



Respiration of Russian soils: Climatic drivers and response to climate change



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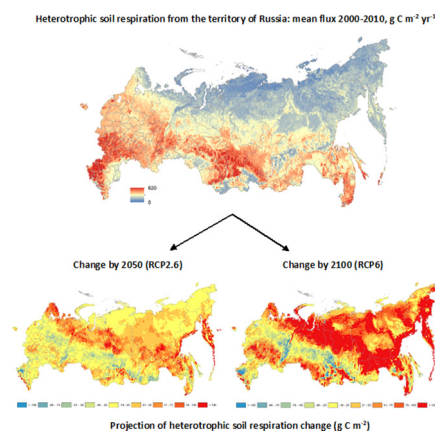
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HIGHLIGHTS

- Regression and random forest models of soil respiration were developed.
- The soil type shapes the soil respiration response to the climate.
- The average heterotrophic soil respiration was estimated to be $190 \pm 0.3 \text{ g C m}^{-2} \text{ yr}^{-1}$
- Maps of current and future projected heterotrophic soil respiration are provided.

GRAPHICAL ABSTRACT



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ABSTRACT

Soil respiration is one of the major ecosystem carbon fluxes and has a strong relationship with climate. We quantified this dependence for the Russian territory based on coupling climate data and in-situ soil respiration (R_s) measurements compiled into a database from the literature using regression and random forest models. The analysis showed that soil properties are a strong factor that mediates the climate effect on R_s . The vegetation class determines the contribution of the autotrophic respiration to the total R_s flux. The heterotrophic soil respiration efflux of Russia was estimated to be 3.2 Pg C yr^{-1} or $190 \text{ g C m}^{-2} \text{ yr}^{-1}$, which is 9–20% higher than most previously reported estimates. According to our modeling, heterotrophic soil respiration is expected to rise by 12% on average by 2050 according to the RCP2.6 climate scenario and at 10% based on RCP6. The total for Russia may reach 3.5 Pg C yr^{-1} by 2050. By the end of the century heterotrophic respiration may reach 3.6 Pg C yr^{-1} (+13%) and 4.3 Pg C yr^{-1} (+34%) based on RCP2.6 and RCP6, respectively. In order to understand to what extent the lack of information on disturbances impact contributes to uncertainty of our model, we analyzed a few available publications and expert estimates. Taking into account the specifics of Russian forest management and regional disturbance regimes, we have found that for the entire territory of Russia, the disturbances are responsible for an increase in heterotrophic soil respiration by less than 2%.

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1. Introduction

Carbon dioxide efflux from soil (soil respiration – R_s) is one of the largest exchanges of carbon to the atmosphere. Recent global estimates suggest that the R_s flux ranges from 68 to 98 Pg C per year (Hashimoto et al., 2015). This is an order of magnitude higher than the emission rates from fossil fuel combustion (Alexander, 1977; Denman et al., 2007), indicating that soils are the predominant source of CO_2 from terrestrial ecosystems. However, despite the importance of this flux, the estimates of its magnitude, and its spatial and temporal variability are still highly uncertain (Bahn et al., 2009).

Carbon dioxide efflux from soil has two main sources: (i) microbial respiration – the heterotrophic part (R_h), and (ii) plant root respiration – the autotrophic flux (R_a). Many researchers have demonstrated a positive linear relationship between CO_2 efflux with the amount of above-ground litterfall (e.g. Wei and Man, 2021), the fine root biomass (Singh et al., 2008; Tang et al., 2020b), and the availability of nutrients (e.g. Nadelhoffer, 2000). Plant communities can be drivers of soil respiration due to the amount of C diverted belowground (Metcalf et al., 2011; Huang et al., 2020; Sun et al., 2020; Fan and Han, 2020).

Among environmental factors, soil temperature and moisture are recognized as the most influential drivers controlling the soil surface carbon dioxide exchange rate. These factors interact, affecting the productivity of terrestrial ecosystems and the decomposition rate of soil organic matter (SOM) (Tang et al., 2020a). Soil temperature strongly affects the CO_2 efflux, providing conditions for SOM decomposition (Chen and Tian, 2005). In dry conditions, root and micro-organism activity is typically low, resulting in low CO_2 emissions (Li et al., 2020; Zheng et al., 2021). Increasing the soil moisture can increase the bio-activity in the soil, but if there is excessive soil moisture, the total soil CO_2 efflux is reduced because of the limited diffusion of oxygen and the subsequent suppression of CO_2 emissions (Bouma and Bryla, 2000; Wood et al., 2013; Du et al., 2020). However, variations in soil moisture around an optimum (i.e., the mesic condition) have little effect on the soil CO_2 efflux (Palmroth et al., 2005). Soil temperature and moisture can also interact, which can lead to both more favorable or less favorable conditions for plant root and microbial activity (Bao et al., 2016; Zheng et al., 2021). For example, a high water content cools the soil down; in contrast, high temperatures can promote evapotranspiration, leading to water deficiency, thereby suppressing biological activity in the soil. Chamber measurements of total ecosystem respiration in a native Canadian grassland ecosystem showed that soil moisture was a dominant environmental factor controlling seasonal and inter-annual variations in the CO_2 efflux (Flanagan and Johnson, 2005).

On a global scale, R_s rates were found to correlate positively with mean annual air temperature and precipitation (Raich and Schlesinger, 1992; Hursh et al., 2017; Zhao et al., 2017; Tang et al., 2020a, 2020b). Furthermore, as shown by some authors, the effect of precipitation on R_s goes beyond its direct effect on soil moisture (Lee et al., 2002; Raich et al., 2002; Curiel Yuste et al., 2003; Matías et al., 2012; Liu et al., 2016; Jeong et al., 2018). Rain controls soil water fluctuations in the surface layers during dry periods and stimulates R_s , i.e., the “drying and rewetting effect” (Lee et al., 2002; Arredondo et al., 2018; Niu et al., 2019). Temperature and precipitation are also considered to be the best climatic predictors of the annual and seasonal dynamics of R_s rates at the regional scale (Li et al., 2020; Kurganova et al., 2020). High positive correlations between CO_2 emissions and soil temperatures have been found in natural and agricultural ecosystems (e.g. Kudryarov and Kurganova, 1998; Meyer et al., 2018). The relationship between R_s and the temperature and moisture conditions has been derived in a number of studies some of that are presented in Table 1.

Usually, R_s increases exponentially with temperature when other factors are not limiting. This direct effect of temperature on R_s is often used as a Q_{10} constant (Raich et al., 2002; Reichstein et al., 2003).

Table 1

Models of soil respiration dependence on climate.

Model	References
$R_s = c_0 e^{(c_1 T + c_2 T^2)}$	(Karhu et al., 2010; Tuomi et al., 2008)
$R_s = c_0 e^{c_1 T} \frac{p}{c_2 + p}$	(Raich and Potter, 1995)
$\ln R_s = c_0 + c_1 T_s + c_2 \theta + c_3 T_s \theta$	(C. Wang et al., 2006)
$\ln R_s = c_0 + c_1 T_s + c_2 T_s^2 + c_3 \theta + c_4 \theta^2 + c_5 T_s \theta$	(Martin et al., 2009)
$R_s = c_0 e^{c_1 T_s} e^{c_2 \theta}$	(Knohl et al., 2008)
$R_s = c_0 e^{c_1 T_s} \theta^{c_2}$	(Qi and Xu, 2001)

Notes: R_s – soil respiration flux, T – air temperature, P – precipitation, T_s – soil temperature, θ – soil moisture, c – coefficients from the models.

Many researchers use the Q_{10} to express the sensitivity of R_s to temperature. However, this coefficient has large variability (Kirschbaum, 1995; Schlesler, 1982; Trumbore et al., 1996; Hamdi et al., 2013; Gritsch et al., 2015). Q_{10} varies among ecosystems and across temperature ranges, partly because the different components of R_s have different temperature responses (Boone et al., 1998; Carey et al., 2016; Meyer et al., 2018). Gaumont-Guay et al. (2009) have shown that for the same soil, Q_{10} can vary in the range from 1.4 to 5.8 during one season. Kurganova (2010) reports that the interannual variation of Q_{10} can range from 1.98 to 5.00 for Umbric Albic Retisol and from 1.72 to 6.20 for Luvic Phaeozem soils. Thus, using this coefficient for R_s modeling is problematic.

