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Vegetation and habitat changes in response to land abandonment: a predicted indirect effect of global warming on Atlantic European Wet grasslands.

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Summary

1. Habitat changes, due to land abandonment, provide a predictive model for vegetation and habitats response to global warming through induced land-use changes in Atlantic European Wet grasslands. The targeted study areas are headwater catchments in Western Brittany with extensively grazed or mown oligo-mesotrophic river marginal and ground water discharge wetlands characterised by sharp-flowered rush Juncus acutiflorus meadows.

2. Changes were analysed as an in natura experiment, in relation to hydrology, oligo-meso-trophic nutrient conditions and land use, by using a paired-site vegetation sampling approach coupled with a diachronic method (1974-1977 and 2003-2004). Environmental variables were identified through a hydrogeomorphic unit approach and Ellenberg species and community indicator values. Species traits were used to identify plant functional types.

3. Among the identified trajectories, the two main trends are those leading to Molinia caerulea meadows followed by Molinia-Myrica fens in poor nutrient and groundwater recharge conditions and to Filipendula stands characterised by spring overland flow and spring groundwater discharge from adjacent areas.
4. The interruption of the ditch network maintenance led to an increase in water retention in slight depressions as well as the natural restoration of Potentilla-Menianthes rafts, an endangered and rare transition mire habitat.

5. Tussock forming Molinia, Deschampsia and Carex habitats were correlated with a decrease in alpha-diversity in the early successional stages. In the late successional stages, ferns and heathland species restored a higher alpha-diversity at the habitat scale and gamma-diversity at the headwater catchment scale.

6. Synthesis and applications. Long-term successions in oligo-mesotrophic headwater catchments showed different trajectories that did not necessarily lead to reforestation. When traditional practices were abandoned in these wetlands, a higher diversity of habitats in relation to geomorphic and hydrological features of the floodplains and adjacent areas was restored. Land use change in such oligo-mesotrophic conditions, might be a positive indirect effect of climate change.

Introduction

Global climate change models (GCMs) have predicted more precipitation and more frequent extreme events in Northern Europe (IPCC 2007). As a result, changes in land use are expected to occur in agricultural lands, natural or semi-natural environments and particularly wetlands. Such climatic changes are likely to increase constraints for traditional agricultural practices (e.g. mowing and grazing) leading to progressive land abandonment, especially in wet grasslands and meadows. Hence, a major concern in applied ecological research is to predict the response of vegetation to direct or indirect effects of climate change by assessing potential habitat changes due to land abandonment (IPCC 2007). Such an assessment requires the existence of habitat references based on classifications developed at either national (e.g. Rodwell 2002; Jennings et al. 2006) or regional scales. At the European scale, habitats are now classified using the EUNIS system (EEA 2005). These classifications are largely based on syntaxonomic definitions of vegetation (Rodwell et al. 2002), which
represent useful indicators of ecological diversity in natural and semi-natural ecosystems (Redžić 2007).

Until recently, agriculture has been a prominent economical activity in Brittany (Western France). More specifically, wet meadows found in headwater catchments with generally poor soils, were contributing towards economical and social poverty, largely explaining the massive rural exodus towards urban areas starting after World War II. This pattern is often recognised as the dominant demographic factor influencing land use (Henry, Boyle & Lambin 2003). More recently, in North-Western Europe and elsewhere, a number of wetlands have been drained for use as agricultural lands. Human activities are the primary cause of wetland loss and degradation, accounting for up to 50% of the loss (Mitsch & Gosselink 2000; Torbick et al. 2006). At the same time, the remnant traditional forms of local wet meadow management in headwater catchments that are less suitable for agriculture intensification are increasingly being abandoned. Similar agricultural practice changes and socio-economic trends have been observed in Europe and elsewhere (Fischer & Stöcklin 1997; Bakker & Berendse 1999; Billeter, Peintinger & Diemer 2007). Climate change is expected to trigger or exacerbate such land-use changes (Dale 1997; Gehrig-Fasel, Guisan & Zimmermann 2007; IPCC 2007). Current and past ecological changes in wet meadows, due to the abandonment of traditional agricultural practices, can be used to assess similar processes that are expected to occur in the future as a result of either direct or indirect climatic changes.

Managed sharp flowered rush *Juncus acutiflorus* meadows (EUNIS habitat type code E3.42) are common plant communities with relatively little variation in moisture content. These meadows constitute one of the main reference habitats in Western European river marginal wetlands maintained by traditional extensive practices. In general, researchers have reported the establishment of natural woody plants (e.g. bush encroachments, reforestation) in response to a decline in traditional agricultural practices (Gellrich et al. 2007; Gallart & Llorens 2004; Baldock et al. 1996; Rudel et al. 2000, Jensen & Schrautzer 1999).

However, this is not always the case, as various other trajectories have been observed (Diemer, Oetiker & Billeter 2001). An example of this can be found in sharp flowered rush
systems which have been previously extensively managed (e.g. grazed or mown), nearly
abandoned, or otherwise disturbed (e.g. beaver encroachment).

