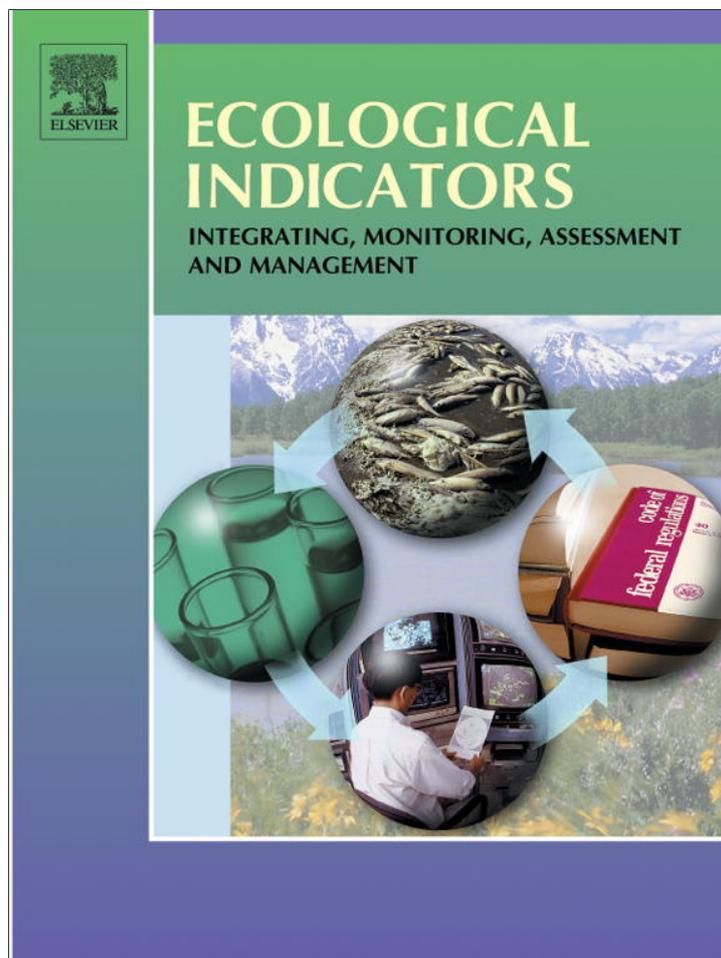


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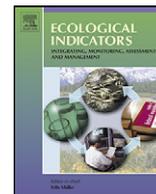
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# Ecological Indicators

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## Disentangling community assemblages to depict an indicator of biological connectivity: A regional study of fragmented semi-natural grasslands

Assu Gil-Tena<sup>a,b,\*</sup>, Rémi Lecerf<sup>c</sup>, Aude Ernoult<sup>a</sup><sup>a</sup> UMR 6553 ECOBIO, CNRS and Université de Rennes 1, Campus de Beaulieu, 35042 Rennes Cedex, France<sup>b</sup> Forest Sciences Center of Catalonia, Crta. Sant Llorenç de Morunys, km 2, 25280 Solsona, Spain<sup>c</sup> UMR 6554 COSTEL, CNRS and Université de Rennes 2, Place du Recteur Henri Le Moal, 35043 Rennes Cedex, France

### ARTICLE INFO

#### Article history:

Received 14 March 2012

Received in revised form 22 May 2012

Accepted 24 May 2012

#### Keywords:

Brittany

Equivalent connected area

Hedgerows

Similarity

Spatial autocorrelation

Stationarity

### ABSTRACT

Under the current context of global change that largely threatens overall biodiversity in increasingly fragmented landscapes, more insights are needed into the drivers of biological connectivity between communities (i.e. the flow of species among a set of local communities responding to landscape structure). This study aims at estimating an indicator of regional biological connectivity of semi-natural grasslands from the expected correlation between the degree of community assemblage (i.e. composition similarity) and landscape features directly related to dispersal among local communities. Large-scale plant distributions characterizing semi-natural grassland communities were gathered from the atlas of Brittany flora (NW France; UTM grid of 10 km × 10 km). The analysed variables were computed considering the focal UTM square and its immediate neighbours, and the modelling encompassed different regression techniques accounting for spatial autocorrelation [Simultaneous Autoregressive (SAR) error models] and non-stationarity [Geographically Weighted Regressions (GWR)].

The degree of community assemblage allocated to biological connectivity was 10.4% (adjusted- $R^2$ ); it was mainly correlated to decreasing hedgerow length and secondly to increasing structural connectivity of semi-natural grasslands once spatial autocorrelation was accounted for. The estimation of the indicator of biological connectivity ( $0.05 \pm 0.01$  from the SAR models) were improved when considering non-stationarity issues, particularly for the Eastern part of Brittany (up to 0.12 in terms of biological connectivity). Overall, the proposed indicator and estimation methodology represent a step ahead in connectivity analysis at the community level, potentially relevant in the detection of hotspots of biological connectivity which can help buffer current large-scale biodiversity threats due to global change.