In this study we collected the most comprehensive database of R_s field measurements and applied data driven approach to investigate the main drivers of the R_s efflux in order i) to understand the effects of climate on R_s efflux, ii) to assess the R_h flux from terrestrial ecosystems in Russia, and iii) predict changes in R_s under future climate. Quantitative information about the R_s efflux from the territory of Russia is necessary for assessing its role in the global carbon cycle. This also helps to model future responses of R_s and R_h to climate change.

Vast territory of Russia covers a wide range of biomes, soils and climatic conditions. Models developed for this area can shed the light on the main drivers of soil respiration fluxes in Northern Eurasia. Fluxes estimated by these models can help to assess contribution of the Russian soils to the global carbon budget under the present and projected conditions.

2. Materials and methods

2.1. Soil respiration database

In situ measurements of R_s reported in peer-reviewed publications have been collected in a database. A large portion of the data was taken from the Global Database of Soil Respiration Data, Version 4.0 by Bond-Lamberty and Thomson (2018). The authors collected 6631 records from 1458 studies; however, we have taken only those records where the annual R_s flux or the mean seasonal rate of R_s was reported, or where the root contribution to R_s was mentioned. Data covering the northern hemisphere, including Russia, were collected from an additional 290 sources using the same criteria. In total, 3822 records on R_s fluxes were collected around the globe from 932 studies, covering the years 1961–2019. This database and the sources are available at <http://dare.iiasa.ac.at/107/> (DOI: 10.22022/ESM/10-2020.107).

The primary data file includes 28 fields. For each of the measurements, the climatic zone, the vegetation class, the soil group and the year of measurement are listed. In addition, 15 climatic characteristics were calculated for the year of measurement (Table S1). The database contains R_s flux in $g\ C\ m^{-2}\ yr^{-1}$, either directly reported in the literature or calculated by us from the mean daily flux for a growing season as follows (Mukhortova et al., 2015):

$$Rs = 101.5309 + 0.5967 \times DT_5 + 0.7087 \times Rs_DT_5, R^2 = 0.81, p < 0.01$$

where R_s is the annual R_s flux, $g\ C\ m^{-2}\ yr^{-1}$; DT_5 – duration of the warm period with mean daily temperature above $5^\circ C$; $R_s_DT_5$ – $C-CO_2$ efflux during the period where mean daily temperature is above $5^\circ C$:

$$Rs_DT_5 = 12 \times Rs_growing \times 10^{-6} \times 60 \times 60 \times 24 \times DT_5,$$

where DT_5 – duration of the warm period with a mean daily temperature above $5^\circ C$; $(60 \times 60 \times 24)$ – recalculation of efflux $\mu mol\ C/m^2 \times s^{-1}$ to the $\mu mol/m^2 \times d^{-1}$; 12 – a molar mass of carbon to convert μmol of C into the gram of C.

The magnitude of the annual R_s flux varies from 1 to $6596\ g\ C\ m^{-2}\ yr^{-1}$ for all ecosystems, while the majority fall between 100 and $1000\ g\ C\ m^{-2}\ yr^{-1}$. The most frequently represented regions are Northern America ($n = 1835$), Europe ($n = 1116$) and Asia ($n = 872$) (Fig. 1). Data from temperate ecosystems dominate the database ($n = 1816$), while the boreal zone is represented in 911 records, and subtropical and tropical biomes are represented in 628 and 400 records, respectively. The majority of the data was collected in forests ($n = 2475$) followed by grasslands ($n = 518$) and arable land ($n = 517$). The distribution of the records in terms of mean annual temperature and mean annual precipitation are near-normal (Fig. S1).

2.2. Long-term climate data

We used historical climate data and data from two future Representative Concentration Pathway (RCP) climate scenarios: RCP2.6 and RCP6. The historical annual climate statistics (1980–2010) were calculated based on AgMERRA daily data (<https://data.giss.nasa.gov/impacts/agmipcf/>). The HadGEM2-ES model (Collins et al., 2011) provides global coverage of climate projection scenarios at a quarter degree spatial resolution. RCP2.6 (IPCC, 2014) is representative of a mitigation scenario aimed at limiting the increase in the global mean temperature

to $2^\circ C$. This scenario forms the low-end in terms of emissions, involving negative emissions from energy use in the second half of the 21st century, assuming full participation of all countries. RCP6 is a mid-way scenario, with emission reductions by the end of the century.

From these sources, we calculated a number of climate attributes (Table S1) related to R_s for each year for the time periods 1980–2010 and 2010–2100. The climate grids were then overlaid onto the sample plot locations and the climate parameters were extracted for each plot for the year of measurement and placed in the database.

2.3. Estimation of the soil respiration flux

R_s was modeled as a function of climate, soil and land cover/land use type. The variety of soils were aggregated into 16 groups according to similar genesis (the full list of soil groups is presented in the table), and by 7 land cover types: coniferous forests, deciduous forests, shrubs, grasslands, arable, other agriculture lands and wetlands. Three modeling approaches were considered: a log-linear additive regression model (LM), a regression tree with a maximum depth of 30 (T1), and a random forest with 300 trees (RF) (Random Forest Code is presented in the Supplementary information as SI_1). While the regression model and the regression tree are easier to interpret, random forest generally performs better when enough data are available (Hastie et al., 2009). Moreover, both the regression tree and random forests are less sensitive to outliers than linear regression. To assess the predictive fit of the three approaches, we used 10-fold cross validation (Hastie et al., 2009) and compared the resulting mean squared errors to choose the best prediction method. The random forest was found to perform the best ($MSE_{RF} = 0.18$, $MSE_{T1} = 0.40$, $MSE_{LM} = 1.01$). The 10-fold cross-validation from RF for the ground data set for Russia showed that there was no systematic error ($MSE = 0.2651$).

In order to estimate the autotrophic component (R_a) of the R_s flux and its dependence on climatic conditions, we use the same database described in Section 2.1 to build the models. The same three methods (LM, T1, and RF) were applied and compared when modeling R_a share as a function of climate, soil and land cover. However, because R_a

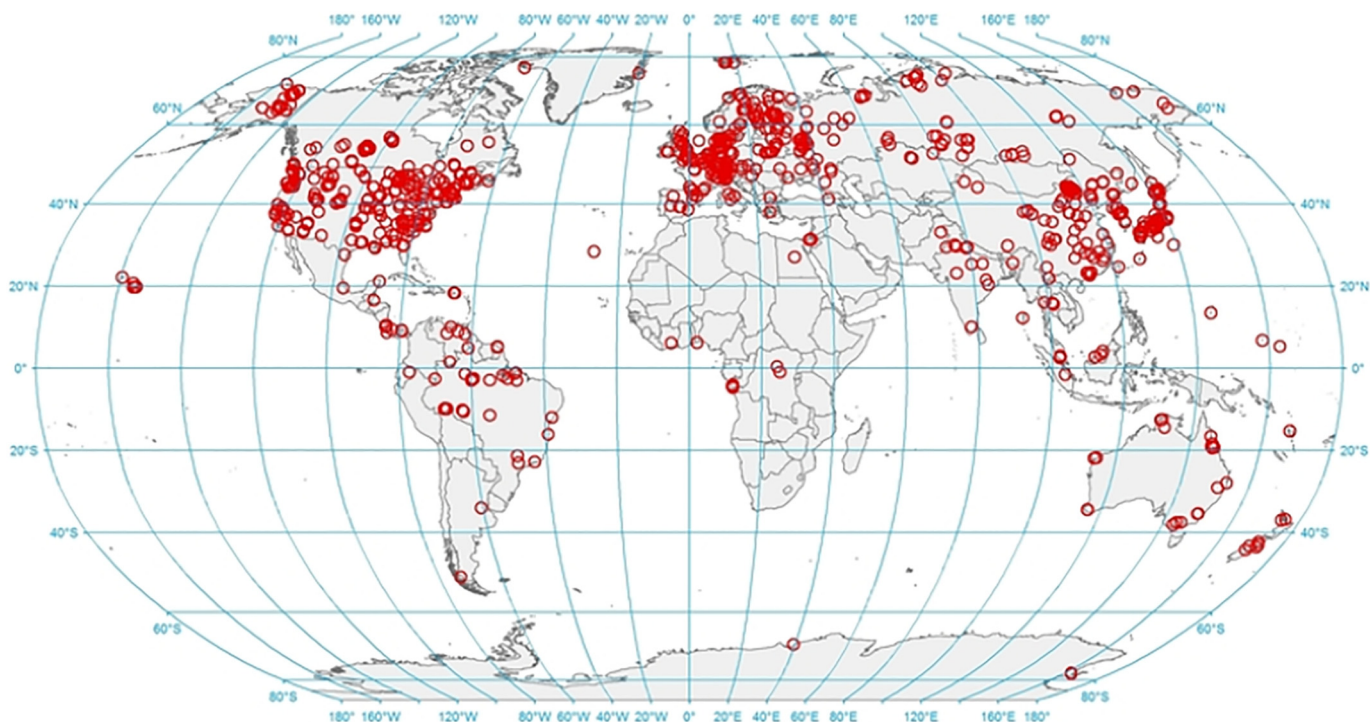


Fig. 1. Location of the soil respiration observations collected in the database used in this study.

