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Response of Soil Surface Respiration to Storm and *Ips typographus* (L.) Disturbance in Boreal Norway Spruce Stands

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Abstract: Disturbances such as storm events and bark beetle outbreaks can have a major influence on forest soil carbon (C) cycling. Both autotrophic and heterotrophic soil respiration may be affected by the increase in tree mortality. We studied the effect of a storm in 2010 followed by an outbreak of the European spruce bark beetle (*Ips typographus* L.) on the soil surface respiration (respiration by soil and ground vegetation) at two Norway spruce (*Picea abies* L.) dominated sites in southeastern Finland. Soil surface respiration, soil temperature, and soil moisture were measured in three types of plots—living trees (undisturbed), storm-felled trees, and standing dead trees killed by *I. typographus*—during the summer–autumn period for three years (2015–2017). Measurements at storm-felled tree plots were separated into dead tree detritus-covered (under storm-felled trees) and open-vegetated (on open areas) microsites. The soil surface total respiration for 2017 was separated into its autotrophic and heterotrophic components using trenching. The soil surface total respiration rates at the disturbed plots were 64%–82% of those at the living tree plots at one site and were due to a decrease in autotrophic respiration, but there was no clear difference in soil surface total respiration between the plots at the other site, due to shifts in either autotrophic or heterotrophic respiration. The soil surface respiration rates were related to plot basal area (living and all trees), as well as to soil temperature and soil moisture. As storm and bark beetle disturbances are predicted to become more common in the future, their effects on forest ecosystem C cycling and CO_2 fluxes will therefore become increasingly important.

Keywords: forest soils; autotrophic respiration; heterotrophic respiration; CO_2 effluxes; decomposition; forest disturbance; tree mortality; storm damage; insect outbreak

1. Introduction

Abiotic disturbances, such as storms, and biotic disturbances, such as bark beetle outbreaks, are important drivers of forest ecosystem functioning [1,2]. Such disturbances increase tree mortality, resulting in—at least temporarily—diminished forest C fixation (CO_2 influx) and autotrophic respiration (CO_2 efflux from plant and rhizosphere metabolism) and, in some cases, increased heterotrophic respiration (CO_2 efflux from organic matter decomposition) due to increased decomposition [2–6]. Over extended periods of time, the effect of natural disturbances on the carbon (C) balance can thus result in a forest turning from being a C sink into a C source and so add to global warming [4,7]. However, the effects on C balance may be less drastic and transient if the productivity of the remaining trees and secondary structure is increased or if decreased forest stand productivity is accompanied

with a reduction in ecosystem respiration [8,9]. Besides disturbance severity, changes in forest ecosystem C fluxes are dependent on several other factors, e.g., pre-disturbance forest composition and structure, growth of the remaining trees and ground vegetation, and tree regeneration [5,8,10–12]. Hence, the responses and recovery of a forest after disturbance may differ among forest management strategies as well as between non-managed and commercially managed forests [3,8,13–15].

Soil respiration is one of the largest terrestrial C fluxes globally [16]. It has been estimated that 55% of the C fixed annually by forests in gross primary production is returned back to the atmosphere as a result of soil respiration [17]. Disturbance may alter soil respiration in several ways. Tree death reduces soil autotrophic respiration due to the cessation of C allocation to roots and soil [18,19]. Disturbance-induced tree mortality also results in changes in litter quality and quantity [20,21], light and water availability and soil temperature and moisture [2,6,12,22,23], soil microbial community dynamics [24–26], and the composition of the ground vegetation [13,27], all of which can be expected to lead to changes in the decomposition process and, hence, soil heterotrophic respiration.

Besides spatial variation in the alterations, the direction and magnitude of these alterations may change with time after the disturbance [5]. As a result, both increases [23,28] and decreases [9,29] as well as no change [6,22,23,30,31] in soil total respiration over periods varying from months to several years after disturbance have been reported. However, few studies have studied the effects of natural disturbance separately on the autotrophic and heterotrophic components of soil respiration. Mayer et al. [6,23] found that storm disturbance increased heterotrophic respiration for some years after the storm and attributed this to increases in soil temperature and associated accelerated decomposition of soil organic matter, whereas in another study [29], storm and bark beetle disturbance was shown to have decreased autotrophic soil respiration but to have had no clear effect on heterotrophic respiration.

Storms and European spruce bark beetle (*Ips typographus* L.) outbreaks are two major forms of disturbance in European forests [32,33], and both are predicted to result in greater tree damage in the future [34,35]. Whilst storms immediately alter the structure and functioning of the forest by breaking and uprooting (killing) trees and mixing soil [1], the changes brought about by bark beetle outbreaks are gradual [2]. Wind disturbance especially creates various microsites [1,36] where tree stand and soil properties differ. For example, undisturbed soil with decomposing residue piles [37] or gaps [38,39] created after disturbance can have different soil properties and dynamics compared to the less affected areas or pre-disturbance conditions. Storm events can predispose forests to insect outbreaks, as wind-fallen trees provide optimal breeding material for bark beetles [40,41]. Where there is more than one disturbance event, changes in the C balance and soil respiration can be expected to be more complicated.

In this study, the effects of a storm event followed by an outbreak of *I. typographus* on soil surface total (SR_{tot}, soil CO_2 efflux from soil and ground vegetation), autotrophic (SR_a), and heterotrophic (SR_h) respiration were investigated at two forest sites in southeastern Finland. The aims of the study were to determine the effect of storm damage and *I. typographus* outbreak on (1) SR_{tot} and its autotrophic and heterotrophic components and (2) the degree to which disturbance-related differences in respiration were due to differences in tree stand characteristics and tree mortality or in environmental conditions. We hypothesized that (1) SR_a from storm-damaged and from *I. typographus*-infested plots would be lower and SR_h higher compared to control (undisturbed) plots; (2) storm-damaged SR_a and SR_h would differ between open microsites having ground vegetation and microsites under storm-felled trees covered with dead tree detritus; and (3) respiration would be related to stand basal area (dead tree basal area resulting from the storm and *I. typographus* disturbances), disturbance-related differences in soil microclimate (temperature and moisture), or both.

