

Spatio-Temporal Variation of Coarse Woody Debris Input in Woodland Key Habitats in Central Sweden

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The persistence of many saproxylic (wood-living) species depends on a readily available supply of coarse woody debris (CWD). Most studies of CWD inputs address stand-level patterns, despite the fact that many saproxylic species depend on landscape-level supplies of CWD. In the present study we used dated CWD inputs (tree mortality events) at each of 14 Norway spruce (*Picea abies*) dominated woodland key habitat sites to analyze the spatial and temporal patterns of CWD additions between 1950 and 2002 within a small landscape in central Sweden. We found that inputs were episodic within sites, where local windstorms created pulses in CWD input. Pulses occurred simultaneously in many sites, yielding landscape-level synchrony of CWD input. These synchronous pulses, and importantly, the breaks between pulses, may have negative implications for saproxylic species that are dependent on large volume inputs of freshly killed Norway spruce. In addition, the inherent small size and relative isolation of these sites may further increase extinction risks due to stochastic events. However, background CWD input rates occurring between pulses varied substantially among sites, presumably the result of the sites' varied histories and structural characteristics. This finding suggests that the different sites have varied abilities to provide habitat for saproxylic species during periods with low landscape-level input of CWD.

Keywords boreal forest, dendrochronology, disturbance dynamics, *Picea abies*, tree mortality, woodland key habitats, windstorms

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1 Introduction

Coarse woody debris (CWD, including snags and down woody debris) provides the critical substrate for a large number of organisms that require deadwood for some or all of their life cycle. Populations of these saproxylic species have declined in Fennoscandia, in large part because intensive and extensive timber extraction over the last century has reduced the volume and diversity of CWD in managed forests (Bader et al. 1995, Rydin 1997, Martikainen et al. 2000, Siitonen 2001, Jonsson et al. 2005, Gärdenfors 2010). As a substrate for saproxylic species, CWD represents a patch-dynamic system, both within stands and at the landscape scale. For example, several threatened species of wood-decay fungi depend on both a stand- and landscape-level supply of deadwood (Gu et al. 2002, Edman et al. 2004a, 2004b, Jönsson et al. 2008). To date, however, most studies of CWD dynamics have addressed only stand-level patterns (e.g., Jonsson 2000, Fraver et al. 2002, Edman et al. 2007, Aakala et al. 2009); much less attention has been directed toward CWD dynamics at larger scales.

In the Nordic countries and the Baltic States, the high-conservation-value forest remnants – namely the *woodland key habitats* (Nitare and Norén 1992, Tenhola and Yrjönen 2000, Jönsson and Jonsson 2007a) – provide an ideal system with which to assess landscape level patterns in CWD dynamics. These key habitats are hotspots of CWD, diversity of CWD, saproxylic species richness and red-listed species (Timonen et al. 2010), constituting a network of potential safe sites for saproxylic species which may serve as ‘stepping stones’ between larger areas of old-growth forest. In Sweden, woodland key habitats have no direct legal protection, but according to the Swedish Forest Stewardship Council (FSC) certification standards, they should be set aside from forest management to support the survival of red-listed species and to serve as reference areas within the managed forest landscape (Swedish FSC... 2010). However, inherent in the key habitats small size (typically only a few hectares) and significant degree of isolation (Aune et al. 2005) is a potential increased extinction risk due to stochastic dynamics within small stands.

Of particular interest when assessing CWD

dynamics at the landscape level is the degree of synchrony in tree mortality (i.e., CWD creation and input) among high-quality forest patches within a landscape. If habitat quality (e.g., volumes of CWD) varies similarly and simultaneously in many high-quality stands, the extinction risk for saproxylic species that are dependent on substantial inputs of fresh CWD or are specialised on living under the bark of recently dead Norway spruce (sensu Ehnström and Axelsson 2002) would increase at the landscape scale. For example, several boreal longhorn beetles (e.g., *Anastrangalia sanguinolenta*, *Pachyta lamed*, *Olisthaerus substriatus*) inhabiting older Norway spruce forest have declined considerably during the past century, with wood of recently dead Norway spruce becoming less and less common on forestry land (Lindhe et al. 2010). Further, spatially correlated disturbances can be detrimental because they may increase fluctuations in the regional carrying capacity of metapopulations (Johst and Drechsler 2003). In contrast, spatial heterogeneity in local environments may promote species persistence by buffering the effects of high levels of temporal environmental stochasticity. For example, local populations of saproxylic species may survive unfavourable periods with limited availability of CWD if suitable substrates are continuously formed elsewhere within the landscape. However, if periods of low CWD input occur synchronously throughout the landscape, the likelihood of neighbouring local populations serving as sources for recolonization (i.e., the rescue effect) would be reduced (Brown and Kodric-Brown 1977).