Our objective was to analyse both current and past habitat dynamics due to land
abandonment in Atlantic European Wet grasslands via an in natura experiment in relation to
hydrology, nutrient and land use, and in particular, the increase of extreme climatic events
(e.g. variability and suddenness of flooding). We used 'plant assemblages', which define
floristically-based communities, as the main habitat indicator based on the EUNIS
classification. The concept of a hydro-geomorphic unit (Maltby, Hogan & McInnes 1996) was
adopted in order to define the spatial extent of habitats and the main hydrological processes.

In order to explain the mechanisms of some of the community and habitat changes,
environmental gradients were analysed using the Ellenberg Indicator Values for plant
communities (Hill et al. 1999; Cingolani et al. 2007). Plants and communities have long been
recognised as potential environmental indicators for detecting assembly rules, with the aim of
identifying the main drivers that govern changes in the composition of plant communities.
(Keddy 1992; Diekmann 2003; Odland & Munkejord 2007). Providing that some precautions
are taken (Thompson et al. 1993; Hawkes, Pyatt & White 1997), there are several
advantages in using plant and community indicators rather than direct physical or chemical
measurements.

The present paper aims to study the role of agricultural abandonment linked to hydrological
alterations as well as to identify the pathways of change through the following comparative
analyses: 1) habitat responses to land abandonment through a plant assemblage analysis, 2)
the determinant factors and mechanisms of those responses and 3) elements of model plant
dynamics in terms of biological and environmental predictors.

Methods

Study area

Five ecologically similar headwater catchments were selected in Western Brittany: four on
the Ellez river (Roudoudour: 48.373°, -3.874°; Roudouhir: 48.379°, -3.897°; Ster Red:
This area has an Oceanic Temperate climate. The geologic substratum consists of siliceous parent rocks (granite, quartzite and sandstone), which generate poor nutrients, acidic water and peaty soils. Groundwater discharge areas and river marginal wetlands are characterised by oligo-mesotrophic wet meadows dominated by the sharp-flowered rush *Juncus acutiflorus*. These wet hay and grazing meadows are classified in EUNIS database (E3.42). Meadows managed by grazing or mowing require drainage via ditches, which need regular maintenance.

In areas that have been abandoned from 5 to more than 30 years, and locally up to 60-70 years, a large array of contrasting vegetation types exists, representing multiple possible trajectories that can be related to different hydro-geomorphic features. In order to study the impact of land abandonment, as an assumed consequence of an increase in the duration and intensity of both flooding and inundation due to global warming, we sampled wet meadows in a very narrow moisture interval. Five hydro-geomorphic units (HGMUs) arranged along elevation gradients from uplands to rivers, with slight differences in elevation, can be described for the whole study area and consist of floodplains (F1 to F4, from high to low elevations) and slopes (S): F1: slight elevations showing groundwater recharge only; F2: moderate elevations with fluctuating groundwater levels; F3: main floodplains with overland flow and water discharge from adjacent areas; F4: slight depressions (10-20 cm deep) with long flooding periods, two or three months later than in the surrounding areas; S1: gentle slopes with fluctuating groundwater levels and runoffs.

**Data collection and sampling design**

The data set comprises 103 relevés from two sampling periods: 1974-1977 (Clément 1978) and 2003-2004. The sampling method for the dataset was based on a diachronic analysis and a space for time substitution analysis (STS). Some relevés were re-sampled when a plot showed a change in land use (especially land abandonment) between the two sampling periods. For the STS, we used a paired-site sampling technique based on *a priori* information.
about the terrain characteristics in order to minimise the differences between the terrain variables.

The relevés, which were distributed via a stratified sampling method based on the hydro-geomorphic conditions, were randomly sampled in each HGMU. The surface area of each relevé was 25 m² (5 x 5 m). We recorded the species present in each relevé and evaluated their cover using the Braun-Blanquet scale (+:<1%; 1: 1-5%; 2: 5-25%; 3: 25-50%; 4: 50-75%; 5: 75-100%). As cover indices are inappropriate for some analyses; these values were transformed into cover percentages, representing the median class value (Cingolani et al. 2007). Botanical nomenclature follows Flora Europaea (Tutin et al. 1968-2001).

**Plant assemblages and communities**

The objective of a species-based phytosociological analysis is to use plant assemblages to define typical communities according to the syntaxonomic hierarchical classification system (see Gehu and Rivas-Martinez 1981 for a detailed description). This approach uses the “fidelity” hypothesis, which assumes that a plant community can be characterised by a specific combination of relatively permanent plant species (Moravec 1992).

The most important species for habitat diagnostics are those, which are present with a medium or high frequency, and are in only one or a few syntaxa (referred to as ‘diagnostic species’). Syntaxa allow the detection of multi-species responses along environmental gradients and ‘can further the understanding of vegetation variation’ (Biondi, Feoli & Zuccarello 2004). According to the present assumption, we expect this method to indicate significant relationships between certain assemblages and drivers, such as field abandonment duration.

