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Understanding Soil Respiration Dynamics in Temperate Forests in Northwestern Mexico

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Abstract: Temperate mixed forests in Mexico are considered highly important ecosystems because of their high levels of biodiversity and capacity to store carbon. The aim of this study was to evaluate temporal and between-forest soil respiration (CO_2 efflux) variability, and to assess the effect of vegetation diversity metrics on soil CO_2 fluxes in mixed-uneven-aged forests in Durango, Northwestern Mexico. Soil CO_2 efflux, soil moisture, and soil temperature were measured in three temperate forest types. A generalized linear model (GLM) was fitted to analyze the relationship between soil CO_2 fluxes and stand variables, diversity metrics, soil moisture, and soil temperature. Furthermore, a two-way analysis of variance was used to assess the effect of forest type, month of the year, and their interaction on soil respiration. Annual average, minimum, and maximum soil CO_2 efflux rate values were 3.81 (±2.94), 2.28 (±1.47), and 7.97 (±2.94) μmol m^{-2} s^{-1}, respectively. Soil respiration was positively related to species richness, aboveground biomass, and quadratic mean diameter; however, forest type did not contribute to understanding the dynamics of soil CO_2 fluxes. The results highlight the importance of seasonality, species diversity and aboveground biomass stocks to preserve the ecosystem processes driving soil respiration in temperate forests.

Keywords: CO_2 efflux; carbon pool; multispecies forest; diversity metrics; forest productivity

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1. Introduction

The soils of forest ecosystems are the main C pool and contain about 1500 Pg worldwide [1], representing about 80% of terrestrial carbon stocks [2]. In this scenario, soil respiration (also known as soil CO_2 efflux) is the second most important carbon flux between forest ecosystems and the atmosphere [3]. It has been observed that variation in soil carbon stocks in forest systems are the result of multiple dynamic processes (e.g., vegetation growth and mortality, litter production, the decomposition of dead organic matter, as well as natural and anthropogenic disturbances), which interact from the scale of a single tree to an entire landscape. Consequently, changes in species diversity and composition, as well as abiotic factors such as temperature and humidity, can significantly affect the dynamics of soil CO_2 fluxes, the atmospheric CO_2 concentration, as well as the overall carbon balance of ecosystems [4,5].

At certain spatial scales, more diverse plant communities tend to show higher primary productivity [6,7]. However, the relationship between plant diversity and soil respiration has not proved to be strong [8], but it has been observed that plant diversity can favour soil respiration by incorporating more C into the system.

Soil CO_2 efflux is conditioned by soil temperature and moisture content, as well as by plant photosynthetic activity [9]. Of these conditioning factors, soil moisture content modifies the soil aeration and the circulation of different gases [10], which leads to variations in the ability of soil microorganisms to carry out organic matter oxidation and litter decomposition [11]. Therefore, environmental conditions and vegetation types, as driving factors that control organic matter inputs and their adjacent processes into the soil, must be taken into account in soil respiration estimates [12]. On the other hand, seasonal fluctuations in soil respiration are commonly found in nearly all ecosystems and are frequently linked to shifts in temperature, moisture, photosynthetic activity, root growth, or a combination of these factors [13]. Conversely, the spatial variability in soil respiration arises from considerable changes in soil physical characteristics, fine-root biomass, fungal and bacterial activity, and nutrient availability [14].

In the future, additional increases in the atmospheric CO_2 concentrations are expected [15]; these changes, together with the expected global temperature increase, may substantially affect the soil CO_2 fluxes in forest soils worldwide. Moreover, some activities, such as land use change, deforestation, and silviculture, increase CO_2 emissions to the atmosphere. For instance, forest management significantly alters soil properties and environmental conditions [16], affecting soil micro-organism activity and, consequently, soil CO_2 dynamics.

The Sierra Madre Occidental in Mexico is considered a special ecological area because of the high levels of biodiversity, which are attributed to diverse physiographic and climatic conditions [17], making it the largest continuous forested area in Mexico. It is also of high importance to forest management for timber production. Despite its ecological, economical, and environmental importance, research on soil CO_2 fluxes in these forests is scarce; consequently, this topic represents a knowledge gap in the carbon cycle in Mexican forests. Based on the above, we selected three forest types in Northwestern Mexico to (i) evaluate temporal and between-forest soil CO_2 efflux variability; (ii) to identify the main environmental determinants of soil CO_2 fluxes; and (iii) to assess the effect of stand variables and diversity metrics on soil respiration.

2. Materials and Methods

2.1. Site Description

The study was conducted in the El Salto forest region, situated in Southwest Durango State, Mexico (23°06′59″ and 24°11′38″ N and 105°55′56″ and 105°10′31″ W) (Figure 1). The elevation in this region varies from 1200 to 3200 m, with an average of 2264 m. The climate of the area is classified according to the Köppen classification modified by García [18] as temperate subhumid C(w2). The temperature ranges from 8.2 to 26.2 °C, with an annual average of 13.3 °C. The mean annual rainfall is 917 mm, varying between 443 and 1452 mm. The study area is characterized by two main soil groups: Luvisol and Umbrisol. These soil types are common in temperate and cold or warm–humid climates with a seasonal pattern of rain and drought, and they are frequently found in the temperate forests of the Sierra Madre Occidental [19]. Regarding vegetation, the area comprises several forest types, including pine forest, pine–oak forest, and associations of pine with other conifer and broadleaved species.

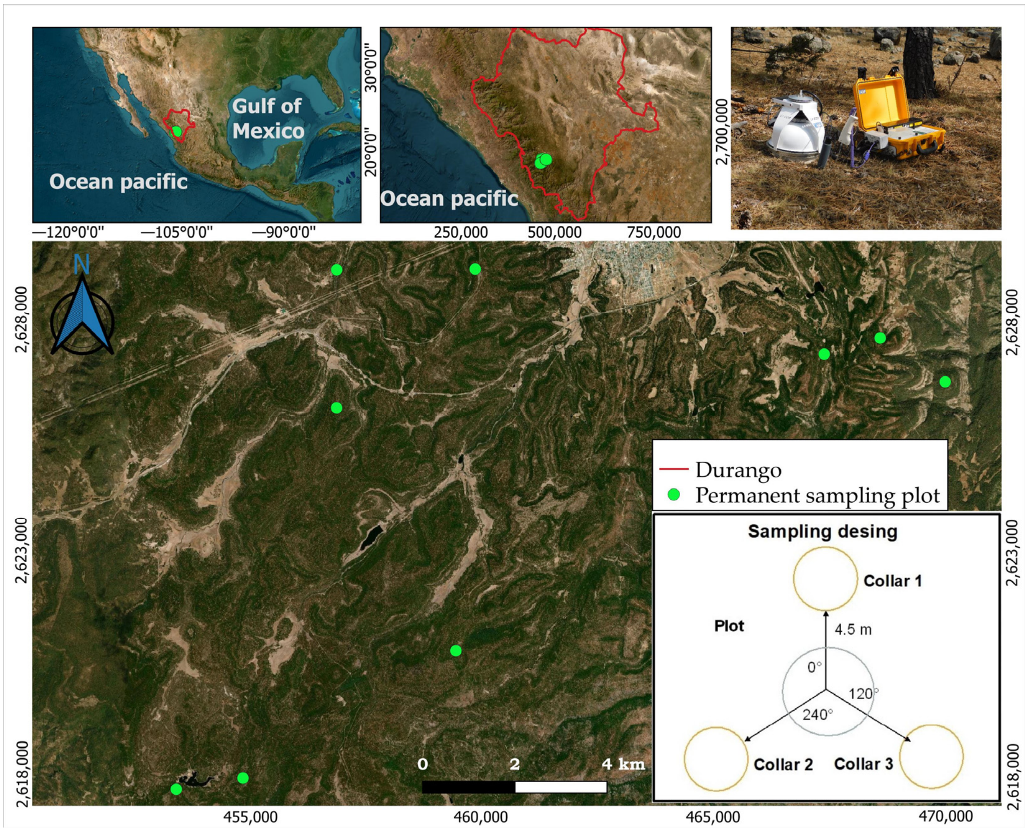

Figure 1. Study area, distribution of the permanent sampling plots, and sampling design.

