

1 Soil CO₂ efflux from mountainous windthrow areas: 2 Dynamics over 12 years post-disturbance

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11 Abstract

12 Windthrow driven changes in carbon (C) allocation and soil microclimate can affect soil carbon
13 dioxide (CO₂) efflux (F_{soil}) of forest ecosystems. Although F_{soil} is the dominant C flux following
14 stand-replacing disturbance, the effects of catastrophic windthrow on F_{soil} are still poorly
15 understood. We measured F_{soil} at a montane mixed forest site and at a subalpine spruce forest
16 site from 2009 until 2012. Each site consisted of an undisturbed forest stand and two adjacent
17 partially cleared (stem fraction harvested) windthrow areas, which differed in time since
18 disturbance. The combination of chronosequence and direct time-series approaches enabled us
19 to investigate F_{soil} dynamics over 12 years post-disturbance. At both sites F_{soil} rates did not
20 differ significantly from those of the undisturbed stands in the initial phase after disturbance (1
21 - 6 years). In the later phase after disturbance (9 - 12 years) F_{soil} rates were significantly higher
22 than in the corresponding undisturbed stand. Soil temperature increased significantly following
23 windthrow (by 2.9 - 4.8 °C) especially in the initial phase post-disturbance when vegetation
24 cover was sparse. A significant part (15 – 31 %) of F_{soil} from the windthrow areas was attributed
25 to the increase in soil temperature. According to our estimates, ~ 500 to 700 g C m⁻² yr⁻¹ are
26 released via F_{soil} from south-facing forest sites in the Austrian Calcareous Alps in the initial 6
27 years after windthrow. With high game pressure suppressing tree regeneration, post-disturbance
28 loss of ecosystem C to the atmosphere is likely to be substantial unless forest management is
29 proactive in regenerating such sites. An increase in the frequency of forest disturbance by
30 windthrow could therefore decrease soil C stocks and positively feedback on rising atmospheric
31 CO₂ concentrations.

1 **1 Introduction**

2 The global carbon dioxide (CO₂) efflux from soil (F_{soil}) was recently estimated at 98 ± 12 Pg
3 carbon (C) yr⁻¹ (Bond-Lamberty and Thomson, 2010), representing the major pathway by which
4 terrestrial ecosystems release CO₂ into the atmosphere (Schlesinger and Andrews, 2000). In
5 forests, F_{soil} typically accounts for roughly 40 to 80% of the total ecosystem respiration (Curiel
6 Yuste et al., 2005b; Davidson et al., 2006; Janssens et al., 2001) and offsets a large part of the
7 CO₂ sequestered via gross primary production (Janssens et al., 2001). The relative contribution
8 of F_{soil} to forest C budgets can however be even greater following forest disturbance (Janssens
9 et al., 2001) thereby reducing the ecosystem C sink strengths (Lindroth et al., 2009). As natural
10 forest disturbance regimes are likely to be altered by climate change (Dale et al., 2001), a
11 detailed understanding of disturbance impacts on F_{soil} is essential if the forest's role in the global
12 C cycle, and thus the climate system, is to be evaluated correctly.

13 Natural and anthropogenic disturbance events, such as stand replacing fires, insect infestations,
14 windthrow or forest harvests, can influence many biotic and abiotic factors (Amiro, 2001;
15 Amiro et al., 2010; Kurz et al., 2008; Lindner et al., 2010; Katzensteiner, 2003; Christophel et
16 al., 2013) which affect F_{soil} . Catastrophic storms are responsible for more than half of the
17 damage in European forests (Gardiner et al., 2010), and the risk of wind damage is expected to
18 increase in the future (Schelhaas et al., 2010; Seidl et al., 2014). According to the conceptual
19 trajectory of Odum (1969) the pre-disturbance ecosystem is sequestering C, until disturbance
20 causes an initial, rather discrete loss of C, which is followed by a period of recovery. In the case
21 of windthrow, the initial C loss is due to the increase in heterotrophic respiration following the
22 sharp decline in photosynthetic C fixation. Considering the windthrow is stand replacing (all
23 trees killed), F_{soil} is likely the main C flux before and during the primary phase of forest
24 recovery (Knohl et al., 2002) and thus determines the magnitude of initial net ecosystem
25 emission/uptake of CO₂. In cases of increased F_{soil} after disturbance, large amounts of
26 ecosystem C can be lost to the atmosphere (Kurz et al., 2008; Covington, 1981). However,
27 where F_{soil} decreases post-disturbance, net ecosystem-atmosphere CO₂ fluxes may show very
28 little difference between pre-, and post-disturbance levels (Moore et al., 2013). Quantifying
29 post-disturbance changes in F_{soil} is therefore crucial in improving our understanding of
30 disturbance impacts on ecosystem C dynamics and the potential risk of ecosystem C loss.

31 Following windthrow, soil initially receives a pulse of organic C inputs in the form of litter and
32 woody debris from killed trees. Roots of dead trees decompose and represent a further source
33 of organic C. However, after this initial C inputs, tree litter production and active transport of

1 labile C from the trees to the rhizosphere cease (Högberg et al., 2001; Levy-Varon et al., 2012;
2 Singh et al., 2008; Olajuyigbe et al., 2012; Tang et al., 2005) with renewed C inputs depending
3 on subsequent vegetation establishment. However, litter from populating pioneer herbs and
4 grasses can differ in quality and quantity to that provided pre-disturbance (Spielvogel et al.,
5 2006). All these dynamic changes in soil C supply will influence the quantity and quality of
6 soil organic matter (SOM) as well as the microbial community (Holden and Treseder, 2013)
7 and thereby affect F_{soil} . Windthrow can also affect microclimatic variables such as soil
8 temperature and moisture, which are key drivers of SOM decomposition (Davidson et al., 1998;
9 Davidson and Janssens, 2006; Lloyd and Taylor, 1994). Complete or partial removal of the tree
10 layer, and the associated changes in insolation at the ground and transpiration demand on the
11 soil can lead to altered soil temperature and soil moisture regimes (Payeur-Poirier et al., 2012;
12 Kulmala et al., 2014; Peng and Thomas, 2006; Pumpanen et al., 2004b; Singh et al., 2008). Due
13 to the complex interplay of various rate limiting factors regarding organic matter
14 decomposition, the overall response of F_{soil} to windthrow depends on many site and ecosystem
15 specific factors. Post-disturbance F_{soil} is thus difficult to estimate with generalized paradigms
16 of ecosystem behaviour. Furthermore, the temporal evolution of F_{soil} post-windthrow is a
17 particularly 'grey' area as many studies have conducted only short (1 – 2 years) measurement
18 campaigns (Vargas, 2012; Vargas and Allen, 2008; Wright and Coleman, 2002; Köster et al.,
19 2011; Thuille et al., 2000).

20 In the European Alps complex topographic preconditions and a tendency towards increasingly
21 aged stands (Seidl et al., 2011) promote susceptibility to larger scale windthrow damage (Seidl
22 et al., 2014). Across Europe soil C stocks increase significantly with altitude (Sjögersten et al.,
23 2011), and the largest organic carbon contents were found in the upper soil horizons of forests
24 in alpine regions (Baritz et al., 2010). High soil C contents and the potential increase in
25 windthrow event frequency mean that these ecosystems could be future hotspots of ecosystem
26 C loss. Despite this threat, the effects of windthrow on F_{soil} in mountainous regions of the
27 European Alps have been rarely quantified.

28 We studied two mountainous forest stands which had been hit by successive larger-scale
29 windthrow events. Together the study sites offered two undisturbed forests and four managed
30 windthrow areas in varying temporal stages after disturbance. Combining time series and
31 chronosequence approaches the areas were investigated to track development of F_{soil} over 12
32 years post-disturbance. Our main objectives were to investigate the effects of windthrow
33 disturbance on soil microclimate and F_{soil} , and to address the post disturbance dynamics in

1 relation to ground vegetation re-establishment. We hypothesized that F_{soil} would decrease in the
2 first years post-disturbance (due to a decrease in autotrophic respiration), and reach pre-
3 disturbance levels with subsequent ground vegetation establishment.

