1 **Testing the relative sensitivity of 102 ecological variables as indicators of woodland condition in**

2 **the New Forest, UK**

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19 **Abstract**

20 Forests globally are facing an increasing number of threats from modified disturbance regimes, novel

21 stressors and changing environmental conditions. This has ultimately resulted in declines in the

22 ecological condition of many forest and woodland ecosystems, leading to widespread tree mortality

23 and stand dieback. Effective indicators of overall woodland ecological condition are therefore needed

24 for environmental monitoring and to support management responses. To test the effectiveness of

25 different variables that could potentially be used as indicators of woodland condition, 102 variables

26 that describe woodland structure, composition, functioning, edaphic conditions and disturbance

27 regimes were assessed along 12 replicate gradients of beech stand dieback. Results indicated that 35

28 variables differed significantly between at least two stages of the dieback gradient, indicating their

29 sensitivity to stand dieback. Seven of these indicators related to woodland species composition, two to

30 functional processes, 20 to structural features, four to edaphic conditions, and two to disturbance

31 regimes. These results demonstrate that effective indicators can potentially be identified for each of

32 the ecological categories. Effective composition indicators included species richness of

33 ectomycorrhizal fungi, ground flora and epiphytic lichens; functional indicators were soil respiration

34 rate and net nitrification rate; edaphic conditions included soil Na:Ca ratio, sodium cation exchange

35 capacity, total carbon, Ca:Al ratio, structural indicators included canopy openness, litter cover, sward

36 height, and volume of deadwood, and for disturbance was *Equus* dung density. Other measures, such

37 as shrub cover and species richness of carabid beetles and spiders, were not found to vary

38 significantly along the dieback gradients, and were therefore not identified as effective indicators.

39 These results demonstrate the value of gradient analysis for evaluating indicators of woodland

40 condition, but also highlight the need for multi-site studies to identify indicators with wide

41 applicability.

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46   **1. Introduction**

47 Forests globally are facing multiple threats related to changing climatic conditions, and to the

48 intensification, interaction and proliferation of disturbance regimes and actors (Allen et al., 2015;

49 Flower and Gonzalez-Meler, 2015; Trumbore et al., 2015; Jung et al., 2018; Ramirez et al., 2018).

50 There is an increasing incidence of large-scale dieback of trees occurring in both tropical and

51 temperate forests as a result of interacting factors such as drought (Allen, 2009; Breshears et al., 2009;

52 Allen et al., 2015; Clark et al., 2016), storms (Csilléry et al., 2017), and the spread of invasive species

53 and novel pests and diseases (van Mantgem and Stephenson, 2007; Sallé et al., 2014; Flower and

54 Gonzalez-Meler, 2015). Such trends have been associated with declines in ecological condition

55 (Gibbons and Freudenberger, 2006), which is defined as an overall product of forest structure,

56 composition and functional processes. Loss of ecological condition is therefore associated with a

57 simplification of forest structure (Noss, 1999), major losses in biodiversity, including native

58 biodiversity (Gao et al., 2015) and/or rapid, detrimental changes in forest dynamic processes such as

59 reduced nutrient cycling rates (Trumbore, 2015). These, in turn, lead to declines in the provision of

60 ecosystem services to human society (MEA, 2005; Foley et al., 2007; Isbell et al., 2015; Trumbore et

61 al., 2015). As a result of interacting pressures, many forest ecosystems are currently considered to be

62 at risk of ecological collapse, which could lead to rapid and long-lasting changes in the state and

63 dynamics of forest ecosystems (Lindenmayer et al., 2016). However, our understanding of the

64 ecological processes occurring during the degradation and collapse of forest ecosystems is still

65 limited, which limits our ability to detect change, recognise tipping points and develop appropriate

66 management and policy responses as counter measures (Breshears et al., 2005; Woodall et al., 2009;

67 Allen et al., 2010; Newton and Echeverría 2014; Lindenmayer et al., 2016).

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69 To be able to maintain or improve forest condition by adopting appropriate management and

70 conservation measures, it is important to determine the ecological condition of forests and how this

71 might be altered as a result of environmental change or human interventions. However, measuring all

72 dimensions of forest or woodland ecological condition is rarely possible owing to the cost and

73 difficulty of collecting data for a large number of different metrics. For this reason, surrogate

74   measures are often used (Hyman and Leibowitz, 2001; Chirici et al., 2012). Rather than measuring

75   ecosystems directly, surrogates can be used as proxies for different ecosystem components such as

76   ecological processes and functions, environmental conditions, and the abundance or diversity of

77   particular groups of species (Lindenmayer et al., 2014). Numerous different measures have been

78   proposed in this context, including single keystone or umbrella species (e.g. Ozaki et al., 2006), taxa-

79   based surrogates (Sabatini et al., 2015; Larrieu et al., 2018) and habitat-based surrogates including

80   vegetation structure, environmental conditions and landscape patterns (Ludwig et al., 2004; Rodrigues

81   and Brooks, 2007). Surrogate measures can relate to a single indicator or a set of multiple indicators

82   derived from different broad categories, each of which can potentially be used to indicate different

83   aspects of ecosystem condition (Noss, 1990; Gao et al., 2015).

84

85   A large number of indicators of forest and woodland condition have been developed in association

86   with various national and international initiatives striving to develop criteria and indicators that reflect

87   progress towards sustainable forest management (SFM) goals and implementing the Convention on

88   Biological Diversity, as well as other intergovernmental policy initiatives (Higman et al., 2005; Gao et

89   al., 2015). For example, a set of Pan-European Indicators for SFM was developed based on set of 34

90   quantitative and 11 qualitative indicators (Forest Europe, 2015). Some of these indicators are relevant

91   for assessing forest condition, such as soil condition, species diversity, dead wood and regeneration,

92   and many of which have been integrated into National Forest Inventories (Chirici et al., 2012). A

93   recent evaluation of the implementation of these indicators showed that they have made a positive

94   contribution to standardising international reporting in the region, and in communicating what SFM

95   comprises. However, their impact has been limited to date by a number of constraints, including a

96   lack of evidence regarding their links with forest management activities, and a failure to define

97   appropriate thresholds or trade-offs among individual indicators (Baycheva-Merger and Wolfslehner,

98   2016). Other sets of indicators of forest condition variables are also widely used with varying degrees

99   of success to support monitoring of forest biodiversity conservation initiatives, in managed and

100   unmanaged woodlands (Gao et al., 2015; Dieler et al., 2017). For example in Europe, the NATURA

101   2000 network of protected areas requires ecological monitoring to ensure that a favourable

102   conservation status of the sites is maintained and this is pursued using specific forest condition

103   indicators (Cantarello and Newton, 2008).