**Environmental features and diversity**

Indicator values (IVs) are derived from a significant relationship between the co-occurrence of species and certain environmental variables (Hawkes et al. 1997). We used the IV database developed by Ellenberg (1992) for Central Europe and updated for the Atlantic...
zone by Hill et al. (1999). Three environmental indicators were used: moisture (F), Nitrogen (N), and soil or water pH (R). The F scale ranges from 1 (plants living in extreme dryness) to 12 (plants permanently or almost continually under water). The N scale indicates trophic conditions such as general fertility (Hill et al. 2000) or biomass production (e.g. Shaffers & Sykora 2000), where a value of 1 indicates extremely low trophic level and 9 indicates extremely rich conditions. The R scale also ranges from 1-9, with 1 indicating extreme acidity and 9 indicating a basic reaction found in calcareous or other high-pH soils or water.

The use of IVs can replace the need for taking direct measurements of variables, saving researchers both time and money. Another advantage of using IVs is that they may be more sensitive to the requirements of a given species than to a selected variable. The IV of a given species does not take into account its ecological amplitude along an environmental axis but rather, corresponds to the mode or optimum i.e. the value of a given environmental factor or indicator, for which the maximum of the given species occurrence is attained (sensu Gauch, Chase & Whittaker 1974). IVs are used at a community level rather than at an individual species level since communities that are representative of a local habitat are more likely to have a stronger indicator value than an individual species. The mean characteristic IV for each relevé was calculated on the basis of the presence/absence of species, following Jongman, ter Braak & van Tongeren (1995).

Plant Functional and Functional Vegetation Types and diversity

The concept of a plant functional type (PFT) assumes that species can be grouped together based on their common response to the environment and/or their similarity in affecting how ecosystem functions (Lavorel & Garnier 2002). Each species was assigned to a PFT according to the species traits provided in the BIOLFLOR database (Kühn, Durka & Klotz 2004), which we adopted with slight modifications. We used 16 traits referring to leaf forms (LM, consisting of grass-like, megafors and other forms), life forms (LF, Geophytes, Hemicryptophytes, Nanophanerophytes and Bryophyta), vegetation propagation modes (VP, including Runners and Rhizomes), storage organs (SO, Tussocks, Runners, Tufts, and
Rhizomes) and rosette types (RO, such as Erosulate, Hemirosette or Rosette plants). Both diversity, which was assessed using the Shannon equations, and evenness were calculated for each relevé. The alpha (\(\alpha\)) as the ‘within’ diversity (Lande 1996) was assessed for each plant assemblage as the mean diversity of the corresponding relevé group. The gamma (\(\gamma\)) diversity was assessed as the ‘total’ species diversity (\(\gamma_T\)) for the entire study area and \(\gamma_{pa}\) for each plant assemblage. Following Lande (1996), beta (\(\beta\)) diversity was calculated as the ‘among’ diversity for the entire study area (\(\beta_T = \gamma_T - \alpha_{mean}\)). A separate beta diversity was calculated for each PA (\(\beta_{pa} = \gamma_{pa} - H_{mean}\)), with \(H_{mean}\) representing the arithmetic mean of the H values of the relevés belonging to a given PA.

**Data analyses**

Plant assemblages, and their corresponding habitat type, were determined through successive classification and ordination analyses using the JUICE software as a data manager and interface programme (Tichy 2002). First, we analysed the data using the TWINSPAN Software package (Hill 1979), which is based on a cluster analysis and reciprocal averaging. This analysis enabled a rearrangement of the rows (species) and columns (relevés) in the data matrix, until a clear hierarchical pattern emerged. In addition to the classification technique, the major gradients were interpreted through vegetation and habitat distribution ordinations using a Detrended Correspondence Analysis (DCA, Hill 1979). The DCA is an indirect gradient analysis ordination which, compared to a Correspondence Analysis (CA), removes non linear dependencies between the axes (Hill & Gauch 1980). The relationship between vegetation and the environment was studied using a direct gradient analysis, i.e. a Canonical Correspondence Analysis (CCA) developed by Ter Braak (1986). The CCA is a two step approach combining an indirect gradient analysis (e.g. DCA) in the first step with a direct gradient analysis in the second step, and which relates the ordination axes to the environmental variables. Each relevé was characterised by 21 environmental variables consisting of three CIVs, plant richness and the Shannon–Weiner evenness indices as well as the 16 trait compositions. The relevé/trait matrix was obtained by
multiplying the species/relevé matrix by the species/trait matrix using the R Software for Statistical Computing (ver. 2.4.1). The DCA and CCA analyses were performed using the CANOCO software (ter Braak & Šmilauer 1998).

Results

Plant assemblages.

The interpretation of the classification and the DCA indirect gradient analyses (Fig. 1) led to the definition of seven mean plant assemblages (PA I to VII), which are summarised in Table 1 (also see S1 in the supplementary material).