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### 1. Introduction

Interactions between climate change and other components of global change such as land-use changes are expected to have strong impacts on the structure of communities (Sala et al., 2000; Thomas et al., 2004). Of the several interplaying processes of global change, land-use change (e.g. agricultural intensification, land abandonment, urbanization) is considered to be one of the main causes of loss, fragmentation and deterioration of many terrestrial ecosystems (e.g. Benton et al., 2003; Eriksson et al., 2002; Sala et al., 2000). In this line, the relevance of landscape connectivity for biodiversity conservation in fragmented landscapes is widely acknowledged

(Kindlmann and Burel, 2008), since it modulates the capacity of movement of organisms among patches (Taylor et al., 1993). Landscape connectivity has also been pointed out as fundamental for species' and ecosystems' adaptation to climate change (Heller and Zavaleta, 2009), potentially allowing species to better face range changes associated with climate change (Opdam and Wascher, 2004).

Given the contemporary and expected global crisis of biodiversity, focusing on community assemblages will be key to preserve as much biodiversity as possible and ultimately to guarantee ecosystem functioning. Dispersal is recognized as a key ecological process on community assemblages, largely dependent on landscape connectivity (Kadoya, 2009). In this sense, a set of local communities that are linked by the dispersal of individuals (or species) forms a metacommunity (Kadoya, 2009; Leibold et al., 2004). We hypothesized that assessing the degree of community assemblages and determining which landscape features are behind it could provide more insights into the species flow or exchange (henceforth called biological connectivity in this study) and, therefore, help

\* Corresponding author at: Forest Sciences Center of Catalonia, Crta. Sant Llorenç de Morunys, km 2, 25280 Solsona, Spain. Tel.: +34 973 48 17 52; fax: +34 973 48 13 92.

E-mail addresses: [assu.gil@ctfc.cat](mailto:assu.gil@ctfc.cat) (A. Gil-Tena), [remi.lecerf@avignon.inra.fr](mailto:remi.lecerf@avignon.inra.fr) (R. Lecerf), [aude.ernoult@univ-rennes1.fr](mailto:aude.ernoult@univ-rennes1.fr) (A. Ernoult).

manage and preserve fragmented habitats. In this study we propose a modelling approach to estimate community assemblages related to landscape heterogeneity, taking advantage of the different approaches for measuring beta diversity in ecology [i.e. the variation in species composition among sites in a geographic area reviewed in Legendre et al. (2005)] and the most recent advances in quantitative landscape ecology such as network connectivity analysis (see Saura et al., 2011). Whittaker (1972) proposed one single metric that averaged composition dissimilarities among sites and in this line a pair-wise approach was used in macroecological studies to compute beta diversity for individual sites, averaging community composition dissimilarity from a focal site and all the remaining neighbouring sites at a given spatial scale and leaving out species richness gradients or nestedness (Gaston et al., 2007; Lennon et al., 2001; Melo et al., 2009). Beta diversity depends on multiple factors such as dispersal constraints and abiotic factors (e.g. environmental heterogeneity and management) (see Melo et al., 2009 for a review). Analogously, assessing the influence of the landscape features impacting dispersal on community similarity will allow estimating a proxy of biological connectivity at the community level (McRae et al., 2008).

Semi-natural grasslands are a clear example of increased fragmented habitats due to modern agriculture and the abandonment of traditional activities (Eriksson et al., 2002; Lindborg et al., 2008). These habitats are characterized by a high biodiversity and a high conservation value, since they harbour very rich communities of plants, some of them very rare (Critchley et al., 2004; Öster et al., 2009). Research on semi-natural grasslands has mainly focused on studying species richness (Reitalu et al., 2009). In many of these studies, present and past landscape structure and management have been shown to influence semi-natural grassland alpha diversity (e.g. Ernoult et al., 2006; Reitalu et al., 2009, 2010). However, the consequences of grassland fragmentation are not restricted to species gains or losses. The decrease in species flows among habitat patches in these fragmented landscapes is also impacting grassland communities (Soons and Heil, 2002) and consequently the plant communities restricted to these habitats have increasing extinction probabilities (Krauss et al., 2010). Biological connectivity is not often considered due to the difficulty in quantifying this ecological dimension, although it is essential to take it into account in order to understand current grassland community functioning.

Under the current changing context there is also an increasing need to apply management practices encompassing large regions, particularly when considering that many management and conservation policies with far-reaching consequences for local biodiversity are determined centrally by governmental authorities. Nevertheless, even a regional management perspective may present a challenge when making inferences from models characterizing ecological processes that encompass large spatial extents (Fortin and Dale, 2005). Therefore, spatial non-stationarity should always be considered in order to avoid incorrect inferences that may not apply to the whole study region (Wagner and Fortin, 2005).

This study aims at estimating an indicator of regional biological connectivity of semi-natural grasslands from the expected correlation between the degree of community assemblage (i.e. similarity) and landscape features related to dispersal. For this purpose, large-scale plant distributions in Brittany (NW France) were gathered from atlas data (10 km × 10 km). Due to the large size of the sampling extent considered, we anticipate that some of the determined relationships will not be stationary and, therefore, our estimates about biological connectivity will not be equally valid for the entire study area. Consequently, our modelling approach accounted for spatial non-stationarity besides considering spatial autocorrelation in order to minimize pockets of deviant residuals.

