



HAL
open science

Spatial patterns of causality in temperate silvopastoral systems: a perspective on nitrification stability in response to flooding

Romane Mettauer, Mathieu Emily, Zita Bednar-Konski, Anaïs Widmer, Olivier Godinot, Lukas Beule, Edith Le Cadre-Barthélemy

► To cite this version:

Romane Mettauer, Mathieu Emily, Zita Bednar-Konski, Anaïs Widmer, Olivier Godinot, et al.. Spatial patterns of causality in temperate silvopastoral systems: a perspective on nitrification stability in response to flooding. *Ecological Processes*, 2024, 13 (1), pp.66. 10.1186/s13717-024-00538-0 . hal-04698408

HAL Id: hal-04698408

<https://hal.science/hal-04698408v1>

Submitted on 16 Sep 2024

HAL is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers.

L'archive ouverte pluridisciplinaire **HAL**, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d'enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.




Distributed under a Creative Commons Attribution 4.0 International License

RESEARCH

Open Access



Spatial patterns of causality in temperate silvopastoral systems: a perspective on nitrification stability in response to flooding

Romane Mettauer^{1*} , Mathieu Emily², Zita Bednar-Konski³, Anaïs Widmer², Olivier Godinot¹, Lukas Beule³ and Edith Le Cadre¹

Abstract

Background Extreme rainfall and flooding events are projected to increase in frequency and disturb biogeochemical cycles such as the nitrogen (N) cycle. By combining trees and grasses, silvopastoral agroforestry is expected to increase the stability of this cycle in response to flooding. However, little is known about the response of nitrification to flooding in silvopastoral systems. Aim of this study was to assess nitrification stability in response to flooding and identify the main causal relations that drive it in temperate silvopastures.

Methods The nitrification stability (i.e., resistance and resilience) was assessed in two silvopastoral systems (i.e., hedgerows and alley cropping) at three positions relative to the trees. The resistance and resilience of nitrification potential were measured in the laboratory after four weeks of flooding stress and four weeks after the end of the stress, respectively. For the first time, we used multigroup latent structural equation modeling (ML-SEM) to explore the spatial structure of causal relations between nitrification stability and soil properties across all positions of the two silvopastoral systems.

Results Tree rows of both systems favored nitrification resistance, while the mean nitrification potential under flooded conditions was on average 27% and 35% higher as compared to non-stressed soils at the two positions assessed in the grass alleys. ML-SEM revealed that the causal relations that explained these results differed between the two systems. The ML-SEM models tested were unable to explain the causal relations in the hedgerow system. However, the model that considered a covariance between soil physical properties and soil resources availability (model A) was able to explain them in the alley-cropping system. It revealed that causal relations explaining nitrification stability varied according to the position relative to the trees: in the tree rows nitrification stability was associated with higher soil organic carbon concentration and earthworm abundance; in the grass alleys it was associated with higher soil organic carbon concentration and soil bulk density.

Conclusions This study indicates that silvopastoral systems help regulate the N cycle near the trees. The results further imply that improvements in soil organic carbon concentration and soil bulk density favor the regulation of N-related processes in grasslands.

Keywords Nitrogen cycle, Soil microorganisms, Agroforestry, Hedgerow, Alley-cropping system, Grassland, Microbial resistance, Microbial resilience, Multigroup latent structural equation modeling, Nitrogen losses mitigation

*Correspondence:

Romane Mettauer
mettauer.romane@gmail.com

Full list of author information is available at the end of the article



© The Author(s) 2024. **Open Access** This article is licensed under a Creative Commons Attribution 4.0 International License, which permits use, sharing, adaptation, distribution and reproduction in any medium or format, as long as you give appropriate credit to the original author(s) and the source, provide a link to the Creative Commons licence, and indicate if changes were made. The images or other third party material in this article are included in the article's Creative Commons licence, unless indicated otherwise in a credit line to the material. If material is not included in the article's Creative Commons licence and your intended use is not permitted by statutory regulation or exceeds the permitted use, you will need to obtain permission directly from the copyright holder. To view a copy of this licence, visit <http://creativecommons.org/licenses/by/4.0/>.

Introduction

Extreme weather events that cause the structure and/or functioning of ecosystems to exceed their usual limits of variability are projected to become strong drivers of ecosystem dynamics (Smith 2011). Extreme weather events have long-lasting impacts on plant–microbe and microbe–microbe interactions, as well as on processes that drive biogeochemical cycles (van der Putten et al. 2013; Kaisermann et al. 2017; Nguyen et al. 2018; Mukhtar et al. 2023). Nonetheless, knowledge of how diverse types of extreme weather events and their legacy disturb biogeochemical cycles is inconsistent (Müller and Bahn 2022; Qu et al. 2023). Authors such as Knapp et al. (2008), Jentsch et al. (2007), and Dodd et al. (2023) highlighted how few studies explore the effects of extreme rainfall events, even though the frequency of extreme rainfall events is projected to increase in some temperate regions. These events are expected to influence critical biogeochemical cycles such as the nitrogen (N) cycle (Greaver et al. 2016), but such events are difficult to predict (Knapp et al. 2008; Ummenhofer and Meehl 2017).

Plant diversity influences N processes and related microbial communities and increases ecosystem stability under extreme stress (Cardinale et al. 2013; Abalos et al. 2019). By planting trees in or around agricultural fields, agroforestry is recommended as one way to increase agroecosystem stability in response to extreme weather events, such as extreme rainfall and flooding (Elrys et al. 2022; IPCC 2022). The stability of soil microbial communities in response to extreme rainfall events depends on the duration, intensity, and frequency of the event as well as on characteristics of microhabitats and the soil microbial community itself (Gionchetta et al. 2019). Since the addition of trees and their understory vegetation alters these characteristics, agroforestry systems are expected to influence the resistance (i.e., ability to remain in a reference state) and resilience (i.e., ability to return to a reference state) of soil microbial communities to extreme weather events. Both resistance and resilience are crucial components of the stability of microbial communities (Shade et al. 2012; van Meerbeek et al. 2021). The influence of trees on the resistance and resilience of soil microbial communities after drying–rewetting and extreme rainfall events has been explored recently in temperate silvoarable systems (Rivest et al. 2013; Guillot et al. 2019; D’Hervilly et al. 2020), but research on other types of agroforestry systems, such as silvopastoral systems (i.e., combination of trees and livestock) is lacking.

By influencing N-related processes, silvopastoral systems are of great interest to mitigate N losses from grazed grasslands (Grimaldi et al. 2012; Kim and Isaac 2022). While inhibiting nitrification [i.e., oxidation of ammonium (NH_4^+) to nitrate (NO_3^-)] has been considered

one way to decrease N losses from grasslands (Di and Cameron 2018), previous studies observed shifts in the microbial communities that perform nitrification (i.e., nitrifying communities) and their activities in response to soil water in grasslands (Hammerl et al. 2019; Hafeez et al. 2023; Dodd et al. 2023). However, the sensitivity of nitrification to extreme rainfall and flooding events is complex and difficult to generalize (Mukhtar et al. 2023), since these events have been observed to decrease (Sun et al. 2016), increase (Waqas et al. 2021), or not influence nitrification rates (Nguyen et al. 2018).

A variety of nitrification pathways have been identified in agricultural soils, and they may respond differently to anoxia. Autotrophic nitrification by ammonia-oxidizing bacteria (AOB), ammonia-oxidizing archaea (AOA), and nitrite oxidizers is particularly reactive to changes in soil water content and oxygen concentration since it requires aerobic conditions (Prosser and Nicol 2012). In addition, heterotrophic nitrification (i.e., oxidation of ammonia or organic N by microorganisms such as bacteria and fungi) may be influenced by changes in the soil redox potential due to extreme rainfall events (Martikainen 2022). Mukhtar et al. (2023) observed that the stability of nitrifying communities in response to extreme rainfall and flooding events depended on the communities’ resource availability, connectivity, and composition. Thus, identifying causal relations that drive the stability of the N cycle within silvopastoral systems during and after extreme rainfall and flooding events is crucial to promote agricultural practices that help decrease N losses from grasslands (Di and Cameron 2018; Thoroughgood et al. 2023).

Identifying causal relations among ecosystem components is a statistical challenge since correlation does not imply causation (Shipley 2016). Studying causal relations among soil biogeochemical processes in agroforestry systems adds another level of complexity, since the relations may be spatially structured. Indeed, differences can be expected among (i) the tree row and its understory vegetation, (ii) the area of the crop alley directly influenced by the tree row, and (iii) the area of the crop alley not directly influenced by the tree row (Cardinael et al. 2020). Structural equation modeling (SEM) is a promising statistical tool to address such issues and is thus increasingly used in ecology (Hoyle 2012; Shipley 2016; Fan et al. 2016). SEM explores and assesses postulated causal relations and is thus a method to acquire systemic understanding of ecosystems (Grace et al. 2016; Fan et al. 2016). In “latent” SEM, abstract attributes of an ecosystem, such as the stability of microbial communities, can be represented by latent variables. Latent variables are described indirectly using a set of measured “manifest” variables. In addition, “multigroup” SEM, a sophisticated type of SEM,

can assess the preservation of causal relations across several compartments in complex agroecosystems by setting fixed parameters across several positions (Hoyle 2012; Rosseel 2021).

The aims of this study were to assess nitrification stability in response to flooding and identify the main causal relations that drive this stability in temperate silvopastoral systems. We hypothesized that the presence of tree rows and their understory vegetation increases nitrification stability in response to flooding due to their positive influence on soil physico-chemical properties. For the first time, we applied multigroup latent SEM (ML-SEM) to explore the spatial structure of causal relations of nitrification stability in the context of flooding in two silvopastoral systems (i.e., hedgerow and alley cropping) in Brittany, France.

Materials and methods

We studied the spatial structure of causal relations that drive nitrification stability in two silvopastoral systems using ML-SEM to assess postulated causal relations and their spatial preservation in temperate silvopastoral systems (Fig. 1).

