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Spatial heterogeneity of soil CO_2 efflux after harvest and prescribed fire in a California mixed conifer forest

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A B S T R A C T

Spatial variability is a key factor when quantifying soil CO_2 efflux and punctual measurements need to be extended to larger stand, ecosystem, or regional scales. Spatial variation also affects comparisons among ecosystems, as when quantifying effects of disturbances on ecosystem carbon dynamics. However, spatial variability of soil CO_2 efflux is still unknown and difficult to predict. We quantified the effects of silvicultural practices (prescribed fire and harvesting) on spatial variability of soil CO_2 efflux in a mixed conifer forest from the central Sierra Nevada in California, USA. Soil CO_2 efflux was measured using a portable chamber system, on 20–29 locations in four treatment sites: an untreated control, a prescribed fire site (burned in 2002 and 2009) and two clear cut sites harvested in 2010. In one of the harvested sites the soils were mechanically ripped to reduce soil compaction, a common practice done on industrial timber forest lands in the Sierra Nevada. Results showed that disturbance increased spatial variability of soil CO_2 efflux. Coefficient of variability increased from an annual average of 32% at the control site to 37% at the burned site, and 49–51% at the harvested sites (without and with soil ripping, respectively), mirroring post-disturbance increases in spatial variability of soil temperature and soil water content. Because of the post-harvest increase in spatial variability, the ability to detect differences became lower, and the number of samples needed to obtain a value representative of the full population mean (within a 10% range) increased by 100%, from 60 to 120 samples. To reduce uncertainty in our soil CO_2 efflux treatment estimates, more than 10–15 randomly selected locations per study site were necessary. Spatial variability of soil CO_2 efflux at our sites was not affected by distance between measurement locations, was correlated to fine root and litter biomass at the control site, negatively correlated to soil bulk density at the fire site, and un-correlated to soil temperature and water content at all sites. The increase of spatial variability in soil CO_2 efflux after disturbance and the requirement for a sufficient number of measurement locations should be considered when quantifying carbon dynamics of disturbed ecosystems, or assessing effects of different forest management practices.

1. Introduction

Soil-surface CO_2 efflux, commonly referred to as soil respiration, is one of the main carbon fluxes in the global carbon cycle (IPCC, 1996), and the largest carbon source to the atmosphere (60–90% of total ecosystem respiration; Liang et al., 2004) in forest ecosystems. Forest ecosystems act generally as sink of carbon, however disturbances can switch forests from carbon sinks to sources (Amiro et al., 2010; Dore et al., 2012; Thornton et al., 2002).

Disturbances can vary in type and intensity. They can range from high intensity events, such as land-use changes, stand replacing fires or clear-cut harvest, to low intensity events, such as thinning and low intensity fires. Thus forest management practices, that include removal of biomass by mechanical methods or by prescribed fire, represent a disturbance to forest ecosystems. The strength and persistence of disturbance effects are greatly determined by their impacts on soil CO_2 efflux, because even if vegetation recovers promptly after the disturbance, the carbon lost in decomposition of old and new material can exceed the newly restored carbon sink (Restaino and Peterson, 2013).

High spatial and temporal variability in soil CO_2 efflux has been found in numerous studies (Han et al., 2007; Ngao et al., 2012; Tedeschi et al., 2006; Vincent et al., 2006) and control of soil CO_2 efflux has been attributed mainly to soil temperature and soil water content (Hanson et al., 1993; Raich and Schlesinger, 1992). While these variables can explain most of the temporal variability

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of soil CO_2 efflux, they are often unable to explain its spatial variability (Tedeschi et al., 2006; Xu and Qi, 2001; Yim et al., 2003). Temporal variation of soil CO_2 efflux is relatively easy to quantify, especially with the development of techniques based on continuous measurements made using chambers (Edwards and Riggs, 2003), below canopy eddy covariance (Law et al., 1999) and CO_2 soil profiles (Jassal et al., 2005). However, spatial variability is still understudied and mostly uncertain (Ngao et al., 2012). Spatial variability of soil CO_2 efflux has been linked to several biotic and abiotic factors, such as species composition, leaf area, fine root biomass, litter depth, soil bulk density, and soil carbon content (Ngao et al., 2012). Nonetheless, the contribution of these factors is highly variable across ecosystems, sites, and seasonally within the same sites. This is because soil CO_2 efflux is the result of both heterotrophic and autotrophic processes, and these processes are controlled independently by different factors (Tang and Baldocchi, 2005).

Improved understanding of the mechanisms and quantification of the spatial heterogeneity of soil CO_2 efflux is essential to scale up from point measurements to the stand and all the way to the global scale, or to verify and/or integrate flux measurements obtained using different techniques (Dore et al., 2003). For example, when using eddy covariance, efflux of CO_2 from soil (though scaled up to the same spatial scale of eddy covariance) can replace low quality night ecosystem respiration measurements (Wohlfahrt et al., 2005), explain heterogeneity in the footprint of measured ecosystem fluxes (Ngao et al., 2012), and help partition the respiratory flux between aboveground and soil fluxes (Baldocchi, 2003). Still, determination of spatial variability is difficult and methods are limited (Tang and Baldocchi, 2005). High spatial variability requires a high number of samples to be taken to obtain meaningful results, especially when studies are aimed to detect differences among ecosystems or treatments. Common use of a relatively small number of measurements could explain in part the lack of agreement among studies quantifying effects of disturbances on soil CO_2 efflux (Kobziar and Stephens, 2006).

In addition to the high number of replicates needed, results are confounded by practical difficulties in the measurement techniques, such as the disturbance of the soil–air interface, effect of leakage, effect of pressure on diffusivity of CO_2 from soil, and the time and labor needed to take measurements in several locations. Also, because most of the factors controlling soil CO_2 efflux lie underground and are difficult to quantify, it is not possible to visually estimate spatial variability and easily evaluate the number and position of soil CO_2 efflux measurement locations.

In our study we analyzed the effect of forest management practices on spatial variability of soil CO_2 efflux. We compared four different treatment types: un-manipulated control, prescribed fire, clear cut harvest, and clear cut harvest followed by mechanical soil ripping (sub-soiling). Clear cut harvests intensely disturbed the ecosystem by totally removing aboveground biomass and affecting the soil during mechanical operations, prescribed fire was a less intense disturbance. Our aim was to: (1) quantify and characterize spatial variability of soil CO_2 efflux and its temporal changes in a mixed conifer forest in the central Sierra Nevada of California; (2) determine if spatial variability of soil CO_2 efflux was affected by the most commonly used fuel treatments and commercial harvesting methods used in these mixed conifer forests; (3) and to analyze the effects of samples size on soil CO_2 efflux estimates. To explore this we compared uncertainty of soil CO_2 efflux estimates using a different number of random subsamples compared to the full measured dataset. Second, we developed a protocol aimed to select a smallest number of soil CO_2 efflux measurement locations among the locations measured initially. Even if our protocol implies an *a priori* assessment of the spatial variability of soil CO_2 efflux, it could be useful for long term monitoring of fewer selected locations to complement/validate continuous soil CO_2 efflux or eddy covariance. Alternatively, it could be used when selecting the location for a permanent, continuous soil CO_2 efflux system, because these systems usually have a low number of chambers and thus a high risk of measuring locations that do not represent a larger area.

