Review on the succession process of *Pinus densiflora* forests in South Korea: progressive and disturbance-driven succession

Yeonsook Choung* , Jongsung Lee, Soyeon Cho and Jaesang Noh

Abstract

Background: Most of the *Pinus densiflora* forests, occupying the largest area, have been restored in South Korea since the 1970s. As young pioneer forests, the succession process is under way. Since the forests are distributed nationwide and are vulnerable to disturbances, the process may differ depending on the geography and/or site conditions. Therefore, we reviewed the direction, the seral communities, and the late-successional species of progressive and disturbance-driven succession nationwide in the cool-temperate zone through meta-analysis and empirical observations.

Main text: As a result of a meta-analysis of the direct succession and vertical structure, we found that the *P. densiflora* forest is in a directionally progressive succession, changing to the broadleaved forest after forming a mixed forest with its overwhelming successor, *Quercus* species (particularly *Q. mongolica* and *Q. serrata*). In dry stands in a relative sense, the *Quercus* species was favored occupying over 80% of the abundance of the succeeding species. Therefore, in dry stands, it is presumed that *Quercus*-dominated stage would last for a long time due to the current dominance and long life span, and eventually, it settles as *Quercus*-broadleaved forest with a site change. Contrary to this, it is presumed that in mesic stands where *Quercus* species do not occur or have low abundance, the late-successional broadleaved species settle early to form a co-dominant forest with multiple species. Due to geographical limits, the species composition of the two late-successional forests is different. Disturbances such as insect pests and fire retrogressed vulnerable *P. densiflora* forest for a while. However, it was mostly restored to the *Quercus* forest and is expected to be incorporated in the pathway of the dry stand.

Conclusions: We revealed the succession process of *P. densiflora* forests according to geography and moisture and found that stand moisture had a decisive effect on the species and abundance of the successor. Although the *P. densiflora* forest is undergoing structural changes, the forest is still young; so within a few decades, physiognomy is not likely to change. Therefore, the decrease in the forest area may be due to other causes such as disturbances and forest conversion rather than due to succession.

Keywords: Human-influenced, Japanese red pine, Korean red pine, Moisture, Oak, *Quercus mongolica*, *Quercus serrata*

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Background

In 1960, 42% (2.2 million ha) of the forest area in South Korea was unstocked, of which 19% (0.52 million ha) was denuded (Lee et al. 2010). The average growing stock was only 10.9 $m^3 ha^{-1}$ in 1972 (Lee et al. 2010; KFS 2018). Historical events such as Japanese colonial exploitation and the Korean War are often pointed out as the major causes of deforestation (e.g., Chun 1999; Chun et al. 2007). However, already in 1910, forests in South Korea covered only 20% area of the country. Most of the mature forests were then distributed in North Korea (Bae and Kim 2019). Therefore, the devastation of the forest would have been attributed to overexploitation of the forests for fuelwood due to long human history, high population density, and cold winter rather than historical events (e.g., Choung and Hong 2006; Lee 2010). Under such difficult circumstances, it was inevitable to depend on forest resources for fuel, timber, and food (Lim 2010).
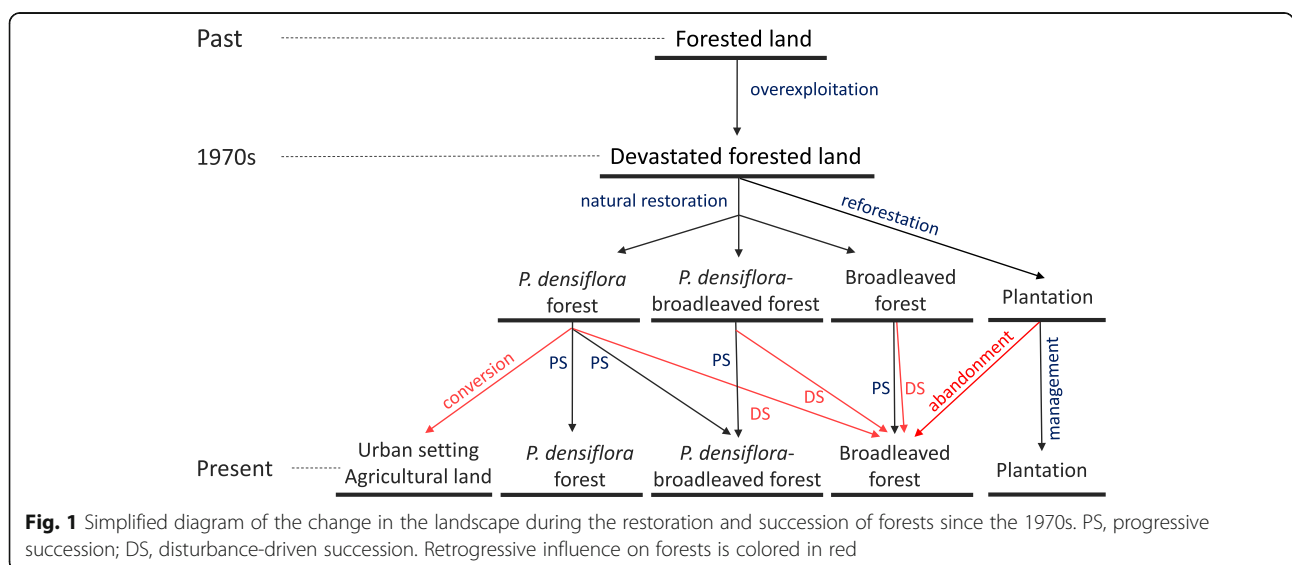
By the way, the average growing stock in South Korea increased dramatically to 157.8 $m^3 ha^{-1}$ in 2018 (KFS 2019). This dramatic restoration of the devastated land was due to the implementation of "The First and Second 10-year Forest Development Plan" (from 1973 to 1987) by the government (Chun 1999; Lee 2010). The two key points of this plan were large-scale reforestation and active protection policy. The latter included substitution of fossil fuels for firewood and clearance of slash-and-burn fields. In addition to the government policies, a large part of the rural population moved to cities as a result of urbanization and industrialization during high economic growth (Lee 2010). This led to an enormous reduction in forest use. Finally, human-arrested and denuded forests were released and restoration started (e.g., Lee 1989; Kamada and Nakagoshi 1993; Hong et al. 1995; Fujihara 1996; Toyohara and Fujihara 1998; Choung and Choung 2019).

The once-forested and devastated lands were restored to mainly three forest types in a short time which are *Pinus densiflora* forests, *P. densiflora*-broadleaved mixed forests, and broadleaved forests (KFRI 2016). The restoration of these forests depended upon preexisting vegetation structures (e.g., species composition, abundance, seed, and sprouting source) and site conditions (moisture and/or nutrients) (Fig. 1). For example, *P. densiflora* forests were developed where soil condition was harsh with little vegetation, while *Quercus* species and/or other broadleaved tree-dominated forests were developed where possibly the area had vegetation or sprouting sources.

Of these three types, the area of *P. densiflora* forests was the largest from the 1970s till today (KFRI 2016), which reflects that the *P. densiflora* settlement has been preferred. It is a light-demanding and typical pioneer species which can germinate in large quantities at even extremely denuded places in a short time to form large, single cohort secondary forests (e.g., Nakagoshi et al. 1987; Keeley and Zedler 1998; Beon and Bartsch 2003; Lee 2006; Park et al. 2010).

At least 111 species belong to the genus *Pinus*. *Pinus* is considered an evolutionarily successful genus because of its broad and dominated distribution in the Northern Hemisphere (Richardson 1998). Among them, *P. densiflora* (Korean red pine) is a two-needled pine geographically distributed in East Asia (Korea, Japan, China, and Russia) (Richardson and Rundel 1998; Lee and Yim 2002; Choung and Hong 2006). The Korean Peninsula is the center of distribution with widespread distribution. In Japan, the species is mainly distributed in Western Honshu, except for Hokkaido, and in China, it is

Fig. 1 Simplified diagram of the change in the landscape during the restoration and succession of forests since the 1970s. PS, progressive succession; DS, disturbance-driven succession. Retrogressive influence on forests is colored in red

distributed in the north of the Korean Peninsula, such as S Heilongjiang, NE Jiangsu, SE Jilin, Liaoning, and E and N Shandong (http://www.efloras.org/).

The area of the *P. densiflora* forests has decreased rapidly from 28% (1.76 million ha) in 1992 to 22% (1.34 million ha) in 2015 (Fig. 2) (KFS 2000; KFRI 2016). By contrast, the areas of the mixed forests and broadleaved forests are increasing (KFS 2019). Although the area is presumed to be the largest since the 1970s, no accurate information is available before 1986. This is because the *P. densiflora* forests were surveyed as a coniferous forest collectively including other coniferous forests and plantations.