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105   Although large numbers of indicators of forest and woodland ecological condition have been

106   developed, many have proved to be impractical for implementation at the scale at which individual

107   woodlands are managed (Franc et al., 2001; Angelstam and Dönz-Breuss, 2004). This is especially the

108   case for those indicators developed to monitor forest biodiversity as an important component

109   underpinning habitat condition (Newton et al., 2007; Chirici et al., 2012). In addition, the scientific

110   validity of many woodland condition indicators is open to question, as they have not been adequately

111   tested or rigorously validated (Noss, 1999; Lindenmayer et al., 2006, 2014; Gao et al., 2015).

112   According to Noss (1990), indicators of biodiversity should ideally be sufficiently sensitive to provide

113   an early warning of change; capable of providing a continuous assessment over a wide range of

114   disturbances; and relevant to ecologically significant phenomena (such as key ecological processes).

115   Information is also needed specifically on how indicators respond to disturbance (Lindenmayer et al.,

116   2000). Further, Simberloff (1997) noted the importance of being able to relate variation in a

117   biodiversity indicator to chemical/physical changes in the environment. However, few indicators of

118   woodland ecological condition have been assessed against these criteria, particularly at local scales.

119   As a result, evidence is lacking on the relative effectiveness and workability of the different indicators

120   that have been proposed (Mahanty et al., 2007; Alexander, 2013; Neupane et al., 2016), leading to a

121   lack of robust guidance regarding how an appropriate group of indicators might best be selected

122   (Niemi and McDonald, 2004; Lawley et al., 2016).

123

124   How might the suitability or effectiveness of a set of woodland ecological condition indicators

125   therefore be tested? One potential approach is to compare woodland stands along gradients of

126   disturbance (Angelstam and Dönz-Breuss, 2004). This would allow the criteria identified by Noss

127   (1990) to be rigorously applied, for example by enabling the sensitivity of indicators to disturbance to

128   be examined. Despite its potential promise, this approach has been relatively little used by

129   researchers. Examples include studies by Liow et al. (2001) who examined bee diversity along a

130   disturbance gradient in tropical lowland forests in South-east Asia; Jones et al. (2003) in South-East

131   Asia who described the collapse of termite assemblages along a land-use intensification gradient in

132   lowland central Sumatra, Indonesia; and Newton et al. (2007), who examined floristic diversity along

133   anthropogenic disturbance gradients in fragmented forests of Latin America. However, we are not

134   aware of any previous study that has evaluated the effectiveness of indicators along gradients of stand

135   dieback. Such gradients enable some of the criteria identified by Noss (1990) to be directly addressed,

136   by providing an opportunity to examine the performance of indicators in relation to a form of

137   disturbance that is ecologically and societally very significant. Dieback gradients also provide a wide

138   range of disturbance intensities over which to evaluate indicator performance. For example, any

139   indicator that is insensitive to complete dieback of a forest stand clearly has little value for monitoring

140   woodland ecological condition.

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142   The aim of this research was therefore to test whether commonly- and easily-measured ecological

143   variables of woodland ecosystem condition are a sensitive reflection of dieback at a stand scale, and

144   could therefore potentially be used as indicators of shifts in ecological condition. To achieve this, we

145   examined a range of potential indicators along a gradient of beech woodland dieback. 102 ecological

146   variables were selected describing forest ecosystem composition, structure and functioning as well as

147   edaphic conditions and primarily herbivore-related levels of disturbance (Noss, 1990; Gao et al.,

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148 2015; Lawley et al., 2016). Examples of structural variables included canopy structure and cover;
149 functional variables included measures of ecological processes, such as the rate of soil nutrient
150 cycling; compositional variables related to the species richness and abundance of different taxonomic
151 groups (Noss, 1990); edaphic conditions included soil structural and chemical properties; and levels
152 of disturbance were assessed, for example, by browsing intensity and dung density. Therefore, our
153 study was undertaken to test the hypothesis that compositional, functional, edaphic, structural, and
154 disturbance variables could be used effectively at the stand scale as indicators for differentiating
155 between the stages of woodland stand dieback. Our objective was also to identify which ecological
156 variable(s) are most effective at highlighting declines in beech woodland condition.

157

158 **2. Methods**

159 2.1. Study area

160 We conducted this study in the New Forest National Park (NFNP), which covers an area of 57,100 ha
161 in southern England (longitude: 1□17'59'' to 1□48'8'' W, Latitude: 50□42'19'' to 51□0'17'' N),
162 and has annual means of 14.8°C (maximum temperature) and 835.2 mm (rainfall) (Met
163 Office, 2015). The NFNP lies upon sedimentary clay and sandy soils, which form a mixture
164 of base-poor acidic, and well-drained clay and loam soils. Continuously-waterlogged marshy
165 bogs and mires are also present (Tubbs, 2001). All survey plots were located within the ancient
166 native woodlands of the NFNP (Fig. 1). The canopies of these ancient woodlands are generally
167 dominated by beech (*Fagus sylvatica*) and pedunculate oak (*Quercus robur*) interspersed with birch
168 (*Betula pendula*), with yew (*Taxus baccata*) and holly (*Ilex aquifolium*) frequently present in the
169 understorey (Tubbs, 2001). Collectively, these woodlands represent one of the most extensive areas of
170 native, semi-natural woodland in England, and are characterised by a diverse structure with many
171 ancient trees and large volumes of deadwood, providing habitat for a high diversity of invertebrates,
172 ectomycorrhizal fungi (ECM) and lichens (Tubbs, 2001; Newton, 2010). The area is also
173 characterised by high densities of large herbivores, including both livestock and deer, owing to its
174 designation as a Royal Hunting Forest and as common land over which livestock are free to roam
175 (Tubbs, 2001; Newton et al., 2013). We selected study areas that were all beech-dominated. These
176 areas of beech woodland are currently undergoing moderate to significant stand dieback. The dieback
177 appears to be related to a combination of changing climate conditions (specifically an increased
178 incidence of summer droughts and winter waterlogging) and the action of fungal pathogens (Martin et
179 al., 2015, 2017; Evans et al., 2017). The variation in levels of beech dieback throughout the NFNP
180 provides a gradient of woodland dieback along which the relative sensitivity of 102 woodland
181 ecological variables as indicators of beech woodland condition could be tested.

