

## RESILIENCE OF EUROPEAN FORESTS: TOWARDS A NON-EQUILIBRIUM VIEW FOR THE MANAGEMENT OF DIVERSITY

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### Introduction

Changes in the environment and in society expose forest managers to new challenges. In the environment, not only the climate is changing but also inputs of nitrogen and air pollution to a forest, for example. In society, not only timber is demanded from a forest but also a wide array of wood and non-wood goods and services. These include carbon sequestration and water holding capacity, biodiversity conservation, and recreation. Changes in the environment mean that the forest is no longer in equilibrium with the prevailing abiotic conditions. Consequently, the genetic composition for functional traits of trees needs adjustment, and it may even mean that the species composition of forests needs adjustment.

Classically, in genetic and ecological theories, the assumption is that the system is in a dynamic equilibrium. For example, in seed collection protocols it is generally assumed that all parent trees contribute alleles to a seed sample in proportion to the allele distribution in the parent population. However, a spa-

tial genetic structure may exist in the forest due to limited dispersal of pollen and seed rather than due to selection caused by local abiotic differences. The distribution of adaptive traits is therefore not yet in equilibrium with the distribution of abiotic gradients, such as moisture and nutrient availability, which influences an optimal sampling protocol. An ecological example of an implicit equilibrium assumption is succession of tree species. This is often considered a predictable sequence of events based on niche differentiation between species. Niche differentiation supposes that species either co-exist, because after a long evolutionary process they are sufficiently dissimilar, so that competitive exclusion is eliminated; or that the better competitor replaces the poor competitor under the prevailing conditions. The implicit equilibrium assumption is that the plant-to-plant interactions operate for a sufficiently long period for competitive exclusion to reach its conclusion. This assumption is disputed by the non-equilibrium explanation of species co-existence, discussed below.

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The validity of assuming equilibrium or non-equilibrium has been largely a rather abstract, academic discussion, especially in ecology. However, climate change requires an urgent response to the question of how to manage forests that are not in equilibrium with the local climate, in terms of both genetic and species composition. This challenging situation demands the rapid integration of genetic, ecological and silvicultural research to arrive at common standards for the evaluation of management options that aim to maintain genetic and ecological diversity in the forest and to provide the goods and services required by society.

A non-equilibrium concept of resilience is proposed in this paper as a tool for such an evaluation of the effects of climate change on forests by different scientific disciplines. With this concept of resilience, existing guidelines on forest management and general forest policies should be re-evaluated for their validity in the context of climate change.

The overall aim of this paper is to provide an introduction to the concepts of equilibrium, non-equilibrium and resilience in genetics and ecology, and to suggest guidelines for the management of forests in the face of climate change and varying societal demands.

### **Equilibrium and non-equilibrium concepts in ecology and genetics**

Equilibrium or non-equilibrium is assumed in many theories in genetics and

ecology, either implicitly or explicitly. The purpose of this section is, firstly, to present a general introduction on equilibrium versus non-equilibrium in ecology considering the co-existence of species and species distribution, and to discuss some of the underlying genetic and evolutionary assumptions. Secondly, this section aims to present a concise introduction to the concept of resilience from both equilibrium and non-equilibrium points of view.

### **Species co-existence**

Many alternative hypotheses on co-existence of plant species exist in the literature. Without going into the details of each of these, only the broad categories are considered here. One hypothesis assuming equilibrium between the species and the abiotic environment is based on the principle of the balance of nature, and another assumes non-equilibrium between the species and the abiotic environment due to variation in space and time in the species' environment. The equilibrium and the non-equilibrium approaches are often considered to be so fundamentally different that they are referred to as different paradigms (Hengeveld and Walter 1999).

The 'balance of nature' paradigm assumes that tree species living together in an area have a long history of joint evolution, which has resulted in each species becoming adapted to a specific set of biotic and abiotic conditions, which

together represent its niche. It is thus assumed that the climate is stationary relative to the rate of adaptation, although it is recognized that the climate and the abiotic environment are variable during that time-span. Abiotic conditions form boundary conditions to which a species must adapt so that it survives and reproduces in the first place. Nevertheless, differentiation between species is ultimately explained by biotic causes. This species differentiation results in prevention of competitive exclusion leading to sustainable coexistence and thereby species communities. Increasing specialization leads to increasing species diversity and increasing community complexity. Population dynamics are thus assumed to be mainly controlled by density-dependent factors leading to numerical equilibria between species. Research should focus on demographic behaviour of species, which is why the equilibrium paradigm is also termed the demographic paradigm in ecology (Hengeveld and Walter 1999).

