Title

Historical ecology and biodiversity conservation of ancient forests in mountain protected areas: a multi-taxonomic approach

Summary

Ancient forests, defined as forest with long temporal continuity according to historical sources (>150 years), are slowly declining despite the twofold increase in forest area in France since 1820. Ancient forests are frequent in protected areas and their heritage value could imply specific conservation measures. However, management recommendations are currently limited to applying precautionary principle. It is thus crucial to provide new knowledge on the heritage value of these forests, so that managers in protected areas can convince the forest sector stakeholders (ONF, CRPF, private owners, townships, CFT, Associations des Communes Forestières ...) to apply appropriate conservation measures.

To provide National parks and forest managers with relevant recommendations, our aim is to understand land use legacies on current forest soil and biodiversity and to clarify the potential interaction between forest management intensity and land use legacies, using historical information available on ancient maps dating back to 1850. Using a multi-taxonomic approach carried out on 5 mountain protected areas, this thesis has three main objectives: (A) to determine whether ancient forests host a higher abundance/number of rare, specialist or threatened species for some taxonomic groups, using a large set of biodiversity databases; (B) to identify which management practices (tree species, regeneration methods, harvesting practices) are detrimental to the conservation of ancient forest species using a multi-taxa approach (vascular plants, fungi, saproxylic beetles and collembola); (C) to investigate whether formerly pastured and cultivated sites have different legacies on current forest soil, understory plant composition and traits, using a functional approach and ancient forests as a reference.

Background and challenges

Forest landscapes are continuously changing under the effect of different drivers and pressures related to global change, and this has happened for centuries: land sealing, agricultural set aside, climate change, soil acidification and eutrophication, tree species change, harvesting intensification or abandonment [1, 2]. Over the last 20 years, several studies have emphasized the importance of including a historical approach in ecological studies to better understand the current structure and functioning of ecosystems, but also to more properly evaluate conservation objectives [3, 4]. These studies gave birth to a new interdisciplinary field of study called "historical ecology" [5, Foster, 2003 #2450, Szabo, 2010 #6521].

These changes also concerned France and forest area varied over the past centuries due to human demographic fluctuations and land requirement for agriculture and livestock. Since the middle of the nineteenth century, forest grew rapidly, which results in dividing forests into "ancient forests" (that remains as a forest since that date) and "recent forests" (afforested on non-forest land after that date). However, recent statistics on 43% of the French territory (where historical land use has been vectorised according to the Etat-Major map [1818-1866], http://www.gip-ecofor.org/cartofora/) indicate that ancient forests represent only 85% of the forests present on the Etat-major map [6]. Ancient forests thus slowly keep on declining and protection actions are required at least at a regional level. The protection of ancient forests has been included in forest regulations in England (one of the lowest forested countries in Europe) and more recently in Belgium [7]. At a global scale, IUCN took initiatives to better integrate forest ancientness in nature conservation policy [8].

National parks aim to preserve the natural heritage of their territory where forests cover 15 to 70% of the conservation area. National parks are concerned by ancient forests for several years: they are involved in the identification of ancient forests and are willing to protect their biodiversity. They would like to provide forest managers with management recommendations in favour of ancient forests. National parks notably operate in the central zone (the restricted zone); for this reason, they can propose specific forest management guidance and may authorize or prohibit silviculture operations. Since 2010, past land use according to mid-nineteenth century historical maps or the Napoleonic cadastre have been progressively vectorised on seven national parks. In 2015, PNF, INRA and Irstea analysed forest cover change for the last 150 years and related the land use changes to topography (altitude, slope and aspect) and historical context [9]. Using forest cover present 150 years ago as a reference, forest decrease amounts to 14% in the Vanoise and 16% in the Pyrenées, but is lower in the Cévennes, Champagne-Bourgogne and Mercantour (4 to 7%). Building on this inter-park study, the present research project will deepen our understanding on the relationships between forest continuity, past land use and forest biodiversity.

