Unveiling the ghosts of landscapes past: changes in landscape connectivity over the last decades are still shaping current woodland plant assemblages

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Abstract

1. In ever-changing landscapes, there is increasing evidence that current plant assemblages are shaped by the temporal dynamics of landscape connectivity. So far, attempts to take the temporal dynamics of connectivity into account have only focused on the degree of connectivity at one or several moments in time, but neglected the cumulative effects of temporal changes in connectivity.

2. We investigated the effects of the temporal dynamics of landscape connectivity (*i.e.*, the degree of connectivity, the magnitude and the variability of its temporal changes) over the last seven decades on current woodland plant herbaceous assemblages. The assemblages were described using a taxonomic approach combined with a functional approach based on four traits linked to the colonisation capacity of plant species.

3. The taxonomic diversity of current woodland assemblages did not respond to the degree of connectivity nor to the magnitude and the variability of temporal changes, but the mean and/or the diversity of trait values linked to their colonisation capacity did. Responses, mainly driven by generalist species, were modulated by the type of connectivity trend experienced by woodlands. In woodlands experiencing an upward connectivity trend, high magnitude of temporal changes in connectivity increased the abundance of species that invest mostly in sexual reproduction at the expense of vegetative reproduction whereas the degree of connectivity and the variability of its temporal changes had no effect. In woodlands experiencing a downward connectivity trend, the diversity of seed mass values was independent on the magnitude but decreased with the variability of temporal changes, and increased with the degree of connectivity.

4. *Synthesis*. Overall, we show that, besides the degree of connectivity, the cumulative effects of decades of changes in connectivity shape woodland plant community assembly by

selecting for particular trait values in plant species. This study opens new perspectives for integrating the temporal dynamics of landscape connectivity in the theoretical framework of plant assembly rules. It should also be considered in the development of management strategies to restore and maintain landscape connectivity.

Résumé

1. Dans des paysages en constante évolution, il existe de plus en plus de preuves que les communautés végétales actuelles sont influencées par la dynamique temporelle de connectivité paysagère. Jusqu'à présent, les tentatives de prise en compte de cette dynamique temporelle de connectivité se sont seulement concentrées sur le degré de connectivité à un ou à plusieurs moments dans le temps, mais ont négligé les effets cumulés des changements temporels de connectivité.

2. Nous avons étudié les effets de la dynamique temporelle de connectivité paysagère (*i.e.*, le degré de connectivité, l'intensité et la variabilité des changements temporels) au cours des sept dernières décennies sur les communautés herbacées boisées actuelles. Les communautés ont été décrites en utilisant une approche taxonomique combinée à une approche fonctionnelle reposant sur quatre traits liés aux capacités de colonisation des espèces végétales.

3. La diversité taxonomique des communautés boisées actuelles n'a pas répondu au degré de connectivité ni à l'intensité et à la variabilité des changements temporels, contrairement à la moyenne et/ou la diversité des valeurs de traits liés à leur capacité de colonisation. Les réponses, principalement déterminées par les espèces généralistes, étaient modulées par le type de tendance de connectivité auxquels les bois ont été soumis. Dans les bois présentant une tendance de connectivité ascendante, une forte intensité des changements temporels de connectivité a augmenté l'abondance des espèces qui investissent principalement dans la reproduction sexuée au détriment de la reproduction végétative, tandis que le degré de connectivité et la variabilité de ses changements temporels n'ont eu aucun effet. Dans les bois présentant une tendance de connectivité descendante, la diversité des valeurs de masse des graines était indépendante de l'intensité mais diminuait avec la variabilité des changements temporels et augmentait avec le degré de connectivité.

4. *Synthèse*. Dans l'ensemble, nous montrons qu'en plus du degré de connectivité, les effets cumulés de décennies de changements de connectivité façonnent l'assemblages des communautés végétales, en sélectionnant des valeurs de traits particulières chez les espèces végétales. Cette étude ouvre de nouvelles perspectives pour intégrer la dynamique temporelle de connectivité paysagère dans le cadre théorique des règles d'assemblage des communautés végétales. Elle devrait également être prise en compte dans l'élaboration de stratégies de gestion visant à restaurer et à maintenir la connectivité paysagère.

Mots-clés: dynamique temporelle, modifications paysagères, règles d'assemblages des communautés végétales, traits fonctionnels, paysages agricoles

1. Introduction

Habitat fragmentation is among the main drivers of global biodiversity loss (Fletcher et al., 2018; Haddad et al., 2015) especially for plant species that are sessile and dispersal-limited (Ibáñez et al., 2014). Species inhabiting fragmented habitat patches are structured in metacommunities, *i.e.*, a set of local communities linked by the dispersal of multiple potentially interacting species (Leibold et al., 2004). Species coexistence within these local communities is driven by the relative importance of dispersal fluxes, niche selection and drift across ecological time scales (Vellend, 2010). High dispersal fluxes increase (re-)colonisation and reduce extinction rates in habitat patches. However, dispersal fluxes strongly depend on landscape connectivity, *i.e.*, the degree to which the landscape elements facilitate the dispersal of plant species (Taylor et al., 2006). Therefore, improving connectivity among habitat patches should promote plant diversity in habitat patches (Damschen et al., 2019).

In ever-changing agricultural landscapes, landscape connectivity is likely to vary over time. The concept of connectivity was integrated into metapopulation theory in the 1990s (Bascompte & Solé, 1996; Hanski, 1994, 1994; Hanski et al., 1994). Since then, authors have called for taking into account its temporal dynamics (Jennings et al., 2021; Kool et al., 2013; Uroy et al., 2021; Zeigler & Fagan, 2014). Indeed, gains or losses of landscape connectivity do not necessarily instantaneously affect plant assemblages in habitat patches but rather entail time-lagged responses over years or even decades (*e.g.*, Bagaria et al., 2019; Bommarco et al., 2014; Helm et al., 2006; Lindborg & Eriksson, 2004). So far, the temporal dynamics of connectivity is only considered by relating current plant assemblages to past connectivity. Degree of connectivity (*i.e.*, the connectivity value of the patch at a given moment in time; Fig. 1a) can be assessed at a single (*i.e.*, one time point; Bagaria et al., 2019; Bommarco et al., 2014; Helm et al., 2006) or at several moments (*i.e.*, several time points; Lindborg & Eriksson, 2004) in the past. One exception is the study of Verheyen et al. (2004). This study

analysed current species occupancy in relation to connectivity with an index incorporating patch turnover. In all the studies referred above, the cumulative effects of temporal changes in connectivity on the dispersal of species are ignored (Uroy et al., 2021). Yet, the dispersal fluxes of species among patches are likely to vary over time, following changes in patches of habitat that are suitable for the dispersal of species within the landscape. Besides the degree of connectivity itself, other components of the temporal dynamics of connectivity are thus likely to determine the ratio between the colonisation and extinction rates of species (Perry & Lee, 2019). These are the magnitude (*i.e.*, the strength at which the connectivity of the patch changes over time; Fig.1b) and the variability (*i.e.*, alternation of periods with the patch being highly connected and periods with the patch being only slightly connected; Fig. 1c) of the temporal changes in landscape connectivity. For instance, in patches experiencing an upward trend in connectivity, a high magnitude of temporal changes in connectivity is likely to increase the ratio between the colonisation and extinction rates of species. It should promote species richness, while inverse effects are expected in patches experiencing a downward trend in connectivity. Predicting the effect of the variability of temporal changes in landscape connectivity is less straightforward. The ratio between colonisation and extinction rates should decrease as low connectivity periods become more frequent and severe due to the increasing probability of extinction (Perry & Lee, 2019), thereby reducing species diversity in patches (Matias et al., 2013; Stier et al., 2019; Valanko et al., 2015).

