



INVITED ARTICLE

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Dedicated to Jianwu (Jim) Tang 唐剑武, who did so much to advance the science of soil respiration.

Key Points:

- Recent decades have seen large advances in measurement methods, experimental approaches, and data availability in soil respiration science
- Lab and field-based experiments have improved our understanding of the integrated effect of environmental change on soil respiration
- Key challenges include broadening access and continuing to explore diverse mechanisms and ecosystems using novel model-experiment approaches

Supporting Information:

Supporting Information may be found in the online version of this article.

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Twenty Years of Progress, Challenges, and Opportunities in Measuring and Understanding Soil Respiration

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Abstract Soil respiration (Rs), the soil-to-atmosphere flux of CO₂, is a dominant but uncertain part of the carbon cycle, even after decades of study. This review focuses on progress in understanding Rs from laboratory incubations to global estimates. We survey key developments of in situ ecosystem-scale Rs observations and manipulations, synthesize Rs meta-analyses and global flux estimates, and discuss the most compelling challenges and opportunities for the future. Increasingly sophisticated lab experiments have yielded insights into the interaction among heterotrophic respiration, substrate supply, and enzymatic kinetics, and extended incubation-based analyses across space and time. Observational and manipulative field-based experiments have used improved measurement approaches to deepen our understanding of the integrated effects of environmental change and disturbance on Rs. Freely-available observational databases have enabled meta-analyses and studies probing the magnitude of, and constraints on, the global Rs flux. Key challenges for the field include expanding Rs measurements, experiments, and opportunities to under-represented communities and ecosystems; reconciling independent estimates of global respiration fluxes and trends; testing and leveraging the power of machine learning and process-based models, both independently and in conjunction with each other; and continuing the field's tradition of using novel experiments to explore diverse mechanisms and ecosystems.

Plain Language Summary “Soil respiration” refers to the flow of carbon dioxide, mostly generated by plant roots and microbes, from the soil to the atmosphere. This flux is large and highly uncertain, and understanding it has significant implications for our ability to predict the effects of land use and climate change. This review summarizes advances, insights, and challenges in soil respiration science. It examines laboratory approaches and findings; documents changes in how researchers measure and understand soil respiration in the natural world; and describes efforts to estimate the global dynamics of soil respiration from openly-available databases of observations. We conclude by discussing the most compelling challenges and opportunities for the future.

1. Introduction

“Soil respiration” (Rs) is conventionally understood to mean the flux of CO₂, as measured at the surface of the litter layer, to the atmosphere (Ryan & Law, 2005). At ecosystem scales, Rs dominates ecosystem respiration (Law et al., 2002). Rs variability can drive the carbon balance of ecosystems (Desai et al., 2022) to entire continents (Ballantyne et al., 2017; Metz et al., 2023). Rs is the second largest carbon flux in the earth system after photosynthesis (Friedlingstein et al., 2022), and almost an order of magnitude larger than anthropogenic carbon emissions (Bond-Lamberty and Thomson, 2010b), and can thus affect the terrestrial carbon cycle (Ballantyne et al., 2017). The links between Rs, carbon allocation, and soil carbon turnover also mean that site-level Rs measurements can be used to calculate or constrain other carbon fluxes such as net biome production (Giasson et al., 2013; Gough et al., 2008; Goulden et al., 2011). In spite of this demonstrated importance of Rs, its underlying processes remain highly uncertain components of Earth System Models (Varney et al., 2022), and ecosystem respiration more generally dominates the uncertainty of terrestrial carbon storage in CMIP6 models (Wei et al., 2022). The interaction between Rs and environmental change thus remains one of the greatest sources of uncertainty in climate and earth system projections (Nissan et al., 2023).

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Previous reviews have synthesized knowledge on ecosystem- to global-scale Rs and reflect the field's evolving research frontiers. Early examples included Raich and Potter (1995) and Schlesinger (1977), as well as quantitative reviews of how Rs interacts with climate change (Rustad et al., 2000; Schlesinger & Andrews, 2000). A 2003 workshop summarized concepts, mechanisms, and above-belowground coupling, with a call for multi-factorial experiments (Ryan & Law, 2005) Luo and Zhou (2006) comprehensively covered many of these topics in their book on Rs. A subsequent workshop in 2007 highlighted the opportunities for using automated soil respiration measurements (Carbone & Vargas, 2007). Focused reviews have surveyed methods to partition autotrophic (Ra) and heterotrophic (Rh) respiration (Hanson et al., 2000; Kuzyakov, 2006; Kuzyakov & Larionova, 2005; J. Zhu et al., 2023), the links between photosynthesis and Rs (Kuzyakov & Cheng, 2001; Kuzyakov & Domanski, 2000; Kuzyakov & Gavrichkova, 2010; Vargas, Baldocchi, et al., 2011), Rs response to elevated CO₂ and temperature (Davidson & Janssens, 2006; Jackson et al., 2009; Pendall et al., 2004; Zak et al., 2000), inferring carbon allocation using isotopes (Brüggemann et al., 2011), above- and belowground Rh under ecosystem disturbance (Harmon et al., 2011), and wetting or thawing effects on Rs (D.-G. Kim et al., 2012). In the last decade, Rey (2015) discussed the importance of considering abiotic Rs sources and transport processes, while M. Xu and Shang (2016) examined the uneven distribution of global Rs measurements, factors affecting Rs computation at different spatial scales, and estimated the global Rs flux. Finally, Phillips et al. (2017) examined how methodological advances in measurement and analysis may improve our mechanistic understanding and modeling of Rs.

Here we survey and synthesize the development of Rs science, focusing on the last two decades. Most previous reviews have treated ecosystem Rs as equivalent to the sum of belowground autotrophic (Ra) and heterotrophic (Rh) respiration. We generally do the same, but emphasize the complexity and diversity of processes generating, transporting, and consuming belowground CO₂ (Figure 1). This review focuses on the growth and application of Rs observational data from laboratory incubations and mesocosms (Section 2); surveys key developments of in situ ecosystem-scale observations and manipulations (Section 3); and synthesizes Rs meta-analyses and flux estimates to assess advances in quantifying and understanding global Rs (Section 4). We conclude by looking to

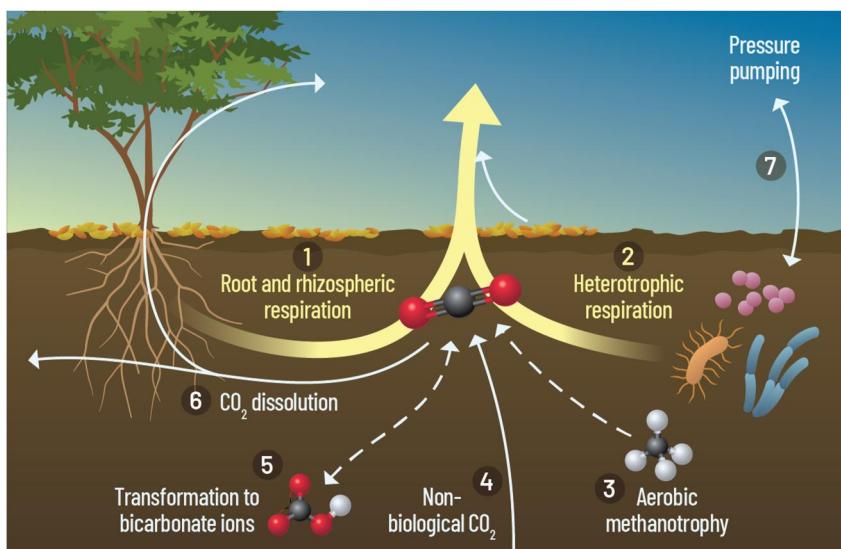


Figure 1. Soil respiration is dominated, in most ecosystems and at most times, by (1) root and rhizospheric respiration and (2) heterotrophic respiration, including surface litter decomposition (Fröberg et al., 2009; X. Yang et al., 2020). However, it may include CO₂ from both (3) aerobic methanotrophy (Serrano-Silva et al., 2014) and (4) non-biological CO₂ production (Rey, 2015; Sánchez-Cañete et al., 2016), processes particularly important in saline and alkaline soils (J. Ma et al., 2013) and geothermally active areas (e.g., F. Liu et al., 2023). In addition, CO₂ produced in soils is not always directly released to the atmosphere (Maier et al., 2011; Sánchez-Cañete et al., 2018), and thus the surface-measured flux may deviate from total belowground CO₂ production due to (5) the transformation to bicarbonate ions under high-pH conditions (Angert et al., 2015); (6) dissolution of resired CO₂ in soil water and subsequent transport (M. S. Johnson et al., 2008; Tamir et al., 2011), potentially via plants' transpiration (Aubrey & Teskey, 2009, 2021); and (7) pressure pumping (Bain et al., 2005; Moya et al., 2019). These and other belowground processes remain important active research areas crucial for reliable estimates of Rs in many ecosystems (Rey, 2015).

the future, discussing what are, in our view, the most compelling challenges and opportunities for this field of research (Section 5).