State-of-art

Mid to long-term land use legacies on present flora and forest soils have been well studied in Western Europe (Koerner, 1997 #1204, Dupouey, 2002 #755, Kirby, 1998 #7378) and North-eastern United States [10, 11]. In these regions, forest areas have largely increased during the last century and a large proportion of forests developed on former agricultural soils (about half of the forest area in France [12]). Two types of forests are thus considered at the landscape scale: ancient forests, which was forested land since the oldest cartographic reference, and recent forests, formerly cultivated or grazed before afforestation. Ancient forests may have a higher frequency of endangered or threatened species compared to recent forests [13]. Ancient forest species have generally low dispersal capacity, are more shade-tolerant and are less tolerant to disturbance compared to those of recent forests [14, 15]. In contrast, recent forests are richer in non-forest or ruderal plant species [16]. Recent forest soils exhibit higher nitrogen and phosphorus content and forest productivity is generally better. Accurate maps of the location of these two types of forest is required for conservation purpose. The 1:40 000 minutes of the Etat-major map (drawn during the assumed date of the minimum forest cover in France) is the most valuable source at the national scale for such reconstruction [17]. Thanks to the recent efforts made by several actors (research laboratories, PNF and PNR, IGN, WWF, CBN), the map of ancient forests, recent forests and deforestation now covers half of the national territory [6].

Despite significant progress made on ancient forest knowledge, important research challenges remain to be explored [6].

What is the heritage value of ancient forests?

The heritage value of ancient forests has been little investigated so far: we expect these forests would not only host an original biodiversity for different taxa compared to recent forests (see a summary in [6]), but could also host more rare, specialist or threatened species [13, 18]. Rare species occupy a central place in conservation biology as they generally run a greater risk of extinction [19]. Knowing more about the biological and ecological traits that characterize rare species is one of the scientific issues of conservation [20, 21]. A study on eight taxonomic groups in Danish forests clearly showed that the species richness of species on the European Red List was better correlated to the forest area in 1810 than to the current forest area [13]. This result was obtained in a context of higher forest fragmentation (3.5% in 1810) compared to France (14% in 1830) and deserves to be explored in other biogeographical and historical contexts. A positive result would strengthen the scientific arguments to recognize a greater heritage value to ancient forests [8]. Few studies in France have investigated the ecological and biological characteristics of rare species [22]. These authors analysed the changes in abundance and distribution of rare plants on the department of Hérault (France) between 1886 to 2001 and showed that rare species tended to be more frequent at higher altitude and in zones with extensive agriculture (permanent grasslands and low-productivity heathlands). Analysing the spatial patterns of rare or threatened forest species according to forest continuity could usefully inform conservation policies.

Interaction between forest management and forest continuity

Even if the role of forest management on biodiversity has been largely documented [23-26], the interaction between forest management and forest continuity has been much less investigated [6]. Can ancient forest properties be disturbed or erased by silvicultural practises? What level of disturbance can an ancient forest tolerate without losing its ancientness status? The few studies on this topic suggest that afforestation with heavy soil preparations and followed by frequent fellings may severely alter ancient forest integrity. In the Champagne valleys, poplar plantations having different land use histories (ancient or recent forest) were found to be much poorer in ancient forest species compared to adjacent sub-natural alluvial forests [27]. Similarly, sessile oak stands have a slightly higher number of forest-dwelling plants compared to Scots pine stands, suggesting the migration or recruitment of some forest plants is delayed in pine plantations, due to the dominant tree species and associated forest management [28]. These results contrast with the relatively efficient migration of herbaceous specialists in recent conifer and hardwood stands [29]. However, they are consistent with experiments emphasizing that acidifying tree species can significantly limit germination and survival of ancient forest species [30]. Further works are thus necessary to define sound silvicultural rules to apply for an efficient conservation of ancient forests.

Role of historical and landscape context on biodiversity response to forest continuity

Recent results [31] indicate smaller differences between ancient and recent forests in mountain and mid-mountain forests compared to lowland forests. However, these results contrast with those found by Brin *et al.* [32] in a region with a lower forest cover, suggesting that the influence of temporal continuity increased with forest fragmentation. In addition, the PhD thesis of J. Abadie on the Luberon PNR [33] showed that the differences in the physico-chemical properties of soils were lower in the Mediterranean than in the temperate region, partly because the landscape is dominated by calcareous substrates. The ecological, historical and landscape context of the study area can therefore explain the differences among studies concerning the effect of forest continuity on current forest soil and biodiversity.

