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Contact CEH NORA team at
noraceh@ceh.ac.uk

1   **Native dominants in British woodland– a potential cause of reduced species-**

2   **richness?**

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4   Rob H. Marrs[*1], Keith J. Kirby[2], Michael G. Le Duc[1], Hugh McAllister[1] Simon M.

5   Smart[3], Jari Oksanen[4], Robert G.H. Bunce[5] and Phillip M. Corney[1,6]

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7   [1]*School of Environmental Sciences, University of Liverpool, Liverpool, L69 7ZB, UK*
8
9   [2]*Department of Plant Sciences, South Parks Road, Oxford, OX1 3RB, UK*
10
11   [3]*Centre for Ecology & Hydrology, Lancaster, LA1 4AP, UK*
12
13   [4]*Department of Biology, University of Oulu, 90014 Oulu, Finland*
14
15   [5]*Alterra, P.O. Box 47, 6700AA Wageningen, The Netherlands*
16
17   [6]*Present address, Hyder Consulting UK Ltd, Stroud GL5 2QG, UK*
18
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21   *Author for correspondence (calluna@liv.ac.uk).

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1   The invasion of native habitats by alien species has received considerable attention.

2   However, in Britain high levels of dominance by a small number of aggressive native

3   plant species may have an equal, or greater, impact on the richness of native

4   woodlands. Here, we examine this hypothesis by modelling the realized niche of

5   native-dominant species along the principal coenocline of British woodlands, and

6   examined niche overlaps with 78 woodland specialist species and two alien species.

7   Four native species had a much greater cover than all other field-layer species, and

8   between them they entirely covered the response range of all other field-layer species,

9   replacing one another along the coenocline. These findings, combined with

10   autecological information suggest that *Hedera helix*, *Mercurialis perennis*, *Pteridium*

11   *aquilinum* and *Rubus fruticosus* have the potential to become 'over-dominant' and

12   perhaps may impinge on other field-layer species. Our results also identified which

13   field-layer species are likely to be impacted by a change in abundance of each of these

14   dominant-species, and as such, provide a novel quantitative method of risk assessment

15   to aid conservation policy. Understanding how woodland communities remain

16   diverse, even in the presence of aggressive native species, may provide insights into

17   how the impact of exotic invasive species can be managed.

18

19   **Keywords:** Invasive species, coenocline, detrended correspondence analysis,

20   woodland field-layer, HOF modelling, national scale conservation policy

21

1   **Introduction**

2   Invasive species are one of the most important threats to biodiversity conservation

3   worldwide (Millennium Ecosystem Assessment, 2005). The recently-published UK

4   National Ecosystem Assessment included invasive species as one of the five major

5   drivers of change in UK ecosystem services over the past 60 years, even though they

6   considered it had had a lesser impact than (a) habitat loss, (b) overexploitation

7   (change in productivity) and (c) air and water pollution (UK National Ecosystem

8   Assessment 2012).

9

10   Most concerns are of the impact of neophytes, i.e. those species that are not native to

11   the area and have invaded in the recent past (Pysek *et al*., 2003; Richardson *et al.,*

12   2005). However, the conservation of ecosystems may also be significantly affected by

13   native species that develop high biomass and necromass and reduce the abundance of

14   other species, in some places becoming almost mono-cultures (Bobbink & Willems

15   1987; Pakeman & Marrs 1992; Milligan *et al*. 2004). This is especially problematic

16   against a background of changing impacts on vegetation, with reports of country-wide

17   biotic homogenization (Smart *et al*. 2005, 2010; Keith *et al.* 2009) and increased

18   abundance of species typical of high fertility (Smart *et al*. 2006). Thus, there is a need

19   to assess the impact of potentially dominant species (whether native and neophyte) on

20   the indigenous flora, and for policy-making this should be done through assessment at

21   the countrywide-scale (Corney *et al.* 2006; Lewis *et al*. 2013).

22
23   Here, therefore, we assess the potential *impact*, using the realised niche-breadth of

24   selected dominant species and those other species that might be at risk if they should

25   increase in abundance. We measured the realised niche-breadth of field-layer species

26   along the major coenocline in the vegetation of ancient, broad-leaved woodland in

1   Great Britain (GB). The data were derived using a stratified-random sampling design

2   that covered the entire broad-leaved, woodland resource in GB, carried out under the

3   National Woodland Survey (NWS) in a baseline survey in 1971. Marrs *et al.* (2010)

4   demonstrated that the NWS survey did cover a wide range of the variation in British

5   woodland as it existed in 1971, with samples from 20 of the 25 woodland National

6   Vegetation Classification (NVC) types (Rodwell 1992), although three were detected

7   in only one plot. The missing classes comprised four *Salix*-dominated shrub

8   communities (W1, W2, W3, W20), and the fifth was the W18 *Pinus sylvestris-*

9   *Hylocomium splendens* community, typical of Scottish native pine woods (Rodwell

10   1991), which were not included in this survey of broad-leaved woodlands.

