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Sixty-year post-windthrow study of stand dynamics in two natural forests differing in pre-disturbance composition

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Abstract. We examined the dynamics of stand structure and composition over 60 years in two natural secondary forest plots in central Hokkaido, Japan, that had been severely disturbed by a stand-replacing windthrow in 1954. We determined temporal trends in tree density, species richness, species diversity, successional composition, and stand developmental stage. One of the plots contained a coniferous stand prior to the disturbance; the second plot contained a mixed stand. Tree density and species richness increased after the windthrow, and peaked in both stands in 1991, 37 years after the windthrow. Based on the dynamics of tree density and species richness, the stand development phase of both plots remained within the stand initiation stage until 1991, and then progressed to the stem exclusion stage by 2014, 60 years after the windthrow. Based on patterns of increasing tree density by species in both plots, vegetative regeneration was presumed to have contributed abundantly to the recovery of the stand after the windthrow. Species diversity increased after the windthrow as species richness increased in both stands; diversities peaked 23 or 32 years after the windthrow and declined slightly thereafter. Although the successional composition of the pre-disturbance coniferous stand regressed to an early stage under the influence of the windthrow, the relative importance of late-successional species approached the pre-disturbance value as the plot recovered. In contrast, the successional composition of the mixed conifer/hardwood plot was unaffected by the windthrow, but gradually changed to an early stage over several decades following the windthrow. The difference in successional composition between plots was likely a result of differences in pre-disturbance stand conditions between stands. Our 60-year permanent plot study determined stand and population dynamics, the duration of the stand initiation stage, and the interrelationships between diversity and species richness. Long-term permanent plot studies contribute crucial data for the interpretation of forest dynamics following disturbance.

Key words: diversity; pre-disturbance stand; species richness; stand developmental stage; stand-replacing windthrow; successional composition; tree density.

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Introduction

Severe disturbances massively alter forest stand structure on very short timescales; the effects of the perturbations persist for centuries (Henry and Swan 1974). In 1954, a severe, large-scale windthrow occurred across Hokkaido, which is the northernmost main island in the Japanese archipelago. Typhoon No. 15 uprooted or snapped off a tree volume of 21.1 × 10^6 m^3 and disrupted 651,844 ha of land in Hokkaido (Forestry Agency of Japanese Government 1959). The effects of the windthrow are still visible >60 years after the event. Evaluation of the

long-term effects of severe windthrows on forests requires detailed examinations of stand dynamics. Most studies of forest dynamics following severe windthrows have investigated changes in stand structure and composition (Foster and Boose 1995, Shibuya et al. 1997, Zhao et al. 2006).

The dynamics of tree density, stem volume (or basal area), and size structure have often been examined in studies of stand structure after disturbance (Weaver 1986, Bellingham and Tanner 1995, Arévalo et al. 2000). The temporal trends in stand structure vary among climatic zones and pre-disturbance stand structures. For example, tree density peaked 15–20 years after a severe disturbance in Puerto Rico (Crow 1980, Weaver 1989, Lugo 2008), after 25 years in a coniferous stand in Oregon (Lutz and Halpern 2006), and after 25–35 years in temperate rain forests of southeastern Alaska (Nowacki and Kramer 1998). Thus, forest recovery rate after a disturbance varies by location and stand. Therefore, classification of stand development stages enables studies of secondary forest succession after a stand-replacing disturbance, especially studies that compare temporal trends in stand structure and composition. Oliver (1980/1981) proposed a stand development model to describe processes following a stand-replacing disturbance; the model classified development into four stages based on the dynamics of tree density, species richness, and size structure:

1. Stand initiation stage: Tree density and species richness increase.
2. Stem exclusion stage: Tree density and species richness decrease as a result of intense competitive interactions and canopy closure.
3. Understory re-initiation stage: Understory vegetation (including shade-tolerant tree seedlings) reestablishes as the overstory trees grow.
4. Old-growth stage: A multi-aged, mosaic stand structure develops through a process of gap-phase dynamics.

In temperate rain forests of southeastern Alaska that had been strongly impacted by logging and fire, the durations of the stand initiation and stem exclusion stages were 25–35 and 100 years, respectively (Alaback 1982, Nowacki and Kramer 1998). However, as indicated above, the duration of each stage varied among the stands that were examined.