The non-equilibrium paradigm, in contrast, recognizes that nature is variable in space and in time at all scales, and that stochastically occurring disturbances drive that variability. Hence, the adaptive response of species ever lags behind trends in both the climate and abiotic factors. Co-existence between tree species that share limiting resources is then explained by the fact that competitive exclusion is slow relative to ongoing disturbances that make these resources

available again, such as nutrients, water and space. A tree species must therefore 'track' the availability of suitable sites to regenerate, establish, grow and reproduce for its sustainable existence. This tracking of suitable sites can be either through dispersal of seeds and vegetative propagules to find those suitable sites at other locations, or by using a 'wait-and-see' strategy by establishing dormant seeds in a seed bank at the location where the adult plant is eventually replaced. In the non-equilibrium paradigm, evolution shapes a plant species with life history traits so that it uniquely responds to competitors, climatic factors and the availability of regeneration sites created by disturbances. The non-equilibrium paradigm thus focuses on the individualistic behaviour of tree species, which is why this paradigm is also called the autecological paradigm (Hengeveld and Walter 1999).

### **Geographic range of tree species**

Much of the assessments of the impact of climate change on species distribution are based on modelling studies that ignore genetic processes. Species distribution models can be grouped into two general classes: climatic envelope models, and dynamic models.

Climatic envelope models assume, firstly, that climate exerts a dominant control over the natural distribution of species (Pearson and Dawson 2003), and, secondly, that the current species range is

in equilibrium with its climatic potential area. If valid, statistical correlations between climate variables at the limits of the species' geographical distribution can be used to describe current ranges. Critical macroclimatic factors include minimum frost temperature, duration of the growing season, and indicators of water stress during the growing season. Implicitly it is thus assumed in these models that physiological mechanisms have evolved, such as (1) frost hardiness of vulnerable tissues to tolerate frosts; (2) perception of cues from the environment, such as photoperiod or chilling, and forcing requirements to break dormancy for the synchronization of the climatic seasonality of the site with the active growing phase of the tree; and (3) stomatal mechanisms or a hydrological architecture to avoid or tolerate water stress.

Dynamic models for the range of tree species can again be broadly divided into two classes. One class of models dynamically considers physiological limiting mechanisms for winter cold tolerance, drought tolerance, and either photoperiod or forcing and chilling requirements to break dormancy and start the growing season (Sykes et al. 1996). These limiting mechanisms are often also represented by bioclimatic variables, hence with essentially the same genetic assumptions on tolerance as the envelope models. The second class considers forest succession models that include not only descriptions of the physiological limiting factors, but

also biotic interaction, including competition for limiting shared resources such as light, water and nutrients (Prentice et al. 1991), and dispersal of propagules and the occurrence of stochastic disturbance events (Kramer et al. 2003). In addition to implicit genetic assumptions on adaptation to abiotic factors, forest succession models assume adaptation to biotic interactions too. These models are therefore explanatory tools for transient dynamics following environmental changes, as well as for eventual equilibrium states.

Both the climatic envelope models and the dynamic models based on bioclimatic variables thus follow the equilibrium paradigm, whereas the forest succession models based on gap-phase replacement assume the non-equilibrium hypothesis. In the face of climate change, land use change, nutrient deposition and pollution, equilibrium models cannot produce a reliable future projection of even the potential distribution of plant species or biomes, and we therefore need to apply non-equilibrium approaches.

### **Resilience**

The concept of resilience differs fundamentally between the equilibrium and non-equilibrium paradigms. In equilibrium theory, resilience is the time required to return to a stable state (Pimm 1991). The quicker the return time, the larger the resilience, and therefore the system is more predictable. In genetics and ecol-

ogy, much of the theory is developed to determine equilibrium conditions, and therefore the return rate to a stable state. In ecology, examples of equilibrium approaches include the widely-used Lotka-Volterra equations and refinements thereof, and the resource-ratio equations of Tilman (1985) to assess the possible co-existence of plant species. In genetics, stable states are described by the Hardy-Weinberg equilibrium of allele frequencies, and assessments of the effects of selection pressure thereon. The time to return to pre-disturbed equilibria can be calculated based on first-order derivatives. A technical but crucial point of this theory is that it applies only to *small* deviations from the stable state.

This notion of resilience is equivalent to stability, or, more precisely, to neighbourhood stability (Lewontin 1969). Neighbourhood stability needs to be distinguished from temporal stability, which refers to constancy or lack of variability.

