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RESEARCH ARTICLE

Title

Distribution of soil properties along forest-grassland interfaces: influence of permanent environmental factors or land-use after-effects?

Author names and affiliations

Maxime Burst[ab], Sandrine Chauchard[a], Etienne Dambrine[c], Jean-Luc Dupouey[a], Bernard Amiaud[a]

[a]Université de Lorraine - AgroParisTech - INRA, UMR Silva, 54506 Vandoeuvre-les-Nancy, France

[b]Université Clermont Auvergne - CNRS, GEOLAB, 63000 Clermont-Ferrand, France

[c]Université Savoie Mont Blanc - INRA, CARRTEL, 74200 Thonon-les-Bains, France

Burst, M. (corresponding author, maxime.burst@uca.fr)

Chauchard, S. (sandrine.chauchard@univ-lorraine.fr)

Dambrine, E. (etienne.dambrine@inra.fr)

Dupouey, J.-L. (jean-luc.dupouey@inra.fr)

Amiaud, B. (bernard.amiaud@univ-lorraine.fr)

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Abstract

Soil properties vary spatially according to land use; both because land users have selected specific soil properties for specific land uses, and land uses modify the soil properties. However, permanent environment factors and land-use effects are unlikely to display the exact same spatial patterns. Study of the spatial and historical patterns of distribution of soil properties could help to separate between these two causes. In this aim, we studied 22 forest-grassland interfaces with controlled historical configurations in northeast France. In each land use (forest and grassland), three distances to the edge (edge, periphery and core) and two land-use histories (ancient and recent) were studied.

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Along forest-grassland interfaces, forests were usually located slightly upslope of grasslands, and mainly because this non-random topographic position the topsoil texture was significantly more silty in forests, and clayey in grasslands. After statistically controlling for the effects of topography and soil texture, we observed two main gradients of variation in soil properties according to the distance-to-edge (acidity in forest and nutrient content in grassland). In forest, pH and Ca dropped from the edges to the peripheries (15 m distance), while in grassland, C, N, P and Na sharply increased from the edges to the cores (25 m distance). These results demonstrate, through the edge effect, the strong influence of the land use on a part of soil properties. Furthermore, less than two centuries after grassland afforestation or deforestation, we observed that soil properties in recent forests and recent grasslands were respectively closer to their current land use than to their former land use. These results demonstrate a rapid change in soil properties after land-use change. However, recent forests and recent grasslands kept a legacy of soil texture from their former land use, respectively. Recent grasslands also kept a lower soil density, N and Na content compared to ancient grasslands.

Hence, this study of forest-grassland interfaces show strong and short-scale relationships between land use and soil properties and suggest that they express both original choices of land users for specific soil properties and land-use after-effects. The non-random topographic position of the forest-grassland interfaces indicates a conscious choice of this positioning by the land users, for agronomic reasons. Beyond that, land use, through vegetation composition and management practices, also has a strong impact on soil properties. The fact that land-use changes affect most soil properties after only a few decades confirms the existence of land-use effects over time.

Keywords

soil; forest; grassland; land use; edge effect; land-use change

1. Introduction

Five soil-forming factors, *i.e.* climate, geology, topography, land use and time have been identified as the source of the heterogeneity of soils in current landscapes (Jenny, 1941). Macro-climate, geology and time mainly affect soil and humus properties at intermediate and large scales (McKenzie and Ryan, 1999; Ponge *et al.*, 2011). At the local scale of a hillslope or a small catchment, geology, topography and land use (including micro-climate) are generally the dominant factors affecting soil properties (McBratney *et al.*, 2003). As man has increasingly changed his environment during the Holocene, the effect of current and past land uses is a central question of ecology.

In most temperate regions, landscapes are currently marked by mosaics of open (*e.g.* grassland, cropland) and closed (*e.g.* forest) land uses. Although relatively small compared to forest-cropland contrast, differences in soil properties have been reported between forest and grassland: forests generally have lower pH, thicker humus, higher C/N and lower P than grasslands (Joimel *et al.*, 2016). However, the distribution of soil properties along forest-grassland interfaces remains poorly known.

Differences in vegetation and management practices, *i.e.* land-occupation and land-use influence, may be intrinsically responsible for most of these differences in soil properties (Jenny, 1941). Differential erosion, leaching, and bioturbation may modify the transport and redistribution of soil particles and elements (Wang *et al.*, 2001). Grassland harvesting or grazing may decrease soil fertility, whereas mineral fertilization and manuring may increase it, by increasing nutrient (N, P, K) contents relative to forests (Chantigny, 2003). By spillover, fertilizer applications can also induce edge effects on soil properties within the forest edges adjacent to the grasslands (Piessens *et al.*, 2006). In addition, between forest and grassland, differences in tree, shrub and herb cover, as well as in taxonomic and functional composition may be the source of different plant-soil feedbacks (Ehrenfeld *et al.*, 2005; Harrison and Bardgett, 2010). Consequently, the species turn-over observed in plant communities along forest-grassland interfaces (Burst *et al.*, 2017) can both induce and reflect an edge effect on soil properties.

To properly study land-use effects on soil properties, all other soil-forming factors (climate, geology, topography and time) should be equal (Motzkin *et al.*, 1996), but in most studies this condition is rarely met. Time effects or slight topographical variations are often neglected. Yet, following the catena concept (Hook and Burke, 2000), topography finely controls for erosion, mobilization and redistribution of water, particles and nutrients along hillslopes (Seibert *et al.*, 2007). Indeed, in valley bottoms, soils are better supplied with water and nutrient-richer than on slopes and uplands (Brubaker *et al.*, 1993; Hook and Burke, 2000). Consequently, strong relationships between topography, soil properties and vegetation composition due to these processes have been observed (Binkley and Fisher, 2013; Solon *et al.*, 2007). However, in the absence of topographic homogeneity, it is thus difficult to attribute the variation in soil properties to a present land-use effect (Schimel *et al.*, 1985). Soil texture is a typical soil characteristic which is both strongly linked to topographical position and modified by land use and which affects most of soil physical and chemical properties (Hassink, 1997; Laganière *et al*., 2010). As a result, the non-random spatial distribution of soil properties, and more specifically their agronomic and forest values, may have played a crucial role in the spatial distribution of past and current land use.