11   Broad-leaved woodlands in Britain tend to be late-successional ecosystems; they

12   have been subject to only low-intensity management in the last 50 years following

13   often significant canopy disturbances during the Second World War (Hopkins &

14   Kirby 2007). Hence their plant species composition might be expected to exhibit high

15   resistance to change. Thus, the data-set provides of reasonable basis for exploring the

16   impact of different dominant species at the GB-scale

17   Within Great Britain, there are several neophytes known to cause local

18   conservation problems in woodlands, for example, *Rhododendron ponticum* (Dehnen-

19   Schmutz *et al*. 2004) (Stace 1997 for nomenclature), planted conifers (including

20   *Pseudotsuga menziesii* and *Picea sitchensis*), *Fallopia japonica*, *Heracleum*

21   *mantegazzianum, Impatiens glandulifera, Acer pseudoplatanus* and *Prunus*

22   *laurocerasus* (Beerling *et al*. 1994; Dawson & Holland 1999; Peterken 2001; Willis &

23   Hulme 2002). Within the NWS survey, only *A.pseudoplatanus, I.glandulifera, R.*

24   *ponticum* produced significant effects on the field-layer species (Marrs *et al.* 2010).

1   Recently, however, it has been postulated that some native plant species, may pose

2   an equal, or even greater, threat to woodland communities than neophytes (Pearman

3   2004; Pearman & Lockton 2004). The species identified were: *Hedera helix* (subspp.

4   *helix* and *hibernica*; McAllister and Rutherford 1990), *Pteridium aquilinum*, *Rubus*

5   *fruticosus* agg. and *Urtica dioica*. Whilst there is no doubt that these species have

6   conservation value in their own right (Kirby & Woodell 1998; Marrs & Watt 2006;

7   Metcalfe 2005), where they occur as dominants, often in mono-cultures, there is a

8   reduction in plant species-richness and hence reduced conservation value (Pakeman &

9   Marrs 1992). The term "Thug" has been used to describe the behaviour of these

10   species in the past (Pearman 2004; Pearman & Lockton 2004; Marrs *et al.* 2010), but

11   as this term is rather emotive, here we refer to these species as native-dominants.

12   In a previous analysis of the NWS survey (Marrs *et al.* 2010), the top four species

13   in terms of rank abundance were in order: *R. fruticosus*, *P. aquilinum*, *M. perennis,*

14   and *H. helix*, i.e. three of the four previously-identified native-dominants (Marrs *et al.*

15   2010). *U. dioica* had a much lower mean rank-abundance (14th) and all were

16   considerably greater than the neophytes (*A. pseudoplatanus* = 38th*, R, ponticum* =

17   70th, *I. parviflora* > 200th). In this paper, we consider five species of native-dominant

18   (*R. fruticosus*, *H. helix*, *M. perennis*, *P. aquilinum*, *U. dioica*); i.e. the four identified

19   by Pearman (2004) and Pearman and Lockton (2004) plus *M. perennis*. We included

20   *M. perennis* because of its abundance in the NWS and because it has also been

21   identified as a species that suppresses other woodland ground flora species (Pigott

22   1977; Rackham 2006). All of these native-dominants have been described by Grime *et*

23   *al.* (1988) as either stress-tolerator/competitors or competitors.

24   Marrs *et al.* (2010) then used variation partitioning to measure the relative

25   importance of the native-dominant field-layer species with invading neophytes (*A.*

5

1 *pseudoplatanus, I. glandulifera, R. ponticum*) in terms of explaining the variation in

2 the field-layer plant communities. The native-dominant species accounted for four

3 times the variation of the significant alien species (*A. pseudoplatanus, I. glandulifera,*

4 *R. ponticum*). Thus, native-dominants had a greater influence on native, broad-leaved

5 woodland field vegetation than neophytes. Clearly, if this is the case it is essential for

6 conservation managers to know where any impact is likely to occur and what species

7 might be at risk if the native-dominants increase either in range (areal extent) or in

8 terms of their cover/biomass (point-intensity).

9 We, therefore, carried out further analyses to explore the following three

10 hypotheses:

11 (1) That the five native dominants chosen would show niche separation within the

12 overall woodland resource;

13 (2) That neophytes would fit into a vacant niche-space between the native species

14 dominants.

15 (3) That they would grow alongside different suites of field-layer species, thus this

16 method could provide a way of identifying which species might be affected by any

17 change in abundance of the native-dominants and nepophytes

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1 **Methods**

2 *Survey methods*

3   The survey methods used in the National Woodland Survey (NWS) are detailed in

4 Bunce & Shaw (1973). Briefly, 103 woodlands were selected objectively from a

5 sample of 2,463 broad-leaved woodlands across Great Britain (Fig. 1) inspected as

6 part of the Nature Conservation Review (Ratcliffe 1977; Kirby *et al.* 2005). In 1971,

7 16 plots (200 m^2) were placed randomly in each site and the vegetation assessed;

8 cover of field-layer vegetation and the shrub and canopy layer were estimated, full

9 details available in Corney *et al*. (2006). However, as the NWS only sampled 103