For plants, seed production, dispersal and establishment are key processes in shaping their colonisation capacity (Eriksson, 2000) and thus, the ratio between colonisation and extinction rates. Considering variation in colonisation capacity may help to obtain better insights into the processes involved in how current plant assemblages respond to the temporal dynamics of connectivity. For instance, higher species' sensitivity to temporal changes in connectivity can be related to trait values that characterise low colonisation capacity

(Zambrano et al., 2019). It might result from a high investment in vegetative reproduction rather than in sexual reproduction (Kolb & Diekmann, 2005) with dispersal of clonal fragments occurring mainly over short distances (Starfinger & Stöcklin, 1996; Zobel et al., 2010). Higher species' sensitivity may also result from the low production of seeds (fewer seeds, Verheyen et al., 2004), the size of seeds which influences their ability to be dispersed over long distances (heavier seeds with limited-distance dispersal, Lindborg et al., 2012), and their limited success in germinating when seeds arrive in a patch (low seed germination rate, Favre-Bac, Lamberti-Raverot, et al., 2017). Thus, lower connectivity may led to lower abundance of species with low colonisation capacity, affecting the mean and reducing the diversity of involved-traits values (Zambrano et al., 2019).

The present study evaluated the effects of the temporal dynamics of landscape connectivity (*i.e.*, the degree of connectivity, the magnitude and the variability of the temporal changes in connectivity; Fig. 1) on the taxonomic diversity and on the functional structure of current woodland herbaceous assemblages. Woodland herbaceous assemblages are known to display long-lasting lagged responses to landscape changes, *i.e.*, over decades even centuries (Naaf & Kolk, 2015; Vellend et al., 2006), which makes them good candidate species to test our predictions. We analysed the effect of connectivity dynamics using landscape datasets in six time points (1952 to the present) to examine these relationships in post-agricultural woodlands experiencing upward or downward trend of connectivity. The functional structure of woodland herbaceous assemblages was evaluated using the mean and the diversity of trait values for four traits related to the colonisation capacity of plant species. We specifically tested the following hypotheses:

H1: The taxonomic diversity of herbaceous assemblages in woodlands experiencing an upward connectivity trend increases with a high degree of connectivity, a high magnitude and a low variability of temporal changes in connectivity. In woodlands experiencing a downward

connectivity trend, the taxonomic diversity increases with a high degree of connectivity, a low magnitude and a low variability of temporal changes in connectivity.

H2: Mean trait values are affected and trait diversity increases with a high degree of connectivity, a high magnitude and low variability of temporal changes in connectivity in woodlands experiencing an upward connectivity trend, because the abundance of species with trait values that confer low colonisation capacity increased. Such response is also expected in plant assemblages of woodlands experiencing a downward connectivity trend in response to a high degree of connectivity, a low magnitude and a low variability of temporal changes.

2. Materials and Methods

2.1 Study site and history of wooded habitats

This study was conducted in the Long-Term Socio-Ecological Research (LTSER) site of "Zone Atelier Armorique" (ZAAr, ca. 130km²) in Brittany, France (48°36′N, 1°32′W). The topology is flat, the soil is underlain by granitic and sandstone bedrocks and the climate is temperate oceanic. The study site is an agriculture-dominated landscape, interspersed with woodlands and a more or less dense network of hedgerows that are more or less connected to woodlands. The main crops are winter cereals (wheat and barley), maize and temporary (1 to 5 years) grasslands. The site also includes a large ancient forest in the south that was already present in the middle of the 19th century, according to the ordnance survey map ("État-major"; Dupouey et al., 2007). Most of the woodlands are recent, established on former agricultural lands (*i.e.*, post-agricultural woodlands) after the middle of the 19th century. They were originally planted with *Castanea sativa* Mill., 1768, *Fagus sylvatica* L., 1753 and *Quercus robur* L., 1753. Those species still dominate the current tree composition. Hedgerows are composed of trees including *Quercus robur* L., 1753 or *Castanea sativa* Mill., 1768 generally planted on an earthen bank (Burel et al., 1998). Hedgerows had an average width of three meters (Litza et al., 2022) suggesting that they provide a sufficient amount of shaded habitat for woodland plant species to successfully establish (Lenoir et al., 2021).

The landscape of the study site has undergone major modifications since the mid-late 1950s because of successive policies, particularly the European common agricultural policy (CAP). These policies were designed to accommodate agricultural intensification (*e.g.*, hedgerow clearing due to land reallotment) and were progressively accompanied by greening measures (*e.g.*, planting of post-agricultural woodlands and, to a lesser extent, hedgerows). The consequences of these successive policies on land cover can be traced back in the landscape datasets covering our study area. Land cover maps (ZAAr vector dataset) and the

wooded habitat cover maps (raster dataset produced by the company KERMAP, https://kermap.com/en/) were established from aerial images with a resolution of 5 m. From these landscape datasets, we selected six time points (Fig. S1a), related to the different policies implemented and available aerial imagery: 1952 (the oldest available map, hereafter referred to as the initial state of the landscape), 1974, 1985, 2000, 2006 and 2016 (the most recent available map, hereafter referred to as the current state of the landscape). Overall, these different policies resulted in a sharp decrease (ca. 61%) in hedgerow cover between 1952 and 1985, followed by a slight increase (ca. 15%) between 1985 and 2016. Over the whole period, woodland cover increased slightly (ca. 31%), whereas the mean area of woodland cover patches decreased (ca. 42%) (Fig. S1b-c).

2.2 Assessment of the temporal dynamics of landscape connectivity

2.2.1 Landscape connectivity

We used the circuit theory (McRae et al., 2008) to assess the landscape connectivity of the remaining "old" post-agricultural woodland patches (*i.e.*, patches that have been continuously wooded since 1952) for each time point (*i.e.*, 1952, 1974, 1985, 2000, 2006 and 2016). This modelling method is based on inter-patch distances. It assumes that dispersal follows random walks and includes all possible dispersal pathways between two habitat patches, depending on the resistance (*i.e.*, ecological cost) of the landscape elements to dispersal.

We detected the remaining "old" post-agricultural woodland patches on land cover maps. For each time point, woodland patches located at a distance of less than 20 m from each other, *i.e.*, the short-distance dispersal distance of plants (Howe & Smallwood, 1982), were considered as belonging to the same patch, except patches crossed by a paved road. The geographical union of these woodland patches from all the time points was computed to construct a detailed history of woodland continuity. We selected all woodland patches that

have been continuously wooded since 1952 comprising an area > 0.1 ha, this area covering, on average, at least one-tenth of the area of the woodland patch at each time point studied. A total of 255 "old" post-agricultural woodland patches that fulfilled these criteria were detected at our study site (Fig. 2a).

