

From Observations to Evidence About Effects of Mixed-Species Stands

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Abstract

A critical understanding of the scientific evidence that we have about the effects of tree species diversity on ecosystem properties and processes is required to guide practical forest management as well as future research. However, current understanding is limited by the lack of an appropriate framework for evaluating the reported evidence. In this chapter we outline how research on mixed-species forests may fit into concepts of ecosystem hierarchy and how previous studies may be ranked regarding their level of evidence. We introduce the most important hypotheses and theories underpinning research on the relationship between tree diversity and ecosystem functioning and illustrate how these may be tested by analyses of forest inventories, experiments, and exploratory research platforms or a combination of these.

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2.1 Introduction

It is important to have a framework for assessing the quality and reliability of our knowledge about mixed-species forests. Not all knowledge that we find documented in textbooks, journal articles, or other media is of equal value. The scientific evidence underpinning this information can vary greatly and so does the confidence that we can place in this information (Forrester and Pretzsch 2015). For example, already in 1828 the early forest scientist Heinrich von Cotta claimed ‘Since not all tree species utilise resources in the same manner, growth is more lively in mixed stands and neither insects nor storms can do as much damage; also, a wider range of timber will be available everywhere to satisfy different demands. The quest to establish pure stands everywhere is based on an old and most damaging prejudice ...’ (Cotta 1828, p. 155, translated by authors). At that time, this expert judgement of Cotta was simply a notion and was likely based on observations in the field. Furthermore, since the history of modern scientific experiments in forestry began only at the end of the nineteenth century, we can safely assume that Cotta’s impressions regarding growth in mixtures did not benefit from the rigour of controlled experiments. The foundation of the International Union of Forest Research Organizations (IUFRO) in 1892, which initiated coordinated experiments and international research collaboration, can be regarded as a landmark event in this regard.

Nowadays there is a strong demand to embrace standards of evidence in most scientific fields. The ideas and concepts developed to support ‘evidence-based medicine’ are now central to fields such as ‘evidence-based conservation’ (Sutherland et al. 2004) and are also influencing the forest sciences (Binkley and Menyailo 2005; Petrokofsky et al. 2012). The demand for evidence-based forestry, similar to evidence-based conservation practice, reflects the current situation where most decisions are based upon expert judgement and anecdotal sources, as opposed to evidence, and where very little evidence is collected on the consequences of particular practices (Sutherland et al. 2004). For that reason, Binkley and Menyailo (2005) proposed a rating scheme for the confidence warranted in forestry studies (Fig. 2.1). This scheme can be easily applied to all knowledge on mixed-species

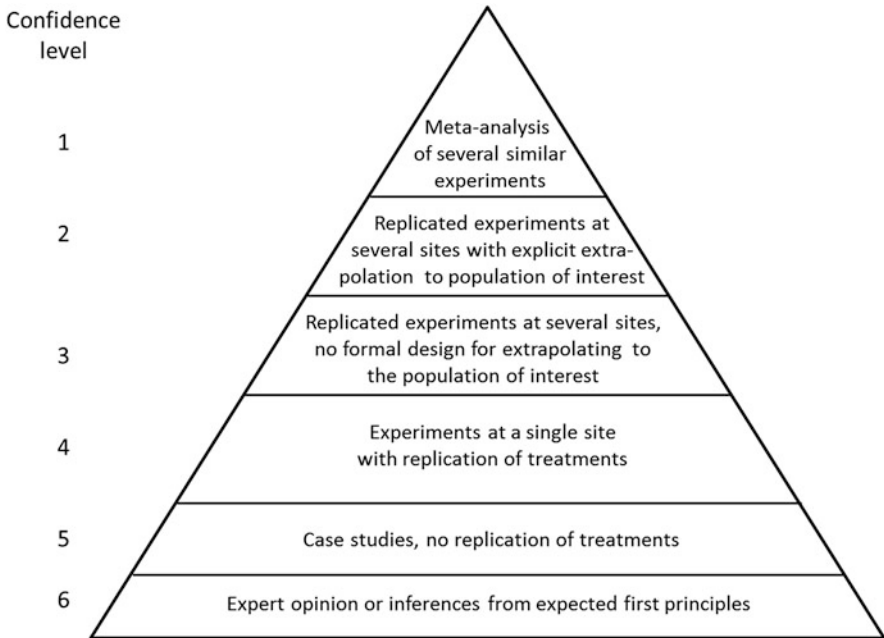


Fig. 2.1 Hierarchy of confidence warranted in forestry studies and experiments ranging from expert opinions (6 = lowest level) to meta-analysis (1 = highest level); adopted from Binkley and Menyailo (2005). See text for examples of these different levels of evidence

forests. In this context, statements by early proponents for mixed-species silviculture can be regarded as expert opinions gained from observations (e.g. Möller 1922, and others in Chap. 1). Replicated experiments at single or multiple sites have greatly improved our understanding of processes and ecosystem functioning in mixed-species stands in tropical, subtropical, and temperate regions (e.g. Bauhus et al. 2000; Scherer-Lorenzen et al. 2007; Potvin and Gotelli 2008; Yang et al. 2013). Whereas, in the past, when studies were conducted at multiple sites, the variation in the response variable among sites was often treated as noise, recent studies explicitly analyse that variation to identify the influence of environmental factors, such as temperature or precipitation on performance of mixed-species communities (e.g. Forrester et al. 2013; Toigo et al. 2015). A high level of evidence has been achieved in particular aspects of mixed-species forests. Meta-analyses have been carried out that confirmed consistent effects of mixtures on productivity (Piotto 2008; Liang et al. 2016), tree nutrition (Richards et al. 2010), or susceptibility to herbivory (Jactel and Brockerhoff 2007; Castagneyrol et al. 2014).

To facilitate a better appreciation of the information provided in this book, we will describe in this chapter the spatial and temporal scales and the different approaches that can be used to study ecological interactions between different tree species and the effects of mixed-species stands on ecosystem properties and processes. Beforehand, we will reflect on some important ecological hypotheses

and theories related to mixed-species stands, since the exploration of these theories and testing of these hypotheses also determines the design of studies in mixed-species forests.

2.2 Hierarchical Levels of Patterns and Processes for Analysing Mixed-Species Stands

Forest ecosystems are enormously complex, self-organised systems that behave in non-linear ways (Messier et al. 2013). They contain vast numbers of species and individuals of a wide range of taxonomic groups that interact continuously with each other and with their abiotic environment. The complexity of such systems typically increases with the number of dominant tree species, which are again associated with specific species of different taxonomic groups (mycorrhiza, herbivores, etc.). In addition, processes in forest ecosystems occur at vastly different temporal and spatial scales, from seconds to thousands of years, and from the cellular to the continental level (Fig. 2.2). Scientists have therefore struggled to find appropriate approaches to analyse such systems (Looijen 1998). One such approach follows a reductionist paradigm. Here, the aim is to simplify complex systems by breaking them down into a number of subsystems that can be analysed separately one after the other. The results of these analyses of subsystems are then tried to be integrated and applied to the whole system. In ecology, this approach has been critiqued for a number of reasons including the possibility of failing to recognise important interactions between the subsystems and emergent properties of the whole system that result from these interactions.

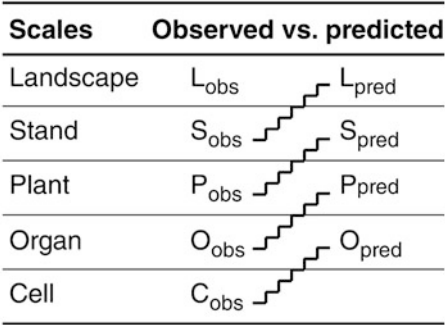


Fig. 2.2 Mixed-species stands’ research by scale-overlapping analysis of structure and processes reaching from cell to organ, plant, stand, and landscape level (denoted C, O, P, S, L). The observed system variables at a certain level ($C_{obs}, O_{obs}, P_{obs}, S_{obs}, L_{obs}$) can be used to predict the expected behaviour for the next higher level ($O_{pred}, P_{pred}, S_{pred}, L_{pred}$) through linear temporal or spatial upscaling (symbolised by the ladders). Deviations between the observed and predicted values at the next higher level indicate knowledge gaps and the limited relevance of lower-level processes for system behaviour at the next higher level (Pretzsch 2009, p 30)

A contrasting approach to deal with complexity of systems is holism, which regards the whole system as more than the sum of its parts or subsystems. This approach explicitly attempts to analyse the interactions between all parts of complex systems and considers all relevant spatial and temporal scales. It is obvious that holistic approaches to analyse complex ecosystems require an enormous amount of effort to study all the possible relationships and interactions between the entities of the system. This is in most cases not achievable.

Given the advantages and disadvantages of these two contrasting approaches, it is not surprising that a complementary approach combining the best aspects of reductionism and holism was developed. In hierarchy theory (Allan and Starr 1988), a reduction in complexity is accomplished on the one hand by concentrating on one single research question and relevant entities of the whole system. On the other hand, this approach considers different hierarchical levels of the system that operate at different spatial and temporal scales and explicitly analyses the processes and interactions between these levels.

The structures and processes at the different hierarchical levels of ecosystems are characteristically interwoven and obey their own principles: the upper levels exert pressure or constraints downwards through regulating processes (top-down control), whereas the lower levels influence the upper levels via other constraints and signals (bottom-up control) (Müller 1992; Ulrich 1994). For example, tree and stand structure regulate atmospheric deposition of elements into forest stands, as well the interception of radiation and precipitation, and determine the initial and limiting conditions for processes at the organ level (e.g. leaf). Processes between trees and the environment such as transpiration or processes at the individual scale such as assimilation and allocation of carbon are dominated by the temporal and spatial processes and structures at the levels above (Fig. 2.2).

Processes that operate on long time scales and moderate to large spatial scales possess a higher level of integration and are more than just the sum of the subordinate processes. The feedback mechanisms between processes at the same or different hierarchical levels shape the characteristic behaviour of biological systems, which cannot be deduced from an isolated view of the underlying elements and processes. Despite all the experimental accuracy, knowledge about soil chemical, biochemical, or physiological processes at a high spatial and temporal resolution (low level of hierarchy) cannot replace investigations at higher levels of integration such as forest growth research at long-term experimental plots. Hence, it is problematic to scale up from lower levels of ecosystem hierarchy to predict system responses at higher levels of hierarchy. For example, in the context of acid rain research, the predictions on growth and productivity of forests that were based on insights about the effects of acid deposition on tree organs, soil chemistry, input-output element balances, fine roots, and other plant organs did not match the actual observations that forest productivity increased over the same period (Spiecker et al. 1996; Pretzsch et al. 2014). Obviously, not all lower-level processes exert a strong enough signal to influence ecosystem behaviour at the higher level, and not all higher-level processes that buffer lower-level processes had been adequately considered.

Likewise, we can observe negative interactions between tree species in mixed stands that can be quantified as lower foliage nutrient concentrations (e.g. Richards et al. 2010) or reduced rooting depth of one species when compared to its performance in monocultures (Schmid and Kazda 2001). Yet, growth of this species, and others for that matter, may still be improved owing to compensatory mechanisms in other organs and at other spatial and temporal scales. Also the growth of individual trees for a given tree size may not differ between monocultures and mixtures. However, owing to niche complementarity, the packing of trees in mixed stands may be higher and thus a higher productivity can be achieved at the community level (e.g. Jucker et al. 2015, and see Chap. 4).

Currently the investigations of tree and stand growth are developing towards higher spatial and temporal resolution and refined causal explanations of structure and functioning. However, often scientific findings at the gene, cell, or organ level do not have any clear relevance at the tree or stand level. For example, stand-level growth across longer periods of time cannot be extrapolated effectively from short-term measurements of small parts of a few trees. Feedbacks between processes either within the same level or between different hierarchical levels influence the characteristic behaviour of ecosystems, which cannot be understood by considering the subprocesses in isolation. A solid understanding of mixed-species stand dynamics requires measurements at multiple hierarchical levels, e.g. stand and tree level, or tree and organ level. To understand the development of organs, trees, or stands, investigations should be conducted at multiple temporal and spatial scales as shown schematically in Fig. 2.2. When the results from observations at the plant level (P_{obs}) (e.g. increment or mortality of individual trees in relation to stand density) are scaled up, they predict certain expected patterns at the stand level (S_{pred}). The temporal or spatial upscaling to the higher level (symbolised through the ladders in Fig. 2.2) may be carried out through simple addition or multiplication or by modelling. If measurements at the stand level (S_{obs}) (e.g. long-term records of stand development based on repeated inventories) do not match the expected pattern ($S_{\text{obs}} \neq S_{\text{pred}}$), this indicates some kind of buffering of the signal from the lower level and is probably attributable to reduced relevance of the processes at the individual plant or species level for explaining the system behaviour at the stand or community level. For example, through competitive reduction, mortality of species A in mixture may be lower than in monoculture. Obviously, the transition from tree to stand level introduces new effects, which cannot be deduced from the individual plant or species level owing to ecological interactions (e.g. facilitation, antagonism) and acclimation of individual species to the situation in mixed-species stands. The discrepancy between predictions and observations at the particular system level can be used as a basis to formulate new hypotheses. Hence, research approaches that integrate over different levels of system hierarchy facilitate assessment of the relevance of results at a certain level for the next higher hierarchical level and often help to identify knowledge gaps. In this book we therefore aim to study the effects of mixing tree species from the organ and tree level (Chaps. 4–6) to the cohort level (Chap. 5), community and stand level (Chap. 6), and even management block and forest company level (Chap. 10).