As the main causes of the decrease in the *P. densiflora* forests, succession (e.g., Chun 1999; Lim 2010; Lee 2010) or disturbance such as insect pests, diseases, and forest fires (e.g., Lee 1989; Choung et al. 2004; Park et al. 2009; Lim and Korea Forest Research Institute 2010; Lee 2010; KFS 2016; Choung and Choung 2019) has been held responsible. As *P. densiflora* is a pioneer species, succession could be considered as logical causes. However, most forests are young, aged under 50 years (KFS 2019), and the lifespan of *P. densiflora* is typically around 150 years (Lee 1995; KFRI 2011). Therefore, it is unlikely that *P. densiflora* in such young forests had been replaced by the next seral communities. Instead, we can assume that socioeconomic and ecological factors, such as forest conversion, plantation failure, and forest

disturbance, have been overlooked as the cause, which have changed the landscape of Korean forests in the last few decades (Fig. 1). With the rapid growth of the Korean economy, significant areas of the forests were either developed into cities or converted to farmlands. Since the *P. densiflora* forests were located at low altitudes near cities and towns, it is most likely that they were lost. Another reason could be disturbances, such as pests, diseases, and forest fires, to which the forests were vulnerable, and had a low restoration capacity as well (Choung et al. 2004).

The dramatic increase of the broadleaved forests may be attributed to the conversion of an abandoned plantation. The total reforestation area after the liberation from Japanese occupation until the year 2000 totaled 5.3 million ha (83% of forest area) including fuel forests and re-planted areas (Lee et al. 2010). However, the current reforestation area covers only 15.5% of the total forest area (NGII 2016). The restoration of failed plantations into broadleaved forests can be commonly observed.

P. densiflora is a very preferred tree species in Korea and an important source of timber (Chun 1999). Nonetheless, except for limited areas such as rock outcrop, it is an inevitable natural process that this species is replaced by the next stage species via succession. There are a number of reports on the succession direction surveyed indirectly and/or stated empirically and intuitively at various scales (e.g., Lee and Lee 1989; Choung and Hong 2006; Chun et al. 2007; Cho and Lee 2011). There are only a few direct studies which have repeatedly observed the same area over time; however, the study periods in those research are only for two decades and are limited to local areas (Lee et al. 2005a; Lee et al. 2006; Lee et al. 2012b). Most of the successional series require at least 100 years to reach a climax stage (Barbour et al. 1999). Such a long time scale in studying succession is a serious challenge to the plant ecologists.

In spite of many limitations, it is necessary to tie up the pieces of information and propose integrated succession progress. Therefore, within the *P. densiflora* distribution range in the cool-temperate zone of South Korea, we collected and meta-analyzed direct and indirect data from across the country and then explored the processes of progressive and disturbance-driven succession according to geographical and moisture conditions, which we believe to be the most affecting factors. In the present study, the key seral communities and associated species composition of these processes have been identified, and the potential tree species of the late-successional stage have been proposed as well.

Progressive succession is defined as an increase in directional change in diversity and biomass over time, with habitats becoming moister (Barbour et al. 1999). On the
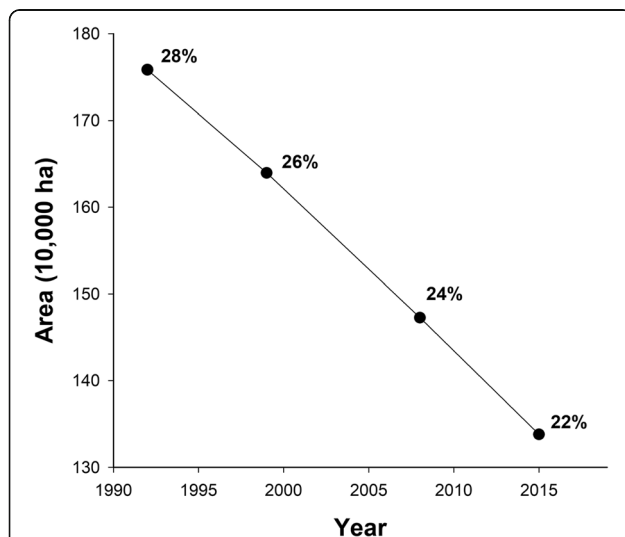
Fig. 2 Changes in the area of *P. densiflora* forests with time in the Republic of Korea. The values in the figure refer to the percent area occupied by *P. densiflora* forests of the total forest area. The area is based on data from 1992 with which forest area occupied by each species was investigated. Data are driven from the national survey on the status of conserved *P. densiflora* forests (KFS 2000), Statistical Yearbook of Forestry (No. 39) (KFS 2009) and the 6th National Forest Inventory Report (KFRI 2016)

other hand, disturbance-driven succession is defined as a directional change through which forests regenerate after undergoing stand-replacing or canopy-remaining disturbances.

Method
Meta-analysis 1: Progressive succession of *P. densiflora* forests over time
Data collection
The available research data on direct succession studies conducted in *P. densiflora* forests were collected. We selected only those data where the abundance of *P. densiflora* was over 15% in the canopy, the strata structure is provided, and the plantation was excluded. Finally, we obtained only 38 stands from 5 sites based on three articles and two databases. The research place and period of each data source are as follows: Mt. Jeombongsan (200–2013, 9 years, Lee et al. unpublished), Mt. Odaesan (2005–2015, 11 years, Choung et al. unpublished), Mt. Namsan (1990–2004, 15 years, Lee et al. 2005a), Nam-hansanseong Fortress (1993–2011, 19 years; 2005–2011, 7 years, Lee et al. 2012b), and Mt. Gayasan (1989–2004, 16 years, Lee et al. 2006). These study forests were estimated between 30 and 60 years old.

Data analysis
The collected stand data were divided into two communities according to the abundance of *P. densiflora*: one over 70% as pure stands (*n* = 24) and the other less than 70% as *P. densiflora-Quercus* mixed stands (*n* = 14). Also, the tree species in the canopy and extended canopy strata were listed as succeeding species in each stand, except for *P. densiflora*. The "Canopy stratum (C)" represented the tree and subtree strata of each stand, while the "Extended Canopy stratum (EC)" was the addition of a shrub stratum to the "Canopy stratum (C)." Here, the classification of "tree species" was based on the NIBR (species.nibr.go.kr).

In each stand, the tree species of C and EC were again assigned to one of the three succeeding groups, viz., (1) with only deciduous *Quercus* species (hereinafter "*Quercus* only"), (2) with deciduous *Quercus* and other trees mixed (hereinafter "*Quercus* & Others"), and (3) case with only other tree species (hereinafter "Others only"). "Others" include deciduous or evergreen, and broad-leaved or coniferous tree species only except for deciduous *Quercus* species.

Due to the various data source, there were also different ways to measure or calculate abundance. In order to make the data comparable, relative abundance was calculated. For data without any stand age information, we made estimations as Jeon et al. (2017).

Meta-analysis 2: Progressive succession estimated from the strata of *P. densiflora* forests according to geography and moisture condition
Data collection
Information on the vertical structure of *P. densiflora* forests was collected, and succession direction was analyzed. In total, we obtained 229 stand data from 46 cases nationwide (44 published articles and 2 unpublished databases) (Table 1). The stand data with a relative abundance of *P. densiflora* over 15% in the canopy stratum were selected, and those with planted trees over 50% were excluded. Only the information from the cool-temperate zone was included, and those from the warm-temperate zone were excluded. In addition, the data from only below 1000 m in elevation were taken. The forests that were analyzed ranged from tree size of DBH 20 to 40 cm, which were presumed to be between 30 and 70 years old based on Jeon et al. (2017).

Categorization of forest zone according to geography and moisture condition
The collected data source covered the cool-temperate zones of the whole nation and included eight provinces (Gangwon-do, Chungcheongbuk-do, Chungcheongnam-do, Gyeonggi-do, Gyeongsangnam-do, Gyeongsangbuk-do, Jeollabuk-do, Jeollanam-do) and four metropolitan cities (Seoul, Busan, Incheon, and Gwangju). Also, data from 14 national parks located within the administrative areas listed above were included.

All data were categorized into four zones (two geographical zones and two moisture conditions) based on what the authors provided. The geography was further divided into northern and southern zones following Eom (2019), who newly proposed the forest zone of Korea. Eom (2019) categorized the forest zone into southern-submontane zone 9~13 °C, central-montane zone 5.5~9 °C, and northern-altimontane zone below 5.5 °C according to the annual mean temperature. Considering the limitation of the number of data, we categorized 9 °C or less as the southern zone and above it as the northern zone. The moisture condition of the stands was categorized into mesic and dry in a relative sense. It was mainly based on the authors' descriptions, and if it was not described, then it was assigned based on species composition, micro-topography, vegetation type (NIE 2017), and/or species ecology data book (Choung and Lee 2019).

