembly during the mid-term stage (2014–2016). Besides, life-history traits such as habitat preferences and propagation patterns play an important role in the utility of space and resources by plants at a particular site.

The limitations of our study included a small-scale observation area and insufficient measurements of major environmental factors associated with successional processes, such as the physical and chemical properties of soils. However, the continuous measurement data over an 11-year period allowed us to investigate the driving ecological processes in this Fagus-dominated young summer-green broadleaved forest, which contributes new knowledge.

### 4.1 Impact of environmental variations and heavy rainfall disturbances

During the study period, a number of record-breaking heavy rainstorms occurred (i.e., there were 3 months with ≥300 mm precipitation between 2009 and 2011, and 3 months with ≥400 mm precipitation between 2014 and 2016). The Albongbunji Basin is a volcanic caldera and is prone to flooding and landslides due to rapid storm runoff through the outer rim of the caldera (Kwon et al., 1994). The large variation in the exposed soil and rock cover is a result of the topographical characteristics of the area (Figure 3). Change patterns with strong variations in bare soil and rock cover are the result of the topographic features (Figure 3). Surface elevation changes caused by soil and rock sediments (in extreme cases, deposition of 50 cm of sediment) and formation of temporary streams were observed after heavy rain. Sedimentation-induced changes in the habitat land surface are disturbances that fundamentally change the existing environment, thereby leading to unique micro-

successional processes that may result in large-scale regeneration of dominant species and the emergence of new plant populations from other area (Pang et al., 2018).

The impacts of the landslides caused by heavy rain on habitat environment were as follows: formation of a new primary or secondary microscale successional space during the secondary successional process; simultaneous formation of communities with different structures at the regional level at the microsites formed by sedimentation; landscape heterogeneity; and species and structural diversity (Elias & Dias, 2009). The survey site in this study included both areas unaffected by sediment transport and newly formed microscale heterogeneous spaces. Thus, in this small-scale survey site, understory plant communities of different successional sequences were observed during the 11-year study period.

Disturbance regimes, which are defined as the accumulated effects of disturbance events occurring through time, usually occur as a stochastic process (Keane, 2013) and show differences in frequency, severity, and extent (Turner, 2010). We recorded heavy rainfalls and mass movement as “disturbance events” over the study period, which were followed by environmental changes at the survey site. However, the study period is deemed insufficient to determine the long-term effects of record-breaking rainfall events and subsequent sediment transport. The recovery dynamics after a disturbance vary depending on the temporary or periodic disturbance characteristics (Miller et al., 2011). Continuous observations are necessary to determine whether sediment transport within the Albongbunji Basin exhibits repetitive characteristics as a disturbance regime and how such disturbances are involved in the regeneration process of the trees, including the dominant Engler’s beech. The successional sequence of the study site was assessed to be transitioning from the stem exclusion stage to the understory re-initiation stage, in which there is regeneration of tree species from the overstory and forest stand continuity is established (Cho et al., 2020; Franklin et al., 2002).

### 4.2 Relative changes in deterministic and stochastic processes

#### 4.2.1 Early observation phase dominated by deterministic processes

In the initial phase of the understory plant community observation, there was little change in forest floor conditions, and the overstory also continued to change in a homogeneous pattern. The species diversity increased after the baseline measurement and peaked, and the final result showed even lower diversity than that of the baseline.
On the other hand, the percentage understory cover gradually increased; however, a temporary peak was observed, presumably because the development of the understory vegetation gradually progressed in line with the relatively homogeneous (predictable) early-phase changing pattern, coupled with a relatively low species turnover rate (≤20%). If a deterministic process is dominant, the species turnover rate in a community over time can be expressed by a relatively stable pattern. In the early observation phase, zeta diversity also showed an increasing trend, with new plant species entering the survey communities (survey site units) (Figure 8, Figure S1). As a supporting result, the NMDS ordination showed a small-scale change in the community composition, and consistent directionality as the overstory density increased from 2009 to 2011. Therefore, during this early part of the study period, deterministic processes were driving the community dynamics of the understory, for example, interactions between environmental conditions and existing plant species (Chesson, 2000; Fargione et al., 2003). On the other hand, the peaks of understory species richness and cover can be attributed to the disturbances caused by the heavy rainfall events and sediment transport that occurred several times during the observation period, rather than to saturation caused by the rainfall (Måren et al., 2018).

