



Double-edged effect? Impact of dual edge proximity on the distribution of ancient woodland indicator plant species in a fragmented habitat

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Abstract: The influence of edge proximity on woodland plants is a well-established research area, yet the influence of dual edge exposure has rarely been investigated. This novel research aims to establish whether proximity to two edges has any additive influence on Ancient Woodland Indicator (AWI) species presence relative to proximity to a single edge. Several AWI species are threatened and thus specific conservation priorities, while Ancient Semi-Natural Woodland (ASNW) itself is often highly fragmented: almost half of remnant patches are less than 5 ha, which increases the potential for dual edge effects. Here, systematic mapping of herbaceous AWI species was conducted in 310 vegetation plots in two formerly-connected ASNW fragments in South-West England. Linear regression modelling revealed that distance to nearest edge and distance to second nearest edge were both univariately positively correlated with AWI species richness. After distance from nearest edge was entered into a multivariate model first, distance from second edge was entered in a second optional step after meeting stepwise criteria. The resultant multivariate model was more significant, and explained more variance, than either variable in isolation, indicating an additive effect of dual edge exposure. Likewise, binary logistic regression modelling showed presence of individual AWI species (*Anemone nemorosa*, *Hyacinthoides non-scripta*, *Lamium galaeobdolon* and *Paris quadrifolia*) was significantly related not only to distance from the nearest and second nearest edges in isolation, but significantly more strongly by the additive effect of distance from both edges in a single model. We discuss the implications of these findings from community ecology and conservation perspectives.

Abbreviations: ASNW – Ancient Semi-Natural Woodland, AWI – Ancient Woodland Indicator.

Nomenclature: IPNI (2015) The International Plant Names Index <http://www.ipni.org/>

Introduction

The presence of scarce and range-restricted flora in Ancient Semi-Natural Woodland (ASNW) (Peterken 1974, Wulf 1997, Honnay et al. 1999, Palo et al. 2013) contributes to its status as an ecosystem of high conservation value (Peterken 1983, Rackham 2003, Goldberg et al. 2007). The ancient woodland concept is well-integrated into forest research and conservation practice, although definitions and date thresholds vary amongst countries (Hermý et al. 1999, Wirth et al. 2009). In England, ASNW is defined as predominantly a native broadleaf canopy established through natural regeneration (Rackham, 2008) on land that has remained continuously woodland since at least the year 1600 (Goldberg et al. 2007).

Ancient woodland indicator (AWI) species are vascular plants that are particularly, but not exclusively, associated with ASNW (Rose 1999, Graves et al. 2009). Regional AWI lists were developed to assist in determining ancient woodland status and are additionally used to assess habitat quality (Graves et al. 2009). AWI species are considered to have low colonisation potential due to poor seed production, low dispersal capability and short-term persistence in the seed bank

(Honnay et al. 1998). As such, AWI species may not be able to colonise alternative woodland habitats if ASNWs are lost or conditions become sub-optimal (Hermý et al. 1999). The limited distribution of AWI species and their specific ecology has promoted extensive use in woodland research (Peterken 1974, Spencer 1990, Wulf 1997, Honnay et al. 1998, Hermý et al. 1999, Rose 1999, Kirby and Goldberg 2002, Rackham 2003, Kirby and Morecroft 2011, Kimberley et al. 2014, Stefańska-Krzaczek et al. 2016).

Landscape fragmentation is a significant threat to ASNW plant communities (Rackham 2008, Corney et al. 2008), not only due to reduction in dispersal potential of AWI species, but also due to increased edge effects. Edge width is defined as the outer part of a woodland compartment where environmental conditions differ significantly from the interior (Honnay et al. 2002). Corney et al. (2008) report that 48% of ancient woodlands are under 5 ha, which means they have a high edge:interior ratio and a large edge width, especially if they deviate from an optimum circular shape (Laurance 2008). Edge environmental conditions are generally considered to be less favourable for persistence of specialist flora, including many AWI species, due to altered abiotic and biotic variables (Matlack 1993, Murcia 1995, Honnay et al. 2002, Willi et al.

2005, Hofmeister et al. 2013, Tinya and Ódor 2016), as well as anthropogenic influences (Corney et al. 2008).

