Development phase convergence across scale in a primeval European beech (*Fagus sylvatica* L.) forest

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ABSTRACT

Despite the recognized influence of spatial resolution on forest life cycle classification typologies, neither the effects of scale (i.e., extent) on development phase assignment nor the pathways of subplot convergence with increasing scale have been quantified. We applied an objective development phase classification protocol to subplots of a 10-ha primeval European beech (*Fagus sylvatica* L.) forest ranging from 156.25 m^2 to 10000 m^2 in extent. The assignment of one of the eight phases [Gap and Regeneration, Establishment, Early Optimum, Mid Optimum, Late Optimum, Terminal, Decay, and Multi-Sized (aka Plenter)] to each subplot was tallied at each scale and the pathways by which subplots in given phases at smaller scales were merged into larger subplots were summarized. As spatial scale increased, the most immature phases (Gap and Regeneration, Establishment, Early Optimum) converged into the mature phases (Terminal, Decay, Multi-Sized) and were no longer assigned by the 1250–2500 scale at which the mature phases dominated. As subplots assigned to one of the eight development phases at a given scale were merged with neighboring subplots to attain the next larger scale, many different possible pathways for convergence emerged but the number of observed combinations declined with increasing scale. Assignment to the most complex phase increased with increasing scale until ultimately all subplots were assigned to this phase. In addition to confirming the scale dependency of development phase assignment, these results support the hypothesis that the immature development phases are assigned predominantly at the smaller scales that correspond to the prevailing disturbance regime while mature phases are assigned predominantly at larger scales. We further observed a convergence with increasing scale on the most structurally complex phase. The convergence of immature phases on more mature phases with increasing scale likely reflects the dual dynamic of fast, short-term gap dynamics predominant at small scales and the slow, long-term dynamics of maturation, maintenance, and persistence that dominate at larger scales. The assignment of development phases at fine spatial resolutions, therefore, is necessary but not sufficient for a comprehensive investigation of the mosaic cycle. Further, examining development phase assignment across spatial scale may enable the identification of the spatial scale of predominant disturbances by investigating and comparing the rate at which phase transitions occur across scales in different primeval forests.

1. Introduction

Scale is defined as the spatial extent and temporal period in which ecosystems integrate, smooth, and dampen signals of ecological processes such as fluxes of energy and matter as they are converted into structures (*sensu* Allen and Starr, 1982). The functional environment of an ecosystem is thus determined by scale, which regulates signal translation (Müller, 1992). Because the conversion of signals into structures takes place at multiple spatial and temporal scales, ecologists distinguish between "fast", short-term processes and "slow", long-term processes (O'Neill et al., 1989). In forest ecosystems, disturbances and senescence result in renewal and express fast (i.e., sudden), short-term (relative to the lifespan of the tree species) processes (e.g., gap formation, germination, establishment), whereas maturation and growth result in persistence and express slow, long-term processes. Together, fast and slow ecological processes create the different forest structures that constitute what has been termed the life cycle of the forest (Watt, 1947). While patches are the smallest spatial units that express different phases of the forest life cycle, the mosaic of patches encompasses the entire life cycle in a forest (Watt, 1947).

In primeval European beech (*Fagus sylvatica* L.) forests, this patch mosaic arises from spatially and temporally asynchronous, small-scale

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canopy disturbances or decaying overstories that initiate new gap-phase patches, which subsequently undergo a sequence of development phases from regeneration, and sometimes multiple releases, through vigorous growth, maturity, and senescence until ultimately breaking down again into gaps with dying, dead, and rotting stems and regeneration (e.g., Watt, 1947; Leibundgut, 1959; Remmert, 1991, Christensen et al., 2007; Diaci et al., 2012). This sequence of upgrade and downgrade phases (Watt, 1947) is commonly distinguished on the basis of micro-structures such as stand volume accumulation [i.e., increasing (initial/growing up), culminating (optimum) or decreasing (decay/breakdown) phases], tree size structure, canopy openness and presence of gaps, number of canopy strata, amount of dead wood, and occurrence of regeneration (Leibundgut, 1993; Korpel', 1995; Tabaku, 2000; Emborg et al., 2000; Král et al., 2010a). Development phases delineated on the basis of micro-structures have great potential for elucidating structural dynamics, regardless of the utility of development phases to capture a temporal sequence within the forest life cycle (Král et al., 2018).

The unequivocal field mapping of development phases based on microstructures, however, is challenging in primeval forests that typically exhibit a complex structure with multi-sized and multi-aged trees forming multi-layered canopies. To excise discrete patches in different phases from a heterogeneous matrix requires a sufficient degree of difference or contrast between the patch and the matrix and among patches, as well as clear boundaries with no spatial overlap of phases among neighboring patches. Excision then relies on classification rules that hierarchically define spatially identifiable, internally homogeneous conditions using threshold values of structural attributes (Kotliar and Wiens, 1990; Emborg et al., 2000; Tabaku, 2000; Král et al., 2010a; Zenner et al., 2016). Such discrete and internally homogeneous patches occur predominantly at fine scales and typically make up the lower levels in the hierarchy of patch structures (Kotliar and Wiens, 1990). Because patch dynamics in primeval European beech forests are largely driven by gap dynamics that open canopy areas of usually less than 200 m^2 (Drößler and von Lüpke, 2005; Zeibig et al., 2005; Trotsiuk et al., 2012; Hobi et al., 2015a), hierarchical classification rules for this forest type typically recognize patch phases at the fine-scale spatial resolutions of 100 to 500 m^2 that are approximately equivalent to the crown projection area of one to several canopy trees (Meyer, 1999; Emborg et al., 2000; Tabaku, 2000; Drößler and Meyer, 2006; Winter and Brambach, 2011; Zenner et al., 2016). Such a fine spatial resolution ensures that all phases are assigned (Winter and Brambach, 2011), is likely to capture the single-layered structure of the Optimum stage thought to occur in small patches in beech forests (Korpel', 1995 p. 169), and avoids frequent assignments of patches into a mixed phase (Emborg et al., 2000).