In light of the foregoing, these traits suggest that the persistence of saproxylic species follows the metapopulation concept, where local extinctions from habitats with sparse or unsuitable substrates are balanced by colonizations from more favourable habitats (Hanski 1999, Hanski and Gaggiotti 2004). In the present study we address the degree of synchrony in tree mortality (i.e., CWD input) within a small landscape in central Sweden. Our assumption is that the spatial and temporal variation in CWD in remnant high-quality habitats strongly influences the population dynamics of saproxylic species dependent on recently dead Norway spruce (the dominant tree in the landscape studied).

Here we assess the synchrony and spatial correlation in CWD input within 14 Swedish wood-

land key habitats dominated by *Picea abies*. We used dendrochronological methods to reconstruct annual CWD inputs from 1950–2002 within each key habitat, followed by landscape-level analyses using all 14 key habitats. Our specific objectives were to: 1) determine if CWD was created stochastically within individual woodland key habitats, and 2) determine to what extent CWD creations occurred synchronously at the landscape level. Finally we discuss the implications of our results for the persistence of metapopulations of saproxylic species dependent on dead Norway spruce trees.

2 Methods

2.1 Study Area

The study was conducted within a 22 km × 36 km area (approximately 800 km²), in Västernorrland County, southern boreal zone of Sweden (Fig. 1). Elevations range from approximately 50

to 440 m above sea level, mean annual temperature is around 3 °C, and the region receives a mean annual precipitation of around 700 mm. *P. abies* is the dominant tree in the study area, with *Pinus sylvestris* as the subordinate forest tree. Fourteen woodland key habitats (WKH1–WKH14) were included in the study (representing the majority of *Picea*-dominated woodland key habitats of mesic site type on SCA forest company land, the major forest owner in the study area), ranging in size from 1 to 50 ha and separated by distances of 0.3 to 34.4 km (Fig. 1, Table 1). *P. abies* is the dominant tree species in all study sites, with *P. sylvestris* and *Betula* species as subordinate species.

The study area has a long history of anthropogenic forest exploitation; in the 1750–1850s forest resources were largely utilized for charcoal production, in the 1850–1900s the region experienced the first wave of commercial diameter-limit and selection timber harvesting, and from the 1900s onward intensive forestry was gradually introduced (Jönsson et al. 2009). The present landscape is dominated by managed for-

