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Session 1: General context and issues on mixed forest ecosystems

Take a walk in the mixed forests complexity with simple questions

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If we consider general data about tree species mixture and forest biomes worldwide, and more in detail in Europe and France with NFI statistics, there are, for sure, mixed forests. Several tree species often grow together, not only in tropical rain forests, but also in temperate managed forests– with respect to very different vertical and horizontal structures and species densities.

Mixed forests are not so easy to define, nor to describe. In temperate forests, when you focus on specific mixtures, most of them appear as transient states of the forest composition, more than less incidentally produced by a specific history and often escaping from the forester's control as they quickly evolve to something else. Actually, the silviculture of tree mixtures is reduced in most silvicultural French guides to general recommendations in their favour.

As mixed forests meet our representation of a generous Nature, a real fact about them is maybe that we love them, what drives us to claim that they are a good thing for many forest ecosystems services. Is it rationally founded? Did we ever though that?

Exploring these paradoxes, we will approach the main issues about mixed forests concerning their distribution, historical and social aspects, dynamics and ecological functioning, and management challenges.

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Session 2.1: Response of trees to environmental factors

Hydraulics and cavitation in trees

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Water transport across the soil-plant-atmosphere-continuum (SPAC) is regulated by different mechanisms in response to environment. After a presentation of the model describing the forces and the parameters affecting this water flow (the Tension-Cohesion theory and the Ohm's analogy), we will focus on the xylem dysfunctions and their consequences on tree hydraulics. Mechanisms of drought- and freezeinduced xylem cavitation, that is loss of functionality, will be described. Examples of plasticity of the xylem water transport properties in response to environment such us light will be provided. The variability in cavitation vulnerability will be analyzed under the light of intra- and inter- specific comparisons. The importance of this parameter on the tree water relations, functioning and ecology will be highlighted. Session 2.1: Response of trees to environmental factors

A few notions about tree response to drought, heat, and elevated CO₂

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Abiotic factors such as water availability or temperature are crucial determinants of species distribution and productivity, and they represent a major selection pressure. Among them, drought is considered as the first limitation to biomass production worldwide. The way the plant will resist to water shortage or high temperature (i.e. the way it will survive or will be able to maintain biomass production under the constraint) is dependent on the strategy it will adopt in response to the stress. The response of the plant is indeed composed of multiple mechanisms, from the molecular scale to the whole plant scale, and from immediate to generation time scales. The objective of this session will be to define a couple of terms about the notions of "stress" and "stress resistance", and to browse rapidly the various consequences of drought, high temperatures, and elevated CO2 on plant physiology. The experimental ways the effects of these factors on plant functioning can be evaluated will also be addressed. The concepts will be illustrated with some examples from the scientific literature.

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Session 2.1: Response of trees to environmental factors

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This session will give an overview of basic knowledge in ecophysiology on the response of tree species to environmental factors (radiation, soil water content, VPD, temperature, CO2 and others) in absence of interspecific competition as a basis in order to understand the potential consequences of species interactions in mixed conditions.

We will look at the responses of trees to various single and mixed changes in environmental conditions at the leaf level and also explore other tissue and organs specific responses. This overview will include responses of the water, carbon and nutrient relations. One focus will be to show how plant responses are imprinted on stable isotope signals. Stable isotopes can be used as a long-term integrating proxies to reconstruct the effects of environmental drivers on the physiology of trees. Moreover we will scale plant reactions towards the environment to the whole tree and will study the integrative above- and below-ground responses

Session 2.2: Impact of climate change on forest dynamics

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Forest dynamics refers to the changes in forest structure and composition over time. The classic model of succession is a typical example of this, where open land is first colonized by pioneer, shade intolerant tree species which are eventually replaced by more shade tolerant trees. In mature forests, smaller gap replacement events (where small scale disturbances or individual tree mortality creates a gap in the canopy which is filled by trees present in the understory) or larger stand replacement events caused by wide scale disturbances are other examples.

Current and future climate change can influence forest dynamics in several ways. Many of the processes involved in tree succession are directly linked to climate, including reproduction, establishment, growth and mortality. Climate is also one of the main limiting factors in determining species ranges, resulting in changes to local and regional species composition. Finally, climate change can indirectly impact forests by altering the frequency and/or intensity of disturbance events, such as fire or bark beetles. This presentation will discuss the impact of climate on various processes, how those processes can result in shifts in species compositions and forest structure, as well as highlighting some potentially unexpected impacts of climate change on forest dynamics.

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Session 3.2: Variability among species in their strategy to acquire and use environmental resources

Session 3.3: Influence of environmental conditions on species interactions

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Understanding species coexistence is a long-standing challenge for forest ecologists. In this session, I will link ecological theory with results from observational and experimental studies to illustrate differences among species' strategies in the use of environmental resources. I will present examples of how spatial heterogeneity of resources and temporal fluctuations of disturbances can promote species coexistence. We will also look at how tree interspecies interactions vary along stress and density gradients, and with stand development. Case studies will be drawn from temperate, boreal and Mediterranean forests.

Session 3.3: Influence of environmental conditions on species interactions

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Mixed-species forests sometimes have greater levels of ecosystem functions and services, including productivity, than monocultures. However, this is not always the case. Whether or not mixtures are more productive depends on the net effects of different types of interactions, and these are dynamic, changing through space and time. Many studies have examined how species interactions influence the growth of mixtures, but few have examined how spatial and temporal differences in resource availability or climatic conditions can influence these interactions. This presentation will discuss these spatial and temporal dynamics. The processes driving the dynamics will be discussed using the production ecology equation, where plant growth is a function of resource availability, multiplied by the fraction of resources that are captured by the trees, multiplied by the efficiency with which the resources are used.

