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Ecological constraints to 'old-growth' lichen indicators: Niche specialism or dispersal limitation?

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ABSTRACT

European landscape conservation includes the recognition of inter-related 'ancient' and 'old-growth' woodland. Ancient woodland is defined by its temporal continuity, which can be measured through its consistent occurrence on historic maps over a period of time, typically several centuries. Old-growth woodland has attributes of both temporal continuity and structural complexity; European old-growth woodland is now extremely rare and a valuable conservation resource. Indicator species provide recognition of old-growth woodland, through traits that are sensitive to its defining features: (i) dispersal limitation demanding temporal continuity of suitable habitat prior to colonisation (as is associated with ancient woodland), and/or (ii) specialist niches associated with old and senescent trees (which may or may not be found in ancient woodland, depending on its past management). To test the response of indicators to each of these features, niche models were developed for lichen epiphytes in an ancient and structurally diverse woodland stand, thus corresponding to 'old-growth' condition. Models were projected for the ancient and an adjacent regenerated stand. There was less suitable habitat in the regenerated stand, and a lower proportion of suitable habitat was occupied. Nevertheless, indicators had colonised from the ancient to the regenerated stand within 50 years. Viewed against the background of previous work, we conclude that landscape context – the spatial relationship between ancient and regenerated woodland – is critical to the interpretation of indicators, which are perhaps better conceptualised as markers of threat and conservation value than independent measures of woodland history.

1. Introduction

European boreal and temperate forest has suffered among the highest global rates of habitat loss and degradation (Hannah et al., 1995; MEA, 2005). Amid this loss, old-growth forest retains two key attributes of temporal continuity and structural complexity (Whittet and Ellis, 2013; Ellis et al., 2015). Remnant fragments of 'old-growth' European temperate woodland provide rare and valuable examples of near-natural forest. Identifying and protecting these habitats is a conservation priority, but their clear recognition is often challenging. Temporal continuity that defines 'ancient woodland' can be confirmed using archival evidence, including historic mapping to identify sites that have been consistently wooded over a long period of time, typically several centuries (Roberts et al., 1992; Spencer and Kirby, 1992). Biological proxies, such as species indicators that are restricted to ancient woodland sites (Peterken, 1974; Peterken and Game, 1984; Hermy et al., 1999), have the additional advantage of incorporating not just the temporal continuity of woodland, but the effects of management on species ecology. The most effective indicators will include species that are sensitive to both 'old-growth' attributes: (i) temporal continuity (as is associated with ancient woodland), which increases the establishment probabilities for dispersal limited species (Dzwonko and Loster, 1992; Matlack, 1994; Brunet and Von Oheimb, 1998), as well as (ii) structural complexity, in particular the occurrence of specialist niches associated with heterogeneous old-growth stands, such as on ancient trees or deadwood (Michel and Winter 2009; Vuidot et al., 2011). In contrast to the use of indicator species, mapping data can only demonstrate the continuous occurrence of woodland; despite their continuity of trees, such ancient stands could represent managed systems without old-

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growth ecological status, e.g. ancient coppice maintained through short cycle rotational forestry.

Lichen epiphytes are a key example of an indicator group widely used for identifying old-growth remnants, and are the subject of this paper. Lists of lichen epiphytes have been developed for species that are assumed to be either niche specialists, with requirement for habitat associated with old-growth stands, or dispersal limited, and which do not colonise into recently regenerated stands. Such species should ideally capture the temporal continuity of specialist niches associated with old-growth woodland. Comparable lichen species lists have been developed for Britain (Rose, 1974, 1976; Coppins and Coppins, 2002) Fennoscandia (Tibell, 1992; Kuusinen, 1996; Nitare, 2000), and North America (Goward, 1994; Selva, 1994). These indicator lists have been proposed based on qualitative analysis combined with expert judgement, and have since received mixed retrospective support (Whittet and Ellis, 2013; Ellis, 2014). Critically, the ecological processes which cause lichens to become restricted to old-growth remnants are unresolved, and this undermines confidence in their application (Nordén and Appelqvist, 2001; Rolstad et al., 2002). Some studies have suggested that species occur in old-growth stands because of the availability of specialist niches (Fritz et al., 2008b; Fritz and Heilmann-Clausen, 2010), while others have suggested that an absence from regenerated stands is related instead to dispersal limitation (Dettki et al., 2000; Sillett et al., 2000). In the former case conservation might focus on creating appropriate habitat, with the expectation that species could colonise over relatively short timespans, while in the latter case improved habitat connectivity over long ecological time scales might be required. These perspectives – habitat loss versus dispersal limitation – can cause discrepancies in the application of conservation strategy.