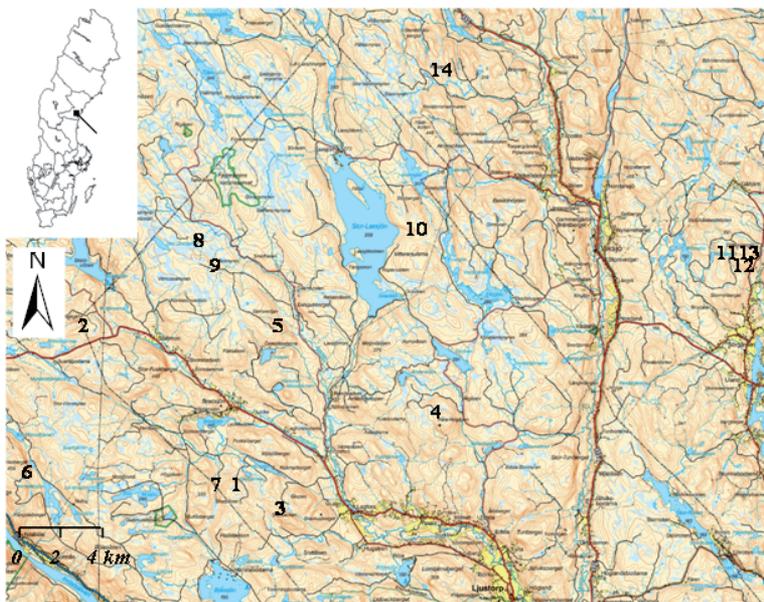


Fig. 1. Location of the study landscape in Västernorrland County, the southern boreal zone of central Sweden. Coarse woody debris inventories and input histories were conducted within key habitats (numbers 1–14) dominated by *Picea abies*.

Table 1. Stand characteristics of the 14 *Picea abies* dominated key habitats studied. All data except coarse woody debris volumes were obtained from the forestry company SCA's stand registers.

Name	Plot abbreviation	Size (ha)	Productivity ($\text{m}^3 \text{ha}^{-1} \text{yr}^{-1}$)	Living trees			Total volume		Coarse woody debris volume ($\text{m}^3 \text{ha}^{-1}$)			
				<i>Picea</i>	<i>Pinus</i>	<i>Betula</i>	<i>Picea</i>	<i>Betula</i>	Standing	Downed	1–2	3–4
Mjösjöområdet	WKH-1	10	5.5	28.7	4.1	8.2	359	7.0	8.3	7.1	6.8	1.4
Stor-Vitberget	WKH-2	9	4.8	24.4	6.6	2.0	273	3.4	0.2	0.5	0.0	3.1
Storbacken	WKH-3	19	6.8	37.2	1.6	1.2	385	6.0	15.2	10.5	6.8	3.9
Häre-Högåsen	WKH-4	15	4.2	24.5	0.3	0.3	207	19.4	20.6	14.8	13.5	11.6
Storsvedjan	WKH-5	25	6.9	29.7	2.0	1.3	349	47.2	56.8	56.4	26.5	24.9
Jerikoberget	WKH-6	8	4.3	34.2	1.1	0.7	329	6.2	2.3	2.2	1.9	4.0
Moaknylen	WKH-7	3	4.0	19.0	0.0	1.0	182	21.9	46.4	20.3	38.2	9.9
Gäddbäcksdammen	WKH-8	31	5.5	27.5	0.7	7.2	317	7.4	12.2	7.5	10.3	1.7
Rotmyran	WKH-9	16	7.4	15.0	0.8	1.3	174	2.1	7.9	5.6	3.9	0.5
Stor-Laxsjön	WKH-10	50	2.8	18.6	1.4	4.0	184	29.7	19.2	11.3	25.3	12.3
Gillersberget	WKH-11	6	4.2	22.8	0.0	1.2	199	16.6	23.6	19.1	15.6	5.6
Gillersberget	WKH-12	1	6.4	33.0	0.0	0.0	334	8.2	20.1	22.2	3.4	2.7
Gillersberget	WKH-13	1	4.2	22.8	0.0	1.2	199	21.7	44.5	26.9	26.9	12.5
Palvara	WKH-14	12	5.1	24.7	1.3	0.0	227	4.2	35.5	32.8	6.6	0.4

ests fragmented by lakes, open mires, cultivated land, roads and sparse settlements. The studied key habitats represent the last remnants (except Fageråsens nature reserve) of old-growth forest in the study area (Jönsson et al. 2009). Remaining mature forest stands (> 120 years old) are few (representing around 5–10% of the forestland) and occur isolated in the matrix of young, efficiently managed forest stands (spatially, around 68% of the forest area is younger than 50 years). Most of the key habitats have been harvested under the selection system in the past, but never completely clear-cut (Jönsson et al. 2009). Forest fires have been effectively suppressed since the 1900s (Jönsson et al. 2009); thus, current disturbance agents include windstorms, fungi and/or insect outbreaks.