The role of the land use before afforestation is another aspect not much addressed in the literature. In lowland forests, recent forests often originated from former crops [34], whereas in the mountains or the Mediterranean area, recent forests often originate from both pastures and crops [35]. Recent forests on former pastures were shown to be in average slightly less nutrient-rich and located on shallower and more stony soils compared to ancient forests, whereas the opposite was true for former crops [35]. A higher species richness of shrubs and herbaceous species was reported in forests with a pastoral history compared to those formerly cultivated, because of a lower disturbance regime on former pastures [36]. Differences in plant composition and traits of the herbaceous layer were observed between ancient crops on one side and ancient pastures and ancient forests on the other one [37]. These differences can be explained by the long-lasting impact of ploughing on former crops, which has disadvantaged species without dispersal agent and rhizomatous plants [37]. Significant differences in plant trait composition between contrasting land use histories (forest, crop, pasture) were observed in the PNR Luberon [38]. In particular, an interesting result is the higher frequency of nano-phanerophytes among the list of species associated to ancient forests, in opposition to the trend in lowland forests [16]. These results emphasize the variability of the effect of forest continuity and its dependence on the historical landscape context [6, 15, 39] and suggest a large-scale study to compare the effect of forest continuity in different ecological and historical contexts.

In addition, plant traits were shown to help elucidate the mechanisms underlying the specific biodiversity of ancient forests. In complement to interspecific trait response, intraspecific variability of species traits can help refine our understanding of land use legacies on current forest understory communities [40]. Post-agricultural forests often exhibit a change in soil characteristics, including phosphorus and nitrogen content [15], which play a role in plant performance [41 Baeten, 2011 #1084]. Plant phosphorus concentration can vary according to forest continuity, with higher concentrations often reported in recent forests [40]. In addition, most of the species tested in that study had a higher individual biomass in recent than in ancient forests [40]. Plant trait response to past land use therefore deserves to be explored in different geographical contexts and considering other former land uses such as grazing.

Work description

This thesis aims at better understanding land use legacies on current forest soil and biodiversity and clarifying the potential interactions between land use legacies and forest management in mountain protected areas. This work should also provide stakeholders and land managers with relevant management recommendations for ancient forests. The specific objectives of this thesis are:

(A) to evaluate the heritage value of ancient forests using existing databases of biotic community or species records available in 5 mountain national parks;

(B) to identify which management practices are favourable to the conservation of ancient forest species following a multi-taxonomic approach;

(C) to investigate how soil and understory vascular plants respond to contrasting land use histories (crop vs. pasture) using a functional approach and ancient forests as a reference.

The thesis is associated to a research project funded by the Agence Française de Biodiversité (https://www.afbiodiversite.fr/).

Part A: Heritage value of ancient forests

Objectives

The objective is to broaden and deepen the analysis of biodiversity differences between ancient and recent mountain forests, focusing on specialized, rare and threatened species and addressing the response of a number of taxonomic groups other than flora. Using available biodiversity databases and including all species (forest but also open-habitat species), we will explore whether ancient forests can host a remarkable biodiversity, beyond vascular plants and ordinary species.

Our main hypothesis is that mountain ancient forests have a greater species richness of specialized, rare and protected species than recent forests for some taxa (lichens, bryophytes, saproxylic insects, fungi, soil fauna), because of the temporal stability of these habitats due to longer forest continuity [42]. For other taxa, such as vascular plants, we assume the reverse trend, *i.e.* rare and protected species are more common in former pastures, since pastures have sharply declined in mountain areas since the 19th century [43, 44].

Content

With the help of project managers of the National parks involved in the project (Cévennes, Ecrins, Vanoise, Mercantour, Pyrénées), you will collect as many biodiversity surveys as possible for several taxa (vascular plants, lichens, bryophytes, fungi, insects, soil fauna, bacteria, mammals, birds, amphibians...). You will also interview a list of institutional partners and NGO that should hold this type of data (the Parks themselves, CEN, CBN, FRAPNA, LPO, ONF, etc…) and the SINP website (http://inventaire.naturefrance.fr/).

All the data collected on the different taxa will be classified according to their location accuracy and other criteria (survey date, quality…). You may have to work with landscape windows of 1x1 km or higher [13]. To complement historical variables (land use in 1850 in case of precise survey or amount of forest in 1850 present in landscape window otherwise), you will collect spatial environmental data following [44]. After listing rare, specialist and threatened species, you will test the effect of historical factors on species richness for these three species attributes at the plot or window scale. You will also include environmental covariates (soil, climate, canopy cover, distance to forest edge or distance to housing) in the statistical analyses to assess the respective weight of different predictors.

Expected results

→ Article 1. Are there more specialists, rare and red-listed species in ancient forests? A multi-taxa approach to conservation in montane forests.