2.2. Inventory Data and Sampling Design

To examine the variation in soil respiration and the relationship between the CO_2 efflux and the vegetation composition, three dominant forest types were selected (pure pine, mixed pine–oak, and mixed oak–pine) (Table 1). Nine permanent sampling plots (50 m × 50 m), three for each forest type, were established. In each plot, the following variables by tree species were recorded: diameter at breast height (DBH, measured at 1.3 m above ground level, cm), total tree height (m), height to the live crown (m), azimuth (°), and radius (m) from the centre of the plot to all trees equal or larger than 7.5 cm in DBH.

Table 1. Description of stand variables of the three forest types evaluated.

Forest Type	Dq (cm)	DBH (cm)	BA (m^2 ha^{-1})	Density (Stems ha^{-1})	GS (m^3 ha^{-1})	AGB (Mg ha^{-1})	Genera	Species	Elevation (m.a.s.l)
Pine	22.1	19.1	20.63	543	191.1	154.1	3	7	2707
Pine–oak	20.2	18.1	23.01	719	203.5	130.7	6	14	2690
Oak–pine	20.7	17.8	24.91	737	202.6	160.1	7	16	2687

Dq = quadratic mean diameter, BA = basal area, GS = growing stock, AGB = aboveground biomass.

A total of 27 CO_2 flux measurement points were located, 3 points within each permanent plot (3 forest types × 3 plots × 3 replicated measurement points); the distance between the measurement points within the plots was 4.5 m (Figure 1). The sample size was determined based on forest types and species composition within each ecosystem. The selection of nine measurement points, each with three replicates in each forest type, was deemed adequate to effectively represent the CO_2 flux across the study area. Furthermore, spatial independence among these locations was ensured. At each measurement point, a polyvinyl-chloride (PVC) collar (20 cm in diameter × 12 cm in height) was installed in the soil at 5 cm depth. To reduce the influence of vegetation and soil disturbances on the CO_2

fluxes, the PVC collars were placed two weeks prior to the first field data collection. At the 27 points, soil CO_2 flux, soil temperature (T_{soil}), and soil moisture (M_{soil}) were measured.

2.3. Soil CO_2 Flux Measurements

Soil CO_2 flux (μmol m^{-2} s^{-1}) was measured in situ with a portable infrared gas analyzer model LICOR-8100A (LI-COR Inc., Lincoln, NE, USA), equipped with a closed dynamic chamber where soil CO_2 emissions are calculated. Measurements were made twice monthly, from January to December 2021, except in September, when the records were lost. On each sampling date, the measurements were made twice daily: 07:00 to 10:00 and 15:00 to 18:00 h. Each measurement lasted 120 s, separated by 60 s between repeated measurements, during which the chamber opened and closed automatically to achieve ambient CO_2 concentrations. At the same time, during the CO_2 flux measurement, T_{soil} (°C) and M_{soil} (%) at 10 cm below the soil surface were measured [20]. T_{soil} was measured with a temperature probe model LICOR 8100-201 Omega (LI-COR Inc., Lincoln, NE, USA), and M_{soil} with a ThetraProbe ML2x (Delta-T Devices Ltd., Cambridge, UK) soil moisture probe, respectively, which were placed adjacent to the soil respiration chamber.

2.4. Diversity Metrics and Aboveground Biomass Estimations

To analyse the species diversity of woody plants, we used Hill numbers, which are a mathematically unified family of diversity indices that incorporate both relative abundance and species richness and overcome many of these shortcomings. In this sense, we calculated $q0$ (species richness [S], $q1$ (Shannon index (H')), and $q2$ (Simpson's index (λ)). The analyses were carried out using the iNEXT library in R 4.3.1 software [21]. In addition, the relative importance of the species composition, the index of importance value (IVI), was computed.

The aboveground biomass (AGB) of live trees in each plot was estimated using species-specific allometric equations based on DBH and total height developed for all major coniferous and broadleaf tree species of Durango forests [22].

2.5. Statistical Analyses

Pearson's correlation coefficient (r) was performed to identify relationships between CO_2 flux and T_{soil}, M_{soil}, and AGB, as well as Hill's number indexes. After that, a generalized linear model (GLM) was fitted to estimate CO_2 efflux based on the measured variables, assuming a gamma distribution of the data. To evaluate the goodness of fit of the GLM model, a cross-validation was performed, fitting the model with 10% of the data to compare it with the null model. Prior to the analysis, the multicollinearity of variables was established to avoid redundancy. Furthermore, a two-way analysis of variance (ANOVA) was used to assess the effects of forest types, months, and the interaction between these both on soil CO_2 fluxes; then, the means of soil CO_2 fluxes by forest type and month were compared with Tukey's multiple means comparison test. Statistical analyses were performed with the R software [21].

3. Results

3.1. Diversity Metrics and Aboveground Biomass

A total of 1499 trees (DBH $\geq$ 7.5 cm) belonging to twenty species, seven genera, and five families were recorded. The abundance among forest types was distributed as follows: 553 trees in oak–pine forest, 539 in pine–oak forest, and 407 in pine forest. The richness estimated with a similar number of individuals (150) was 13.27 (CI = 12.20–14.33; cover estimator C.hat = 0.98) for oak–pine forest, 11.55 (CI = 10.73–12.37; cover estimator C.hat = 0.983) for pine–oak forest, and 6.86 (CI = 6.52–7.20; cover estimator C.hat = 0.78) for pine forest. The Shannon index (H') showed the highest values in the oak–pine forest (2.14, CI = 2.06–2.22), followed by the pine–oak forest (1.95, CI = 1.88–2.03) and the pine forest (1.14, CI = 1.03–1.24). According to the H' values, the oak–pine and pine–oak forests were in the medium-diversity range, while the pine forest had low diversity. Conversely, Simpson's diversity index (λ) showed that the pine forests had a higher dominance of one species assemblage (0.47, CI = 0.42–0.52) than the oak–pine (0.17, CI = 0.15–0.2) and pine–oak (0.19, CI = 0.17–0.21) forests.

The most important species in the oak–pine and pine–oak forests were *Q. sideroxila* (26.9% and 23.3%), *P. durangensis* (13.7% and 19.6%), and *P. teocote* (10.2% and 12.4%). These three species together accounted for 50.8% and 55.2% of the IVI in these forests. In pine forests, the most important species was *P. cooperi* (53.9%) (Figure 2). The maximum AGB values by forest type were recorded in the oak–pine forest (211.83 Mg ha^{-1}), followed by pine forest (208.33 Mg ha^{-1}) and pine–oak forest (177.36 Mg ha^{-1}).