The species composition analysis showed that all PAs comprises a common large group of 24 plant species and confirming that the dataset can be used to identify changes in vegetation structure and composition within the same ecological context.

PA I corresponds to sharp-flowered rush (*Juncus acutiflorus*) meadows that are still managed by mowing and are occasionally extensively grazed in summer. This PA, which can include recently abandoned fields (less than 5 years), is considered to be the managed control for the whole study. A variant of this PA is recognised based on the abundance of Bryophytes, and especially *Sphagnum* ssp. This PA occurs in all HGMUs, except at slight elevations (F1)

PA II corresponds to meadow-sweet stands with tall herb communities of humid meadows which are differentiated by *Filipendula ulmaria* and related species, and megaforbs such as *Urtica dioica*, *Galium aparine* and *G.* mollugo. Two variants of this PA are characterised by the tussock-forming *Deschampsia caespitosa* and the purple moorgrass *Molinia caerulea*, respectively. PA II exclusively occupies the main floodplains (F3).

PA III relates to acid-purple moor-grass meadows. Great tussocks of *Molinia caerulea* structure its physiognomy. A sub-group can be distinctly identified, comprising heath species (e.g. *Narthecium ossifragum*, *Erica tetralix*, *Erica ciliaris*, *Calluna vulgaris*, *Ulex gallii*).
PA IV refers to bog-myrtle scrub on poor fens. *Myrica gale* thickets often colonise abandoned wet meadows. Then, the system changes into a tussock-based mosaic of *Molinia caerulea* and/or *Deschampsia caespitosa* with clones of *Myrica gale*. This vegetation type is poor in terms of its botanical composition, which depends on the density of the previous species.

Both PA III and IV are found in floodplains (F2) and on gentle slopes (S1).

PA V corresponds to *Menyanthes trifoliata* and *Potentilla palustris* rafts, which are transition mire communities constituted by forbs (*M. trifoliata*, *P. palustris*, *Hypericum helodes*, etc.) and graminoids such as *Carex rostrata* and *Eriophorum angustifolium*. These communities are located in slight depressions (F4) within *Juncus acutiflorus* or *Molinia caerulea* meadows.

PA VI relates to a tussock-based formation of the sedge *Carex paniculata*, which usually occur on gentle slopes with permanent groundwater discharge or in floodplain depressions that are partly connected with a river. Like other ferns, *Osmunda regalis* primarily grows on the tussock sides of *Carex paniculata*.

PA VII corresponds to *Carex nigra* fens and red fescue meadows that occur on the slight elevation of the floodplain (F1) within *Juncus acutiflorus* or *Molinia caerulea* wet meadows.

**Environmental and diversity gradients**

Each PA was characterised from an environmental point of view using the Ellenberg IVs (Table 2). The community mean values for moisture primarily ranged from 7 (i.e. intermediate between mainly constantly moist or damp habitat) to 9 (wet habitat, often water-saturated). While these habitats showed such a relatively small moisture range, the difference between habitats was significant (p<0.001).

The mean community F, N and R values in PA I are very similar to the total data set values. The bryophyte-based sub-group (I-1) corresponds to a lower nutrient level as indicated by the presence of *Sphagnum* ssp. The other two variants are differentiated based on their trophic levels.
PA II has a higher N value, as revealed by the presence of megaforbs, which are good indicators of higher nutrient conditions. The diagnostic species group from PA III is the most relevant according to its trophy indicator values between extremely infertile and more or less infertile sites. Some species showing an N value between 2 and 4 are of intermediate fertility. An exacerbation of this process is shown in sub-group III-3, where the presence of heath species indicates a hyper oligotrophic condition (the N S-IV value is between 1 and 2). Some of oldest (i.e. abandoned for 30-40 years) great tussock meadows have also been colonised by ferns, such as Athyrium felix-femina, which usually grow on the sides or top of old tussocks (Peach & Zelden 2006). Especially old tussocks may enhance species richness by increasing the surface area or by providing multiple microhabitats. However, grass tussocks may reduce species richness through high litter production and accumulation; especially at low fertility levels with slow decomposition and mineralisation processes.

PA IV This species group is comprised of a combination of ferns and small shrubs, indicating an intermediate level of fertility and late successional stands. When previously efficient drainage practices (linked to man-made ditches) were stopped, natural habitats (PA V) were restored, allowing mire fens to expand their distribution. PA VI Water fluxes create wetter conditions in the higher trophic level of the habitat. PA VII has the lowest levels of humidity, due to micro-elevations (about 10 cm) with high species richness. In some cases, the tufted Festuca rubra and Carex nigra resemble small tussocks in old abandoned fields.