We had the opportunity to characterize the spatial and temporal variability of soil CO_2 efflux in an area subject to a range of disturbance severity but with generally the same climate, vegetation, management history, and soil type. In addition, the treatments created conditions ranging from the high autotrophic contribution of an undisturbed, dense forest, to the single heterotrophic contribution of a clear cut harvested stand.

2. Methods

This study was conducted at Blodgett Forest (38°54′N, 120°39′W), a University of California Research Station in the central Sierra Nevada near Georgetown, California, that is actively managed as a commercial timberland. Total annual precipitation in the mixed-conifer forest located between 1100 and 1410 m a.s.l. averages about 1600 mm, falling between September and May, and almost absent in the summer (Stephens and Collins, 2004). The average minimum daily temperature in January is 0.6 °C and the average maximum daily temperature in July is 28.3 °C. The winter is wet and cold with an average of 254 cm of snow (Xu et al., 2001). The most common tree species in this forest include sugar pine (*Pinus lambertiana*), ponderosa pine (*Pinus ponderosa*), white fir (*Abies concolor*), incense-cedar (*Calocedrus decurrens*), Douglas-fir (*Pseudotsuga menziesii*), and California black oak (*Quercus kelloggii*). The mineral soils are underlain by Mesozoic granitic material and are predominantly classified as the Holland and Musick series (fine-loamy, mixed, semiactive, mesic Ultic Haploxeralfs; Olson and Helms, 1996).

This study compares soil CO_2 efflux from four different treatment types: prescribed fire (FIRE), un-manipulated control (UND), and clear cut harvest (HARV) with and without mechanical soil ripping (RIP and NO_RIP; Fig. 1). The sites are generally subject to the same climatic and edaphic conditions because of their close proximity (less than 10 km apart). The FIRE and UND sites were established in 2001 as part of the Fire and Fire Surrogate Study (FFS), which investigated the effects of fuel treatments on vegetation structure and fuel loads at 13 locations across the US (Stephens and Moghaddas, 2005; McIver et al., 2013). The FIRE site was burned initially in the fall of 2002 and burned a 2nd time in the fall of 2009. In addition, we used four small clear cut harvest areas treated in summer 2010 (each between 2000 and 7000 m^2). In these areas all trees were removed and the residual material was piled and burned. In two of the four units soils were mechanically ripped (sub-soiled), a common post-harvesting practice used in the region to prepare the soil for tree planting. Data on forest structure (Table 1) shows conditions at all sites were similar prior to treatments. The prescribed fire treatments in 2002 and 2009 decreased stand canopy cover and tree density compared to the UND site (Table 1 and Stephens et al., 2012). Clear cut harvest removed almost all aboveground biomass except for down wood that was not consumed in the burn piles (Table 1). In fall 2010, the logged areas were planted with 1 year old saplings (in couples) on a 5 × 5 m grid (840 plants per ha). The saplings in 2012 had diameter of circa 3 cm at the plant base, and height of circa 50 cm.

We measured soil CO_2 efflux using a Li-6000 and later a Li-6400 with the soil chamber attachment (Li-Cor, Lincoln, USA) every two weeks at 110 locations (at each of the four sites we measured 20–29 locations and each measurement covered an area of 80 cm^2) over a two-day period during snow free periods, starting in June

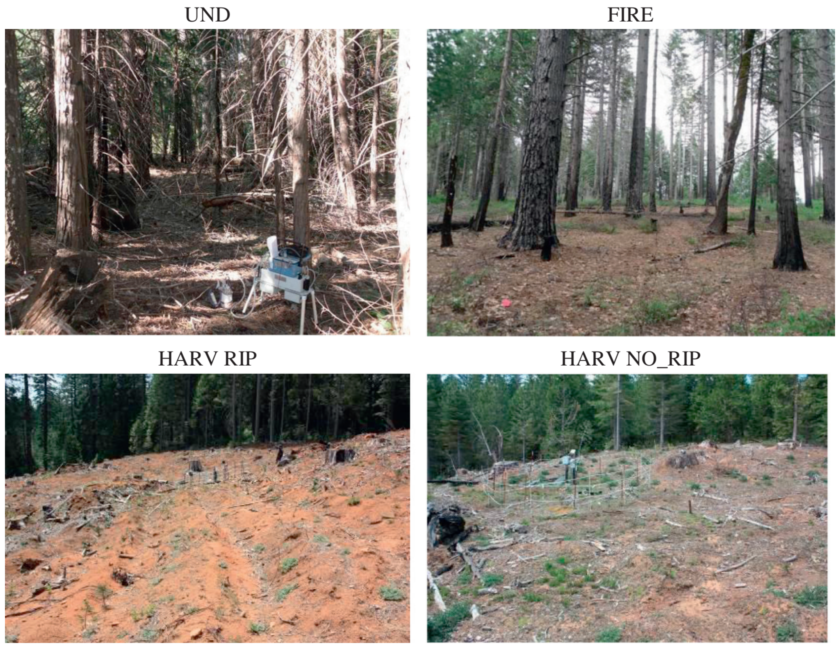

Fig. 1. Photographs illustrating the four sites at Blodgett Forest: UND control site; FIRE prescribed burned site and the post clear cuts harvest treatment (HARV), with (RIP) or without (NO_RIP) soil treatment preparation before the plantation of new trees.

Table 1
Stand biotic and abiotic characteristics (± standard error) of undisturbed-control (UND), prescribed fire (FIRE), and harvest sites (HARV).

				UND	FIRE	Avg	HARV NO_RIP	RIP
Tree density		(N ha^{-1})	PRE	558 (±47)	476 (±52)	550 (±110)		
			POST1	549 (±45)	393 (±43)	840		
			POST7	534 (±36)	282 (±19)	632 (±20)		
Biomass		(Mg ha^{-1})	PRE	426 (±44)	389 (±20)	534 (±145)		
			POST1	444 (±43)	389 (±26)	1×10^{-6} (±0.2×10^{-6})		
			POST7	500 (±47)	398 (±27)			
Canopy cover		(%)	PRE	70	69	68		
			POST1	75	65	0		
			POST7	78	66	0		
Soil C	0–5 cm			2435 (±183)	2453 (±162)		2866 (±304)	2321 (±222)
	5–15 cm	(g m^{-2})		3906 (±280)	3186 (±172)		3958 (±721)	3025 (±250)
	0–15 cm			6341 (±269)	5639 (±228)		6824 (±605)	5346 (±303)
Litter		(g m^{-2})		702 (±75)	383 (±41)		408 (±91)	126 (±37)
Soil bulk density	0–5 cm	(g cm^3)		0.65 (±0.03)	0.92 (±0.02)		0.76 (±0.05)	0.82 (±0.05)
	5–15 cm			0.79 (±0.04)	0.74 (±0.08)		0.85 (±0.1)	0.89 (±0.02)
Soil temperature		(°C)		9.7 (±0.3)	10.7 (±0.3)		12.9 (±0.3)	14.3 (±0.4)
Soil water content		(m^3 m^{-3})		0.26 (±0.006)	0.29 (±0.005)		0.29 (±0.005)	0.33 (±0.004)
Fine roots		(g m^{-2})		517 (*±162*)	583 (*±203)*		143 (±66)	191 (*±137*)