However, like any measure of heterogeneity and diversity, forest structure is scale dependent (Peterken, 1996; Zenner, 2005; Král et al., 2010b). Further, it is well established that discrete and internally homogeneous patches are rarely observed beyond the scale of gap dynamics (Smith and Urban, 1988) and that structurally heterogeneous mosaics of patches within patches occur over a broad range of scales (Wiens, 1976; Kotliar and Wiens, 1990). When phases are differentiated on the basis of internal structural variation, their relative frequency and the relative area they occupy can thus be expected to be a function of spatial resolution. Although spatial resolution/scale has been identified as a critical weak point of classification typologies (Standovár and Kenderes, 2003; Zenner et al., 2015), its influence on the relative frequency of patch assignment to different phases has not yet been explored, nor has the transition with increasing scale to more structurally heterogeneous phase-patches been quantified. While it is precisely the existence of scaled structure in complex forests that permits the separation of fast and slow processes (O'Neill et al., 1989), the disadvantage of using a single scale is that the importance of short-term dynamics may be emphasized too much if the scale is too fine, whereas it may be entirely missed if the scale is too coarse.

In this study we take advantage of a unique stem-mapped primeval European beech stand in the central Transcarpathian region of southwestern Ukraine (Commarmot et al., 2005) of sufficient size (10 ha) to take a multiscale perspective on the influence of spatial resolution on the relative frequencies and areas assigned to different phases. The hypotheses empirically tested in this stand are that (1) phases associated with patches of relatively homogeneous structure (i.e., the immature phases reflecting gap dynamics) are assigned predominantly at smaller scales, whereas the more complex structures in the mature phases are assigned predominantly at larger scales and (2) convergence with increasing scale is ultimately on the most structurally complex phase. Based on the modified classification typology of Tabaku (2000) presented by Zenner et al. (2016), the immature phases include the Gap/Regeneration, Establishment, Early-, Mid-, and Late-Optimum phases that are dominant in reserves of previously managed European beech forests (e.g., Emborg et al., 2000; cf. Winter and Brambach, 2011), whereas the mature phases are the Terminal, Decay, and Multi-Sized/Plenter phases found predominantly in unmanaged primeval beech dominated forests (Drößler and Meyer, 2006; Peck et al., 2015).

2. Material and methods

2.1. Study area

The Uholka-Shyrokyi Luh reserve is situated on the southern slopes of the Krasna mountain range (400–1400 m a.s.l.) in central Transcarpathia, the south-westernmost region of the Ukraine. The reserve is part of the Carpathian Biosphere Reserve, with ca. 9000 ha considered to be virgin forest of almost pure European beech. The geology is characterized by Cretaceous and Paleogene flysch formations and is comprised of Jurassic limestone, calcareous conglomerates, marls and sandstone. A nearby meteorological station at 430 m altitude has recorded a mean temperature of 7.7 °C (−2.7 °C in January, and 17.9 °C in July) and an annual precipitation of 1134 mm, of which more than half falls between May and October (Hamor and Brändli, 2013).

2.2. Sampling

In 2000, a 10 ha (200 × 500 m) inventory plot was established in the Uholka-Shyrokyi Luh reserve (48° 16′ N, 23° 37′) on an exposed southeast slope of 20–40% at an altitude of 700–800 m a.s.l. (Commarmot et al., 2005). All trees (live, dead standing snags, and dead lying trees attributable to a stump) with a minimum diameter at 1.3 m in height (DBH) of 6 cm were numbered and their positions (spatial coordinates), species, and DBH recorded. Tree heights were measured on all snags and a random sub-sample of 200 live trees distributed throughout the plot. For all standing live tree, crown length and four crown radii in the cardinal directions were measured to estimate crown projection areas based on a non-linear regression between DBH and crown diameter (KD) (KD = exp(0.69302 + 0.39183*ln (DBH) with R^2 = 0.55 and RMSE = 1.29 m). The volumes of snags and dead lying trees (stump + log) with bases within the cell were calculated according to Abegg et al. (2013). In 2010, re-measurements of DBH were taken and new trees (ingrowth to 6 cm DBH) were stem-mapped; the updated 2010 measurement data were used in this study. At the 10-ha scale, this primeval beech forest was composed of 290 trees ha^{-1} that amounted to a basal area of 37.0 m^2 ha^{-1} and a volume of 654 m^3 ha^{-1}. The forest contained 22.7 trees ha^{-1} that were at least 80 cm in DBH, had a mean (± standard deviation) DBH of 29.4 (± 27.6) cm (range: 6–129.9 cm), a mean height of 21.6 (± 14.7) m (range: 3.8–47.9 m), and a deadwood share (based on total stand basal area) of 21.5%.

2.3. Phase assignment

Although subjective development phase assignment in the field

creates irregular patches, these rule-based objective phases were assigned to non-overlapping adjacent grid cells within the 10 ha plot. Given that the vast majority of gaps in this beech forest are less than $200\,m^2$ in extent (Hobi et al., 2015a), we chose to assign phases down to the smallest spatial resolution for which phases are typically assigned (e.g., Tabaku, 2000; Drößler and Meyer, 2006), which at $156.25\,m^2$ is roughly equivalent to the crown projection area of a mature beech tree of 70 cm (Meyer 1999). A fixed grid of increasing mesh size was placed over the 10 ha inventory plot to create a non-overlapping net of square subplots of the following sizes: $12.5 \times 12.5\,m$ ($156.25\,m^2$, n = 640), $12.5 \times 25\,m$ ($312.5\,m^2$, n = 320), $25 \times 25\,m$ ($625\,m^2$, n = 160), $25 \times 50\,m$ ($1250\,m^2$, n = 80), $50 \times 50\,m$ ($2500\,m^2$, n = 40), $50 \times 100\,m$ ($5000\,m^2$, n = 20), $100 \times 100\,m$ ($10000\,m^2$, n = 10), $100 \times 250\,m$ (2.5 ha, n = 4), $100 \times 500\,m$ (5 ha, n = 2), and $200 \times 500\,m$ (10 ha, n = 1).