2. Laboratory Incubations and Mesocosms

Laboratory experiments are foundational to our mechanistic understanding of soil heterotrophic respiration and carbon mineralization processes. These studies occur in tightly controlled environments and are usually manipulative rather than observational, enabling causal attribution and mechanistic understanding (Vicca et al., 2014). Laboratory conditions differ from the real world (Henry, 2007), however, and are typically disturbed, small-volume soil samples isolated from the pedosphere and effects of roots, litter, and soil fauna (Kampichler et al., 2001). Results can be affected by experimental protocols (X. Chen et al., 2010) as well as experiment length (Birge et al., 2015; Hamdi et al., 2013). Extrapolating such results to *in situ* conditions, or using them to parameterize models, must be done with caution (J. Chen et al., 2023; Patel et al., 2022).

Laboratory incubations are frequently used to manipulate a single aspect of the soil biotic or abiotic environment in isolation. One of the most extensively studied of these is the temperature sensitivity of Rh, often expressed as Q_{10} , the relative change of respiration with a 10°C temperature increase. This is a voluminous literature to which we cannot do justice here; Hamdi et al. (2013) synthesized a broad range of such experiments. However, the field has increasingly recognized limits to this approach because of its intrinsic simplicity (Subke & Bahn, 2010) and because environmental change comprises far more than temperature increases. This has shifted both research (Bradford et al., 2010; Qu et al., 2023; Y. Zhang et al., 2023b) and inspired a new generation of process-focused models (Abramoff et al., 2018; Davidson et al., 2012; Sulman et al., 2014; Wieder et al., 2013) toward microbial responses to temperature variation more generally, and the degree to which microbial growth and turnover, substrate supply, and enzymatic kinetics control Rh acclimation (Bradford et al., 2010). Other studies have analyzed the responses of specific bacterial taxa and proposed that community-assembled traits of microbial taxa may enable enhanced prediction of carbon cycling feedbacks to climate change in ecosystems across the globe (C. Wang et al., 2021). These more recent studies have emphasized the need to incorporate multiple drivers and response variables in Rh incubations.

The response of soil Rh to temperature is contingent upon water availability, which is intricately linked with soil type (Hartley et al., 2021; Maia et al., 2019; Singh et al., 2021; X. Xu et al., 2016). Moyano et al. (2012) summarized hundreds of different Rh ~ soil moisture responses from 90 different soils and found consistent effects of soil texture, organic carbon content, and bulk density. Other innovative studies have looked at the differential effects of top-down wetting simulating rainfall (Lee et al., 2004), versus bottom-up as a proxy for groundwater rise (Patel et al., 2021b), and how rewetting history and frequency affect microbial C and N dynamics (Fierer & Schimel, 2002; Hawkes et al., 2017). The maximum response of Rs to temperature is valid only when there is no water stress, an important factor in water-limited ecosystems (Almagro et al., 2009; Leon et al., 2014). Rh may also be limited by high soil moisture due to energetic and enzymatic constraints on microbial activity under short-term anaerobic conditions (Freeman et al., 2001), a relationship often used in ecosystem- and Earth system models (Sulman et al., 2014). Models may thus underestimate greenhouse gas emissions in high-moisture environments that experience redox oscillations, particularly in the face of altered frequency and intensity of precipitation (W. Huang & Hall, 2017).

Carbon accessibility to microbes is influenced by mineralogy (Rasmussen et al., 2018) and substrate characteristics (Leinweber et al., 2008; Lugato et al., 2021; Moinet et al., 2020; Zimmermann et al., 2012) in addition to soil moisture and temperature. It is increasingly recognized that soil physicochemical characteristics determine carbon stabilization mechanisms, including organo-mineral associations (Kleber et al., 2007) and physical protection within aggregates (Pulleman & Marinissen, 2004). This limits soil organic matter (SOM) availability to microbes (Doetterl et al., 2015; Glassman et al., 2017; González-Domínguez et al., 2019; Torn et al., 1997). Uroz et al. (2015) proposed the term “mineralosphere” to reflect the strong mineralogical control on the distribution and function of mineral-associated bacterial communities.

The temperature sensitivity of SOM decomposition decreases with increasing stability of SOM (Jia et al., 2023; Leinweber et al., 2008), implying that physicochemical protection of SOM constrains the temperature sensitivity of SOM decomposition under field conditions (Moinet et al., 2020). Because of the complex nature of SOM (Trumbore, 2000; Rocci et al., 2024), separating soil carbon into particulate and mineral-associated organic matter may be crucial to understanding its vulnerability (Lugato et al., 2021; Zimmermann et al., 2012).

Analytical techniques such as Fourier transform ion cyclotron resonance mass spectrometry (Cooper et al., 2022; Wilson & Tfaily, 2018) and soft X-ray spectromicroscopy (C. Chen et al., 2014) can identify specific mineral-organic associations of SOM, a frontier that Rs researchers are only beginning to explore (Seyfferth et al., 2020). In addition, because microbial activity in soil is carbon-limited (Hobbie & Hobbie, 2013), changes in primary productivity produce a “priming effect,” increasing Rh above that derived from the substrate directly (Kuzyakov, 2006). B. Zhu and Cheng (2011) showed how plant-carbon inputs to the rhizosphere create a priming effect and simultaneously increase the temperature sensitivity of SOM decomposition. In bulk soil, substrate availability also positively affects the temperature sensitivity of soil carbon mineralization (Gershenson et al., 2009; Jia et al., 2023). Researchers are increasingly incorporating microscale physicochemical properties (Abramoff et al., 2018; Moyano et al., 2013; Yan et al., 2018) and biological processes (Davidson et al., 2006; Soong et al., 2020; Tao et al., 2023; Wieder et al., 2013; Wutzler et al., 2023) into models (Rocci et al., 2024).

Moving upwards in scale, innovative studies have extended incubations across space and time. Continental-scale comparative incubations have examined magnitudes, variability, and drivers of respiration rates (Colman & Schimel, 2014; Tian et al., 2022) as well as temperature sensitivity (Craine et al., 2010; Q. Wang et al., 2016), microbial community structure (Karhu et al., 2014), and carbon use efficiency (Ye et al., 2019). Y. Liu et al. (2018) incubated 25 soils from tropical to cold-temperate forests to quantify how the temperature of optimal Rh varies by region and other factors. Incubation studies have also shown how Q_{10} depends on ecosystem type, with alpine grasslands showing higher temperature sensitivity than tropical forests in China (M. Liu et al., 2017). Soil carbon priming has also been characterized at the global scale—Bastida et al. (2019) found that positive priming effects were associated with drier, lower-carbon ecosystems—although work remains to be done on interactive effects between priming and other factors such as temperature (B. Zhu & Cheng, 2011). This increased understanding of microbial catabolism is critical for correctly implementing microbial processes in Earth system models (Soong et al., 2020).