We assessed the dispersal distance between pairs of "old" post-agricultural woodland patches as a function of the presence of suitable habitats for the dispersal of woodland plant species, that is, wooded habitats (*i.e.*, woodlands and hedgerows), considering a habitat patch-matrix landscape model (*sensu* Brudvig et al., 2017). We did not define the presence of suitable habitats for dispersal (*i.e.*, wooded habitats) based on the environmental conditions within them. Indeed, we do not have environmental data for all of the wooded habitats within the study site to integrate these variables. We then calculated resistance maps based on wooded habitat cover maps for each time point (giving a total of six resistance maps), by classifying wooded habitats with a resistance value of 1 (*i.e.*, habitat, highly suitable for dispersal) and the matrix with a resistance value of 50 (*i.e.*, non-habitat, hardly suitable for dispersal) (Fig. 2b). The centre-to-centre distance between pairs of patches was then assessed from each resistance map as the resistance distance using the R package "gdistance" (van Etten, 2017) (Fig. 2c). As the R package "gdistance" computes resistance distance between points, we used patch centre-to-centre distances rather than edge-to-edge distances as they are easier to obtain. Given the small area of "old" post-agricultural woodland patches in our study area, the difference between these two ways of measuring distance is inconsequential (Moilanen & Nieminen, 2002).

For each time point t studied, the connectivity of each "old" post-agricultural woodland patch i (N = 255) was assessed using the "Potential Dispersal Flux" index ($PCflux_{i,t}$, Saura & Rubio, 2010). This index corresponds to the dispersal flux (Urban & Keitt, 2001) through the connections of a given woodland patch i with all other patches in the

landscapes for a time point t. It is given by: $PCflux_{i,t} = \sum_{j=1, j \neq i}^{n-1} p_{ij,t}^{*}$, where $p_{ij,t}^{*}$ is the maximum product probability of all potential paths between pairs of woodland patches, i and j, in the landscape for a time point t Saura & Pascual-Hortal, 2007). The probability of dispersal (p_{ij}, t) between pairs of woodland patches at a given time point t was modelled as a negative exponential function of the dispersal distance between woodland patches (Saura & Pascual-Hortal, 2007). We calculated the $PCflux_{i,t}$ index using a potential maximum dispersal distance of 500 m (Fig. 2d), as it is often considered to be the spatial extent at which landscape processes best predict herbaceous woodland plant species (*i.e.*, the "scale of effect", Jackson & Fahrig, 2015, *e.g.*, Bagaria et al., 2019; Petit et al., 2004; Usher et al., 1992; van Ruremonde & Kalkhoven, 1991; Vanneste et al., 2019). The potential maximum distance of 500 m was converted into resistance distance using the maximum resistance distance observed over the whole period (*i.e.*, all time points combined) between pairs of patches separated by a Euclidean distance smaller than 500 m. This "converted" potential maximum dispersal distance was then used to set the decay rate of the negative exponential function at p_{ij} = 0.01. These calculations were made using Conefor 2.6 software (Saura & Torné, 2009). $PCflux_{i,t}$ index obtained was overly correlated between each time point (Pearson's correlations, $0.82 \leq r \leq 0.98$).

2.2.2 Temporal dynamics of connectivity

The temporal dynamics of landscape connectivity of each "old" post-agricultural woodland patch over the whole study period were assessed using the connectivity indices obtained for each individual time point. In particular, the temporal dynamics of landscape connectivity was described using three components: (i) the degree of connectivity (ii) the magnitude and (iii) the variability of the temporal changes in connectivity (Fig. 1; Fig. 2e). First, the degree of connectivity of each woodland patch i was evaluated by the initial state of landscape

connectivity using the "Potential Dispersal Flux" index obtained for the first time point, 1952 ($PCflux_{i,1952}$). Since $PCflux_{i,1952}$ were overly correlated with the $PCflux_{i,t}$ of other time points t (see above), we assumed it reflects the degree of connectivity of a given woodland patch i. Second, the magnitude and the variability of the temporal changes in the connectivity of each woodland patch i were quantified by performing an ordinary least squares (OLS) regression model for each woodland patch i, with $PCflux_{i,t}$ as the dependent variable and time point t (1952, 1974, 1985, 2000, 2006 and 2016) as the independent variable. We then used the absolute value of the slope ($|slope_i|$) and the residual standard error (RSE_i) of each OLS regression model as proxies of the magnitude and the variability of the temporal changes in the connectivity of each woodland patch i, respectively. The higher the (i) $PCflux_{i,1952}$, (ii) $|slope_i|$ and (iii) RSE_i, the higher (i) the degree of connectivity (ii) the magnitude and (iii) the variability of the temporal changes in the connectivity of the woodland patch i. The sign of the slope of each OLS regression model was also extracted to obtain information about the trend of connectivity values (*i.e.*, upward or downward) to select the "old" post-agricultural woodland patches to be sampled.

2.3 Sampling design

To compare the effect of the temporal dynamics of the landscape connectivity on woodland assemblages between upward and downward trends, we selected a total of 50 woodlands to be sampled out of the 255 "old" post-agricultural woodlands in our study site. We specifically selected 20 and 24 woodlands characterised by upward and downward connectivity trends, respectively. Six woodlands remained completely isolated during the study period ($PCflux_{i,t} = 0$) and were characterised by a null trend ($PCflux_{i,1952} = 0$, $|slope_i| = 0$ and $RSE_i = 0$). Further details about the trend of connectivity experienced by each selected woodland are given in Supplementary information, Fig. S2.

The 50 selected woodlands were distributed across the study site, with a distance of at least 200 m between woodland edges. Their area (mean: 1.11 ha, range: 0.16–5.78), their dominant tree species composition, and their management regime (*i.e.*, extensively managed) were also standardised according to the typical characteristics of these woodlands in our study site. We also checked that the distribution of values of the three components of the temporal dynamics of landscape connectivity of the selected woodlands (N = 50) was consistent with those of all the "old" post-agricultural woodlands detected in our study site (N = 255; Supplementary information, Fig. S3).

Floristic surveys were conducted in the 50 woodlands from late-May to mid-June 2019. We identified each vascular herbaceous species and estimated its abundance (as percentage cover) using eight 10 m x 8 m quadrats (six quadrats for the three smallest woodlands), following the minimum recommended sampling area for woodland assemblages (Mueller-Dombois & Ellenberg, 1974). Nomenclature followed the French taxonomic register TAXREF (Gargominy et al., 2021). The species accumulation curves generated for the 50 woodlands (using Kindt's exact method in the function specaccum of the "vegan" R package, Oksanen et al., 2019) appeared to be asymptotic, suggesting that sampling effort was sufficient (Fig. S4).

These quadrats were evenly distributed within the woodland at least 5 m from the edge. The species composition and species abundance were pooled at the woodland level from the quadrats. We then weighted the total abundance of each species by the number of quadrats, to account for the disequilibrium in subsequent analyses. Woody species were not recorded due to their dependence on the initial planting composition and management regime of the woodland. In addition, woody species are probably less sensitive than herbaceous ones to the temporal dynamics of connectivity over the last seven decades owing to their longer lifespans.