The "modified TC Method" of Zenner et al. (2016) was used to assign grid cells to phases. In this revision of the previously established and widely employed method of Tabaku (2000), grid cells were assigned to one of eight phases within the forest life cycle: a combined Gap and Regeneration phase (GR), Establishment (E), Early Optimum (EO), Mid Optimum (MO), Late Optimum (LO), Terminal (T), Decay (D), and the Plenter phase [hereafter referred to as the Multi-Sized (MS) phase to avoid confusion with the managed plenter system/structure]. The five standard classification criteria were computed for each grid cell: (1) openness/gaps directly through canopy projection area, as the proportion (%) of a grid cell area covered by at least a single layer of projected crowns; (2) canopy height indirectly through the maximum DBH of standing trees within a grid cell; (3) mortality through the deadwood share, as the proportion (%) of the total basal area in a cell grid comprised of dead standing and lying trees (stumps + logs); (4) growth indirectly through the mean DBH of standing live trees; and (5) complexity of canopy layering through the normalized quartile DBH difference (NQD), which assesses variability in trees as the size difference (in DBH) of the tree of the 75th percentile and that of the 25th percentile, divided by median DBH. Threshold values for these criteria were then used to assign grid cells to a phase. Details of the calculations, explanations of modifications, and a discussion of their implications can be found in Zenner et al. (2016).

2.4. Statistical analyses

All phase assignment computations and classifications were performed in Matlab (v 8.2.0; Mathworks Inc., Natick,MA, US). In order to obtain an average with an estimate of error for the frequency of phase assignments (Table 1), those computations were conducted at the 1 ha scale (n = 10). As subplots were merged to scale up from the 156.25 to each larger spatial scale, the phases assigned to the resulting larger subplots were noted. For each spatial scale, we tallied the number of different observed convergence pathways (i.e., the number of different combinations of phases assigned to the subplots prior to and after the merger). Statistical summaries were performed in Matlab and SAS (v

Table 2
Maximum contiguous area across the 10 ha plot assigned to the same phase, by scale. GR = Gap/Regeneration, E = Establishment, EO = Early Optimal, MO = Mid Optimal, LO = Late Optimal, T = Terminal, D = Decay, MS = Multi-Sized.

| Scale, m^2 | Stand phase | | | | | | | |
	GR	E	EO	MO	LO	T	D	MS
156.25	312.5	312.5	625	468.75	2968.75	468.75	468.25	1093.75
312.5	312.5	312.5	625	312.5	1875	1250	1875	6250
625	0	0	0	625	2500	2500	3125	6875
1250	0	0	0	0	1250	2500	2500	65,000
2500	0	0	0	0	0	2500	5000	82,500
5000	0	0	0	0	0	5000	5000	90,000
≥10000	0	0	0	0	0	0	0	100,000

9.4; SAS Institute Inc., Cary, NC, US).

3. Results

3.1. Phase assignment

Phase diversity was highest at the smallest spatial scale and decreased steadily with increasing scale. The number of phases assigned decreased abruptly between the 312.5 and 625 scales (from 8 down to 5 phases) and then gradually decreased thereafter until at the largest scale only one phase was assigned (Table 1). All of the immature phases were assigned at the smallest scales ($\leq 312.5\,m^2$) but the first three phases (Gap/Regeneration, Establishment, and Early Optimum) were also the first to decrease in frequency and area (Table 2) until they dropped out at the 625 scale. As subplots merged to ever larger extents, the remaining phases dropped out in order, with the MO phase last assigned at 625, LO at 1250, and T and D last assigned at the 5000 scale. Although the most complex phase was assigned at all spatial scales, the area in MS consistently increased with increasing scale (Table 2).

At the finest spatial scale, most phases were assigned in roughly similar, relatively modest frequencies (7–14%); only the LO (33%) phase was more common (Table 1). Already by the 312.5 scale, however, with the exception of the LO phase (still 25% but already less than MS), the first three phases had become rare (less than3.5%). The mature phases peaked in abundance around 20% (both T and D at the 625 scale), or in the case of MS exceeded all other phases by the 312.5 scale and eventually accounted for 100% of subplots (Tables 1 and 2).

3.2. Convergence pattern

As scale increased, the first phases converged into the next subsequent phases such that the former generally lost in frequency and area while the latter gained (e.g., E to EO and MO to LO at all scales, LO to T at 1250, and T to D at 312.5, 625, and 2500) (Tables 1 and 2).

Table 1
Mean (across the 10 1ha subplots) proportion (standard error) of subplots (in %) classified in different stand phases, by scale. GR = Gap/Regeneration, E = Establishment, EO = Early Optimal, MO = Mid Optimal, LO = Late Optimal, T = Terminal, D = Decay, MS = Multi-Sized.