Furthermore, historical land-use changes (*e.g.* afforestation and deforestation) may blur the influence of current land use by reducing differences in soil properties between forests and grasslands. Indeed, after afforestation of former grasslands, topsoil properties of recent forests should gradually tend towards those of the ancient forests (Li *et al.*, 2012) and display intermediate values between those of ancient grasslands and ancient forests. Similarly, after deforestation, soil properties of recent grasslands should display intermediate values between those of ancient forests and ancient grasslands. Thus, depending on the resiliency of the former soil properties after land-use change, a temporary mismatch between current land use and soil properties can be observed (Peña *et al.*, 2016). With the acceleration of land-use changes in the last decades (Alstad *et al.*, 2016), it is becoming urgent to better understand the effects of these changes on soil properties.

To decipher the influence of permanent environment factors and of land-use effects on soil properties, we focused our study on forest-grassland interfaces and sought to answer the following questions:

1. How are soil properties distributed along forest-grassland interfaces? To what extent land use and/or distance-to-edge impact soil properties?

2. To what extent afforestation and deforestation modify soil properties? Do soil properties of recent land uses (forest or grassland) remain closer to those of their former land use or rapidly became similar to those of their new land use?

2. Materials and Methods

2.1. Study area and site selection

The study was conducted in two sectors of the Lorraine regional natural park (PNRL) in northeast France (figure 1, 215-277 m a.s.l.). The climate is semi-continental with annual rainfall and temperature averaging 775 mm and 10.4°C, respectively, for the period 1981-2010. The geological substrate is mainly a clayey marl from the Oxford Clay formation in the western sector and the Keuper formation in the eastern sector. All soils studied are vertic cambisols (IUSS Working Group WRB, 2015), derived from post-Holocene aerial deposits of silts of various thickness overlaying the clayey marl material (Antoine *et al*., 2003).

Vectorized land-use maps (scale 1:40,000) over the PNRL allowed us to preselect forest-grassland interfaces. Land-use changes were characterized by comparing the land use on French Etat-Major map (established from 1826 to 1831 in the area, see Favre *et al*. 2013 for the vectorization) and the current land-use map (vectorized since 1998 by the PNRL and updated in 2014, with a typology of land-uses more detailed but included in that of the Etat-Major map) using a geographic information system (ArcGIS®, v.10.2, ESRI, France). When the land use had not changed since 1826-1831, a date which is close to the minimum forest area in northeast France, we categorized it as ancient, and when the land use was different, we qualified it as recent. For each preselected forest-grassland interface, series of aerial photographs (spaced by ten years maximum between 1931 and 2014, http://www.geoportail.gouv.fr) were photo-interpreted to confirm the origin and the stability of the forest, the grassland and the edge over time. As a result, we could confirm that the land-use changes, and therefore recent habitats, were all over 50 and under 188 years old.

To avoid confounding factors other than present land-use effect, edge effect and land-use change effect, the interfaces were then selected according to several environmental criteria, including: homogeneity of topographic positions within and between interfaces (mainly wide and open valley bottoms and footslopes), minimum area of both adjacent land uses (≥ 1 ha) to ensure to have a core area, linearity of the edge to avoid multiple edge effect and absence of disturbances (*e.g.* paths, streams, trenches). Forests were only mature deciduous forests, treated as high forests or former coppices with standards now in conversion to high forests, mainly dominated by oaks, beech and hornbeam *(Carpinion betuli* Issler 1931*)* without recent logging. Grasslands were mesophilous to meso-hygrophilous mowing grasslands, dominated by tall grasses *(Arrhenatherion elatioris* Luquet 1926 and *Bromion racemosi* Tx. in Tx. et Preising ex de Foucault 2009) *i.e.* temporarily wet meadows (Mucina *et al.* 2016), most of which are flooded each year. Unlike forests managed for the most part by the National Forestry Office, grasslands were owned by private farmers who may have varying management practices. In the last decades, most meadows were mowed once a year around June 15th, and some were fertilized by manure application and / or chemical fertilizers (NPK granules). Traces of burrowing activities (mainly due to earthworms and wild boars) were regularly observed in the periphery of grasslands. After field surveys, 22 interfaces conforming exactly to the above criteria were retained for our study (11 in the eastern sector and 11 in the western sector of the PNRL, figure 1).

2.2. Study design

We sampled three types of interfaces with different historical configurations (figure 1): (i) stable interfaces (8 sites) corresponding to ancient forest adjacent to ancient grassland, (ii) afforestation interfaces (7 sites) with recent forest (developed on a former grassland) adjacent to ancient grassland, and (iii) deforestation interfaces (7 sites) with ancient forest adjacent to recent grassland (formerly forested). Therefore, we sampled four land-use histories combining two histories (ancient, recent) and two land uses (forest, grassland). Each interface included six plots, three in forest and three in grassland, positioned at three increasing distances from the forest-grassland boundary and referred according to plot position as edge, periphery and core (appendix A). Each plot had an area of 2 m x 50 m (100 m²) and was oriented parallel to the forest-grassland boundary. As the distance of influence of the edge effect is recognized as lower in grassland compared to forest (Schmidt *et al.*, 2017), periphery and core plots were placed closer to the boundary in grassland (5 m and 25 m, respectively) than in forest (15 m and 50 m). A total of 132 plots in the 22 forest-grassland interfaces were sampled.

2.3. Soil sampling and soil analyses

In each plot (appendix A), three equally spaced topsoil samples (excluding litter) were collected in September 2014 to a depth of 4.5 cm with a steel cylinder of 250 cm^3 volume (8.4 cm in diameter, and 4.5 cm in height). The choice of the sampling at depths of 0 to 4.5 cm makes it possible to focus only on the first soil horizon, which is the one most influenced by the land uses and which interacts most with the composition of the vegetation and the management practices. Samples were bulked, homogenized and air-dried. Samples were then sieved to 2 mm to remove roots, pebbles (< 1 %) and other debris.

For each of the 132 topsoil samples, the following soil properties were measured: (i) the particle size distribution in three fractions *i.e.* clay (0-2 µm), silt (2-50 µm) and sand (50-2000 µm) using the pipette method without organic matter destruction, (ii) the dry bulk density (hereinafter simply mentioned soil density or density) based on the residual weight of an aliquot of 30 g of fine soil dried in an oven (105°C, 48h), then extrapolated to the total 750 cm^3 soil sample, (iii) the total organic carbon (C) and the total nitrogen (N) using dry combustion, (iv) the available phosphorus (P), (v) the cation exchange capacity (CEC) and the exchangeable cations (Ca, Mg, Na, K, Fe, Mn and Al) after cobaltihexamin extraction, and (vi) the soil pH in water. By adding the calculated C/N ratio, a total of

17 soil properties were used in subsequent analyses (see appendix B for the list of soil properties and references for the methods used).