The study did not require ethical approval or licences. All woodland owners gave us permission for fieldwork.

2.4 Taxonomic diversity and functional structure of woodland plant assemblages

The taxonomic diversity of each "old" post-agricultural woodland assemblage was assessed using total species richness and Piélou's evenness, using the "vegan" R package (Oksanen et al., 2019).

Four functional traits related to colonisation capacity were chosen: the number of seeds per plant, seed dry mass, seed germination rate, and type of reproduction (Table 1). We did not consider seed bank persistence nor life-span, as most woodland herbaceous plant species are perennials (89.89% of the species recorded in our study according to the Biolflor database, Kühn et al., 2004) and have a transient seed bank (80.90% of the species recorded according to the LEDA database, Kleyer et al., 2008). Continuous traits (number of seeds per plant, seed dry mass and seed germination rate) were obtained from the TRY global plant trait database (Kattge et al., 2011). Trait values with an error risk < 4 (Kattge et al., 2011) were averaged per trait and per species, following an outlier detection and removal procedure assuming normal distribution of values per trait and per species (4.3% of the continuous trait values dataset). The ordinal trait (type of reproduction, describing the investment in vegetative reproduction) was obtained from the BiolFlor database (Kühn et al., 2004). We estimated missing trait values using multivariate imputation with the chained equation procedure (Penone et al., 2014; Taugourdeau et al., 2014), using the family of each species as nested blocks assuming phylogenetic conservatism (Baeten et al., 2015). This procedure was performed with the "mice" R package (van Buuren & Groothuis-Oudshoorn, 2011). Continuous traits were transformed before analysis to achieve normality (Table 1). The

correlations between selected traits either non-significant or low (Pearson's correlations, -$0.39 \leq r \leq 0.17$).

To assess the functional structure of each "old" post-agricultural woodland assemblage, we quantified the mean and the diversity of the trait values using community-weighted mean (CWM; Garnier et al., 2004) and Rao's quadratic entropy (RaoQ; Rao, 1982). CWM expresses the mean trait value in the community weighted by the relative abundances of the species. RaoQ combines both functional richness (*i.e.*, the range of trait values) and divergence (*i.e.*, the position of dominant species relative to the centre of the trait range) (Botta-Dukát & Czúcz, 2016; Mason et al., 2005) by quantifying the sum of pairwise distances between species weighted by their relative abundance. CWM and RaoQ were calculated for each trait and each woodland assemblage using the R package "FD" (Laliberté et al., 2014).

To obtain additional information on the habitat preference of woodland herbaceous plant species, we collected the forest affinity in France, Atlantic region, for each species from the European Forest Plant Species List (EuForPlant; Heinken et al., 2019, 2022) with the following typology: specialist forest species (species that occur only in forests), generalist forest species (species that occur both in and outside forests) and species of open habitats. Specialist forest species correspond to forest affinity categories "1.1" (species of forest interiors) and "1.2" (species of forest edges and forest openings). Generalist forest species correspond to forest affinity categories "2.1" (species that can be found in forest as well as open habitat) and "2.2" (species that can be found partly in forest, but mainly in open habitat). Species of open habitats correspond to category "O". Missing forest affinity values (*i.e.*, 3.37% of the dataset) were estimated from Dumé et al. (2018).

2.5 Statistical analysis

We investigated the effects of the temporal dynamics of landscape connectivity (*i.e.*, the degree of landscape connectivity, magnitude and variability of its temporal changes) on the taxonomic diversity and the functional structure of current woodland plant assemblages for each type of connectivity trend. Models described below were performed on the upward connectivity trend dataset (N = 20), and on the downward connectivity trend dataset (N = 24) separately. Woodlands characterised by a null trend (N = 6) were included in both datasets for subsequent analysis, as they remained isolated during the study period. We hereafter referred to woodlands characterised by an upward and a null connectivity trends as woodlands experiencing an upward connectivity trend, and to woodlands characterised by a downward and a null connectivity trends as woodlands experiencing a downward connectivity trend.

First, we investigated the effects of the temporal dynamics of connectivity on the taxonomic diversity of woodland herbaceous plant assemblages. We used a (i) binomial generalised linear model with a logit link-function and (ii) a multiple ordinary least squares (OLS) regression model to assess the effects of the temporal dynamics of connectivity on species richness and Piélou's evenness, respectively. These metrics were not correlated (Pearson's correlations, $r = 0.14$, P > 0.05 and $r = 0.07$, P > 0.05 in woodlands experiencing upward and downward connectivity trends, respectively). Second, we used multiple OLS regression models to assess the effects of the temporal dynamics of connectivity on the functional structure of woodland plant assemblages (CWM and RaoQ of the number of seeds per plant, seed dry mass, seed germination rate and type of reproduction). The CWM (Table S1) and RaoQ (Table S2) of the four selected traits were not or weakly correlated.

Prior to model optimisation, collinearity between independent variables (*i.e.*, degree of landscape connectivity, magnitude and variability of its temporal change) was tested using the variance inflation factor (VIF). Despite correlations between independent variables (Pearson's correlations, $0.53 \leq r \leq 0.73$ and $0.67 \leq r \leq 0.72$ in woodlands experiencing upward and

downward connectivity trends, respectively), VIF values were all < 5, indicating negligible collinearity (Hair et al., 2014; O'Brien, 2007). Using the "ncf" R package (Bjørnstad, 2020), we found no evidence of residual spatial autocorrelation in any of these models. All the models were optimised using a multi-model inference based on the bias-corrected Akaike information criterion (AICc). In this way, we built all possible candidate models based on all additive combinations of independent variables and assigned them Akaike weights. We retained as the most parsimonious, models with a ΔAICc < 2 according to Burnham and Anderson (2002). When more than one model was retained, we used a model averaging approach to account for uncertainty in the selection process (Burnham & Anderson, 2002). The full-model averaged estimates and 95% confidence intervals of each independent variable were generated across the most parsimonious models. This model optimisation procedure was repeated for all models, by including the degree of landscape connectivity in all candidates model to account for the potential dependence of the magnitude and/or the variability of temporal changes in connectivity to the degree of connectivity. Model(s) retained systematically include the degree of connectivity. Independent variables were considered significant if their 95% confidence intervals did not overlap zero. Model averaging was performed using "MuMIn" R package (Barton, 2018).

There was no evidence that detected effects were attributable to the area of woodland patches nor to the presence of a species-area relationship in those patches. Specifically, the mean area of woodland patches did not differ significantly between woodlands experiencing an upward (1.37 ha) and a downward (0.80 ha) connectivity trend (permutation Student's t-test, t = -1.71, P > 0.05). The area of woodland patches was not correlated with any components of the temporal dynamics of landscape connectivity (Table S3). It was also not correlated with the taxonomic and the functional structure (Table S4) of woodland assemblages.

All statistical analyses were conducted in R version 3.5.1.

