Soil Respiration in Temperate and Tropical Ecosystems: The Role of Abiotic and Biotic Factors

Yulin Liu

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Soil Respiration in Temperate and Tropical Ecosystems: The Role of Abiotic and Biotic Factors

Yulin Liu

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Thesis Abstract

Soil respiration (R_s) represents a major carbon flux from terrestrial ecosystems to the atmosphere and an important component of ecosystem carbon cycling. The magnitude and temporal variation of R_s are influenced by a combination of environmental and biological factors. Despite the important role of R_s in the global C cycle, field-based observations across diverse ecosystems remain limited, constraining our understanding of how environmental and biological factors regulate soil CO_2 efflux. The current project explored the variations of R_s across temperate dairy grassland, temperate *Pinus radiata* plantation forest, and tropical forest systems through comparative field-based measurements under natural conditions. The objective was to identify how R_s co-varied with temperature, moisture, and broader site context, and to examine the extent to which these relationships differed among ecosystems.

In New Zealand dairy grasslands, observed R_s rates at the sampled sites were higher than the global temperate grassland values used for comparison. Seasonal variation was apparent with higher R_s in summer than in winter. Soil temperature and soil type were more strongly associated with R_s variation than soil moisture, although these relationships differed among sites and should be interpreted within the limits of short-term sampling and site-specific conditions.

In *Pinus radiata* plantation forests, seasonal R_s was more strongly related to soil moisture than soil temperature. Stand age was associated with shifts in soil microbial community composition, including changes in dominant bacterial and fungal groups, while stand-age-related differences in R_s were less consistent. These findings suggest that the changes in microbial community across stand development were more clearly observable than a straightforward trend in R_s with stand age under the sampled conditions.

In the tropical forest study, R_s varied among forest types and landscape positions. Plantation and native forest sites showed overlapping ranges of R_s, but the observed patterns were affected by co-varying environmental gradients, such as elevation, moisture, and site context. Vegetation type should therefore be interpreted as an integrated indicator of multiple environmental and site factors rather than as a standalone driver.

In summary, this thesis shows that R_s responses varied depending on the context across all three ecosystems. Temperature and moisture were significant factors influencing R_s, but their apparent impact depended on site conditions, soil characteristics, and broader environmental setting. Within clearly defined interpretive limits, this thesis offers comparative evidence that supports more cautious, context-aware interpretation of soil respiration patterns across ecosystems, rather than universal or mechanistic claims.

Keywords: Soil respiration, agriculture, plantation, soil microbial and fungal communities, soil temperature, soil moisture, soil type, stand age, tree species, temperate forests, tropical forests, temperate grassland

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Attestation of Authorship

I hereby declare that this submission is my own work and that, to the best of my knowledge and belief, it contains no material previously published or written by another person (except where explicitly defined in the acknowledgements), nor used artificial intelligence tools or generative artificial intelligence tools (unless it is clearly stated, and referenced, along with the purpose of use), nor material which to a substantial extent has been submitted for the award of any other degree or diploma of a university or other institution of higher learning.

Yulin Liu

18th March 2025

Co-Authorship Declaration

STUDENT AND SUPERVISOR APPROVALS

By signing you are confirming that the co-author contributions stated in the table(s) below are accurate.

Student Name	**Yulin Liu**	**Signature**	**Date**	26/03/2025
Supervisor Name	**Sebastian Leuzinger**	**Signature**	**Date**	26/03/2025

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AUTHOR SURNAME: (order as per manuscript)	**CONTRIBUTION** (May copy from the guidelines above)
Liu	**Conception and design of the project; Acquisition of research data; Contribution of knowledge; Analysis or interpretation of research data; Drafting significant parts of the research output.**
Zhang	**Analysis or interpretation of research data; Critically revising the research output so as to contribute to its quality and interpretation.**
Bader	**Conception and design of the project; Critically revising the research output so as to contribute to its quality and interpretation.**
Leuzinger	**Conception and design of the project; Contribution of knowledge; Critically revising it so as to contribute to its quality and interpretation.**

STUDENT AND SUPERVISOR APPROVALS

By signing you are confirming that the co-author contributions stated in the table(s) below are accurate.

Student Name	**Yulin Liu**	**Signature**	**Date**	26/03/2025
Supervisor Name	**Sebastian Leuzinger**	**Signature**	**Date**	26/03/2025

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AUTHOR SURNAME: (order as per manuscript)	**CONTRIBUTION** (May copy from the guidelines above)
Liu	**Conception and design of the project; Acquisition of research data; Contribution of knowledge; Analysis or interpretation of research data; Drafting significant parts of the research output.**
Archer	**Conception and design of the output; Acquisition of research data; Critically revising it so as to contribute to its quality and interpretation.**
Lee	**Analysis or interpretation of research data; Critically revising it so as to contribute to its quality and interpretation.**
Zhang	**Analysis or interpretation of research data; Critically revising the research output so as to contribute to its quality and interpretation.**
Bader	**Conception and design of the project; Critically revising the research output so as to contribute to its quality and interpretation.**
Smaill	**Conception and design of the project; Critically revising it so as to contribute to its quality and interpretation.**
Hu	**Contribution of knowledge; Critically revising it so as to contribute to its quality and interpretation.**
Leuzinger	**Conception and design of the project; Contribution of knowledge; Critically revising it so as to contribute to its quality and interpretation.**

STUDENT AND SUPERVISOR APPROVALS

By signing you are confirming that the co-author contributions stated in the table(s) below are accurate.

Student Name	**Yulin Liu**	**Signature**	**Date**	26/03/2025
Supervisor Name	**Sebastian Leuzinger**	**Signature**	**Date**	26/03/2025

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Sabetian	**Conception and design of the project; Acquisition of research data.**
Leuzinger	**Conception and design of the project; Contribution of knowledge; Critically revising it so as to contribute to its quality and interpretation.**

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Chapter 1. Introduction

Soil respiration (R_s) is the process of carbon dioxide (CO_2) release from the soil into the atmosphere (Luo & Zhou, 2006). It primarily consists of the respiration of microorganisms (e.g., bacteria and fungi) that decompose organic matter (R_h) and the respiratory processes by root system and microbes in the rhizosphere (R_a), which is influenced by root metabolism and closely coupled rhizosphere processes (Lambers et al., 2009; Pandey et al., 2018). While the partitioning of rhizosphere microbial respiration between R_a and R_h remains debated (Hanson et al., 2000; Kuzyakov, 2006), R_a is generally defined to include root respiration and associated rhizosphere activity due to their strong dependence on recent photosynthate supply (Kuzyakov & Gavrichkova, 2010). In this way, soil respiration is a major player in the global carbon (C) cycle as it connects belowground C activity to the exchange of greenhouse gases with the atmosphere (Xu & Shang, 2016). By measuring soil respiration and analysing its response to environmental changes, we gain insights into how soil ecosystems function, how C is allocated through soil, and how climate change can alter these processes (Ryan & Law, 2005; Zhou et al., 2016).

Apart from a purely academic interest of accurately describing the global C cycle, quantifying soil respiration is of importance in a land-use context. Farmers and land managers can utilise knowledge on soil respiration to improve soil health and land productivity. Healthy soils contain diverse microbial communities that can break down organic matter more effectively and thereby release nutrients for crop growth (Bill et al., 2021). At a broader scale, informed land and soil management can support soil functioning, sustain long-term productivity, and enhance the resilience of agricultural systems by maintaining soil structure, nutrient cycling, and biological activity (Guo et al., 2020; Wang et al., 2017b).

Across terrestrial ecosystems, soil respiration can be applied as an indicator of ecosystem functioning and condition, including forest health (Gatica-Saavedra et al., 2023; Ratcliffe et al., 2018). High soil respiration can indicate that microbial communities are actively breaking down leaf litter and wood debris, thereby recycling nutrients (Bani et al., 2018). Conversely,

abnormally low or high respiration rates can suggest environmental stressors including drought, pollution or invasive pests (Nikolova et al., 2009; Pérez Castro et al., 2019; Schaeffer et al., 2016).

At both global and local scales, soil respiration is closely related to climate change and C sequestration as the shifts in soil respiration patterns can potentially influence atmospheric CO_2 levels. Policymakers and environmental agencies use soil respiration data primarily to constrain and parameterise terrestrial carbon models, which underpin national greenhouse gas (GHG) inventories and land-use change assessments (Lugato et al., 2014; Smith et al., 2020). Empirical knowledge of soil respiration responses to temperature, moisture, vegetation, and management improves model representations of soil carbon turnover and heterotrophic respiration, thereby reducing uncertainty in country-specific estimates of soil carbon dynamics. Such model-based approaches are encouraged under Tier 2 and Tier 3 methodologies of the IPCC Guidelines, which rely on higher-order models and national data rather than default emission factors (IPCC, 2019). Practices such as agroforestry and cropping systems that incorporate rotations, cover crops, or reduced soil disturbance can enhance soil carbon inputs and promote the resilience of agricultural and natural systems (Kay et al., 2019; Sharma et al., 2021).

Soil respiration is a tangible and measurable process that has profound long-term implications for agriculture, forestry, and climate policy, which allows us to make more informed decisions about how we manage our lands and thus mitigate the negative effects of climate change for future generations.

Studies have focused on understanding R_s through its components, measurement methods, and environmental drivers in various ecosystems (Bond-Lamberty & Thomson, 2010a; Davidson & Janssens, 2006; Raich & Schlesinger, 1992; Subke et al., 2006). The components of R_s show various responses to environmental changes. Plant productivity and belowground C allocation primarily influence R_a, while temperature and SOM quality mainly affect heterotrophic respiration (R_h) (Wang et al., 2017a; Yan et al., 2021). To quantify R_s, multiple measuring techniques have been utilised. Chamber measurements are cost effective, portable, and the most

widely used methods, which include static, dynamic, and open chamber designs (Davidson et al., 2002b). These chamber methods tend to underestimate or overestimate R_s due to design limitations and gas exchange dynamics (Davidson et al., 2002b; Venterea, 2010). Technological advancements (e.g., infrared gas analysers) have improved accuracy but have not resolved all uncertainties. Gradient and eddy covariance methods provide alternative approaches, which enable in-depth and large-scale observations, but are hindered by soil disturbance and the need for indirect estimation (Myklebust et al., 2008). Soil temperature and moisture are widely recognised as the primary environmental drivers of soil respiration. In many ecosystems, soil respiration increases linearly or exponentially with rising soil temperature, reflecting enhanced microbial and root metabolic activity; however, this temperature response is strongly modulated by soil moisture, which can either enhance respiration under optimal conditions or constrain it under drought or saturation (Fang & Moncrieff, 2001). For example, optimal soil moisture enhances R_s by enhancing microbial activity and soil gas diffusion, while extremes in soil moisture suppress R_s (Manzoni et al., 2012). Plant productivity, vegetation type, and the composition of microbial community also influence R_s by determining belowground C allocation (Carney & Matson, 2005; Kaiser et al., 2011; Metcalfe et al., 2011). Previous studies have shown that soil respiration in dairy grasslands is influenced by grazing intensity, nutrient availability, and seasonal variation in soil temperature and moisture; in this thesis, I focus on the role of temperature, moisture, and soil type in driving R_s dynamics. (Bahn et al., 2008; Matías et al., 2021). In plantation forests, soil respiration varies with stand age and management practices (e.g., thinning and harvesting) by affecting soil structure and carbon inputs (Cheng et al., 2021; Epron et al., 2006). Bacteria and fungi regulate R_s through SOM decomposition and nutrient cycling, and their community composition and environmental stressors further influence these processes (Chen et al., 2020; Hicks et al., 2021; Nuccio et al., 2013). Integrating abiotic and biotic interactions into R_s predictive models is crucial for improving our understanding of R_s and its role in the global and regional C cycle.

Despite decades of studies, R_s research gaps remain on the effects of land use and vegetation, the interactions between abiotic and biotic factors, and the integration of the underrepresented

ecosystems into global R_s models (Bond-Lamberty et al., 2024). Land-use changes and vegetation dynamics can impact R_s, yet their effects are not fully understood. For example, agricultural practices and vegetation type influence soil basal respiration (microbial respiration under substrate limitation) and substrate-induced respiration (microbial respiration following labile carbon addition), but the variations between land-use systems remains inadequately quantified (Ebrahimi et al., 2019). Similarly, spatial variations in R_s due to canopy gaps, root biomass, and understory plants in forests need further exploration to improve C flux models (Han et al., 2020; Jarvi & Burton, 2020; Zhao et al., 2018). In temperate grasslands, seasonal variability in temperature and moisture affects the root and microbial contributions to R_s, which is critical for assessing the carbon balance under warming scenarios but lacks temporal and spatial coverage (Li et al., 2018). Grassland conversion to cropland or restoration to forest alters soil structure, organic matter, and microbial communities, but the long-term effects remain poorly understood (Chen et al., 2022; Zhang et al., 2023b). In plantation forests, tree-species effects, age-dependent variability, and management practice (e.g., thinning and harvesting) influence R_s through root biomass, litter quality, microclimate, and microbial communities (Parsapour et al., 2018; Peng et al., 2020b). The interactive effects of these are not fully studied for C cycling implications. Additionally, in tropical plantation forests, high temperatures and fluctuating soil moisture conditions, including recurrent wet-dry cycles driven by rainfall pulses, introduce substantial variation in R_s (Vargas-Terminel et al., 2022). Their effects on R_s, along with the consequence of conversion from primary to plantation forests, remain understudied. Moreover, the limited availability of soil respiration data in underrepresented ecosystems and areas, such as southern hemisphere and tropical regions, hinders their inclusion in global C models and induces uncertainty in R_s predictions (Bond-Lamberty et al., 2024).

In this thesis, I conducted three field-based research projects to study R_s in temperate dairy grassland, temperate plantation forest, and tropical plantation forest in New Zealand and Solomon Islands, using the closed-static chamber method. The research objectives were to (1) quantify the magnitude of R_s across these ecosystems, (2) identify the most influential abiotic (e.g., soil temperature, soil moisture, soil type) and biotic (e.g., vegetation characteristics, stand

age, and soil microbial communities) factors driving R_s, and (3) examine how R_s responds to environmental gradients and land-use contexts, including seasonal variation, stand age, and ecosystem type. The major contributions of this thesis, arising from the research objectives outlined above, include: (1) the inclusion of underrepresented Southern Hemisphere ecosystems in R_s research; (2) improved understanding of the roles of abiotic (e.g., soil temperature and moisture) and biotic (e.g., microbial communities and vegetation characteristics) factors influencing R_s; and (3) a comparative analysis of R_s across contrasting land-use types and climatic regions. By investigating managed grasslands and forests, and temperate and tropical ecosystems, this thesis provides critical insights into how R_s varies with land-use types, biome characteristics, soil microbial communities, stand ages, and plantation versus native forest ecosystems. Moreover, this thesis highlights the implications of environmental changes on R_s trends and offers valuable perspectives for C management practices and climate change mitigation. Together, these contributions address some gaps in global R_s datasets and enhance our understanding of soil C fluxes across ecosystems.

The remainder of this thesis is structured as follows: it begins with a comprehensive literature review on the global carbon cycle, the process of R_s, methodologies commonly used in R_s research, and factors influencing R_s. This is followed by three research chapters detailing the field studies conducted: the first focuses on R_s in New Zealand dairy grasslands and examines its variation across diverse soil types; the second explores R_s in New Zealand *Pinus radiata* plantation forests and emphasizes the difference of R_s and microbial communities across stand ages in monocultural forestry systems; and the third investigates R_s in tropical plantation forests and native forests in Solomon Islands. The thesis concludes with a general discussion that synthesizes the findings, compares R_s across managed grassland and forests, temperate and tropical ecosystems, and addresses the implications of environmental change on R_s.

Chapter 2. Literature Review

2.1. Global carbon flux and storage

Greenhouse gas emissions have caused global warming. Net atmospheric CO_2 has grown at a rate of 5.2 gigatons of carbon (Gt C) per year during 2013–2022, primarily due to anthropogenic fossil fuel combustion and land-use changes, which contribute 9.6 and 1.3 Gt C per year, respectively (Friedlingstein et al., 2023). This net CO_2 increase has driven global surface temperatures to rise by 1.1°C from 1850–1900 to 2011–2020, exhibiting a greater increase over land than oceans (1.59°C vs. 0.88°C, IPCC, 2023). Despite the anthropogenic emissions, biological carbon (C) fluxes, such as photosynthesis (i.e., gross primary production, GPP) and soil respiration (R_s), are about tenfold larger than human C contributions and the net balance between GPP and R_s can potentially offset a great portion of these human-induced CO_2 emissions (IPCC, 2023b). These processes form part of the global C cycle, which regulates the atmospheric CO_2 balance through exchanges between four major C reservoirs: ocean, land, atmosphere, and fossil fuels (Ciais et al., 2013). Oceans store the largest amount of biologically relevant C (38,703 Gt C), primarily in the deep layers of the oceans (Hansell et al., 2009), while terrestrial ecosystems rank second and hold 3,950–5,450 Gt C, of which soils store over 80%, comprising soil organic matter (41%), wetlands (11%), and permafrost (36%) (Batjes, 2014; Bridgham et al., 2006; Griggs & Noguer, 2002; Tamocai et al., 2009). Fossil fuel reserves and atmospheric CO_2 contain comparatively smaller amounts, at 1,002-1,940 Gt C and 831.9 Gt C, respectively (Joos et al., 2013; Prather et al., 2012; Rogner et al., 2012).

Atmospheric C exchanges are most extensive with terrestrial and oceanic reservoirs, driven by processes such as photosynthesis, soil respiration, and oceanic CO_2 uptake. Within terrestrial ecosystems, photosynthesis is the largest C flux and account for 123 Gt C annually, which converts atmospheric CO_2 into organic compounds in plants (Beer et al., 2010). In contrast, soil respiration, the second-largest flux, releases about 98 Gt C annually through the metabolism of plant roots, soil microbes, and soil animals (Bond-Lamberty & Thomson, 2010a). The dynamic balance between these processes largely influences net atmospheric CO_2 sequestration. Other terrestrial processes, such as forest fires, also influence the terrestrial carbon balance by rapidly

releasing stored biomass carbon to the atmosphere and reducing ecosystem carbon stocks, although their contribution to the long-term global carbon budget is episodic and spatially heterogeneous. Ocean-atmosphere exchanges, driven by CO_2 pressure gradients, result in average annual fluxes of 78.4 Gt C from ocean to atmosphere and 80 Gt C in the reverse direction (Ballantyne et al., 2012). While anthropogenic fossil fuel C fluxes (~9.4 Gt C per year) are smaller than terrestrial or oceanic fluxes, their net contribution is disproportionately large because C is released rapidly from long-term geological stores and present-day sequestration into comparable reservoirs operates on much longer timescales, resulting in a strong imbalance in these C fluxes (Boden et al., 2017). This anthropogenic influence, alongside land-use changes (1.5 Gt C per year), has driven atmospheric CO_2 growth, while net oceanic and terrestrial C uptakes (2.5 and 3.8 Gt C per year, respectively) mitigate some of this increase (Friedlingstein et al., 2022). However, the accelerating CO_2 growth rate is not fully offset by these sinks, as terrestrial and oceanic C uptakes have only partially kept pace with rising emissions (Le Quéré et al., 2018). Therefore, understanding the R_s response to environmental changes is critical for global warming mitigation efforts, due to its potential to exacerbate atmospheric CO_2 increases.

2.2. Soil respiration

2.2.1. Global soil respiration and its components

The estimation of global soil respiration (R_s) varies significantly among studies, ranging from 68 to 98 GtC annually (Adachi et al., 2017; Bond-Lamberty & Thomson, 2010b; Hashimoto et al., 2015; Raich & Schlesinger, 1992). This large variance is caused by differences in R_s measurement timescales and modelling approaches. For example, Jian et al. (2018) applied Random Forest and exponential models with different timescales of R_s and climate data to quantify the R_s variability. They found that using annually aggregated R_s data can inflate global R_s estimates, as annual means often obscure seasonal extremes. In contrast, monthly or daily R_s data capture sub-annual variability and yield lower, more constrained estimates. They also found that the Random Forest model significantly underestimated global R_s. Additionally, R_s measurements during a full year are rare, with growing season data being more common and potentially skewing results.

Soil respiration (R_s) primarily consists of belowground autotrophic respiration (R_a) and heterotrophic respiration (R_h) (Xu & Shang, 2016). Autotrophic respiration describes soil CO_2 loss from the metabolic activity of plant roots, mycorrhizae, and the rhizosphere, relying on root exudates and influenced by plant biological characteristics such as fine root biomass, GPP, net ecosystem production (NEP), and vegetation type. These factors affect R_a dynamics and magnitude through the quality and quantity of carbon input, soil temperature, and soil moisture (Hanson et al., 2000; Tang et al., 2020b). Heterotrophic respiration represents CO_2 loss from microbial decomposition of dead plant material and soil organic matter (SOM), which is primarily influenced by climate and ecosystem type (Subke et al., 2010). At the global scale, the relationship between heterotrophic respiration (R_h) and soil organic matter (SOM) is complex and shaped by variations in SOM quality and availability, as well as climatic factors such as temperature and moisture across different biomes. Soil organic matter (SOM) shows scale-dependent effects on heterotrophic respiration (R_h). At the global scale, R_h can be negatively correlated with SOM because ecosystems with the largest carbon stocks, such as peatlands and permafrost soils, often exhibit low decomposition rates due to constraints imposed by temperature, oxygen availability, and SOM quality. At site-specific or ecosystem levels, SOM positively influences R_h, because environmental conditions such as temperature, moisture, and oxygen availability are relatively consistent, allowing substrate availability to become the dominant control on microbial decomposition. (Tang et al., 2020a).

Although productivity and respiration must be roughly equal over a long spatiotemporal scale assuming constant soil C, R_a and R_h together constitute the majority of R_s, accounting for 85–90% of GPP annually (Kirschbaum et al., 2001), with global R_a and R_h of 41.2 and 51.5 Gt C per year respectively (Hashimoto et al., 2015). Bond-Lamberty et al. (2018) showed that the global R_h/R_s ratio had increased over time, rising from 0.54 in the 1990s to 0.63 in the 2010s. This suggested that enhanced SOM mineralization accelerated R_h and decreased soil C under rising global temperatures. Different responses of R_a and R_h to abiotic factors show the importance of R_s partitioning. For example, a warming treatment (2°C increase) showed that R_h increased by 21% and remained elevated, while R_a initially remained stable before declining

(Wang et al., 2014). Partitioning methods such as root exclusion, physical separation, and isotope techniques provide insights on the contribution of R_a and R_h to R_s but mostly require soil disturbance (Bond-Lamberty et al., 2004; Kuzyakov, 2006; Subke et al., 2006). Understanding dynamics and driving factors of R_a and R_h is important to predict the responses of R_s to climate change.

2.2.2. Methods to measure soil respiration

Methods used to estimate soil respiration include chamber-based measurements, soil CO_2 concentration gradient approaches, and micrometeorological techniques; however, only chamber methods directly measure soil CO_2 efflux, whereas gradient and micrometeorological approaches infer R_s through additional assumptions (Subke et al., 2010). Among these, chamber measurements are the most common methods due to their low cost and high portability. Chamber measurements can be further categorised into closed static, closed dynamic, and open chamber methods (Pumpanen et al., 2010).

The closed static chamber method involves sealing a chamber to the soil surface and estimating R_s from the rate of CO_2 accumulation within the chamber over time; internal fans are commonly used to ensure adequate air mixing (Collier et al., 2014; Pumpanen et al., 2004). The closed dynamic chamber systems continuously circulate air between the chamber and an infrared gas analyser, and soil respiration is calculated from changes in CO_2 concentration under controlled airflow conditions (Baneschi et al., 2023). The open chamber method, first introduced by Porkka (1931), calculates R_s using the CO_2 concentration difference between the inlet and outlet air (Bekku et al., 1997). Later developments on these methods, such as the use of infrared gas analysers (IRGA) or gas chromatography (GC), have drastically improved R_s measurement accuracy and enabled continuous readings (Janssens et al., 2000). However, soil respiration differences between these chamber methods still exist. For example, the closed static chamber often yields lower R_s values compared to the open chamber method (Pumpanen et al., 2004).

The concentration gradient method calculates R_s mainly by the diffusion of CO_2 from soil to the atmosphere and the differences in CO_2 concentrations between multiple soil layers and air. This

method depends on molecular diffusion efficiency, which is influenced by soil depth, diffusivity, moisture, and sampling location (Maier & Schack-Kirchner, 2014). However, it causes severe soil disturbance and thus makes replication challenging. Variability in soil properties (e.g., soil porosity) can also result in inaccuracies and limit its broader application.

The eddy covariance method measures net vertical CO_2 fluxes by analysing the covariance between fluctuations in vertical wind velocity and CO_2 concentration and using a sonic anemometer and an infrared gas analyser (Skinner & Wagner-Riddle, 2012). Although this method can provide continuous ecosystem-scale CO_2 measurements, it does not directly measure R_s. Soil respiration rate must be estimated by subtracting aboveground R_a from total ecosystem respiration, which complicates soil respiration measurement in forests where stem respiration needs to be measured separately. Fixed-location measurements further constrain spatial coverage and replication in the study (Baldocchi, 2003).

In summary, chamber methods remain the most widely used approach for estimating soil respiration due to their practicality and flexibility; however, they require careful installation (e.g., collar insertion, vegetation clipping) to minimise contributions from aboveground plant tissues and ensure that measured fluxes represent belowground respiration. The gradient and eddy covariance methods are effective but less commonly applied to R_s measurement due to soil disturbance, sensitivity to environmental conditions, and indirect R_s estimation.

2.3. Driving factors of soil respiration

2.3.1. Soil temperature and soil moisture

Soil temperature and moisture are the most influential environmental factors to R_s (Zhang et al., 2023c). Soil respiration generally shows an exponential increase with soil temperature, mostly caused by the positive temperature effect on R_h (Lloyd & Taylor, 1994). The temperature sensitivity of R_s is often defined as Q_{10}, which quantifies the rate increase of R_s with a 10°C temperature rise (Meyer et al., 2018). Alternative formulations, such as the Lloyd-Taylor model and macromolecular rate theory (MMRT), have also been used to describe Rs-temperature relationships, particularly where non-linear responses or thermal acclimation are considered

(Alster et al., 2020; Lloyd & Taylor, 1994). Global mean Q_{10} values range between 1.5 and 3.0, with a decreasing trend at higher temperatures (Raich & Schlesinger, 1992; Zhou et al., 2009). However, confounding factors like soil moisture and plant productivity often affect Q_{10}'s accuracy in reflecting temperature effects (Xu & Shang, 2016). For example, Xu & Qi (2001) found that low soil moisture limited the temperature effect on R_s in Californian forests during summer, which led to low Q_{10} value. Additionally, ecosystem types and interactions with soil moisture also influences R_s-temperature relationship, resulting in different R_s patterns than the generic exponential response (Sierra et al., 2015).

Optimal soil moisture for highest R_s rate is near field capacity, where soil macropores are air-filled and micropores are water filled, allowing adequate O_2/CO_2 diffusion and substrate availability to microbes (Luo & Zhou, 2006). Lower or higher moisture levels result in lower R_s rates. Soil moisture also impacts microbial community. For example, under soil water deficit, aerobic microbes are more active due to increased soil O_2 diffusion, while saturation beyond field capacity decreases microbial activity due to oxygen limitations (Skopp et al., 1990). Rainfall and soil texture can cause the spatial and temporal variations of soil moisture, which complicate R_s predictions (Burns et al., 2016). For instance, clayey soils show higher water holding capacity than sandy soils do (Bruand & Tessier, 2000). Seasonal soil moisture correlates with temperature and precipitation, and annual precipitation has been identified as the most important factor for explaining global R_s variation (Chen et al., 2014). Studies have shown that soil moisture rather than soil temperature dominates in certain biomes such as temperate forests (Hursh et al., 2017).

