Life on deadwood: cut stumps as a model system for the succession and management of lichen diversity

Vérèna BLASY and Christopher J. ELLIS

Abstract: Coarse deadwood provides an important habitat for a suite of niche-specialist lichens in old-growth forests, for example, snags (standing dead trees) and fallen logs. Conversely, the scarcity of deadwood in managed forests is a limiting factor to lichen diversity, though cut stumps may provide an alternative habitat for deadwood species. The surface of cut stumps is an ecologically useful study system, facilitating standardized sampling with which to determine the pattern and process of dead-wood succession. This study examined vegetation patterns for the surface of cut stumps at Abernethy RSPB Reserve in northern Scotland. We demonstrate the interrelationship between key topographic, management and edaphic factors during a successional process of terrestrialization. Consequently, we recommend that deadwood diversity might be maximized by 1) creating managed plots with varying degrees of canopy openness for sites with different levels of topographic exposure, and 2) providing cut stumps at different heights within plots, to ensure that during a rotational period the process of terrestrialization operates at different speeds among individual microhabitats. The study examined successional processes on cut stumps using two recently accessible and powerful statistical methods: 1) nonparametric multiplicative regression (NPMR), and 2) multivariate regression trees (MRT). The principles on which these techniques are based are becoming the preferred statistical framework with which to provide robust interpretation of field-sampled data; they are unconstrained by prior assumptions as to the form of a species' niche response, and are data-led models evaluated based on cross-validated performance, thereby avoiding the complication of multiple hypothesis tests.

Key words: bryophyte, deadwood management, multivariate regression trees, nonparametric multiplicative regression, terrestrialization

Introduction

Deadwood is a key structural component that underpins forest biodiversity and ecosystem function (Ferris & Humphrey 1999). It is a resource that often occurs in lower volumes or is absent from managed production forest systems (Kirby *et al.* 1998; Gibb *et al.* 2005; Lommi *et al.* 2010), with this scarcity of deadwood microhabitat limiting the occurrence of niche-specialist lichens (McCune *et al.* 2000; Lõhmus & Lõhmus 2001; Meier & Paal 2009). Floristic analysis suggests that up to 10% of 'epiphytic' lichens are dead-

wood obligates (alternatively termed 'epixylic' lichens), with an additional 33% of species occurring facultatively on deadwood (Spribille *et al.* 2008). Accordingly, the occurrence of deadwood increases lichen species richness among forest stands (Moning *et al.* 2009). Furthermore, deadwood habitat is a dynamic system, with lichen community turnover and *β*-diversity related to contrasting size and decay stage among a variety of structural attributes, for example snags, logs and stumps (Crites & Dale 1998; Humphrey *et al.* 2002; Nascimbene *et al.* 2008*a*).

Naturally-occurring coarse deadwood structures such as snags and logs are often absent from managed forests, though in contrast cut stumps may be plentiful, enabling a suite of deadwood species to persist in habitats from which they would otherwise be excluded. Previous studies have indicated that

V. Blasy: Mount Revelstoke and Glacier Field Unit, Parks Canada, P.O. Box 350, Revelstoke, B.C., V0E 2S0, Canada.
C. Ellis (corresponding author): Royal Botanic Garden Edinburgh, 20A Inverleith Row, Edinburgh EH3 5LR, UK. Email: c.ellis@rbge.org.uk

the community composition of stumps may be intermediate between, and overlap with, that of fallen logs and snags (Nascimbene *et al.* 2008*a*), yet may be qualitatively different from, and more species rich than, other types of remnant post-harvest material such as slash (Caruso *et al.* 2008). These previous findings strongly suggest that cut stumps may be a valuable conservation resource. Additionally, the surface of a cut stump usefully represents a standardized template for species colonization and establishment, enabling deadwood succession to be quantified without the confounding influence of extreme microhabitat complexity, such as highly variable small-scale topography, aspects, angles of lean etc., which characterizes the three-dimensional surface structure of snags and logs. Given an opportunity provided by cut stumps, both in practical terms for the conservation of deadwood lichens, and as an ecological study system, this paper asks whether it is possible to identify an optimum procedure for the management of stumps during a transition from intensively harvested to sustainable and conservation-orientated forestry. The aim is therefore to isolate factors that would maximize species diversity for stumps at different successional stages in a matrix of forest plots.

FIG. 1. The location of Abernethy RSPB Reserve in northern Scotland (57°15′N, 3°40′W). The climate is relatively continental (Summers *et al.* 1997): July mean temperature = 14·1°C; January mean temperature = −0·5°C; annual precipitation = 804 mm.

Materials and Methods

Field sampling

Field sampling was carried out at Abernethy RSPB Reserve (Royal Society for the Protection of Birds), north-east Scotland (Fig. 1). The Reserve forms part of a relatively large area in Strathspey (*c*. 458 km²) including both recent and long-established Scots pine (*Pinus sylvestris*) plantations, with pockets of ancient semi-natural forest (Summers *et al.* 1997). The study area comprised clearcut plantation forestry, in addition to former plantation that is now undergoing active conservation management to achieve a more complex forest structure. This includes an ambition for increased deadwood, which is currently measured at 10% relative to comparable old-growth forests in Scandinavia (A. Amphlett, pers. comm.).

Field sampling was split into two phases. Phase 1 field sampling provided a broad measure of the vegetation structure associated with deadwood stumps, while Phase 2 sampling provided a more detailed assessment by quantifying species community composition and richness.

For Phase 1 sampling, 17 managed forest plots with cut stumps were identified from the same contiguous area of forest (*c*. 7 km²), selected to represent a range of age-classes since harvesting (plot area varied from *c*. 0·1–1·0 ha), and corresponding to different management types:

a) Clearcut; all trees were harvested,
b) Retention; a small number of trees were retained within the cleared plot,
c) Selective; limited thinning in order to recreate a 'natural' forest structure.

We estimated the proportional cover across the horizontal cut stump surface of 1) vascular plants plus bryophytes, and 2) macrolichens (fruticose and foliose species). A maximum of 50 stumps was randomly selected and surveyed within each of the 17 plots, though limited to a minimum of 30 stumps for plots with low variance in proportional cover values. Vegetation sampling was accompanied by three types of environmental data as follows.