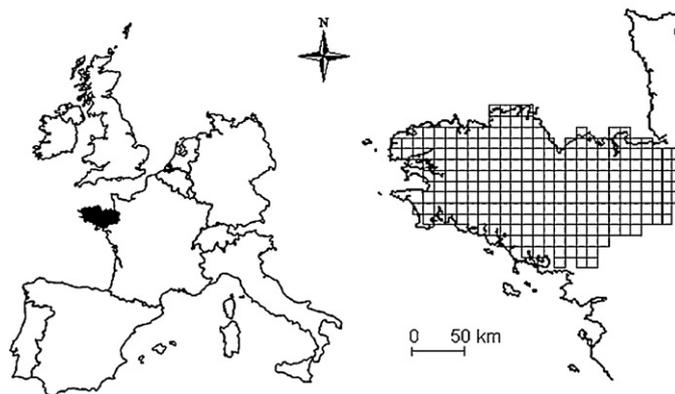


Fig. 1. Geographic location of the study area (Brittany, NW France) (left) and representation of the sampling units (248 10 km × 10 km UTM squares) (right).

## 2. Materials and methods

### 2.1. Study area and dataset

The study was carried out in Brittany (about 27,200 km<sup>2</sup>), a region located in north-western France (Fig. 1). The climate is temperate oceanic and strongly influenced by Atlantic depressions. The agricultural context of the region is dairy-cattle farming based on a gradient of intensive cereal/maize fields, managed and semi-natural grasslands and forests. The characteristic “*Bocage*” landscape of this region is composed of grasslands surrounded by a well-developed hedgerow network. This typical landscape has been in regression because of the increasing agricultural intensification which has favoured more open landscapes dominated by crops. In Brittany, about 70% of semi-natural grasslands have disappeared (Agreste Bretagne, 2009). The decrease in the semi-natural grassland area as well as in its structural connectivity has induced the regression of many plant species, particularly those most specialist of this habitat.

To measure the degree of community assemblage of semi-natural grasslands, we used data from the Atlas of Brittany Flora, a survey conducted between 1985 and 2004 by volunteers. The presence of plants was recorded in Universal Transverse Mercator (UTM) squares throughout Brittany at the 10 km × 10 km spatial resolution. From the regional species pool, we selected species that characterize the plant community of semi-natural grasslands (*Bromion racemosi*, *Ranunculo repentis*–*Agropyron repentis*, *Arrhenatherion elatioris* and *Cynosorion cristati* grasslands), explicitly excluding species that can be frequently found in other non-grassland habitats. This selection was based on representative literature of the regional flora under study (Bournérias et al., 2001; Lambinon et al., 2004) while taking into account the criteria of an expert botanist in the region. A total of 35 species were selected (Appendix A), which minimized the effect on semi-natural grassland community assemblage of environmental and management factors not linked to this type of habitat.

A regional land-use map was reconstructed by using image time series from the Moderate Resolution Imaging Spectroradiometer (MODIS; 250 m × 250 m). We considered MODIS imagery from 9 consecutive summer seasons (2000–2008), the final result being the statistical mode of the nine time series (Lecerf et al., 2005, 2008). Seven categories of land-use were identified: crops, semi-natural grasslands, managed grasslands, forests, urban areas, moors and heathlands and water. The hedgerow network was also identified from the vector geographic database BDTopo<sup>®</sup> (2003–2006) produced by the French National Geographic Institute.

A total of 248 UTM 10 km × 10 km squares were selected for subsequent analysis because ≥10% of their surface was occupied by land and they were entirely situated within the administrative boundaries of Brittany. The land-use map, hedgerow network and plant data were stored on ArcGIS version 9.3 (ESRI Inc.: 1999–2005).

## 2.2. Measuring the degree of community assemblage

We considered a similarity measure ( $S$ ) from spatial turnover (dissimilarity) analysis often applied in macroecology (e.g. Gaston et al., 2007; Lennon et al., 2001; Melo et al., 2009). Measures of spatial turnover can be derived from three matching/mismatching components: continuity ( $a$ ; the total number of species shared by two areas), gain ( $b$ ; the number of species present in the other area but not in the focal one) and loss ( $c$ ; the number of species present in the focal area but absent from the other one) (Gaston et al., 2007). For this study, we considered the modified Simpson's index of beta diversity [ $a$  dissimilarity measure,  $D(S = 1 - D)$ ], which quantifies the relative magnitude of the species gains and losses [ $\min(b, c)/(\min(b, c) + a)$ ] (Lennon et al., 2001). This measure allows us to determine true differences in species composition among sites, separating the influence on species composition due to local richness gradients (i.e. nestedness). Based on Koleff et al. (2003), we computed a dissimilarity matrix in R (<http://www.r-project.org>) by means of the “betadiver” function in the “vegan” library. For each UTM square we averaged similarity values ( $1 - D$ ) from comparison with its  $n$  (a maximum of eight) immediate neighbours (Appendix B).

## 2.3. Descriptors of landscape structure

Landscape structure was characterized for semi-natural grasslands, managed grasslands, crops, forests and hedgerows, which represent the main land-uses in the region with a potential effect on community assemblages of semi-natural grasslands. Correspondingly to the community assemblage metric (i.e. similarity), the landscape descriptors were measured considering the focal UTM square and its immediate neighbours (see also Gaston et al., 2007; Melo et al., 2009). Therefore, further statistical analysis explicitly considered the number of different neighbours per UTM square (Fig. 1).