The relationship between R_s and soil temperature or moisture is confounded by biotic and abiotic interactions across scales (Reichstein & Beer, 2008). At field scales, these interactions can hinder the R_s response to individual factors, while at regional and global scales, confounding factors like vegetation growth and climatic controls covary, which compromise the effectiveness of predictive models. Some studies highlight the role of temperature and precipitation in explaining R_s (Raich & Potter, 1995), whereas others emphasize plant productivity (Janssens et al., 2001). Incorporating both soil moisture and temperature dynamics

is crucial for refining R_s models and reducing uncertainties in projecting carbon dynamics globally.

2.3.2. Plant productivity and vegetation type

Plant productivity and vegetation type are closely related, with their effects on soil respiration (R_s) primarily driven by belowground C allocation. Plant productivity directly contributes over 50% of R_s by supplying photosynthates to roots, mycorrhizae, and rhizospheric microbes (Litton & Giardina, 2008). Litterfall, root biomass, and species richness can be the indicators of plant productivity and represent C assimilation, production and allocation as these processes are difficult to measure (Metcalfe et al., 2011). Studies have shown a positive correlation between plant productivity and soil respiration at the global scale, reflecting strong coupling between aboveground carbon assimilation and belowground carbon allocation through litter inputs and root activity (Bond-Lamberty et al., 2018; Hashimoto et al., 2015; Jian et al., 2018; Raich & Nadelhoffer, 1989; Raich & Potter, 1995). For example, Caprez et al. (2012) found that total annual litter production explained 41% and 39% of R_s at high and low elevations respectively, emphasizing that productivity, rather than temperature, often drives R_s, highlighting that plant productivity can be a stronger driver of Rs than temperature alone. This relationship reflects the role of litter quantity and quality in supplying labile carbon substrates to soil microbial communities. Fast-growing plants produce nitrogen-rich, easily decomposable litter, stimulating microbial activity and R_s (Wardle et al., 2004). At broader scales, warm and humid climates support higher productivity and litter production thereby higher R_s, as evidenced by the contribution of litter to R_s, which is 33% in tropical forests and 15% in boreal forests (Chen et al., 2011). This difference is drastic, given that overall R_s is higher in tropical areas than in boreal areas (Bond-Lamberty & Thomson, 2010a). Root biomass allocation increases under infertile soils, enhancing belowground autotrophic respiration (Poorter et al., 2012). Moreover, plant species richness correlates positively with R_s due to enhanced productivity (Craine et al., 2001; Dias et al., 2010; Hooper et al., 2005; Zak et al., 2003). During droughts, reduced aboveground productivity drives R_s reduction, while the abundant species richness and root biomass alleviates this R_s reduction (Burri et al., 2018).

Vegetation type (e.g., forests and grasslands) influences R_s by altering soil structure, microclimate, detritus quality, and root activity (Raich & Tufekcioglu, 2000). Grasslands generally show higher R_s rates than forests (Metcalfe et al., 2011). Compared to grasslands, spatial variation in R_s is more pronounced in woody vegetation, where fine root and rhizomorph biomass show greater variation (Vargas & Allen, 2008). In both forests and grasslands, warming and increased precipitation typically stimulate R_s by promoting microbial activity and fine root development, while in grassland, grazing and drought reduce R_s by diminishing biomass and substrate availability (Oertel et al., 2016a; Zhou et al., 2019).

2.3.3. Soil bacteria and fungi

Bacterial and fungal activities determine soil organic matter (SOM) decomposition and nutrient cycling, thereby affecting soil respiration (R_s). Soil microbes break down complex polymers in SOM into dissolved organic carbon (DOC) and nitrogen (DON) by secreting extracellular enzymes for growth and maintenance, releasing CO_2 in the process (Berg & McClaugherty, 2020). Decomposition rates are influenced by the chemical composition of SOM, showing positive correlations with nitrogen and negative correlations with lignin (Song et al., 2010). Microbial composition also influences R_s. For example, compared to bacteria, fungi specialize in decomposing complex organic matter, require less nitrogen, and have higher carbon content per biomass. The fungal-to-bacteria ratio has been linked to the soil C:N ratio and can serve as an indicator of decomposition dynamics (Fierer et al., 2009).

Soil microbes influence plant productivity and R_s through mutualistic relationships. Rhizospheric microbes exchange litter-derived nutrients for photosynthetic carbon from plants, with mycorrhizal fungi and nitrogen-fixing bacteria providing up to 80% of nitrogen and 75% of phosphorus in forest ecosystems (Van Der Heijden et al., 2008). Arbuscular mycorrhizal (AM) fungi facilitate up to 90% of phosphorus uptake, doubling plant productivity in some grasslands (Van Der Heijden et al., 2006). Soil microbial biomass, influenced by plant carbon input and soil organic carbon, correlates positively with R_s (Fierer et al., 2009). Factors such as clay content and soil aggregates enhance microbial biomass by providing structural stability and

moisture retention (Six et al., 2006). Additionally, environmental stressors (e.g., temperature and moisture) regulate microbial effects on R_s (Romero-Olivares et al., 2017; Zhang et al., 2020).

The taxonomy of soil bacteria and fungi and their diverse characteristics show varying effects on R_s. Key bacterial phyla include Proteobacteria, Actinobacteria, and Acidobacteria. Proteobacteria are versatile, participating in nitrogen fixation, denitrification, and pathogen suppression (Kersters et al., 2006). Yang et al. (2018) found that R_s slightly negatively correlated with Proteobacteria richness and was related to microbial communities rather than DOC in an estuarine wetland. Actinobacteria are known for decomposing organic matter and producing antibiotics (Schrempf, 2013). Liu et al. (2017) sampled and artificially warmed forest soils (+4 ℃) and found that Actinobacteria abundance increased. Frey et al. (2008) and DeAngelis et al. (2015) found similar increases in the abundance of Actinobacteria under long-term warming, enhancing soil respiration. In grasslands, Peng et al. (2020a) investigated the changes in soil respiration and soil microbial communities under warming. They found that the relative abundance of Actinobacteria in warmed plots negatively correlated with R_s in deep soil layers (10–50 cm). They suggested that Actinobacteria in the study favored recalcitrant carbon, and the labile carbon increase due to root biomass led to the reduction in Actinobacteria. Acidobacteria adapt to varied pH levels and decompose complex organic matter (Kalam et al., 2020). Chen et al. (2021) explored microbial communities and R_s variability across elevational gradients in an alpine forest. They found that Acidobacteria are a dominant microbial phylum influencing soil respiration (R_s) patterns along elevation gradients, likely due to their role in carbon mineralization. A significant negative correlation between Acidobacteria abundance and R_s was observed, suggesting high carbon-use efficiency. While typically considered oligotrophic, their influence may reflect efficient carbon processing with lower CO_2 loss.

Mycorrhizal fungi include AM and ectomycorrhizal (ECM) fungi and form critical symbiotic relationships with plant roots, enhancing nutrient acquisition and carbon cycling. AM fungi boost nutrient availability and R_s by increasing root exudation and altering microbial communities (Fall et al., 2022). Liu et al. (2024a) explored the effects of summer precipitation pulses on AMF and soil respiration under drought. They found that AMF biomass significantly

increased and positively correlated with R_a after precipitation pulses, which contributed to enhanced substrate availability, nutrient uptake, and transportation through AMF-plant symbiosis. Jin et al. (2024) investigated R_a and R_h changes in Moso bamboo forests under intensive management (e.g., annual deep tillage, understory plant removal, and fertilization). They found that the abundance and respiration rate of AMF increased significantly, likely due to stimulated hyphae development for limited soil nitrogen and phosphorus and increased photosynthetic carbon input under intensive management. ECM fungi significantly contribute to R_s in forest ecosystems by facilitating carbon allocation and nutrient uptake. Yan et al. (2019) quantified ECM respiration and its drivers in a temperate larch plantation. They found that ECM respiration represented a large portion of R_a, averaging 41% across stand ages, and was positively correlated with soil temperature and annual fine root increments due to increases in ECM mycelial production, root colonization, and photosynthetic carbon allocation. Wang & Wang (2018) compared R_s between monocultural AM and ECM fungi-associated temperate tree species. They found that R_s in AM stands was significantly higher than in ECM stands due to higher soil temperature and water content under more open canopies in AM stands. Biotic factors, such as microbial growth and fine root biomass, drove R_s in AM stands, while litter quality and nitrogen availability predominantly influenced R_s in ECM stands. Similar findings were supported by Zhang et al. (2023a) in tropical forests.

The interactions between soil bacteria and fungi include both competitive and mutualistic relationships. Soil bacteria and fungi compete for limiting soil resources including nutrients, space, and organic matter. One competitive strategy is the production of secondary metabolites (i.e., antibiotics) by both groups. Bacteria, particularly Actinobacteria, produce antibiotics and inhibit fungal growth (van der Meij et al., 2017). Similarly, certain fungi produce antimicrobial secondary metabolites, including polyketides and non-ribosomal peptides, which can inhibit bacterial growth and shape microbial competition in soils (Frac et al., 2018). Mutualism mainly exists between fungi and plants where mycorrhizal fungi enhance nutrient uptake for plants while receiving organic carbon from them in return.

2.4. Soil respiration in New Zealand

A few studies reporting R_s data from New Zealand have been published. In the global soil respiration database, most R_s measurements in New Zealand focused on native forest, managed forest, dairy grassland, and mangrove (Bond-Lamberty & Thomson, 2010a). The rest included managed grassland and unmanaged shrubland. Forests showed high annual R_s variation (Leopold et al., 2013; Thomas et al., 2000). Managed forest showed higher annual R_s than native forest (Arneth et al., 1998b, 1998a; DeLucia et al., 2003; Lovelock, 2008; Tate et al., 1993; Thomas et al., 2000). Managed grasslands showed lower annual R_s than in forests, while shrublands showed higher annual R_s than in forests (Brown et al., 2009; Graham et al., 2014; Hedley et al., 2013). These studies were relatively less representative than the studies in the USA, China, and Canada in terms of regional R_s. This was due to comparatively lower numbers of studies, less spatial coverage, and the type of ecosystem studied.

2.4.1. Grassland

Grassland soil respiration (R_s) in New Zealand is influenced by climate, grazing, nutrient availability, and management practices. While the mechanisms governing R_s are broadly consistent with grasslands globally, this section emphasises findings from New Zealand systems, drawing on international studies where NZ-specific evidence is limited. Soil moisture plays a predominant role in controlling R_s in grasslands and shows great temporal variation during the growing season (James et al., 2003). Both very dry and very wet conditions inhibit R_s - the former through limited substrate availability and the latter via air-filled pores replaced by water. The resulting response curve is therefore of a reversed U-shape, with highest R_s values observed at intermediate soil moisture (Barnard et al., 2015). The duration and intensity of drought show significant negative correlations with grassland R_s (Gao et al., 2019). Soil temperature further influences R_s and becomes significant only when moisture is sufficient (Moinet et al., 2017). Consistent with observations from New Zealand grasslands, seasonal R_s typically peaks in spring when soil moisture is substantially higher than during summer drought periods, while during dry summers R_s may increase with temperature until soil water availability becomes limiting (Hunt et al., 2002; Rutledge et al., 2014).

Grazing affects R_s through both aboveground and belowground carbon dynamics and its effects depend on grazing intensity and pattern. Light or managed grazing (e.g., seasonal or rotational grazing) can reduce soil physical disturbance and maintain plant cover and litter inputs, thereby sustaining soil microbial biomass and organic carbon stocks compared to continuous or unrestricted grazing. Recent field evidence shows that managed grazing preserves soil structure, microbial respiration, and soil C pools more effectively than unlimited grazing, largely by minimizing compaction and maintaining belowground carbon inputs (Bastani et al., 2023; Byrnes et al., 2018). Conversely, continuous grazing increases R_s by reducing plant productivity and stimulating microbial turnover on soil carbon stocks (Jordon et al., 2024; Zhou et al., 2019). In New Zealand grasslands, grazing-induced root damage reduces both aboveground carbon (e.g., grass biomass) and belowground carbon (e.g., roots and exudates) and leads to decreased R_s (Kirschbaum et al., 2015). The negative effects of grazing on soil carbon are exacerbated by high temperatures, longer grazing durations, and reduced soil water availability (Zhou et al., 2017).

Nutrient availability, particularly nitrogen (N) and phosphorus (P), influences R_s by enhancing plant and microbial activity. An increase of N and P stimulates R_s through increased root biomass, fungal-related root activity, belowground carbon allocation, soil substrate availability, decreased soil pH, and shifts in microbial composition (Zeng et al., 2018). An increase of P promotes both N and P cycles, which leads to significant increases in available soil ammonium and phosphorus for plants and microbes (Lu et al., 2022). However, the effect of nitrogen on R_s remains debated due to conflicting findings, showing that nitrogen addition increased R_s (Graham et al., 2014), while others reported no significant effect on seasonal R_s (Moinet et al., 2017).

Grassland R_a and R_h contribute differently to total R_s. In New Zealand grasslands, more than half of gross primary production (GPP) is lost through R_a, with an additional one-fifth attributed to R_h (Kirschbaum et al., 2015). Temperature and nitrogen additions can influence the balance between R_a and R_h. For example, soil warming increased R_s by 12% and R_h by 37% in experimental tussock grasslands, but nitrogen additions alone had no effect on R_h (Graham et

al., 2014). Substrate limitations further constrain R_s contributions, as observed in dry tussock grasslands where R_h accounted for only 26% of R_s (Hunt et al., 2004).

2.4.2. Forest

Soil respiration in forests is influenced by age-related stand structure, soil disturbance, nutrient availability, and tree species composition. Compared to natural forests, plantation stands store 50% less soil carbon, allocate more carbon to aboveground biomass, and result in lower R_s (Noormets et al., 2015). Carbon allocation patterns change over time. Greater belowground allocation during early stand development enhances root growth and substrate availability, increasing both R_a and R_h (Diochon & Kellman, 2009; Genet et al., 2010). Over time, R_h declines due to substrate depletion until increased aboveground litterfall contributes to soil C inputs. Soil disturbances (e.g., harvesting) redistribute aboveground and belowground C pools, increase microbial exposure, and thus enhance R_s, particularly in fast-growing species with short rotations. These practices can double R_h and reduce forest floor carbon pools by 30%, while R_a decreases due to the decline of root production and exudation (Harmon et al., 2011; Nave et al., 2010). Conversely, thinning often has limited long-term effects on soil respiration because initial reductions in stand density are offset by enhanced growth of residual trees and understory vegetation (Zhou et al., 2013a). Increased light availability and reduced competition for water and nutrients following thinning can stimulate photosynthesis, fine root production, and litter inputs (Wang et al., 2019), thereby sustaining belowground carbon allocation and microbial activity. Although thinning may cause short-term changes in R_s due to soil disturbance or altered microclimate, these effects are frequently transient, and R_s often returns to pre-thinning levels as vegetation productivity recovers (Zhang et al., 2018).

Nitrogen deposition influences R_s by altering carbon allocation, plant productivity, and microbial activity, but its effects are highly dependent. Elevated N enhances photosynthesis, directs C to coarse roots and stem wood at the expense of fine roots and exudates, and thereby reduces substrate availability and microbial activity, which decreases both R_a and R_h under nitrogen-saturated conditions (Janssens & Luyssaert, 2009; Maier et al., 2004). However, nitrogen addition can also stimulate R_s, particularly in nitrogen-limited ecosystems or under

short-term enrichment, by enhancing plant growth, microbial biomass, and substrate availability (Fu et al., 2021).

Native forest R_s is strongly linked to soil temperature and biomass, though temperature poorly predicts temporal R_s variation (Schwendenmann & Macinnis-Ng, 2016). Urban forests show high intra-city variability in R_s but exhibit similarities across cities due to shared management practices, mirroring native forest R_s in New Zealand (Weissert et al., 2016). In *Pinus radiata* plantations, R_s is limited by microbial activity under low soil moisture and reduced by insufficient wind when soil moisture is adequate (Arneth et al., 1998a).

Mangroves are large carbon sinks and their R_s patterns are influenced by sedimentation, nutrient enrichment, and temperature. Enhanced sedimentation increases microbial activity and R_s, but R_s decreases at temperatures above 26 °C due to suppressed activity of soil-surface photosynthetic organisms (Barbier et al., 2011; Lovelock, 2008; Lovelock et al., 2007). Older mangrove stands allocate more carbon belowground and show higher R_s despite declining tree growth rates, while intact and cleared mangroves show no significant difference in R_s (Lovelock et al., 2010).

Chapter 3. Soil type and temperature determine soil respiration seasonal dynamics in dairy grassland

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3.1. Introduction

Soil respiration (R_s), the CO_2 flux from soil to atmosphere, is the second-largest carbon flux on earth (Friedlingstein et al., 2022). It plays an important role in regulating terrestrial carbon cycling, both at a regional and global scale (Green & Byrne, 2004). Plant roots together with their mycorrhizal partners (autotrophic respiration, R_a) and soil microbes (heterotrophic respiration, R_h) are the major components that make up R_s (Bond-Lamberty et al., 2004; Subke et al., 2006). The amount of R_s per unit surface area is usually calculated by CO_2 increases inside a dark measuring chamber placed over a known surface area with the aboveground biomass removed (Pumpanen et al., 2004). Over long time periods and integrated over large areas, soil respiration is ultimately driven by plant productivity (Caprez et al., 2012; Raich & Tufekcioglu, 2000), as 'you can only eat as much food as you have produced' (Raich & Nadelhoffer, 1989). In the short term however, R_s is influenced by soil characteristics (e.g., soil type; Cable et al. 2008), environmental factors (e.g., soil temperature and moisture; Lloyd & Taylor 1994; Moyano et al. 2013), and the present microbial communities (Bardgett et al., 2008). In response to climate warming, shifts in these short-term drivers can modify R_s rates and may contribute to positive feedback between terrestrial ecosystems and atmospheric CO_2 concentrations.

Soil respiration increases exponentially with temperature and displays a seasonal pattern with higher summer rates if moisture does not become limiting (Lloyd & Taylor, 1994; Suseela et al., 2012). Warming often stimulates decomposition, contributing to increases in soil heterotrophic respiration (Moonis et al., 2021; Sierra et al., 2015). Temperature can also influence R_s indirectly through the availability of soil substrate according to seasonally varying litter input (Zhang et al., 2020). These substrate changes may affect rhizosphere microbial activity and

microbial biomass. Newly produced carbohydrates are largely composed of labile carbon that is readily consumed by soil microbes, thereby contributing to R_s variation (Wan & Luo, 2003).

Both soil moisture and soil organic matter are correlated with temperature as well as with each other, as soils often become drier with rising temperature, and soil water status influences the availability and decomposition of soil organic matter (Borken & Matzner, 2009; Manzoni et al., 2012). Soil respiration rates are often highest near field capacity, when macropores remain air-filled and micropores retain sufficient water to support microbial and root activity (Davidson et al., 2000). Soil moisture alters R_s through physiological effects on soil microbes and roots, as well as through its influence on substrate transport and soil gas diffusivity. Drained soil pores limit the movement of soil microbes (Yang & van Elsas, 2018) and the availability of water-soluble substrate for microbial consumption. Additionally, dry conditions can reduce the efficiency of microbes using soil resources (Schimel, 2018) or even induce dormancy in non-sporulating bacteria (Jones & Lennon, 2010). Water scarcity in soils may thus reduce microbial biomass and/or activity, and hence soil respiration. Conversely, when soil water content exceeds optimal conditions, the overabundance of water-filled soil pores suppresses soil gas diffusion, thus limiting soil O_2 availability (Iiyama et al., 2012), while the effect on microbial respiration depends on the composition of the microbial community, i.e., the proportion of obligatory aerobes, facultative anaerobes, and obligatory anaerobes (Keiluweit et al., 2017). Because of its close link to water-holding capacity, soil texture is recognised as a driver of R_s, although its effects were not explicitly evaluated in this study.

At ecosystem scales, high grassland coverage combined with elevated CO_2 emission rates means that grasslands can contribute substantially to the atmospheric CO_2 pool. Grassland covers c.a. 25% of global soil carbon stocks (FAO, 2023; Jordon et al., 2024). Globally, soil CO_2 efflux rates are often higher in grassland than in forests and croplands under similar climatic conditions (Raich & Tufekcioglu, 2000). Mean R_s rates of global temperate grassland were estimated at around 1.03 -1.61 μmol CO_2 m^{-2} s^{-1} (Raich & Potter, 1995; Wang & Fang, 2009), though these values represent gross soil CO_2 fluxes and do not provide information on net ecosystem carbon balance (NEP). In New Zealand, grassland is the most common type of

land cover, accounting for about 40 % of the total land area (Ministry for the Environment & Stats NZ, 2021). In 2021, the net carbon emissions from grassland (excluding livestock emissions) amounted to over 4 million t CO_2-equivalent, of which around 98 % originated from CO_2 emissions, and only 2 % were due to N_2O and CH_4 from biomass burning and nitrogen mineralisation. The estimated net CO_2-equivalent emission rate was around 4 times higher in 2021 (0.01 μmol CO_2 m^{-2} s^{-1}) than in 1990 (0.003 μmol CO_2 m^{-2} s^{-1}; Ministry for the Environment 2023). New Zealand dairy accounts for about 42% of export revenue in primary industries in 2023 (Ministry for Primary Industries, 2023b). The profitability of the dairy industry has driven decades of agricultural intensification, e.g., dairy cattle numbers have doubled from 1990s to 2019 (Ministry for the Environment & Stats NZ, 2021). As a result, quantifying soil CO_2 emission and investigating the driving factors in dairy grassland are essential for understanding the impact of dairy farm intensification to soil C stock and are prerequisite to soil C sequestration in such land use. A previous New Zealand study by Brown et al. (2009) measured soil respiration using chamber-based approaches, while many others focused primarily on ecosystem carbon exchange, with soil respiration often estimated or treated as a secondary variable (Giltrap et al., 2020; Hunt et al., 2002; Kirschbaum et al., 2015). The present study provides additional field measurements of R_s to characterise its seasonal patterns and examine relationships with short-term environmental drivers. Two research questions to address include: 1) What are the rates of R_s in New Zealand dairy grasslands? 2) What are the major factors influencing the magnitude and temporal dynamics of R_s in New Zealand dairy grasslands? Correspondingly, I propose the following hypotheses.

1) Mean R_s rates are higher than those in global temperate grassland due to the intensified dairy farming.

2) Seasonal and diurnal variability in soil temperature and moisture help explain temporal changes in R_s.

3) Soil temperature explains summer R_s best, while soil water affects winter R_s the most.

4) Soil respiration rates differ among soil types.

3.2. Materials and methods

3.2.1. Study sites

The study sites included four dairy farms in New Zealand. Three in the North Island (Mangakura, Tauhei, Rotorua) and one in Teviotdale, North Canterbury (*Figure 1*) with soil types ultic (U), organic/gley (OG), pumice (Pu) and pallic (Pa) respectively (*Table 1*). Soil taxonomy was following the New Zealand Soil Classification system (Hewitt, 2010). The corresponding soil classifications were Acrosols, Gleysols, Arenosols, and Cambisols in FAO world reference database (IUSS Working Group WRB, 2022). The study took place in early January to mid-February (summer) and early to mid-July (winter) within year 2020. The sites were no more than 400 metres above sea level, and all were dominated by the temperate oceanic climate. Ryegrass (*Lolium perenne*) and white clover (*Trifolium repens*) were the two most abundant species. Fertilisers were not applied. No tillage happened in the paddocks measured in this study. The herd size of each dairy farm was around 300 cows. Multi-paddock rotational grazing was scheduled to 1 to 3 days per paddock. Soil type, drainage, texture, carbon stock, phosphorus retention rate, and pH were retrieved from S-Map Online website, Landcare (Lilburne et al., 2012), while climate information (i.e., windspeed, air pressure, hourly sunlight duration, weekly rainfall, monthly rainfall, three-monthly rainfall) was retrieved from National Climate Database, NIWA (National Institute of Water and Atmospheric Research, n.d.) (*Table 1*).

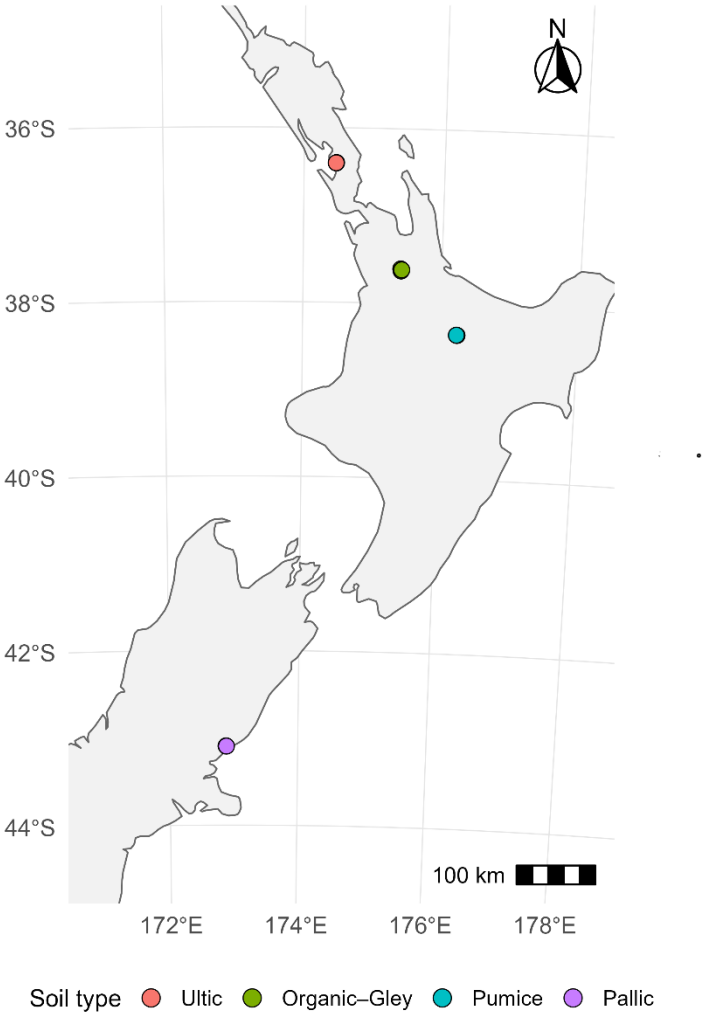


Figure 1. Location of grassland study sites in New Zealand. Coloured points indicate site soil type.

3.2.2. Experimental design

Twelve plots (10 × 10 m) were randomly selected across four study sites (three plots per site). Each plot contained four sub-plots (polyethylene collars) and was measured one day in summer and another in winter (except missing winter measurements at the Pa site). During any given measurement day, soil respiration at each sub-plot was measured six times i.e., at two-hourly intervals from 8:00 until 18:00. These measurements were repeated across plots on different sampling days rather than representing continuous or replicated diurnal observations at a single plot. No temporal averaging across hours was applied. Every soil respiration measurement was coupled with three soil temperature and three soil water content measurements. Overall, I carried out 496 individual R_s measurements.