TABLE 1. *Assessment of stump decay and characterization into five decay-stage classes, compilation based on previous qualitative field assessment techniques, cf. Söderström (1988), Humphrey* et al. *(2002), Ódor & van Hees (2004) & Caruso & Rudolphi (2009)*

Decay stage	Bark	Sap-wood		Heart-wood	
		Knife penetration	Decay description	Knife penetration	Decay description
1	100%, intact and not loose	1–2 mm	No decay, hard wood	1–2 mm	No decay, hard wood
2	75–100%, loose	<10 mm	Minimal decay	1–2 mm	No to minimal decay
3	50–75%, loose	10–50 mm	Moderate decay	<10 mm	Minimal decay
4	25–50%, separated from wood	50–90 mm	Considerable decay	10–90 mm	Moderate decay
5	0–25%, separated from wood	>100 mm	Considerable decay	>100 mm	Considerable decay

1. *Stump-size.* Including, a) minimum height from the forest floor to the cut stump surface, and b) stump diameter at the widest point.

2. *Managed and topographic variables.* Including, a) age since felling, b) annual potential direct radiation (megajoules.cm^{-2}.yr^{-1}) calculated as a function of latitude, aspect and slope measured centrally within each plot over a distance of 20 m using a clinometer (McCune & Keon 2002), c) exposure index, measured using the UK Forestry Commission's 'DAMS scores' (Gardiner *et al.* 2006) developed by integrating observed wind speeds with elevation, aspect and an index of topographic exposure (Quine & White 1994; Suárez *et al.* 1999), and ranging from a score of 0 (very sheltered) to 22 (severely exposed), d) canopy openness, measured for five locations within each plot, including the central stump and four positions that were 5 m towards the plot centre from stumps at each of the corner boundaries. At each position, canopy openness (the reciprocal of canopy closure) was measured using a spherical densiometer (Lemmon 1956; Englund *et al.* 2000; Paletto & Tosi 2009) and the mean value calculated.

3. *Edaphic index variables.* Estimated values for edaphic factors were derived from indicator plant species. The vascular plant vegetation was sampled in quadrats of 1 m^2 at the five locations from which canopy measurements were collected (see above). Species presence-absence was used to derive a mean index value based on Ellenberg indicators corrected for the British Isles (Hill *et al.* 1999), for a) soil moisture, and b) soil nutrient status, as both soil pH and soil nitrogen.

Phase 2 field sampling was based on the sub-selection of 25 stumps (5 stumps within each of 5 plots), aiming to capture a gradient in vegetation succession. The sub-selection of stumps was designed to incorporate a range of values in the colonization of vascular plants plus bryophytes. Proportional cover previously established during Phase 1 sampling was grouped into five classes: I (0 cover), II (0·01–0·25), III (0·26–0·50), IV (0·51–0·75), and V (0·76–1·00). The proportion of stumps falling within each cover class was calculated for each plot; the five sample sites selected had the highest proportion of stumps within a unique cover class (I through to V) while also having at least one stump in each of the other classes. A single stump from each cover class was then randomly selected from each of the five selected plots, to provide a range of contrasts in terms of deadwood succession: two of the plots selected were from Selective and Clearcut management types, with a single plot from the Retention management type. Mean plot area, determined by the distance between randomly selected stumps, was 0·29 ha, varying from 0·88 ha to 0·09 ha.

For detailed vegetation sampling (Phase 2), a transect was established along the largest diameter of the stump (or north-south if the stump was circular). Further transects were then aligned perpendicularly, and at 5 cm intervals, starting at a position that was 5 cm inwards from the edge of the stump. Circular 'quadrats' with a diameter of 1·5 cm (area = 1·77 cm^2) were sampled at 5 cm intervals along the length of all transects, so that the sampling effort was correlated with the area of the stump surface ($r = 0.978$, $P < 0.0001$ with 23 df). Presence-absence by species was recorded for all lichens, bryophytes and vascular plants within an individual quadrat, with specimen collection and subsequent determination at RBGE (Royal Botanic Garden Edinburgh) if required. Taxonomic nomenclature follows Smith *et al.* (2009) for lichens, Smith (2004) for mosses and Paton (1999) for liverworts.

Phase 2 habitat variables included the stump size (see above) combined with an additional assessment of stump decay categorized into five classes (Table 1) on the basis of evidence incorporating both visual inspection and semi-quantitative tests. Edaphic index values (soil moisture and soil nutrient status) were resampled at the scale of each stump, using Ellenberg values for a 1 m^2 quadrat positioned at 1 m to the west of the stumps selected. Of

the managed and topographic variables, canopy open-
ness was resampled for each individual stump, using a
spherical densiometer positioned 1 m from the stump at
four cardinal points.

Statistical analysis: Phase 1 sampling

First, we tested for significant differences in the man-
aged, topographic and edaphic index variables among
harvest types, using box plots and a Kruskal-Wallis non-
parametric analysis of variance (R base-package: R De-
velopment Core Team 2012). Secondly, we compared
the managed and topographic variables (age since fell-
ing, radiation, exposure index and canopy openness) us-
ing Spearman's rank correlation (R Development Core
Team 2012). We then used multiple linear regression
(R Development Core Team 2012) to examine the rela-
tionship between edaphic index variables, and the topo-
graphic and managed variables (age since felling, radia-
tion, topographic exposure and canopy openness).
Stepwise selection was used to optimize fixed effects by
minimizing the Akaike Information Criterion (AIC)
among sequentially tested models. We also compared
the proportional cover of vascular plants plus bryophytes,
and macrolichens, using Spearman's rank correlation.