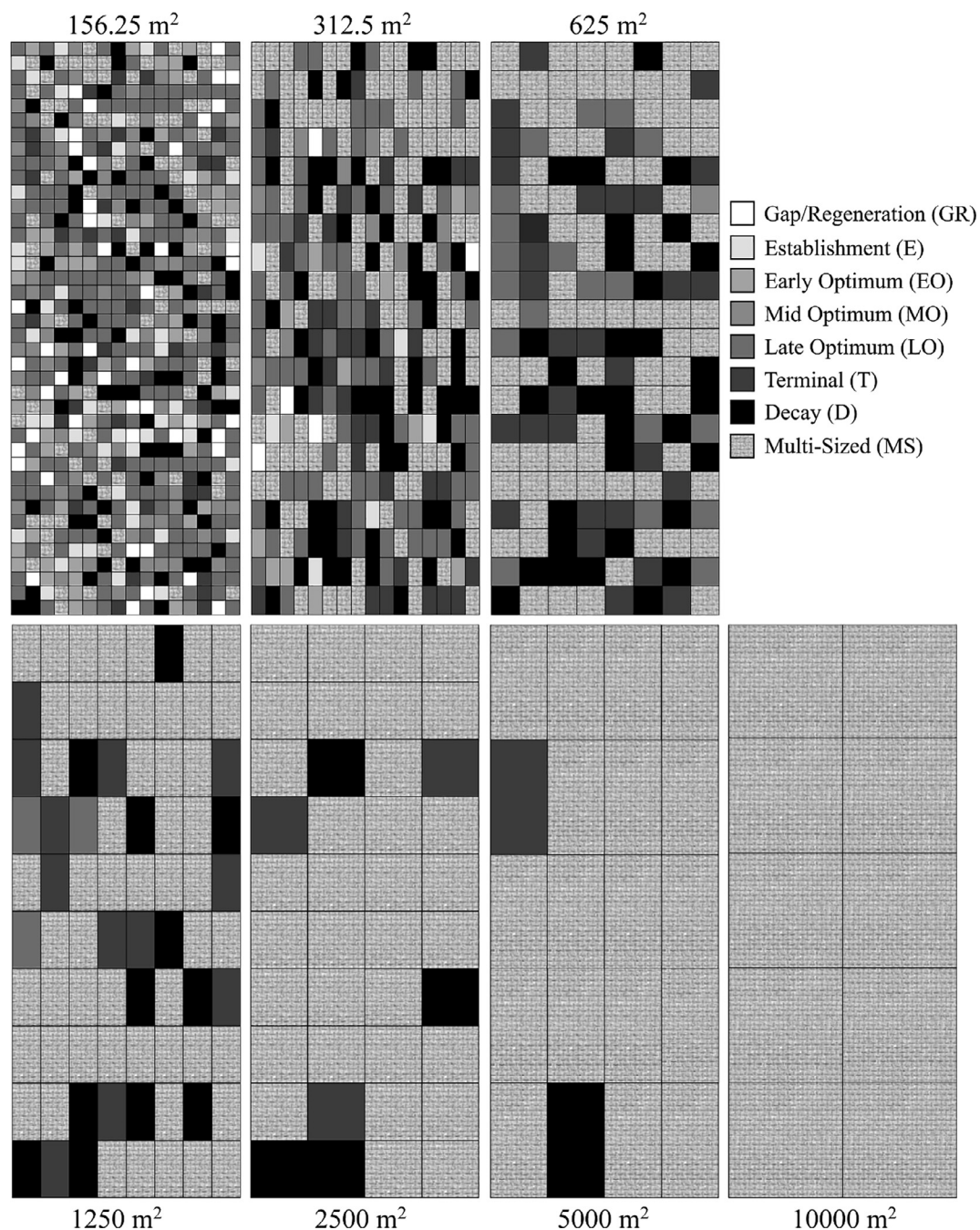| Scale, m^2 | Stand phase | | | | | | | |
	GR	E	EO	MO	LO	T	D	MS
156.25	7.0 (1.0)	7.5 (1.1)	8.8 (1.3)	11.9 (1.4)	33.3 (2.1)	5.2 (0.7)	12.5 (1.6)	13.9 (2.5)
312.5	1.6 (1.0)	1.9 (0.5)	3.4 (1.8)	3.1 (1.3)	25.3 (2.9)	10.9 (1.6)	19.4 (2.9)	34.4 (4.8)
625	0	0	0	0.6 (0.6)	11.9 (2.9)	19.4 (1.6)	20.0 (4.1)	48.1 (4.4)
1250	0	0	0	0	3.8 (2.7)	15.0 (4.1)	15.0 (4.1)	66.3 (7.2)
2500	0	0	0	0	0	7.5 (3.8)	10.0 (5.5)	82.5 (8.4)
5000	0	0	0	0	0	5.0 (5.0)	5.0 (5.0)	90.0 (6.7)
≥10000	0	0	0	0	0	0	0	100 (0)

Fig. 1. Actual phase assignment to subplots at the 156.25–10000 scales. Note the absence of the first two phases (Gap/Regeneration, Establishment) after the 312.5 scale and the ultimate convergence on the Multi-Sized phase.

While the immature phases consistently decreased in frequency and area with increasing scale, the T and D phases initially increased in frequency before decreasing again, even as the contiguous areas assigned to these mature phases continued to increase. The MS phase consistently increased in frequency and area with increasing scale.

At the smallest scale, the minimum contiguous area (or patch size) for any phase ranged from only 312.5 m^2 (two adjoining 156.25 subplots) for the GR and E phases to nearly 2969 m^2 (19 such adjoining subplots) for the LO phase (Table 2). Although patch sizes naturally increased with increasing scale through the merger of neighboring subplots into larger spatial units (Fig. 1), the maximum patch size for the GR and E phases never exceeded 312.5 m^2, the EO phase peaked at 625 m^2, and MO phase patches were never greater than 469 m^2. In other words, these immature phases expanded to at most four adjoining

subplots and were typically surrounded by subplots assigned to some other phase. In contrast, the LO phase initially had the greatest contiguous area of any phase, but with increased scale adjacent subplots were increasingly assigned to other phases such that LO patch size never exceeded 3000 m^2. Although the maximum patch size of the T phase increased steadily up to the 5000 scale, typically no more than 2–4 adjoining subplots were ever assigned to that phase. Patch size also consistently increased with increasing scale for subplots assigned to the D phase even as the proportion of subplots declined. The Multi-Sized phase was never observed in a patch size of less than 1000 m^2 at any scale, less than 6000 m^2 above the 312.5 scale, or less than 80,000 m^2 above the 0.25-hectare scale. The area of both contiguous and non-contiguous patches assigned to the Multi-Sized phase dominated at all but the very smallest scale.
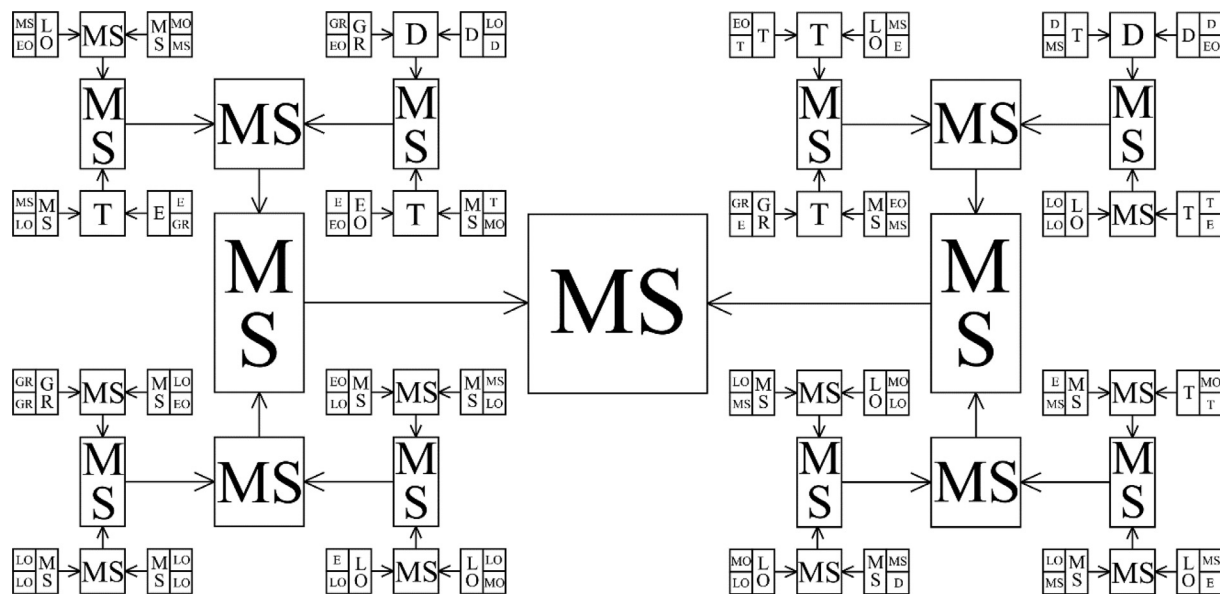
Fig. 2. Visualization of the observed convergence of phases (in five steps →) from the 156.25 to 10,000 scale in one of the 1 ha subplots. As was typical of all 10 1 ha subplots, in most cases phases partially overlapped across scales until the intermediate scales when phase assignment began to converge on the Multi-Sized phase. GR = Gap/Regeneration, E = Establishment, EO = Early Optimal, MO = Mid Optimal, LO = Late Optimal, T = Terminal, D = Decay, MS = Multi-Sized.