2.3 Some Basic Ecological Concepts Related to Mixed-Species Stands

2.3.1 Biodiversity and Ecosystem Functioning

Prior to reflecting on how knowledge about mixed-species forests has developed over time from observations, forest inventories, and experiments, it is important to reflect on some ecological hypotheses and theories related to mixed-species forests, because this will inform us about the adequacy of the different approaches to study mixed-species forests.

Most relevant to our considerations are the concepts that link biodiversity to ecosystem functioning. Here we will concentrate on the effects of tree species richness and diversity, which may also be expressed as the diversity of functional traits, on ecosystem processes. This is not a new question and has occupied ecologists and forest scientists for quite some time (Scherer-Lorenzen et al. 2005a). In ecology, this question has been mostly driven by the concern about the loss of biodiversity. A typical question that has been asked is: what happens to ecosystem functioning if we lose species from the ecosystem or community? This focus on the relationship between biodiversity and ecosystem functioning can be regarded as a paradigm shift in ecology, where previously a major objective was to understand the regulation and maintenance of biological diversity. Hence, biodiversity moved from a response variable to an explanatory variable (Hillebrand and Matthiessen 2009). The book by Schulze and Mooney (1993) on biodiversity and ecosystem functioning is often regarded as a landmark publication that represents this shift.

In forest sciences, the focus on mixtures started earlier, and this was initially not motivated by the question of what happens if we lose tree species from a forest community, but by the question of what can be achieved, mostly in relation to productivity and ecological stability, if we reintroduce species to forests that had previously been simplified, for example, through conversion to monocultures (see previous chapter). This has often resulted in the study of two-species mixtures (e.g. Wiedemann 1942; Pretzsch 1995, 1997; Forrester et al. 2006). Today, where forestry is concerned about providing the whole range of ecosystem goods and services, and where we are experiencing the loss of tree species from large regions, forest scientists have equally embraced the biodiversity and ecosystem functioning paradigm to carry out interdisciplinary studies jointly with ecologists to study the effects of tree species diversity on ecosystem functioning (e.g. Baeten et al. 2013; van der Plas et al. 2016; Verheyen et al. 2016). While a large range of response variables such as those related to nutrient and water cycles, herbivory, pathogens, decomposition, dependent taxonomic diversity, and many others are typically being analysed in these studies, they all include productivity as an important and integrative measure of ecosystem functioning. Productivity may be regarded as an important ‘performance currency’ of vegetation communities of forest stands (*sensu* McGill et al. 2006) and will therefore feature as an important dependent variable in this chapter and book.

Many different theories exist about how the magnitude of ecosystem processes or properties could respond to changes in species or functional diversity (e.g. Naeem 2002). The patterns of this relationship depend on a range of factors including the degree of dominance of the species lost/removed from, or added to a community, the type and strength of interactions with other species, the functional traits of species lost from the community, added to it, and from those remaining, and the relative strength of biotic versus abiotic control over the ecosystem process or property (Hooper et al. 2005).

Theories describing the relationship between species diversity and ecosystem functioning vary in attribution of importance to individual species effects on ecosystem functioning. For example, the **redundancy hypothesis** assumes that the magnitude of ecosystem processes or properties increases with the number of species in the ecosystem, but only up to a point beyond which additional species become redundant and do not have any further effect on the magnitude of the particular ecosystem process or property (Fig. 2.3). Or if we follow the curve from the right side, the loss of (redundant) species is compensated by other species remaining in the community that have similar functional traits to those that have been lost. The lower the total number of species in a community, the lower is the probability that species are functionally similar, for example, in a mixed-species boreal forest, where most genera are represented only by one or two species (Pastor et al. 1996). Hence, the redundancy hypothesis is closely linked to the insurance hypothesis, which assumes more stable ecosystem functioning at higher levels of species richness in the face of stress and disturbances (Yachi and Loreau 1999).

A similar response pattern may also be attributed to a **sampling effect** for dominant species, where the maximal magnitude of the response variable is also achievable with particular combinations of species at low levels of diversity or species richness. The increase in average magnitude of the response variable is attributable to the increasing probability of including the most effective species with increasing species richness (Wardle 1999; Hooper et al. 2005).

The **complementarity hypothesis** assumes that the magnitude of ecosystem processes and properties increases with the number of species through positive interactions such as complementarity or facilitation among species. Each species added to an ecosystem contributes to the magnitude of ecosystem processes, although the increase in the magnitude of a particular process increases decrementally as more species are added to the system, following the law of diminishing marginal benefit.

In addition, one might assume that there is no fixed relationship between species richness/diversity and ecosystem functions. This may be the case if the latter are dominated by abiotic factors, or when there is a strong overlap of resource use by different species, or if the ecosystem property or process is strongly dominated by one particular species that is present at all levels of diversity (Hooper et al. 2005). In this case, not the number but the identity of species present in a given community would be important.

Which of these and other theories receives most empirical support is not certain. This varies, for example, with the particular ecosystem process or property that is

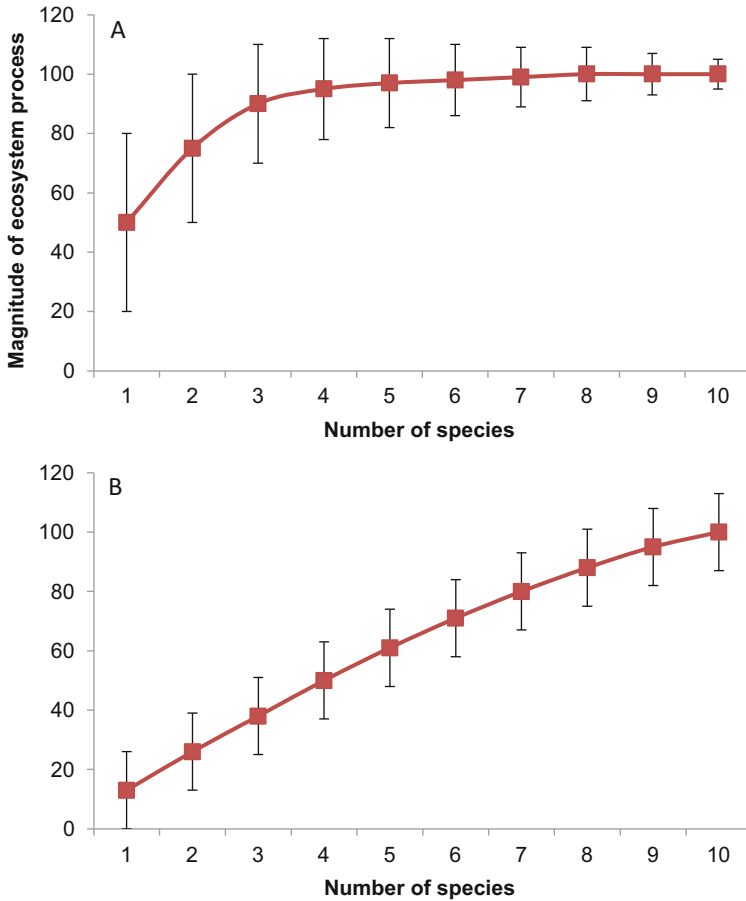


Fig. 2.3 (a and b) Some hypotheses considering the relationship between species numbers and ecosystem functioning. (a) **Redundancy hypothesis**: magnitude of ecosystem processes increases with the number of species in the ecosystem, but only up to a point beyond which more species are redundant and do not have any additional effect on the average magnitude of the particular ecosystem process; however, the variability of that process may still decrease further with species richness. A similar response pattern may also be attributed to a **selection effect** for dominant species, where the maximal magnitude of the response variable is also achievable with particular combinations of species at low levels of diversity or species richness. The increase in average magnitude of the response variable is attributable to the increasing probability of including the most effective species with increasing species richness (Hooper et al. 2005). (b) **Complementarity hypothesis**: The magnitude of ecosystem processes increases with number of species through positive interactions such as complementarity or facilitation among species. Each species added to an ecosystem contributes to the magnitude of ecosystem processes, although the increase in the magnitude of a particular process increases decrementally as more species are added to the system. Once there is at least one representative species of each functional type, the effect of increasing species numbers should begin to saturate. At which point the relationship saturates depends on the degree of niche overlap among the different species (Hooper et al. 2005). Below this saturation point, any change in species numbers leads to a change in the magnitude of the ecosystem process

being regarded as a response variable and with the scale at which species richness or diversity is being analysed. In communities with few species, the left parts of Fig. 2.3a and b, it may be difficult to differentiate between the different response patterns and hence theories. This may be the case for many forest ecosystems in boreal and temperate regions (see Chap. 1). To identify which of these different hypotheses apply for certain ecosystems, it is necessary to compare the performances of individual species in mixtures and monocultures (e.g. Loreau and Hector 2001; Bruelheide et al. 2014).

Often relationships between tree diversity or species richness and ecosystem functioning are depicted for a measure of productivity, which is our ‘performance currency’ of tree communities *sensu* McGill et al. (2006). On average, this relationship between tree diversity and forest productivity is positive across the major biomes (Forrester and Bauhus 2016; Liang et al. 2016). When other ecosystem functions are being regarded, the relationships between tree diversity/species richness and the particular ecosystem property or process are often less clear or follow different patterns; they may decline with high levels of species diversity (e.g. Gamfeldt et al. 2013), or there may be outright negative effects between species diversity and ecosystem functioning, for example, with regard to drought resistance or groundwater recharge in forest ecosystems (Grossiord et al. 2014).

The effects of tree species richness or diversity on ecosystem functioning depend largely on the type and intensity of ecological interactions that occur within particular species mixtures at a given site, and this is in turn driven by the particular attributes of species or their functional traits (Forrester and Bauhus 2016). For example, the magnitude of a range of ecosystem pools and processes in a mixed-species forest consisting only of evergreen coniferous species is likely to be less than in a forest consisting of the same number of species but covering a wider range of functional types, e.g. including pioneer small-leaved hardwood species, shade-tolerant and deep-rooting deciduous species, etc. Functional traits such as rooting depth, shade tolerance, wood density, specific leaf area, etc. determine the niches that species can occupy (fundamental niche), and the ecological interactions such as competition determine the actual niche of a species within a community at a given site (realised niche).

In the next sections we will therefore cover the concepts of niches, functional traits, and ecological interactions.

2.3.2 Fundamental and Ecological Niches

The concept of fundamental and realised niches as n -dimensional spaces, where every factor that influences the survival and fitness of a species such as temperature, moisture, or soil chemical reaction represents one dimension of this space, is commonly traced back to Hutchinson (1957). The fundamental niche describes the multidimensional space in the environment, where a species could potentially grow and reproduce. It is largely determined by the physiology of a given species,

which reflects its evolutionary adaption to environmental conditions such as temperature, and the availability of water, light, and nutrients.

Fundamental niches are typically quantified by measuring growth or surrogates for it in relation to the variation of environmental variables, for example, to develop physiological response curves such a growth in relation to light availability (McGill et al. 2006). To describe the full physiological niche of a species, growth response curves would have to be determined in relation to all other factors that influence growth. The fundamental niche of a species is not constant and may change with the ontogeny of individuals (Poorter 2007). For example in trees, shade tolerance is often higher in seedlings than in mature trees of the same species. Hence, analyses of species differences commonly focus on a particular attribute, e.g. photosynthesis in relation to light availability or transpiration in relation to soil water potential, but do not attempt to quantify complete niches, which would be extremely difficult if not impossible.