10 woods, an independent check on the abundance of the five native-dominants across

11 the range of variation within GB woodlands was carried out. To do this, the

12 frequencies of occurrence of the five native dominant species (*H. helix, M. perennis,*

13 *P. aquilinum, R. fruticosus, U. dioica*) were extracted from the tables in the National

14 Vegetation Classification (NVC, Rodwell 1991).

15

16 *Ordination of the field-layer community data – derivation of the coenocline*

17 The ordination procedure used here was based on the same approach used by Corney

18 *et al*. (2006), where an iterative process was used to refine the field-layer cover

19 dataset, essentially because preliminary analyses showed extensive distortion within

20 the ordinations caused by the inclusion of plots with a non-woodland flora. These

21 outliers were identified using an iterative approach combining ordination, regression

22 and classification (Corney *et al.* 2006), and the overall process reduced the dataset

23 from 1648 to 1438 plots.

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1   The resultant dataset (ln(y+1) transformed) was then analysed using Detrended

2   Correspondence Analysis (DCA, Hill & Gauch 1980; ter Braak & Šmilauer 2002);

3   species occurring only once in the dataset were removed. DCA is an iterative

4   algorithm that produces an unconstrained ordination of multivariate ecological data,

5   and is, therefore, a useful for data exploration tool and summary in community

6   ecology (ter Braak & Šmilauer 2002).

7

8   The first axis, which accounts for the greatest variation in the dataset and is scaled in

9   standard deviation units, was extracted here to produce a coenocline for calculating

10   the species response curves. However, for the analysis of individual species response

11   curves, there is an inevitable problem of non-independence with the coenocline; i.e

12   the abundance of the most influential species (here the native-dominants) are used to

13   calculate the coenocline where they effect the greatest influence on the position of

14   both plots and other species.

15

16   To minimize this problem DCA ordinations were calculated with and without the five

17   native-dominant species. These analyses were performed using the 'decorana'

18   function in the 'vegan' package (Oksanen 2010) within the R statistical environment

19   (R Core Team 2012). During these analyses a further three quadrats and one species

20   (*Trifoium dubium*) produced severe distortions in the analyses without the native

21   dominants so they were removed. The graphical outputs of these revised analyses

22   were almost identical to that published by Corney *et al*. (2006). A linear regression

23   between the plot scores on axis 1 of the revised analyses derived from the DCA

24   analysis without the native-dominants (y-variable) against those with all species (x-

25   variable) produced an intercept approximating to zero (0.014±0.001) and a slope

1 approximating to 1 (1.084±0.007) ($F_{1,1433}=2082$; $r^2=0.94$). Nevertheless, the response

2 curves and all subsequent calculations in this paper are based on the coenocline

3 derived from the DCA analysis where the native-dominants were removed.

4
5 *Production of species response curves*

6 The responses of the 216 most frequent species in the NWS (present in more than 5%

7 of quadrats) were then modelled along the first DCA axis using the HOF modelling

8 approach (Huisman *et al.* 1993). The HOF protocol fits an hierarchical set of five

9 increasingly complex response models (Model I, the null model, i.e. no trend; Model

10 II, increasing or decreasing trend; Model III, increasing or decreasing trend below

11 maximum attainable response; Model IV, symmetrical response curve; Model V,

12 skewed response curve).

13

14 The models are fitted sequentially; Model I and II are fitted and the deviance

15 calculated; if the more complex model reduces the AIC statistic then it is selected, if

16 not the simpler model is chosen. The procedure is repeated until all five models have

17 been fitted. The aim is to select the most parsimonious model, i.e. one that is not over-

18 fitted. This technique provides one of the most robust methods for estimating niche

19 characteristics of plant species (Lawesson & Oksanen 2002).

20

21 Here, all model fitting and subsequent calculations were performed within the 'gravy'

22 package (Oksanen 2011) within the R statistical environment (R Core Team 2012).

23 The HOF models were fitted using the 'HOF' function with a Poisson error structure

24 and information on response curve characteristics (maximum cover predicted by

25 model, optimal point on the coenocline where the maximum cover was predicted and

26 the Gaussian tolerance, a measure of spread) was estimated using the 'GaussPara'

1　function. For the symmetric unimodal model IV the Gaussian tolerance (t) is equal

2　both sides of the optimal point but for the skewed model different lower and upper

3　estimates are produced. Thereafter, niche range overlaps for each species pair were

4　calculated using the 'nichelap' function. This function calculates the proportion of the

5　HOF-response range area of species *a* covered by the response range area of species *b*

6　and *vice-versa* by integrating under the selected response curves (Fig. 2, Lawesson &

7　Oksanen 2002).

8　　We tested the first and second hypotheses by inspection of the response curves and

9　measuring the mutual overlaps between the five native-dominant and neophyte

10　species. We also produced a response curve for the mean cover of all native-

11　dominants in each plot along the coenocline. We tested the third hypothesis, assessing

12　the potential threat of the native-dominants to indigenous field-layer species by

13　measuring the amount of the niche of the indigenous species overlapped by each of

14　the seven invasive species.

