Forest Ecology and Management 356 (2015) 41–53

Contents lists available at ScienceDirect

Forest Ecology and Management

journal homepage: www.elsevier.com/locate/foreco

Tamm Review: On the strength of evidence when comparing ecosystem functions of mixtures with monocultures

David I. Forrester [a,*], Hans Pretzsch [b]

[a] Chair of Silviculture, Faculty of Environment and Natural Resources, Freiburg University, Tennenbacherstr. 4, 79108 Freiburg, Germany
[b] Chair of Forest Growth and Yield Science, Technische Universität München, Germany

ARTICLE INFO

Article history:
Received 3 June 2015
Received in revised form 10 August 2015
Accepted 13 August 2015
Available online 18 August 2015

Keywords:
Allometry
Biodiversity
Complementarity
Mixed-species forest
Stand density

ABSTRACT

The diversity of dominant tree species in a forest might strongly influence ecosystem functions and services, but the current evidence is not strong enough to provide general insights on when and where these diversity effects will be large or small for a given combination of species. With this goal in mind, the aim of this study is to discuss some of the factors that may need to be considered when designing studies or judging the strength of evidence provided in studies about tree-species mixing effects in forests. While the focus is on productivity, other ecosystem functions relating to light, water and nutrients are also considered. Firstly we consider the implications of stand-level spatial replication, the effects of stand density and tracking mixing effects through time in the same stand or by using chronosequences. Mixing effects at single sites (or ages) can represent significant increases in productivity while the mean mixing effect for the same mixture across a wide range of sites (or a whole rotation) can be much smaller and insignificant. The use of tree- and neighbourhood-level analyses to expand the range of treatments compared with stand-level analyses is then discussed before examining upscaling issues relating to inter- and intra-specific variability in morphology, allometry, physiology and phenology. Ignoring intra-specific variability between individuals in monocultures and mixed-species stands when upscaling to the stand level can strongly distort mixing effects, resulting in very misleading conclusions. The difference between correlations and causality is then discussed using the production ecology equation and mass balance approaches. We also discuss some of the methodological considerations when calculating mixing effects. All of these factors can have significant implications for the calculation and interpretation of mixing effects in forests.

Contents

1. Introduction . . . 42
2. Definitions and calculations . . . 42
   2.1. Level of analysis – tree, neighbourhood, species, total stand and community . . . 42
   2.2. Empirical data sources – planted experiments, specific forest plots or inventory . . . 43
   2.3. Types of interactions . . . 43
   2.4. Mixing effects . . . 43
   2.5. Quantification of mixing proportions using stand density . . . 45
3. Replication at the stand level . . . 46
   3.1. Spatial replication . . . 46
   3.2. Temporal replication . . . 47
   3.3. Stand density and structure . . . 47
4. Tree- and neighbourhood-level replication . . . 49
5. Scaling issues relating to intra-specific variability . . . 49
   5.1. Intra-specific variability in morphology/allometry . . . 50

* Corresponding author.
E-mail address: david.forrester@waldbau.uni-freiburg.de (D.I. Forrester).

http://dx.doi.org/10.1016/j.foreco.2015.08.016

5.2. Intra-specific variability in physiology . . . 50
5.3. Intra- and inter-specific variability in phenology . . . 50
6. Correlations and causality . . . 50
7. Conclusions . . . 51
Acknowledgements . . . 51
References . . . 51

1. Introduction

Forest growth depends not only on broad-scale drivers of climate and soil fertility, but also on species composition. Monocultures of different species often differ in productivity on a given site and interactions between species in mixtures can also influence forest dynamics. Most of the forests of the world are mixtures, so the overall patterns and processes of ecosystem functions and services in relation to species composition are fundamental in forest ecology and management.

Many of the processes and species interactions occurring in mixtures have been reviewed (Binkley, 1992; Kelty, 1992; Forrester et al., 2006b; Richards et al., 2010) and conceptual models have been developed to generalise when and where a given species may perform better or worse in mixtures than monocultures (Forrester, 2014). The development of such concepts requires many studies that are carefully designed, analysed and interpreted. Inappropriate assumptions made when designing or analysing such studies lead to biased calculations of mixing effects, which hamper progress to develop our understanding about these effects. This study combines insights from case studies with general approaches that are powerful tools for quantifying mixing effects.