The CCA is illustrated by three ordination diagrams representing the relevé groups and the main species (Fig. 2), plant traits and environmental variables (Fig. 3). Fig. 2 shows that the main PAs (Table 1) presented in the DCA analysis remain more or less distinct. PAs VI (Carex tussocks), II (Filipendula stands) and IV (Myrica scrubs) are more or less separate. On the first axis (Fig. 2), which mainly refer to vegetation dynamic stages, the positive scores correspond to abandoned old fields (Molinia grasslands (PA III), Myrica scrubs (PA IV) and D. caespitosa grasslands. Similarly, the positive eigen-values on the second axis correspond
to mature stands after the abandonment of *Filipendula* stands (PA II) and *Carex* tussocks (PA VI). This dynamic trajectory is correlated with an increase in productivity, as indicated (Table 2) by the N and R indicator values, and with a slight increase in moisture (F). Species richness and evenness are clearly associated with managed and pioneer plant communities (Table 2). The lowest richness values were found in old grasslands, especially those forming tussock habitats (e.g. *Molinia* and *Deschampsia* grasslands, *Carex* tussocks and *Myrica* scrubs). For instance, tall forbs (LMM) are expected to relate to an increase in fertility, which is associated with the second axis (Fig. 3). ROg (rosette plant) and SOtu (tussocks) related variables have a higher correlation with the first axis (0.854 and 0.892, respectively). Rich (species richness) and Eve (evenness or equitability) have nearly the same significance and are both highly and negatively correlated with the first axis (-0.629 and -0.636). ROh (hemi-rosette plant) and ROg have a high negative correlation (-0.731) and plot at opposite ends from one another. Conversely, ROh and SOrh (rhizome) are positively correlated (0.776).

**Discussion**

*Plant assemblages and environmental gradients*

Wetland plant communities are highly sensitive to three main drivers: 1) hydrology, especially flooding duration and/or soil wetness during spring; 2) nutrient availability, both nitrogen and phosphorus, during plant growth periods (i.e. the trophic level); and 3) land use, either mowing and/or grazing versus the abandonment of agricultural practices in situ. Hydrological features refer to the period of time from late winter to early summer, i.e. when plant growth and survival may be affected. For example, F2 and S1 are defined by groundwater fluctuations, but if overland flow occurs in winter, plant growth should be not affected because of the desynchronisation of these two events. Land use is itself dependent in physical or abiotic constraints, hydrological processes and trophic levels, but in the case of abandonment, this type of change may affect hydrology and the nutrient transfer within the system; e.g. the abandonment of ditches could increase flush
or overland flows and subsequently, nutrient fluxes, thereby changing the trophic level of the system.

Old field succession trends primarily refer to a differentiation from woodlands (Gellrich et al. 2007), especially Salix-based ones in most wetlands. In the present work, and only in PA VI, Salix cinerea indicates a potential trajectory to mire grey willow scrub (EUNIS code F9.21). When wet meadows are grazed in spring and when grazing coincides with willow seed dispersal, trampling produces microhabitats that promote germination and seedling development (Touzard, Clément & Lavorel 2002). This scenario does not occur in the present study, with the exception of PA VI. If the wet meadow is then mown or grazed in summer, the undisturbed perennial herb mat prevents willow seedlings from colonising. Grasslands are still present more than 30-60 years after abandonment, especially in oligotrophic conditions.

When starting from control-managed fields (Juncus meadows), plant assemblage dynamics may follow various trajectories (Fig. 4) with four main trends (T1 to T4):

T1: Molinia meadows are successful in HGMUs where groundwater recharge occurs in spring and then fluctuates with low nutrient availability. Later (more than 30 years), Myrica scrubs and ferns could be present.

T2: following abandonment, Filipendula stands are established in HGMUs (type F3) characterised by overland flow and groundwater discharge. Water coming from adjacent areas does not contain a higher nutrient content, but it releases, in terms of cumulative load amount, more nutriments to plants that require a higher nutrient flux (such as megaforbs).

Such mesotrophic conditions are not only the consequence of abandonment; but this type of HGMU existed previously and can also be observed in certain habitat variants within Juncus acutiflorus meadows.

T3: On slopes with local, permanent or high groundwater discharge, or in depressions within a floodplain where surface water occurs for more than six months of the year, late successional Carex paniculata tussocks could be found; mesotrophic conditions linked to
water flux explain this local habitat type. It should be noticed that this type of habitat may be found outside oligotrophic headwater catchment systems.

T4: In floodplains, slight depressions, such as old abandoned ditches, with longer durations of surface water retention offer an opportunity for the development of *Potentilla palustris* raft habitats. This pioneer habitat is highly important as many of these pioneer species are both rare and endangered in most European wetlands and abandonment processes provide an opportunity for the natural restoration of this kind of biodiversity.

Marginal wetlands in headwater catchments refer to those generated by headwaters rather than by rivers, due to their small size. Notice that the term “marginal” wetland refers here to the space location in relation to the body of water (e.g. river or lake), rather than the economic meaning of a wetland at the margin of economic viability (Brouwer *et al*. 1997).