4 **2 Materials and methods**

5 **2.1 Study sites**

6 The study took place in the Rax mountain area (henceforth 'Rax'; 47°43'37" N, 15°41'20" E)
7 and in the Höllengebirge mountain range (henceforth 'Höllengebirge'; 47°47'19" N,
8 13°38'21" E), located in the eastern and the central part of the Austrian Calcareous Alps,
9 respectively (Fig. 1). Rax is a subalpine, coniferous dominated forest site at an altitude of 1470
10 m a.s.l., and Höllengebirge is a montane, mixed forest site at an altitude of around 1000 m a.s.l.
11 Both sites are south to south - west exposed. Climatic conditions at the sites are cool and humid,
12 characterized by distinctive precipitation maxima during summer and precipitation minima
13 during spring and fall (Kilian et al., 1994). Average (2002 – 2012) air temperature and
14 precipitation were 3.8 °C and 1424 mm at the Rax site (closest climate station ~ 7 km apart at
15 similar altitude) and 6.6 °C and 1964 mm at the Höllengebirge site (interpolated values from
16 the closest climate stations both ~ 10 km apart) respectively (ZAMG, 2013). Growing season
17 at both sites is between May and September.

18 The forest stand at the Rax site was dominated by Norway spruce (*Picea abies*) with a stand
19 age of 185 years in 2012. The ground vegetation cover consisted of a very sparse herbal and
20 grass layer (*Lycopodium sp.*, *Luzula luzuloides*). The forest stand at Höllengebirge was
21 dominated by Norway spruce (*Picea abies*), European beech (*Fagus sylvatica*) and Silver fir
22 (*Abies alba*) and intermixed by Sycamore (*Acer pseudoplatanus*) and European ash (*Fraxinus*
23 *excelsior*). The average stand age was 219 years in 2012. Ground vegetation was also very
24 sparse composed of herbs (*Mycelis muralis*, *Prenanthes purpurea*), grasses (*Calamagrostis*
25 *varia*) and a few, infrequently occurring understory trees (*Picea abies*).

26 In winter 1999/2000 the Rax site was affected by a storm event where several hectares of the
27 forest stand were either blown over or destroyed by wind-snap. A subsequent windthrow in
28 winter/spring 2007 then worked its way from the exposed forest edge eastwards (Fig. 1a).
29 Respective areas are henceforth denoted as 'Rax windthrow 2000' (RW00) and 'Rax windthrow
30 2007' (RW07) treatments. The unaffected intact stand adjacent to the windthrow areas served
31 as a control (RC). At the Höllengebirge site a windthrow in winter/spring 2007 and subsequent
32 bark beetle events totally destroyed roughly 25 ha of forest. This was then followed by
33 subsequent windthrow disturbance in winter/spring 2009, which opened up a further 4 ha (Fig.

1 1b). The denotation of these specific areas is ‘Höllengebirge windthrow 2007’ (HW07) and
2 ‘Höllengebirge windthrow 2009’ (HW09) treatments accordingly. The unaffected stand beside
3 the windthrow areas again served as a control (HC). The area comprised of pits and mounts
4 contributed only slightly (<5 %) to the total area of each windthrow site.

5 The windthrow areas at both sites were actively managed. Sites were partially cleared of
6 stemwood immediately after the disturbance events in order to prevent bark beetle infestations.
7 About 15 % of the stem fraction was left in place. Branches and stumps were kept on site. Wind
8 snapped trees were cut, and the logs were harvested as well. Only a marginal number of mature
9 trees survived the disturbance events at both sites, which were not harvested after the
10 windthrow. Ground vegetation reestablishment at the disturbed areas at both sites comprised
11 initially herbaceous plants (*Senecio jacobaea*, *Adenostyles glabra*, *Eupatorium cannabinum*,
12 *Cirsium arvense*, *Urtica dioica*) followed by grass vegetation (*Luzula luzuloides*,
13 *Calamagrostis varia*, *Calamagrostis villosa*). Except for sparse groups of spruce (*Picea abies*)
14 remaining from a pre-disturbance understory tree layer at HW07, natural tree regeneration was
15 largely inhibited at both sites.

16 The Rax and the Höllengebirge sites were similar to one another regarding bedrock and soil
17 conditions. The parent bedrock was mainly limestone in paragenesis with dolomite. Chromic
18 Cambisols, Rendzic Leptosols and Folic Histosols (WRB, 2006) were the dominant soil types
19 and Moder and Tangel (Zanella et al., 2011) the main humus forms. A slope line transect
20 showed that Folic Histosols and Rendzic Leptosols tended to occur at steeper terrain and
21 Chromic Cambisols at flatter areas. Nonetheless, the heterogeneous conditions typical of *Karst*
22 meant the above soil- and humus types were often found within meters of one another.
23 According to forest inventory data from both sites, pre-disturbance stand conditions (tree
24 species composition, stand age, stand structure) of the windthrown areas were similar to those
25 of the respective adjacent control stands. Furthermore, at both sites exposition, slope, soil types
26 and humus forms were similar between respective disturbed and undisturbed areas. Detailed
27 information about the soil characteristics is given in Table 1.

28 **2.2 Experimental design**

29 The assessment of F_{soil} at undisturbed areas and windthrown areas which differed in time since
30 disturbance, together with 3 to 4 years of repeated measurements of F_{soil} at all windthrow and
31 stand areas allowed us to combine time series and chronosequence approaches. Time series of
32 F_{soil} were measured at both sites, but spatial and temporal resolution of measurements was
33 higher at the Höllengebirge site which was a core site of the INTERREG project ‘SicAlp’. At

1 the Rax site six to eight plots were established at the individual treatments. Plots were defined
2 by a rectangular area of 1 x 1 m and were arranged along slope line transects (Fig. 1a).
3 Measurements of F_{soil} and soil temperature at Rax started in July 2009 and were supplemented
4 by soil moisture measurements from July 2010 onwards. Measurements were accomplished at
5 irregular intervals (monthly to three month) during the snow-free periods and ended in
6 November 2012. At Höllengebirge 65 1x1 m plots were arranged in a nested (multi – stage)
7 sampling scheme (Fig. 1b large crosses), composed of different distance stages (Webster and
8 Oliver, 2007). The distance stages were 25 m, 12.5 m and < 12.5 m. In sum 13, 29 and 23 plots
9 were established at HC, HW09 and HW07 respectively. The higher number of plots and large
10 spatial extent of the sampling area at Höllengebirge site was partially due to concurrent eddy
11 covariance measurements at this site (data not presented here), and the subsequent need to cover
12 the flux footprint. Measurements of F_{soil} , soil temperature and soil moisture were taken
13 biweekly to monthly from August to November 2010 and monthly from April to November
14 2011 and May to November 2012 (during snow free conditions). Additional measurements
15 were carried out in January 2011 due to snow free conditions.

16 **2.3 Measurements of soil CO₂ efflux, soil microclimate, and ground vegetation**

17 Two weeks prior to the first F_{soil} measurements, a single PVC collar (4 cm height, 10 cm inner
18 diameter) was installed in the centre of each plot at each site. The collars were inserted 3 cm
19 into the soil surface (including litter layer) and were kept in place throughout the whole study.
20 Establishing vegetation inside the collars was clipped regularly at both sites. Measurements of
21 F_{soil} were conducted by means of the closed chamber technique, using a portable infrared gas
22 analyser (model EGM-4, PP Systems International, Inc. Amesbury, MA, USA) and an attached
23 mobile respiration chamber (model SRC-1, PP Systems International, Inc. Amesbury, MA,
24 USA). For each plot the chamber was placed over the respective collar and measured the
25 concentration increase in the chamber headspace. The temporal CO₂ increase inside the
26 chamber headspace was measured over a maximum period of 120 seconds, though the period
27 was cut short once the temporal increase of CO₂ exceeded 50 ppm. The recording interval of
28 CO₂ efflux [ppm] was 4.8 to 5 seconds. These were the standard settings from the company
29 (EGM4, PP-Systems International, Inc. Amesbury, MA, USA) which was shown to produce
30 reliable soil CO₂ efflux rates (Pumpanen et al., 2004a). Within each plot, soil temperature and
31 soil moisture were measured simultaneous to the F_{soil} measurements. Soil temperature was
32 measured at a soil depth of 5 cm (including litter layer) using a handheld thermometer. Soil
33 moisture, measured as volumetric water content, was determined for 0 to 7 cm soil depth