Abiotic and biotic variables commonly exhibit an edge width of between 10–60 m in temperate forests (Palik and Murphy 1990, Matlack 1993, Matlack 1994, Gehlhausen et al. 2000, Honnay et al. 2002). Additionally, studies seeking to avoid edge influence, have situated sample plots at > 20 m from the edge (Bossuyt and Hermy 2000), > 30 m (Brunet et al. 2012), and > 50 m (Gelhausen 2000, Coote et al. 2012). Exceptionally, edge effects have been evidenced over 100 m from the edge (Hofmeister et al. 2013, Pellissier et al. 2013) but such findings are not comparable to small ancient woodland fragments in the UK. Land use in the matrix (Gove et al. 2007), prevailing wind direction (Smithers 2000) and aspect (Murcia 1995, Honnay et al. 2002) influence the extent to which edge effects permeate woodland.

This is the first study to investigate multiple edge effects in relation to AWI species and ancient woodland. The impact of multiple edges is an important but overlooked factor (Ries and Sisk 2004). Few studies have explicitly gathered primary data to analyse this in relation to any species or ecosystem (Fletcher et al. 2005), instead measuring linear distance to the closest edge only. A small number of studies have been completed with explicit focus on AWI response to nearest edge proximity (Willi et al. 2005, Hofmeister et al. 2013, Pellissier et al. 2013, Kimberley et al. 2014). Despite the potential importance of edge effects on AWI species, both in their own right as specialist species, and in terms of their efficacy of indicators, a search of the literature revealed no studies relating to multiple edge effects on these species. This is surprising given that the highly-fragmented nature of ANSW means that the potential for exposure to multiple edge effects is considerable.

We test for relationship with the nearest edge, as well as any additional contribution of the second edge to take account of double exposure within fragment corners. We hypothesised that (1) AWI richness will increase with distance from any edge; (2) the second nearest edge would also correlate with AWI richness so that a multivariate model with both distances would be superior to a univariate model using either in isolation; (3) the patterns for AWI species richness would also hold true for specific AWI species analysed on a presence/absence basis.

Methods

The study site was a fragmented species-rich ANSW in the South-West UK. The two discrete fragments comprising the site were situated near Cheltenham on the Cotswold Hills escarpment of Jurassic oolitic limestone, at 265 m above sea level and centred on 51°53'35.5"N, 2°00'34.60"W (Fig. 1). The mean diurnal temperature was 8.6–14.7°C and annual precipitation was 843 mm (MET office, 1981–2010). The fragments have comparable geology, edaphic variables and topography. The coppice-with-standards woodland classifies as National Vegetation Classification W8b (Rodwell 1991),

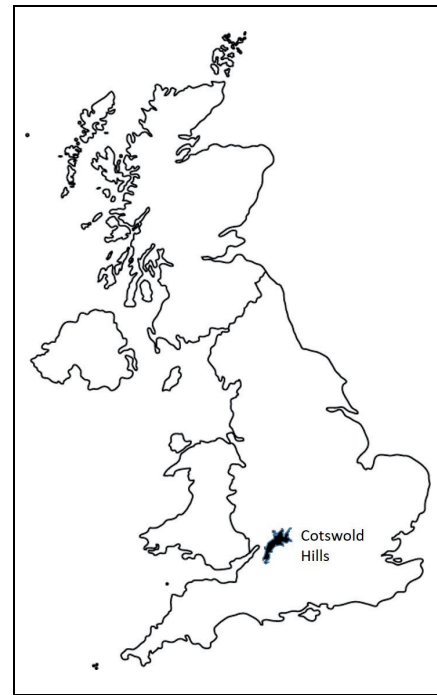


Figure 1. Study site location of the Cotswold Hills, UK.

with a canopy dominated by *Fraxinus excelsior* and *Quercus robur*.

Both fragments, henceforth referred to as Fragment 1a and 1b were located within an agricultural (arable and equine) matrix. Fragment 1a was 4.8 ha and of approximately rectangular dimension (190 m × 255 m). Fragment 1b was a remnant of 0.6 ha located 25 m from the eastern edge of Fragment 1a. Historic map evidence showed that both fragments formed a single woodland until c. 1965. Both fragments are classified by DEFRA (2016) as ANSW.

In order to assess any influence of dual-edge effect in Fragment 1a, presence of AWI species was mapped and recorded via a total of 256 2 m × 2 m plots. Plots were located in the corners of Fragment 1a within 60 m of both the nearest edge (Edge 1) and second nearest edge (Edge 2). The distance of 60 m was deemed a conservative upper limit for detection of edge effects based on previous studies (Murcia 1995, Gelhausen et al. 2000, Honnay et al. 2002, Vallet et al. 2010). Plots were located at 0, 5, 10, 20, 30, 40, 50 and 60 m on transects perpendicular to the Western and Eastern edges, with 0 m defined as the commencement of woody species' stems (Murcia 1995). Changing the sampling distance from 10 m to 5 m at the edges of the fragment allowed small-scale change to be better detected (Honnay et al. 2002). Recorded species were restricted to herbaceous and semi-woody plants (Brunet et al. 2011) identified as Ancient Woodland Indicators in the South-West UK (Rose 1999). To complement analysis of the larger fragment and demonstrate any difference in species richness and presence between the two fragments, Fragment 1b was surveyed on the same system with plots at 0, 5, 10 and 20 m from the Eastern and Western edges (n = 54). All statistical analyses apply to Fragment 1a.