Development of the directed acyclic graph

In the first step of ML-SEM, we developed a directed acyclic graph to test postulated causal relations among latent and manifest variables identified in the literature (Rivest et al. 2013; Fan et al. 2016). Hence, we reviewed studies on nitrification stability and overall microbial stability, especially in temperate agroforestry systems, using Web of Science and Google Scholar (see Appendix 1: Box 1 for the combinations of keywords used). We considered reviews and articles published from 2000–2022 and screened their titles and abstracts to select those that provided insights into nitrification or microbial stability under flooding stress. In total, we identified 45 relevant articles (Appendix 1: Table S1).

Four main soil properties that drive nitrification were identified as potential latent variables for the directed acyclic graph: (i) intrinsic properties of the nitrifying community (i.e., community composition, size, and activity level), (ii) resource availability for the nitrifying community, (iii) soil physical properties that drive soil oxygenation and structure, and (iv) soil microclimate. These properties are partly modulated by plant traits and agricultural practices (Hallin et al. 2009; Abalos et al. 2019; Jia et al. 2020; Clark et al. 2020). Soil microclimate was not included as a latent variable due to experimental and statistical constraints. Ultimately, the directed acyclic graph (Fig. 2) included three latent variables: NITRIFICATION STABILITY, RESOURCE AVAILABILITY, and SOIL PHYSICAL PROPERTIES. Since ML-SEM

is constrained by the number of replicates (Deng et al. 2018), latent variables were informed by ecologically accurate and easily measured manifest variables. For NITRIFICATION STABILITY, nitrification resistance (RS) and nitrification resilience (RL) were considered (Orwin and Wardle 2004; Shade et al. 2012). One manifest variable for the size of the nitrifying community was also included, since intrinsic characteristics of the microbial community can explain RS and RL (Bérard et al. 2011; Thion and Prosser 2014). Since we detected no AOA *amoA* genes at the study site using real-time PCR (Mettauer et al. 2024) and could not distinguish nitrifying fungi from non-nitrifying fungi, AOB *amoA* genes were used to represent the size of the nitrifying community. RESOURCE AVAILABILITY was informed by three manifest variables known to influence nitrification activity through the limitation of resources for nitrifying communities and known to vary according to the position to the trees: soil organic carbon (SOC) concentration (Cardinael et al. 2017; Fikri et al. 2021), $N-NH_4^+$ concentration (Pardon et al. 2017; Clark et al. 2020), and soil pH (Gao et al. 2022; Mettauer et al. 2024). SOIL PHYSICAL PROPERTIES that limit aeration and soil water holding capacity were informed by proxies of soil aeration and structure known to impact soil nitrification and to vary according to the positions to the trees: soil bulk density (Danielson and Sutherland 1986; Mettauer et al. 2024), earthworm abundance (Sharma et al. 2017; Vaupel et al. 2023), and root biomass (Freschet et al. 2021; Siegwart et al. 2023). Since SOIL PHYSICAL PROPERTIES and RESOURCE AVAILABILITY may influence each other, we tested model A, which considered covariance (β_3) between them, and model A', which did not (Fig. 2).

The directed acyclic graph developed met the requirements for identification of ML-SEM models: (i) positive degrees of freedom ($df=27$ and 28 for models A and A', respectively), (ii) all latent variables scaled by setting their variances equal to 1, and (iii) all latent variables informed by more than two manifest variables (Fan et al. 2016).

Data acquisition

The manifest variables were measured in April and May 2022 on two neighboring plots in the south of the Ille-et-Vilaine department, in Brittany, France ($47^\circ 45' 36.3''$ N, $1^\circ 54' 54.0''$ W). Each plot contained a silvopastoral system typical for the region, with trees on a 4-year temporary grassland (*Lolium* spp. and *Trifolium pratense*): (i) a hedgerow (H) system or (ii) an alley-cropping (AC) system (Fig. 3). The systems differed in the density of trees planted in the tree row (every 4 m, with shrubs every 1 m between them, in H; every 6 m in AC), diversity of tree species (9 in H; 6 in AC), and number of tree rows per plot (one in H; two spaced 27 m apart in AC). Both plots

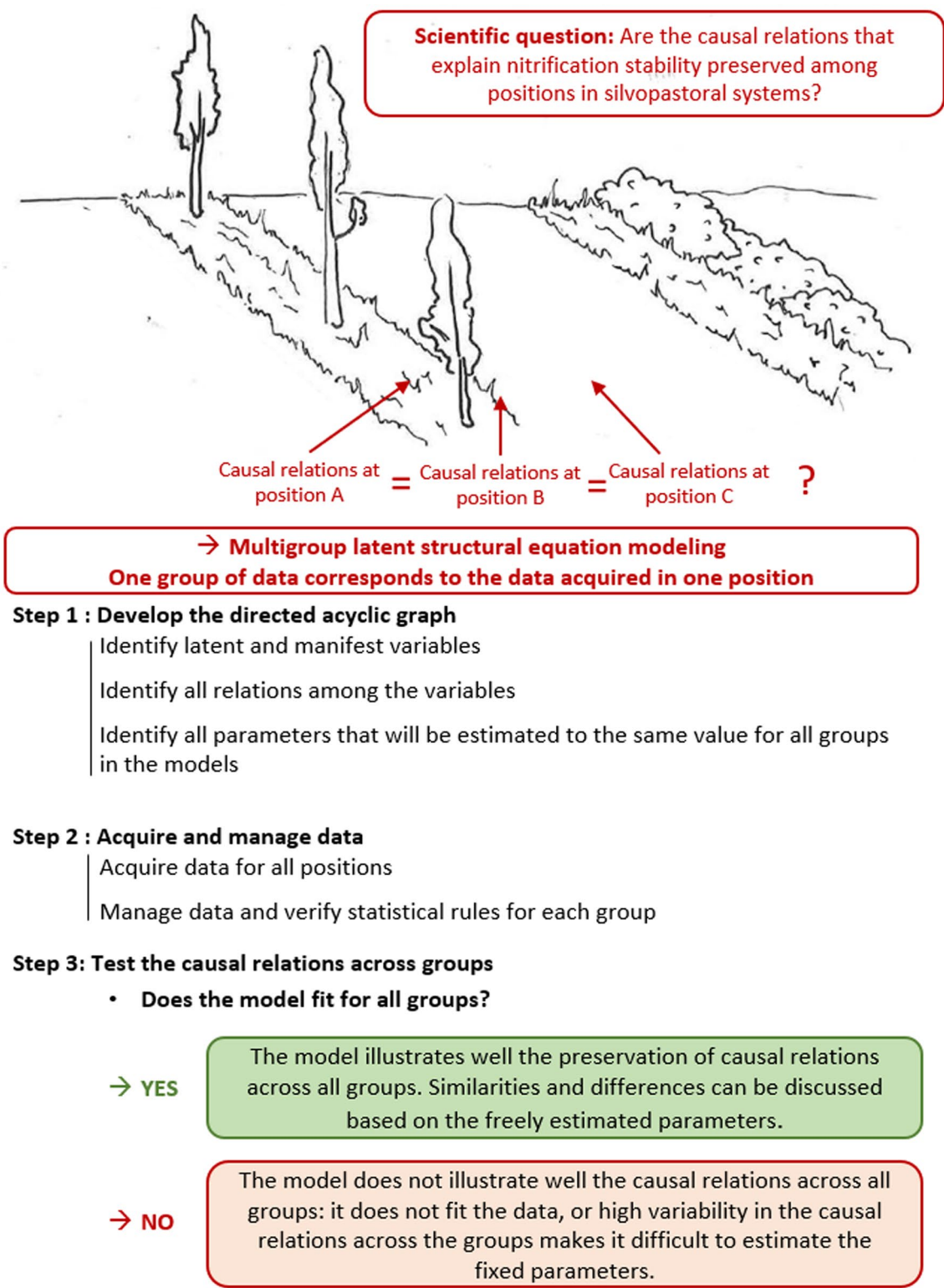


Fig. 1 Overview of the multigroup latent structural equation modeling (ML-SEM) used in the study

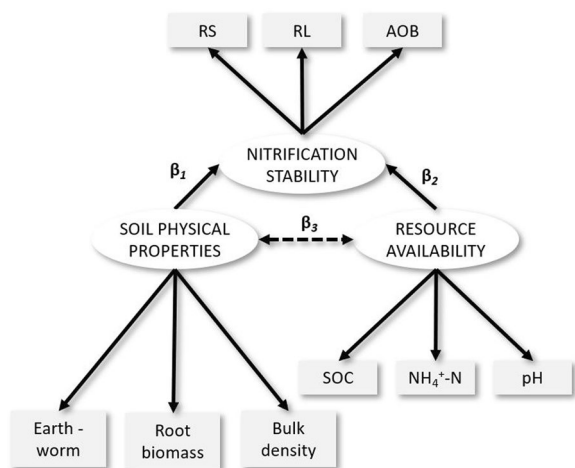


Fig. 2 Directed acyclic graph developed to study nitrification stability in two silvopastoral systems (alley cropping vs. hedgerows) and for three positions relative to the trees. Rectangles represent the manifest variables, ovals the latent variables, and solid arrows the causal relations. The dashed arrow represents the potential covariance between the latent variables SOIL PHYSICAL PROPERTIES and RESOURCE AVAILABILITY (considered when testing model A but not when testing model A'). RS, nitrification resistance; RL, nitrification resilience; SOC, soil organic carbon; AOB, ammonia-oxidizing bacteria *amoA* gene abundance; Earthworm, earthworm abundance

are under a temperate oceanic climate on a silty-loam Luvisol soil. In winter, the plots were regularly flooded for several days due to rainfall events. See Mettauer et al. (2024) for further details on the management of both plots.

Following Mettauer et al. (2024), 30 trees were selected in each plot, and the manifest variables were measured in a 1 m² area at three positions relative to each tree (Fig. 3): (i) in the tree row at 1 m from the tree (position A), (ii) in the grass alley at 1.5 m from the tree (position B), and (iii) in the grass alley at 10 m from the tree (position C). Consequently, the dataset was categorized into six groups by the type of system (H or AC) and position relative to the tree (A, B, or C): H-A, H-B, H-C, AC-A, AC-B, and AC-C.