1 (including litter layer) by means of time domain reflectometry (TDR) using a calibrated soil
 2 moisture meter (model Field Scout, Spectrum Technologies, Inc. Plainfield, IL, USA). The
 3 measurement cycles took ~ 2 h at Rax and ~ 8 h at Höllengebirge. Plots at both sites were
 4 measured in the same order throughout the study. The long duration of measurements at the
 5 Höllengebirge site posed the risk of bias due to changing soil conditions (temperature, moisture)
 6 throughout the day. To account for that and to ensure comparability between undisturbed and
 7 disturbed sites, measurements were undertaken in an uphill-crisscross fashion. After every
 8 seventh plot, the treatment (HC, HW09, HW07) was changed, thus essentially moving across
 9 the slope and between all three the treatments before each movement to the plots further
 10 upslope. Soil temperature in 5 cm depth (including litter layer) was continuously measured with
 11 thermocouple elements at RC and at HW09 as well. The data were recorded by Minicube data
 12 loggers (EMS, Brno, Czech Republic) at 15 min and 30 min storage intervals at RC and HW09,
 13 respectively (Fig 1). Ground vegetation surface cover in percentage was assessed at Rax during
 14 the growing seasons of 2009 and 2011 and at Höllengebirge during the growing seasons of 2010
 15 and 2012. Percentages of herbs, grass and young trees were estimated within the 1 x 1 m area
 16 of each plot.

17 **2.4 Data analysis**

18 Effects of windthrow on F_{soil} , soil temperature, and soil moisture were tested by means of
 19 ANOVA and subsequent Tukey's HSD tests with a mixed effects model structure (Pinheiro and
 20 Bates, 2000) at each site. To account for the repeated measurement structure within the data,
 21 the plots were assumed as random effects and the treatments were assumed as fixed effects in
 22 each ANOVA and subsequent Tukey's HSD tests. Mixed effects ANOVA and Tukey's HSD
 23 tests were calculated by means of the R package 'NLME' (Pinheiro et al., 2014).

24 Soil CO₂ efflux was strongly correlated with soil temperature (Fig. 2). We fitted a simple Q_{10}
 25 function to the F_{soil} and soil temperature data (Janssens et al., 2003):

$$26 \quad F_{\text{soil}} = F_{10} Q_{10}^{\left(\frac{T-10}{10}\right)}, \quad (1)$$

27 where F_{soil} and T are the soil CO₂ efflux rates [$\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$] and soil temperature [°C] at
 28 5 cm soil depth respectively, F_{10} represents the basal soil CO₂ efflux at a soil temperature of 10
 29 °C, and Q_{10} represents the temperature sensitivity of the soil CO₂ efflux (the factor by which
 30 the F_{soil} increases during a temperature rise of 10 °C). To account for soil moisture (Fig. 3b,
 31 3e), we added an exponential soil moisture term (Knohl et al., 2008; Soe and Buchmann, 2005)
 32 to Eq. (1). This however only marginally improved the model. Therefore, only parameters from

1 Eq. (1) were used for further analysis in this study. Non-linear fitting was done by means of the
2 R package ‘minpack.lm’ (Elzhov et al., 2013). Equation (1) was fitted to the data of each plot
3 as well as to the daily averages of each treatment. In order to dig deeper into processes related
4 to basal CO₂ efflux and temperature sensitivity of F_{soil} , the data were also separated into
5 seasonal windows. Equation 1 was accordingly fitted to the daily averages of each treatment
6 for a mid - season (01.06 to 31.08) and for an early/late – season (01.09 to 31.05). Student t-
7 tests were used to test for treatment differences in the parameters of Eq. (1).

8 We used the continuous soil temperature data to obtain approximations of annual sums of F_{soil}
9 for all treatments. As soil temperature was only measured continuously at RC and HW09, we
10 first had to generate continuous soil temperature estimates for all plots. We used simple linear
11 relationships between the plot-specific manually gathered soil temperature measurements and
12 the continuous measurements during the corresponding time (R^2 ranged from 0.71 to 0.93), in
13 order to simulate hourly soil temperatures for the study period. Plot specific model parameters
14 derived from Eq. (1) together with the simulated hourly soil temperature were subsequently
15 used to calculate hourly F_{soil} for each plot. Model simulations were summed up per plot and
16 mean values and respective standard errors were calculated for each treatment. Annual sums
17 were calculated for 2012, as dry conditions during summer weakened the model performance
18 in 2011.

19 In order to disentangle the effects of altered soil temperature on F_{soil} at the different windthrow
20 areas, annual courses in F_{soil} rates at the windthrow areas were also modelled under theoretical
21 pre-disturbance soil temperature conditions. For this purpose we used the plot specific
22 (windthrow plots only) model parameters of Eq. (1) together with the interpolated hourly
23 average soil temperature from the respective undisturbed control stands.

24 Relative F_{soil} rates were calculated for the windthrow areas in order to compare both sites within
25 one longer term disturbance chronosequence. Daily average F_{soil} rates of the windthrow areas
26 were divided by the daily average F_{soil} rates of their respective control stand. This procedure
27 should minimize possible site differences (stand differences, differences in air temperature) but
28 nonetheless indicate longer-term dynamics in F_{soil} following disturbance of such ecosystems.

29 Correlation analysis was performed to investigate the influence of plant functional types on
30 F_{soil} . Plot specific annual mean values of F_{soil} were correlated with the plot specific ground
31 vegetation surface coverage in 2009 and 2011 at Rax and in 2010 and 2012 at Höllengebirge.

1 All statistical analysis and plotting were done in R, an environment for statistical computing
2 and graphics (R Core Team, 2013). The level of significance for the statistical analysis was a
3 p-value < 0.05.

4 **3 Results**

5 **3.1 Soil microclimate**

6 Soil temperature in 5 cm depth showed typical seasonal patterns at both sites and at each
7 treatment (Fig. 3a, Fig. 3d). Average soil temperatures over the whole study period were 8.1,
8 12.9, and 11.3 °C at RC, RW07 and RW00, and 13.1, 17.2 and 16.0 °C at HC, HW09 and
9 HW07 respectively. Soils in the disturbed treatments were significantly warmer compared to
10 the soils in the undisturbed stands (Table 2). Soil temperature was significantly higher at HW09
11 than at HW07, whereas soil temperatures at the windthrow areas at Rax did not differ
12 significantly. No clear seasonal patterns in soil moisture were detected for either Rax or
13 Höllengebirge throughout the measurement campaign (Fig. 3b, Fig. 3e). Apart from discrete
14 drought periods at Höllengebirge in August 2011 and at Rax in October 2011, soil moisture
15 was rather stable around 40 to 50 vol% at both sites. At Rax no significant differences in soil
16 moisture could be shown for the treatments (Table 2). Average soil moisture over the whole
17 study period was 43 vol%, 43 vol%, and 46 vol% at RC, RW07 and RW00 respectively. At
18 Höllengebirge soil moisture was roughly 6 vol% and 5 vol% lower at HC than HW09 and
19 HW07 (Table 2). No significant difference in soil moisture could be determined between the
20 disturbed treatments. Average soil moisture over the whole study period was 38 vol%, 44 vol%,
21 and 43 vol% at HC, HW09 and HW07 respectively.

22 **3.2 Soil CO₂ efflux**

23 F_{soil} showed clear seasonal variations at all treatments, strongly following the patterns in soil
24 temperature (Fig. 3). F_{soil} was significantly higher at RW00 when compared to RC and RW07,
25 but no significant difference in F_{soil} was determined for RC and RW07 (Table 2). At
26 Höllengebirge, F_{soil} was slightly lower at the windthrow areas, but the difference between intact
27 stand and windthrow areas was statistically not significant (Table 2).

