Agriculture, Ecosystems and Environment 258 (2018) 154–161

Contents lists available at ScienceDirect

Agriculture, Ecosystems and Environment

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

How does grazing management influence the functional diversity of oak woodland ecosystems? A plant trait approach

Hilary Ford*, John R. Healey, Lars Markesteijn, Andrew R. Smith

School of Environment, Natural Resources and Geography, Bangor University, Bangor, LL57 2DG, UK

ARTICLE INFO

Keywords:
Atlantic oak woodlands
Ecosystem resilience
Forest pasture
Herbivory
Stress tolerance
Wood pasture

ABSTRACT

Traditional approaches to conservation often focus on plant species composition. In contrast, trait-based approaches highlight the role plant species play in ecosystem function, with a focus on functional diversity and its importance for ecosystem resilience. Here we utilise a plant-trait approach to explore the association between livestock grazing intensity and plant functional diversity in Atlantic oak woodlands, a conservation priority habitat. In two historically un-grazed woodlands (subject to periods of light sheep grazing in winter) paired with two grazed woodlands (intensively grazed by sheep or feral goats), in north-west Wales, UK, field plant-trait data were recorded in three (30 × 4 m) plots per woodland for trees, saplings and understory plants. For trees and saplings, plant-trait data from the field (specific leaf area (SLA) and leaf dry matter content (LDMC)) were combined with plant tolerance indices from the scientific literature (shade, drought and water-logging tolerance) and used to calculate community weighted means (CWM) and functional diversity for plot-level communities. Three plant traits (LDMC, mean foliage height and growth form) and two Ellenberg indices (light and moisture) were combined to calculate CWM and functional diversity for understory plant communities. Tree and sapling communities from grazed woodlands were characterised by response traits associated with grazing avoidance strategies (high LDMC, low SLA), and higher shade – and drought-tolerance scores but lower water-logging-tolerance scores than in un-grazed woodlands. Tree and sapling communities in the un-grazed woodlands had greater seedling establishment, sapling recruitment and functional diversity than in the grazed woodlands. Plant-trait values and functional diversity did not differ with grazing intensity for understory plants. Land managers are increasingly being asked to manage semi-natural habitats for 'resilience to future events' such as droughts or floods. Here we demonstrate how a plant-trait approach, including assessment of community-level tolerance indices, allows us to infer potential associations between grazing management, functional diversity and ecosystem resilience.

1. Introduction

Atlantic oak woodlands are a priority ecosystem for conservation within Europe (European Commission, 2015), characterised by high rainfall, base-poor soils and biodiverse bryophyte communities. Despite their high conservation importance many are listed as having unfavourable conservation status, threatened by fragmentation, inappropriate grazing management and invasive species (JNCC, 2013). Traditional approaches to woodland conservation focus on plant community composition and diversity (Hansson, 2001; McEvoy et al., 2006) and sapling recruitment (Palmer et al., 2004), with poor regeneration of oak (*Quercus* spp.) of particular concern (Shaw, 1968a,b). More recently, trait-based approaches to plant community ecology have been advocated, as a basis for conservation management, in a range of terrestrial ecosystems (Cadotte et al., 2011) including forests (Andersen et al., 2012; Craven et al., 2016; Mokany et al., 2015). These trait-based approaches highlight the role plant species play in ecosystem function, exploring the emerging relationship between functional diversity and resilience to future perturbations (Standish et al., 2014). Here we define *resilience* as the degree to which ecosystem function can resist or recover rapidly from environmental perturbations (Oliver et al., 2015) as mediated by plant functional traits.

Plant functional traits can be defined in two broad ways: i) as any measurable characteristics at the individual level that directly or indirectly affect plant fitness (Lavorel et al., 1997; Violle et al., 2007); or ii) characteristics of individuals or species that influence ecosystem-level properties and processes (Petchey and Gaston, 2006). Plant traits are commonly categorised as either: i) *response traits* – traits associated with an individual or species response to environmental change such as grazing, drought or flooding; or ii) *effect traits* – traits that determine the

* Corresponding author.
E-mail address: hilary.ford@bangor.ac.uk (H. Ford).

https://doi.org/10.1016/j.agee.2018.02.025
Received 11 October 2017; Received in revised form 21 February 2018; Accepted 22 February 2018
0167-8809/

Table 1
Characteristics of the four study woodlands in north-west Wales, UK.

Location	Ceunant Llennyrch		Nant Gwynant	
Woodland	Llennyrch (L)	Coed Felinrhyd (F)	Hafod y Llan (H)	Llyndy Isaf (I)
Lat/Long (WGS84)	52°55′30.07″N	52°56′06.85″N	53°02′07.49″N	53°01′26.21″N
Elevation (of plots)	~100 m	~70 m	~70 m	~70 m
Grazing category	G	U	G	U
Grazing history	Intensively sheep grazed (80–100 years)	Un-grazed or light sheep grazing in winter only (80–100 years)	Feral goat grazed but sheep excluded (40 years +)	Un-grazed or light sheep grazing in winter only (25 years +)
Condition	Unfavourable	Favourable	Unfavourable	Favourable

Condition was reported according to Common Standards Monitoring (CSM) criteria set by the Joint Nature Conservation Committee (JNCC) for Ceunant Llennyrch (Woodland Trust, 2016) and Nant Gwynant (Allen and Brash, 2012; Hearn, 2004; Nouvet et al., 2000). Information on grazing history was also obtained from these References.

effect of plants on ecosystem functions such as nutrient or biogeochemical cycling (Lavorel and Garnier, 2002). A greater functional diversity (i.e. variation in functional traits within a community) of effect traits is expected to result in enhanced community-level plant productivity and resource-use efficiency (Díaz et al., 2001). For response traits, greater functional diversity can enhance a community's resilience to a range of environmental disturbances (Díaz et al., 2001; Elmqvist et al., 2003; Loreau et al., 2001; Standish et al., 2014), such as grazing by large herbivores, flooding or drought, by providing a higher response diversity.