Finally, larger mesocosms and ecotrons can include flora and fauna in an experiment, providing a higher degree of realism by manipulating both Ra and Rh (Stewart et al., 2013; Tingey et al., 2008). This allows for unusual and/or complicated experiments probing various biotic effects on Rs, for example, earthworms (Jouquet et al., 2012), plant diversity (D. Johnson et al., 2008; M. Liu et al., 2017), and litter characteristics (Fröberg et al., 2009; Jonasson et al., 2004). As an intermediate step between laboratory and field experiments, mesocosms can be used to test precipitation gradients (Yu et al., 2017), extreme precipitation events (Petrakis et al., 2017), the role of hydrology and salinity (Krauss et al., 2012), or CO₂ fertilization (Mikan et al., 2000) on Rs. Ecotrons have also been proposed as a crucial intermediate scale between small-scale laboratory or pot experiments and our understanding of ecosystem processes (Chapin et al., 2009; Curiel Yuste et al., 2010; Roy et al., 2021; Ryan & Law, 2005). We suggest that future research take advantage of the balance between control, replication, and realism that mesocosms and ecotrons provide (Stewart et al., 2013).

3. In Situ Measurements and Manipulations

3.1. Methodological Advances

Both observational and manipulative studies of in situ Rs begin with the act of measurement (Figure 2), and substantial research has gone into accurately quantifying Rs (Luo & Zhou, 2006). Manual and automated chamber methods, in which the changing CO₂ concentrations over time in a closed chamber (Pumpanen et al., 2004) are used to calculate the Rs flux using an infrared gas analyzer (Mills et al., 2012; Parkinson, 1981; Pongracic et al., 1997) or gas chromatograph (Mondini et al., 2010), are most common. Chambers are set into collars embedded in the soil surface; methodological studies have shown that collar properties generally do not introduce bias (Jian et al., 2020), but long-term installations may be problematic (X. Ma et al., 2023). Low mixing and turbulence velocity may also bias chamber-based Rs measurements (Brændholt et al., 2017). M. Xu and Shang (2016) discussed methods and challenges of such chamber-based Rs measurements.

Manual measurements are labor-intensive but can capture Rs spatial variability within an ecosystem and, to a limited extent, across time (La Scala et al., 2000; Leon et al., 2014; Panosso et al., 2009). Such measurements dominate the extant Rs literature. This approach is laborious, however, and for convenience researchers often measure once a month (Jian et al., 2018), likely biasing their observations to days and times when conditions are best for fieldwork (Cueva et al., 2017). Such sampling may not capture temporal trends (Vargas & Le, 2023) and inadequately samples Rs pulses driven by rain or atmospheric pressure (Bain et al., 2005; Lee et al., 2004; Leon

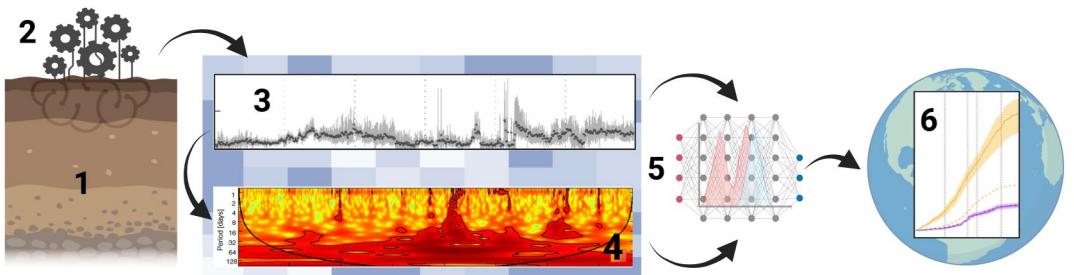


Figure 2. Technological and experimental improvements have revolutionized our understanding and prediction capabilities of soil respiration over time and space. We have seen refinement of (1) experiments (Bahn et al., 2006; Cao et al., 2004; Höglberg et al., 2001; Tremblay et al., 2018), continued (2) technological advances (Carbone & Vargas, 2007), and the advent of global databases (Bond-Lamberty et al., 2020; Jian et al., 2021b). These advances have allowed (3) analyses of long-term records or soil respiration (Bernhardt et al., 2006; Giasson et al., 2013; Kurganova et al., 2020) and (4) quantifying its temporal variability in unprecedented ways (Bond-Lamberty et al., 2019; Vargas, Dettò, et al., 2010). New mechanisms have been identified and incorporated in (5) process-based models (Abramoff et al., 2022; Sulman et al., 2018), building on a widening pool of global researchers (D.-G. Kim et al., 2022). Finally, these new approaches have (6) improved predictions of soil respiration from local to global scales (Jian et al., 2021a; H. Lu et al., 2021; Stell et al., 2021a).

et al., 2014; Pumpanen et al., 2010; K. Savage et al., 2014). This may bias the functional relationships researchers estimate between R_s and soil temperature or moisture as well as the calculation of annual flux estimates (Bond-Lamberty et al., 2019; Giasson et al., 2013; Vargas & Le, 2023; M. Xu & Shang, 2016).

Continuously-measuring automated systems provide detailed information about the temporal variability of R_s (Vargas, Carbone, et al., 2011). Early custom-made systems were engineered as chambers powered by pneumatic mechanisms and connected to infrared-gas analyzers (Brumme & Beese, 1992; Goulden & Crill, 1997; McGinn et al., 1998; Vose et al., 1995). Commercial automated chamber systems available by the mid 2000s, albeit at a high cost, were initially used in forests (Shi et al., 2009; Xiang et al., 2007) and their application has expanded to ecosystems worldwide (Bond-Lamberty et al., 2020). Other automated methods have been developed in the last 20 years (e.g., the forced diffusion method; Risk et al., 2011). R_s may be calculated from the concentration of CO_2 at different soil depths, based on Fick's first law of diffusion (J. Tang et al., 2003 and references therein); early applications of this method include studies in temperate (Hirano et al., 2003; Schindlbacher et al., 2007) and water-limited ecosystems (J. Tang et al., 2003; Vargas & Allen, 2008b). The National Ecological Observatory Network network implemented this “gradient method” across its sites (<https://data.neonscience.org/data-products/DP1.00095.001#documentation>). R_s can also be calculated using a “gas-snake,” a flexible micro-polyvinylidene difluoride membrane that is pushed into the soil and equilibrates with soil air (Heinemeyer et al., 2012).

The large volume of temporally-detailed observations from automated systems has enabled new types of analyses (Figure 2). This has revealed the importance of seasonal temperature patterns, synoptic events such as weather fronts, and individual precipitation events (Thomey et al., 2011; Vargas, Carbone, et al., 2011). Automated measurements have also characterized diel patterns as well as decouplings from soil temperature (Gaumont-Guay et al., 2006; Misson et al., 2009; Vargas & Allen, 2008c) that may be due to the Kok effect, a temporary light inhibition of respiration (Wehr et al., 2016). These measurements have thus contributed to our understanding of how plant photosynthesis influences R_s (J. Tang et al., 2005; Vargas, Baldocchi, et al., 2011). Temporal lags between R_s and temperature/moisture have been detected using time-series techniques such as cross-correlation and wavelet analysis (Stoy et al., 2013; Vargas, Baldocchi, et al., 2010; Vargas et al., 2018; Q. Zhang et al., 2018). Automated R_s measurements provided the basis for demonstrating, via a physical process model, that diel phase lags between R_s and soil temperature can be explained by physical heat and gaseous transport through porous media (Phillips et al., 2011). Finally, the data density of automated systems has opened new opportunities for leveraging eddy covariance data that have only begun to be exploited (Barba et al., 2018; Hill et al., 2021; Phillips et al., 2017; X. Wang et al., 2017).

Automated systems also impose constraints and demand new protocols, however. Many analyses depend on continuous time series, and automated measurements of R_s inevitably have gaps due to loss of power, physical obstructions, or instrument measurement error (e.g., out of detection limit, spikes). A few studies have suggested approaches for gap-filling R_s time series (Gomez-Casanovas et al., 2013; Zhao et al., 2020); it has been proposed

that nighttime eddy covariance data could be used, but the substantial differences in magnitude and pattern between nighttime Reco and Rs (Barba et al., 2018; Renchon et al., 2018) present an obstacle for gap-filling even at sites where paired measurements are available. The community still needs to standardize methods and protocols in this area and develop consistent infrastructure and reporting formats for dealing with large data sets (Bond-Lamberty et al., 2021).

