forests

MDPI

Article

Black Alder (*Alnus glutinosa* (L.) Gaertn.) on Compacted Skid Trails: A Trade-off between Greenhouse Gas Fluxes and Soil Structure Recovery?

Hannes Warlo [1,*], Klaus von Wilpert [2], Friederike Lang [1] and Helmer Schack-Kirchner [1]

1 Institute of Forest Sciences, University of Freiburg, D-79085 Freiburg, Germany
2 Department of Soil and Environment, Forest Research Institute of Baden-Württemberg, D-79100 Freiburg, Germany
* Correspondence: hannes.warlo@bodenkunde.uni-freiburg.de; Tel.: +49-761-203-3816

Received: 16 July 2019; Accepted: 23 August 2019; Published: 24 August 2019

check for updates

Abstract: The compaction of forest soils can deteriorate soil aeration, leading to decreased CH_4 uptake and increased N_2O efflux. Black alder (*Alnus glutinosa*) may accelerate soil structure regeneration as it can grow roots under anaerobic soil conditions. However, symbiotic nitrogen fixation by alder can have undesirable side-effects on greenhouse gas (GHG) fluxes. In this study, we evaluated the possible trade-off between alder-mediated structure recovery and GHG emissions. We compared two directly adjacent 15-year old beech (*Fagus sylvatica*) and alder stands (loamy texture, pH 5–6), including old planted skid trails. The last soil trafficking on the skid trails took place in 1999. GHG fluxes were measured over one year. Undisturbed plots with beech had a moderately higher total porosity and were lower in soil moisture and soil organic carbon than undisturbed alder plots. No differences in mineral nitrogen were found. N_2O emissions in the undisturbed beech stand were 0.4 kg ha^{-1} y^{-1} and 3.1 kg ha^{-1} y^{-1} in the undisturbed alder stand. CH_4 uptake was 4.0 kg ha^{-1} y^{-1} and 1.5 kg ha^{-1} y^{-1} under beech and alder, respectively. On the beech planted skid trail, topsoil compaction was still evident by reduced macro porosity and soil aeration; on the alder planted skid trail, soil structure of the uppermost soil layer was completely recovered. Skid trail N_2O fluxes under beech were five times higher and CH_4 oxidation was 0.6 times lower compared to the adjacent undisturbed beech stand. Under alder, no skid-trail-effects on GHG fluxes were evident. Multiple regression modelling revealed that N_2O and CH_4 emissions were mainly governed by soil aeration and soil temperature. Compared to beech, alder considerably increased net fluxes of GHG on undisturbed plots. However, for skid trails we suggest that black alder improves soil structure without deterioration of the stand's greenhouse gas balance, when planted only on the compacted areas.

Keywords: soil compaction; skid trails; black alder; *Alnus glutinosa*; greenhouse gas fluxes; soil structure recovery

1. Introduction

Compaction and deformation of forest soils is a widespread issue caused by fully mechanized logging. When soil trafficking during forest operations is restricted to permanent skid trails [1], the remaining forest stand is fully protected from soil compaction. In practice, spacing between skid trails is often in the range of 20 and 40 m. When distances are 20 m, around 12–16% of the total operational stand area is affected by soil physical changes [2]. As a result, coarse soil porosity decreases and pore continuity is interrupted, leading to reduced soil aeration [3,4]. Although it is well documented that reduced soil aeration can increase greenhouse gas (GHG) emissions from forest soils, the persistence of such changes is mostly unclear and little is known regarding tree species effects on soil structure recovery.

In well aerated forest soils, methanotrophic bacteria oxidize atmospheric methane (CH_4) to carbon dioxide (CO_2) and water. On a global scale, this sink consumes 1–9% of the annual CH_4 emissions [5]. When the degradation of organic matter occurs in poorly aerated soils under anaerobic conditions, methanogenic bacteria release CH_4 [6]. Oxygen availability is also a key factor for N_2O formation in soils [7]. N_2O is mainly produced by aerobic nitrification and anaerobic denitrification with the latter being considered the dominant process [8]; however, many other biotic and abiotic processes releasing N_2O were identified [9]. Highest N_2O emissions were reported when >60% of pore spaces were water-filled, i.e., low oxygen availability [8,10,11], whereas completely anerobic soil conditions can lead to reduced or even negative N_2O fluxes [12]. On skid trails, Teepe et al. [2] found N_2O emissions up to 40 times higher compared to undisturbed plots. CH_4 oxidation rates were significantly lower and in some cases positive CH_4 fluxes were measured. Similarly, Frey et al. [13] reported reduced CH_4 oxidation rates and positive CH_4 fluxes on skid trails. In contrast, Epron et al. [14] found no significant changes in CH_4 fluxes in a soil trafficked with heavy forest machinery.

In compacted soils, natural structure recovery can take several decades [15,16]. Recent research focuses on biological soil structure formation induced by plants. The benefit of planting tree species [17,18] or herbs [19] tolerant to poor soil aeration or "stagnic" [20] soil conditions has been assessed. Proposed processes of structure formation caused by plant roots are (i) shrinkage by water extraction, (ii) the introduction root litter and other rhizo-deposition promoting soil fauna or acting as a binding agent between soil particles, and (iii) the formation of macropores by root penetration [21,22].

Concerning biological soil regeneration, promising results were obtained with black alder (*Alnus glutinosa* (L.) Gaertn.). Its roots can penetrate anaerobic soils due to an aerenchyma that enables transport of oxygen to the roots via diffusion and stem photosynthesis [23,24]. Meyer et al. [17] showed that seven years after planting, black alders had developed a vital root system in a compacted sandy loam soil on a skid trail. Soil recovery was observed to a depth of 70 cm by the generation of air-conducting porosity. At another site with a silty to clayey loam texture, Flores Fernández et al. [18] found positive effects on soil aeration by several tree species tolerant to poor soil aeration including black alder.

Based on these findings, recovered soil structure, improved soil aeration, increased CH_4 oxidation, and a reduction of N_2O production in alder stands can be assumed. However, alder species live in symbiosis with nitrogen-fixing actinomycetes *Frankia alni* [25]. Via this pathway, input of more than 100 kg N ha^{-1} y^{-1} is possible [26], providing large amounts of substrate for the N_2O releasing processes of nitrification and denitrification. Mogge et al. [27] reported 15 times higher N_2O emissions from a drained black alder forest compared to a beech forest due to higher contents of water-soluble OC and nitrate contents. This is in accordance with findings of Bühlmann et al. [28] who measured on average 12 times higher N_2O emissions under different alder species compared to non-N_2-fixing species. Reay et al. [29] found reduced CH_4 oxidation rates under black alder, presumably due to elevated nitrate (NO_3) or ammonium (NH_4) contents in the soil, caused by N-fixation. Several other studies reported an inhibition of CH_4 oxidation by NH_4 [30,31].

The aim of the present study was to evaluate how black alder planted on skid trails affects GHG fluxes and soil physical and chemical parameters compared to skid trails planted with beech. Gas flux measurements in two adjacent 15-years-old single species stands of black alder and beech were conducted over a period of one year, followed by destructive sampling to carry out soil physical and chemical analyses.

2. Materials and Methods

2.1. Study Site and Experimental Design

The study site was in the Tepfenharder Wald (47°46′12″ N 9°28′11″ E, 540 m asl) near Ravensburg in Southern Germany. The mean annual temperature between 2007 and 2017 at the closest meteorological station was 9.6 °C and mean annual precipitation was 900 mm [32]. The soil developed on glacial tills and was classified as a eutric Gleysol (Loamic, Humic) according to IUSS Working Group WRB [20] with a texture in the upper 20 cm consisting of 32% sand, 45% silt, 23% clay. Across the studied area, there was no slope gradient.

Until 1999, the study site was planted with a 90-year-old stand consisting of 65% spruce (*Picea abies* (L.) Karst.), 20% silver fir (*Abies alba* Mill.), and 15% beech (*Fagus sylvatica* L.). The whole stand was thrown by a hurricane in 1999. In 2001, two neighboring single-species stands of beech and black alder, respectively were established. The area was planted manually in 2001 without application of fertilizer or lime. In 2016, timber stocks in the beech stand were 95 $m^3\ ha^{-1}$ at an average tree height of 12 m and 183 $m^3\ ha^{-1}$ in the alder stand at an average tree height of 15 m.

In 2016, an abandoned skid trail (to that point at least 15 years without trafficking) traversing both stands was chosen as research object. The former skid trail was included in the planting area as no difference between undisturbed and disturbed soil was made during planting (Figure 1). For our measurements, five transects were established perpendicular to the skid trail in both stands, respectively, and each transect was subdivided in three strata: (i) undisturbed stand, (ii) wheel track, the part of the skid trail where direct contact between machine and soil occurred, and (iii) center bulge (strip between the wheel tracks).

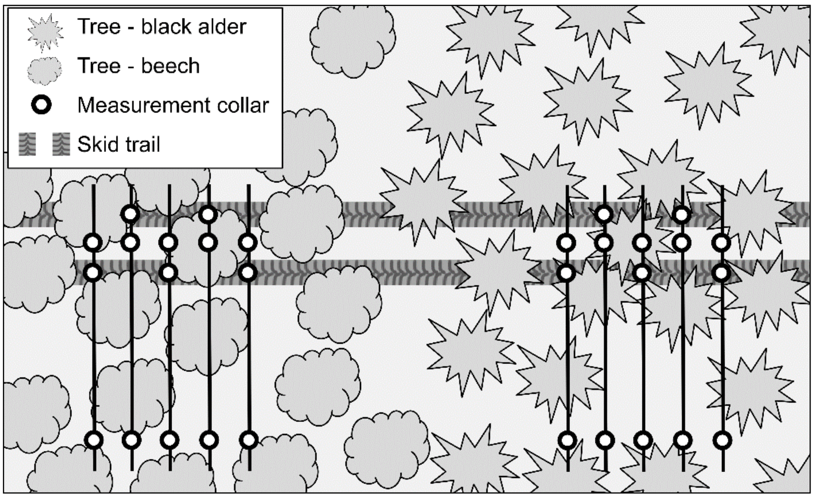

Figure 1. Sketch of the two adjacent stands of black alder and beech with an abandoned skid trail. Measurement collars were installed along five stratified transects per stand: undisturbed stand, wheel track and center bulge.