Pre-treatment data (PRE) was collected in 2001 for control and fire treatment sites, and 2010 for harvested sites. Post-treatment data were collected the first year after treatment (POST 1) and seventh year after treatment (POST 7). Biomass was the sum of aboveground and coarse root biomass. For the FIRE and UND sites, biomass and tree density data represent the average of three units where trees >5 cm diameter were measured in 20, 0.40 ha plots. At the HARV site we measured 4, 0.40 plots. Litter and soil bulk density were collected in proximity of each soil CO_2 efflux collar (20–29 samples per site). Soil carbon was collected at 18 randomly selected locations per site among the soil CO_2 efflux collars, and fine root (<2 mm diameter, 0–30 cm) at 10 randomly selected locations per site among the soil CO_2 efflux collars. Soil temperature (at 10 cm in the mineral soil) and soil water content (0–5 cm) represent the mean of daily data for 2012.

2011 and continued until end of 2012. In spring 2012, measurements made in the field using the Li-6000 and Li-6400 were compared and consequently 2011 data were corrected for the 15% difference ($r^2 = 0.95$) found between the two instruments. Measurements were restricted to the interval from 9:00 to 17:00 h to limit the effect of daily fluctuations in soil CO_2 efflux and the order of the sites and plots changed randomly, always measuring the UND and FIRE site and the RIP and NO_RIP sites in the same day. During measurements the chamber was positioned on 10-cm diameter PVC soil collars, installed 1 cm in the soil to avoid disturbance during measurements and allowing the repeated measurement of the same locations. Soil CO_2 efflux was calculated from the change of CO_2 concentration over time and averaged for two cycles over a 10 ppm range encompassing the ambient CO_2 concentration. Soil water content (SWC, measured at 0–5 cm depth using a HH2 and ML2x, DeltaT devices, Cambridge, UK) and soil temperature (Ts, measured at 10 cm depth using a 6000–09TC, Licor, Lincoln, USA) were measured nearby each soil CO_2 efflux collar.

Measurements in the FIRE and UND treatments were collected on 29 different locations at each of the two sites. In the harvested areas, we measured soil CO_2 efflux in 20 different locations at both the RIP an NO_RIP treatments. Twelve additional collars were positioned in the untreated forest adjacent to the harvested area (total of 110 locations). Measurement locations at each treatment site were distributed in 4 different plots (circa 30 $\times$ 30 m each), each with 6–11 randomly selected locations. The four plots per treatment site were scattered throughout the sites to sample different slopes, vegetation type and density, and fire intensity. The plots were located 30–200 m apart in the UND and FIRE sites, and in two different plots located 300 m apart at the HARV sites. At the UND and FIRE sites, the four plots were scattered over a total area of circa 150×200 m and at the HARV site over an area of circa 150×400 m. At the HARV site collars were randomly positioned relative to the saplings and the mounds produced by the soil ripping. One-way analysis of variance (ANOVA) was performed among plots at each treatment site at every measurement date. No differences were found among any of the four plots for the UND, FIRE, and at the HARV sites for any dates, so we treated single measurement locations as independent. Distance between each pair of collars was recorded at each site at 1 m precision.

Fine root biomass was measured in summer 2012. Samples of 5 cm diameter were collected on 10 locations adjacent to randomly selected soil CO_2 efflux collars at each of the four sites, at two depths (0–15 cm and 15–30 cm). Fine roots were hand-picked and separated in <2 mm, and 2–5 mm diameter classes, without distinction between live and dead roots. Dry weight was determined after drying samples at 70 °C until constant weight. Litter was collected inside each soil CO_2 efflux collar at the end of 2012. Dried litter (70 °C for 4 days) was divided into leaves and woody components. Bulk density was determined on 5 cm diameter and 5 cm high soil samples collected inside each soil CO_2 efflux collar after removing the litter.

Spatial variability was expressed in terms of the coefficient of variation (CV). To assess the ability of the measurement locations to capture the spatial variability in soil CO_2 efflux, at each site we quantified the number of samples necessary to reach a mean within 10% and 20% (95% confidence levels) of the full population mean (Davidson et al., 2002). To calculate this we used the following equation

$$n = \left[\frac{t \cdot s}{range/2}\right]^2 \quad (1)$$

where n is the sample size, t is the t-statistic (two-way test) for a given confidence level (in our case 95% confidence level) and degrees of freedom, s is the standard deviation of the full population (all locations during one day), *range* is the width of the desired interval around the full population mean in which a smaller sample mean is expected to fall (±10%, ±20% of the full population mean).

By rearranging the above equation, considering the number of plots effectively used at each site, the minimum detectable soil CO_2 efflux difference from the measured mean δ can be calculated as (Zar, 1999):

$$\delta = \sqrt{\frac{s^2 \cdot t}{n}} \quad (2)$$

In addition, to characterize soil CO_2 efflux variability in space, we quantify how the distance between measurement locations was correlated with the soil CO_2 efflux rate. We considered that if soil CO_2 efflux was dependent on its location, the difference between rates measured in locations separated by a set distance would be on average different from zero, and this difference would increase at increasing distances. We applied the concept of drift (first-order moment of the respiration increments) using the following equation (Vauclin et al., 1982):

$$D(k) = \frac{1}{n(k)} \sum_{i=1}^{n(k)} (Rs_1 - Rs_{i+k}) \quad (3)$$

where D is the drift, Rs the soil CO_2 efflux, and n the number of pairs of locations at distance k (i and $i + K$).

We also applied the Moran's I test (Moran, 1950; Chen, 2013) to investigate whether the observed value of the variable at one locality is dependent on the values at neighboring localities. If such dependence exists, the variable is said to exhibit spatial autocorrelation. I varies from -1 to +1, the expected value approaching zero in the absence of autocorrelation.

For each site and date with highest spatial variability, we calculated the difference in soil CO_2 efflux rates for each pair of measurement locations and their relative distance. We then averaged the soil CO_2 efflux differences between pairs of locations over 5 m distance classes between 5 and 50 m, and in 100 m classes between 100 and 300 m. In general, shortest distances were found within the plots, medium between the farthest locations in the plots, and maximum among plots. We selected only classes with more than 10 measurements.

As a way to optimize the number of samples needed to obtain a representative estimate of soil CO_2 efflux at each site, we quantified the uncertainty of subsets of increasing number of samples using a bootstrapping resampling (with replacement) exercise. We randomly selected 1000 times, 5, 10, 15, 20, 25, samples over the 29 total at the UND and FIRE sites, and 5, 8, 11, 14, 17 samples over the 20 total at the HARV sites. For each different number of samples, we calculated the mean and 95% confidence interval of the 1000 randomly determined subset.