Table 1. Soil characteristics and climate data of the study sites. Mean air temperature and precipitation data were retrieved from the National Climate Database, NIWA based on the records of the month when the R_s measurement took place. Soil type, texture, carbon stock and pH were obtained from S-Map Online website, Landcare and were not measured directly at the study sites. "S" represents summer, while "W" for winter

Site	Coordinates	Mean Air Temperature (°C)	Mean Precipitation (mm/month)	Soil type	Soil texture	Soil pH	Soil carbon storage (t ha^{-1})	Soil drainage	Dominant species
Mangakura	36°24'11.6"S 174°26'60.0"E	18.4 (S) 12.9 (W)	6.0 (S) 110.8 (W)	ultic (U)	Clay	5.5~5.6	92.7~105.6	Imperfectly	Ryegrass Kikuyu
Tauhei	37°37'15.6"S 175°24'26.4"E	18.3 (S) 9.9 (W)	14 (S) 77.7 (W)	organic/gley (OG)	Peat/Loamy Peat over Clay	4.4~5.3	90.3~167.7	Very poorly	Ryegrass White clover Annual blue grass
Rotorua	38°20'52.7"S 176°14'39.8"E	18.4 (S) 8.4 (W)	11.6 (S) 135.6 (W)	pumice (Pu)	Sand/Loam over Sand	5.4~5.6	83.1~84.8	Well	Ryegrass White clover
Teviodale	43°05'23.9"S 172°52'54.6"E	18.8 (S) N/A (W)	35.2 (S) N/A (W)	pallic (Pa)	Silt over Clay	5.8~6.0	124.5~139.1	Imperfectly	Ryegrass White clover

3.2.3. Field measurement of soil respiration, temperature, and moisture

Soil CO_2 efflux was measured by the closed static chamber method. Chamber design and construction followed the method proposed by Bader & Körner (2010). The chamber housing (diameter × height: 19.0 × 29.4 cm) had an internal volume of 8.34 L and featured a sealable vent to minimize pressure fluctuations involved with chamber placement on soil collars (*Figure 2*, Gschwend Kunststoff AG, Basel, Switzerland). Prior to the initial measurement for each season (24 hours), the aboveground grasses were trimmed to ca. one centimetre and the polyethylene collars (height: 7.0 cm) were inserted 2 to 3 cm into the soil. This protocol was used to minimise both aboveground autotrophic respiration and extra CO_2 release from potentially damaged plant roots (wound respiration) following the insertion of the collars into the soil. For the duration of the R_s measurement, the customised chamber was placed on the collar. A 5V electric fan was attached inside the chamber to gently rotate the air, avoiding CO_2 accumulation at the soil surface. The chamber was equipped with a CO_2 probe (GMP343, Vaisala, Finland) coupled with a temperature/humidity (T/RH) probe (HMP75B, Vaisala, Finland) to correct for the effect of water vapour on CO_2 measurements (*Figure 2*). Both probes were connected to a hand-held data logger (*Figure 2*, MI70, Vaisala, Finland), which stored temporal changes in air temperature, air humidity and CO_2 concentration inside the chamber. For each R_s measurement, both probe readings were recorded at an interval of 5 seconds with a 5-minute duration. First-minute recordings were excluded for R_s calculation to account for flux disturbances involved with chamber placement.

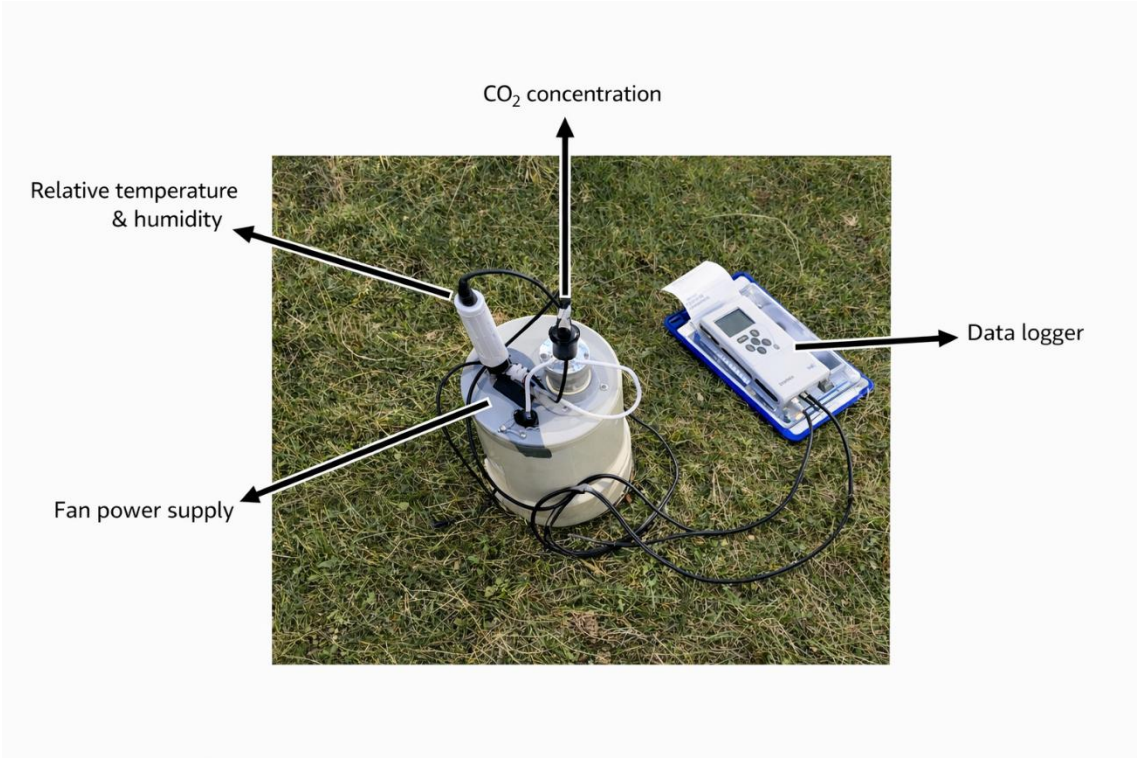


Figure 2. Chamber-based system used for in situ soil respiration measurements. The setup comprised a custom closed static chamber mounted on a polyethylene soil collar inserted 2-3 cm into the soil, with an internal fan to promote air mixing, a CO_2 probe, a temperature/relative humidity probe, and a handheld data logger for recording chamber conditions during each measurement.

Soil CO_2 fluxes were calculated from the linear rate of change in CO_2 concentration over time using least-squares linear regression. Measurements showing non-linear concentration patterns were visually screened and excluded. Then, the resulting slopes were corrected for air temperature and pressure using the ideal gas law, scaled by effective chamber air volume (including collar volume and excluding probe volumes), and normalised to collar surface area to obtain areal fluxes.

Soil temperature was measured using a Pocket Digital Thermometer (FOOD FM10, DigiMate, Digitron, UK) at a depth of 10 cm. Soil water content was measured by a handheld time domain reflectometry (TDR) soil moisture sensor (HydroSense II, HS2, Campbell Scientific, USA) integrated over a depth of 0-12 cm. Soil temperature and soil water content were measured within 30 cm radius outside the collar.

3.2.4. Statistical analysis

Exploratory data analysis

Multi-panel scatterplots with spearman correlation coefficients were used for exploratory data analysis to visualise the relationship between R_s and covariates. Two-way ANOVA followed by a post-hoc test based on Tukey contrasts was used to check for significant differences in R_s between each site and each season. Variance Inflation Factors (VIFs) were calculated to identify strong correlations among explanatory variables (multicollinearity) that can reduce the reliability of regression estimates.

Variable screening and selection

The explanatory variables considered included season, soil characteristics (i.e., temperature, water content, type, drainage, phosphorus retention rate, pH, carbon stock), climatic information (i.e., windspeed, air pressure, hourly sunlight duration, weekly rainfall, monthly rainfall, three-monthly rainfall), time of the day, air temperature in the chamber. Variables with high VIF values (≥10) were excluded. Then multiple regression with ANOVA was used to calculate the significance of the remaining variables. The non-significant predictors were excluded. Principal component analysis (PCA) was used to validate the selection of variables. Soil temperature, soil water content, and soil type were selected as independent variables for further analysis. Soil carbon storage and soil pH were examined separately using one-way ANOVA with soil type as the factor.

Generalised additive modelling

Because soil respiration likely follows a non-linear relationship with its predictor variables (e.g., soil temperature) and the rates are distinct between seasons, I used a generalised additive modelling (GAM) approach to model R_s with those selected independent variables, and the goal was to determine the most influential variables and then investigate the R_s trends in summer and winter separately. I checked for concurvity to detect multicollinearity among smoothed non-linear predictors (i.e., soil temperature and soil water content) and used a backwards model

selection procedure and the Akaike Information Criterion (AIC) to find the most parsimonious model.

Parametric temperature-respiration modelling

I also applied R_s parametric models to investigate the relationship between R_s and temperature. The equation is as follows,

$$Rs = A * e^{BT}$$

Where R_s is soil respiration rate (μmol CO_2 m^{-2} s^{-1}), T is soil temperature (°C), A is the intercept parameter representing basal respiration at T = 0 °C, and B is the temperature sensitivity coefficient describing the exponential response of respiration to temperature (Lloyd & Taylor, 1994; van't Hoff, 1898).

The entire dataset, season-grouped, and soil-type-grouped data were fitted to the above equation, respectively. F tests were performed to compare the full model and grouped models, with null hypothesis 'the more grouped model does not explain significantly more variation'. I used a generalised nonlinear least-squares framework (GNLS) with variance modelling to address the residual heterogeneity (Pinheiro et al., 2023). AIC comparisons identified the optimal variance structure.

Model diagnostics

I checked for model assumptions using standard diagnostic plots. Residual vs. fitted values were plotted to assess the variance homogeneity assumption. Residuals were also plotted against each predictor variable to detect model misfits. No gross violations of model assumptions were detected. All statistical analyses were performed using the statistical software R (version 4.0.5) and the "mgcv" package (R Core Team, 2021; Wood, 2021).

3.3. Results

3.3.1. Soil respiration rates

Overall, soil respiration rates (R_s) ranged from 0.29 to 14.58 μmol CO_2 m^{-2} s^{-1} with a mean of 5.38 ± 0.13 μmol CO_2 m^{-2} s^{-1}. Both maximum and minimum observed R_s occurred during summer sampling, while winter R_s ranged from 0.51 to 8.03 μmol CO_2 m^{-2} s^{-1}. The seasonal R_s means were significantly different with 6.84 ± 0.20 and 3.67 ± 0.09 μmol CO_2 m^{-2} s^{-1} in summer and winter, respectively ($F_{1, 494}$ = 190.96, P < 0.001; GNLS, P < 0.001) (*Figure 3A*). Mean R_s differed significantly between all four measured sites, except between the organic/gley (OG) and the pumice (Pu) sites (*Figure 3B*), with means of 3.17, 6.59, 6.51 and 4.71 μmol CO_2 m^{-2} s^{-1} for the ultic (U), organic/gley, pumice, and pallic (Pa) soils, respectively ($F_{3, 492}$ = 52.47, P < 0.001; GNLS, P < 0.001). The interaction between seasons and sites was significant ($F_{2, 489}$ = 129.95, P < 0.001). In summer, the mean R_s at the OG and Pu sites were significantly higher than those at the U and Pa sites (P < 0.001), while in winter, the mean R_s at the OG and Pu sites were significantly higher than that at the U site (P < 0.001 and P = 0.03 respectively). Slight within-day patterns in R_s were found based on soil types and seasons (*Figure 4*). Although measurements were taken at fixed two-hour intervals (08:00-18:00), these observations represent discrete sampling times across different plots and sampling days to to illustrate within-day variability under field conditions, rather than continuous diurnal measurements at individual plots. In general, the mean soil respiration rate was lowest in the morning and increased by 43.5 % to reach a maximum around noon, followed by a decrease in the afternoon. Soil pH had a significantly negative effect on R_s ($F_{1, 494}$ = 52.24, P < 0.001), while soil carbon had no direct effect on R_s ($F_{1, 494}$ = 1.17, P > 0.1).

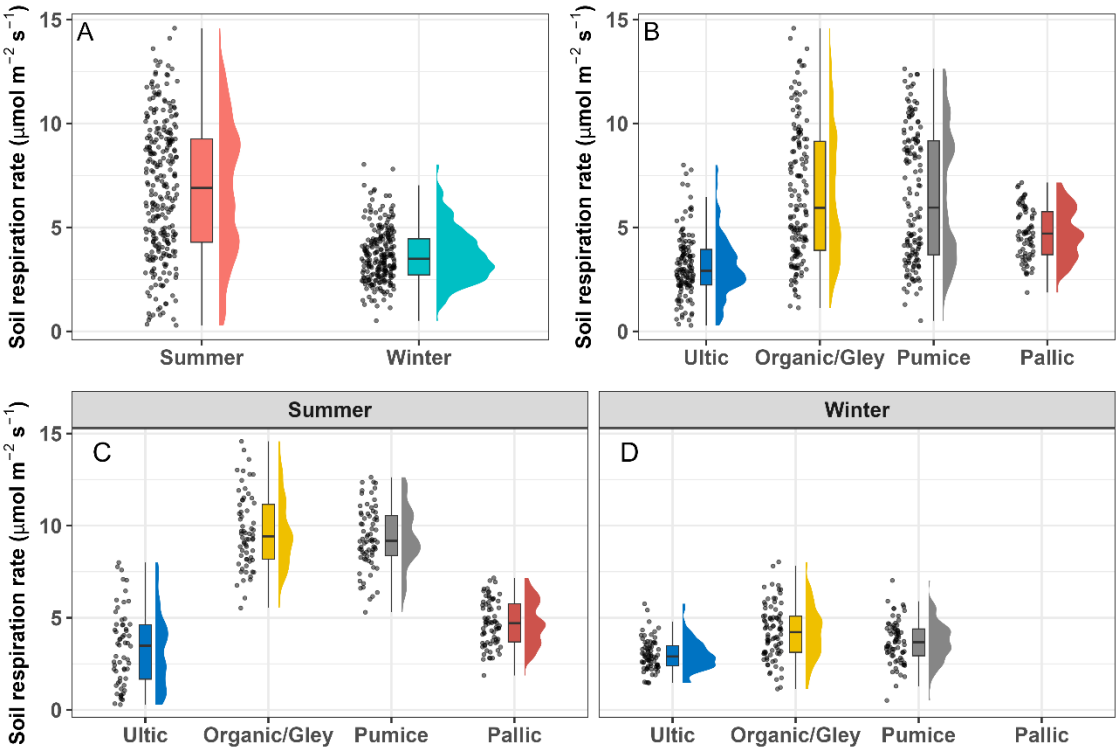


Figure 3. Soil respiration rates categorised by seasons (A), sites (B) and both (C, D). The density plots indicate the sample sizes.

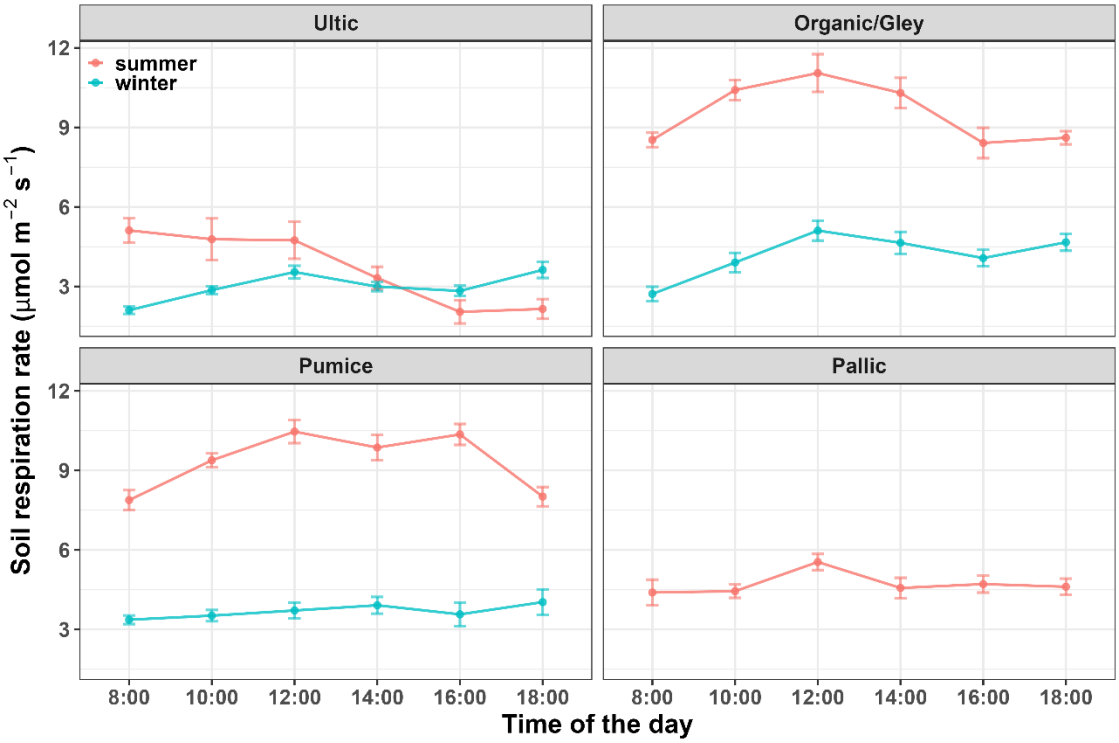


Figure 4. Mean soil respiration (R_s) measured at fixed two-hour intervals (08:00-18:00) during sampling days in summer and winter across the four soil types. Points represent means across

three plots per site at each sampling time, with error bars showing standard error. Data are presented for visualisation of within-day variability only; no temporal averaging applied in subsequent analyses, and measurements do not represent continuous diurnal observations at individual plots.

3.3.2. Microclimate and soil data

Soil temperature and soil water content shifted in response to seasonal and site-specific differences. Soil temperature (T_s) ranged from 17.3 to 26.7 °C in summer and from 6.7 to 13.1 °C in winter. During summer sampling days, mean soil temperature ranged from 19.9 ± 0.2 °C at the U site to 22.1 ± 0.3 °C at the Pa site. During winter sampling days, mean soil temperature ranged from 8.9 ± 0.2 °C at the OG site to 11.6 ± 0.1 °C at the U site. These differences reflect conditions on the respective sampling days rather than site-level effects, as soil temperature measurements were conducted on different dates and were strongly influenced by prevailing weather conditions.

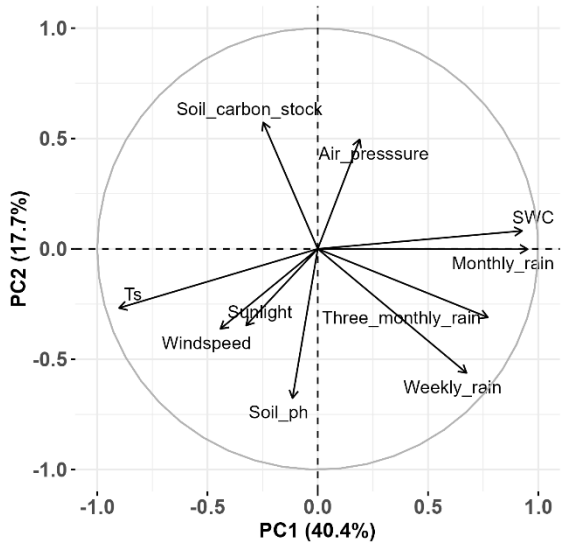
Soil water content (SWC) was high in winter (28.1 % to 49.6 %) and low in summer (4.4 to 28.6 %) across all sites. In summer, mean soil water content (in descending order) was 19.6 % 16.5 %, 10.9 %, and 5.9 % at the Pu, U, OG and Pa sites respectively, while during winter, values increased to 42.0 %, 40.6 %, and 38.4 % for the U, OG, and Pu sites respectively. The Pa site was not measured during winter due to COVID-19 lockdown.

Soil carbon storage and soil pH showed strong loading on PC2 (*Figure 5*) and were significantly different among sites (ANOVA, $P < 0.001$ respectively). Mean soil carbon storage (in descending order) was 142.4, 129.4, 96.3 and 84.2 tonnes per hectare (t/ha) at the OG, Pa, U, and Pu sites respectively (Post-hoc, all $P < 0.001$). Mean soil pH (in ascending order) was 4.7, 5.5, 5.6, and 5.9 at OG, Pu, U, and Pa sites respectively (Post-hoc, all $P < 0.001$).

3.3.3. The R_s dependence on soil temperature, moisture, type, and others

PCA results showed that the first and second axes (PC1 and PC2) explained 40.4% and 17.7% of variance, respectively. PC1 primarily reflected a hydro-climatic gradient, dominated by soil water content and supported by antecedent rainfall metrics (weekly, monthly, and three-monthly), which were included to provide contextual information on moisture conditions at the

time of measurement rather than as independent controls on soil respiration. Soil temperature loaded negatively along this axis. PC2 was more strongly associated with soil properties, particularly soil carbon stock and soil pH (*Figure 5*). Soil respiration was sensitive to soil temperature changes, but the relationship varied strongly with soil type (*Figure 6A*). The relationship between soil respiration and soil temperature was mostly following a pattern of increasing R_s with T_s until around 21 °C, beyond which R_s decreased. Soil respiration rates were less temperature sensitive in the low-temperature range (6 - 13 °C) and responded differently at low vs. high SWC (*Figure 6B*). At low to medium SWC (≤ 30 %), soil respiration rate generally increased with SWC. Soil respiration peaked around 10 and 25 % SWC, then decreased. At high SWC (> 30 %), soil respiration rates remained low and steady until they decreased at 45 % SWC and beyond. Soil pH had a negative correlation with R_s (linear regression, adjusted R^2: 0.096; $P < 0.001$), while soil carbon storage had no significant effect on R_s (linear regression, $P > 0.1$). Soil pH had a significantly negative effect on R_s ($F_{1, 494} = 52.24$, $P < 0.001$), while soil carbon had no direct effect on R_s ($F_{1, 494} = 1.17$, $P > 0.1$).



	PC1	PC2
Soil_ph	-0.057	-0.508
Soil_carbon_stock	-0.123	0.430
SWC	0.461	0.061
Ts	-0.448	-0.201
Sunlight	-0.162	-0.260
Air_presssure	0.095	0.373
Windspeed	-0.220	-0.272
Weekly_rain	0.336	-0.422
Monthly_rain	0.474	-0.001
Three_monthly_rain	0.384	-0.233

Figure 5. Principal Component Analysis (PCA) of overall soil respiration as explained by soil temperature (T_s), soil water content (SWC), soil carbon stock, soil pH, hourly sunlight duration (Sunlight), air pressure, as well as one-week, one-month and three- month rainfall volume prior to measurement (Weekly_rain, Monthly_rain, and Three_monthly_rain, respectively).

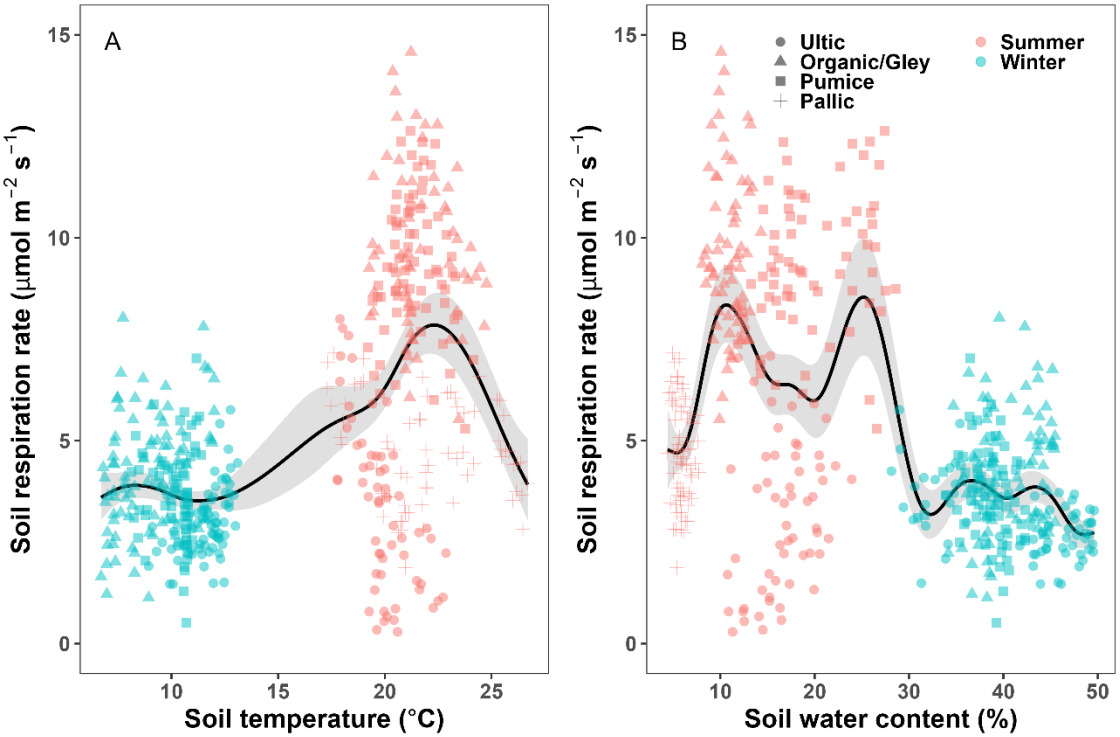


Figure 6. Response of soil respiration to soil temperature (A) and to soil water content (B) during summer and winter. Solid lines represent generalised additive model fits, and the grey surrounding areas indicate the 95 % confidence intervals.

At a seasonal scale, soil type had a significant effect on R_s according to GAM model comparison and GNLS model (likelihood ratio comparison between models with soil type interaction vs. without, $P < 0.001$; GNLS, $P < 0.001$). Soil temperature and soil type best explained the variation in both summer (79 %) and winter R_s (27 %) (*Figure 7*). The typical hump-shaped R_s-T_s relationship was only seen during summer in pumice soil (Pu site) with peak R_s values around 21 °C (*Figure 7A*). Summer respiratory CO_2 release from the ultic grassland soil (U site) showed an exponential decline with increasing T_s, while the two remaining soil types displayed no distinctive pattern (*Figure 7A*). During winter, R_s increased slightly with soil temperature in the U and OG soils, while R_s in the Pu soil remained unchanged until 11°C, then increased (*Figure 7C*). The relationship between R_s and SWC was generally steady but with some site-specific changes. During summer, R_s increased slightly with SWC in the U and Pu soils, while there were no distinctive patterns in the OG and Pa soils (*Figure 7B*). During winter, at the U soils, R_s decreased slightly with SWC, opposite to the increasing R_s-SWC trend in the

OG soils. At the Pu site, R_s remained unchanged until SWC reached around 36 %, then slightly decreased (*Figure 7D*).

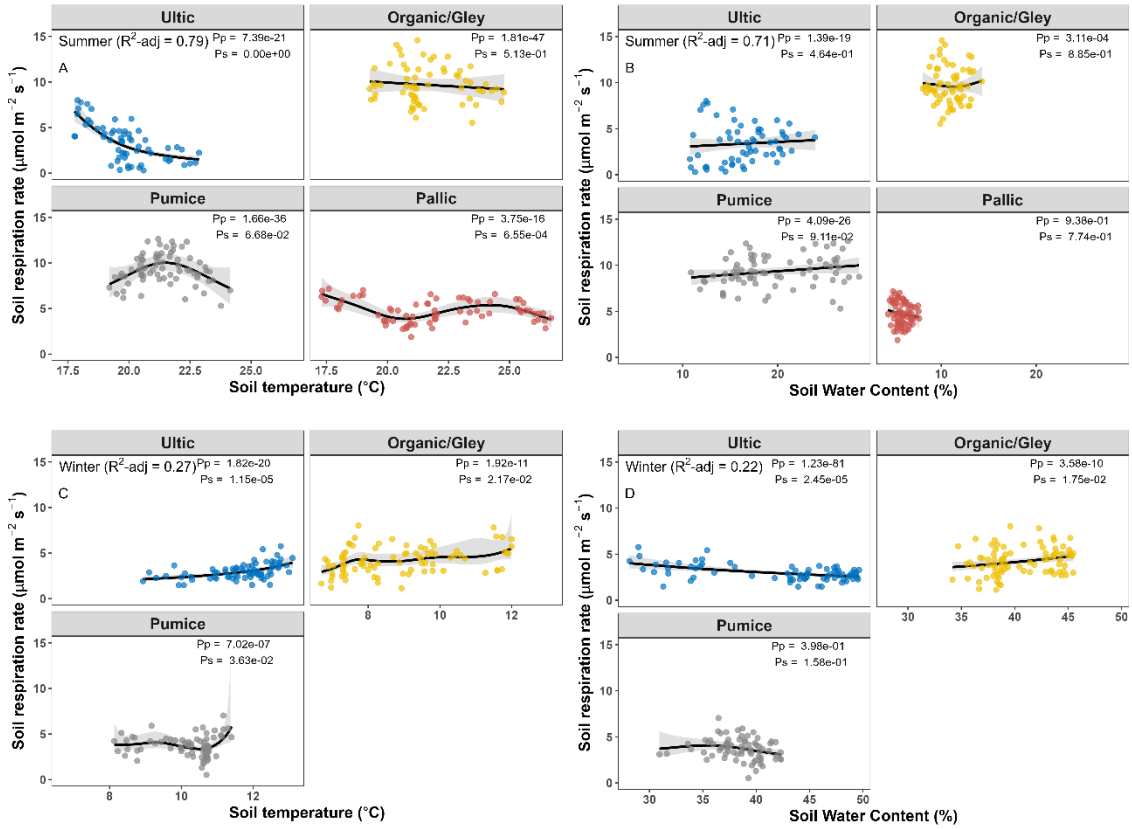


Figure 7. The relationship of soil respiration with summer soil temperature (A), summer soil water content (B), winter soil temperature (C) and winter soil water content (D). Solid lines represent generalised additive model fits, and the grey surrounding areas indicate the 95 % confidence intervals. Pp is the abbreviation of p value for parametric term and Ps is the abbreviation of p value for smoother.