2.4. Humus and soil description

In each plot, in addition to soil sampling to analyses of soil properties, we also described the humus, dug a soil pit down to 30 cm and probed the soil with an auger down to 1 m to describe the different horizons by visual estimation and to the touch for texture, color, structure, compaction, root density, effervescence and redoximorphic features. The humus types were mainly mulls (from dysmull to eumull), except two plots characterized as eumoder type (Jabiol *et al.*, 2009). For all the plots, soil texture was clayey-silty to clayey with less than 10 % of sand on average. As soils derived from the overlay of silty deposits over a clayey material, they all showed a more or less abrupt textural change in the soil sampling, at various depth (Brêthes, 1976). Upslope, the depth to which this transition occurred was 30 cm on the average (10 to 60 cm), while downslope, this depth was about 10 cm (0 to 60 cm). Close to the valley bottoms, pseudogley features were observed from an average depth of 10 cm (0 to 50 cm).

2.5. Topographic data collection

Within each site, two complementary topographical observations were collected for each plot: (i) the topographic position was noted as an ordered factor (4 levels: bottom = 1, footslope = 2, mid-slope = 3 and upper slope = 4), and (ii) the slope percentage from the forest-grassland boundary measured with a Suunto® clinometer (accuracy < 0.5 % of slope). Slopes along the 75 m long interfaces were low, 2.3 % on average and 5.7 % at the maximum (see also appendix C). It is interesting to note that in all the sampled cases, the ancient forests were located upslope from the ancient grasslands.

2.6. Data analysis

To identify the main soil gradients along the forest-grassland interfaces and take into account collinearities between soil variables, a principal component analysis (PCA) was performed on all the 17 soil properties. Due to the major influence of topography and soil texture on most physical and chemical soil properties, a partial PCA was then performed in order to partial out the effects of these two variables. The topography *i.e.* the topographic position was included as an ordered factor with four levels (bottom, footslope, mid-slope and upper slope) and the soil texture as a continuous variable, the soil clay content.

To examine how land use, distance to edge and land-use change influenced soil properties along the forest-grassland interfaces, three linear mixed models (LMMs) were fitted:

LMM1: Y ~ Position + History:Position + Topography + (~1|Sector/Site)

LMM2: Y ~ Position + History:Position + Topography + Clay content (~1|Sector/Site)

LMM3: Y ~ Position + History:Position + (~1|Sector/Site)

The first model (LMM1) applied to the three textural properties (clay, silt and sand contents) included as fixed effects: the position along the interfaces (6 levels: forest core, forest periphery, forest edge, grassland edge, grassland periphery and grassland core), the interaction of the history (2 levels: ancient and recent) with the position, and topography as a categorical ordered control variable. This first model allowed us to check whether the land use *per se* had an effect on soil texture, once removed the influence of topography on the particle size distribution along the slopes. The second model (LMM2) applied to all the other soil properties included as fixed effects: the position, the interaction of the history with the position and the control variables topography and clay content. The third model (LMM3) was applied to the first two axes of the partial PCA and included as fixed effects: the position and the interaction of the history with the position. The last two models allowed us to evaluate the influence of land use on the soil properties by controlling for the effects associated with the non-random distribution of land uses along the slopes, which depends on topographic position and soil texture. Topography and clay content were not included in LMM3, because the effects of these control variables had already been removed by partialling them out of the PCA. In a second step, to check to what extent the control for topography and soil texture within the first two models (LMM1 and LMM2) affected our results, the third model was also applied to each soil property. For the three models, the site (22 levels) nested in the sector (2 levels: east and west of the PNRL) was introduced as a random effect.

For each each soil property and the first two partial PCA axes, the goodness-of-fit of LMMs was assessed using two indicators: (i) the marginal r^2 (*i.e.* variance explained by fixed effects only) and (ii) the conditional r^2 (*i.e.* variance explained by both fixed and random effects) (Nakagawa and Schielzeth, 2013). The part of random (site) effects relative to the total of random and fixed effects was calculated as: 1 - marginal r^2/conditional r^2, and expressed in percentage. To determine the statistical significance of fixed effects in models, type-III analyses of variance were performed.

Contrast analyses were then performed to test for more specific assumptions using the interaction of the history with the position. Firstly, to properly test for the present land-use effect (*i.e.* test for differences between and due to current forests and grasslands) and notably avoid any confounding effects linked to land-use change and distance-to-edge, only plots from cores of ancient land uses (15 plots of ancient forest cores *vs.* 15 plots of ancient grassland cores, AFC-AGC) were compared. Secondly, to test for the edge effect in each land use, we compared the ancient forest cores *vs.* ancient forest edges (AFC-AFE, both 15 plots) and the ancient grassland cores *vs.* the ancient grassland edges (AGC-AGE, both 15 plots). Thirdly, to test for the land-use change effect in recent forests and in recent grasslands, cores and peripheries of each land-use having the same history were grouped in order to improve the power of the tests. The edges of the two land uses were excluded from these groups because of their close physical proximity. We tested for the legacy of soil properties after land-use change by contrasting the recent forests against the ancient forests (RFCP-AFCP, 14 *vs.* 30 plots) and the recent grasslands against the ancient grasslands (RGCP-AGCP, 14 *vs.* 30 plots). We then tested for the change of soil properties after land-use change by contrasting the recent forests against the ancient grasslands (RFCP-AGCP, 14 *vs.* 30 plots) and the recent grasslands against the ancient forests (RGCP-AFCP, 14 *vs.* 30 plots). All the p-values associated with contrast analyses were adjusted by controlling for the false discovery rate (Benjamini and Hochberg, 1995).

Statistical analyses were carried out with R 3.2.3 (R Foundation for Statistical Computing, Vienna, AT) and the following packages were used: *vegan* for PCA, *nlme* for LMMs, *piecewiseSEM* to calculate the r² and assess the quality of models, *car* for analyses of variance and *lsmeans* for the least-squares means estimations and the contrasts tests.

3. Results

3.1. Effects of topography and soil texture on soil properties

The topography showed a significant influence (p-value ≤ 0.05) on clay, silt and sand (table 1), but only on sodium among the other soil properties. Besides, the soil texture, *i.e.* the soil clay content, showed a significant influence on most of the other soil properties (table 1), except on Al and Fe. The goodness-of-fit of models was high for most soil properties (conditional $r^2 \geq 0.5$) (table 1). Only the goodness-of-fit for Al and Fe contents was lower (conditional $r^2 = 0.39$ and 0.36, respectively).