A different analysis describes a protocol intended to select fewer appropriate measurement locations among an initial larger sample. Also in this case we aimed to reduce sample size, for example to reduce costs when monitoring long term soil CO_2 efflux or when selecting the best location for a continuous measurement system. The method involved an initial period to assess spatial variability and the selection of specific locations at each site, as opposed to the random selection of locations of the previous analysis. The selected subsample should represent the full sampled soil CO_2 efflux population and should reproduce its seasonal variations. Due to the different spatial variability among treatment sites, a different number of plots would be needed at each site. We defined as sufficiently accurate the subsample that would produce a mean that included a range of ±1% of the total soil carbon released over the 6 months measurement period in 2012, and would explain >90% of the variability observed in the field (over the 11 measurement dates in 2012). We calculated the total soil carbon emission between the first and the last measurement date (May to October 2012) using a linear extrapolation of soil CO_2 efflux rates between consecutive dates. We believe the 6 months total soil CO_2 efflux is an appropriate metric because in the sum of soil CO_2 soil fluxes are weighted by their seasonal frequency and importance. To develop our protocol we analyzed the soil CO_2 efflux seasonal rates measured at each location (Fig. 2). The specific contribution of each location was maintained for most of the growing season, even if absolute values of fluxes varied seasonally. Thus, at each site and every measurement date, soil CO_2 efflux locations were ranked by their relative magnitude. We expressed the order as percentage rank to take into account missing data. Ranks were averaged over all measurement dates in 2012 to minimize the effects of outliers. Thus every site had a general order of its measurement location, where the location ranked first was the location with, on average, highest fluxes and the last the location with, on average, lowest fluxes. At each site we selected an increasing number of locations. Selections started with plots that were the closest to the median (ranking in the middle of the order) and then adding plots that ranked increasingly farther above/below the 50% value. For each subset we computed the total, May–October soil CO_2 efflux, and the coefficient of determination (r^2) between the mean soil CO_2 efflux measured each date on the sub-sample and on the full dataset. We determined the minimum number of samples necessary to obtain a total soil flux that was less than 1% from the total calculated

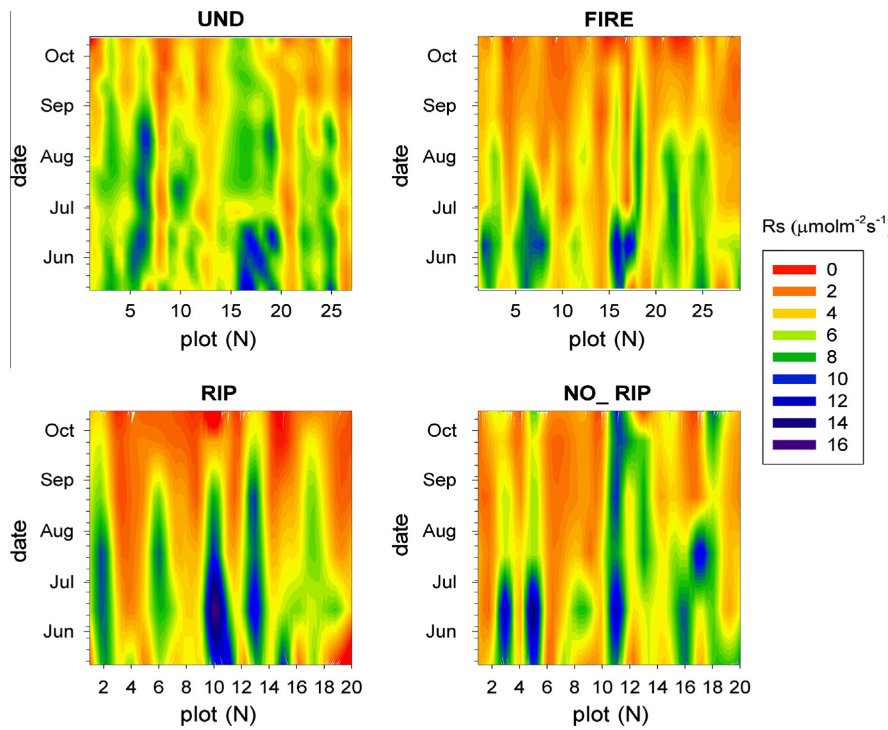

Fig. 2. Soil CO_2 efflux (Rs) measured during April–October 2012 at each of the locations at the control (UND), fire (FIRE), and harvested soil ripped (RIP) and not ripped (NO_RIP) sites.

on the full set of locations (around 10 g C m^{-2} over a 6 month period), and a $r^2 > 0.9$ over the 11 measurements dates in 2012.

Repeated measures ANOVA was used to assess differences in CV among sites. We analyzed the relationship between abiotic factors (soil temperature and water content) and the seasonal variation of CV of soil CO_2 efflux. In addition, we analyzed the relationship between biotic and abiotic factors and the fluxes measured at each collar. A stepwise backward regression was used to analyze multiple regressions between biotic and abiotic variables and soil CO_2 efflux CV or single locations fluxes at each site. We also performed this analysis on data pooled from all sites.

Soil temperature (at 10 cm depth) and water content (0–5 cm) relationships with soil CO_2 efflux were analyzed at each site for each measuring date and in addition, for the average of 2012, for the period with most active soil CO_2 efflux (May and June), and the period when water availability and temperature were more limiting (September and October).

At each site we analyzed the Pearson correlation coefficient between litter (woody, leaves and total), root biomass (<2 and <5 mm diameter on a 0–15 cm and 0–30 cm depth), superficial soil bulk density (in the first 5 cm), soil carbon (0–5 cm, 5–15 cm and 0–15 cm), soil temperature and water content, and the mean soil CO_2 efflux in 2012. We assumed variations of soil carbon or soil bulk density on a time scale shorter than the year are difficult to detect (Jandl et al., 2013), and litter layer differences among locations were preserved through the seasons. However, fine root biomass varies seasonally, especially relative to the soil CO_2 efflux measurement collars. Thus, we also analyzed the relationship between fine root biomass and soil CO_2 efflux averaged over July 2012, when fine roots were sampled.

3. Results

Soil CO_2 efflux varied in space, and this spatial variability differed among treatments ($p < 0.001$) and in time. Coefficient of variation (CV) was lowest at the UND site, was slightly higher at the FIRE site and highest at the HARV sites, mirroring the intensity of disturbance (Fig. 3). CV in soil CO_2 efflux was highest at the beginning of both spring and fall.

We can be confident that the higher CV at the HARV site was not caused by a difference in the site characteristics, such as a different topography and hydrology, because the CV of soil CO_2 efflux measured in the undisturbed forest immediately adjacent to the harvested areas ($n = 12$) was significantly lower than the CV at the harvested sites ($p < 0.01$), and not different ($p = 0.78$) than the CV of soil CO_2 efflux in the UND site (data not shown). There was not a strong relationship between CV of different treatments, even when they were only 100 m apart. When we analyzed the relationship between the CV at the FIRE and HARV sites and the simultaneously determined CV at the UND site we found a weak association between the variables. The correlation coefficient of the relationship between CV at the UND and CV at the HARV and FIRE sites was between −0.13 and 0.13 (data not shown). The correlation coefficient of the relationship between the CV at the HARV site and the CV of the measurements at the un-treated forest immediately adjacent to the HARV site fell in the same range. However, the correlation coefficient between the CV at the UND site and the CV at the un-treated forest adjacent to the HARV site was 0.83, showing that the low correlation between undisturbed and disturbed forests was due to the treatments and not to the different location of the sites.