3.4. Discussion

3.4.1. Limitations

Several limitations should be considered when interpreting the results of this study. Measurements at each plot were conducted within a single sampling day in both summer and winter, which limited the ability to characterise long-term seasonal R_s variability and capture the full range of the environmental drivers influencing R_s. Consequently, observed relationships between R_s and its drivers reflect short-term patterns instead of long-term seasonal dynamics. Additionally, reported maximum and minimum R_s values represent instantaneous chamber

measurements collected during individual sampling days and should not be viewed as seasonal extremes.

Soil temperature varied in a relatively narrow range due to the short sampling periods, which constrained the inference about the R_s response across the full temperature range. In contrast, soil moisture displayed broader variation and its effects cannot be completely separated from soil temperature, site-specific weather, and soil conditions, since these factors were not experimentally controlled.

Soil type, soil carbon stocks, and soil pH were derived from S-map datasets rather than direct field measurements at collar locations. At a plot scale, mapped classifications and values may not accurately represent local soil heterogeneity, which may introduce uncertainty into soil type comparisons and limit the site-scale inference about the relationship between R_s, soil carbon stock, and soil pH.

Because sites were sampled on different days under naturally varying weather conditions, measurements across soil types and locations (sites and plots) may introduce confounding effects between soil properties and climatic conditions. Thus, variations in site microclimate during the measurement periods may be partially responsible for the soil-type-associated differences in R_s.

Together, these limitations restrict the generalisation of findings beyond the observed short-term conditions during field sampling periods and emphasize the long-term requirement for repeated and controlled sampling approaches to confidently evaluate seasonal drivers and soil-type variations in R_s.

3.4.2. Comparison of soil respiration to global data and studies from comparable climatic zones

Mean summer and winter R_s rates at the investigated sites were 178 % and 564 % higher than those reported for global temperate grassland, respectively (Jian et al., 2020). Mean R_s rates observed in this study were 111% and 53% higher than those reported by Francioni et al. (2019)

and Mukumbuta et al. (2019), respectively, based on studies conducted in grassland systems within broadly comparable climatic zones but at different locations. In New Zealand, mean summer R_s at my study sites was 19% higher than that measured at an extensive sheep farming grassland in Canterbury, South Island, by Moinet et al. (2016), while mean winter R_s was about three times higher than that measured at the same place by Moinet et al. (2017).

This overall higher R_s values may be associated with differences in soil type and management intensity between the present study and many of the reference sites. For example, higher soil organic carbon stocks associated with organic and gley soils may contribute to greater respiration under favourable conditions. Elevated soil organic carbon is generally associated with increased microbial biomass and higher potential for microbial respiration (Zarafshar et al., 2023). Nonetheless, in this study, soil carbon stock estimates were derived from S-map datasets, which provide spatially averaged, profile-scale values for soil units rather than plot-level measurements. These values should be interpreted as contextual indicators and do not capture fine-scale or labile carbon pools that more directly support microbial activity.

Soil type is likely to reflect a suite of co-varying physical and chemical properties, including soil pH, compaction, and organic matter content, which are known to be associated with variation in R_s (Lohila et al., 2003). In addition, soil type may be indirectly associated with R_s patterns through its influence on soil temperature and moisture dynamics (Howard & Howard, 1993). Accordingly, differences in R_s observed among sites are best viewed as soil-type-associated patterns rather than direct effects of individual soil properties.

3.4.3. The effect of soil type on soil respiration

In this study, soil type was strongly associated with differences in R_s, with higher R_s observed at the OG and Pu sites, compared to U and Pa sites. At the OG site, these higher R_s values are consistent with elevated soil organic matter stocks (max: 167.7 t ha^{-1}, *Table 1*). OG soils are formed on the remains of wetlands and are thus high in organic matter and shrinkage potential (Hewitt et al., 2021a). These characteristics may predispose OG soils to higher R_s under aerobic conditions (i.e., oxidation and biodegradation).

At the Pu site, relatively high R_s rates were associated with favourable soil moisture conditions. Pumice soils are characterised by high water-holding capacity and seasonal moisture variability (Hewitt et al., 2021c), which can promote microbial activity under non-saturated conditions (Evans et al., 2022). Soil water content at the Pu site was higher during the summer sampling period and lower during winter relative to the other sites, reflecting site-specific weather conditions interacting with the high porosity and water-holding capacity of Pumice soils, which in turn supported overall high R_s at Pu site. In general, soil respiration has been shown to increase with increasing soil water content under dry conditions, exhibit weak or no relationship under wet conditions, and decline once field capacity is exceeded, as reported in previous studies (Smith et al., 2003; Xu & Shang, 2016). Thus, at my Pu site, high SWC promoted R_s in summer when soil moisture levels are usually low. In contrast, low SWC facilitated soil diffusivity thus R_s in winter when soil moisture was often high at the other sites (> 30 % vol.).

In contrast, lower R_s at the U and Pa sites is likely influenced by a combination of soil physical properties (e.g., clay content) and moisture conditions; however, given the observational nature of the dataset and the co-variation among soil texture, soil water content, and site-specific conditions, these effects cannot be disentangled definitively. At the U site, high clay content might confine soil organic matter and microbes in small pores, inducing a protective effect on C mineralisation (Rutherford & Juma, 1992; Wang et al., 2003). At the Pa site, the low SWC observed during the summer probably indicated a seasonal discrepancy between precipitation and evapotranspiration, with minimal rainfall and elevated evaporative demand. Additionally, the naturally low water-holding capacity of Pallic soils may have exacerbated this moisture shortage (Hewitt et al., 2021b; Hewitt, 2010)

3.4.4. The effect of soil type and temperature on soil respiration

Soil temperature, together with soil type, explained a large proportion of the variation in R_s, accounting for 79 % of the variance during summer and 27 % during winter. In this study, overall R_s increased with soil temperature at lower temperature ranges but levelled off or declined at moderate temperatures (~20-22 °C, *Figure 6A*), rather than continuing to increase toward higher temperatures (25 °C) as commonly reported for grassland systems. (Carey et al.,

2016). The initial rise in R_s occurred alongside increasing soil temperatures, consistent with the well-established non-linear response of soil respiration to temperature, whereby incremental increases at the lower temperature range result in proportionally larger increases in R_s (Graham et al., 2012; Wang et al., 2009). However, the relative contributions of autotrophic and heterotrophic respiration cannot be resolved with the present dataset.

The early declining trend was mainly driven by low rates of R_s at the Pa site, which might be due to the low metabolic activity of plant roots and microbes, caused by the low SWC levels. In summer, the rapid R_s decrease at the U site was likely due to drought-induced soil desiccation as a result of low midsummer rainfall during the measurement period (*Table 1*). The restrictive effect of drought on R_s was probably largely confined to the topsoil, while in the typically clay-rich and well-moistened ultic subsoil, oxygen-poor conditions due to low gas diffusivity are likely to suppress R_s (Hewitt et al., 2021d).

At the OG site, the non-significant R_s-T_s relationship indicated that R_s remained high but showed a slight decreasing trend with increasing soil temperature. Similar temperature-insensitive R_s responses have been reported in systems where substrate availability or microbial acclimation constrain temperature sensitivity (Crowther & Bradford, 2013); however, these mechanisms cannot be resolved with the present dataset.

At the Pu site, the hump-shaped relationship between R_s and T_s was probably due to high soil porosity and a low level of organic matter in the topsoil (Hewitt et al., 2021c). The high level of macropores facilitated the O_2/CO_2 pathways, allowing the plant roots and soil microbes to produce more respiratory CO_2 in an aerobic environment. The peak and decreasing part might be due to the limitation of soil organic matter. Under rising soil temperatures and high soil microporosity, low organic matter content in the topsoil was likely to decrease to the extent that adversely affected R_s. The weak R_s-T_s relationship at the Pa site was possibly due to limiting soil water availability, which may also explain the lack of a temperature effect.

During winter, an R_s increase with soil temperature was expected. Low magnitudes of this increase might be due to high soil moisture and a narrow range of soil temperature change, which may have limited temperature sensitivity during this period.

3.4.5. The effect of soil type and moisture on soil respiration

Soil water content only explained 22.3 % of the variance in winter R_s, with higher rates at the OG and Pu sites. These patterns are consistent with differences in soil type and moisture conditions during winter, although the underlying mechanisms cannot be resolved with the present dataset. Higher winter R_s at the OG and Pu sites co-occurred with higher soil water content and greater soil organic matter stocks, which may be associated with increased respiration under non-saturated conditions.(Hewitt et al., 2021c).

The decreasing trend beyond 45 % SWC was largely influenced by low R_s rates at the U site. Ultic soils are characterised by high clay content and water-holding capacity (Hewitt et al., 2021d), which are commonly associated with reduced soil permeability and gas diffusion under wet conditions. The high soil water content observed at the U site during winter (approximately 30-50%) coincided with lower R_s, a pattern consistent with diffusion-related constraints on soil respiration, although direct measurements of soil aeration or gas diffusivity were not available.

At the OG site, R_s showed a weak increasing trend with SWC. This response may reflect soil-type-specific properties, including high organic matter content and distinct physicochemical characteristics of organic/gley soils (Hewitt et al., 2021a). Potential explanations include enhanced microbial activity under improved moisture conditions, as reported in a previous study (Liu et al., 2009); however, these processes cannot be evaluated directly given the absence of measurements of microbial activity, nutrient availability, or soil chemical dynamics.

At the Pu site, the R_s-SWC relationship was weak and non-significant, suggesting that SWC was not a primary constraint on R_s under the sampled conditions. This pattern is consistent with the high porosity and rapid drainage characteristic of pumice soils (Hewitt et al., 2021c), which may buffer R_s against short-term variation in SWC.

During summer, R_s-SWC relationships were generally weak across sites. In the U and Pu soils, R_s appeared relatively insensitive to SWC, suggesting that moisture was not strongly limiting R_s during the sampling period. In the OG and Pa soils, summer R_s-SWC relationships were difficult to interpret due to the narrow range of SWC observed.

3.5. Conclusion

At the sampled dairy grassland sites, the observed R_s rates were higher than the global temperate grassland values used for comparison. However, this trend should not be generalised beyond the specific conditions and locations assessed in this study. Soil temperature and soil type can best explain the magnitude and trend of seasonal R_s. In ultic soils, a low R_s was linked to clay-dominant soil conditions, which might have limited decomposition and the diffusion of soil gases under the conditions sampled. The observed decrease in R_s with increasing soil temperature at the ultic site during summer may reflect site-specific conditions during the sampling period, but the underlying mechanism cannot be concluded from the present dataset. In organic soils, high R_s was associated with high soil organic matter content, consistent with the wetland-derived origin of these soils. In pumice soils, high R_s was associated with favourable moisture conditions, likely reflecting the combined influence of recent weather and the high porosity and water-holding capacity characteristic of pumice soils. My findings showed that soil type can play an important role in R_s estimation at local scale.

Chapter 4. Stand age affects microbial biodiversity but not soil respiration rates in *Pinus radiata* plantations

Under Review @ Frontiers in Plant Science

4.1. Introduction

Forests represent the largest terrestrial carbon pool globally, storing 662 to 861 Pg C, with soil carbon contributing 45% (FAO, 2020). Temperate forests, despite storing only 14% of the global forest carbon in soil and plant biomass, account for 47% of the global net forest sink (Harris et al., 2021). The net sink results from a dynamic balance between soil and aboveground plant respiration (C losses), and photosynthesis (C input). Forest soil respiration (R_s), the primary pathway to release CO_2 to atmosphere, has two major components – belowground heterotrophic and autotrophic respiration. Heterotrophic respiration (R_h) is linked to the microbial and meso-faunal decomposition process of soil organic matter (SOM). Autotrophic respiration (R_a) is associated with respiratory processes in plant roots, rhizospheric microbes and fungi. Both components are sensitive to environmental changes. Global warming can promote forest soil respiration and hence weaken the forest CO_2 sink, indicated by positive temporal trends in evergreen forest R_s and global R_h over the past two decades (Lei et al., 2021).

Planted forests can enhance soil and biomass C input thereby boost the global forest net CO_2 sink, with their increasing land cover and C sequestration potential. Plantation forests covered 131 million hectares (ha) globally in 2020, up from 55.8 million ha in 1990 (FAO, 2020). For example, driven by the demand in Australia and New Zealand's wood supply, annual wood harvests have doubled from 1990 to 2018 in Oceania (Australasia, Melanesia, Micronesia, and Polynesia; FAO, 2020). In New Zealand, the total plantation forest area showed a steady increase over time and was estimated to be 1.81 million ha in 2022, with *Pinus radiata* D. Don (radiata pine) covering 90% of this area (Ministry for Primary Industries, 2023a). The selection of fast-growing tree species in these plantations increases stand productivity and thereby soil C inputs (Noormets et al., 2015). Conversely, plantation forest soil respiration (i.e., C loss) can potentially increase atmospheric CO_2 and is affected by decomposition of soil organic matter

(SOM) (Ekblad et al., 2013; Raza et al., 2023; Talbot et al., 2008), tree characteristics (e.g., species, age, genotype, and litter input) (Madritch et al., 2007; Mahmoodi et al., 2023; Saiz et al., 2006), environmental factors (e.g., soil temperature and moisture) (Melillo et al., 2017; Reichstein et al., 2003), and management practices (e.g., thinning, and harvest) (Jandl et al., 2007). Investigating the influence of these R_s drivers can provide a better estimation of the net global forest net CO_2 sink.

Decomposition is a core process in soil respiration, where soil bacteria and fungi break down polymeric organic substrates and metabolise the subsequent simpler compounds (Talbot et al., 2008). Soil nutrients and microbial diversity determine the efficiency of decomposition, both of which are closely related to the species and productivity of plants and microbes (Raczka et al., 2021). A plant-fungi symbiotic relationship enables fungi to acquire nutrients by decomposing biomass and exchange these nutrients for carbon fixed by plants (Raza et al., 2023). During nutrient acquisition, N and P uptake by mycorrhizal fungi may cause nutrient limitations for other microbes, thus slowing down the bacterial decomposition rate (Ekblad et al., 2013). Mycorrhizal fungi can potentially utilise soil C for survival when photosynthate supply is low and accelerate soil C decomposition due to a priming effect when photosynthate supply is high (Talbot et al., 2008). High microbial diversity enhances SOM decomposition through diverse trophic niches. Greater richness of fungi fosters enzymatic breakdown of lignocellulose, similarly, increased richness of bacteria helps break down smaller components (Alessi et al., 2018). Bacteria rapidly decompose labile organic matter, while fungi specialise in decomposing more recalcitrant organic matter like cellulose and lignin (Raza et al., 2023). Soil decomposition dynamics highlight the complex roles of bacteria and fungi in soil respiration.

Soil respiration typically shows a U-shaped response to stand age in forests. Juvenile stands often exhibit high R_s because rapid stand development is associated with high C allocation to fine root biomass and turnover, which increases autotrophic root respiration and stimulates rhizosphere microbial activity through root exudation (Gong et al., 2012; Pregitzer & Euskirchen, 2004; Zhao et al., 2016). As stands age, R_s decreases with reduced fine root biomass (Saiz et al., 2006). Eventually, mature stands exhibit high R_s due to accumulated litter

input and nutrients (Xiao et al., 2014). In plantation forests with short rotation times and fast-growing genotypes, this R_s-age trend may be altered, which merits further investigation. Genotype affects soil respiration by influencing nutrient availability and microbial communities (Hoeksema & Classen, 2012; Madritch et al., 2007). For example, Norway spruce (*Picea abies*) genotypes affect ectomycorrhizal (ECM) fungal diversity through the quality of leaf litter and photosynthetic C allocation (Korkama et al., 2006). Temperature sensitivity of R_s varies among genotypes, with high temperature sensitivity often increasing fine root turnover (Tyree et al., 2014). In New Zealand, research on radiata pine has traditionally focussed on improving stand quality and productivity (Burdon & Moore, 2018), disease tolerance (Gapare, 2014), and stability (Lasserre et al., 2005; Mason, 2023). The effects of genotype on R_s remain underexplored.

Soil temperature positively correlates with R_s, with decreasing temperature sensitivity at higher temperatures due to thermal acclimation (Melillo et al., 2017; Peng et al., 2009). Thinning and harvesting increase soil temperature and thereby SOM decomposition, enhancing soil respiration through organic input from harvest residuals (Jandl et al., 2007). Soil moisture affects R_s with a hump-shaped relationship: respiration is constrained under very dry conditions, increases as soil moisture rises toward optimal levels, and declines again under water-saturated conditions due to oxygen limitation (Luo & Zhou, 2006; Ngaba et al., 2023). While soil moisture controls respiration during dry conditions, soil temperature dominates in non-drought conditions (Almagro et al., 2009; Mo et al., 2008; Rey et al., 2002). Soil moisture impacts R_s through substrate availability and soil oxygen delivery (air-filled pore space), particularly affecting R_h (Davidson et al., 2012).

Growing forests are net C sinks, but soil CO_2 dynamics in plantation forests remain poorly understood. Harvest rotation, disturbance, and management practices influence soil C processes, potentially misrepresenting the C sequestration potential. Here, I present a field-based study to investigate R_s responses to environmental and microbial changes in radiata pine stands of varying ages in Kaingaroa forest in New Zealand, one of the world's largest conifer plantations. I hypothesise that 1) the highest and lowest mean R_s occurs in juvenile stands and mature stands

respectively, i.e. a decreasing R_s-age relationship; 2) soil microbial richness and diversity affect soil respiration, and the magnitude and direction of this effect depends on microbial community shifts among stand ages; and 3) because soil water availability at the study site during the summer and winter sampling periods was not expected to be persistently limiting, soil temperature potentially explains more variation in R_s than other environmental drivers (e.g. soil moisture, pH, organic C availability).

4.2. Materials and Methods

4.2.1. Study sites

The study sites are situated in Kaingaroa Forest, central North Island of New Zealand (38°24′27″S, 176°35′00″E; 465 m a.s.l.; *Figure 8*). The forest is a large, long-established Pinus radiata plantation that has been managed under successive short-rotation cycles. Understorey species include but are not limited to rough tree fern (*Dicksonia squarrosa*), broad leaved fleabane (*Conyza albida*), and wall lettuce (*Mycelis muralis*). The forest experiences a temperate oceanic climate, with a mean annual temperature of ca. 11 °C and annual precipitation of ca. 1,500 mm. The forest soil is classified as pumice (Hewitt et al., 2021c). Information on soil type, carbon stock, phosphorus retention rate, and pH (*Table 2*) were obtained from the S-Map Online website, Landcare (Lilburne et al., 2012), while air temperature and precipitation data (*Table 2*) were retrieved from the National Climate Database, NIWA (National Institute of Water and Atmospheric Research, 2021).

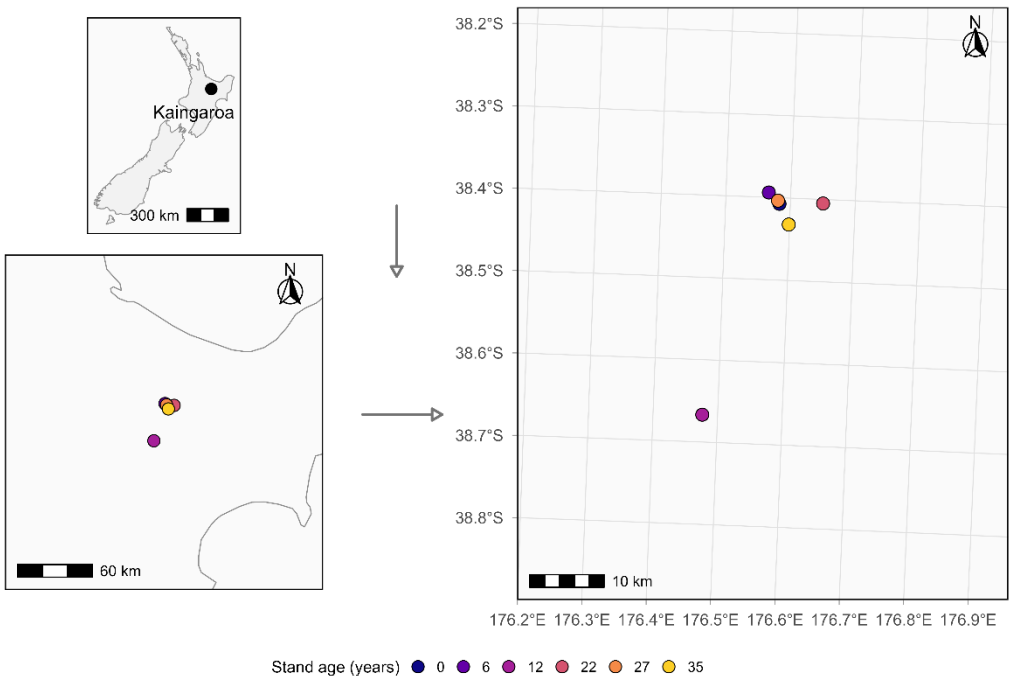


Figure 8. Spatial distribution of Pinus radiata plantation study sites within the Kaingaroa Forest, New Zealand. The inset map (top left) shows the location of Kaingaroa Forest within New Zealand; the intermediate panel (bottom left) provides regional context; and the main panel (right) shows the individual sampling sites. Points denote site locations and are coloured by stand age (0, 6, 12, 22, 27, and 35 years).

Table 2. Site characteristics across six Pinus radiata plantation age classes, including coordinates, mean measured air temperature, mean monthly precipitation, soil pH, total soil carbon storage, and soil phosphorus retention rate. Climatic data are reported separately for summer (S) and winter (W) where available.

Site	Coordinates	Mean measured air temperature (°C)	Mean monthly precipitation (mm/month)	Soil pH	Soil carbon storage (t ha^{-1})	Soil phosphorus retention rate
0-year-old stand	38°24′27″S 176°35′00″E	29.4 (S) NA (W)	42.2 (S) 76.3 (W)	5.3	94.7	57%
6-year-old stand	38°23′39″S 176°33′58″E	18.3 (S) 14.2 (W)	42.2 (S) 76.3 (W)	5.4	95.4	57%
12-year-old stand	38°40′01″S 176°28′35″E	16.3 (S) 11.3 (W)	59.4 (S) 78.0 (S)	5.4	72.5	60%
22-year-old stand	38°24′19″S 176°39′02″E	23.6 (S) NA (W)	42.2 (S) 76.3 (W)	5.3	85.3	52%
27-year-old stand	38°24′14″S 176°34′51″E	17.9 (S) 14.5 (W)	42.2 (S) 76.3 (W)	5.3	94.7	57%
35-year-old stand	38°25′56″S 176°35′56″E	23.63 (S) NA (W)	42.2 (S) 76.3 (W)	5.3	86.9	57%

4.2.2. Soil respiration measurements

Soil CO_2 efflux was measured by the closed static chamber method. Chamber design and construction followed (Bader & Körner, 2010). The chambers were custom-built from polyethylene by a plastics manufacturer (Gschwend Kunststoff AG, Basel, Switzerland), which does not specialise in flux chambers but fabricated the units according to the specified design. Each chamber had an internal diameter of 19.0 cm, a height of 29.4 cm, and an internal volume of 8.34 L, and was fitted with a sealable vent to minimise pressure artefacts during placement. The polyethylene collars (height: 7.0 cm) were inserted 2 to 3 cm into the soil at least 24 hours before the first measurement to prevent additional CO_2 release from potentially damaged plant roots (wound respiration). Then, the chambers were carefully placed on the collars, where closed cell neoprene gaskets on the chamber flange provided an airtight seal. A 5V electric fan was attached inside the chamber to ventilate the air, avoiding the accumulation of CO_2 above soil surface. The chamber was equipped with a temperature/relative humidity (T/RH) probe (HMP75B, Vaisala, Finland) and a CO_2 probe (GMP343, Vaisala, Finland) to correct for the effect of water vapour and temperature on the CO_2 measurements. Both probes were connected to a hand-held data logger (MI70, Vaisala, Finland), which stored temporal changes in air temperature, air humidity and CO_2 concentration inside the chamber. For each R_s measurement, both probe readings were recorded at an interval of 5 seconds with a 5-minute duration. First-minute recordings were excluded for R_s calculation to account for slight flux disturbances during chamber placement (Bader & Körner, 2010; Davidson et al., 2002b).

Soil temperature (T_s) was measured using a pocket digital thermometer (FOOD FM10, DigiMate, Digitron, UK) at a soil depth of 10 cm. Volumetric soil water content (SWC) was measured by a handheld soil moisture sensor (HydroSense II, HS2, Campbell Scientific, USA) at the soil depth of 12 cm.

All measurements were conducted during early to mid-September 2020 (late winter) and early to late-March 2021 (late summer).

4.2.3. Experimental design

Six radiata pine sites were selected with stand ages of 0 (less than 1 year), 6, 12, 22, 27, and 35 years. Each stand age class was represented by one study site. Genotype information (i.e., radiata pine breeding line) was available only for the 6- and 12-year-old sites. The 6-, 22-, and 35-year-old sites were located 5-7 km apart; the 0- and 27-year-old sites were approximately 500 m apart and 2-5 km from the others; the 12-year-old site was about 30 km away from all other sites. Of these, the 6-, 12-, and 27-year-old sites each consisted of a single stand, within which three plots were established per stand (n = 9 total plots across these three age classes). The plots were spaced 20-50 meters apart to ensure spatial independence and treated as experimental units in the analysis. Each plot was approximately 10 × 10 meters in size. Within each plot, four soil collars were installed for R_s measurements, with 3-5 meters between collars, and chamber-based soil respiration rates were measured with a two-hour interval from 8:00 to 16:00 within one day per season. This provided 20 measurements per plot per season, and for replicated age classes measured across both seasons, a total of 345 R_s measurements were collected after excluding unreliable measurements (3 age classes × 3 plots × 2 seasons × 5 time points × 1 day).

The remaining sites, i.e., 0-, 22-, and 35-year-old stand sites, were each represented by one unreplicated plot with five collars installed. These collars were measured only once during the summer due to COVID-19 logistical constraints, which added an additional 15 R_s measurements (3 plots × 5 collars × 1 time point).

All plots of a given age were located within the same stand. Stand density is in the typical range for Pinus radiata plantations from ca. 500 for older stands to 1000 stems per ha for young stands before thinning (usually around year 7-8). Stand area was estimated using GIS mapping: most stands ranged from approximately 2 to 9 ha, except for the 27-year-old stand, which covered around 119 ha. Field measurements in each stand were conducted within an accessible 2-hectare area.