28 A clear exponential relation between F_{soil} and soil temperature in 5 cm depth was observed for
29 each treatment (Fig. 2). Soil temperature alone explained 79 % to 86 % and 66 % to 87 % of
30 the temporal variation in F_{soil} at Rax and Höllengebirge respectively. However, under dry soil
31 conditions in October 2011 and August 2011 at Rax and Höllengebirge respectively, (soil
32 moisture declined to a minimum of 23 vol% and 27 vol% at Rax and Höllengebirge

1 respectively), soil moisture became a limiting factor for F_{soil} and interfered with the response
2 to soil temperature at each treatment (Fig 3, hatched area). As suggested by e.g. Curiel Yuste
3 et al. (2005a) and Ruehr and Buchmann (2010) respective dates with water limiting conditions
4 were excluded from the data, which strongly improved the relation between F_{soil} and soil
5 temperature, with soil temperature subsequently explaining 91, 83, 85 % of the variation in F_{soil}
6 at RC, RW07 and RW00 respectively, and 83, 86, 90 % of the variation in F_{soil} at HC, HW09
7 and HW07 respectively (Table 3). However, the addition of an exponential soil moisture term
8 to Eq. (1) only marginally improved the explanatory value of the F_{soil} models at the
9 Höllengebirge site, while at Rax no significant model improvement was observed (data not
10 shown).

11 The basal CO₂ efflux, as represented by the F_{10} parameter of Eq. (1), was significantly higher
12 at the undisturbed control stands when compared to the corresponding disturbed treatments at
13 RW07, HW09 and HW07 (Table 3). Only at the oldest windthrow site (RW00) was F_{10}
14 significantly higher when compared to the undisturbed stand (RC) (Table 3). Except for RW00,
15 the same pattern in F_{10} could also be demonstrated when analysing the mid-season (01.06. to
16 31.08) and early/late season (01.09 to 31.05) separately (Table 3).

17 The Q_{10} values during non-water limited conditions were 3.53, 2.44, and 2.40 at RC, RW07
18 and RW00 and 3.08, 2.33, and 2.49 at HC, HW09 and HW07, respectively (Table 3). The
19 seasonal separation of the data also revealed that Q_{10} values across all treatments were lower
20 during the growing season than during the dormant season (Table 3).

21 Average annual sums of F_{soil} for the sampling year 2012 of 626 ± 37 (\pm SE, $n = 8$), 696 ± 56 (n
22 $= 6$) and 1130 ± 115 ($n = 6$) $\text{g C m}^{-2} \text{yr}^{-1}$ were calculated for the Rax treatments RC, RW07, and
23 RW00 respectively. For the Höllengebirge site, corresponding values of 551 ± 72 ($n = 13$), 463
24 ± 29 ($n = 29$) and 492 ± 37 ($n = 23$) $\text{g C m}^{-2} \text{yr}^{-1}$ were calculated for HC, HW09 and HW07
25 respectively. The annual sums were corrected for surface rock outcrops, which on average
26 accounted for 13 % and 27 % of the total area at Rax and Höllengebirge respectively.

27 By means of the modelling approach with two temperature scenarios (actual soil temperature
28 and stand soil temperature), 31 %, 20 %, 15 %, and 20 % of the annual CO₂ efflux was
29 attributed to warmer soil conditions at RW07, RW00, HW09, and HW07 respectively (Fig. 4).

30 According to the longer term chronosequence of relative F_{soil} rates, the efflux tended to be rather
31 similar until the sixth year after disturbance followed by a rebound and increase during years 6
32 to 12 post-disturbance (Fig. 5).

1 3.3 Ground vegetation cover

2 Ground vegetation surface cover was clearly higher at older than younger windthrow areas (Fig.
3 6). Ground vegetation was dominated by herbaceous plants in the first years after disturbance,
4 followed by a transition to a dominating grass community within roughly the first decade after
5 disturbance. Except of HW07 practically no tree regeneration was present at the disturbed areas.
6 Total ground vegetation cover and F_{soil} as well as grass vegetation cover and F_{soil} were strongly
7 correlated at HW07, although these relationships were only significant for data from 2012
8 (Table 4). At HW09, RW07 and RW00 no correlation between vegetation variables and F_{soil}
9 could be detected.

10 4 Discussion

11 The hypothesized initial decrease in post-disturbance F_{soil} was not confirmed at both sites. F_{soil}
12 showed no significant decline throughout the first six years post disturbance, and remained
13 close to pre-disturbance levels (Table 2, Fig. 5). We hypothesized that the reduced F_{soil} would
14 be driven by a large decrease in autotrophic respiration which would outweigh the additional
15 CO_2 release from the decomposition of litter from killed trees (needles and dead fine roots).
16 The basal CO_2 efflux at 10°C (F_{10}) was 30 to 40 % lower when compared to the control stands
17 (Table 3). This percentage roughly corresponds to the autotrophic contribution to F_{soil} in intact
18 forest ecosystems similar to ours (Hanson et al., 2000; Ruehr and Buchmann, 2010;
19 Schindlbacher et al., 2009). However, as measured F_{soil} rates between the young windthrow
20 areas and control stands were not statistically different (Table 2), it appears that the decrease in
21 autotrophic soil respiration was in fact offset by accelerated heterotrophic soil respiration i.e.
22 SOM decomposition. Rates of SOM decomposition are driven by changes in the soil microbial
23 community (Holden and Treseder, 2013), substrate availability and/or changes in soil
24 microclimate (Davidson and Janssens, 2006; Davidson et al., 1998). Although all such changes
25 are likely to have occurred at our windthrow areas, it could be shown that the increase in soil
26 temperature was key in maintaining F_{soil} rates at pre-disturbance levels (Fig. 4, Fig. 5). The
27 higher than hypothesized F_{soil} in the initial years post disturbance thus appears to be primarily
28 driven by rate-accelerating soil microclimatic conditions.

29 During the CO_2 measurement campaigns, soil in the windthrow areas was on average 4.8 ± 0.7
30 $^\circ\text{C}$ (RW07) and 3.2 ± 0.7 $^\circ\text{C}$ (RW00) warmer than in the undisturbed treatment (RC) at Rax,
31 and 4.2 ± 0.4 $^\circ\text{C}$ (HW09) and 2.9 ± 0.4 $^\circ\text{C}$ (HW07) warmer than in the undisturbed treatment
32 (HC) at Höllengebirge (Table 2). Such an increase in soil temperature after stand disturbance
33 is a commonly observed response in forest ecosystems (Payeur-Poirier et al., 2012; Kulmala et

1 al., 2014; Classen et al., 2005; Pumpanen et al., 2004b; Singh et al., 2008; Vanderhoof et al.,
2 2013), driven by the loss of shading by the tree canopy and subsequently higher insolation at
3 the forest floor. The decreasing temperature difference between windthrow areas and
4 undisturbed stands with increasing time post disturbance is likely connected to increased
5 shading by the developing ground vegetation. In addition to soil temperature effects, removal
6 or dieback of the tree layer can lead to changes in the soil moisture regime, often producing
7 wetter soil conditions post-disturbance (Payeur-Poirier et al., 2012; Classen et al., 2005; Peng
8 and Thomas, 2006; Pumpanen et al., 2004b). This effect, which is mainly due to the ceased
9 water uptake by trees, was observed at Höllengebirge but not at Rax. This may have been due
10 to the smaller transpiration demand on soil of the Norway spruce dominated stand at Rax
11 compared to that of the Beech dominated stand at Höllengebirge (Hietz et al., 2000). A higher
12 ground vegetation coverage and a consequently higher water demand at the Rax windthrow
13 areas (Fig. 6a) is also likely to decrease soil moisture, since evapotranspiration is increasing
14 rapidly with vegetation reestablishment following forest disturbance (Williams et al., 2014).
15 As mentioned already, the above changes in soil microclimate were substantial factors in
16 maintaining higher F_{soil} after disturbance. Simulations with two soil temperature scenarios (with
17 soil temperature from the windthrow areas and from the control stands respectively) revealed
18 that disturbance-induced changes in soil microclimate were responsible for 15 to 31% of the
19 CO_2 flux magnitude of the windthrow areas (Fig. 4). Especially during warmer periods in
20 summer, the temperature related effect on F_{soil} was pronounced. Although soil moisture was
21 also higher at the Höllengebirge windthrow areas, the effect on F_{soil} rates was marginal ($\sim 2\%$,
22 data not shown).