The realised (or ecological) niche describes the multidimensional, not physical, space in the environment that is actually occupied by a species. Hence, it is a functional concept that describes the role that a species plays in an ecosystem and the factors that are required for its growth and survival. In most cases, the realised niche is a subset or proportion of the fundamental niche, where the actual occurrence of a species is limited by dispersal, disturbances, and biotic interactions. However, biotic interactions such as facilitation (see below) that benefit a species may also expand its realised niche, even if only in one or few dimensions of the environmental space. Current approaches to depict realised niches involve, for example, habitat modelling, where the occurrences of species are related to geographically referenced environmental variables. These concepts will be explained below using a two-species model.

The overlap in fundamental niches of species is a necessary, though insufficient prerequisite for determining whether species can co-occur in mixtures (Fig. 2.4a). A mixture of species may occur only at sites, where their fundamental niches overlap in terms of resource availability and environmental conditions (Fig. 2.4b, grey area). In man-made ecosystems such as plantations, these may be species that do not occur together in the natural environment, for example, when they originate from different forest types or even continents.

It is often assumed that, under steady-state conditions, the fitness of a species, measured as growth, reproductive rate, etc., is highest near the centre of the fundamental niche. If only one dimension of the niche space is depicted, this may be illustrated as an optimum curve in relation to the respective environmental variable (Fig. 2.5). Based on this concept we can assume that if a site lies near the centre of the fundamental niche of species 1 (Fig. 2.4b, site p), then intraspecific competition among individuals of this species is higher than interspecific competition with individuals from species 2, because species 2 occurs at the fringe of its niche at site p. However, under changing environmental conditions (Fig. 2.4c), site p represents the area of worst possible conditions or mortality for species 2.

Through the competitive influence of the two species on each other (e.g. shading, physical damage), the width of the fundamental niche of each species may be

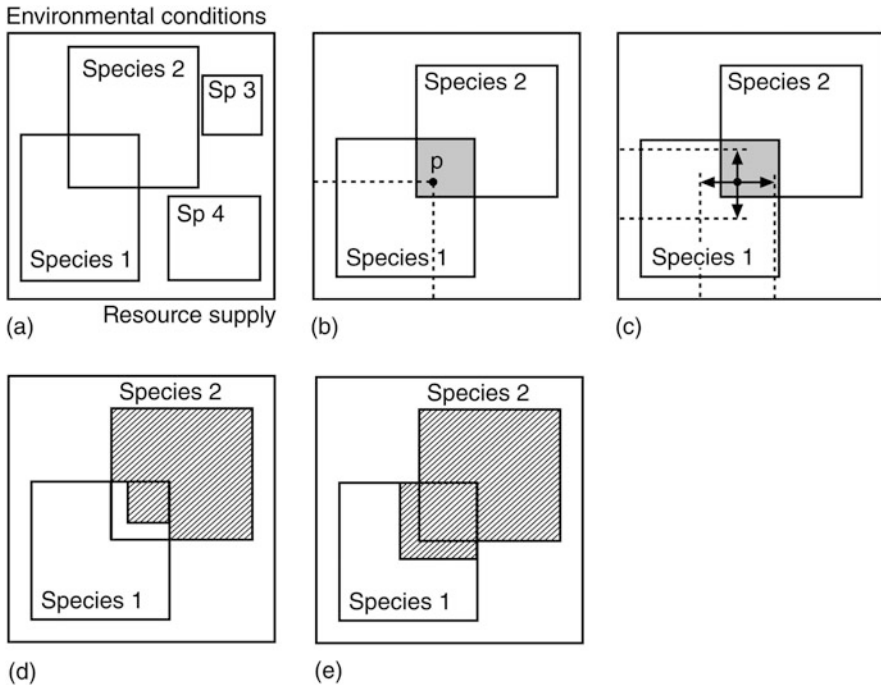


Fig. 2.4 (a–f) Overlap of fundamental and realised niches as a prerequisite for a stable, productive species mixture: (a) fundamental niches of species defined by their potential occurrence in a matrix of resource supply and environmental conditions, (b) species 1 and 2 have a common niche (grey area) which includes site p, (c) resource supply or environmental conditions at site p can fluctuate (arrows) so that they extend beyond the fundamental niches of species 1 and 2, (d) the realised niche of species 2 can be restricted (hatched area) due to competition by species 1, or (e) the realised niche of species 2 can be extended (hatched area) with the admixture of species 1

restricted to a realised niche that is narrower than the fundamental niche. The area of possible coexistence of two species, therefore, may be smaller than the intersection of their fundamental niches. For example, species 1 causes a reduction in the fundamental niche of species 2, so that species 1 and 2 can coexist only in the hatched area (Fig. 2.4d). This reduction of the realised niche, or even the competitive exclusion of a species, occurs frequently when species differ greatly in competitive strength. In the case of trees, this may be related to differences in height growth development (species-specific ontogenesis), final height, and shade tolerance. The limited access of the inferior species to light can lead to a permanent decline and, ultimately, in the absence of disturbance, to the elimination of a species from a forest stand.

The realised niche of a species can also be extended through facilitative interactions with other species. For example, N-fixing species may facilitate establishment and growth of a species at nutrient poor sites where it could not otherwise

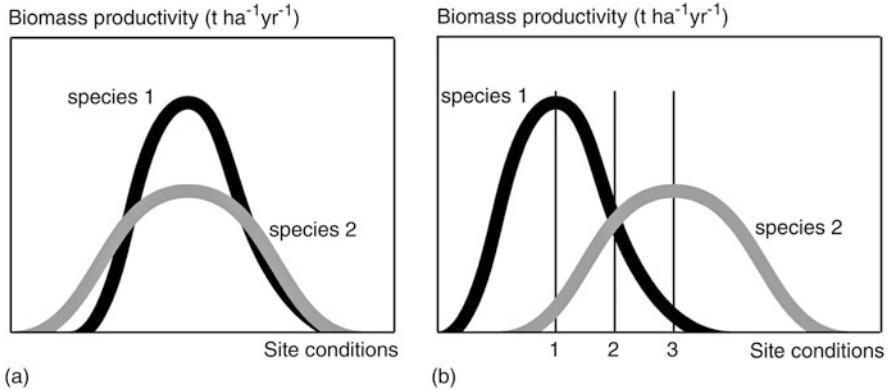


Fig. 2.5 (a, b) Dry biomass productivity of different tree species in relation to site conditions: (a) growth of two tree species with similar fundamental niches but different levels of productivity; in this situation, species 1 would likely dominate the mixture at most site conditions, except at lower site quality; (b) growth of two tree species with different fundamental niches. Numbers 1–3 below the abscissa represent different site conditions with different growth responses by species 1 and 2; here species 2 would become increasingly dominant in mixture when moving from site condition 1 to 3 (Pretzsch 2005)

thrive. Figure 2.4e depicts this arrangement. Here, the area of possible coexistence of species 1 and 2 extends beyond the fundamental niche of species 2.

Coexistence of two or more species in the same niche does not mean that they use the same strategies to access the available resources, as has been mentioned above under the complementarity hypothesis. For a given site condition (site *p* in Fig. 2.4 a and b), species 1 and 2 may access resources in spatially and temporally different ways.

In contrast, in pure stands, genetically similar individuals with similar phenology, morphology, and physiology compete in space and time for the same pool of resources. The greater the niche differentiation achieved by mixing species, and hence the greater the diversity of functional traits, the higher the probability for complementary resource use and relaxed interspecific resource competition (Fig. 2.6). Considering the niche space of an ecosystem, depicted as two-dimensional space using two resource gradients, it is obvious that this niche space is more easily filled to a larger degree by many species rather than one or few (Fig. 2.6), even though some species might be very dominant and occupy a large share of the niche space; see also chapter one on natural forests that are almost monospecific. This filling of the niche space with additional species represents a complementary use of available resources. Clearly, the picture becomes much more complex, when we have mixtures of many species and consider the whole range of environmental factors.

Niche differentiation is also an important factor contributing to the **insurance hypothesis** in relation to biodiversity. On the one hand, a high level of niche differentiation in a community with few species reduces redundancy. This means

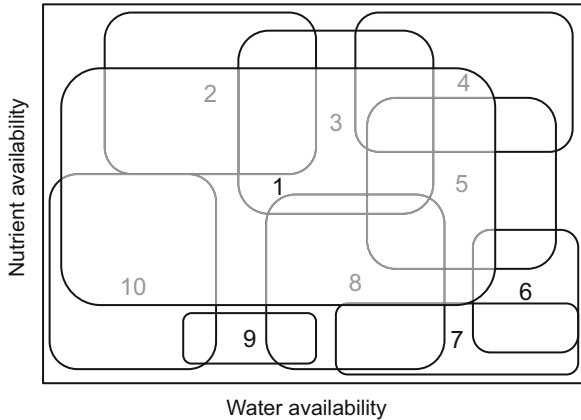
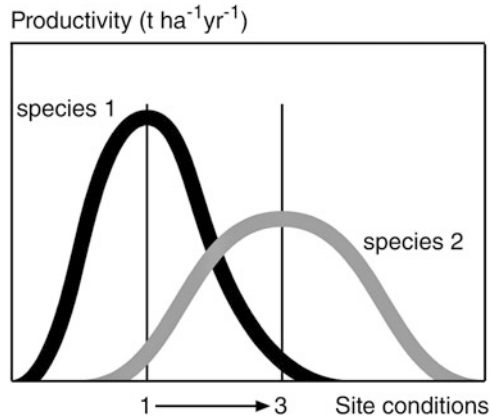


Fig. 2.6 Two-dimensional niche space of an ecosystem with the fundamental niches of ten different species. Within an ecosystem, water and nutrient availability are not constant, and thus site conditions are variable. Under most situations one species such as species 1 in this example may be dominant (depicted by the shading of the niche space of other species). However, with changes in space or time and thus in resource availability, other species may gain dominance. Within this heterogeneous system, all species may coexist and the niche space provided within the ecosystem is filled to a large extent, leading to complementary resource use. The resources are used more fully by the whole community than by any single species or subset of species. Removing or losing one species from this system can be partially compensated by other species that share part of the fundamental niche

that the loss of one species with certain functional attributes cannot be fully compensated by another species with different functional attributes. On the other hand, in the case of changes in the type, frequency, or intensity of stress or disturbance factors, there is a greater likelihood that some species within the community can cope with the new conditions, when compared to a community with a low level of niche differentiation or diversity in functional traits. We can envisage this as a shift in the combination of environmental factors such as those depicted in Fig. 2.6 from one part of the niche space to another part; it is likely that there will be one or few species that can thrive under the new conditions. The greater the niche variation between the constituent species of a mixed stand, the more elastic its response will be to disturbances (Yachi and Loreau 1999). Returning to our example of a two-species mixture, if one species is more sensitive to a particular stress, the more robust species may then, on account of its better adaptation, profit from the weakening or mortality of the inferior species. Assuming a shift in environmental factors and resource availability reduces the fitness of species 1 (Fig. 2.7, arrow 1→3), this would lead to a significant decrease in productivity of pure stands of this species. However, if the same shift in environmental factors affected a stand where species 1 was mixed with a second species that was better adapted to the new growth conditions, stand growth would be much less affected. Species 2 would make better use of the available resources, and,

Fig. 2.7 Dry biomass productivity for species 1 and 2 (black and grey lines, respectively) in relation to site conditions. The shift in site conditions from 1 to 3 (arrows) results in considerable growth loss for species 1. If species 1 and 2 are mixed, species 2 is able to compensate for a loss in biomass productivity



consequently, species 2 can improve its productivity and space sequestration. The same would happen if one species disappeared completely after a disturbance or through natural mortality (Fig. 2.8). In this case, the species remaining would contribute to ecosystem recovery and maintenance of ecosystem functioning through accelerated growth. This buffering or compensatory effect of the remaining species would be positively related to the density and regularity of its spatial distribution within the stand; it would be higher if the remaining species occurred in evenly spaced single tree or small group mixture rather than in irregular large patches. Managing forests in the form of mixed stands represents therefore a risk distribution through silvicultural diversification (Brang et al. 2014).

While fundamental and realised niches may provide a useful ecological concept, their use in quantitative analyses of the relationship between diversity and ecosystem functioning is limited. The concept has been widely applied to understand the coexistence of species within communities or to predict species distributions along environmental gradients or range shifts under future climatic conditions (Morin and Lechowicz 2008). It has had some success in explaining interactions in two or few-species systems, but has not been successful in providing general principles about interactions in and performance of communities with many species (McGill et al. 2006). One problem is that fundamental niches are rarely measured owing to the difficulty to quantify the performance of a species over a sequence of life stages and a large number of continuous abiotic gradients under controlled environmental conditions. This is one reason why different approaches based on functional traits have been proposed to study diverse communities (e.g. Violle and Jiang 2009). In addition, for many communities, interactions are diffuse, and considering each pairwise interaction between species in a highly diverse community as a separate process is difficult or impossible (McGill et al. 2006).