Part B: Interaction between management and forest continuity on biodiversity using a multi-taxa approach

Objectives

The aim is to evaluate the role of current (and past) forest management practices on ancient forest biodiversity using a multi-taxa approach, in particular to evaluate the potential negative impact of introduced coniferous plantations. In other words, the objective is to identify to what degree the ecological attributes of an ancient forest are modified or maybe deleted by silvicultural practises and what disturbance intensity an ancient forest can support without losing its specific biodiversity. Our hypothesis is that the more intensive silviculture (stand regeneration associated with heavy soil preparation), the higher the detrimental effect on ancient forest species pool [27, 28].

Content

First, you will review the combined effects of forest continuity and stand management on biodiversity [27-30]. Then, you will carefully prepare a sampling design of 100 sites in adult forests to cross the two factors "forest continuity" and "forest stand type", in close relation with the forest project managers of the different National Parks and AFB. The study area encompass the five mountain National Parks (Cévennes, Ecrins, Vanoise, Mercantour, Pyrénees) but may be extended in a later stage to adjacent areas where the historical land use have been vectorised. The idea is to sample various stand types (broadleaved *vs.* coniferous, plantations *vs.* natural regeneration, even-aged *vs.* uneven-aged high forest, several harvesting methods more or less destructive for the understory and litter layers) while crossing with a gradient of forest continuity. Historical data will be collected from the Etat-major maps, which have been digitised and vectorised by AFB [9]. You will also carefully control as far as possible for climate, topography, soil and landscape variations in the selected sites. You will reconstitute management history of the selected sites using forest archives (recent and past management plans) and determine forest stand origin, regeneration practises, and if possible, the silviculture applied since then.

On the selected sites, you will sample vascular plants, fungi, saproxylic beetles and stringtails in year 1. You will perform soil physico-chemical analyses to control between-sites variations. You will collect the environmental DNA of fungi and stringtails by molecular meta-barcoding of soil samples, an effective technique to analyse soil biodiversity [45-47].

Statistical analyses will focus on the response of species richness (total and for each trait) and of species composition (for each taxonomic group) to forest continuity and forest management. You will test variation in species richness using a two-way analysis of variance with interaction and variation in species composition using ACC [48].

Expected results

→ Article 2. To what extent can intensive forest practices threaten ancient forest species? A multi-taxa approach in montane ancient forests.

Part C: Role of land use history (forest, pasture or crop) on current soil, understory plant composition and traits

Objectives

We ask whether soil, plant composition and traits differ between forested sites with contrasting land use histories (pasture vs. culture), using ancient forests as a reference. In particular, we will specify (a) how intraspecific plant traits explain population response to former land use (nitrogen content, SLA, LMDC, ...) and (b) how interspecific plant traits explain community response to former land use (colonisation capacity, dispersal mode, life-form, habitat requirement,…).

A first hypothesis is that the long-term impact of land use history on plant communities, plant traits and soil (pH, carbon, nitrogen and phosphorus content) is higher in forests that were previously ploughed and fertilized than in forests that did not experience these types of soil disturbances [36-38, 49]. An alternative hypothesis is that the natural processes of forest succession could mitigate land use legacies [49]. A second hypothesis is that within-species plant traits also vary according to past land use (forest, pasture or crop) [40].

Content

Part C1 – You will sample around 70 forest sites with different former land uses using historical maps (forest, crop, pasture) while controlling for recent forest age. To capitalize on Part B investment, you will reuse some of the sites sampled in Part B and complement them with new sites corresponding to the objectives of Part C1. Forest stand structure, tree composition, topography and soil properties will be characterised on each site. You will survey plant communities in spring-summer of year 1 and 2. You will measure functional traits on 3 to 4 forest plants associated to ancient and recent forests. You will analyse leaf traits related to growth capacity (SLA, nitrogen and chlorophyll content), fertility (C:N and P:C ratios) and response to grazing (LDMC, chemical compounds of defence such as flavonoids or anthocyanins by *in situ* measurement with DUALEX clamp).

Part C2 – You will follow the same approach (excluding *in situ* trait measurements) on a larger scale using IGN-Ifn and CBNA survey plots, with the objective to analyse about 1500 plots, a significantly larger sample compared to previous works in mountain forests [48]. You will collect plant traits (related to persistence, regeneration, dispersal and ecological preferences) by querying the LECA plant trait database for alpine flora, but you will also have to query other plant trait databases such as TRY [50] and Baseflor. You will also gather existing environmental geodata (topography, geology, soil, climate, current land use) available at Irstea and from the project partners. You will recycle the surveys previously collected in the FORGECO project on the PNR Vercors [51] and query the floristic survey database of the CBNA. Past land use and environmental variables (altitude, soil, topography ...) will be characterised for each site using GIS treatment.