For each position, RS and RL were determined by comparing the potential nitrification rates (PNR, ISO 15685, see Mettauer et al. 2024 for details) of soil samples exposed to flooding stress to that of soil samples not exposed to flooding stress. Before determining RS and RL, soil samples were collected from each position, air-dried, stored at ambient temperature for two months, and then sieved at <1 mm. Next, four 10 g soil samples per position were prepared by slowly rewetting them for 2 weeks at 20 °C to reach 60% water holding

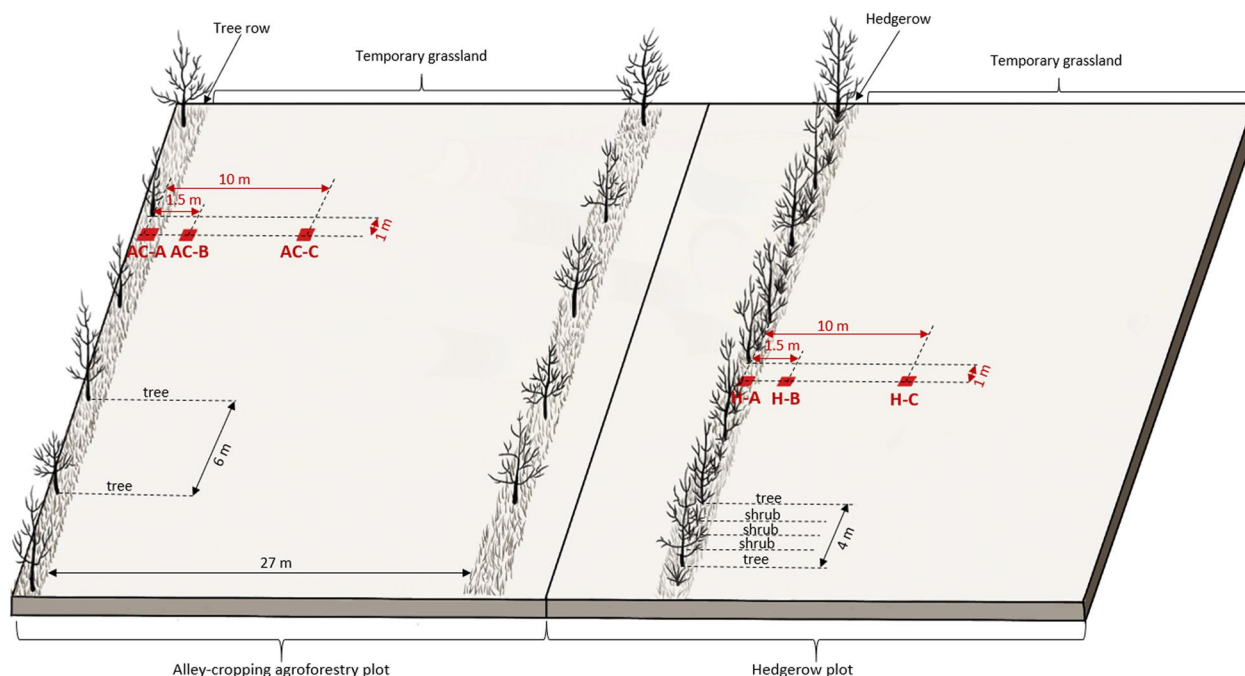


Fig. 3 The experimental design of the two silvopastoral systems studied in Brittany, France (adapted from Mettauer et al. 2024). Soil and vegetation were measured at three positions relative to each tree: at 1 m in the tree row (A), in the grass alley at 1.5 m from the tree (B), and in the grass alley at 10 m from the tree (C). AC, alley cropping; H, hedgerow

capacity. Two of the four soil samples were kept at 20 °C and 60% water holding capacity for the entire experiment and served as control soil samples. The other two samples were exposed to flooding stress by adding ultra-pure water until they reached 200% water holding capacity, at which they were held for 4 weeks. At the end of the stress period, the soils were air-dried for 2 days at 20 °C to reach 60% water holding capacity. Immediately after this step, one control sample and one stressed sample were analyzed to determine the RS. The other two samples were kept for 4 additional weeks under control conditions to determine the RL. The 4-week duration was chosen based on several studies that had observed high resilience four weeks after the end of an applied stress (Bérard et al. 2011; de Oliveira et al. 2020; Guillot et al. 2019; Nguyen et al. 2018; Rivest et al. 2013).

RS and RL were then calculated:

$$RS = \frac{PNRs(T_0)}{PNRc(T_0)} \quad (1)$$

$$RL = \frac{PNRs(T_4)}{PNRc(T_4)} \quad (2)$$

where PNRs and PNRc are the PNR of the stressed and control soils, respectively; T_0 is the measurement immediately after the end of the stress; and T_4 is the measurement after the additional four weeks under control conditions. Thus, RS and RL equaled 1 when the stress

did not influence the PNR, were greater than 1 when the stress stimulated the PNR, and were less than 1 when the stress decreased the PNR.

Several protocols were used to collect data on the manifest variables that described SOIL PHYSICAL PROPERTIES and RESOURCE AVAILABILITY and to determine AOB *amoA* gene abundance (Table 1).

Data management and statistical analysis

Data management and statistical analysis were performed using R software v.4.2.0 (R Core Team 2022).

Detection of outliers

ML-SEM requires that each group of data considered follow a multivariate normal distribution (i.e., multinormality) (Fan et al. 2016). We considered all six groups H-A, H-B, H-C, AC-A, AC-B, and AC-C in the ML-SEM. Multinormality of the groups was assessed based on skewness and kurtosis using Mardia's test (function 'mvn()' of the 'MVN' package; Korkmaz et al. 2014). If a group was not multinormal, we identified multivariate outliers by calculating the Mahalanobis square distance (function 'outlier()' of the 'psych' package) for each observation. Four outliers were detected and removed from the dataset. The final dataset contained 30 observations each for groups AC-A and AC-C and 29 observations each for the other groups AC-B, H-A, H-B, and H-C. Since this procedure considered multivariate normal distribution,

Table 1 Protocols used to measure the manifest variables that informed latent variables

Variable	Method used	References
Ammonium (N-NH ₄ ⁺)	Soil NH ₄ ⁺ concentration was determined in the laboratory from fresh and sieved (< 2 mm) soil samples. NH ₄ ⁺ was extracted by agitating samples for 1 h in a 1 M KCl solution and then measured using a discrete analyzer (SmartChem 200)	ISO 1425-6
Soil organic carbon (SOC)	Soil samples were air-dried upon arrival from the field and then homogenized using a gravimetric grinder. SOC was determined by dry combustion (FlashEA® 1112 analyzer) of the total soil carbon concentration	ISO 10694
Soil pH	Soil samples were air-dried upon arrival from the field and sieved at < 2 mm. Soil pH was determined after agitating samples for 5 min in a 1 M KCl solution	ISO 10390
Soil bulk density	Soil samples were collected in the field using a volumetric cylinder (8 cm in diameter; 15 cm tall). They were then dried at 105 °C for 48 h and weighed. Bulk density was calculated as the ratio of the sample's dry mass to its volume	Blake and Hartge (1986)
Earthworm abundance	In the field, soil blocks (25 cm L × 25 cm W × 30 cm D) were extracted and hand-sorted to count the number of earthworms. Since the soil was shallow, no mustard solution was added to collect earthworms below a depth of 30 cm	ISO 23611-1, adapted
Root biomass	Soil samples were collected in the field using a volumetric cylinder (8 cm in diameter; 15 cm tall) and stored frozen. They were then hand-washed to collect the roots, which were dried at 65 °C for at least 48 h and weighed	Freschet et al. (2021)
AOB <i>amoA</i> gene abundance	Microbial DNA was extracted from the soil samples, inspected for quality and quantity, and diluted at 1:50 (v/v) in double-distilled water. The population size of nitrifying communities [i.e., ammonia-oxidizing bacteria (AOB) and archaea (AOA)] was then determined by quantifying <i>amoA</i> genes using real-time PCR. AOA <i>amoA</i> genes were not detected	Beule et al. (2020)

These manifest variables informed the latent variables SOIL PHYSICAL PROPERTIES (Earthworm abundance, Root biomass, Soil bulk density), RESOURCE AVAILABILITY (SOC, NH₄⁺-N, pH), and NITRIFICATION STABILITY (AOB *amoA* gene abundance). See Mettaufer et al. (2024) for more details about the measurements

some individual data points may look like outliers when considering only one variable.

Univariate analysis of nitrification resistance and resilience

Effects of the type of silvopastoral system (H or AC) and position relative to the tree (A, B, and C) on RS and RL were tested using linear regression models. Since the groups' data did not have normally distributed residuals or homoscedasticity, Kruskal–Wallis tests were followed by Wilcoxon tests with Bonferroni correction of p -values. Effects of the silvopastoral system and position relative to the tree were considered significant at $p < 0.05$. In addition, to assess whether the PNR of stressed soils differed from that of control soils, Student's t -tests ('t.test' function of the 'stats' package) were performed to compare RS and RL to 1.

ML-SEM

ML-SEM was performed with models A and A' using a standardized dataset (function 'scale' of R) that excluded the four outliers. Models A and A' were estimated (i.e., free parameters were calculated to fit the data) using the 'sem' function of R ('lavaan' package, Rosseel 2012). To test whether the spatial structure of causal relations between nitrification stability and the other latent variables was preserved across groups, parameters for causal relations β_1 , β_2 , and β_3 (Fig. 2) were each assigned the same estimated value for the groups considered. First, β_1 , β_2 , and β_3 were each assigned the same estimated value for all six groups. Next, they were each assigned the same estimated value for all positions given a silvopastoral system (H-A, H-B, and H-C vs. AC-A, AC-B, and AC-C). Finally, they were each assigned the same estimated value for each position relative to the tree (H-A and AC-A vs. H-B and AC-B vs. H-C and AC-C). We calculated χ^2 - p -values ('pchisq' function of the 'stats' package) for each group using a χ^2 test and the degrees of freedom of the given model. Models were non-rejected at χ^2 - $p > 0.05$. The Akaike Information Criteria (AIC) was used to compare models A and A' and identify the more plausible one (Bollen et al. 2014).