## 2. Materials and Methods

2.1. Research Area

The study was carried out in two Norway spruce (*Picea abies* L.) dominated forest sites, Paajasensalo (56 ha) and Viitalampi (73 ha), located in the municipality of Ruokolahti (61°17′30″ N, 28°49′10″ E) in southeastern Finland. The distance between the two sites is about 6 km. A large-scale storm occurred in the region in July 2010 and was followed by an outbreak of *I. typographus* from 2011 onwards. The forests at the Paajasensalo site were in commercial use until 2010 and those in the Viitalampi site until 2011, but afterwards they were conserved as METSO (Forest Biodiversity Program for Southern Finland) sites and no forest management actions have been carried out since. Thus, contrary to normal forestry practice, all the trees killed by the storm and bark beetle were left in the forest after the disturbance events, making the sites ideal for the purposes of this research.

The soils at the study sites were Podzols, mostly cambic, and developed in till deposits. The soil texture (fine-earth fraction) was either sandy loam or loamy sand, and the thickness of the surface humus layer varied between 2.3 and 8.0 cm. According to the Cajanderian site type classification [42], which describes site stand productivity, the sites were mainly medium-rich Myrtillus (MT) and rich Oxalis-Myrtillus (OMT) types. The ground vegetation under closed canopy was dominated by blueberry (*Vaccinium myrtillus* L.), with lingonberry (*Vaccinium vitis-idaea* L.) and several herbaceous species (e.g., small cow-wheat (*Melampyrum sylvaticum* L.), twinflower (*Linnea borealis* L.), wood sorrel (*Oxalis acetosella* L.), and oak fern (*Gymnocarpium dryopteris* L. Newman)) being present. The forest floor moss layer was dominated by red-stemmed feather-moss (*Pleurozium schreberi* (Brid.) Mitt.), stairstep moss (*Hylocomium splendens* (Hedw.) BSG), and fork-moss (*Dicranum* sp.). The storm and, to a lesser degree, the bark beetle outbreaks modified the ground vegetation composition towards more light-demanding pioneer species such as fireweed (*Chamerion angustifolium* L.), wavy hair-grass (*Deschampsia flexuosa* L. Trin), and raspberry (*Rubus ideaus* L.). Although dominated by spruce, isolated Scots pine (*Pinus sylvesteris* L.), silver birch (*Betula pendula* Roth), downy birch (*Betula pubescens* L.), European aspen (*Populus tremula* L.), grey alder (*Alnus incana* L.), common alder (*Alnus glutinosa* L. Gaertn), rowen (*Sorbus aucuparia* L.), and willow (*Salix* spp.) trees also grew within the stands. The long-term (1981–2010) mean annual air temperature for the study sites was 4.2 °C and the mean annual precipitation was 653 mm [43]. The mean air temperature and precipitation for the study months (May–Oct) were 12.3 °C and 38 mm in 2015, 13.0 °C and 52 mm in 2016, and 11.3 °C and 61 mm in 2017 [44].

2.2. Study Layout

After exploring both study sites, three types of disturbance areas were identified: those having living trees with no clear signs of storm or bark beetle damage (LT), areas with fallen trees resulting from the storm (SF), and areas of living and dead standing trees showing bark beetle attack (ID). A circular plot (radius 11.28 m, area 400 m^2) was then established in each of three areas in both study sites in June 2015 (Figure 1), resulting in a total of 12 plots (6 in Paajasensalo and 6 in Viitalampi). In order to have a more encompassing data set, another set (block) of plots were established in both study sites in June 2016 (Figure 1). Photographs of each plot type (LT, SF, and ID) are presented in Figure S1. As the three plots (disturbance treatments) were spatially interspersed within the two blocks and the blocks were replicated at two study sites, bias and problems of pseudoreplication were reduced [45].
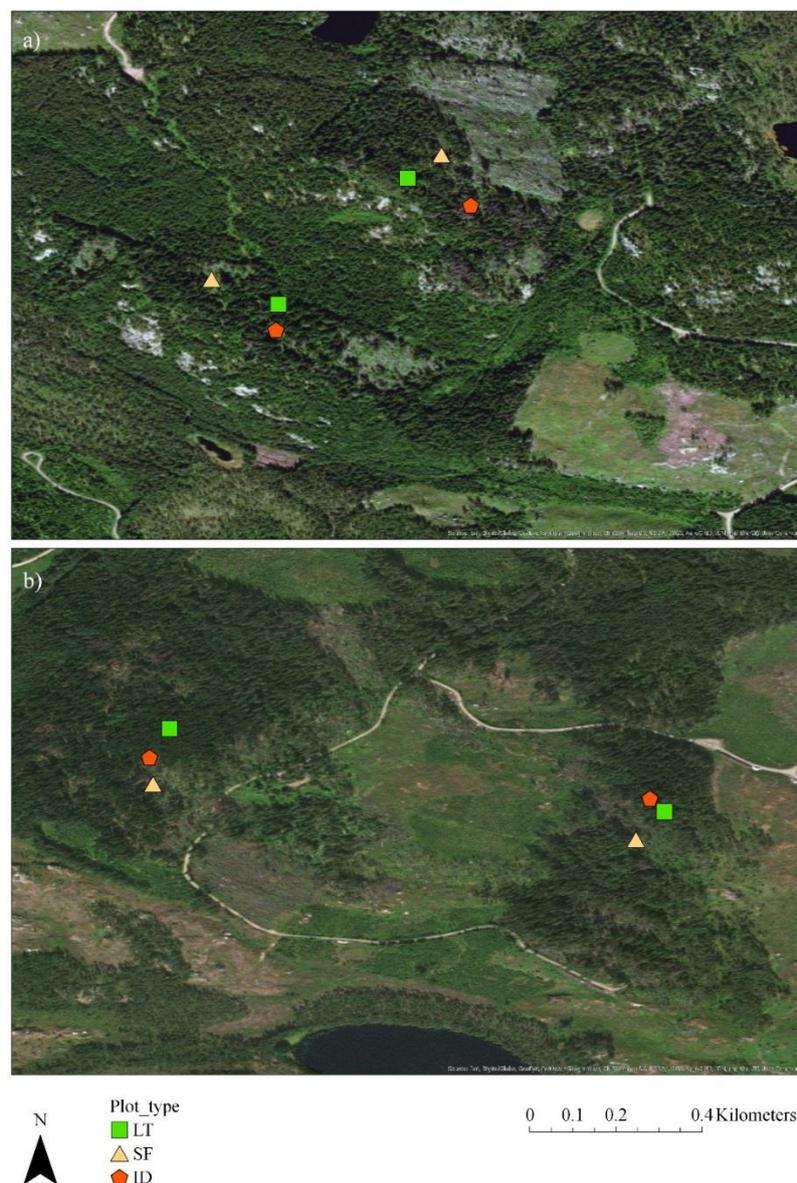
Figure 1. Locations of study plots in Paajasensalo (**a**) where plots established in 2015 are on the left and plots established in 2016 are on the right, and Viitalampi (**b**) where plots established in 2015 are on the right and plots established in 2016 are on the left. LT = living tree plot (green squares), SF = storm-felled tree plot (light brown triangles), and ID = tree killed by *I. typographus* plot (red pentagons). Created using ArcGIS (ESRI, Redlands, CA, USA).