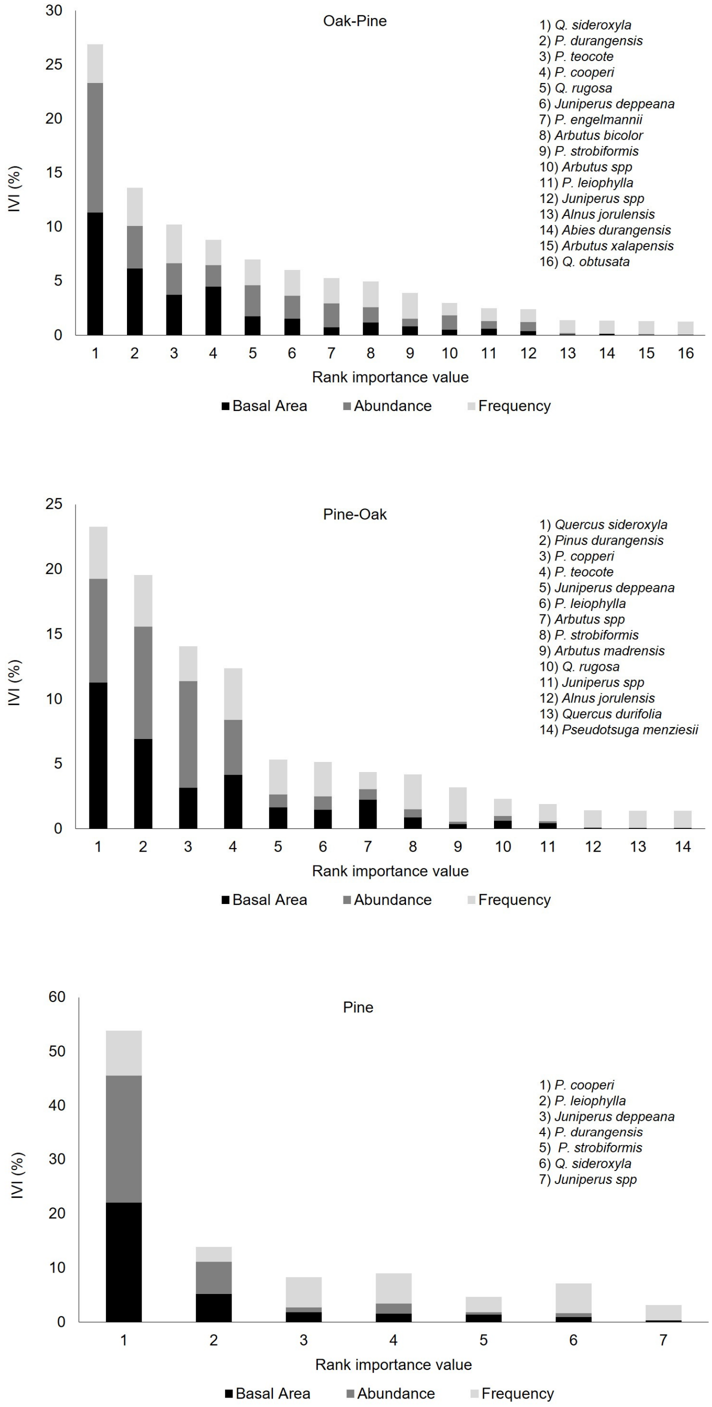

Figure 2. Importance value index (IVI) for the species identified in the three forest types.

3.2. Monthly CO_2 Efflux

The mean soil respiration in the study area was 4.97 (±3.07) µmol m^{-2} s^{-1}. Between January and December, CO_2 fluxes spanned from 0.04 (May) to 15.5 µmol m^{-2} s^{-1} (June). Across the measurement period, T_{soil} ranged from around 5.1–20.6 °C, with an average of 11.9 °C (±2.96), whereas M_{soil} also varied temporally from around 8.8 to 95% (Figure 3). Mean CO_2 efflux reached its highest value in July (8.79 ± 1.8 µmol m^{-2} s^{-1}), while the lowest occurred in April (2.28 ± 1.47 µmol m^{-2} s^{-1}) (Table 2). From January to April, the average CO_2 efflux values showed no significant variation, with a value around 2.2–2.8 µmol m^{-2} s^{-1}. From June, the mean CO_2 efflux increased considerably, reaching about four times higher (July) than in the previous months (Table 2).

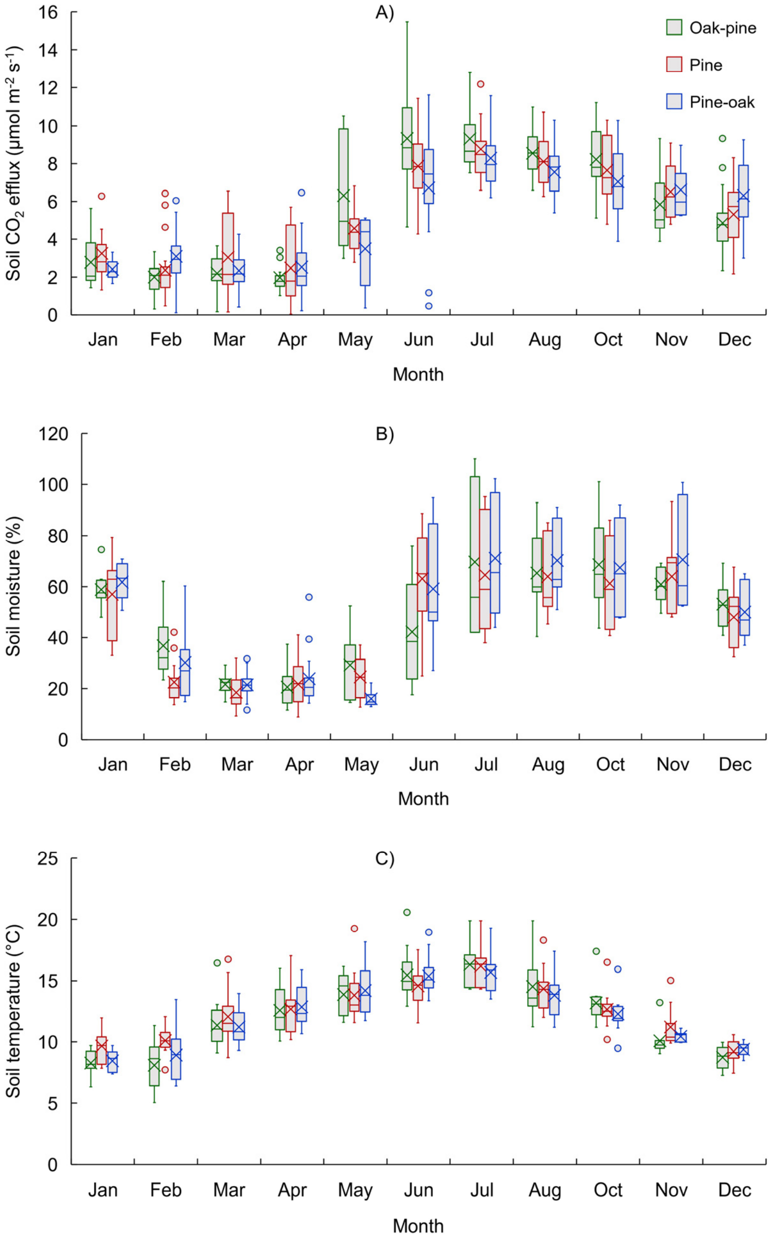

Figure 3. Monthly soil respiration (**A**), soil moisture (**B**), and soil temperature (**C**) for the three forest types evaluated.