Post-disturbance species composition varies among the agents of disturbance (fire, wind storm, flooding and insect outbreak, etc.) and the magnitudes of their impacts (Schulze et al. 2005, Swanson et al. 2011). Recovery after wind damage is much more dependent on surviving sources of regeneration, such as standing trees and advance regeneration, than recovery following perturbations caused by fire and volcanic activity (Franklin et al. 2002, Swanson et al. 2011). After a wind disturbance, early-successional tree species sometimes become dominant through seedling recruitment (Batista and Platt 2003, Woods 2004), but late-successional species may become dominant under other circumstances (Webb and Scanga 2001). The disparity among cases is likely attributable to differences in major sources of regeneration (Peterson 2000, Schulze et al. 2005), but a consistent model of the differences in composition between pre- and post-disturbance stands is not available. Traditionally, disturbance has been viewed as a mechanism that sets back succession to an earlier stage (Abrams and Scott 1989); however, changes in composition before and after a disturbance may depend on the stand structure and species composition of the pre-disturbance forest (Peterson 2000, Cowden et al. 2014). Therefore, a detailed examination of compositional change before and after a disturbance in a permanent plot study is necessary to construct a consistent model of the compositional change. In addition, trends in compositional change are assessed quantitatively based on the change in the relative importance of early-, intermediate, and late-successional species (White et al. 2015), which indicates changes in successional composition.

Changes in species diversity accompany changes in species composition after wind disturbance. Species richness and diversity increased for 19 and 14 years, respectively, after a hurricane in Puerto Rico (Crow 1980). In central New England, species diversity increased rapidly through 10 years following a hurricane and then decreased; species richness also decreased after 10 years (Hibbs 1983). However, Zhao et al. (2006) found that species diversity was close to stable in the hardwood forests of South Carolina in the 12 years following a hurricane. Therefore, patterns of change in species composition and diversity after wind disturbance can vary, and a comprehensive model describing trends in community

structure before and after wind disturbance has yet to be developed (Peterson 2000). Long-term observations necessary to develop such a model are scarce; protracted studies in permanent plots are especially rare (Burslem et al. 2000, Lorimer and Halpin 2014). Peterson (2000) showed that pre-disturbance stand conditions and the severity of disturbance effects influence species composition and diversity after a perturbation. Therefore, improved understanding of forest vegetation recovery requires long-term studies of stand dynamics (after disturbance) that take account of pre-disturbance stand conditions.

We examined the stand structures and compositions of two natural forest plots on Hokkaido (with different pre-disturbance compositions) following a massive perturbation by No. 15 typhoon in 1954. Our permanent plot study spanned 60 years following the event. The aims of this study were:

1. to describe changes in stand structure and composition in the 60 years following the disturbance;
2. to determine the development stages of post-disturbance stands using Oliver's (1980/1981) model;
3. to examine temporal trends in species diversity and changes in relative importance by successional category.

Several studies have examined stand dynamics after forest disturbances in permanent plots (Spurr 1956, Crow 1980, Woods 2004, Lutz and Halpern 2006, Fisher and Fisher 2012); however, long-term studies (more than 40 years in duration) are rare. Weaver's studies (1986, 1989) in Jamaica and Puerto Rico spanned 49 years, and Mabry and Korsgren's study (1998) in the northeastern United States spanned 53 years. We present 60 years of permanent plot data on the long-term dynamics of stand structure and the composition of natural temperate forests after a stand-replacing disturbance.

Methods

Study sites

The study was conducted in the Tomakomai (42°43′ N, 141°27′ E) and Jozankei (42°57′ N, 141°12′ E) permanent plots in the Japanese National Forest, which is located in central Hokkaido.

The Tomakomai plot was on a flat slope at an elevation of approximately 300 m. The annual mean temperature and precipitation in the period 1981–2010 were 6.7°C and 1766 mm, respectively, at the Shikotsukohan meteorological station located 6 km from the plot at an elevation of 290 m. The soil is volcanic in origin and immature. Only shallow soil (approximately 10 cm depth) is available for plant growth (Shin and Shibuya 2007), and the area around the Tomakomai plot is vulnerable to wind damage (Koizumi et al. 2007). The pre-disturbance forest comprised a natural coniferous stand in which conifers, such as *Picea jezoensis* and *Abies sachalinensis*, accounted for 93% of basal area. The conifers were mixed with 13 hardwood species, such as *Magnolia obovata*, *Quercus crispula*, *Acer pictum* (including *A. pictum* ssp. *mono* and *A. pictum* ssp. *mayrii*), and *Phellodendron amurense*. No. 15 typhoon removed 85% of standing trees (diameter at breast height [DBH] ≥ 5 cm) and 94% of basal area in September 1954; this level of disturbance was stand-replacing. A permanent plot was set up in the damaged zone in 1956 without salvage logging. The plot area was 0.50 ha (50 × 100 m); a surrounding buffer zone of 1.17 ha was established. Wind disturbance occurred again in 2004, when 6% of trees and 7% of the basal area were damaged.