2.2 Field Sampling

To inventory CWD at each key habitat, we established 5-m wide belt transects, positioned to lie perpendicular to the aspect on steeper slopes or in a north-south orientation on flatter sites. To avoid subjectivity in transect placement, we simply let the first inventory line cross the approximate geographical centers of each key habitat. A second and sometimes a third transect, depending on stand size, were thereafter established at approximate regular spacing between the centre transect and the edge of the key habitat. Due to time constraints in collecting, preparing and cross-dating deadwood samples we did not establish a third transect if the number of deadwood samples exceeded 50 within the two first transects. All standing (snags and high stumps) and fallen (logs) dead trees of *P. abies* with a diameter at base ≥ 10 cm and height or length ≥ 1.3 m that originated within the transects were inventoried. For each dead tree we recorded diameters at large and small ends, length or height, and decay class (using an eight-class system with class 1 being least decayed and class 8 most decayed; modified after McCullough 1948). We calculated the volume of dead trees and logs using the conic-paraboloid formula, which has greater accuracy than more commonly used formulae (Fraver et al. 2007).

Logs that had passed beyond decay class 6 were not inventoried or sampled as these are often too

decayed for dendrochronological cross-dating to determine the year of death (below). We collected two wood samples from each dead tree, taking complete stem cross-sections from logs and partial sections or 12-mm diameter increment cores from snags and high-stumps. In total, 353 logs and 356 standing dead trees were inventoried, from which we collected wood samples from all but 56 logs of decay class 6. Fieldwork was conducted in the fall of 2003.

2.3 Determining the Year of Tree Death

We used dendrochronological methods to determine the year of death for each collected wood sample. Samples were sanded to a fine polish using standard methods. Ring widths were measured on a Velmex sliding-stage stereomicroscope to the nearest 0.01 mm. Cross-dating was conducted following the marker-year method of Yamaguchi (1991), with verification by COFECHA (Holmes 1983). The master chronology and set of marker years used in cross-dating were provided from a detailed companion study conducted on six of these fourteen key habitats (see Jönsson et al. 2009). The year of the outermost ring was taken as the year of death, although we acknowledge that if trees that had died slowly, as evident by narrow outermost rings, they may have failed to produce annual rings in the years prior to death (Mast and Veblen 1994, Aakala et al. 2007). Thus, the year of death obtained is regarded as a conservative measure (possibly underestimating by several years), but dating uncertainties should not be sufficient to obscure the overall synchrony among stands (Mast and Veblen 1994).

2.4 Testing for Landscape-Level Synchrony

To determine if CWD was being created synchronously among key habitats, we first assessed the degree of spatial autocorrelation in annual input rates. Autocorrelation is generally expected to decline with distance, meaning that samples that are closer in space are more similar than those further apart. We used autocorrelation analysis to determine if our time series of year-to-year and 5-year periods of CWD input (i.e., tree mortality)

rates from 1950–2002 exhibited any such spatial pattern. More specifically, we used covariance functions with non-parametric Spearman correlation to assess the similarity of the overlapping time series obtained from the various key habitats. We used Spearman correlation because it uses ranks of tree mortality abundances rather than the values themselves and may therefore be less affected by extreme values. We produced a matrix of pairwise coefficients of covariance between key habitats, and thereafter averaged these coefficients to obtain an *observed* regional measure of synchrony (e.g., Bjørnstad et al. 1999, Fortin and Dale 2005). To analyze the statistical significance of this observed measure, we produced a *random* regional measure of synchrony. This regional measure was derived from randomization trials in which the observed values from time-series obtained from each key habitat were shuffled at random and re-sampled with replacement. This procedure was repeated 100 times to yield the average random regional measure of synchrony. Analyses were performed in the statistical program R (<http://www.r-project.org>).

We then plotted the pairwise coefficients of covariance against the geographical distances between pairs of key habitats to visualize the overall relationship between distance and the cross-correlation coefficients. We further evaluated the overall relationship between the geographic distance matrix and the cross-correlation coefficient matrix using the Mantel R-statistic (with 1000 random permutations). The R-statistic represents the Pearson correlation coefficient between all the entries in the two matrices. The reported P value is one-tailed. Mantel tests were conducted using the PAST software package (version 1.57; Hammer et al. 2001).