15

16　　For this last analysis, the niche overlap values were ranked into five classes (I=0-

17　20%, II=20-40%, III=40-60%, IV=60-80%, 80-100% overlap). A field-layer species

18　that is in Class V is likely to be under threat from an increase in that invasive species.

19　Here, we concentrate on those field-layer species that have been proposed as

20　woodland specialist species, and hence of most conservation interest because of their

21　strong association with ancient woodland (list derived from an unpublished collation

22　of 'ancient woodland indicator' lists by K J Kirby, summarised in Rose *et al*. (2006).

23

1   **Results**

2   The five native-dominant species are all among the twenty species (out of 334

3   vascular plant species) that occur in more than half the twenty-five communities in the

4   woodland and scrub section of the National Vegetation Classification, with *R.*

5   *fruticosus* and *H. helix* being the two most widespread. They are more likely to be

6   frequent in communities where they do occur. Compared to the distribution of

7   frequency scores for all vascular plant records across all communities (Table 1a) the

8   five make up 3.5% of the records for frequency class 1, but 30% of those for class 5

9   (present in 81-100% of samples). At least one of them is frequent (class 3) or constant

10 (classes 4, 5) in 17 of the 25 communities (Table 1b), the exceptions being five of the

11 wet types (W1-4, W7) and three montane/boreal types (W18, 19, 20). The five species

12 are broadly spread out over the different communities: in most only one of the five

13 species is a 'constant species' (frequency score of 4 or 5) and never more than two.

14 Individually and collectively, therefore , they have the potential to impact on a wide

15 range of other field-layer species.

16

17 *Assessing the woodland community composition from the NWS (1971)*

18 The DCA analysis of Corney *et al.* (2006) produced eigenvalues of 0.528 and 0.325,

19 and gradient lengths of 5.8 and 5.0 for the first two axes respectively. The species plot

20 (Fig. 1a) showed a transition along axis 1 from those with low scores that tend to be

21 shade-tolerant woodland species, associated with fertile, base-rich soils (e.g.,

22 *Glechoma hederacea*, *Circaea lutetiana* and woodland specialist species *M. perennis*

23 and *Galium odoratum*); through a region with species typical of moderately open

24 woodland (*Veronica chamaedrys*, *Viola reichenbachiana, Deschampsia cespitosa*),

25 suggesting increasing illumination, intermediate fertility and neutral to slightly acid

soils through to species with high scores which tend to be associated with acidic, infertile soils and well-lit habitats such as heathland communities and moorlands (*P. aquilinum, Vaccinium myrtillus*).

The correlation between the mean cover of all five 'native-dominants' and the species richness in each sample was negative (Pearson's r= -0.33, df=1436, P< 0.0001).

Species response along the coenocline

The responses of the 'native dominant' species and the two 'Alien' species are shown on Fig.4. The native-dominants show a progression along the coenocline; *H.helix* was most abundant at the negative end of the gradient, followed by *M. perennis*, *R.fruticosus* and *P. aquilinum* at the positive end; *U. dioica* has a much lower mean cover and appeared to peak around the same point as *M. perennis*. *H. helix* exhibited the simplest response with a reduction along the axis (Type II model: ΔDeviance (ΔD, the reduction in Deviance from the null model) = 19.7%), *P. aquilinum* increased to an asymptote below the maximum possible value (Type III model: ΔD = 34.9%), and the other species showed either an unimodal response (Type IV: *M. perennis*, ΔD=57.3%) or skewed response (Type V: *R. fruticosus*, ΔD= 13.7%; *U.dioica*, ΔD=31.5%).

The mean value of the five 'native dominant' species was calculated and also modelled (Fig. 4f); this produced a Type II model (ΔD=8.0%) with a slight decline in mean cover from negative to positive ends of the coeonocline. The two 'Alien' species both produced unimodal responses (Type IV: *A. pseudoplatanus* ΔD= 2.5%;

Type V: *R. fruticosus*, ΔD= 11.7%) and showed much lower cover than the native dominants (Fig, 5).

H. helix and *P. aquilinum* at the opposite ends of the coenocline do not show a unimodal response, as they dominate the ends of the axes. However, the other native dominants show a clear progression (Table 2). Here the tolerance values indicate clear separation between the two native-dominants with the largest overall cover values (*M. perennis* -2.9 - -1.6; *R. fruticosus* -1.7- +0.4); *U.dioica* had a lower cover peak subsumed within these ranges (-2.4 - -0.2. The two neophytes peak under *R. fruticosus*, but show different tolerance ranges; *A pseuodplatanus* has a wide tolerance range (-2.0 – +0.1), whereas *R. ponticum* has a narrower range (-0.13 – +0.1).