share is a proportion, a logistic transformation $\log \frac{R_a}{1-R_a}$ was used for the response in the linear regression. Initially, three additive regression models were compared: one including climate, soil and land cover covariates, the second including soil and land cover only, and the third including soil only. The respective cross-validation MSEs were 200.45, 216.89, and 249.52. In addition, the MSEs for T1 and RF were 137.9 and 183.28. Because a limited number of measurements ($n = 279$) were available for the assessment of R_a , the random forest performed poorly, and the regression tree was chosen instead as the best performing method.

Heterotrophic soil respiration (Rh) was calculated as the difference between the total soil respiration (Rs) and the share of autotrophic respiration ($R_{A\%}$) from the total Rs:

$$R_h = R_s \left(1 - \frac{R_{A\%}}{100} \right)$$

To investigate the main climatic drivers for respiration, we used stepwise linear regression. Log-log and log-polynomial linear models were developed for each soil group. To choose the best model, we used the Akaike information criterion (AIC). Statistical analyses were performed using the R software v.3.6.3 (R Core Team, 2013), incl. libraries data.table v.1.12.8 and H2O v.3.30.1.3.

2.4. Impact of disturbances

The following simplifications were made to estimate the impact of disturbances (Ds). First, it was assumed that there is an absence of temporal trends in the disturbance regimes, which allows for constant correction coefficients to be used during the period of restoration (PoR). This assumption corresponds to reality for fire and biogenic Ds during 1998–2017. Second, we used the current age structure of Russian forests (i.e., the areas of age groups of major forest forming species, MFFS) formed by the Ds considered here. Third, all calculations were provided for stand-replacing Ds to minimize the inconsistency in the empirical data for weak and moderate Ds. This includes crown and stable soil (peat) fires. The latter often occur on permafrost, which covers around two-thirds of the area of Russian forests. The length of the PoR was estimated at 60 years, which was divided into 3 age groups of forests used in the Russian forest inventory. The initial data on Russian forests and Ds were derived from IIASA databases (<https://iiasa.ac.at/web/home/research/modelsData/models-tools-data.html>), official forest statistics from the Federal Forest Agency of the Russian Federation, and scientific publications, mentioned in the SI.

Three correction coefficients have been assessed: 1) area share by different Ds (fire, harvest, biogenic); 2) the average corrections of Rh for the PoR; and 3) average corrections with respect to the entire land area of Russia. It is important to point out that all the above coefficients describe the impact of yearly Ds on Rh (see Table S2).

In this analysis, the post-disturbance behavior of Rh was analyzed by temporal phase, which may have similar directional changes in the soil carbon fluxes (i.e., increasing, neutral, decreasing) during the period of forest ecosystem restoration after a Ds (Fig. 2).

Phase I of the immediate post-disturbance response usually lasts from 1–2 to 3–5 years for different types of Ds and continues until the direct consequences of the Ds are realized, e.g., post-fire mortality of trees after a fire. Phase II of the initial restoration ends when the Net Primary Production of a restored young generation of forests returns to the pre-burn value. This is usually defined by indexes of biological productivity, which are estimated by satellites, and lasts 10–20 years after the Ds. During the intermediate (middle-aged) succession Phase III (usually 25–60 years), the soil effluxes become nearly equal to the pre-disturbance values, and major ecosystem characteristics are similar to the indigenous forest types. This phase includes a period of intermediate successions, which in the boreal forests of Northern Eurasia are realized in two ways: without changes in tree species (basically in indigenous

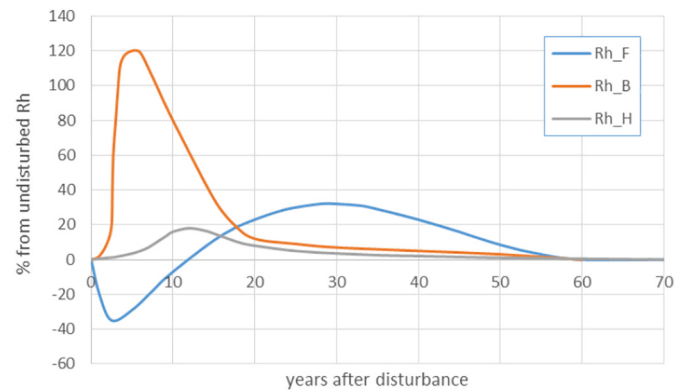


Fig. 2. Conceptual models of changes in Rh after disturbances (in % from undisturbed Rh in these ecosystems): Rh_F – postfire; Rh_B – after biogenic agents; Rh_H – postharvest.

conifer forests of high latitudes) and with changes in dominant species (through a period of dominance of pioneer species like birch and aspen); this latter succession is dominant in the post-disturbance restoration of 70–80% Russia's boreal forest area. This phase coincides temporally with the decomposition of coarse woody debris (CWD), which occurs in two ways: decomposition of direct post Ds residuals (i.e., dead fine roots, biogenic fall of defoliators, etc.) and a period of downing the dry standing trees and snags. The end of this phase means the end of the restoration period. Such phases could be combined with an inventory of forests by age group – young, middle-aged, immature, mature and overmature forests, as used in the official Russian forest inventory system. Our analysis shows that the period of restoration in coniferous and hard wood deciduous forests continues for around 60 years, while for soft wood deciduous forests dominated by pioneer species like birch and aspen, this period lasts 30 years. These periods basically cover two age groups – young and middle-aged forests.

The main purpose of this section was to estimate the impact of Ds on the Rh of forest ecosystems in Russia with a level of certainty. We assessed the correction coefficients that were applied to the data of the system developed here to assess Rh. The calculation was based on matrices that describe the recognized regularities of the temporal dynamics of Rh, taking the specifics of Russian forest management and regional disturbance regimes into account; details are presented in a short review of selected publications and methods in the Supplementary information (SI₂).

3. Results

3.1. The relationship between climate and the annual soil respiration flux

3.1.1. Modeling the soil respiration flux by vegetation class

The average Rs flux by different vegetation classes was calculated based on the measurements collected (Table S3).

The Rs in forest is significantly different ($p < 0.05$) than that found in other vegetation classes. Shrubs and wetlands have the lowest Rs rate among all the vegetation types, which are on average only 41–55% of the forest soil CO₂ efflux. Grassland Rs is 9–19% lower on average compared to forest. Coniferous and deciduous forests are also significantly different ($p < 0.05$) from one another, with higher values of Rs for deciduous forests.

The Rs models that relate climate parameters to different vegetation classes are presented in Table S4. It was found that the Rs in forest ecosystems mostly depends on active temperatures during frost free periods and the moisture conditions of the site. The variation in Rs for coniferous forests is controlled by four climatic variables: (i) the duration and (ii) accumulated temperature for the frost-free period, and (iii) the annual precipitation and (iv) wetting index, where the latter

Table 2

Average annual soil respiration flux in the database by soil groups.