Soil CO_2 efflux rates measured during one season at each location (Fig. 2) displayed how spatial heterogeneity differed among sites. The UND site had similar fluxes at most of the locations, while locations at the RIP site had extreme, mostly very low or high, fluxes.

Soil temperature (Ts) and soil water content (SWC) also showed an increase in CV with increasing disturbance intensity (except for CV of SWC at the fire site, Fig. 3). However, maximum absolute CV of soil CO_2 efflux reached 60%, CV of Ts was 20% and SWC more than 100% (Fig. 3). Effects of disturbances on CV mirrored effects

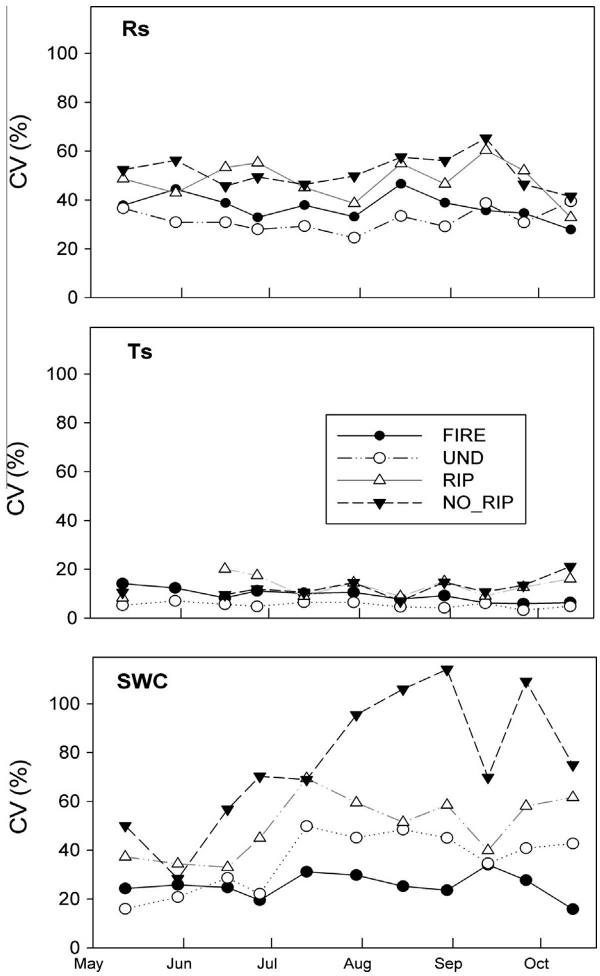

Fig. 3. Coefficient of variation in soil respiration (Rs), soil temperature (Ts), and soil water content (SWC) at the control (UND), fire (FIRE), and harvest no soil ripped (NO_RIP) and soil ripped (RIP) sites. Data were collected from May to October 2012.

on climatic conditions. Disturbances reduced the stand canopy cover, particularly the clear-cut harvest (Table 1), with a consequent increase in the amount of energy reaching the ground and a decrease in the water used by vegetation through transpiration. A comparison of Ts and SWC measured simultaneously at the sites (1 to 1 relationship), showed that, compared to the UND site, Ts was 4% higher at the FIRE and 21% at the HARV site; and SWC was 14% higher at the FIRE and 35% higher at the HARV site (data no shown). In general, the HARV site had the most extreme micro-environment conditions (Ts, SWC), while the UND site the least variable of all sites.

The Moran I test resulted in no spatial autocorrelation and a random distribution of the sampled soil CO_2 efflux locations at each site. The coefficients were −0.088 at the UND site, 0.019 at the FIRE sites, −0.16 at the RIP and −0.064 at the NO_RIP site, values that were not different from the expected value in case of no autocorrelation (−0.036 at the UND and FIRE sites; −0.05 at the RIP and NO_RIP sites). Also the Drift, expressed as the mean soil CO_2 efflux difference between pairs of locations at set distances, had no clear trend of increasing difference for increased distance (Fig. 4). No clear trend was also found for Ts and SWC. Analyzing the relationship between differences in soil CO_2 efflux and the corresponding differences in SWC and Ts at different distances, we found that differences in soil CO_2 efflux at different distances were explained mostly by the corresponding differences in SWC at the UND site ($r^2 = 0.35$; $p = 0.09$), by differences in Ts ($r^2 = 0.53$; $p = 0.01$) at the FIRE site, and was not related to Ts or SWC ($r^2 < 0.1$) at the RIP and NO_RIP sites.

The variability of soil CO_2 efflux found at each site had direct impact on the ability to measure soil CO_2 efflux, and to detect differences among treatments. The number of samples necessary to obtain mean values ±10% from the full population mean ranged between 55 samples at the UND site to 125 at the RIP site (Table 2). Broadening the desired interval to ±20% around the population mean, the number of samples ranged from 14 at the UND site to 31 for the RIP site (Table 2). During 2012, the optimal number of samples was constant at the UND site, but varied with season at the FIRE site, and had the highest seasonal variation, reaching the highest values in the fall at the HARV RIP and NO_RIP sites (Fig. 5a).

The minimum disturbance effect possible to detect, defined as the smallest detectible difference from the measured mean (δ) ranged from 0.7 to 0.8 μmol m^{-2} s^{-1} for the UND and FIRE sites, and 1.15–1.20 μmol m^{-2} s^{-1} for the HARV sites (Table 2). The δ varied seasonally (Fig. 5b), and during 2012 generally decreased from spring (higher fluxes and variability) to the fall (smaller fluxes and variability).

In a bootstrapping resampling exercise, subsamples of increasing size were randomly selected 1000 times. We expressed the uncertainty of the subsamples as coefficient of variability, because it expresses variability independently from the magnitude of the measured fluxes, allowing a better comparison of the four treatment sites. The analysis showed that the uncertainty was highest for subsamples smaller than 10, and highest, and similar, at the FIRE and HARV sites, compared to the UND site. The influence of sample size decreased for subsamples larger than 15 locations (Fig. 6).

Our method to reduce the number of measurement locations, selecting locations based on their relative magnitude, led to large differences among treatments (Table 3). At the UND site, selecting only three locations was sufficient to have a 2 g C m^{-2} difference over the 6 month period and to explain 91% of the variability observed in the same period on the full measurement set ($n = 11$). Eleven measurements were necessary to meet our criteria at the FIRE site, and 13 measurements were needed for both the RIP and NO_RIP sites.