The separation of the native dominants assessed via pair-wise overlaps confirmed mutual separation with the exception of *U.dioica* which was overlapped by three of the native dominants; *H. helix*, *M. perennis,* and *R. fruticosus* (Table 3a). The overlap by native-dominants covered at least 69% of the response curve of *A. pseudoplatanus* and 61% of *R. ponticum* (Table 3b). *A. pseudoplatanus* overlapped 36% of *R. ponticum* band 61% of *R. ponticum* (Table 3b). The relationship between the two neophytes was non-symmetric with 36% of the response of *A. pseudoplatanus* overlapped by *R. ponticum* yet almost 100% of *R. ponticum* was overlapped by *A. pseudoplatanus* (Table 3b).

The overlap of the native-dominants/neophytes with woodland specialist species that fell into the high-impact Class V (overlapped >80% of their range) are highlighted in E.Appendix I. There were more than 75 of the woodland specialists in this high-impact Class V for three of the native dominants (*H. helix*, *R. fruticosus*, *P. aquilinum*); for *M. perennis* and *U. dioica* there were between 46-51 and for the neophytes there were 49 and five for *A. pseudoplatanus* and *R. ponticum* respectively.

1   **Discussion**

2   Where productive species grow well then there is likely to be a suppression of species

3   diversity, particularly of the many slow-growing species that are often found in places

4   with the greatest diversity (Grime 1979). Therefore, the overall high mean cover of

5   three of the proposed native-dominant species, both in the NVC tables and in the

6   analysis of the NWS, suggests that Pearman's hypothesis that they could be affecting

7   species richness is reasonable (Pearman 2004, Pearman & Lockton 2004; Marrs *et al*.

8   2010). The addition of *M. perennis*, an indicator of ancient woodlands (Hermy *et al*.

9   1999; Honnay *et al*. 1998), may seem less obvious but Pigott (1977) showed that

10   removal of *M. perennis* shade was followed by a marked increase in growth of

11   *Hyacinthoides non-scripta* and *Primula vulgaris*. However unlike *H. helix*, *U. dioica*

12   and *R. fruticosus*, it has a very poor mobility (Peterken & Game 1981), which limits

13   its ability to invade and hence become dominant in recently created woodland

14   (Rodwell 1991). Little is known about the spread of *P. aquilinum* under current

15   conditions, except that regeneration through sexual reproduction is relatively

16   uncommon (Marrs & Watt 2006), and hence spread is likely to be localised via

17   vegetative means.

18   Nevertheless, *P. aquilinum*, *R. fruticosus* and *Hedera helix* all occur at a high

19   frequency, both under canopy, where they often form mono-specific stands capable of

20   depressing field-layer vegetation and seedling regeneration (e.g. Fotelli *et al*. 2002;

21   Marrs & Watt 2006; Metcalfe 2005; Phelouzat & Levacher 1981), and outside of the

22   shaded woodland environment. In these open locations, for example in glades or

23   clear-fells, they may exhibit great vigour (Marrs & Watt 2006; Metcalfe 2005;

24   Phelouzat & Levacher 1981), and hence strong competition with other woodland

25   species (McAllister & Rutherford 1990; Kirby & Woodell 1998; Pakeman & Marrs

1992). In favourable conditions, the foliage of *P. aquilinum* and *R. fruticosus* can reach 2-4 m (Marrs & Watt 2006; Taylor 2005), while in western coastal areas, the tetraploid ivy, *H. helix* ssp. *hibernica*, is capable of successfully competing with both *P. aquilinum* and *R. fruticosus* (McAllister & Rutherford 1990). *U. dioica* was retained as a weak-dominant species in this study to be consistent with Pearman (2004) and Pearman and Lockton (2004) as it has the potential to expand, but it has a much lower mean cover across GB (Marrs *et al.* 2010) and is overlapped by the others to a large extent.

We present these initial results as a baseline study. The realized niche has been obtained only with respect to the first axis of the DCA alone, and niche separation of the species would be expected to occur with respect to factors that are represented on other axes. While this is a valid criticism in determining niche separation to determine diversity the first axis presented here does represent a coenocline through the entire woodland resource of Great Britain and the major axis of variation. A further criticism is that at least three of the native-dominant species show some form of sub-specific variation below the taxonomic level assessed during the survey: *H. helix* is known to consist of at least two sub-species *H. helix* ssp. *helix* and ssp. *hibernica,* the genus *Pteridium* has recently been revised and several varieties of *P. aqulinum* ssp. *aquilinum* have been described in GB (reviewed, Marrs & Watt 2006*)* and the apomictic *R. fruticosus* aggregate comprises a complex of closely-related taxa across Europe (Gilli 1986; Matzke-Hajek,1993, 1997). Unfortunately, it was not possible to assess the impact of this level of variation in this study as the taxonomy identification within the NWS was not performed at an appropriate scale. Further consideration of the importance of this variation in ecological terms is sorely needed.

In the initial analyses of the NWS dataset, the 'native-dominant' species were included in the DCA analysis, and as the most frequency and dominant species (Corney *et al.* 2006; Marrs *et al.* 2010) might be expected to be influential in determining this axis (Lawesson & Oksanen 2002). Hence, here the DCA analysis has been re-run without the native dominants species to remove their influence. When this was done the results were essentially the same.