ID	Soil group ^a	N	Average Rs, g C m ⁻² yr ⁻¹ ± 1 SE ^b	
			Global	Extratropical Eurasia
1	Cryosols-soils of cold permafrost regions	49	191 ± 22.6	147 ± 10.6
2	Gleysols or Gleyzems- overwetted soils with gleyic horizon	144	571 ± 28.1	408 ± 40.7
3	Podzol - soils with light podzolic horizon	384	664 ± 20.9	440 ± 19.8
4	Cambic Podzol or Podbur -Al-Fe-Humic cold soils without clear podzolic horizon	54	496 ± 50.6	366 ± 31.6
5	Luvissols and Greyzems - texture-differentiated soils	482	751 ± 22.7	677 ± 21.6
6	Gleysols Gelic - overwetted mineral soils with thick (10–30 cm) organic horizon	53	592 ± 50.9	592 ± 50.9
7	Histosols - overwetted organic soils	287	476 ± 23.6	426 ± 19.5
8	Cambisols or metamorphic soils -soil is made from the weathering of schist, slate, or gneiss without substantial redistribution of Fe in the soil profile	565	746 ± 25.2	740 ± 26.5
9	Phaeozems, Histosols and Leptosols-sod-organic accumulative soils	22	551 ± 77.3	616 ± 90.7
10	Chernozems or Kastanozems - humic- accumulative soils	294	820.2 ± 34.2	834 ± 38.3
11	Andosols - soils on volcanic parent materials	110	1123 ± 62.3	914 ± 59.3
12	Fluvisols - soil is formed under deposition of alluvial material	41	769 ± 109.2	563 ± 66.8
13	Calcisols or Solonetz - low-humic, accumulative calcareous soils. It has a fairly high pH and is alkaline	107	381 ± 34.7	289 ± 22.7
14	Leptosols - shallow weakly developed soils with a short profile	153	699 ± 43.2	644 ± 45.8
15	Umbrisols or Regosols - sod mountain soils	21	423 ± 59.4	422 ± 59.4
16	Ferrallitic	248	1327 ± 50.3	

^a Soil is named in accordance with WRB (2015).^b Standard error.

is related to the wetting conditions during the growing season. The Rs of deciduous forests has a weaker link with climatic variables ($R^2 = 0.12$), where warm seasons with mean daily temperatures above 5 °C and 10 °C are the most statistically significant variable ($p < 0.05$). However, a better relationship between Rs and climatic drivers was observed when deciduous and mixed forests were combined. Yet mixed forests alone have a stronger dependence of Rs on the same climatic variables as the coniferous forest soil carbon dioxide flux. Thus, the multiple regression analysis undertaken separately for the vegetation classes has shown that Rs closely depends on the thermal and moisture conditions during the whole frost-free period of the year. However, the spatial distribution of coniferous and deciduous forests play an important role in the specific Rs responses to the climatic drivers. For example, deciduous forests, which are mostly located south of coniferous forests in the northern hemisphere, have shown that the Rs flux has a stronger dependence on the warmest period conditions ($T > +10$ °C).

The Rs of shrubs and grasslands is driven by similar climatic variables as forest land, but the duration of the warm period does not significantly ($p > 0.05$) influence the amount of annual soil carbon release. The annual flux of arable Rs depends mainly on the duration and hydro-thermal conditions during the warmest period of the year (D_{10} and GTK_{10}) as well as on the hydrothermal conditions during the period with temperatures above 5 °C, the mean annual precipitation (MAP) and the wetting conditions during the frost free period (IndW). Other agroecosystem soils also showed a strong relationship between Rs and the duration of the warmest period during a year.

Wetlands differ from the other ecosystems as their Rs depends only on the conditions of the warmest period ($T > +10$ °C). This is most likely due to the fact that wet soils can be further warmed during this

period. Finally, the close dependence of the Rs of agricultural lands on the duration and moisture supply of the growing season can be explained by the fact that agricultural vegetation is mostly thermophilic.

3.1.2. Modeling the soil respiration flux by soil group

The correlations of the Rs flux and climatic variables by vegetation class were not strong. For this reason, we further analyzed the relationships between Rs and climate by soil group where the average Rs rates are presented in Table 2.

The lowest Rs rate is found in cold arctic tundra soils. Sod mountain and peat soil also have a low Rs efflux. In both cases this is due to the unfavorable conditions for root growth and microbial activity. In sod-mountain soils, the limiting factor is temperature while for peat soils it is overwetting conditions. Warm and wet tropical and subtropical Ferrallitic soil, together with Andosols, have the highest Rs rate compared with other soil groups. Extratropical Eurasia has the lowest level of Rs, excluding sod-organic accumulative soils, and in most cases, a lower standard error compared to the global values.

The highest dependence of Rs on climatic drivers was observed for soil groups independently of vegetation class (Table S5).

3.2. Root contribution to the carbon efflux

According to the records in our database, the average root contribution to the total Rs flux under forest vegetation ($n = 292$) and grasslands ($n = 40$) is 44%, varying from 2 to 96% for forest and from 15 to 90% for grasslands. The Rs of Arable ($n = 38$) and Other agricultural ($n = 2$) ecosystems includes, on average, 31 and 22% of root contributions, respectively.

Table 3

Climatic drivers of root contribution to the total soil respiration flux by vegetation classes.

Vegetation class	N	R ²	p-Level	SD	SE	Model
Coniferous forest	161	0.35	<0.01	16.2	1.2	RC = 213.507 + 0.0656*MAP+0.120*(P_5)-0.146*(P_10)-61.452*(GTK_5) + 47.921*(GTK_10)+ 15.141*(IndW)-51.691*ln(D_5) + 46.944*ln(GTK_5)- 20.802*ln(GTK_10)
Deciduous forest	157	0.22	<0.05	16.3	1.8	RC = -408.392-0.070*(SUM_T_5)+ 0.047*(Sum_T_10) + 98.140*ln(P_5)-29.509*ln(P_10) + 81.471*ln(IndW)
Grasslands	44	0.54	<0.05	12.0	2.0	LnRC = 6.999-0.629*MAT+0.0121*MAP+ 0.0265*(D_5) + 0.0032*(SUM_T_5) + 0.0134*(P_0)- 0.0308*(P_5)-12.4813*(GTK_0) + 16.194*(GTK_5)+ 7.353*ln(P_0)-12.617*ln(P_5) + 1.978*ln(P_10)
Arable	47	0.58	<0.05	9.1	1.5	RC = 966.669-0.14*MAP+0.456*(P_0)-0.344*(P_5) +0.160*(P_10)-166.045*(GTK_10)-184.234*ln(P_0)+ 49.217*ln(P_10) + 280.158*ln(P_5)

Table 4

Distribution of the average share of autotrophic respiration by bioclimatic zones and land cover types for the territory of Russia.

Bioclimatic zones	Autotrophic soil respiration by land cover type, %						
	Forest	Shrubs	Grassland	Arable	Rangeland & hayfield	Wetland	Average
Tundra	40	44	49	28	41	44	47
SF & NT	39	40	40	37	40	40	39
MT	39	39	41	29	38	41	39
ST	38	41	45	39	40	41	39
TF	39	41	45	35	38	45	39
Steppe	33	34	37	29	33	41	32
DSD	40	39	40	29	39	42	38
Total	39	41	46	31	36	42	40
Russia							

The main climatic factors driving root contributions to the Rs flux in coniferous forests ($n = 177$) are the mean annual precipitation and the precipitation during a period with mean daily temperatures above 5 and 10 °C, and hydro-thermal conditions during these periods, as well as the duration of the period with temperature above 5 °C and the wetting conditions of the site (Table 3).

The root contribution of deciduous forests ($n = 86$) depends on the accumulated temperatures during the period when the temperature is above 5 and 10 °C, and the amount of precipitation during these periods. The root contribution of grassland vegetation ($n = 38$) depends mainly on periods when the temperature is above 0 and 5 °C. For agricultural plants, the root contribution is derived mainly from the precipitation during different periods in the year.

The average contribution of autotrophic respiration to Rs varies from 31% for Arable lands to 46% for Grasslands with an average across Russia of around 40% (Table 4).

3.3. Heterotrophic soil respiration flux

Using the models developed in this study, we calculated the average soil efflux and the distribution of Rh over Russia (Fig. 3 and Table S6).

Grasslands in the Tundra have the lowest Rh flux. In contrast, soils in Forest and Arable land cover types in the temperate forest and steppe zones have the highest Rh activity. Forests in Russia contribute around 58% of the total Rh flux while the share of shrubs and grasslands is 17%, agricultural lands contribute about 18%, and wetlands and the

rest around 7%. The estimated average heterotrophic soil respiration for Russia is $190 \pm 0.3 \text{ g C m}^{-2} \text{ yr}^{-1}$ (Table 5).