3.2. Main soil gradients along the forest-grassland interfaces

The first PCA axis (44.7 % of the total variation) showed a gradient from coarser textured soils (high silt and sand contents) to soils of finer texture (high soil clay content) (appendix D). The second PCA axis (15.4 % of the total variation) showed a gradient from acidic soils (with relatively high Fe and Al contents and high C/N) to more neutrophilic soils (with a higher pH). After controlling for topography and soil texture (figure 2a), the first partial PCA axis (28.2 % of the total variation) showed a gradient from acidic soils to more neutrophilic soils, the same as the previous second PCA axis obtained without topography and soil texture control. The distribution of types of humus along this axis confirmed its interpretation as an acidity axis (figure 2a). The second partial PCA axis (19% of the total variation) showed a K-Na opposition, the soils richer in Na being also higher in Mg, Mn and P, and displaying a higher organic matter content (C and N concentrations). Correlations of the first two partial PCA axes with soil properties are given in appendix E. Both the first two partial PCA axes reflected a forest-grassland gradient (figure 2b). Along the forest-grassland interfaces, both the first (soil acidity) and the second (gradient of nutrient variations) partial PCA axes were significantly influenced by the plot position (appendix F), but only the second one was also significantly influenced by the interaction of history with plot position.

3.3. Soil texture

From ancient forest cores to ancient grassland cores, the clay content increased while the silt content decreased linearly (figure 3, appendix G and H3), with a pronounced gap between forest edges and forest peripheries. Significant land-use and edge effects were found for these two texture properties (table 1). In recent land-uses (both forest and grassland), clay and silt contents were intermediate between those of ancient forest and ancient grassland (figure 3). Thereby, land-use change also had a significant effect, but the recent land uses were closer to their former land uses than to their current ones (table 1 & 2). For clay, silt and sand, the goodness-of-fit of models was very high (conditional $r^2 > 0.8$), but reflected a high or moderate site effect (table 2).

3.4. Soil acidity

Within interfaces, Fe and Al were higher in ancient forest compared to ancient grassland (appendix G), with a remarkable gap between the two edges, although located a few meters apart. In accordance, pH was higher in ancient grassland than in ancient forest and showed a decline from edges to cores in forest (figure 3). These three soil properties showed a significant position effect (table 1), but none for the interaction of history with plot position. However, the land-use and edge effects were not significant (table 2). After afforestation, we observed no significant change or legacy in recent forest, but after deforestation, Fe was significantly lower (appendix G) and pH higher (figure 3) in recent grassland compared to ancient forest (table 2). A relatively strong site effect was found for these three soil properties (table 2).

3.5. Soil nutrients, organic matter and density

From ancient forest cores to ancient grassland cores, density, C/N and K decreased, and conversely C, N, P and Na increased (figure 3 and appendix G). Most of these soil properties showed a significant position effect, except for density and C (table 1). Thereby, C/N, N, P, Na, K, but also C showed a significant land-use effect (table 2). For almost all of these soil properties, a significant edge effect was observed in grassland, but not in forest (table 2), except for K for which the opposite was found. Indeed, for K, in addition to a decreasing gradient (not significant) from ancient grassland edges to ancient grassland cores, a significant decreasing gradient was observed from ancient forest edges to ancient forest cores (table 2 and figure 3).

Interacting with plot position, land-use history showed a significant influence on the density, C/N, C, N and Na (table 1). After afforestation, density, C/N, but also K were higher in recent forest cores and peripheries compared to ancient grassland cores and peripheries, while C, N, Na and P were lower (figure 3 and appendix G). Thereby, significant changes for all these soil properties (including K and P) were observed in recent forest compared to ancient grassland (RFCP-AGCP comparisons, table 2), while no significant differences (legacies of previous land use) were found between recent forest and ancient forest (RFCP-AFCP comparisons, table 2). After deforestation, C/N and K were lower in recent grassland compared to ancient forest, while density, N, Na and P were higher (figure 3). However, only the changes for C/N, P and K were significant (RGCP-AFCP comparisons, table 2). Besides, significant differences for density, N and Na were observed between recent grassland and ancient grassland (RGCP-AGCP comparisons, table 2), with a lower N and Na and a higher density in recent grassland (figure 3). It is remarkable to note that none of these soil properties showed both a significant change and a significant legacy, either after afforestation or after deforestation.

For all these soil properties (*i.e.* density, C/N, C, N, Na and K), except P, a low site effect was found (table 2).

3.6. Effectiveness of topography and soil texture control and validity of the results

The use of the third model LMM3 on each of the soil properties, *i.e.* without topography and soil texture control, confirmed the results obtained with the two previous models LMM1 and LLM2 (appendix H). Indeed, apart from two rare exceptions, one for Fe and one for K, the control of topography and soil texture in the first two models simply led to a general decrease in the significance of most of the results (appendix H). We can also note that in the absence of topography and texture control, the goodness-of-fit of the third model was weaker for most soil properties except Sand, Fe and Al (appendix H).

4. Discussion

4.1. Land-use and edge effects

4.1.1. Soil texture

In the smooth landscapes of the PNRL plains, texture variations are first related to the occurrence of silt deposits, overlying the clays of the Keuper and Oxfordian marlstone (Antoine *et al.*, 2003). We showed that these textural variations are spatially organised along the slopes, ranging from coarser texture upslope to finer texture downslope (Brubaker *et al.*, 1993; Hook and Burke, 2000) even at very slight slopes (average slope: 2.3 %), and that they overlap with the distribution of forests (upslope) and grasslands (downslope). This non-random correlation between soil texture gradients, slopes and relative position of forests and grasslands in the landscape could be partly the result of past land-use choices based on soil texture and topography. The main reason is that grasslands were always located in the most favorable places in terms of soil moisture to promote fodder growth. However, the abrupt textural change from the forest peripheries to the edges (at 15 meters apart) also suggests a possible effect of land use. Several explanations for this land-use after-effect may be proposed: (1) the rapid erosion mainly due to rainfall of the silty layer of grassland soils, but also adjacent forest edge soils, in the years following logging and before the establishment of perennial herbaceous cover, (2) the burrowing activity of earthworms, moles and boars in grasslands raises clay from deeper clayey horizons to silty surface horizons and decrease the silt percentage, and (3) the possible illuviation of clay particles in forest soils, although this is generally more common in sandy soils. The erosion of the soil silt cover after forest clearing has indeed been demonstrated by various authors (since the bronze or the Roman ages) in northeast France (Etienne, 2011), Belgium (Vanwalleghem *et al.*, 2006) and south Germany (Houben, 2008), but still poorly reported within footslopes and valley bottoms at forest-grassland interfaces. Besides, the impacts of the burrowing activity on soil surface texture in grasslands are well known, while the slightly acid deciduous forest soils are known to favor the illuviation of clay particles into a clay-enriched B horizon (Binkley and Fisher, 2013).