23 F_{soil} showed a strong relationship to soil temperature in all treatments but apparent Q_{10} values
24 were higher for the intact stands (Table 3); a pattern which has also been observed after clear-
25 cut (Zu et al., 2009; Payeur-Poirier et al., 2012). This however does not necessarily mean that
26 the real temperature sensitivity of SOM decomposition differed at windthrow and stand areas.
27 More likely, the higher Q_{10} in the intact stand to an extent reflect the seasonal trend of
28 autotrophic soil respiration, which often correlates with the seasonal development of soil
29 temperatures, and hence increases apparent Q_{10} (Schindlbacher et al., 2009). Similar mid -
30 season Q_{10} values within each site (Table 3) therefore suggest a rather small disturbance effect
31 on the real temperature sensitivity.

32 Together with soil microclimate, C availability is likely to have influenced the temporal
33 development of the soil CO_2 efflux post-windthrow. Initial C input due to dead tree foliage and

1 fine roots is typically high after windthrow. Our results however do not point towards a flush
2 in heterotrophic decomposition during the first years after windthrow. As ground vegetation
3 cover was quite sparse in the initial period post-disturbance (Fig. 6), heterotrophic respiration
4 was thus assumed to be the dominant contributor to F_{soil} . Hence the additional C input during
5 disturbance seems to be slowly, but continually utilised, thus maintaining high decomposition
6 rates.

7 F_{soil} and F_{10} from the oldest windthrow area (RW00) were significantly higher when compared
8 to both, F_{soil} and F_{10} from the more recent windthrow (RW07) and F_{soil} and F_{10} from the
9 undisturbed stand (RC). The oldest windthrow site was characterized by dense grass vegetation
10 which fully covered the soil surface (Fig. 6). The development of this dense grass community
11 and the correspondingly increasing autotrophic respiration and litter input, as well as an input
12 of easily decomposable exudates to the heterotrophic community is likely responsible for the
13 higher CO₂ efflux observed after 9 – 12 years post-disturbance, as reported by Pumpanen et al.
14 (2004b). A significant positive relation between F_{soil} and grass cover at HW07 also supports
15 this explanation (Table 4). Williams et al. (2014) reported an autotrophic contribution of ~ 30
16 % after four years post-clearcut. Their site was however nearly 100 % covered by ground
17 vegetation already after four years, while it took much longer at the sites in our study region.
18 In addition to the effects of ground vegetation cover, a delayed decomposition of woody debris
19 might have contributed to higher F_{soil} rates in a later phase post-disturbance as well.

20 Average annual F_{soil} (during 2012) was estimated at ~ 6.3 and 5.5 t C ha⁻¹ yr⁻¹ for RC and HC
21 respectively, which is comparable with values reported for other temperate forest sites (Etzold
22 et al., 2011; Knohl et al., 2008; Ruehr et al., 2010; Schindlbacher et al., 2012). Annual estimates
23 for F_{soil} from the more recent windthrow areas were within this range (4.6 – 7.0 t C ha⁻¹ yr⁻¹).
24 In the intact forest stands, the loss of C through soil CO₂ efflux was likely offset by the C gain
25 by photosynthesis and growth (Luyssaert et al., 2008). At the windthrow areas, the F_{soil}
26 estimates indicate a substantial loss of C from the ecosystem, especially during the initial stage
27 when ground vegetation cover was sparse. Our C loss estimates from the windthrow areas is
28 somewhat lower than that from Knohl et al. (2002) who observed an annual C release of 8 t ha⁻¹
29 ¹ from a windthrow area in a boreal forest. At their site, roughly 1/3 of the released CO₂ was
30 from dead-wood decomposition, whereas at our sites, most dead wood was removed. The
31 comparably high F_{soil} rates at our windthrow areas were primarily related to the warm soil
32 conditions created by loss of canopy shading (Fig. 4). All windthrow areas in our study were
33 on steep, south exposed slopes, thus receiving large amounts of solar radiation. The effects of

1 windthrow on soil temperatures may be less pronounced for other aspects. On north exposed
2 slopes for example, disturbance may have little or no effect on soil temperature. Finally, while
3 the above annual estimates are subject to a number of uncertainties (e.g. uncertainties in model
4 parameters (Eq. 1), uncertainties in simulated temperatures), they nonetheless point toward
5 substantial C losses from such sites after windthrow disturbance.

6 The respiratory C loss of $\sim 11.1 \text{ t C ha}^{-1} \text{ yr}^{-1}$ at RW00 is high for forest ecosystems, but is within
7 the range of annual F_{soil} rates estimated for European grasslands (Bahn et al., 2008).
8 Considering almost 100 % grass vegetation cover at this site, the above estimates are thus
9 plausible. Whether this 12 year old windthrow area acts as a C sink or source cannot be assessed
10 with our data. Rhizosphere respiration will contribute a large share of the overall F_{soil} (Chen et
11 al., 2006; Subke et al., 2006) and the dense grass cover produces comparatively high amounts
12 of above and below ground litter (Freschet et al., 2013). Therefore, it is likely that the old
13 windthrow area is losing comparatively less C than the more recently disturbed areas.

14 It has been shown that it takes 10 – 25 years until forest ecosystems return to C sinks after stand
15 replacing disturbances (Amiro et al., 2010; Pfeifer et al., 2011). This recovery time depends on
16 disturbance effects on (soil) respiratory processes and on the recovery of vegetation
17 productivity. If disturbance largely reduces ecosystem respiration, than the disturbance effects
18 will be small and a balance in net C flux can be restored quickly (Moore et al., 2013). If the
19 respiration does not decrease post-disturbance as observed in our study (soil respiration only)
20 and elsewhere (Knohl et al., 2002; Köster et al., 2011; Morehouse et al., 2008; Toland and Zak,
21 1994) then the recovery of the C sink capacity strongly depends on forest re-growth. At none
22 of the sites of our windthrow chronosequence, could significant tree seedling establishment or
23 tree re-growth be observed (Fig. 6). The study regions, just like much of Austria's mountain
24 forests, are characterized by high population densities of roe deer, red deer, and chamois and
25 are thus subject to high browsing pressures (Ammer, 1996; Reimoser and Gossow, 1996;
26 Reimoser and Reimoser, 2010). Therefore, a fast re-establishment of forest stands on
27 windthrow areas is extremely difficult without post-disturbance management such as artificial
28 regeneration and subsequent fencing against browsing. If such measures are not undertaken
29 forest re-growth is hardly feasible. As carbon uptake in the successional phase of pioneer
30 vegetation is lower compared to the phase of tree recovery (Williams et al., 2014), the C uptake
31 at such windthrow sites is likely to be low. Consequently, more frequent forest disturbance by
32 windthrow in mountainous regions (Seidl et al., 2011; Seidl et al., 2014) poses a significant risk

1 to soil C stocks in the European Alps and may positively feedback on rising atmospheric CO₂
2 concentrations.

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1 **Table 1.** Mean soil characteristics of the undisturbed control stands at Rax and Höllengebirge.

	Rax	Höllengebirge
Soil C stock (kg m ⁻²) O - horizon	8.3 (1.5)	7.5 (0.9)
C content (%) O - horizon	45 (2)	42 (2)
C:N ratio O - horizon	24.9	19.1
pH (H ₂ O)	5.3	4.7
Layer thickness (cm) O - horizon	12 (2)	15 (2)
Total soil depth (cm)	17 (4)	38 (3)

2 Values in parentheses represent standard error.

1 **Table 2.** Site specific effects of windthrow on soil temperature (T) [°C], soil moisture (M)
 2 [vol%], and soil CO₂ efflux (F_{soil}) [$\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$], as assessed by Tukey's HSD tests with
 3 mixed effects model structure.