Data analysis
The distinction between the canopy and extended canopy strata is the same as those of meta-analysis 1. Among the total 229 data, there were 223 canopy and 229 extended canopy data as some canopies in the data had only *P. densiflora* with no other trees present.

Table 1 List of the references cited for meta-analyses 1 and 2

Moisture	Northern zone	Southern zone
Mesic	Back et al. (2013), Jo et al. (1995), Kim and Choo (2005), Kim et al. (2012), Lee et al. (1994), Lee et al. (1996), Lee et al. (2012c), Noh et al. (2013), Oh et al. (2005), Oh et al. (2017), Park and Kang (2016) Park and Oh (2015), Park et al. (1988), Shin et al. (2014), Yoon et al. (2014)	Ahn and Cho (2000), Choi and Cho (2001), Choi and Cho (2006), Choi and Cho (2009), Choi et al. (2009), Han et al. (2001), Han et al. (2014), Kang and Choi (2008), Kang et al. (2012), Kim and Um (2009), Lee et al. (1995), Lee et al. (2012a), Lee et al. (2013), Lee et al. (2014a), Oh and Shim (2006), Park and Kang (2016), Park and Oh (2015), Shin et al. (2014), Yoon et al. (2014)
Dry	An and Choo (2010), Cho and Choi (2002), Jo et al. (1995), Kim and Choo (2005), Kim et al. (1995), Kim et al. (2012), Kim et al. (2017), Lee et al. (1996), Lee et al. (1997), Lee et al. (2012c), Oh et al. (2005), Park and Kang (2016), Park and Oh (2015), Shin et al. (2014), Yoon et al. (2014),	Byeon and Yun (2018), Choi and Cho (2001), Choi and Cho (2006), Choi and Cho (2009), Choi and Kang (2006), Choi et al. (2009), Choo et al. (2008), Kang and Choi (2008), Kim and Choi (2004), Kim and Um (2009), Kim et al. (2006), Lee et al. (2002), Lee et al. (2009b), Lee et al. (2012a), Lee et al. (2013), Lee et al. (2014a, 2014b), Park et al. (1989), Park and Kang (2016), Park and Oh (2015), Shin et al. (2014), Yoon et al. (2014)

Species with relative abundance over 15% were considered as the succeeding species. Three types of succeeding groups were considered the same as those in meta-analysis 1. One thing different, this data set includes *Q. acuta*, an evergreen *Quercus* tree. As it is distributed only in the southern regions and not in the other forest zones, this species was included as "others" for comparison.

Nonmetric Multidimensional Scaling (NMS) ordination was performed by using species composition of the canopy and extended canopy according to the geographical and moisture conditions (PC-ORD ver. 6, PC-ORD 2011). The relative abundance of succeeding tree species was used, and no transformation was conducted. Species with less than two out of eight data sets were excluded from the analysis.
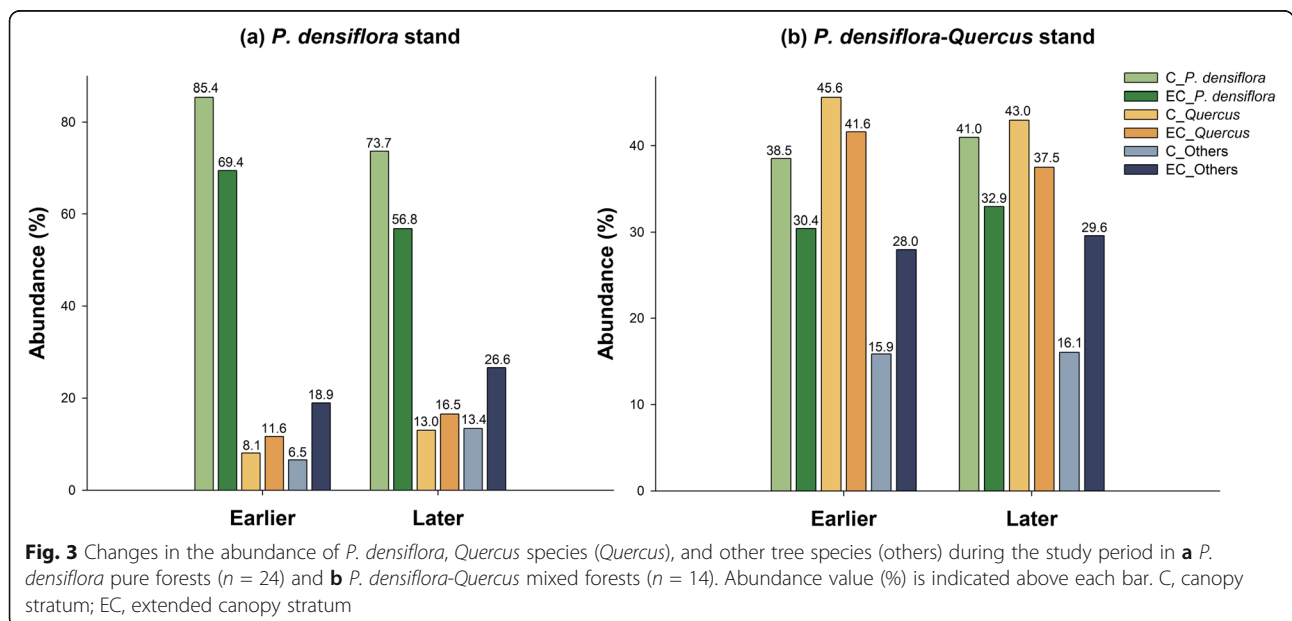
The number of species was compared according to moisture condition only for the north ($n = 53$ for mesic,

$n = 58$ for dry) by ANOVA (SPSS ver. 24, SPSS 2017). Data with the same plot size (15×15 m^2) was used, and no analysis was done for the south due to the small data size. The number of species in the canopy and extended canopy data was analyzed by pairwise t test (SPSS ver. 24, SPSS INC).

Main text

Meta-analysis 1: Progressive succession from *P. densiflora* forests over time

The abundance changes of major trees, *P. densiflora*, *Quercus*, and others, were compared in *P. densiflora* pure forests and *P. densiflora-Quercus* mixed forests for 7–19 years (Fig. 3). The typical succession was under way in which the abundance of *P. densiflora* decreased while those of *Quercus* and other species increased.

Fig. 3 Changes in the abundance of *P. densiflora*, *Quercus* species (*Quercus*), and other tree species (others) during the study period in **a** *P. densiflora* pure forests ($n = 24$) and **b** *P. densiflora-Quercus* mixed forests ($n = 14$). Abundance value (%) is indicated above each bar. C, canopy stratum; EC, extended canopy stratum

Nevertheless, due to the low mortality of *P. densiflora*, the forest type was not changed.

The mortality rate of *P. densiflora* trees, which were thicker in DBH and of lower density, was only 5% for 10 years in the forests of Mt. Jeombongsan and Mt. Odaesan (Table 2). On the contrary, the mortalities of *Quercus* and broadleaved species, whose density was high, were greater due to the effect of density-dependent thinning in the mixed forests (Barbour et al. 1999). The thinner trees in both the forests declined, and the surviving trees, especially *Quercus* and others, grew better than *P. densiflora*.

The succeeding group was analyzed (Table 3). The initial frequency of the "*Quercus* only" stand decreased later, common in both forests, while those of the "*Quercus* & Others" and "Others only" stands increased later. The change was slight, but it did show the direction of the change clearly. The results were the same for the extended canopy also. The extent of changes was greater in the mixed forests, which are in advanced stages.

On tracking the changes by stand, the species level changes could be identified. Addition of trees such as *Carpinus laxiflora*, *Sorbus alnifolia*, and *Acer pseudosieboldianum* to early "*Quercus* only" stands resulted in changes to "*Quercus* & Others" stands, whereas the *Quercus* species disappeared from the "*Quercus* & Others" stands to become "Others only" stands. This tendency was the same in the extended canopy with the change being larger, particularly when *A. pseudosieboldianum* was added to the multiple stands of the extended canopy.

Meta-analysis 2: Progressive succession estimated from the strata of *P. densiflora* forests according to geography and moisture condition

The vertical structures of *P. densiflora* forests across the country were analyzed and compared according to geographical and moisture conditions (Fig. 4). "*Quercus* only" stands showed the highest frequency in the three zones except for the southern mesic zone, and it was followed by "*Quercus* & Others" and "Others only" stands in the descending order. The frequency of "*Quercus* only" stands was lower for the extended canopy than for the canopy, while that for the "Others only" increased. This result was the same as that of the direct succession study.