3. Results

A total of 89 herbaceous plant species were recorded, with 83 and 56 species found in woodlands experiencing upward (null included, N = 26) and downward (null included, N = 30) connectivity trends, respectively. We recorded 64 generalist forest species, 24 specialist forest species, and one species of open habitats in total. The three most common forest specialist species were *Circaea lutetiana* L., 1753 (present in 50% of woodlands), *Euphorbia amygdaloides* L., 1753 (42%) and *Hyacinthoides non-scripta* (L.) Chouard ex Rothm., 1944 (40%), and the three most common forest generalist species were *Holcus mollis* L., 1759 (present in 64% of woodlands), *Galium aparine* L., 1753 (46%) and *Geranium robertianum* L., 1753 (36%). We recorded 60 generalist forest species, 22 specialist forest species and one species of open habitats in woodlands experiencing upward (N = 26) connectivity trends and 38 generalist forest species and 18 specialist forest species in woodlands experiencing downward (N = 30) connectivity trends (Table S5). Woodland plant assemblages experiencing an upward connectivity trend (N = 26) contained from one to 28 herbaceous plant species, with 11.00 ± 1.57 (mean ± SE) species on average, whereas those experiencing a downward connectivity trend (N = 30) contained from zero to 14 species, with 7.30 ± 0.72 species on average. The Pielou's evenness of assemblages ranged from zero to 0.94 (mean ± SE: 0.67 ± 0.04) in woodlands experiencing upward connectivity trends (N = 26), and from zero to 0.98 (mean ± SE: 0.65 ± 0.04) in woodlands experiencing downward connectivity trends (N = 28). The taxonomic diversity of woodland plant assemblages for generalist and specialist forest species are provided in Table S6. The distributions of the mean (CWM) and the diversity (RaoQ) of the trait values for the four traits studied are summarized in Table 2.

3.1 Taxonomic diversity

The degree of landscape connectivity, the magnitude and the variability of the temporal changes in landscape connectivity did not affect species richness nor Piélou's

evenness of plant assemblages regardless the connectivity trend (upward or downward) (Table 3). When models systematically included the degree of landscape connectivity, we noted a negative effect of the variability of the temporal changes in landscape connectivity on Piélou's evenness in woodlands experiencing downward connectivity trends (Table S7; Fig. S5a).

3.2 Functional structure

Two traits were significantly related to the temporal dynamics of landscape connectivity: the type of reproduction in woodlands experiencing an upward connectivity trend and seed dry mass in woodlands experiencing a downward connectivity trend. In woodlands experiencing upward connectivity trends, the CWM of type of reproduction was negatively related to the magnitude of the temporal changes in landscape connectivity. In woodlands experiencing downward connectivity trends, the RaoQ of seed dry mass was positively related to the degree of landscape connectivity and negatively related to the variability of the temporal changes in landscape connectivity (Table 3, Fig. 3). Another trait, seed germination rate, was significantly related to the temporal dynamics of landscape connectivity in woodlands experiencing a downward connectivity trend when including systematically the degree of landscape connectivity in models. Specifically, the RaoQ of seed germination rate was positively related to the magnitude of the temporal changes in landscape connectivity (Table S7; Fig. S5b).

4. Discussion

Using landscape datasets over seven decades, we showed that accounting for the independent effects of the degree of connectivity, the magnitude and the variability of temporal changes in landscape connectivity improved our ability to predict the functional response of current woodland herbaceous plant assemblages to the temporal dynamics of connectivity, but not their taxonomic response. Our dataset comprises a few specialist forest species (*e.g.*, *Anemone nemorosa L.*, 1753, *Hyacinthoides non-scripta* (L.) Chouard ex Rothm., 1944) typical of ancient forests (Hermy et al., 1999; Honnay et al., 1998), which are known to strongly depend on woodland connectivity (Butaye et al., 2001; Honnay et al., 2002; Petit et al., 2004). However, responses of current woodland plant assemblages to the temporal dynamics of connectivity were mainly determined by generalist forest species, which represent 72% of the total species pool.

4.1 The temporal dynamics of connectivity only drives current woodland plant functional assemblages

Contrary to our first hypothesis, the taxonomic diversity of current woodland herbaceous plant assemblages did not respond to either the degree of connectivity nor the magnitude nor the variability of temporal changes in connectivity, regardless the trend of connectivity. However, this absence of effect was inconsistent, as we found evidence of lower evenness of current woodland plant assemblages in response to higher variability of the temporal changes in landscape connectivity in woodland assemblages experiencing upward connectivity trends when models systematically included the degree of connectivity. Our results suggest that the temporal dynamics of connectivity did slightly affect species coexistence in woodland patches but rather drove a shift in species composition. This shift in species composition may be driven by particular trait values related to the colonisation

capacity of plant species, hence warranting further investigation into the functional structure of woodland plant assemblages.

The functional structure of current woodland plant assemblages responded to the temporal dynamics of connectivity supporting our second hypothesis. These findings support Brudvig's hypothesis (2016) that connectivity may affect species composition by acting on traits related to extinction and colonisation, even when no relationship between connectivity and species richness exists. The present work extends this hypothesis to the temporal changes in landscape connectivity (*i.e.*, its magnitude and variability).

4.2 Plant functional response to the temporal dynamics of connectivity is modulated by the type of connectivity trend

We found plant responses to be modulated by the type of connectivity trend experienced by woodlands. Specifically, in woodland assemblages experiencing upward connectivity trends, we demonstrated that a high magnitude of the temporal changes in connectivity did not affect the diversity of trait values for any given trait, but increased the abundance of species investing mostly in sexual reproduction at the expense of vegetative reproduction. The woodland with the highest magnitude of temporal changes in connectivity was dominated by *Galium aparine* L., 1753 (24% of the total abundance in the woodland) that reproduces by seeds and by *Circaea lutetiana* L., 1753 (22%) that reproduces by seed or vegetatively. In contrast, woodlands with the lowest magnitude of temporal changes were dominated by species that either reproduce by seed and vegetatively (*i.e.*, *Teucrium scorodonia* L., 1753, *Circaea lutetiana* L., 1753) or mostly vegetatively, rarely by seed [*i.e.*, Hyacinthoides non-scripta (L.) Chouard ex Rothm., 1944, *Anemone nemorosa* L., 1753, *Holcus mollis* L., 1759]. This suggests that, by promoting long dispersal distance events, a higher investment in sexual reproduction in woodland herbaceous species (Starfinger &

Stöcklin, 1996) may favour faster colonisation of woodland patches (Brunet et al., 2012). Species that reproduce sexually may thus benefit most from a marked increase in connectivity over time (Naaf & Kolk, 2015). Besides, by arriving first in woodland patches, these species may have a competitive numerical advantage over others (*i.e.*, priority effects, Drake, 1991), that could be the slow and hence late-arriving colonists, characterised by higher investment in vegetative reproduction.