Manual and automated measurements of Rs are thus complementary, but the community needs to better reconcile information from these approaches for robust temporal (to annual fluxes) and spatial (to eddy covariance tower footprints) upscaling. Random heterogeneity can be addressed through Rs power analyses (Davidson et al., 2002; Pennington et al., 2020; Rodeghiero & Cescatti, 2008) and then adequate sampling, but must also take into consideration the shifting tower footprint (Barba et al., 2018; Phillips et al., 2017) and statistical structure of the random error of measurements (Cueva et al., 2015; K. Savage et al., 2008; Wutzler et al., 2020). In temporal scaling, annual estimates from manual measurements may differ from those based on automated systems (Capooci & Vargas, 2022; M. Xu & Shang, 2016). Relatedly, the apparent strong temperature-Rs relationship derived from sparse manual Rs measurements becomes more complex when hundreds of observations are available (N. K. Ruehr et al., 2010; K. E. Savage & Davidson, 2003). This difference extends to uncertainty, where automated measurements incorporate natural temporal variability along with systematic and random errors (Berryman et al., 2018; Cueva et al., 2015), but are more vulnerable to spatial uncertainty and variability (Rodeghiero & Cescatti, 2008; Teixeira et al., 2012).

3.2. Observational and Manipulative Studies Across Space and Time

Observational studies have used combinations of manual and automated measurements to examine the Rs coupling with various biotic and abiotic factors. These include chronosequence studies looking at disturbance (Campbell & Law, 2005; Czimczik et al., 2006; O'Neill et al., 2006; C. Wang et al., 2002) and ecosystem development (Dacal et al., 2022; Gough et al., 2007; Marañón-Jiménez et al., 2011; Tedeschi et al., 2006); pre-versus post-disturbance effects (T. Hu et al., 2017; Vargas & Allen, 2008a); topographic complexity (Berryman et al., 2015; Kopp et al., 2022; Riveros-Iregui et al., 2012; Webster et al., 2008); and tree mortality (Avila et al., 2019; Borkhuu et al., 2015; Curiel Yuste et al., 2019; Mathes et al., 2023). Links between vegetation and soil respiration are frequently observed: Rs is higher closer to trees (Pennington et al., 2020; J. Tang & Baldocchi, 2005) and shrubs (Cable et al., 2013; Vargas et al., 2018), with different contributions from its source fluxes (Grossiord et al., 2012), as the roots and canopies of plants respire belowground, exude photosynthate, drop leaf litter, and change the micrometeorological environment (B. Wang et al., 2014). Across 18 forested ecosystems in Europe, Rs was significantly correlated with photosynthesis and total ecosystem respiration; disturbed sites deviated from this pattern (Janssens et al., 2001). The challenge with all observational studies, however, is the problem of confounding variables and ascertaining causality (Dacal et al., 2022; Detto et al., 2012; Larsen et al., 2019; Vargas et al., 2018).

Site-scale manipulative studies have significantly advanced our understanding of the biology and biogeochemistry driving Rs over the last two decades. Probably the most common manipulation aims to quantify the distinct sources of Rs, which have varying responses to environmental conditions and different implications for global climate change (Bond-Lamberty et al., 2018; Högberg, 2010; X. Tang et al., 2021). Separating Rs into its distinct components poses technical challenges, and methods include isotopes (Andrews et al., 1999; Schuur & Trumbore, 2006), component integration, tree girdling (Högberg et al., 2001), and root exclusion (including root removal, gap analysis, trench, and deep collar) (Jian, Frissell, et al., 2022). Root exclusion is the most commonly used due to its cost-effectiveness and ease of implementation (Chin et al., 2023; Jassal & Black, 2006), but each technique has its distinct advantages and disadvantages. Despite the potential benefits, integrating or comparing multiple methods remains infrequent (Bond-Lamberty et al., 2004; Comeau et al., 2018; Phillips et al., 2017; Subke et al., 2006).

Disturbance manipulations aim to mimic processes such as fire, harvest, hurricanes, insect mortality, and organic matter change. Early ecosystem-scale experiments simulated hurricane blowdown (Bowden et al., 1993; Millikin & Bowden, 1996) and watershed-scale forest fires (Y. Kim & Tanaka, 2003), an experimental approach that has been applied in other ecosystems such as pine forests (Grady & Hart, 2006), grasslands (Knapp et al., 1998), and tropical savannas (Andersson et al., 2004). Tree girdling showed that the impact of tree mortality events on Rs is proportional to the loss of overstory canopy (Mathes et al., 2023), building upon early studies that first

demonstrated the tight link between live trees and Rs (Högberg et al., 2001) (2001). Harvesting experiments observe strong effects on Rs (Gough et al., 2007; Singh et al., 2021; Ćater et al., 2021; Parro et al., 2019). The landmark Detrital Input and Removal Treatment network experiment applied consistent methodologies and manipulations at sites worldwide; litter addition stimulated priming effects, increasing Rs (Lajtha et al., 2018). The common thread among these disturbances is their tendency to disrupt the existing carbon balance in soils, frequently leading to a prolonged reduction in Rs and soil organic carbon (SOC) in spite of often-elevated soil temperatures after disturbance (Aust & Lea, 1991; Siwek, 2021; Williams et al., 2016).

A second category of manipulation experiments has aimed to change soils' in situ environmental conditions through heating, drought or water additions, fertilization, or CO₂ enrichment. Soil heating experiments have examined changes in Rs magnitude and sources, the durability of any changes, and how they are linked with for example, changes belowground allocation (Giasson et al., 2013) and/or the soil microbial community (Nyberg & Hovenden, 2020; Schindlbacher et al., 2011). For example, soil warming can induce modifications in microbial activity, facilitating thermal adaptation and influencing SOC decomposition rates, ultimately impacting Rs (Bradford et al., 2008). Several meta-analyses have synthesized warming experiments (see below), but substantial uncertainty remains about the in situ Rs response to temperature changes (Nissan et al., 2023). Novel experiments have challenged conventional wisdom on the importance and vulnerability to warming of deeper soil horizons (Hanson et al., 2017; Hicks Pries et al., 2017; Soong et al., 2021; Q. Zhang et al., 2023a).

Manipulative drought experiments consistently report strong negative effects on Rs (Morris et al., 2022; X. Wang et al., 2014). Substantial CO₂ pulses can occur upon soil rewetting (D.-G. Kim et al., 2012; Thomey et al., 2011), and in some ecosystems annual fluxes are dominated by "hot moments" of rainfall-driven Rs pulses (Delgado-Balbuena et al., 2023; Metz et al., 2023; Vargas et al., 2018). Rainfall/drought experiments are crucial because of the confounding effect between soil temperature and moisture (Davidson et al., 1998; Lellei-Kovács et al., 2011), and interactive effects between drought and CO₂ enrichment have also been reported (Reinthalter et al., 2021). Vicca et al. (2014) synthesized 38 manipulation experiments to examine whether Rs changes due to natural soil temperature and moisture variability would accurately predict Rs under altered rainfall, and concluded that generally, the answer was yes—except for studies with high-frequency Rs data. Vicca et al. (2014) suggest that high-frequency data capture short-duration shifts and pulses in the Rs response, increasing the variance of the data (cf. Vargas & Le, 2023). This emphasizes the importance, noted above, of consistently treating and reconciling these different measurement strategies.

In the last two decades, Free-Air CO₂ Enrichment (FACE) experiments have generally reported 20%–40% Rs increases in elevated-CO₂ plots (Bernhardt et al., 2006; King et al., 2004; Pendall et al., 2001), but the durability of this effect varies (Norby et al., 2010). Tradeoffs between building plant biomass versus increasing SOC storage may partially explain this variable response of Rs to elevated CO₂, but what drives this tradeoff is not well understood (Terrer et al., 2021). FACE experiments have generally been performed in developmentally young ecosystems, but recent studies in mature woodlands are more equivocal (Drake et al., 2018); there is also evidence of publication bias in this area (Dieleman & Janssens, 2010). These factors, combined with the high value of such experimental data for ecological to earth system modeling (Keenan et al., 2013; Medlyn et al., 2015; Norby et al., 2016), mean that CO₂ enrichment experiments remain crucial for our understanding of how elevated atmospheric CO₂ concentrations may affect Rs, carbon cycling, and climate feedbacks.