2.3. Tree Measurements

All trees growing on the plots were numbered and the diameter at breast height (dbh) of each living and dead tree, both standing and fallen, with a dbh of >6 cm was measured. All spruce trees were inspected for symptoms of *I. typographus* colonization (discoloration, defoliation, entrance and exit holes, resin flow spots, and bark loss) [46] to confirm the initial cause of each spruce tree's death as *I. typographus* and to monitor the population level of the living trees during the study. Although some spruce trees on the LT plots showed incipient symptoms caused by *I. typographus*, they remained living and vigorous during the study period. We are not able to identify the specific time of death of the *I. typographus*-killed trees in our plots, but it took place during 2013–2014 [47]. In addition to the storm in July 2010, the warm summers of 2010, 2011, and 2013 [48] likely contributed to the development of the *I. typographus* outbreak. The two disturbance types also interacted on some of the

plots. For example, 50% of the standing dead trees on the Viitalampi ID plot established in 2015 broke and fell due to another storm in October 2015. On the other plots, however, only single standing dead trees and none of the living trees fell during the study period. In addition, many of the wind-thrown trees on the SF plots had maternal galleries of *I. typographus*. However, the initial cause of tree death on SF plots was the storm in 2010 and the beetle outbreak on the ID plots that occurred from 2011 onwards. Some dead trees were also found at the LT plots, but they had already died before the 2010 storm and start of the beetle outbreak.

2.4. Soil Surface Respiration, Temperature, and Moisture Measurements

Soil surface respiration, soil temperature, and soil moisture were measured at a number of locations in each plot. For the LT and ID plots, the location of the sampling point was based on a random selection of the numbered trees. A stone-free sampling area ≥2 m from the randomly selected tree stem (or other measurement point) was selected. In the case of the SF plots, all fallen tree(s)–detritus-covered microsites (SF_d) and ground vegetated–open (i.e., no fallen trees above) microsites (SF_o) were identified and numbered, and then a set of each microsite type was chosen using a random number sequence generator. These two types of microsite reflected a clear dichotomy in conditions created by the storm. If a respiration measurement point was considered unsuitable (stony or <1.5 m to another measurement point or tree), it was rejected and the next measurement point in the random sequence was chosen. Accordingly, 30 soil respiration measurement points were established in each study site in summer 2015: eight in the LT plots, seven each in the SF_d and SF_o microsites, and eight in ID plots at each forest (Figure S2). A PVC collar (diameter = 20.1 cm, height ~ 15 cm) for respiration measurements was installed at each selected measurement point by pressing the collar into the ground to a depth of ca. 1 cm and sealed from the outside with sand (Figure 2, Figure S2). At this stage, vegetation was not removed from inside the collars so that SR_{tot} measurements included respiration by soil and ground vegetation. In 2016, collars were installed in the new plots using the same procedure as in 2015: three collars in the LT plots, three in each of the two microsites in the SF plots, and three in ID plots at both study sites.

Figure 2. Soil surface respiration chamber darkened with aluminum foil and containing the CARBOCAP® GMP343 CO_2 probe and a data logger on the ground in front. The measurement point is one of the trenched measurement points. Photo: Maiju Kosunen.

In order to quantify the proportions of SR_a and SR_h, 15 of the measurement points in the plots established in 2015 (4 in LT, 3 or 4 in SF_d and 3 or 4 in SF_o, and 4 in ID selected at random in both study sites) were trenched in July–August 2016. A knife and a spade were used to cut the roots in an area of ca 0.25 m^2 surrounding the selected collars to a depth of ca. 30 cm, the maximum depth of most *P. abies* roots in Finnish conditions [49]. A 30 cm wide strip of strong fabric was then inserted into the cut to inhibit further root ingrowth. After trenching, the ground vegetation was carefully removed from inside the collars. Mosses were, however, left growing in the collars to avoid direct radiation from topsoil, but were not considered to have significantly affected the respiration measurements. Any regrowth of vegetation was removed inside the trenched collars before each measurement.

Trenching may bias soil autotrophic and heterotrophic respiration estimates, for example, because of changes in the soil microclimate brought about by root decease [50]. In our study, trenching, however, had no clear effect on soil moisture and increased the soil temperature only slightly at some plots. Nevertheless, for example, re-sprouting of the clipped vegetation at trenched points in between measurements as well as inclusion of ground vegetation respiration to measurements at intact collars may have also caused inaccuracy to estimations. Thus, the SR_a and SR_h values should only be considered as estimates of the proportions.