Results

Nitrification stability

For both silvopastoral systems, the PNR in the tree row after stress were comparable to those from control soils (RS at position A, 1.13 ± 0.38), but it was found higher as compared to the control soils at positions B (1.35 ± 0.61) and C (1.27 ± 0.38) ($p < 0.001$) (Fig. 4a). This indicates that the PNR was stimulated by the flooding stress in the grass alleys only. Although the type of system did not influence RS in response to the flooding stress (Fig. 4a), the RS of the alley-cropping system varied less (standard

deviation = 0.33–0.52) than that of the hedgerow system (standard deviation = 0.43–0.79). In the alley-cropping system, RS was influenced by the position, with lower RS in the tree row (position A, 1.01 ± 0.52) than in the middle of the grass alley (position C, 1.30 ± 0.33) ($p < 0.001$) (Fig. 4a). RL did not differ significantly from 1 for either system and all positions (Fig. 4b), indicating that four weeks after experiencing flooding stress, stressed soils had similar PNR as control soils.

Preservation of the causal relations that explain nitrification stability across silvopastoral systems

When parameters β_1 , β_2 , and β_3 were each assigned the same estimated value for all six groups (AC-A, AC-B, AC-C, H-A, H-B, and H-C), model A was rejected for groups AC-B, H-A, H-B, and H-C (χ^2 - $p = 0.018$, 0.027, 0.016, and 0.001, respectively), while model A' was rejected for groups AC-B, AC-C, H-B, and H-C (χ^2 - $p = 0.012$, 0.032, 0.004, and 0.001, respectively) (Fig. 5b). These results indicate that the causal relations that explained NITRIFICATION STABILITY were not preserved among groups.

When considering models A and A' for only the alley-cropping system, model A was always accepted (χ^2 - $p > 0.05$ for AC-A, AC-B, and AC-C), while model A' was always rejected (χ^2 - $p < 0.05$ for AC-A, AC-B, and AC-C) (Fig. 5c). In addition, model A had a better AIC (1909) than model A' (1946) for the alley-cropping system, indicating that NITRIFICATION STABILITY was explained well for all positions of this system when considering covariance between SOIL PHYSICAL PROPERTIES and RESOURCE AVAILABILITY. Both models A and A' were rejected when considering only the hedgerow system (χ^2 - $p < 0.05$ for H-A, H-B, and H-C) (Fig. 5c), which indicates that neither model could explain nitrification stability across all positions of the hedgerow system.

When parameters β_1 , β_2 , and β_3 were each assigned the same estimated value for AC-A and H-A, AC-B and H-B, or AC-C and H-B, sequentially, both models were accepted for position A (χ^2 - $p > 0.05$ for AC-A and H-A) (Fig. 5d). Model A had a better AIC (1457) than model A' (1462), but causal relations β_1 between NITRIFICATION STABILITY and SOIL PHYSICAL PROPERTIES ($p = 0.67$) and β_2 between NITRIFICATION STABILITY and RESOURCE AVAILABILITY ($p = 0.54$) were non-significant for model A (Appendix S2). Both model A and A' were rejected when estimating β_1 , β_2 , and β_3 equally for positions B and C (χ^2 - $p < 0.05$ for AC-B and H-B as well as for AC-C and H-C) (Fig. 5d). Thus, none of the models was able to explain nitrification stability well in the grass alleys of either silvopastoral system when estimating β_1 , β_2 , and β_3 equally for positions B and C.

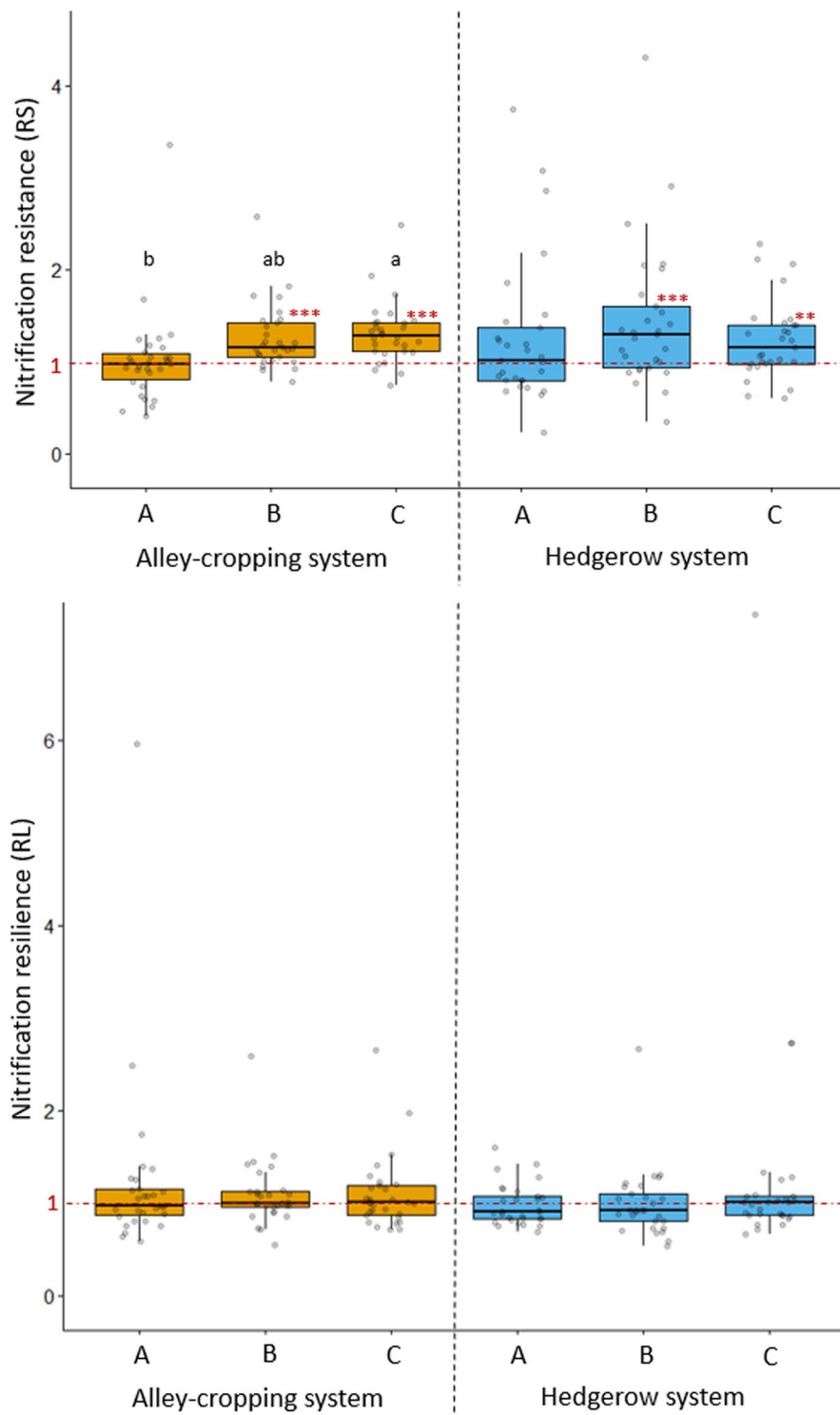
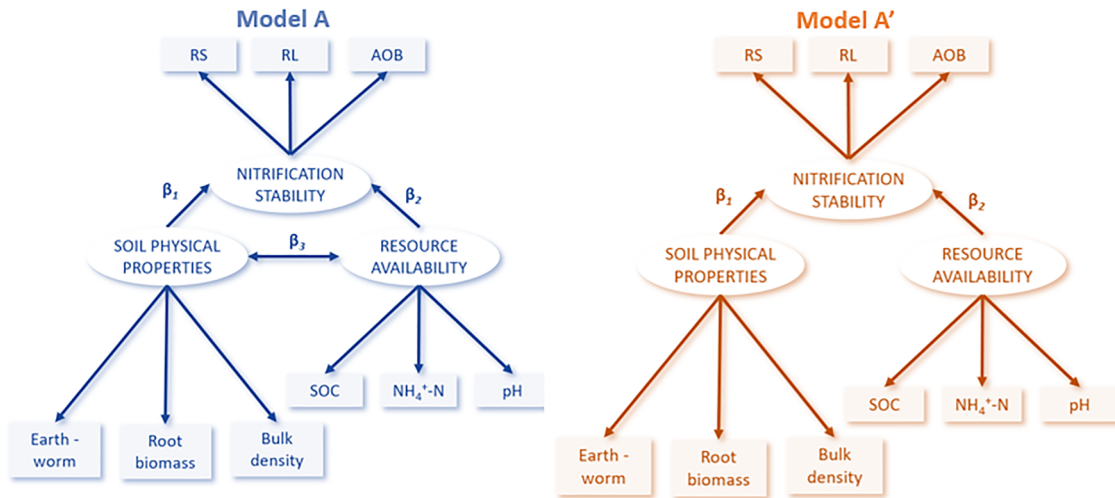


Fig. 4 Boxplots with jittered data points ($n = 176$) of **(a)** nitrification resistance (RS) and **(b)** resilience (RL) as a function of the silvopastoral system and the position relative to the trees: at 1 m in the tree row (A), in the grass alleys at 1.5 m from the tree (B), and in the grass alleys at 10 m from the tree (C). Whiskers represent 1.5 times the interquartile range. Boxplots concerning RS and RL in the alley-cropping system are colored in orange and the ones concerning the hedgerow system are colored in blue. Different letters above the boxplots indicate significant differences ($p < 0.05$). Red asterisks indicate significant differences from 1: * $p < 0.05$, ** $p < 0.01$, and *** $p < 0.001$

(a) Two tested Directed Acyclic Graphs



(b) β_1 , β_2 and β_3 are assigned the same value for all groups AC-A, AC-B, AC-C, H-A, H-B and H-C.