The Jozankei plot was located on a 35° slope at an elevation of 400–500 m. Annual mean temperature and precipitation in the 1981–2010 period were 8.9°C and 1107 mm, respectively, at the Sapporo meteorological observatory located 16 km from the plot at an elevation of 20 m. Mesic brown forest soil occurs at the site. Before the windthrow in 1954, conifers and hardwoods in the mixed forest accounted for 57% and 43% of tree basal area, respectively. *Abies sachalinensis* was dominant in the plot, where 18 other tree species, such as *Picea* spp., *Acer pictum*, *Q. crispula*, and *Tilia japonica*, occurred. Of the trees (DBH ≥ 5 cm) standing before the storm, 82% were windthrown and 86% of basal area was lost; this level of disturbance was stand-replacing. A permanent plot measuring 70 × 70 m (0.49 ha) was set up in 1956 without salvage logging; a buffer zone of 1.46 ha was established.

The taxonomic nomenclature used here follows Yonekura and Kajita (2003–).

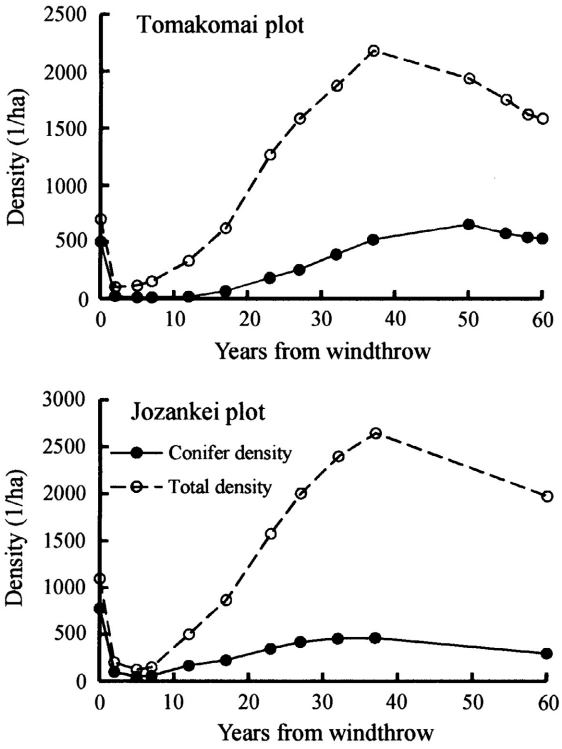


Fig. 1. Tree density dynamics in 60 yr after stand-replacing windthrow. Values at year = 0 indicate the pre-disturbance stands. In Tomakomai plot, a slight windthrow (6% of trees and 7% of basal area lost) occurred in year = 50.

Measurements of trees and assessments of diversity and relative importance

Trees were measured 13 times from 1956 to 2014 at 2- to 13-year intervals in the Tomakomai plot (Fig. 1). The pre-disturbance stand condition was reconstructed in the 1956 measurements, which included both standing and fallen trees with DBH ≥ 5 cm. Trees with DBH ≥ 5 cm were tagged, identified, and measured for girth on every census occasion. The heights of DBH measurements were marked on the stems. DBH was measured with an accuracy of 2 cm in the 1956–1966 period, and to an accuracy of 0.1 cm thereafter.

Measurement procedures on trees (DBH ≥ 5 cm) in the Jozankei plot were identical to those in the Tomakomai plot. Measurements were taken on 10 occasions at 2- to 23-year intervals (in the 1956–2014 period) in the Jozankei plot (Fig. 1). The pre-disturbance stand reconstruction procedure was identical to that used in the Tomakomai plot. Many trees lost their tags on the 2014 measurement occasion, due to the long measurement interval (23 yr).

Species diversities for trees were estimated with the Shannon index (H'):

$$H' = -\sum p_i \ln p_i$$

where p_i is the relative basal area of species i.

We used the relative importance (RI; White et al. 2015) of successional categories (early-, intermediate, and late-successional species) to examine changes in the successional composition of pre- and post-disturbance stands:

$$\text{RI} = \text{relative density} + \text{relative dominance (relative basal area)}.$$

Trees were classified into three successional categories (early-, intermediate, and late-successional species) based on Kikuzawa (1983), Koike (1988), Hanada et al. (2006), Nonoda et al. (2008), and Iwasaki and Shibuya (2013), using photosynthetic characteristics, leaf emergence patterns, suitable regeneration site, and shade tolerance (Appendix S1).