Land-use structural connectivity was computed through a recent proposed habitat availability (reachability) metric based on graph theory that simultaneously accounted for inter- and intra-patch connectivity, using the software Conefor Sensinode 2.6 (Saura and Torné, 2009; available at <http://www.conefor.org>). The measure of structural connectivity was the Equivalent Connected Area (ECA, Saura et al., 2011), which is based on the Probability of Connectivity (PC; Saura and Pascual-Hortal, 2007) and defined as the attribute of a single habitat patch (maximally connected) that would provide the same value of the PC than the actual habitat pattern in the landscape. PC is defined as the probability that two points randomly placed within the landscape fall into habitat areas that are reachable from each other (interconnected) given a set of  $n$  habitat patches and the links (direct connections) among them.

$$PC = \frac{\sum_{i=1}^n \sum_{j=1}^n a_i a_j p_{ij}^*}{A_L^2}$$

where  $a_i$  and  $a_j$  are the attributes of the habitat patches.  $A_L$  is the maximum landscape attribute. The product probability of a path (where a path is a sequence of patches in which no patch is visited more than once) is the product of all the values of  $p_{ij}$  (probability of direct dispersal) for all the links in the path.  $p_{ij}^*$  is the maximum product probability of all the possible paths between patches  $i$  and  $j$  (including direct dispersal between the two patches). If patches  $i$

and  $j$  are distant enough or have a direct weak connection and the best path comprises several steps through intermediate stepping stone patches, then  $p_{ij}^* > p_{ij}$ . When two patches are completely isolated from each other, either by being too distant or by the existence of a land cover impeding the movement between both patches (e.g. a road), then  $p_{ij}^* = 0$ . When  $i = j$  then  $p_{ij}^* = 1$ , since it is certain that a patch can be reached from itself, which is related to the habitat availability concept that applies for PC, in which a patch itself is considered as a space where connectivity exists. The final choice for computing ECA was because it does not depend on  $A_L$ , which in some cases may be arbitrary, and therefore, it has the same units as the patch attributes [i.e. land-use area (km<sup>2</sup>) in this study; Saura et al., 2011].

In this case, the dispersal probabilities  $p_{ij}$  were given by a negative exponential as a function of interpatch edge-to-edge distance (Bunn et al., 2000):

$$p_{ij} = e^{-kd_{ij}}$$

where  $d_{ij}$  is the edge-to-edge interpatch distance (m) and  $k$  is a constant. For this study, we set as the maximum dispersal distance ( $p = 0.01$ ; Saura and Pascual-Hortal, 2008) the distance from edge-to-edge of an eight-neighbourhood polygon of UTM squares (i.e. 42.4 km).

For each sampling unit (UTM square), hedgerow length (km) was calculated as the sum at the focal square plus that of its respective immediate neighbours. Landscape structure metrics were standardized to zero means and unit variances in order to eliminate the effect of differences in the measurement scale in subsequent analyses.

## 2.4. Modelling approach to estimate an indicator of biological connectivity

The indicator of biological connectivity was obtained through regressing semi-natural grassland similarity with the variables of landscape structure. If significant predictors of semi-natural grassland similarity are detected, the model estimates for each sampling unit once subtracted the intercept of the adjusted equation will depict the value of the biological connectivity indicator. The regressions encompassed Ordinary Least Squares (OLS) and Simultaneous Autoregressive (SAR) error modelling (see also Melo et al., 2009). A backward step-wise OLS model selection was performed to adjust the final OLS model; the most complex potential OLS model included all the explanatory variables (ECA of semi-natural grasslands, ECA of managed grasslands, ECA of crops, ECA of forest and hedgerow length) and the number of neighbours. We also checked that variance inflation factors in the OLS models were under the desired threshold of 10, which indicates the absence of strong linear dependencies among these variables.

After fitting the OLS model, we explicitly considered spatial autocorrelation in the modelling in order to prevent biased estimates and incorrect model specifications (Dormann et al., 2007). If a significant predictor ( $p \leq 0.05$ ) of the OLS model was not more significant in the SAR model, then it was discarded for estimating the biological connectivity indicator according to the fitted SAR equation. According to Kissling and Carl (2008), the SAR error model takes the form

$$Y = X\beta + \lambda Wu + e$$

where  $\lambda Wu$  represents the spatial structure ( $\lambda W$ ) in the spatially dependent error term ( $u$ ).  $\lambda$  is the spatial autoregression coefficient,  $W$  is the spatial weights matrix,  $\beta$  is a vector representing the slopes associated with the explanatory variables in the original predictor matrix  $X$ , and  $e$  represents the (spatially) independent errors. The neighbourhood relationship was expressed as a row-standardized

**Table 1**

Landscape structure descriptors behind biological connectivity of semi-natural grasslands according to the OLS and SAR models and spatial variability assessment of the studied relationships through GWR.

	OLS		SAR		GWR
	Regression coefficient	p-Value	Regression coefficient	p-Value	Spatial variability
Intercept	0.866		0.878		*
Number of neighbours	0.009	<0.001	0.007	<0.001	**
Hedgerow length	−0.016	<0.001	−0.012	0.001	**
ECA of SN grasslands	0.006	0.032	0.006	0.044	n/s

n/s, lack of spatial variability.