	χ^2 p-value						AIC
	AC-A	AC-B	AC-C	H-A	H-B	H-C	
Model A	0.142	0.018	0.153	0.027	0.016	0.001	4114
Model A'	0.171	0.012	0.032	0.051	0.004	0.001	4134

(c) β_1 , β_2 and β_3 are assigned the same value for the positions A, B and C given one silvopastoral system.

	χ^2 p-value			AIC
	AC-A	AC-B	AC-C	
Model A	0.185	0.086	0.091	1909
Model A'	0.002	0.006	0.032	1946
	H-A	H-B	H-C	
Model A	0.011	0.027	0.005	2203
Model A'	0.023	0.007	0.001	2211

(d) β_1 , β_2 and β_3 are assigned the same value for both silvopastoral systems given one position.

	χ^2 p-value		AIC
	AC-A	H-A	
Model A	0.225	0.163	1457
Model A'	0.171	0.094	1462
	AC-B	H-B	
Model A	0.017	0.039	1305
Model A'	0.012	0.041	1307
	AC-C	H-C	
Model A	0.028	0.006	1353
Model A'	0.045	0.000	1360

Fig. 5 Causal space exploration and model selection using multigroup latent structural equation modeling (ML-SEM). (a) Two latent causal structures were tested. Model A considered potential covariance between the latent variables SOIL PHYSICAL PROPERTIES and RESOURCE AVAILABILITY, while model A' did not. Tables (b), (c) and (d) show the χ^2 -p-value and Akaike Information Criteria (AIC) for all models. Models were not rejected when χ^2 -p > 0.05 (in bold). RS = nitrification resistance, RL = nitrification resilience, SOC = soil organic carbon, AOB = ammonia-oxidizing bacteria *amoA* gene abundance, Earthworm = earthworm abundance

Spatial causal relations between latent and manifest variables in the alley-cropping system according to model A

The latent variable NITRIFICATION STABILITY was significantly and positively informed by RS at positions A and B (Fig. 6). Since the RS was greater than 1 and related to stimulation of PNR, the stability of PNR decreased as RS increased. In contrast, NITRIFICATION STABILITY was significantly and negatively informed by RS at position C. RL significantly informed NITRIFICATION STABILITY only at position B, while AOB did not significantly inform NITRIFICATION STABILITY at any position. At all positions, NITRIFICATION STABILITY was significantly related to RESOURCE AVAILABILITY (negatively) and SOIL PHYSICAL PROPERTIES (positively).

Depending on the position, RESOURCE AVAILABILITY was significantly informed by different manifest variables. At position A, RESOURCE AVAILABILITY was positively informed by SOC and soil pH. At position B, it was positively informed by SOC, while at position C, it was significantly and negatively informed by SOC. Furthermore, the absolute value of the contribution of SOC to RESOURCE AVAILABILITY decreased from position A (0.826) to B (0.423) to C (0.270). SOIL PHYSICAL PROPERTIES was significantly and positively influenced by earthworm abundance only at position A. Soil bulk density significantly influenced SOIL PHYSICAL PROPERTIES in the grass alleys at positions B (negatively) and C (positively), with similar absolute values of contribution at both positions (0.581 and 0.504, respectively). In addition, RESOURCE AVAILABILITY and SOIL PHYSICAL PROPERTIES significantly influenced each other.

The latent variable NITRIFICATION STABILITY was mostly positively related to the manifest variable RS (i.e., stimulation of PNR after flooding). By extension of the relations between NITRIFICATION STABILITY and RESOURCE AVAILABILITY and SOIL PHYSICAL PROPERTIES, RS was negatively related to high SOC and soil pH at position A. Moreover, RS was positively related to earthworm abundance in the tree row (position A) and negatively related to SOC and soil bulk density in the grass alleys (positions B and C).

Discussion

Trees improve nearby nitrification stability when soil faces flooding stress

This study demonstrates that trees in temperate grasslands can favor nitrification stability when flooding occurs. Although PNR may not reflect the in situ activity of the nitrifying communities due to laboratory conditions, it is a valid method to explore and compare nitrification potentials between several conditions (e.g., position relative to the trees) (Hazard et al. 2021). First,

the PNR was resilient at all positions relative to the tree in both silvopastoral systems studied. This study indicates that, unlike other C- and N-cycle processes, flooding stress has no long-term effect on nitrification or nitrifying communities, consistent with the results of other studies (Nguyen et al. 2018; Fikri et al. 2021).

In the present study, NITRIFICATION STABILITY was most sensitive to variations in nitrification resistance. Immediately after the flooding stress, PNR was stimulated in the grass alleys, indicating that nitrification was not resistant in these positions in the plots. This result is consistent with that of Dodd et al. (2023), who concluded that flooding stress strongly influences ecosystem processes in temperate grasslands; however, the present study highlights that tree rows of both alley-cropping and hedgerow systems prevented such stimulation. Previous studies argued that after anaerobic conditions, nitrification can be stimulated by the $N-NH_4^+$ that had accumulated through nitrate reduction during the anaerobic conditions and additional mineralization of organic N inputs from cell lysis (Unger et al. 2009; De-Campos et al. 2012; Dodd et al. 2023). Since SOC contributed greatly to nitrification stability in the ML-SEM of the alley-cropping system, we speculate that additional N mineralization was inhibited by litter inputs in the tree rows, which consequently inhibited $N-NH_4^+$ production during the flooding stress (Lado-Monserrat et al. 2014; Rivest et al. 2015).

Hedgerows and tree rows are considered to help improving microclimate conditions by intercepting, draining, and taking up water, as well as by decreasing wind speeds (Benhamou 2012; Kanzler et al. 2019; van Ramshorst et al. 2022; Brandle et al. 2004). Thus, we speculate that nitrification may also be stimulated in grass alleys because the nitrifying communities there are more accustomed to flooding stress than those in tree rows (Guillot et al. 2019; Evans and Wallenstein 2012).

Finally, we expected a strong relation between nitrification stability and the size of the nitrifying community (i.e., AOB) from the ML-SEM. However, results of the present study are consistent with those of Nguyen et al. (2018), who observed no influence of flooding on AOB community size in agricultural soils. Further analysis of the composition of AOB communities and other nitrifying organisms may supplement our results for nitrification stability. Moreover, PNR measurements neglect the impact of heterotrophic nitrifiers (Hazard et al. 2021), although heterotrophic nitrification may be of importance, especially in grassland soils (Martikainen 2022). Hence, further studies considering the role of heterotrophic nitrifying communities in the causal relations explaining nitrification stability in silvopastoral systems are needed.

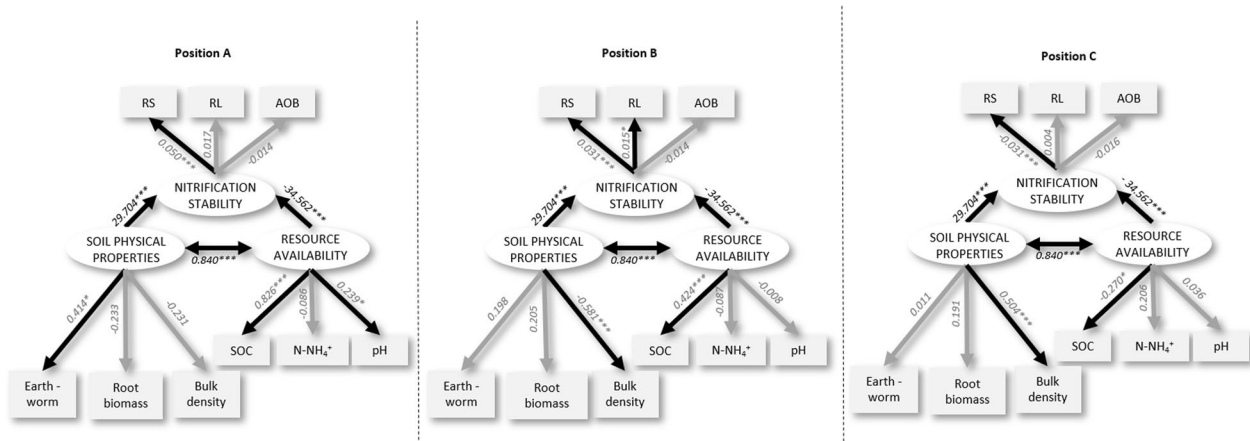


Fig. 6 Validated models obtained for positions in the alley-cropping system: at 1 m in the tree row (A), in the grass alleys at 1.5 m from the tree (B), and in the grass alleys at 10 m from the tree (C). Values in italics indicate regressions between latent (ovals) and manifest (rectangles) variables. Asterisks indicate significant regressions: * $p < 0.05$, ** $p < 0.01$, and *** $p < 0.001$. Black arrows represent significant regressions ($p < 0.05$), while gray arrows represent non-significant regressions. RS, nitrification resistance; RL, nitrification resilience; SOC, soil organic carbon; AOB, ammonia-oxidizing bacteria *amoA* gene abundance; Earthworm, earthworm abundance

Agroforestry systems differ in the spatial causal relations that drive nitrification stability when soil faces flooding stress

Silvopastoral systems are often considered a homogeneous type of agroforestry system, but several studies revealed high heterogeneity among silvopastoral systems (e.g., Mayer et al. 2022; Terasaki Hart et al. 2023). In the present study, both silvopastoral systems were managed in the same way, differing only in characteristics of the tree rows (i.e., tree species, tree density, and number of tree rows per plot). Univariate analysis revealed that the two systems had similar spatial patterns of nitrification resistance and resilience, but the ML-SEM revealed that different underlying causal processes explained their nitrification stability. In the first step of the ML-SEM, most models were rejected when assigning the same estimated value for the causal relations among NITRIFICATION STABILITY, SOIL PHYSICAL PROPERTIES, and RESOURCE AVAILABILITY for all six groups (H-A, H-B, H-C, AC-A, AC-B, and AC-C). The second and third steps of the ML-SEM in particular revealed that the directed acyclic graph developed did not reflect the causal relations that explained nitrification stability for the hedgerow system, but that it did for the alley-cropping system. Thus, ML-SEM was sufficient for identifying the main factors that explained nitrification stability in the alley-cropping system (i.e., soil physical properties and resource availability), but further research is necessary to identify those that explain it in the hedgerow system.