3.3. Convergence pathways

In most cases, subplot mergers to increase spatial scale did not result in entirely new phase assignments: merging two neighboring subplots into the next larger subplot scale usually resulted in the larger subplot being assigned the same phase as at least one of the two smaller subplots (e.g., Fig. 2). Only at the 312.5 and the 625 scales did notable proportions of mergers result in an entirely new phase assignment (22% and 12% of the time, respectively). By the 1250 scale the proportion was down to 2.5%, and at larger scales new phases were always identical to at least one of their constituent phases.

Merging neighboring subplots from the 156.25 to the 312.5 scale resulted in 77 different convergence pathways. The number of possible combinations declined with increasing scale, such that merging neighboring subplots at the 312.5, 625, 1250, 2500, and 5000 scales resulted in 42, 20, 9, 5, and 3 unique combinations at the next larger scale, respectively. Merging the same two constituent phases could result in either the original phase or up to three different phases (e.g., when merged, neighboring EO and LO subplots could result in a larger subplot assigned to any of the LO, T, D or MS phases, Table 3). Consistent with the hierarchical definition of the phases, combinational retrogression was extremely rare: only once did the merger of two subplots assigned to immature phases result in the assignment of an even more immature phase (EO with EO to E at the smallest scale). Likewise, mergers involving subplots in the mature T or D phases invariably resulted in the assignment of the T or more mature phases at all scales (Tables 3 and 4). Although mergers involving the MS phase sometimes resulted in the assignment of a more immature phase (most often LO) through the 625 scale, in most cases at all scales mergers involving at least one subplot assigned to the MS phase resulted in the larger subplot also being assigned to the MS phase.

4. Discussion

Our results confirm earlier indications that the delineation of forest cycle phases is sensitive to the spatial scale of assessment in European beech forests (Korpel', 1995; Tabaku, 2000; Winter and Brambach, 2011). Although not previously systematically investigated for development phases, the importance of scale has long been recognized. At inception, unequal representation of phases was expected (Watt, 1947), with short-lived phases (anticipating fast vs. slow processes *sensu* O'Neill et al., 1989) envisioned to occupy a lower proportion of the total landscape than longer-lived phases (Leibundgut, 1993), and broad stages to be more applicable at large scales and fine phases at smaller scales (Korpel', 1995). Early suppositions as to the extents of patches in a given stage (e.g., 0.5–2 ha for the Optimum stage) or those required to capture all phases (5–10 ha) (Korpel', 1995) also established scale expectations that shaped subsequent work.

At the same time, the extremely small extent of disturbances in European beech stands dictated gap-patches the size of a single mature tree crown as the basic unit of developmental dynamics (Meyer, 1999), inevitably rendering phase assignment scale-dependent (Tabaku, 2000). Characterizations of phase patches as very small (Establishment), small (Optimum), larger (Multi-Sized/Plenter), or extensive (Terminal) set expectations of the spatial scales required to capture different phases, as did initial reports that primeval beech forests had relatively small amounts of early phases and were dominated by later phases (Tabaku, 2000). Further, empirical classifications demonstrated greater proportions of "mixed" phases at larger (greater than 200 m^2) sampling scales (Emborg et al., 2000) and scale-dependency of the Multi-Sized/Plenter phase (Tabaku, 2000). More recently, observations of more phases assigned at smaller scales as well as of greater areas assigned to later phases with increasing scale (Winter and Brambach, 2011) sparked our explicit test of the hypothesis that the immature forest cycle phases (Gap/Regeneration, Establishment, and Optimum) would be assigned predominantly at very small spatial scales while the more mature phases (Terminal, Decay, Multi-Sized) would be primarily assigned at larger spatial scales.

Support for this hypothesis was found in the (1) assignment of the immature phases at only the two smallest spatial scales, (2) decreasing proportion and area of immature phase patches with increasing scale, and (3) increasing proportion and area of mature phase patches with increasing scale. The tendency at the 156.25 scale toward low proportions of the immature phases (G/R, E, EO, and MO) and higher proportions of the more mature D and MS phases observed in the current study appears to be consistent across older European beech forests (cf. Tabaku, 2000; Drößler and Meyer, 2006). The prevalence of immature phase patches at the finest scale is consistent with the small scale of gaps in the reserve (Hobi et al., 2015b). The close spatial intermingling of phase patches (Drößler et al., 2016), further facilitated

Table 3
Phases (number out of 320 subplots) that resulted from merging subplots from the 156.25 to the 312.5 scale, by initial phases. Merging across neighboring subplots at this scale resulted in 77 different convergence pathways (e.g., four convergence pathways were observed when a GR subplot was merged with an LO subplot, resulting in either an LO, T, D, or MS phase at the 312.5 scale). Bold indicates that the new phase at the larger scale is the same as one or both of the constituent phases assigned at the smaller scale. GR = Gap/Regeneration, E = Establishment, EO = Early Optimal, MO = Mid Optimal, LO = Late Optimal, T = Terminal, D = Decay, MS = Multi-Sized.