\* Spatial variability was significant at  $p < 0.01$ .

\*\* Spatial variability was significant at  $p < 0.01$ .

$n \times n$  matrix ( $W$ ) with elements ( $w_{ij}$ ) representing a measure of the connection between sampling units  $i$  and  $j$ . The inverse of the geographic distances ( $1/d_{ij}^\alpha$ ) among sampling units was used to define the spatial relationship in order to minimize spatially autocorrelated model residuals (i.e. spatially modelled component of variation not considered by the independent variables). In this study,  $\alpha$  was set to 1 since our particular focus was on the factors behind the similarity aspect related to biological connectivity (e.g. landscape structure) and not on other non-considered factors driving community assemblages (e.g. environment). The SAR modelling, the Moran's  $I$  coefficients of the OLS and SAR model residuals and the model assumptions' checking were performed using the software of Spatial Analysis in Macroecology (SAM) ver. 4.0 (Rangel et al., 2010; available at <http://www.ecoevol.ufg.br/sam/>).

### 2.5. Detection of spatial non-stationarity

To detect if the estimation of the biological connectivity indicator was based on stationary relationships among semi-natural grassland similarity and landscape structure, local Geographically Weighted Regressions (GWR) were performed including each of the significant ( $p \leq 0.05$ ) variables in the SAR model, apart from the number of neighbours. According to Fotheringham et al. (2002), the GWR model takes the form

$$Y = \beta_0(u_i, v_i) + \sum_k \beta_k(u_i, v_i) x_{ik} + e_i$$

where  $(u_i, v_i)$  denotes the coordinates of the  $i$ th point in space and  $\beta_k(u_i, v_i)$  is a realization of the continuous function  $\beta_k(u, v)$  at point  $i$ . Therefore, GWR provides local estimates of the predictors and their significance at each regression point and may allow revisiting and refining the indicator of biological connectivity in case significant spatial variability in the considered relationships is detected.

In the GWR modelling, the distance (bandwidth) within which surrounding observations are included in the analysis can be defined according to a fixed Gaussian kernel, or by using an adaptive kernel that alters the inclusion distance to encompass a defined number of data points. The influence of the observations is weighted with a distance-decay-function from the location being predicted (see Fotheringham et al., 2002 for an extensive mathematical overview). In this study, bandwidth selection matched the spatial range of semi-natural grassland similarity (Guo et al., 2008) which was based on Moran's  $I$  zone of influence (Fortin and Dale, 2005). The lag distance defined to calculate Moran's  $I$  coefficients of spatial autocorrelation was 15 km (i.e. a maximum of eight neighbours). The bandwidth was determined according to the distance at which the value of spatial autocorrelation crosses the expected value  $E(I)$  for the absence of spatial autocorrelation, indicating the spatial range of the studied pattern (i.e. bandwidth = 75 km). GWR analyses were performed in the GWR 3.0 software (Charlton et al., 2003), selecting a Monte Carlo significance testing procedure to examine the significance of the spatial variability in the local parameter estimates (Fotheringham et al., 2002). In order

to assess the parameter significance in GWR and to avoid potential problems caused by multiple hypothesis tests, we adjusted the family-wise error rate (i.e.  $p = 0.05$ ) dividing it by the effective number of parameters (Dr. Martin Charlton, personal communication; Martín-Queller et al., 2011).