The NVC tables and the HOF model species response curves indicate that the five native-dominant species considered are capable of dominating the local flora, achieving very high rates of cover relative to other field-layer species, and frequently developing mono-specific stands where other vegetation is excluded. Four of these species (*H. helix*, *M. perennis*, P. *aquilinum*, *R. fruticosus*) show clear sequential niche separation across the primary coenoclinal woodland gradient in the UK (Hypothesis 1 accepted). The response range areas of these native-dominants almost entirely overlapped, or completely covered, the ranges of all other field-layer species. These species may, therefore, have the potential to respond to any change in the abundance of the native-dominants, either as a result of a changes in amplitude of the niche (increased intensity in mid range) or as a result of a change in niche width (niche range expansion). This could affect the field layer species positively, including the potential for niche width expansion (Bolnick *et al.* 2010), if the 'native dominants' were to be reduced in abundance, or negatively if they increase. The two neophytes did not appear to fit neatly between the native dominants, both peaking under *R. fruticosus*. *A. pseudoplatanus*, the species with the longer history in GB has a relatively wide niche compared to the relatively recent *R. ponticum*.

Our methodology provides an objective assessment of the species likely to be impacted by each of the 'native dominants' species at the countrywide scale at the

1   time of survey. It can also be used to assess future change in niche size and range

2   status of both native and alien species. Thus, hypothesis 3 is accepted, but requires

3   further observations to determine its relevance with respect to changing impacts

4   through time.

5   Whilst HOF models provide a robust mathematical means of describing species

6   relationships, they do not identify the factors that may be driving those relationships,

7   for example resource availability, physiological adaptations or limitations,

8   competitive interactions with other organisms and human interference. Variations in

9   these factors may also help explain how despite the abundance and competitive ability

10   of these five species a wide range of woodland ground flora species are able to co-

11   exist with them (Table 1b). Thus, *M. perennis* is sensitive to trampling (Rodwell

12   1991) or equivalent disturbance such as falling branches which may break up stands

13   and allow other species to co-exist; full canopy cover of *P. aquilinum* does not

14   develop till mid-summer so vernal species such as *H. non-scripta* can grow and

15   flower unshaded; *R. fruticosus* and *H. helix* are both favoured browse species such

16   that a degree of grazing may reduce their competitive ability (Kirby 2001). *U. dioica*

17   is known to have a high phosphorus requirement (Pigott & Taylor 1964), and it is

18   possible that its potential to dominate is reduced by low soil fertility. The patchy

19   nature of the woodland environment in terms of light availability, soil conditions and

20   disturbance factors are thus critical in maintaining species diversity at local scales in

21   woodland.

22   Increased homogenisation of the environment might lead to increased potential for

23   dominance by one or other of these species, enhancing biotic homogenization (Smart

24   *et al.* 2006). A clear signal of increased eutrophication has been detected recently

1 within the flora of the British countryside (Smart *et al.* 2005, 2010); although not so

2 clear for undisturbed European woodlands (Verheyen *et al.* 2012).

3   Other types of models have considered the likely response of different woodland

4 species under the various climate change projections as part of the BRANCH project

5 (Hayhurst *et al.* 2007). Of the five 'native dominants' *R. fruticosus* appears to be the

6 most sensitive with a potential major loss of climate niche space by 2080; smaller

7 losses of climate space in eastern and southern England may occur for *U. dioica* and

8 *M. perennis*, but the whole of GB remains within the climate envelope for *H. helix*

9 and *P. aquilinum*. If these projections prove correct then there could significant

10 changes in the balance of British ground flora because of changes in competition from

11 these native dominants but particularly the reduced competitiveness of *R. fruticosus*,

12 irrespective of the direct effects of climate change on the individual species. However,

13 removal of one or more of the current set of dominants might just clear the way for

14 another set of species with similar traits (Smart *et al.* 2006).

15   Much of the concern about invasive species is that they become over-dominant in a

16 community. Identifying mechanisms by which species cope with dominance by native

17 species may provide pointers to how rich communities may be maintained in the face

18 of future increases in invasive aliens but also likely changes in abundance of native

19 species under changing future environmental conditions

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Table 1 The distribution of the five native-dominant species within the National Vegetation Classification (Rodwell 1991): (a) number of records for different frequency scores for the five species and for all vascular plant species in the NVC woodland community tables: frequency scores represent: 1 = present in 5-20% of samples; 2= present in 21-40%; 3 = present in 41-60%; 4 = present in 61-80%; 5 = present in 81-100% of samples for a community. (b) Frequency classes for each NVC woodland community for each native-dominant species and the number of vascular plants listed from the NVC woodland communities sampled in this study. W1, W2, W3, W18, and W20 were not sampled in the NWS survey.