3.4. Impacts of disturbances on heterotrophic soil respiration

We applied a simplified calculation to provide an illustrative assessment of the impacts of Ds on the Rh of Russian forest ecosystems; details can be found in the SI in the section entitled Impact of Disturbances. We found that the major types of Ds will increase the Rh of disturbed areas during the period of restoration (PoR) by an annual average increase of +9.89%, including +12.2% in burnt areas, +14.9% of areas affected by insects and pathogens, and +3.1% in harvested areas. Assuming stable disturbance regimes, the current structure of Russian forests and the length of the PoR of 60 years, then the increase in Rh due to Ds for all years and for all of Russia is estimated at around +1.76%.

The uncertainties in these results cannot be estimated by formal methods. Expert estimates of the impacts of uncertainty on the results due to simplifications in the accounting, shortcomings in the available information, inconsistency and contradictions in empirical estimates used, etc., lead to the conclusion that the overall error could be estimated within limits of 30–40%.

3.5. Projection of heterotrophic soil respiration

Our calculation of Rh is based on the models that use climatic parameters as inputs. This allows us to use available climate records or future climate projections to identify the variability in Rs and possible future developments at the national level. We used the RCP2.6 and RCP6 scenarios for the time interval 2010–2100 with a spatial resolution of a quarter degree as inputs to our Rh model. Some of the climatic parameters together with Rh are presented in Table S7.

According to our modeling results, the Rh of Russian soils will increase by an average of 12% by 2050 according to the RCP2.6 scenario and by 10% based on RCP6. Hence, the total Rh may reach 3.56 and 3.48 Pg C yr⁻¹ by 2050 for the two scenarios, respectively. By the end of the century, Rh will reach 3.58 Pg C yr⁻¹ (+13%) and 4.33 Pg C yr⁻¹ (+34%) for the two scenarios. The Rh will rise both by 2050 and by 2100 for all bioclimatic zones, except for the southern taiga due to limitations in precipitation. The interannual variation of Rh is also expected to be higher as shown in Fig. 4.

One can observe areas of both intensive growth and local reductions in Rh in Fig. 5. A reduction is usually associated with a lack of

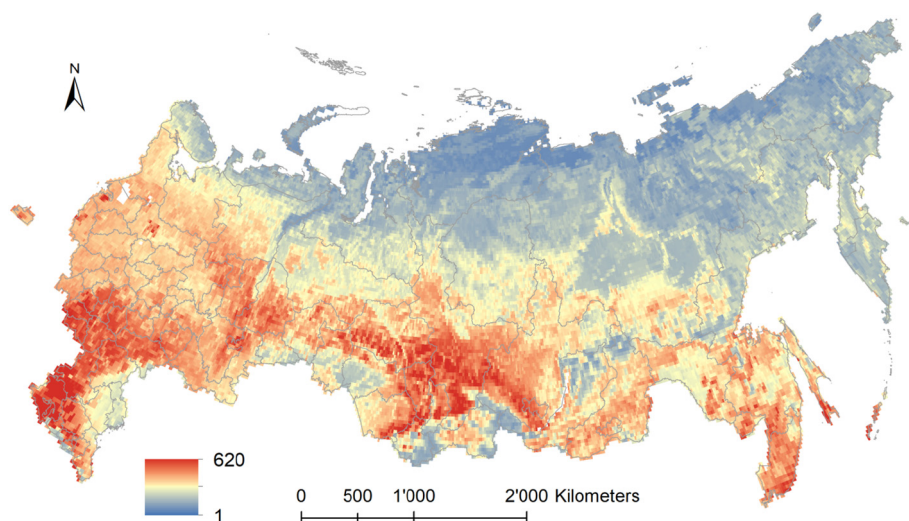


Fig. 3. The spatial distribution of the heterotrophic soil respiration for the period 2000–2010, $\text{g C m}^{-2} \text{ yr}^{-1}$.

Table 5
Average heterotrophic soil respiration for the territory of Russia by bioclimatic zones and land cover types for the years 2000–2010.

Bioclimatic zone	Heterotrophic soil respiration by land cover type, $\text{g C m}^{-2} \text{yr}^{-1} \pm \text{SE}$						Average
	Forest	Shrubs	Grassland	Arable	Rangeland & hayfield	Wetland	
European Russia							
Tundra	139 ± 3.9	110 ± 2.2	87 ± 5.2	–	55 ± 19.8	113 ± 2.9	101 ± 1.5
SF & NT	206 ± 1.4	164 ± 2.6	171 ± 2.1	216 ± 19.1	197 ± 4.7	163 ± 1.5	190 ± 0.8
MT	259 ± 1.2	246 ± 1.9	244 ± 2.3	259 ± 6.3	249 ± 2.7	215 ± 1.9	254 ± 0.8
ST	267 ± 1.4	250 ± 1.6	268 ± 1.5	237 ± 2.3	234 ± 1.5	227 ± 2.7	258 ± 0.8
TF	318 ± 3.1	256 ± 3.6	294 ± 2.4	309 ± 2.7	271 ± 2.2	211 ± 7.1	300 ± 1.0
Steppe	301 ± 3.7	250 ± 3.9	275 ± 2.3	357 ± 1.8	285 ± 1.7	220 ± 11.8	324 ± 6.0
DSD	262 ± 46.6	177 ± 21.3	184 ± 18.4	279 ± 21.6	215 ± 15.8	183 ± 28.3	210 ± 17.6
Total Europe	258 ± 0.7	150 ± 1.4	180 ± 2.4	333 ± 1.3	256 ± 1.0	172 ± 1.0	250 ± 0.4
Asian Russia							
Tundra	120 ± 1.4	85 ± 0.8	80 ± 0.8	277 ± 57.0	84 ± 4.9	87 ± 1.4	84 ± 0.4
SF & NT	158 ± 0.7	124 ± 0.9	134 ± 1.3	277 ± 32.6	210 ± 4.5	143 ± 1.1	147 ± 0.4
MT	209 ± 0.5	136 ± 0.6	134 ± 0.7	301 ± 6.4	205 ± 1.6	173 ± 1.0	185 ± 0.2
ST	304 ± 1.2	255 ± 1.6	263 ± 2.4	295 ± 3.6	280 ± 1.8	224 ± 1.7	288 ± 0.7
TF	303 ± 6.1	257 ± 5.5	254 ± 5.3	249 ± 5.7	250 ± 3.8	225 ± 7.7	280 ± 3.2
Steppe	279 ± 2.4	246 ± 2.4	219 ± 2.2	234 ± 2.2	225 ± 1.6	173 ± 3.8	236 ± 1.1
DSD	178 ± 9.1	158 ± 10.0	110 ± 7.6	212 ± 9.5	148 ± 6.4	153 ± 12.1	155 ± 4.4
Total Asia	216 ± 0.4	122 ± 0.4	107 ± 0.5	244 ± 1.8	225 ± 1.0	150 ± 0.6	173 ± 0.3
Total Russia	224 ± 0.3	124 ± 0.4	117 ± 0.5	308 ± 1.1	242 ± 0.7	154 ± 0.5	190 ± 0.3

precipitation. In contrast, the most intensive growth is expected in the tundra and the northern taiga where current temperatures limit Rh at present.

4. Discussion

4.1. Effect of climate on the annual soil respiration flux

The models developed for the individual soil groups show that the Rs flux is closely dependent on climate, but that the soil properties are a very important factor influencing the rate of carbon dioxide release from soils. The main influencing variables are most likely the limiting factors for Rs within the area of these soils. For example, in cold arctic tundra soils, Rs negatively depends on the duration of the frost-free period in a non-linear way, positively with the duration of the period when temperatures reach above 5 °C, and negatively on precipitation during this period. This means that the main Rs flux from these soils is generated while the temperature is above 5 °C. This is because in the arctic permafrost regions, the winter emissions of CO₂ are very low due to the ice crust on the soil surface, which creates a barrier for carbon dioxide efflux (Kononov, 2006). Moreover, closing of the permafrost from the bottom and seasonal frost layers from the top in wintertime limits the microbiological activity and root respiration in the whole soil profile. Cold seasons with temperatures from 0 °C to 5 °C do not

play a substantial role in the annual CO₂ emissions due to the low microbial activity in cold, overwetted soils. Precipitation during the period when the temperature rises above 5 °C leads to overwetting of the thawed soil because of the low temperatures and a waterproof frost layer that is near the surface. During this period, Rs depends mainly on the ratio between precipitation and temperature. The duration of the warmest period, above 10 °C, positively influences the Rs. The total respiration of these soils positively depends on MAT and MAP, which are characteristic of the region where the soil developed. The sum of active temperatures is most likely not a limiting factor for the Rs of these soils because their specificity has a very narrow range of thermal conditions (MAT of the records varied from –16 to +2 °C). These represent cold conditions, so the vegetation and microbial communities are well adapted to this climate.