In contrast, in woodland assemblages experiencing downward connectivity trends, a high degree of connectivity increased the diversity of seed mass values but without affecting the mean value. Our findings are in line with previous study demonstrating that higher connectivity leads to divergent trait values in seed mass (Favre-Bac, Mony, et al., 2017). As seed mass displays competitive ability during establishment (Leishman et al., 2000), higher diversity in trait values may indicate that the increase in dispersal fluxes, and hence in the colonisation rates in the woodland patches promote local coexistence of heavy- and light-seeded species. Seed mass is also closely related to dispersal syndromes (Moles et al., 2005; Westoby et al., 1996) and – for zoochory – to dispersal agents (Kelly, 1995). The increase in seed mass diversity may thus also indicate a wider range of dispersal syndromes, or even of dispersal agents, as seed mass is related to both factors. Of note, animal-dispersed woodland assemblages in the study site have already been shown to be particularly sensitive to connectivity (Mony et al., 2018; Uroy et al., 2019).

We also observed that, in woodlands experiencing downward connectivity trends, current woodland assemblages displayed a reduced diversity of seed mass values in response to the high variability of the temporal changes in landscape connectivity, with no change in the associated mean values. This finding might suggest that species with extreme seed mass values, whether low or high, would be less able to colonise these woodlands. Two non-mutually exclusive hypotheses could explain this observation. First, species with light seeds

generally disperse over long distances (Muller-Landau et al., 2008) but an increasing proportion of their seeds is lost in the inhospitable matrix among patches in low connectivity periods (Ouborg et al., 2006). Because light seeds do not survive long during the early stage of seedling establishment (Moles & Westoby, 2004), the probability of their successful establishment along the dispersal pathway may decrease, preventing them from pursuing their dispersal in a context of ever-changing connectivity where only some periods are favourable for dispersal. Second, species with heavy seeds may also experience increased difficulty dispersing as connectivity declines over time, especially during low connectivity periods, due to their short-distance dispersal (Muller-Landau et al., 2008). The limited persistence of heavy seeds in the soil (Leishman et al., 2000) combined with the increased risk of predation (Orrock et al., 2003) or parasitism (Sullivan et al., 2011) of seeds immobilized along the dispersal pathways during low connectivity periods means they cannot postpone a new dispersal event until the occurrence of high connectivity period.

Lastly, we found no and slight evidence that the number and germination of seeds played a role in the strategies used by woodland species to overcome the temporal dynamics in landscape connectivity, respectively. Seed germination rate was indeed involved in woodland species response to the variability of the temporal changes in landscape connectivity in woodlands experiencing downward connectivity trends, with increased diversity in seed germination rates in response to the high magnitude of the temporal changes in connectivity, but only when the degree of connectivity was systematically included in models. This finding suggests that two processes that influence the colonisation capacity of plant species, *i.e.*, the production of seeds and their successful germination once they arrive, are not, or are only marginally, among the strategies used by woodland community assemblages facing connectivity changes.

4.3 Current plant assemblages are haunted by the cumulative effects of decades of connectivity changes

This study suggests that, besides the degree of connectivity, the cumulative effects of seven decades of connectivity changes exert an influence in shaping woodland plant community assembly, by selecting species with particular trait values involved in the colonisation process. In particular, the magnitude and the variability of these changes drive functional traits values in the community. Although conducted within post-agricultural woodlands dominated by generalist species, this works shows the potential of historical trends in connectivity to provide new mechanistic insights to spatial variation in diversity. Next step would be to validate these results on a larger set of samples, and eventually in ancient forests. We could expect stronger effects of the temporal dynamics of connectivity on current plant herbaceous assemblages in ancient forests, as they are likely to harbour a higher number of specialist species that are expected to be more sensitive to landscape changes (Kuussaari et al., 2009). This could be done by incorporating information on environmental conditions of the patches, and associated suitability of the patches for specialist species, in connectivity indices (*e.g.*, Verheyen et al., 2004, 2006).

Overall, our findings underline the need to better integrate landscape connectivity temporal dynamics in metacommunity theory, as its role in driving the temporal intensity and the fluctuation of dispersal fluxes over time and subsequently in shaping community assembly has not yet been incorporated. This study also opens up new perspectives for connectivity research and application. It underlines the need to use a new method, which simultaneously accounts for the different components of the temporal dynamics of landscape connectivity to reveal the real dispersal processes of plants. Strategies to conserve and restore landscape connectivity, which are often based on moments in time, should go further by including the cumulative effect on biodiversity of past changes in connectivity.

Conflict of Interest

The authors declare no conflict of interest.

Authors' contributions

Léa Uroy, Aude Ernoult, Audrey Alignier and Cendrine Mony conceived the idea and designed methodology; Léa Uroy collected the data. Léa Uroy analysed the data, with help of Aude Ernoult, Audrey Alignier and Cendrine Mony. Léa Uroy led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

Data Availability Statement

Data and R scripts used for this study are available on Figshare: https://doi.org/10.6084/m9.figshare.19122410.v1 (Uroy et al., 2023). Land cover and the wooded habitat cover maps are available on Osuris (https://accueil.osuris.fr/) using the following links:

1952	https://www.osuris.fr/geonetwork/srv/metadata/24a136fc-5935-4424-8198-0f23daf2eaeb https://www.osuris.fr/geonetwork/srv/metadata/493497e0-2332-4cdb-8d0f-22536d8bd790
1974	https://www.osuris.fr/geonetwork/srv/metadata/bdec305c-217d-4051-9686-60e9f88d2db0 https://www.osuris.fr/geonetwork/srv/metadata/64cdc9fc-da9c-420e-99b0-b8df96526d52
1985	https://www.osuris.fr/geonetwork/srv/metadata/3c96ee46-b84e-4fa8-840d-7d58628c46a1 https://www.osuris.fr/geonetwork/srv/metadata/5d638060-4ce5-48d5-905c-674be4166b8e
2000	https://www.osuris.fr/geonetwork/srv/metadata/efb47da2-76ed-4bf7-8254-beba09d2c0e4 https://www.osuris.fr/geonetwork/srv/metadata/087795f4-3b24-4ea0-b5de-0f037d76ed5
2006	https://www.osuris.fr/geonetwork/srv/metadata/e4617185-4f84-48e2-b486-9a1712cfe80a https://www.osuris.fr/geonetwork/srv/metadata/ca33df79-6f67-443b-9cc8-a1e23cd81750

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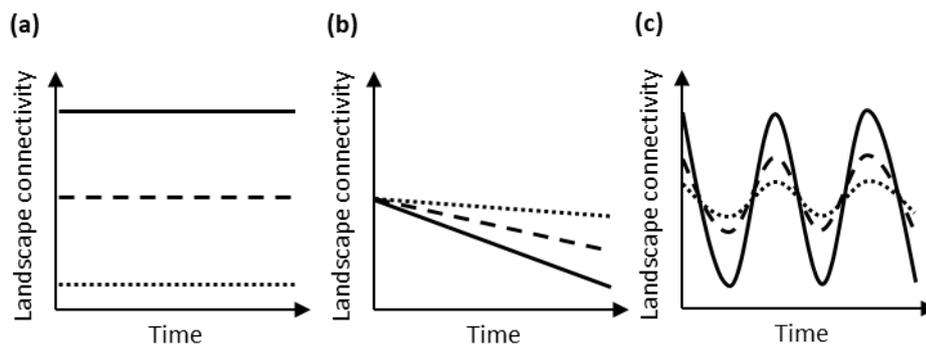
Figures and Tables