The power of ecosystem-scale manipulations arises from integrating the effects of experimental treatment(s) across abiotic drivers, biogeochemical cycles, and biological processes. Their weakness lies in their complexity and cost, and thus they are rarely sustained beyond a few years. One interesting compromise to address this problem is soil transplant experiments, which are field-based but feature core- to monolith-scale experimental units moved between different elevations (Ayres et al., 2009; Mills et al., 2014), ecotones (Sjogersten & Woockey, 2002; Tremblay et al., 2018), or for example, saltwater exposure (Capooci et al., 2019; Hopple et al., 2022). While laborious to implement and limited in scale, the altered environmental conditions come "for free" and thus long-term field transplants can be highly cost-effective (Bond-Lamberty et al., 2016).

3.3. The Importance and Potential of Long-Term Measurements

Long-term observations are crucial for drawing robust scientific inference about the Earth system (Luo et al., 2011; Mori et al., 2023; Müller et al., 2016; Ward et al., 2017). While short-term observations provide insight into how Rs responds to perturbations, any extrapolation to long-term system behavior is problematic.

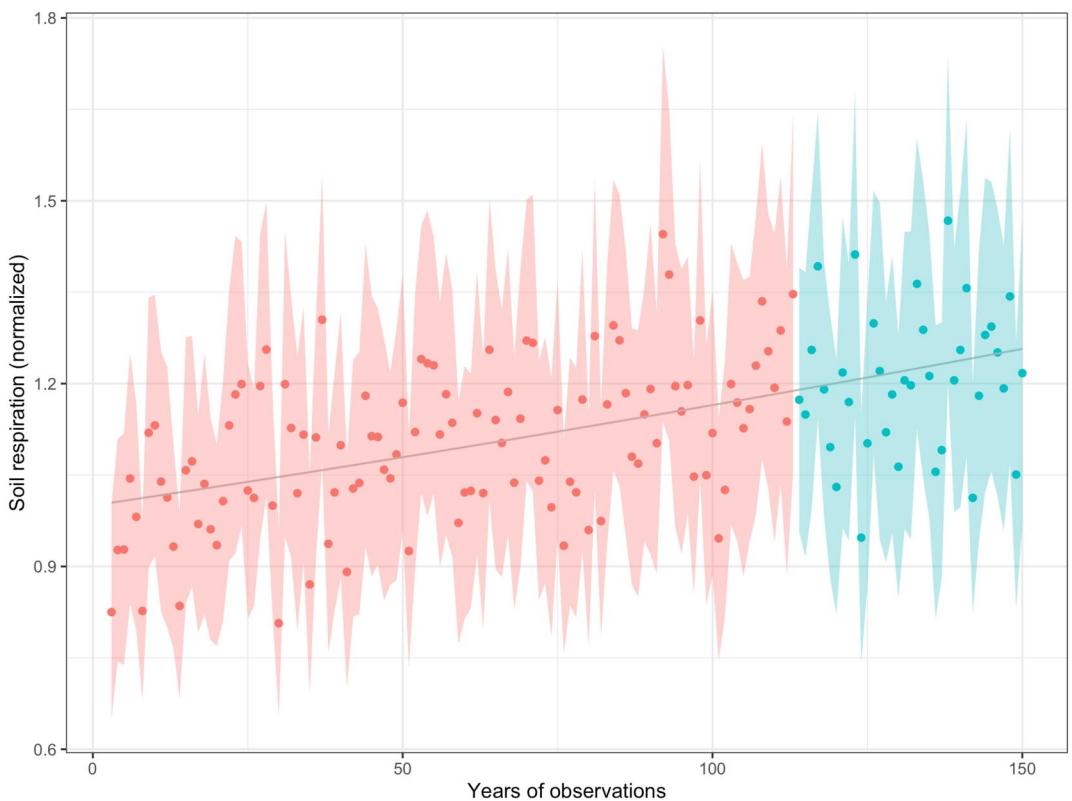


Figure 3. An example of the length of soil respiration (Rs) observations required to observe a statistically significant trend from environmental warming. This back-of-the-envelope analysis assumes a Q_{10} temperature sensitivity of 2.0, an initial Rs rate of 1.0 (unitless, as this is a normalized example), and a warming rate of $0.022^{\circ}\text{C year}^{-1}$ based on contemporary climate change observations (Morange et al., 2021). The flux uncertainty, shaded region, comes from a combination of measurement error, calculated from COSORE (Bond-Lamberty et al., 2020) data, and typical inter-annual variability driven by weather, from SRDB-V5 (Jian et al., 2021b). The figure shows the resulting 150-year-long simulated Rs time series, with the Theil-Sen trend significance calculated iteratively at each year. In the red section of the time series, the observed trend is not yet statistically significant.

This is due in part to the different response times of the Rh and Ra components of Rs: soil microfauna can rapidly adapt to changing conditions (Barron-Gafford et al., 2014; Carbone et al., 2011; L. Zhou et al., 2016), whereas slower-growing plants are restricted in their plasticity. Empirical evidence suggests that the response of Rs to environmental changes (e.g., warming, precipitation change, and N enrichment) can vary with the length of the study (Melillo et al., 2017; Morris et al., 2022; Zheng et al., 2022), and most manipulation experiments tend to be short-term (X. Ma et al., 2023; Morris et al., 2022). In addition, the combined effects of observational error, Rs variability, and buffered soil response mean that climate change effects may be confidently attributed only over long observational periods (Figure 3).

The longer-term impacts of environmental change on Rs are only beginning to be understood. Many global change experiments suggest an acclimation of Rs in the long-term following warming or precipitation shifts: for example, an initial elevation in Rs in response to warming dissipated over 10 years in a mid-latitude forest (Melillo et al., 2002). Similar results were found for a meta-analysis of 32 sites, with statistically significant increases in Rs in the first 3 years subsequently fading (Rustad et al., 2001). Recent work synthesizing 81 warming experiments corroborates short-term increases in Rs in response to warming but did not include any studies lasting longer than 18 months (Y. Zhang et al., 2023b). The long-term Rs response to precipitation change seems similarly variable, with some studies indicating little change in Rs response over time (L. Liu et al., 2016; Wu et al., 2011) and others finding long-term acclimation to increased precipitation and gradual exacerbation of drought effects, depending on the ecosystem (Morris et al., 2022). One meta-analysis incorporating long-term data on Rs under multiple global change drivers found highly significant interactive effects of factors such as

temperature and drought (L. Zhou et al., 2016). Due to the complexity of processes driving Rs and high variability of site conditions, addressing the long-term nature of Rs response and model prediction will be crucial.

4. Global-Scale Data and Analyses

A crucial trend over the last 20 years has been the rapidly increasing volume of observational Rs data (Hashimoto et al., 2023), driven by an expanding scientific community (D.-G. Kim et al., 2022) and the rising use of automated, continuous measurement systems (Vargas, Carbone, et al., 2011). Early data assemblages by individual authors (Hibbard et al., 2005; Raich & Schlesinger, 1992; Schlesinger, 1977) were valuable but one-time efforts. In contrast, the global Soil Respiration Database (SRDB) was first released as a fully-public resource in 2010 and has been periodically updated (Bond-Lamberty and Thomson, 2010a; Jian et al., 2021b). Subsequent studies have collected Rs data from the African continent (Epule, 2015), Russia (Mukhortova et al., 2021), and China (D.-G. Kim et al., 2022; Song et al., 2014). There have also been nascent efforts to compile data from automated systems into standardized formats and databases (Bond-Lamberty et al., 2020, 2021).

This explosion in available Rs data has been paired with equally rapid growth in satellite data products, reanalysis data sets, multi-model intercomparisons, plant trait databases, and other resources (Reichstein et al., 2003), resulting in many openly-available gridded, global Rs and Rh data sets (S. Chen et al., 2014; Hashimoto et al., 2015; Stell et al., 2021b; Warner et al., 2019; Yao et al., 2021). Advances in remote sensing of soil moisture variability (Y. Liu & Yang, 2022), an important driver of Rs at the biome and ecosystem scale (Hursh et al., 2017) but not typically used in global upscaling efforts, could lead to a more direct consideration of soil moisture in global Rs estimates. Remote sensing estimates of gross primary production (GPP) from novel metrics, such as solar-induced fluorescence (SIF; Bowman et al., 2017; Houweling et al., 2015) combined with inversion models of net CO₂ exchange have led to independent and improved estimates of Rh as the residual of these observationally constrained fluxes (Konings et al., 2019). As a result, far more Rs science papers involve modeling or remote sensing than in the past.