3 Results

3.1 Determining the Year of Tree Death

We successfully cross-dated 474 (73%) of the 653 dead trees sampled. In most cases we failed to cross-date because of advanced decay, weathering of outer rings and/or short tree-ring series with insufficient numbers of marker years. Given these

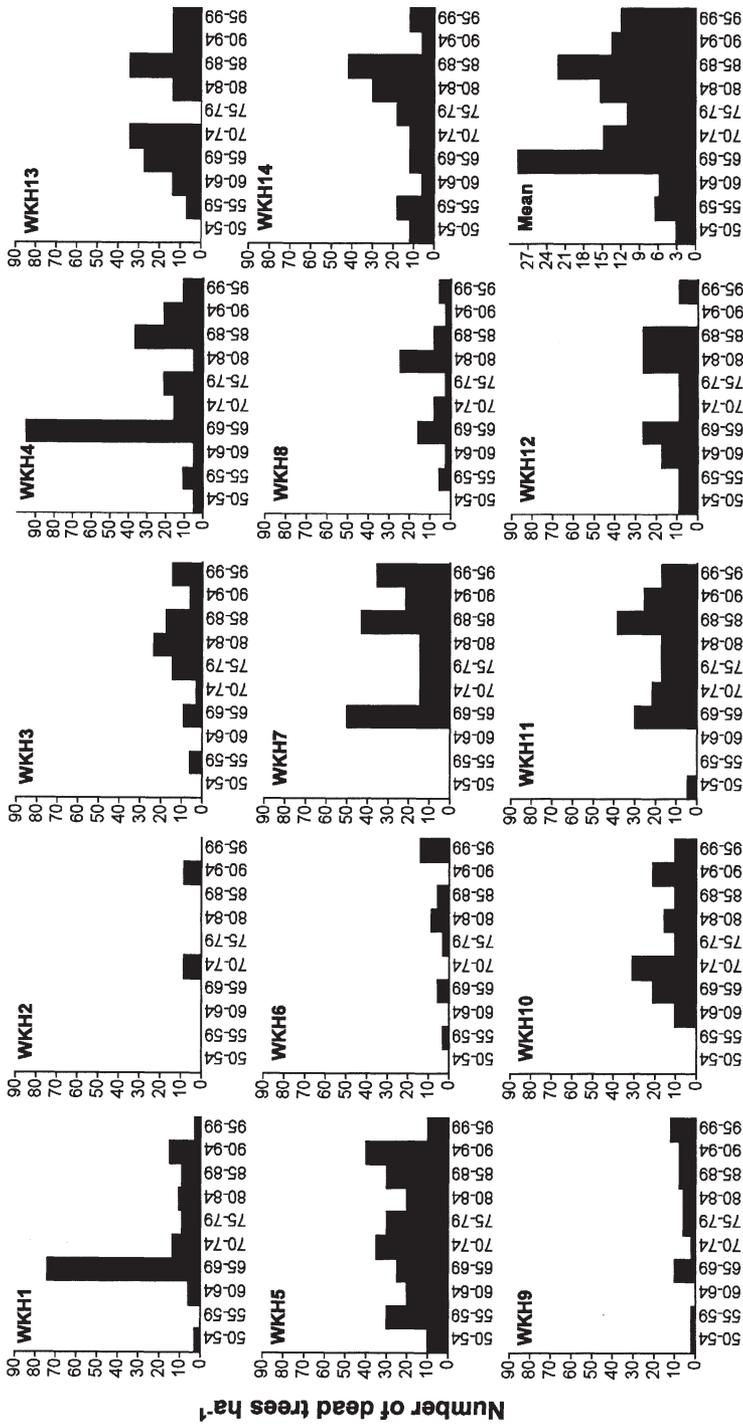
varied causes of cross-dating failure, undated samples were more or less equally spread over decay classes 1–5. The undated samples do not compromise this study, because our intent was to capture overall large-scale trends in the CWD input. We believe this was achieved by dating the vast majority of the wood samples.