Figure 1. Illustration of the: **(a)** degree of connectivity (*i.e.*, the connectivity value of the patch at a given moment in time), **(b)** magnitude (*i.e.*, the strength at which the connectivity of the patch changes over time) and **(c)** variability (*i.e.*, alternation of periods with the patch being highly connected and periods with the patch being only slightly connected) of the temporal changes in landscape connectivity, when all other components are fixed. The magnitude of the temporal changes in landscape connectivity is represented for a patch experiencing a downward trend in connectivity. Solid, dashed and dotted lines represent their high, medium and low levels, respectively. Adapted from Uroy et al. (2021).
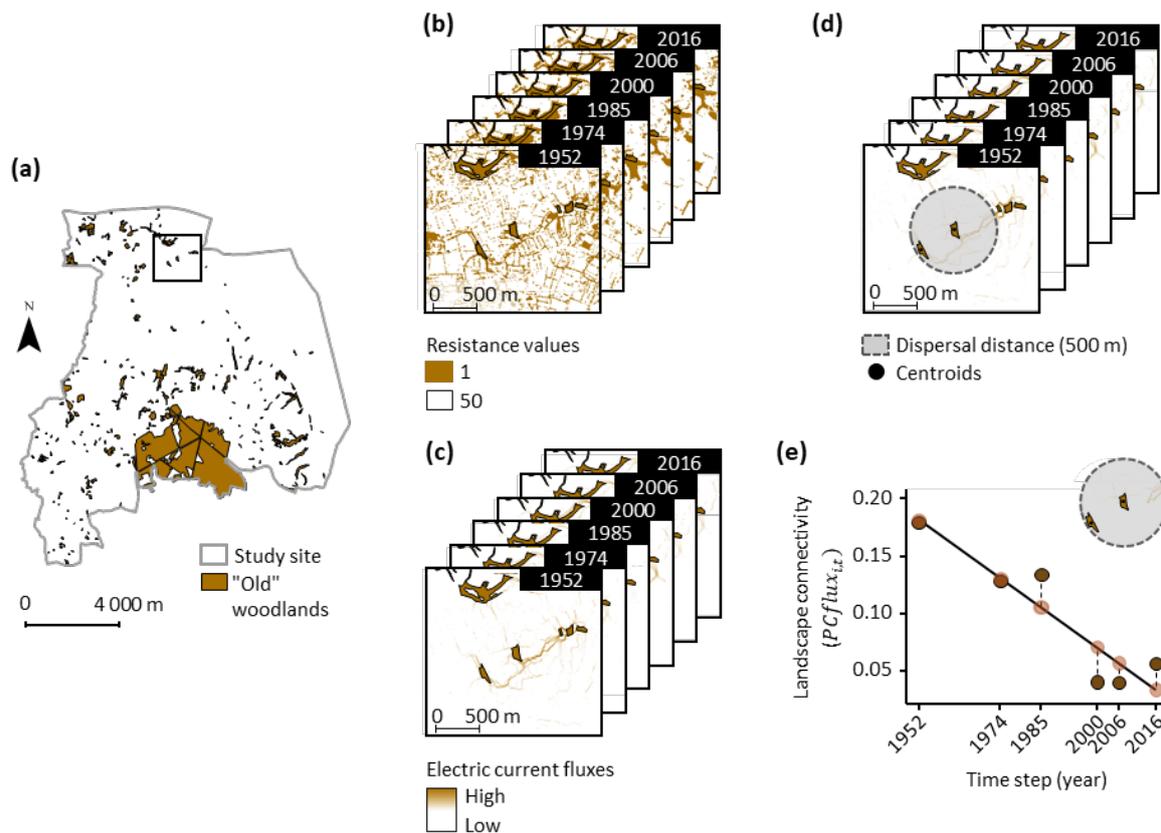
Figure 2. Illustration of the method used to model landscape connectivity and its temporal dynamics in the remaining "old" post-agricultural woodland patches (N = 255). **(a)** Detection of the "old" post-agricultural woodland patches in our study site. **(b)** Design of the resistance maps for each time point t (1952, 1974, 1985, 2000, 2006 and 2016). Wooded habitats obtained a minimum resistance value of 1, whereas other types of habitats obtained a maximum resistance value of 50. **(c)** Calculation of the resistance distance between pairs of woodland patches for each time point t from the circuit theory, here graphically represented by the cumulative electric current fluxes using the Circuitscape 4.0.5 software (McRae et al. 2008). For a given woodland i: **(d)** Assessment of the landscape connectivity using the potential dispersal flux ($PCflux_{i,t}$) index for each time point t. For a dispersal distance of 500 m around the given woodland i, only resistance distance(s) between woodland patches annotated by their respective centroids were included; **(e)** Assignment of the initial state of landscape connectivity ($PCflux_{i,1952}$), the slope ($|slope_i|$) and the residual standard error (RSE_i) – the two latter derived from the single ordinary least squares regression model – as

the degree of landscape connectivity, the magnitude and the variability of the temporal changes in landscape connectivity, respectively.
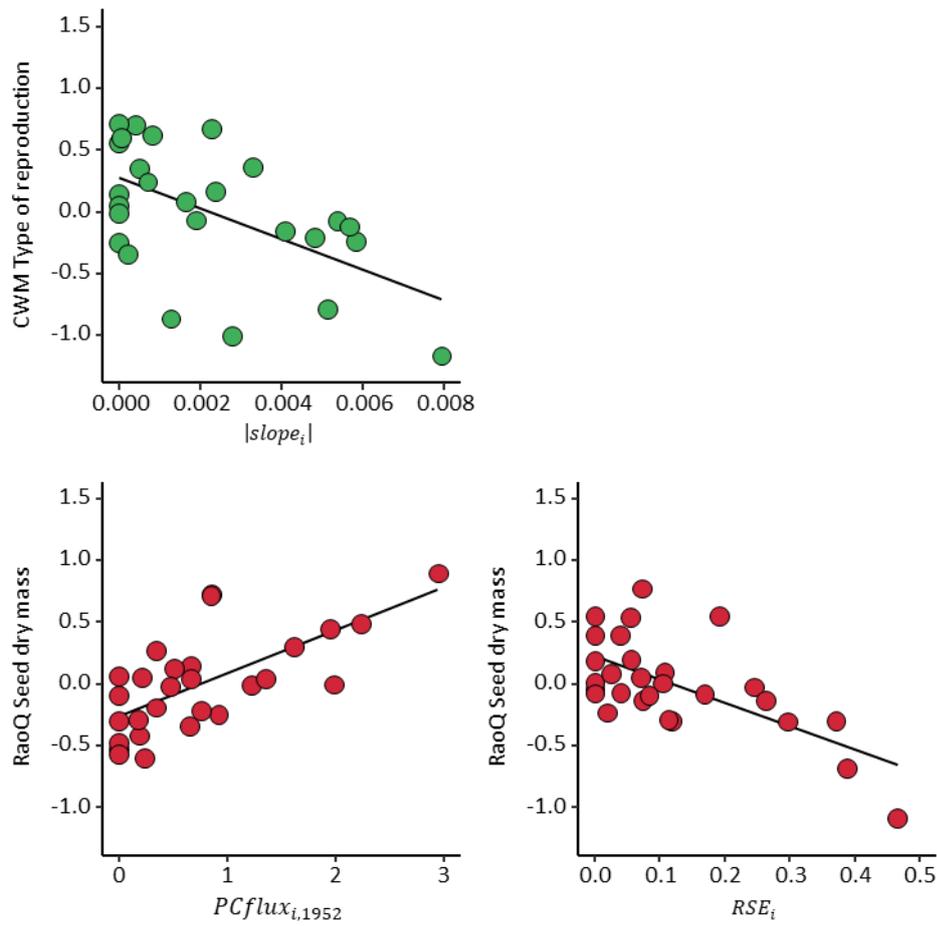
Figure 3. Partial residual plots showing the significant effects of the temporal dynamics of landscape connectivity on woodland plant assemblages for woodlands characterised by an upward (green dots, N = 26) and a downward (red dots, N = 28) trend of connectivity. Models did not systematically include the degree of landscape connectivity. CWM = community weighted mean. RaoQ = Rao's quadratic entropy. $PCflux_{i,1952}$ = degree of landscape connectivity. $|slope_i|$ = the magnitude of temporal changes in landscape connectivity. RSE_i = the variability of temporal changes in landscape connectivity.