Fig. 2.8 Bark beetles have killed all Norway spruce (*Picea abies*) trees in a mixed spruce-beech (*Fagus sylvatica*) forest. This biotic disturbance agent is specific to the conifer species and does not affect the deciduous hardwood species. The surviving beech trees maintain forest condition and ecosystem functioning (Photo: J. Bauhus)

2.3.3 Species Traits and Functional Diversity

A trait is a well-defined, measurable property of organisms, which is ideally measured as a continuous variable and in well-defined units at the individual level. To be useful for the purpose of analyses of diversity effects, traits should vary more between than within species. Functional traits are those that strongly influence organismal performance, i.e. plant attributes that enhance establishment, growth, survival, reproduction, etc. Functional traits are, for example, important drivers of the distribution of species along environmental gradients (McGill et al. 2006). The underlying concept of trait-based approaches is that traits, not species identity, are fundamental units of species sorting from a regional pool of species

and that therefore traits should be a relevant tool to quantify niches. This may be applied by tracking plant functional traits related to the performance of individuals (Violle and Jiang 2009). There has been increasing support for the idea that many ecological questions can be addressed effectively by understanding how and why functional traits are related, and how these traits affect ecological outcomes. In the context of this book, relevant questions to which this concept has been applied comprise the vegetation community change along environmental gradients, effects of plants and communities on ecosystem functioning, and ecological interactions between species. An important question is which of the many possible traits have the strongest influence on the fundamental and realised niche of species. Fortunately, there is already some agreement about important plant traits that should form the basis of functional plant classifications, either because they have strong predictive power in relation to important ecosystem responses to environmental change or these traits themselves have a strong influence on ecosystem processes (Cornelissen et al. 2003). Based on the identification of important functional traits, protocols and databases have been developed to measure and document these traits and to make them available for trait-based analyses (Kattge et al. 2011). In concrete analyses of niche similarities and competitive abilities of species within a community using functional traits, however, the potentially long list is often reduced to a few key functional traits such as leaf mass per unit area (LMA), wood density (WD), seed mass (SM), and tree maximum height (Kunstler et al. 2012).

In the previous section, we have seen that a complementary effect in diverse communities would be maximised if all species contributed, with increasing species richness, proportionately to the increase of an ecosystem response variable such as productivity (Fig. 2.3b). This may be achieved by effective niche differentiation between the species. Applying a trait-based approach to this concept, maximum complementarity would be expected with maximum divergence of traits in the community. Hence, it may be expected more generally that strong relationships between response variables of ecosystem functioning and species richness are more likely in communities with trait divergence and hence high functional diversity, i.e. with great variation in specific leaf area, shade tolerance, maximum height, etc. In contrast, in communities with a high degree of trait convergence across participating species, ecosystem functioning may not be or only weakly related to species richness. Thus, instead of species richness or diversity, measures of functional diversity may be used as independent variables in approaches to quantify ecosystem functioning responses (e.g. Tilman et al. 1997). Accordingly, experimental designs have been developed that allow the separation between species richness and functional diversity (e.g. Tobner et al. 2014, Fig. 2.13).

It may be due to this difference between species and functional diversity that we see also different influences on the magnitude of ecosystem properties and processes between biodiversity experiments and culturally influenced production ecosystems on the one side and between natural communities on the other side. In natural communities, a convergence of traits, for example, those related to leaf morphology and function, are often observed (Reich et al. 1999) where plants share a similar life history, morphology, and physiology (Grime 2006). In contrast,

experiments that have tested biodiversity ecosystem functioning relationships have often selected specifically different functional groups to include a high degree functional diversity (Scherer-Lorenzen et al. 2005b). Likewise, in cultivated forests, managers have used insights from empirical evidence to combine functionally different species, such as light-demanding and fast growing with shade-tolerant and slow growing species (e.g. Scots pine and European beech; Pretzsch et al. 2015) or nitrogen-fixing with non-nitrogen fixing species (e.g. eucalypts with acacias; Forrester et al. 2006). Although some of the combinations of tree species or genera also occur in nature (e.g. eucalypts with acacias), it has to be kept in mind when evaluating the majority of these experiments that their results should not be directly extrapolated to natural plant communities (Wardle 2016).

In the past, plant functional groups have often been used to depict different niches, and there have been many studies demonstrating the strong influence of functional group richness on ecosystem processes such as primary productivity (e.g. Hooper et al. 2005). Such plant functional groups can be defined as sets of species which perform similarly in an ecosystem based on a set of common traits. They can be defined either in relation to the role of species for certain ecosystem processes (such as C assimilation or nutrient cycling) or to the response of species to biotic and abiotic environmental factors such as temperature, pathogens, etc. (Lavorel et al. 1997). The number of functional groups represented by the different species within a community has been commonly used as a measure of functional diversity (e.g. Hector et al. 1999). However, owing to the large number of traits that may characterise the role of a species within an ecosystem, unambiguously assigning species to certain groups is not trivial and has been criticised as arbitrary. Therefore, other measures of functional diversity have been developed, which are based on the measured traits of species and their distance and provide a continuous measure of the natural variation among species (Petchey and Gaston 2002; Laliberté and Legendre 2010). However, measuring all relevant traits of all species in a community can be an onerous task, if these data are not already available. To overcome this, phylogenetic diversity has been used as a proxy of functional diversity. The underlying assumption of this approach is that plant function is phylogenetically conserved (Swenson and Enquist 2009), i.e. that species that are closely related have similar expression of functional traits because these traits are the results of the evolutionary history and inherited from ancestors (Cadotte et al. 2009). However, trait variation may be only partially related to phylogenetic distances between species, and hence values for functional diversity of plant communities may be only partially correlated with phylogenetic diversity (Flynn et al. 2011). Importantly, the use of phylogenetic diversity alone does not provide a mechanistic understanding of the relationships between species and their environment or the ecological interactions among species.

Functional traits determine the fundamental niche of species, and they shape the ecological interactions in mixed-species forests and thus also influence the ecological niche. In the following we will discuss some important ecological interactions in mixed-species communities.

2.3.4 Important Ecological Interactions

There is a range of positive and negative ecological interactions that may occur between different species in a community. In the context of interactions between tree species, the most important interactions comprise competition, facilitation, and tolerance. Competition can be defined as the ecological interaction in which one organism or species consumes a resource that would have been available to and could have potentially been consumed by the other, and hence the fitness of one is lowered by the presence of another (Begon et al. 1996). The limited resource for which conspecific or heterospecific individuals compete, comprise, in the case of plants, light, water and nutrients. Competition among individuals of the same species is defined as intraspecific competition, whereas competition between individuals of different species is interspecific competition. Negative net effects may occur between tree species in mixtures, when the **competition** for resources between species is stronger than any competitive reduction or facilitation (Fig. 2.9c) (Callaway and Walker 1997). In this case, the interspecific competition is stronger than the intraspecific competition. In other words, for a given subject tree, a tree neighbour from the other species exerts more competition for resources than a conspecific neighbour.

Positive, **complementary** effects that result from mixing trees species can be expected, when competitive reduction or facilitation between the species participating in a mixture outweigh any negative effects of competition (Kelty 1992). In the case of **competitive reduction**, interspecific competition in the mixture is lower than intraspecific competition in the monocultures (Fig. 2.9d). Competitive reduction may occur through a range of differences in patterns and processes between monocultures and mixed-species stands both above ground as well as below ground (e.g. Bauhus et al. 2000; Lei et al. 2012). These differences in patterns and processes may be the result of niche separation, where different species use either different resources or the same resources but at different points in space or time. This enables more of the total available resources to be used by the mixed-species stand when compared to monocultures of the participating species (Vandermeer 1989). If competitive reduction relates to resources that limit growth, then this mechanism should lead to greater total productivity and possibly also a decreased loss of resources from the ecosystem (e.g. through nutrient leaching) (Hooper et al. 2005). An example of above-ground competitive reduction may be when a tall light-demanding species that uses a relatively small proportion of the available light is mixed with a shorter shade-tolerant species that can use a large proportion of the light that is transmitted through the canopy of the light-demanding species (e.g. Bauhus et al. 2004). The competition between light-demanding and shade-tolerant species may be further reduced, if they have different growth dynamics such that the light-demanding species grows much faster initially and thus can achieve a large proportion of its final height, before the shade-tolerant species catches up (Fig. 2.10). A typical example for this pattern can be seen in mixtures of *Betula* or *Populus* with more shade-tolerant conifers such as *Picea* and *Abies* (e.g. Man and Lieffers 1999). In Sweden, the productivity of the *Picea abies*

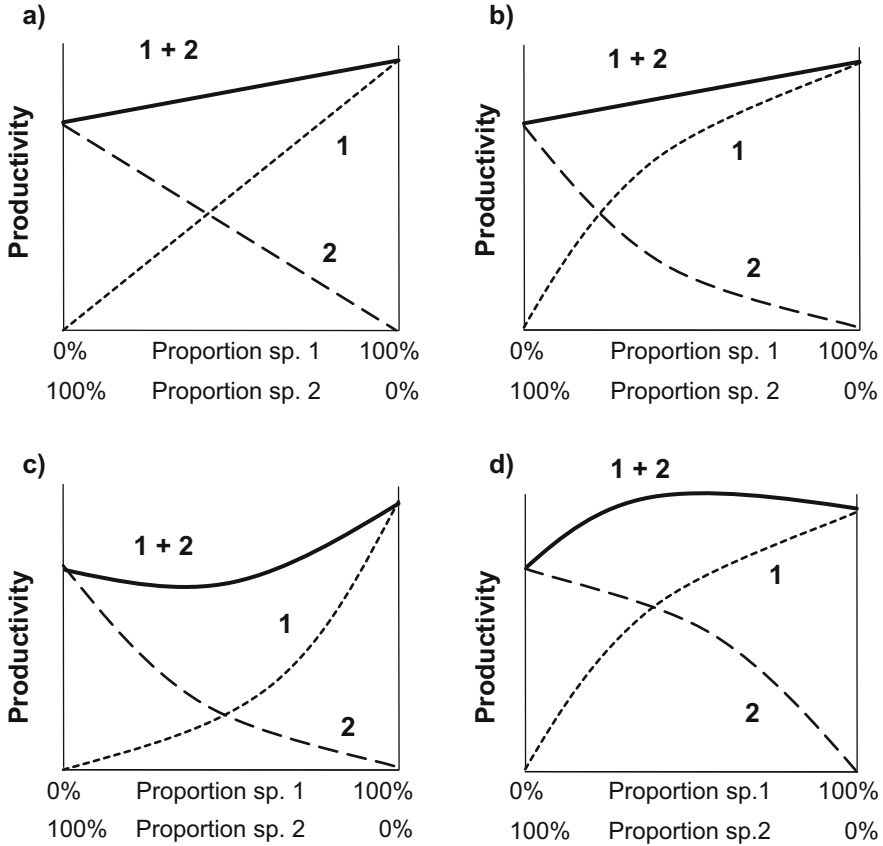


Fig. 2.9 Different effects of mixing two tree species on the total productivity of the mixture (*fat line*) and the individual productivities of the participating species 1 and 2 (*dotted lines*) (after Harper 1977). The graphs can be thought of as depicting species replacement series, where the density of the mixture is the same as the monocultures and always 100% and where one species is gradually replaced by the other. In monoculture, species 1 is more productive than species 2. We can distinguish four different situations. (a) The two species do not interact, they tolerate each other. Interspecific competition equals intraspecific competition. Total productivity is the additive effect of the productivities of the individual species. (b) Species 1 benefits from the interaction, e.g. through facilitation or competitive reduction. The intraspecific competition for species 1 is higher than the interspecific competition with species 2; the reverse applies to species 2. However, these effects compensate each other so that the net effect for the mixture appears to be purely additive. (c) Interactions between the two species are antagonistic. Interspecific competition is higher than intraspecific competition for both species. At the level of the mixture, this leads to under-yielding. (d) Interactions between the two species are synergistic or mutualistic. Intraspecific competition is higher than interspecific competition for both species. This may result from facilitation or competitive reduction. This leads to overyielding at the level of the mixture

component in mixtures with a nurse canopy of 600 *Betula* trees ha⁻¹ was, up to the stand age of 25 years, not different from the productivity of pure *P. abies* stands (Tham 1994). Below-ground, competitive reduction may occur when trees with