The impact of livestock grazing on community-level plant traits has been summarised by several classic plant-resource models: Grime's (1977) CSR (Competitor, Stress-tolerator, Ruderal) model, Coley et al.'s (1985) resource availability model and Westoby's (1998) LHS (leaf-height-seed) model. These models predict that: i) selective or low-intensity grazing favours unpalatable plants with low specific leaf area (SLA) (Cornelissen et al., 1999; Coughenour, 1985) and higher leaf dry matter content (LDMC) (grazing avoidance); and ii) intensive non-selective grazing favours short, often palatable, plants with high SLA indicating fast regrowth of high-quality tissue with low structural defence (grazing tolerance), particularly in humid or productive grassland systems (Díaz et al., 2001). This framework, particularly relevant in woodlands to understory plant species, may also be affected by canopy openness with more open woodlands characterised by fast-growing understory species with traits indicative of grazing tolerance strategies such as high SLA (Le Brocque et al., 2009). For sapling communities, grazing avoidance strategies may be favoured, with low SLA and high LDMC effective at deterring herbivory (Westoby et al., 2002) as these traits tend to be coupled with the allocation of more tannins, phenols or other defensive compounds to leaves (Coley, 1983). Indeed, under open-canopy and intensive livestock-grazing conditions, sapling SLA was found to be lower than in un-grazed forests (Carlucci et al., 2012).

In addition to commonly studied response traits such as SLA and LDMC, traits linked to plant response to variation in the physical environment, e.g. tolerance of shade, drought and water-logging, have recently been incorporated into studies evaluating the impact of land-use intensity on functional diversity and ecosystem resilience (Carreño-Rocabado et al., 2012; Carreño-Rocabado et al., 2016; Craven et al., 2016). Some studies have focused on how grazing interacts with response plant-traits related to the physical environment, especially drought tolerance (Deléglise et al., 2015, Leiva et al., 2013; Plieninger et al., 2011; Tucker et al., 2011). In a further advance, Niinemets and Valladares (2006) developed proxies for environmental response plant-traits based primarily on Ellenberg indices of shade, drought and water-logging tolerance which they extrapolated to over 800 species of trees and shrubs from the northern hemisphere, in lieu of trait-specific information.

The effect of grazing on plant functional diversity has been discussed through the lens of 'environmental filtering' where strong abiotic or biotic filtering effects (e.g. heavy grazing pressure) are expected to select for convergent trait values for co-occurring species, leading to a loss of functional diversity (Ackerly and Cornwell, 2007; Cavendar-Bares et al., 2004; Kraft et al., 2008). Most studies on the impact of livestock grazing on functional diversity in woodland ecosystems have focused on the understory plant community, finding that an increase in grazing intensity leads to either increased (Mandle and Ticktin, 2015) or decreased (de Bello et al., 2006) functional diversity. Results from studies of the response of grassland functional diversity to livestock grazing are also inconsistent, with grazing either reducing plant functional diversity by favouring a limited set of trait values related to either avoidance or tolerance strategies (Catorci et al., 2014) or enhancing it, when compared to un-grazed grasslands where tall grasses dominate (Komac et al., 2015; Vandewalle et al., 2014).

In this study we utilised a plant-trait approach to explore the association between livestock grazing and plant community response traits, tolerance indices and functional diversity in oak woodlands. We expected: 1) in the understory plant community of grazed woodlands response trait values associated with grazing tolerance strategies (low LDMC, low mean foliage height) to dominate; 2) in the tree and sapling communities of grazed woodlands response traits linked to grazing avoidance strategies (e.g. low SLA, high LDMC) to dominate; 3) in the tree and sapling communities of both grazed and un-grazed woodlands trait values associated with shade and water-logging tolerance scores to be greater than those associated with drought tolerance due to the high year-round rainfall in the study area; 4) in the un-grazed woodland plant communities functional diversity to be greater due to the effect of environmental filtering on the grazed woodlands.

2. Methods

2.1. Study area and sampling design

Two pairs of Atlantic oak woodlands, identified as upland oakwood, a priority habitat for conservation and designated as Site(s) of Special Scientific Interest (SSSI), were selected in north-west Wales, UK. One pair is in the area of Ceunant Llennyrch and the other 15 km away in Nant Gwynant (Table 1).These woodlands are managed by the government conservation agency Natural Resources Wales (NRW), alongside two non-governmental organisations: the Woodland Trust (at Ceunant Llennyrch) and the National Trust (at Nant Gwynant). These woodlands are remnants of natural woodland that originally covered most of the Atlantic fringe of Europe, influenced by the Gulf Stream to create the warm, wet microclimate of a temperate rainforest with > 200 days per year of precipitation ≥1 mm (JNCC, 2013). Annual precipitation is ~3400 mm with mean, maximum and minimum temperatures of ~10, 19 and −1.5C respectively (Robinson et al., 2017). These woodlands are dominated by *Quercus petraea*, with lower abundance of *Betula pubescens*, *Corylus avellana*, *Fraxinus excelsior*, *Sorbus aucuparia* and *Ilex aquifolium*. Within each of the two study areas, one woodland was selected that had a known history of intensive grazing (managed sheep or feral goat) for at least the past 25 years, and the other managed with no or only light winter grazing over the same time period due to fencing to exclude the animals (Table 1). Sheep and feral goats were the only large mammal herbivores in the study area over this