In addition to the effects of tree diversity and identity (Abalos et al. 2019), differences in microclimate induced

by tree density (Jian et al. 2018; 33% higher density in the hedgerow system than in the alley-cropping system) may have contributed to the differences in causal relations observed between the two systems. Due to experimental and statistical constraints, we were unable to consider data on soil microclimate in the ML-SEM, although we observed a trend for higher temperature in the hedgerow system than in the alley-cropping system (Appendix S3). Future studies that relate the functional traits of trees and their understory vegetation to microclimate and microbial communities may help understand the observed differences in causal relations. Moreover, affiliates of the fungal phylum Ascomycota may be involved in heterotrophic nitrification, especially at low pH (Martikainen 2022). Since we could not distinguish nitrifying from non-nitrifying Ascomycota, we were not able to include this information in the directed acyclic graph.

Understanding the effects of biodiversity-based practices on ecological processes in order to develop agroecological systems requires considering causal complexity (Carof et al. 2022; Thorogood et al. 2023). Many replicates (i.e., > 50; Marsh et al. 1998) are necessary for SEM to capture the high variability induced by such complexity. Despite our sampling effort, the directed acyclic graph may have been invalid for the hedgerow system due to this system's high variability in RS. Thus, causal relations in the hedgerow system may be more uncertain than those in the alley-cropping system. Despite the difficulties in acquiring datasets with many replicates, the power of SEM is promising, since univariate analyses of nitrification stability concluded that the two silvopastoral systems were highly similar, while the present study's

ML-SEM highlighted a variety of multifactorial relations that drive nitrification stability in these systems.

Perspectives on the regulation of nitrification stability in grass alleys in temperate agroforestry systems

Although rainfall or flooding events that last for four weeks remain rare in temperate regions, they are expected to increase in frequency as the climate changes (Knapp et al. 2008; Beier et al. 2008; Soubeyroux et al. 2020; Qu et al. 2023). Studies like ours that focused on a “press” flooding stress (i.e., a continuous long-term event; Dodd et al. 2023; Unger et al. 2009) often recorded a stimulation of nitrification immediately after flooding, which has rarely been observed in studies that focused on “pulse” flooding stresses (i.e., discrete short-term events) (Sereni et al. 2022; Nguyen et al. 2018). The present study’s results highlight risks of hot spots and hot moments for nitrification (i.e., locations where nitrification rates are high for short periods) (McClain et al. 2003) in grazed grass alleys. Since the PNR is considered as a proxy of losses in soil function (Sereni et al. 2022) and provides insights on potential N losses (Cameron et al. 2013), the present study’s results suggest that agroforestry can mitigate spikes in N losses from grass alleys. However, our previous study of PNR under non-stressed conditions found higher PNR in the tree rows of the alley-cropping system than that in its grass alleys or in the hedgerow system (Mettauer et al. 2024). We thus argue that alley-cropping systems may have trade-offs between a high risk of N losses under non-stressed conditions and limitation of spikes in N losses under stressed conditions, while hedgerow systems seem to promote more stable and lower PNR. Thus, based on the present study’s results, hedgerow systems may be more likely to decrease N losses from grazed grasslands than alley-cropping systems.

More specifically, ML-SEM helps identify factors that decrease PNR under flooding, which is important since certain types of agriculture, such as organic farming, cannot use nitrification inhibitors to decrease N losses (Norton and Ouyang 2019). Indeed, our study revealed that causal relations explaining nitrification stability in the alley-cropping system varied according to the position relative to the trees: in the tree rows nitrification stability was associated with higher soil organic carbon concentration and earthworm abundance; in the grass alleys it was associated with higher soil organic carbon concentration and soil bulk density. The present study thus encourages considering agricultural practices in the grass alley that enhance SOC (e.g., organic fertilization, agroforestry practices) to limit hot spots and hot moments of nitrification in grazed grasslands. In addition, soil bulk density contributed significantly to nitrification stability

in grass alleys, likely due to bulk density’s influence on the structure of nitrifying communities in grazed grasslands (Pan et al. 2018). Unfortunately, SOC and bulk density are usually excluded when modeling nitrification in agricultural systems since variations of nitrification are often calculated based on variations in NH_4^+ concentration, soil temperature, soil water content, and soil pH (Brisson et al. 2008; Taylor et al. 2017; Norton and Ouyang 2019). Furthermore, our study indicates the spatial variation in the main factors that influence nitrification stability in the alley-cropping system, which highlights the complexity of process stability in agroecological systems. Meanwhile, the rejection of model A’ (i.e., no covariance between SOIL PHYSICAL PROPERTIES and RESOURCE AVAILABILITY) for the alley-cropping system highlights the importance of feedback loops in regulating nitrification stability (Placella and Firestone 2013; Jia et al. 2020; Clark et al. 2020; Bei et al. 2021). Feedback loops need to be considered when identifying management options for regulating soil processes (van der Putten et al. 2013) and PNR under non-flooded conditions. Modeling nitrification processes would be useful to assessing agricultural practices that decrease N losses from grazed grasslands. However, we argue that such models need improvements before they can be applied robustly to complex agroecological systems (e.g., agroforestry systems). These improvements include representing the spatial heterogeneity of soil processes, effects of plant traits, and feedback loops between soil physical properties and resource availability.

Conclusions

This study found that temperate silvopastoral systems improve the stability of nitrification in the context of extreme rainfall and flooding events. Trees in both the hedgerow and alley-cropping systems promoted nearby nitrification stability. Furthermore, the ML-SEM highlighted that the causal relations that drive nitrification stability are spatially structured in silvopastoral systems and differ between the two systems studied. Overall, hedgerow systems seem to be a better option for mitigating N losses through nitrification regulation in grazed grasslands. By using ML-SEM, this study raises novel research questions about the relations among SOC, soil bulk density, and nitrification stability, as well as about shifts in microbial communities during extreme weather events in complex agroecosystems. Future research using factorial experiments and modeling will help to address these questions.

Abbreviations

AC	Alley-cropping system
AOA	Ammonia-oxidizing archaea
AOB	Ammonia-oxidizing bacteria

H	Hedgerow
N	Nitrogen
NH ₄ ⁺	Ammonium
NO ₂ ⁻	Nitrite
NO ₃ ⁻	Nitrate
PCR	Polymerase chain reaction
PNR	Potential nitrification rate
RL	Resilience
RS	Resistance
(ML-)SEM	(Multigroup latent) structural equation modeling
SOC	Soil organic carbon

Supplementary Information

The online version contains supplementary material available at <https://doi.org/10.1186/s13717-024-00538-0>.

Supplementary Material 1. **Appendix 1.** Literature review of nitrification stability used to develop the directed acyclic graph. **Appendix 2.** Validated structural equation models obtained for the alley-cropping system and hedgerow system at position A. Values in italics indicate regressions between latent and manifest variables. Asterisks identify significant regressions: * $p < 0.05$, ** $p < 0.01$, and *** $p < 0.001$. **Appendix 3.** Example of soil temperature measured over 24 h at a depth of 15 cm in the alley-cropping system and hedgerow system. Points represent means, while error bars represent minima and maxima. Data came from an 8-day survey (i.e. 5–12 April 2022) at four locations per silvopastoral system.

Acknowledgements

The authors thank their colleagues from INRAE and Institut Agro Rennes-Angers who helped with field preparation as well as sampling and laboratory work. We extend special thanks to our colleagues from UMR STLO, who welcomed us to their laboratory for part of the experiment.

Author contributions

RM, OG and ELC contributed to the conception and design of the study. RM performed the laboratory work to determine nitrification resistance and resilience with the help of OG and ELC. LB and ZB performed laboratory work to determine the size of the soil microbial community. RM performed the statistical analysis with the help of ME and AW. RM and ELC wrote the first draft of the manuscript, which was critically revised by LB, ZB, OG, ME, and AW. All authors read and approved the final manuscript.

Funding

This study was financially supported by La Fondation de France (grant no. 00117721/WB-2021-35937).

Availability of data and materials

All data generated during the study and R script used for data management and statistical analysis are available at: <https://doi.org/10.57745/ZNUPPX>.

Declarations

Ethics approval and consent to participate

Not applicable.

Consent for publication

Not applicable.

Competing interests

The authors declare they have no competing interest.

Author details

¹SAS, Institut Agro, INRAE, 35000 Rennes, France. ²Institut Agro, Univ Rennes, CNRS, IRMAR, 35000 Rennes, France. ³Julius Kühn Institute (JKI)-Federal Research Centre for Cultivated Plants, Institute for Ecological Chemistry, Plant Analysis and Stored Product Protection, Berlin, Germany.