2.2. Field Measurements

Two months before the first gas flux measurement, five PVC collars (15.5 cm inner diameter and 9 cm in height) were installed in each stratum, resulting in a total of 30 measurement collars (Figure 1). Inserted into the soil to a depth of 5 cm, the collars served as permanent anchors for the chambers during soil gas flux measurement. Flux measurements of CO_2, CH_4, and N_2O were conducted between June 2016 and June 2017. A total of 17 measurement campaigns were carried out with a temporal resolution of at least one measurement per month. Closed chambers with a volume of 1800 cm^3 and a basal area of 179 cm^2, equipped with a vent, three small fans, a temperature sensor, and a sampling cannula were installed on the PVC collars. During 30 min chamber closure time, six gas samples were drawn at minutes 1, 3, 7, 13, 20, and 30 with evacuated glass vials (10 ml) sealed with butyl stoppers. Samples were analyzed in the laboratory with a gas chromatograph (8000 series, Fisons, Loughborough, UK) equipped with a CarbonPLOT column (J&W Scientific, Folsom, CA, USA) and pure nitrogen as carrier gas (flow rate 13.2 mL s^{-1}). A flame ionization detector (FID) was used for CH_4 measurements and an electron capture detector (ECD) was used for N_2O and CO_2 measurements [33].

Soil-surface fluxes were calculated according to Hutchinson & Livingston [34] using robust linear regressions [35] of gas concentration change over time within the chambers. CO_2 equivalents of CH_4 and N_2O fluxes were calculated by assuming a global warming potential over a 100-year horizon of 28 (CH_4) and 265 (N_2O) times higher than that of CO_2 [36].

Volumetric soil moisture θ was measured close to each chamber with a FD probe (ML1, Delta-T Devices Ltd, Cambridge, United Kingdom) and chamber air temperature was measured with a digital thermometer (GTH 1160, GHM Messtechnik GmbH, Regenstauf, Germany) connected to a temperature sensor inside the chamber. Soil temperature at 5 cm depth was monitored continuously during each measurement campaign with a penetration probe connected to a precision thermometer (GMH 3700, GHM Messtechnik GmbH, Regenstauf, Germany) at a constant location. A transfer function using the air temperature and the soil temperature at 5 cm depth was applied to calculate an estimated soil temperature under each chamber.

2.3. Soil Sampling and Laboratory Analyses

Following the last measurement campaign in June 2017, soil rings (200 cm^3) were taken from 1–6 cm and 9–14 cm depth at the position of each collar. Vacuum pycnometry was used to calculate the percentage of air-filled soil fraction at field water content ε_{field} as a fraction of air-filled volume V_{air} from the volume of the soil cylinder V_{tot} (200 cm^3). To assess macro porosity (pores > 20 µm equivalent capillary diameter), the soil rings were saturated with water and then equilibrated to a water potential of −160 hPa (pF = 2.2) on a filter bed [37]. Macro porosity ε_{160} in percent was then calculated from ε_{field} and the percentage of mass difference between the soil sample at field water content m_{field} and the mass of the sample after equilibration to a water potential of −160 hPa m_{160}. Similarly, total porosity Φ was calculated based on ε_{field} and the percentage of mass difference between m_{field} and the mass of the soil sample after drying at 105 °C m_{dried}. Dried samples were also used to calculate bulk density ρ by dividing m_{dried} by V_{tot}. To calculate the water filled pore space (WFPS) in 1–6 cm soil depth, Φ was assumed constant over the whole measurement period. WFPS for every measurement chamber and month was calculated as the proportion of θ from Φ. Based on the assumption of constant Φ over the year, a calculated air-filled soil fraction ε_{calc} was derived for every month and measurement chamber by subtracting θ from Φ. Soil gas diffusivity D_S/D_0 of the soil rings at field fresh moisture state and equilibrated at a water potential of −160 hPa was measured in the laboratory with a method described by Kühne et al. [38]. To obtain D_s/D_0 data for the whole measurement period and for every measurement chamber, an empirical model for forest soils in south-west Germany proposed by Schack-Kirchner et al. [39] was applied to estimate $D_s/D_{0\,calc}$ based on ε_{calc}:

$$D_s/D_{0\,calc} = 0.496 \times [\varepsilon_{calc}/100]^{1.661} \tag{1}$$

Fine roots (<2 mm in diameter) were separated from each soil ring, then dried at 105 °C and weighed. Dividing the root mass by the volume of the soil sample resulted in root mass density (RMD) in mg cm^{-3} soil.

Samples for the analysis of pH value, total carbon (C), total nitrogen (N), and mineral nitrogen (N_{min}) contents were taken together with the soil rings at 1–6 and 9–14 cm depth. N_{min} samples were cooled immediately after extraction. Measurements of pH were conducted with air dried soil samples eluted in H_2O. Total C and N contents were measured with an elemental analyzer (Vario EL cube, Elementar, Germany) after grinding and drying the samples at 105 °C. N_{min} was quantified according to Bassler & Hoffmann [40].

2.4. Statistical Analyses

All calculations and statistics were done with R version 3.2.3 (R Foundation for Statistical Computing, Vienna, Austria) [41]. For soil gas flux calculations, the R package "robustbase" [35] was used to run robust linear regression models. Differences in gas fluxes, soil physical and soil chemical properties between treatments were tested for significance ($p < 0.05$) with Dunn's test for multiple comparison using the R package "dunn.test" [42]. Confidence intervals of median values were calculated according to McGill et al. [43].

The R package "nlme" [44] was used to assess the effect of tree species on CH_4 and N_2O fluxes with linear mixed effects models. We chose linear models since there was no indication of non-linear relationships between dependent and independent variables. To fulfill the criterion of normal distribution, a log-modulus transformation [45] was applied on the values of N_2O fluxes. Predicted N_2O fluxes were reconverted by an inverse log-modulus transformation. Model performance was optimized based on Akaike information criterion (AIC) and conditional R^2 calculated with the R package "piecewiseSEM" [46]. Fixed effects were tested for collinearity beforehand and considered significant when $p < 0.05$. The spatial replicates of measurement collars were considered as *random effect*. By this means, pseudo replication by repeated measurements of the same collars during the course of the year was avoided. Model validation was performed by comparison of gas fluxes measured in the field with the fluxes derived from the models and by calculation of the resulting root mean square error (RMSE).

3. Results

3.1. Environmental Conditions during the Measurement Period

Temperature in 5 cm soil depth ranged between 1.5 °C in December 2016 to 20.5 °C in June 2016 and did not differ between stands or strata (Figure 2A–C). Although the soil was not frozen to this depth, in December 2016, January 2017, February 2017, and April 2017, air temperature was below or close to zero and the upper few cm of the soil were frozen. In January, a snow cover was present and in February and April, measurements took place under thawing conditions.

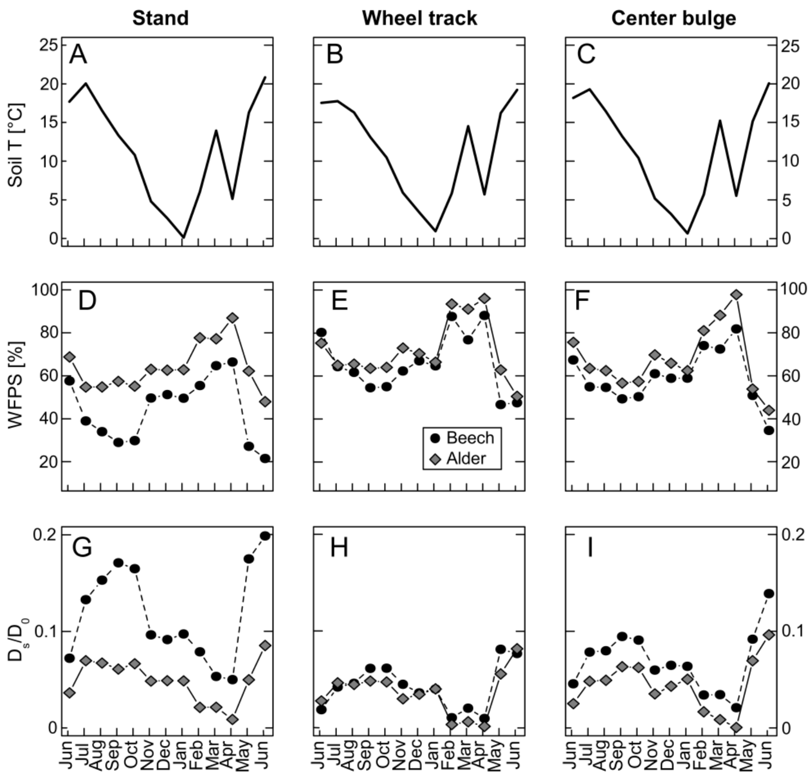

Figure 2. Monthly mean values of soil temperature (**A**–**C**), water filled pore space (WFPS; **D**–**F**), and D_s/D_0 (**G**–**I**) during the measurement period between June 2016 and June 2017 in each stratum for beech and black alder.

Volumetric soil moisture measured in the field was higher under alder than under beech with greatest differences in the undisturbed stand. Here, median values over the whole measurement period were 41% in the undisturbed alder stand and 34% in the beech stand. On the wheel track and on the center bulge, differences were less pronounced (wheel track alder 44% compared to 40% under beech and center bulge alder 43% compared to 41% under beech) but still significant. According to this, WFPS was significantly higher under alder compared to beech throughout the year in all strata (Figure 2D–F). $D_s/D_{0\ calc}$ was negatively correlated with WFPS (Figure 2G–I) with most distinct differences between beech and alder on the undisturbed plots (Figure 2G). Soil diffusivity measured in soil rings was in good agreement with $D_s/D_{0\ calc}$ estimated by the empirical model ($R^2 = 0.79$, $p < 0.05$).