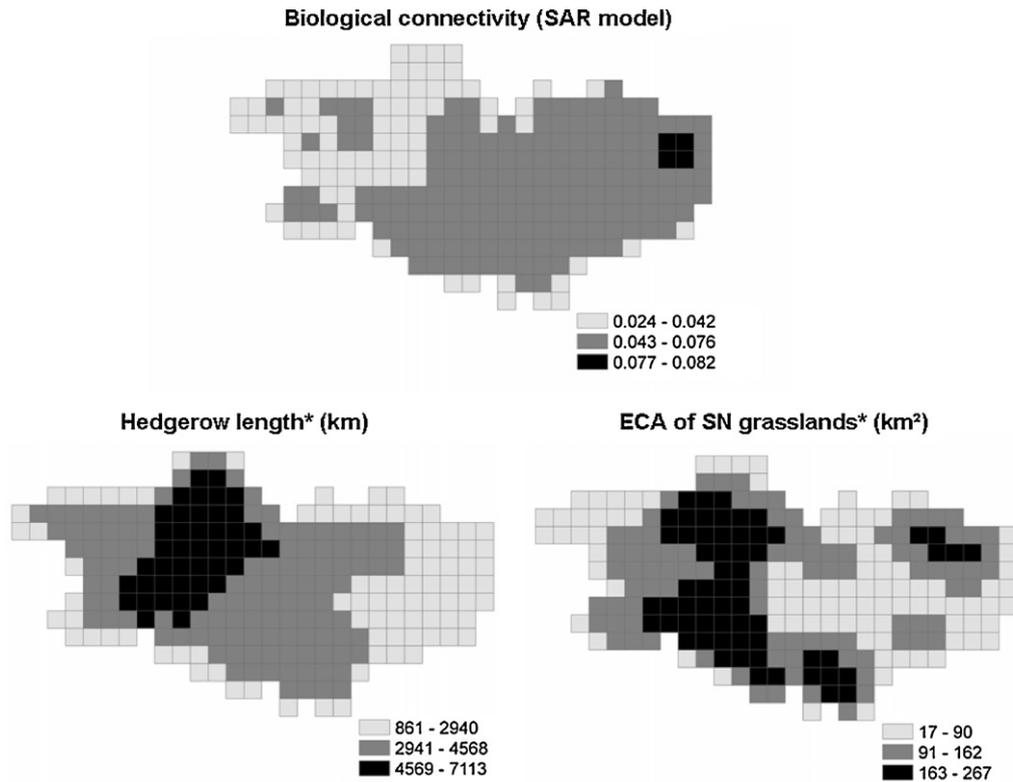
### 3. Results

The OLS model considering the whole extent of Brittany explained 10.4% of similarity in terms of adjusted- $R^2$  ( $p < 0.001$ ; Table 1), which according to our assumptions corresponded to the degree of community assemblage allocated to biological connectivity. This model showed that after considering the number of neighbours ( $p < 0.001$ ), biological connectivity of semi-natural grasslands was negatively associated with the neighbourhood hedgerow length ( $p < 0.001$ ) and positively with the neighbourhood structural connectivity (ECA) of semi-natural grasslands ( $p = 0.032$ ). When explicitly considering spatial autocorrelation issues in the modelling through the SAR models (Table 1), the prediction capacity of hedgerow length and structural connectivity of semi-natural grasslands was confirmed as well as their relative importance in terms of standardized regression coefficients and sign (the negative influence of hedgerow length was stronger than the positive one of ECA of semi-natural grasslands). For each estimate of the SAR model, we obtained the indicator of semi-natural grassland biological connectivity once subtracted the intercept value of the SAR model equation (see Table 1 and Fig. 2). The values of the indicator of biological connectivity ranged from 0.023 to 0.082 ( $0.048 \pm 0.012$ ), and were higher eastwards (see Fig. 2). This increasing pattern fairly matched the decreasing eastern trend of hedgerow length and semi-natural grassland structural connectivity (Fig. 2).

The GWR modelling indicated the presence of non-stationarity in the influence of hedgerow length (see Table 1). The new local GWR models refined our results in terms of biological connectivity, obtaining greater estimations for the Eastern part of Brittany than in the SAR modelling (up to 0.121; see Fig. 3a). Accordingly, the negative relationship between hedgerow length and biological connectivity was stronger eastwards (Fig. 3b). For a few sampling units in Western Brittany, it was impossible to estimate the biological connectivity indicator of semi-natural grasslands because the values were close to zero but negative (Fig. 3a).

### 4. Discussion

This study proposes a modelling approach to estimate biological connectivity in terms of species flows as a function of the landscape structure directly related to species dispersal among local communities. Semi-natural grasslands are increasingly fragmented due to global change processes and more insights are needed into community functioning beyond alpha diversity. Hedgerow length and structural connectivity of semi-natural grasslands fairly matched



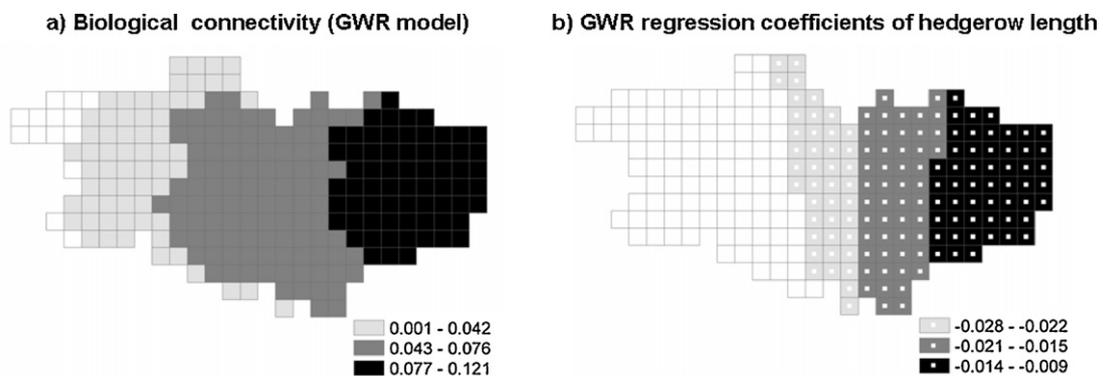
**Fig. 2.** Estimates of the biological connectivity indicator of semi-natural (SN) grasslands according to the SAR modelling (top) and the significant landscape structure descriptors ( $p \leq 0.05$ ) in the OLS and SAR model (bottom). The asterisks indicate that the landscape structure descriptors were calculated including the UTM square neighbourhood (a maximum of eight).

the degree of community assemblages, allowing the depiction of biological connectivity at the regional scale while taking into account the influence of non-stationary relationships and spatial autocorrelation.

