Forest Ecology and Management 382 (2016) 244–256

Contents lists available at ScienceDirect

Forest Ecology and Management

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

Diversity, functional structure and functional redundancy of woodland plant communities: How do mixed tree species plantations compare with monocultures?

N. Barsoum[a,*], L. Coote[b], A.E. Eycott[c], L. Fuller[d], A. Kiewitt[a], R.G. Davies[e]

[a] Forest Research, Alice Holt Lodge, Farnham, Surrey GU10 4LH, UK
[b] Department of Botany, School of Natural Sciences, Trinity College Dublin, Dublin 2, Ireland
[c] Institute of Biology, University of Bergen, Thormøhlensgate, 53A, Bergen N-5006, Norway
[d] Biological and Environmental Sciences, University of Stirling, Stirling FK9 4LA, UK
[e] School of Biological Sciences, University of East Anglia, Norwich NR4 7TJ, UK

ARTICLE INFO

Article history:
Received 25 July 2016
Received in revised form 26 September 2016
Accepted 2 October 2016
Available online 15 October 2016

Keywords:
Diversification
Functional traits
Functional redundancy
Ground vegetation
Pinus sylvestris
Quercus robur

ABSTRACT

Managing forest plantation stands in a way that retains productivity targets, but that also fosters biodiversity and stand resilience are key sustainable forest management goals. Current forestry policy advocates a diversification of forest stands to achieve these goals, favouring mixed age structures and polycultures over single-aged monocultures. Evidence is lacking, however, to support this management recommendation for biodiversity gains and related ecosystem service delivery. We used indices of taxonomic diversity and functional structure to compare ground vegetation communities in mixed and pure stands of Scots pine (*Pinus sylvestris*) and pedunculate oak (*Quercus robur*) in each of three study regions. We categorised the 91 vascular plant species identified into functional effect and response groups. We tested the hypotheses that ground vegetation communities (i) differ significantly in structure and composition between Scots pine and oak monocultures and (ii) show enhanced levels of taxonomic and functional diversity and functional redundancy in mixed stands of Scots pine and oak compared with monocultures. We explored the implications of any differences in the functional structure of ground vegetation communities in the different stand types on two ecosystem services: nutrient availability and levels of resource provisioning for herbivores. Nine functional response groups (RG) and seven functional effect groups (EG) were identified with considerable overlap in the RG and EG species grouping. Three RGs had traits characteristic of forests (spring flowering herbs, tree saplings and shrubs/climbers), one RG had traits characteristic of open habitats (annual ruderals) and the remaining RGs had more generalist traits (anemochorous perennials, graminoids and short perennials). No significant differences were found among stand types in terms of taxonomic diversity or richness of the different functional trait groups. Ground vegetation communities in the three study regions also had similar levels of functional redundancy across stand types. However, Scots pine and oak monocultures harboured significantly different abundances of species with distinct functional traits. In all three study regions, anemochorous perennials were significantly more abundant in Scots pine monocultures than oak monocultures, while two core forest groups (shrubs/climbers, spring flowering herbs) were significantly more abundant in oak monocultures. Mixed stands had intermediate abundances of these functional groups. These differences have implications for the comparative availability of food resources and shelter for wildlife, but also the mobilisation and temporal availability of nutrients in the two monocultures. Thus, mixtures of Scots pine and pedunculate oak can temper significant tree species identity influences on ground vegetation functional diversity.

1. Introduction

Plantations make up 7%, i.e. 264 million ha, of forest cover worldwide and this area is increasing rapidly with a growing reliance on plantations for wood products, carbon management, the

* Corresponding author.
E-mail addresses: nadia.barsoum@forestry.gsi.gov.uk (N. Barsoum), cootel@tcd.ie (L. Coote), Amy.Eycott@uib.no (A.E. Eycott), lauren.fuller@stir.ac.uk (L. Fuller), andrea.kiewitt@gmail.com (A. Kiewitt), Richard.G.Davies@uea.ac.uk (R.G. Davies).

http://dx.doi.org/10.1016/j.foreco.2016.10.005
0378-1127/

protection of soil and water and the rehabilitation and diversification of impoverished landscapes (FAO, 2010; Pawson et al., 2013). In some countries, plantations constitute a significant proportion of the total forest area, resulting in a strong anthropogenic influence on the composition of forest stands. Often the composition, structure and function of plantations are highly simplified; e.g. in Europe, 29% of forests are composed of a single tree species and many of these are plantations comprised of a single age cohort (Forest Europe, UNECE & FAO, 2011). This raises concerns over the implications for biodiversity, particularly for the many forest dependent species that are in decline (Shvidenko et al., 2005). Also of concern is the resilience of these simplified forests to environmental change (e.g. drought, invasive species, pests and diseases) and their capacity to deliver anticipated ecosystem services (e.g. nutrient cycling, erosion control, shelter and food resources for wildlife) (Thompson et al. 2009; Kanninen, 2010).