This increasing data availability has supported many statistical meta-analyses related to Rs. Following early quantitative reviews of topics such as global patterns of root turnover (Gill & Jackson, 2000) and separating sources of Rs (Hanson et al., 2000), the first formal meta-analysis synthesized data from 32 experimental warming sites, most in the US and Europe (Rustad et al., 2001). Subsequent studies have examined the effects of a range of global change factors, as well as environmental features, on both Rh and Rs (Table 1). Broad patterns that emerge are: (a) warming consistently produces a strong increase, and drought a reduction, of Rh and Rs; (b) precipitation addition increases Rs overall, but the effect on Rh is unclear; (c) the picture for nitrogen addition is less clear. One meta-analysis suggested that N deposition impedes organic matter decomposition and thus reduces Rs (Janssens et al., 2010), but a subsequent study found a more complex response (L. Zhou et al., 2014). A recent global analysis found that, overall, N deposition enhances Rs except in hotspots where the effect is negative, mostly in acid soils and at high levels of N deposition (C. Chen & Chen, 2023). Finally and importantly, (d) in recent years, increasing numbers of studies have considered the interaction between different factors that regulate Rs (Gao et al., 2020; Raich et al., 2023; Yue et al., 2018; L. Zhou et al., 2016).

Quantifying the large-scale Rs flux is useful for understanding and constraining other parts of the global carbon cycle (Friedlingstein et al., 2022; Jian, Bailey, et al., 2022) the expansion of global observing networks and remote sensing data products has led to a proliferation of global Rs estimates using different model approaches (Figure 4; cf. Hashimoto et al., 2023). Upscaling techniques pioneered by Raich and Schlesinger (1992) to derive estimates of global mean Rs developed into more sophisticated multivariate regression (Raich et al., 2002) and then Bayesian approaches (J. Hu et al., 2016) and machine learning (ML) algorithms (Bond-Lamberty et al., 2012). Concurrently, increased resolution of atmospheric inversion estimates of net biome productivity, combined with an array of satellite-derived primary productivity estimates, have been combined to produce “top-down” Rh estimates (Konings et al., 2019).

Despite these advances, Rs remains one of the most uncertain global fluxes, both operationally and statistically. In evaluating global estimates of respiration, it is critical to evaluate which flux is being estimated because total ecosystem respiration is often compared with Rs, and Rh often assumes that aboveground heterotrophic fluxes are negligible. Recent estimates of global gross primary productivity have converged to 123 ± 8 Pg C year⁻¹ with a coefficient of variation (CV) of 0.07 (Beer et al., 2010) 89.9 ± 13.3 Pg C year⁻¹ (CV of 0.15) (Ballantyne et al., 2017; Jian, Bailey, et al., 2022). More observations may improve uncertainties at the regional scale, but do

Table 1

Effect of Global Change Factors on Soil Heterotrophic Respiration (R_H) and Total Soil Respiration (R_S) According to Individual Meta-Analysis Studies

Study	N	Duration (years)	Global change factors				
			Warming	Nitrogen	Precip.	Drought	CO_2
Heterotrophic soil respiration (R_H)							
Janssens et al. (2010)	36			↓			
X. Wang et al. (2014)	50	1–19	↑↑			↓	
L. Zhou et al. (2014)	62	1–35		↓↓			
Zhong et al. (2016)	132			↓			
L. Zhou et al. (2016)	150	1–6	—	—	—	↓	↑↑
Morris et al. (2022)	128/141	1–13			↑↑	↓	
Y. Yang, Li, et al. (2022)	83	1–20+		↓			
Y. Liu et al. (2023)	222			↑↓			
L. Yang et al. (2023)	187		↑				
Total soil respiration (R_S)							
Rustad et al. (2001)	32	2–9	↑↑				
M. Lu et al. (2011)	150			↑			
Wu et al. (2011)	Various	2–14	↑		↑	↓	
X. Wang et al. (2014)	50	1–19	↑			—	
L. Zhou et al. (2014)	257	1–35		↑↓			
L. Liu et al. (2016)	113/105				↑	↓	
Zhong et al. (2016)	431			↑↓			
L. Zhou et al. (2016)	150	1–6	↑	↑	↑	—	↑↑
Feng et al. (2017)	Various		↑	↑	↑↑		
Xiao et al. (2020)	333	0.2–2.6		↑			
Morris et al. (2022)	128/141	1–13			↑↓	↓	
Y. Yang, Li, et al. (2022)	335	1–20+		↓			
Y. Liu et al. (2023)	1,060			↑			
X. Xu (2023)	23/80				↑	↓	
Z. Zhang et al. (2023c)	178/134	0.1–1.4	↑		↑↑		

Note. Factors shown include experimental warming, nitrogen addition, precipitation addition, drought or precipitation reduction, and CO_2 addition. Table entries show statistical significance: strong positive effect (typically $P < 0.01$, double up arrow, bright green), weak positive effect ($P < 0.05$, single up arrow, light green), no effect (double dash, gray), mixed effect (up and down arrows, olive), weak negative effect (single down arrow, light red), strong negative effect (double down arrow, bright red). These symbols and colors convey only a simplified, qualitative summary of results, and we encourage readers to read the individual studies. Additional columns give the number of experimental pairs (N) and range of study durations (years) in each meta-analysis. Meta-analyses of more rarely examined factors such as fire (Gu et al., 2023; M. Hu et al., 2020), phosphorous (Feng & Zhu, 2019; X. Lu et al., 2022), topography (Y. Zhang et al., 2021), litter inputs (X. Chen & Chen, 2018; Y. Zhang et al., 2020), vegetation (X. Chen & Chen, 2019; Y. Zhang et al., 2021), microplastics (X. Liu et al., 2023), metallic nanoparticles (He et al., 2024), and acid rain (Feng et al., 2017) are not shown.

not necessarily reduce uncertainty of global R_S estimates (Stell et al., 2021a; M. Xu & Shang, 2016), because they are concentrated in “redundant” ecoregions (e.g., temperate forests and grasslands in North America, Europe, and eastern Asia) rather than underrepresented ecoregions (e.g., arctic, boreal, tropical, desert). Furthermore, errors can arise from the approach used to estimate global R_S , as well as the distributional assumptions made about the aggregated fluxes (Wutzler et al., 2020). Hursch et al. (2017) found a wide range of global R_S estimates derived from a mechanistic model ($108.6 \pm 69.6 \text{ Pg C year}^{-1}$) compared to a statistical model ($80.3 \pm 24.6 \text{ Pg C year}^{-1}$), using the same SRDB observations. Perhaps what is most disconcerting about global R_S estimates is their apparent divergence over time (Hashimoto et al., 2023 and Figure 4). It is thus crucial to have clearly reported