Similar to the arctic tundra soils, the cold podbur Rs also positively depends on the duration of the period with mean daily temperatures above 5 °C and the duration of the warmest period. The dependence on the duration of the period with temperature above 0 °C has a nonlinear character. Precipitation during cold periods (from 0 °C to 5 °C) has a negative effect on Rs. During a period with mean daily temperatures from 5 °C to 10 °C, precipitation has a positive effect on Rs. In contrast, precipitation during the period with temperatures above 10 °C has a negative effect on respiration, most likely due to the cooling of soil temperature during rainy weather; however, the ratio between the precipitation and the temperature during this period positively affects the CO₂ efflux. The sum of the active temperatures during the warmest period also has a positive effect on the respiration of these soils. In sum, whether there is a significant effect ($p < 0.05$) on the respiration rate of these soils will depend on the balance between precipitation and active temperatures (i.e., HTC indices) during different periods of the frost-free season. A positive effect of this ratio during the period with temperatures from 0 to 5 °C can be connected with faster thawing of the soil because precipitating water has a higher temperature than frosted soil and penetrates through the moss litter, bringing more rapid heat energy into the soil. During the period with temperatures above 10 °C, this balance is important for providing favorable hydro-thermal conditions for microbial activity.

The Rs from usually wet Gleyzems depends positively and nonlinearly on the regional MAP, which is likely due to stagnant wetting – the most important feature of this soil group – developed mostly at different depths of the soil profile. Surface soil layers are mostly influenced by atmospheric moisture, where wetting conditions during the warmest period are one of the most important driving factors for Rs.

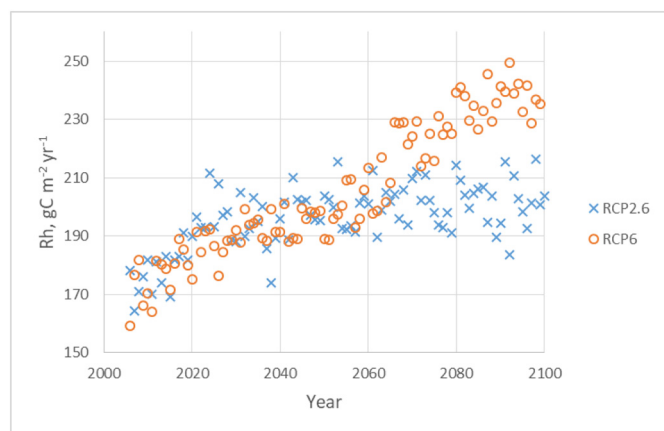


Fig. 4. The projection of the country average heterotrophic soil respiration based on RCPs 2.6 and 6.

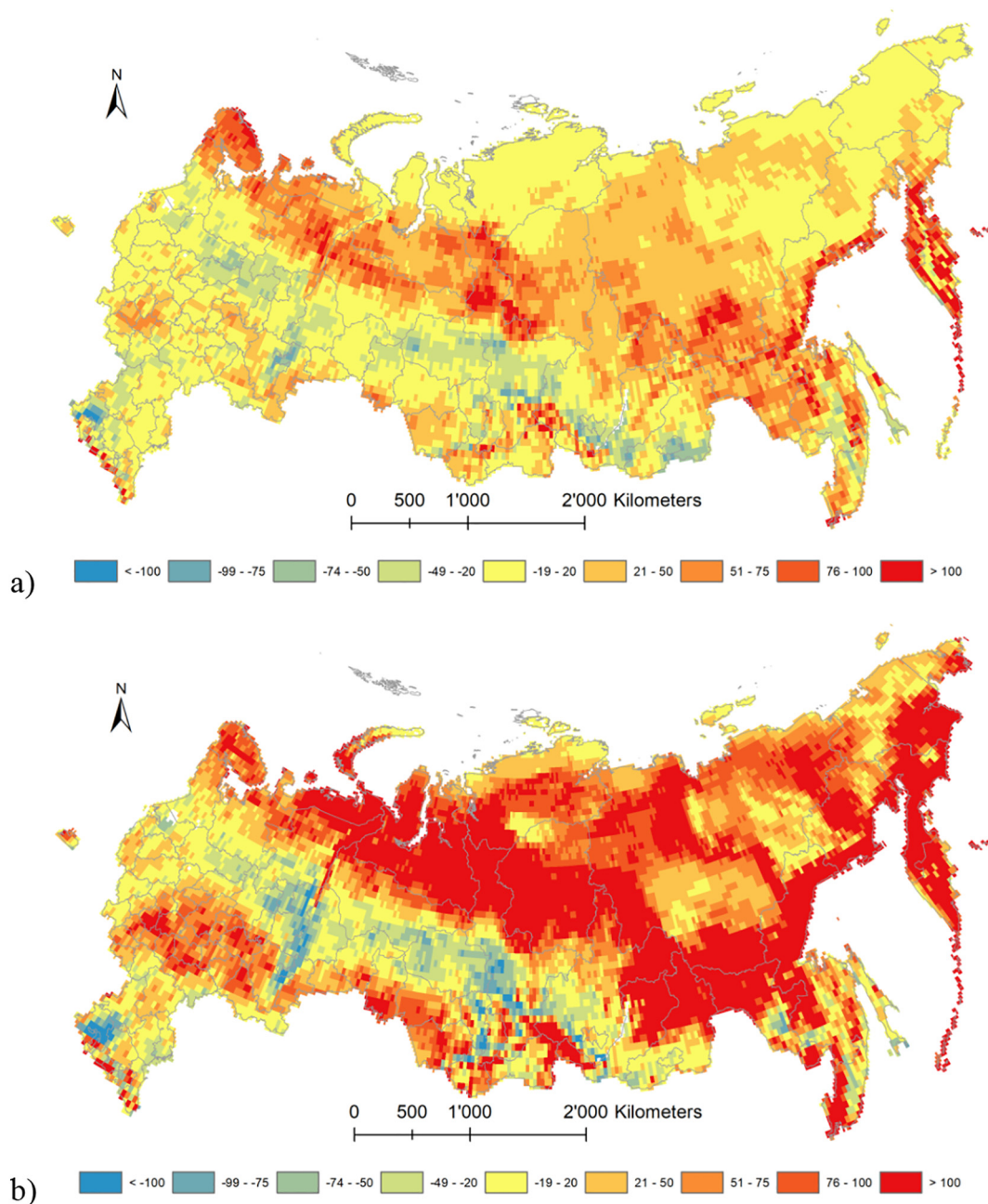


Fig. 5. The projection of heterotrophic soil respiration change (g C m^{-2}) for a) 2010–2050 according to the RCP2.6 climate scenario and for b) 2010–2100 according to the RCP6 climate scenario.

The duration of this warmest period has a positive nonlinear effect on R_s . The sum of the active temperatures during the frost-free period and the period with temperatures above 5°C have nonlinear positive and negative effects, respectively.

It seems reasonable that the effect of precipitation on the respiration flux from soil depends significantly on its physical properties and the drainage conditions. On coarse-textured and well drained soils, the excessive soil wetting by precipitation will not sufficiently depress the R_s because the overwetting for such soils by rainfall is a short-term phenomenon. For such soils, water deficiency is of more importance (Kurganova et al., 2020), which can mostly be observed in dry regions. Fine-textured soils (dominance of clay and silt) and the waterproof layer situated close to the active soil layer can be reasons for overwetting and blocking the R_s under conditions of high precipitation. In such a case, the return of the soil to optimal moisture conditions can

require much more time because water outflow is limited both by the waterproof layer and decreased evaporation due to the soil structure, which impacts the retention of water.