Finally, we examined the response of vascular plant
plus bryophyte cover, and macrolichen cover, to all of
the managed, topographic and edaphic index variables,
in addition to stump height and diameter. The cover of
vascular plants plus bryophytes was included as an addi-
tional explanatory variable in the response of macroli-
chens. Response curves were generated using nonpara-
metric multiplicative regression (NPMR: McCune 2006)
implemented in the program Hyperniche v. 2 (McCune
& Mefford 2009). See McCune (2011) for a detailed
explanation of NPMR; here we provide a summary.
NPMR applies a smoother referred to as a kernel func-
tion to weight the observed response at a target data
point, and provide a fit to the explanatory variables. Key
attributes are the shape of the kernel in terms of the
weightings that are applied to the surrounding data, the
selection of sampled data surrounding the target point
(whether this reflects local trends in the dataset), and its
width or 'neighbourhood', that is, the span of data points
across environmental space. We used a local linear model
to capture the data within a 'neighbourhood' around a
target point, with weightings applied using a 'bell-shaped'
Gaussian kernel, and with the kernel width measured by
referencing 1 SD of the Gaussian response in environ-
mental space, referred to as the 'tolerance'. Explanatory
variables are combined multiplicatively, so that their indi-
vidual effects depend on the simultaneous values of other
variables, and a tolerance is specified for each variable.

A single best model is selected by an iterative search,
which adds and subtracts variables and adjusts kernel
tolerances. This procedure is constrained in several im-
portant ways, to make the procedure computationally
tractable and to control parsimony and prevent over-
fitting. Multiple models are accumulated by requiring a
minimum improvement in model fit when a new explan-
atory variable is added, and with model complexity con-
strained by a minimum data:predictor ratio, that is, the
number of sample units divided by the number of pre-
dictors in the model. Model fitting is controlled by 1)
setting a minimum average neighbourhood size to con-
trol kernel width, 2) setting a maximum allowance for
missing estimates, to avoid inflating the model fit by
ignoring data-poor regions of environmental space, and
3) setting a minimum neighbourhood size when extrap-
olating a response surface. From among alternative
models with different combinations of explanatory vari-
ables and contrasting tolerances, an $n - 1$ cross-validated
R^2 ($x - R^2$) is used to identify an optimum solution.

We used 'conservative' default options in Hyperniche
v. 2 to accumulate models. Having selected an optimum
model, the sensitivity of explanatory variables is assessed
by systematically nudging their values (at 5% intervals)
with respect to the observed range, and calculating the
shift in the response with respect to its observed range.
Optimum models were assessed using a randomization
test, with 100 permutations used to estimate model sig-
nificance.

Statistical analysis: Phase 2 sampling

Community structure was summarized as the fre-
quency of occurrence for individual species, calculated
among quadrats sampled from the cut stump surface.
Species that occurred on ≤2 stumps were excluded from
analysis. A matrix of species frequencies was used to cal-
culate pairwise values of Bray-Curtis dissimilarity among
stumps.

First, the dissimilarity matrix formed the basis for an
analysis of community structure using distance-based
multivariate regression trees (MRT: De'ath 2002). MRT
is analogous to the widely applied technique of univariate
regression trees (De'ath & Fabricius 2000), in splitting
the initial data matrix into mutually exclusive clusters of
samples (nodes) along axes of the explanatory variables.
Homogeneity within these clusters is then measured as
the sum of squared dissimilarities among samples within
a cluster, aiming to maximize the shift towards homoge-
neity at a given split. This procedure is followed to pro-
duce an 'over-fitted' tree, which is then pruned to an op-
timum number of splits using predictive cross-validation;
this is calculated as the sum of squared distances to the
predicted sample, when compared to all other samples,
minus the within-cluster sums of squared distances. The
explanatory variables used included stump-size (height
and diameter) and decay class, and the full suite of
managed, topographic and edaphic index variables.

Automated procedures were used to control MRT
analysis within the R package '*mvpart*' (De'ath 2002).
During each individual run, multivariate trees of
increasing complexity were individually assessed using a
10-fold cross-validated error (xE), and an optimum con-
figuration was selected as the least complex tree whose
xE was within 1 SE of the overall minimum. Because
this individual run is based on a randomized cross-vali-
dation, it was repeated 1000 times and the most consis-
tently sized tree was selected. Having selected the most
frequently derived optimum tree, indicator species analy-
sis (Dufrêne & Legendre 1997) was performed for groups

consistent with MRT sample clusters (PC-ORD: McCune & Mefford 2011), with significance assessed using a permutation test with 10 000 randomizations. A nonparametric Kruskal-Wallis test (R Development Core Team 2012) was used to compare community clusters in terms of their broad-scale vegetation structure, and lichen species richness.

Secondly, the Bray-Curtis dissimilarity matrix was used to perform multivariate ordination using nonmetric multidimensional scaling (NMDS: McCune & Grace 2002). This provided a necessary check because community partitioning by MRT is constrained by measured environmental variables; an MRT solution may be validated by plotting equivalent samples in ordination space unconstrained by environmental variables, and then examining to confirm that optimum clusters form coherent groups. NMDS operates by assigning samples to ordination space randomly, and iteratively nudging the position of samples to improve the monotonicity between sample distances in ordination space, and distances contained within the original dissimilarity matrix; 'stress' is calculated as the departure from monotonicity (McCune & Grace 2002). NMDS was implemented in PC-ORD v. 6 (McCune & Mefford 2011) using 100 separate runs with random start points, to avoid convergence on anomalous local stress minima, and with 50 iterations to assess stability of the solution, up to a maximum of 500 iterations. The optimum solution (minimum number of ordination axes, for a stable low stress solution) was tested using a permutation test, with 1000 randomized runs. The solution was rotated to orthogonal principal axes, so information was displayed on axes in descending order of importance.

NMDS sample scores were tested among the clusters identified by MRT using a Kruskal-Wallis test, and plotted for each axis along with the individual species scores calculated using weighted averaging.

Thirdly, the species richness on cut stumps was compared to the suite of managed, topographic and edaphic index variables, in addition to stump height, diameter and decay class, using NPMR as described above.

Results

Analysis of sampled environmental variation confirmed a highly significant difference in canopy openness among harvest types, reflecting the different management strategies in creating the forest plots (Fig. 2). There was a less strongly significant difference in the soil moisture index among harvest types, with soil moisture declining from the clearcut through the retention and selectively thinned plots (Fig. 2). Although there was no significant difference in the age since felling among harvest types, and values overlapped considerably, the retention and selectively thinned plots tended to include some representation of progressively older stumps (Fig. 2); this is also reflected by the negative correlation between age since felling and canopy openness (Table 2). None of the other topographic (radiation, exposure) or edaphic variables (pH index, soil-N index) was significantly different among harvest types. Tested using multiple regression, only the soil moisture index was significantly related to the measured topographic and managed variables; soil moisture increased as topographic exposure (DAMs scores) decreased, and canopy openness increased (adj-$R^2 = 0.28$, $P = 0.039$, on 14 df).