Variable	Rax			Höllengebirge		
	Differences					
	RC – RW07	RC – RW00	RW07 – RW00	HC – HW09	HC – HW07	HW09 – HW07
<i>T</i>	-4.80 (0.69) ^b	-3.22 (0.70) ^b	1.59 (0.75) n.s.	-4.16 (0.38) ^b	-2.89(0.39) ^b	1.27(0.32) ^b
<i>M</i>	0.75 (2.49) n.s.	-2.84 (2.49) n.s.	-3.59 (2.67) n.s.	-6.31 (1.60) ^b	-5.36(1.66) ^a	0.95(1.34) n.s.
F_{soil}	-0.36 (0.42) n.s.	-2.21 (0.42) ^b	-1.85 (0.45) ^b	0.42 (0.35) n.s.	0.57(0.36) n.s.	0.15(0.29) n.s.

4 Values in parentheses represent standard error. Significance levels:
 5 n.s., not significant;
 6 ^a p value<0.01;
 7 ^b p value<0.001.

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1 **Table 3.** Seasonality of basal soil CO₂ efflux at 10 °C soil temperature and temperature
 2 sensitivity for the different treatments of the Rax and Höllengebirge site. Model results of Eq.
 3 (1) (F_{10} , Q_{10} , R^2) for the whole campaign (All), for a mid - season (01.06. – 31.08.), and for an
 4 early/late - season (01.09. – 31.05.). Letters indicate statistical differences (p-value < 0.05)
 5 between the model parameters within one site and season.

Site	Treatment	F_{10}	Q_{10}	R^2	Season
Rax	RC	2.94 (0.15) a	3.53 (0.50) a	0.91	All
	RW07	2.10 (0.28) b	2.44 (0.38) b	0.83	All
	RW00	3.96 (0.39) c	2.40 (0.29) b	0.85	All
	RC	3.31 (0.42) a	2.46 (0.96) a	0.52	Mid
	RW07	2.55 (0.76) b	2.02 (0.60) a	0.49	Mid
	RW00	5.38 (0.79) c	1.67 (0.30) a	0.54	Mid
	RC	3.74 (0.44) a	6.91 (1.85) a	0.90	Early/late
	RW07	1.99 (0.21) b	4.45 (1.74) b	0.79	Early/late
	RW00	4.13 (0.15) a	8.62 (1.46) a	0.98	Early/late
Höllengebirge	HC	2.28 (0.12) a	3.08 (0.35) a	0.83	All
	HW09	1.44 (0.12) b	2.33 (0.19) b	0.86	All
	HW07	1.42 (0.09) b	2.49 (0.17) c	0.90	All
	HC	2.93 (0.22) a	2.02 (0.29) a	0.75	Mid
	HW09	2.00 (0.40) b	1.80 (0.32) a	0.51	Mid
	HW07	1.79 (0.17) b	2.02 (0.18) a	0.86	Mid
	HC	2.14 (0.14) a	3.37 (0.65) a	0.79	Early/late
	HW09	1.42 (0.12) b	2.17 (0.24) b	0.82	Early/late
	HW07	1.36 (0.13) b	2.53 (0.39) c	0.80	Early/late

6 Values in parentheses represent standard errors. All model parameters shown in the table were
 7 significant (p-value < 0.05).

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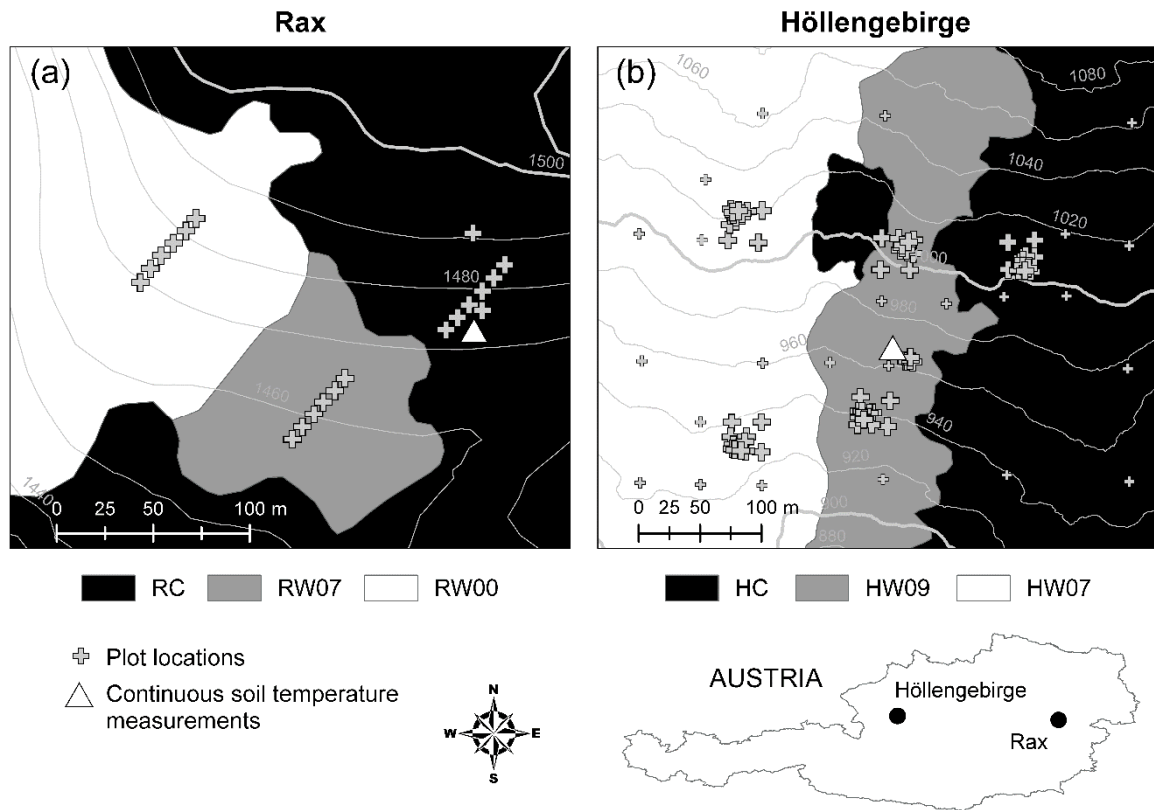
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1 **Table 4.** Pearson's correlation coefficients between F_{soil} and the ground vegetation surface
 2 cover of different plant functional types (Herbaceous vegetation, grass vegetation, tree
 3 regeneration) for the disturbed areas at Rax and Höllengebirge. Surveys were performed during
 4 the growing seasons of 2009 and 2011 at Rax and during the growing seasons of 2010 and 2012
 5 at Höllengebirge.

Variable	Rax				Höllengebirge			
	RW07		RW00		HW09		HW07	
	2009	2011	2009	2011	2010	2012	2010	2012
Herbs (%)	-0.310	0.620	0.259	-0.378	-0.169	0.141	-0.222	0.016
	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
Grasses (%)	-0.275	-0.241	0.544	0.606	0.333	-0.263	-0.337	0.426
	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	*
Trees (%)	-	-	-	-	-	-	0.373	0.188
							n.s.	n.s.
Total (%)	-0.335	0.244	0.427	0.620	-0.003	-0.081	-0.166	0.475
	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	*

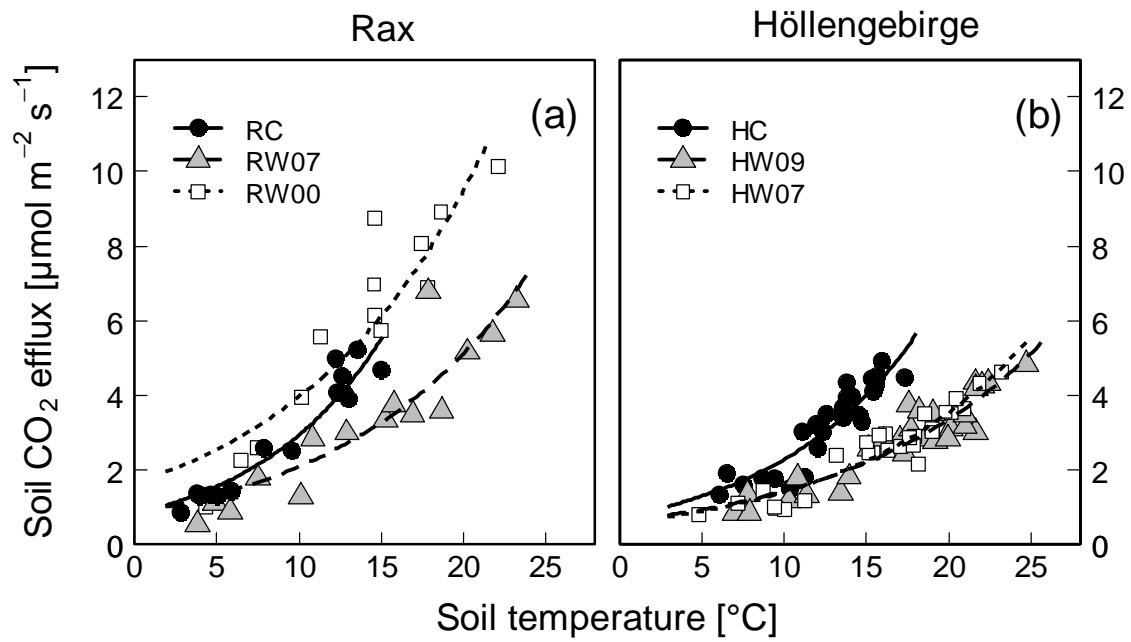
6 Significance levels: n.s., not significant; *, p-value < 0.05;