To clarify evidence around the use of lichen indicators, this study directly tested the degree to which niche specialism or dispersal limitation might constrain their occurrence. We compared patterns of habitat occupancy for adjacent stands, including ancient woodland that was structurally diverse (old-growth like), and recently regenerated woodland, in western Scotland. We assume that the pattern of species habitat occupancy in the ancient stand is at equilibrium; this habitat response was then captured in predictive models, which were projected onto the regenerated stand. Within the specific context of our study system, but replicating across multiple old-growth indicators, we hypothesised that:

1. If dispersal limitation is a factor, indicator lichens that occurred in the ancient stand, will not yet have colonised into the regenerated stand;
2. Or, if these species had colonised into the regenerated stand, they should have failed to occupy a similar proportion of their suitable habitat space, relative to the ancient stand;
3. And, the spatial pattern of habitat model residuals should show a degree of aggregation consistent with local dispersal limitation.

2. Methods

2.1. Species and study site

The study site – Shian Wood – is located on Scotland's west coast (Fig. 1A), and represents a geographically-isolated area of mixed oakwood (Baarda, 2005) that can be divided into two distinct stands (Fig. 1B). First, an area of c. 4 ha that is classified as semi-natural 'ancient woodland' (Walker and Kirby, 1987; Roberts et al., 1992); it occurs consistently on historic mapping since the mid-18th century and is therefore known to be > 250 yr old. Second, an area of c. 11 ha adjoined with and directly adjacent to the ancient woodland that was once wooded (appearing on maps in the mid-18th century), but from which woodland was completely removed (absent on maps in the mid-19th century), having since regenerated to the native woodland that is present today. Close examination of historic mapping (Whittet et al., 2015), revealed that the regenerated woodland stand was open and without trees on the Ordnance Survey maps surveyed in 1863–1871 (with revisions in 1895 and 1904), 1924–1926 (with a revision in 1947), and 1954–1960. The current woodland is present on maps surveyed in 1973, and on maps revised thereafter (in 1999 and 2007). This places the age of the regenerated woodland as c. 40–50 yr old.

2.2. Field sampling

We selected 14 epiphytic lichen species that were easily located and identified under field conditions, which had contrasting physiologies and dispersal modes (Table 1), and which are expected to be indicators of old-growth woodland (≈ecological continuity) for Scotland's western zone of oceanic climate (Ellis, 2016). Thus, the species are used as indicators within either: (i) the Revised

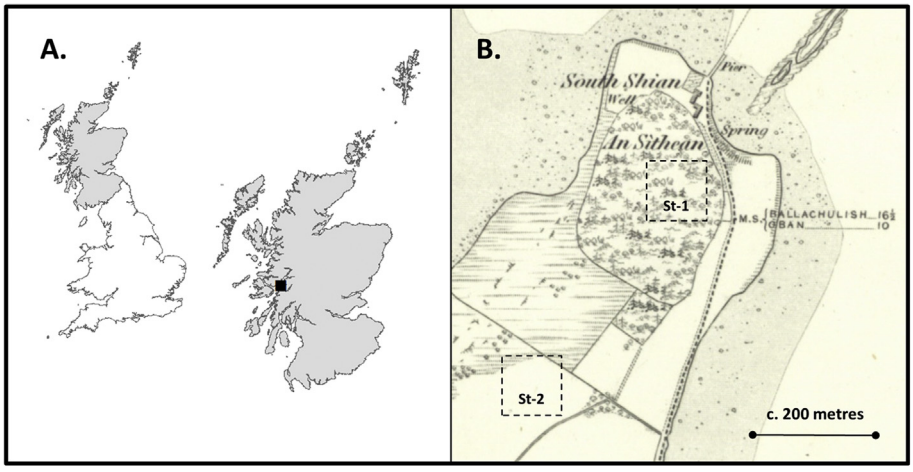

Fig. 1. A. The position of the Shian Wood study site in western Scotland (c. 56.52 N; −5.41 E), and B. The extent of woodland from the Ordnance Survey first six-inch series (1843–1882), with the position of the sampling plots in the ancient woodland, and in an area of open ground (without trees) that has regenerated to woodland in the past c. 50 yr. Reproduced with permission of the National Map Library of Scotland.