During Phase 1 of the study, a total of 805 individual stumps was sampled to characterize broad-scale vegetation structure. The proportional cover values for macrolichens, and vascular plants plus bryophytes, were significantly negatively correlated (Spearman's-rank $r = -0.647$, $P < 0.0001$, on 803 df). Nonparametric multiplicative regression (NPMR) produced significant models explaining the cover of macrolichens, and of vascular plants plus bryophytes (Table 3). For vascular plants plus bryophytes, proportional cover decreased with stump height, though this decrease was less pronounced under moderate values of canopy openness (Table 3, Fig. 3A), and cover increased for stumps of a given height under wetter soil moisture conditions (Table 3, Fig. 3B). For macrolichens, proportional cover increased with stump height, especially in situations with low cover values for vascular plants plus bryophytes (Table 3, Fig. 3C).

During Phase 2 of the study, vegetation sampling of the cut stump surface included 82 species, with 46 lichens, 29 bryophytes (mosses and liverworts) and 7 vascular plants. Analysis using a multivariate regression tree (MRT) indicated an optimum solution with two nodes (87% of outcomes generated), resulting in three clusters, which explained 46% of variance, and with xE $= 0.88$. The first split was determined by stump height, and the second by physical exposure (Fig. 4). Stump decay was not selected as an explanatory variable.

Cluster 1 (associated with stumps <13.5 cm in height) had *Hypnum jutlandicum* (Holmen & Warncke) as an indicator species (Fig. 4), and was characterized by signifi-
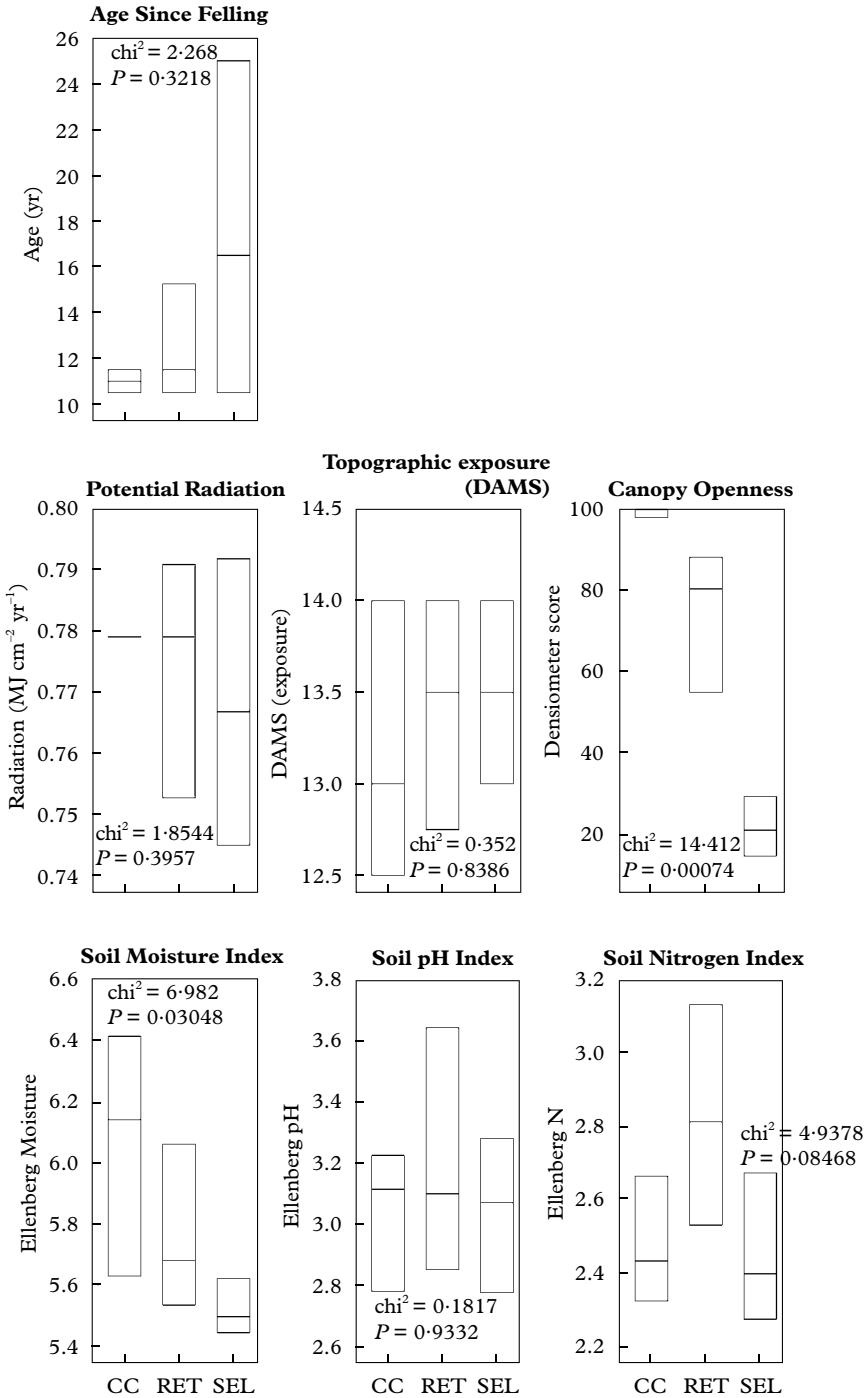
Fig. 2. The box plot comparison of managed, topographic and edaphic environmental variables measured for three different harvest types: CC = clearcut, RET = retention, and SEL = selective thinning. Significance values refer to a Kruskal-Wallis test among harvest types (2 df)

TABLE 2. *Spearman's rank correlation coefficients for managed and topographic variables across sampled plots (*n = 17 *in all cases). The significant correlation is highlighted in bold*

Age [1]	1			
Radiation [2]	0·029	1		
Exposure [3]	−0·41	−0·359	1	
Canopy openness [4]	**−0·53***	0·286	−0·045	1
	[1]	[2]	[3]	[4]

* P < 0·05

cantly higher values for vascular plant plus bryophyte cover, lower values for macrolichen cover and significantly lower values of total lichen richness (Fig. 5). Cluster 2 (associated with stumps >13·5 cm in height, in topographically exposed plots) had five lichen indicator species (Fig. 4), and was characterized by significantly lower vascular plant plus bryophyte cover, higher cover of macrolichens, and significantly higher values of total lichen richness (Fig. 5). Cluster 3 (associated with stumps >13·5 cm in height, in less exposed plots), had two moss species indicators (Fig. 4), and was characterized by significantly higher values for vascular plant plus bryophyte cover, lower values for macrolichen cover and significantly lower values of total lichen richness (Fig. 5).