Table 2. Monthly mean CO_2 efflux, soil temperature and soil moisture, and Tukey's test of soil CO_2 efflux by month.

Month	Soil CO_2 Efflux (μmol m^{-2} s^{-1}) [†]	Soil Temperature (°C)	Soil Moisture (%)
January	2.81 ± 1.24^{a}	8.81 ± 1.28	59.2 ± 10.9
February	2.49 ± 1.46^{ab}	9.05 ± 1.98	29.9 ± 13.7
March	2.46 ± 1.42^{ab}	11.6 ± 1.95	20.5 ± 5.66
April	2.28 ± 1.47^{ab}	12.7 ± 1.72	22.1 ± 9.69
May	4.15 ± 2.57^{ac}	13.8 ± 2.16	22.8 ± 10.1
June	7.97 ± 2.94^{d}	15.1 ± 1.85	54.8 ± 23.1
July	8.79 ± 1.81^{de}	16.1 ± 1.80	68.4 ± 25.8
August	8.07 ± 1.47^{def}	14.2 ± 2.21	66.4 ± 16.5
October	7.64 ± 1.94^{dfg}	12.7 ± 1.70	65.7 ± 18.2
November	6.38 ± 1.74^{fgh}	10.7 ± 1.43	64.4 ± 16.6
December	5.53 ± 1.86^{h}	9.8 ± 0.82	51.7 ± 11.5

[†] Mean ± standard deviation. Means labelled with the same letter (in the same column) are not significantly different ($p > 0.05$).

There were statistically significant differences in CO_2 efflux among months (F-value = 71.113, $p < 0.0000$, $\alpha = 0.05$), as well as in the interaction forest type: month (F-value = 2.547, $p < 0.0003$, $\alpha = 0.05$); forest type had no significant effect on CO_2 efflux (F-value = 0.847, $p = 0.429$, $\alpha = 0.05$). Through Tukey's means comparison test, a significant difference in CO_2 fluxes between most months (Table 2) was observed. Similarly, the CO_2 efflux in July and August was significantly higher than in the other months. The ANOVA for T_{soil} and M_{soil} also indicated significant differences between months (F-value = 80.464, $p < 0.0000$, $\alpha = 0.05$; F-value = 65.645, $p < 0.0000$, $\alpha = 0.05$, respectively). It is worth noting that significant differences in T_{soil} among months mainly occurred between seasons; for example, soil temperature in spring (March, April, and May) was not significantly different between those months, but it was different from the winter months (January and February) and the beginning of summer (June). The maximum monthly T_{soil} occurred in June (20.6 °C) and the minimum occurred in February (5.1 °C). Soil moisture was significantly different between months, except January and June. The dynamic of M_{soil} showed a maximum in July (68.4%) and a minimum in April (9.05%) (Figure 3).

3.3. Soil Respiration by Forest Type

Mean CO_2 efflux by forest type was 5.08 (±3.40), 5.03 (±2.96), and 4.81 (±2.84) μmol m^{-2} s^{-1}, in oak–pine, pine, and pine–oak forest, respectively (Table 3). The three forest types showed a similar monthly CO_2 efflux trend (Figure 3).

Table 3. Mean values and Tukey's test of soil CO_2 efflux, soil temperature, and soil moisture in the three forest types evaluated.

Forest Type	Soil CO_2 Efflux (μmol m^{-2} s^{-1}) [†]	Soil Temperature (°C)	Soil Moisture (%)
Pine	5.03 ± 2.96^{a}	12.2 ± 2.71^{a}	42.4 ± 23.9^{a}
Pine–oak	4.81 ± 2.83^{a}	11.9 ± 2.82^{a}	45.2 ± 24.9^{a}
Oak–pine	5.08 ± 3.40^{a}	11.7 ± 3.27^{a}	43.7 ± 22.3^{a}

[†] Mean ± standard deviation. Means labelled with the same letter (in the same column) are not significantly different ($p < 0.05$).

The maximum value of CO_2 efflux was found in the oak–pine forest (15.5 μmol m^{-2} s^{-1}), while the lowest was in the pine forest (0.04 μmol m^{-2} s^{-1}). The mean soil CO_2 flux reached peaks of 7.87 μmol m^{-2} s^{-1} (pine), 6.72 μmol m^{-2} s^{-1} (pine–oak), and 9.32 μmol m^{-2} s^{-1} (oak–pine). The maximum values of CO_2 flux recorded in June corresponded to the highest average T_{soil} (14.58, 15.37, and 15.46 °C) in pine, pine–oak, and oak–pine forest, respectively.

As for temperature, the highest average CO_2 flux values coincided with the monthly highest M_{soil} records (June) in the three forest types: 88.61 (pine), 94.85 (pine–oak), and 75.94% (oak–pine) (Figure 3).

3.4. Relationships of Soil CO_2 Fluxes with Forest Diversity Metrics, Soil Temperature, Soil Moisture, and Forest Stand Variables

Forest type had no statistically significant effects on soil CO_2 (F-value = 1.586, $p = 0.2068$, $\alpha = 0.05$), T_{soil} (F-value = 1.776, $p = 0.175$, $\alpha = 0.05$), or M_{soil} (F-value = 0.423, $p = 0.656$, $\alpha = 0.05$). However, the analysis of variance indicated that the interaction between forest type and months had a significant effect on soil CO_2 flux (F-value = 13.28, $p = 0.0001$, $\alpha = 0.05$) and on M_{soil} (F-value = 4.21, $p = 0.0002$, $\alpha = 0.05$). T_{soil} and M_{soil} did not differ significantly among forest types.

Soil respiration was positively correlated with soil temperature ($r = 0.44$) and soil moisture ($r = 0.45$) at 0.1 m depth. Likewise, CO_2 flux showed significant positive correlations with stand variables, such as basal area ($r = 0.48$), tree density ($r = 0.48$), and aboveground biomass ($r = 0.36$) (Figure 4). Soil respiration was similarly positively correlated with diversity metrics (species richness, $r = 0.25$; Shannon, $r = 0.25$; and Simpson, $r = 0.13$). In contrast, T_{soil} was negatively correlated with basal area ($r = -0.51$, $p = 0.003$), biomass ($r = -0.45$, $p < 0.000$), number of species ($r = -0.35$, $p = 0.033$), and Shannon ($r = -0.18$, $p = 0.037$) and Simpson indices ($r = -0.23$, $p = 0.016$). Regarding M_{soil}, a positive correlation was observed with aboveground biomass ($r = 0.48$, $p = 0.021$), basal area ($r = 0.42$, $p = 0.029$), Simpson's index ($r = 0.35$, $p = 0.016$), and species richness ($r = 0.31$, $p = 0.021$).