4.2. R_a contribution to R_s and its response to climate

Root respiration is attributed to plant physiological functions, so it seems reasonable that the R_a flux depends mainly on the vegetation class and that the plant growth activity can influence this flux (Han et al., 2017; Ru et al., 2018; Sagar et al., 2019; Liu et al., 2019). The root growth and root mortality are highly seasonal, with active growth from the late spring to early summer and a substantial mortality in the fall (Fitter et al., 1998; McNaughton et al., 1998; Pregitzer et al., 2000; Wang et al., 2009). Root respiration increased during this time and it is assumed that higher root respiration rates may have resulted from

high physiological activity associated with root growth (Miao et al., 2020). Wang et al. (2009) found that the pattern of root productivity was similar to that of Rs.

In our calculations, we did not use absolute values of the autotrophic respiration but rather the contribution of this flux to the total Rs. This means that the value of the contribution of the autotrophic component can change not only as a result of changes in root respiration, but it also depends on changes in the Rh flux. The seasonal variation in the contribution of the autotrophic respiration has been reported as ranging from <10% to >90% of the total Rs (Fu et al., 2002; Hanson et al., 2000; Tomotsune et al., 2013). Some authors have suggested that root growth respiration, which is associated with the synthesis of new tissue, fluctuates irrespective of environmental conditions such as temperature (Högberg et al., 2001; Ohashi et al., 2000); however, other researchers found positive correlations between Ra and the mean annual temperature and precipitation (Tang et al., 2020b). The log-linear regression models developed here for the share of the autotrophic component to the total Rs (Table 3) showed that the contribution of the root respiration in coniferous forests and arable lands was not related to the temperature. The most important factors in coniferous forests are the wetting conditions during the growing season (when the temperature exceeds +5 °C) and during the warmest period of the year (with temperatures above +10 °C). A negative dependence from the duration of the growing season can reflect the seasonality of root growth activity.

In deciduous forests, the contribution of the autotrophic component depends on active temperatures during the whole growing season and on the warmest seasons. The root contribution to the total Rs decreases if the spring is warm (negative relationship with SumT_5), which is most likely due to warm conditions at the beginning of the growing season as well as increases in Rh that decrease the share of the autotrophic component. We assume that hot summers (SumT_10) can decrease the Rh due to enhanced evaporation and soil drying, which results in an increased autotrophic contribution (Zheng et al., 2021). In contrast, the dependence on precipitation during these periods has been confirmed previously: with enough precipitation during the warmest period of the year, Rh can be stimulated, which results in a decreased contribution to root respiration, while increased precipitation during the cool period can decrease microbial activity due to overwetting and thus increase the contribution of the autotrophic component.

Similar differences between coniferous and deciduous forests were observed in experimental studies that reported that elevated temperatures did not lead to large changes in autotrophic respiration in coniferous forests (Zou et al., 2018), but to increased root respiration in cool temperate deciduous forests (Noh et al., 2016).

The autotrophic contribution in grasslands also depends partly on temperature. There are two temperature parameters included in the log-linear regressions for this vegetation class: MAT and SumT_5. A negative dependence of the root contribution to the total Rs on MAT most likely reflects the higher sensitivity of Rh to temperature (Li et al., 2013; Verburg et al., 2005; Wang et al., 2014), which can be more pronounced at low temperatures (Díaz-Raviña et al., 1994; Kirschbaum, 1995; Koven et al., 2017). The grasslands vegetation class includes tundra ecosystems, which develop in cold climatic conditions. These ecosystems are limited by temperature and this is most likely one of the reasons why active temperatures and the duration of the period with temperatures above +5 °C positively influence the relative value of the root respiration. Other variables used in the regression are connected to the moisture conditions of the site. The most important periods appear to be spring or autumn when the average temperatures are in the range between 0 and +5 °C, and the warmest period (when temperature is at or exceeds +10 °C). During these periods, the contribution of the autotrophic respiration increases with an increase in precipitation. This can also be connected to changes in the dependence of Rh on soil moisture. The complex hysteretic response of Rh on soil moisture in grasslands has been reported previously by Suseela et al. (2012).

The average estimates of the autotrophic contribution to Rs varies between 40 and 45% and 60% for forest and non-forest vegetation, respectively (Hanson et al., 2000; Högberg et al., 2001, 2005; Yevdokimov et al., 2010). The average root contribution estimated by random forest in our study was 39% for forests and 30–45% for other vegetation classes. The highest root contribution was calculated for grassland vegetation in the tundra (49%). Grasslands have the highest root contribution among all land cover classes at all bioclimatic zones. The lowest contribution from the roots was obtained for arable lands. In total, the average root contribution to the total soil respiration was higher in cold tundra conditions in comparison with other bioclimatic zones. Measured by four different methods, the contribution of root respiration to the total soil respiration flux in the tundra zone was reported to be 30–60% for forest ecosystems, 29–58% for wetlands and 15–70% for grass-dwarf shrubs-moss-lichen tundras (Goncharova et al., 2019). Our calculated values (40–49%) fall inside of these ranges.

A high share of forests to the total Rh flux from the territory of Russia (Table S6) is related to the large area occupied by forested land because the average Rh for forest soils is similar to other land cover classes (Table 5). The middle and southern taiga and the temperate regions have the highest Rh flux in both parts of Russia, indicating more favorable climatic conditions in these bioclimatic zones for decomposing activity in the soil. Soil respiration in the more northern ecosystems (northern taiga, forest-tundra and tundra) are limited by temperatures and duration of the vegetation period while the more southern semiarid zones (steppe and deserts or semi-deserts) have a lack of precipitation.

The average rate of heterotrophic soil respiration in the European part of Russia is almost 45% higher than in the Asian part, probably due to the milder climate in the European part. However, the much larger area of the Asian part results in a relatively low annual average heterotrophic respiration rate for the whole territory of Russia ($190 \pm 0.3 \text{ gC m}^{-2} \text{ yr}^{-1}$).

Arable lands occupy a small part of the territory of Russia (6.3%) but they have the highest rate of heterotrophic respiration in both parts of the country (Table 5). The heterotrophic respiration rate on these lands is 33 and 38% higher than the average regional rate in the European and Asian parts, respectively. Soils used for agricultural production should have high fertility to provide high levels of agricultural plant productivity. Fertile soils have high respiration activity. Additionally, arable lands that are mostly situated in bioclimatic zones with favorable climatic conditions can explain the high rate of heterotrophic respiration on these soils. Tillage practices increase the turnover of soil aggregates and accelerate the decomposition of aggregate-associated soil organic matter, additionally increasing the heterotrophic soil respiration of cultivated soils (Paustian et al., 2000). An increase in the soil CO₂ efflux was observed after the conversion of forests to agricultural lands (Fan and Han, 2020).

Overall, the estimation of Rh in this study is higher by 7–20% than reported previously for the territory of Russia (Table 6).

4.3. Impacts of disturbances on Rh

Within this study, it is assumed that 1) standard measurements of Rs were not provided in stands with clear recent signs of Ds (with the

Table 6
Estimation of heterotrophic soil respiration for the territory of Russia by different authors.

Rh total, Pg C yr ⁻¹	Mean Rh, g C m ⁻² yr ⁻¹	Source
3.20	196	(Nilsson et al., 2000; Stolbovoi, 2003)
2.78	171	(Kudeyarov and Kurganova, 2005; Kurganova, 2003; Kurganova, 2010)
2.73	168	(Golubjatnikov et al., 2005; Golubjatnikov and Svirezhev, 2008)
2.7–3.0	158–175	(Kudeyarov, 2018)
3.16	190	Our estimation

exception of certain studies of Ds impacts, e.g., fire chronosequences); 2) the efflux caused by decomposition of CWD is not included in soil respiration but estimated separately; and 3) under the joint impact of several Ds, e.g., fires in stands that were previously destroyed by defoliators (so called *shelkopryadniki*), the estimates have been accounted for by impacts from a primary destructive agent.

A diversity of factors controls the impacts of Ds on Rs and Rh. However, due to incomplete knowledge on important ecosystem processes coupled with often biased spatial and temporal information on the extent and the severity of Ds, it is difficult to undertake an accurate quantitative assessment of the impact of Ds on soil effluxes at large scales (Harmon et al., 2011). This is particularly true for a large and heterogeneous country such as Russia. However, we tried to use some approximation to estimate the rate of the impacts of Ds on the soil carbon efflux. This estimation can help to understand how much the lack of information about Ds would impact the uncertainty of the practical implementation of the system designed to assess Rs and Rh.

