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Title of symposium

Current Challenges in Landscape Ecology: Habitat Amount, Landscape Connectivity, Landscape History

Main organizer of the symposium

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Session description

The current dominant paradigm in landscape ecology assumes that habitat fragmentation generally has negative effects on biodiversity and thus emphasizes the importance of landscape connectivity to mitigate this effect. Connectivity measurements have received a huge scientific attention, and a broad array of methods and approaches have been provided in order to test for its impact (Rayfield et al. 2011). After twenty years of research, strong empirical validation of this positive effect is not obvious, especially when considering multispecies assemblages, which feeds the debate on the importance of connectivity for driving biodiversity.

Recent works stress a certain number of explanations dealing with:

(1) The need to separate habitat loss *versus* habitat fragmentation *per se*, that is the breaking apart of the habitat patches independently of the amount of habitat. Edges have additionally been demonstrated as an additional key element determining processes involved in connectivity.

(2) The importance of considering the delay with which populations and communities respond to landscape change through time (extinction debt, colonization credit). An increasing number of evidences have reported that historical landscape patterns affects more present species diversity than current landscape patterns (Lindborg et al. 2004). Temporal dynamics of land-cover change, in particular the key components of land-cover regimes (frequency of land-cover changes over time, sequence of land-cover types, duration of each land-cover type and magnitude of difference between land-cover types, cf. Watson et al. 2014) may contribute to connectivity dynamics.

This session addresses three objectives: (1) a synthesis on how measuring connectivity in space and time while taking into account the recent limitations highlighted in the current debates on the topic (Talk 1), (2) a synthesis of the effect of edges in biological processes involved in species response to connectivity (Talk 2), and (3) a state-of-art on the integration of the temporal dimension in landscape ecology discipline. In this latter section, talks include both metapopulation and metacommunity dynamics response (Talks 3 & 4) and synthesize how species richness and functional traits of communities respond to the temporal change in connectivity (Talks 5 & 6).

Fahrig, L. 2017. Ecological responses to habitat fragmentation per se. *Annual Review of Ecology, Evolution, and Systematics* 48: null.
Lindborg, R. & Eriksson, O. 2004. Historical landscape connectivity affects present plant species diversity. *Ecology* 85: 1840-1845.
Rayfield, B., Fortin, M.J. & Fall, A. 2011. Connectivity for conservation: a framework to classify network measures. *Ecology* 92: 847-858.
Watson, S.J., Luck, G.W., Spooner, P.G. & Watson, D.M. 2014. Land-use change: incorporating the frequency, sequence, time span, and magnitude of changes into ecological research. *Frontiers in Ecology and the Environment* 12: 241-249.

Speakers

Talk 1. SAURA Santiago, European Commission, Joint Research Centre (JRC), Directorate D – Sustainable Resources, Via E. Fermi 2749, I-21027 Ispra, VA, Italy
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“The amount of reachable habitat: jointly measuring habitat amount and connectivity” (Key-note speaker, 30 min)

There is a long-lasting discussion on the relative importance of habitat amount and connectivity for species persistence and diversity patterns. While some scientists argue that habitat amount may be enough to explain the responses of species to landscape change, others emphasize the prominence of habitat fragmentation and connectivity loss as major drivers of species distributions and population declines. I here argue that is unnecessary, and possibly inconvenient, to see habitat amount and connectivity as competing hypothesis. Instead, I suggest that the amount of reachable habitat provides an overarching hypothesis that integrates both habitat amount and connectivity, and hence provides a more solid and enriched view of the landscape, and of the species needs and responses, than that provided by any of the two factors alone. I describe how metrics of the amount of reachable habitat, also referred to as habitat availability or habitat reachability metrics, can provide improved insights in landscape and seascape ecology, compared to assessments focusing only on the amount of habitat or on inter-patch connectivity. I provide examples of related empirical, modelling and applied studies, ranging from the explanation of species distribution or diversity patterns to the delivery of indicators for the Digital Observatory for Protected Areas of the Joint Research Centre of the European Commission. Finally, I discuss and illustrate how the spatial and temporal dimensions can be integrated to account for the possibilities of reaching habitat resources through space and time and, therefore, to better explain species distribution and persistence in dynamic landscapes.