Results

Stand structure, composition, and stand development stage

Tree density in the Tomakomai plot was 700/ha before the 1954 windthrow (Fig. 1). Immediately after the windthrow, tree density decreased, then increased continually to a peak of 2178/ha in 1991. Tree density decreased again after 1991 (Fig. 1). Temporal trends in tree density differed between conifers and hardwoods; conifer densities increased until 50 years after the windthrow, while hardwood density increased until 37 years after the windthrow (Fig. 1). Two years after the windthrow, species richness fell to 10, then increased to a peak of 33 in the 32- to 37-year period. After 1991, species richness fell to 31 by 60 years, which was more than double the richness of the pre-disturbance stand (Fig. 2). The basal area fell from 34.9 to 1.3 m^2/ha 7 years after the windthrow, but increased continually thereafter, reaching 30.6 m^2/ha after 60 years, which is equivalent to 88% of the pre-disturbance area (Fig. 2).

Tree density in the Jozankei plot before the 1954 windthrow was 1096/ha, which decreased

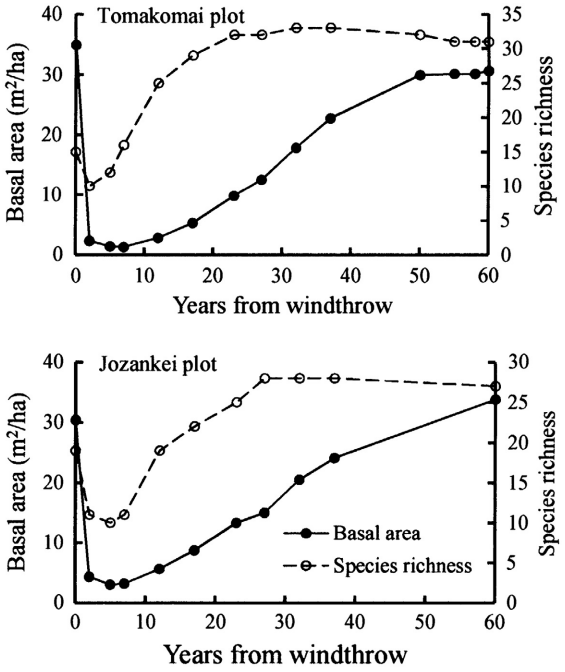


Fig. 2. Dynamics in basal area and species richness in 60 yr after stand-replacing windthrow. Note: See Fig. 1.

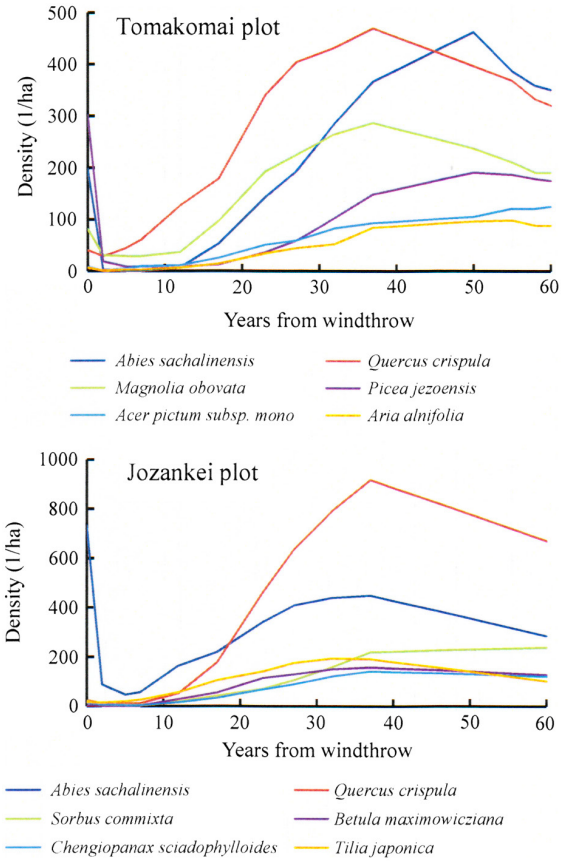


Fig. 3. Density of major tree species in 60 yr after stand-replacing windthrow. The density of the most abundant six species at year = 60 (2014) is shown.

for the first 5 years and then increased to 2643/ha 37 years (1991) after the windthrow. Tree density was 1973/ha after 60 years (Fig. 1). Conifers and hardwoods increased until 1991 (Fig. 1). Five years after the windthrow, species richness fell to 10, then increased to a peak of 28 in the 27- to 37-year period (1981–1991). Species richness during the final measurement was 27 (Fig. 2). The basal area decreased from 30.4 to 3.0 m^2/ha due to the windthrow, but increased to 33.8 m^2/ha after 60 years, equivalent to 111% of the pre-disturbance area (Fig. 2).