An optimum NMDS solution of the Phase 2 stumps based on species composition was significant ($P = 0·01$) with three orthogonal axes (Fig. 6), final stress = 10·67, and instability <0·00001. Ordination axes described *c.* 74% of variation in the dissimilarity matrix:

axis one = 31·2%, axis two = 30·5% and axis three = 12·7%. The MRT clusters were well supported by unconstrained community ordination along NMDS axes one and two, though with no separation along axis three (not shown in Fig. 6). NMDS axis one separated out the lichen rich Cluster 2, from the vascular plants and bryophytes associated with Clusters 1 and 3 (Fig. 6). NMDS axis two separated out Cluster 3, from Clusters 1 and 2; the weighted-average position of species suggesting a separation of mixed-guild assemblages including vascular plants, bryophytes and certain lichens (especially *Cladonia* species) towards the left of NMDS axis two, with fewer bryophytes relative to lichens towards the right of NMDS axis two.

Species richness on cut stumps was best explained by vascular plant plus bryophyte abundance and canopy cover (Fig. 3D), which were cautiously identified in an optimized two-parameter NPMR model ($xR^2 = 0·356$, $P = 0·059$) as the best explanatory variables [canopy cover, T = 32·03 (40%), S = 0·145; vascular plant plus bryophyte cover, T = 85 (85%), S = 0·157].

Discussion

The deadwood habitat is critically important for forest biodiversity, though naturally-occurring deadwood is structurally complex, making it difficult to achieve standardized sampling and thereby isolate ecological patterns and processes. By sampling the cut stump surface, this study has provided ecological data for a deadwood microhabitat with

TABLE 3. *Model diagnostics for the response of vascular plant plus bryophyte proportional cover, and macrolichen proportional cover, on cut stump surfaces, using nonparametric multiplicative regression (McCune 2006; McCune & Mefford 2009)*

Response	Explanatory variables			xR^2	P
Vascular plant plus bryophyte cover	Stump height T = 62·55 (45%)*, S = 1·168*	Canopy cover T = 9·19 (10%), S = 2·19	Soil moisture T = 0·476 (40%), S = 0·82	0·569	<0·01
Lichen cover	Stump height T = 48·65 (35%), S = 0·506	Vascular plant and bryophyte cover T = 20 (20%), S = 0·67		0·227	<0·01

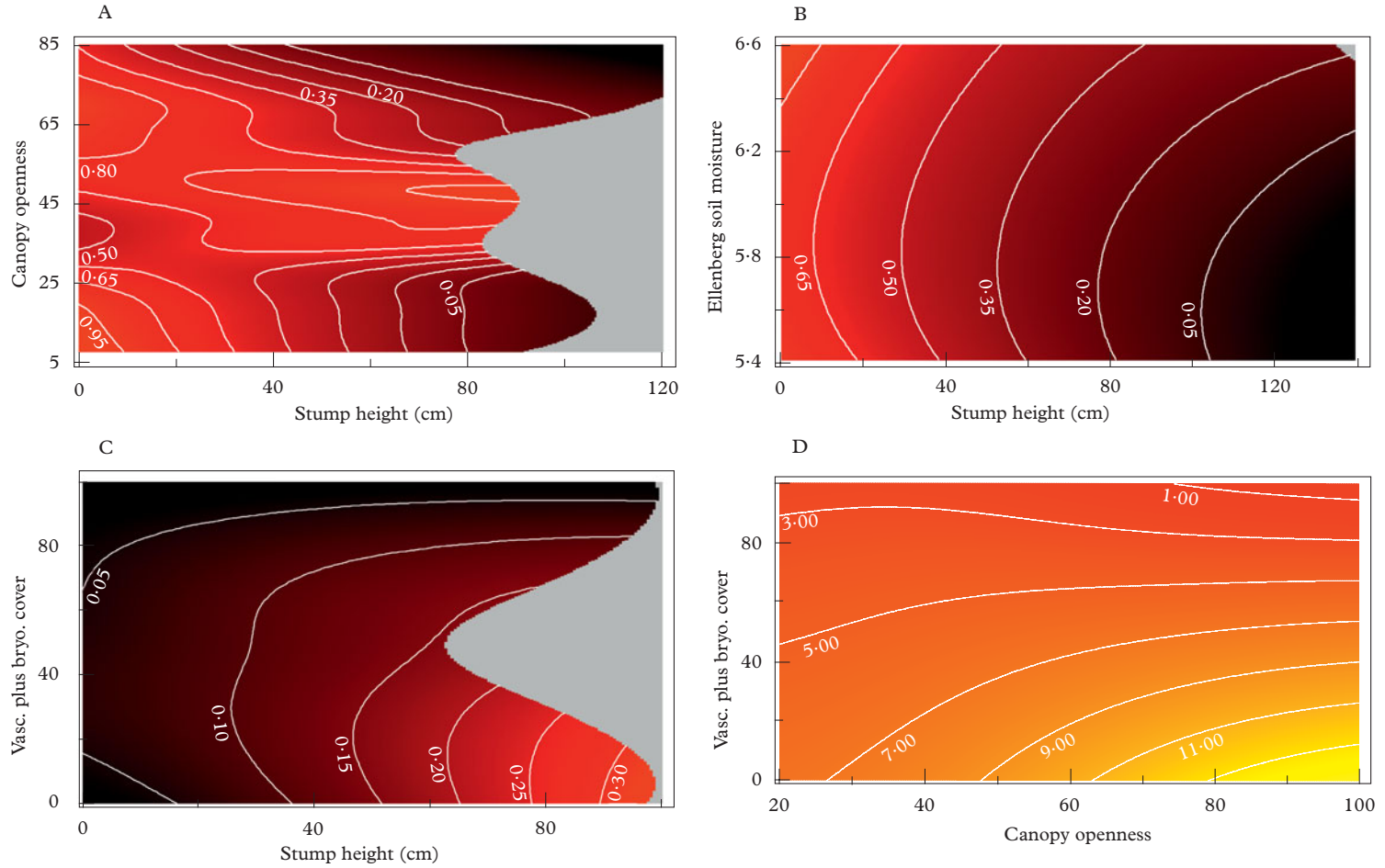** T = tolerance (% of data range), S = sensitivity*