3.2. Soil Physical Properties

Fifteen years after soil trafficking, soil compaction was still evident in both soil depths under beech. Total porosity in 1–6 cm was around 20% lower on the wheel track and 10% lower in the center bulge compared to the undisturbed stand (Figure 3 left). A similar pattern was visible in 9–14 cm depth, albeit less pronounced. Under alder, total porosity in 9–14 cm depth was reduced by 10% on the wheel track and by 5% in the center bulge. In 1–6 cm however, no significant difference between trafficked and untrafficked soil was apparent.

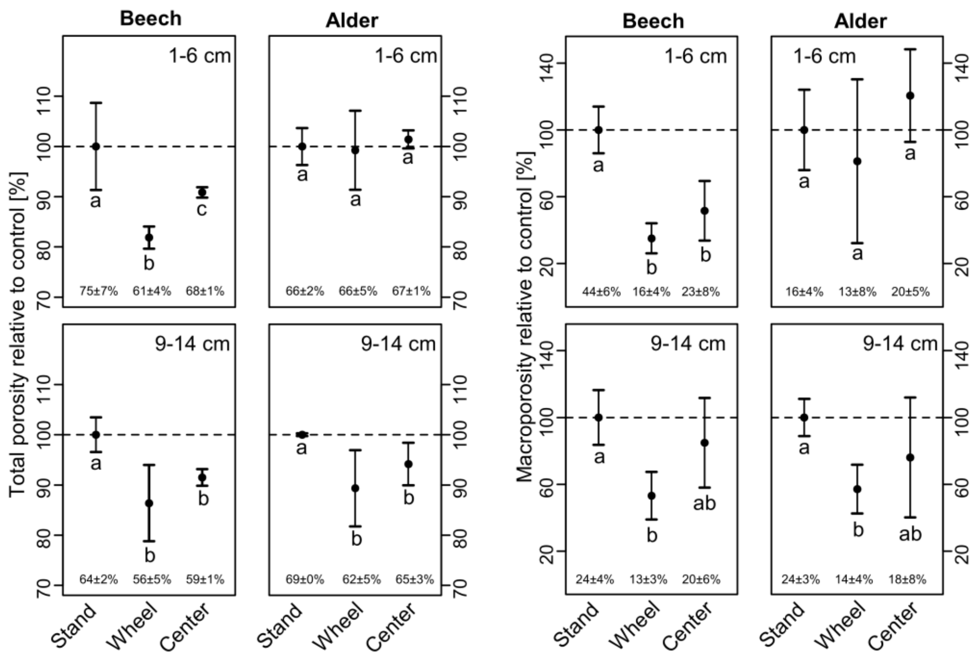

Figure 3. Relative changes of total porosity (left) and macro porosity (right) compared to the respective undisturbed stand (100%). Error bars indicate the ±95% confidence interval of medians. Significant differences between median values of strata within tree species are denoted by different letters. Absolute values as volume percent (median ±95% confidence interval) are given at the bottom of each bar.

Macro porosity in the skid trail under beech was distinctly lower compared to the undisturbed stand in both depths (Figure 3 right). Similarly, under alder macro porosity in 9–14 cm depth was lower compared to the undisturbed stand, whereas in 1–6 cm, no significant difference between undisturbed and disturbed soil was apparent.

Bulk density was significantly lower on the wheel track under alder than under beech in both depths (Table 1). In the center bulge, the difference was only significant in 9–14 cm depth. Within both stands, variability of root mass density was high and no significant differences between tree species or strata were found.

Table 1. Median values of bulk density (DB) [g cm^{-3}] and fine root mass density (RMD) [mg cm^{-3}] ± 95% confidence intervals for each tree species and stratum in 1–6 and 9–14 cm soil depth. Significant differences between tree species within same strata are indicated by different letters.

	Depth [cm]	Stand		Wheel Track		Center Bulge	
		Beech	Alder	Beech	Alder	Beech	Alder
DB	1–6	0.76 ± 0.04 ^{a}	0.92 ± 0.02 ^{b}	1.05 ± 0.00 ^{a}	0.94 ± 0.03 ^{b}	0.95 ± 0.02 ^{a}	0.93 ± 0.00 ^{a}
	9–14	1.06 ± 0.02 ^{a}	0.87 ± 0.00 ^{b}	1.20 ± 0.02 ^{a}	1.07 ± 0.04 ^{b}	1.20 ± 0.01 ^{a}	0.96 ± 0.02 ^{b}
RMD	1–6	0.88 ± 0.38 ^{a}	0.89 ± 0.30 ^{a}	1.34 ± 0.45 ^{a}	0.63 ± 0.26 ^{a}	1.93 ± 2.31 ^{a}	0.93 ± 0.43 ^{a}
	9–14	1.00 ± 0.65 ^{a}	0.66 ± 0.14 ^{a}	0.13 ± 0.27 ^{a}	0.57 ± 0.23 ^{a}	0.47 ± 0.87 ^{a}	0.30 ± 0.34 ^{a}

3.3. *Soil Chemical Properties*

Under alder, pH values and C and N contents were significantly higher than under beech within every stratum and in both depths (Table 2). Averaged over all strata and depths, 34% less C and 30% less N were found under beech. In both stands, C and N contents decreased with increasing depth. N_{min} contents determined at the end of the whole measurement period in June 2017 differed neither between tree species nor between different strata (data not shown) and no significant difference in the NO_3/NH_4 ratio was found (beech 0.24, alder 0.22).

Table 2. Median pH values, C and N contents and C/N ratio ± 95% confidence interval for each tree species and stratum in 1–6 and 9–14 cm soil depth. Significant differences between tree species within same strata are indicated by different letters.

	Depth [cm]	Stand		Wheel Track		Center Bulge	
		Beech	Alder	Beech	Alder	Beech	Alder
pH	1–6	5.0 ± 0.02 ^{a}	5.7 ± 0.03 ^{b}	5.6 ± 0.04 ^{a}	5.9 ± 0.04 ^{b}	5.2 ± 0.08 ^{a}	5.6 ± 0.01 ^{b}
	9–14	5.0 ± 0.09 ^{a}	5.9 ± 0.02 ^{b}	5.7 ± 0.02 ^{a}	6.1 ± 0.02 ^{b}	5.6 ± 0.02 ^{a}	6.0 ± 0.03 ^{b}
C [mg g^{-1}]	1–6	41.2 ± 0.3 ^{a}	57.7 ± 0.4 ^{b}	38.4 ± 0.3 ^{a}	58.2 ± 0.5 ^{b}	41.0 ± 0.4 ^{a}	54.5 ± 0.3 ^{b}
	9–14	36.8 ± 0.4 ^{a}	47.9 ± 0.6 ^{b}	22.6 ± 0.3 ^{a}	47.4 ± 0.6 ^{b}	25.7 ± 0.3 ^{a}	41.6 ± 0.2 ^{b}
N [mg g^{-1}]	1–6	3.2 ± 0.2 ^{a}	4.4 ± 0.1 ^{b}	3.0 ± 0.2 ^{a}	4.4 ± 0.4 ^{b}	3.2 ± 0.20 ^{a}	4.3 ± 0.1 ^{b}
	9–14	2.8 ± 0.2 ^{a}	3.5 ± 0.3 ^{b}	1.9 ± 0.2 ^{a}	3.4 ± 0.4 ^{b}	2.2 ± 0.2 ^{a}	3.1 ± 0.2 ^{b}
C/N	1–6	13.1 ± 0.5 ^{a}	12.8 ± 1.0 ^{a}	12.6 ± 0.63 ^{a}	13.0 ± 0.2 ^{a}	12.5 ± 0.64 ^{a}	12.4 ± 0.5 ^{a}
	9–14	12.2 ± 1.4 ^{a}	13.8 ± 0.5 ^{a}	11.7 ± 0.4 ^{a}	14.0 ± 0.7 ^{b}	11.7 ± 0.2 ^{a}	13.0 ± 0.2 ^{b}

3.4. *Greenhouse Gas Fluxes*

3.4.1. Carbon Dioxide

In both stands and in all strata, soil respiration was correlated with soil temperature ($R^2 = 0.37$, $p < 0.05$). Higher respiration rates were measured under alder than under beech in all strata during spring and summer (Figure 4A–C). At lower soil temperatures between October 2016 and April 2017, differences in CO_2 efflux between beech and alder were not significant. Cumulative CO_2 fluxes in the undisturbed stands during the whole measurement period were significantly higher under alder (20.8 Mg CO_2 ha^{-1} y^{-1}) than under beech (16.7 Mg CO_2 ha^{-1} y^{-1}). Within the alder stand, no difference between trafficked and untrafficked soil was found, whereas cumulative fluxes under beech were around 30% lower on the wheel track (11.7 Mg CO_2 ha^{-1} y^{-1}) compared to the undisturbed stand.