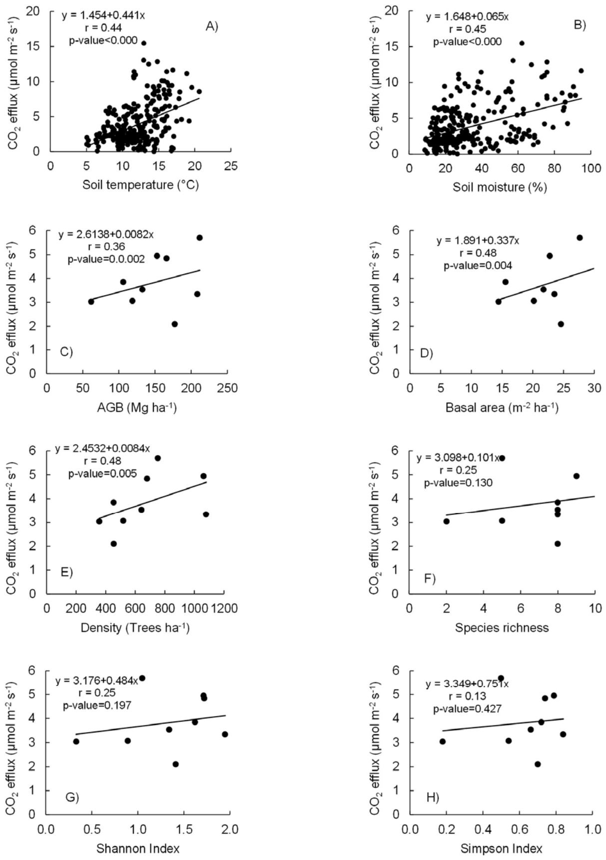

Figure 4. Relationships between soil respiration and soil temperature (**A**), soil moisture (**B**), aboveground biomass (**C**), stand variables (**D**,**E**), and diversity metrics (**F**–**H**). The solid line represents the fitted linear regression.

3.5. Model for Estimating Soil Respiration

Soil CO_2 efflux was estimated with the following generalized linear model:

$$CO_2 \text{ efflux} = b1\,(T_{soil}) + b2\,(M_{soil}) + b3\,(S) + b4\,(\text{Simpson}) + b5\,(Dq) + b6\,(AGB)$$

The model explained 48.3% of the variance in soil CO_2 flux in the three forest types. All parameters were highly significant at a 99% confidence level. The sign of the parameters was, in all cases, biologically logical, so the model is considered adequate (Table 4). The residuals of the model did not show any trends indicating no problems of heteroscedasticity.

Table 4. Estimates and goodness-of-fit of the GLM procedure for estimating CO_2 efflux in temperate forests.

					Cross-Validation	
Parameter	**Estimate**	**Std. Err.**	**$t_{(262)}$**	***p*-Value**	**RMSE**	**R^2**
b1	0.1030	0.0075	13.6992	<0.0000	2.483	0.483
b2	0.0166	0.0011	16.5048	<0.0000		
b3	0.0599	0.0190	3.1613	<0.0000		
b4	−1.2549	0.2572	−4.8799	<0.0000		
b5	−0.0328	0.0055	−5.9732	<0.0000		
b6	0.0039	0.0007	5.2337	<0.0000		

4. Discussion

Despite the importance of soil organic carbon in terrestrial carbon cycle dynamics, few studies have analysed the influence of forest type, soil temperature, and soil moisture on CO_2 fluxes in managed forests in Mexico. This study provides key information for understanding the dynamics of soil respiration in three forest types.

The average CO_2 effluxes observed for the three forest types fell within the range of soil respiration values reported in similar research [4,23–27]. Likewise, the mean values of CO_2 effluxes obtained in our study were similar to those reported by Yáñez-Díaz et al. [28], who found CO_2 effluxes of 3.86 and 4.33 µmol m^{-2} s^{-1} in *Eucalyptus camaldulensis* and *E. microtheca* forest plantations in Northeastern Mexico, respectively.

The observed CO_2 efflux patterns showed no significant differences between forest types. The fact that no differences in CO_2 efflux were identified might be a result of the low variability in species diversity in such forests [29] and the observed IVI values of some species (Figure 2). Our results come from three forest types defined by the dominance of species belonging to genus *Pinus* and *Quercus*. However, the three forest types are mixed pine–oak forests, even the one named pine forest. In addition, since the studied forests are located close to each other under same edaphic and climatic conditions, T_{soil} and M_{soil} showed little differences among them; we may expect low differentiation in the microbial community, both in total microbial biomass and community structure (fungi, bacteria, and actinomycetes) due to the similar amount of litterfall and mixtures in forest floor litter, and therefore, low differences in soil CO_2 efflux since soil microorganisms are highly important in affecting this process [30]. Furthermore, the absence of significant differences in CO_2 efflux patterns suggests that certain dominant species, such as *Quercus siredoxyla* in the pine–oak and oak–pine forests and *Pinus durangensis* and *Pinus cooperi* in the pine forest, along with *P. durangensis*, which is common to all three forest types, may strongly influence the autotrophic respiration processes. Consequently, soil respiration rates could be remarkably similar across the different forest types. The statement by Peng et al. [31] supports our findings, since they point out that the differences in soil respiration among stands also result from the prevailing tree species.

Despite the lack of statistical differences among the three forest types, the highest CO_2 efflux was found in the forest with the highest aboveground biomass (AGB) stocks (oak–pine forest). Such dynamics of soil respiration in this forest type are due to the fact that mixed broadleaved forests produce more readily decomposable litter than coniferdominated forests [32], and that mixed forests have higher net primary productivity than pine [4], which means that the higher AGB in the oak–pine forest is associated with increased microbial soil respiration. These results are reasonable and support the assumption that autotrophic respiration is closely related to aboveground productivity, due to the C input from plants functioning as a substrate for root respiration [33], whereby AGB positively conditions soil respiration.

Although many studies have reported different soil respiration rates, our findings are in line with prior research reporting that CO_2 effluxes do not significantly differ among forest types. For instance, Borken et al. [2] found that soil respiration was not significantly different among *Fagus sylvatica*, *Picea abies*, and *Pinus sylvestris* forest stands in Germany. Similarly, Hibbard et al. [23] reported that soil CO_2 fluxes did not differ between deciduous broadleaf and conifer forests, and Kim et al. [34] observed no statistical differences in CO_2 efflux among deciduous, conifer, and mixed forests in South Korea. The above means that other factors such as soil moisture, rainfall intensity and frequency, temperature, litter decomposition rate, and the amount of carbon derived from organic matter regulate CO_2 effluxes in forest ecosystems [35].

While the main aim of this study was to explore the effect of forest types, we observed that seasonal variation could be an important aspect to consider in understanding carbon dynamics in the forests evaluated. Soil respiration was constant and relatively low during the first months of the study period (January–April). This may have been due to the fact that during the winter season and the first months of spring, the CO_2 efflux is affected by low temperatures, although M_{soil} remains relatively high. From March to mid-May, soil M_{soil} decreased due to the increase in environment temperature, lack of precipitation, and the beginning of physiological activities of plants, drastically reducing the CO_2 efflux. From mid-May onwards, the CO_2 efflux gradually increased, reaching a peak in June. Normally in this region of Mexico, at the end of May, the first rainfall favours the biological activities in the soil profile, reactivating microbial activity. This is the factor suggesting the high soil moisture and nutrient supply throughout the growing season led to the highest CO_2 efflux in June [5].