FIG. 3. Response surfaces with isoclines showing the proportional cover of vascular plants plus bryophytes (A and B), macrolichens (C) and lichen species richness (D), compared to explanatory environmental variables identified using nonparametric multiplicative regression (cf. Table 3)
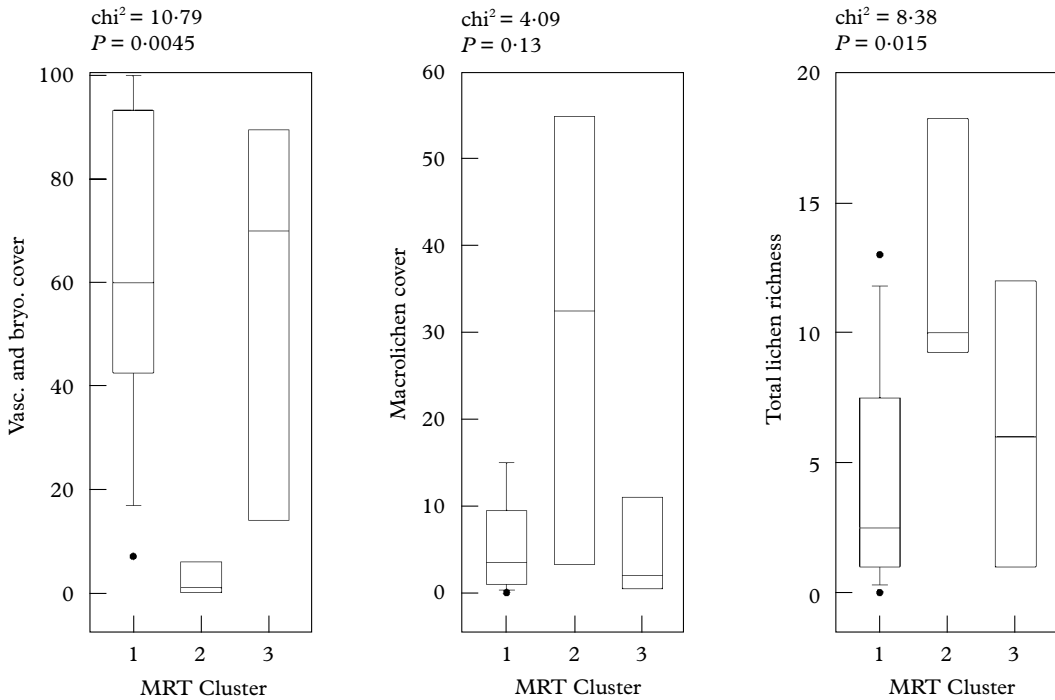
Stump height

< 13·5 cm   > 13·5 cm

Exposure (DAMS)

≥ 12·5   < 12·5

Cluster 1

Hypnum jutlandicum ($P = 0.0024$)
$n = 12$

Cluster 2

Bryoria fuscescens ($P = 0.0049$)
Cladonia coniocraea ($P = 0.0091$)
Hypogymnia physodes ($P = 0.0001$)
Parmelia spp. ($P = 0.0203$)
Platismatia glauca ($P = 0.0443$)
$n = 8$

Cluster 3

Pseudoscleropodium purum ($P = 0.0019$)
Rhytidiadelphus triquetrus ($P = 0.0072$)
$n = 5$

Fig. 4. The most consistently produced and optimum multivariate regression tree, which identifies three community clusters occurring on cut stump surfaces, partitioned according to associated environmental variables. Significant indicator species are included with their respective clusters.

limited complexity, in order to gain a better understanding of key drivers controlling deadwood vegetation, especially lichens. Although the cut stump is an artificial habitat entirely dependent on human intervention, cut stumps are potentially important as a conservation resource because they provide deadwood within managed forest systems, and are the primary habitat for several rare species of conservation concern. In Great Britain, this famously includes the Biodiversity Action Plan species *Cladonia botrytes* (K. G. Hagen) Willd.] (Yahr *et al.* 2013), and during this study we discovered relatively large populations of *Lecidea globulispora* (Nyl.) (syn = *L. antiloga*, cf. Fryday 2009), on four stumps across three different plots, a nationally rare species which has received

IUCN 'Vulnerable' classification in an assessment of the British lichen flora (Woods & Coppins 2012).

Deadwood ecological processes

In sampling the cut stump surface, our study has focused on 'epixylic' (deadwood occurring) lichens, and does not encompass a full transition from corticolous to lignicolous communities. Nevertheless, our results fit broadly within an established scheme of deadwood succession that describes a process of increasing terrestrialization (Söderström 1988; Crites & Dale 1998), marked by the negative relationship between 1) the cover and richness of deadwood lichens, and 2) the abundance of ground-layer vascular

FIG. 5. Box–plot comparison of broad-scale vegetation structure among the three clusters identified using MRT (cf. Fig. 4). Significance values refer to a Kruskal–Wallis test (2 df).

plants and bryophytes. Additionally, our analyses clearly demonstrated a sequence of environmental interrelationships that constrain patterns in vegetation structure on cut stumps (Fig. 7), and which might therefore be manipulated within a site management plan.

First, the proportional cover ($\approx$abundance) of vascular plants plus bryophytes was explained by factors including soil moisture index, canopy cover and stump height. Stump colonization through the direct process of spread from the existing ground flora explained why vascular plants and bryophytes were more abundant on low-cut stumps. This process of colonization was facilitated by understorey abiotic conditions (cf. Anderson *et al.* 1969; North *et al.* 2005) pointing to an increased physical stature of the vegetation on moister sites with moderate light levels. Soil moisture was in turn re-

lated to canopy cover and physical exposure, with lower values at more exposed sites (increased evapotranspiration) and where canopy cover was greatest (increased canopy interception of rainfall, and transpiration).