Table 1. Overview of the functional traits investigated. The distribution of traits [mean ± SE (standard error of the mean); min-max] are indicated before the transformation of any continuous trait. Availability denotes the percentage of species for which the trait value was available in plant trait databases before multivariate imputation using the chained equation (MICE) procedure. See the Methods section for more details.

Trait	Type	Transformation	Unit	Mean ± SE	Min – Max	Availability (%)
Number of seeds per plant	Continuous	Log	1/plant	4964.1 ± 1311.1	10.0 – 70250.0	87.6
Seed dry mass	Continuous	Log	mg	2.8 ± 0.7	0.0 – 47.6	97.8
Seed germination rate	Continuous	Logit	%	91.9 ± 1.0	55.0 – 100.0	82.0
Type of reproduction	Ordinal	–	1: by seed; 2: mostly by seed, rarely vegetatively; 3: by seed and vegetatively; 4: mostly vegetatively, rarely by seed	2.6 ± 0.1	1 – 4	97.8

Table 2. Functional characteristics of woodland plant assemblages. The distribution of each community-weighted mean (CWM) and Rao's quadratic entropy (RaoQ) are given for each trait studied (number of seeds per plant, seed dry mass, seed germination rate and type of reproduction). [1] and [2] indicates traits that were, respectively, log- and logit-transformed beforehand to meet normality. SE = standard error of the mean.

Trait	CWMs		RaoQ	
	Mean ± SE	Min – Max	Mean ± SE	Min – Max
Upward trending woodlands (N = 26)				
Number of seeds per plant[1]	5.81 ± 0.19	4.47 – 8.19	0.49 ± 0.10	0.00 – 2.26
Seed dry mass[1]	0.40 ± 0.14	-0.95 – 2.12	0.49 ± 0.08	0.00 – 2.08
Seed germination rate[2]	2.21 ± 0.12	1.10 – 3.66	0.81 ± 0.11	0.00 – 1.85
Type of reproduction	3.12 ± 0.10	2.08 – 3.97	0.79 ± 0.12	0.00 – 2.38
Downward trending woodlands (N = 28)				
Number of seeds per plant[1]	5.91 ± 0.16	4.45 – 8.23	0.44 ± 0.10	0.00 – 2.26
Seed dry mass[1]	0.38 ± 0.17	-1.57 – 2.12	0.51 ± 0.08	0.00 – 1.65
Seed germination rate[2]	1.96 ± 0.11	0.98 – 3.00	0.84 ± 0.10	0.00 – 1.78
Type of reproduction	3.17 ± 0.08	2.35 – 3.80	0.60 ± 0.11	0.00 – 2.51

Table 3. Summary of the model-averaged estimates ± 95% confidence interval (CI) and relative importance (RI) of the effects of the temporal dynamics of landscape connectivity [the degree of landscape connectivity ($PCflux_{i,1952}$), magnitude ($|slope_i|$) and variability (RSE_i) of the temporal changes in landscape connectivity] on the taxonomic diversity (species richness, Piélou's evenness) and the functional structure [community-weighted mean (CWM) and Rao's quadratic entropy (RaoQ) of the number of seeds per plant, seed dry mass, seed germination rate and type of reproduction] of woodland plant assemblages. Models did not systematically include the degree of landscape connectivity. Models with only intercept values indicate a null model (*i.e,.* a model with no independent variables). 95% confidence intervals that did not encompass zero are in **bold**.

	Model	Intercept	$PCflux_{i,1952}$		$|slope_i|$		RSE_i	
	N		Estimate ± 95% CI	RI	Estimate ± 95% CI	RI	Estimate ± 95% CI	RI
Taxonomic diversity								
Upward trending woodlands								
Species richness	26	2.35			19.75 ± 89.54	0.32		
Piélou's evenness	26	0.66	0.02 ± 0.13	0.29				
Downward trending woodlands								

Species richness	30	2.10	-0.09 ± 0.30	0.38			-0.41 ± 1.52	0.31
Piélou's evenness	28	0.69	0.04 ± 0.13	0.37	6.62 ± 19.47	0.44	-0.87 ± 1.10	0.87

Functional structure

Upward trending woodlands

CWM

Number of seeds per plant	26	5.81						
Seed dry mass	26	0.47			-15.77 ± 82.63	0.25	-0.62 ± 3.19	0.25
Seed germination rate	26	2.16			19.54 ± 81.07	0.35		
Type of reproduction	26	3.22	0.14 ± 0.51	0.30	**-123.78 ± 107.59**	**1**	1.58 ± 4.39	0.44

RaoQ

Number of seeds per plant	26	0.55					-0.96 ± 3.17	0.42
Seed dry mass	26	0.47	0.05 ± 0.27	0.29				
Seed germination rate	26	0.91			25.98 ± 103.69	0.28	-2.19 ± 5.04	0.60
Type of reproduction	26	0.67			40.07 ± 110.90	0.46	0.36 ± 2.36	0.18

Downward trending woodlands

CWM

Number of seeds per plant	28	5.91						
Seed dry mass	28	0.43	-0.04 ± 0.25	0.22			-0.19 ± 1.43	0.21
Seed germination rate	28	1.94			14.59 ± 48.64	0.46	-0.47 ± 2.13	0.23
Type of reproduction	28	3.14	0.02 ± 0.12	0.21			0.17 ± 0.89	0.26

RaoQ

Number of seeds per plant	28	0.44						
Seed dry mass	28	0.37	**0.35 ± 0.26**	**1**	21.96 ± 40.45	0.67	**-1.90 ± 1.56**	**1**
Seed germination rate	28	0.91	-0.08 ± 0.31	0.30	40.10 ± 64.53	0.73	-1.77 ± 2.86	0.73
Type of reproduction	28	0.60						