Disturbance-related impacts on terrestrial ecosystems may substantially change Rs and its major constituents (Pereira et al., 2019; Ribeiro-Kumara et al., 2020). The diversity of such impacts is very broad, as it depends on the land use/land cover type, the biometric and ecological characteristics of the vegetation, the buffering capacity and adaptive thresholds of the ecosystems, and from a disturbance perspective, on the type, extent, frequency and severity of the disturbances (Ds). For agricultural land (arable, pastures, hay fields), major Ds are associated with land management and soil treatment under relatively stable, long period regimes of land use. This has resulted in the development of a specific type of human-transformed soil on which the impact of other Ds (other than land management) is relatively small over large areas and for long time periods (≥ 1 year). Hence, the impacts are within the uncertainty limits of the assessment of the basic environmental factors controlling Rs. Of all potential Ds that can occur in natural grasslands and shrubs, which occupy vast territories in Russia's high latitudes and the subboreal ecotone, the most dangerous Ds are wildfires and grazing. However, such Ds were historically an inherent feature of the evolution of this land cover class under relatively stable land-use systems, and the majority of the empirical data on soil respiration already directly or indirectly includes the impacts of these Ds. Treeless bogs are burnt only during catastrophic events in fire danger years; the return interval of such fires under current conditions exceeds hundreds of years (Shvidenko and Schepaschenko, 2013).

In contrast to the aforementioned land cover classes, Ds in forests do impact both Rs and Rh. Around 20–50% of all Rh losses in boreal and temperate forests are the result of Ds (Harmon et al., 2011). As the most extreme case, deforestation usually increases the carbon release from soil at various scales due to increases in soil temperature (Hirsch et al., 2004; Schlesinger and Andrews, 2000; Townsend et al., 1992). However, over the long-term, deforestation may reduce the soil carbon efflux due to the removal of the aboveground vegetation and the destruction of the root respiration before recovery to a full canopy (Alexander, 1977; Boone et al., 1998). That said, deforestation in Russia (in a land use change sense) is observed only over small areas, about 100–150 thousand ha per year (Pan et al., 2011). The area of planted forests does not currently exceed 200×10^3 ha year⁻¹ (0.03% of the Russian forested area), so the impact of deforestation and reforestation is negligible for the assessment of the total Rs flux of forests for Russia. Three types of Ds – fires, biogenic factors and harvest – occur on about 20 mio. ha of land in Russia annually, of which about 3 mio. ha leads to stand replacement (Shvidenko and Schepaschenko, 2013).

According to our estimates for the entire territory of Russia, the disturbances are responsible for an increase in heterotrophic soil respiration by only 1.76% under the stable disturbance regime. Altering of this regime due to climate change will increase the contribution of disturbances to the total flux of Rh. For example, McDowell et al. (2018) have predicted a doubling of drought frequency by 2100, even in areas that historically have had limited drought disturbances. Drought causes

vegetation stress, increasing vulnerability to insects and pathogens (Seidl et al., 2014), and the drying of fuel for wildfires (Flannigan et al., 2016). According to the output from six Global Climate Models for the territory of Russia, the number of days with fire danger conditions are expected to increase by 12–30% for the southern forest zone boundary in both the European region and in Siberia. However, in the Baykal and Primoriye regions, the change in fire danger in the twenty-first century will be quite small for the entire fire season (Malevsky-Malevich et al., 2008). These authors also projected that the areas of maximum fire danger risk will double by the middle of the century. However, the relatively low contribution of disturbances to the total Rh flux does not consider any crucial effects on this emission under climate change, except in the situation where these changes are catastrophic.

4.4. Projection of Rh

Our results showed that climate warming may change the Rs flux as well as the contribution of different biomes to the total Rh across Russia by the middle of the century (Table S7). The maximum changes in Rh are expected for soils in the European part of Russia (25 ± 1.5 g C m⁻² year⁻¹). Temperate forests and the Middle taiga bioclimatic zones are forecast to have the maximum increase in Rs due to climate change (28 ± 0.3 and 27 ± 0.1 g C m⁻² year⁻¹, respectively). In the Asian part of the country, the maximum changes will be observed in the Steppe biome (32 ± 0.3 g C m⁻² year⁻¹). Maximum changes are also expected in grasslands and arable lands over the entire Russian territory. Minimal changes are forecasted for Wetlands in the whole European part of Russia and in the northern biomes (boreal and tundra ecosystems) in the Asian part of Russia. Changes in the Rs flux in the southern biomes of the Asian part of Russia will be substantial (23 – 26 g C m⁻² year⁻¹). The main reason for such differences between wetlands can be due to different hydrological regimes in different bioclimatic zones. The European part of the country receives more precipitation during a year. The soils in the northern regions of the Asian part of Russia can supplement their water reserves owing to permafrost melting. In the southern biomes of the Asian part, such sources of water will be unavailable due to low amounts of precipitation and increased evapotranspiration due to the expected changes in the climate. This can lead to the lowering of the ground water table and mean that wetlands will become a considerable source of CO₂ under climate warming (Kurbatova et al., 2009). The expected increase in droughts and climate variability might lead to more frequent and severe peat fires. Some authors have projected that the melting of the permafrost will lead to an alteration in the hydrological and temperature regime of northern peatlands. As a result, permafrost peatland might additionally emit 8 – 10 Tg CH₄ yr⁻¹ (Minayeva and Sirin, 2012).

The business-as-usual scenario for arable land will result in a loss of 9–12% of carbon in the 0–20 top layer during the course of this century (Romanenkov et al., 2009). The abandonment of arable land in 1990–2015 has led to a substantial accumulation of carbon, estimated to be as much as 74 ± 22 Mt. C year⁻¹ (Kurganova et al., 2010, 2014). However, this process will not be that intensive in the future, even with a stationary climate (Romanovskaya, 2008).

Our model suggests an increase in Rh due to climate change (based on the RCP2.6 and RCP6 scenarios) by 10–12% in forest ecosystems by the middle of the century; however, rises in productivity (Gu et al., 2017; Madani et al., 2018) will likely exceed this amount. Using machine learning tools, Naidu and Bagchi (2021) predicted a net soil-C gain in most parts of the territory of Russia in near-future scenarios (2020–2040). The outputs from 13 Earth system models projected small impacts from droughts on the Gross Primary Production for most parts of the territory of Russia during 2075–2099 (Xu et al., 2019). However, taking into account the expected increase in harvests and the extent and severity of wildfires and insect dynamics, in

particular, we expect a reduction in C sequestration in forests (FAO, 2016; Komarov et al., 2006; Xu et al., 2019).

5. Conclusions

According to the results obtained here, soil properties are a strong factor in determining the climatic effect of changes in Rs. Without any disturbances, soil properties develop over a very long time in comparison with changes in vegetation. Soil features influence both the root respiration and heterotrophic activity, providing favorable or unfavorable conditions for root growth and SOM decomposition. However, different vegetation growing on similar soils can have different autotrophic respiration fluxes and varying inputs of organic substances into the soil. Natural disturbance and anthropogenic activity can lead to a shift in the vegetation cover on the soil and hence to changes in the respiration flux.

The most intensive degree of planetary climate change has been observed during the few last decades (IPCC, 2014). Changes in soil properties take hundreds and thousand years compared to changes in vegetation composition and productivity. This means that predictions of changes in the Rs flux that are based on genetic soil properties can be a promising avenue to pursue in the future because the main characteristics of soil groups and their spatial distribution will be more stable than vegetation parameters in a rapidly changing environment.

CRedit authorship contribution statement

Liudmila Mukhortova: Methodology, Investigation, Data curation; Statistical analysis, Writing- Original draft preparation. **Dmitry Schepaschenko:** Methodology, Investigation, Data curation, Writing-Reviewing and Editing. **Elena Moltchanova:** Statistical analysis, Investigation, Software, Writing- Reviewing and Editing. **Anatoly Shvidenko:** Conceptualization, Reviewing and Editing. **Nikolay Khabarov:** Climate data processing. **Linda See:** Writing- Reviewing and Editing.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Supplementary information

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