3.2 Temporal Patterns within Key Habitats

Our first objective was to determine if CWD input occurred stochastically within individual key habitats. Several key habitats had too few CWD pieces to properly address this objective. However, the remaining habitats exhibited pulses with elevated tree mortality, some with three-fold or greater increases over the background levels (Fig. 2). Tree mortality rates averaged 6.2 trees $\text{ha}^{-1} \text{yr}^{-1}$ during these disturbance peaks. In contrast, tree mortality rates averaged 2.2 trees $\text{ha}^{-1} \text{yr}^{-1}$ in periods outside of episodic windstorm events.

3.3 Synchrony within the Landscape

Our second objective was to determine if pulses in both year-to-year and 5-year periods of tree mortality occurred simultaneously across key habitats, yielding a landscape-level synchrony in CWD input. Covariance functions with Spearman correlation revealed that both year-to-year and 5-year periods of mortality rates from 1950–2002 exhibited a clear synchronized temporal pattern. The average observed regional measure of synchrony of 25.8 was significantly greater than the random average regional measure of 0.4 ($n=91$, $P<0.000$), based on 100 random resamples of the observed stand year-to-year mortality. The regional measure of synchrony was 46.7 compared to a random average of -2.6 ($n=91$, $P<0.000$) based on 5-year periods of mortality. To visualize this landscape-level synchrony, we plotted the pairwise coefficients of covariance against the geographical distances between key habitats, illustrating that autocorrelation did not decline with distance within this landscape (Mantel $R=0.10$, $P=0.223$; Fig. 3). The absence of such a decline precludes any analysis of the geographical



Year 1950-2000

Fig. 2. Number of coarse woody debris inputs (i.e., tree mortality events) $\text{ha}^{-1} \text{5-yr}^{-1}$ period (based on decay classes I–V) as measured between 1950 and 2000 at the 14 key habitats studied. Note difference in vertical scale for the mean-value plot.

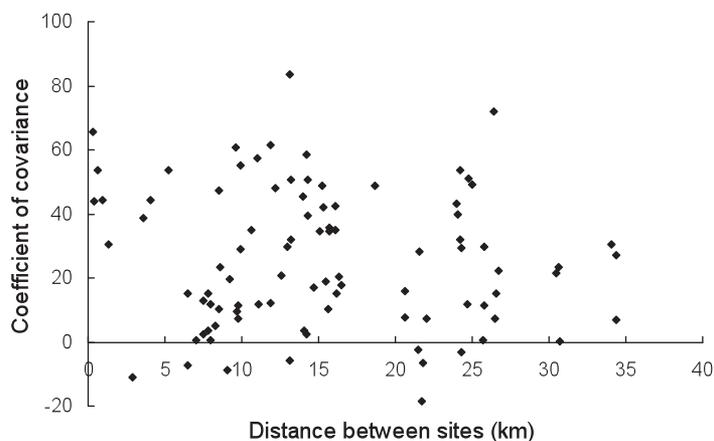


Fig. 3. Relationship between pairwise coefficients of covariance (91 pairs of key habitats) of annual mortality rates (i.e., coarse woody debris input) and distance between sites, assessed between 1950 and 2002 at the 14 key habitats. The general positive coefficients indicate synchrony among habitats, and the absence of a declining trend over distance suggests the lack of spatial autocorrelation.

extent of spatial autocorrelation. Nonetheless, the habitat-to-habitat distances of the present study are well within the migration distances physiologically possible for some threatened saproxylic insects (Jonsson 2003, Jonsson and Nordlander 2005) and dispersal distances for wood-decay fungi (Edman et al. 2004a, b) and thus relevant in a metapopulation context.

4 Discussion

4.1 Temporal Patterns within Key Habitats

Windstorm records from the region provided evidence that local storms caused the disturbance peaks within key habitats, with substantial storm damage occurring in 1966–67, 1981 and 1992–93 (Holmberg 2005). These episodic disturbances create considerable variation in the number of existing dead trees and the rate at which CWD is created. The role of wind as a disturbance agent did not come as a surprise, as forest fragments and harvest-created edges generally tend to experience more severe wind disturbance, resulting in

elevated rates of tree mortality (Chen et al. 1992, Harper et al. 2005, Jönsson et al. 2007b).