Species composition in the Tomakomai and Jozankei plots changed considerably after the windthrow in 1954 (Fig. 3; Appendix S1). In the Tomakomai plot, conifers (*P. jezoensis* and *A. sachalinensis*) dominated before the windthrow. However, hardwoods such as *Q. crispula*, *M. obovata,* and *A. pictum* subsp. *mono* increased after the windthrow and accounted for 67% of the tree density at the final measurement (2014; Appendix S1). *Abies sachalinensis* was the predominant species in the Jozankei plot before the windthrow, while the dominant hardwood was *A. pictum* (Appendix S1). After the windthrow, *Q. crispula* and *A. sachalinensis* increased rapidly, and were the dominant species after 60 years (Fig. 3). Based on tree density, the hardwood ratio was 29% before the windthrow and 85% at the final measurement (Appendix S1). The most abundant six species in the Jozankei plot in the final measurement included one early-successional (*Betula maximowicziana*) and two intermediate (*Sorbus commixta* and *Chegiopanax sciadophylloides*) species, although one intermediate species (*S. commixta*) was present before the windthrow (Appendix S1).

In agreement with Oliver's (1980/1981) model of forest stand development after a stand-replacing disturbance, we found that tree density and species richness in the stand initiation stage increased after the disturbance, but were reduced by intensive competition between trees after canopy closure. Tree density and species richness in

the Tomakomai plot peaked after 37 years (1991) and 32–37 years (1986–1991), respectively. They decreased after 1991 (Figs. 1 and 2). Thus, the secondary vegetation in the Tomakomai plot was in the stand initiation stage for 37 years after the windthrow, and the stem exclusion stage after 1991. Tree density in the Jozankei plot increased until 37 years after the windthrow (1991; Fig. 1); species richness was highest in the 27- to 37-year period (1981–1991; Fig. 2). Tree density and species richness after 60 years were lower than those after 37 years. Thus, the stand initiation stage continued through the 1954–1991 period in the secondary stand in the Jozankei plot. The stem exclusion stage spanned the 1991–2014 period.

Species diversity and relative importance by successional category

The species diversity value (H') in the Tomakomai plot increased due to the windthrow, and continued increasing to 2.49 until 32 years before declining gradually until 60 years (Fig. 4). H' values were 1.60 and 1.79 in the Jozankei plot before and after the windthrow, respectively; they increased to a peak of 2.31 at 23 years. H' decreased slightly at 60 years (Fig. 4).

In the Tomakomai plot, the RIs of the successional categories changed after the windthrow (Fig. 5). The RI of late-successional species was decreased rapidly by the windthrow after 5 years (1954–1959). In the same period, the RI of intermediate species increased. After 1959, the RIs of late-successional and intermediate species continued to increase and decrease, respectively, until 60 years. The RI of early-successional species (0.03–0.21) remained low over the observation period (Fig. 5). Temporal trends in RI differed between the Jozankei and Tomakomai plots. The RIs of all three successional categories were relatively stable until 7 years (1961) in the Jozankei plot (Fig. 5). After 1961, the RIs of early-successional and intermediate species increased; however, the RI of late-successional species decreased from 1.88 to 1.34 in the 60 years after the windthrow.

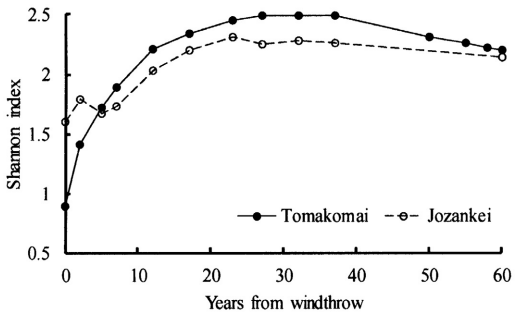


Fig. 4. Temporal trends in species diversity in 60 yr after stand-replacing windthrow.