You will define the lists of ancient and recent forest species thank to statistical models using past land use as a predictor and controlling for other sources of environmental variability [16]. Finally, you will identify plant traits that discriminate understory species response to past land use [38]. Unlike previous works that applied RLQ coupled with Fourth-corner analysis [28, 52], you will attempt to analyse the relationships between historical/ecological factors and plant traits using a multi-species generalised linear model [53, 54].

Expected results

Depending on the results, we will focus on the valorisation of the results of Part C1 or C2.
→ Article 3. Are land use legacies detectable on within-species trait variability in montane understory vegetation?
→ Article 4. Former land use, forest continuity and other ecological factors shape understory plant composition and traits in montane forests: a multispecies generalised linear model analysis.

Schedule

Part	Task	Year 1				Year 2				Year 3			
	Committee meeting		●				●				●		
A	In-depth statistical analysis of the data collected during the Master in 2019									—			
	Article 1 draft										—		
B	Bibliography	—											
	Sampling preparation (site selection)	—	—										
	Taxonomic inventories		—	—									
	Statistical analysis				—	—							
	Article 2 draft					—							
C	Bibliography	—											
	Sampling prep. and field data coll. (comm., traits)						—	—					
	Statistical analysis							—	—				
	Article 3 or 4 Draft								—				
	Correction of submitted manuscripts											—	
	Thesis manuscript											—	—

Collaborations

PhD thesis will be co-supervised by Irstea and INRA Nancy (UMR Silva). Collaboration: Ecole d'Ingénieurs de Purpan, Laboratoire PACTE, UMR LECA, Conservatoire Botanique National Alpin, ONF and National Parks (AFB).

Project benefits

• Planned applications

- Updated list of plants associated with ancient forests and publication of a list of species for mountain national parks;
- Arguments for the integration of the network of ancient forests as biodiversity reservoirs or as sub-network of the green and blue infrastructure;
- Recommendations of ancient forest management to preserve as much as possible their ecological integrity, to elaborate in collaboration with protected mountain area managers;
- Raising awareness of the heritage value of ancient forests in cooperation with AFB and forest stakeholders (WWF, REFORA, FRAPNA, LPO, CEN, ONF, CRPF, private owners, communities, CFT, Associations des Communes Forestières).

• Proposed publications with choice of scientific support and impact factor

n°	Draft title	Target journal	IF_{2017}
A	Are there more rare and red-listed species in ancient forests? A multi-taxa approach to conservation in montane forests	*Biological Conservation*	4.66
B	To what extent can intensive forest practices threaten ancient forest species? A multi-taxa approach in montane forests	*Ecosystems*	4.03
C	Are land use legacies detectable on within-species trait variability in montane understory vegetation? Former land use, forest continuity and other ecological factors shape understory plant composition and traits in montane forests: a multi-species generalized linear model analysis	*Journal of Vegetation Science*	2.66

Organisation

• Supervision: ● Thesis supervisor: Laurent Bergès, UGA - Irstea UR LESSEM ● Co-supervision: J.-L. Dupouey - INRA UMR Silva Nancy ● Irstea management: Georges Kunstler (HDR), Marc Fuhr, UGA - Irstea UR LESSEM

• Funding: Thesis grant and related expenses funded by AFB and Irstea (AFB-Irstea contract 2019-2021).

• Candidate profile: Master in plant ecology or landscape ecology and - if possible - interested in geo-historical approaches. Knowledge of statistical analyses (preferably with *R*) and skills in GIS. The candidate will prepare and coordinate a field campaign including multi-taxa surveys (vascular plants, fungi, saproxylic beetles and stringtails), measurements of environmental parameters (soil, forest stand) and measurements of vascular plant functional traits.

References

Management team (and people involved)

Abadie, J., Avon, C., **Dupouey, J.-L.**, Lopez, J.-M., Tatoni, T. & **Bergès, L.** 2018. Land use legacies on forest understory vegetation and soils in the Mediterranean region: Should we use historical maps or in situ land use remnants? *Forest Ecology and Management* 427: 17-25.