Phase	GR	E	EO	MO	LO	T	D	MS
Phases at 156.25 scale merged to phases at 312.5 scale (n = 320)								
GR	**GR (3)**	**GR (1)** **E (1)**	**GR (1)** E (1) **EO (3)**	**MO (2)** LO (1) D (2)	**LO (12)** T (3) D (3) MS (1)	**T (1)**	**D (3)**	EO (1) **MS (4)**
E		**E (4)**	**EO (2)** MS (1)	**MO (3)** D (2) MS (1)	**LO (6)** D (5) MS (5)	**T (1)**	**D (3)**	LO (4) T (1) **MS (4)**
EO			E (1) EO (4)	**MO (1)**	**LO (9)** D (1) MS (5)	**T (3)**	LO (1) T (1) **D (9)**	LO (3) D (1) **MS (5)**
MO				**MO (3)** MS (1)	**LO (17)** T (2) MS (13)	**T (3)** MS (4)	T (1) **D (7)**	LO (2) **MS (6)**
LO					**LO (21)** MS (15)	**T (4)** MS (1)	T (9) **D (9)** MS (6)	**LO (5)** **MS (22)**
T						**T (3)**	**T (1)** **D (5)** MS (1)	**MS (3)**
D							**D (6)**	T (3) **D (4)** **MS (5)**
MS								LO (1) **MS (8)**

the very rapid loss with increasing scale of the immature phases, which was nearly complete at intermediate scales ($1250\,m^2$) and involved their outright absorption into the mature phases at the 2500 scale.

The loss of immature phases by the 1250–2500 scales is consistent with a prevailing small-scale disturbance regime, which could involve more-or-less continuous micro-gap formation through limb breakage and the mortality of a single or just a few old canopy trees (Drößler and von Lüpke, 2005; Zeibig et al., 2005) or intermediate-intensity disturbances (e.g. windthrow Nagel and Diaci, 2006; and/or ice Standovár and Kenderes, 2003) affecting canopy trees to a greater extent than understory regeneration (Nagel and Diaci, 2006). Two disturbance events are known to have occurred in the adjacent reserve during the study period: a wind storm in March 2007 and a heavy wet snow fall in October 2009 (local forest service personnel, *pers. comm.*). Such disturbances often result in incomplete overstory mortality with persistent large residual trees, large amounts of deadwood, and release of advance regeneration (Nagel and Svoboda, 2008), which could leave a structural signature corresponding to the Decay phase. In the current study, a strong presence of the Decay phase at the 1250 scale, which persisted to the 0.5 ha extent, might point to either synchronized mortality of individual trees or past intermediate-scale disturbance paired with more recent gap formation. Although clarity would require detailed dendroecological reconstructions, the current study reconfirms previous findings of the predominance of fine-scale disturbance impacts and developmental dynamics.

The increase with increasing scale in the proportion of subplots assigned to mature phases, which doubled from 36% at the smallest scale to 70% at the 312 scale and greater than 90% by the 625 scale, largely reflected a substantial and consistent increase in the internally heterogeneous Multi-Sized phase. Nearly half of subplots were assigned to this phase by the 625 scale, consistent with the ~50% of $500\,m^2$ inventory subplots throughout the entire reserve (Peck et al., 2015), and it predominated (60%) by the 1250 scale, dominated (90%) by the 10,000 scale, and was the only phase assigned at larger scales. This clear support for the hypothesis of convergence with increasing scale on the most complex phase is consistent with previous observations of the

scale dependency of structurally complex phases (cf., the "mixed" phase of Emborg et al., 2000), including substantial increases in the proportion of the Multi-Sized phase between the 156 and 2500 scales (Tabaku, 2000). Convergence in this forest to the Multi-Sized phase with increasing scale may reflect (1) anomalous conditions specific to this case-study, (2) the interaction of stochastic stand development with phase classification rules, (3) the effect of merging scale-dependent structures resulting from hierarchically layered processes, and/or (4) the background matrix structure of an ecosystem dominated by extremely small-scale disturbance and developmental dynamics.

Because a systematic and comprehensive assessment of scale impacts dictated an unusually large stem-mapped research plot, the current study was not able to replicated at this time in any other of the few remnants that remain of unmanaged primeval European beech forest. While this constraint necessarily limits the inferences that can be drawn from current study, the potential applicability of our results to natural beech forest may be inferred from the similarity of the Uholka plot to other old-growth European beech forests. First, despite some variation in the mean values of stand structural metrics, the proportions of phases within the 10-ha plot have previously been found to be similar to those in the surrounding 10,000 ha Uholka reserve (Peck et al., 2015). The live-tree forest structures (e.g., basal area, density, mean tree sizes) within the 10-ha plot (Zenner et al., 2015) as well as of the overall Uholka reserve (Hobi et al., 2015a) are typical of primeval European beech forest, as is the shape of the diameter distribution, the lack of evidence of large historic disturbances (Zenner et al., 2015), the multi-layered canopy structure, and deadwood volume (Hobi et al., 2015b). Previous reports of the ubiquity of beech seedlings in Uholka (Commarmot et al., 2005) and of multiple-releases (Hobi et al., 2015b; Trotsiuk et al., 2012) are consistent with generalizations about natural beech forests (e.g., Wagner et al., 2010), and the large span in ages among comparably sized trees has also been reported for other primeval beech forest (see Hobi et al., 2015b; Trotsiuk et al., 2012). Although gap fractions and mean gap sizes reported for Uholka are on the low end of those reported for old-growth beech (Hobi et al. 2015a), the small spatial scale of the disturbance regime is consistent with other

Table 4

Phases (number out of 160, 80, 40, 20, and 10 subplots, respectively) that resulted from merging subplots into the next larger scale, starting from the 312.5 scale, by initial phases. Bold indicates that the new phase at the larger scale is the same as one or both of the constituent phases assigned at the smaller scale. GR = Gap/Regeneration, E = Establishment, EO = Early Optimal, MO = Mid Optimal, LO = Late Optimal, T = Terminal, D = Decay, MS = Multi-Sized.