### 4.2.2 Mid-term and late observation phases dominated by stochastic processes

From the fourth year of observation onwards, a substantial change was observed in the understory vegetation development pattern along with large-scale variations in environmental factors. The basic background of this change is the impact of heavy rainfall and sediment transport in the Ulleungdo area. In 2013, a large directional change in the species composition began to occur, returning to the initial state of observation, followed by a dramatic increase in the average distance of change and the irregularity of direction. A gradual increase in tree density leads to a more closed canopy and less light reaching the forest floor; in turn, this leads to the suppression of light-demanding species of the understory community and increases in the shade-tolerant plant species (Franklin et al., 2002). During the successional process, however, the understory plant community cover increased steadily, and the overstory environment was independent of the species turnover rate (Figure 7).

Exponential and power law forms of zeta diversity decline are framed by distinct hypotheses regarding ecological processes; that is, hypotheses of stochastic (exponential zeta) or niche differentiation processes (power-law zeta) for species turnover (Scheiner et al., 2011). Deterministic processes were observed in the early phase of the experiment, whereas the overall decline in zeta diversity was more closely fitted to an exponential (i.e., stochastic) rather than a power law function. Rapid changes in understory species turnover rate (in particular, an increase) and species composition can be due to stochastic processes driven by environmental disturbances.

### 4.3 Importance of disturbances and plant traits

The initial composition of the understory plant community is also important in determining the changes in the community, irrespective of the overstory structure (Halpern & Lutz, 2013). Particularly, overstory tree species such as Engler’s beech became abundant during the study period. Moreover, Engler’s beech seedlings dominated the survey site, while natural regeneration of Engler’s beech has been rarely observed in Engler’s beech forest at the mountain slope near the basin (Han et al., 2019). Due to the large-scale inflow of seeds through sediment transport (Guariguata, 1990; Shiels & Walker, 2003), seeds from outside the area can also enter the stand. These results suggest the importance of the dispersal and colonization processes of species through disturbances over the filtering effect, such as the maturation process of the overstory, from the mid-term onwards.

It was also verified that the importance of plant life-history strategies, such as plant propagation and habitat preference, along with stochastic factors, was maintained throughout the successional process by the rapid utilization of the disturbed environment (Halpern, 1989). During the observation period, woody vines with high shade tolerance (such as the rocky hydrangea vine) and ferns that spread through underground rhizomes (Owens & Lund, 2009) continuously expanded. Hence, traits related to life-history strategies, such as habitat preference and propagation mechanisms, can be evaluated as important characteristics of understory plant community changes by using stochastic events or increasing the chance of retention after disturbance.

### 4.4 Implications for research

Our records of understory vegetation dynamics during observations of the mid-term phase revealed shifts in the relative roles of deterministic and stochastic processes under the influence of disturbances. Although the
responses of different species to niche and environmental conditions are closely associated with deterministic processes, the stochastic processes, such as fluctuations in species colonization and extinction, can be more important, especially in environmental conditions with strong abiotic and biotic filters (Chase & Myers, 2011). Although it is currently accepted that both deterministic and stochastic factors contribute equally to the community composition at the regional level (Chase, 2010; Chase & Myers, 2011; Oñaterra et al., 2010; Stegen et al., 2016), it is necessary to continue the efforts to understand their relative importance in determining community structure, successional processes, and biogeography as the core of this discussion (Stegen et al., 2015; Vellend et al., 2014; Zhou et al., 2013; Zhou et al., 2014).

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CONFLICTS OF INTEREST
The researcher claims no conflicts of interest.

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