4.1.2. Soil acidity and soil nutrients content

Controlling for the effects of topography and soil texture, two main soil gradients related to soil acidity and soil nutrients content were observed along the forest-grassland interfaces. Forest soils, particularly in ancient forests, were slightly more acidic than grassland soils, possibly because of the litter input on the topsoil (Glatzel, 1991) and cation leaching (von Oheimb *et al.*, 2008). However, we found no land-use effect or edge effect on this soil acidity gradient. The small differences in pH and humus (mainly mull type) that we found along the forest-grassland interfaces can probably explain these results.

Besides, C, N, P and the C/N ratio showed a land-use effect associated with a strong edge effect in grassland. The highest C and N observed in grassland topsoils (especially in grassland cores) are likely due to a greater root biomass decomposition compared to forest soils (Hook and Burke, 2000). Indeed, the annual turnover of soil organic matter derived from tree and shrubs in forests could be lower than that from annual and perennial herbs in grasslands (Guo *et al.*, 2007; Guo and Gifford, 2002). The unilateral edge effect for soil nutrients content, found only in grassland, probably also reflects the influence of management practices such as grassland fertilization. This seems particularly true for P (Brubaker *et al.*, 1993), which also exhibited a strong site effect which could be due to varying fertilization levels among grasslands. It should be noted that other influences could also contribute to these results, such as differences in net productivity between forest and grassland, bioturbation by ants and worms higher in grassland, or even greater abundance of leguminous plants in grassland.

A land-use effect associated with a strong edge effect was also observed for Na with increasing values from grassland edges to grassland cores. Unlike the previous ones, Na is the only element having shown a topography effect. It likely highlights the well-known local presence of salt and gypsum lenses within or near the clayey marls of our sites (BRGM 2001). In the lower lands, these salt lenses can cause extensive salinization of near-surface soil horizons by dissolution within groundwater and frequent rise of the water table. In the natural region of Saulnois, on the same geological substratum and a few kilometers away from several of our study sites, these salt lenses are known to be at the origin of resurgence of salt water and the presence of mainland salt meadows (Duvigneaud 1967). In our sites, the extensive salinization observed in the grassland cores could thus be related to the increasing soil moisture from forest to grassland, confirmed by plant bio-indication (Burst *et al.*, 2017), resulting from a lower topographic position and probably also from a lower evapotranspiration of grasslands compared to forests (Nosetto *et al.*, 2007).

We also found a land use effect for K, but unlike the previous ones, it was mainly associated with a strong edge effect in forest. This result could be due to a spillover of mineral fertilizers applied to adjacent grasslands (Kepfer-Rojas *et al.*, 2015; Piessens *et al.*, 2006). Indeed, it was showed that many elements can penetrate into forest edges during and after grassland fertilization, in particular by aerial deposits (Thimonier *et al*., 1992). However, we also observed a slight edge effect in grassland, and the lowest K contents were found in grassland peripheries and cores. These results are possibly due to the higher abundance of grasses within grassland peripheries and cores we observed (Burst *et al.* 2017), which are better competitors and extractors of K compared to forbs (Bezemer *et al.*, 2006; Tilman *et al.*, 1999). Because our grasslands are at least annually subject to the export of plant biomass by mowing, K is probably here a limiting element, although this is sometimes not the case in low-intensity grasslands (Swacha *et al*., 2018). Another explanation is the increasing clay contents found in soils towards grassland cores, which retain the exchangeable K. Note also that the highest K was found in forest edge soils. This could be due to the fact that the trees and shrubs, whose highest densities were found at the forest edges, can (i) affect the distribution of cations such as K through uptake from deep soil horizons and transport to topsoil horizons by deposition of a cation-rich litter (Jobbágy and Jackson, 2004), but also (ii) increase the K-rich throughfall inputs (Thimonier *et al*., 1992).

4.2. Land-use change effects

4.2.1. Land-use legacy and gradual change of soil texture

After afforestation and deforestation, soil texture remained closer to the former land use than to the new land use. Obviously, recent forests were established on grassland clayey soils while recent grasslands resulted from the deforestation of silty forest soils. We assume that the afforestation could not rapidly change the silt content of former clayey grassland soils, except if newly established forests have preserve silt colluviation from upsloping ancient forests. Besides, in case of deforestation, the fact that recent grasslands were enriched in clay compared to ancient forest cores may be related to a rapid land-use effect after land-use change, here probably an erosional redistribution of silt and clay particles after clearance of the forest.

4.2.2. Rapid change of soil properties after afforestation

In contrast to many studies showing the long-term persistence of soil properties after afforestation of former cultivated parcels (Blondeel *et al*., 2018; Dupouey *et al*., 2002; Koerner *et al*., 1997), no legacy in soil properties was found from ancient grassland to recent forest after afforestation of grassland. As observed in some previous studies (Graae *et al*., 2003; von Oheimb *et al*., 2008 for recent forest developed on former grazed heathland), in recent forest, most soil properties became similar to those found in ancient forest in less than two centuries. One explanation is that the differences in soil properties would be lower between forest and grassland than forest and cultivated field (Janssen *et al*., 2018; Joimel *et al.*, 2016). Another explanation would be that traditional management practices were not as intensive as modern practices (Flinn and Marks, 2007; Kepfer-Rojas *et al.*, 2015). For example, the fertilizer inputs in grassland, mainly from organic matter, were relatively low before the 20th century (Green, 1990).

Besides, we showed higher density, C/N and K, as well as lower C, N, P and Na in recent forest compared to ancient grassland. Because these values were mostly higher (density) or lower (particularly P and Na) than those found in ancient forest, these results could likely reflect the existence of a short period of cultivation before or after grassland use, followed by afforestation. Indeed, cultivation generally increases soil density and greatly depletes former forest soils in organic matter and nutrients (Murty *et al.*, 2002). We can also think of an increase of fertilizer inputs in grassland in the modern period (supported by higher C/N and lower C, N and P in recent forest) and/or a rapid decline in soil nutrients after afforestation. Indeed, after afforestation, soil nutrients are progressively depleted through their sequestration within perennial plant tissues, in particular in the tree and shrub trunks and roots (Laganière *et al*., 2010). Regarding the decline of Na in recent forest, it has also been shown that increased evapotranspiration due to trees and shrubs after afforestation could result in a lowering of groundwater (Nosetto *et al*., 2007) and consequently limit the intake of Na in topsoils.