Soil respiration was positively related to species richness; consequently, the results highlight the importance of maintaining species diversity and aboveground biomass stocks in order to preserve the ecosystem processes driving soil respiration. The highest species diversity was observed in the oak–pine forest (Table 2), which corresponded to the highest CO_2 efflux. This positive relationship between species richness and CO_2 efflux can be understood under the assumption that more diverse sites are more productive in the multiplicity of ecosystem processes, due to species complementarity [36]. In this context, Bréchet et al. [37] highlighted that tree species are one of the most important factors in the variation in soil respiration. Our results are consistent with those reported by Hirota et al. [38], who pointed out that vegetation properties, including plant biomass and species richness, determined the small-scale heterogeneity of soil CO_2 fluxes. Likewise, litter decomposition rate is directly related to diversity, a process that is also directly related to a higher diversity of decomposer microorganisms [39]. Authors such as Li et al. [40] found that soil CO_2 fluxes are directly influenced by species diversity, as a result of facilitation in soil microbiota, which, by decomposing leaf litter, increase soil respiration. Similarly, Salahuddin et al. [41] highlighted that plants invest more energy in intraspecific competition for belowground resources and, therefore, autotrophic respiration shows an increasing trend with decreasing plant diversity. Moreover, aboveground biomass influences CO_2 efflux due to the amount of litter and nutrients incorporated into the system, both in broadleaf forest soils [42] and in conifer forest soils [15]; consequently, a higher litter input favours the interaction of microorganisms and increases soil respiration [43].

We observed a positive correlation between CO_2 efflux and T_{soil}. This finding is consistent with those reported in other studies, in which T_{soil} was the main factor controlling soil respiration [30,44,45]. Furthermore, Cantú-Silva et al. [46] reported that soil CO_2 fluxes are directly influenced by T_{soil}, where microorganisms responsible for the decomposition of soil organic matter are involved. Nevertheless, Sugasti et al. [47] point out that, although there is a positive correlation between CO_2 efflux and T_{soil}, variations in this variable are not the only factor driving soil CO_2 fluxes; therefore, each particular forest depends on a balance of conditions such as soil moisture content, belowground biomass and microorganisms, which play an important role in CO_2 production and transport to the soil surface.

Based on the aforementioned statement, we identified a correlation between soil water content, measured through M_{soil}, and CO_2 efflux ($r = 0.45$). This is consistent with the findings reported by Li et al. [48] and Zhang et al. [49], who emphasize that soil moisture is a key factor controlling soil respiration since it inhibits the diffusion of CO_2. The lowest soil CO_2 fluxes were found in March, April, and May, when the M_{soil} reached its minimum values of 9.23, 9.05, and 8.78%. This finding is congruent with the observations by Darenova and Čater [3], who highlight that soil moisture is not sufficient to explain the variability of soil respiration, but it is one of main drivers for temporal CO_2 efflux variation in forests. Similar conclusions have been reached by authors such as Kosugi et al. [50] and Darenova et al. [51].

Soil respiration was positively correlated with canopy cover, assessed by tree density (trees ha^{-1}) and basal area. This correlation is explained in a study by Tscharntke et al. [52], who described the shading effect caused by forest structures, particularly the upper canopy species, leading to favourable microclimatic conditions with reduced temperatures in the understory. Consequently, plants in the canopy filter and absorb a portion of the solar radiation, mitigating its impact and thermally regulating the soil surface while maintaining adequate water availability. These optimal temperature conditions support the proliferation of soil microorganisms and facilitate their metabolic processes, including respiration.

The developed Generalized Linear Model (GLM) was designed to consider the effect of T_{soil}, M_{soil}, stand-related factors and diversity metrics on CO_2 efflux, and it showed good performance. The fitted model explained more than 48% of the variability of the soil respiration in the three forest types evaluated. The explained CO_2 efflux variance was higher than the reported in similar studies, such as the one conducted by Yan et al. [4] ($R^2 = 0.38$), who used the soil temperature as an explanatory variable. Similarly, in studies such as those by Chen et al. [53], Wang et al. [54], and Tian et al. [55], soil temperature alone accounted for about 40% of the seasonal fluctuations in soil respiration. However, these models often rely on single-factor associations, which can be confounded by other factors. In contrast, our model significantly enhanced its performance by including species richness, Simpson's diversity index, stand quadratic diameter, and aboveground biomass as explanatory variables. These additions contributed approximately 10% to explaining the variation in CO_2 efflux data.

This is of particular importance, because it indicates that soil temperature and soil moisture are not necessarily the sole controlling factors over soil respiration in forest ecosystems. This perspective is consistent with Reichstein et al. [56], who formulated nonlinear regression models that encompassed, in addition to soil temperature and soil moisture, factors such as leaf area index, leaf biomass, leaf productivity, aboveground biomass and soil carbon stock, as well as precipitation and air temperature, achieving acceptable model performance.

5. Conclusions

Soil respiration showed consistent rates across forest types, suggesting uniformity in CO_2 efflux processes. The absence of significant differences in CO_2 efflux patterns could be explained by the presence of one or two dominant species common to the three forest types, which may strongly influence the autotrophic respiration processes. Within the temperate forests of Northwestern Mexico, fluctuations in CO_2 efflux over time seem to be controlled mainly by soil temperature and soil moisture. Nevertheless, this study also highlighted the significance of not only such biophysical controls, but also other ecological parameters, such as diversity metrics (e.g., species diversity and richness), structural stand indicators such as the quadratic mean diameter and basal area, as well as aboveground biomass. GLM regression analysis yielded suitable estimates of CO_2 efflux, providing information that can be used as a basis for soil CO_2 emissions. Although the focus of the study was to identify differences in CO_2 fluxes among forest types, the results also may establish a baseline for future research to assess the impact of human (e.g., forest management practices) and natural disturbances on CO_2 dynamics within the soil–atmosphere relationship of these temperate forests. This holds particular importance due to the direct influence of forest management practices, such as harvesting and thinning, on regional and global carbon balance.