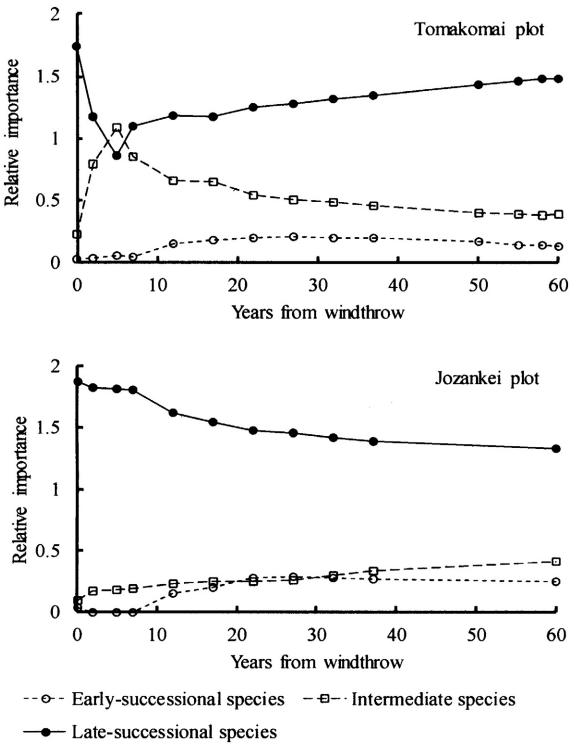


Fig. 5. Temporal trends in relative importance by successional category in 60 yr after stand-replacing windthrow. Relative importance: See in the text; successional category: See Appendix S1.

Discussion

Based on the dynamics of tree density and species richness, we conclude that the Tomakomai and Jozankei plots were in the stand initiation stage for 37 years after the 1954 stand-replacing windthrow, after which they transitioned to the stem exclusion stage. In a temperate deciduous hardwood stand (42°40′ N, 141°36′ E) in Tomakomai City (central Hokkaido), tree density (DBH ≥ 5 cm) and species richness peaked 35 years after a stand-replacing windthrow, the same event experienced in our study sites, and

declined thereafter (Shibuya et al. 1997). Although the intervals between the 1991 measurement and the next in the Tomakomai and Jozankei plots in this study were long (13 and 23 yr, respectively), we suggest that tree density (DBH ≥ 5 cm) and species richness in natural secondary stands in central Hokkaido reach maxima 35–40 years after a stand-replacing windthrow, regardless of pre-disturbance stand structure or composition. Our estimations indicate that the duration of the stand initiation stage is 35–40 years in central Hokkaido. However, as indicated in the *Introduction*, the time to maximum tree density after a severe disturbance (i.e., the duration of the stand initiation stage) varies among climatic zones and forest types (Crow 1980, Weaver 1989, Nowacki and Kramer 1998, Lutz and Halpern 2006, Lugo 2008). Additional long-term permanent plot studies are required to develop a comprehensive understanding of stand dynamics after a stand-replacing disturbance. Basal areas continued to increase 60 years after the windthrow in both plots (Fig. 1). The temporal trends in basal area differed from those of tree density and species richness in the initial 60-year period of secondary succession in both plots.

In the Tomakomai plot, typical early-successional species such as *Alnus hirsuta* and *Betula* spp. and intermediate species such as *Cornus controversa* and *Morus australis*, which had been absent from the pre-disturbance stand, were present in 1966, 12 years after the windthrow (Appendix S1). Late-successional species such as *Q. crispula* and *Acer* spp. began to increase in number in the 5- to 7-year period (1959–1961; Appendix S1) before the appearance of fast-growing early-successional species. This suggests that vegetative regeneration (i.e., advance regeneration and resprouting) was frequent in the first 10 years following the windthrow in the Tomakomai plot. Many species appeared in the 12- to 37-year period (1966–1991). The recruitment of fast-growing early-successional trees (*Betula* spp. and *A. hirsuta*) was observed in 1966 in the Jozankei plot. Intermediate (*S. commixta*, *C. sciadophylloides*, and *M. obovata*) and late-successional (*Q. crispula*, *A. sachalinensis*, and *T. japonica*) species increased rapidly after 1966, following the same timing as the occurrence of the early-successional species (Appendix S1). This suggests that vegetative regeneration contributed abundantly to the initial stand recovery of the Jozankei plot. Many species absent from the pre-disturbance stand were observed after 1966, 12 years after the windthrow (Appendix S1). Osawa (1992) reported that advance regeneration was a major source of a secondary coniferous stand after the 1954 windthrow based on the tree-based measurements in a permanent plot located near our Tomakomai plot. Stand recovery from vegetative regeneration after a stand-replacing windthrow may be major process in central Hokkaido.