To predict the influence of Edge 1 and Edge 2 on AWI richness, separate univariate linear regression analyses were performed ($n = 256$). To test any additive influence of both edges, a hierarchical multivariate model was created where Edge 1 was entered via forced entry and Edge 2 was available as a candidate variable in a second step using a stepwise approach (entry criterion $\alpha = 0.05$, except *L. galaeobdolon* $\alpha = 0.1$) (De Keersmaecker et al. 2004). Normality assumptions were met, and collinearity was within accepted limits: VIF < 10 (Myers 1990) and tolerance > 0.2 (Menard 1995). The same principles were followed using binary logistic regression to test the influence of Edge 1 and Edge 2, separately and additively, on the presence AWI species (those found in > 10% of plots) ($n = 256$). The R^2 (linear regression) and Nagelkerke pseudo R^2 (logistic regression) statistics were calculated to measure the relative influence of single and additive edges on, respectively, AWI richness and species presence.

Results and analysis

Mapping of Fragment 1a, showed clear spatial patterns in AWI richness in relation to edge proximity (Fig. 2). AWI richness was very low at the edge, and increased gradually up to 60m; this effect was most pronounced at the corners where a distinct edge effect was apparent up to 20–30 m, rather than 5–10 m on transects located mid-edge. Within the very

small Fragment 1b, AWI richness is lower throughout than in Fragment 1a, with no clear edge or corner pattern (Fig. 2).

Regression analysis showed significant positive directional relationships between AWI richness and distance from the edge in Fragment 1a (Table 1). When tested independently, Edge 1 and Edge 2 were both shown to be significantly positively related to AWI richness, but Edge 1 was related more strongly than Edge 2. Used in a hierarchical framework, Edge 2 met the stepwise criteria for entry as a second variable into a multivariate model after Edge 1 had already been entered. This, together with the resultant multivariate model being more significant and explaining more variance than either Edge 1 or Edge 2 in isolation, strongly suggests dual-edge exposure is important for AWI richness.

Repeating the above analytical framework using hierarchical multiple logistic regression for the seven most prevalent species (those present in > 10% of plots) showed that the presence of four species increased significantly with increasing distance from edge (Table 1). For each of these species (*A. nemorosa*, *H. non-scripta*, *L. galaeobdolon* and *P. quadrifolia*) Edge 1 and Edge 2 were both significant when analysed separately and again the R^2 statistic for Edge 2 was slightly lower than Edge 1. In all four cases, running a stepwise model with Edge 2 available as a candidate variable resulted in a multivariate model being created that had a substantially lower P value and substantially higher R^2 value than either edge tested alone. For where species Edge 2 was not entered us-