Secondly, macrolichen cover was explained by the abundance of vascular plants plus bryophytes and stump height, while total lichen richness was explained by vascular plant plus bryophyte abundance and canopy cover. The persistent effect of vascular plant plus bryophyte abundance on both macrolichen cover and total lichen richness is consistent with asymmetric competition, whereby the larger-statured vascular plants and bryophytes overtop and therefore out-compete lichens during deadwood succession towards terrestrialization (McCullough 1948; Söderström 1988; Crites & Dale 1998). It is indicative that key elements of the bryophyte flora [e.g., *Pseudoscleropodium purum* (Hedw.)
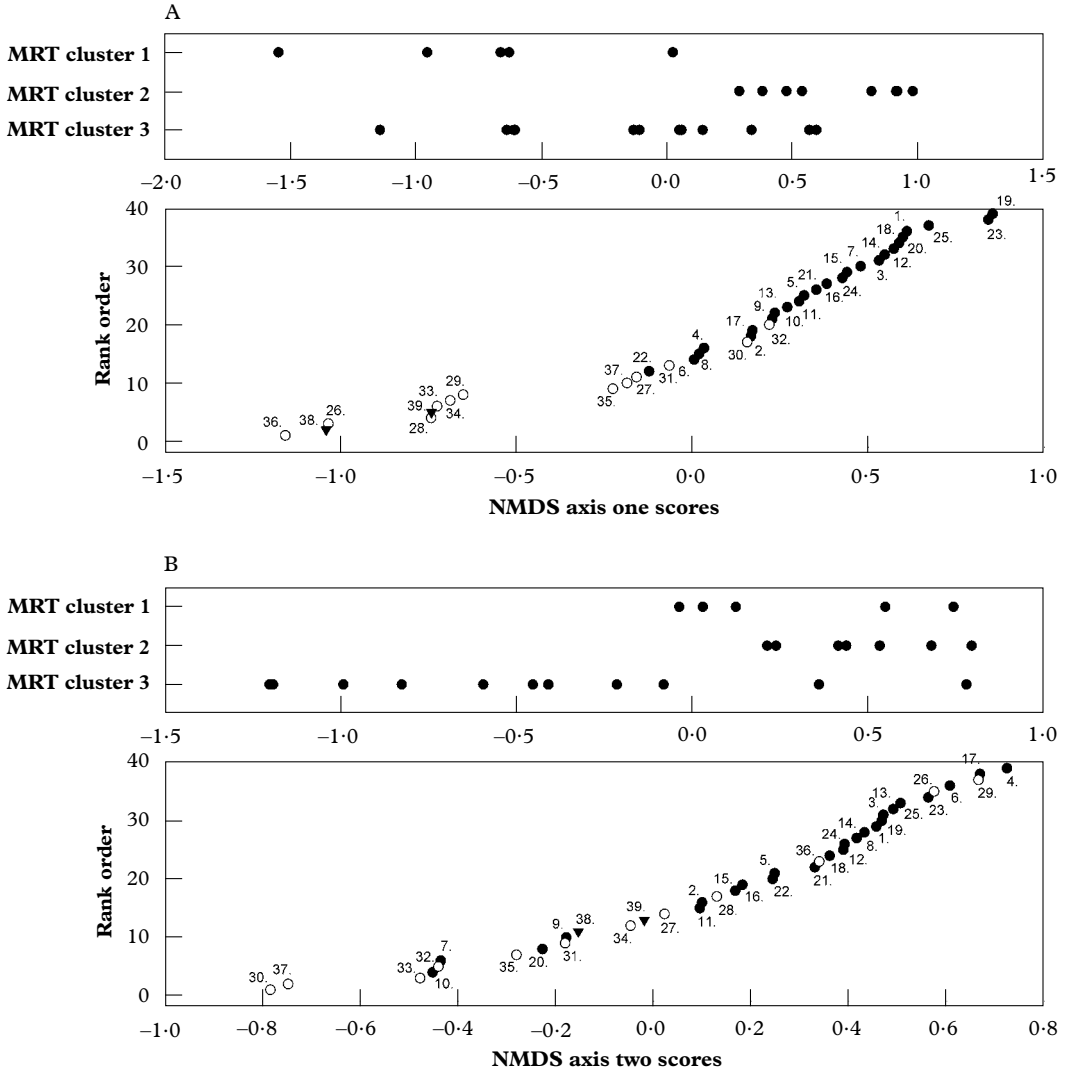
Fig. 6. NMDS scores for axis one (A) and two (B). In the upper graphs for each axis, the scores for individual cut stumps are compared among MRT community clusters (Clusters 1–3). In the lower graphs for each axis, weighted average scores for individual species are displayed on an expanded subset of their equivalent ordination axis, in order to better discriminate species optima (●, lichens, spp 1–25; ○, bryophytes, spp 26–37; ▼, vascular plants, spp 38 & 39): 1. *Bryoria fuscescens*, 2. *Cladonia chlorophaea*, 3. *Cladonia coniocraea*, 4. *Cladonia cornuta*, 5. *Cladonia fimbriata*, 6. *Cladonia gracilis*, 7. *Cladonia macilenta*, 8. *Cladonia polydactyla*, 9. *Cladonia portentosa*, 10. *Cladonia ramulosa*, 11. *Cladonia sp.* (squamules), 12. *Hypogymnia physodes*, 13. *Lecanora pulicaris*, 14. *Lecidea globulispora* (syn = *L. antiloga*), 15. *Lecidea hypopta*, 16. *Lecidea turgidula*, 17. *Micarea misella*, 18. *Parmelia sp.*, 19. *Parmeliopsis hyperopta*, 20. *Pertusaria pupillaris*, 21. *Placynthiella dasaea*, 22. *Placynthiella icmalea*, 23. *Platismatia glauca*, 24. *Tuckermanopsis chlorophylla*, 25. *Xylographa vitiligo*, 26. *Aulacomnium palustre*, 27. *Dicranum scoparium*, 28. *Hylocomium splendens*, 29. *Hypnum cupressiforme*, 30. *Hypnum jutlandicum*, 31. *Lophocolea bidentata*, 32. *Nowellia curvifolia*, 33. *Pleurozium schreberi*, 34. *Pseudoscleropodium purum*, 35. *Rhytidiadelphus squarrosus*, 36. *Rhytidiadelphus triquetrus*, 37. *Riccardia palmata*, 38. *Deschampsia flexuosa*, 39. *Galium saxatile*.
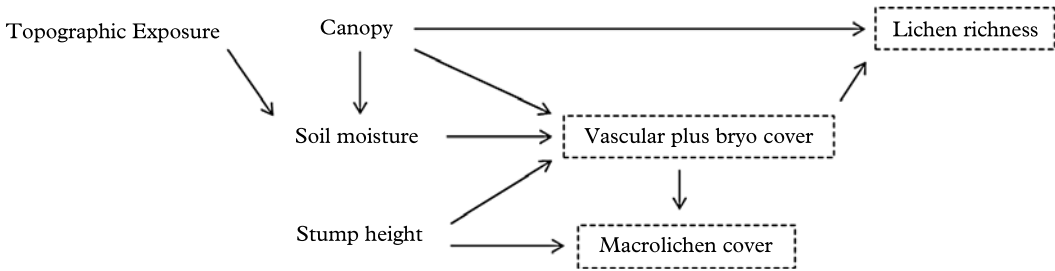
Fig. 7. Interrelationships among topographic (physical exposure), managed (canopy openness, stump height) and edaphic (soil moisture index) variables, and vegetation response variables (hatched boxes): vascular plant plus bryophyte cover, macrolichen cover, and total lichen richness.