Abadie, J., **Dupouey, J.-L.**, Avon, C., Rochel, X., Salvaudon, A., Tatoni, T. & **Bergès, L.** 2017. Déterminants du changement du couvert forestier depuis 1860 dans le parc naturel régional du Luberon et implications pour la répartition des forêts actuelles. *Revue Forestière Française* 69: 371-386.

Abadie, J., **Dupouey, J.-L.**, Avon, C., Rochel, X., Tatoni, T. & **Bergès, L.** 2018. Forest recovery since 1860 in a Mediterranean region: drivers and implications for land use and land cover spatial distribution. *Landscape Ecology* 33: 289-305.

Bergès, L. & **Dupouey, J.-L.** 2017. Ecologie historique et ancienneté de l'état boisé : concepts, applications, avancées et perspectives de la recherche. *Revue Forestière Française* 69: 297-318.

Bergès, L., Avon, C., Arnaudet, L., Archaux, F., Chauchard, S., **Dupouey, J.L.**, 2016. Past landscape explains forest periphery-to-core gradient of understory plant communities in a reforestation context. *Diversity and Distributions* 22(1): 3-16

Bergès, L., Feiss, T., Avon, C., Martin, H., Rochel, X., Dauffy-Richard, E., Cordonnier, T. & **Dupouey, J.-L.** 2017. Response of understorey plant communities and traits to past land use and coniferous plantation. *Applied Vegetation Science* 20: 468-481.

Janssen, P., Bec, S., **Fuhr, M.**, Taberlet, P., Brun, J.J. & Bouget, C. 2018. Present conditions may mediate the legacy effect of past land-use changes on species richness and composition of above- and below-ground assemblages. *Journal of Ecology* 106: 306-318.

Janssen, P., Cateau, E., **Fuhr, M.**, Nusillard, B., Brustel, H. & Bouget, C. 2016. Are biodiversity patterns of saproxylic beetles shaped by habitat limitation or dispersal limitation? A case study in unfragmented montane forests. *Biodiversity and Conservation* 25: 1167-1185.

Thomas, M., Bec, R., Abadie, J., Avon, C., **Bergès, L.**, Grel, A. & **Dupouey, J.-L.** 2017. Changements à long terme des paysages forestiers dans cinq parcs nationaux métropolitains et le futur Parc National des Forêts de Champagne et Bourgogne. *Revue Forestière Française* 69: 387-404.

Rochel, X., Abadie, J., Avon, C., **Bergès, L.**, Chauchard, S., Defever, S., Jeanmonod, J., Leroy, N. & **Dupouey, J.-L.** 2017. Quelles sources cartographiques pour la définition des forêts anciennes en France ? *Revue Forestière Française* 69: 353-370.

Other references

1. McGrath, M.J., et al., *Reconstructing European forest management from 1600 to 2010.* Biogeosciences, 2015. **12**(14): p. 4291-4316.
2. Kaplan, J.O., et al., *Large scale anthropogenic reduction of forest cover in last glacial maximum Europe.* Plos One, 2016. **11**(11).
3. Szabo, P. and R. Hedl, *Advancing the integration of history and ecology for conservation.* Conservation Biology, 2011. **25**(4): p. 680-687.
4. Vellend, M., et al., *Historical ecology: using unconventional data sources to test for effects of global environmental change.* American Journal of Botany, 2013. **100**(7): p. 1294-1305.
5. Peterken, G., *Woodland conservation and management*. 1981, London, UK: Chapman et Hall.
6. Bergès, L. and J.-L. Dupouey, *Ecologie historique et ancienneté de l'état boisé : concepts, applications, avancées et perspectives de la recherche.* Revue Forestière Française, 2017. **69**(4-5): p. 297-318.
7. Kervyn, T., et al., *La gestion patrimoniale des forêts anciennes de Wallonie (Belgique).* Revue forestière Française, 2017. **69**(4-5): p. 545-560.
8. Vallauri, D., et al., *Ancienneté : perspectives pour la conservation des forêts.* Revue Forestière Française, 2017. **69**(4-5): p. 560-570.
9. Thomas, M., et al., *Changements à long terme des paysages forestiers dans cinq parcs nationaux métropolitains et le futur Parc National des Forêts de Champagne et Bourgogne.* Revue Forestière Française, 2017. **69**(4-5): p. 387-404.
10. Bellemare, J., G. Motzkin, and D.R. Foster, *Rich mesic forests: Edaphic and physiographic drivers of community variation in western Massachusetts.* Rhodora, 2005. **107**(931): p. 239-283.
11. Flinn, K.M., M. Vellend, and P.L. Marks, *Environmental causes and consequences of forest clearance and agricultural abandonment in central New York, USA.* Journal of Biogeography, 2005. **32**(3): p. 439-452.
12. Mather, A.S., C.L. Needle, and J.R. Coull, *From resource crisis to sustainability: the forest transition in Denmark.* International Journal of Sustainable Development and World Ecology, 1998. **5**(3): p. 182-193.
13. Flensted, K.K., et al., *Red-listed species and forest continuity – A multi-taxon approach to conservation in temperate forests.* Forest Ecology and Management, 2016. **378**: p. 144-159.
14. Flinn, K.M. and M. Vellend, *Recovery of forest plant communities in post-agricultural landscapes.* Frontiers in Ecology and the Environment, 2005. **3**(5): p. 243-250.
15. Hermy, M. and K. Verheyen, *Legacies of the past in the present-day forest biodiversity: a review of past land-use effects on forest plant species composition and diversity.* Ecological Research, 2007. **22**(3): p. 361-371.
16. Bergès, L., et al., *Past landscape explains forest periphery-to-core gradient of understorey plant communities in a reforestation context.* Diversity and Distributions, 2016. **22**(1): p. 3-16.
17. Dupouey, J.L., et al., *Vers la réalisation d'une carte géoréférencée des forêts anciennes de France.* Le Monde des Cartes, 2007. **191**: p. 85-98.
18. Fritz, O., L. Gustafsson, and K. Larsson, *Does forest continuity matter in conservation? A study of epiphytic lichens and bryophytes in beech forests of southern Sweden.* Biological Conservation, 2008. **141**(3): p. 655-668.