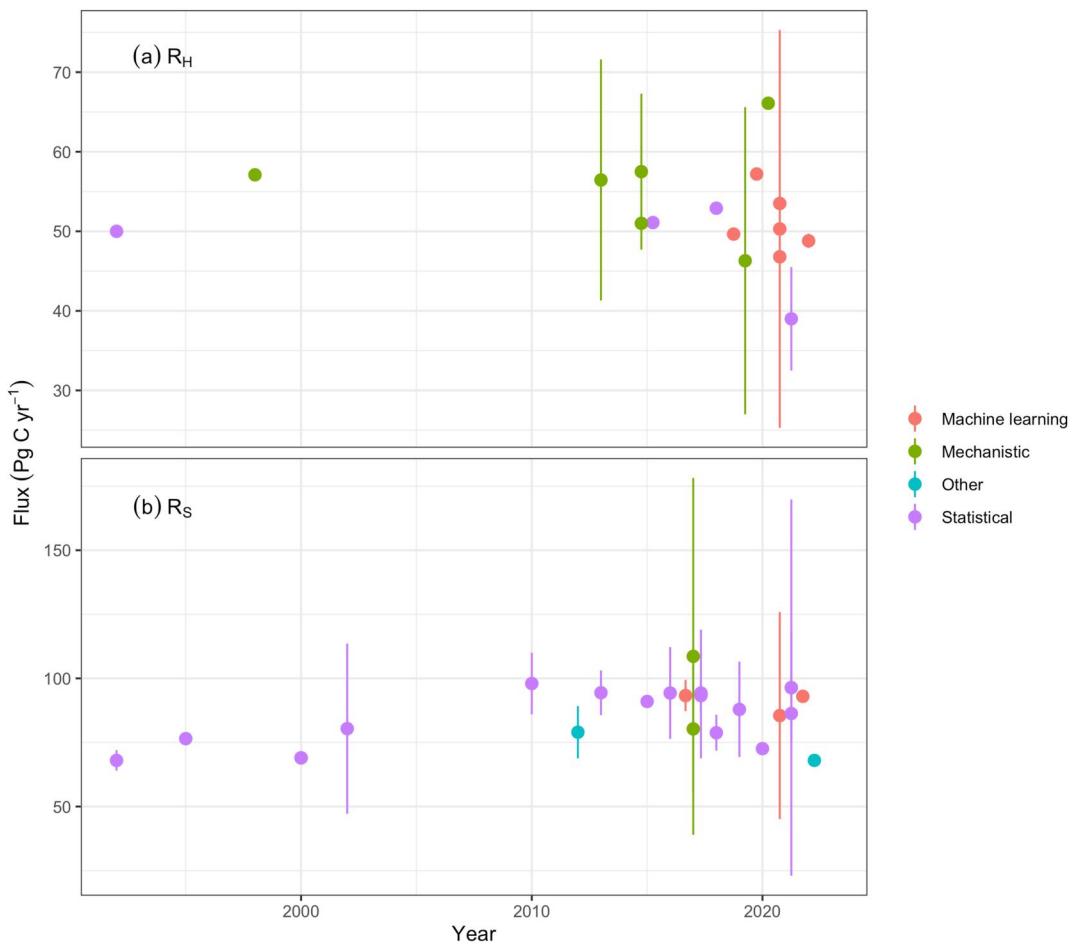


Figure 4. Published global flux estimates for (a) heterotrophic respiration (R_H) and (b) total soil surface respiration (R_S) plotted by year of estimate and by method of estimation (machine learning model, process-based or mechanistic model, statistical model, or other). Median values for studies in the last 20 years (2004–2023) are 51.1 and $93.3 \text{ Pg C year}^{-1}$ for R_H and R_S , respectively. For visual clarity, panel (b) cuts off one early estimate of $75 \text{ Pg C year}^{-1}$ (Schlesinger, 1977).

respiration fluxes, additional R_S observations in underrepresented ecosystems (e.g., tropics, semi-arid, and arctic), and reporting estimates from an ensemble of statistical models to advance our understanding of global R_S .

The global R_S flux appears to be increasing over decadal timescales (Hashimoto et al., 2023), but the underlying cause remains unknown. Based on upscaled soil respiration data, Bond-Lamberty and Thomson (2010b) first suggested that global R_S is rising at $\sim 0.1 \text{ Pg C year}^{-1}$, likely driven by temperature changes (e.g., N. Huang et al., 2020). This has been corroborated by top-down estimates of total respiration, with decadal variability possibly driven by soil moisture (Ballantyne et al., 2017; Green et al., 2019). Current explanations of this increase are an acceleration of the C cycle (i.e., increased C inputs belowground and thus R_a) and/or increasing mineralization of historically stable soil C (increased R_h). Lei et al. (2021) inferred strong R_S growth at the end of the twentieth century, followed by a hiatus, even as global R_h steadily increased from 1987 to 2016. This is consistent with analyses reporting a rising $R_h:R_S$ ratio (Bond-Lamberty et al., 2018; X. Tang et al., 2021) and suggests soil C losses to the atmosphere, although this is difficult to reconcile with a strengthening net terrestrial carbon sink (S. Ruehr et al., 2023). Full attribution of the cause of large-scale R_S and R_h changes remains an important research frontier.

5. Challenges and Opportunities

Enormous progress in measurement and analytical techniques, observational networks, and cross-disciplinary research has been made over the last two decades. These developments highlight substantial challenges and exciting opportunities going forward.

The first major challenge and opportunity for Rs research centers around biases and gaps in our observational data and the community of Rs researchers itself. Most of our inferences about temporal changes in the global Rs flux depend on a space-for-time substitution that assumes the spatial gradient in current-day Rs is a reliable proxy for future change, but this is questionable and untested (Blois et al., 2013; Dunne et al., 2004; Knapp et al., 2017). A related problem is the distorted distribution of extant Rs data (Jian et al., 2021b; Stell et al., 2021a; M. Xu & Shang, 2016) and how it limits our ability to understand mechanisms, regional dynamics, and global-scale fluxes in an era of global environmental change. This can be dramatically seen in Figure 5: the spatial distribution of SRDB records (a close proxy for the overall published Rs literature) does not match with either observed climate change or the urban ecosystems in which most people live in the twenty-first century (Lerman & Contosta, 2019; Velasco et al., 2021).

We posit that expanding diversity, equity, and access in Rs research will enable scientists in these regions to fill these gaps in our knowledge of soil respiration, because regions where we have the fewest Rs measurements (Figure 5) coincide with lower-income regions where we have the fewest earth scientists. Infrastructure and publications related to Rs and greenhouse gas science have been expanding in less-developed countries (D.-G. Kim et al., 2022), and novel instrumentation approaches continue to lower monetary costs (Forbes et al., 2023; Risk et al., 2011). Expanding the size and diversity of the pool of Rs-focused scientists and networks (Vargas et al., 2013) will encourage novel and imaginative ideas, leverage community-specific knowledge, and lead to stronger science teams and results (Dwivedi et al., 2022; Y. Yang, Tian, et al., 2022). It cannot be done in isolation, however, and will depend on continuing improvements in the diversity, equity, and accessibility of global science (McGill et al., 2021).

Reconciling independent estimates of global respiration fluxes and trends is a second major challenge and may hold the key to diagnosing latent carbon cycle processes and their sensitivities to climate. We are now able to compare abundant bottom-up estimates of Rs and Rh with emergent top-down estimates over space and time to identify regions or processes that remain poorly understood. For instance, Jian, Bailey, et al. (2022) reported that Rs constrained by GPP was significantly lower than independent estimates of Rs. Similarly, recent advances in remote sensing and data assimilation have yielded top-down estimates of global Rh that tend to be higher than bottom-up estimates derived from soil respiration observations, with the greatest mismatch being in tropical latitudes where dense observations of Rs and Rh are still lacking (Konings et al., 2019). A recent regional carbon assessment based on a detailed accounting of C pools and fluxes estimated global soil Rh to be $39 \text{ Pg C year}^{-1}$, slightly lower than previous top-down estimates but possibly higher than bottom-up estimates upscaled from soil respiration observations (Ciais et al., 2020). It may be possible to aggregate soil respiration data at similar continental scales as these regional assessments to evaluate to what extent spatial aggregation of observations may contribute to these mismatches in Rh fluxes (Butman & Raymond, 2011; Kicklighter et al., 1994; Tan et al., 2020).

A third challenge concerns the power, applicability, and interpretability of ML algorithms (Dramsch, 2020; Reichstein et al., 2019). The large size of many Rs data sets, combined with the large number of environmental variables influencing Rs, has made Random Forests a popular algorithm in Rs research (e.g., H. Lu et al., 2021; Warner et al., 2019; Yao et al., 2021) but other approaches have also been applied. However, it is not clear that ML provides more utility over simple approaches: a study of Rs gap-filling algorithms found that ANNs exhibited larger errors than nonlinear least squares and other techniques (Zhao et al., 2020). Another analysis found no significant differences or biases among Rs estimates derived from semi-empirical, statistical or ML approaches (Hashimoto et al., 2023). We suggest that the field needs convincing demonstrations of what ML approaches add to more interpretable mechanistic or empirical approaches (Peters et al., 2014), careful consideration of the interpretability of ML models, and awareness of their potential biases (Perry et al., 2022). ML may be particularly useful for large-scale assessments of the importance of parent material (Aka Sagliker et al., 2018; Dacal et al., 2022), geochemistry (Doetterl et al., 2015), and presence of soil carbonates (Gallagher & Breecker, 2020). For all these reasons, ML remains an intriguing frontier but one that has yet to reveal new patterns to advance our theoretical understanding of Rs.