M. Fleisch in Broth., *Rhytidiadelphus triquetrus* (Hedw.) Schimp.] were characteristically terrestrial species (Smith 2004; Atherton *et al.* 2010), while the vascular plants sampled were also common elements of the surrounding ground flora [e.g., *Deschampsia flexuosa* (L.) Trin., *Galium saxatile* L.]. In our study system, this process of terrestrialization did not appear to be driven primarily by wood decay (*cf.* Muhle & LeBlanc 1975), but rather because stumps became progressively overtopped and buried within a luxuriant ground-layer vegetation. It is possible that our qualitative field measurements of decay stage were too coarse to detect subtle but important changes (Table 1); however, previous studies on cut stumps have shown that shifts in lichen composition and richness may be only weakly related to decay stage (Nascimbene *et al.* 2008*b*, though see also Caruso & Rudolphi 2009), and it is perhaps likely that, for our system, colonization of the surrounding vegetation onto low-cut stumps was more rapid than decay rates. Nevertheless, consistent with previous studies on cut stumps (Daniels 1993; Nascimbene *et al.* 2008*b*), the shift towards terrestrialization includes compositional variation within the lichen community (cf. Figs 4, 5 & 6), with certain species [e.g., *Cladonia cornuta* (L.) Hoffm., *C. gracilis* (L.) Willd., *C. portentosa* (Dufour) Coem.] associated with conditions approaching terrestrialization and contrasting in their community position with species that are more directly representative of the deadwood substratum [e.g., *Lecidea globulispora*, *Xylographa vitiligo* (Ach.) J. R. Laundon].

In addition to the direct effect of vascular plants plus bryophytes, macrolichen cover tended to increase on taller stumps, which may be less easily overtopped by the established ground flora, and which may also provide a periodically drier and more exposed microhabitat, slowing the establishment of vascular plants and bryophytes, and favouring the persistence of desiccation-tolerant lichens (Kranner *et al.* 2008). Pronounced desiccation tolerance and lichen photosynthetic ability may also be a factor in explaining the increased total lichen richness with decreasing canopy cover (see also Humphrey *et al.* 2002; Paltto *et al.* 2008) through a lowered overall humidity and higher light regimes.

In summary, there is a strong effect of topographic (exposure), managed (canopy openness, stump height) and edaphic (soil moisture index) variables on deadwood community structure. In extrapolating the findings of this study, it is important to acknowledge that our results focus on cut stumps as a simplified system relevant to managed forest habitats. In natural forests, the deadwood resource is more heterogeneous and becomes increasingly variable in terms of size and decay-stage as stands mature (Crites & Dale 1998). Lichen richness may be lower on cut stumps (and fallen logs) than on standing structures such as snags (Humphrey *et al.* 2002; Nascimbene *et al.* 2008*a*). However, differences observed in deadwood vegetation among these contrasting structures may partly reflect the height of the surface sampled above the ground-layer (*cf.* Söderström 1988), which is captured in our study by the

wide range of stump heights, and the consequent effect on lichen cover, composition and richness. On this basis, we suggest that forest managers could intervene to promote deadwood species richness on cut stumps through the following key recommendations applied on a rotational basis: 1) create plots with varying degrees of canopy openness (from small areas of clearcut, through retention to selective thinning), considering how these might represent contrasting forest processes (stand replacing disturbance, or local gap dynamics), and apply these techniques to sites with different levels of topographic exposure, using the DAMs scores (Gardiner *et al.* 2006); 2) provide cut stumps at different heights (e.g., 10–100 cm), to ensure that during the rotational period the process of terrestrialization operates at different speeds among individual microhabitats. Across a network of plots this approach should generate contrasting successional patterns associated with environmental heterogeneity (Fig. 7), yielding higher levels of species richness.

Development of statistical methods

As a secondary aim, the study provided information on deadwood vegetation by using statistical procedures that are likely to become increasingly important in the analytical tool-kit employed by lichen ecologists. In particular, the use of nonparametric multiplicative regression (McCune 2006, 2011) and multivariate regression trees (De'ath 2002), coupled with NMDS, provide representations of ecological datasets (dependent and explanatory variables) that are unconstrained by prior assumptions as to the particular form of a species' niche, and the emergent patterns of community variation. This flexibility is coupled with an avoidance of multiple null hypothesis tests when optimizing statistical models, with a focus instead on predictive performance achieved by data partitioning (cross-validation). These approaches reflect the fundamental difference between strict hypothesis testing within a highly controlled experimental framework, and the inductive exploration of field-sampled datasets, leading to an ability to usefully project species or

community responses based on contrasting environmental scenarios.

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