The respiration measurements were carried out approximately weekly during 18 Jun–6 Oct 2015 and 24 May–27 Sept 2016 and approximately biweekly during 16 May–19 Oct 2017 (intervals varying from 4 to 18 days) using a closed and darkened chamber (D = 19.0 cm, height = 24.7 cm) made of Perspex fitted with a CARBOCAP®GMP343 CO_2 probe (Vaisala Ltd., Vantaa, Finland) and an air mixing fan (Figure 2). After carefully placing the chamber on top of the collar, the increase in the CO_2 concentration inside the chamber was recorded every 5 seconds over a 5 minute period. The lower edge of the chamber was fitted with a rubber O-ring washer so as to prevent any airflow between the collar and chamber. The air in the chamber was mixed during each measurement by means of a small fan fitted inside the chamber. Between each measurement, the chamber was ventilated by exposing the chamber to the air. Immediately following the respiration measurements, soil temperature and moisture were measured at three spots around each collar (ca. 0.2 m distance from the collar). Soil temperature (°C) was measured at a depth of 10.5 cm using a S3 11B thermometer (Fluke corp., Everett, WA, USA) probe and the soil moisture (% vol) was measured at a depth of 6.0 cm with a ML3 ThetaKit soil moisture meter (Delta-T devices Ltd., Cambridge, UK).

2.5. Calculation of Soil Surface Total, Heterotrophic, and Autotrophic Respiration

Respiration (mg CO_2 m^{-2} s^{-1}) was calculated as the slope of the linear regression between CO_2 concentration in the chamber and time. Respiration measurements from the intact (non-trenched) collars ($n = 30$ in both Paajasensalo and Viitalampi until Aug 2016, after which $n = 27$) in both study sites over the whole study period in 2015–2017 were taken to be SR_{tot}. Respiration measured from the trenched collars ($n = 15$ in both Paajasensalo and 15 in Viitalampi) was considered to be SR_h, and the difference between SR_{tot} and SR_h was therefore assumed to be SR_a.

However, as we observed a difference in the mean SR_{tot} values between the intact collars and the collars to be trenched already before the trenching for some plots, we used linear regression to estimate the SR_{tot} values for the trenched collars in order to correct for this baseline difference. Thus, for each plot established in 2015, a linear regression model was computed using pre-trench data (up to June 2016) to predict the SR_{tot} of the collars to be trenched from that of the collars that would remain intact. These regression models were then used to derive post-trenching SR_{tot} values for the trenched collars as if they had not been trenched. All regression models had high R^2 values (0.73–0.96). The difference between the predicted mean SR_{tot} values and the measured mean values from the trenched collars (SR_h) was then taken to be SR_a. Values of SR_a were thus weekly treatment means, including one value that was negative. The SR_h values were individual collar measurements; however, weekly treatment means of SR_h for each plot were used to compare with SR_a values.

The disturbance caused by root cutting and fast decay could be expected to keep the levels of respiration high for some time after trenching. In our treatments, respiration of the trenched collars in comparison to the intact collars decreased mostly 1–3 weeks (but ca. 2 months at the latest) after the root cutting; therefore, only the respiration measurements starting from 2017 were used to estimate the proportions of SR_a and SR_h.

2.6. Statistical Analyses

For comparing SR_{tot} and SR_h (measured and temperature-adjusted), temperature, and moisture between treatments, analyses of variance (ANOVA) with a linear mixed-effects model structure followed by Scheffe's post hoc tests were used. Treatment (LT, SF_o, SF_d, and ID) was set as a fixed variable, and measurement date (running number of days cumulated over the study period) and collar number were set as random crossed variables. If the produced linear mixed model did not fulfil the assumptions of normality and homogeneity of residuals, appropriate transformations were applied. Because there was only one value for SR_a at each treatment for each measurement day in 2017, it was not appropriate to test for differences in SR_a between treatments.

To control for the effect of treatment differences in soil temperature on respiration, each measured SR_{tot} and SR_h value was adjusted to a soil temperature value of 10 °C. This was done by fitting a nonlinear regression [51] between soil temperature and respiration for each collar separately. The adjusted flux at a soil temperature at 10 °C was then calculated by adding the estimated value of respiration at 10 °C of each collar to the residual of each measurement.

Spearman's rank correlation coefficients were computed to describe the relationship between the plot ($n = 16$) mean SR_{tot} (measured and temperature-adjusted), soil temperature and soil moisture, and plot basal area (living, dead, and total), i.e., across treatments. Basal area values of the entire SF plots were used for both SF_d and SF_o microsites. Spearman's rank correlation coefficients were also computed to describe the relationship between plot ($n = 8$) mean SR_a and SR_h and plot basal area, i.e., across treatments.

All the analyses were done using the R statistical computing environment [52] with utilization of *lme4* [53] for the mixed modeling, *car* [54] for ANOVA, and *emmeans* [55] for the post hoc tests.

3. Results

3.1. Tree Mortality

The characteristics of the stands on each plot are shown in Table 1. Spruce was the dominant species, although several plots also had a considerable proportion of pine (*Pinus sylvestris* L.) and broadleaved trees (mostly silver birch, *Betula Pendula* Roth) present. An exception was the Viitalampi LT plot established in 2016, where only 45% of the trees were spruce; however, 59% of the living trees on that plot were spruce. The Viitalampi ID plot established in 2016 had the highest stem density, and the Viitalampi SF plot established in 2015 had the lowest, with all being dead. Of the disturbed plots (SF and ID), the greatest proportion of dead trees was in the Viitalampi SF plot established in 2015 (100%) and the lowest was in the Viitalampi ID plot established in 2015 (69%). The proportion of dead trees on the LT plots varied between 8% and 27%.

Table 1. Study plot disturbance and stand characteristics (mean ± standard deviation). Abbreviations: Year = year of plot establishment, dbh = tree diameter at breast height, Stems/ha = number of trees per hectare, Basal area = basal area of trees, Species (%) = percentage of basal area of certain tree species from all measured trees on plot, Sp = spruce, Pi = pine, De = deciduous, PS = Paajasensalo, VL = Viitalampi, LT = living trees, ID = trees killed by *I. typographus*, SF = storm-felled trees, MT = medium-rich Myrtillus type, OMT = Oxalis-Myrtillus type.