For each R_s collar, T_s and SWC were measured by taking three readings at three points within a 30 cm radius, and the average was used to represent the collar-level environmental condition at that time point. These measurements were taken immediately before or after each R_s reading. In replicated plots (6-, 12- , and 27- year-old stands), T_s and SWC were measured at five time points during the day (8:00, 10:00, 12:00, 14:00, and 16:00), resulting in five averaged values per collar per day, based on a total of 15 raw readings per collar. In unreplicated plots (0-, 22-, and 35-year-old stands), T_s and SWC were measured only once during the day, with three readings taken per collar and averaged to produce a single mean value.

4.2.4. Microbial sampling and DNA sequencing

Two 25 mL litterfall-free soil samples were collected aseptically at the soil surface (1-3 cm) in each plot during summer. All soil samples were stored on ice in the field and frozen to -20 °C in the laboratory until extractions. DNA was extracted by a modified CTAB bead-beating method (Archer et al., 2015). DNA purification was achieved through CTAB-based extraction, organic solvent clean-up, and alcohol precipitation, as a part of the extraction. The extracted DNA was quantified by Qubit 2.0 Fluorometer (Invitrogen, Life Technologies, US), then diluted to 5ng/μL. Protocols for lab analysis followed Archer et al. (2019). Polymerase chain reaction (PCR) amplification of 16S rDNA was performed as per manufacturer's protocol (16S Metagenomic Sequencing Library Preparation; Part # 15044223; Rev. B [Illumina; San Diego, CA, USA]) using forward primer 341F (5'-CAGCCTACGGGNGGCWGCAG-3') and reverse primer 785R (5'-GACTACHVGGGTATCTAATCC-3'), while that of ITS rDNA was performed using ITS1-F (5'-CTTGGTCATTTAGAGGAAGTAA-3') and ITS2 (5'-GCTGCGTTCTTCATCGATGC-3') primers from (Bellemain et al., 2010; Klindworth et al., 2013). These primers target the V3 and V4 region of 16S, and fungal ITS1 region between 18S and 5.8S rRNA genes. The PCR mixture for each soil sample consisted of 2.5 μL genomic DNA (5ng/μL), 2.5 μL Reverse primer (1 μM), 2.5 μl forward primer (1 μM), and 12.5 μl KAPA HiFi HotStart ReadyMix. PCR conditions were as following sequentially: a) 95 °C for 3 mins, b) 25 cycles of 95 °C (30 s), 55 °C (30 s) and 72 °C (30 s), c) 72 °C for 5 mins, and d) hold at 4 °C. A 2% agarose gel electrophoresis was performed after PCR to confirm the amplicon specificity.

Sequence libraries were prepared using Illumina Miseq v3 600 cycle chemistry as per manufacture's protocol.

4.2.5. Data processing and analysis

Primer sequences and amplicon sequence variants were removed using cutadapt and the resultant libraries were formed by dada2 (Callahan et al., 2016; Martin, 2011). After rarefaction curves were reviewed to ensure sufficient sequencing depth, samples with less than 1000 reads were excluded to guarantee the accuracy in bacterial and fungal community structure. Beta regression was performed to investigate the relationship between relative abundance and stand age, and differential abundance analysis was used to show relative abundance difference between stand age groups. Alpha diversity was calculated with Chao1 and Shannon's diversity index. Beta diversity was visualised with Principal Coordinate Analysis (PCoA) based on Bray Curtis community dissimilarities. Generalised linear model (GLM) was formed to investigate the relationships between alpha diversity and stand age. Permutational multivariate analysis of variance (PERMANOVA) and analyses of multivariate homogeneity of group dispersions (PERMDISP) were used to test the significant differences of the spread of the bacterial and fungal community among stand age groups, respectively.

Multi-panel scatterplots with Spearman's correlation coefficients were used to visualise the R_s relationship with soil temperature, soil water content, and chamber air temperature. Variance inflation factors (VIF) were calculated to initially assess multicollinearity among predictors, namely soil temperature, soil moisture, stand age (continuous and categorical respectively), measuring time of the day, precipitation (weekly, monthly, and 3-monthly), soil pH, and soil carbon storage. A generalized linear mixed-effects modelling (GLMM) approach was used to test for differences in R_s according to season and stand age class, with stand age included as a categorical fixed effect. The model employed a Gamma distribution with an identity link and included plot and collar as random effects to account for spatial structure and repeated observations. Post hoc pairwise comparisons were conducted using Tukey contrasts.

To examine non-linear relationships between R_s and environmental variables, we used generalized additive mixed models (GAMMs) stratified by season. Separate models were fitted for soil water content (SWC) and soil temperature (T_s). We tested plot, collar, and age class as potential random effects, both individually and in combination, and found that including plot and collar together provided the best fit based on Akaike Information Criterion (AIC). The SWC model used a Gamma distribution with an identity link, while the T_s model used an inverse Gaussian distribution with an inverse link. Predictor selection was guided by variance inflation factor (VIF) analysis, and statistical assumptions for all models were checked using standard diagnostic plots.

All statistical analyses were preformed using the statistical software R (version 4.3.2, R Core Team, 2023). R packages 'phyloseq' (McMurdie & Holmes, 2013), 'vegan' (Oksanen et al., 2022), 'ANCOMBC' (Lin & Peddada, 2020) were used for microbial abundance calculations, statistical tests, and visualisations. GAMs were fitted with the 'mgcv' package (Wood, 2021).

4.3. Results

4.3.1. Soil respiration

Overall, R_s rates ranged from 0.37 to 6.87 μmol CO_2 m^{-2} s^{-1} with an overall mean of 2.20 ± 0.06 μmol CO_2 m^{-2} s^{-1} (± standard error). Mean summer R_s was significantly higher than mean winter R_s by 61% ($F_{1,358}$ = 111.7, P < 0.001). Both maximum and minimum R_s occurred in summer. The mean summer R_s rate was 2.69 ± 0.08 μmol CO_2 m^{-2} s^{-1}. Winter R_s ranged from 0.64 to 4.63 μmol CO_2 m^{-2} s^{-1} with a mean and standard error of 1.67 ± 0.05 μmol CO_2 m^{-2} s^{-1}. Stand age affected R_s differently in summer and winter (likelihood ratio test, GAM with age-season interaction vs. GAM with a common age smoother only, df = 3.0, F = 206.93, P < 0.001). In summer, the R_s rate did not vary linearly with stand age. Mean R_s rates in stands aged 6 and 12 years were significantly higher than those in other stands, except age 35 stands. In winter, R_s rates decreased with stand age (*Figure 9*). In 6- and 12-year-old stands, genotype significantly affected R_s with no seasonal interaction but only explained 1.8% of R_s variation (GLM, L_2 =

6.19, P = 0.045). Mean R_s with genotype G1 and G3 were significantly higher than stands with G2 (*post hoc* test, P < 0.05, respectively, *Figure 10*).

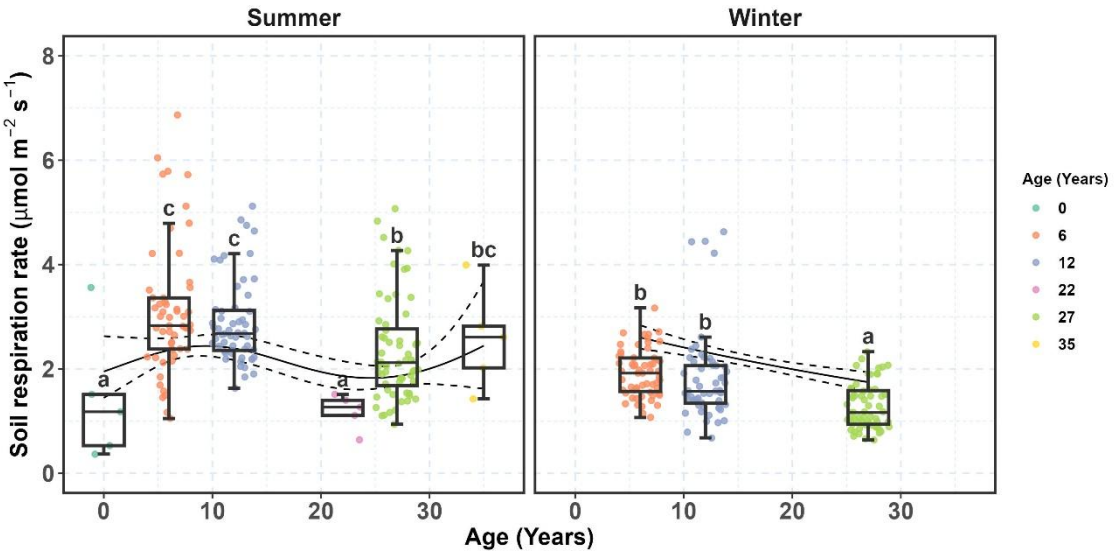


Figure 9. Seasonal soil respiration changes with Pinus radiata stand age (0, 6, 12, 22, 27, and 35 years old) in Kaingaroa Forest, central North Island, New Zealand. A total of 360 R_s measurements were included in summer (early to late-March 2021; n=185) and winter (early to mid-September 2020; n=175), as indicated by the individual data point. The GAM model-based regression lines represent the trend between soil respiration and age. The areas between the dashed lines represent a 95% confidence interval. The letters represent significant differences between age groups in each panel (differing letters indicating significance at a 5% alpha threshold).

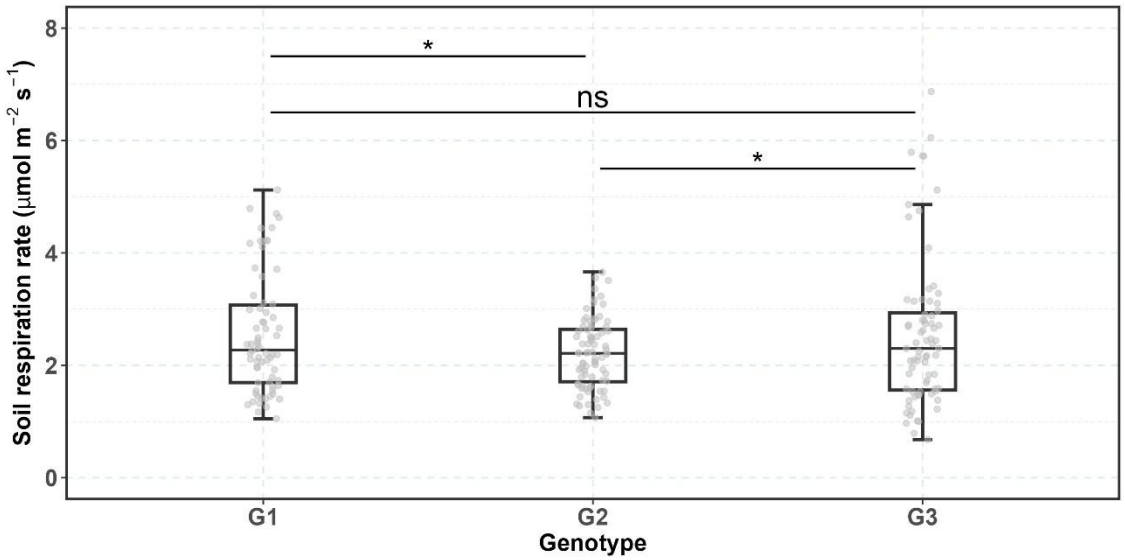


Figure 10. Soil respiration rates under genotype G1 (n=70), G2 (n=80), and G3 (n=75). All measurements taken from young (6- and 12-year-old) stands. Asterisks indicate the significance levels ('', < 0.05; 'ns', non-significant).*

4.3.2. Soil bacteria and fungi

Soil bacterial phyla in the study were dominated by Proteobacteria, Acidobacteriota, Actinobacteriota and Verrucomicrobiota with mean relative abundance of 37.6%, 20.8%, 12.2% and 7.7% across stand age (*Figure 11A*). The relative abundance of Proteobacteria, Actinobacteriota and Verrucomicrobiota showed decreasing trends with stand age, while that of Acidobacteriota showed an age-related increase (Beta regression, Z = -0.68, -0.43, -0.92 and 1.18 respectively, all P > = 0.05; ANCOM-BC2 global analysis, W = 6.81, 4.28, 4.16, and 8.23 respectively, all adjusted P > 0.05 except Acidobacteriota P = 0.03 with high sensitivity). Mean relative abundance of Patescibacteria was 1.3% across stand age and its relative abundance showed a significant decrease with stand age (Beta regression, Z = -13.83, P < 0.001; ANCOM-BC2 global analysis, W = 26.35, P < 0.001). The relative abundance of Patescibacteria in age 27 stands was significantly lower than these in age 6 and 12 stands (ANCOM-BC2 pairwise analysis, W = –3.91 and –3.20 respectively, both adjusted P < 0.05).

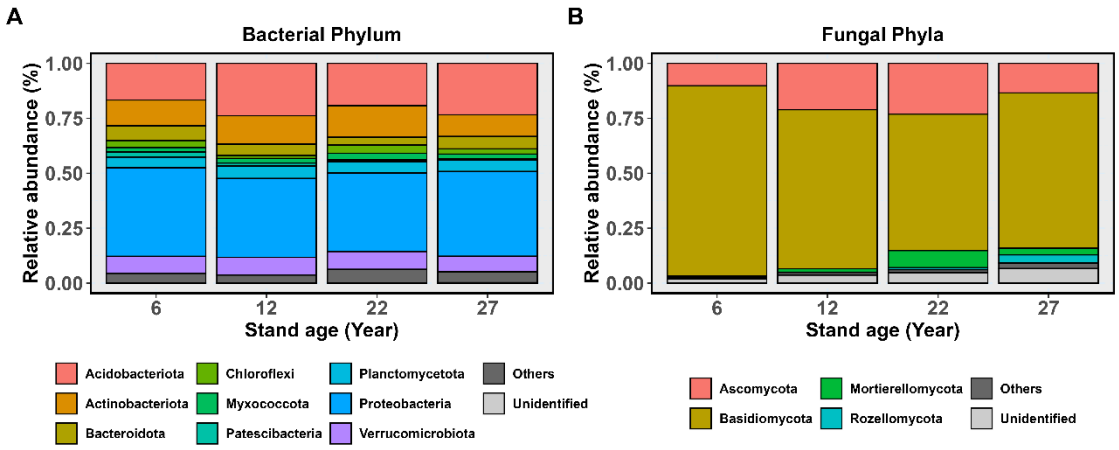


Figure 11. Phylum-level composition of soil microbial communities across Pinus radiata stand ages in Kaingaroa Forest, New Zealand. Stacked bars show mean relative abundance of dominant bacterial phyla based on 16S rRNA gene sequencing (A) and dominant fungal phyla based on ITS sequencing (B) for each stand age class (6, 12, 22, and 27 years). Low-abundance taxa (≤ 1%) were grouped as "Others", and sequences not assigned at phylum level are shown as "Unidentified".

At family level, Xanthobacteraceae, Burkholderiaceae, Acidobacteriaceae (Subgroup 1), and Chthoniobacteraceae were predominated, with mean relative abundances of 9.7%, 4.3%, 4.0%, and 3.2% respectively across stand age. The relative abundance of Xanthobacteraceae and Chthoniobacteraceae increased (Beta regression, $Z = 2.76$ and 0.40, $P < 0.01$ and >0.05, respectively; ANCOM-BC2 global analysis, $W = 1.17$ and 7.89 respectively, both adjusted $P > 0.05$), while those of Burkholderiaceae and Acidobacteriaceae (Subgroup 1) decreased with stand age (Beta regression, $Z = -1.95$ and -0.44, $P = 0.05$ and > 0.05 respectively; ANCOM-BC2 global analysis, $W = 33.25$ and 21.06 respectively, both adjusted $P < 0.001$; *Figure 12*). The relative abundance of Burkholderiaceae and Acidobacteriaceae (Subgroup 1) in age 22 stands were significantly lower than those in age 6 and age 12 stands respectively (ANCOM-BC2 pairwise analysis; Burkholderiaceae: $W = –5.57$ and –3.73, both adjusted $P < 0.05$; Acidobacteriaceae (Subgroup 1): $W = –3.33$ and –4.54, both adjusted $P < 0.05$).

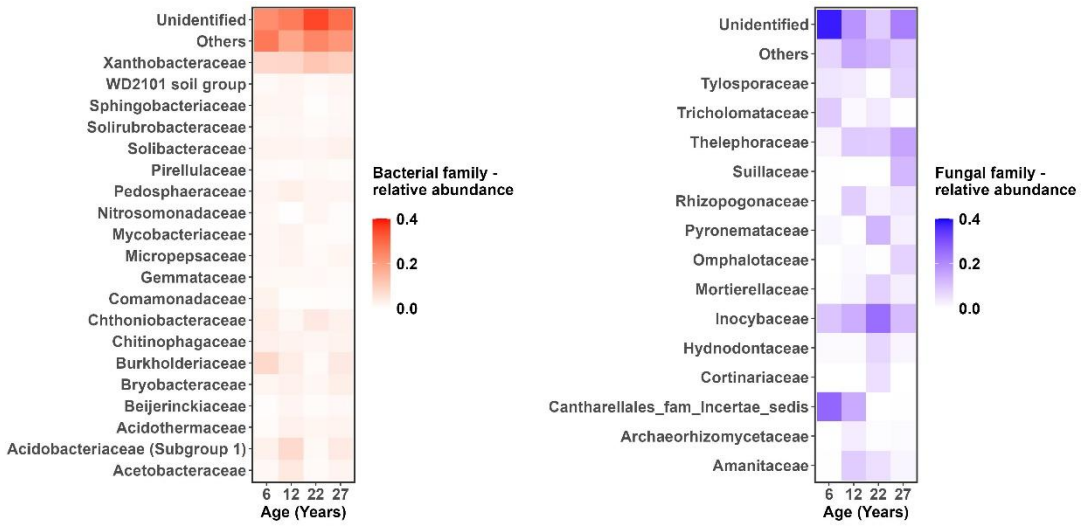


Figure 12. Relative abundance of bacterial (left) and fungal (right) families in age groups 6, 12, 22, and 27 of Pinus radiata stands. Families with more than 1% relative abundance across the soil samples are labelled, while families with less than or equal to 1% relative abundance are combined in 'Others'.

Soil fungal phyla in my study sites were dominated by Basidiomycota and Ascomycota with mean relative abundance of 72.9% and 17.0% respectively across stand age (*Figure 11B*). The relative abundance of Basidiomycota decreased while that of Ascomycota increased with stand age (Beta regression, $Z = -2.29$ and 0.59, $P < 0.05$ and > 0.05 respectively; ANCOM-BC2 global analysis, $W = 0.52$ and 11.63, adjusted $P > 0.05$ and < 0.01 respectively).

At family level, Inocybaceae, an unknown family in Cantharellales (Cantharellales Incertae sedis), and Thelephoraceae prevailed with relative abundances of 15.2%, 10.3%, and 8.7%, respectively. The relative abundance of Inocybaceae and Thelephoraceae increased (Beta regression, $Z = 0.74$ and 3.41, $P > 0.05$ and < 0.001, respectively; ANCOM-BC2 global analysis, $W = 1.58$ and 15.03, adjusted $P > 0.05$ and $P < 0.05$ with high sensitivity, respectively), while that of Cantharellales Incertae sedis decreased with stand age (Beta regression, $Z = -4.58$, $P < 0.001$, ANCOM-BC2 global analysis, $W = 112.88$, adjusted $P < 0.001$ with high sensitivity, *Figure 12*). The relative abundance of Thelephoraceae in age 27 stands was significantly higher than that in age 6 stands (ANCOM-BC2 pairwise analysis, $W = 3.57$, adjusted $P < 0.05$ with high sensitivity), while those of Cantharellales Incertae sedis in age 22 and 27 stands were

significantly lower than that in age 6 stands (ANCOM-BC2 pairwise analysis, W = -10.10 and -7.07, respectively; both adjusted $P < 0.001$ with high sensitivity).

Alpha diversity of both bacteria and fungi indicated by the Chao1 and Shannon index showed no significant trend with stand age (GLM, $L_1 = 3.48$, 1.69, 1.61, and 0.82 for bacterial Chao1, bacterial Shannon, fungal Chao1, and fungal Shannon respectively, all $P > 0.05$; *Figure 13*). Bacterial richness decreased, while fungi richness increased with stand age. Beta diversity indicated by Bray-Curtis dissimilarity index showed bacterial and fungal communities significantly differed with stand age (PEMANOVA, bacterial $F_{3,19} = 2.40$, fungal $F_{3,16} = 2.21$, both $P = 0.001$, *Figure 14*), with no dispersion between any two age groups (PERMDISP2, *post hoc* test, all $P > 0.4$). In both bacterial and fungal communities, compositions in various age groups were significantly different from each other (Pairwise PEMANOVA, all $P < 0.05$), except those between age 12 and 27 stands (Pairwise PEMANOVA, bacterial $P = 0.081$, fungal $P = 0.085$).

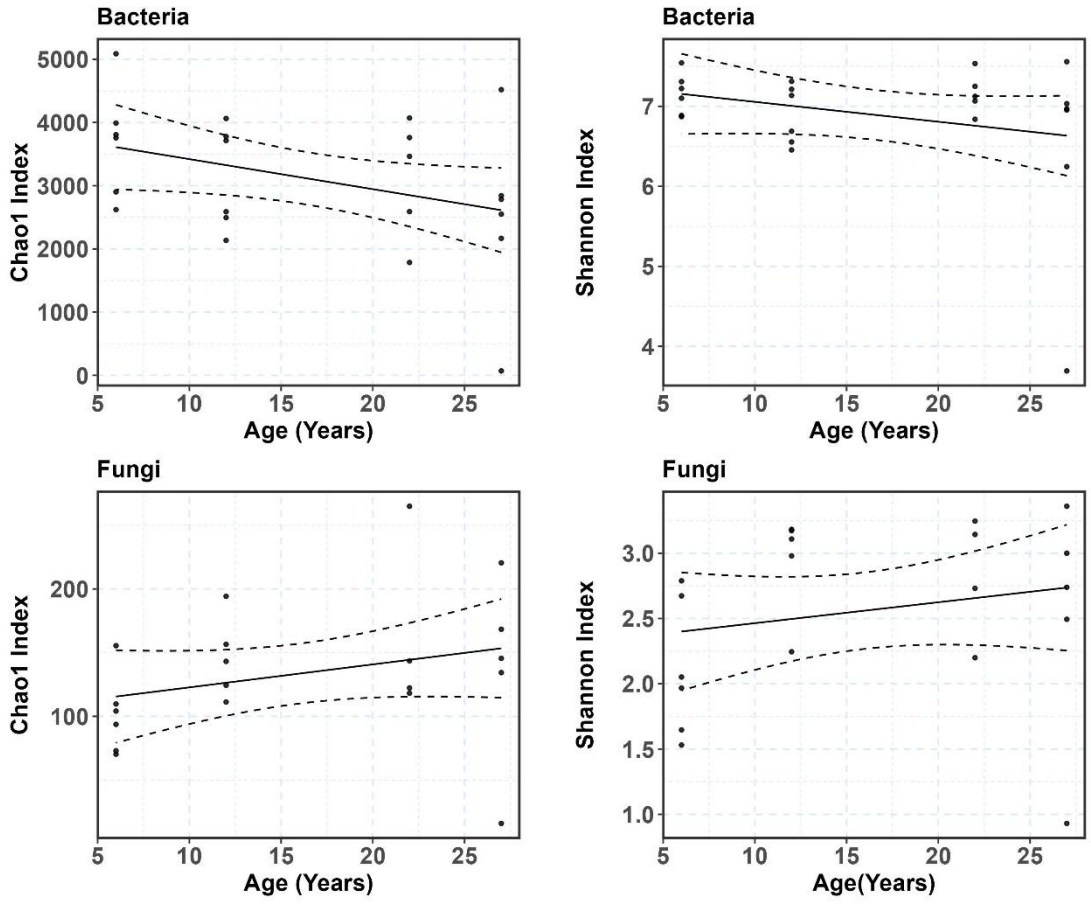


Figure 13. Effects of stand ages (6 to 27 years) on the richness of soil bacteria and fungi respectively, indicated as the Chao1 and Shannon Indices. Each point represents the index value in one plot. Regression lines (generalised linear regression models, GLMs) are shown between stand age and the index values. The areas between the dashed lines represent 95% confidence intervals.

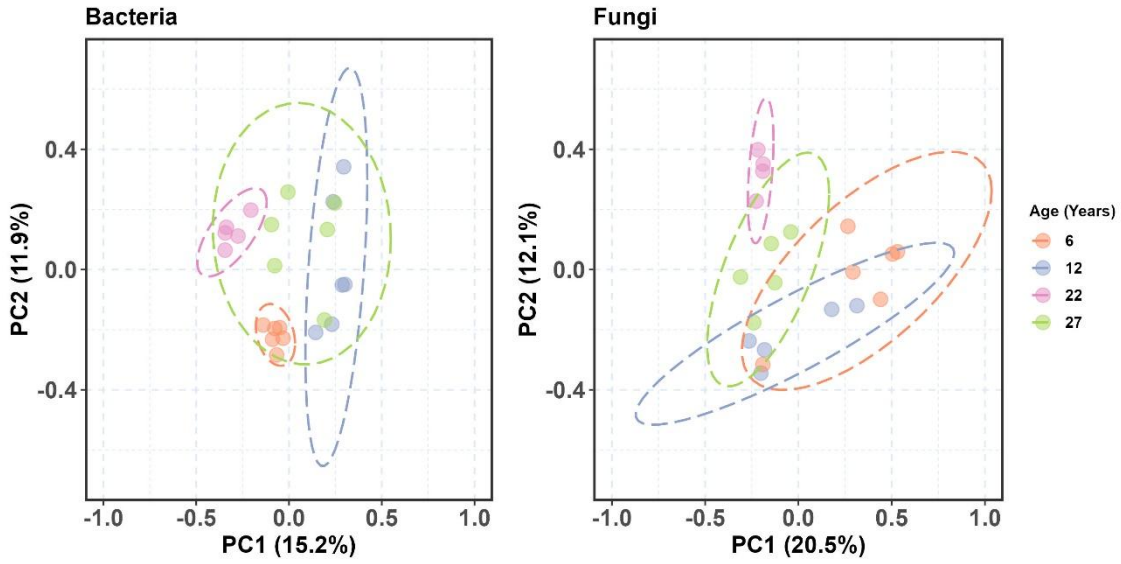


Figure 14. Principal coordinates analysis (PCoA) plot. Results of PCoA with Bray-Curtis index, presenting the first two principal coordinates, explaining 27.1% and 32.6% of the observed genetic variation in soil bacteria and fungi respectively. Colours correspond to the stand ages.

4.3.3. Soil temperature and soil water content

Soil temperature (T_s) varied strongly with season, ranging from 12.2 to 16.0 °C in summer and from 6.1 to 10.3 °C in winter. Mean soil temperatures measured during the summer sampling period were 13.8 ± 0.1 °C, while those measured during the winter sampling period were 8.1 ± 0.1 °C. Soil temperature varied significantly with stand age in both seasons (Linear regression, summer: slope = -0.05, $F_{1,183} = 63.36$, $P < 0.001$; winter: slope = 0.02, $F_{1,173} = 4.77$, $P < 0.05$). However, because measurements were conducted on different days across stands, these patterns reflect combined effects of stand age and short-term meteorological conditions. In summer, T_s showed a significant and decreasing trend with stand age, while in winter, T_s showed slight but significant increase with stand age. Soil water content (SWC) was significantly different between seasons ($F_{1,358} = 142.56$, $P < 0.001$), ranging from unmeasurable points (< 0.5 % due to sandy texture) to 25.83 % in summer and from 6.67 to 32.03% in winter, with a mean value of 9.78 ± 0.56 % and 18.75 ± 0.50 % respectively. In summer, SWC showed a statistically

significant decrease with stand age ($F_{1,183}$ = 79.36, P < 0.001, slope = -0.44), while in winter, SWC decreased only slightly but still significantly with stand age ($F_{1,173}$ = 24.54, P < 0.001, slope = -0.26).