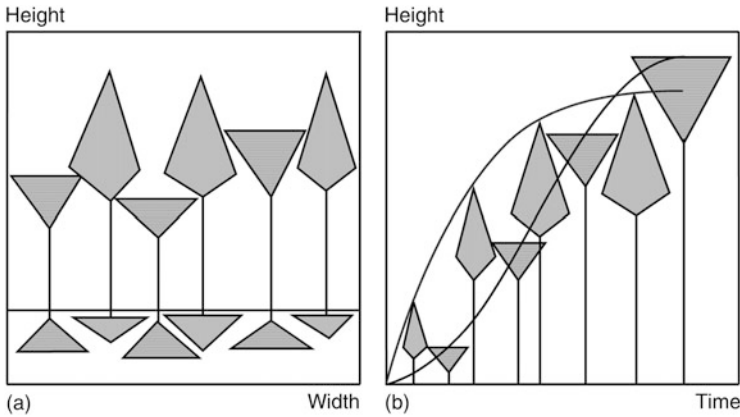


Fig. 2.10 (a, b) Coexistence of species 1 and 2 can be facilitated and productivity increased through competitive reduction in the form of spatial or temporal niche differentiation by (a) stratification in the crown or root space or (b) asynchronous growth patterns of the species. Asynchronous growth may also take place below ground through different rates of the expansion of root systems, but this has so far not been documented

different root architectures and rooting depths (Fig. 2.10) take up water (e.g. Schwendenmann et al. 2014) or nutrients (Lang et al. 2014) from different soil horizons or take up different forms of the same nutrient (see Richards et al. 2010). In both cases, competitive reduction may also occur through differences in phenology, when evergreen and deciduous species are mixed or the seasonal growth of fine roots differs between species. In both cases, species will differ with regard to the time at which they can take up resources such as light, water, or nutrients. For example, evergreen species will benefit from mixtures with species that are deciduous during a seasonal drought period (Schwendenmann et al. 2014). Similarly evergreen species will likely benefit from adjacent leafless deciduous trees during periods in spring and fall, when they photosynthesise at higher levels of light availability when compared to situations with other evergreen trees as neighbours.

The concept of niche complementarity also comprises **facilitation**, which can lead to an increase in the magnitude of ecosystem pools or processes as species numbers or functional richness increase. Facilitation can be defined as a form of interaction among species that benefit at least one of the participants and cause harm to neither of the participating species. It can be classified as mutualism, in which both species benefit (Fig. 2.9d), or commensalism, in which one species benefits and the other remains unaffected (Stachowicz 2001). Facilitative interactions among species occur when certain species improve environmental conditions for others, for example, through accelerating litter decomposition (Gartner and Cardon 2004), through reducing damage to foliage or other organs through abiotic factors, such as lowering the probability of frost events through sheltering (e.g. Örlander 1993; Scowcroft et al. 2000), or biotic agents, such as

disguising plants from insect herbivores (e.g. Castagneyrol et al. 2013), or where one species supplies a critical resource such as nitrogen through fixation to others (e.g. Forrester et al. 2006). Although mixing of N-fixing and non-N-fixing species represents differences in resource acquisition and benefits initially primarily the individuals of the N-fixing species, in the longer term, the N-enrichment of the system increases the turnover of plant material (nutrients in transported leaves and fine roots) and thereby the amount of resources introduced into the nutrient cycle (not just N), which become available to individuals of other species (Rothe and Binkley 2001; Piotta 2008). This does not mean, however, that the net effect of interactions between the N-fixing and non-N-fixing species is always positive for the latter (see examples in Callaway and Walker 1997).

The Stress-Gradient Hypothesis

The ecological interactions discussed above are not constant in space and time (Figs. 2.5 and 2.10; Chap. 3). That is one reason why it is so important to consider the extrapolation to the population of interest in the design of experiments on mixed species (Fig. 2.1). For example, synergistic effects between two species at an unfavourable site may not be representative for the same species combination at a site more favourable for plant growth, where the overall effect between the same species may be antagonistic.

Questions relating to how and why these interactions change, spatially or temporally, have received a considerable amount of attention, particularly in non-forest ecosystems (Bertness and Callaway 1994; Holmgren et al. 1997; Brooker 2006; Holmgren and Scheffer 2010). These interactions are often described using the stress-gradient hypothesis, which suggests that facilitation will increase and competition will decrease with increasing abiotic and biotic stress (Bertness and Callaway 1994). Hundreds of experiments have tested the stress-gradient hypothesis. While its generality has been questioned (Maestre et al. 2009), a recent meta-analysis that included 727 tests of shifts in the magnitude and type of ecological interactions between plant species concluded that there is a global generality of the stress-gradient hypothesis. It showed that plant interactions change with increasing stress through an outright shift to facilitation, when facilitation is quantified in terms of survival, or a reduction in competition, when facilitation is quantified in terms of growth and reproduction (He et al. 2013). A small number of studies found no change in ecological interactions to increasing stress but no studies found a shift towards increased competition.

It is important to note that there is usually a fundamental difference in the quantification of facilitation in forests, when compared with studies outside forests that were used to develop the stress-gradient hypothesis (Forrester 2014; Forrester and Bauhus 2016). In the latter, facilitation has been usually quantified by comparing the survival, growth, or fitness of a plant of a certain species with neighbours to a plant of the same species without neighbours, and these studies were often carried out in environments that are too harsh for forests to exist, either too cold or too dry. Under such harsh growing conditions, plants growing in a situation ‘without neighbours’ may not be unusual. However, this situation ‘without neighbours’ is

rarely found in environments that support forests, which have higher stand densities. Therefore, facilitation or competitive reduction is often assumed to have occurred in forests, when growth (or survival) is greater with inter- than with intraspecific competition. As a result of this difference in quantification, the meta-analysis by He et al. (2013) did not include any studies of tree-tree interactions unless the trees were in open woodlands (not forests) or seedlings of tree species were examined.

It is often assumed that as stress increases, productivity will decline, and so facilitation will be more common in ecosystems with lower productivity, and this has been suggested for forest ecosystems (Toigo et al. 2015; Pretzsch et al. 2013). However, while this may often be the case, there are also many exceptions such that complementarity increases with resource availability or site quality and often the interactions that occur in forests are competitive reduction and not facilitation, including all interactions that influence light absorption (see Table 1 in Forrester and Bauhus 2016). It is therefore problematic to apply the stress-gradient hypothesis, which is based on facilitation as opposed to competitive reduction, to forests unless most of the complementarity effect resulted from facilitation and not competitive reduction, and this is rarely known. Therefore, Chap. 3 (Sect. 3.6, Fig. 3.4) uses an alternative framework to the stress-gradient hypothesis to describe the spatial and temporal dynamics of complementarity in forests. This framework, which includes the stress-gradient hypothesis as a special case, is consistent with all mixed-forest studies in the literature and can be used to explain when and why complementarity can increase or decrease along spatial or temporal gradients in resource availability or climatic conditions.

In the context of this chapter, it is important to consider that, if we want to study the ecological interactions between certain combinations of species, this should ideally be done for the entire range of site conditions at which these species combinations occur (Confidence level 2 in Fig. 2.1). Otherwise we cannot extrapolate the results to the whole population of mixed stands of this species combination.

2.3.5 Tree Diversity and Diversity at Other Trophic Levels

Foundation species have been characterised as those individual species that define much of the structure of a community by creating locally stable conditions for other species and by modulating and stabilising fundamental ecosystem processes (Dayton 1972). Trees are often foundation species in forested ecosystems, because they shape forest structure, create a forest microclimate, and through their functional and physiological characteristics have a large influence on material cycling and energy flow (Ellison et al. 2005). Through their species-specific traits, they control ecosystem dynamics. Owing to specific interactions with symbionts, pathogens, herbivores, etc., a large number of other taxa typically depend on specific tree species. Hence, the loss of such foundation species might have dramatic consequences for the stability and functioning of forest ecosystems (Ellison et al. 2005). However, the number of other taxa that depend on individual tree species is difficult if not impossible to ascertain. For example, some early

estimates of the global number of tropical forest beetles and other arthropods were based on the fogging with insecticide of the crowns of individual tropical tree species (Erwin 1982). Based on the count of arthropod species that were knocked down, which amounted to many hundreds and in some cases more than 1000 species per tree, estimates were derived for the richness of beetles and other arthropods based on an assumption of the proportion of host-specific species. In the early study of Erwin (1982), that proportion was estimated at 13.5%. The resulting number of species was then multiplied with the number of known tropical tree species to yield an estimate of 30 million arthropod species for tropical forests. However, owing to the unknown range of plant host-specificities of tropical insects, particularly of non-herbivore species, this and subsequent similar estimates are associated with very high uncertainty (Stork 1988). Although this figure has since been corrected downwards, recent studies, which have found close associations between floristic diversity and both herbivore and non-herbivore species richness in tropical forests, confirmed that the general modelling approach to scale up from plant species richness appears to be valid (Basset et al. 2012). The estimates of species richness in insect communities in the crowns of temperate forests are lower than those of tropical forests, but still in the order of hundreds of species (e.g. Southwood et al. 2004). If we consider host specificity or preference of additional taxonomic and functional groups such as fungal pathogens, wood inhabiting fungi (e.g. Unterseher et al. 2005; Purahong et al. 2014), saproxylic beetles (e.g. Floren et al. 2014), decomposers (e.g. Lodge 1997), mycorrhizal fungi (Ishida et al. 2007), root herbivores, and so forth, we can see that each tree species may provide habitat and resources for hundreds of other species at different trophic levels within the ecosystem. If we add or remove these tree species, these other species may be also added (if they can colonise the tree species) or lost from the system. Even non-native, introduced tree species can contribute substantially to species richness and diversity in forest ecosystems, when they are admixed in small proportions, for example, admixed *Pseudotsuga menziesii* in stands of native *Fagus sylvatica* (e.g. Goßner and Ammer 2006). Hence, many tree species can be viewed as foundation species that add much complexity to the ecological communities in forest ecosystems. Therefore, with increasing tree species richness, the number and frequency of interactions and feedbacks also increases, and this might buffer mixed-species forests against stressors and disturbances (Messier et al. 2013, see also Chap. 7). Increased stability of communities is of course not just linked to species-specific, dependent diversity. Generalist species add also to the complexity and stability of ecological networks, which typically increases with number of interactions between participating species. The strength of interactions typically decreases with the number of links between species in networks (Vázquez et al. 2007). The increased stability with increasing species richness is most likely to occur at the level of community and ecosystem processes and less at the level of populations of individual species, as has been observed for grasslands (Tilman 1996). However, increased stability with increasing complexity of ecological networks may be effective only in case of random removal of species. Complex networks may be very fragile in case of selective removal of the most connected species (Solé and Montoya 2001).

In terms of ecosystem hierarchy (Fig. 2.2), increasing species and functional diversity at the different levels of ecosystem organisation may dampen the signal from one level to the other.

2.4 Analysing Ecosystem Properties and Processes in Tree Species Mixtures Based on Experiments and Inventories

2.4.1 General Considerations Regarding Tree Diversity Experiments

Quantitative information about the effects of tree species diversity on ecosystem properties and processes stems mostly from the analyses of large-scale, permanent forest inventories that capture gradients in tree species richness (e.g. Caspersen and Pacala 2001; Gamfeldt et al. 2013; Villà et al. 2013) and from controlled experiments or long-term forest plots comparing monocultures and tree species mixtures, mostly two-species mixtures (e.g. Forrester et al. 2006; Piotta 2008; Pretzsch et al. 2015). Whereas the first source of data stems mostly from all forms of forests (native, seminatural, and plantations), the latter stems mostly from plantations or seminatural forests. Only relatively recently have experiments been established that permit the analyses of tree species diversity and ecosystem functioning relationships for a wider range of species richness levels and functional diversity (e.g. Scherer-Lorenzen et al. 2007; Potvin and Gotelli 2008; Tobner et al. 2014; Bruelheide et al. 2014). In relation to the longevity of trees, these experiments can so far only provide information on the initial phase of stand development and species interactions.