In non-equilibrium theory, resilience refers to the conditions that allow a system to absorb changes in the environment and still persist (Holling 1973). This notion of resilience recognizes that random events, spatial heterogeneity and changes in external drivers can bring a system to a state far from equilibrium. Changes in climate, land use, nutrient deposition and pollution may very well push the system so far from equilibrium that stability analysis is no longer applicable.

Therefore, an alternative approach is needed to the classical theory on return time to a pre-disturbed stable state.

In ecology, much research is done on the importance of spatial processes, including disturbances (Tilman and Kareiva 1997) and dispersal limitation in fragmented landscapes, as exemplified by many studies on metapopulation dynamics (Hanski and Gilpin 1997). A general condition for a resilient metapopulation is that there should be sufficient connectivity between habitat islands to allow a metapopulation to persist despite recurring local extinction.

In forest genetics, an example of this notion of resilience is the often-stressed importance of having sufficient genetic variation in a forest as a general condition to allow adaptation. However, relatively new is the insight that populations are not in Hardy-Weinberg equilibrium for adaptive traits, nor for genetic markers. Indeed, spatial genetic structure in both adaptive traits and genetic markers (see case study below) is often found, violating the elementary assumption of the Hardy-Weinberg equilibrium. This urges us to study gene flow through pollen and seeds, which is now possible as a result of techniques using the highly polymorphic genetic markers that are available for many tree species.

Hence, in both genetics and ecology, the scientific approaches move from the demographic, population-genetic,

equilibrium point of view towards the individualistic, autecological and non-equilibrium point of view. However, scientific insight has not yet resulted in refined forest management strategies to maximize adaptive potential of tree species. An example of a study that aimed to provide the first steps in that direction is outlined below.

### Case study on the management of European beech

The DynaBeech project was aimed to bridge genetics and ecology to provide management recommendations for sustainable management of European beech (*Fagus sylvatica*) (Kramer 2004). The interactions between selection for adaptive traits, gene flow and management practice were studied to evaluate the impacts of forest management on the dynamics of genetic and ecological diversity of European beech. The overall aim was to assess the adaptive potential of beech, as a model tree species, to environmental changes based on its genetic and ecophysiological characteristics. Three sub-aims were formulated: (1) the development of a coupled genetic–ecological individual-tree model and its parameterization for beech, either based on field studies performed within the DynaBeech project or obtained from literature sources; (2) the evaluation of the adaptive response of a beech stand to environmental changes (through sensitivity analyses of (a) initial genetic diversity, (b) pollen dispersal distance, (c) herita-

bility of selected phenotypic traits, and (d) forest management, ranging from the least intensive system without management to the most intensive system represented by so-called sheltercut management); and (3) the evaluation, by model simulation, of the responses of selected phenotypic traits and their genetic diversity to a range of management systems applied at the study plots.

In summary, the main results of the DynaBeech project were:

**Gene flow:** a substantial proportion of pollen was coming in from outside the stands (44.6% and 71.8% for the Sainte-Baume and Ventoux sites, respectively (G.G. Vendramin, personal communication). The results of the sensitivity analyses showed that, with a short pollen dispersal distance, the genetic diversity decreases over time, and more so in the sheltercut system compared with a no-management system. Thus, long-distance gene flow can be an important mechanism to counteract the loss in genetic diversity caused by selection and drift (Hamrick 2004).

**Heritability of phenotypic traits:** selective responses are low if the heritability is low, and vice versa. The results of the sensitivity analysis show that genetic diversity indeed declines with increasing heritability of a functional trait under the sheltercut system. In that system, selection on emerging recruitment is allowed to operate about every 120 years,

thereby removing poorly adapted saplings and thus reducing genetic diversity. Such a trend is much less apparent in the no-management system because effective selection moments are determined by the longevity of beech, i.e. about 250 years.

**Selection pressure on a trait:** a given environmental change will not affect all traits similarly. In DynaBeech, we evaluated four types of trait: (1) a neutral trait, which is selected neither for nor against, and changes due to genetic drift only; (2) bud burst day, which changes due to natural selection only; (3) spiral grain, which changes due to artificial selection only; and (4) height growth rate, changing due to both natural and artificial selection. Based on the simulated responses, the selection pressure imposed on the selected traits increases in this order and genetic diversity decreases proportionally to the selection pressure. Of the adaptive traits, bud burst day shows a small response, and height growth rate shows a strong one, even though the heritabilities were set to the same value in the model.