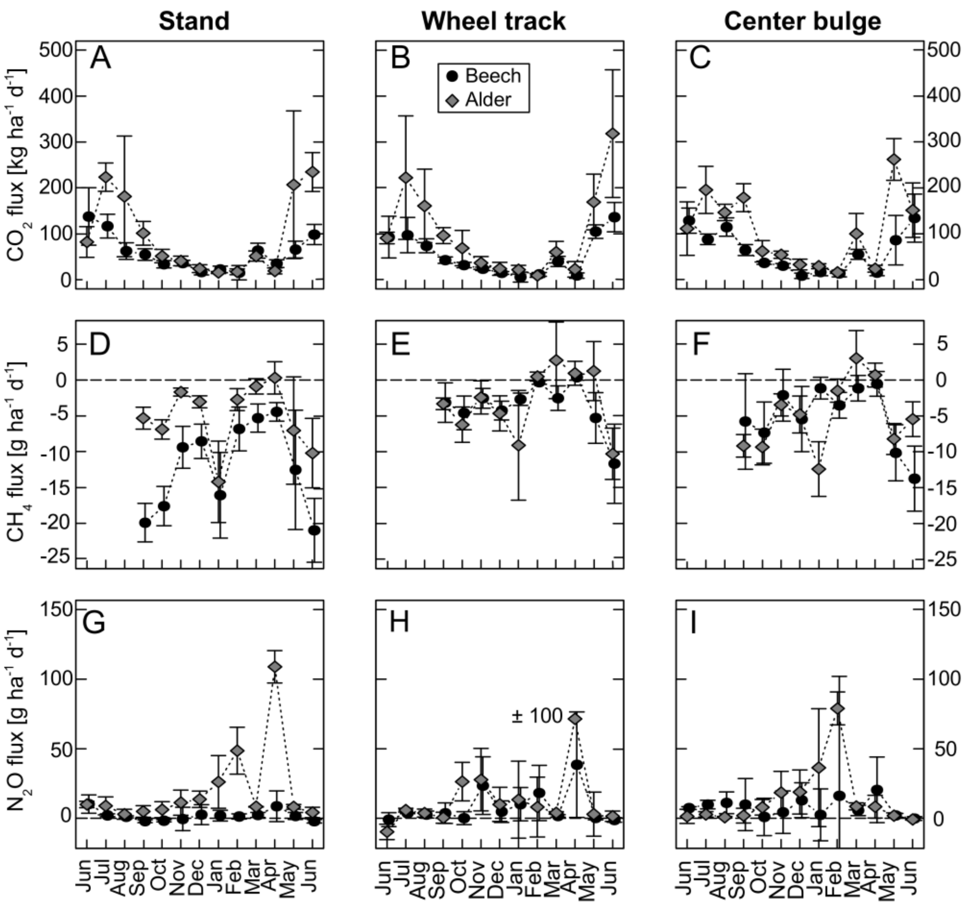

Figure 4. Monthly fluxes of CO_2 (**A**–**C**), CH_4 (**D**–**F**), and N_2O (**G**–**I**) during the measurement period between June 2016 and June 2017 in each stratum for beech and black alder. Median values of five field replicates ±95% confidence intervals are shown.

3.4.2. Methane

CH_4 fluxes from June to August 2016 were discarded because a batch of butyl stoppers of the vials emitted CH_4, leading to biased concentration measurements. Throughout the rest of the year, CH_4 fluxes were mostly negative under both tree species indicating microbial methane oxidation, best explained by WFPS ($R^2 = 0.38$, $p < 0.05$) and D_s/D_0 ($R^2 = 0.39$, $p < 0.05$). Between February and April, at very wet soil conditions with WFPS around 80%, net CH_4 emission was measured (Figure 4D–F). Cumulative CH_4 fluxes over the entire measurement period (Figure 5) were significantly lower in the undisturbed alder stand (−1.5 kg CH_4 ha^{-1} y^{-1}) compared to the beech stand (−4.0 kg CH_4 ha^{-1} y^{-1}). In contrast, no significant differences between CH_4 fluxes under beech and alder were found on the wheel track or on the center bulge (Figure 4E,F). When relative differences between undisturbed soil and skid trail within the two stands are considered, the effect of soil trafficking was more pronounced under beech compared to alder. On the skid trail under beech, CH_4 oxidation was 75% lower in the wheel track and 57% lower in the center bulge compared to the uncompacted stand. Under alder, with 20% decreased CH_4 oxidation in the wheel track (−1.1 kg CH_4 ha^{-1} y^{-1}) compared to the stand, this effect was less clear and not significant in the center bulge (−2.0 kg CH_4 ha^{-1} y^{-1}).

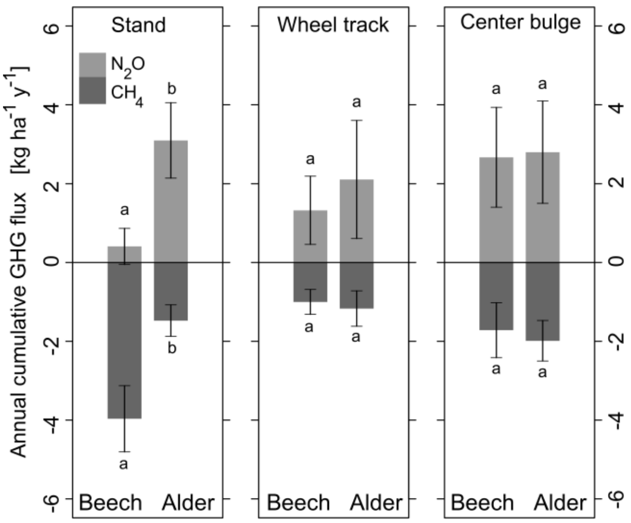

Figure 5. Annual cumulative fluxes of N_2O and CH_4. Bars represent median values of the spatial replicates with their 95% confidence interval. Different letters indicate significant differences between beech and alder within strata.

3.4.3. Nitrous Oxide

Throughout the year, N_2O fluxes were predominantly positive with emission peaks >100 g ha^{-1} d^{-1} under alder in April 2017 when WFPS was around 80% (Figure 4G). In some cases, slightly negative fluxes were measured in spring and summer, while the highest emissions occurred between October 2016 and May 2017 in the alder stand. Cumulative emissions between November 2016 and April 2017 accounted for 75% of the annual N_2O fluxes under beech and for 85% under alder. Significant differences between beech and alder were observed in the undisturbed stand, where cumulative annual emissions (Figure 5) were nearly eight times higher under alder (3.1 kg N_2O ha^{-1} y^{-1}) than under beech (0.4 kg N_2O ha^{-1} y^{-1}). In the alder stand, N_2O fluxes were neither higher on the wheel track (2.1 kg ha^{-1} y^{-1}) nor on the center bulge (2.8 kg ha^{-1} y^{-1}) compared to the undisturbed stand (Figure 5G–I). Under beech, cumulative annual N_2O emissions were more than three times higher in the wheel track (1.3 kg ha^{-1} y^{-1}) and nearly seven times higher in the center bulge (2.7 kg ha^{-1} y^{-1}) than in the undisturbed stand (0.4 kg ha^{-1} y^{-1}).

3.4.4. Greenhouse Gas Fluxes on Stand-Level

In Table 3, GHG emissions in CO_2 equivalents are shown, based on the assumption that 14% of a stand's area is occupied by skid trails [2] and that wheel track and center bulge make up 50% of a skid trail, respectively. Significant differences in N_2O and CH_4 fluxes between beech and alder are only present in the undisturbed stands. For CO_2, higher emissions are found in all strata under alder.

Table 3. Median values of annual CO_2 fluxes and fluxes of N_2O and CH_4 in CO_2 equivalents according to the respective area-percentage of a forest stand ±95% confidence interval. Significant differences between tree species within same strata are indicated by different letters. $\sum$ CO_2 eq is calculated for CO_2 equivalents of N_2O and CH_4 fluxes.

	Stand (86%)		**Wheel Track (7%)**		**Center Bulge (7%)**	
	Beech	**Alder**	**Beech**	**Alder**	**Beech**	**Alder**
CO_2 [kg ha^{-1} y^{-1}]	14,359 ± 2093 ^{a}	17,862 ± 5700 ^{b}	820 ± 267 ^{a}	1697 ± 430 ^{b}	988 ± 238 ^{a}	1933 ± 572 ^{b}
N_2O in CO_2 eq [kg ha^{-1} y^{-1}]	93.0 ± 104.4 ^{a}	706.0 ± 218.4 ^{b}	24.6 ± 16.1 ^{a}	39.1 ± 27.8 ^{a}	49.5 ± 23.5 ^{a}	51.9 ± 24.1 ^{a}
CH_4 in CO_2 eq [kg ha^{-1} y^{-1}]	−95.5 ± 20.0 ^{a}	−35.5 ± 9.6 ^{b}	−2.0 ± 0.6 ^{a}	−2.3 ± 0.9 ^{a}	−3.4 ± 1.4 ^{a}	−3.9 ± 1.0 ^{a}
$\sum$ CO_2 eq [kg ha^{-1} y^{-1}]	**−2.5**	**670.5**	**22.6**	**36.8**	**46.1**	**48**

3.5. Mixed Effects Models for CH_4 and N_2O Fluxes

Tested variables to describe CH_4 and N_2O fluxes were *soil temperature, soil moisture, diffusion coefficient, total porosity, macro porosity, air-filled porosity*, and *WFPS*. C, N, and N_{min} contents and pH values were not continuously monitored during the measurement period and thus not included in the models. Best model fit indicated by AIC and conditional R^2 was achieved with the fixed effects *soil temperature* and *diffusion coefficient* ($D_s/D_{0\ calc}$). As $D_s/D_{0\ calc}$ was estimated based on ε_{calc} (Equation (1)), it included information on soil moisture and pore structure, making it a more powerful predictor than simple *soil moisture* or *WFPS*. The resulting model with the replicates of measurement collars as *random effect* accounting for unexplained spatial variability was:

$$gas\ flux = f(soil\ temperature + diffusion\ coefficient + random\ effect) \quad (2)$$

This model was applied separately for datasets of CH_4 and N_2O under beech and alder respectively, resulting in four individual models with acceptable values of conditional R^2, ranging between 0.26 and 0.64 (Table 4). Additionally, we present the relative susceptibility of the gas fluxes to a change of model parameters. This is calculated as the quotient of the fixed effects divided by the model coefficient. It represents the relative change of the gas flux of N_2O and CH_4 when soil temperature is increased by 1 °C and $D_s/D_{0\ calc}$ by 0.01.

Table 4. Summary of the linear mixed effects models for CH_4 and N_2O fluxes under beech and alder.

CH_4 Flux Beech	Estimate	Standard Error	Effect [%]	*p*-Value	Conditional R^2	RMSE
Intercept	0.56	0.68	-	n.s.		
Soil T [°C]	−0.04	0.06	−7.1 per 1 °C	n.s.	0.64	4.13
D_s/D_0 [−]	−93.6	6.57	−167.1 per 0.01	***		
CH_4 Flux Alder	**Estimate**	**Standard Error**	**Effect [%]**	***p*-Value**	**Conditional R^2**	
Intercept	0.71	0.81	-	n.s.		
Soil T [°C]	0.13	0.07	18.3 per 1 °C	*	0.26	4.99
D_s/D_0 [−]	−115.08	14.78	−162.1 per 0.01	***		
N_2O Flux Beech	**Estimate**	**Standard Error**	**Effect [%]**	***p*-Value**	**Conditional R^2**	
Intercept	2.73	0.31	-	***		
Soil T [°C]	−0.04	0.02	−1.5 per 1 °C	*	0.48	1.26
D_s/D_0 [−]	−13.36	2.50	−4.9 per 0.01	***		
N_2O Flux Alder	**Estimate**	**Standard Error**	**Effect [%]**	***p*-Value**	**Conditional R^2**	
Intercept	4.21	0.27	-	***		
Soil T [°C]	−0.12	0.02	−2.9 per 1 °C	***	0.50	1.25
D_s/D_0 [−]	−19.80	3.93	−4.7 per 0.01	***		

Significance codes: <0.001 '***', <0.01 '**', <0.05 '*', > 0.05 'n.s.'.