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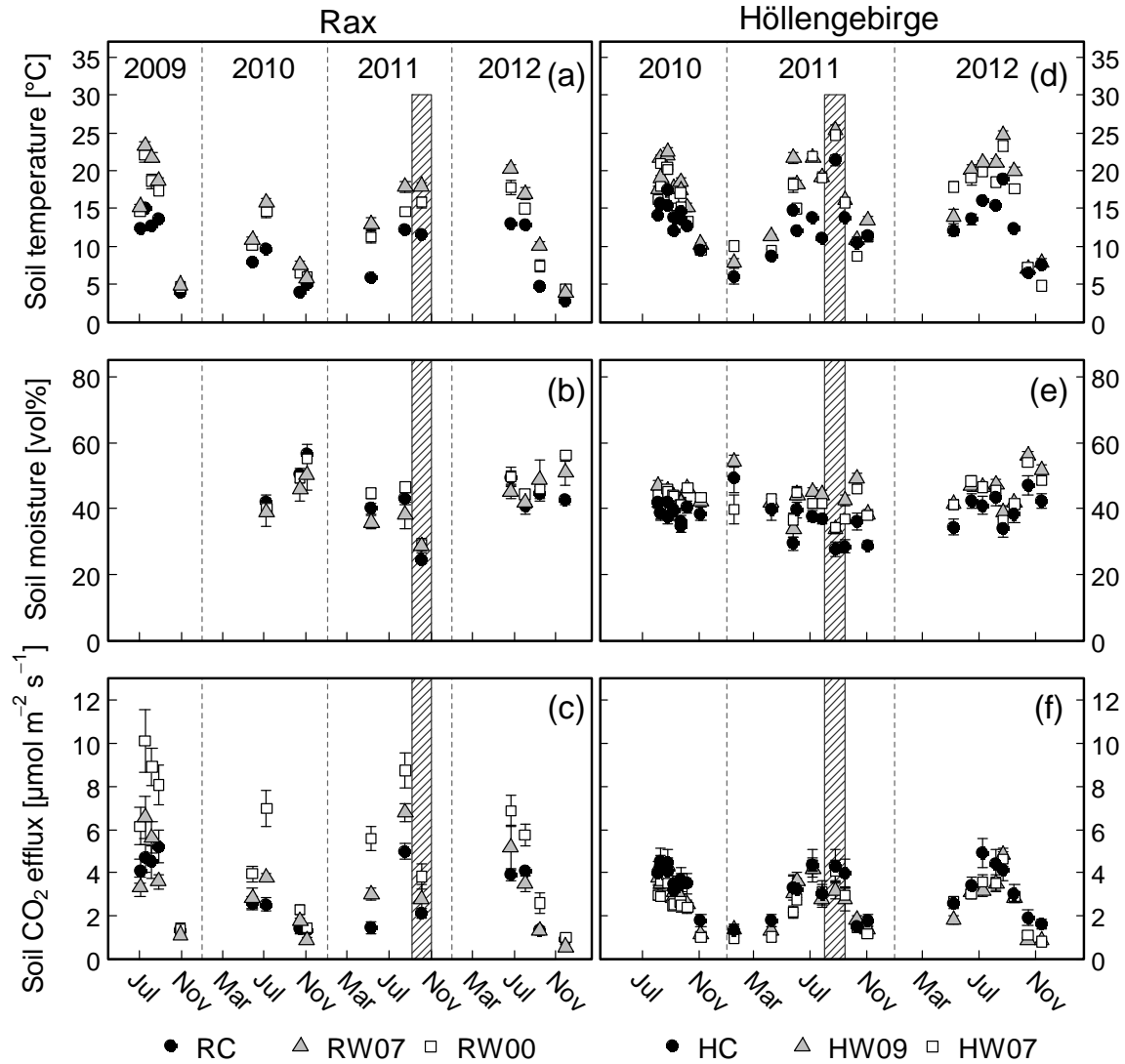
2 **Fig. 1.** Windthrow areas (white, grey) and unaffected forest stands (black) at the two study sites
 3 (a) Rax (RC, control; RW07, windthrow 2007; RW00, windthrow 2000) and (b) Höllengebirge
 4 (HC, control; HW09, windthrow 2009, HW07, windthrow 2007). Crosses represent the plot
 5 locations for soil CO₂ efflux, soil temperature and soil moisture measurements. Only plots
 6 represented by a large cross were used for analysis at the Höllengebirge site. Small crosses
 7 represent plots which were only measured in 2010 and 2011 as part of a different investigation.



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2 **Fig. 2.** Relationship between mean soil temperature and mean soil CO₂ efflux under
 3 non-limiting soil moisture conditions at **(a)** Rax (control, RC; windthrow 2007, RW07;
 4 windthrow 2000, RW00) and **(b)** Höllengebirge (control, HC; windthrow 2009, HG09;
 5 windthrow 2007, HG07). Curves show the fit of a Q_{10} function (Eq. (1)).