Comparing the frequency of each succeeding group in the southern and northern regions, that of "*Quercus* only" stands was markedly high in the latter (Fig. 4a, b), whereas that of the "*Quercus* & Others" stands was higher in the southern mesic zone (Fig. 4c). On the other hand, the difference between the mesic and dry stands was large. While the frequency of "*Quercus* only" in dry stands was two times higher than in the mesic stands (Fig. 4a, c), the frequency of the "Others only" in the mesic stands was eight times higher than that in the dry stands (Fig. 4b, d). That is, 86% of the mesic stands were in the "Others only" succeeding group. This meant that other species, not *Quercus*, settled early as the succeeding species in most of the *P. densiflora* forests developed at the mesic sites.

The composition of the succeeding species in the *P. densiflora* forests of the four zones was clearly separated in the NMS ordination space (Fig. 5). The northern and southern zones were separated on axis 1 which accounted for 82.8% of the total variance, while the mesic and dry sites were separated on axis 2. The *Quercus* species such as *Q. mongolica*, *Q. variabilis*, and *Q. dentata* dominated in the northern zone, whereas the *Q. serrata* dominated in the southern mesic stands. The difference in species composition in the south and north was due to the species distributed only in the south, such as *Styrax japonicus*, *Carpinus tschonoskii*, *Q. acuta*, *Acer palmatum*, *Lindera erythrocarpa*, *Stewartia koreana*, and *P. thunbergii*.

Table 2 Tree population dynamics and diameter (DBH) growth in *P. densiflora* pure forests and *P. densiflora-Quercus* mixed forests in Mts. Jeombong and Odae during the study period

Stand	Tree species	No. of trees (ha^{-1})				DBH (SE) (cm)		
		Total	Survived	Dead	Dead (%)	Earlier	Later	Dead
P. densiflora stand (*n* = 11)	*P. densiflora*	454.5	436.4	18.2	4.0	28.8 (1.1)[1]	32.4 (1.0)	15.9 (0.6)
	Quercus	225.0	213.6	11.4	5.1	11.3 (1.1)	13.3 (1.2)	9.1 (2.4)
	Others	365.9	352.3	13.6	3.7	9.7 (0.3)	11.6 (0.3)	8.2 (1.6)
	Total	1045.5	1002.3	43.2	4.1	18.3 (0.6)	21.0 (0.6)	11.2 (1.8)
P. densiflora-Quercus stand (*n* = 10)	*P. densiflora*	182.5	172.5	10.0	5.5	33.0 (2.5)	38.8 (2.6)	12.4 (1.9)
	Quercus	887.5	660.0	227.5	25.6	15.0 (0.9)	17.8 (0.9)	9.9 (0.7)
	Others	70.0	52.5	17.5	25.0	12.2 (2.0)	14.0 (2.5)	11.2 (2.4)
	Total	1140.0	885.0	255.0	22.4	17.3 (1.0)	20.8 (1.1)	10.0 (0.6)

Plot size, 20 × 20 m^2
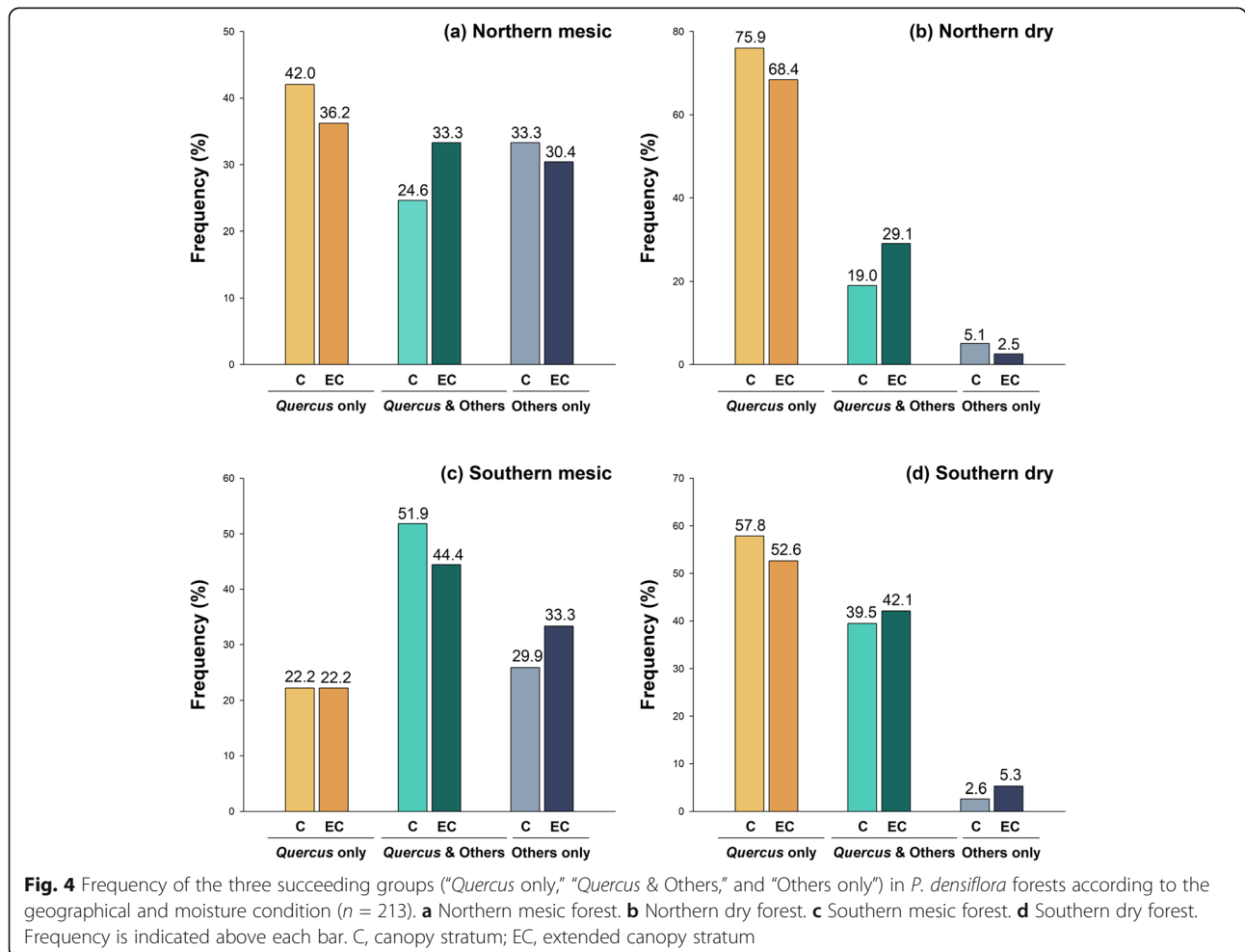[1]Mean and standard error are indicated

Table 3 Changes in the relative frequency of three succeeding groups in *P. densiflora* forests

Stand	Succeeding group	Earlier		Later	
		C (%)	EC (%)	C (%)	EC (%)
P. densiflora stands (*n* = 24)	*Quercus* only	35.0	25.0	30.0	25.0
	Quercus & Others	45.0	50.0	45.0	50.0
	Others only	20.0	25.0	25.0	25.0
P. densiflora-Quercus stands (*n* = 14)	*Quercus* only	71.4	71.4	64.3	42.9
	Quercus & Others	14.3	14.3	21.4	42.9
	Others only	14.3	14.3	14.3	14.3
Total (*n* = 38)	*Quercus* only	50.0	44.1	44.1	32.4
	Quercus & Others	32.4	35.3	35.3	47.1
	Others only	17.6	20.6	20.6	20.6

C canopy stratum, *EC* extended canopy stratum

Such difference can be compared in detail by species composition and abundance data of the four zones (Tables 4 and 5). The most predominant species was *Quercus* species. Especially, it occupies over 80% of the total abundance in the dry stands and about 50% in the mesic stands. *Q. mongolica* was the most frequent and overwhelmingly dominant species in three zones except the southern mesic zone. In particular, in the northern dry zone, the abundance of *Q. mongolica* exceeded 50%, while *Q. variabilis* was more dominant in the dry stands