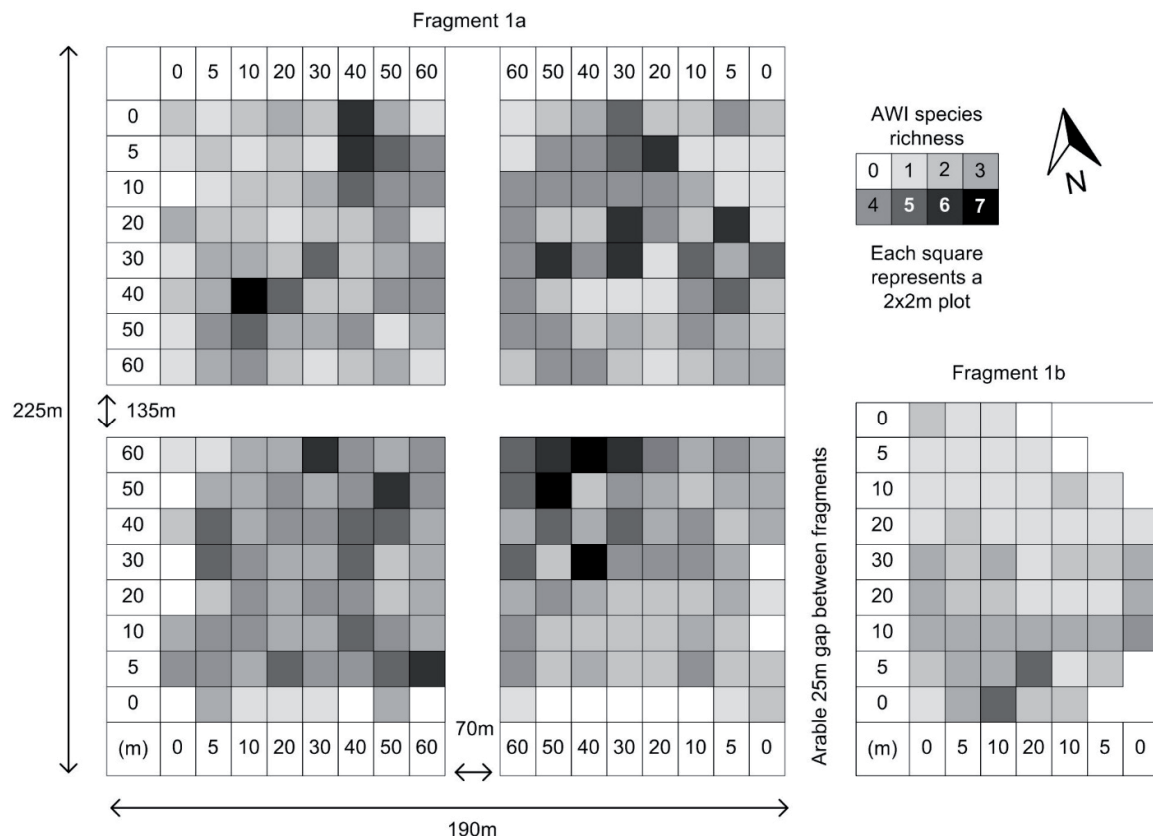


Figure 2. Richness of Ancient Woodland Indicator species in a total of 310 2 m × 2 m plots within two fragments of ancient semi-natural woodland.

ing standard stepwise criteria ($\alpha = 0.05$ or 0.10), forcing this variable into the model did not improve it relative to using Edge 1 alone and all models were non-significant.

Thirteen AWI species were recorded within Fragment 1a sample plots and eight within Fragment 1b (Appendix 1). The four species significantly associated with distance showed clear reductions in prevalence in Fragment 1b, in comparison to 1a (Appendix 1). Presence of *A. nemorosa* and *H. non-scripta* in Fragment 1b was half of that in 1a, while *L. galaeobdolon* and *P. quadrifolia* were absent from Fragment 1b. Of prevalent species not significantly associated with distance, only *A. ursinum* occurred considerably more frequently in Fragment 1b than in Fragment 1a.

Discussion

The above results show that not only are edge conditions less suitable for the majority of AWI species present, but the AWI community is vulnerable to a dual-edge effect whereby the combined influence of two edges is amplified and permeates further into a woodland near corners. The distance to the nearest two edges combined explained 11% of the variation in AWI richness and up to 17% of the variation in the presence/absence of specific AWI species (Table 1). Dual-edge exposure explained a significant, and consistent, additional 1-3% of the variation in AWI richness and presence of some species than the single nearest edge alone (Table 1). The findings reinforce the need to protect ancient woodlands from fragmentation. Two species with conservation designations, *H. non-scripta* and *L. galaeobdolon*, were especially adversely affected by edge proximity (Table 1). At 4.8 ha, Fragment 1a is among the larger of the 48% of ancient woodlands that are smaller than 5 ha (Corney et al. 2008), with a considerable area exposed to single and dual-edge effects. Fragment 1b is smaller still, and mapping suggests is influenced in its entirety by edge conditions.

Both woodlands reinforce the edge:interior ratio theory proposed by Laurance (2008). For this reason, some AWI species might not be appropriate indicators in small fragments where there is a high proportion of edge habitat, as they may be absent even from small ancient woodlands. Our findings show a lower richness count and predominantly lower prevalence of AWI species in Fragment 1b despite its adjacent position and history of connectivity with 1a. However, both fragments have what is considered to be an acceptable AWI score (Fragment 1a = 13; Fragment 1b = 8). Thresholds of 10-12 AWI species (including woody species, forbs and ferns) are used by organisations for allocating conservation priority, while ASNWs under 2 ha with > 5 AWI species were recommended for inclusion in a county ancient woodland inventory (Glaves et al. 2009). If AWI species counts are used in small fragments, consideration should be given to only using the subset of species that are not seemingly affected by edge effects.