4.1. What is new in the proposed biological connectivity indicator?

Landscape connectivity has been traditionally distinguished according to its structural and functional aspect (Kindlmann and Burel, 2008; Taylor et al., 2006). Both types of connectivity implicitly account for landscape elements and the main difference among them resides in the consideration of species' ecological requirements in the latter such as minimum area, dispersal capacities or effective movement. Although the structural aspect of connectivity

is relatively easy to analyse and less data demanding, increasing attention is given to the need to consider a more functional aspect of connectivity. Recent advances in network connectivity analysis through graph theory have increased and improved the quantification of functional connectivity (e.g. Baranyi et al., 2011; Galpern et al., 2011; McRae et al., 2008; Saura et al., 2011; Saura and Pascual-Hortal, 2007; Watts and Handley, 2010). The proposed indicator of biological connectivity represents a step ahead in connectivity analysis at the community level, estimating the species flows from the degree of community assemblage and its response to landscape heterogeneity affecting dispersal, thus feeding on either functional or structural connectivity. Similarities to this indicator of biological connectivity measures can be found in the promising studies of gene divergence according to habitat heterogeneity (e.g. McRae, 2006; McRae et al., 2008).



**Fig. 3.** (a) Estimates of the biological connectivity indicator of semi-natural grasslands according to the modelling approach considering non-stationarity (GWR, being the bandwidth = 75 km). In the case of 14 UTM squares the indicator of biological connectivity could not be estimated since it was negative (hollow squares). (b) Significant GWR regression coefficients of hedgerow length were also represented (filled squares); significance was set after multiple testing corrections (see Section 2.5).

In addition, our indicator of biological connectivity deals with the similarity aspect explicitly boosted by dispersal at the community level. Therefore, this indicator can also complement the existing assessment of community assemblages (e.g. Gaston et al., 2007; Melo et al., 2009), thus being potentially relevant in the detection of hotspots of biological connectivity which can help buffer current large-scale biodiversity threats due to global change.

#### 4.2. Drivers of biological connectivity of semi-natural grasslands

To understand how landscape structure determines biological connectivity of semi-natural grasslands, it is essential to focus on long-distance dispersal since it plays a major role in determining the species flow between local communities within a meta-community (Levine and Murrell, 2003; Nathan et al., 2008). Thus, at a large scale, this type of dispersal determines the persistence of communities in fragmented landscapes (Trakhtenbrot et al., 2005). However, its quantification is difficult, so few studies have worked on it (Nathan et al., 2001, 2003). The plant response to landscape fragmentation varies according to the long-distance dispersal vector (Jordano et al., 2007; Spiegel and Nathan, 2007). In our study, the selected species were characteristic of semi-natural grasslands and predominantly dispersed over long distances by wind (Ozinga et al., 2004). This dispersal vector may be important for regional survival (Hodkinson and Thompson, 1997) but it is almost impossible to measure (Bullock and Clarke, 2000; Cain et al., 2000). In addition, non-standard vectors (Higgins et al., 2003) are also well known to disperse grassland species over long distances such as in the case of farm machinery (Bullock and Nathan, 2008) or livestock (Bullock et al., 2006; Manzano and Malo, 2006). At local scales (i.e. within farms) but also at larger scales, the farming activities have many effects on the dispersal of grassland species (Wichmann et al., 2009).

According to our results, the closed landscape characterized by a long hedgerow network seems to provide unfavourable conditions for long-distance dispersal (decreased biological connectivity), especially by wind in this case, due to the presence of obstacles that prevent the movements of seeds (Nathan et al., 2008). Ozinga et al. (2004) also showed a clear positive correlation between long-distance dispersal and an index of landscape openness. The vegetation structure of a site and its spatial organization affect the wind speed and its direction, modifying the dispersal capacity of plant communities (Bullock et al., 2003; Clark, 1998). In fact, grasslands may promote dispersal by wind because of their low vegetation (Bullock et al., 2003). Therefore, an increase in grassland structural connectivity can effectively improve long-distance dispersal by creating corridors for seeds besides boosting dispersal by non-standard vectors. Nevertheless, this effect on biological connectivity of semi-natural grasslands in Brittany was weak compared with that of hedgerow length.

Anyway, our results did not contradict the studies that underlined the key role of hedgerows for maintaining or increasing grassland diversity. These studies have considered the whole community of grassland species including forest species (Ernault et al., 2006; Le Viol et al., 2008). For forest species, hedgerows are actually corridors and represent a source of species for grasslands (Ernault and Alard, 2011; Jamoneau et al., 2011). Conversely, in our study these linear landscape elements did not increase the biological connectivity for the considered grassland species because they were unsuitable for seedling establishment and acted as barriers for the migration of wind-dispersed plants (Van Dorp et al., 1997).

#### 4.3. Regional analysis and drawbacks

Due to the importance of semi-natural habitats for maintaining and enhancing biodiversity, Sullivan et al. (2011) recently called

for reliable yet easy-to-use methods for accurately identifying priority areas for conservation actions and monitoring biodiversity on a large spatial scale while considering spatial issues. Considering non-stationarity in the modelling allowed us to better estimate biological connectivity at the regional scale, particularly in Eastern Brittany. This result is probably due to the different landscape spatial grains in Eastern and Western Brittany and the fact that the size of the sampling units (i.e. 10 km × 10 km) better matched the Eastern landscape grain. Eastern Brittany is a quite homogeneous zone dominated by farmlands devoted to intensive agricultural practices (maize and cereal being the most widespread crops) whereas the Western part is made up of a mosaic of different types of landscapes (grasslands with a dense hedgerow network, forests and moors) with a more extensive management.