The maximum Shannon index (H') values occurred 32 and 23 years after the windthrow in the Tomakomai and Jozankei plots, respectively (Fig. 4). The maximum in the Tomakomai plot was coincident with the maximum species richness, but the maximum H' value in the Jozankei plot occurred 4 years before the peak in species richness (Figs. 2 and 4). Thus, H' increased as species richness increased (excluding 1956 values from the Jozankei plot). Therefore, species diversity probably increased after the windthrow because many large trees had been removed. After peaking, H' tended to decrease slightly in both plots: one or two species disappeared. Hence, species diversity increased as species richness increased during the stand initiation stage and decreased during the stem exclusion stage. Increases in tree species diversity after a severe disturbance have been reported frequently, but the duration of the period of the increase varies, for example, 14 years in Puerto Rico (Crow 1980), 10 years in a hardwood stand in central New England (Hibbs 1983), and several years at another Puerto Rico site (Lugo 2008). The duration of the increase in H' in this study was relatively long (32 and 23 yr), possibly due to the climatic zone, stand type, and measurement size (DBH ≥ 5 cm).

Trends in RI among successional categories differed between the plots (Fig. 5). The RIs of intermediate and late-successional species increased and decreased, respectively, and successional composition regressed to an earlier stage following the windthrow in the Tomakomai plot. These changes were strongly influenced by the decrease in late-successional trees (Appendix S1). However, the RI of the Jozankei plot was stable during the 7 years following the windthrow (1954–1961), and the successional composition was not affected by the windthrow. The stability in this plot is explained by the high relative abundances of

A. sachalinensis and *A. pictum* before and after the windthrow (Appendix S1). The RIs of intermediate and late-successional species increased and decreased, respectively, after 7 years in the Jozankei plot. The successional composition of the Jozankei plot continued to change gradually toward an early stage for several decades after the windthrow. However, we do not expect the RI of intermediate species to increase over the long term because the most abundant species, *S. commixta* and *C. sciadophylloides* (Fig. 3), are subcanopy trees. The RI of late-successional species is expected to increase in the Jozankei plot into the future if the stand remains undisturbed for several decades. The RIs of successional categories in the Tomakomai plot after 60 years were similar to those pre-disturbance, and the successional composition in the secondary stand was very similar to that in the pre-disturbance stand just 60 years after the windthrow. Temporal trends in successional composition of both plots appeared not to be related to dynamics in tree density, species richness, and stand development stage (Figs. 1 and 5). Considering that vegetative propagation was presumed to be abundant in stand recovery in both plots, the differing trends in successional composition between plots are probably attributable to the difference in composition of trees with DBHs < 5 cm in pre-disturbance stands; this will be examined in a future study.

Our 60-year permanent plot study described (1) stand and population dynamics, (2) the duration of the stand initiation stage, and (3) the interrelationships between diversity and species richness. Such long-term permanent plot studies provide crucial information on stand dynamics after disturbances.

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Supporting Information

Additional Supporting Information may be found online at: http://onlinelibrary.wiley.com/doi/10.1002/ecs2.1571/full

Appendix S1

Table S1. Tree density by species (DBH ≥ 5 cm).