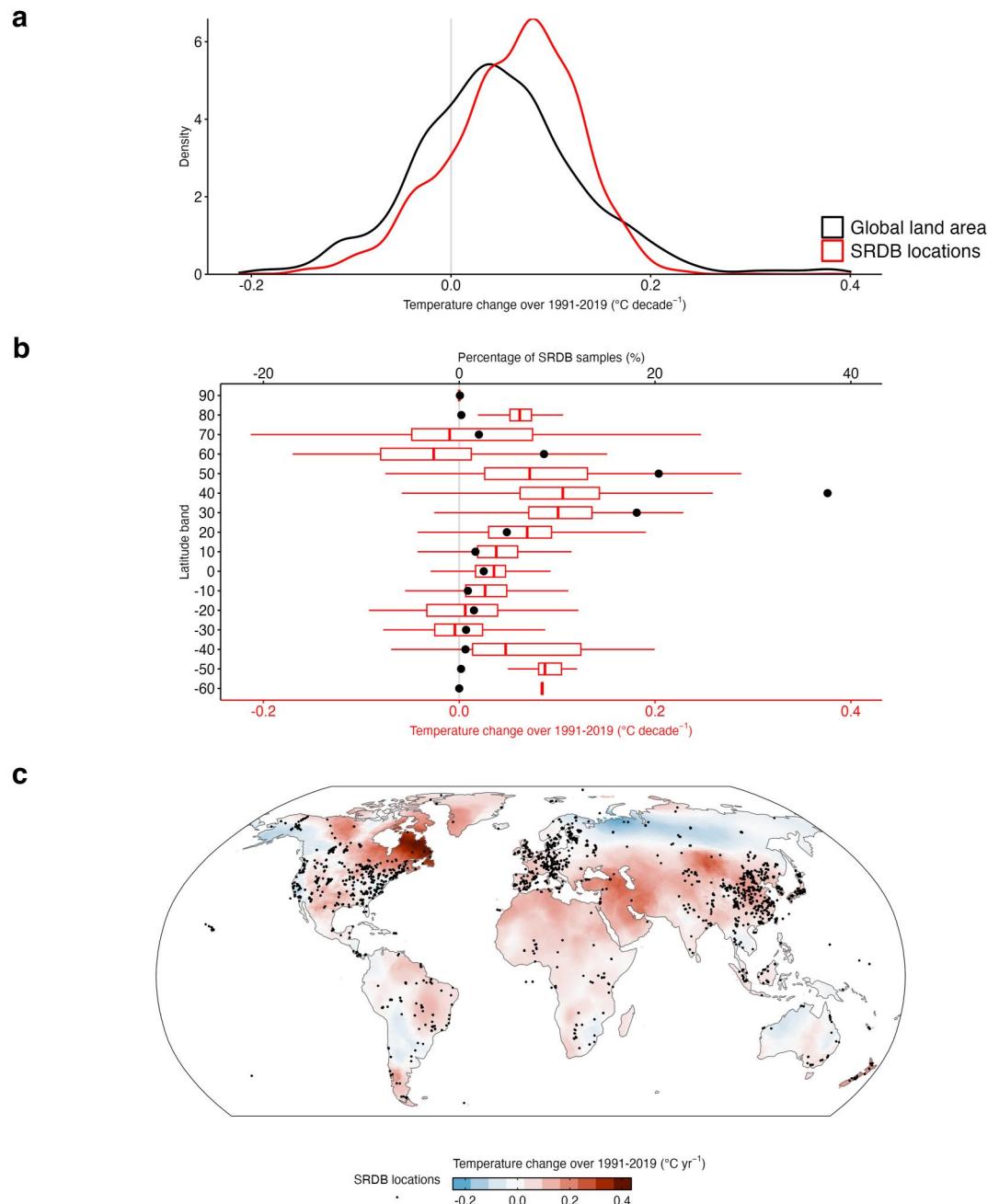


Figure 5. (a) Comparison of the density distribution of air temperature linear slope over 1991–2019 between Soil Respiration Database (SRDB) v5 (Jian et al., 2021b) locations and the global land surface area. The differences between the distributions (two-tailed K-S test; $D = 0.15569$, p -value $<2.2e-16$) show that SRDB samples well areas with a warming trend since 1991, while it under-samples regions with cooling trends. (b) Comparison of SRDB locations across 10-degree latitudinal bands showing the over-representation of northern temperate latitudes in soil respiration measurements, while warming in southern latitudes are not well captured by measurements. (c) Geographic distribution of SRDB sites over the global background showing large undersampled regions having both undergone warming and cooling trends. Temperature trend was estimated from GSWP3-W5E5 which itself was generated from GSWP3 v1.09 (Cucchi et al., 2020; Dirmeyer et al., 2006; H. Kim, 2017; Lange et al., 2021). Notably, SRDB under-samples regions experiencing the largest temperature trends over the last three decades. SRDB locations only include measurements collected after 1991.

In addition to ML, Rs researchers should challenge themselves to increasingly employ creative and rigorous mechanistic modeling. This includes using model-experiment synthesis instead of model benchmarking (Hanson & Walker, 2019; Medlyn et al., 2015; Norby et al., 2016); investing in multi-model testbeds to accelerate progress

(Wieder et al., 2018); favoring models based on fundamental and measurable pools and processes (Abramoff et al., 2018; Davidson et al., 2012); and rigorously assessing the value of data for models (Keenan et al., 2013). Novel approaches such as probabilistic modeling, which aim to represent a complex system's behavior based on the underlying probability distribution of its controlling factors, should be explored. Such work has for example, been able to predict and partition Rs (X. Zhou et al., 2010), determine the temperature dependence of Rs (Le & Vargas, 2024), and study its response to elevated CO₂ (Gao et al., 2020) or extreme heat events (Anjileli et al., 2021). The central point is that progress will not come solely through numerical methods; integrating novel process models with manipulative field and lab experiments will be crucial (Kyker-Snowman et al., 2021; Medlyn et al., 2015).

The continued exploration of understudied mechanisms and ecosystems using diverse, novel experimental approaches constitutes a final, crucial challenge. Expanded research on the importance and complexity of hysteresis (Li et al., 2017; Phillips et al., 2011; N. K. Ruehr et al., 2010; B. Wang et al., 2014) and antecedent conditions (Barron-Gafford et al., 2014; Cable et al., 2010; Hawkes et al., 2017; Patel et al., 2021a) will be crucial to account for the factors driving carbon-cycle twenty-first-century changes. This is particularly true given the expanding focus on nature-based climate solutions (Vargas & Le, 2023) and carbon capture and storage (Tao et al., 2023) as potential techniques for slowing climate change. Links among terrestrial, riverine, and aquatic carbon cycling are under-appreciated but potentially important pathways (Butman & Raymond, 2011; Tan et al., 2020), particularly with increasing disturbances such as storms and floods (Wen et al., 2022). Finally, as hinted at in Figure 5, certain types of ecosystems and environments merit focused research: for example, organic soils and wetlands, both managed and unmanaged; areas with thawing permafrost, and complex coastal interfaces. Including some of these key processes in models will be crucial to understand the driving mechanisms and controls of Rs, and to make testable predictions about its likely evolution in the changing earth system of the twenty-first century.

Data Availability Statement

All data and code necessary to reproduce the table and figures, including information on package and R (R Core Team, 2023) versions used, are available at <https://github.com/bpbond/jgr20> and permanently archived with a Digital Object Identifier (DOI) of [10.5281/zenodo.10620030](https://doi.org/10.5281/zenodo.10620030).

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