The factors presented in this study are generally not new but they are sometimes forgotten or ignored. It is also important to note that many of the factors mentioned are only relevant under certain circumstances. Therefore it is important to know which factors, and under which circumstances, there could be significant consequences for mixing effect calculations when these factors are ignored, and these circumstances are also discussed.

2. Definitions and calculations

Since its beginnings, forest science has developed standards for the evaluation of experiments, standardized variables for reporting mean tree and stand characteristics, and standards for the transparency and documentation of calculation procedures (Pretzsch, 2009). However, such standards have focused on the analysis of monocultures, in terms of spacing, thinning and fertiliser application experiments. Comparable standards for the calculation and analysis of mixing effects have proven more difficult to achieve, not least due to the complexity of stand structural effects on estimating mixing proportions as well as definitions and algorithms for dominant height, site indices, stand density in mixed stands and approaches for upscaling from stem volume to tree mass.

This relatively slow development of standards contrasts with the long history of studies about mixing effects in forests. For example, studies by Schwappach (1909), Wimmenauer (1914), Dietrich (1928), Hofmann (1923), and Flury (1926, 1931) provided basic growth and yield data and highlighted the divergence of growth curves at the tree and stand level by mixing. They also showed a stabilising effect on productivity and stand structure in the event of disturbances. However, their comparisons with monocultures were questionable because they were based on yield tables and not neighbouring monocultures with equivalent site conditions. Given this long history, and the many questions that have been examined in relation to mixtures, it is not surprising that a wide range of approaches has been developed and used to calculate mixing effects and each calculation can result in a different mixing effect from a given data set. This section provides definitions of different levels of analyses, different sources of data, and different types of species interactions, as well as definitions and calculations of mixing effects and stand density, all of which will be referred to throughout this paper.

This study does not aim to review experimental designs or discuss statistical analyses. This has been the focus of many previous studies that present the advantages and disadvantages of designs such as replacement series, additive series, biodiversity experiments and many others (Vandermeer, 1989; Kelty and Cameron, 1995; Scherer-Lorenzen et al., 2005; Bruelheide et al., 2014) and in studies that discuss statistical analyses in ecology (e.g. Zuur et al., 2010).

2.1. Level of analysis – tree, neighbourhood, species, total stand and community

The consideration of different levels in a given study enables an examination of how changes at one level influences patterns at another level (Forrester, 2015; Pretzsch et al., 2015a). For example, a large change in the leaf-level physiology of a species in mixture compared with its monoculture may or may not result in a large change in growth or other functions at the stand level, depending on how other processes change, such as carbon partitioning. Combining tree- and stand-level analyses helps to determine which mixing effects are most important for forest functioning. They can also be used to indicate potential sources of error when comparing measurements of a given processes at different levels and when scaling up or down between each level (Pretzsch et al., 2015a). It is therefore important to define the main levels that are referred to in this study.

Tree-level analyses are those that examine individual trees e.g. when regression is used to examine whether the relationship between tree diameter and height varies between treatments. *Neighbourhood-level* analyses are a type of tree-level analysis that account for the characteristics of the trees' neighbourhood (e.g. in terms of basal area, species composition; Boyden et al., 2005; Vanclay, 2006a; Forrester et al., 2011; von Oheimb et al., 2011). This contrasts with typical tree-level analyses where the characteristics of the trees' neighbourhood are ignored or only considered in terms of the stand-level treatment, such that all trees within the plot have the same (mean plot) neighbourhood.

Stand-level analyses consider totals and means of all trees within the plot, such as total basal area (BA_T) or mean tree diameter. Stand-level analyses include *species-level* and *total stand-level* analyses. For species-level analyses the total stand is simply divided by species to provide the totals and means for each species within the stand. For example, in a two-species mixture, $BA_T = BA_{species1} + BA_{species2}$; a total stand-level analysis would consider BA_T, while a species-level analysis would consider $BA_{species1}$ or $BA_{species2}$. Total stand-level analyses are also sometimes referred to as *community-level* analyses because they consider the totals or means of the whole community. Many other levels exist, including finer scales such as leaf-level and organ-level (e.g. branches, roots)