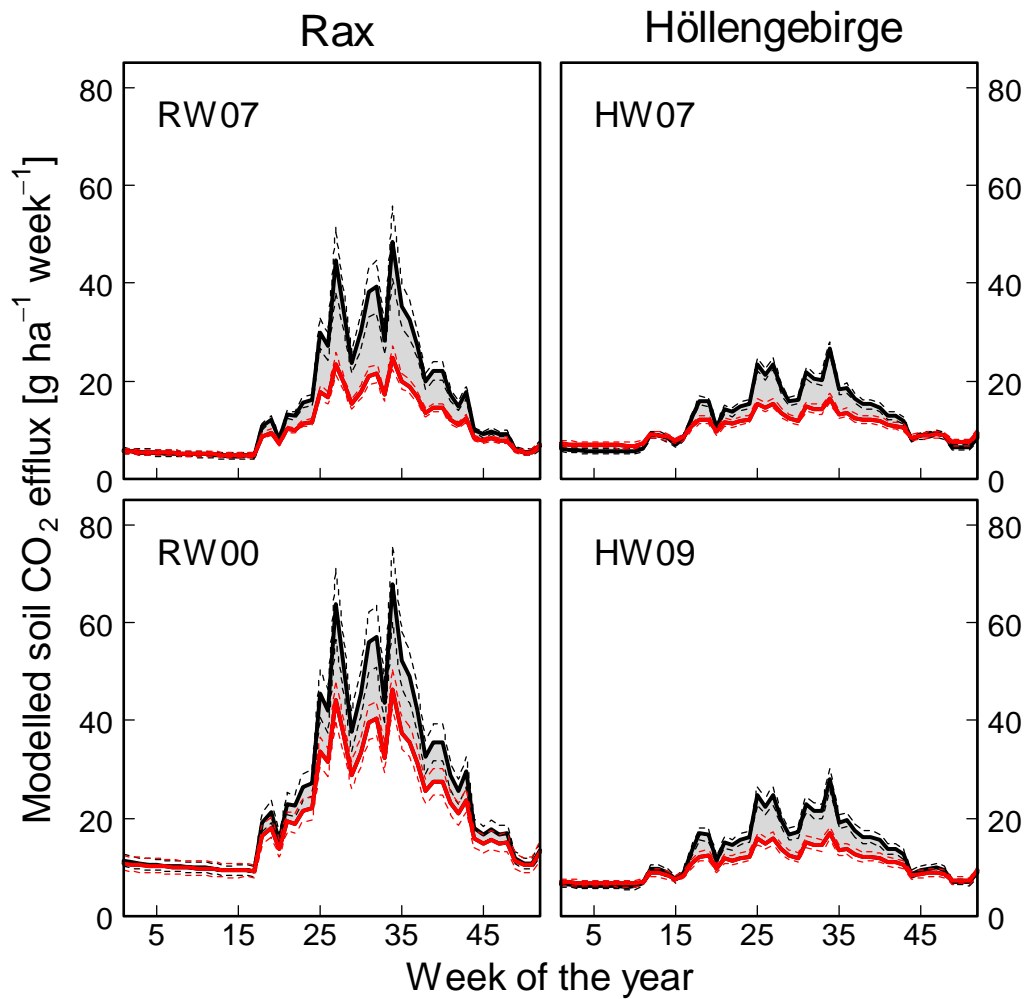
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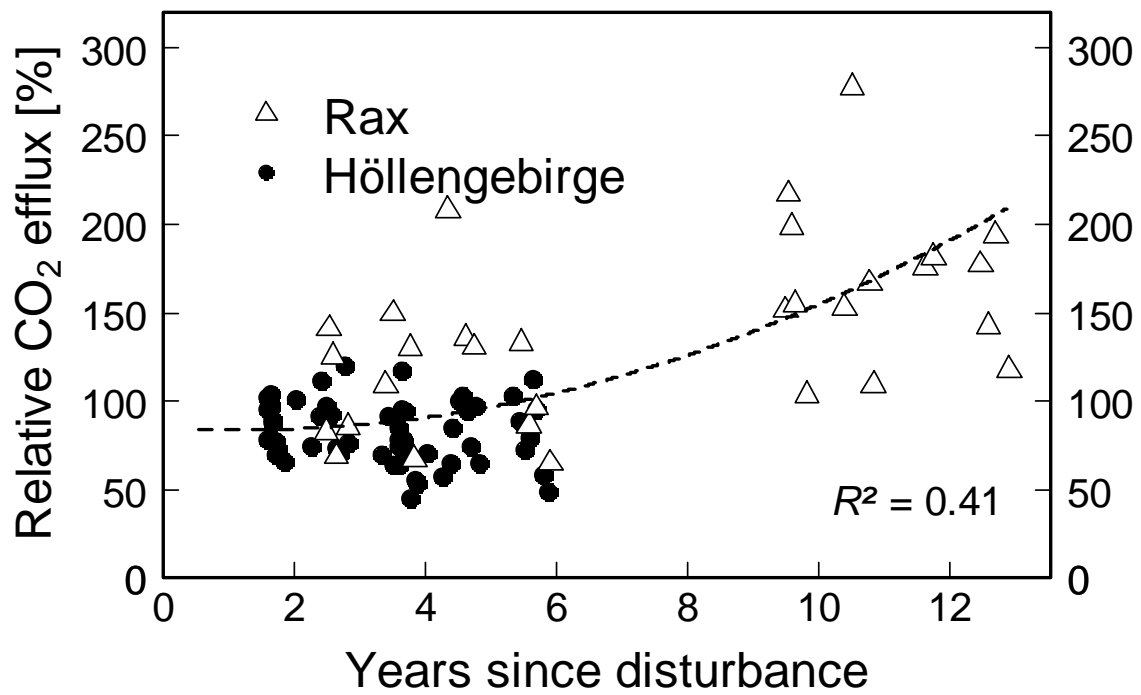
2 **Fig. 3.** Soil temperature, soil moisture and soil CO₂ efflux (F_{soil}) at Rax (a, b, c) and
 3 Höllengebirge (d, e, f) for the years 2009 to 2012. Plotted are mean values for each
 4 measurement date for Rax (control, RC; windthrow 2007, RW07; windthrow 2000, RW00) and
 5 Höllengebirge (control, HC; windthrow 2009, HW09; windthrow 2007, HW07). Error bars
 6 represent standard error of the mean (RC: n = 8, RW07: n = 6, RW00: n = 6, HC: n = 13, HW09:
 7 n = 29, HW07: n = 23). The hatched areas highlight measurement periods during water-limiting
 8 conditions.

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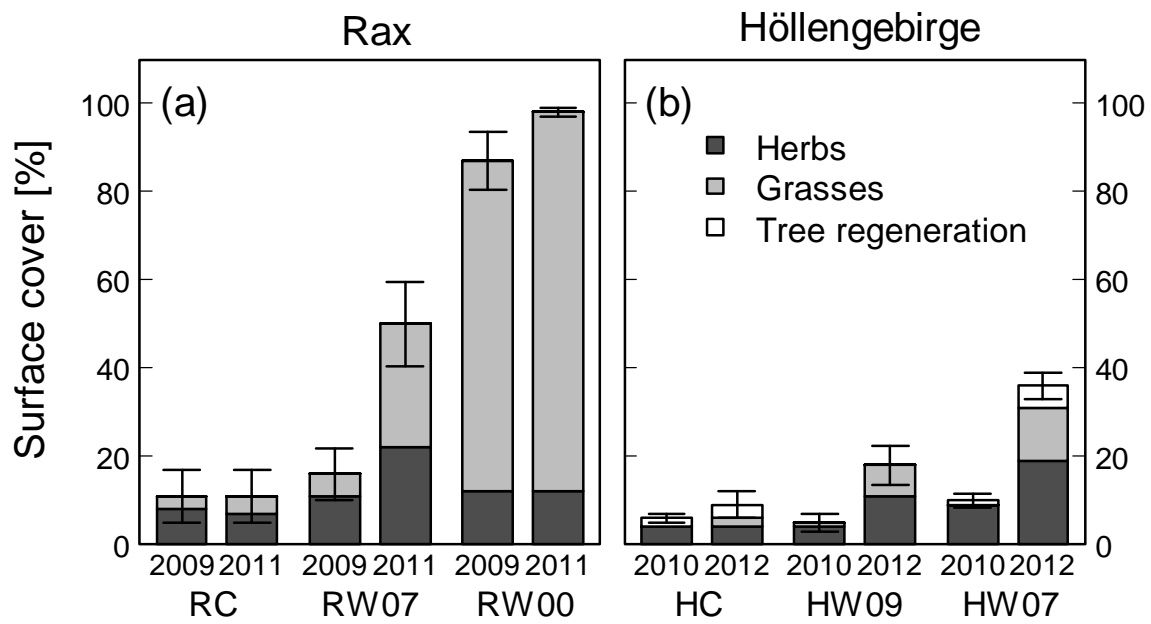
2 **Fig. 4.** Modelled annual courses of soil CO₂ efflux for the Rax (windthrow 2007, RW07;
 3 windthrow 2000, RW00) and the Höllengebirge (HG09; HG07) windthrow areas for the year
 4 2012 using actual soil temperature (black) and soil temperature of the adjacent undisturbed
 5 stand (red). The grey area represents the effect of increased soil temperature on the soil CO₂
 6 efflux of the respective windthrow areas. Dashed lines represent standard error of the mean.



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2 **Fig. 5.** Post-disturbance development of soil CO₂ efflux relative to the respective undisturbed
 3 control treatments at the Rax and Höllengebirge chronosequence.

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2 **Fig. 6.** Ground vegetation surface cover of the different treatments at **(a)** Rax (control, RC;
3 windthrow 2007, RW07; windthrow 2000, RW00) and **(b)** Höllengebirge (control, HC;
4 windthrow 2009, HW09; windthrow 2007, HW07) determined in 2009 and 2011 at Rax, and in
5 2010 and 2012 at Höllengebirge respectively. Bars represent mean values of the plant type's
6 surface cover. Error bars represent standard error of the mean total cover of the plots (RC: n =
7 8, RW07: n = 6, RW00: n = 6, HC: n = 13, HW09: n = 29, HW07: n = 23).