Fig. 4 Frequency of the three succeeding groups ("*Quercus* only," "*Quercus* & Others," and "Others only") in *P. densiflora* forests according to the geographical and moisture condition (*n* = 213). **a** Northern mesic forest. **b** Northern dry forest. **c** Southern mesic forest. **d** Southern dry forest. Frequency is indicated above each bar. C, canopy stratum; EC, extended canopy stratum
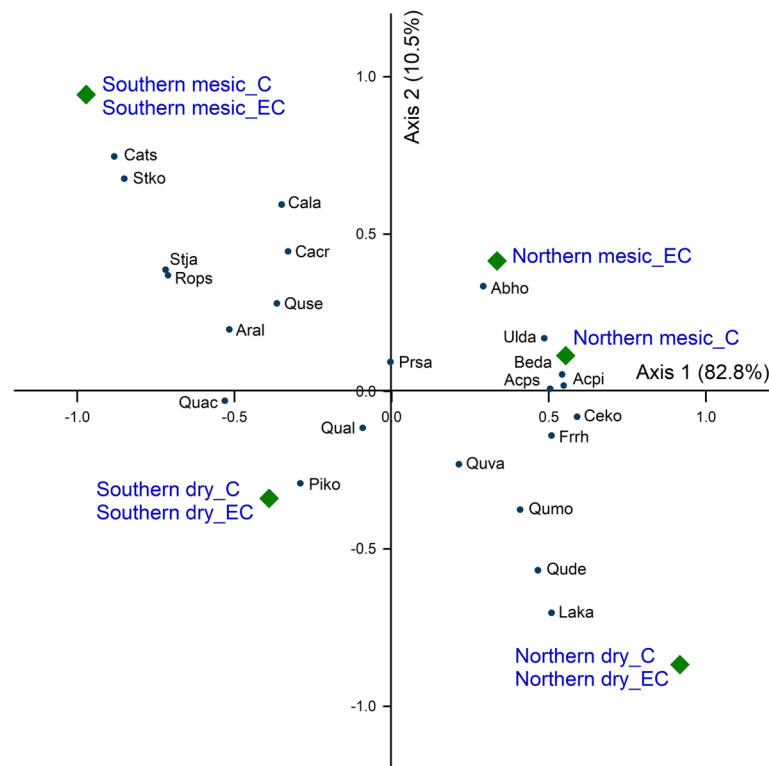
Fig. 5 Nonmetric Multidimensional Scaling (NMS) ordination showing the spatial relationship among the succeeding tree species composition in *P. densiflora* forests according to the geographical and moisture condition. The number next to the axis represents the variance of each axis relative to the total variance. C, canopy stratum; EC, extended canopy stratum; Abho, *Abies holophylla*; Acpi, *Acer pictum* var. *mono*; Acps, *Acer pseudosieboldianum*; Aral, *Aria alnifolia*; Beda, *Betula dahurica*; Cacr, *Castanea crenata*; Cala, *Carpinus laxiflora*; Cats, *Carpinus tschonoskii*; Ceko, *Celtis koraiensis*; Frrh, *Fraxinus rhynchophylla*; Laka, *Larix kaempferi*; Piko, *Pinus koraiensis*; Prsa, *Prunus sargentii*; Quac, *Quercus acutissima*; Qual, *Quercus aliena*; Qude, *Quercus dentate*; Qumo, *Quercus mongolica*; Quse, *Quercus serrata*; Quva, *Quercus variabilis*; Rops, *Robinia pseudoacacia*; Stja, *Styrax japonicas*; Stko, *Stewartia koreana*; Ulda, *Ulmus davidiana* var. *japonica*

in both south and north. In contrast to the above two *Quercus* species, *Q. serrata* was more frequent in the southern zone and more dominant in the mesic stands. *Q. dentata* appeared in dry stands, and *Q. acutissima* and *Q. aliena* were more abundant in the southern dry stands.

F. rhynchophylla among the other species, except for *Quercus* species, was the most dominant and frequent species, especially in the north. *Prunus sargentii* appears in similar abundance and frequency in all the four zones. *C. laxiflora* mainly appears in the mesic stands of the northern and southern zones with greater abundance and frequency in the southern zone. *A. pseudosieboldianum* and *Betula dahurica* mainly dominated the northern zone. On the contrary, *S. japonicus*, *C. tschonoskii*, *Q. acuta*, and *A. palmatum* seemed to be the characteristic succeeding species of the southern *P. densiflora* forests as they are distributed only in the southern zone.

There was a little difference in the abundance of *Q. mongolica* between the canopy and extended canopy (Table 5). However, *Q. serrata*, *F. rhynchophylla*, *A. pseudosieboldianum*, and *Q. aliena* showed the

possibility to increase in the future as they had greater abundance in the extended canopy. By contrast, *Q. variabilis* is predicted to decrease in all the zones.

The number of other broadleaved species in the canopy of mesic stands was three times larger than that in the dry stands (Table 6). The trend was the same in the extended canopy. When the number of species between the canopy and extended canopy was compared, it was not significantly different in mesic stands (Table 7). However, the number of the *Quercus* species or others was significantly greater in the extended canopy than that in the canopy in the dry stands. This implied that the species which did not exist in the canopy were distributed in the understory in the dry stands, and there is a high possibility of changes in the future.

Disturbance-driven succession from *P. densiflora* forests: acceleration to broadleaved forests

Direct human influence on forests had decreased greatly since the 1970s. Nonetheless, since then, disturbances, such as insect pests, disease, forest fire, and landslide,

Table 4 Succeeding tree species composition in the canopy stratum of *P. densiflora* forests according to the geographical and moisture condition

Succeeding tree species	Northern mesic (%, n = 70)		Northern dry (%, n = 79)		Southern mesic (%, n = 27)		Southern dry (%, n = 38)	
	RA	RF	RA	RF	RA	RF	RA	RF
Quercus mongolica	28.7	22.4	50.7	42.8	6.5	3.3	30.3	24.7
Quercus variabilis	15.5	13.4	26.1	25.2	13.5	18.0	19.1	22.1
Quercus serrata	7.2	10.4	3.6	5.0	22.8	21.3	15.4	16.9
Fraxinus rhynchophylla	7.4	6.7	4.6	5.9			0.7	1.3
Prunus sargentii	5.7	3.7	3.4	3.4	4.6	3.3	3.7	3.9
Quercus dentata	1.6	1.5	6.5	7.6			4.1	2.6
Carpinus laxiflora	3.4	4.5	0.9	1.7	6.9	8.2		
Styrax japonicus					10.7	9.8	7.7	7.8
Acer pseudosieboldianum	3.4	5.2	1.7	3.4				
Carpinus tschonoskii					11.8	13.1	1.9	2.6
Quercus acutissima					2.7	3.3	7.0	5.2
Betula dahurica	3.9	3.7	0.6	0.9				
Cornus controversa	1.8	3.7						
Quercus aliena	2.0	1.5					4.1	3.9
Ulmus davidiana var. *japonica*	2.7	3.0						
Abies holophylla	2.9	3.0						
Aria alnifolia	0.4	0.7			1.8	1.6	1.7	2.6
Juglans mandshurica	2.3	3.0						
Castanea crenata	1.1	1.5			1.1	1.6	0.7	1.3
Celtis koraiensis	1.3	1.5	0.2	0.9				
Quercus acuta					6.3	4.9		
Pyrus ussuriensis	2.0	2.2						
Larix kaempferi			0.8	1.7			0.7	1.3
Acer pictum var. *mono*	1.1	1.5						
Robinia pseudoacacia					1.8	1.6	0.7	1.3
Acer palmatum					4.1	3.3		
Maackia amurensis	1.1	1.5						
Pinus koraiensis	0.2	0.7					1.2	1.3
Populus koreana	1.4	0.7						
Betula schmidtii			0.3	0.9				
Alnus hirsuta							0.9	1.3
Fraxinus mandshurica	0.6	0.7						
Kalopanax septemlobus	0.7	0.7						
Alnus japonica					1.8	1.6		
Stewartia koreana					1.4	1.6		
Tilia amurensis			0.7	0.9				
Salix koreensis	0.8	0.7						
Pinus thunbergii					0.8	1.6		
Lithocarpus edulis					1.3	1.6		
Cornus walteri	0.8	0.7						
Carpinus cordata	0.2	0.7						
Total	100	100	100	100	100	100	100	100

RA relative abundance, *RF* relative frequency

Table 5 Comparison of the succeeding tree species composition in the canopy (C) and extended canopy stratum (EC) in *P. densiflora* forests according to geographical and moisture conditions

	Succeeding tree species	Northern mesic (%)		Northern dry (%)		Southern mesic (%)		Southern dry (%)	
		C (n = 70)	EC (n = 73)	C (n = 79)	EC (n = 80)	C (n = 27)	EC (n = 28)	C (n = 38)	EC (n = 39)
Quercus	*Quercus mongolica*	28.7[1]	29.5	50.7	50.5	6.5	6.5	30.3	29.9
	Quercus variabilis	15.5	11.4	26.1	23.5	13.5	11.6	19.1	17.1
	Quercus serrata	7.2	10.0	3.6	4.7	22.8	25.7	15.4	14.7
	Quercus dentata	1.6	1.5	6.5	6.8			4.1	4.4
	Quercus acutissima					2.7	1.8	7.0	6.2
	Quercus aliena	2.0	2.6					4.1	5.1
	Subtotal	55.0	55.0	86.9	85.5	45.5	45.6	80.0	77.4
Others	*Fraxinus rhynchophylla*	7.4	10.4	4.6	5.6		0.9	0.7	1.8
	Prunus sargentii	5.7	4.4	3.4	2.5	4.6	5.7	3.7	3.1
	Carpinus laxiflora	3.4	3.1	0.9		6.9	5.6		
	Acer pseudosieboldianum	3.4	7.0	1.7	1.5				0.6
	Betula dahurica	3.9	2.5	0.6	0.6				
	Styrax japonicus					10.7	9.8	7.7	7.0
	Carpinus tschonoskii					11.8	9.8	1.9	1.8
	Quercus acuta					6.3	6.3		
	Acer palmatum					4.1	4.1		
	Subtotal	45.0	45.0	13.1	14.5	54.5	54.4	20.0	22.6
Total		100	100	100	100	100	100	100	100

[1]Relative abundance of the succeeding species is shown. The species is chosen where is ≥ 3% in any temperate zone and moisture condition

have affected the landscape, and the structure of the forests have been destroyed (Chun 1999; Park et al. 2009; Lim 2010). The damaged area by pests was overwhelmingly large (Park et al. 2009). Especially, pine moth (*Dendrolimus spectabilis*) and pine needle gall midge (*Thecodiplosis japonensis*) caused extensive damage, but they are currently under control. These insects selectively killed or weakened *P. densiflora* trees, but the entire stand rarely declined to death.