The effect of $D_s/D_{0\ calc}$ on CH_4 and N_2O fluxes was high compared to the effect of soil temperature (Table 4). Under beech and alder, an increase of D_s/D_0 by 0.01 resulted in in a reduction of CH_4 emissions, i.e., an increase of CH_4 oxidation by 167% and 162%, respectively, whereas a decrease of N_2O emissions by 5% can be expected under beech and alder.

To allow comparison of pure tree species effects, all models were run with an averaged $D_s/D_{0\ calc}$ of 0.05 and soil temperature of 10 °C (Figure 6). Modeled N_2O fluxes at standardized soil temperature and D_s/D_0 were higher under alder than under beech (Figure 6). This effect was evident in all strata and most distinct in the undisturbed stand, where around three times more N_2O can be expected under alder compared to beech. Differences in modeled CH_4 fluxes were significant but less pronounced than for N_2O. Within all strata under alder, under standardized conditions, a slightly higher CH_4 uptake was found compared to beech. However, predicted CH_4 fluxes for all treatments ranged in a relatively small margin between −1.2 and −1.6 kg ha^{-1} y^{-1}.

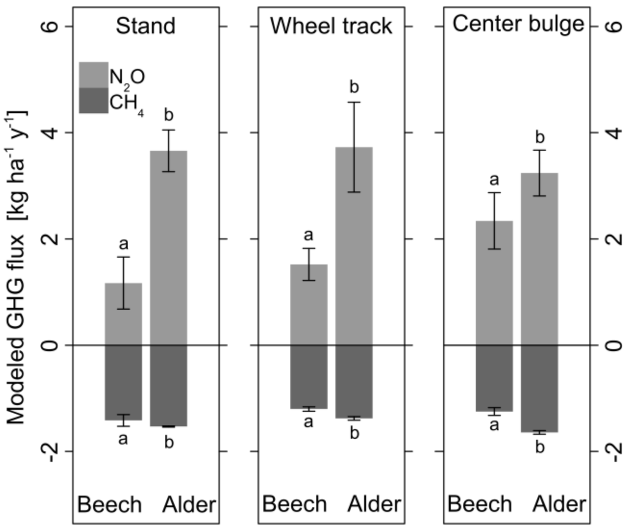

Figure 6. Modeled CH_4 and N_2O fluxes at standardized soil temperature (10 °C) and D_s/D_0 (0.05). Bars represent medians of the values predicted by the respective linear mixed effects models with their 95% confidence interval. Different letters indicate significant differences between beech and alder within strata.

4. Discussion

4.1. Soil Chemical Parameters

Elevated C contents associated with N fixation are frequently reported [47–49]. However, the exact mechanisms behind C-accumulation under N-fixing tree species are unclear [50]. Possibly, an increase in pools of new carbon and lower decomposition rates of old carbon under N-fixing trees favor accumulation of organic carbon (OC) [51]. In forests, 20–70% of net primary production (NPP) is allocated to fine roots, making fine root turnover a main source of OC [52–54]. For beech, turnover rates vary between 0.4–0.8 y^{-1} [55] and 0.8–1.2 y^{-1} [56]. Only few data is available on fine root turnover rates of alder, but considerably higher values of 6.2 y^{-1} reported by Rytter [53] suggest that differences in root turnover rates might explain higher OC contents found under alder than under beech.

Reduced soil acidity under alder was surprising, as high nitrification rates due to N-richness of alder litter were expected to promote soil acidification [57,58]. However, reduced soil acidity was possibly caused by a favorable lignin to N ratio of alder litter and consequential fast litter decomposition [59]. During fast decomposition, less organic acids are released than during slow decomposition, resulting in reduced soil acidification [59–61].

4.2. Soil Physical Parameters

On the skid trail under beech, the effect of soil trafficking was still obvious in elevated bulk density and lower total and macro porosity compared to the untrafficked stand in both depths. Under alder, however, differences compared to the untrafficked stand were found only in the deeper soil region, whereas in the upper centimeters, macro and total porosity did not differ between trafficked and undisturbed soil. Therefore, we suggest that the topsoil under alder was fully recovered. Even though root mass densities did not differ significantly between tree species, alder roots may have contributed to soil structure formation also due to higher fine root turnover rates, not visible in root mass densities. Ebeling et al. [15] observed full structure recovery 20 years after trafficking at a site with high biological activity, whereas at a site with low biotic activity, soil recovery was not completed after 40 years. In our case, high biological activity under alder was indicated by elevated soil respiration during the growing period. We presume that besides a possible higher root turnover rate, biological activity and thus structural regeneration under alder was promoted by fixation and assimilation of nitrogen and carbon as well as by reduced soil acidity [62,63].

Higher soil moisture and WFPS under alder caused a reduction of soil diffusivity, i.e., soil aeration. Possibly, up to 2% higher contents of OC have significantly increased water retention [64]. For "medium-textured" soils (0–40% clay, 0–52% sand), 2% more OC are expected to increase soil moisture by 4.2 vol% at field capacity and by 7.2 vol% at water saturation [65]. This is in the range of differences observed between beech and alder in the present study and can therefore explain elevated WFPS and thus lower D_s/D_0 under alder.

4.3. Greenhouse Gas Fluxes

4.3.1. Carbon Dioxide

A favorable N to lignin ratio of alder litter, high rhizomicrobial activity due to N-fixation by *Frankia alni*, elevated OC and possibly a higher root turnover could explain elevated soil respiration rates under black alder [60,66,67]. Throughout winter, soil temperature was the limiting factor for biological activity [68] leading to equally low soil respiration rates under beech and alder.

Regarding CO_2 efflux measured at the soil surface, it should be considered that it does not represent ecosystem respiration which would include the CO_2 uptake by above-ground plant tissue via photosynthesis. Therefore, elevated soil respiration under alder during the growing season may include an elevated authotrophic (root) respiration, accompanied by higher rates of aboveground photosynthetic C-fixation. However, evidence for higher C-fixation, i.e., NPP in the alder stand can be seen in timber stocks twice as high as in the beech stand. Therefore, a rough estimate of the CO_2 balance in the undisturbed stands can be given by assuming an annual CO_2-fixation by timber growth of 12.3 Mg ha^{-1} y^{-1} in the alder stand and 7.9 Mg ha^{-1} y^{-1} in the beech stand based on (i) the timber stocks measured in 2016, (ii) a C-content of 50% in woody biomass, and (iii) a wood density of 0.55 g cm^{-3} for alder and 0.68 g cm^{-3} for beech. CO_2-fixation in the alder stand was 4.4 Mg ha^{-1} y^{-1} higher than in the beech stand and hence completely offsets higher cumulative CO_2 emissions of 4.1 Mg ha^{-1} y^{-1} measured under alder. This is in agreement with Kutsch et al. [66] who stated that rhizomicrobial respiration, comprising respiration of roots, mycorrhizal fungi and microorganisms associated with roots, is closely correlated with primary production.

Several studies report a reduction of soil respiration in compacted soils due to anoxic conditions and subsequent decrease of biological activity [14,69,70]. This was evident in the present study under beech but not in the alder stand. Bringing this observation together with observations discussed above, the assumption of soil regeneration under alder is supported.

4.3.2. Methane

Cumulative CH_4 oxidation rates during the measurement period in the undisturbed plots ranged between −1.5 and −4.0 kg CH_4 ha^{-1} y^{-1} and were in the typical range of forest sites in northern Europe (−0.1 to −9.1 kg CH_4 ha^{-1} y^{-1}) [71]. The observed reduction of methane oxidation on the wheel track under beech is in accordance with Teepe et al. [2], who found CH_4 oxidation on wheel tracks reduced by 77% to >100% shortly after compaction. This is remarkable since our measurements took place 17 years after the last soil trafficking event and in contrast to Teepe et al. [2], the skid trail was planted with trees. Under alder, the impact of soil trafficking was much less pronounced, which can be attributed to the lack of a difference in the state of soil aeration between compacted and uncompacted strata. Lower absolute CH_4 oxidation in the undisturbed alder stand compared to the beech stand is related to lower values of D_s/D_0. Even though differences in the predicted CH_4 fluxes between tree species were statistically significant, the small range of modelled values within all treatments shows that soil temperature and D_s/D_0 explain CH_4 fluxes to a great extent.

An inhibition of methane oxidizing bacteria by high NO_3 or NH_4 contents was reported in several studies [30,31,72]. Yet contrary to our expectations, N_{min} contents in June 2017 were not elevated due to N-fixation under alder. As seasonal variability of N_{min} is high [27,73], no assessment can be made whether during the rest of the year, differences were present. However, slightly higher CH_4 oxidation under alder than under beech when D_s/D_0 and soil temperature were standardized (Figure 5) indicate that, even if N_{min} was elevated, it had no detrimental effect on CH_4 oxidation.

We note that a well-developed aerenchym in black alder reaching from the stem base to the roots can mediate gas transport between soil and atmosphere [74]. Also for *Fagus sylcatica*, evidence for a transport link between soil and atmosphere via the root system was suggested by Maier et al. [75]. If only soil-to-atmosphere fluxes are regarded, total CH_4 (and N_2O) fluxes of forest stands may be underestimated under certain circumstances. However, it was beyond the scope of this study to include stem fluxes. Until now, only few studies have included these fluxes and it is not fully understood under which conditions they are relevant or not.