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2.2. Experimental design

We established survey plots along a gradient of beech woodland condition in twelve replicate woodland blocks. The gradient of beech woodland condition covered five stages of stand dieback ranging from Intact (i.e. a closed canopy beech stand) to Total dieback (where no living beech remained). All survey plots were assumed to have had a similar starting (i.e. closed canopy) density as they were all in ancient native woodlands. The stages of dieback were determined primarily by the basal area (BA) of living trees. However, essential secondary criteria for site selection included the presence of standing or lying dead wood, beech snag presence in the Total dieback stage, increased canopy openness associated with tree mortality, and degradation of the remaining beech crowns, following (Roloff, 1989). Any prospective survey plots, other than the Intact plot, which did not meet the secondary criteria as well as the primary criterion were not used. Survey plots were positioned to provide linear gradients of BA of the canopy dominant species (beech), as calculated by Cantarello and Newton (2008). The mean BA of 12 Intact beech stands was first calculated, then used to define the BA of four other stages along each gradient, namely Slight dieback (defined as 75% of the mean BA of Intact stands); Moderate dieback (50%), Major dieback (25%), and Total dieback (0%). For ease of reference, 1-5 represent the individual dieback stages in numeric form, with 1 indicating Intact stands and 5 indicating Total dieback. This provided 12 replicates of each gradient stage, totalling 60 survey plots overall, each of which was 20 x 20 m (0.04 ha) in area.

2.3. Ecological variables measured

We recorded 102 ecological variables in each of the 60 survey plots (Table 1). The variables included condition measures that have been found to be useful at multiple woodland locations and woodland types. For example, due to their utility, metrics relating to dead wood (e.g. Angelstam and Dönz-Breuss, 2004; JNCC, 2004; Rondeux and Sanchez, 2010), tree canopy health (Zarnoch et al., 2004; Gao et al. 2015), soil productivity (Amacher et al., 2007; Thiffault et al., 2011; Forest Europe, 2015), and browsing disturbance and regeneration (Angelstam and Dönz-Breuss, 2004; Forest Europe, 2015) have frequently been used in woodland condition assessments. Overall, the variables used in this study included 35 of stand composition, 4 of functional processes, 29 of edaphic (physical and chemical) conditions of the forest floor to a mineral layer depth of 15 cm, 22 measures of woodland stand structure, and 12 of environmental disturbances (e.g. herbivory). For the methods used, see the Methodology section in the Supplementary Material. The selection of ecological variables was based on variables that had been previously applied as indicators to describe an element of forest condition (see Noss, 1999; Angelstam and Dönz-Breuss, 2004; Cantarello and Newton, 2008; Thiffault et al., 2011; Forest Europe, 2015; Gao et al., 2015).
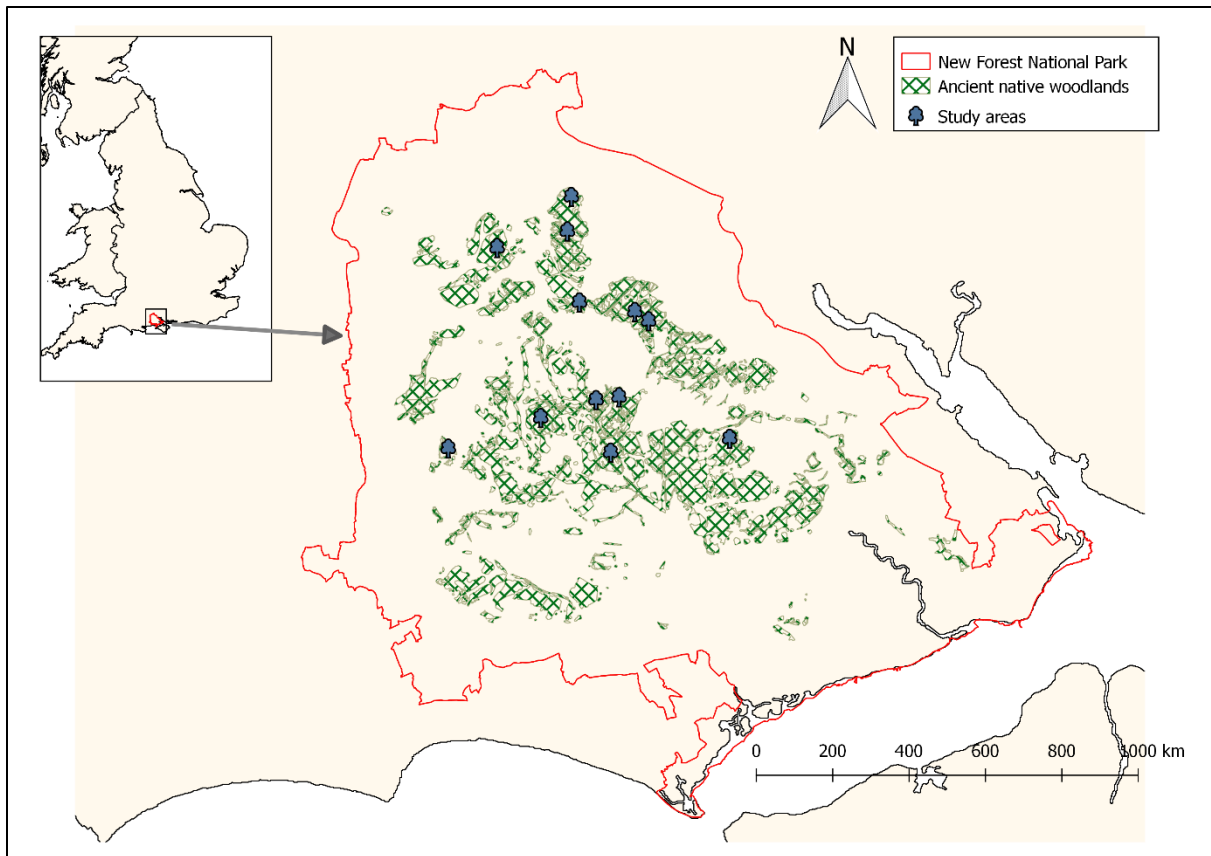
Fig. 1: Map of the New Forest National Park (red outline) the ancient native woodlands (green), in Hampshire, UK, and the central location of each study area (blue trees). Map was produced using QGIS 2.18.19.

2.4. Statistical analysis

One-way ANOVAs were used to analyse each variable to identify significant differences between mean values associated with the different stages of dieback. To test whether the data matched the assumptions of ANOVA, Shapiro-Wilk tests were conducted to test the normality of each variable at each stage over the gradient, and Levene's test was used to test for homogeneity of variance (Fox and Weisberg, 2011; R 'car' package). Where the ANOVA assumptions were met, one-way factorial ANOVAs were performed with the indicator as the response variable and the dieback stages as the independent variable. When the homogeneity of variances assumption was not met, or the variables had unequal sample sizes, Welch's one-way ANOVA was used. For variables that did not exhibit normality, even after transformations, the non-parametric Kruskal-Wallis test was used. If ANOVA results calculated significant differences at a 0.05 level, Tukey's, Games-Howell (Games and Howell, 1976) or Dunn's (Dunn, 1964) post-hoc pairwise comparison tests were carried out for ANOVA, Welch's ANOVA and Kruskal-Wallis tests, respectively. To reduce the chance of a false positive (a Type I error), Bonferroni-corrected p-values were calculated in addition to the standard p-values. All

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238   statistical analyses were carried out using R (version 3.2.3; R Development Core Team, 2015,

239   http://www.r-project.org/).