Session 3.4: Functional traits and community assemblage

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Plant ecologists seek to understand where plants grow and why they grow there, which species, present in a larger geographical region, will be found at a local site, ... And then, ultimately, how different species can survive in the same environment (i.e. in mixed forests). These questions are at the interface of Community Ecology and Functional Ecology because plant functional traits reflect trade-offs that determine species performance in a given environment and consequently species abundances along environmental gradients.

During this talk, I will present the fundamental bases that explain why functional traits are important to explain community assemblage and give illustrations largely based on the numerous studies done so far in tropical rainforests. I will not directly speak about species interactions, but the ecological concepts presented here (environmental filtering, neutral theory ...) are necessary to understand the ecology of mixed forests.

Session 4.1: Relationship between diversity and productivity

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Nearly all of the world's plantations are monospecific, and many of these plantations are composed of species that naturally occur in monocultures (excluding the understory), at least in some parts of their natural distribution. However, many of the world's forests are mixtures, and productivity often (but not always) increases with increasing tree species diversity. This is obviously of great interest to forest and plantation managers as well as scientists. However, productivity – biodiversity relationships need to be interpreted carefully when attempting to identify the causality within this relationship. This presentation will discuss these relationships, the advantages and disadvantages of different data sources that can be used to examine them e.g. inventory data, experiments in existing forests, planted experiments. Some of the causes, such as evenness of species compositions, selection effects and complementary effects will also be discussed.

Session 4.2: Relationship between diversity and other ecosystem functions

Mixed forests do foster tree quality development related to high value timber production

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Several studies had been done on influence of mixed temperate forests on ecosystem services such as biomass, nutrients, biodiversity, water, stand stability etc. However; tree quality which is albeit a very important ecosystem service related to high value timber production, had not been comprehensively studied in mixed stands by comparing monocultures. In this presentation, I will show how tree quality development occurs in mixed forest created by cluster planting. I will present the results from a meta-analysis which combined oak cluster planting trials from Germany, Austria and Switzerland. In addition to the oak cluster planting experiments, I will also present the results from the Europe wide experiments (FunDIVEurope) on relationship between tree species diversity and tree quality. The presentation will focus on the general trend of tree quality development in mixtures and future research potential in this field.

Session 4.2: Relationship between diversity and other ecosystem functions

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Biodiversity is known to support and boost a wide range of forest ecosystem functions and services like productivity and resistance against insect pests and diseases. However whether tree species diversity also promotes water and carbon acquisition and use in forest ecosystems is still unclear. Furthermore, in the actual context of global warming, information on how tree species diversity can influence the response of forest ecosystems to extreme climatic events such as drought are urgently needed. During this session, I will present results from field observations showing how tree species diversity influences important functions of the water and carbon cycle including transpiration and drought exposure at the tree- and ecosystem-scale under contrasting soil water conditions. Based on these observations, I will discuss the potential mechanisms of species interactions that may explain diversity effects.

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Session 4.3: Are diverse ecosystems more resilient to biotic and abiotic factors?

A retrospective study on growth and growth responses of beech and oak in mixed forests

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The relevance of antagonistic biotic factors most often is tree species specific, i.e. in the case of insect or fungi attack. Hence, mixed stands should display greater resilience than pure stands. Whether abiotic factors such as storm, snow, frost, stagnant water or drought affect mixed stands less than pure stands is not that obvious. Due to tree species' different rooting architecture resistance to storm damage varies greatly. As a result mixed stands should be less susceptible to storm damage. But if we know that an exposed site is at risk of storm damage, should we plant only deep rooting, storm-proof tree species? The question becomes even more complex, when it comes to drought and heat. From the natural distribution of tree species we know that some species are more adapted to high temperatures and low precipitation than others. But does this mean, that they are also more resilient to episodic droughts?

To answer this question in the context of mixed beech (Fagus sylvatica) and oak (Quercus petraea) forests, we analyzed their resistance, resilience and recovery using a dendroecological approach. The results show, that differences between beech and sessile oak regarding their drought reaction are not as distinct as expected. In the view of recently published literature on the same topic it becomes obvious, that consideration of soil properties, species selection and methodological approaches is crucial for the correct interpretation of the results.

Session 5: Modelling approaches for mixed forest ecosystems

Modelling the role of biodiversity on community ecology and ecosystem functioning in mixed forest ecosystems

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Understanding the link between biodiversity and ecosystem functioning is pivotal in the context of global biodiversity loss. Yet, this task is especially difficult in forest ecosystems for which long-term monitoring is required to assess underlying mechanisms. In this context, modelling appears as a relevant alternative to study the biodiversity-ecosystem processes relationships. Here, I'll present an approach recently proposed to explore the long-term relationship between diversity and productivity, through the use of a process-based forest succession model (ForClim) based on competition for light. Virtual experiments have been carried-out, in which community composition and forest productivity are emergent properties based on environmental filtering and competition in the long-term. These simulations show that tree species richness and functional diversity promote productivity in European temperate forests across a large climatic gradient, mostly through strong complementarity between species. The results further highlight that this biodiversity effect emerges because species richness promotes higher diversity in shade tolerance and growth ability, which results in forests responding faster to mortality events. This study thus demonstrates that competition for light alone can entail a positive effect of biodiversity on productivity. I'll further discuss how such an approach may provide a new angle for studying mixed forest ecosystems in general (e.g. understanding why some species can co-exist in a same stand while other cannot), and the consequences of environmental changes on ecosystem functioning and services in particular.

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