Talk 2. BARBARO Luc¹ (luc.barbaro@inra.fr), BROCKERHOFF Ecki G.², VAN HALDER Inge³, CHARBONNIER Yohan³, LAFORGE Alexis⁴, ANDRIEU Emilie⁴, DECONCHAT Marc⁴

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“Forest edges as keystone structures for animal biodiversity and their ecological functions in mosaic landscapes” (15 min)

Mosaic forest landscapes are characterized by intermediate levels of fragmentation, providing high amount of edges between wooded and adjacent open habitats. Edge effects are considered as the second most important cause of both negative and positive effects of fragmentation on animal biodiversity. These edge effects occur through a large variety of ecological processes, including trophic interactions and animal movements. Modern forestry creates such large-scale heterogeneous landscapes driven by short-term clear-cutting of even-aged stands. These forest edges can be considered as keystone landscape structures offering both supporting and regulating ecosystem services linked to biodiversity. Here, we summarize several studies conducted in mosaic forest landscapes of France and New Zealand. We first highlight the role of forest edges as provisioning key habitats for the conservation of bat, bee, bird and butterfly diversity in France as well as bird diversity in New Zealand, where native and exotic species coexist at edges. In addition, we found that in both countries, the regulating service of natural biocontrol provided by avian insectivory was higher at forest edges and depended on bird functional evenness. In France, the biological control exerted on pine-defoliating moths by insectivorous birds and bats was also enhanced at plantation edges because prey accessibility to foraging predators was higher at edges. Our results suggest that edge effects increase functional diversity and trait complementation within insectivore assemblages in mosaic forest landscapes. We therefore advocate for considering adequately managed forest edges as keystone structures benefiting biodiversity and associated supporting and regulating ecosystem services.

Talk 3. BARRY Pierre¹, MANEL Stéphanie¹ (stephanie.manel@cefe.cnrs.fr), COULON Aurélie^{1,2}

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“Time lags of demo-genetic responses to landscape changes” (15 min)

Landscape perturbations modify the stability of allelic composition (i.e. genetic equilibrium), which take some time before being recovered. Indeed, there is a time-lag in the genetic response of populations to landscape changes. Although the existence of this time-lag is widely acknowledged, little is known about how different types of landscape changes affect time-lags. In this study, we tested the hypothesis that time-lag after an event of

fragmentation is larger than after an event of creation of connectivity, because of the different evolutionary processes involved (drift vs. gene flow). We also tested the effects of life-history traits on time lag. To do so we used a spatially explicit individual-based approach. We simulated theoretical amphibian-like species and compared the effects of i) adding a barrier, ii) removing a barrier, iii) adding barrier and connectivity at the same time, for different migration abilities, effective population sizes and permeability of barriers. Time-lags were quantified using indexes of genetic differentiation based on allele fixation (G_{ST} , G'_{ST}), allele composition (Josts' D , Mutual Information) and Mantel tests. Time-lags ranged from 49 to more than 2000 years. We found that reaching a new equilibrium was extremely faster after removing a barrier or adding connectivity than after adding a barrier (20 – 90% faster). This highlights the strong impacts of past perturbations on current genetic differentiation long after their occurrence, especially for strong barriers and species with short dispersal abilities.

Talk 4. JABOT Franck¹ (franck.jabot@irstea.fr), **ARCHAUX Frédéric²**

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“Spatial biodiversity patterns: non-stationary investigations”

Landscape and metacommunity ecology have been two major fields of developments in the last decade. Many studies have focused on static spatial patterns in metapopulations and metacommunities, often with an implicit assumption that communities are at a dynamical equilibrium. We will here present two lines of research that aim at relaxing this assumption. The first line of research complements static biodiversity data with landscape history data. Such coupled information enables to calibrate dynamical metapopulation models and to project metapopulation responses to landscape (and climate) changes. We will present applications of these ideas to forest plant metapopulations in the Ile-de-France region. Our results highlight the interactions between past and current landscape spatial structure in shaping current biodiversity patterns, and the interaction between current spatial structure and climate changes in shaping future biodiversity responses to climate changes. The second line of research relies on temporal biodiversity data in order to better understand the drivers of metacommunity dynamics. We present the results of a simulation study to assess the benefits of using temporal rather than static biodiversity data in order to disentangle the respective influences of ecological processes on community assembly.

Talk 5. CLOSSET-KOPP Déborah (deborah.closset-kopp@u-picardie.fr), **DECOCQ Guillaume**, Université de Picardie Jules Verne, UMR CNRS 7058 Ecologie et Dynamique des Systèmes Anthropisés (EDYSAN), 1 rue des Louvels, F-80037 Amiens Cedex 1, France

“Connectivity between forest patches in changing agricultural landscapes: time also matters!”