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Species composition	Functional process	Edaphic conditions	Stand structure	Disturbance intensity
• Ant species richness	• Net ammonification per month	• Ammonium concentration (mineral layer)	• Aboveground woody tree biomass	• Bare ground and moss cover
• Beech sapling density	• Net N mineralisation	• Ammonium concentration (organic layer)	• Average height of beech trees	• Cervus dung density (proportional)
• Beech seedling density	• Net nitrification	• Ca/Al ratio	• Beech biomass	• *Cervus* dung density (total)
• Beech tree density	• Soil respiration rate	• Clay percentage of soil	• Beech tree canopy discolouration	• Debarking of trees
• Bracken cover		• Electrical conductivity	• Beech tree leaf loss	• Dung density (proportional)
• Carabid beetle species richness		• Loss on ignition (mineral layer)	• Beech tree structural canopy loss	• Dung density (total)
• Click beetle species richness		• Loss on ignition (organic layer)	• Canopy openness	• *Equus* dung density (proportional)
• ECM species richness		• Moisture content (mineral layer)	• Live wood to dead wood ratio	• *Equus* dung density (total)
• Grass cover		• Moisture content (organic layer)	• Living biomass of holly	• Holly shrubs browsed
• Ground flora species richness		• Nitrate concentration (mineral layer)	• Lying dead wood volume (all species)	• Palatable tree browseline
• Ground-dwelling invertebrates species richness		• Nitrate concentration (organic layer)	• Lying dead wood volume of beech	• *Rubus* sp. eaten by herbivores
• Holly sapling density		• Organic soil depth	• Mean (quadratic) diameter at breast height of beech	• Unpalatable tree browseline
• Holly seedling density		• Potentially mineralisable N (mineral layer)	• Sward height	
• Holly shrub cover		• Potentially mineralisable N (organic layer)	• Total C in stand	
• Holly tree density		• Sand percentage of soil	• Understorey openness	
• Large beech trees (68.32 cm < DBH < 74.97 cm) density		• Silt percentage of soil	• Unhealthiness of beech trees	

- Lichen richness on holly
- Lichen richness on non-holly and non-beech trees
- Lichen species richness on beech
- Litter cover
- Oak seedling density
- Palatable seedling density
- Rove beetle species richness
- *Rubus* sp. ground cover
- Seedling and ground flora species richness
- Small beech trees (10 cm < DBH < 59.59 cm) density
- Spider species richness
- Total lichen species richness
- Total sapling density
- Total tree seedling density
- Tree seedling species richness
- Tree species richness
- Very large beech trees (74.97 cm < DBH < 103 cm) density
- Weevil species richness
- Woodlouse species richness

- Soil exchangeable aluminium
- Soil available phosphorus
- Soil bulk density
- Soil C/N ratio
- Soil exchangeable calcium
- Soil exchangeable iron
- Soil exchangeable magnesium
- Soil exchangeable manganese
- Soil Na/Ca ratio
- Soil pH
- Soil exchangeable potassium
- Soil exchangeable sodium
- Total N in soil

- Volume of lying holly dead wood
- Volume of lying oak dead wood
- Volume of standing beech dead wood
- Volume of standing dead wood
- Volume of standing holly dead wood
- Volume of standing oak dead wood

241

242   Table 1: Ecological variables measured split into five different categories. DBH is the diameter at breast height.

243

3. Results

35 of the 102 measured ecological variables differed significantly between at least two stages of the beech dieback gradient. All five categories of ecological variables tested (i.e. compositional, structural etc) had at least two variables that showed a significant response to beech decline (Table 2).