**Plant assemblage dynamics and biodiversity**

The succession from *Juncus acutiflorus* managed meadows to *Molinia* and *Myrica* abandoned ones shows a decrease in species richness. A possible explanation for this is that after the disturbances have stopped, the degree of inter-specific competition becomes more intense (Shipley, Keddy & Lefkovitch 1991). Grime (1979) hypothesised that the relationship between plant species richness and biomass is unimodal, with richness being highest at intermediate levels of biomass. At high biomass levels, after abandonment, species richness decreases and only one or a few species dominate via competitive exclusion. This was statistically significant in several types of wetlands (Vermeer and Berendse 1983; Moore and Keddy 1989; Garcia *et al*. 1993; Clément and Maltby 1996). Goldberg and Miller (1990) suggested that the low availability of light for sub-canopy plants would increase plant mortality and decrease diversity by excluding low-growing or shade-intolerant species, which is what we observed in the present study. An increase in litter mass is highly correlated to a decrease in plant diversity (Xiong and Nilson 1999; Nilson *et al*. 1999) and primary productivity (Touzard *et al*. 2002). Litter creates a physical barrier, preventing seeds from reaching the soil or seedlings from emerging.
Most of the plants in wet grasslands are perennials. Many exhibit a perennial clonal growth strategy. *Molinia caerulea* and *Deschampsia caespitosa* function as “ecosystem engineers” in that they significantly modify the environment to their advantage by forming dense tussocks that often reach more than half a meter above the general surrounding features. These tall-grass tussocks compete against small forbs (*Viola palustris, Hydrocotyle vulgaris*) and grass (*Agrostis canina*) via a reduction in light and an increase in litter accumulation. Tussock mounds play an important role in terms of nutrient cycling and retention as well as in competitiveness (Grime, Hodgson, & Hunt 1988; Ryser and Urbas 2000; Michalet 2001). *Molinia* has a number of physiological traits that are particularly well adapted to nutrient poor soils (Berendse, Oudhof & Bol 1987; Clément 1987).

Along the trajectory towards *Filipendula* early successional stands in mesotrophic conditions, most of small oligotrophic plant species were eliminated primarily due to high megaforb species, such as *Filipendula*, restricting light. There might not have been a significant litter effect given that this species has a rapid decomposition rate.

When considering levels of species diversity, we can conclude that there is a small number of species (mainly bryophytes, ericaceous and fern species groups) that appear locally after abandonment, all of the oligotrophic heathland and shrubland species indicate a potential dynamic from oligotrophic meadows to heathland vegetation types (southern wet heath EUNIS code F4.12).

Mowing or grazing in managed sites induces an apparent standardisation of habitats (e.g. *Juncus acutiflorus* meadows and *Festuca rubra* meadows on slight elevations in floodplains); even if different sub-groups of relevés in each habitat type exhibit variations in the species assemblage in relation to hydrological and trophic variations.

In abandoned study sites, the main factors, which explained the different dynamics trajectories, were plant community dynamics and the interruption of hydrological network maintenance, which lead to an increase in the flooding duration. As a result (Fig. 4), early successional, late successional and pioneer plant community grasslands, in addition to *Salix*
shrublands which were locally present but not studied here, support a higher Gamma
diversity within oligo-mesotrophic wetlands localised in headwater catchment systems.
The main results discussed in this study refer to oligo-mesotrophic wetlands found in
headwater catchments in the Atlantic European region. We assumed that human activities in
upland areas within the catchment did not have an impact on the nutrient input into these
ecosystems.

In our case, the vegetation cover found in the uplands is heathlands, bogs, or extensively
grazed grasslands. Other than atmospheric deposition, there is very little nutrient input.
Ecosystems are either P or N limited, as described by Maltby et al. (1996) and Murphy et al.
(1994) in the UK, under the same conditions. On gentle slopes, *Molinia* grasslands occur in
low nutrient input zones, while *Filipendula* stands with more nutrient requirements are found
in flush zones, thanks to drainage disruption. This indicates that habitat changes are also
related to a lack of ditch management, which functions as an integral part of the global
abandonment process (Clément et al. 1996).

In headwater catchments, the main concern is that upland areas with high nutrient loads will
release nutrients into oligotrophic wetlands when they are intensively cultivated.

Maintenance of the ditch network protects most of these systems, and thus, water and
nutrient fluxes are controlled from the source (fields) to the sink (river). The ditch
maintenance cessation could increase the nutrient flux within oligotrophic plant communities,
thereby causing a negative change towards more nutrient rich plant communities that,
however, constitute a buffer zone improving water quality (Maltby et al. 1996).