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References

1. Lal, R. Sequestration of atmospheric CO_2 in global carbon pools. *Energy Environ. Sci.* **2008**, *1*, 86–100. [CrossRef]
2. Nielsen, U.N.; Ayres, E.; Wall, D.H.; Bardgett, R.D. Soil biodiversity and carbon cycling: A review and synthesis of studies examining diversity-function relationships. *Eur. J. Soil Sci.* **2011**, *62*, 105–116. [CrossRef]
3. Darenova, E.; Čater, M. Effect of spatial scale and harvest on heterogeneity of forest floor CO_2 efflux in a sessile oak forest. *CATENA* **2020**, *188*, 104455. [CrossRef]
4. Yan, W.D.; Xu, W.M.; Chen, X.Y.; Tian, D.L.; Peng, Y.Y.; Zhen, W.; Zhang, C.; Xu, J. Soil CO_2 flux in different types of forests under a subtropical microclimatic environment. *Pedosphere* **2014**, *24*, 243–250. [CrossRef]
5. Finderup, N.T.; Rand, R.N.; Michelsen, A. Increased CO_2 efflux due to long-term experimental summer warming and litter input in subarctic tundra—CO_2 fluxes at snowmelt, in growing season, fall and winter. *Plant Soil* **2019**, *444*, 365–382. [CrossRef]
6. Chase, J.M.; Leibold, M.A. Spatial scale dictates the productivity-biodiversity relationship. *Nature* **2002**, *416*, 427–430. [CrossRef]
7. Bohdalková, E.; Toszogyova, A.; Šímová, I.; Storch, D. Universality in biodiversity patterns: Variation in species–temperature and species–productivity relationships reveal a prominent role of productivity in diversity gradients. *Ecography* **2021**, *44*, 1366–1378. [CrossRef]
8. Van Ruijven, J.; Berendse, F. Positive effects of plant species diversity on productivity in the absence of legumes. *Ecol. Lett.* **2003**, *6*, 170–175. [CrossRef]
9. Lellei-Kovács, E.; Kovács-Láng, E.; Botta-Dukát, Z.; Kalapos, T.; Emmett, B.; Beier, C. Thresholds and interactive effects of soil moisture on the temperature response of soil respiration. *Eur. J. Soil Biol.* **2011**, *47*, 247–255. [CrossRef]
10. Smith, K.; Ball, T.; Conen, F.; Dobbie, K.; Massheder, J.; Rey, A. Exchange of greenhouse gases between soil and atmosphere: Interactions of soil physical factors and biological processes. *Eur. J. Soil Sci.* **2003**, *54*, 779–791. [CrossRef]
11. Luo, Y.; Zhou, X. *Soil Respiration and the Environment*; Elsevier: Berkeley, CA, USA, 2006. [CrossRef]
12. Adachi, M.; Ito, A.; Yonemura, S.; Takeuchi, W. Estimation of global soil respiration by accounting for land-use changes derived from remote sensing data. *J. Environ. Manag.* **2017**, *200*, 97–104. [CrossRef] [PubMed]
13. Acosta, M.; Darenova, E.; Krupková, L.; Pavelka, M. Seasonal and inter-annual variability of soil CO_2 efflux in a Norway spruce forest over an eight-year study. *Agric. For. Meteorol.* **2018**, *256–257*, 93–103. [CrossRef]
14. De Carlo, N.D.; Oelbermann, M.; Gordon, A.M. Carbon dioxide emissions: Spatiotemporal variation in a young and mature riparian forest. *Ecol. Eng.* **2019**, *138*, 353–361. [CrossRef]
15. Jílková, V. Soil respiration in temperate forests is increased by a shift from coniferous to deciduous trees but not by an increase in temperature. *Appl. Soil Ecol.* **2020**, *154*, 103635. [CrossRef]
16. Merino, A.; Edeso, J.M.; González, M.J.; Marauri, P. Soil properties in a hilly area following different harvesting management practices. *For. Ecol. Manag.* **1997**, *103*, 235–246. [CrossRef]
17. Challenger, A. *Use and Conservation of Mexico's Terrestrial Ecosystems: Past, Present and Future*; Comisión Nacional para el Conocimiento y Uso de la Biodiversidad/Instituto de Biología, UNAM-Agrupación Sierra Madre: Mexico City, Mexico, 1998.
18. García, E. *Modificaciones al Régimen de Clasificación Climática de Köppen*; Instituto de Geografía, UNAM: Mexico City, Mexico, 1988.