3.1. Composition variables

Seventeen out of 35 composition indicators differed significantly across the dieback gradients (Table 2). The density of beech trees (X^2 (4) = 47.846, p <0.001) differed significantly in seven out of 10 pairwise stages comparisons. ECM species richness (F (4,55) = 13.974, p < 0.001) (Fig. 2a), total ground flora species richness (F (4,55) = 13.059, p < 0.001) (Fig. 2b) and ground flora species richness excluding woody plants (F (4,55) = 14.542, p < 0.001) differed significantly in five pairwise stages comparisons. Lichen species richness on beech (F (4,55) = 17.429, p < 0.001) (Fig. 2c), grass cover (F (4,55) = 11.981, p < 0.001), ant species richness (X^2 (4) = 14.554, p = 0.006) (Fig. 2d) and the density of palatable seedlings (X^2 (4) = 14.322, p = 0.006) differed significantly in four pairwise stages comparisons. Two indicators differed significantly in three pairwise stages comparisons, namely total lichen species richness (F (4,55) = 4.207, p = 0.005) and density of beech seedlings (X^2 (4) = 10.046, p = 0.040). Bracken cover (X^2 (4) = 14.290, p = 0.006) (Fig. 2e) differed significantly in two pairwise stages comparisons, while seedling species richness (F (4,55) = 4.003, p = 0.006) and ground-dwelling invertebrate species richness (F (4,55) = 3.782, p = 0.019) (Fig. 2f) differed significantly in one of the pairwise stages comparisons. Litter cover (X^2 (4) = 40.496, p < 0.001) (Fig. 3a) differed significantly in six pairwise stages comparisons, as did the percent of bramble cover (X^2 (4) = 33.230, p < 0.001).
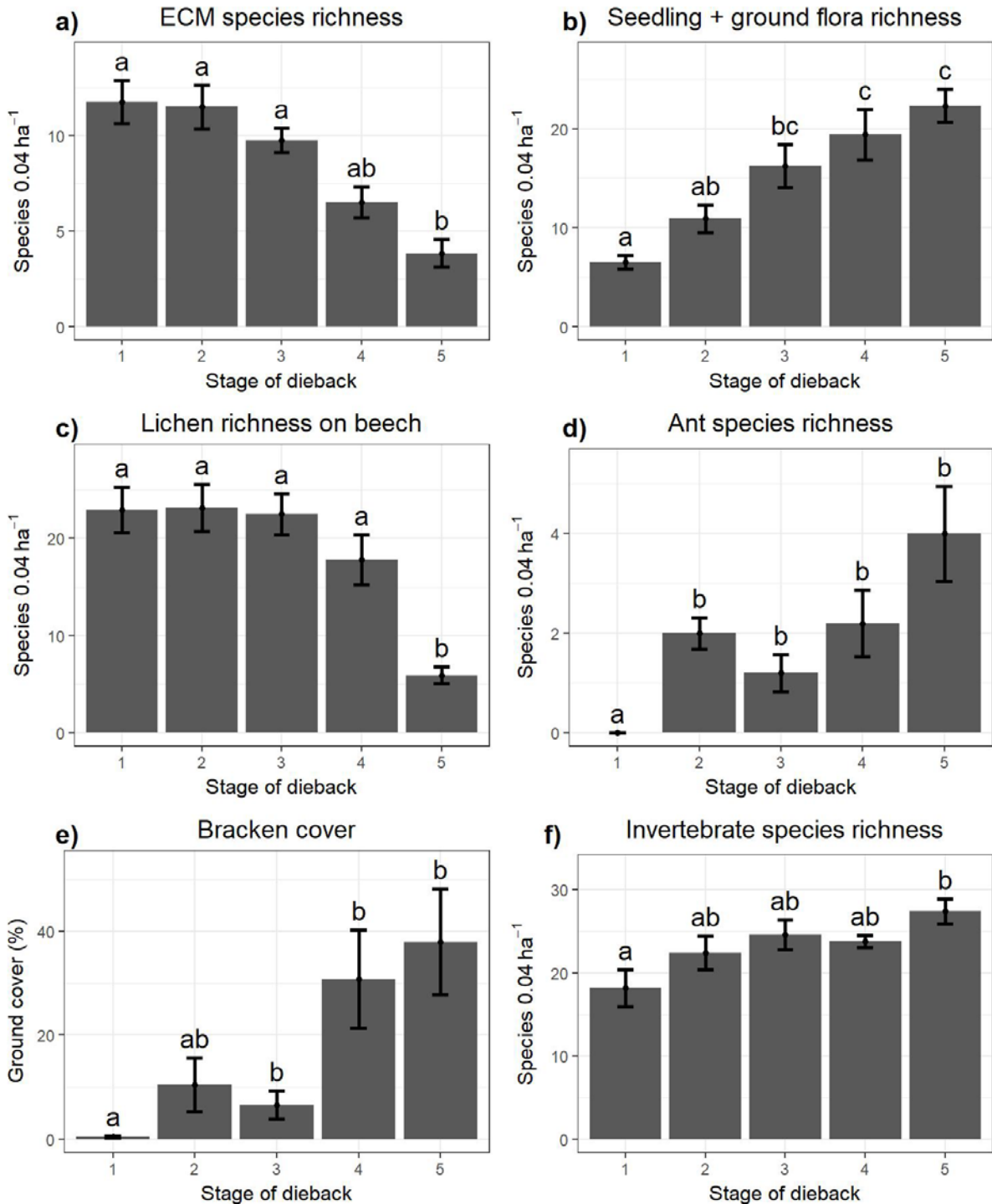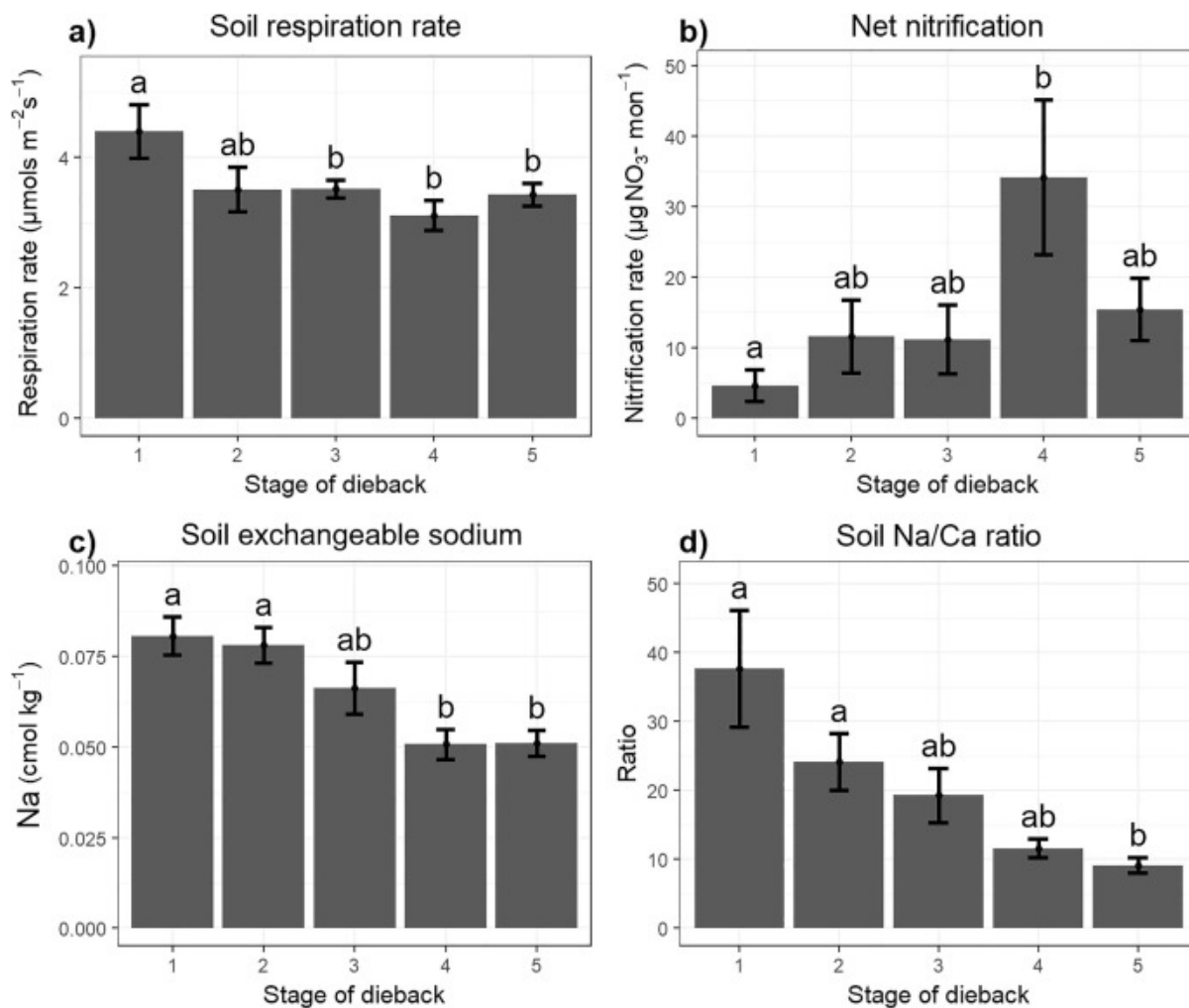
Fig. 2: Mean values of composition variables measured across the stages of dieback (1=Intact; 5=Total dieback). The black bars indicate the standard error of the mean. Means grouped by the same letter are not significantly different (p < 0.05, Tukey HSD test or Dunn's test).

3.2. Functional process variables

Two out of four functional processes variables differed significantly over the dieback gradient. These were the soil respiration rate (X^2 (4) = 12.875, $p = 0.012$) (Fig. 3a), which differed significantly in three pairwise stages comparisons, and net nitrification (X^2 (4) = 2.616, $p = 0.046$) (Fig. 3b), which

275   differed significantly in one pairwise stages comparison. The net ammonification rate and net N

276   mineralisation rate did not differ significantly.