4.2.3. Land-use legacy or rapid change of soil properties after deforestation

After deforestation, density, C, N and Na have shown a legacy from forest past land use to grassland. The higher soil density in recent grassland compared to ancient grassland could be the result of forestry work during harvesting and a short period of tillage. Indeed, even if this higher density was partly related to lower C, the density was also higher in recent grassland compared to ancient forest, which is likely the result of soil compaction (Batey, 2009). Besides, the lower C and N in recent grassland compared to ancient grassland can be explained by a relatively shorter period of accumulation of nutrients and belowground organic matter and/or a better decomposition of organic matter. Indeed, we showed that ancient grassland has the wettest soils (Burst *et al.*, 2017), which are frequently and annually flooded. Consequently, the decomposition of organic matter is likely lower in ancient grassland due to seasonal anaerobic periods (Hassink, 1997, 1994). Note that in their meta-analysis, Guo and Gifford (2002) have reported an increase in organic matter and especially C in recent grassland after deforestation. However, these authors found an increase in C in high-precipitation zones, with 2000-3000 mm, but not in drier zones with less than 2000 mm. Finally, the lower Na soil concentration in recent grassland compared to ancient grassland could be explained by a deeper water table and consequently less frequent upwelling of dissolved salts in topsoils (Nosetto *et al.*, 2007).

Unlike the previous soil properties, C/N, P and K have undergone a rapid change in recent grassland compared to ancient forest. These results reflect the impact of management practices in recent grassland. Indeed, the increase in P and the decline of C/N likely reflect the introduction of fertilization in recent grassland. Besides, the decline in K demonstrates the impacts of both a higher potassium content in the hay exported from grassland, in comparison with its very low level in wood, and the higher rhythm of biomass exportation from grassland.

Conclusions

On a very short scale and despite low slopes, soil texture varied from silty clay to clay along the forest-grassland gradient. This change was related to a thinning of the silty deposits overlaying the clayey material derived from the marlstone. This may be due to initial land-use choices by farmers, to land use after-effects, or both. Various arguments suggest that this gradient result from both. Naturally, clayey soils downslope add value to the production of fodder while silty well-drained soils upslope are better used for hardwood forest. However, ancient grasslands have been probably repeatedly tilled, and tillage increase erosion. A strong effect of land use is suggested by (i) the abruptness of the textural gradient compared to the very smooth topographic gradient, and (ii) the fact that the soil texture of recent grasslands which developed for less than 150 years on former forests was already enriched in clay compared to forests from which they derived.

In the study area, the present land use influenced soil acidity, soil organic content and concentration in nutrients. Soil acidity decreased with the distance-to-edge in forest and increased in recent grassland after deforestation. Soil organic content and nutrients generally increased with distance-to-edge in grassland, decreased in case of afforestation and increased more or less rapidly after deforestation. Besides these general trends, some exceptions were found, for example for K. For various reasons, mainly related to differences in vegetation composition and management practices between forest and grassland, soil properties change strongly according to both distance-to-edge and land-use change. However, traces of former land uses persist on some soil properties. The legacy of ancient land-use was stronger in case of deforestation than afforestation. The legacy of former forests in current grasslands is a new result that has implications for conservancy of grasslands.

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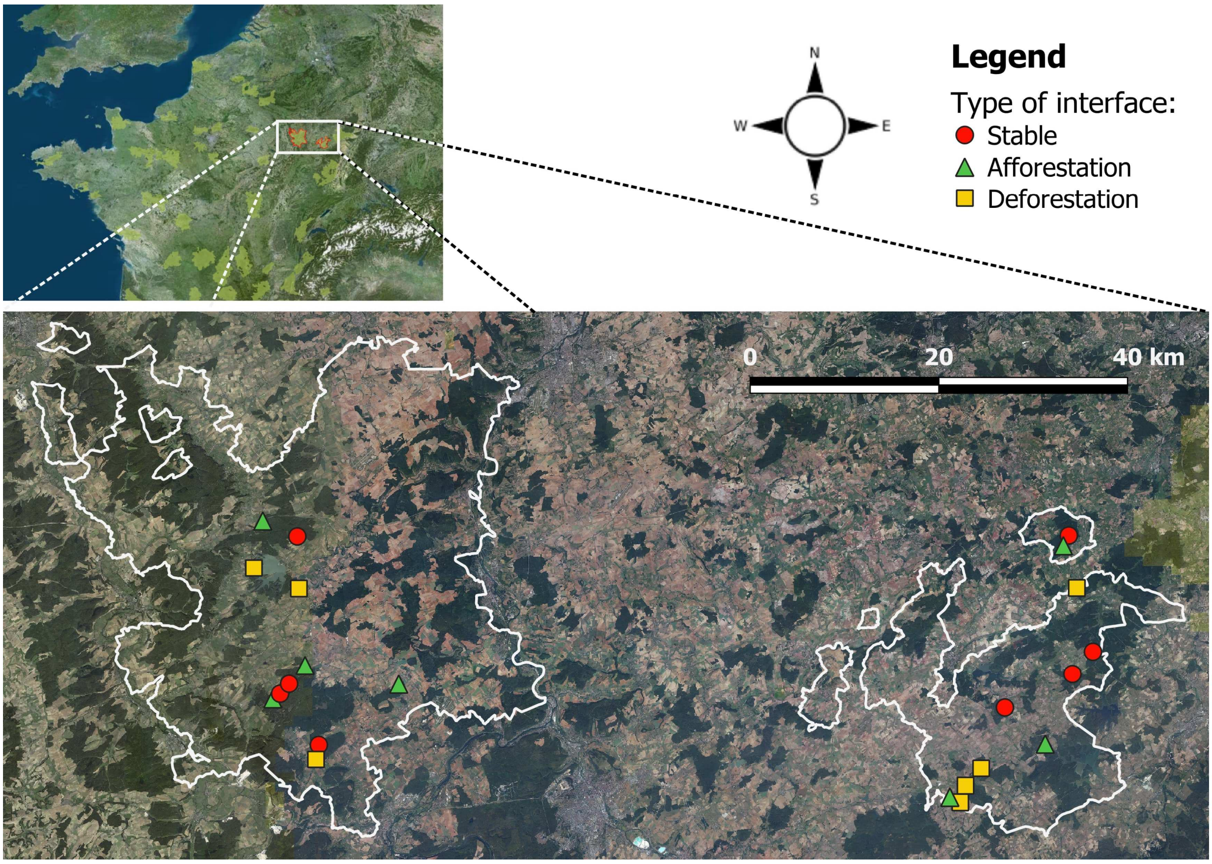

Fig. 1. Study area and location of the three types of forest-grassland interfaces studied. All the study sites (forest-grassland interfaces) were selected within the Lorraine Regional Natural Park in northeast France (inside the white lines). The red circles show the stable interfaces (ancient forest vs. ancient grassland, 8 sites), the green triangles show the afforestation interfaces (recent forest vs. ancient grassland, 7 sites) and the yellow squares show the deforestation interfaces (ancient forest vs. recent grassland, 7 sites).