Phase	GR	E	EO	MO	LO	T	D	MS
Phases at 312.5 scale merged to phases at 625 scale (n = 160)								
GR					D (1) MS (1)		**D (2)**	T (1) **MS (1)**
E						D (1)	**D (2)**	T (2)
EO				**MO (1)**	**LO (3)** MS (2)		**D (1)**	LO (2) T (1) **MS (1)**
MO					**LO (1)** MS (1)		**D (4)** MS (1)	LO (1) T (1)
LO					**LO (6)** MS (5)	**T (10)** MS (2)	T (7) **D (3)** MS (1)	**LO (6)** T (1) **MS (21)**
T						**T (4)** MS (1)	**D (4)** MS (2)	**T (2)** **MS (5)**
D							**D (7)**	T (2) **D (8)** **MS (11)**
MS								**MS (22)**
Phases at 625 scale merged to phases at 1250 scale (n = 80)								
MO						**T (1)**		
LO					**LO (1)**	**T (2)** MS (1)	T (1) **D (1)** MS (2)	**MS (10)**
T						**T (3)** MS (1)	**T (2)** **D (1)** MS (4)	**T (2)** **MS (10)**
D							**D (3)**	T (1) **D (7)** **MS (9)**
MS								**MS (18)**
Phases at 1250 scale merged to phases at 2500 scale (n = 40)								
LO						T (1)		**MS (2)**
T						**T (1)**	T (1) **D (3)** MS (1)	**T (1)** **MS (5)**
D								**MS (7)**
MS								**MS (19)**
Phases at 2500 scale merged to phases at 5000 scale (n = 20)								
T							**D (1)**	**T (1)** **MS (1)**
D								**MS (3)**
MS								**MS (14)**
Phases at 5000 scale merged to phases at 10,000 scale (n = 10)								
T								**MS (1)**
D								**MS (1)**
MS								**MS (8)**

natural European beech stands (Hobi et al., 2015b). Finally, the spatial smoothing observed in the current study and previously reported for Uholka (Hobi et al. 2015b) is consistent with that reported for other old-growth beech (Král et al., 2010a).

Alternatively, convergence on the mature phases with increasing scale could partially reflect the delineation of development phases by this classification protocol. Phases, by definition, are surrogates for temporal development, and thus age in primeval forests (where increment boring is largely prohibited), which inherently introduces a degree of uncertainty. Likewise, just as the original application of development phases as subjectively identified patches of irregular shape and extent with unquantified characteristics (Leibundgut, 1959, 1993; Korpel', 1995) was subject to irreplicability, the transcription of the phase concept onto objectively delineated discrete grid cells using a rule-based classification protocol is inevitably subject to debate over chosen criteria and thresholds (e.g., Zenner et al., 2016). For example,

regardless of the threshold value chosen, it is questionable as to whether the addition of a single tree exceeding a size threshold warrants assignment of an entire patch to a more mature development phase. Further, although the NQD indirectly captures canopy layering, the traditional threshold of 100 may lead to the assignment of two-storied structures to the Multi-sized phase that might otherwise have been assigned to the Late Optimum or Terminal phases. Consequently, the classification protocol employed in the current study would benefit from future refinements such as a more direct incorporation of canopy layering and the use of relative rather than absolute classification thresholds.

Nonetheless, although minor modifications of the classification thresholds in the current study would have resulted in different proportional abundances of development phases, the general trend in convergence across scale to the more mature phases would likely have persisted. For example, although 13% of grid cells (at the smallest scale) that were assigned to the Decay phase could also have qualified as Multi-Sized, shifting the assignment away from the Decay phase would have only increased the convergence on the complex Multi-Sized phase. Likewise, while it is theoretically possible for grid cells with very simple structures (i.e., only trees of the smallest size classes) to be assigned to the Multi-Sized phase rather than the Late Optimal or Terminal phases, at the smallest scale only one such grid cell (1%) was observed, while less than 10% had bimodal size distributions (data not shown)—which are arguably no longer simple in structure. However, a tendency for convergence of natural beech forest on breakdown (*sensu* Korpel', 1995) phases at larger scales may have also arisen because the mixed-phase patches captured at larger scales are more likely to contain the structural features that define mature phases, such as size diversity (Multi-Sized), trees of large diameters (Terminal), or, at least at intermediate scales, a larger share of deadwood (Decay). Although an assessment of the influence of scale dictated the use of consistent classification criteria across all scales, this may nonetheless explain why, despite multiple potential pathways for assembling neighboring phase-patches, it was extremely rare for mergers to result in immature phases but not uncommon to result in mature phases. Further, convergence on the Multi-Sized phase could be due to the increasing difficulty at larger scales of meeting classification thresholds for other phases. For example, despite a stand average of 18% of deadwood in the current study, deadwood in individual subplots was often below the 30% threshold for assignment to the Decay phase.

However, in an ecosystem dominated by extremely small-scale dynamics including single-tree canopy gaps (regardless of their origin), *any* scale greater than 156.25 m^2 would involve the merger of heterogeneous patches. Likewise, the tendency for shade tolerant beech (Wagner et al., 2010) to layer may have lessened the likelihood of assignment to the relatively more homogeneous phases. Given the basic tenet of hierarchy theory (Allen and Starr, 1982), that patches at any scale reflect the internal patchiness expressed at yet finer scales (Kotliar and Wiens,1990), these mixed-phase patches will inevitably contain both the 'among-component' variation between phases and the 'within-component' variation of each phase (*sensu* Smith and Urban, 1988). This phenomenon has previously been observed through the trend toward spatial smoothing of diameter distributions, which often converge on a reverse-J or rotated sigmoid distribution with increasing scale in temperate hardwood forests (Janowiak, et al. 2008; Alessandrini et al., 2011; Zenner et al., 2018). Such high heterogeneity aggregations are likely to be classified into the Multi-Sized phase, which is why some previous authors have sought extremely fine spatial resolutions to minimize the assignment of a seemingly artificially derived mixed phase (e.g., Emborg et al., 2000) while others have allocated this variability to other phases (e.g., Decay, Begehold et al., 2016) or explicitly omitted it entirely (Winter and Brambach, 2011).