Forest fragmentation is widely acknowledged as a major threat to biodiversity. Connectivity (i.e. the degree to which the landscape facilitates or impedes species movement among habitat fragments) is thought crucial to metacommunity functioning. However, connectivity

often refers to the spatial connection of habitat patches within a landscape (structural connectivity) and its interaction with species-specific traits (functional connectivity), whilst time is often ignored. Yet, in many temperate regions of the world, landscapes have been patterned by a long history of forest fragmentation and reforestation of former agricultural lands, so that contemporary forests consist of fragments of different age, size, and isolation, embedded in a more or less intensively managed landscape. Here, we highlight the crucial importance of temporal connectivity for understanding biodiversity and functioning of forest metacommunities.

Temporal connectivity emerged as a major issue when plant ecologists evidenced strong differences of species composition between recent and ancient forests that cannot be explained by recruitment but dispersal capacities; and that current patterns of species distribution were better explained by past landscape features than by the current ones. These results led to influential concepts such as *extinction debt* (and its counterpart, the *colonization credit*) and *dark diversity*. These patterns applied not only to forest patches and their edges, but also to hedgerow corridors. Results found at the community level were confirmed at the metacommunity scale, with a number of studies showing that temporal connectivity strongly interact with spatial connectivity to drive biodiversity patterns, providing empirical support to the Species-Time-Area relationship. More importantly, spatio-temporal connectivity of local (meta-)communities surpasses macroecological gradients in explaining local plant diversity at a biome scale. Not only plants, but also other taxonomic groups (e.g. fungi, arthropods) are affected by temporal connectivity, so that the latter deserve more attention when ecologists aim to assess ecosystem functioning and associated-ecosystem services in fragmented forests.

Talk 6. MONY Cendrine¹ (cendrine.mony@univ-rennes1.fr), **BERGÈS Laurent²** (laurent.berges@irstea.fr), **ALIGNIER Audrey³**, **BAUDRY Jacques³**, **BUREL Françoise¹**, **ERNOULT Aude¹**, **LECOCQ, Lucie¹**, **UROY Léa^{1,3}**, **AVON Catherine⁴**, **ARCHAUX Frédéric⁵**, **CHAUCHARD Sandrine⁶**, **DUPOUEY Jean-Luc⁶**

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“Time as a driver of biodiversity response to landscape connectivity”

Since a couple of decades, maintaining or restoring connectivity in forested and agricultural landscape has been considered as a key issue for preserving biodiversity. Evidence has been provided on the positive impact of connectivity on some species of ecological interest but also in simplified experimental landscape manipulations. However, empirical analyses investigating the role of landscape connectivity on the whole plant or animal assemblages are scarce and do not result in a global consensus on the way organisms respond to connectivity loss.

Most of these studies investigated the effect of current connectivity on biodiversity. But landscape elements are dynamics over time. In agricultural landscapes, such dynamics include i.) intra-annual changes, e.g. linked with crop phenology, ii.) inter-annual changes, e.g. linked with crop rotation and agricultural practices (crop/grassland turnover, field margin and hedgerow management) and iii.) inter-decades changes, e.g. linked with land-use change and planting or removal of wooded elements. In forested landscapes, land use change and the large reforestation process that occurred in France since the middle of the 19th century resulted in edge shift. All these temporal dynamics interplay with different biological processes linked with organism's movement and reproduction and therefore affect their occurrence in the landscape, in particular the potential delayed recolonisation of the forest understory communities in the recent post-agricultural forests (i.e. colonisation credit).

In this presentation, we will develop how time is taken into account in the connectivity assessment in agricultural and forested landscapes. We will also present how temporal dynamics impact organism responses to connectivity. We will illustrate that these responses may include a preferential effect of past rather than current connectivity on species biodiversity. We will then demonstrate how the use of functional traits may help to better understand these responses. To illustrate the range of biological responses we will give examples linked with plants, carabids and birds studied in the LTER site "ZA Armorique" and with plants in three regions of northern France (Lorraine, Nord-pas-de-Calais, Centre-Ile de France). For example, we will show that the distance to the nearest forest edge in 1830 better explain the spatial pattern of ancient forest species than distance to the nearest present forest edge.

Through this presentation, we will develop the conceptual perspectives and current issues linked with temporal dynamics connectivity assessment and the interest of taking time into account while preserving and restoring connectivity in landscape management.