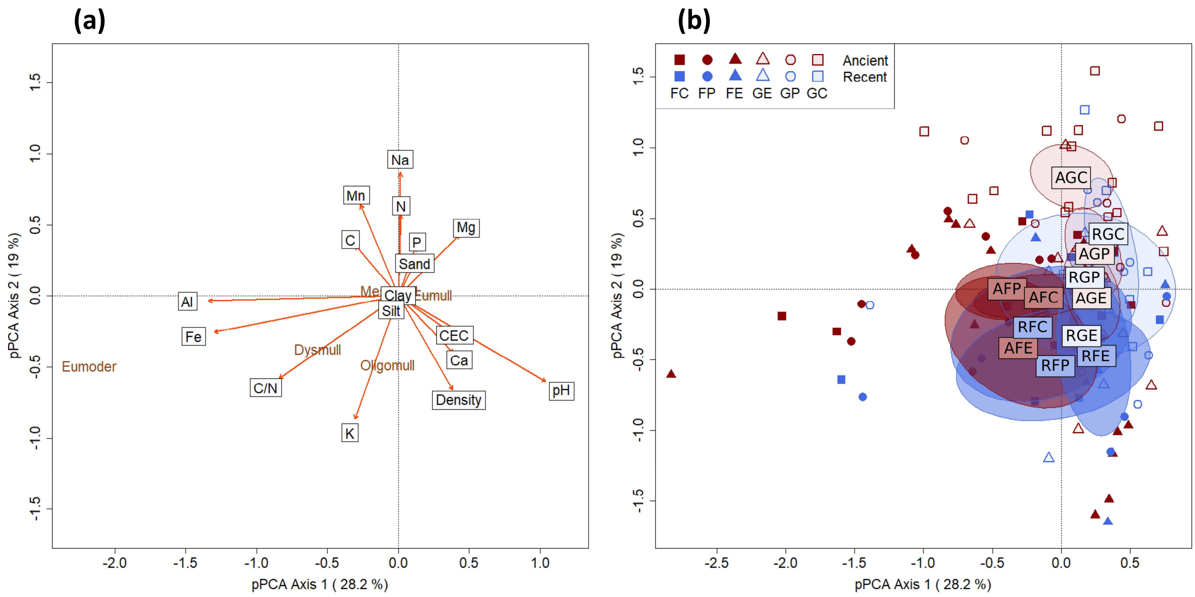

Fig. 2. Partial principal component analysis of soil properties. The effects of topography (factor with 4 levels) and soil texture (*i.e.* soil clay content) were partialled out before PCA. Projection of soil properties (see appendix B for their list) is shown in figure (a) and the humus types have been projected as supplementary variables. Plots are shown in figure (b) and dispersion ellipses are added for the interaction of the history with the position (12 levels) using a confidence interval of 0.95. Ellipse labels are the combination of history and plot position and were sometimes slightly shifted for better readability. History: A (ancient) and R (recent). Plot position: FC (forest core), FP (forest periphery), FE (forest edge), GE (grassland edge), GP (grassland periphery) and GC (grassland core).

Table 1. Goodness-of-fit of linear mixed models (LMMs) and analyses of variance of fixed effects for soil properties.

	LMM goodness-of-fit		Position		History:Position		Topography		Clay content	
	Marginal r²	Conditional r²	chi²	p-value	chi²	p-value	chi²	p-value	chi²	p-value
LMM1										
Clay	0.32	0.84	25.1	***	28.9	***	16	**		
Silt	0.3	0.83	23.2	***	35.5	***	13.9	**		
Sand	0.08	0.81	4.9	ns	3.5	ns	10.1	*		
LMM2										
Density	0.5	0.62	10.5	.	19.6	**	7	.	22.1	***
C/N	0.61	0.79	134.7	***	13.6	*	1.2	ns	6.7	**
C	0.64	0.73	10	.	14.4	*	2	ns	68.7	***
N	0.78	0.82	45.7	***	13.4	*	3	ns	109.6	***
P	0.25	0.76	35.2	***	6.3	ns	0.7	ns	7.2	**
CEC	0.79	0.88	16.8	**	3.9	ns	3.4	ns	192.2	***
Ca	0.61	0.82	13.3	*	2.8	ns	2.4	ns	101.7	***
Mg	0.19	0.91	1.5	ns	2.5	ns	7.7	.	54.4	***
Na	0.71	0.81	89.3	***	32.9	***	12.8	**	16.3	***
K	0.5	0.57	79.2	***	8.2	ns	2.9	ns	25.5	***
Fe	0.14	0.36	12.3	*	8.4	ns	4.1	ns	1	ns
Mn	0.13	0.65	4.5	ns	6.5	ns	7.5	.	5.6	*
Al	0.18	0.39	11.5	*	9.3	ns	2.1	ns	0.8	ns
pH	0.26	0.5	15.6	**	3.9	ns	3.5	ns	10.3	**

Marginal r^2: fixed effects only. Conditional r^2: fixed and random (site in sector) effects. *** $P < 0.001$, ** $0.001 \leq P < 0.01$, * $0.01 \leq P < 0.05$ and '.' $0.05 \leq P < 0.1$.

Table 2. Contrast analyses of the land-use, edge and land-use change effects for 14 soil properties. The contrasts were performed between selected levels of the interaction of the history with the position (12 levels), which was one of the fixed effects of the linear mixed models (LMMs). The number of plots used in each contrast analysis is indicated in the 'Number of plots' line.