**Management implication**

In headwater catchments, and in an oligo-mesotrophic context with non-intense agricultural
practices, *Juncus acutiflorus* meadows are the reference habitat type for the Atlantic region,
from Northern Portugal to Northern Scotland. Land abandonment does not always result in a
process of natural reforestation in these climate and ecological conditions. Depending on
natural processes, the establishment of *Molinia*-dominant tussock vegetation is a common
succession trend on gentle slopes and in floodplains with water-table fluctuations. A reduction in species richness is compensated for by an increase in \( \beta \) diversity and a progressive colonisation by local ferns, heathland and peatland species, more than 30 years after abandonment. In mesotrophic conditions linked with overland flow in winter and spring, \( F. \) stands succeed \( J. \) meadows. The abandonment of ditch management, a direct impact of human activity change, provides a potential for the natural restoration of \( P. \) rafts, which represent an endangered and rare habitat in Western Europe.

All of the habitats resulting from land abandonment have enhanced the total gamma diversity (\( \gamma \)) for the entire headwater catchment landscape. The biomass accumulation is also an opportunity for the restoration of the carbon sink and for the maintenance of a high water quality in those ecosystems.

On a local scale, and mainly in the uplands, land abandonment due to climate change, could be seen as a positive opportunity for the natural restoration of some of the major biochemical and ecological functions of wetlands, thereby enhancing their values within the framework of river-basin management.

### Acknowledgements

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Table 1. Correspondence between plant assemblages and EUNIS habitat codes.

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<tr>
<th>PA</th>
<th>EUNIS code</th>
<th>EUNIS habitat designation</th>
<th>Abridged name</th>
</tr>
</thead>
<tbody>
<tr>
<td>I</td>
<td>E3.42</td>
<td>Sharp-flowered rush meadows</td>
<td>Juncus meadows</td>
</tr>
<tr>
<td>II</td>
<td>E5.421</td>
<td>Western nemoral tall-herb communities of humid meadows</td>
<td>Filipendula stands</td>
</tr>
<tr>
<td>III</td>
<td>E3.512</td>
<td>Acidoclone purple moorgrass meadows</td>
<td>Molinia meadows</td>
</tr>
<tr>
<td>IV</td>
<td>D2.2A</td>
<td>Bog-myrtle scrub on poor fens</td>
<td>Myrica scrubs</td>
</tr>
<tr>
<td>V</td>
<td>D2.39</td>
<td>Bog bean and marsh cinquefoil rafts</td>
<td>Potentilla rafts</td>
</tr>
<tr>
<td>VI</td>
<td>D5.216</td>
<td>Greater tussock sedge tussocks</td>
<td>Carex tussocks</td>
</tr>
<tr>
<td>VII</td>
<td>D2.223</td>
<td>British black-white-star sedge acidic fens</td>
<td>Festuca meadows</td>
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</table>
Table 2. Environmental and diversity parameters for the habitats

<table>
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<tr>
<th>Ellenberg IV</th>
<th>Total</th>
<th>I</th>
<th>II</th>
<th>III</th>
<th>IV</th>
<th>V</th>
<th>VI</th>
<th>VII</th>
<th>F</th>
<th>P</th>
<th>Mean</th>
<th>CI 0.05</th>
<th>Mean</th>
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<th>Mean</th>
<th>CI 0.05</th>
<th>Mean</th>
<th>CI 0.05</th>
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</thead>
<tbody>
<tr>
<td>F Mean</td>
<td>7.66</td>
<td>7.66</td>
<td>7.58</td>
<td>7.60</td>
<td>7.69</td>
<td>8.13</td>
<td>8.13</td>
<td>7.13</td>
<td>11.20</td>
<td>&lt;0.001</td>
<td></td>
<td>0.08</td>
<td>0.13</td>
<td>0.14</td>
<td>0.12</td>
<td>0.31</td>
<td>0.26</td>
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<tr>
<td>N Mean</td>
<td>3.58</td>
<td>3.39</td>
<td>4.51</td>
<td>3.23</td>
<td>3.34</td>
<td>3.50</td>
<td>4.30</td>
<td>3.25</td>
<td>9.22</td>
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<td>0.16</td>
<td>0.44</td>
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<td>0.31</td>
<td>0.66</td>
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<tr>
<td>R Mean</td>
<td>4.71</td>
<td>4.59</td>
<td>5.49</td>
<td>4.40</td>
<td>4.17</td>
<td>4.81</td>
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<td>12.59</td>
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<td>0.12</td>
<td>0.30</td>
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<td>0.23</td>
<td>0.57</td>
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<tr>
<td>Rich Mean</td>
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<td>16.13</td>
<td>13.53</td>
<td>10.32</td>
<td>6.78</td>
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<td>11.33</td>
<td>19.50</td>
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<td>1.12</td>
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<td>1.42</td>
<td>1.93</td>
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<tr>
<td>H Mean</td>
<td>-</td>
<td>2.82</td>
<td>2.31</td>
<td>1.29</td>
<td>0.95</td>
<td>2.95</td>
<td>1.87</td>
<td>3.06</td>
<td>28.84</td>
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<td>-</td>
<td>0.3</td>
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<td>0.23</td>
<td>0.6</td>
<td>0.31</td>
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<tr>
<td>Eve Mean</td>
<td>-</td>
<td>0.71</td>
<td>0.62</td>
<td>0.38</td>
<td>0.60</td>
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<td>-</td>
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<td>γpa</td>
<td>-</td>
<td>4.14</td>
<td>3.79</td>
<td>1.91</td>
<td>2.25</td>
<td>4.58</td>
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<td>-</td>
<td>1.32</td>
<td>1.48</td>
<td>0.63</td>
<td>1.30</td>
<td>1.63</td>
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<tr>
<td>βpa</td>
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<td></td>
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<td></td>
<td>γT = 4.70</td>
<td></td>
<td>βT = 2.52</td>
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</table>