A consistent mitigation measure that is advocated under current forestry policy is the diversification of forest management units to derive greater structural and/or compositional heterogeneity (Puettmann, 2011); structural diversity is generally accepted to enhance levels of biodiversity through the provision of a greater diversity of microhabitats (Simpson, 1949; Tews et al., 2004). A mixed tree species approach is a particularly attractive option as it combines recommendations for increased stand heterogeneity while potentially retaining, or even enhancing levels of productivity where there is complementary resource use by the tree species in a polyculture (Pretzsch and Schütze, 2009; Thompson et al., 2009; Jucker et al., 2014). There is inconsistent supporting evidence, however, of the comparative benefits of mixed stands over monocultures for forest biodiversity and ecosystem functioning (e.g. resistance to disturbance, or element cycling) (Nadrowski et al., 2010; Cavard et al., 2011; Gamfeldt et al., 2013; Scherer-Lorenzen, 2014); this is related to the difficulty in disentangling tree diversity effects from confounding factors such as substrate and topographic heterogeneity (Nadrowski et al., 2010). Moreover, the respective roles of tree species identity and tree species richness in influencing wider forest species diversity and ecosystem functioning are not fully understood, making it difficult to predict the likely consequences of various proposed tree species combinations on ecosystem service provision and the functional resilience of associated communities. Differences in traits between tree species, such as canopy phenology, have been shown in some studies to have a greater influence on wider forest species diversity than tree species richness (Barbier et al., 2008; Scherer-Lorenzen, 2014). Tree species identity has also been found to have stronger effects than tree species richness on forest ecosystem functioning and associated ecosystem service provisioning (e.g. resistance to herbivory, decomposition) (Nadrowski et al., 2010).

Ground vegetation is a highly influential component of forest ecosystem processes (Gilliam, 2007). It has an impact on recruitment patterns of the overstorey, nutrient cycling and disturbance mediation; it also plays an important role in the provisioning of habitat and foraging material (e.g. pollen, nectar, foliage) for many associated species (Royo and Carson, 2006; Gilliam, 2007). Ground vegetation, in turn, is strongly influenced by the composition and structure of the overstorey, responding to differences in temperatures and the availability of light, water and soil nutrients at the forest floor level (Barbier et al., 2008). Thus, a greater understanding of tree compositional influences on ground vegetation species diversity and functional structure should contribute greatly to the improved management of this component of forest biodiversity and associated ecosystem functions and services. Existing evidence for monoculture compared with mixed tree species effects on ground vegetation is largely based on taxonomic indices of diversity (i.e. species richness, diversity, evenness) with no consistent trends found. Taboada et al. (2010) and Augusto et al. (2003), for example, found limited significant influences of tree species mixtures compared with pure stands on taxonomic indices of ground vegetation diversity, unlike some other authors (e.g. Simmons and Buckley, 1992; Saetre et al., 1997). Furthermore, where stand age was considered as an explanatory variable in some studies, significant positive correlations between tree species richness and ground vegetation species diversity were not consistently found across all growth stages (Auclair and Goff, 1971; Pharo et al., 2000).

Regional differences in species pools and the need for research results to be easily transposable across regions argue in favour of adopting a functional diversity approach which relies on describing the functional traits, rather than the taxonomic identity, of species to help explain forest composition and biodiversity-ecosystem function relationships (Hooper et al., 2005). The functional structure of communities can be defined by categorising species both according to functional *response* traits, which reflect the way species respond to the abiotic and biotic environments (e.g. resource availability, disturbance), but also according to functional *effect* traits which characterise species effects on dominant ecosystem functional processes and the related delivery of ecosystem services (e.g. nutrient cycling, disturbance mediation, pollination). A functional diversity approach can also be used as an indirect measure of resilience by assessing levels of functional redundancy in the delivery of one or more ecosystem services among associated communities. This can be achieved, for example, by assessing the number of species present in different functional effect trait groups and the number of distinct functional effect trait groups represented in a community (Díaz and Cabido, 2001; Laliberté et al., 2010).

A functional diversity approach is achievable with ground vegetation considering the significant species-specific physiological and morphological knowledge that has been acquired, documented and linked to functional processes (Pérez-Harguindeguy et al., 2013). There is also a good understanding of traits that typify forest-dependent species and those with the highest conservation value (Hermy et al., 1999; Hérault et al., 2005). Functional diversity analyses represent an alternative approach, therefore, to information-poor species richness analyses on the one hand, and analyses based on taxonomic composition for which results are hard to generalise, on the other.

This study compared ground vegetation communities in mixed and pure stands of Scots pine (*Pinus sylvestris* L.) and pedunculate oak (*Quercus robur* L.) across three study regions. These species were selected for their contrasting evergreen and deciduous habits and because they are known successful polycultures. The study objectives were to investigate the influences of tree species identity (Scots pine or oak) and plantation complexity (i.e. monocultures or two species mixtures of Scots pine and oak) on the functional structure and levels of taxonomic diversity and functional redundancy of ground vegetation communities. Functional structure was described by categorising ground vegetation species according to two alternative functional classifications, based on species functional response and functional effect traits, respectively. This allowed for inferences to be made about ground vegetation community responses to environmental conditions, but also their potential influences on forest ecosystem functioning in mixed and pure stands of Scots pine and oak. Functional redundancy served as a proxy for the functional resilience of communities to environmental change. The same tree species identity and monoculture/polyculture comparisons were repeated in three study regions selected for their differing environmental conditions, particularly for differences in environmental variables known to have a strong influence on ground vegetation community composition (e.g. levels of N deposition, rainfall). This was to check for the consistency of any significant stand type effects on ground vegetation communities, but also to test for any significant stand type and region interactions. Hence, this study aims to contribute towards