4.3.3. Nitrous Oxide

With 3.1 kg N_2O ha^{-1} y^{-1}, cumulative N_2O production in the undisturbed alder stand was higher than emissions of 0.8–1.6 kg N_2O ha^{-1} y^{-1} observed in black alder stands in southern Germany [76] but lower than emissions of 7.7 kg N_2O ha^{-1} y^{-1} from a black alder stand in northern Germany [27]. In the undisturbed beech stand, cumulative emissions of 0.4 kg N_2O ha^{-1} y^{-1} are in agreement with observations by Mogge et al. [27] but lower than measurements by Butterbach-Bahl et al. [77] during four consecutive years in a beech stand (1.6–10.4 kg N_2O ha^{-1} y^{-1}) and several other authors [78,79]. The only study quantifying N_2O emissions from skid trails under comparable conditions reported cumulative N_2O effluxes between 1.8 and 4.3 kg ha^{-1} during the growing season [2], which is in the range of our observations on the skid trail.

Seventeen years after soil trafficking, N_2O emissions were not increased on the skid trail planted with alder compared to the non-compacted soil under alder, probably because soil structure was not different from the undisturbed alder stand within the upper 1–6 cm. On the skid trail planted with beech, similar N_2O production rates at comparable WFPS suggest that limited soil aeration enhanced N_2O production by denitrification, while good soil aeration in the undisturbed beech stand caused lower N_2O emissions. Standardization in the tree-species specific models showed that D_s/D_0 was the main variable controlling N_2O fluxes and that the effect of D_s/D_0 on N_2O fluxes was of similar size for beech and alder. Consequently, up to three times higher N_2O emissions predicted by the model under alder after standardizing D_s/D_0 and soil temperature point towards an additional factor that has contributed to elevated N_2O emissions. Possibly, available nitrogen originating from N-rich alder litter may have been provided, resulting in a boost of microbial nitrification and denitrification [27,28,76]. Because this microbial activity consumes the available N in the soil solution, this hypothesis does not contradict the rather uniform N_{min} observations at the sampling date in June 2017. An increase of N_2O emissions under alder in all strata with begin of litterfall in October/November 2016 lasting until April 2017 corroborates the hypothesis of elevated N-availability.

Besides nitrogen availability and restricted soil aeration, freeze/thaw cycles could explain enhanced emissions of N_2O during winter in both stands. When measurements took place under thawing conditions as it was the case in February 2017 and April 2017, formerly entrapped N_2O may have been discharged [80], or the release of N-rich intracellular content after death of bacteria or fungi [81] and subsequent decomposition by surviving microbes may have boosted N_2O emission [82,83]. The resulting temporal pattern of N_2O fluxes with emission outbursts during winter dominating annual emissions is in agreement with observations by many authors [84–86].

It should be highlighted that, despite differences in N_2O fluxes between tree species and between strata, annual N_2O production was in no case extraordinarily high compared to other studies. Even in the treatment with highest annual emissions, N_2O fluxes were lower compared to up to 10 kg N_2O ha^{-1} y^{-1} measured in a beech stand by Butterbach-Bahl et al. [77] or to 6.8 kg N_2O ha^{-1} y^{-1} measured in a beech stand by Zechmeister-Boltenstern et al. [79]. N_2O emissions from fertilized and unfertilized German agricultural soils reported in a review by Jungkunst et al. [87] range up to 27 kg N_2O ha^{-1} y^{-1}.

5. Conclusions

A main goal of this study was to reveal the tree species effect on GHG exchange in disturbed and undisturbed forest soils. With the results, a basic problem of such comparisons in more or less established forest ecosystems becomes obvious. The manifold soil–plant interactions make it difficult to reduce observed effects to single factors. This was particularly apparent in soil physical parameters of the undisturbed stands of alder and beech. To overcome this problem, we used multiple regression models to approximate a standardization of factors. We observed clear differences in the GHG fluxes between undisturbed stands of alder and beech and also between recovered and non-recovered soil compaction. Taking into account all variables, it became obvious that N_2O and CH_4 fluxes were mainly governed by soil aeration and soil temperature. Under alder, available nitrogen might additionally have modified N_2O emissions. The comparison of undisturbed beech and alder stands shows that alder affected soil structure formation and the amount of soil organic carbon and nitrogen turnover, leading to increased N_2O emission and decreased CH_4 oxidation (however, for available nitrogen we did not find evidence for higher concentrations under alder). On the skid trail, we conclude that there was no trade-off between structure recovery and undesired side-effects on GHG fluxes since black alder was suitable to improve soil structure without changing the stand's GHG balance.

Author Contributions: Funding acquisition, K.v.W. and H.S.-K.; Investigation, H.W.; Methodology, H.W. and H.S.-K.; Project administration, H.W. and H.S.-K.; Supervision, F.L. and H.S.-K.; Writing–original draft, H.W.; Writing–review & editing, K.v.W., F.L. and H.S.-K.

Funding: This research was funded by the German Federal Ministry of Food and Agriculture, grant number FNR-22029114.

Acknowledgments: We are grateful to Felix Hugo and Moritz Kramer for their assistance in field and laboratory work. Many thanks to Kenton Stutz and Thomas Laemmel for fruitful discussions. We also thank Christoph Schaaf and ForstBW for assistance in finding and accessing the study site.

Conflicts of Interest: The authors declare no conflict of interest.

References and Notes

1. Garland, J.J. *Designated Skid Trails Minimize Soil Compaction*; Oregon State University, Extension Service: Corvallis, OR, USA, 1983.
2. Teepe, R.; Brumme, R.; Beese, F.; Ludwig, B. Nitrous Oxide Emission and Methane Consumption Following Compaction of Forest Soils. *Soil Sci. Soc. Am. J.* **2004**, *68*, 605. [CrossRef]
3. Ampoorter, E.; De Schrijver, A.; De Frenne, P.; Hermy, M.; Verheyen, K. Experimental Assessment of Ecological Restoration Options for Compacted Forest Soils. *Ecol. Eng.* **2011**, *37*, 1734–1746. [CrossRef]
4. Horn, R.; Vossbrink, J.; Peth, S.; Becker, S. Impact of Modern Forest Vehicles on Soil Physical Properties. *For. Ecol. Manag.* **2007**, *248*, 56–63. [CrossRef]
5. Ciais, P.; Sabine, C.; Bala, G.; Bopp, L.; Brovkin, V.; Canadell, A.; Chhabra, R.; DeFries, R.; Galloway, J.; Heimann, M.; et al. Carbon and Other Biogeochemical Cycles. In *Climate Change 2013: The Physical Basis. Contribution of Working Group I to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change*; Stocker, T.F., Qin, D., Plattner, G.-K., Tignor, M., Allen, S.K., Boschung, J., Nauels, A., Xia, Y., Bex, V., Midgley, P.M., Eds.; Cambridge University Press: Cambridge, UK; New York, NY, USA, 2013; pp. 465–570.
6. Le Mer, J.; Roger, P. Production, Oxidation, Emission and Consumption of Methane by Soils: A Review. *Eur. J. Soil Biol.* **2001**, *37*, 25–50. [CrossRef]
7. Dobbie, K.E.; Smith, K.A. Nitrous Oxide Emission Factors for Agricultural Soils in Great Britain: The Impact of Soil Water-filled Pore Space and Other Controlling Variables. *Glob. Chang. Biol.* **2003**, *9*, 204–218. [CrossRef]
8. Bateman, E.J.; Baggs, E.M. Contributions of Nitrification and Denitrification to N2O Emissions from Soils at Different Water-Filled Pore Space. *Biol. Fertil. Soils* **2005**, *41*, 379–388. [CrossRef]