277

278

279   Fig. 3: Mean values of functional processes and edaphic variables measured across the stages of

280   dieback. The black bars indicate the standard error of the mean. Means grouped by the same letter are

281   not significantly different ($p < 0.05$, Tukey HSD test or Dunn's test).

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283   3.3. Edaphic variables

284   Three out of 29 woodland edaphic condition variables differed significantly across the dieback

285   gradient (Table 2). Soil exchangeable sodium ($F (4,55) = 8.307$, $p < 0.001$) (Fig. 3c) differed

286   significantly in four pairwise stages comparisons, and the sodium/calcium ratio ($F (4,55) = 8.787$, $p <$

287   0.001) (Fig. 3d) and calcium/aluminium ratio each differed significantly in two pairwise stages

288   comparisons.

289

3.4. Structure variables

Ten out of 22 of the woodland structure variables differed significantly across the dieback gradients. Aboveground woody tree biomass ($F (4,55) = 11.748$, $p < 0.001$) and beech biomass ($X^2 (4) = 53.528$, $p < 0.001$) differed significantly in all stages, as did canopy openness ($F (4,55) = 193.434$, $p < 0.001$ (Fig. 4a). Sward height ($X^2 (4) = 37.566$, $p < 0.001$) (Fig. 4b), differed significantly in seven pairwise stages comparisons. Understorey openness ($X^2 (4) = 19.516$, $p = 0.001$) differed significantly in five pairwise stages comparisons. Total lying dead wood ($F (4,55) = 11.755$, $p < 0.001$) (Fig. 4c) and beech dead wood volume ($F (4,55) = 9.602$, $p < 0.001$) differed among four pairwise stage comparisons. The other woodland structure indicators that varied significantly over the dieback gradient were the density of large and small beech trees, and the amount of leaf loss from beech (Table 2).
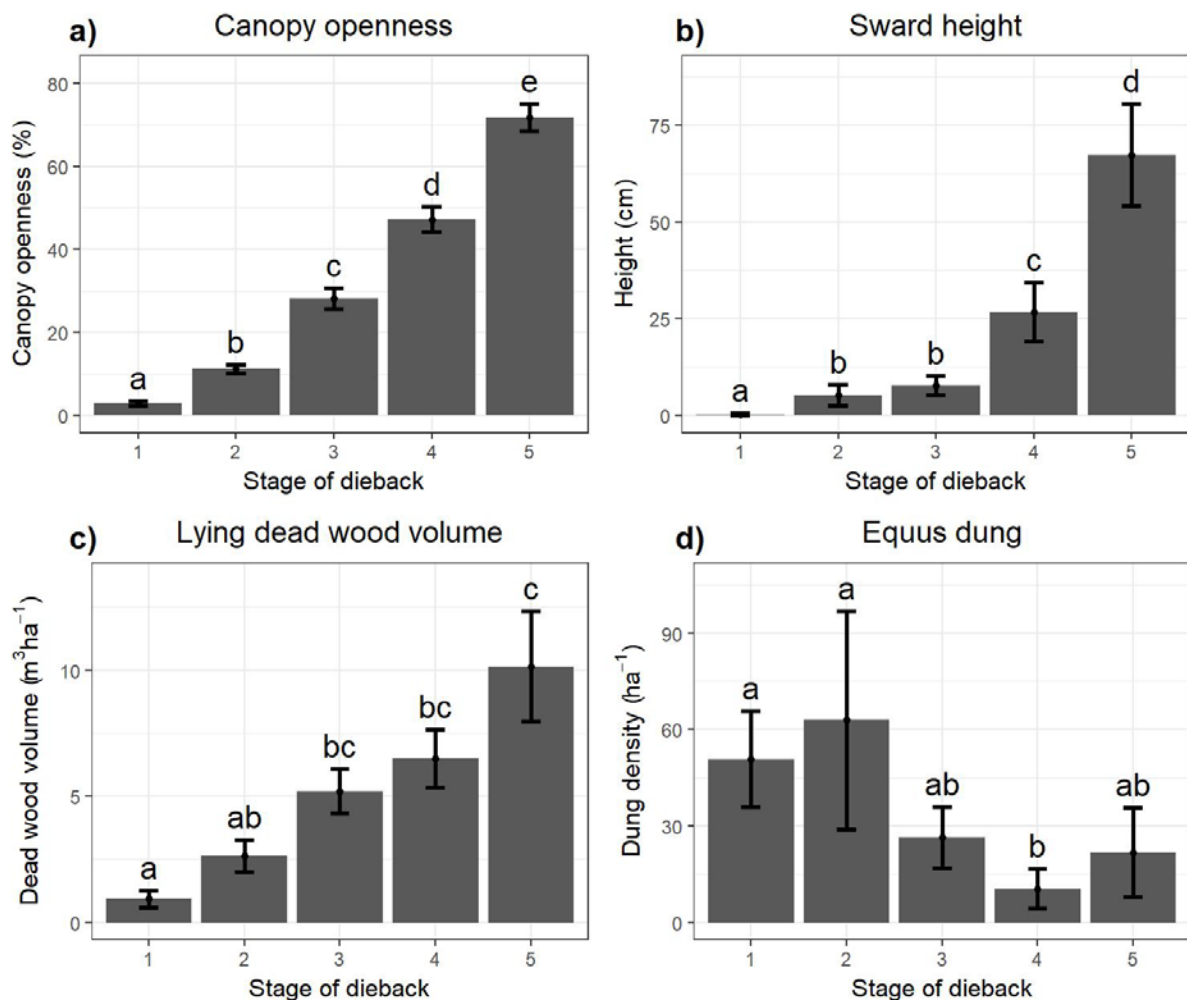
Fig. 4: Mean values of structure variables measured across the stages of dieback. The black bars indicate the standard error of the mean. Means grouped by the same letter are not significantly different (p < 0.05, Tukey HSD test or Dunn's test).