1) Tomakomai plot

Species	SC*	1954	1956	1959	1961	1966	1971	1977	1981	1986	1991	2004	2009	2012	2014
Conifer															
Abies sachalinensis	L	198	2			6	52	142	192	284	366	462	386	358	350
Picea jezoensis	L	302	18	8	8	8	12	36	58	102	148	190	186	178	174
Taxus cuspidata	L											2	2	2	2
Hardwood															
Quercus crispula	L	40	28	44	60	126	178	340	404	432	470	396	368	332	320
Magnolia obovata	I	82	30	28	28	36	96	192	224	264	286	236	210	190	190
Acer pictum subsp. *mono*	L	8		4	8	10	24	50	58	82	92	104	120	120	124
Aria alnifolia	L	6		2	2	6	14	34	44	52	84	96	98	88	88
Betula ermanii	E	6	2	2	2	8	20	36	52	66	76	74	60	58	56
Ulmus dabidiana var. *japonica*	I	6	6	8	12	28	34	42	42	42	42	42	36	36	32
Acer amoenum var. *matsumurae*	L						2	4	8	18	18	26	28	30	32
Prunus spp.**	L				2	8	12	38	68	80	88	38	32	28	26
Fraxinus lanuginosa	L					2	4	10	12	16	18	14	14	18	20
Tilia japonica	L	4			4	18	26	52	50	48	50	28	24	20	18
Acer japonicum	L				2	6	8	10	10	12	12	12	18	18	18
Acer pictum subsp. *mayrii*	L	4	4	4	4	4	4	6	10	12	16	16	18	18	18
Alnus hirsuta var. *hirsuta*	E	8				12	32	46	50	40	40	24	16	16	14
Phellodendron amurense	I	12	6	6	6	4	10	26	40	40	44	24	20	16	14
Acer ukurunduense	L			2	6	10	22	56	82	78	94	26	18	14	14
Cornus controversa	I					16	22	26	26	26	26	22	20	12	12
Betula maximowicziana	E					2	8	28	42	54	58	30	22	14	10
Chengiopanax sciadophylloides	I				2	2	2	8	12	14	14	12	12	10	10
Kalopanax septemlobus	I	12	4	4	4	6	8	12	12	14	22	10	8	8	8
Betula platyphylla var. *japonica*	E					4	6	8	8	6	6	6	6	6	6
Salix caprea	E							14	16	18	24	12	8	8	6
Magnolia kobus var. borealis	I						10	16	18	20	20	6	6	6	6
Cercidiphykkum japonicum	I	2	2	2	2	2	2	2	2	2	2	2	2	4	4
Padus ssiori	L						2	2	2	2	2	4	4	4	4
Toxicodendron trichocarpum	E							6	8	8	16	2	2	2	2
Fraxinus mandshurica	I							2	2	4	4	4	2	2	2
Carpinus cordata	L						2	2	2	2	2	2	2	2	2
Morus australis	I					2	2			2	2				2
Sorbus commixta	I	10				2	2	8	14	22	30	10			
Hydrangea paniculata	I					2	2	6	10	6	4	2	2	2	
Sambucus racemosa subsp. *kamtschatic*	I							6	6	2	2				

2) Jozankei plot

Species	SC*	1954	1956	1959	1961	1966	1971	1977	1981	1986	1991	2014
Conifer												
Abies sachalinensis	L	733	86	45	55	163	218	341	408	439	449	284
Picea jezoensis	L	37	6			2	2	4	6	10	8	8
Picea glehnii	L	8	4	2	2	2	2	2	4	4	4	2
Hardwood												
Quercus crispula	L	22	10	10	10	51	176	463	635	792	918	671
Sorbus commixta	I	20	6	4	4	18	39	69	104	157	218	237
Betula maximowicziana	E	2				27	53	114	129	149	157	127
Chengiopanax sciadophylloides	I	12	6	2	2	14	31	67	88	120	141	120
Tilia japonica	L	16	12	18	24	55	102	139	173	192	190	100
Magnolia obovata	I	6				16	35	71	73	88	94	82
Acer pictum ***	L	178	57	31	33	51	53	35	49	63	59	80
Acer japonicum	L	2	8	8	10	39	43	55	63	65	69	69
Fraxinus lanuginosa	L					4	4	4	6	6	14	45
Prunus spp.**	L	2				8	18	29	51	73	82	41
Aria alnifolia	L	4						16	22	31	31	24
Kalopanax septemlobus	I	10	2	2	2	8	18	22	22	24	27	20
Alnus hirsuta var. *hirsuta*	E					14	27	41	47	45	43	14
Ulmus laciniata	I				2	2	2	2	4	8	8	8
Styrax obassia	L		2	2	4	6	6	6	8	10	10	8
Betula platyphylla var. *japonica*	E	6										6
Betula ermanii	E	2				8	16	33	37	35	35	6
Carpinus cordata	L						4	6	6	6	6	6
Salix spp.****	E	12				6	12	35	45	47	49	4
Toxicodendron trichocarpum	E								4	10	8	2
Juglans mandshurica var. *sachalinensis*	I							4	6	6	6	2
Phellodendron amurense	I								2	2	2	2
Padus ssiori	L	8						2	2	2	2	2
Tilia maximowicziana var. *yesoana*	L									4	6	2
Aralia elata	E						2	2	2			
Ostrya japonica	I							2	2	2	2	
Cornus controversa	I								2	4	4	
Maackia amurensis	L	12										

Tree density: 1/ha.

*: succcessional category. E: early-successional species, I: intermediate species, L: late-successional species.

**: *Prunus* spp. include *Cerasus sargentii* and *C. maximowiczii*.

***: *Acer* spp. include *A. pictum* subsp. *mono* and *A. pictum* subsp. *mayrii*.

****: Excluding 2014, *Salix* spcies are identified to genus level.