						Basal Area (m^2/ha)			Species (%)		
Site	Year	Plot Type	Site Type	dbh (cm)	Stems/ha	Living	Dead	Total	Sp	Pi	De
PS	2015	LT	MT	21 ± 8	1350	42.2 ± 0.6	9.3 ± 1.4	51.5 ± 0.8	65	22	13
PS	2015	SF	MT	22 ± 7	925	13.6 ± 0.7	24.6 ± 0.6	38.2 ± 0.7	81	14	5
PS	2015	ID	OMT	25 ± 8	625	5.5 ± 1.2	27.4 ± 0.7	33.0 ± 0.8	96	0	4
PS	2016	LT	MT	20 ± 10	925	34.3 ± 0.8	0.9 ± 0.2	35.2 ± 0.8	89	0	11
PS	2016	SF	MT	17 ± 7	1725	10.6 ± 0.3	36.8 ± 0.7	47.4 ± 0.6	88	0	12
PS	2016	ID	MT	15 ± 7	1525	2.3 ± 0.3	29.3 ± 0.5	31.7 ± 0.5	100	0	0
VL	2015	LT	MT	21 ± 7	975	35.9 ± 0.4	0.4 ± 0.0	36.3 ± 0.5	97	0	3
VL	2015	SF	MT	25 ± 3	600	0 ± 0.0	28.6 ± 0.3	28.6 ± 0.3	100	0	0
VL	2015	ID	MT	24 ± 4	650	9.8 ± 0.4	20.1 ± 0.3	30.0 ± 0.3	100	0	0
VL	2016	LT	MT	20 ± 10	1275	39.8 ± 0.8	9.5 ± 1.0	49.2 ± 0.9	45	4	51
VL	2016	SF	MT	19 ± 9	800	0.7 ± 0.1	26 ± 0.8	26.7 ± 0.8	63	0	38
VL	2016	ID	OMT	19 ± 9	1800	22.8 ± 0.7	39.7 ± 0.7	62.5 ± 0.7	96	0	4

### 3.2. Soil Surface Total Respiration, Soil Temperature, and Soil Moisture

At Paajasensalo, the mean SR$_{tot}$ of the three disturbed treatments was lower than that of the LT treatment, although only significantly so in the case of the SF$_o$ treatment (Table 2). At Viitalampi, the disturbed treatment mean SR$_{tot}$ was also lower than that of the LT treatment, but none of the differences were significant. After adjusting SR$_{tot}$ for soil temperature, the differences in mean values between treatments were reduced, but LT and SF$_o$ still significantly differed from each other at Paajasensalo (Table 2). Adjusting the respiration values for soil temperature did not change the pattern in SR$_{tot}$ among the treatments at Viitalampi.

Table 2. Treatment mean total soil surface respiration (SR$_{tot}$) and soil-temperature-adjusted soil surface total respiration values (SR$_{tot\_ST adj.}$), soil temperature (ST) and soil moisture (SM; non-trenched collars 2015–2017 data only), and heterotrophic soil respiration (SR$_h$) and soil-temperature-adjusted heterotrophic soil respiration (SR$_{tot\_STadj}$; 2017 data from trenched collars only) for the Paajasensalo and Viitalampi study sites. Values are linear mixed-effects model adjusted means. Treatment means followed by the same subscript letter are not significantly different (*p* = 0.05; Scheffe's post hoc tests). LT = living trees, SF$_d$ = storm damaged, tree detritus, SF$_o$ = storm damaged, open-vegetated, ID = trees killed by *I. typographus*.

	LT		SF$_d$		SF$_o$		ID	
Paajasensalo								
SR$_{tot}$ (mg CO$_2$ m^{-2} s^{-1})	0.28	a	0.23	ab	0.18	b	0.22	ab
SR$_{tot\_STadj.}$ (mg CO$_2$ m^{-2} s^{-1})	0.24	a	0.22	ab	0.17	b	0.20	ab
ST (°C)	10.7	a	10.2	b	10.2	b	10.5	ab
SM (% vol/vol)	13.3	a	18.3	b	22.8	bc	26.0	c
SR$_h$ (mg CO$_2$ m^{-2} s^{-1})	0.14	a	0.13	ab	0.10	b	0.12	ab
SRh$_{\_STadj.}$ (mg CO$_2$ m^{-2} s^{-1})	0.15	a	0.15	a	0.12	a	0.13	a
Viitalampi								
SR$_{tot}$ (mg CO$_2$ m^{-2} s^{-1})	0.22	a	0.18	a	0.21	a	0.20	a
SR$_{tot\_STadj.}$ (mg CO$_2$ m^{-2} s^{-1})	0.20	a	0.17	a	0.19	a	0.17	a
ST (°C)	10.5	a	10.3	a	10.6	a	11.0	b
SM (% vol/vol)	20.1	a	26.1	a	26.3	a	26.3	a
SR$_h$ (mg CO$_2$ m^{-2} s^{-1})	0.11	a	0.14	a	0.12	a	0.11	a
SRh$_{\_STadj.}$ (mg CO$_2$ m^{-2} s^{-1})	0.12	a	0.15	a	0.12	a	0.11	a

Mean soil temperatures were slightly lower, but significantly so only at SF_d and SF_o for the disturbed treatments compared to the LT treatment at Paajasensalo (Table 2). At Viitalampi, mean soil temperatures were significantly highest in the case of the ID treatment. The mean soil moisture content at Paajasensalo was significantly higher for the three disturbed treatments compared to the LT treatment. At Viitalampi, the disturbed treatment mean soil moisture was also higher than the LT treatment mean value, but not significantly so (Table 2). The mean SR_{tot}, temperature, and moisture of plots established in 2015 and 2016 as well as those of the to-be-trenched and intact collars are presented in Table S1.