Received: 21 March 2024 Accepted: 6 August 2024

Published online: 14 September 2024

References

- Abalos D, van Groenigen JW, Philippot L et al (2019) Plant trait-based approaches to improve nitrogen cycling in agroecosystems. *J Appl Ecol* 56:2454–2466. <https://doi.org/10.1111/1365-2664.13489>
- Bei S, Tian Y, Zhao J et al (2021) Temperature-dependent changes in active nitrifying communities in response to field fertilization legacy. *Biol Fertil Soils* 57:1–14. <https://doi.org/10.1007/s00374-020-01500-w>
- Beier C, Emmett BA, Peñuelas J et al (2008) Carbon and nitrogen cycles in European ecosystems respond differently to global warming. *Sci Total Environ* 407:692–697. <https://doi.org/10.1016/j.scitotenv.2008.10.001>
- Benhamou C (2012) Modélisation de l'effet des interactions haies-cultures sur les transferts d'eau et d'azote à l'échelle d'un petit bassin versant agricole. Institut supérieur des sciences agronomiques agroalimentaires horticoles et du paysage
- Bérard A, Bouchet T, Sévenier G et al (2011) Resilience of soil microbial communities impacted by severe drought and high temperature in the context of Mediterranean heat waves. *Eur J Soil Biol* 47:333–342. <https://doi.org/10.1016/j.ejsobi.2011.08.004>
- Beule L, Lehtsaar E, Corre MD et al (2020) Poplar rows in temperate agroforestry croplands promote bacteria, fungi, and denitrification genes in soils. *Front Microbiol* 10:3108. <https://doi.org/10.3389/fmicb.2019.03108>
- Blake GR, Hartge KH (1986) Bulk density. In: *Methods of Soil Analysis*. John Wiley & Sons, Ltd, pp 363–375
- Bollen KA, Harden JJ, Ray S, Zavisca J (2014) BIC and Alternative Bayesian information criteria in the selection of structural equation models. *Struct Equ Modeling* 21:1–19. <https://doi.org/10.1080/10705511.2014.856691>
- Brandle J, Hodges L, Zhou X (2004) Windbreaks in North American agricultural systems: new visitas in agroforestry. *Agrofor Syst* 61:65–78. <https://doi.org/10.1023/B:AGFO.0000028990.31801.62>
- Brisson N, Launay M, Mary B, Beaudouin N (2008) Conceptual Basis, Formalisations and Parameterization of the Stics Crop Model, Quae. Éditions Quae, 78026 Versailles Cedex, France
- Cameron KC, Di HJ, Moir JL (2013) Nitrogen losses from the soil/plant system: a review. *Ann Appl Biol* 162:145–173. <https://doi.org/10.1111/aab.12014>
- Cardinael R, Chevallier T, Cambou A et al (2017) Increased soil organic carbon stocks under agroforestry: a survey of six different sites in France. *Agr Ecosyst Environ* 236:243–255. <https://doi.org/10.1016/j.agee.2016.12.011>
- Cardinael R, Mao Z, Chenu C, Hinsinger P (2020) Belowground functioning of agroforestry systems: recent advances and perspectives. *Plant Soil* 453:1–13. <https://doi.org/10.1007/s11104-020-04633-x>
- Cardinale BJ, Gross K, Fritschie K et al (2013) Biodiversity simultaneously enhances the production and stability of community biomass, but the effects are independent. *Ecology* 94:1697–1707. <https://doi.org/10.1890/12-1334.1>
- Carof M, Godinot O, Le Cadre E (2022) Biodiversity-based cropping systems: a long-term perspective is necessary. *Sci Total Environ* 838:156022. <https://doi.org/10.1016/j.scitotenv.2022.156022>
- Clark DR, McKew BA, Dong LF et al (2020) Mineralization and nitrification: archaea dominate ammonia-oxidising communities in grassland soils. *Soil Biol Biochem* 143:107725. <https://doi.org/10.1016/j.soilbio.2020.107725>
- D'Hervilly C, Marsden C, Hedde M, Bertrand I (2020) Sown understory vegetation strips impact soil chemical fertility, associated microorganisms and macro-invertebrates in two temperate alley cropping systems. *Agrofor Syst* 94:1851–1864. <https://doi.org/10.1007/s10457-020-00501-w>
- Danielson RE, Sutherland PL (1986) Porosity. *Methods of soil analysis*. John Wiley & Sons Ltd, pp 443–461
- de Oliveira AB, Cantarel AAM, Seiller M et al (2020) Short-term plant legacy alters the resistance and resilience of soil microbial communities exposed to heat disturbance in a Mediterranean calcareous soil. *Ecol Indic* 108:105740. <https://doi.org/10.1016/j.ecolind.2019.105740>
- De-Campos AB, Huang C, Johnston CT (2012) Biogeochemistry of terrestrial soils as influenced by short-term flooding. *Biogeochemistry* 111:239–252. <https://doi.org/10.1007/s10533-011-9639-2>

- Deng L, Yang M, Marcoulides KM (2018) Structural equation modeling with many variables: a systematic review of issues and developments. *Front Psychol* 9:580. <https://doi.org/10.3389/fpsyg.2018.00580>
- Di HJ, Cameron KC (2018) Ammonia oxidisers and their inhibition to reduce nitrogen losses in grazed grassland: a review. *J R Soc N Z* 48:127–142. <https://doi.org/10.1080/03036758.2017.1354894>
- Dodd RJ, Chadwick DR, Hill PW et al (2023) Resilience of ecosystem service delivery in grasslands in response to single and compound extreme weather events. *Sci Total Environ* 861:160660. <https://doi.org/10.1016/j.scitotenv.2022.160660>
- Elrys AS, Uwiragiye Y, Zhang Y et al (2022) Expanding agroforestry can increase nitrate retention and mitigate the global impact of a leaky nitrogen cycle in croplands. *Nat Food* 4:109–121. <https://doi.org/10.1038/s43016-022-00657-x>
- Evans SE, Wallenstein MD (2012) Soil microbial community response to drying and rewetting stress: does historical precipitation regime matter? *Biogeochemistry* 109:101–116. <https://doi.org/10.1007/s10533-011-9638-3>
- Fan Y, Chen J, Shirkey G et al (2016) Applications of structural equation modeling (SEM) in ecological studies: an updated review. *Ecol Process* 5:19. <https://doi.org/10.1186/s13717-016-0063-3>
- Fikri M, Joulain C, Motelica-Heino M et al (2021) Resistance and resilience of soil nitrogen cycling to drought and heat stress in rehabilitated urban soils. *Front Microbiol* 12:727468. <https://doi.org/10.3389/fmicb.2021.727468>
- Freschet GT, Roumet C, Comas LH et al (2021) Root traits as drivers of plant and ecosystem functioning: current understanding, pitfalls and future research needs. *New Phytol* 232:1123–1158. <https://doi.org/10.1111/nph.17072>
- Gao W, Chen M, Xu X (2022) Tracing controls of autotrophic and heterotrophic nitrification in terrestrial soils. *Eur J Soil Biol* 110:103409. <https://doi.org/10.1016/j.ejsobi.2022.103409>
- Gionchetta G, Romani AM, Oliva F, Artigas J (2019) Distinct responses from bacterial, archaeal and fungal streambed communities to severe hydrological disturbances. *Sci Rep* 9:13506. <https://doi.org/10.1038/s41598-019-49832-4>
- Grace JB, Anderson TM, Seabloom EW et al (2016) Integrative modelling reveals mechanisms linking productivity and plant species richness. *Nature* 529:390–393. <https://doi.org/10.1038/nature16524>
- Greaver TL, Clark CM, Compton JE et al (2016) Key ecological responses to nitrogen are altered by climate change. *Nat Clim Chang* 6:836–843. <https://doi.org/10.1038/nclimate3088>
- Grimaldi C, Fossey M, Thomas Z et al (2012) Nitrate attenuation in soil and shallow groundwater under a bottomland hedgerow in a European farming landscape. *Hydrol Process* 26:3570–3578. <https://doi.org/10.1002/hyp.8441>
- Guillot E, Hinsinger P, Dufour L et al (2019) With or without trees: resistance and resilience of soil microbial communities to drought and heat stress in a Mediterranean agroforestry system. *Soil Biol Biochem* 129:122–135. <https://doi.org/10.1016/j.soilbio.2018.11.011>
- Hafeez F, Clément J-C, Bernard L et al (2023) Early spring snowmelt and summer droughts strongly impair the resilience of bacterial community and N cycling functions in a subalpine grassland ecosystem. *Oikos* 2023:e09836. <https://doi.org/10.1111/oik.09836>
- Hallin S, Jones CM, Schloter M, Philippot L (2009) Relationship between N-cycling communities and ecosystem functioning in a 50-year-old fertilization experiment. *ISME J* 3:597–605. <https://doi.org/10.1038/ismej.2008.128>
- Hammerl V, Kastl E-M, Schloter M et al (2019) Influence of rewetting on microbial communities involved in nitrification and denitrification in a grassland soil after a prolonged drought period. *Sci Rep* 9:2280. <https://doi.org/10.1038/s41598-018-38147-5>
- Hazard C, Prosser JL, Nicol GW (2021) Use and abuse of potential rates in soil microbiology. *Soil Biol Biochem* 157:108242. <https://doi.org/10.1016/j.soilbio.2021.108242>
- Hoyle RH (2012) Handbook of structural equation modeling. Guilford Press
- IPCC (2022) Climate Change 2022: Impacts, Adaptation and Vulnerability. Contribution of Working Group II to the sixth Assessment Report of the Intergovernmental Panel on Climate Change [H.-O. Pörtner, D.C. Roberts, M. Tignor, E.S. Poloczanska, K. Mintenbeck, A. Alegria, M. Craig, S. Langsdorf, S. Löschke, V. Möller, A. Okem, B. Rama (eds.)]. Cambridge University Press, Cambridge, UK and New York, NY, USA, p 3056
- Jentsch A, Kreyling J, Beierkuhnlein C (2007) A new generation of climate-change experiments: events, not trends. *Front Ecol Environ* 5:365–374. [https://doi.org/10.1890/1540-9295\(2007\)5\[365:ANGOCE\]2.0.CO;2](https://doi.org/10.1890/1540-9295(2007)5[365:ANGOCE]2.0.CO;2)
- Jia Z, Zhou X, Xia W et al (2020) Evidence for niche differentiation of nitrifying communities in grassland soils after 44 years of different field fertilization scenarios. *Pedosphere* 30:87–97. [https://doi.org/10.1016/S1002-0160\(19\)60803-9](https://doi.org/10.1016/S1002-0160(19)60803-9)
- Jian Z, Bo L, Mingyue W (2018) Study on windbreak performance of tree canopy by numerical simulation method. *J Comput Multiphase Flows* 10:259–265. <https://doi.org/10.1177/1757482X18791901>
- Kaisermann A, de Vries FT, Griffiths RI, Bardgett RD (2017) Legacy effects of drought on plant–soil feedbacks and plant–plant interactions. *New Phytol* 215:1413–1424. <https://doi.org/10.1111/nph.14661>
- Kanzler M, Böhm C, Mirck J et al (2019) Microclimate effects on evaporation and winter wheat (*Triticum aestivum* L.) yield within a temperate agroforestry system. *Agroforest Syst* 93:1821–1841. <https://doi.org/10.1007/s10457-018-0289-4>
- Kim D-G, Isaac ME (2022) Nitrogen dynamics in agroforestry systems: a review. *Agron Sustain Dev* 42:60. <https://doi.org/10.1007/s13593-022-00791-7>
- Knapp AK, Beier C, Briske DD et al (2008) Consequences of more extreme precipitation regimes for terrestrial ecosystems. *Bioscience* 58:811–821. <https://doi.org/10.1641/B580908>
- Korkmaz S, Goksuluk D, Zararsiz G (2014) MVN: an R package for assessing multivariate normality. *R J* 6:151. <https://doi.org/10.32614/RJ-2014-031>
- Lado-Monserrat L, Lull C, Bautista I et al (2014) Soil moisture increment as a controlling variable of the “Birch effect”: Interactions with the pre-wetting soil moisture and litter addition. *Plant Soil* 379:21–34. <https://doi.org/10.1007/s11104-014-2037-5>
- Marsh HW, Hau K-T, Balla JR, Grayson D (1998) Is more ever too much? The number of indicators per factor in confirmatory factor analysis. *Multivar Behav Res* 33:181–220. https://doi.org/10.1207/s15327906mbr3302_1
- Martikainen PJ (2022) Heterotrophic nitrification—an eternal mystery in the nitrogen cycle. *Soil Biol Biochem* 168:108611. <https://doi.org/10.1016/j.soilbio.2022.108611>
- Mayer S, Wiesmeier M, Sakamoto E et al (2022) Soil organic carbon sequestration in temperate agroforestry systems—a meta-analysis. *Agr Ecosyst Environ* 323:107689. <https://doi.org/10.1016/j.agee.2021.107689>
- McClain ME, Boyer EW, Dent CL et al (2003) Biogeochemical hot spots and hot moments at the interface of terrestrial and aquatic ecosystems. *Ecosystems* 6:301–312. <https://doi.org/10.1007/s10021-003-0161-9>
- Mettaufer R, Beule L, Bednar Z et al (2024) Influence of two agroforestry systems on the nitrification potential in temperate pastures in Brittany, France. *Plant Soil* 494:651–667. <https://doi.org/10.1007/s11104-023-06309-8>
- Mukhtar H, Wunderlich RF, Muzaffar A et al (2023) Soil microbiome feedback to climate change and options for mitigation. *Sci Total Environ* 882:163412. <https://doi.org/10.1016/j.scitotenv.2023.163412>
- Müller LM, Bahn M (2022) Drought legacies and ecosystem responses to subsequent drought. *Glob Change Biol* 28:5086–5103. <https://doi.org/10.1111/gcb.16270>
- Nguyen LTT, Osanai Y, Anderson IC et al (2018) Flooding and prolonged drought have differential legacy impacts on soil nitrogen cycling, microbial communities and plant productivity. *Plant Soil* 431:371–387. <https://doi.org/10.1007/s11104-018-3774-7>
- Norton J, Ouyang Y (2019) Controls and adaptive management of nitrification in agricultural soils. *Front Microbiol* 10:1931. <https://doi.org/10.3389/fmicb.2019.01931>
- Orwin K, Wardle D (2004) New indices for quantifying the resistance and resilience of soil biota to exogenous disturbances. *Soil Biol Biochem* 36:1907–1912. <https://doi.org/10.1016/j.soilbio.2004.04.036>
- Pan H, Liu H, Liu Y et al (2018) Understanding the relationships between grazing intensity and the distribution of nitrifying communities in grassland soils. *Sci Total Environ* 634:1157–1164. <https://doi.org/10.1016/j.scitotenv.2018.04.117>
- Pardon P, Reubens B, Reheul D et al (2017) Trees increase soil organic carbon and nutrient availability in temperate agroforestry systems. *Agr Ecosyst Environ* 247:98–111. <https://doi.org/10.1016/j.agee.2017.06.018>
- Placella SA, Firestone MK (2013) Transcriptional Response of nitrifying communities to wetting of dry soil. *Appl Environ Microbiol* 79:3294–3302. <https://doi.org/10.1128/AEM.00404-13>