Typical hypotheses to be addressed in such studies are (Baeten et al. 2013):

1. Ecosystem functioning is higher in tree species mixtures than in monocultures. This may be related to complementarity and selection effects (see above).
2. Species interactions and hence the mixing or diversity effects are not consistent along environmental gradients (Forrester et al. 2013) and with development of mixtures over time (Pretzsch and Schütze 2009).
3. Tree species mixtures have a higher resistance and resilience than monospecific stands to abiotic stress and disturbances as well as to pests and diseases.
4. Fewer tree species or a lower level of diversity is required to maximise a single ecosystem function such as productivity when compared to maximising multiple ecosystem functions simultaneously (e.g. van der Plas et al. 2016).

To be effective and make efficient use of resources for research, tree diversity studies should ideally be designed to permit addressing all of the above questions. Such an ideal design should consider and optimise three basic criteria, which have been termed orthogonality, comprehensiveness, and representativeness (Fig. 2.11) (Baeten et al. 2013).

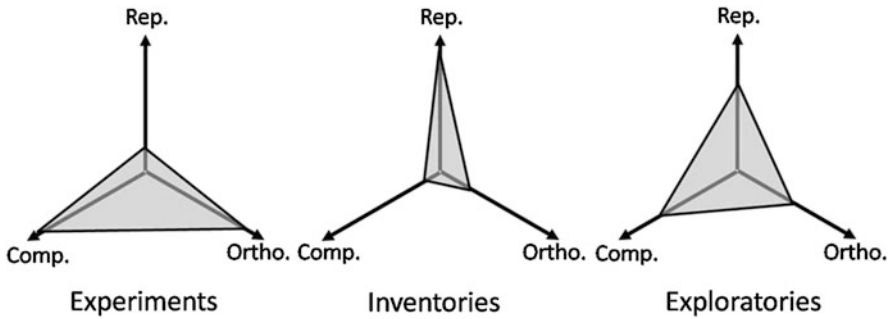


Fig. 2.11 The relative differences in representativeness (Rep.), comprehensiveness (Comp.), and orthogonality (Ortho.) of three types of study designs used to quantify the effects of biodiversity: experiments, inventories, and exploratory plots in forests. This figure is reproduced with permission from the FunDivEUROPE project consortium (http://www.fundiveurope.eu/?page_id=30)

Orthogonality refers to the statistical independence of species diversity effects from other factors. Orthogonal designs allow the effects of species diversity to be completely uncorrelated with those of other variables and covariates (e.g., species identity, environmental gradients, management influences) (Nadrowski et al. 2010; Baeten et al. 2013). However, it is extremely difficult to design studies in which tree species diversity is completely independent (orthogonal) from other variables due to unavoidable biological correlations. For example, orthogonality would be reduced in an inventory-based analysis of tree diversity effects, if species diversity was not independent of successional stage or stand age, which in turn influences productivity. Orthogonality would be also reduced in a design, where the more diverse species mixtures can be found at the most productive sites (Vilà et al. 2005).

Comprehensiveness refers to the spectrum of ecosystem properties and processes and hence ecosystem functions quantified in a study (Nadrowski et al. 2010). Since forests are managed for many different functions and related ecosystem services, we would typically like to know how tree species diversity affects these functions. Therefore, it is desirable to design tree diversity studies in a way that as many as possible of these ecosystem functions (e.g. biomass production, carbon sequestration, nutrient cycling, provision of non-wood products, etc.) can potentially be analysed simultaneously (e.g. Gamfeldt et al. 2013). This typically requires large interdisciplinary teams of researchers to quantify these different functions. Inventory-based, observational studies have typically a low comprehensiveness because only a limited set of variables, from which ecosystem properties and processes can be derived, is quantified on inventory plots. However, these inventories are currently evolving towards multipurpose resource surveys to include increasingly more variables that are relevant for biodiversity (Corona et al. 2011). Low comprehensiveness is not a characteristic of any particular design per se; however, it is much easier to measure many functions in planted experiments, which are relatively small in area and have fewer trees, compared

with inventory datasets, which can cover very large areas and include very high numbers of trees.

Representativeness refers to the proportion of the variation in the population of interest that is captured by the design. It indicates to which extent the results from the study may be extrapolated to the population of interest. For example, if we wanted to study tree diversity effects in temperate deciduous forests of Europe, then we would require a design that reflects the different existing forest types, soil types, stand density, and age structure to allow a transfer of the results to real-world conditions. This could be considered confidence level 2 in Fig. 2.1. A representative design relates also to the relevance of the results for policy and decision makers. Representativeness is typically high in large-scale, permanent inventories, which are designed to capture the entire variation of the population of interest, whereas experiments are likely to be far less representative because they tend to focus on a small range of environmental conditions, species compositions, stand densities, ages etc.

2.4.2 Forest Inventories

Forest inventories typically adopt sampling schemes in accordance with a spatial design in which sampling points are randomly selected, for example, as grid points, from the population of interest about we wish to infer certain properties (e.g. Corona et al. 2011). In many National Forest Inventories or forest enterprise-level inventories, sample plots with a sufficiently large radius or angle counts with a predefined basal area factor are established with their centres at the selected points, and a range of attributes are recorded for the trees included in the plots or in the angle counts (e.g. Schreuder et al. 1993). At the same sample points, smaller plots or angle counts with a low basal area factor may be established to capture regeneration and smaller tree individuals. A traditional focus of these inventories has been on the assessment of growing stock and its changes through periodical growth, recruitment, harvesting, and mortality and on tree species composition. More recently, forest inventories have broadened their scope to include variables related to forest carbon pools and carbon sequestration, forest health, and biodiversity (Corona et al. 2011). Typical forest inventories are theoretically designed to monitor forest changes through periodic remeasurements at 5–10 year periods. It has to be kept in mind, however, that the statistical design of these inventories is related to the sampling probability of important variables related to the original purpose of the inventory. Some variables that might be of interest with regard to additional ecosystem functions might not be sampled with sufficient intensity to provide reliable estimates for the population of interest. It may be very difficult, for example, to estimate the growth of rare tree species that contribute less than 0.1% to the total growing stock from nationwide forest inventories. One other problem that may be encountered in some regions when analysing forest inventory data for relationships between tree species richness or diversity and ecosystem functions is that the gradient in tree species richness can be rather

short, because plots with high diversity are uncommon, either because the original sampling design did not take this into account or because the average stand condition on the landscape is relatively species poor. Therefore, most inventory plots cover only the lower end of the tree diversity gradient (e.g. Vilà et al. 2007). For example, in Europe, the probability of sampling plots with more than three species is less than 25% and to sample plots with more than five species is less than 10% (see Fig. 1.1 in Chap. 1). Another shortcoming of inventories is that 5–10 year measurement periods may be too long to examine relationships between growth and short-term climatic variability. For example, the effect of particular drought years on forest of different composition may not be captured through such inventories. However, the same problem applies to experiments or other plots, where processes are not recorded at a higher temporal resolution, for example, through measurement of tree growth through permanent dendrometer bands.

The strength of inventory datasets is their representativeness (Fig. 2.11). They typically cover a very wide range of environmental conditions, forest ages, species compositions and forest types, management approaches, and stand densities. Because they represent real-world ecosystems, they can help to put results obtained from artificial communities, such as created in experiments, into perspective. For example, in real-world ecosystems, species richness, if it is primarily related to the occurrence of rare species that contribute little to function, may not be a strong determinant of ecosystem functioning and ecosystem services provision (Winfree et al. 2015). However, inventories often only include data about a small number of ecosystem properties and processes, such as growth and standing wood volumes, biomass, and carbon stocks. They can also lack orthogonality, which can require careful consideration when interpreting the results (Vilà et al. 2005). Several studies have shown that variables such as edaphic and climatic conditions, stand age, and density can influence relationships between diversity and productivity and need to be considered when analysing inventory data (Firn et al. 2007; Vilà et al. 2007, 2013; Belote et al. 2011; Paquette and Messier 2011). For example, Caspersen and Pacala (2001) found an asymptotical increase of growth with increasing tree species richness when plotting the number of canopy tree species against stand growth using national forest inventory data from the USA. From their study, one might conclude that tree species richness enhances productivity owing to functional differences between species in accordance with the niche complementarity hypothesis outlined above (Sect. 2.3.1). However, one might also conclude that more productive sites that support more productive stands simply permit the coexistence of more species. Thus, cause and effect cannot be disentangled from observational and comparative studies in the absence of additional information (Scherer-Lorenzen et al. 2005b). In another inventory-based study by Vilà et al. (2013), no effect of species richness was observed in *Pinus sylvestris*-dominated forests, but a positive effect was detected in *Pinus halepensis* stands of Catalonia. In the latter case, however, tree species richness was no longer a significant independent variable, when climate, bedrock types, radiation, and successional stage of inventory plots were considered.

Also thinning may be heavier in stands, where tree species diversity effects accelerate the growth rate, to harvest the additional increment and to adjust species composition. This is often done to release the inferior and rare tree species from competition to keep them in the forest community. When inventory plots represent mainly managed stands, their stand density may be considerably below the maximum density which may best reveal any mixing effects. Hence, mixing effects may be eliminated or reduced by thinning (Chaps. 4 and 9).

Approaches such as structured equation modelling may be used to account for these confounding factors when analysing inventory data, for example, that basal area had a greater effect on productivity than tree species diversity (Paquette and Messier 2011; Vilà et al. 2013). However, extracting the signal of tree species diversity from forest inventory data requires a large amount of additional information.

When accounting for possible confounding factors, most analyses of large-scale forest inventories have found positive relationships between tree species richness and forest productivity, from Mediterranean, to temperate and boreal forests. Productivity is also the variable that has been most commonly addressed in these studies. However, additional variables that served as proxies for biodiversity and ecosystem services such as soil carbon storage, bilberry production, game production potential, understorey plant species richness, and dead wood have also been related to tree species richness on the basis of data from the National Forest Inventory of Sweden and the Swedish Survey of Forest Soils and Vegetation (Gamfeldt et al. 2013). In addition to the analyses of relationships between species richness and ecosystem properties and processes, inventory data might also be used to address other hypotheses, for example, regarding the interaction between site quality and complementarity. For example, Toïgo et al. (2015) were able to show with data from the French National Forest Inventory that for a number of two-species mixtures exhibiting overyielding, this effect was higher at sites of lower productivity.

2.4.3 Mixed-Species and Tree Species Diversity Experiments

Here we distinguish between experiments to study the mixing effects of two species, which we call mixed-species experiments, which have a long tradition in forest sciences (Pretzsch 2005), and tree diversity experiments, which comprise more than two tree species and permit the separation of diversity effects from species identity effects (Scherer-Lorenzen et al. 2005b). The latter type of experiment aims at identifying and quantifying relationships between biodiversity and ecosystem functioning, so-called BEF experiments (Bruelheide et al. 2014). Large-scale experiments with higher species richness levels have much less tradition than the former and have only been installed since the beginning of this century, which is currently still a weakness of this approach. The experimental designs can be broadly divided into (1) planted experiments and (2) exploratory plots in forests (Baeten et al. 2013; Bruelheide et al. 2014; Verheyen et al. 2016). Each of these has

advantages and disadvantages, also when compared to inventories, and these can be summarised as depicted in Fig. 2.11.

Experiments are typically designed to analyse the influence of one or a few independent variables, here chiefly tree species richness, tree diversity, and functional diversity, and to exclude or control the influence of other factors and hence to maximise orthogonality (Fig. 2.11). Thus the particular strength of experiments is to detect effects of diversity per se and to identify and quantify the underlying mechanisms. The greater the extent to which they consider the population of inference, e.g. by replicating the diversity gradients along environmental gradients such as different site or soil types, the higher the level of confidence we can place in the results from these experiments (see Fig. 2.2). The compact nature of experiments with shared infrastructures typically permits the quantification of a wide range of ecosystem properties and processes, hence they provide for high comprehensiveness. In the following, we will discuss some commonly used designs for such experiments.

2.4.3.1 Planted Experiments

By using planted experiments, it is possible to carefully control species compositions and proportions, functional diversity, stand density, and edaphic and climatic factors. This is a clear advantage over inventories and so-called exploratories (see below), where these factors can be confounded with diversity. Over the last two decades, a rapidly increasing number of planted biodiversity experiments have been established, and many of these have joined to form extensive networks (e.g. Verheyen et al. 2016). While all of these experiments are primarily interested in the influence of biodiversity on ecosystem functions, they also have their own unique design features. Some consider genetic diversity or functional diversity instead of, or in addition to, species diversity (e.g. Scherer-Lorenzen et al. 2007; Tobner et al. 2014). In addition to tree species diversity, some include understorey diversity treatments (Bruelheide et al. 2014).