F: moisture; N: trophy; R: reaction; Rich: richness; H: Shannon index; Eve: evenness; H; γT: Total species diversity; βT: among' species diversity for the whole study area; γpa: gamma species diversity of each PA; βpa: Beta diversity of each PA.
Fig. 1. Ordination diagram of the DCA analysis (Axis 1-2 Plane).

The dotted ellipses represent the relevé groups corresponding to the plant assemblages (PAs) I: *Juncus* meadows; II: *Filipendula* stands; III: *Molinia* meadows; IV: *Myrica* scrubs; V: *Potentilla* rafts; VI: *Carex* tussocks and VII: *Festuca* meadows. Ev = Axis Eigen-value.
Fig. 2. Ordination diagram of the CCA analysis (Axis 1-2 Plane).

Only dominant species are represented. The dotted ellipses represent the relevé groups corresponding to the plant assemblages (PAs): I: Juncus meadows; II: Filipendula stands; III: Molinia meadows; IV: Myrica scrubs; V: Potentilla rafts; VI: Carex tussocks and VII: Festuca meadows. \( \text{Ev} = \) Axis Eigen-value.
Fig. 3. Ordination diagram for the environmental variables used in the CCA

Rich = species richness, Eve = evenness; Ellenberg Indicators: 'F' for moisture, N for trophical level, R for pH or reaction. Species trait are indicated by 3 or four letters: trait group by the two first letters and sub-group by the 3rd and/or 4th letters as follows: LM = leaf forms (LMgr = grass-like, LMM = megaforbs and LMo = other forms), LF = life forms (LFG = Geophytes, LFH = Hemicryptophytes, LFN = Nanophanerophytes and LFBr = Bryophyta), VP = vegetation propagation modes (VPa = Runners, VPrh = Rhizomes), SO = storage organs (SOt = Tussocks, SOa = Runners, SOh = Tufts, and SOrg = Rhizomes), and RO = rosette types (ROr = Erosulate, ROh = Hemirosette or ROg = Rosette plants).

Each variable is represented by an arrow explaining the occurrence of such a trait. The longer the arrow, the greater the relevance of the considered variable. The position of the head of the arrow depends on the Eigenvalues of the axes and the intra-set correlations of that environmental variable with the axes. The direction of the arrow shows the gradient increase. The distance and the correlation between two variables or between a variavle and an axis, are inversely proportional.
Figure 4. A trajectory scheme for wet grasslands in headwater catchments subjected to land abandonment in the Atlantic European zone.

T1 to T4: successional trajectories; GW = ground water; SW = surface water; in square brackets: EUNIS habitat code; increasing trophic level from 'o' = low, '+' = moderate, to '++' = high.
Supplementary material.

Table S1. Phytosociological matrix

<table>
<thead>
<tr>
<th>Species</th>
<th>I</th>
<th>II</th>
<th>III</th>
<th>IV</th>
<th>V</th>
<th>VI</th>
<th>VII</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Nardus stricta</em></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Carex rubra</em></td>
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<td></td>
<td></td>
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</tr>
<tr>
<td><em>Juncus trifidus</em></td>
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</tr>
<tr>
<td><em>Carex remota</em></td>
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<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Juncus effusus</em></td>
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<tr>
<td><em>Carex nigra</em></td>
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<td><em>Juncus arcticus</em></td>
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<td></td>
</tr>
</tbody>
</table>

Note: The table contains data on phytosociological traits for different species, with columns indicating specific conditions or measurements.
The matrix consist of 103 relevés (25 m² : 5 x 5 m each) sampled during two periods: 1974-1977 (Clément 1978) and 2003-2004.
In the upper part are given, general information on the relevés (sampled plots): plant trait type (forb, graminoid, tussock, moss), richness, diversity index and evenness, Ellenberg mean IVs.
For each species are indicated its Ellenberg Indicator Value for moisture (F), trophic level (N) and pH (R). The botanical nomenclature is given according to Flora Europaea (Tutin et al. 1968-2001).
For a given relevé, the cover of each species is assessed according to the Braun-Blanquet scale (+:<1%; 1: 1-5%; 2:5-25%; 3: 25-50%; 4: 50-75%; 5: 75-100%).
A relevé group corresponds to a plant assemblage (numbred between I and VII) of whose diagnostic species groupe was coded between A to K.