9. Butterbach-Bahl, K.; Baggs, E.M.; Dannenmann, M.; Kiese, R.; Zechmeister-Boltenstern, S. Nitrous Oxide Emissions from Soils: How Well Do We Understand the Processes and Their Controls? *Philos. Trans. R. Soc. B Biol. Sci.* **2013**, *368*, 20130122. [CrossRef] [PubMed]
10. Weier, K.L.; Doran, J.W.; Power, J.F.; Walters, D.T. Denitrification and the Dinitrogen/Nitrous Oxide Ratio as Affected by Soil Water, Available Carbon, and Nitrate. *Soil Sci. Soc. Am. J.* **1993**, *57*, 66. [CrossRef]
11. Linn, D.M.; Doran, J.W. Effect of Water-Filled Pore Space on Carbon Dioxide and Nitrous Oxide Production in Tilled and Nontilled Soils1. *Soil Sci. Soc. Am. J.* **1984**, *48*, 1267. [CrossRef]
12. Chapuis-Lardy, L.; Wrage, N.; Metay, A.; Chotte, J.-L.; Bernoux, M. Soils, a Sink for N_2O? A Review. *Glob. Chang. Biol.* **2007**, *13*, 1–17. [CrossRef]
13. Frey, B.; Niklaus, P.A.; Kremer, J.; Lüscher, P.; Zimmermann, S. Heavy-Machinery Traffic Impacts Methane Emissions as Well as Methanogen Abundance and Community Structure in Oxic Forest Soils. *Appl. Environ. Microbiol.* **2011**, *77*, 6060–6068. [CrossRef] [PubMed]
14. Epron, D.; Plain, C.; Ndiaye, F.K.; Bonnaud, P.; Pasquier, C.; Ranger, J. Effects of Compaction by Heavy Machine Traffic on Soil Fluxes of Methane and Carbon Dioxide in a Temperate Broadleaved Forest. *For. Ecol. Manage.* **2016**, *382*, 1–9. [CrossRef]
15. Ebeling, C.; Lang, F.; Gaertig, T. Structural Recovery in Three Selected Forest Soils after Compaction by Forest Machines in Lower Saxony, Germany. *For. Ecol. Manag.* **2016**, *359*, 74–82. [CrossRef]
16. Von Wilpert, K.; Schäffer, J. Ecological Effects of Soil Compaction and Initial Recovery Dynamics: A Preliminary Study. *Eur. J. For. Res.* **2006**, *125*, 129–138. [CrossRef]
17. Meyer, C.; Lüscher, P.; Schulin, R. Recovery of Forest Soil from Compaction in Skid Tracks Planted with Black Alder (*Alnus glutinosa* (L.) Gaertn.). *Soil Tillage Res.* **2014**, *143*, 7–16. [CrossRef]
18. Flores Fernández, J.L.; Hartmann, P.; Schäffer, J.; Puhlmann, H.; von Wilpert, K. Initial Recovery of Compacted Soil—Planting and Technical Treatments Decrease CO_2 concentrations in Soil and Promote Root Growth. *Ann. For. Sci.* **2017**, *74*. [CrossRef]
19. Haas, J.; Kühne, A.; Schack-Kirchner, H.; Lang, F. Does Juncus Effusus L. And Carex Brizoides L. Help to Regenerate a Sufficient Aeration in Compacted Forest Soils? *Allg. For. Jagdzeitung* **2017**, *188*, 85–94. [CrossRef]
20. IUSS Working Group WRB. *World Reference Base for Soil Resources 2014, Update 2015. International Soil Classification System for Naming Soils and Creating Legends for Soil Maps*; Word Soil Ressource Reports; FAO: Rome, Italy, 2015.
21. Angers, D.A.; Caron, J. Plant-Induced Changes in Soil Structure: Processes and Feedbacks. *Biogeochemistry* **1998**, *42*, 55–72. [CrossRef]
22. Bardgett, R.D.; Mommer, L.; De Vries, F.T. Going Underground: Root Traits as Drivers of Ecosystem Processes. *Trends Ecol. Evol.* **2014**, *29*, 692–699. [CrossRef]
23. Gill, C.J. The Ecological Significance of Adventitious Rooting as a Response to Flooding in Woody Species, with Special Reference to *Alnus glutinosa* (L.) Gaertn. *Flora* **1975**, *164*, 85–97. [CrossRef]
24. Armstrong, W.; Armstrong, J. Stem Photosynthesis Not Pressurized Ventilation Is Responsible for Light-Enhanced Oxygen Supply to Submerged Roots of Alder (*Alnus glutinosa*). *Ann. Bot.* **2005**, *96*, 591–612. [CrossRef]
25. Kätzel, R. Zum Physiologischen Anpassungspotenzial Der Schwarz-Erle (*Alnus glutinosa* [L.] GAERTN.). *Eberswalder Forstl. Schriftenr.* **2003**, *17*, 39–46.
26. Bühlmann, T.; Körner, C.; Hiltbrunner, E. Shrub Expansion of Alnus Viridis Drives Former Montane Grassland into Nitrogen Saturation. *Ecosystems* **2016**, *19*, 968–985. [CrossRef]
27. Mogge, B.; Kaiser, E.A.; Munch, J.C. Nitrous Oxide Emissions and Denitrification N-Losses from Forest Soils in the Bornhoved Lake Region (Northern Germany). *Soil Biol. Biochem.* **1998**, *30*, 703–710. [CrossRef]
28. Bühlmann, T.; Caprez, R.; Hiltbrunner, E.; Körner, C.; Niklaus, P.A. Nitrogen Fixation by Alnus Species Boosts Soil Nitrous Oxide Emissions. *Eur. J. Soil Sci.* **2017**, *68*, 740–748. [CrossRef]
29. Reay, D.S.; Nedwell, D.B.; McNamara, N.; Ineson, P. Effect of Tree Species on Methane and Ammonium Oxidation Capacity in Forest Soils. *Soil Biol. Biochem.* **2005**, *37*, 719–730. [CrossRef]
30. MacDonald, J.A.; Skiba, U.; Sheppard, L.J.; Ball, B.; Roberts, J.D.; Smith, K.A.; Fowler, D. The Effect of Nitrogen Deposition and Seasonal Variability on Methane Oxidation and Nitrous Oxide Emission Rates in an Upland Spruce Plantation and Moorland. *Atmos. Environ.* **1997**, *31*, 3693–3706. [CrossRef]

31. Gulledge, J.; Doyle, A.P.; Schimel, J.P. Different NH4+-Inhibition Patterns of Soil CH4 Consumption: A Result of Distinct CH4-Oxidizer Populations Across Sites? *Soil Biol. Biochem.* **1997**, *29*, 13–21. [CrossRef]
32. Deutscher Wetterdienst, DWD. Monthly Mean of Air Temperature, 1 km Grid for Germany. Available online: http://werdis.dwd.de/werdis/retrieve_data.do?pidpat=de.dwd.nkdz-grid.TAMM17.30.00&toplevel=false (accessed on 15 February 2019).
33. Loftfield, N.; Flessa, H.; Augustin, J.; Beese, F. Automated Gas Chromatographic System for Rapid Analysis of the Atmospheric Trace Gases Methane, Carbon Dioxide, and Nitrous Oxide. *J. Environ. Qual.* **1997**, *26*, 560–564. [CrossRef]
34. Hutchinson, G.L.; Livingston, G.P. Soil-Atmosphere Gas Exchange. In *Methods of Soil Analysis: Part 4 Physical Methods*; Soil Science Society of America: Madison, WI, USA, 2002; pp. 1159–1182.
35. Maechler, M.; Rousseeuw, P.; Croux, C.; Todorov, V.; Ruckstuhl, A.; Salibian-Barrera, M.; Verbeke, T.; Koller, M. Robustbase: Basic Robust Statistics, 2016.
36. Myhre, G.; Shindell, D.; Bréon, F.-M.; Collins, W.; Fuglestvedt, J.; Huang, J.; Koch, D.; Lamarque, J.-F.; Lee, D.; Mendoza, B.; et al. Anthropogenic and Natural Radiative Forcing. In *Climate Change 2013: The Physical Science Basis. Contribution of Working Group I to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change*; Stocker, T.F., Qin, D., Plattner, G.-K., Tignor, M., Allen, S.K., Boschung, J., Nauels, A., Xia, Y., Bex, V., Midgley, P.M., Eds.; Cambridge University Press: Cambridge, UK; New York, NY, USA, 2013; pp. 659–740.
37. Hartge, K.H.; Horn, R. *Die Physikalische Untersuchung von Böden*, 3rd ed.; Ferdinand Enke Verlag: Stuttgart, Germany, 2011.
38. Kühne, A.; Schack-Kirchner, H.; Hildebrand, E.E. Gas Diffusivity in Soils Compared to Ideal Isotropic Porous Media. *J. Plant Nutr. Soil Sci.* **2012**, *175*, 34–45. [CrossRef]
39. Schack-Kirchner, H.; Gaertig, T.; Wilpert, K.V.; Hildebrand, E.E. A Modified Mcintyre and Phillip Approach to Measure Top-Soil Gas Diffusivity in-Situ. *J. Plant Nutr. Soil Sci.* **2001**, *164*, 253–258. [CrossRef]
40. Bassler, R.; Hoffmann, G. Bestimmung von Mineralischem, (Nitrat-) Stickstoff in Bodenprofilen, Nmin-Labormethode. In *VDLUFA Methodenbuch Band I*; Deller, B., Ed.; VDLUFA-Verlag: Darmstadt, Germany, 1997.
41. R Development Core Team. *R: A Language and Environment for Statistical Computing*; Foundation for Statistical Computing: Vienna, Austria, 2016.
42. Dinno, A. Dunn.Test: Dunn's Test of Multiple Comparisons Using Rank Sums, 2016.
43. McGill, R.; Tukey, J.W.; Larsen, W.A. Variation of Box Plots. *Am. Stat.* **1978**, *32*, 12–16.
44. Pinheiro, J.; Bates, D.; DebRoy, S.; Sarkar, D.; R Core Team. Nlme: Linear and Nonlinear Mixed Effects Models, 2016.
45. John, J.A.; Draper, N.R. An Alternative Family of Transformations. *J. R. Stat. Soc.* **1980**, *29*, 190–197. [CrossRef]
46. Lefcheck, J.S. PiecewiseSEM: Piecewise Structural Equation Modelling in R for Ecology, Evolution, and Systematics. *Methods Ecol. Evol.* **2016**, *7*, 573–579. [CrossRef]
47. Wang, F.; Li, Z.; Xia, H.; Zou, B.; Li, N.; LIu, J.; Zhu, W. Effects of Nitrogen-Fixing and Non-Nitrogen-Fixing Tree Species on Soil Properties and Nitrogen Transformation during Forest Restoration in Southern China. *Soil Sci. Plant Nutr.* **2010**, *56*, 297–306. [CrossRef]
48. Uri, V.; Aosaar, J.; Varik, M.; Becker, H.; Ligi, K.; Padari, A.; Kanal, A.; Lõhmus, K. The Dynamics of Biomass Production, Carbon and Nitrogen Accumulation in Grey Alder (*Alnus incana* (L.) Moench) Chronosequence Stands in Estonia. *For. Ecol. Manag.* **2014**, *327*, 106–117. [CrossRef]
49. Rothe, A.; Kermit Cromack, J.; Resh, S.C.; Makineci, E.; Son, Y. Soil Carbon and Nitrogen Changes Under Douglas-Fir With and Without Red Alder. *Soil Sci. Soc. Am. J.* **2002**, *66*, 1988–1995. [CrossRef]
50. Binkley, D. How Nitrogen-Fixing Trees Change Soil Carbon. In *Tree Species Effects on Soils: Implications for Global Change*; Binkley, D., Menyailo, O., Eds.; Implications for Global Change, NATO Sciences Series; Kluwer Academic Publishers: Dordrecht, The Netherland, 2005; pp. 155–164.
51. Resh, S.C.; Binkley, D.; Parrotta, J.A. Greater Soil Carbon Sequestration under Nitrogen-Fixing Trees Compared with Eucalyptus Species. *Ecosystems* **2002**, *5*, 217–231. [CrossRef]
52. Rytter, L.; Rytter, R.M. Growth and Carbon Capture of Grey Alder (*Alnus incana* (L.) Moench.) under North European Conditions—Estimates Based on Reported Research. *For. Ecol. Manag.* **2016**, *373*, 56–65. [CrossRef]
53. Rytter, R.M. The Effect of Limited Availability of N or Water on C Allocation to Fine Roots and Annual Fine Root Turnover in *Alnus incana* and Salix Viminalis. *Tree Physiol.* **2013**, *33*, 924–939. [CrossRef]