**Recruitment interval:** the rate of adaptation of trees to environmental changes depends not so much on the longevity of individual trees, but on successful recruitment events during the lifetime of a tree. Recruitment interval is in most forests determined by the management practice rather than through natural forest dynamics. Our modelling analysis

on the effects of forest management at 10 study sites showed that the loss of genetic diversity is directly related to management activity, which increases from the no-management system to the sheltercut system (with several management regimes of intermediate intensity). The results indicated that selection mainly operates during recruitment events. Hence, the duration of the interval between the recruitment events is an important factor determining the adaptive response of the forest.

Overall, the modelling results indicated that the highest level of genetic variation is maintained in a forest by applying no forest management. However, the no-management regime also led to a spatial genetic structure for some traits, hence inbreeding circles. If environmental conditions change, this system is the least suitable, as there are few moments in time where adaptation most effectively operates, i.e. the recruitment stage. These adaptive moments occur more frequently with increasing management intensity, thereby increasing the selective response of adaptive traits. This takes place with a minor loss of both genetic diversity and potentially adaptive alleles.

Hence, by spatial-explicit modelling of competitive interactions between individual trees, dispersal of seeds and pollen, and including a simple genetic model to allow adaptive responses of functional traits, the non-equilibrium approach to the dynamics of a beech forest

is applied, while allowing equilibria in frequencies of alleles for adaptive traits. The modelling tool, named FORGEM, can be used to assess transient responses of tree populations and tree species composition to climate change and to determine optimal forest management to meet multiple goals.

An interesting observational result was that in the virgin forest site of Dobra, indications existed of a spatial structure for bud burst phenology. This suggests that so-called 'inbreeding circles' of closely related adults occur in a group rather than throughout the forest. In the half-sib experiments of DynaBeech, phenology was found to have a relatively high narrow-sense heritability (Teissier du Cros et al. 2004), and in the full-sib trial, indications of quantitative trait loci were found for bud burst (Scalfi et al. 2004). This makes bud burst phenology a good candidate to assess phenotypically whether a spatial genetic structure exists in a forest, without extensive laboratory tests. It is still under debate whether bud burst phenology of beech is also a good candidate for the evaluation of climate change effects because the experimental findings on a control by either photoperiod or temperature or both are conflicting (Falusi and Calamassi 1990, 1996; Heide 1993a, b).

### Conclusions and recommendations

Society demands today from forest managers not only a reliable supply of

timber in sufficient quality and amount, but also a wide array of goods and services, ranging from carbon sequestration, biodiversity conservation, water retention and purification to aesthetic values. Guidelines for forest management to optimize the genetic diversity in a stand for a sustainable yield must therefore be embedded in guidelines for the management of other forest functions.

Changes in climate, land use, nitrogen deposition and air pollution occur simultaneously, resulting in a situation where stands, forests and species distributions are no longer in equilibrium with the prevailing abiotic conditions. This situation demands that forests be managed in a way that enables adaptation (in a genetic sense) and adjustment (in an ecological sense) to such changes. Genetic diversity, structural diversity and species diversity are, in general terms, conditions that allow the forest to adapt and adjust.

From a research point of view, more integration between genetic, ecological and silvicultural disciplines for the management of diversity is required. This should include studies on stand productivity, tree species composition of forests, biogeochemical cycling at the landscape scale, and changes in geographic distributions of tree species. It is essential that both field studies, e.g. provenance trials, and modelling studies, should be used simultaneously to complement each other. Additionally, common quantifica-

ble concepts should be developed. Here the concept of resilience, defined as the conditions that allow a system to absorb disturbances and environmental stress, should be made operational and quantified for both genetic and ecological aspects of diversity at the stand, landscape and regional scales. From a genetic point of view, the resilience concept is already quite well developed at the stand scale with the importance of maintaining genetic diversity, whilst taking a spatial genetic structure and limitations of gene flow into account. Matching ecological concepts may, however, need further attention.

From a forest policy point of view, the current situation is that international policies on biodiversity, such as the Convention on Biological Diversity (CBD), recognize that humans have caused a dramatic loss in biodiversity. This has led to the development of policies and management guidelines aiming to prevent ongoing loss and to restore biodiversity. Such guidelines, protocols and (inter-)national policies on forest genetics should reflect the realization that classical equilibrium concepts may no longer be valid for systems that are now essentially in non-equilibrium due to climate change. Implementation of policies aiming at returning to a pre-disturbed reference situation may therefore not be feasible and the resilience of forests to ongoing environmental change becomes of central importance.

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