This phenomenon can rather promote forest succession because it increases the growth of succeeding species such as *Quercus* or broadleaved species. There are several reports that the forests damaged by insect pests have rapidly restored to broadleaved forests. For example, Lee (1989) reported that the forests damaged by the pine gall midge across the country were restored to *Quercus* forests within 20 years. In Japan, 25% (650,000 ha) of *P. densiflora* forests were damaged by pine wilt

Table 6 Number of succeeding tree species along the moisture condition in *P. densiflora* forests of the northern temperate zone

	Canopy stratum			Extended canopy stratum		
	No. of species[1] (mean ± SE)	F	p	No. of species (mean ± SE)	F	p
Total		13.67	< 0.01		6.9	0.01
Northern mesic	1.9 ± 0.13			2.0 ± 0.12		
Northern dry	1.4 ± 0.07			1.6 ± 0.08		
Quercus		2.05	0.16		2.00	0.17
Northern mesic	0.9 ± 0.12			1.0 ± 0.12		
Northern dry	1.1 ± 0.06			1.2 ± 0.06		
Others		18.74	< 0.01		13.45	< 0.01
Northern mesic	1.0 ± 0.16			1.0 ± 0.14		
Northern dry	0.3 ± 0.07			0.4 ± 0.08		

[1]Number of plots for northern mesic is 53, and those for northern dry is 58 (plot size, 15 × 15 m²)

Table 7 Pairwise *t* test on the number of succeeding tree species (plot size, 15 × 15 m²) in the canopy and extended canopy strata of the northern *P. densiflora* stands

	Northern mesic (*n* = 53)			Northern dry (*n* = 58)		
	No. of species[1] (mean ± SE)	*t*	*p*	No. of species (mean ± SE)	*t*	*p*
Total		− 0.45	0.65		− 3.24	< 0.01
Canopy	1.9 ± 0.13			1.4 ± 0.07		
Extended canopy	2.0 ± 0.12			1.6 ± 0.08		
Quercus		− 1.07	0.29		− 2.06	0.04
Canopy	0.9 ± 0.07			1.1 ± 0.06		
Extended canopy	1.0 ± 0.07			1.2 ± 0.06		
Others		− 0.20	0.84		− 2.21	0.03
Canopy	1.0 ± 0.09			0.3 ± 0.07		
Extended canopy	1.0 ± 0.08			0.4 ± 0.08		

[1]Number of plots for northern mesic is 53 and those for northern dry is 58 (plot size: 15 x 15 m²)

disease (Mamiya 1983), and they have been restored to *Q. serrata* forests in many areas of southwestern Japan where the damage was extremely severe (Sakamoto et al. 1995; Fujihara 1996; Toyohara and Fujihara 1998; Fujihara et al. 2002).

Forest fires have occurred around 500 times annually since 1970 (KFS 2017). The damage grew larger with an increase in forest growing stocks. The East Coast fire which took place in 2000 had the largest damaged area of 23,794 ha (Ro et al. 2000), and the Goseong fire in 1996 had the 2nd largest damaged area of 3762 ha (KFS and KFRI 1996). Two thirds of the forest fires initiated from the *P. densiflora* forests (Lee et al. 2005b) as they are vulnerable to fire (Seo and Choung 2010; Seo and Choung 2014).

Once burned by stand-replacing fire, the forests retrogressed unlike those damaged by insects and pests. However, they can initiate succession fast with the species having sprouting ability (Vesk and Westoby 2004). To note, 81% of all prefire species had sprouting ability in the East Coast fire regions (Choung and Choung 2019). It resulted in the restoration to *Quercus* forests but not to *P. densiflora* forests. Although most were short-term studies, *Q. serrata* trees were regenerated in the burned *P. densiflora* forests in the southern province (e.g., Kim 1983; Kim et al. 1983; Kim and Cho 1984; Cho and Kim 1991; Cho and Kim 1992; Kim et al. 1999). The northern East Coast region, where large forest fires are frequent, had commonly been restored to *Q. mongolica*- and *Q. variabilis*-dominated forests (e.g., Mun and Choung 1997; Lee and Hong 1998; Choung et al. 2004; Lee et al. 2004; Lee 2007; Shin 2015). Some extreme sites, poor and dry, such as ridges or shallow erosive soils, were restored to *P. densiflora-Quercus* mixed forests.

This demonstrates that disturbances occurring in *P. densiflora* forests with sprouting understory species succeeded mostly into *Quercus* forests by skipping over the *P. densiflora*-broadleaved mixed stage (Abrams and Scott 1989; Fujihara 1996; Choung and Choung 2019).

Integrated succession process from *P. densiflora* forest

We synthesized the succession process of the *P. densiflora* forests based on the results of meta-analysis and literature review (Fig. 6). As mentioned by Finegan (1984), a directional change along three distinct seral communities in the species composition and vegetation physiognomy occurred.

Establishment of the *P. densiflora* forest

P. densiflora can germinate and settle at denuded sites where mineral soil is exposed and little sprouting source of broadleaved species (Lee and Chung 1998; Lee 2006; Lim 2010; Park et al. 2010). The *P. densiflora* grows slowly and takes 5 to 10 years to grow up to 2 to 3 m high. However, later, it grows exponentially and forms a cohort monospecific stand (Park et al. 2010). The abandoned fields in Jinbu, Gangwon province, took about 20 to 30 years to develop into *P. densiflora* forests (Lee 1995c; Lee 2006).