A common and major focus of most of these BEF experiments is the question whether random species loss can affect ecosystem functioning (Hooper et al. 2005). This can be examined using extinction scenarios, whereby certain species from the total species pool are left out of the less diverse treatments (Fig. 2.13) while maintaining the same total initial tree density in experimental plots. In this regard, these BEF experiments usually follow a substitutive (also called replacement series) design (see below) rather than additive series, where diversity is confounded with density.

The extinction scenarios used in the experiments may follow a random pattern, if there is inadequate information about the drivers of extinction or when those drivers do not lead to a biased extinction of species (Bruelheide et al. 2014). Alternatively, non-random scenarios may be employed to reflect the preferential loss of species with certain traits and thus a particular contribution to the ecosystem and its functional diversity (Bruelheide et al. 2014). For example, in the BEF-China experiment, two types of non-random extinction scenarios were implemented. One removes species in the order of rarity starting with the rarest species, which

may resemble what might happen in case of forest loss and fragmentation in the landscape. The other removes species in relation to the expression of the functional trait specific leaf area (SLA) starting with the highest SLA, assuming that they will be the first to decline in vitality as the climate becomes drier and warmer (Bruelheide et al. 2014). It is also important to have several extinction scenarios to separate diversity effects from those of a particular community composition, and in experiments such as BEF-China (Fig. 2.12), there are three overlapping random extinction scenarios at each of two sites.

The International Diversity Experiment Network with Trees (IDENT) focusses on the separation of tree species richness and functional diversity effects (Tobner et al. 2014) (Fig. 2.13).

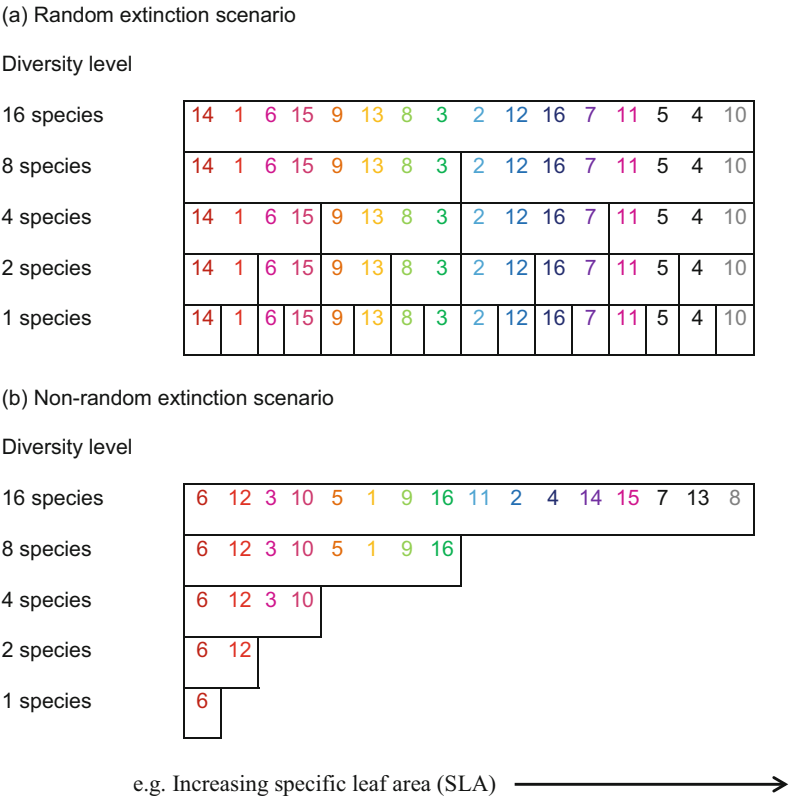


Fig. 2.12 (a) The random extinction design used in the BEF-China experiment. Each number represents a different species. A pool of 16 species is randomly partitioned into two mixtures that each contains eight species. This partitioning is continued down to monocultures. Each species is included at each diversity level. (b) A non-random extinction scenario based on increasing specific leaf area. Most studies contain several extinction scenarios, and when they contain only one they are referred to as a dilution diversity gradient. Modified from Bruelheide et al. (2014)

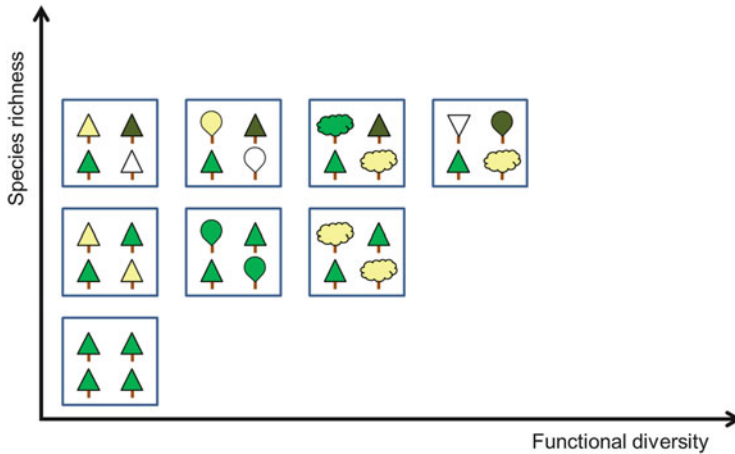


Fig. 2.13 Outline of an experimental design used in the International Diversity Experiment Network with Trees (IDENT) comprising gradients of species richness (SR) and functional diversity (FD) (Tobner et al. 2014). The design includes monocultures of all species and mixtures of increasing species richness that have different degrees of functional diversity. For example, a two-species combination with low functional diversity may consist of two species of the same family with similar traits (e.g. *Picea abies* and *Pinus sylvestris*), whereas a higher level of functional diversity would be represented by a combination of a broadleaved deciduous species with an evergreen conifer, e.g. *A. pseudoplatanus* with *Picea abies*. A four species mixture representing a high level of functional diversity may comprise an evergreen (*P. sylvestris*) and deciduous conifer (*Larix europaea*) as well as a shade-tolerant broadleaved (*A. pseudoplatanus*) and a shade-intolerant deciduous species (*Quercus robur*) (see Wein et al. (2016) for the whole range of species combinations). Levels of functional diversity are repeated using different species combinations. For analytical purposes, these levels of functional diversity can be pooled in groups of similar value

In contrast to other experiments, the basic design of IDENT experiments comprises gradients in both, species richness and functional diversity, and it focusses on the early stages of stand development through employing a high planting density. The high-density design reduces the space required to implement the experiment and time needed for trees to start interacting. The variation of functional diversity within levels of constant species richness also allows the testing for underlying mechanisms such as complementarity or selection effects on ecosystem properties and processes (Tobner et al. 2014). Functional traits used to compute indices of functional diversity in some of these experiments included wood density, seed mass, and foliage N content; however, one could think of many other traits to be used for that purpose. For two-species combinations, the calculated functional diversity, measured as the extent of functional differences (distance) among species in the community (Laliberté and Legendre 2010), ranged from 0.3 in congeneric mixtures of *Picea glauca* and *P. abies* to 2.23 in mixtures of *Quercus robur* with *P. glauca*. The latter value was higher than in the six species mixtures of this experiment, indicating how species richness and functional diversity might diverge.

The IDENT network with a number of experiments in North America and Europe using the same design allows for later meta-analysis and synthesis that can provide a high level of evidence for possible findings (see Fig. 2.1).

2.4.3.2 Planting Designs

The most common experimental designs to study species diversity effects are 'substitutive' or 'additive'. In the case of short-lived plants, which are often already planted with the final spacing between individuals and species, such designs can be kept through the whole rotation until the final harvest (if that is intended). This is typically not possible with long-lived plants such as trees, which continue to increase in size and typically at different rates, so that the initial composition of plots with regard to species proportions and density will change as the experiment progresses.

Establishment of a substitutive design (de Wit 1960) comprises the planting of monocultures of each species participating in mixed plots. This is a prerequisite to answer the question whether the average performance across all species is higher at higher levels of species diversity (the complementarity effect) or whether diverse species mixtures have a higher probability to contain particular species with a very high contribution to the performance of the community with regard to certain ecosystem processes or properties (sampling or selection effect). When monoculture plots of all species are included in the experiment, the additive partitioning method of Loreau and Hector (2001) can be employed to separate complementarity and selection effects.

In its most simple form with two species, the mixed stand can be established by planting half of the tree positions (or any other defined proportion) with one species and the remaining positions with the other species (Fig. 2.14), thus keeping the density constant across monocultures and mixtures of the replacement series. Ideally, the replacement series are also established at different densities to allow the separation of mixing and density effects. However, in practice such substitutive designs are mostly established at one density only and also at one site only, which limits their representativeness.

In experiments with a substitutive design, three main types of planting patterns may be employed to establish plots with an identical initial number of trees. For a two-species mixture, these are tree-by-tree (ABABABAB) (Fig. 2.15 top right), patches (AAABBBAAABBB), or random (ABBABAABA). Tree-by-tree or row-by-row mixing patterns, in which each individual has at least two heterospecific neighbours, maximise interactions between species during the early stages of development. This also has the advantage that for certain types of measurements, e.g. soil properties, fine roots, or light, a measurement point can be selected that represents the influence of the different species in that particular neighbourhood situation based on the distance to the surrounding trees (e.g. Bauhus et al. 2000). However, owing to differences in growth dynamics between species, it is possible that some species may outcompete others. To avoid this, the patch-planting design is sometimes used so that some individuals of a given species are surrounded by individuals of the same species (even in the diverse treatments) to ensure that some

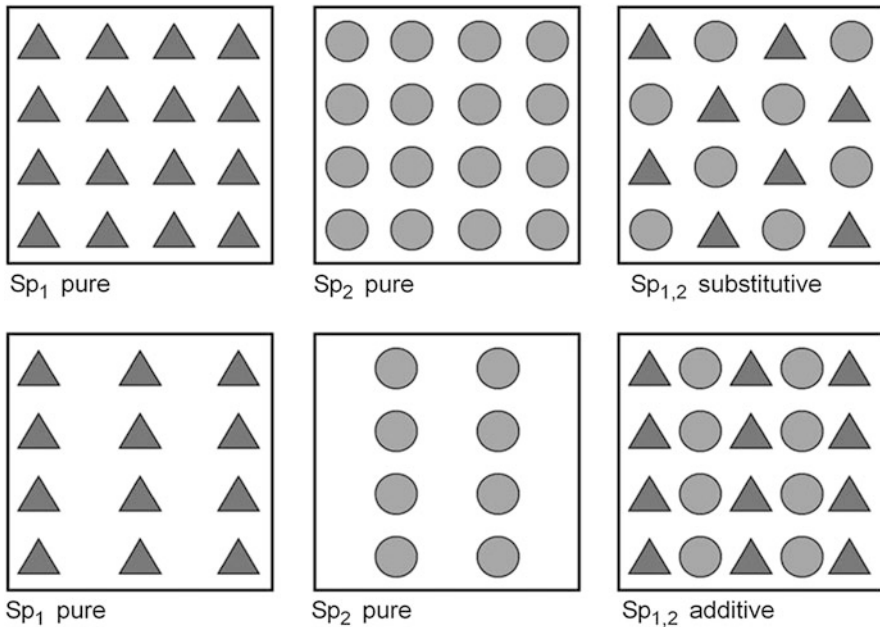


Fig. 2.14 Illustration of substitutive design (above) and additive experimental design (below) for a simple two-species mixture. In case of the substitutive design, the monocultures are established by planting two species in a defined pattern (density, distribution), and the mixed stand is established by planting half of the positions (or any other defined proportion) with one species and the remaining positions with the other. Here we have depicted a 50:50 mixture; often mixtures of 25:75 percent have also been included in replacement series. The additive design also bases on the distribution pattern in the pure stands. But for creating the mixture, the plants are not substituted by the other species but both patterns are added

individuals initially experience only conspecific competition. This is done with the expectation that as the stand develops, the diversity treatment will be retained for longer without losing the less competitive species completely (Scherer-Lorenzen et al. 2007). The disadvantage of such a patch-planting design is that most of the early interactions among trees within the diverse plots will actually be intraspecific. Some studies try to avoid both of these disadvantages by using random patterns (e.g. BEF-China; Bruelheide et al. 2014). This also creates more variability at the tree level in terms of the neighbourhood compositions of individual trees.

In tree diversity experiments with more than two species, the population sizes per species decrease inversely with increasing species richness, while the community density within plots remains unchanged. The substitutive design avoids confounding community density and diversity effects, a problem that is encountered with additive designs.

The additive design also starts with the distribution pattern of trees in pure stands. However, in mixed-species plots the planting positions of one species are not partially substituted by the other species, but both patterns are added (Fig. 2.14).