	Site effect	Land-use effect	Edge effect		Land-use change effect			
					Afforestation (recent forest)		Deforestation (recent grassland)	
	Marginal r² / Conditional r²		Forest	Grassland	Change	Legacy	Change	Legacy
		AFC-AGC	AFC-AFE	AGC-AGE	RFCP-AGCP	RFCP-AFCP	RGCP-AFCP	RGCP-AGCP
Number of plots		15-15	15-15	15-15	14-30	14-30	14-30	14-30
LMM1								
Clay	62 %	***	***	***	*	**	*	***
Silt	64 %	***	***	***	.	***	*	***
Sand	90 %	ns	ns	ns	ns	ns	ns	ns
LMM2								
Density	19 %	.	ns	**	**	ns	ns	**
C/N	23 %	***	ns	**	***	.	***	ns
C	12 %	*	ns	***	*	ns	ns	.
N	5 %	***	ns	***	***	ns	ns	*
P	67 %	*	ns	*	***	.	*	ns
CEC	10 %	ns	ns	ns	ns	ns	ns	ns
Ca	26 %	ns	ns	ns	ns	ns	ns	ns
Mg	79 %	ns	ns	ns	ns	ns	ns	ns
Na	12 %	***	ns	***	***	ns	.	***
K	12 %	**	**	.	***	ns	**	ns
Fe	61 %	.	ns	ns	ns	ns	*	ns
Mn	80 %	ns	ns	ns	ns	ns	ns	ns
Al	54 %	ns	ns	ns	ns	ns	ns	ns
pH	48 %	ns	.	ns	ns	ns	*	ns

Planned contrasts. Land use effect: ancient forest core *vs.* ancient grassland core (AFC-AGC). Edge effect: ancient forest core *vs.* ancient forest edge (AFC-AFE) and ancient grassland core *vs.* ancient grassland edge (AGC-AGE). Land-use change effect: recent forest core and periphery *vs.* ancient grassland core and periphery (RFCP-AGCP), recent forest core and periphery *vs.* ancient forest core and periphery (RFCP-AFCP), recent grassland core and periphery *vs.* ancient forest core and periphery (RGCP-AFCP) and recent grassland core and periphery *vs.* ancient grassland core and periphery (RGCP-AGCP). *** $P < 0.001$, ** $0.001 \le P < 0.01$, * $0.01 \le P < 0.05$ and '.' $0.05 \le P < 0.1$.

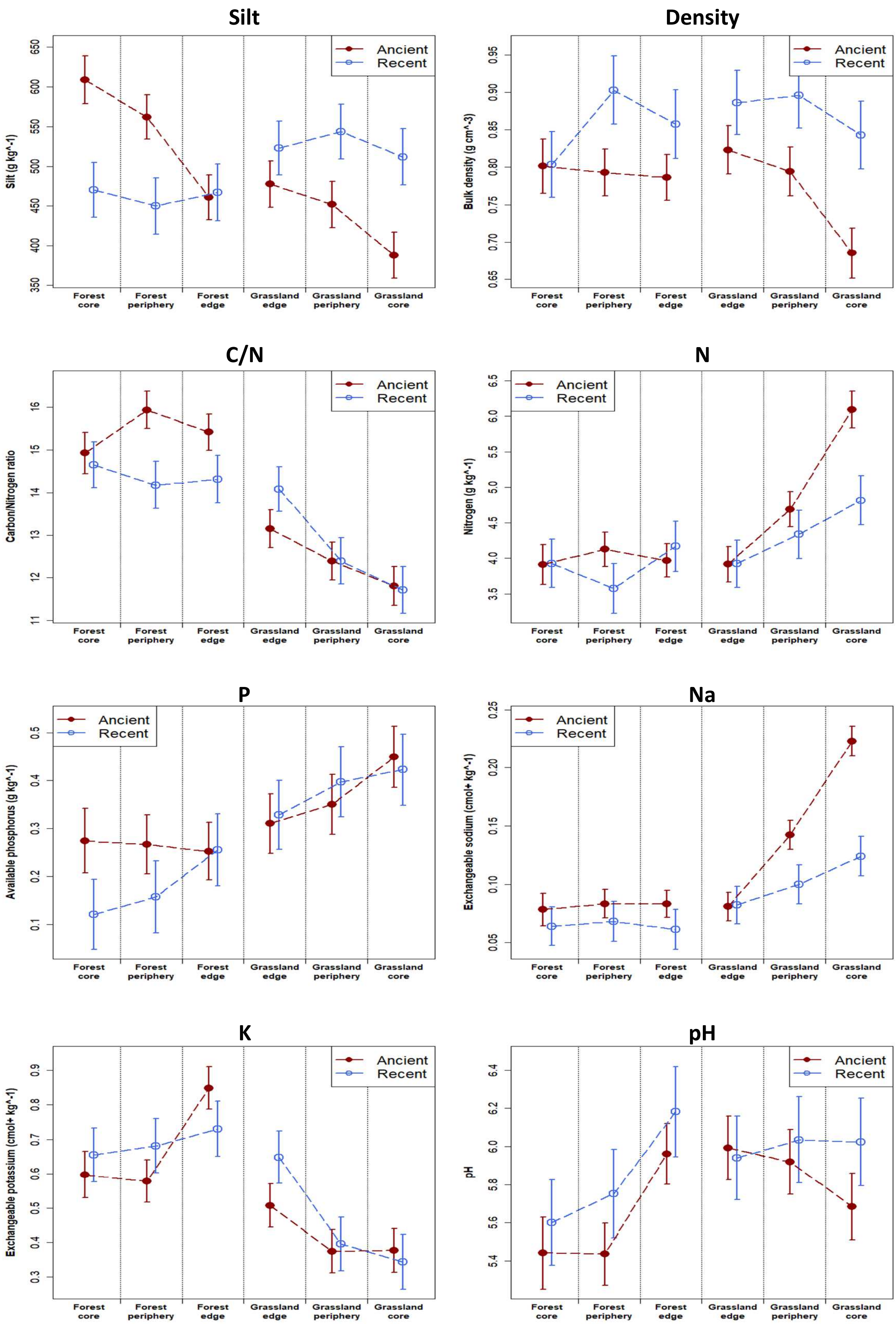

Fig. 3. Least-squares means and standard errors of eight soil properties by position along forest-grassland interfaces for each land-use history. Least-squares means, which are means adjusted for the means of others factors, were calculated using only the topography as a categorical control variable (factor with 4 levels) for the silt content (LMM1), and in addition using the soil texture *i.e.* the soil clay content as a numerical control variable for other soil properties (LMM2).