Variable	F-value	p-value		Variable	F-value	p-value
Ground flora species richness	14.542	**< 0.001**		Canopy openness	193.434	**< 0.001**
ECM species richness	13.974	**< 0.001**		Beech biomass	53.528	**< 0.001**
Seedling and ground flora species richness	13.059	**< 0.001**		Sward height	37.566	**< 0.001**
Beech tree density	47.846	**< 0.001**		Lying dead wood volume (all species)	11.755	**< 0.001**
Rubus sp. ground cover	33.23	**< 0.001**		Lying dead wood volume of beech	9.602	**< 0.001**
Grass cover	11.981	**< 0.001**		Aboveground woody tree biomass	11.748	**< 0.001**
Litter cover	40.496	**< 0.001**		Total C in stand	32.912	**< 0.001**
Lichen species richness on beech	17.429	**< 0.001**		Understorey openness	19.516	**0.001**
Total lichen species richness	4.207	**0.005**		Beech tree leaf loss	10.889	**0.012**

Large beech trees (68.32 cm < DBH < 74.97 cm) density	12.916	**0.005**		Unhealthiness of beech trees*	4.023	**0.019**
Ant species richness	14.554	**0.006**		Bare ground and moss cover	7.276	**0.001**
Tree seedling species richness	4.003	**0.006**		*Equus* dung density (proportional)	12.63	**0.013**
Palatable seedling density	14.322	**0.006**		Soil Na/Ca ratio	8.787	**< 0.001**
Bracken cover	14.29	**0.006**		Soil exchangeable sodium	8.307	**< 0.001**
Ground-dwelling invertebrates species richness	3.782	**0.019**		Ca/Al ratio	3.815	**0.022**
Beech seedling density	10.046	**0.04**		Soil respiration rate	12.875	**0.012**
Small beech trees (10 cm < DBH < 59.59 cm) density	8.072	**0.045**		Net nitrification	2.616	**0.046**

307   Table 2: Significant ANOVA results of the ecological variables tested as indicators across the stages

308   of woodland stand dieback, sorted by ecological category. Bold values indicate significant results.

309   D.f. = 4 in each case, except where indicated (*), where d.f. = 3 owing to there being no beech

310   individuals present in the Total dieback survey plots. All ANOVA results are found in Table S3.

311

312 3.5. Disturbance variables

313 Three of the 12 disturbance variables measured changed significantly over the gradient of dieback.

314 These were the bare ground and moss cover ($F_{(4,25)} = 7.276$, $p = 0.001$), which differed significantly

315 in three pairwise stages comparisons, and the related measures of total ($X^2(4) = 11.614$, $p = 0.020$)

316 (Fig. 3d) and proportional *Equus* dung density ($X^2(4) = 12.630$, $p = 0.013$).

317

318 **4. Discussion**

319 The results presented here support our initial hypothesis that a selection of ecological variables,

320 representing a diversity of components of the woodland ecosystem (i.e. from edaphic conditions to

321 species composition), can be used at the stand scale as indicators of woodland ecological condition

322 (Noss, 1990; Gao et al., 2015; Lawley et al., 2016). We were able to show this based on their

323 sensitivity to a gradient of stand dieback. We observed some ecological variables that changed

324 systematically (either positively or negatively) across most of the sequential stages of dieback. In

325 addition, some variables changed significantly between two or more stages, but not in a systemic way

326 over the dieback gradient.

327

328 Variables describing forest composition are often considered a key indicator of woodland condition.

329 While they are included in the monitoring schemes of numerous national and international forest

330 health monitoring programmes (e.g. EEA, 2012; the ICP framework (Michel and Seidling, 2016);

331 National Forest Inventories (Chirici et al., 2012)), this is typically restricted to assessments of tree

332 species composition due to the need for taxonomic expertise for other taxonomic groups. In this study,

333 ecological variables demonstrating the strongest potential as condition indicators included the species

334 richness of ECM fungi and epiphytic lichens, which both declined over the gradient of dieback,

335 decreasing by 67% and 32%, respectively, by the final stage of the dieback gradient. Additionally, the

336 species richness of vascular ground flora and ground-dwelling arthropods demonstrate potential as

337 indicators as they increased with dieback, increasing by over 14 (420%) and nine (50%) species,

338 respectively, by the Total dieback stage as canopy cover decreased (see Supplementary Material).

339 Changes in ECM fungal species richness over spatial and temporal gradients of forest condition have

340 also been explored by other authors. For example, Treu et al. (2014) found that ECM species richness

341 declined as the BA of lodgepole pine (*Pinus contorta* var. *latifolia*) declined in Canadian forests,

342 following a stand-destroying beetle attack. Other studies have highlighted a decline in ECM diversity

343 over certain gradients, including temperature, nitrogen deposition and the health of individual trees

344 (Power and Ashmore, 1996; Kovács et al., 2000; Lilleskov et al., 2002; Cox et al., 2010; Suz et al

345 2014; van der Linde et al., 2018).

346

347 Similarly, the occurrence of epiphytic lichen have been found to decline significantly along gradients

348 of increasing forest disturbance in the form of management level, from 'natural' to 'very altered'

349 (Angelstam and Dönz-Breuss, 2004). In Romania, Ardelean et al. (2015) also found that management-
350 induced disturbance significantly decreased lichen species richness in forest landscapes with long
351 stand continuity. While the two aforementioned studies focused largely on management intensity
352 gradients, the results from our study indicate that stand dieback has a similar effect. Thus, our results
353 further support the suggestion made by Keddy and Drummond (1996) that epiphytic lichen
354 communities can provide a useful indicator of the condition of temperate forest ecosystems.
355
356 Floristic diversity studies that examined light gradients in European and North American forests show
357 similar trends to the findings in this study (Tinya et al., 2009; van Couwenberghe et al., 2011; Neufeld
358 and Young, 2014; Sabatini et al., 2014); that is, observed increases in plant species richness are
359 positively related to an increase in light availability.
360
361 Although some of ecological variables assessed in this study are potentially useful indicators of beech
362 woodland dieback, none of these measures differed systematically between every dieback stage.
363 Therefore, there may be a need to use a suite of indicators, rather than a single indicator in isolation
364 (e.g. Ferris and Humphrey 1999; Aubin et al., 2013; Sabatini et al., 2016), a finding that has been
365 found in other ecosystems subject to disturbance (Fournier et al., 2015). However, as recorded here,
366 ECM and ground flora species richness exhibited negative and positive trends with dieback,
367 respectively. These contrasting trends suggest that using combination measures of the two taxa in
368 assessments may be of value in detecting changing woodland condition.
369
370 We show that some soil functional processes and edaphic condition variables properties are relatively
371 sensitive to stand dieback and therefore could be used as indicators of condition. For example, the soil
372 exchangeable sodium varied significantly across the dieback gradient, decreasing by 37% when
373 comparing the Total dieback stage to the Intact stage. Similarly, the sodium/calcium ratio decreased
374 by > 75% from Intact to Total dieback stages. Soil respiration rate was another variable that showed
375 significant variation, decreasing by approximately a third between the Intact and Major dieback
376 stages. However, while the soil variables measured here could potentially be used as indicators of
377 woodland ecosystem condition, further research is required to verify the extent to which they are
378 generally applicable. Previous research has demonstrated that soil respiration in temperate forest
379 stands can be very variable (Priwitzer et al., 2013) and rates are influenced by a wide range of factors
380 including soil moisture and temperature, as well as the species present (Smith and Johnson, 2004).
381
382 Effective structural woodland condition indicators identified in this study included stand biomass,
383 sward height, canopy openness and the volume of lying dead wood. The biomass of beech was very
384 sensitive to dieback and declined sequentially at each stage over the gradient, while lying dead wood
385 increased positively with dieback. However, owing to the spatial variability in dead wood volume,