(a)

Frequency score	1	2	3	4	5
All species, all communities	1037	205	101	43	20
Hedera helix	12	5	2	1	0
Mercurialis perennis	7	2	1	2	1
Rubus fruticosus	5	6	3	4	4
Pteridium aquilinum	6	1	5	3	1
Urtica dioica	6	5	4	1	0
% of total records	3.5	9.3	14.9	25.6	30

(b)

Community number	Woodland community name	*Mercurialis perennis*	*Hedera helix*	*Urtica dioica*	*Rubus fruticosus*	*Pteridium aquilinum*	No of vascular plants (no of samples)
W13	*Taxus baccata*	3	1	1	1		15(22)
W12	*Fagus sylvatica–Mercurialis perennis*	4	3	1	3		65(109)
W9	*Fraxinus excelsior–Sorbus aucuparia–Mercurialis perennis*	4	1	1	1	1	86(117)
W8	*Fraxinus excelsior– Acer campestre –Mercurialis perennis*	5	3	2	4	1	108(425)
W21	*Crataegus monogyna – Hedera helix*	2	4	3	4	1	54(115)
W22	*Prunus spinosa – Rubus fruticosus*	1	2	2	3	3	40(49)
W24	*Rubus fruticosus – Holcus lanatus*	2	2	3	5		68(39)
W6	*Alnus glutinosa – Urtica dioica*	1		4	3		64(58)
W5	*Alnus glutinosa – Carex paniculata*		1	3	4		83(107)
W10	*Quercus robur – Pteridium aquilinum – Rubus fruticosus*	1	2	1	4	4	79(379)
W14	*Fagus sylvatica – Rubus fruticosus*	1	2	1	5	3	44(49)
W7	*Alnus glutinosa – Fraxinus excelsior–Lysimachia nemorum*	1	1	2	2	1	84(102)
W25	*Pteridium aquilinum–Rubus fruticosus*	1	1	3	5	5	44(54)
W23	*Ulex europaeus–Rubus fruticosus*		1		5	3	36(32)
W4	*Betula pubescens–Molinia caerulea*		1		2	1	51(72)
W15	*Fagus syvatica – Deschampsia flexuosa*		1		2	3	22(59)
W16	*Quercus spp – Betula spp – Deschampsia flexuosa*		1		2	4	32(149)
W17	*Quercus petraea – Betula pubescens – Dicranum majus*		1		1	3	54(303)
W19	*Juinperus communis – Oxalis acetosella*	1		1		2	56(69)
W11	*Quercus petraea – Betula pubescens – Oxalis acetosella*				1	4	64(139)
W1	*Salix cinerea – Galium palustre*		2		2		47 (38)
W2	*Salix cinerea – Betula pubescens – Phragmites australis*		1	2	2		65(44)
W3	*Salix pentandra – Carex rostrata*		1	2	1		67 (18)
W18	*Pinus sylvestris – Hylocomium splendens*					1	23(77)
W20	*Salix lapponum – Luzula sylvatica*						55(19)

Table 2. Parameters of the selected unimodal HOF models selected for the native-dominants along the coenoclinal axis (DCA axis 1) of the National Woodland Survey of Great Britain field-layer cover data in 1971: Model type; IV = symmetric, V = skewed; maximum point is the maximum cover modelled, optimal point is the distance on the coenocline the maximum point occurred and the Gaussian tolerance range has been calculated as the Optimal point ± the tolerance ranges (Lawesson & Oksanen 2002).

Species	Model type	Maximum point	Optimal point on coenocline	Tolerance range on coenocline	
				Minimum	Maximum
Mercurialis perennis	IV	0.427	-2.246	-2.883	-1.609
Urtica dioica	V	0.056	-1.862	-2.391	-0.173
Acer pseudoplatanus	IV	0.004	-0.333	-2.022	1.356
Rubus fruticosus	V	0.163	-0.062	-1.677	0.136
Rhododendron ponticum	V	0.004	0.067	-0.131	0.067

Table 3. Mutual pair-wise overlap in niche response range area of the native-dominant and neophyte species along the coenoclinal axis (DCA axis 1) of the National Woodland Survey of Great Britain field-layer cover data in 1971. (a) Overlaps between native-dominants; shaded boxes show contrasting responses: *U. dioica* overlaps 33% of the range of *M. perennis* whereas *M. perennis* overlaps 100% of the range of *U. dioica*. Overlapping mean = the degree to which the niche of this species overlaps the niches of the other four species; the Overlapped mean = the degree to which the niche of this species is overlapped by the other four species. (b) Overlap between neophytes species and the five native-dominant species.

(a)

	Hedera helix	*Mercurialis perennis*	*Urtica dioica*	*Rubus fruticosus*	*Pteridium aquilinum*	Overlapped Mean
Hedera helix	NA	83.5	32.7	81.1	30.4	56.9
Mercurialis perennis	35.2	NA	13.8	33.6	6	22.1
Urtica dioica	100	100	NA	100	28.5	82.1
Rubus fruticosus	40.4	39.8	16.3	NA	38.6	33.8
Pteridium aquilinum	12.6	5.9	3.9	32.1	NA	13.6
	47.0	57.3	16.6	61.7	25.9	-

(b)