As an example, we describe results of the application of our method to the harvested NO_RIP site, where spatial variability was high compared to the other sites, and thus the reduction of the number of location more uncertain. We applied the method to the 2012 data and, as a result, our full dataset was reduced from 20 locations to 11 selected locations. We then tested our results using the six available date in 2011. The difference between the full dataset mean fluxes and the subset mean fluxes (Fig. 7) was on average 0.09 μmol m^{-2} s^{-1} of CO_2 (−1.3%) in 2011, reaching a maximum value of 0.18 μmol m^{-2} s^{-1} of CO_2 (1.7%). Over the entire period 2011 and 2012, the difference between the full dataset mean flux and the subset mean flux was 3% ($r^2 = 0.98$; Fig. 7), with a maximum difference of 0.4 μmol m^{-2} s^{-1} of CO_2.

In the analysis linking spatial variability of soil CO_2 efflux to abiotic and biotic factors (Table 4), only few significant relationships were found. Relationships and factors differed among sites. Soil temperature and SWC were not able to clearly explain spatial variation of soil CO_2 efflux at any measuring date at any treatment sites. However, they were in part associated with the seasonal trend of CV of soil CO_2 efflux (Table 4 a). At the UND site, only fine root and litter biomass were significantly correlated with soil CO_2 efflux. At the FIRE site, only soil bulk density (0–5 cm) was correlated (negatively) to soil CO_2 efflux. At the HARV site, soil CO_2 efflux was un-correlated with fine root biomass, litter, surface soil bulk density or soil temperature and water content. There was no significant correlation with soil temperature or water content even when the relationship was restricted to temperature or water limiting periods.

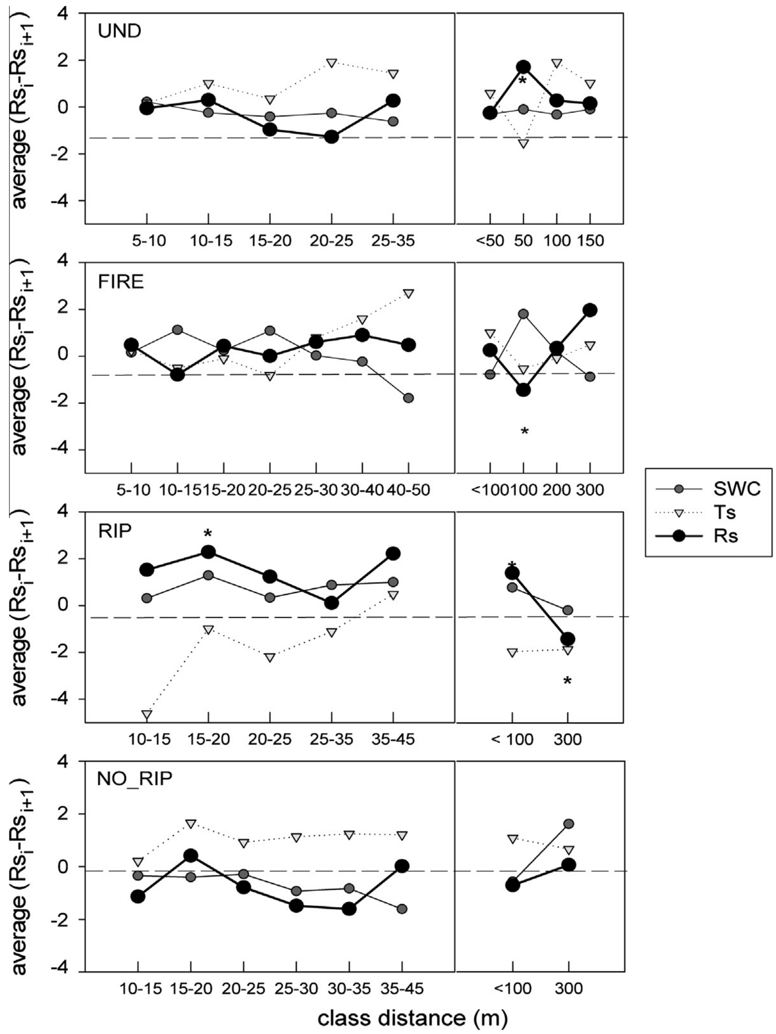

Fig. 4. Trend of the average difference of the soil CO_2 efflux (Rs, in μmol m^{-2} s^{-1}), soil temperature (Ts, in C°) and soil water content (SWC, in vol.%) between pairs of locations over 5 m distance classes (in the left panels) and 50–100 m classes (in the right panels), at the control (UND), fire (FIRE) and harvested soil ripped (RIP) and not riped (NO_RIP) sites. * Indicates difference statistically different from zero (α = 0.05).

Table 2
Number of measurements of soil CO_2 efflux required to be within ±10 and ±20% of the full population mean at the 95% confidence level (in the first two columns) and minimum detectable difference from the measured soil CO_2 efflux mean (α = 0.05 and 0.1) in the last two columns.

Treatment site	±10% Of mean (N)	±20% Of mean (N)	δ 95% (μmol m^{-2} s^{-1})	δ 90% (μmol m^{-2} s^{-1})
UND	60	15	0.69	0.57
FIRE	55	14	0.81	0.67
NO_RIP	121	30	1.16	0.95
RIP	125	31	1.22	1.01

Data are the average of all measurement dates.

4. Discussion

In this study we quantified the effects of silvicultural practices (prescribed fire and harvesting) on spatial variability of soil CO_2 efflux in a mixed conifer forest in the central Sierra Nevada. Spatial variability increased after disturbance, particularly after harvest, despite the harvested site being less complex and heterogeneous than the undisturbed stand. The harvested areas had minimal vegetation cover, consisting of one year old conifer seedling planted on a 2.5 m grid, and thus minimal autotrophic respiration, fine root biomass, and litter layer. The increase in spatial variability of soil CO_2 efflux after disturbance may be explained by the lack of the buffering effect of the canopy primarily, followed by the litter layer, in this forest ecosystem.

Harvest or prescribed burn reduced or removed the overstory canopy, allowing more energy to reach the ground. Post-disturbance soil temperature and soil water content were higher compared to the undisturbed forest, and they were characterized by a higher spatial variability. This may have created conditions that strongly impacted soil processes and small scale heterogeneity. That treatment increased sensitivity to environmental factors was also found by Kobziar and Stephens (2006). A second cause of the increased spatial variability of soil CO_2 efflux can be the high heterogeneity of belowground carbon pools as a consequence of