19. Murray, B.R., et al., *How plant life-history and ecological traits relate to species rarity and commonness at varying spatial scales.* Austral Ecology, 2002. **27**(3): p. 291-310.
20. Cofre, H.L., K. Bohning-Gaese, and P.A. Marquet, *Rarity in Chilean forest birds: which ecological and life-history traits matter?* Diversity and Distributions, 2007. **13**(2): p. 203-212.
21. Gabrielova, J., et al., *Can we distinguish plant species that are rare and endangered from other plants using their biological traits?* Folia Geobotanica, 2013. **48**(4): p. 449-466.
22. Lavergne, S., *Les espèces végétales rares ont-elles des caractéristiques écologiques et biologiques qui leur sont propres ?* Acta Botanica Gallica, 2004. **151**(3): p. 319-323.
23. Kuuluvainen, T., *Forest management and biodiversity conservation based on natural ecosystem dynamics in northern Europe: the complexity challenge.* AMBIO, 2009. **38**.
24. Paillet, Y., et al., *Biodiversity differences between managed and unmanaged forests: meta-analysis of species richness in Europe.* Conservation Biology, 2010. **24**(1): p. 101-112.
25. Schall, P., et al., *The impact of even-aged and uneven-aged forest management on regional biodiversity of multiple taxa in European beech forests.* Journal of Applied Ecology, 2018. **55**: p. 267-278.
26. Schulze, E.D., *Effects of forest management on biodiversity in temperate deciduous forests: An overview based on Central European beech forests.* Journal for Nature Conservation, 2018. **43**: p. 213-226.
27. Chevalier, R., et al., *Le concept de forêt ancienne s'applique-t-il aux peupleraies cultivées? Test de pertinence avec la flore des vallées de Champagne.* Revue Forestière Française, 2013. **65**(4): p. 375-388.
28. Bergès, L., et al., *Response of understorey plant communities and traits to past land use and coniferous plantation.* Applied Vegetation Science, 2017. **20**(3): p. 468-481.
29. Wulf, M. and T. Heinken, *Colonization of recent coniferous versus deciduous forest stands by vascular plants at the local scale.* Applied Vegetation Science, 2008. **11**(3): p. 307-316.
30. Thomaes, A., et al., *Tree species determine the colonisation success of forest herbs in post-agricultural forests: Results from a 9 yr introduction experiment.* Biological Conservation, 2014. **169**: p. 238-247.
31. Janssen, P., *Influences relatives de l'ancienneté et de la maturité sur la biodiversité : implications pour la conservation en forêts de montagne*, in *ED EDISCE*. 2016, UGA: Grenoble.
32. Brin, A., et al., *Effects of forest continuity on flying saproxylic beetle assemblages in small woodlots embedded in agricultural landscapes.* Biodiversity and Conservation, 2016. **25**(3): p. 587-602.
33. Abadie, J., *Écologie historique des forêts méditerranéennes : déterminants du changement du couvert forestier et effets des usages passés sur les sols et la flore actuels [Historical ecology of Mediterranean forests: drivers of forest cover change and effects of past land use on current soils and vegetation]*. 2018, Aix-Marseile Université: Aix-Marseille. p. 322.
34. Verheyen, K., et al., *Response of forest plant species to land-use change: a life-history trait-based approach.* Journal of Ecology, 2003. **91**(4): p. 563-577.
35. Abadie, J., et al., *Land use legacies on forest understory vegetation and soils in the Mediterranean region: Should we use historical maps or in situ land use remnants?* Forest Ecology and Management, 2018. **427**: p. 17-25.