4.3.4. Response of R_s to soil bacteria and fungi, soil temperature and soil water content

The richness and diversity of bacteria and fungi affected soil respiration. In regard to bacterial community, R_s showed strong correlations with PC2 in PCoA and the Shannon Index (Spearman, rho = -0.32 and 0.24 respectively, both P < 0.01). For fungal community, R_s showed strong correlations with Chao1 Index and PC2 (Spearman, rho = -0.24 and -0.18 respectively, both P < 0.05).

Seasonal changes in soil water content explained more variation in R_s across stand ages (GAM, adjusted R^2 = 0.33) than seasonal soil temperature fluctuations (GAM, adjusted R^2 = 0.28, *Figure 15*). In summer, R_s showed a bimodal trend with SWC peaking at ca. 5% and 18%, while a slightly positive relationship between R_s and T_s was observable. In winter, R_s remained unchanged with varying SWC and T_s.

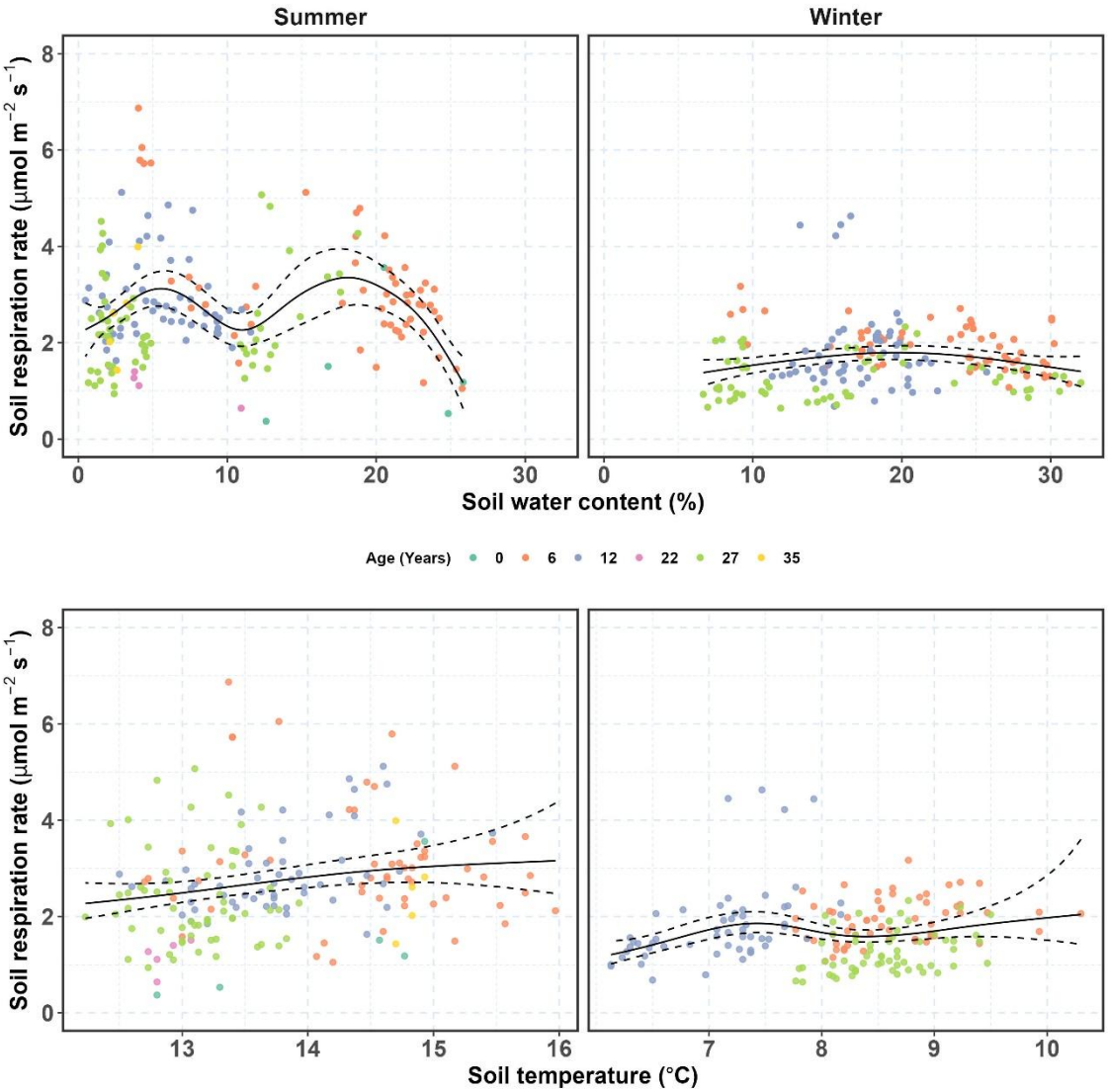


Figure 15. Generalised additive model (GAM) plot showing the effects of soil water content and soil temperature on soil respiration rates at my study sites during summer and winter. Each point represents one R_s measurement and colours correspond to stand ages. The smoothed regression lines are drawn from GAM predictions. The areas between dashed lines represent 95% confidence intervals.

4.4. Discussion

4.4.1. Limitations

The findings discussed in this chapter should be interpreted considering various limitations that are common to field-based R_s studies (Sumpter et al., 2023). These limitations mainly relate to the representativeness of the site, the timing and duration of sampling, the characterization of the site, and the ability to disentangle the interacting environmental drivers.

The sampled locations may not have fully represented the wider variety of *Pinus radiata* plantation conditions in New Zealand. All study sites were located within Kaingaroa Forest in the central North Island, which reduced variability in regional climate but also restricted spatial generalisability. Differences in soil type, management history, and climatic conditions in other plantation regions may result in differing R_s and microbial responses.

The timing of sampling may not have fully represented the longer-term R_s dynamics. Measurements of R_s were taken on a limited number of days during summer and winter, instead of being conducted continuously or throughout complete seasonal cycles. Consequently, the differences observed among stand ages may be influenced by short-term weather conditions at the time of measurement, rather than solely by the effects of stand age. In this regard, stand age should be viewed as a proxy for a group of co-varying biotic and structural attributes (e.g. canopy development, root distribution, and litter inputs), rather than as a singular causal driver.

The sampling programme lacked sufficient duration to capture natural temporal variability in R_s and microbial dynamics. Soil respiration is highly responsive to short-term changes in soil temperature and moisture, and microbial communities can also exhibit seasonal and event-driven variability. The restricted temporal coverage constrained the ability to characterise intra-annual variability or to evaluate R_s responses to environmental drivers.

Soil physicochemical properties were not completely characterised at the study sites. Key soil characteristics, such as soil carbon stock, bulk density, porosity, and nutrient availability were missing or not directly measured at each site. Instead, these characteristics were obtained from regional soil databases and used for contextual comparison rather than site-specific inference. Although these data provided useful background information, they did not capture fine-scale heterogeneity within and among stands, which limited the mechanistic interpretation of R_s patterns.

Other potentially important factors were not specifically quantified. Stand age-related patterns in R_s can be affected by interacting factors such as understory vegetation, the distribution of root biomass, litter inputs, and management practices, which were not measured in this study. As a

result, relationships between R_s, stand age, and microbial variables should be viewed as correlative rather than causal.

The information on microbial communities was limited in both spatial and temporal scope. The composition of microbial communities was evaluated for a subset of stand ages and was not temporally aligned with all R_s measurements. Considering that microbial communities respond actively to environmental conditions, the microbial data presented here represented relative differences among stands rather than comprehensive microbial influences on R_s.

These limitations revealed the challenges of isolating specific drivers influencing R_s under field conditions. Although this study provides insights into patterns of R_s and microbial diversity across different stand ages of *Pinus radiata* plantations, the results should be viewed as indicative of associations observed under operational forestry conditions, where experimental control is inherently limited. Future studies that include extended measurement periods, direct characterization of soil properties, and temporally aligned microbial sampling would provide a more thorough evaluation of the mechanisms driving R_s dynamics in plantation forests.

4.4.2. Comparison of R_s to global and New Zealand Forest studies

Mean R_s reported in the present study generally matches values reported from other forest studies. For example, my R_s rates lie 3.4 % lower than the values in global temperate forests under similar climate, but 25.4% higher than R_s rates from global evergreen conifer forests under different climatological conditions (Wei et al., 2010). These differences must be viewed with care, as they represent large-scale comparisons instead of direct statistical differences. However, the closer alignment of R_s with research carried out in similar temperature conditions indicates that the climatic context, especially temperature, plays a key role in R_s magnitude in forest ecosystems.

Long-term increases in R_s under climate warming and historical differences in measurement techniques provide important background context. Lei et al. (2021) found that R_s in evergreen forests increased at a yearly rate of 0.05 μmol CO_2 m^{-2} s^{-1} during 2000-2016, while the meta-analysis conducted by Wei et al. (2010) included the studies in early 2000s and before

(dominated by potassium hydroxide-based trapping and gas chromatography approaches), when infrared gas analysers (IRGA) were not widely implemented in R_s measurements.

Mean R_s rate in the present study was close to the R_s in radiata pine stand reported by other studies in New Zealand. For example, the overall mean R_s rate was 3% lower than that reported by Tate et al. (2000). Mean seasonal R_s rates at my sites were 2% to 18% lower than those measured by Scott et al. (2006) in radiata pine forests with different stand densities, likely due to lower soil temperature at my sites.

4.4.3. The effects of stand age on soil respiration

In winter, mean R_s was lower in the older sampled stands compared to younger stands (*Figure 9*). This pattern is based on measurements from three stand ages, each represented by a single stand, and should therefore be interpreted as a site-specific observation rather than a general stand-age trend. Although R_s showed no clear trend with stand age in summer, R_s in the juvenile stands (6- and 12-year-old) was higher than those in the mature stands (22- and 27-year-old). This is probably a result of decreasing R_h with stand age (Pregitzer & Euskirchen, 2004). Saiz et al. (2006) found that a higher decomposition rate in the 10- and 15-year-old stands than those in 31- and 47-year-old stands due to higher microbial biomass in Ireland Sitka spruce forests. Moreover, canopy closure in mature stands might cause decreased light exposure and temperature, adversely affecting soil substrates and microbial activity respectively (Tanaka & Hashimoto, 2006). This is supported by my result that summer soil temperature decreased with stand age. I have not measured fine root biomass but decreasing fine root biomass in the later stages of stand development resulting in a decrease in R_h have previously been reported (Yan et al., 2015). Fewer fine roots imply reduced belowground allocation of labile C from photosynthesis and consequently limited microbial activity (Davidson et al., 2002a; Giardina & Ryan, 2002).

The lack of a clear trend in R_s with stand age in summer came as a surprise (*Figure 9*). Juvenile stands generally emit more soil CO_2 due to extensive fine root biomass and higher metabolic intensity during the early stages of stand development, mostly followed by decreasing R_s with

increasing stand age (Yan et al., 2011). However, at my sites, the coarse-textured pumice soils have limited soil C reserves and high macro-porosity, leading to rapid decomposition of post-harvest residue and thus limiting soil C availability further (Hewitt et al., 2021c). While soil C data do not resolve plot-scale or labile carbon availability, they suggest that constrained soil carbon supply may have contributed to limiting R_s during the early stages of stand development. Previous studies have shown that soil carbon pools in plantation forests often increase with stand development due to litter accumulation but may stabilise in coarse-textured soils where leaching and limited mineral protection constrain long-term carbon retention (Dłużewski et al., 2024; Xu et al., 2024). In the present study, these processes were not directly measured and are therefore discussed as potential mechanisms rather than demonstrated drivers of the observed R_s patterns.

4.4.4. The relationships between soil microorganisms and soil respiration

Soil bacterial community

As hypothesized, microbial community shifts among stand ages (*Figure 12, Figure 13*). The relative abundance of Acidobacteriota phylum generally increased with the stand age, while that of Proteobacteria and Actinobacteriota phyla decreased. The Acidobacteriota phylum is often associated with complex carbohydrate degradation and nitrogen fixation, thus likely promotes plant growth and soil respiration (Kalam et al., 2020). Within this phylum, the Acidobacteriaceae family was found to favour unsaturated, low nutrient/carbon, acidic soils such as pumice, enhancing the above functions (Campbell, 2014; Hansel et al., 2008; Kielak et al., 2016). The decreasing relative abundance of Proteobacteria was primarily due to a reduced abundance of the Burkholderiaceae family, specifically the genus of Burkholderia, and Caballeronia at my sites, which include many known plant pathogens, while the Xanthobacteraceae family associated with nitrogen fixation and autotrophic plant growth, increased in proportion (Kersters et al., 2006).

Bacterial species richness showed a decreasing trend with stand age (*Figure 13*). This pattern is consistent with previous findings that copiotrophic bacteria decline under nitrogen-limited

conditions (Li et al., 2021). Although soil nitrogen availability was not directly measured in this study, the observed reduction in copiotrophic taxa such as Proteobacteria with stand age suggests a shift toward more nutrient-limited microbial communities. As stand age increases, soil N can decline through plant and fungal uptake, leaching, and mineralisation (Kirschbaum et al., 2008). This soil N reduction can adversely affect the survival and growth of bacteria, worsened by uptake-induced fungal growth and subsequential nutrient competition (Bai et al., 2021; Kirschbaum et al., 2008). Previous study has shown that declining soil nitrogen availability can be associated with an increase in substrate C:N ratios, resulting in lower-quality organic inputs that are decomposed less efficiently by bacteria (Wang et al., 2021). While substrate quality was not directly measured in this study, such mechanisms provide a plausible explanation for the observed decline in bacterial richness with stand age.

Soil fungal community

The relative abundance of Basidiomycota decreased with stand age, while that of Ascomycota increased with stand age (*Figure 12*). The decreasing Basidiomycota trend was inconsistent with the finding of Wan et al. (2021). Previous study suggested that declining soil nitrogen availability with stand development can constrain Basidiomycota-mediated lignin decomposition and reduce carbon-nutrient exchange with host plants (Smith & Read, 2008). In the phylum Basidiomycota, Cantharellales *incertae sedis* decreased due to SWC decreased, which negatively affected the decomposition by mycelium (Floudas, 2021), while Thelephoraceae increased due to their brown or dark hypha as mechanisms to tolerate soil drying (De Miguel et al., 2016)

The increasing Ascomycota trend could be associated with accumulated litter input, as they specialise in decomposing cellulose and hemicellulose (Hannula et al., 2012; Manici et al., 2024). Species belonging to the Ascomycota phylum can also contain darkly pigmented hyphal walls, known as dark septate endophytes (DSE) (Poteri et al., 2021). The functions of DSE included stimulated plant nutrient use and inhibitory effect against plant pathogens (Alberton et al., 2010; Terhonen et al., 2016). Alberton et al. (2010) found that DSE fungi led to double or triple belowground respiration along with 17% plant biomass increase in Scot pine seedlings.

Therefore, the increase Ascomycota might result in R_s increase at an early stage of stand development.

Fungal richness increased with stand age at my sites (*Figure 13*). This is in line with the general trend of juvenile stands being initially mainly colonised by opportunistic fungi with a subsequent increase in fungal species richness (Genevieve et al., 2019). Increasing plant productivity has been shown to support high fungal richness in mature stands, especially ectomycorrhizal fungi, which may stimulate R_s (Hiiesalu et al., 2017). Moreover, decreasing soil N and an increasing soil C:N ratio restrict plant productivity and belowground C allocation, which might favour the generally oligotrophic ascomycetous fungi.

4.4.5. The effects of soil water content and temperature on soil respiration

Contrary to our hypothesis, soil moisture explained the most seasonal R_s variation, followed by soil temperature (*Figure 15*). In summer, the bimodal relationship between R_s and SWC likely reflects the combined influence of stand age, spatial heterogeneity in SWC, and site-specific soil characteristics (e.g. soil carbon availability and physical structure) that were not explicitly quantified at the plot scale. Age 6 stands contributed to the peaks at around 5% and 18% SWC, exhibiting high R_s rates, possibly reflecting the increased fine root biomass under sufficient soil water conditions (Claus & George, 2011), although fine-root biomass was not measured in this study. Conversely, age 27 stands contributed to the dip at around 11% SWC. These stands were characterised by their wide SWC range and perhaps showed a lower sensitivity of R_s to SWC changes compared the younger stands. The decreasing R_s trend beyond 20% SWC during summer was likely associated with reduced soil aeration and oxygen diffusion rather than absolute volumetric thresholds. Because soil porosity varies among sites and soil types, volumetric SWC values cannot be directly translated into moisture stress without information on water-filled pore space (WFPS), which was not quantified in this study. In winter, slow stand development may be largely responsible for the weak R_s-SWC trend (Harsch et al., 2014).

Rates of R_s increased with soil temperature in summer. This relationship is consistent with temperature-driven increases in substrate availability associated with higher net biomass

production in temperature-limited systems (Caprez et al., 2012; Liu et al., 2006). Temperature-induced increases in soil enzyme activity generally enhance R_s rates (Song et al., 2014; Zhang et al., 2023c). Moreover, the decomposition rate of SOM and microbial metabolism commonly increases with temperature, thus stimulating R_s (Davidson & Janssens, 2006). Soil respiration rates in winter showed no significant change with temperature. This is most likely due to a winter-related downregulation of tree physiological activity and temperature-driven reductions in soil enzymatic activity. The composition of the soil enzyme pool is determined by the soil microbial community, which can be affected by temperature changes (Bradford, 2013; French et al., 2009).

4.5. Conclusion

The current investigation provides new insights into soil microbiome dynamics in New Zealand *Pinus radiata* stands, and their implications for soil C cycling in relation to plant characteristics and environmental factors. Seasonal R_s was best explained by soil moisture, with a non-linear R_s-age trend in summer and an R_s decline with stand age in winter. I observed a decrease in bacterial richness and an increase in fungal richness as stands aged, reflecting plausible shifts in the soil nutrient environment and the opportunistic fungal development. These changes, along with the increase in Acidobacteriota and Xanthobacteraceae, enhance complex carbohydrate degradation and nitrogen fixation, promoting plant growth and soil respiration. My findings contribute to the understanding of the relationship between stand age and changes in soil microbial community composition in *Pinus radiata* plantations. It also suggests that these microbial alterations were more readily observable than the differences in R_s related to stand age under the conditions sampled.

Chapter 5. No elevated soil respiration in recently planted tropical plantation forests compared to adjacent native forests

5.1. Introduction

Soil respiration (R_s) serves as the major pathway for the CO_2 release from soil to atmosphere (Xu & Shang, 2016). This process primarily comprises belowground autotrophic respiration (root metabolism, R_a) and heterotrophic respiration (microbial decomposition of organic matter, R_h) (Subke et al., 2006). Globally, soil respiration represents the second-largest terrestrial C flux after gross photosynthesis, releasing approximately 90 Gt C annually (Bond-Lamberty & Thomson, 2010b; Hashimoto et al., 2015). Tropical forest ecosystems play a crucial role in global C cycling due to their large C storage and high C turnover. These forests store 25% of global terrestrial C with nearly 50% in soils and show the highest net primary productivity (NPP) per year among all biomes due to year-round favorable growing period and climatic conditions (Pan et al., 2011). Optimal temperatures, high moisture availability, and high biodiversity in tropical forests promote high NPP-induced belowground allocation, stimulating microbial and root activity and contributing to 40 Gt C per year through soil respiration (Nottingham et al., 2022; Poorter et al., 2015; Zimmermann et al., 2009).

The clearing of tropical forests acts as a C source but is partly compensated by the C sink of the remaining intact forests, making a near-neutral contribution to the global C budget (Baccini et al., 2017; Liu et al., 2015). However, with increasing deforestation, tropical forests may quickly turn from a balanced C budget to a net contributor of atmospheric CO_2, particularly with rising temperature and decreasing moisture availability over the coming decades (Hubau et al., 2020; Mitchard, 2018). Apart from the removal of aboveground biomass, tropical deforestation reduces transpiration and thereby weaken moisture transport from ocean, contributing to regional warming and drying (Davin & de Noblet-Ducoudre, 2010). This deforestation-induced increase in air temperature may suppress photosynthesis and enhance autotrophic respiration in the remaining tropical forests, reducing NPP and aboveground biomass (Doughty & Goulden, 2008; Sullivan et al., 2020). Additionally, deforestation-induced fragmentation and edge effects

in tropical forests lead to further C loss due to microclimate changes in wind turbulence, increased fire risk, and higher tree mortality rates (Li et al., 2022). Although new trees at the forest edges exhibit adaptability, a post-fragmentation C equilibrium can be reached within 6 to 15 years after deforestation, but with lower canopy height, basal area, and aboveground biomass compared to adjacent intact areas. (Silva et al., 2020).

Establishing plantations can remediate soil CO_2 emissions by enhancing C sequestration in areas where primary forests have already been cleared, as these fast-growing species rapidly convert photosynthetic C to plant biomass (Kongsager et al., 2013). However, the net C balance is uncertain as decomposing root systems and debris at deforested sites obviously constitute a C source. Therefore, understanding soil respiration dynamics during the transition from native forests to plantation forests, which represents an adverse land-use change associated with ecological degradation and carbon losses, is critical for evaluating how altered soil C processes influence the net C balance.

While deforestation and plantation establishment affect the functional properties of tropical forest ecosystems in C cycling, abiotic and biotic factors influence the trend and feedback of C cycling. Soil temperature (T_s) can have indirect effects on R_s through its influence on soil moisture, aboveground litter production, and photosynthetic activity in tropical forests as well as plantations. While R_s often shows positive linear or exponential relationship with T_s in temperate and boreal regions, the lack of seasonal temperature variation in tropical forests show little temperature governance over R_s (Kosugi et al., 2007; Wood et al., 2013a). Temperature-induced soil water deficits, however, can adversely affect microbial activity, thus limiting the R_s and its responses to temperature (Li et al., 2024). High aboveground litter production and decomposition in tropical forests positively correlates with T_s, providing nutrients (N and P) and supporting belowground microbial activity and plant growth (Krishna & Mohan, 2017; Sayer et al., 2007; Zhao et al., 2022). Additionally, most CO_2 emissions from decomposition in tropical forests originate from short-lived SOM and C fixed less than one year ago (Riutta et al., 2021). This shows the rapid turnover of photosynthetic C in tropical forests and suggests a strong

correlation between temperature-induced photosynthetic activity and soil respiration (Zhou et al., 2013b).

Soil moisture directly affects both R_a and R_h through root and soil microbial activity and indirectly affects them by C and N availability. Generally, soil moisture suppresses R_s by limiting decomposition under moisture deficiency and restricting oxygen availability under saturation, while moisture levels near field capacity are optimal for microbial metabolism, resulting in a peak in soil CO_2 emissions (Suseela et al., 2012). In dry tropical forests, reduced moisture can suppress R_a more than R_h due to root biomass limitations (Huang et al., 2018). In humid tropical forests, the direction of soil respiration responses to precipitation depends on baseline moisture conditions. Moderate precipitation reductions can stimulate heterotrophic respiration by relieving oxygen limitation (Cleveland et al., 2010; Waring & Hawkes, 2015; Wood et al., 2013b), whereas increased precipitation can promote soil respiration by enhancing substrate and nutrient availability under non-saturated conditions (Guo et al., 2024). In tropical forests, soil P rather than N availability often limits soil microbial activity, and thereby SOM decomposition (Mori et al., 2018). Litterfall P, along with litterfall C, can alleviate soil P shortage and improve soil C availability through water infiltration and increased rainfall frequency, stimulating R_s (Deng et al., 2018).

Tree species determine litterfall availability and decomposability, fine root production, and microclimates, thus affecting root activity and microbial decomposition. Differences in litter chemistry among tree species affect substrate quality for decomposition and substrates with low C:P ratios result in higher R_s (Wieder et al., 2008). High fine root production facilitates labile substrates via root exudation, thus promoting R_s (Valverde-Barrantes, 2007). Tree species can alter the microclimate through variations in canopy cover and root structure. For example, species with dense crowns reduce soil temperature and increase soil moisture by limiting evaporation, affecting R_s (Ontong et al., 2023). Deep-rooted species can access water unavailable to co-existing plants, influencing plant productivity and soil C stocks (Stahl et al., 2013).

The rapid C turnover in tropical forests and the significant potential for C sequestration in tropical plantations underscore the importance of understanding soil respiration dynamics and the factors that influence them. In this study, I conducted a field-based investigation of soil respiration across tropical moist plantations to compare them with tropical native forests under similar climatic conditions. My objective was to examine whether R_s differed following the transition from native forests to plantation forests. I also examined variation in R_s across tropical forests in relation to soil temperature, soil moisture, tree species, elevational gradients, and stand age. I hypothesise that (i) soil respiration in tropical plantation forests is higher than that in native forests; (ii) variation in soil respiration is more strongly associated with soil moisture than with soil temperature; and (iii) soil respiration rates vary significantly among tree species.

5.2. Materials and Methods

5.2.1. Study sites

The study area was located in the southwest of Kolombangara Island, Solomon Islands (8°03'35"S, 156°58'06"E; *Figure 16*). The study period ranged from December 2022 to January 2023. The region experiences a warm, year-round tropical climate. Based on long-term monthly climatological data, mean surface air temperatures at the study site vary only modestly throughout the year, ranging from approximately 25.2 °C in the coolest months (July-August) to 26.4 °C in the warmest months (January), with corresponding monthly minimum and maximum temperatures ranging from ~21.5-22.6 °C and ~28.9-30.4 °C, respectively (Harris et al., 2020). Long-term monthly precipitation data indicate a clear seasonal pattern, with higher rainfall during the wet season (November-April) and reduced rainfall during the drier months (May-October), resulting in an annual precipitation total of approximately 3000 mm (Harris et al., 2020). Study sites spanned a low-elevation gradient from sea level to approximately 120 m ASL. The typic haplorthox soils in the area were low in pH (<5.0) and high in organic compounds (Wairiu & Lal, 2003). Intensive logging removed 90% of the primary rainforest and subsequent leaching and erosion led to the increased concentration of aluminium and iron oxide in the soils (Katovai et al., 2012). Plantation tree species in the study area mainly include Eucalyptus (*Eucalyptus deglupta* Blume), Teak (*Tectona grandis* L.f.), and Mangium (*Acacia*

mangium Willd). Native tree species include Pacific Maple (*Aglaia cucullata* (Roxb.) Pellegr.), Brown Terminalia (*Terminalia brassii* Exell.) and Pink Birch (*Schizomeria serrata* Hochr.). Various understory plant species are present such as *Alsophila crassicaula* Holttum. and *Areca novohibernica* (Lauterb.) Becc. The grass species is Kangaroo Grass (*Themeda australis* (R.Br.) Stapf.).