We acknowledge that our indicator of biological connectivity is based on distribution data (i.e. species presence according to an atlas), which implies that colonization success is inherently taken into account. Species flow among local communities implies the movement of species through dispersal but in fact if the species were not able to colonize then they cannot be considered in our biological connectivity indicator. At the community level it is difficult to only focus on movement for the many caveats related to the dispersal assessment (see Section 4.2) and because of the large number of species involved (see also McRae et al., 2008). In addition, the estimated biological connectivity from current distribution data can partially rely on past species flow potential no longer available, as underlined in recent studies showing a time lag in semi-natural grassland community response to landscape changes (e.g. Ernault et al., 2006; Helm et al., 2006). In this sense, the availability of the Atlas of Brittany Flora allowed to test the approach presented here for assessing biological connectivity at the regional scale despite the former biases and the extra ones related to differences in sampling effort, which are inherent to this type of monitoring programs. Historical data often are not available with enough detail either (Johansson et al., 2008), so further efforts will be needed in order to consider them when analysing fragmented habitats at large scales, such as those encompassing entire regions (e.g. semi-natural grasslands in Brittany).

## 5. Conclusions and further research

The modelling approach proposed here accounting for spatial autocorrelation and non-stationarity allowed us to estimate the indicator of biological connectivity at the regional scale through disentangling the landscape factors related to dispersal behind the degree of community assemblages (i.e. similarity). The proposed indicator and estimation methodology represent a step ahead in connectivity analysis at the community level that could be valuable in many ecological fields (e.g. landscape ecology, community functioning, biological conservation). Further research concerning the indicator of biological connectivity will focus on (1) analysing finer spatial scales than the one utilized here in terms of both grain and extent, (2) assessing its comparability with other proposed methodologies (e.g. McRae et al., 2008), (3) explicitly considering in the landscape structure analysis community species traits such as dispersal distances, habitat requirements (e.g. matrix heterogeneity) or historical data when necessary (e.g. semi-natural grasslands), and (4) testing its relevance in the detection of hotspots of biological connectivity. This will help buffer current biodiversity threats in a changing world, adding an extra value to the application of this biological connectivity indicator.

## Acknowledgements

B. Clement, S. Croci and J. Nabucet helped select the species under study and calculate the landscape descriptors. F. Burel, M. De

Cáceres, M.J. Fortin, M.E. Grillet, E. Petit, S. Saura and two anonymous reviewers provided valuable comments on some manuscript ideas and data analysis. Data from the Atlas of Brittany Flora were provided by the *Conservatoire Botanique National de Brest*. A. Gil-Tena was funded by the MEC (*Programa Nacional de Movilidad de RRHH, Plan Nacional de I-D+i 2008–2011*).

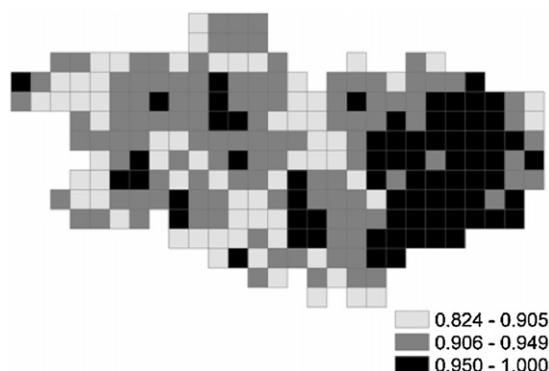
## Appendix A.

List of 35 species characterizing semi-natural grassland vegetation in Brittany.

Semi-natural grassland species	
<i>Achillea ptarmica</i>	<i>Hypericum perforatum</i>
<i>Agrimonia procera</i>	<i>Juncus acutiflorus</i>
<i>Allium vineale</i>	<i>Lathyrus pratensis</i>
<i>Anthemis nobilis</i>	<i>Lotus uliginosus</i>
<i>Anthoxanthum odoratum</i>	<i>Lychnis flos-cuculi</i>
<i>Arrhenatherum elatius</i>	<i>Oenanthe lachenalii</i>
<i>Avenula pubescens</i>	<i>Oenanthe peucedanifolia</i>
<i>Briza media</i>	<i>Oenanthe pimpinelloides</i>
<i>Bromus racemosus</i>	<i>Oenanthe silaifolia</i>
<i>Carum verticillatum</i>	<i>Orchis palustris</i>
<i>Centaurea gr. nigra</i>	<i>Origanum vulgare</i>
<i>Centaurea gr. pratensis</i>	<i>Peucedanum lancifolium</i>
<i>Cerastium fontanum</i>	<i>Polygala vulgaris</i>
<i>Cynosurus cristatus</i>	<i>Ranunculus acris</i>
<i>Festuca arundinacea</i>	<i>Ranunculus bulbosus</i>
<i>Gaudinia fragilis</i>	<i>Rhinanthus minor</i>
<i>Heracleum sphondylium</i>	<i>Stellaria graminea</i>
<i>Hieracium pilosella</i>	

## Appendix B.

Semi-natural grassland similarity ( $0.93 \pm 0.04$ ).



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