The *P. densiflora* forests still cover the largest area as a single species-dominated stand even though its area is decreasing (Fig. 2; KFRI 2016). This means that the settlement of *P. densiflora* in the 1970s was the preferred environment. In meta-analysis 1, as a result of 7–19 years of succession in the *P. densiflora* forests of 30–60 years of age, the physiognomy of *P. densiflora* forests and *P. densiflora*-broadleaved mixed forest remained unchanged during this period. It is because the mortality rate of *P. densiflora* was low. *Quercus* and other species grew throughout density-dependent thinning. Lee et al. (1998) predicted that *P. densiflora* forests would be maintained in Mt. Seoraksan for a considerable period of time.
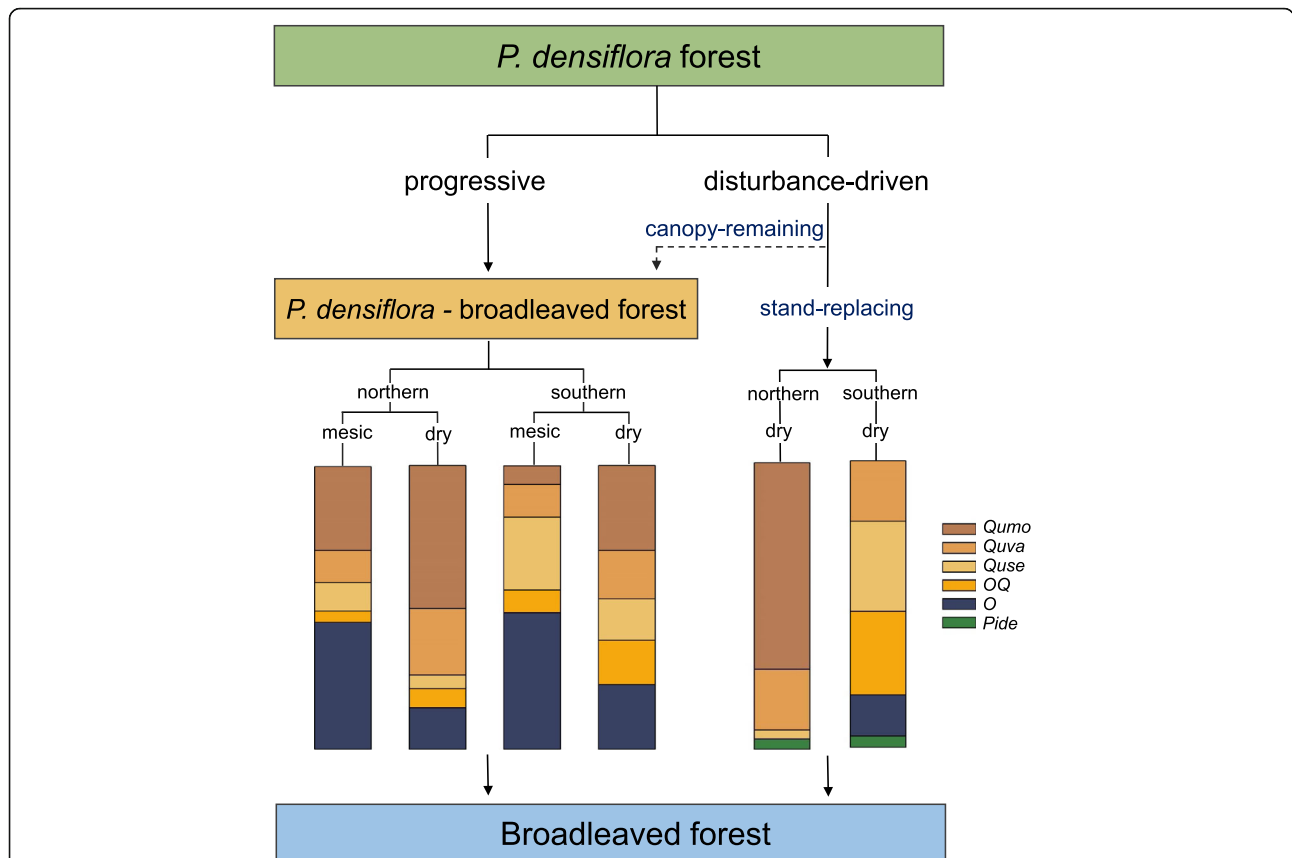
Fig. 6 Schematic diagram of the progressive and disturbance-driven succession process in the cool-temperate *P. densiflora* forest. Stacked bar graphs indicate the composition (the relative abundance) of succeeding tree species or succeeding groups. The four stacked bars from the left were drawn from the meta-analysis data 2 for this study. The fifth bar was drawn from a forest that had been restored for 20 years after a stand-replacing fire (East Coast fire occurred in 2000) from the prefire *P. densiflora* forests, Samcheok, Gangwon province (Choung et al. unpublished). The sixth bar was drawn from a forest that had been restored for 5 years after a stand-replacing fire (occurred in 1986) from prefire *P. densiflora* forest, Daegu-si (Cho and Kim 1991). "Canopy remaining disturbance" is less severe than "stand-replacing disturbance" and refers to the state in which canopy stratum remains even after disturbance. O, other broadleaved species except for *Quercus* species; OQ, other *Quercus* species except for three *Quercus* species (Qumo, Quva, and Quse); Pide, *Pinus densiflora*; Qumo, *Quercus mongolica*; Quse, *Quercus serrata*; Quva, *Quercus variabilis*

Succession to P. densiflora-broadleaved mixed forest: mainly P. densiflora-Quercus mixed forest

Since *P. densiflora* is shade-intolerant, relatively tolerant *Quercus* species and/or other tree species settled as succeeding species underneath (Higo et al. 1995; Beon and Bartsch 2003). A series of processes such as thinning and formation of forest gap are typical processes in which *P. densiflora* forests were changed to *P. densiflora*-broadleaved mixed forests. Since the most mature *P. densiflora* grows slowly, whereas the young *Quercus* and other species grow fast, the latter species eventually replace the *P. densiflora*. Kato and Hayashi (2006) observed that *Q. mongolica* ssp. *crispula* reached the canopy stratum in *P. densiflora* forests in about 30 years, and as a result, *P. densiflora* began to die under competitive pressure.

Our meta-analysis 2 revealed that the composition of the succeeding species differed depending on the geography and moisture condition of the stands. Among them, the deciduous *Quercus* species, such as *Q. mongolica*, *Q. serrata*, and *Q. variabilis*, were surprisingly widely distributed and predominant. In particular, the relative abundance of *Quercus* species was over 80% in the southern and northern dry stands and about 50% in the mesic stands, suggesting that it is the exclusive succeeding genus of *P. densiflora* forests. Therefore, the next stage of *P. densiflora* forests is *P. densiflora*-*Quercus* mixed forests in most of the stands. However, in some mesic stands, other broadleaved species without *Quercus* appeared as the succeeding species. This means that in the mesic stands, succession to broadleaved forest can proceed faster by passing through the *Quercus* stage.

Succession to early broadleaved forest: Quercus-dominated forest and Quercus-broadleaved forest

The natural death of *P. densiflora* in *P. densiflora*-broadleaved mixed forests should lead to broadleaved forests

(Fig. 6). Unlike the previous two seral stages, more tree species co-dominate in this stage. Depending upon the distribution and abundance of mainly the *Quercus* species, the physiognomy and the duration of this stage will vary (e.g., *Quercus*-dominated forests, *Quercus*-broad-leaved forests, and/or broadleaved forests).

In dry or disturbed stands, the early forests will mainly be *Quercus* dominated in the canopy with several broad-leaved species of low abundance. Since most of the mountain slopes and ridges are relatively dry, this forest type should sustain over a large area for a long time. In the long-term, however, as forests are preserved and sites develop in a more fertile and mesic direction ("mesophication"; Nowacki and Abrams 2008), the *Quercus* species will coexist with other broadleaved species.

On the other hand, in the mesic or moist stand, our meta-analysis 2 revealed that the *Quercus* species either did not exist or was just present in low abundance. Therefore, the late-successional species can settle earlier in the mesic or moist stand than in the dry ones. These mesic or moist stands are only a valley or lower parts of mountains, so the area is small.

Late-successional broadleaved forest: climax community

The species composition of late-successional forests has long been the subject of interest (Lee 2011). Late-successional forest refers to the forests with minor fluctuating changes in structure but little change in species composition after the current *P. densiflora* forests go through the process in a series of predicted directions (Barbour et al. 1999). Considering the young age of the current forests and the life span of *Quercus* species, which is presumed to be a few hundred years, it is estimated that it will take a considerable time to reach the late-successional forest (KFRI 2011).
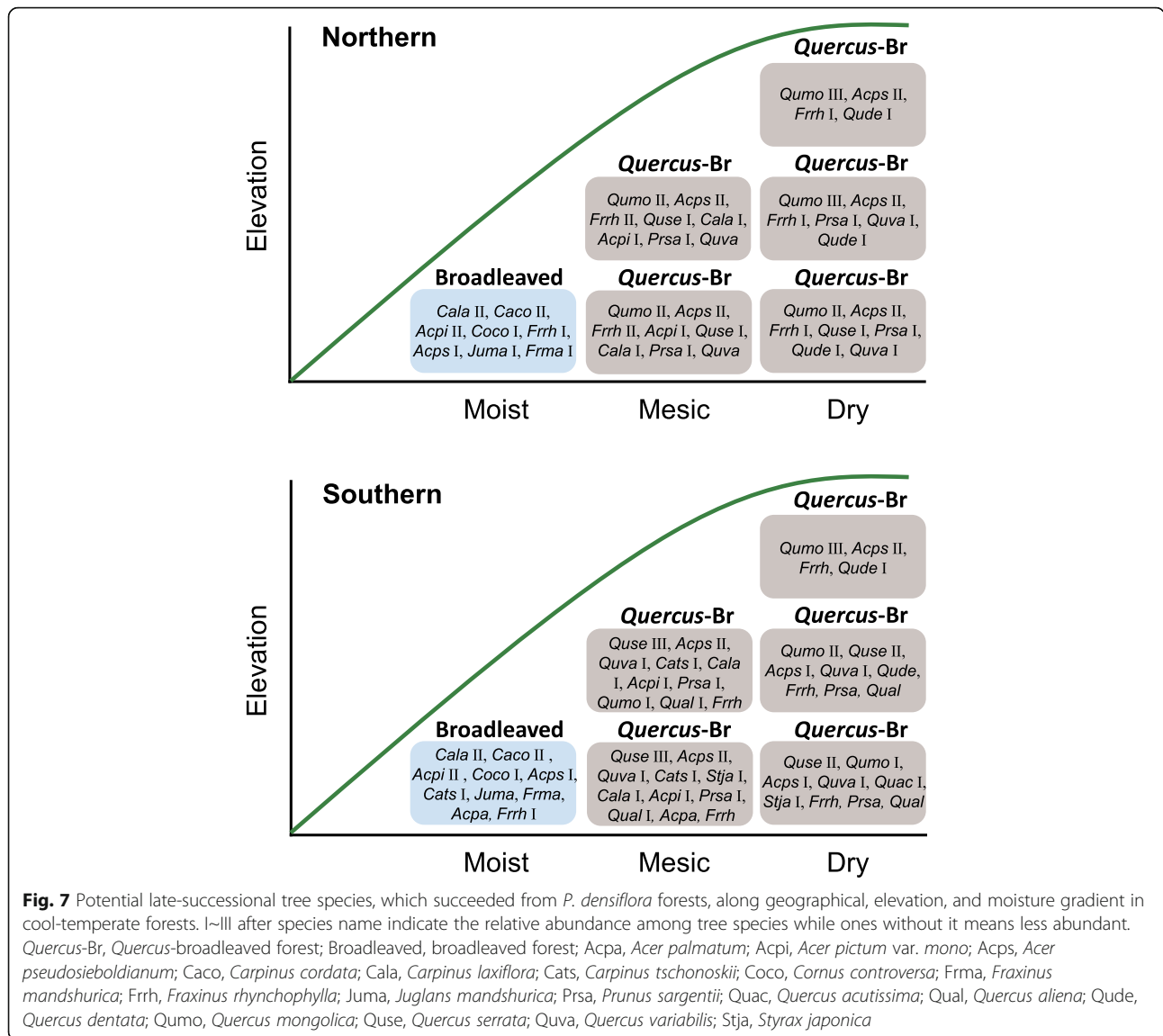
The composition of the tree species in the late-successional forests will depend on the characteristics of the species, such as distributional potential, life span, dispersal opportunity, and/or site conditions. We suggest some potential tree species according to the geography, elevation, and moisture condition (Fig. 7). The major forest types are categorized into two divisions: *Quercus*-broadleaved forests ("*Quercus*-Br") and other broad-leaved forests ("Broadleaved"). Although the abundance of *Quercus* species is presumed to decrease over time, the said abundance would sustain for quite a long time, considering the current abundance and longevity of the species, and slow change in the site condition. *Q. mongolica* in the north and both *Q. serrata* and *Q. mongolica* in the south are the representative species of the forests. *Q. serrata* is widely distributed in both dry and mesic stands in the south (Lee and Lee 1989; Choung et al. 2000; Choung and Hong 2006; Chun et al. 2007; Cho and Lee 2011).