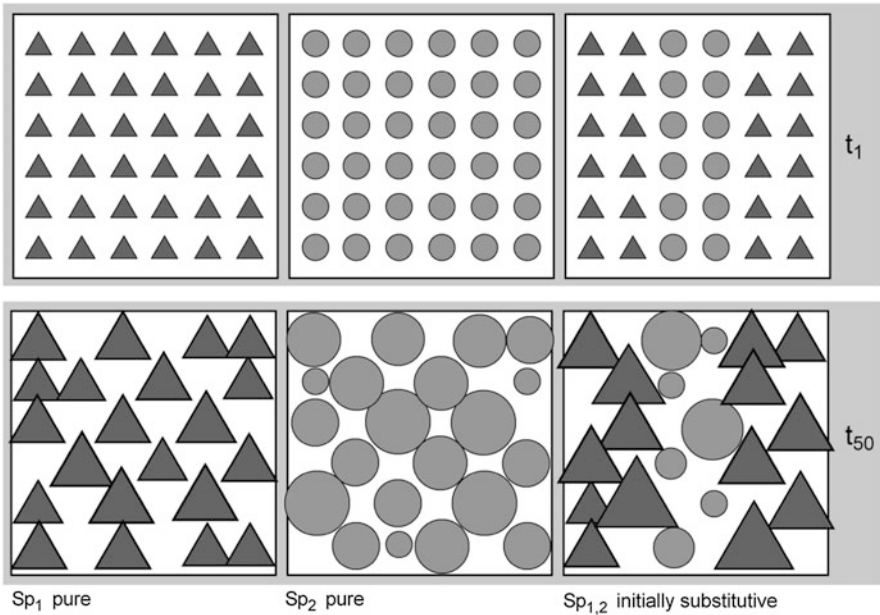


Fig. 2.15 Possible development of an ‘initially substitutive design’ with two tree species, where the experiment starts with an unpaired substitutive design with double rows. The spatial pattern progressively deviates from the initial design owing to species-specific size growth, density-dependent mortality, disturbances, and silvicultural interference in the course of stand development (below). In the analogue case of an additive design (not shown), this would be called ‘initially additive design’

The substitutive design is common in even-aged forests, where the participating species with similar growth dynamics are planted at the same time (e.g. Forrester et al. 2004). In contrast, the additive design is more suitable in two-layered stands, where, for example, a shade-tolerant species may be planted beneath the canopy of a shade-intolerant species, e.g. *F. sylvatica* under *P. sylvestris*, and both species are also represented in monoculture as reference.

In planted experiments it is also possible to quantify the influence of site heterogeneity before any of the species have influenced the edaphic and climatic factors (Bruehlheide et al. 2014). These details can be included as covariates later, and it also enables the examination of how the diversity treatments modify these environmental factors (Bruehlheide et al. 2014).

Pot trials are also planted experiments that offer many of the same characteristics of planted experiments. An advantage of pot trials, where different species are placed in the same pot, is that it is easier to carefully control water and nutrient availability as well as climatic conditions. However, the pots restrict growth, in particular of the root systems, and the interactions between small plants growing in pots may often not resemble those of larger plants.

2.4.3.3 Development of Initially Substitutive or Additive Designs in Forest Stands

Experiments in long-lived forest stands are often established either with a substitutive or an additive design but with stand development they progressively deviate from it. Since the original design in terms of stand density, mixing pattern, or proportion of the species commonly changes due to species-specific size growth, mortality, and thinning, the respective designs might be more appropriately called ‘initially substitutive design’ or ‘initially additive design’ (Fig. 2.15). This deviation from the original design can be accounted for by frequent surveying of pure and mixed plots to record their productivity, current species proportions, stand density, mixing patterns, and other variables as confounding factors for later analyses of the temporal variation of mixing effects during stand development (see Sect. 6.5). Another alternative to deal with this development is to move away from plot-based measurements and focus on diversity effects in tree neighbourhoods, where the tree species diversity may then be defined by the species identity, dimension, and distance of all neighbours of a subject tree (e.g. Forrester et al. 2013; Forrester 2015). However, when moving from the plot level to the neighbourhood level, only those properties and process in relation to tree species diversity can be analysed that occur at that spatial scale. These may be interactions regarding the competition for resources such as light, water, and nutrients. The neighbourhood scale is likely not relevant for questions regarding the interactions between tree diversity and ecological disturbances. In addition, the maximum tree species richness that may be analysed is likely limited to the number of immediate neighbours, which would typically be not more than eight.

An advantage of the longevity of experiments is that the tree species diversity effects can evolve and be studied much longer. When closed canopies can be maintained by only permitting self-thinning or light silvicultural thinnings, the effect of tree diversity on productivity and site carrying capacity in terms of maximum stand density can be quantified. In this sense, the longevity of experiments increases their representativeness since the results obtained over the course of the experiment can then be extrapolated to all ages or developmental stages covered in the study. Exceptions, where the initial planting design can be maintained during a complete rotation of the experiment, are short-rotation plantations.

Another interesting question is how much forest stands can change their maximum stand density and carrying capacity through species interactions and modifications of site conditions (see Chap. 4). To answer this question, it is necessary that mixed pure and mixed-species plots remain unthinned or fully stocked. However, as shown above leaving plots unthinned means that they will gradually drift away from the initially substitutive design with equal density, mixing proportions, and defined mixing pattern.

2.4.4 Exploratories

The third approach of **exploratories** represents a hybrid strategy, where existing mature stands are explicitly selected for diversity gradients with otherwise comparable environmental conditions and management regimes. This approach considers all three criteria of orthogonality, comprehensiveness, and representativeness, but without fully maximising them.

Exploratories combine some of the attributes of planted experiments with those of inventories and complement these approaches. Like inventories, they are done in existing forests so that tree size distribution, stand structures, and species compositions may be more representative for real-world systems than in planted experiments, and this representativeness may be improved further if the plots are replicated at different sites and comprise different stand ages. However, unlike inventories, and consistent with planted experiments, there is usually some control to ensure a gradient in species diversity at a given site, thereby making them more orthogonal than inventories. This diversity gradient may use existing stand variability or be created manually.

One older example using this approach is situated in a central *F. sylvatica* forest with a small-scale mosaic of tree diversity and otherwise similar soils and climatic conditions (Leuschner et al. 2009). A weakness of that research platform, apart from no replication, was related to the lack of monocultures for all tree species in the species pool, except for *F. sylvatica*, and the presence of one species, *F. sylvatica*, in all mixtures. The design might therefore be regarded as dilution design (Nadrowski et al. 2010) in which the effects of tree species richness or diversity could not be separated from the effects of *F. sylvatica* abundance.

Another possible approach is the adjustment of different levels of species richness in removal experiments, where different degrees of tree diversity at the stand level are created through removing one or more individual species from an initially species-diverse forest ecosystem. These types of experiments, which may emulate the loss of species as has happened as a result of specific pests or pathogens in the past, could potentially yield very interesting results. They may also be implemented in older stands, and they would permit the study of before and after effects in relation to a reduction in species diversity. However, there are a number of strong limitations and conceptual problems with removal experiments (see also Díaz et al. 2003):

- It will be extremely difficult to find large enough natural stands with a homogeneous distribution of a diverse range of species of similar abundance. These would have to be reasonably young stands capable of rapid canopy closure following species removal. Otherwise the removal of species would create gaps, and thus the removal/diversity effect could not be separated from a disturbance effect.
- The distribution of species in natural stands is in most situations not homogeneous or random but clumped or clustered, and many species in species-rich and

diverse stands are rare, making it very difficult to establish different tree species diversities at a scale (neighbourhood), where trees do interact.

- This type of experiment would have to be based on the assumption that the distribution of species within a stand is random and not affected by site factors or other (unknown) co-variables.
- In order to analyse the effect of different diversities after removing a certain number of species, a similar biomass must be removed or a similar stand density retained in all treatments. Otherwise the diversity effect cannot be separated from a stand density effect. This would be extremely difficult to achieve in practice.
- The removal of a species would leave legacies, such as litter or the root system, which may not be desirable for analysis of species diversity effects following the removal.
- Such an experiment would have to be established as a long-term endeavour, since its value would be in the analysis of before and after removal effects. However, this requires the description of the baseline conditions through extensive measurements, which may need several years to capture temporal variation, before removal of one or more species.

When an adequate range of diversity or density already exists, it is not necessary to thin or plant in order to alter the diversity and density of the stands. An example of this is the exploratory platform within the FunDivEUROPE project (Baeten et al. 2013). This design includes study areas in six forest ecosystem types in different European regions, from boreal forests (Finland) to mediterranean (Spain). Here, many plots were established to explore the relationships between tree species diversity and ecosystem functioning. For that purpose, three to five co-occurring, important tree species were selected for each region, and then plots were identified in existing forest representing monocultures of each species and species mixtures with two to five species. Each species is usually represented at each level of diversity (to avoid dilution designs), and each of these species combinations is replicated in two or more plots. In practice, it is of course difficult to translate this design on the ground, since some combinations of species are very rare or clearly violate the attempt to have *ceteris paribus* conditions with regard to other environmental variables.

Take-Home Messages

1. Much of our knowledge about the effects of mixed-species forests stems from experiments and exploratory research plots with replications of species richness levels at the same site. In recent years, this knowledge has been greatly expanded by analyses of forest inventories using tree species richness or diversity as an independent variable. However, these latter analyses are restricted to those ecosystem properties and processes that are recorded in forest inventories; often they are limited to measures of productivity. Our

knowledge will gain substantially from a considerable number of experiments on the function of tree species diversity that have been established in the last one or two decades. However, compared to the longevity of trees, these experiments are still relatively young, and the results so far restricted to the initial phase of the growth of even-aged stands. In future, these experiments will facilitate meta-analyses of tree species diversity effects for a range of ecosystem functions and hence provide a high level of evidence for these findings. Owing to the different strengths and weaknesses of inventories, exploratories, and experiments, an approach based on a combination of these research platforms is likely to yield the most comprehensive information in the short term. The level of evidence for tree diversity effects will increase with the temporal and spatial variation that is captured in experiments or networks of experiments.

2. Tree diversity studies should optimise three basic criteria: orthogonality, comprehensiveness, and representativeness. An optimal combination of these criteria is likely not achievable at the level of individual studies but more so at the level of networks of coordinated experiments with a wide geographical coverage. Orthogonality refers to the statistical independence of species diversity effects from other factors, comprehensiveness refers to the spectrum of ecosystem properties and processes and hence ecosystem functions quantified in a study, and representativeness refers to the proportion of the variation in the population of interest that is captured by the design. Ideally, any experiment on the effects of tree diversity on ecosystem functioning should be established in a way that permits the comparison of structures and processes between mixtures (of different diversity) and monocultures at all levels of organisation from cells to the stand (or possibly landscape) scale to facilitate a mechanistic understanding of the underlying processes. To analyse the effects of tree diversity on ecosystem functioning, mixtures with different degrees of tree species richness or functional diversity are typically established. For tree diversity experiments, a number of different planting designs are available; most commonly substitutive designs are being used.
3. A number of ecological theories exist to explain the changes in ecosystem functioning (or properties and processes) with increasing tree species richness or diversity. The most relevant of these is the complementarity hypothesis which postulates that the magnitude of ecosystem processes increases decrementally with the number of species. Each species added to a community, which is functionally different from the species already present, contributes to the magnitude of ecosystem processes. However, this increase follows a saturating curve as more species are added to the system, because the overlap between species in functionality increases.
4. The most important ecological interactions between species in mixture are competition, competitive reduction, and facilitation; the latter two lead to complementary effects. The degree of competition or complementarity is likely dependent on the functional traits of the participating species and the

functional diversity of the community. Functional traits are an expression of the fundamental and realised niche of species. We assume that the lower the functional diversity between species the higher the competition and the lower the complementarity.

5. Since many tree species are foundation species in forest ecosystems, they have a strong influence on the diversity of other taxonomic groups and hence through the increasing complexity of ecological networks will influence ecosystem properties and processes at many levels of ecosystem hierarchy.
6. Diversity effects in mixed tree communities are not constant in space and time. They may be more pronounced on infertile sites, where species interactions improve nutrition of individual species, or they may be more pronounced on sites with good nutrient and water availability, if interactions improve the light use of participating species. The relative importance of the different mechanisms of species interactions further change with stand development. This spatial and temporal variation in interactions even within the same mixture or community makes it difficult to generalise and predict the outcomes of specific tree species mixtures.

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