AWI species have been considered as a guild (Hermy et al. 1999), but in this study the response of the community and individual species in relation to edge proximity indicates

Table 1. AWI richness (all species) and species presence (most frequently occurring species in > 10% of plots) relationship with distance from Edge 1, Edge 2, and both edges together. In all cases, the additive model was a hierarchical one whereby Edge 1 was entered first and then Edge 2 was available as a candidate variable for inclusion following a stepwise approach; the model was not calculated if the addition of Edge 2 into the model did not significantly improve it.

		<i>p</i>	R ²	Dir.	
AWI richness	Edge 1	< 0.001	0.099	+	
	Edge 2	< 0.001	0.069	+	
	Additive	< 0.001	0.115	+	
Species		Chi (df)	<i>p</i>	R ²	Dir.
<i>A. ursinum</i>	Edge 1	0.357 (1)	0.425	0.030	
	Edge 2	0.187 (1)	0.666	0.080	
	Additive	Model not calculated			
<i>A. nemorosa</i>	Edge 1	23.117 (1)	< 0.001	0.126	+
	Edge 2	19.572 (1)	< 0.001	0.107	+
	Additive	29.292 (2)	< 0.001	0.158	+
<i>G. odoratum</i>	Edge 1	0.077 (1)	0.781	0.000	
	Edge 2	0.002 (1)	0.968	0.000	
	Additive	Model not calculated			
<i>H. non-scripta</i>	Edge 1	27.550 (1)	< 0.001	0.141	+
	Edge 2	20.323 (1)	< 0.001	0.105	+
	Additive	33.100 (2)	< 0.001	0.168	+
<i>L. galaeobdolon</i>	Edge 1	11.866 (1)	0.001	0.064	+
	Edge 2	9.321 (1)	0.002	0.036	+
	Additive	14.417 (2)	0.001	0.077	+
<i>P. quadrifolia</i>	Edge 1	16.698 (1)	< 0.001	0.095	+
	Edge 2	16.117 (1)	< 0.001	0.092	+
	Additive	22.287 (2)	< 0.001	0.126	+
<i>V. reichenbachiana</i>	Edge 1	0.699 (1)	0.403	0.005	
	Edge 2	2.044 (1)	0.153	0.014	
	Both	Model not calculated			
Dir. - direction of relationship for significant models. R ² - Nagelkerke					
Species present with conservation designations: <i>Hyacinthoides non-scripta</i> - Wildlife and Countryside Act, schedule 8; <i>Lamium galaeobdolon</i> - Vascular Plant Red List for Great Britain nationally scarce, vulnerable. Vascular Plant Red List for England, vulnerable; <i>Viola reichenbachiana</i> - Scottish Biodiversity List. <i>Primula vulgaris</i> (Wildlife Order Northern Ireland schedule 8); <i>Sanicula europaea</i> (Vascular Plant Red List for Great Britain, near threatened)					

variation in niche requirements. Of the species significantly influenced by edge proximity, all increased in prevalence with distance from the edge (Table 1). The preference of *P.*

quadrifolia for woodland interior may be accounted for by its adaptation for vegetative growth during low light periods (Bjerketvedt et al. 2003). Similarly to this study, Honnay et al. (2002) found *A. nemorosa* to have a positive edge-distance distribution in ancient woodland study sites in Belgium. Of those not exhibiting significant relationships with edge, only *V. reichenbachiana* decreased in prevalence with distance from either and both edges, possibly accounted for by its greater light requirement for a summer second leafing period (Rackham 2003).

This study has demonstrated dual-edge proximity has a substantial effect on AWI community composition, and has highlighted the species-specific nature of the response to different plants to the edge. It has also emphasised the effects of edge orientation and woodland size on floral response to edge conditions. Future research on the influence on multiple-edge biotic and abiotic variables in small ASNWs would be beneficial in further explaining spatial distribution of AWI species and for development of conservation management practices.

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Appendix 1. Comparative frequency occurrence of AWI species in Fragments 1a and 1b. Total herbaceous AWI count of both fragments.

	Fragment 1a	Fragment 1b
Frequency occurrence		
<i>Anemone nemorosa</i>	73%	35%
<i>Hyacinthoides non-scripta</i>	66%	33%
<i>Allium ursinum</i>	51%	96%
<i>Lamium galaeobdolon</i>	31%	Absent
<i>Galium odoratum</i>	25%	Absent
<i>Paris quadrifolia</i>	22%	Absent
<i>Viola reichenbachiana</i>	15%	2%
<i>Conopodium majus</i>	4%	2%
<i>Primula vulgaris</i>	2%	7%
<i>Euphorbia amygdaloides</i>	1%	Absent
<i>Orchis mascula</i>	1%	2%
<i>Veronica montana</i>	1%	2%
<i>Sanicula europaea</i>	< 1%	Absent
Total AWI count	13	8