The seasonal patterns in SR_{tot}, soil temperature, and soil moisture contents for the three study years are shown in Figure 3. At Paajansensalo, the LT treatment had higher SR_{tot} values compared to the disturbed treatments during the mid-summer to autumn months, whereas the differences between treatments were not that visible in the early summer periods (Figure 3a). At Viitalampi, no clear differences in the seasonal pattern of SR_{tot} among the treatments were observed (Figure 3b). However, at both Paajasensalo and Viitalampi, SR_{tot} followed the seasonal pattern in soil temperature (Figure 3c,d). The seasonal pattern in soil moisture in each year was similar at both Paajasensalo and Viitalampi. At Paajasensalo, soil moisture was consistently the highest in the ID treatment and lowest in the LT treatment throughout each year (Figure 3e). While the treatment differences in soil moisture at Viitalampi during 2015 were similar to those at Paajasensalo, the differences evened out during 2016 and 2017 (Figure 3f).
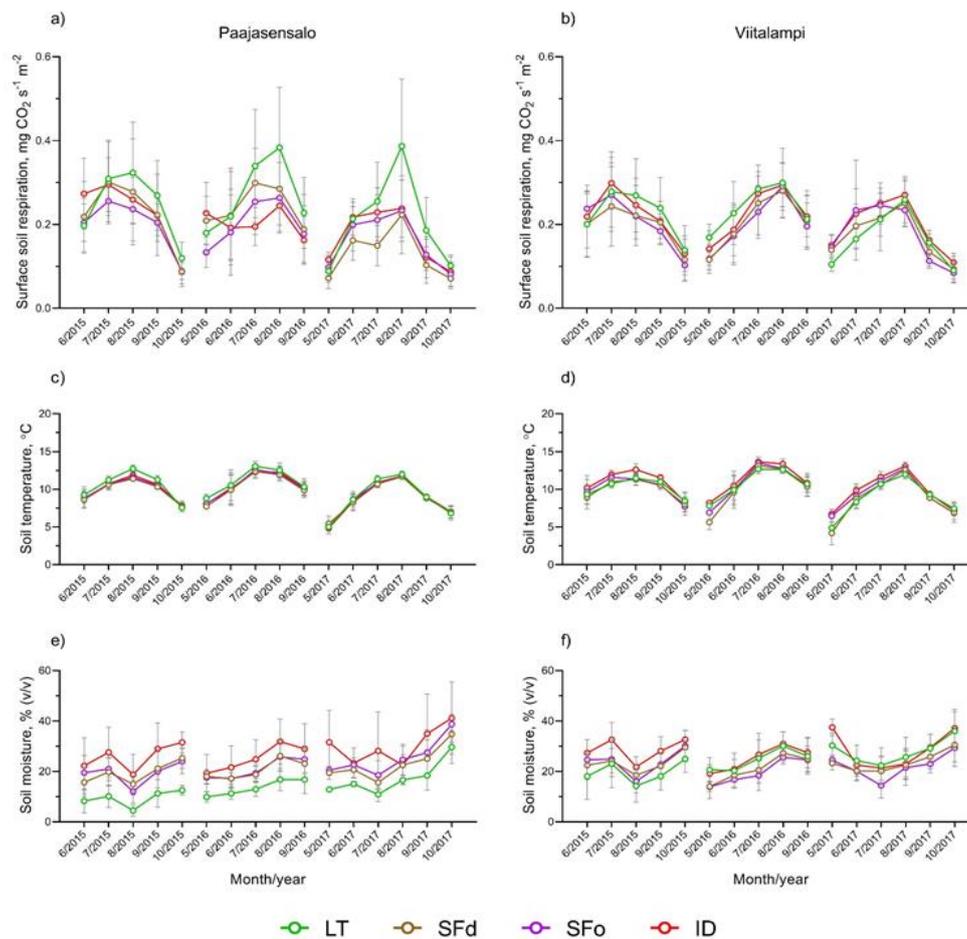
Figure 3. Monthly means and standard deviations for soil surface total respiration (**a,b**), soil temperature (**c,d**), and soil moisture (**e,f**) of each treatment in Paajasensalo (left) and Viitalampi (right). Values are based on measurements from the intact collars on plots established in 2015, i.e., the data set is consistent throughout 2015–2017. LT = living trees, SF_d = storm dead tree detritus, SF_o = storm open-vegetated, and ID = trees killed by *I. typographus*.

3.3. Heterotrophic and Autotrophic Soil Respiration

At Paajasensalo, the mean SR_a values from the disturbed plots were 23% (SF_d), 39% (SF_o), and 57% (ID) of the mean value from LT. At Viitalampi, the mean SR_a value from the SF_d treatment was 45% of the mean value in LT, whereas the mean values from the SF_o microsite and ID plot were 195% and 124%, respectively, of the mean value of LT. The mean SR_h at Paajansensalo was lowest in SF_o (70% of the mean in LT) (Figure 4) and differed significantly from LT. The respective soil-temperature-adjusted mean respiration values, however, did not differ significantly from each other (Table 2). At Viitalampi, the highest mean SR_h was found in SF_d (124% of mean in LT), but the mean did not differ significantly from those of other treatments (Table 2).
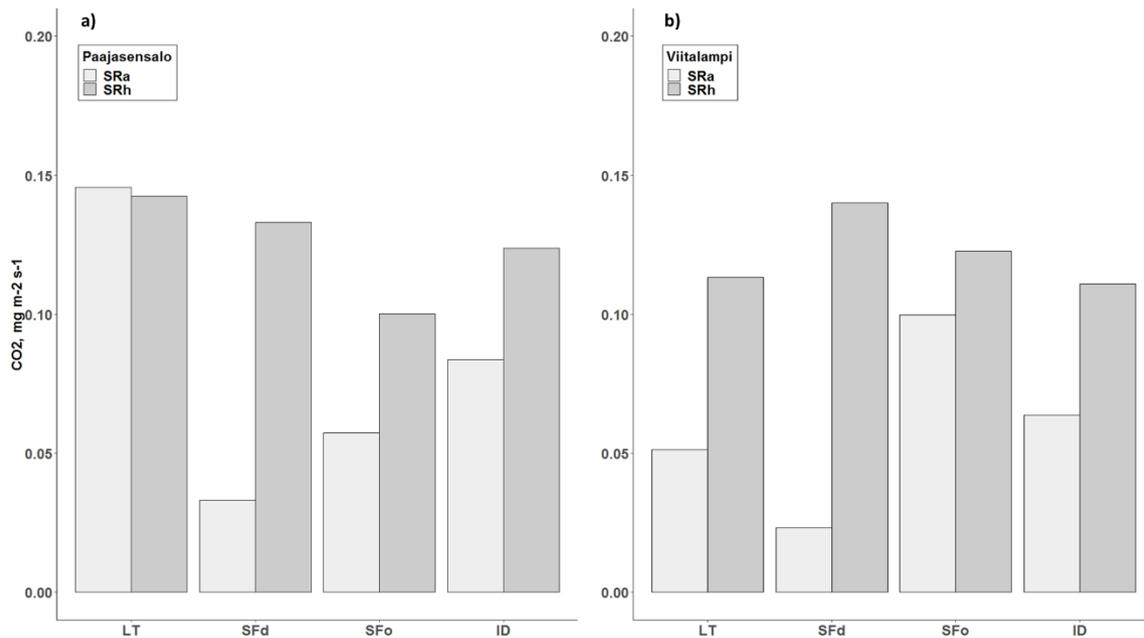
Figure 4. Means of autotrophic (SR_a) and heterotrophic (SR_h) soil surface respiration, based on the measurements in May–Sept 2017, of each treatment (one weekly mean value per treatment) in plots established in 2015 for (**a**) Paajasensalo and (**b**) Viitalampi. LT = living trees, SF_d = storm dead tree detritus, SF_o = storm open-vegetated, ID = trees killed by *I. typographus*.