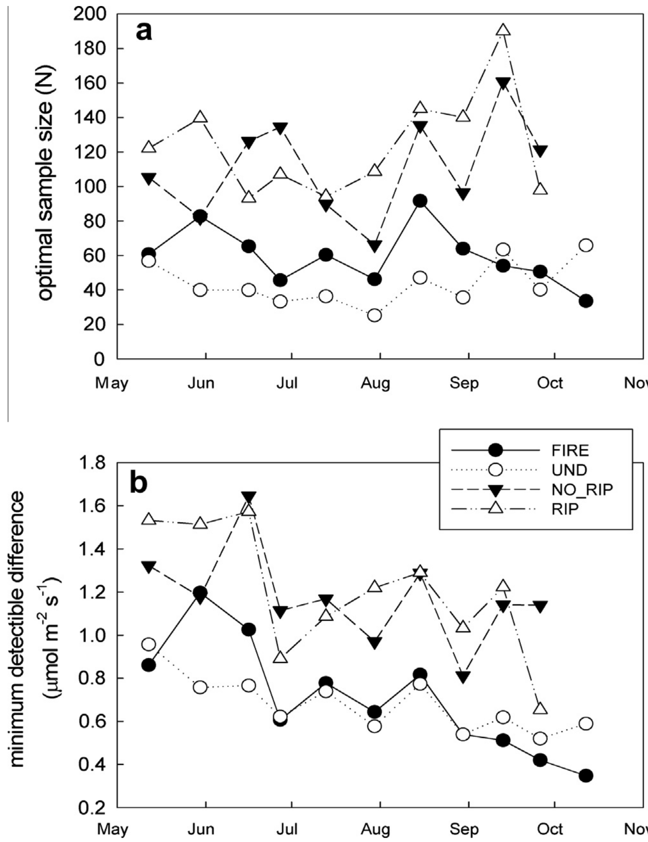

Fig. 5. Seasonal trend (2012) at the control (UND), fire (FIRE), harvested soil ripped (RIP) and not soil ripped (NO_RIP) sites of a) the number of random locations of soil CO_2 efflux measurements needed to obtain a mean value included in a 10% range of the full population mean (95% confidence level), (b) minimum difference from the mean detectable (with 95% confidence), considering the number of plots effectively used at each site (29 at the UND and FIRE sites, 20 at the RIP and NO_RIP sites).

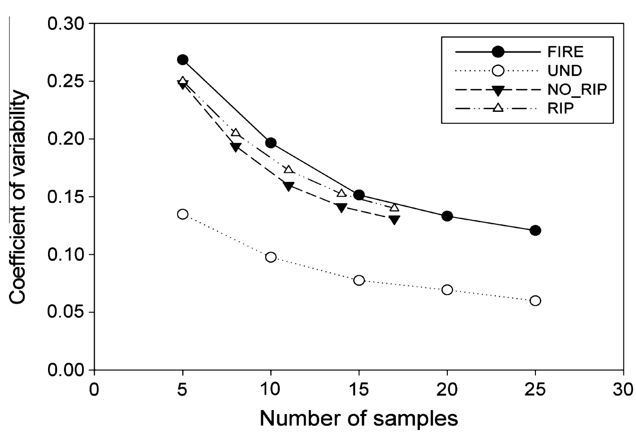

Fig. 6. Coefficient of variability for 1000 randomly selected locations of subsamples of increasing size at the control (UND), fire and harvested soil ripped (RIP) and not ripped (NO_RIP) sites.

the harvest practices. During the mechanized clear cut harvest with soil ripping, the fine roots, litter, superficial organic soil layer, coarse woody debris, and herbaceous vegetation were displaced or buried under the soil surface, creating highly localized below-ground pools.

Our undisturbed forest soil CO_2 efflux CV compared well with CV of forest ecosystems in previous studies. For example, several studies (Adachi et al., 2005; Ngao et al., 2012; Ohashi and

Table 3
Effect of increasing sample size of selected few locations among the full sampled population.

		All	$N = 3$	$N = 5$	$N = 7$	$N = 9$	$N = 11$	$N = 13$
UND	r^2		0.91	0.91	0.96	0.97	0.95	0.93
	Diff (g C m^{-2})		2	−1	−8	−12	3	−4
	Tot (g C m^{-2})	924	922	924	932	935	921	928
FIRE	r^2		0.77	0.94	0.92	0.93	0.96	0.96
	Diff (g C m^{-2})		39	50	39	40	−0.3	0.0
	Tot (g C m^{-2})	781	742	731	742	741	781	781
RIP	r^2		0.96	0.78	0.84	0.95	0.97	0.99
	Diff (g C m^{-2})		87	38	78	80	65	5
	Tot (g C m^{-2})	760	673	722	683	680	695	755
NO RIP	r^2		0.44	0.50	0.86	0.85	0.93	0.95
	Diff (g C m^{-2})		90	87	61	40	27	−5
	Tot (g C m^{-2})	779	689	691	718	739	752	784

Cumulative soil flux is compared (Diff) to the 6 months total (Tot). Coefficient of determination r^2 between daily mean and sub-sample mean, at the control (UND), prescribed fire (FIRE), and harvested ripped and not ripped (RIP and NO_RIP) sites. In bold the minimum number of location required to reach 1% difference from the total soil flux, and $r^2 > 0.9$.

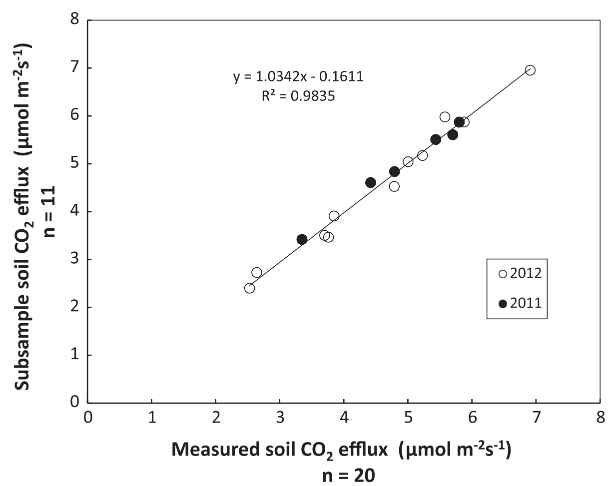

Fig. 7. Relationship between the daily mean soil CO_2 efflux calculated over the full measured set of locations ($n = 20$) and a selected subset of location ($n = 11$) at the harvested NO_RIP site. The locations were selected using data collected in 2012 (open symbols). The same selected locations were used in 2011 (black symbols).

Gyokusen, 2007; Singh et al., 2008; Song et al., 2013; Tang and Baldocchi, 2005) found that spatial variability of soil CO_2 efflux varied seasonally, that soil CO_2 efflux CV reached up to ~40%, and finally that CV of soil temperature was much lower than CV of soil CO_2 efflux and soil water content. Higher CV in disturbed stands was not found by Adachi et al. (2005), who did not find any difference in soil CO_2 efflux CV between a tropical natural forest and a plantation. However, Tedeschi et al. (2006) found higher soil CO_2 efflux CV (up to 50%) in a one-year old oak coppice compared to older stands, and Han et al. (2007) found high soil CO_2 efflux CV (58%) in a maize crop. Singh et al. (2008) compared CV in a post-fire chronosequence and found higher CV in the youngest, 10 year old, stand. Finally, Kobziar and Stephens (2006), found soil CO_2 efflux maximum CV increased from 42%, to 49%, and 66% in a control, burn only, and burn plus mechanical shredding of understory vegetation, respectively, in a mixed coniferous forest similar to ours. The dimension of the chamber used to measure soil CO_2 efflux could have, in part, determined the high spatial variability detected in these studies. However all previously cited

Table 4
Relationship between spatial variability of soil CO_2 efflux and biotic and abiotic variables.