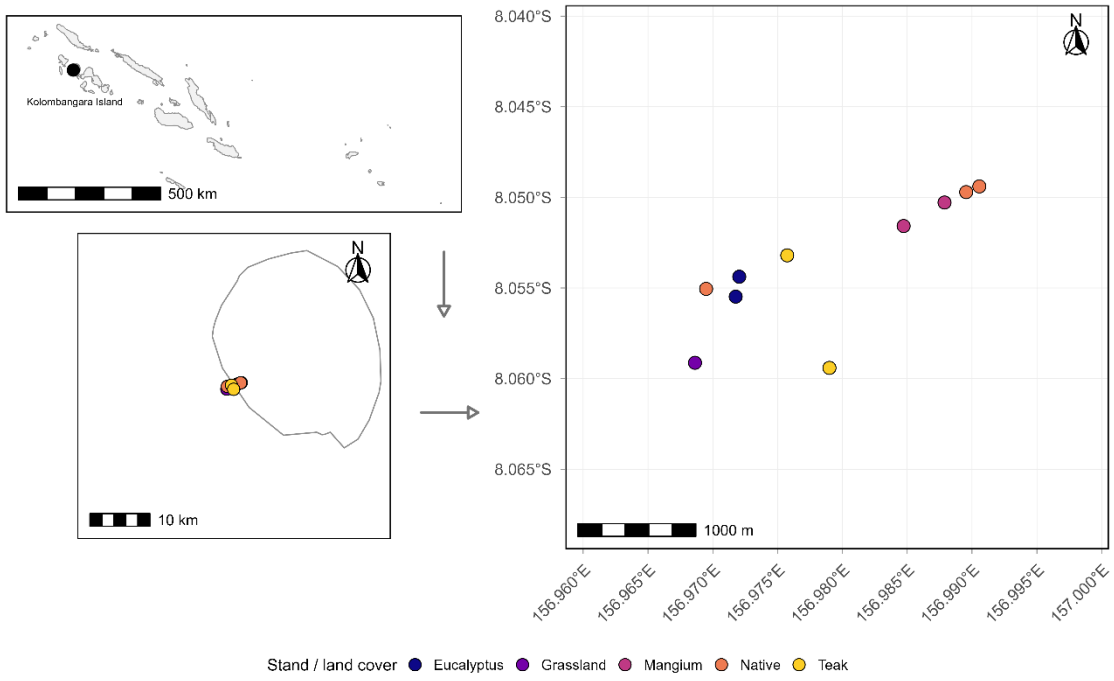


Figure 16. Location of study sites on Kolombangara Island, Solomon Islands. The regional inset (top left) shows the position of Kolombangara within the Solomon Islands; the island-scale panel (bottom left) provides geographic context; and the main panel (right) shows the spatial distribution of individual sampling sites. Points indicate site locations and are coloured by stand/land-cover type (Eucalyptus, grassland, mangium, native forest, and teak).

5.2.2. Experiment design

A total of 80 measuring points were distributed across 26 plots in 10 study sites (*Figure 16*), which included Eucalyptus plantations (2 sites, 10-20 vs. 20-30 years old), Teak plantations (2 sites, 20-30 years old), Mangium plantations (2 sites, more than 50 years old), native mixed forest (3 sites, more than 50 years old) and grassland (1 site, unknown age). At each site, three plots were randomly selected and each contained three measuring points. Exceptions were the grassland site and one of the native mixed forest sites, where a single plot with four measuring points was established.

At each measuring point, data collection included a single soil respiration measurement, along with three replicates each for soil temperature and soil water content. A 4-day rotation schedule was implemented to cover Eucalyptus, Teak, Mangium and two remote native mixed forests, with two sites measured per day. This rotation was repeated three times during the study period, while the grassland site and the remaining native mixed forest were measured periodically, three to four times throughout the study.

5.2.3. Soil respiration measurement

Soil respiration was measured using the closed static chamber method, following the design by Bader & Körner (2010) and the measuring procedure by Liu et al. (2024b). Chamber (19.0 × 29.4 cm, 8.34 L; Gschwend Kunststoff AG, Basel, Switzerland) was equipped with a CO_2 probe (GMP343, Vaisala, Finland), a temperature/humidity probe (HMP75B, Vaisala, Finland), and a handhold data logger (MI70, Vaisala, Finland). It was also fitted with a sealable vent to minimize pressure fluctuations. Aboveground biomass was trimmed 24 hours before measurements, and polyethylene collars (7.0 cm in height) were inserted 2-3 cm into the soil to reduce wound respiration from plant roots. CO_2 concentrations were recorded at 5-second intervals for 5 minutes with the first minute excluded to minimize disturbances. Soil temperature at a 10 cm depth was measured using a Pocket Digital Thermometer (FOOD FM10, DigiMate, Digitron, UK), while soil moisture was assessed using a handheld TDR sensor (HydroSense II, HS2, Campbell Scientific, USA) at 0-12 cm depth. Both parameters were measured within a 30 cm radius outside the chamber.

5.2.4. Statistical analysis

Soil respiration data were checked for normality using the Shapiro-Wilk test. The differences among measurements were tested for significance using one-way analysis of variance (ANOVA) and Kruskal-Wallis tests between continuous variables (i.e., R_s, T_s, and SWC) and categorical variables (tree species, stand age group, and elevation). Once significance was detected, post-hoc tests were performed to evaluate pairwise group differences.

A generalized additive modelling (GAM) approach was used to explore the non-linear R_s relationship with soil temperature and soil water content. Multiple generalised linear mixed models (GLMM) were formed to determine which variables best explained R_s. Fixed effects included T_s, SWC, while random effects were tree species, stand age group, elevational level, site, and plot. A backward selection approach guided by Akaike's information (AIC) was used to identify the best-fitting model. The final model incorporated an interaction between SWC and tree species, with study plot as a random effect, as indicated by the lowest AIC value. A gamma distribution with log-link function was applied to further reduce the residual variation.

5.3. Results

5.3.1. Soil respiration rates

Soil respiration (R_s) rates ranged from 0.78 to 10.98 μmol CO_2 m^{-2} s^{-1} with a mean and standard error of 4.53 ± 0.10 μmol CO_2 m^{-2} s^{-1} across forest types. Land use type affected R_s significantly ($F_{4, 292}$ = 54.65, P < 0.001, *Figure 17*). Mean R_s in grassland was significantly higher than that in any forest stand (post-hoc tests, all P < 0.001), while R_s showed no significant difference among tree species (post-hoc tests, all P > 0.1). Stand age affected R_s significantly ($F_{2, 254}$ = 5.52, P = 0.004). Mean R_s in 20-30 year-old forests was significantly higher than those in 10-20 year-old and more than 50 year-old stands (post-hoc tests, both P = 0.01).

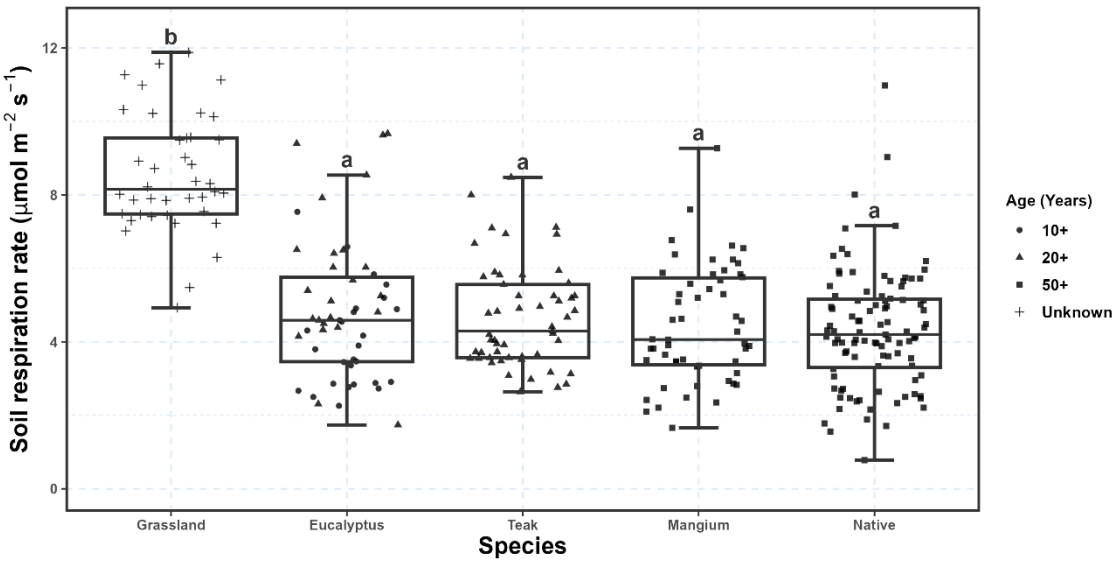


Figure 17. Soil respiration rates (µmol CO_2 m^{-2} s^{-1}) across different land cover types: grassland (n = 40), Eucalyptus (n = 51), Teak (n = 53), Mangium (n = 54), and native mixed forests (n = 99). Symbols represent data points categorised by age: 10+ years (●), 20+ years (▲), 50+ years (■), and unknown age (+). Different letters (a and b) above the boxplots indicate statistically significant differences between groups (p < 0.05, post-hoc tests with Tukey's contrasts).

5.3.2. Microclimate and soil information

Soil water content (SWC) was significantly different among land use types ($F_{4, 292}$ = 144.33, P < 0.001, *Figure 18*). Mean SWC in grassland was significantly higher than that in any forest stand (post-hoc tests, all P < 0.001). Among tree species, mean SWC in Mangium and native forests was significantly higher than in Eucalyptus and Teak (post-hoc tests, all P < 0.01), and mean SWC in Teak was significantly higher than in Eucalyptus (Post-hoc test, P < 0.001).

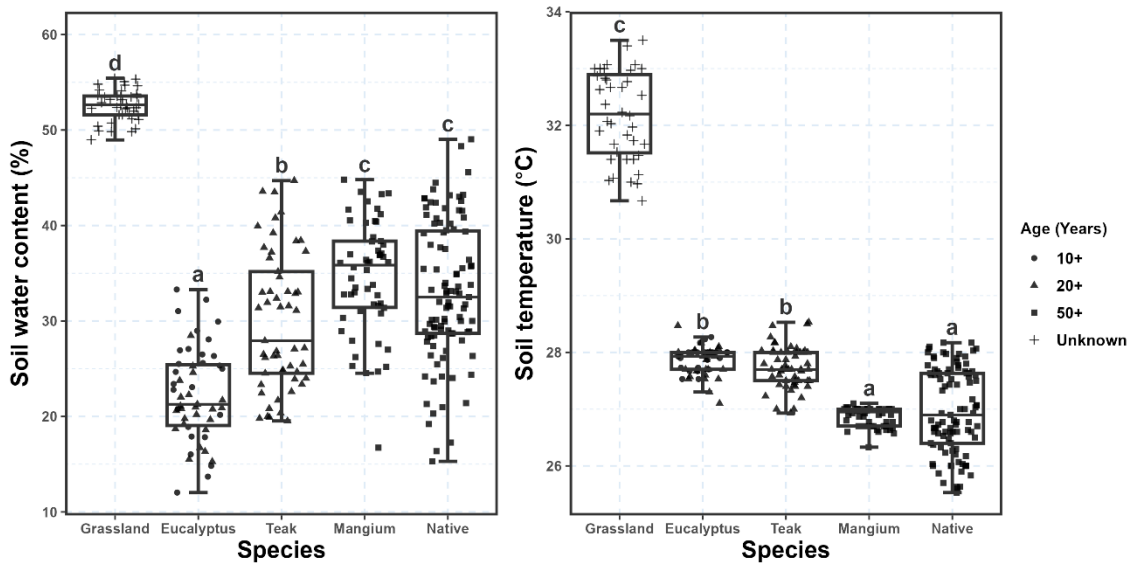


Figure 18. Soil water content (%, left panel) and soil temperature (°C, right panel) across different land cover types: grassland, Eucalyptus, Teak, Mangium, and native mixed forests. Data points are categorised by age: 10+ years (●), 20+ years (▲), 50+ years (■), and unknown age (+). Different letters above boxplots (a, b, c, and d) indicate statistically significant differences between groups (p < 0.05, post-hoc tests with Tukey's contrasts).

Soil water content varied significantly with elevation ($F_{8, 248}$ = 25.64, P < 0.001). Mean SWC were significantly higher at elevations above or equal to 70 metres above sea level (ASL) compared to lower elevations (post-hoc tests, all P < 0.05). Below 70m ASL, mean SWC at 20m ASL was significantly greater than those at 30, 50 and 60m ASL (Post hoc tests, all P < 0.05).

Overall, SWC showed a significant positive correlation with elevation (Adjusted $R^2 = 0.23$, slope = 0.09, $F_{1, 255} = 78.80$, $P < 0.001$).

Soil water content varied significantly with stand age ($F_{3, 254} = 37.50$, $P < 0.001$). Mean SWC in more than 50 year-old stands was significantly higher than those in 10-20 year-old and 20-30 year-old stands (post-hoc tests, both $P < 0.001$), and mean SWC in 20-30 year-old stand was significantly higher than that in 10-20 year-old stand (post-hoc test, $P = 0.03$).

Soil temperatures (T_s) were significantly different among land use types ($F_{4, 292} = 712.96$, $P < 0.001$; *Figure 18*). Mean T_s in grassland was significantly higher than that in any forested sites (post-hoc tests, $P < 0.001$). Among tree species, mean T_s in Eucalyptus and Teak were significantly higher than those in Mangium and native forests (post-hoc tests, $P < 0.001$).

Soil temperature varied significantly among elevation ($F_{8, 248} = 95.53$, $P < 0.001$). Mean T_s were significantly higher at elevations below 70m ASL (post-hoc tests, all $P < 0.001$). Above 70m ASL, mean T_s at 120m was significantly lower than those at 70, 80, 100, 110m (post-hoc tests, $P < 0.001$). Overall, T_s showed a significant negative correlation with elevation (Adjusted $R^2 = 0.68$, slope = -0.01, $F_{1, 255} = 541.9$, $P < 0.001$).

Soil temperature varied significantly with stand age ($F_{2, 254} = 89.27$, $P < 0.001$). Mean T_s in more than 50 year-old stands was significantly lower than those in 10-20 year-old and 20-30 year-old stands (post-hoc tests, both $P < 0.001$).

5.3.3. The R_s dependence on soil temperature and moisture

Overall, soil respiration was slightly sensitive to soil moisture but remain largely unchanged to soil temperature. The relationship between R_s and SWC followed a non-linear pattern (GAM, adjusted $R^2 = 4.4\%$, $P_{\text{smooth term}} < 0.05$; *Figure 19*). Soil respiration rate decreased until ca. 30% SWC, remained unchanged between 30 to 40% SWC, and then decreased again beyond 40% SWC. The R_s-T_s relationship was marginally significant and R_s remained unchanged until 27.5 °C, after which it slightly increased (GAM, adjusted $R^2 = 3.2\%$, $P_{\text{smooth term}} = 0.05$; *Figure 19*).

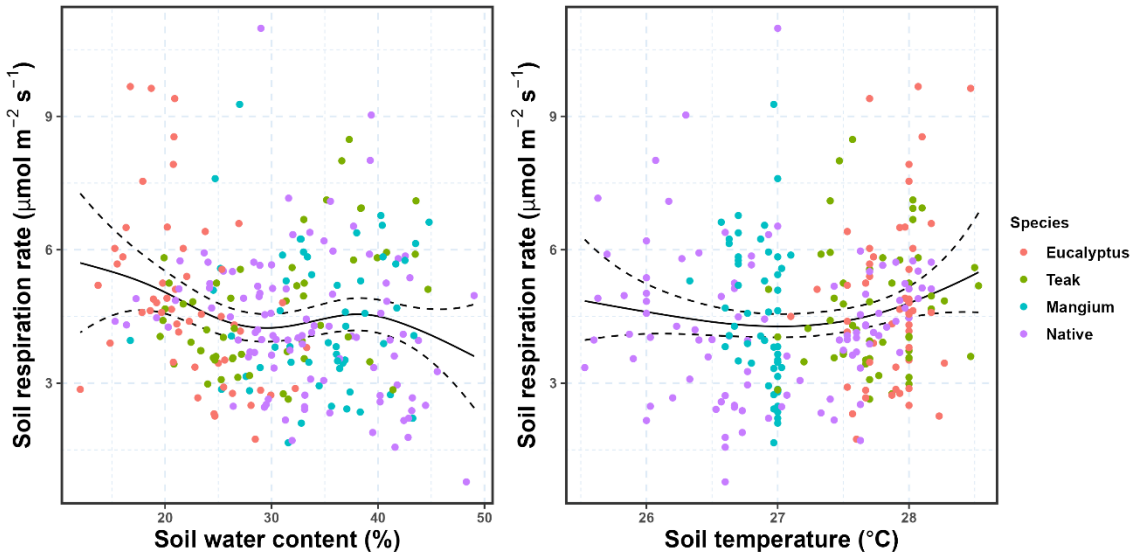


Figure 19. Relationship between soil respiration rate (μmol CO_2 m^{-2} s^{-1}) and soil water content (%, left panel) and soil temperature (°C, right panel) across four land cover types: Eucalyptus (red), Teak (green), Mangium (blue), and native mixed forests (purple). Coloured points represent individual measurements. The solid black lines indicate the best-fit curves for the overall relationship. Dashed lines represent 95% confidence intervals.

The optimised GLMM explained 26% of R_s variance, where the interaction between SWC and tree species accounted for 13% of R_s variance and the plot (random effect) explained the rest. The SWC-species interaction significantly affected R_s (GLMM, Chisq = 19.36, df = 3, P < 0.001; *Figure 20*). Soil respiration strongly decreased within 10-30% SWC in Eucalyptus and moderately decreased within 15-50% SWC in native forests, while R_s moderately increased in Teak and slightly increased in Mangium within 15-45% SWC.

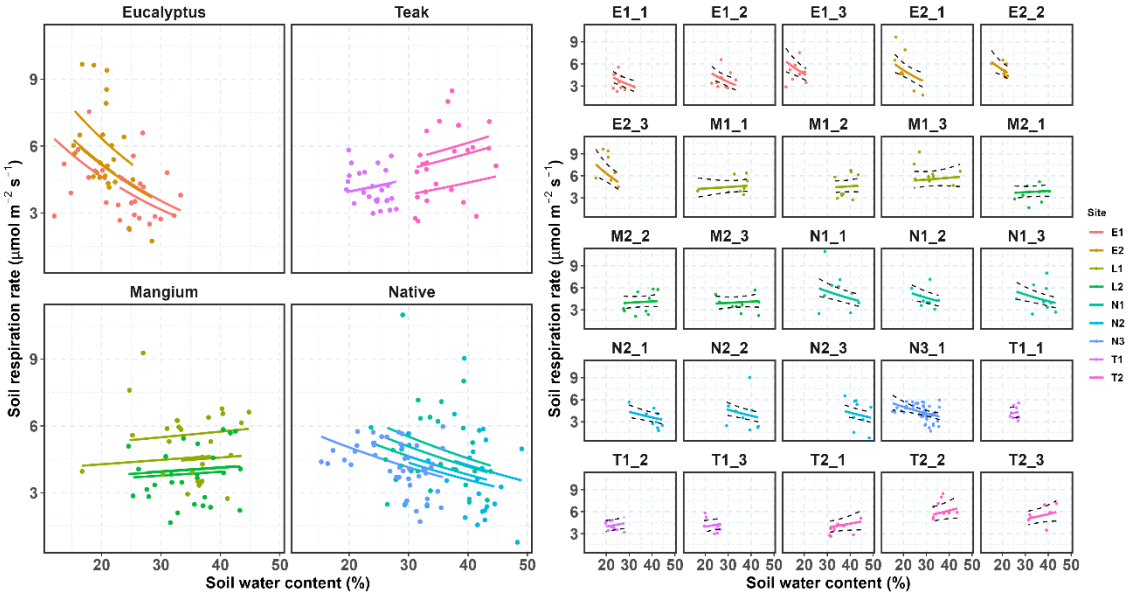


Figure 20. Relationship between soil respiration rate (µmol CO_2 m^{-2} s^{-1}) and soil water content (%) across different species (left panel) and individual study plots (right panel). The left panel depicts species-level trends for Eucalyptus, Teak, Mangium, and native mixed forests. The right panel presents plot-specific relationships, with site-specific trends color-coded. Plot labels follow the pattern of 'Species Site number – Plot number'. For example, 'E1-2' means Plot 2 at Site 1 in Eucalyptus plantations. 'E' stands for Eucalyptus, 'T' for Teak, 'M for Mangium', and 'N' for native mixed forests. Solid lines indicate the best-fit regression for each species or site, while dashed lines represent 95% confidence intervals.

5.4. Discussion

5.4.1. Limitations

The main limitation of this study arises from the spatial structure of the tropical study site, which restricted the ability to separate the effects of vegetation effects on R_s. Unlike the temperate plantation study presented in Chapter 4, where primary limitations were due to temporal and abiotic co-variation, the key constraint here was landscape-level confounding that is intrinsic to the field environment (Sumpter et al., 2023).

Plantation and native forests were spread across an elevation and distance-from-coast gradient on Kolombangara Island. This spatial distribution likely created systematic variations in soil temperature, soil moisture, drainage conditions, and microclimate that could not be

experimentally controlled. Consequently, differences in soil respiration observed among forest types may reflect landscape position as much as, or more than, the characteristics of vegetation.

In this context, tree species should be considered as an integrated indicator that includes co-varying environmental and structural attributes rather than as an independent experimental variable. Since species were not replicated across similar elevations and soil moisture conditions, The effects of vegetation were partially inseparable from microclimatic and hydrological differences among landscape positions. Comparisons between plantation species and between plantation and native forests reflect spatial associations rather than providing direct evidence of species-driven effects on soil respiration.

The interpretation was further constrained by limited site characterisation. Soil physicochemical and hydrological properties, including soil carbon stock, texture, bulk density, porosity, and indicators of soil water repellency, were not measured. This hinders the ability to mechanistically explain contrasting soil moisture-respiration relationships, which requires that proposed explanations are worked as hypotheses consistent with observed patterns rather than confirmed mechanisms.

Measurements were taken during a single season field campaign, which recorded soil respiration responses under existing conditions but did not include seasonal variability. In tropical environments, where soil respiration responds strongly to rainfall-driven wet-dry cycles, this temporal constraint interacts with spatial heterogeneity to further limit inference.

The biotic factors such as root biomass distribution, litter inputs, and soil microbial community composition were not measured. These factors may vary with both vegetation type and landscape position and could contribute to observed soil respiration patterns apart from the measured abiotic variables.

The findings of this chapter should be viewed as describing spatially structured patterns of soil respiration across a diverse tropical landscape, rather than merely focusing on the effects of vegetation or specific species. Therefore, the lack of statistically significant differences between

mature native forests and plantation stands should not be considered as proof of functional equivalence in belowground carbon processes. Instead, it reflects a pattern under the spatial and measurement constraints of this study. To accurately attribute soil respiration differences to forest conversion or plantation species, experimental designs should control for elevation and hydrological gradient, such as replicated sites across landscape positions, together with direct soil measurements and extended temporal coverage.

5.4.2. Compare our soil respiration rate to those in other studies

The mean R_s of 4.5 μmol CO_2 m^{-2} s^{-1} at our study sites aligns closely with the values reported in both global and local studies. Grace et al. (2014) conducted a meta-analysis of carbon budgets in tropical ecosystems and estimated a mean annual soil respiration rate in the range of 3 and 6 μmol CO_2 m^{-2} s^{-1} in global tropical forests (Luyssaert et al., 2007; Oertel et al., 2016b). A recent study by McFarlane et al. (2024) performed experimental warming and drying in Panama tropical forests and soil respiration in the control plots ranged from 3.8 to 7.8 μmol CO_2 m^{-2} s^{-1}. Similarly, Bae et al. (2013) and Pacaldo & Aydin (2023) reported soil respiration rates from 4.8 to 5.8 μmol CO_2 m^{-2} s^{-1} in Philippines tropical forests. These consistent R_s values across studies likely result from little temperature variation, sufficient moisture and sustained inputs of labile C substrates derived from continuous litterfall and root turnover in tropical moist forests. On the contrary, Lima et al. (2023) investigated soil respiration rates in the semiarid Brazilian tropical forests. They reported a much lower mean R_s of 2.4 μmol CO_2 m^{-2} s^{-1} and found that soil moisture positively controlled R_s.

5.4.3. No significant difference in soil respiration between native and plantation forests

In contrast to my hypothesis, soil respiration rates showed no significant difference among forest types under the sampled conditions. This may reflect the co-varying influence of environmental factors (e.g., soil temperature and moisture), while other unmeasured factors such as rapid root decomposition prior to R_s measurements, and similar litter quantity remain possible but untested explanations (Huang et al., 2014).

Tropical forests generally experience high and stable temperatures with abundant rainfall. At my study sites, mean soil temperature exceeded 26°C and soil water content remained above 20% across native and plantation forests. Eucalyptus and Teak showed high temperatures and low soil water content, while Mangium and native forests displayed low temperatures and high soil water content. These optimal and complementary conditions may have contributed to the observed similarity in R_s across native and plantation forests, making species-related differences more difficult to distinguish within this dataset. For example, Bréchet et al. (2009) investigated the influence of tree species on soil respiration in tropical forests and found no significant spatial and seasonal R_s relationship with tree species-specific characteristics such as root biomass. Similarly, Murphy et al. (2008) reported that R_s variations in tropical forests were more strongly driven by canopy-induced changes in soil microclimate (e.g., temperature and moisture) than by tree species or root biomass, suggesting a limited effect of tree species on R_s in tropical forests.

Additionally, residual root decomposition following forest conversion may have declined substantially before the time of measurement, particularly in the older plantation stands (Saha et al., 2023). However, because autotrophic and heterotrophic components of soil respiration were not partitioned, the extent to which decomposing roots influenced the observed fluxes cannot be determined here. These processes should therefore be treated as possible contextual explanations rather than direct inferences from the present data. In tropical regions, fine root biomass ($\leq$ 2 mm diameter) typically decomposes within 3 to 5 years after deforestation, potentially contributing to 40% of soil respiration (Huaraca Huasco et al., 2021; Silver & Miya, 2001), while coarse roots (> 10 mm diameter) require 10 to 25 years or even longer to fully decompose (Anderson et al., 2018; Ohashi et al., 2019). Given that the plantation forests at my study sites ranged from 10 to 50 years old, only a small portion of recalcitrant coarse roots likely remained after years of decomposition, contributing little to R_s due to their slow decay rates. Although these decomposing coarse roots may still have increased R_h, plantation forests generally have smaller root systems compared to native forests, leading to comparatively lower R_a (Cai et al., 2019) and therefore balancing overall R_s. This increased R_h and reduced R_a

together may have cancelled each other out. Together, these scenarios suggest that the root system of deforested native forests may have largely been decomposed prior to my measurements and the disturbance to soil and aboveground biomass inevitably caused soil C loss shortly after deforestation.

Furthermore, tropical forests are typically N-rich and P-limited, which can be attributed to N-fixing plants, atmospheric N deposition, and P leaching via highly weathered tropical soils (Fujii et al., 2018). This may also be consistent with the possibility that litter inputs and nutrient context did not differ strongly enough among the sampled forest types to produce clear contrasts in R_s, although neither litterfall nor soil nutrient status was measured directly in this study. For example, Wang et al. (2015) investigated the soil organic carbon (SOC) turnover rate between tropical native forests and plantation forests and found that plantation forests did not change the SOC stock, compared to native forests. They explained this finding by the similar amount of litterfall input of tropical native and plantation forests. Similarly, Kerdraon et al. (2020) assessed the R_s relationship with litter types and their decomposition and found that there was no effect of litter type on soil respiration, despite difference in litter properties. They also found a decline in microbial activity and biomass in the absence of litter inputs. This may indicate that litter quantity can be an important correlate of R_s in tropical forests, although the present study does not allow litter quantity and litter quality effects to be separated.

5.4.4. Limited influence of soil temperature on soil respiration under the observed conditions

As hypothesised, soil moisture proved to be a stronger R_s predictor than soil temperature, with the interaction between soil moisture and tree species explaining the most R_s variation.

The observed lack of a significant R_s-T_s relationships contrasts with previous studies that predominantly reported a positive correlation between soil respiration and soil temperature in tropical forests (Wood et al., 2013a; Zimmermann et al., 2015; Zimmermann & Bird, 2012). The limited variability of high T_s (25.5–28.5 °C) during our study period likely contributed to the lack of R_s response to temperature, which can be also attributed to low temperature sensitivity

resulting from possible soil thermal acclimation (Anjileli et al., 2019; Krause et al., 2013). In line with the findings of Kosugi et al. (2007), my results of a weak but significant R_s decline with SWC under limited T_s effect can be explained by reduced soil CO_2 diffusivity and soil microbial activity in saturated soils (Gui et al., 2023).