Although the tendency toward convergence on a single phase has led some to conclude that forests appear more homogeneous than they really are (Feldmann et al., 2018), the internally heterogeneous nature

of the Multi-Sized phase actually reflects the greater degree of structural complexity captured at larger scales. Subsequently, the inverse may be equally true: disregarding how phases assemble across scales by limiting the spatial perspective to tree-crown extents could lead to overestimating the importance of simple, immature phase patches and underestimating the more complex mature phase patches. Perhaps more importantly, by discounting the significance of heterogeneous patches the outcomes of the fast, short-term dynamics (Tikhonov, 1950 presented in English by Plant and Kim, 1975) of disturbance/renewal may be emphasized over the slow, long-term dynamics of maturation/maintenance/persistence. This emphasis on fast dynamics (i.e., gap-phase replacement) likely shaped past considerations of the mosaic cycle (Remmert, 1991) viz. the frequency distributions of phases expected to achieve a dynamic "phasic equilibrium" (Watt, 1947) or a "shifting mosaic steady state" (Bormann and Likens, 1979). In this investigation of the mosaic cycle at multiple scales, however, slow dynamics appear to be as prevalent as fast dynamics.

The importance of the slow, long-term dynamics at larger scales may be seen in the rapid convergence with increasing scale of fast, short-term, small-scale immature phases on the more complex mature phases. Additionally, however, the assignment of the Multi-Sized phase at even the smallest scale and its prevalence (over a third) already at the 312 scale indicates that complex structures persist across scales. Delineated as a phase out of necessity (because the existence of complex structures could not be denied, Leibundgut, 1993) rather than deduced from developmental dynamics, a Multi-Sized phase continues to be designated because of the widespread importance of prevalent, complex structures (e.g., Král et al., 2016, 2018). If indeed complex structure is a persistent feature of natural beech forests regardless of development stage (Peck and Zenner, 2019) at all spatial scales, the transitions in phase that resulted from merging subplots across scale observed in the current study, as well as temporal transitions in and out of the Multi-Sized/Steady State phase (Král et al., 2018), may best be interpreted as structural developmental dynamics rather than temporal developmental dynamics. Toward that end, a potentially more useful classification protocol might conceptually distinguish not only between the immature and mature phases within a developmental framework, but also focus on teasing apart the purely structural differences among the mature phases.

The prevalence of a structural phase that alternately absorbs from, and contributes to, other gap-patch phases to weave the textural fabric of the forest obviously complicates the application of a hierarchical, high-resolution classification typology intended to carve out homogeneous phases. Temporal development phases, by design, necessarily try to discretize a "mostly continuous" dynamic (Meyer, 1999), which may resist attempts to identify discrete transitions (e.g., Glatthorn et al., 2018). Our results reconfirm the necessity of a very fine spatial perspective to successfully discern the immature, and thus all, phases (Tabaku, 2000; Emborg et al., 2000; Winter and Brambach, 2011), likely reflecting the obligate link between the spatial scale of sampling and the predominant scale of disturbance (Peterken, 1996). However, 156.25 m^2 (proposed by Meyer, 1999 and adopted by Tabaku, 2000; Drößler and Meyer, 2006) is a compromise between the desire for fine-scale mapping of gap-dynamics on the one hand and the need to reasonably represent the stand structure on the other (Král et al., 2010b). Our results remind us that this scale is not sufficient to reliably identify phases with complex structures. Further, when phase becomes functionally synonymous with the extent of a single tree while beech forests converge on a single complex phase by operational scales (e.g., the compartment), the application of phases ceases to be managerially useful. Nonetheless, while the loss of phases with increasing scale clearly exposes the strong control of spatial resolution in phase assignment, it also points to assigning phases across multiple scales as a tool to more thoroughly examine the mosaic cycle and the emergent properties of forest communities such as resistance, resilience, and stability.

Confirmation of spatial scaling may also render the North-American approach of structural stages a potentially suitable model for primeval European beech. Although the focus has often been on development following catastrophic disturbance towards a structurally diverse, uneven-aged, patchy "steady-state" (Bormann and Likens, 1979), "old-growth" (Oliver and Larson, 1996) or "shifting-gap" (Spies and Franklin, 1996) phase, the structurally diverse "endpoint of stand development" (Franklin et al., 2002) is useful for characterizing old-growth forests subject to frequent light to moderate disturbances. We agree with Franklin et al. (2002) that it is more useful to regard the late successional mosaic of small structural units as a collective entity than to focus on individual structural units. Although very small structural units may provide insight into the spatial and perhaps even temporal patterns of disturbance events, the placement of structural phases within a larger context provides a more direct management guide because it incorporates the biological legacies of disturbance that shape future structure.

5. Conclusions

The convergence of phase assignment across spatial scale in this primeval European beech stand presents both a challenge and an opportunity. If this pattern proves typical, a single, fine scale of assessment may yet be suitable when the objective is to delineate patches belonging to all stages of development, emphasizing the structurally more homogeneous, immature phases reflective of fast dynamics such as gap formation. However, assessments at a single scale bias estimates of phase extents: small scales underestimate mature phases, while large scales eliminate immature phases. It is thus only through trans-scale assessments that stand dynamics *per se* can be elucidated. Multi-scale assessments may also help move beyond unhelpful traditional concepts about the "steady-state" (Mori 2011) by shifting attention away from the small scales in which fast, short-term dynamics are most evident to also include the scales at which slow, long-term dynamics are expressed. Consequently, the assignment of phases at only very fine spatial resolutions is necessary, but not sufficient, for a comprehensive investigation of the mosaic cycle in such structurally heterogeneous forests.

At the same time, the awareness of a foreseeable convergence on the most complex phase with increasing spatial scale opens the window to a new approach to exploring developmental dynamics, including identifying the actual spatial scale of dominant disturbances, by investigating and comparing the rate at which phase transitions occur across scales in different forests. Rather than delineating sequential phases of temporal dynamics, structural phases may capture the cumulative diversity of structures that arise through a variety of developmental dynamics at different spatial and temporal levels. The spatial convergence of phase assignment thus reiterates the utility of understanding forest structural dynamics, which extends beyond the tree-attributes used to assign phases to the imprint of disturbance on the landscape.

CRediT authorship contribution statement

Eric K. Zenner: Conceptualization, Methodology, Formal analysis, Data curation, Writing - original draft, Writing - review & editing, Visualization. **JeriLynn E. Peck:** Methodology, Formal analysis, Writing - original draft, Writing - review & editing, Visualization. **Martina L. Hobi:** Methodology, Validation, Resources, Writing - review & editing, Data curation.

Research data

While the analysis datasets are on file with the lead author, the primary data are available at https://esajournals.onlinelibrary.wiley.com/doi/full/10.1002/ecy.2845 as a data paper by Stillhard et al. (2019).

Declaration of Competing Interest

Acknowledgements

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.foreco.2020.117889.

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