54. Kalyn, A.L.; Van Rees, K.C.J. Contribution of Fine Roots to Ecosystem Biomass and Net Primary Production in Black Spruce, Aspen, and Jack Pine Forests in Saskatchewan. *Agric. For. Meteorol.* **2006**, *140*, 236–243. [CrossRef]
55. Hertel, D.; Strecker, T.; Müller-Haubold, H.; Leuschner, C. Fine Root Biomass and Dynamics in Beech Forests across a Precipitation Gradient—Is Optimal Resource Partitioning Theory Applicable to Water-Limited Mature Trees? *J. Ecol.* **2013**, *101*, 1183–1200. [CrossRef]
56. Burke, M.K.; Raynal, J. Fine Root Growth Phenology, Production, and Turnover in a Northern Hardwood Forest Ecosystem. *Plant Soil* **1994**, *162*, 135–146. [CrossRef]
57. Uri, V.; Lõhmus, K.; Mander, Ü.; Ostonen, I.; Aosaar, J.; Maddison, M.; Helmisaari, H.S.; Augustin, J. Long-Term Effects on the Nitrogen Budget of a Short-Rotation Grey Alder (*Alnus incana* (L.) Moench) Forest on Abandoned Agricultural Land. *Ecol. Eng.* **2011**, *37*, 920–930. [CrossRef]
58. Van Miegroet, H.; Cole, D.W. Acidification Sources in Red Alder and Douglas Fir Soils-Importance of Nitrification. *Soil Sci. Soc. Am. J.* **1985**, *49*, 1274–1279. [CrossRef]
59. Dilly, O.; Munch, J.C. Microbial Biomass Content, Basal Respiration and Enzyme Activities during the Course of Decomposition of Leaf Litter in a Black Alder (*Alnus glutinosa* (L.) Gaertn.) Forest. *Soil Biol. Biochem.* **1996**, *28*, 1073–1081. [CrossRef]
60. Wedderburn, M.E.; Carter, J. Litter Decomposition by Four Functional Tree Types for Use in Silvopastoral Systems. *Soil Biol. Biochem.* **1999**, *31*, 455–461. [CrossRef]
61. De Vries, W.; Breeuwsma, A. Relative Importance of Natural and Anthropogenic Proton Sources in Soils in The Netherlands. *Water. Air. Soil Pollut.* **1986**, *28*, 173–184. [CrossRef]
62. Neirynck, J.; Mirtcheva, S.; Sioen, G.; Lust, N. Impact of *Tilia platyphyllos* Scop., *Fraxinus Excelsior* L., *Acer pseudoplatanus* L., *Quercus robur* L. and *Fagus sylvatica* L. on Earthworm Biomass and Physico-Chemical Properties of a Loamy Topsoil. *For. Ecol. Manag.* **2000**, *133*, 275–286. [CrossRef]
63. Haynes, R.J.; Naidu, R. Influence of Lime, Fertilizer and Manure Applications on Soil Organic Matter Content and Soil Physical Conditions: A Review. *Nutr. Cycl. Agroecosyst.* **1998**, *51*, 123–137. [CrossRef]
64. Rawls, W.J.; Pachepsky, Y.A.; Ritchie, J.C.; Sobecki, T.M.; Bloodworth, H. Effect of Soil Organic Carbon on Soil Water Retention. *Geoderma* **2003**, *116*, 61–76. [CrossRef]
65. Minasny, B.; McBratney, A.B. Limited Effect of Organic Matter on Soil Available Water Capacity. *Eur. J. Soil Sci.* **2018**, *69*, 39–47. [CrossRef]
66. Kutsch, W.L.; Staack, A.; Wötzel, J.; Middelhoff, U.; Kappen, L. Field Measurements of Root Respiration and Total Soil Respiration in an Alder Forest. *New Phytol.* **2001**, *150*, 157–168. [CrossRef]
67. Butnor, J.R.; Johnsen, K.H.; Oren, R.; Katul, G.G. Reduction of Forest Floor Respiration by Fertilization on Both Carbon Dioxide-Enriched and Reference 17-Year-Old Loblolly Pine Stands. *Glob. Chang. Biol.* **2003**, *9*, 849–861. [CrossRef]
68. Lloyd, J.; Taylor, J.A. On the Temperature Dependence of Soil Respiration. *Funct. Ecol.* **1994**, *8*, 315–323. [CrossRef]
69. Goutal, N.; Parent, F.; Bonnaud, P.; Demaison, J.; Nourrisson, G.; Epron, D.; Ranger, J. Soil CO_2 concentration and Efflux as Affected by Heavy Traffic in Forest in Northeast France. *Eur. J. Soil Sci.* **2012**, *63*, 261–271. [CrossRef]
70. Conlin, T.S.S.; Driessche, R. Response of Soil CO_2 and O_2 Concentrations to Forest Soil Compaction at the Long-Term Soil Productivity Sites in Central British Columbia. *Can. J. Soil Sci.* **2000**, *80*, 625–632. [CrossRef]
71. Smith, K.A.; Dobbie, K.E.; Ball, B.C.; Bakken, L.R.; Sitaula, B.K.; Hansen, S.; Brumme, R.; Borken, W.; Christensen, S.; Priemé, A.; et al. Oxidation of Atmospheric Methane in Northern European Soils, Comparison with Other Ecosystems, and Uncertainties in the Global Terrestrial Sink. *Glob. Chang. Biol.* **2000**, *6*, 791–803. [CrossRef]
72. Reay, D.S.; Radajewski, S.; Murrell, J.C.; McNamara, N.; Nedwell, D.B. Effects of Land-Use on the Activity and Diversity of Methane Oxidizing Bacteria in Forest Soils. *Soil Biol. Biochem.* **2001**, *33*, 1613–1623. [CrossRef]
73. Gallardo, A.; Rodr, J.J.; Covelo, F.; Fern, R.; Rodriguez-Saucedo, J.J.; Fernandez-Ales, R. Soil Nitrogen Heterogeneity in a Dehesa Ecosystem. *Plant Soil* **2000**, *222*, 71–82. [CrossRef]
74. Rusch, H.; Rennenberg, H. Black Alder (*Alnus glutinosa* (L.) Gaertn.) Trees Mediate Methane and Nitrous Oxide Emission from the Soil to the Atmosphere. *Plant Soil* **1998**, *201*, 1–7. [CrossRef]

75. Maier, M.; Machacova, K.; Lang, F.; Svobodova, K.; Urban, O. Combining Soil and Tree-Stem Flux Measurements and Soil Gas Profiles to Understand CH_4 Pathways in Fagus Sylvatica Forests. *J. Plant Nutr. Soil Sci.* **2017**, 1–5. [CrossRef]
76. Eickenscheidt, T.; Heinichen, J.; Augustin, J.; Freibauer, A.; Drösler, M. Nitrogen Mineralization and Gaseous Nitrogen Losses from Waterlogged and Drained Organic Soils in a Black Alder (*Alnus glutinosa* (L.) Gaertn.) Forest. *Biogeosciences* **2014**, *11*, 2961–2976. [CrossRef]
77. Butterbach-Bahl, K.; Willibald, G.; Papen, H.; Gasche, R. Exchange of N-Gases at the Spruce and Beech Sites at the Höglwald Forest—A Summary. *Plant Soil* **2002**, *240*, 117–123. [CrossRef]
78. Borken, W.; Beese, F. Methane and Nitrous Oxide Fluxes of Soils in Pure and Mixed Stands of European Beech and Norway Spruce. *Eur. J. Soil Sci.* **2006**, *57*, 617–625. [CrossRef]
79. Zechmeister-Boltenstern, S.; Hahn, M.; Meger, S.; Jandl, R. Nitrous Oxide Emissions and Nitrate Leaching in Relation to Microbial Biomass Dynamics in a Beech Forest Soil. *Soil Biol. Biochem.* **2002**, *34*, 823–832. [CrossRef]
80. Teepe, R.; Brumme, R.; Beese, F. Nitrous Oxide Emissions from Soil during Freezing and Thawing Periods. *Soil Biol. Biochem.* **2001**, *33*, 1269–1275. [CrossRef]
81. Bierderbeck, V.O.; Campbell, C.A. Influence of Simulated Fall and Spring Conditions on Soil System. I. Effect on Soil Microflora. *Soil Sci. Soc. Am. J.* **1971**, *35*, 474–479. [CrossRef]
82. Müller, C.; Martin, M.; Stevens, R.J.; Laughlin, R.J.; Kammann, C.; Ottow, J.C.G.; Jäger, H.J. Processes Leading to N_2O Emissions in Grassland Soil during Freezing and Thawing. *Soil Biol. Biochem.* **2002**, *34*, 1325–1331. [CrossRef]
83. Risk, N.; Snider, D.; Wagner-Riddle, C. Mechanisms Leading to Enhanced Soil Nitrous Oxide Fluxes Induced by Freeze–Thaw Cycles. *Can. J. Soil Sci.* **2013**, *93*, 401–414. [CrossRef]
84. Papen, H.; Butterbach-Bahl, K. A 3-Year Continuous Record of Nitrogen Trace Gas Fluxes from Untreated and Limed Soil of a N-Saturated Spruce and Beech Forest Ecosystem in Germany 1. N_2O Emissions. *J. Geophys. Res.* **1999**, *104*, 18487–18503. [CrossRef]
85. Luo, G.J.; Brüggemann, N.; Wolf, B.; Gasche, R.; Grote, R.; Butterbach-Bahl, K. Decadal Variability of Soil CO_2, NO, N_2O, and CH_4 fluxes at the Höglwald Forest, Germany. *Biogeosciences* **2012**, *9*, 1741–1763. [CrossRef]
86. Wu, X.; Bruggemann, N.; Gasche, R.; Shen, Z.; Wolf, B.; Butterbach-Bahl, K. Environmental Controls over Soil-Atmosphere Exchange of N_2O, NO, and CO_2 in a Temperate Norway Spruce Forest. *Global Biogeochem. Cycles* **2010**, *24*, 1–16. [CrossRef]
87. Jungkunst, H.F.; Freibauer, A.; Neufeldt, H.; Bareth, G. Nitrous Oxide Emissions from Agricultural Land Use in Germany—A Synthesis of Available Annual Field Data. *J. Plant Nutr. Soil Sci.* **2006**, *169*, 341–351. [CrossRef]