5.4.5. The interactive effects of soil moisture and tree species on soil respiration

My finding of an interactive SWC-species effect on soil respiration is consistent with that of Raich (2017), who found non-linear relationships between soil respiration and SWC across five different tree species in tropical plantation forests. This interactive effect, coupled with no significant differences in R_s among tree species at my sites, suggests that species-specific phenological traits can influence soil water dynamics in tropical moist forests, thus indirectly affecting soil respiration.

The decreasing R_s-SWC trend observed in Eucalyptus soils at my sites likely reflects soil physical constraints under wetter conditions. Previous study by Walden et al. (2015) has shown that Eucalyptus reforestation can be associated with soil water repellence, with the incidence and severity of repellence increasing with stand age. They suggested that hydrophobic compounds from Eucalyptus, rather than land-use change, caused soil water repellence Although soil water repellence was not measured in the present study, the 10-20 and 20-30 year-old Eucalyptus stands at my sites may exhibit similar soil physical characteristics. Under high soil moisture conditions, such properties can promote uneven wetting, reduced gas diffusivity, and localized oxygen limitation, particularly in surface soils where repellence is often most pronounced (Piyaruwan & Leelamanie, 2020), thereby constraining microbial and root respiration despite increasing bulk SWC.

The increasing R_s-SWC trend observed in Teak soils at our sites is consistent with previous studies reporting higher soil porosity and water-holding capacity under Teak plantations, although these soil physical properties were not measured directly in the present study. Greater soil porosity and water-holding capacity reported for some Teak systems may help explain the

positive R_s-SWC trend observed here by promoting favourable moisture conditions without strongly restricting gas exchange, although these soil properties were not measured directly at the present sites (Franzluebbers, 2020). For example, Masnang et al. (2023) assessed and compared the water holding capacity in tropical Teak monoculture and tropical Teak mixed forests with agroforestry and found that tropical Teak monoculture soils showed greater soil porosity and water retention due to Teak-induced low soil bulk density. Similarly, Takahashi et al. (2009) found that in tropical Teak plantations with different stand ages (1-, 6-, and 21-year-old), soil respiration showed a significantly positive correlation with soil water content in the 0-30 cm soil layer.

Few studies have investigated the R_s-SWC relationship in Mangium, especially under high SWC conditions. Konda et al. (2010) evaluated the seasonal and spatial CO_2 fluxes variation in Mangium plantations. They found that soil respiration increased with soil litter amount without a significant R_s-SWC relationship. This suggested that soil litter amount, rather than soil moisture, controlled soil respiration in their plots. Similarly, at my sites, the weak response of R_s to SWC suggested soil moisture was not a main driver of R_s within the observed Mangium plots, and that other unmeasured site factors may also have contributed to the pattern.

The decreasing R_s-SWC trend observed in native forests likely reflects soil physical constraints under persistently wet conditions rather than soil moisture magnitude alone. Although mean SWC in native forests was higher than in Eucalyptus and Teak, SWC ranges overlapped substantially among forest types. Notably, R_s declined with increasing SWC in native forests at moisture levels where R_s increased in Teak and showed little response in Mangium. This suggests that differences in the R_s-SWC response among forest types are more strongly related to species-specific forest structure and soil physical context than to absolute soil moisture levels. Native forests typically have denser canopies and thicker organic matter and litter layers, which can enhance water retention and reduce soil aeration, thereby promoting reduced gas diffusivity and localized oxygen limitation under wet conditions (Colmer & Greenway, 2005; Kagawa et al., 2009). These mechanisms are discussed here as plausible explanations, as soil physical properties were not measured in this study.

5.5. Conclusion

This study evaluated how soil respiration varied between tropical native forests and plantation forests and how that variation related to soil moisture, soil temperature, and tree species under the sampled field conditions. Our findings revealed that tropical plantations showed comparable R_s rates in tropical native vs. plantation forests. This suggests that, following the initial post-deforestation disturbance phase, soil respiration rates in established plantations can recover to levels comparable to native forest systems. Any similarity in soil respiration rates likely reflects a combination of co-varying environmental conditions and other unmeasured belowground and litter-related factors, which could not be separated within this study. Soil moisture served as the primary driver of R_s variations, while soil temperature showed little effects on R_s due to its limited variation. The interaction between soil water content and tree species explained the greatest proportion of variation in soil respiration, with contrasting, non-linear R_s-SWC response patterns among forest types. For example, an increasing R_s-SWC trend was observed in Teak, which is consistent with literature reporting higher soil porosity and water-holding capacity in Teak plantations, likely associated with lower soil bulk density and greater organic matter inputs. These observed non-linear relationships between R_s and SWC across tree species point out the joint importance of species-specific traits and environmental changes in regulating soil C dynamics. These findings demonstrate that mature, minimally managed plantation forests have great potential to mitigate soil C loss at tropical deforested sites, and the tree species traits and soil moisture dynamics are crucial at regulating soil respiration at these sites.

Chapter 6. Discussion

6.1. Purpose and scope

Soil respiration represents a major pathway of CO_2 exchange between terrestrial ecosystems and the atmosphere and is widely used as an indicator of ecosystem C cycling. This chapter brings together the findings from the three empirical chapters in this thesis (Chapters 3, 4, and 5), which examine R_s across temperate dairy grasslands, temperate radiata pine plantations, and tropical forest ecosystems. These studies were conducted using observational approaches that differ in spatial scale, environmental context, and study design. Rather than restating individual results, the aim of this general discussion is to integrate findings across systems to identify consistent patterns, key differences, and shared constraints influencing R_s under field conditions.

The focus of interpretation in this chapter is on patterns and consistencies, rather than on mechanistic explanations. Across the three empirical chapters, R_s was examined in relation to climatic variables, soil properties, vegetation characteristics, and landscape context; however, none of the studies involved experimental manipulation or direct partitioning of respiration components. As a result, the synthesis presented here is based on associative relationships, and causal drivers of observed patterns cannot be disentangled with confidence.

The scope of inference is further limited by the observational nature of the datasets, the influence of site-specific conditions, and the short time periods over which measurements were collected. Accordingly, patterns discussed across chapters reflect responses under the sampled conditions rather than long-term or universal ecosystem behaviour. Differences among systems are therefore interpreted as context-dependent outcomes arising from co-varying environmental and structural factors, rather than as evidence of general controls on R_s.

Within these constraints, this chapter aims to synthesise what can be robustly inferred from the combined evidence, clearly indicate where interpretation is limited, and place the findings of this thesis into a broader comparative context while acknowledging remaining uncertainty.

6.2. Cross-system patterns

Throughout Chapters 3-5, R_s displayed consistent patterns, despite great variations in ecosystem type, spatial scale, and research design. Notably, R_s varied systematically with season, soil temperature, and soil water content across all studied systems. In each empirical chapter, elevated R_s was observed during warmer periods compared to cooler ones, with summer values typically exceeding those of winter. However, the extent and nature of seasonal responses differed among sites and ecosystems, consistent with global evidence that seasonal R_s sensitivity varies across biomes and environmental contexts (Bond-Lamberty & Thomson, 2010b). This shared seasonal signal provides a basis for comparison, while the differences in response strength highlight system-specific constraints related to soil properties, structural characteristics, or landscape context.

The empirical chapters also collectively showed that R_s was consistently associated with soil temperature and soil water content, but these relationships were non-linear and highly context-dependent, consistent with previous evidence of context-dependent R_s responses to temperature and moisture (Davidson & Janssens, 2006; Moyano et al., 2012). In the temperate dairy grasslands discussed in Chapter 3, R_s displayed non-linear responses to both temperature and moisture, which varied greatly among soil types under broadly similar climatic conditions. In contrast, in the radiata pine plantation chronosequence examined in Chapter 4, R_s-temperature relationships were more uniform across various sites, despite the stand age difference. In Chapter 5, which focused on tropical forest systems, R_s was most influenced by moisture availability and landscape position, while temperature effects were relatively inhibited within the narrow thermal range. Overall, these differences indicate that while temperature and moisture are common correlates of R_s, the primary constraint associated with R_s variations differs across systems.

Soil type, stand age, and landscape position emerged as important sources of variation in R_s across the chapters, but their impact varied in how they integrated underlying environmental conditions. In Chapter 3, soil type captured co-varying physical and chemical properties that distinguished R_s among grassland sites, even where climate conditions were broadly similar. In

Chapter 4, stand age served as an indicator for forest structural development, but R_s remained relatively comparable across ages despite differences in microbial community composition. In Chapter 5, R_s variability was primarily associated with soil moisture and its interaction with tree species, while altitudinal differences reflected broader microclimatic gradients rather than discrete species effects.

Despite the differences in studied ecosystems, R_s responses were limited to comparable ranges in relation to the environmental conditions observed across managed grasslands, plantation forests, and tropical forest systems. Higher or lower R_s values were often linked to site-specific conditions (e.g., soil properties, moisture levels, or landscape context) than with ecosystem type solely. This suggests that similar R_s patterns can arise across ecosystems, even when the influencing factors differ.

Importantly, in Chapters 3-5, factors such as soil type, stand age, species identity, and landscape position served as proxy variables that represented groups of co-varying environmental and structural characteristics. As a result, the patterns observed across ecosystems here indicate associative relationships instead of direct proof of process-level control. These similarities come from different dominant constraints and encourage a more detailed investigation into the reasons why patterns differ among systems.

6.3. Why patterns differ

6.3.1. Site-level co-variation constraining attribution of R_s drivers

In Chapter 3, the variation in R_s patterns was strongly influenced by the soil characteristic of each site, which co-varied with local climatic conditions. The differences among grassland sites were mainly linked to soil type, which encompassed a range of physical and chemical properties instead of a single controlling factor. As soil types varied across sites, observed R_s variability represented a combination of environmental contexts rather than individual soil attributes.

Importantly, climatic factors such as temperature and moisture did not vary independently of soil characteristics throughout the study sites. Soil texture, drainage ability, and organic matter

content were closely linked to site-level climate and management conditions, resulting in overlapping impacts on R_s. Consequently, it was not possible to separate the relative effects of soil and climate on observed R_s patterns. Therefore, R_s responses reflect the relationships from co-varying drivers rather than proof of direct causal control.

In addition, the context of managed grazing added further complexity. Grazing intensity, vegetation structure, and short-term weather conditions differed among sites and seasons, which could affect belowground C inputs and soil physical conditions. These management-related factors were not experimentally controlled and likely interacted with soil and climatic variability, further limiting the ability to draw conclusions. As a result, seasonal and spatial R_s patterns observed in Chapter 3 should be viewed as the result of the interplay between soil, climate, and management practices.

In summary, Chapter 3 shows a system where high site heterogeneity and strong co-variation among environmental drivers limited the ability to attribute R_s variability to specific controlling factors. The differences in R_s patterns did not stem from inconsistent respiration behaviors, but from the prevailing soil-climate associations within the grassland system, unlike the more structurally limited systems analysed in the following chapters.

6.3.2. Stand age as a proxy for structural development

In Chapter 4, R_s showed a relatively stable trend throughout a plantation forest chronosequence, even with differences in stand age and microbial community composition. This observation suggests that stand age acted as an indicator of more extensive structural development, rather than an independent factor influencing R_s. Therefore, comparisons among age classes illustrate integrated changes in forest structure and belowground C allocation, rather than isolated effects of age.

Although there were clear age-related variations in the composition of microbial community, these variations did not lead to similar changes in R_s. This separation indicates that variation in microbial diversity metrics did not result in equivalent changes in ecosystem-level CO_2 efflux. Instead, R_s appeared mainly limited by the structural context at the stand level, suggesting that

the overall forest characteristics had a stronger impact on R_s patterns than microbial diversity alone within this plantation system.

The interpretation of these patterns is inherently constrained by the observational nature of the study. Stand age included various co-varying factors, such as canopy closure, root system development, litter inputs, and microclimate, which could not be independently separated. As a result, the lack of strong R_s differences among age classes should not be viewed as proof that R_s is unresponsive to forest development, but instead it suggests that dominant structural constraints likely obscured fine-scale biological variations.

In summary, Chapter 4 presents a system where R_s patterns vary from those observed in Chapters 3 and 5, as integrative structural characteristics dominate variability over strong soil-climate or landscape gradients. This shows how the proxy variables influencing R_s variability can differ between ecosystems, even when overall R_s rates remain comparable.

6.3.3. Landscape position as a dominant integrative constraint

In Chapter 5, the variation in R_s was primarily linked to landscape position, where species identity, soil moisture, and topographic context were closely connected. Despite the presence of multiple tree species throughout the study sites, species identity was not independent of landscape position, which resulted in overlapping environmental conditions among forest types. Thus, observed R_s patterns reflected combined landscape-scale conditions rather than distinct species-level effects.

Within the tropical forest system, there were no consistent main effects of tree species on R_s detected. Instead, R_s variability was more closely related to gradients in soil moisture and topography that co-varied with elevation and landscape position. While Chapter 5 noted an interaction between soil moisture and tree species, this interaction occurred within landscape gradients where species identity and hydrological conditions co-varied, which limited independent attribution. Therefore, species-associated R_s responses should be viewed as conditional on landscape position rather than as independent species effects.

Additionally, the interpretation is limited by the observational design, which restricts the ability to separate species effects from their landscape positions. Soil moisture availability, drainage characteristics, and microclimatic conditions were influenced by topography and elevation, while the distributions of tree species were partially organised along these same gradients. Species identity thereby worked as a contextual factor integrated within wider landscape controls, rather than as an independent factor affecting R_s variability.

To summarise, Chapter 5 demonstrates a system where R_s patterns are different from those observed in grassland and plantation, as landscape and hydrological constraints tend to overshadow fine-scale biological differences. This contrasts with the proxy masking discussed in Chapter 4 and the soil-climate co-variation presented Chapter 3, showing that differences in R_s patterns are due to changes in dominant constraints, not inconsistencies in R_s behavior across ecosystems.

6.4. Limits of inference and generalization

The results outlined in this thesis are achieved from observational field studies and should thus be interpreted within the limits of non-experimental inference. In Chapters 3-5, R_s responses were measured under naturally varying environmental conditions. These included grassland systems defined by different soil types and site contexts (Chapter 3), plantation forests that covered gradients in stand age and structural development (Chapter 4), and tropical forest systems where moisture level and landscape position were important factors (Chapter 5). Since no experimental manipulation of individual drivers was performed, the observed relationships represent statistical associations instead of proof of direct causal influence. In addition, R_s was measured as a total CO_2 efflux, and the relative contributions of autotrophic (root-derived, R_a) and heterotrophic (microbial, R_h) respiration were not separated. This limits the interpretation of whether observed variability in R_s indicates changes in root activity, microbial decomposition, or a combination of both across the studied systems. Consequently, the conclusions drawn in this thesis emphasise comparative patterns of co-variation among environmental factors throughout Chapters 3-5, rather than pinpointing specific process-level controls.

A primary limitation on the interpretation across this thesis comes from the strong covariation among environmental factors that affect R_s. In all three empirical chapters, variables such as soil temperature, soil water content, soil physical properties, vegetation structure, and site context did not change independently, but instead formed interconnected environmental gradients. In Chapter 3, soil type differentiated grassland sites that also differed in drainage, texture, and moisture regimes under generally similar climatic conditions. In Chapter 4, stand age acted as a proxy for forest structural development, integrating changes in canopy structure, rooting patterns, and local microclimate rather than representing one single controlling factor. In Chapter 5, landscape position and soil moisture were closely linked to topography and species distribution, which made it difficult to separate species-level effects from broader hydrological and terrain influences. Consequently, the key explanatory variables in each chapter functioned as proxy indicators of integrated site conditions. This strong covariation limits the ability to disentangle individual drivers and indicates that observed R_s patterns are a reflection of dominant environmental constraints specific to each system, rather than direct effects of individual factors.

Soil respiration measurements in this thesis were based on short-term, chamber-based observations across all three empirical chapters. These measurements provide snapshot fluxes during discrete sampling intervals rather than continuous time series data. Therefore, the reported R_s values show responses under the environmental conditions present at the time of measurement but do not account for seasonal extremes and variability. In Chapters 3-5, the observed relationships between R_s and the environment thus indicate short-term associations during sampling periods rather than longer-term sensitivities that are likely to differ among grassland, plantation forest, and tropical forest systems. Although repeated measurements were conducted within sampling periods, the overall temporal coverage is still inadequate to fully characterise seasonal patterns or delayed ecosystem responses beyond the sampled conditions, for example, winter-summer contrasts in temperate systems (Chapters 3 and 4) or wet-dry variability in tropical forests (Chapter 5). This limitation is particularly important given the varying seasonal dynamics and hydrological regimes across the studied systems. Consequently,

long-term R_s dynamics, including potential lag effects or cumulative responses to extended environmental variation, remain unresolved within the scope of this research. Spatial resolution further limits inference. Replication within sites was restricted, which means that measurements at the plot scale may not fully capture fine-scale heterogeneity in soil properties, root distribution, or microclimatic variation. This limitation is expected to be more serious in heterogeneous grassland and tropical forest environments than in relatively uniform plantation stands. While multiple sites were included within each system, cross-system comparisons were meant to be intentional and comparative rather than spatially exhaustive. As a result, the contrasts among grasslands, plantation forests, and tropical forest systems reflect conditions at the sampled sites rather than complete spatial characterisation.

Soil respiration measurements in this thesis represent gross CO_2 efflux at the plot scale, derived from short-term, chamber-based observations. Therefore, they do not serve as direct indicators of soil C sequestration or balance. In Chapters 3-5, R_s quantifies the rate of CO_2 release from soils in relation to observed variations in temperature, moisture, and site context during discrete sampling periods, but does not account for concurrent C inputs or long-term changes in soil C pools. Processes such as belowground C allocation and litter-derived C inputs occur over time that extend beyond the sampling periods and were not included the scope of this study. As a result, the differences in R_s observed among sites, seasons, or ecosystems cannot be interpreted as evidence of net soil C gain or loss. This distinction is important, considering the carbon-cycle framework of the thesis and the cross-system comparisons among grasslands, plantation forests, and tropical forest systems. Net soil C represents the balance between inputs and losses over time, whereas the R_s measurements show instantaneous flux responses under sampled conditions. Thus, no inference is made regarding climate mitigation potential or long-term C storage based on R_s alone. A further limitation comes from the scale mismatch between measurements and inference where R_s was measured at the plot scale, while many of the broader questions that motivate this work relate to C dynamic at the ecosystem or landscape scale. In addition, several soil properties used for interpretation were derived from mapped datasets that represent spatial averages for wide soil units rather than plot-level heterogeneity.

This discrepancy limits the understanding beyond sampled conditions and shows that the contribution of this thesis is in comparative analysis of R_s patterns across systems, rather than in estimating ecosystem-scale C budgets or balances.

The findings outlined in this thesis are context-dependent and are specifically relevant to the grassland, plantation forest, and tropical forest systems discussed in Chapters 3-5. Therefore, the observed relationships between R_s and temperature, soil moisture, and integrative site context are not directly applicable to regional or national estimates of soil C fluxes. The differences among ecosystems represent distinct combinations of climate, soil properties, vegetation structure, management history, and landscape position, which are unlikely to be uniformly replicated beyond the sampled conditions. Consequently, ecosystem-specific results should not be viewed as general responses, particularly where management intensity, climatic regimes, or soil characteristics differ greatly from those examined in this thesis. Within these limitations, the thesis provides comparative evidence of how R_s patterns co-vary with temperature, moisture, and site context across ecosystems. By applying consistent chamber-based measurements and comparative analytical processes across systems that differ in climate, land use, and spatial scale, this work offers a coherent cross-system synthesis of R_s behaviour.

6.5. Implications for interpreting soil respiration

6.5.1. Interpreting soil respiration as an ecosystem indicator

The results in this thesis show the importance of careful interpretation of R_s as an indicator of ecosystem functioning. In three empirical chapters, R_s varied with environmental conditions, but these responses were strongly influenced by site-specific contexts rather than by individual controlling factors. In such cases, R_s values and patterns give meaning only when considered along with the broader environmental settings in which they are measured.

Specifically, the results indicate that explanations based on individual factors for R_s variability are insufficient across ecosystems. In grassland systems (Chapter 3), R_s patterns were closely linked to soil type and local climatic conditions that co-varied across sites. In plantation forests (Chapter 4), stand age reflected the structural development, yet R_s remained generally similar

despite differences in microbial diversity. In tropical forest systems (Chapter 5), R_s variability was strongly linked to soil moisture and tree species, with landscape position playing a secondary role. These findings indicate that R_s reflects integrated environmental constraints rather than isolated drivers.

Thus, R_s should be viewed as an integrative response that shows combined influences of climate, soil characteristics, vegetation structure, and landscape context. Interpreting R_s without considering these interacting factors can oversimplify ecosystem processes and misrepresent the conditions in which soil CO_2 effluxes are measured. The implication is not that R_s lacks value as a metric, but that its interpretation must be closely related to system-specific contexts and observational limits.

6.5.2. Avoiding over-simplified interpretations of R_s patterns

The comparative structure of this thesis also has implications for how R_s patterns are interpreted across ecosystems. While similar R_s sensitivities to temperature and moisture were observed across grasslands, plantation forests, and tropical forests, the primary constraints that shape these responses differed among systems. This suggests that similar R_s patterns can be caused by different environmental conditions, rather than by process-level controls.

Across Chapters 3-5, variables such as soil type, stand age, and landscape position worked as proxy indicators that captured groups of co-varying physical, biological, and climatic characteristics. As a result, the relationships between R_s and these variables should not be seen as proof of direct mechanistic control. They reflect how primary environmental constraints function within specific systems. This has implications for explanatory frameworks that aim to link R_s variability to individual drivers, especially when relying on observational data.

These results show the importance of caution when developing mechanistic narratives from R_s observations. The value of cross-system comparisons lies in identifying recurring patterns of co-variation and context dependence, rather than in forming universal explanations for R_s behaviour.

6.5.3. Implications for cross-system synthesis and modelling studies

When soil respiration results. like those discussed in this thesis, are used in cross-system comparisons or modelling applications, it is essential to be careful to assume that similar response patterns indicate shared underlying controls. In Chapters 3-5, similar non-linear relationships between R_s and environmental variables were observed across ecosystems, despite these patterns emerging under different dominant constraints, which linked to soil properties, vegetation structure, and landscape setting. This suggests that similarities in R_s responses do not imply that response functions can be directly transferred across systems.

For modelling studies, this has implications for how R_s-environment relationships are pooled, parameterised, or extrapolated across spatial scales, land-use types, or biomes. Methods that apply common response functions without consideration of system-specific constraints (e.g., moisture limitation in tropical forests, structural development in plantation stands, or soil-type-associated variability in grasslands) can potentially mask the conditions where observed R_s patterns occur. Thereby, generalised parameterisations may inaccurately represent the respiration dynamics when applied outside the environmental contexts from which they were derived.

The findings of this thesis support a constraint-oriented approach to cross-system R_s comparison, where primary limiting factors are identified before aggregation or scaling. Instead of viewing similar response as proof of shared controls, synthesis and modelling efforts are enhanced by recognising where apparent similarities reflect different underlying constraints.

6.5.4. Implications for future interpretation-oriented study design

The patterns observed across the grassland, plantation forest, and tropical forest systems examined in this thesis indicate that the value of R_s measurements is strongly shaped by study design choices. The interpretation is strengthened when measurement strategies are aligned with the primary constraints in each system, as demonstrated in Chapters 3-5. This has implications for the design and evaluation if future R_s studies, particularly in cross-system contexts.

In all systems examined here, R_s responses reflected short-term environmental conditions during discrete sampling periods. This implies that snapshot chamber-based measurements are insufficient to some extent and their interpretive capacity depends on how effectively temporal variability is address in relation to the study objectives. In situations where seasonal dynamics, moisture patterns, or phenological changes are expected to influence R_s variability, conducting repeated sampling under varying conditions offers greater interpretive strength than isolated measurements. Designs that account for temporal variability thereby improve inference when long-term continuous monitoring is not available.

Another implication is about the strong covariation among environmental drivers observed throughout this thesis. Soil temperature, soil moisture, soil physical properties, vegetation structure, and site context consistently varied together. This covariation should be treated as a fundamental characteristic of field-based R_s studies. Where possible, future studies could enhance interpretability by selecting sites or sampling methods that minimise unnecessary overlap among key drivers. Where covariation is inherent to the system, interpretation is improved by clearly identifying which constraints are predominant, rather than trying to isolate individual drivers that cannot be meaningfully separated under natural conditions.

The results of this thesis show the value of incorporating biological, physical, and chemical context alongside R_s measurements. The strength of interpretation comes from situating R_s responses within the broader environmental and structural conditions in which they occur. This integration supports more robust cross-system comparison and reduces the risk of overgeneralisation. Importantly, these implications relate to how R_s evidence is interpreted rather than prescribing ecosystem management actions or inferring causal mechanisms beyond the limits of observational data.

6.6. Conclusion

This thesis investigated how soil respiration (R_s) varies across different ecosystems through a comparative observational approach that included temperate dairy grasslands, temperate plantation forests, and tropical forest systems. By using consistent chamber-based field

measurements, the study focused on identifying patterns of variation and the primary environmental factors influencing R_s responses. The objective was to facilitate cross-ecosystem comparisons by contextualizing the observed R_s within the specific environmental conditions where it was measured, thereby offering a foundation for interpretation across systems.

Throughout the studied ecosystems, R_s displayed similar patterns of variation. The observed variation was primarily associated with temperature and moisture conditions, with non-linear responses under different environments. Seasonal differences were most noticeable, indicating that variations in R_s responses might reflect changes in dominant constraints. In grasslands, the variation in R_s corresponded with environmental gradients linked to soil types, which served as integrated site contexts. In plantation forests, the structural development, indicated by stand age, did not correspond to a clear distinction in the observed R_s patterns, suggesting that the stand structural development alone was insufficient to explain R_s variation. In tropical forests, the patterns of R_s were more related to moisture gradients and landscape position than to temperature. Thus, the apparent similarity in R_s responses coexisted with variations in environment factors, showing the necessity for careful interpretation of similarities across different ecosystems.

The interpretive scope of these findings is shaped by the observational, non-manipulative design of the study. Chamber-based measurements provide temporally discrete snapshots of flux rather than continuous tracking of processes, and soil respiration was not partitioned into autotrophic and heterotrophic components, which limits the attribution of biological sources. Environmental drivers often covaried across different sites, making it difficult to isolate independent effects. Therefore, the results serve as comparative evidence of structured co-variation rather than causal mechanisms. The thesis does not aim to quantify long-term carbon balance or ecosystem-scale carbon dynamics. Rather, it clarifies how empirical R_s observations can be interpreted within their environmental conditions while clearly defining the limits of inference.

This work indicates that soil respiration can show similar responses across diverse ecosystems while being influenced by different dominant factors. The similarity in response does not imply

uniform environmental control or shared mechanisms. To achieve comparability across systems, it is essential to acknowledge the environmental conditions that shape these responses. Proxy variables like soil type, stand age, or landscape position should be viewed as integrated representations of site condition rather than isolated influences. By focusing on constraint-aware interpretation, the thesis frames cross-ecosystem R_s comparison as a matter of contextual alignment instead of generalised functional consistency, providing a basis for integrating observational data across different systems.

This comparative design offers cross-ecosystem empirical data to clarify how soil respiration varies under various environmental constraints. Situating R_s measurements within their primary environmental context allows for the interpretation of similarities and differences without overextending inference. The contribution of this thesis is not to suggest universal explanations, but to enhance the interpretive conditions where R_s observations can be compared across systems. By highlighting the patterns alongside defined limits of inference, this work supports a context-aware synthesis of soil respiration evidence.

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