By contrast, in the moist or mesic stands of the low-lands of the south and north, multiple species such as *C. laxiflora*, *Q. serrata*, *Cornus controversa*, *Juglans mandshurica*, *Carpinus cordata*, *Fraxinus rhynchophylla*, *Fraxinus mandshurica*, *A. pseudosieboldianum*, *Acer pictum* var. *mono*, *P. sargentii*, *C. tschonoskii*, *S. japonicus*, and *A. palmatum* constitute the coexisting broadleaved forests. Of these, the last three species are distributed only in the south to characterize the influence of geography.

Krestov et al. (2006) and Cerny et al. (2015) stated that *Q. mongolica* forests are the core of cool-temperate forests in Korea. Many studies on Mts. Bukhansan (Lee 1997), Odaesan (Byun et al. 1998; Choi et al. 2014), Sobaeksan (Lee et al. 1993), Weoraksan (Lee et al. 2015a; Lee et al. 2015b), Deogyusan (Oh et al. 2013; Choi et al. 2013a; Choi et al. 2013b), Naejangsan and Seonunsan (Kim and Yim 1987; Kim and Yim 1988), and Mudeungsan (Kim et al. 1994) indicated *Q. mongolica* as the "climax species" throughout the whole region or in the high elevation slopes. Even though *Q. mongolica* is distributed all over the country, it is more predominant in the dry stands as we found in meta-analysis 2. While in the mesic and moist stands, it has a low abundance or is not presented. Even in the dry stands, regeneration of *Q. mongolica* was slow, and other broad-leaved occupy the understory stratum (Lee 2015). As the succession progresses, the site becomes more fertile and moister (Barbour et al. 1999; Nowacki and Abrams 2008). Such conditions would reduce the current dominance of the genus *Quercus* and become co-dominant with the other broadleaved trees.

C. laxiflora has also been frequently suggested as a climax species. For example, studies on Mt. Bukhansan (Lee 1997), Namhansanseong (Lee et al. 2012b), Mt. Sobaeksan (Lee et al. 1993), Mt. Songnisan (Lee et al. 2009a), Mt. Deogyusan (Oh et al. 2013; Choi et al. 2013b), Mt. Naejangsan and Mt. Seonunsan (Kim and Yim 1987; Kim and Yim 1988), and Mt. Gayasan (Park et al. 1989; Lee et al. 2006) have stated it as climax species. It may form a monospecific stand in a particular small-scale location. However, it is commonly observed to form forests with *F. mandshurica*, *J. mandshurica*, *C. controversa*, and *F. rhynchophylla* in valley forests or lower mountain slopes (Lee 2015; Choung and Lee 2019).

In meta-analysis 2, *C. laxiflora* appeared in the mesic stands in the north and south and was relatively more abundant in the southern mesic stands. Here, however, the abundance of *C. laxiflora* was lower than those of the *Q. serrata* and *Q. variabilis*, as well as *C. tschonoskii*. Even in an extended canopy, it has not increased, so it is unlikely that it will increase in the future. Therefore, we have not found any ground to consider it as a

Fig. 7 Potential late-successional tree species, which succeeded from *P. densiflora* forests, along geographical, elevation, and moisture gradient in cool-temperate forests. I~III after species name indicate the relative abundance among tree species while ones without it means less abundant. *Quercus*-Br, *Quercus*-broadleaved forest; Broadleaved, broadleaved forest; Acpa, *Acer palmatum*; Acpi, *Acer pictum* var. *mono*; Acps, *Acer pseudosieboldianum*; Caco, *Carpinus cordata*; Cala, *Carpinus laxiflora*; Cats, *Carpinus tschonoskii*; Coco, *Cornus controversa*; Frma, *Fraxinus mandshurica*; Frrh, *Fraxinus rhynchophylla*; Juma, *Juglans mandshurica*; Prsa, *Prunus sargentii*; Quac, *Quercus acutissima*; Qual, *Quercus aliena*; Qude, *Quercus dentata*; Qumo, *Quercus mongolica*; Quse, *Quercus serrata*; Quva, *Quercus variabilis*; Stja, *Styrax japonica*

representative species across a wide area. *C. laxiflora* is sure to be one of the co-dominant species of late-successional forests in the northern or southern mesic region.

Conclusions

As we have intuitively known from observations on nearby plots of different ages, young pioneer *P. densiflora* forests are undergoing progressive succession of the species composition and physiognomy. The process direction of the seral communities is *P. densiflora* cohort forest → *P. densiflora*-broadleaved mixed forests → broadleaved forests. The time span and species composition of the process would vary depending on the geographical and site conditions. In particular, stand moisture has a decisive effect on the distribution and abundance of the successor of *P. densiflora*. In dry

stands, *Quercus* species are favored occupying over 80% of the abundance of the succeeding species, suggesting as an overwhelming successor.

Therefore, the process in the dry stands, which covers most of the area, is characterized by a long *Quercus*-dominated stage due to the current dominance and long life span. Therefore, the modified process appears as *P. densiflora* forests → *P. densiflora-Quercus* mixed forests → *Quercus*-dominated forests → *Quercus*-broadleaved forests. The *P. densiflora* forests, which have been affected by insects, pests, or forest fires, are often restored to the *Quercus*-dominated forests after retrogression. Contrary to this, in the mesic stands where *Quercus* species does not occur or occurs in low abundance, the late-successional species establish and settle earlier.

Eventually, the late-successional stage will stabilize into two forest types, viz., the *Quercus*-broadleaved

forest and broadleaved forest in the dry and mesic stands, respectively. The former species composition will be co-dominance of *Quercus*, and other broadleaved species even though the abundance of *Quercus* decreases with time. The broadleaved forests will comprise stands composed of a larger number of broadleaved species. The composition of the broadleaved species will vary depending upon the geography, moisture condition, and elevation that limit the distribution of the species. *Q. mongolica* or *C. laxiflora* has been referred to as a climax species in a number of studies; however, no such evidence was found in the present study. They will compose late-stage forests as co-dominated species.

Overall, *P. densiflora* forests are changing on the track of progressive succession. As a pioneer, it will be eventually replaced along the succession process, but it is still young and developing. Therefore, we have not found any evidence that the forest area is decreasing due to succession during the recent several decades.

Authors' contributions
YC designed, reviewed, and wrote the manuscript. JL, SC, and JN analyzed the data and edited the manuscript. All the authors approved the manuscript.

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