386   only the Total dieback stage was found to be associated with significantly higher values when

387   compared to the other stages. Increases in dead wood volume and canopy openness have obvious

388   links to mortality of canopy dominant tree species, and are therefore closely associated with dieback

389   (Anderegg et al., 2013). It is therefore unsurprising that these variables increased with stand dieback

390   and were therefore found to be effective indicators of condition. It has previously been observed that

391   both dead wood volume and canopy openness often correlate with biodiversity measures (Gao et al.,

392   2014, 2015), making them consistently important aspects of forest and woodland condition

393   assessments (Noss, 1999; Hagan and Whitman, 2006; Rondeux and Sanchez, 2010). This is especially

394   true for dead wood, which provides habitats for many forest-dwelling species, including invertebrates

395   (Jabin et al., 2004), lichens (Humphrey et al., 2002) and wood-inhabiting fungi (Nordén and Paltto,

396   2001; Penttilä et al., 2004). However, as pointed out by Rondeux and Sanchez (2010) in their review

397   of commonly-used biodiversity indicators, while dead wood volume is a useful measurement, it often

398   displays greater variability than other structural forest metrics. Site-specific information may therefore

399   be required to support its effective use as an indicator.

400

401   It is also pertinent to consider those variables that did not vary significantly across the dieback

402   gradient. These included a number of composition variables, including total density of tree seedlings,

403   species richness of invertebrate groups such as spiders and carabid beetles, and density of oak or

404   beech saplings. The lack of any significant impact on carabids and spiders is particularly surprising, as

405   previous research in conifer plantations in the UK and Canada identified a significant negative

406   relationship between carabid diversity and canopy cover (Spake et al., 2016), and spider diversity and

407   harvesting amount (Aubin et al., 2013). However, both these studies used a trait-based approach,

408   which is different to the approach taken here. Furthermore, the reason for carabid beetle trends

409   observed in this study is possibly due to different carabid species favouring different levels of canopy

410   cover (e.g. Taboada et al., 2006), which cannot be analysed using species richness measures.

411

412   Interpretation of these results should consider the particular characteristics of the field site examined

413   here; as a Royal Hunting Forest that is also used for livestock 'commoning' (the right to release

414   animals into the forest), herbivore pressure is universally high (Newton et al., 2013), and

415   consequently both seedling and sapling densities were very low throughout the dieback gradients.

416   Interestingly, based on dung counts, woodland dieback was associated with an increase in browsing

417   by horses (*Equus* sp.) but not by deer (*Cervus* sp.); *Equus* dung decreased by almost 80% by the

418   Major dieback stage. However, the dramatic decrease may be due to increased decomposition rates in

419   areas with less canopy cover; to determine how much of an effect decay rates have, studies are needed

420   to be carried out in the specific ecosystem first (Zabek et al., 2016). Many functional measures also

421   did not vary significantly along the gradients, including net N mineralisation, soil C/N ratio, nitrate

422   concentration, soil pH or electrical conductivity. Examples of structural variables that did not vary

423   significantly included understorey cover, soil bulk density, soil organic matter content, and mean tree

424   height. This indicates that some of those variables that are standard measures of woodland

425   ecosystems, such as canopy height and shrub cover (Angelstam and Dönz-Breuss 2004), are not

426   necessarily effective as indicators. Again, however, the particular characteristics of this field site need

427   to be borne in mind when interpreting the results; for example soil bulk density values were relatively

428   high throughout the dieback gradients, reflecting the pervasive influence of trampling by large

429   herbivores.

430

431   While this investigation has demonstrated that degradation of woodland condition can be identified

432   using a number of ecological variables that are sensitive indicators of dieback, and the potential value

433   of using gradients of forest and woodland condition to test the effectiveness of different indicators, the

434   results should clearly be interpreted with caution. Limitations of the study included the choice of

435   measurement variables; although a large number of variables were included, additional potentially

436   highly sensitive ecological variables along a woodland dieback gradient could potentially have been

437   selected. Comparison with lists of indicators proposed by Angelstam and Dönz-Breuss (2004) and

438   Keddy and Drummond (1996) show a close correspondence with those measured in this study, but

439   these lists included populations of specialised vertebrates (e.g. bat and woodpecker species) and

440   epiphytic bryophytes, which were not considered here. A further limitation relates to replication.

441   While twelve replicate beech dieback gradients were surveyed in the current study, these were all

442   located within a single protected area; application of the results obtained here to other geographical

443   areas would require additional verification. Previous multi-site comparison of indicator performance

444   has highlighted pronounced variation between areas. For example, in their evaluation of forest

445   biodiversity indicators across a range of European sites, Angelstam and Dönz-Breuss (2004) found

446   that only two indicators gave consistent results across all sites, namely the amount of dead wood and

447   the frequency of occurrence of uprooted trees. Similarly, in an examination of forest disturbance

448   gradients in four study areas in Latin America, Newton et al. (2007) found contrasting responses in

449   different areas. For example, in the Highlands of Chiapas in Mexico, highly significant correlations

450   were obtained between BA and both soil organic matter content and bulk density, but no such

451   correlations were found in two of the other study areas, supporting the results of the current

452   investigation. With respect to floristic species richness, a significant correlation with BA was found in

453   only one of the four areas. Such variation implies that individual indicator sets may need to be

454   adapted and tested for each individual forest area of interest.

455

456   **5. Conclusion**

457   This original work indicates which ecological variables changed significantly over a specific gradient

458   of declining woodland condition, enabling the detection of important changes at and between different

459   stages of degradation. The major findings suggest that several different structural, functional and

compositional variables could all be used as indicators of woodland condition. However, focusing on variables which are not typically closely associated with dieback and therefore the primary criterion of BA change (e.g. beech biomass), it is the composition variables, most notably ECM fungi and ground flora species richness, which could be used as condition indicators, as these variables demonstrated large significant declines over the dieback gradient. Functional variables including the soil respiration rate, Na/Ca soil ratio and net nitrification also all changed significantly over the dieback gradient and therefore could also be used as indicators of condition.

When developing monitoring plans in order to achieve effective woodland management and conservation strategies, results here suggest that at least ECM fungi and ground flora species richness should be recorded, together with a few cheap-to-measure structural indicators that changed significantly over the gradient, such as canopy openness. With additional resources, measuring soil function and content as well could yield a fuller evaluation of condition. Other things which are important to note for inclusion in future plans are that the results here detail changes in the ecological condition of the forest without any management interventions, and that the cost and time requirements and difficulty of continued measurement need to be considered (see sections 2 and 3 in Supplementary Material for more detail). This research could be further enhanced in future by using complementary studies or a greater range of indicators, such as additional measures of faunal diversity (Gao et al. 2015).

496 **Declarations of interest**

497 None

498

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