Site	Variables	Correlation coefficient (r)
Simple linear correlation		
(a) Seasonal variation of CV of soil CO_2 efflux		
HARV	Ts	0.44 (p = 0.098)
	SWC	−0.24 (p = 0.17)
UND	Rs	0.43 (p = 0.08)
	CV_{Ts}	0.67 (p = 0.007)
Fire	Rs	(p = 0.14)
Multiple regression		
		Regression function
Fire	Ts and SWC	CV_{Rs} = 0.000596 + 0.0177·Ts + 0.00835·SWC (r^2 = 0.65; p = 0.02)
All sites	Ts, SWC and CV_{Ts}	CV_{Rs} = 0.0774 + 0.00573SWC + 0.03Ts + 0.81CV_{Ts} (r^2 = 0.43; p < 0.001)
Simple linear correlation		
		Correlation coefficient (r)
(b) Spatial variation of soil CO_2 efflux		
UND	Fine root	
	<5 mm; 0–15 cm	0.76 (p = 0.01)
	<2 mm; 0–15 cm	0.83 (p = 0.003)
	<5 mm; 0–30 cm	0.66 (p = 0.05)
	<2 mm; 0–30 cm	0.74 (p = 0.02)
	Litter	
	Leaves	0.40 (p = 0.033)
	Leaves + wood	0.43 (p = 0.023)
FIRE	Soil bulk density	−0.34 (p = 0.07)

Relationships between (a) spatial variation of soil CO_2 efflux (CV_{Rs}); (b) soil CO_2 efflux, and soil temperature (Ts) soil water content (SWC) spatial variation of soil temperature (CV_{Ts}), soil bulk density, litter (leaves or total) and fine root biomass with different root diameter and sampling depth. Relationships were analyzed at the control (UND), fire and harvested sites (HARV, including both the RIP and NO_RIP sites) and combining all sites. Only relationship with $r > \pm 0.2$ and $p < 0.2$ are showed. A stepwise backward selection method was applied to identify covariables for inclusion in the multiple regression model.

studies used a 10 cm diameter circa chamber (except for the 24 cm diameter in Ohashi and Gyokusen, 2007) and most of them (except Ohashi and Gyokusen, 2007; Tedeschi et al., 2006) used the same instrument.

Our study was based on 29 locations at the UND and FIRE sites, and 20 at the HARV sites. For the UND and FIRE sites, these actual sample sizes were higher than the optimal sample size needed to provide a sample mean within 20% of the full population mean (14 and15 samples respectively), but lower than the optimal sample size needed to be 10% from the full population (60 and 55 samples, respectively). At the HARV sites, our 20 measurement locations were always lower than the optimal sample size (∼30 samples to be 20%, or 120 to be 10% from the full population mean). The HARV sites optimal size of 100–200 samples is very difficult to obtain, or to maintain on a regular basis. Our optimal size was in the range of the optimal size of 150 observed by Ohashi and Gyokusen (2007), 85 of Adachi et al. (2005), and slightly higher than the 35 in Knohl et al. (2008). Using a small sample size in soil CO_2 efflux measurements, especially when using a small chamber as in our case, can be a determining factor when scaling up estimates to the stand, to the region or to the global level. It can be a determinant when soil CO_2 efflux estimates validate or integrate eddy covariance measurements, and are especially important when comparing different ecosystems, as when assessing effects of disturbances, treatments, or stand age. Past studies quantifying the effects of disturbances on soil CO_2 efflux, often characterized by labor and time constraints required to compare several treatments, reported number of replicates equal or less than 10 (Concilio et al., 2005; Kobziar and Stephens, 2006), or most of the time, between 10 and 20 samples (Hart et al., 2006; Howard et al., 2004; Humphreys et al., 2006; Irvine et al., 2007; Ma et al., 2004; Sullivan et al., 2008). Unless the disturbance has a strong and clear effect on soil CO_2 efflux, such small sampling sizes, plus the fact that spatial variability varies seasonally, could limit the ability to detect differences among treatments. In addition, it could cause an underestimation of the variability of soil CO_2 efflux, and lead to inaccuracies in the calculation of annual soil CO_2 efflux budgets. In our case, to be able to detect an effect of a treatment, differences between the RIP and NO_RIP treatments should be circa 50% higher than the difference between the UND and FIRE sites (>1 μmol m^{-2} s^{-1} and 0.6 μmol m^{-2} s^{-1}, respectively) even if at these intensely disturbed sites fluxes are lower.

In an effort to reduce the number of soil CO_2 efflux measurement locations, we determined that having more than 10–15 random samples reduced the uncertainty and gave results similar to what was obtained using the full dataset. In particular cases, such us when monitoring soil CO_2 efflux over the long period after an intense initial campaign, or when selecting few permanent measurement locations after an initial period characterized by high spatial resolution, it could be possible to further reduce the number of samples, while still obtaining an accurate soil CO_2 efflux mean and reproducing its changes in time. In our case only 3 samples were necessary at the UND site and 11–13 at the FIRE and HARV sites. The same methodology would allow for a good fit of any subset of locations that were selected for convenience, distance, or position. However, this would reduce greatly the sampled soil CO_2 efflux variability and would not allow the comparison among treatments or sites.

As in several other studies (Ngao et al., 2012; Song et al., 2013; Tedeschi et al., 2006; Yim et al., 2003), we observed that soil temperature and soil water content were not able to clearly explain spatial variability in soil CO_2 efflux. It is possible that soil temperature and water content control temporal, but not spatial variability, or that this control is very hard to quantify because it is extremely difficult to measure these variables at the right position and vertical depth, due to the large vertical gradient and time lags of soil temperature and fine scale spatial variability of soil water content. Relationships with fine root biomass, litter, and bulk density changed among sites. At the UND site we found a significant correlation only with fine root biomass, as Han et al. (2007), Knohl et al. (2008), Singh et al. (2008) did, and with litter biomass. At this site litter and fine root biomass represented a significant contribution of the respiratory pools. At the FIRE site soil CO_2 efflux was only correlated (negatively) with surface soil bulk density, as in Ngao et al. (2012). The lack of a clear relationship with any biotic factor at the HARV sites can be explained by the minor contribution of litter and fine root biomass at those sites.

Our results could extend to other forest ecosystems subject to silvicultural management practices, especially in conifer forests in Mediterranean regions, or in areas where water availability is a limiting factor. This is because such practices commonly aim to reduce the canopy cover, and consequently increase the energy reaching the ground and alter the environment for respiratory processes. Also, when post-disturbance vegetation does not regenerate by sprouting, heterotrophic respiration prevails. And heterotrophic processes are driven mainly by soil temperature and moisture (Tang and Baldocchi, 2005).

In conclusion, we hypothesized that the highly complex, undisturbed forest, consisting of different tree species, sizes and ages, and numerous carbon pools, needed intense sampling compared to the simplified bare soil resulting from the clear cut harvest. However, soil CO_2 efflux of the ecosystem where natural complexity was reduced artificially by disturbance was more spatially heterogeneous and difficult to assess. These findings should be considered when quantifying effects of management or treatments on soil CO_2 efflux, when the absence of an effect could be due to the lack of an appropriate sampling size.

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