19. Instituto Nacional de Estadística Geográfica e Informática (INEGI). *Uso del Suelo y Vegetación Escala 1:250 000 Serie V, Información Vectorial*; INEGI: Mexico City, Mexico, 2012.
20. Borken, W.; Xu, Y.J.; Davidson, E.A.; Beese, F. Site and temporal variation of soil respiration in European beech, Norway spruce, and Scots pine forests. *Glob. Change Biol.* **2002**, *8*, 1205–1216. [CrossRef]
21. R Core Team. *R: A Language and Environment for Statistical Computing*; R Foundation for Statistical Computing: Vienna, Austria, 2020.
22. Vargas-Larreta, B.; López, S.C.; Corral-Rivas, J.J.; López, M.J.; Aguirre, C.C.; Álvarez-González, J.G. Allometric equations for estimating biomass and carbon stocks in the temperate forests of North-Western Mexico. *Forests* **2017**, *8*, 269. [CrossRef]
23. Hibbard, K.A.; Law, B.E.; Reichstein, M.; Sulzman, J. An analysis of soil respiration across northern hemisphere temperate ecosystems. *Biogeochemistry* **2005**, *73*, 29–70. [CrossRef]
24. Adachi, M.; Bekku, Y.; Konuma, A.; Kadir, W.; Okuda, T.; Koizumi, H. Required sample size for estimating soil respiration rates in large areas of two tropical forests and of two types of plantations in Malaysia. *For. Ecol. Manag.* **2005**, *210*, 455–459. [CrossRef]
25. Se-Hoon, J.; Dong-Joo, K.; Chan-Woo, P.; Seong-Deog, K. Appropriate sampling points and frequency of CO_2 measurements for soil respiration analysis in a pine (*Pinus densiflora*) forest. *Anim. Cells Syst.* **2015**, *19*, 332–338. [CrossRef]
26. Pantani, O.L.; Fioravanti, F.; Stefanini, F.M.; Berni, R.; Certini, G. Accounting for soil respiration variability—Case study in a Mediterranean pine-dominated forest. *Sci. Rep.* **2020**, *10*, 1787. [CrossRef] [PubMed]
27. Barba, J.; Yuste, J.C.; Martínez-Vilalta, J.; Lloret, F. Drought-induced tree species replacement is reflected in the spatial variability of soil respiration in a mixed Mediterranean forest. *For. Ecol. Manag.* **2013**, *306*, 79–87. [CrossRef]
28. Yáñez-Díaz, M.I.; Cantú-Silva, I.; González-Rodríguez, H.; Marmolejo-Monsiváis, J.G.; Jurado, E.; Gómez-Meza, M.V. Soil respiration in four land use systems. *Rev. Mex. Cienc. For.* **2017**, *8*, 123–149.
29. Čater, M.; Darenova, E.; Simončič, P. Harvesting intensity and tree species affect soil respiration in uneven-aged Dinaric Forest stands. *For. Ecol. Manag.* **2021**, *480*, 118638. [CrossRef]
30. Zhang, Y.; Zou, J.; Meng, D.; Dang, S.; Zhou, J.; Osborne, B.; Ren, Y.; Liang, T.; Yu, K. Effect of soil microorganisms and labile C availability on soil respiration in response to litter inputs in forest ecosystems: A metaanalysis. *Ecol. Evol.* **2020**, *10*, 13602–13612. [CrossRef]
31. Peng, Y.; Thomas, S.C.; Tian, D. Forest management and soil respiration: Implications for carbon sequestration. *Environ. Rev.* **2008**, *16*, 93–111. [CrossRef]
32. Wang, C.; Yu, G.; Zhon, G.; Yan, J.; Zhang, L.; Wang, X.; Tang, X.; Sun, X. CO_2 flux elevations over the evergreen coniferous and broadleaved mixed forest in Ginghushan, China. *Sci. China Ser. D Earth Sci.* **2006**, *49* (Suppl. S2), 127–138. [CrossRef]
33. Wertin, T.M.; Belnap, J.; Reed, S.C. Experimental warming in a dryland community reduced plant photosynthesis and soil CO_2 efflux although the relationship between the fluxes remained unchanged. *Funct. Ecol.* **2017**, *31*, 297–305. [CrossRef]
34. Kim, D.G.; Mu, S.; Kang, S.; Lee, D. Factors controlling soil CO_2 effluxes and the effects of rewetting on effluxes in adjacent deciduous, coniferous, and mixed forests in Korea. *Soil Biol. Biochem.* **2010**, *42*, 576–585. [CrossRef]
35. Yan, T.; Qu, T.; Song, H.; Sun, Z.; Zeng, H.; Peng, S. Ectomycorrhizal fungi respiration quantification and drivers in three differently-aged larch plantations. *Agric. For. Meteorol.* **2019**, *265*, 245–251. [CrossRef]
36. Tilman, D.; Knops, J.; Wedin, D.; Reich, P.; Ritchie, M.; Siemann, E. The Influence of functional diversity and composition on ecosystem processes. *Science* **1997**, *277*, 1300–1302. [CrossRef]
37. Bréchet, L.; Ponton, S.; Roy, J.; Freycon, V.; Coûteaux, M.; Bonal, D.; Epron, D. Do tree species characteristics influence soil respiration in tropical forests? A test based on 16 tree species planted in monospecific plots. *Plant Soil* **2009**, *319*, 235–246. [CrossRef]
38. Hirota, M.; Zhang, P.; Gu, S.; Shen, H.; Kuriyama, T.; Li, Y.; Tang, Y. Small-scale variation in ecosystem CO_2 fluxes in an alpine meadow depends on plant biomass and species richness. *J. Plant Res.* **2010**, *123*, 531–541. [CrossRef] [PubMed]
39. Gessner, M.O.; Swan, C.M.; Dang, C.K.; McKie, B.G.; Bardgett, R.D.; Wall, D.H.; Hättenschwiler, S. Diversity meets decomposition. *Trends Ecol. Evol.* **2010**, *25*, 372–380. [CrossRef]
40. Li, Q.; Tian, Y.; Zhan, X.; Xu, X.; Wang, H.; Kuzyakov, Y. Labile carbon and nitrogen additions affect soil organic matter decomposition more strongly than temperature. *Appl. Soil Ecol.* **2017**, *114*, 152–160. [CrossRef]
41. Salahuddin, R.B.; Razaq, M.; Li, J.; Khan, F.; Jie, Z. Root order-based traits of Manchurian walnut & larch and their plasticity under interspecific competition. *Sci. Rep.* **2018**, *8*, 9815. [CrossRef]
42. Kammer, A.; Schmidt, M.W.; Hagedorn, F. Decomposition pathways of 13C-depleted leaf litter in forest soils of the Swiss Jura. *Biogeochemistry* **2012**, *108*, 395–411. [CrossRef]
43. Shaver, G.R.; Johnson, L.C.; Cades, D.H.; Murray, G.; Laundre, J.A.; Rastetter, E.B.; Nadelhoffer, K.J.; Giblin, A.E. Biomass and CO_2 flux in wet sedge tundras: Responses to nutrients, temperature, and light. *Ecol. Monogr.* **1998**, *68*, 75–97. [CrossRef]
44. Reth, S.; Reichstein, M.; Falge, E. The effect of soil water content, soil temperature, soil pH-value and the root mass on soil CO_2 efflux—A modified model. *Plant Soil* **2005**, *268*, 21–33. [CrossRef]
45. Wei, W.; Weile, C.; Shaopeng, W. Forest soil respiration and its heterotrophic and autotrophic components: Global patterns and responses to temperature and precipitation. *Soil Biol. Biochem.* **2010**, *42*, 1236–1244. [CrossRef]
46. Cantú-Silva, I.; González-Rodríguez, H.; Gómez-Meza, M.V. CO_2 efflux in vertisol under different land use systems. *Trop. Subtrop. Agroecosystems* **2010**, *12*, 389–403.

47. Sugasti, L.; Eng, B.; Pinzón, R. Medición continúa de flujo de CO_2 en suelo en una parcela de bosque tropical en Isla Barro Colorado, Canal de Panamá. In Proceedings of the 16th LACCEI International Multi-Conference for Engineering, Education, and Technology: Innovation in Education and Inclusion, Lima, Peru, 19–21 July 2018. [CrossRef]
48. Li, Y.L.; Otieno, D.; Owen, K.; Zhang, Y.; Tenhunen, J.; Rao, X.Q.; Lin, Y.B. Temporal variability in soil CO_2 emission in an orchard forest ecosystem. *Pedosphere* **2008**, *18*, 273–283. [CrossRef]
49. Zhang, P.; Tang, Y.; Hirota, M.; Yamamoto, A.; Mariko, S. Use of a regression method to partition sources of ecosystem respiration in an alpine meadow. *Soil Biol. Biochem.* **2009**, *41*, 663–670. [CrossRef]
50. Kosugi, Y.; Mitani, T.; Itoh, M.; Noguchi, S.; Tani, M.; Matsuo, N.; Takanashi, S.; Ohkubo, S.; Nik, A.R. Spatial and temporal variation in soil respiration in a Southeast Asian tropical rainforest. *Agric. For. Meteorol.* **2007**, *147*, 35–47. [CrossRef]
51. Darenova, E.; Pavelka, M.; Macalkova, L. Spatial heterogeneity of CO_2 efflux and optimization of the number of measurement positions. *Eur. J. Soil Biol.* **2016**, *75*, 123–134. [CrossRef]
52. Tscharntke, T.; Clough, Y.; Bhagwat, S.A.; Buchori, D.; Faust, H.; Hertel, D.; Hölscher, D.; Juhrbandt, J.; Kessler, M.; Perfecto, I.; et al. Multifunctional shade-tree management in tropical agroforestry landscapes—A review. *J. Appl. Ecol.* **2011**, *48*, 619–629. [CrossRef]
53. Chen, X.Y.; Eamus, D.; Hutley, L.B. Seasonal patterns of soil carbon dioxide efflux from a wet-dry tropical savanna of northern Australia. *Aust. J. Bot.* **2002**, *50*, 43–51. [CrossRef]
54. Wang, C.K.; Yang, J.Y.; Zhang, Q.Z. Soil respiration in six temperate forests in China. *Glob. Chang. Biol.* **2006**, *12*, 2103–2114. [CrossRef]
55. Tian, D.L.; Peng, Y.Y.; Yan, W.D.; Fang, X.; Kang, W.X.; Wang, G.J.; Chen, X.Y. Effects of thinning and litter fall removal on fine root production and soil organic carbon content in Masson pine plantations. *Pedosphere* **2010**, *20*, 486–493. [CrossRef]
56. Reichstein, M.; Rey, A.; Freibauer, A.; Tenhunen, J.; Valentini, R.; Banza, J.; Casals, P.; Cheng, Y.; Grünzweig, J.; Irvine, J.; et al. Modeling temporal and large-scale spatial variability of soil respiration from soil water availability, temperature and vegetation productivity indices. *Glob. Biogeochem. Cycles* **2003**, *17*, 1104. [CrossRef]