- Prosser JI, Nicol GW (2012) Archaeal and bacterial ammonia-oxidisers in soil: the quest for niche specialisation and differentiation. *Trends Microbiol* 20:523–531. <https://doi.org/10.1016/j.tim.2012.08.001>
- Qu Q, Xu H, Ai Z et al (2023) Impacts of extreme weather events on terrestrial carbon and nitrogen cycling: a global meta-analysis. *Environ Pollut* 319:120996. <https://doi.org/10.1016/j.envpol.2022.120996>
- R Core Team (2022) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna
- Rivest D, Lorente M, Olivier A, Messier C (2013) Soil biochemical properties and microbial resilience in agroforestry systems: Effects on wheat growth under controlled drought and flooding conditions. *Sci Total Environ* 463–464:51–60. <https://doi.org/10.1016/j.scitotenv.2013.05.071>
- Rivest D, Paquette A, Shipley B et al (2015) Tree communities rapidly alter soil microbial resistance and resilience to drought. *Funct Ecol* 29:570–578. <https://doi.org/10.1111/1365-2435.12364>
- Rosseel Y (2012) lavaan: an R package for structural equation modeling. *J Stat Softw* 48:1–36. <https://doi.org/10.18637/jss.v048.i02>
- Rosseel Y (2021) Evaluating the observed log-likelihood function in two-level structural equation modeling with missing data: from formulas to R code. *Psych* 3:197–232. <https://doi.org/10.3390/psych3020017>
- Sereni L, Guenet B, Crouzet O et al (2022) Responses of soil nitrification activities to copper after a moisture stress. *Environ Sci Pollut Res* 29:46680–46690. <https://doi.org/10.1007/s11356-022-19093-2>
- Shade A, Peter H, Allison S et al (2012) Fundamentals of microbial community resistance and resilience. *Front Microbiol* 3:417
- Sharma DK, Tomar S, Chakraborty D (2017) Role of earthworm in improving soil structure and functioning. *Curr Sci* 113:1064–1071. <https://doi.org/10.18520/cs/v113/i06/1064-1071>
- Shipley B (2016) Cause and correlation in biology: a user's guide to path analysis, structural equations and causal inference with R. Cambridge University Press
- Siegwart L, Jourdan C, Piton G et al (2023) Root distribution and properties of a young alley-cropping system: effects on soil carbon storage and microbial activity. *Plant Soil* 482:601–625. <https://doi.org/10.1007/s11104-022-05714-9>
- Smith MD (2011) An ecological perspective on extreme climatic events: a synthetic definition and framework to guide future research. *J Ecol* 99:656–663. <https://doi.org/10.1111/j.1365-2745.2011.01798.x>
- Soubeyroux J-M, Bernus S, Corre L, et al (2020) Les nouvelles projections climatiques de référence DRIAS 2020 pour la Métropole. Météo-France
- Sun F, Pan K, Tariq A et al (2016) The response of the soil microbial food web to extreme rainfall under different plant systems. *Sci Rep* 6:37662. <https://doi.org/10.1038/srep37662>
- Taylor AE, Giguere AT, Zobebelein CM et al (2017) Modeling of soil nitrification responses to temperature reveals thermodynamic differences between ammonia-oxidizing activity of archaea and bacteria. *ISME J* 11:896–908. <https://doi.org/10.1038/ismej.2016.179>
- Terasaki Hart DE, Yeo S, Almaraz M et al (2023) Priority science can accelerate agroforestry as a natural climate solution. *Nat Clim Chang* 13:1179–1190. <https://doi.org/10.1038/s41558-023-01810-5>
- Thion C, Prosser JI (2014) Differential response of nonadapted ammonia-oxidizing archaea and bacteria to drying–rewetting stress. *FEMS Microbiol Ecol* 90:380–389. <https://doi.org/10.1111/1574-6941.12395>
- Thorogood R, Mustonen V, Aleixo A et al (2023) Understanding and applying biological resilience, from genes to ecosystems. *NPJ Biodivers* 2:16. <https://doi.org/10.1038/s44185-023-00022-6>
- Ummenhofer CC, Meehl GA (2017) Extreme weather and climate events with ecological relevance: a review. *Philos Trans R Soc B* 372:20160135. <https://doi.org/10.1098/rstb.2016.0135>
- Unger IM, Motavalli PP, Muzika R-M (2009) Changes in soil chemical properties with flooding: a field laboratory approach. *Agr Ecosyst Environ* 131:105–110. <https://doi.org/10.1016/j.agee.2008.09.013>
- van der Putten WH, Bardgett RD, Bever JD et al (2013) Plant–soil feedbacks: the past, the present and future challenges. *J Ecol* 101:265–276. <https://doi.org/10.1111/1365-2745.12054>
- Van Meerbeek K, Jucker T, Svenning J-C (2021) Unifying the concepts of stability and resilience in ecology. *J Ecol* 109:3114–3132. <https://doi.org/10.1111/1365-2745.13651>
- van Ramshorst JGV, Siebicke L, Baumeister M et al (2022) Reducing wind erosion through agroforestry: a case study using large eddy simulations. *Sustainability* 14:13372. <https://doi.org/10.3390/su142013372>
- Vaupel A, Bednar Z, Herwig N et al (2023) Tree-distance and tree-species effects on soil biota in a temperate agroforestry system. *Plant Soil* 487:355–372. <https://doi.org/10.1007/s11104-023-05932-9>
- Waqas MA, Li Y, Ashraf MN et al (2021) Long-term warming and elevated CO₂ increase ammonia-oxidizing microbial communities and accelerate nitrification in paddy soil. *Appl Soil Ecol* 166:104063. <https://doi.org/10.1016/j.apsoil.2021.104063>

Publisher's Note

Springer Nature remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.