36. Wulf, M., *Plant species richness of afforestations with different former use and habitat continuity.* Forest Ecology and Management, 2004. **195**(1-2): p. 191-204.
37. Dyer, J.M., *Land-use legacies in a central Appalachian forest: differential response of trees and herbs to historic agricultural practices.* Applied Vegetation Science, 2010. **13**(2): p. 195-206.
38. Abadie, J., et al., *Mediterranean forest plant species: different vegetation communities and plant traits according to time since abandonment and past land use.* Biological Conservation, in prep.
39. De Frenne, P., et al., *Interregional variation in the floristic recovery of post-agricultural forests.* Journal of Ecology, 2011. **99**(2): p. 600-609.
40. Baeten, L., et al., *Former land use affects the nitrogen and phosphorus concentrations and biomass of forest herbs.* Plant Ecology, 2011. **212**(5): p. 901-909.
41. Vellend, M., *Land-use history and plant performance in populations of Trillium grandiflorum.* Biological Conservation, 2005. **124**(2): p. 217-224.
42. Norden, B., et al., *Effects of ecological continuity on species richness and composition in forests and woodlands: A review.* Ecoscience, 2014. **21**(1): p. 34-45.
43. Sitzia, T., P. Semenzato, and G. Trentanovi, *Natural reforestation is changing spatial patterns of rural mountain and hill landscapes: A global overview.* Forest Ecology and Management, 2010. **259**(8): p. 1354-1362.
44. Abadie, J., et al., *Forest recovery since 1860 in a Mediterranean region: drivers and implications for land use and land cover spatial distribution.* Landscape Ecology, 2018. **33**(2): p. 289-305.
45. Thomsen, P.F. and E. Willerslev, *Environmental DNA - An emerging tool in conservation for monitoring past and present biodiversity.* Biological Conservation, 2015. **183**: p. 4-18.
46. Pansu, J., et al., *Landscape-scale distribution patterns of earthworms inferred from soil DNA.* Soil Biology and Biochemistry, 2015. **83**: p. 100-105.
47. Orgiazzi, A., et al., *Soil biodiversity and DNA barcodes: opportunities and challenges.* Soil Biology and Biochemistry, 2015. **80**: p. 244-250.
48. Janssen, P., et al., *Present conditions may mediate the legacy effect of past land-use changes on species richness and composition of above- and below-ground assemblages.* Journal of Ecology, 2018. **106**(1): p. 306-318.
49. Holmes, M.A. and G.R. Matlack, *Forest micro-environment develops through time: Changes in physical and structural heterogeneity follow abandonment from two forms of agriculture.* Forest Ecology and Management, 2017. **404**: p. 55-64.
50. Kattge, J., et al., *TRY - a global database of plant traits.* Global Change Biology, 2011. **17**(9): p. 2905-2935.
51. Dupouey, J.L., et al., *Identifier les facteurs historiques de vulnérabilité dans la relation sylviculture-biodiversité. Projet FORGECO, programme ANR Systerra, Compte-rendu de fin de projet, Annexe Ia*. 2014. p. 52.
52. Dray, S., et al., *Combining the fourth-corner and the RLQ methods for assessing trait responses to environmental variation.* Ecology, 2014. **95**(1): p. 14-21.
53. Brown, A.M., et al., *The fourth-corner solution - using predictive models to understand how species traits interact with the environment.* Methods in Ecology and Evolution, 2014. **5**(4): p. 344-352.
54. Warton, D.I., B. Shipley, and T. Hastie, *CATS regression - a model-based approach to studying trait-based community assembly.* Methods in Ecology and Evolution, 2015. **6**(4): p. 389-398.