Several studies have illustrated the importance of small-scale disturbance events, namely gap dynamics, within boreal forests, where frequent deaths of individual trees or small groups of trees may be more important for stand dynamics and structure than infrequent large-scale disturbances (Kuuluvainen 1994, McCarthy 2001, Aakala et al. 2007, Fraver et al. 2008, Caron et al. 2009). Apart from the episodic pulses in tree mortality caused by windstorms, our results further illustrated that the background mortality rate that occurred in periods outside of episodic mortality events varied substantially between stands. This is presumably the result of their varied histories and structural characteristics, where many previously managed stands may only recently have begun to develop characteristic of old-growth forests (Jönsson et al. 2009). Thus, the background mortality rates are likely to increase within these stands in the future as these stands advance toward old-growth status with increased levels of self-thinning and gap dynamics. On the other hand, episodic disturbances caused by wind will likely continue, given the

relatively open, thus wind exposed, matrices in which these key habitats are located.

The risk of stand-level extinctions for saproxylic species increases with breaks in CWD input, which over time results in low CWD volumes in certain decay stages. The pronounced breaks seen at WKH-2 (Fig. 2), as well as the low extant CWD volume (Table 1), likely represents a risk of local extinctions for this key habitat. Indeed, the prevalence of managed forests with similarly low volumes of CWD has been implicated in the reduced richness and abundance of saproxylic species in Fennoscandia (Bader et al. 1995, Rydin et al. 1997, Martikainen et al. 2000, Jonsson et al. 2005). In contrast, the relatively high background input rates, the episodic pulses in input, and the attendant high extant CWD volume seen at WKH-5 (Fig. 2, Table 1) suggests a safe site for saproxylic species. In fact, the down woody debris volume at this key habitat ($56.8 \text{ m}^3 \text{ ha}^{-1}$) places it within or near the natural range of variability for old-growth *Picea* forests of this region (Jonsson 2000, Fraver et al. 2008).

4.2 Synchrony within the Landscape

Most studies of CWD input address stand-level patterns (Fraver et al. 2002, Edman et al. 2007, Aakala et al. 2009), despite the fact many saproxylic species are highly dynamic in their distributions and dependent on a landscape-level supply of CWD (see Gu et al. 2002, Jonsson 2003, Edman et al. 2004a, b). In addition, most forestry planning takes place at the landscape level (Fries et al. 1997, Raivio et al. 2001), suggesting that natural disturbance dynamics must also be analysed at this scale. This study is unique in analysing the degree of synchrony in CWD input in remaining high-quality patches at the landscape level over a longer time period (1950–2002). Our results illustrated that local windstorms produced stochastic tree mortality patterns within key habitats, yielding episodic pulses in CWD inputs that were synchronous across the landscape.

Critical to the survival of saproxylic organisms is a relatively stable supply of CWD substrate somewhere within colonization distance. Synchronized pulses of CWD input suggest complementarily synchronized breaks occurring between

pulses. This implies that unfavourable periods with very little CWD input, and hence low CWD volumes, may reduce all local populations in a similar way. Thus, the synchronized pulses in CWD input, and importantly, the attendant breaks between pulses, may increase the fluctuations in the regional carrying capacity of metapopulations of saproxylic species dependent on recently killed Norway spruce trees, potentially increasing landscape-level extinction risk (Hanski 1999, Johst and Drechsler 2003). The rate of CWD input between pulses did, however, vary substantially among key habitats, which suggests they have varied buffering potentials during such landscape-level breaks. Also, inherent in the small size and significant degree of isolation of most key habitats is an increased extinction risk due to stochastic dynamics and edge effects within small areas (Aune et al. 2005, Berglund and Jonsson 2005, Junninen and Kouki 2006). In view of the foregoing, saproxylic species at highest extinction risk from landscape-level synchronous breaks in CWD input are those with small populations, contracted distributions, and/or limited dispersal abilities. Also, saproxylic species associated with highly ephemeral substrates (e.g., a certain state of decay) or specific character (e.g., large diameter) may also experience higher extinction risks.

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