The proportion of SR_a relative to SR_{tot} at Paajasensalo was 51% for LT, 20% for SF_d, 36% for SF_o, and 40% for ID treatment. The corresponding proportions at Viitalampi were 31% for LT, 14% for SF_d, 45% for SF_o, and 36% for ID. This resulted in a shift in SR_{tot} towards SR_h at disturbed plots with exception of the SF_o microsite and ID plot in Viitalampi, where the proportions of SR_a were higher than at the LT plot.

3.4. Relationships between Variables

Combining data from both sites, the plot mean (treatment mean in SF) SR_{tot} was significantly and positively correlated with the basal area of living trees (Table 3). SR_a or SR_h, however, were not significantly correlated with the basal area of living trees or that of all trees. Neither did soil temperature correlate with the tree stand variables, but soil moisture showed a significant negative correlation with both basal areas of living and all trees (Table 3). Using soil-temperature-adjusted SR_{tot} values for correlations did lower the correlations. Across both sites, treatment and plot mean soil temperature also showed a significant positive correlation with soil total respiration (Table 3), as it did inside each treatment (Table S2). Mean soil moisture, on the contrary, showed significant negative correlations with SR_{tot} and SR_h across both sites and treatments (Table 3) but showed weaker correlations inside each treatment (Table S2).

Table 3. Spearman's correlation coefficients between various plot mean soil surface respiration and soil temperature, soil moisture, and stand basal area. BA_L = living, BA_D = dead, and BA_{tot} = all trees, ST = soil temperature, SM = soil moisture, SR_{tot} = soil surface total respiration, $SR_{tot\_STadj.}$ = temperature-adjusted soil surface total respiration (Aug–Oct 2016 and May–Oct 2017 data, *n* = 16). SR_a = autotrophic respiration, SR_h = measured, and $SR_{h\_STadj.}$ = soil-temperature-adjusted heterotrophic respiration (May–Oct 2017 data, *n* = 8).

	BA_L	BA_D	BA_{tot}	ST	SM
SR_{tot}	0.55 *	−0.41	0.40	0.54 *	−0.67 **
$SR_{tot\_STadj.}$	0.43	−0.36	0.31	-	−0.69 **
SR_a	0.14	−0.12	0.17	-	-
SR_h	0.02	0.17	0.12	−0.29	−0.83 *
$SR_{h\_STadj.}$	0.16	0.13	0.33	-	−0.88 **
ST	0.17	−0.18	−0.01	-	−0.13
SM	−0.56 *	0.25	−0.59 **	−0.13	-

* = $p < 0.05$ and ** = $p < 0.01$.

4. Discussion

4.1. Soil Surface Total, Autotrophic, and Heterotrophic Respiration

We hypothesized that the loss of living trees (roots) resulting from storm damage (5–7 years ago) and *I. typographus* infestation (tree mortality circa 2–4 years ago) would result in reduced SR_a, while the death of trees and roots would increase the amount of surface organic debris and soil organic matter available for microbial decomposition and hence increase SR_h. Our results went some way to supporting this hypothesis. Thus, SR_a at both the *I. typographus*-infested and storm-damaged plots was lower than at the living tree plot in Paajasensalo, and the same was true for the storm-damaged SF_d microsite, but not for the storm-damaged SF_o microsite and *I. typographus*-infested plot, at Viitalampi. Furthermore, the lower SR_a/SR_{tot} ratios of the disturbed plots compared to the living tree plots supported the hypothesis that disturbance results in a shift in total respiration away from SR_a towards SR_h at Paajasensalo, but not at Viitalampi. Although significant differences in SR_h were only found between the SF_o and LT treatments in Paajasensalo, the values at disturbed treatments were mainly lower in Paajasensalo and higher in Viitalampi in comparison to LT. As a result of these patterns in SR_a and SR_h, significant differences (lower) in SR_{tot} compared to living tree plots were only associated with the storm-damaged open microsites at Paajasensalo.

The higher-than-expected level of SR_a at the Viitalampi SF_o microsite and ID plot might have been due to a response of ground vegetation cover and/or the remaining living trees to changes brought about by the tree mortality. As the ground vegetation at the Viitalampi SF_o microsite was observed to be more developed than at the other plots, the higher-than-expected SR_a value was however probably due to the inclusion of the associated autotrophic respiration. The ID plot was also damaged by a storm which broke and felled 50% of the beetle-killed standing dead trees, resulting in increased light to the forest floor and subsequent development of the ground vegetation, which is typical especially after wind disturbance [27]. The effect of developing ground vegetation after disturbance (bark beetle, storm and clearance) has been implicated in increased autotrophic soil respiration observed in a study carried out in Norway spruce stands in Austria [50]. In addition, the productivity of the remaining living trees at the ID plot may have been stimulated by an increase in light, water, and nutrient availability after the death of surrounding trees by *I. typographus*, as was shown in a study on mountain pine beetle (*Dendroctonus ponderosae* Hopkins) attack on lodgepole pine stands in British Columbia [8], and resulted in increased SR_a. Also, seedlings which were growing at all plot types may have contributed to some extent to the SR_a at the disturbed treatment plots. However, rather than stimulating growth, mechanical damage to the remaining living trees caused by the storm-felled trees may have hampered their growth [56], resulting in the lower SR_a in SF_d plot compared to the ID plot at Paajasensalo. That

there was still relatively high SR_a in the SF_d microsite in Viitalampi in spite of there being no living mature trees, may be because some of the respiration measurement points also had living ground vegetation, which would have contributed to the SR_a component.

That the difference in SR_h rates between treatments was weaker than expected may be related to the length of time since tree mortality. Following tree mortality, the C/N and lignin/N ratios of the needle litter decrease [20,22], while litterfall [21] and the mortality of fine roots and ectomycorrhizal fungi [19,57] increase, all of which could potentially stimulate decomposition and SR_h. With time after disturbance, the more easily decomposable compounds would be utilized, leaving more recalcitrant debris and lowering the rate of decomposition [24]. The SR_h rates at our disturbed plots may thus have been considerably higher in the first weeks, or even years, following the death of the trees, i.e., before our measurements started. Nevertheless, small branches and twigs on the SF_d microsites were probably a sufficiently good substrate for decomposition, keeping SR_h rates relatively high even seven years after the storm. However, such an effect could be expected to be less visible in the case of managed forests where trees are cleared away after disturbance. Increasing ground vegetation growth accompanied with lowering heterotrophic respiration can considerably mitigate C emissions already three to six years after storm and beetle disturbance and clearing of damaged trees [50]. In our study, the higher SR_a at the SF_o microsite in comparison to LT at Viitalampi and lower (although not significantly) SR_h at SF_o microsite in comparison to SF_d at both sites could indicate such a pattern. However, we have no data to support this possibl effect.

On a larger spatial scale with greater variability in tree mortality, forest structure and composition, and disturbance-created microhabitats, different or more notable effects in soil surface respiration after the two disturbance types could possibly be found. Although our disturbed study plots on average had a similar dead tree basal area, storm- and *I. typographus*-induced tree mortality patterns across the study forests were rather heterogeneous, varying from individual to stand-level tree decease. Noteworthy also is that at our sites, trees were not cleared away after the events, which would be expected to lead to differing response and recovery patterns of C balance compared to managed forests, due to differences in, e.g., litter quantity, incoming radiation, and ground vegetation changes [13,27].

4.2. Relationships between Basal Area, Soil Microclimate, and Respiration

Although we hypothesized that respiration would be related to the amount of dead tree biomass resulting from the disturbances, SR_{tot} was more strongly correlated to the basal area of living trees than to that of the dead trees. The weaker correlations with dead tree basal area are probably because much of the dead fine root biomass, needles, and small branch detritus that decompose much faster than the bigger tree parts [58,59] had already decomposed by the time of our respiration measurements. Also, since detritus for decomposition is also supplied by the living trees, SR_h cannot be attributed to dead trees only; therefore, correlations with basal area likely were relatively weak.

As we had hypothesized, soil temperature and moisture conditions differed among the treatments. The higher soil moisture contents in the disturbed plots compared to the living tree plots in Paajasensalo are likely related to a reduction in transpiration resulting from tree mortality. The effect of tree mortality on transpiration and soil moisture contents was also clearly indicated by a significant negative correlation between soil moisture content and living tree basal area. However, in Viitalampi, the diminishing soil moisture differences between treatments during the study period may be related to the dense herbaceous ground vegetation further developing during the study and potentially enhanced tree growth taking up moisture from the soil. Soil temperature did not differ so clearly between treatments as moisture, but the higher soil temperatures recorded in Viitalampi ID treatment compared to other treatments may be explained by an increase in light (radiation) conditions brought about by the storm felling of dead trees, as discussed earlier.

To assess the extent to which soil surface respiration were determined more by soil temperature than by plant metabolism and the supply of detritus (living and dead basal area), we examined temperature-adjusted respiration values. However, adjusting respiration for temperature had little

effect on the treatment mean respiration rates, indicating that treatment differences in soil surface respiration were determined more by differences in plant metabolism and the supply of detritus than by differences in soil temperature per se.

Collar-wise correlations between soil moisture and SR_{tot} were generally poor, which is why we were not able to examine the effect of soil moisture on respiration differences between treatments. There were, however, clear differences in mean soil moisture contents between treatments, and plot-wise mean SR_{tot} and SR_h rates were strongly and significantly correlated to plot mean soil moisture contents, indicating that disturbance-driven effects on soil surface respiration are related to changes in soil moisture conditions. However, as basal area and soil moisture were also strongly correlated, it is not possible to determine whether differences in respiration were due to differences in basal area or soil moisture.

5. Conclusions

We found no consistent effect of either storm or *I. typographus* disturbances (tree mortality) on SR_{tot} and SR_h. However, SR_a was lower and SR_{tot} rates showed a shift towards a greater proportion of SR_h in the disturbed forest areas, except at the SF_o microsite and ID plot at Viitalampi, where SR_a was higher than expected. These higher-than-expected SR_a values may have been related to the development of ground vegetation and growth stimulation of remaining living trees. Soil surface respiration was found to be related to basal area (living trees) and soil moisture and temperature conditions, factors which would further relate to plant metabolism, the supply and availability of organic matter for decomposition, forest floor light (radiation) conditions, and stand transpiration.

Despite the mainly similar effects of the two disturbances on soil C dynamics found in this study, the influence of the disturbances on tree mortality patterns, stand structure and composition, and created microsites differs over larger areas. Since storm and bark beetle disturbances are predicted to become more common in the future, their effects on forest C dynamics may become even more complex and considerable. Therefore, for future research, studies concentrating on several disturbances and their effects on forest C fluxes and C balance at greater spatial and temporal scales would be important in order to clarify and estimate the potential effects of disturbances on forest C dynamics.

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