Focal species	Niche range of neophyte species which is overlapped by focal species range		Niche range of neophyte species that overlaps the focal species range	
	A. pseudoplatanus	*R. ponticum*	*A. pseudoplatanus*	*R. ponticum*
Hedera helix	100	100	5.9	2.2
Mercurialis perennis	75.3	60.8	1.9	0.6
Urtica dioica	68.9	45.7	12.5	3
Rubus fruticosus	100	100	3	1.1
Pteridium aquilinum	100	100	2.5	0.9
Acer pseudoplatanus	-	99.8	-	36.2
Rhododendron. ponticum	36.2	-	99.8	-
	80.1	84.4	19.3	7.5
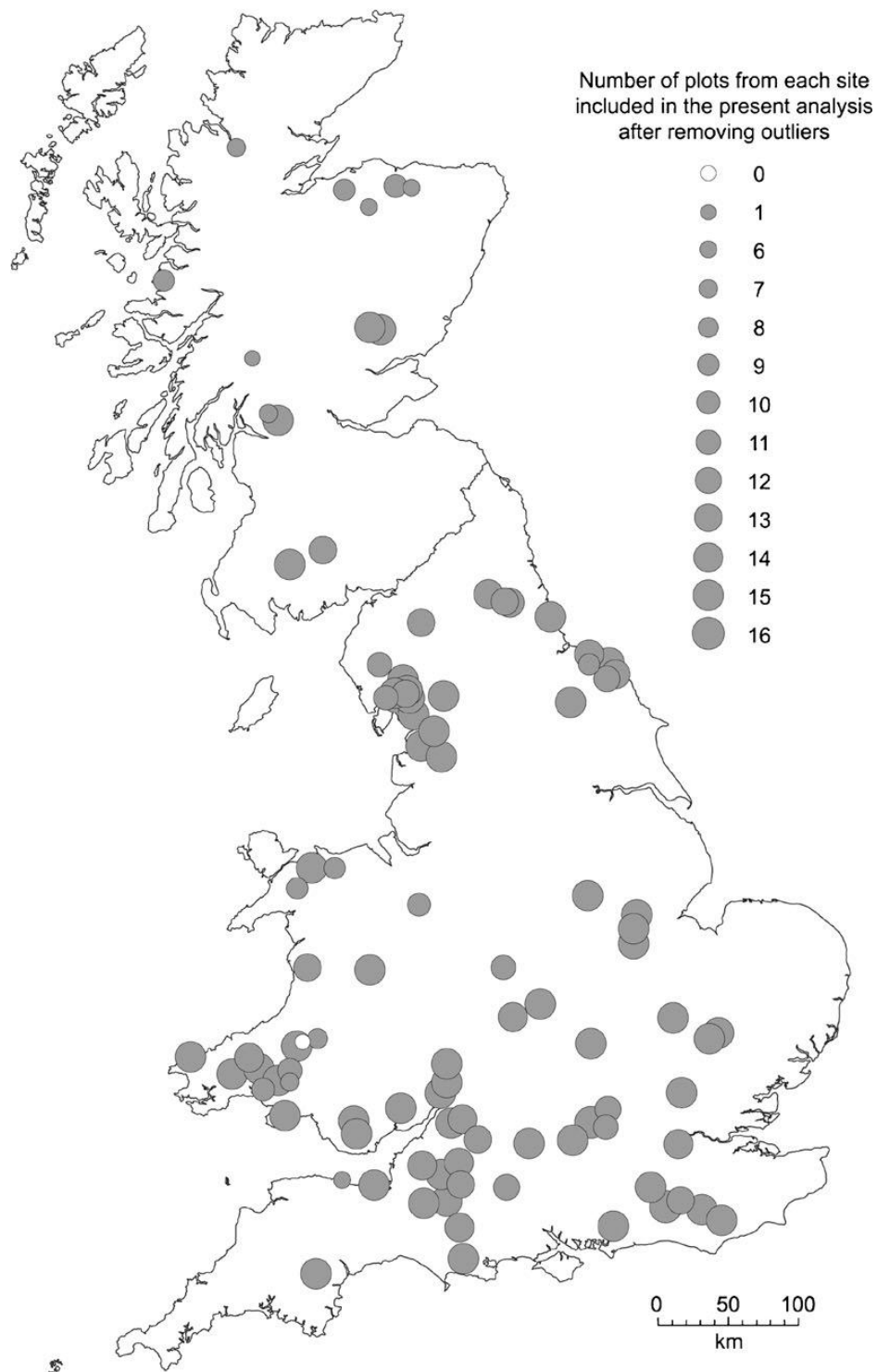
Figure 1 Distribution of sites surveyed in the 1971 National Woodland Survey (NWS) of Great Britain. Circle size represents the number of plots from each site included in the present analysis after removing outliers (adapted from Corney *et al*. 2006).

Fig.2. Hypothetical diagram outlining the measurement of niche overlap; the area under the curve for species 1 (a+o) and species 2 (b+o) are calculated by integration along with the overlapped area (o). The proportion of species 1 niche overlapped by species 2 = o/(o+a) and the proportion of the species 2 overlapped by species 1 = o/(o+b) (adapted from Lawesson & Oksanen 2002).

(a)

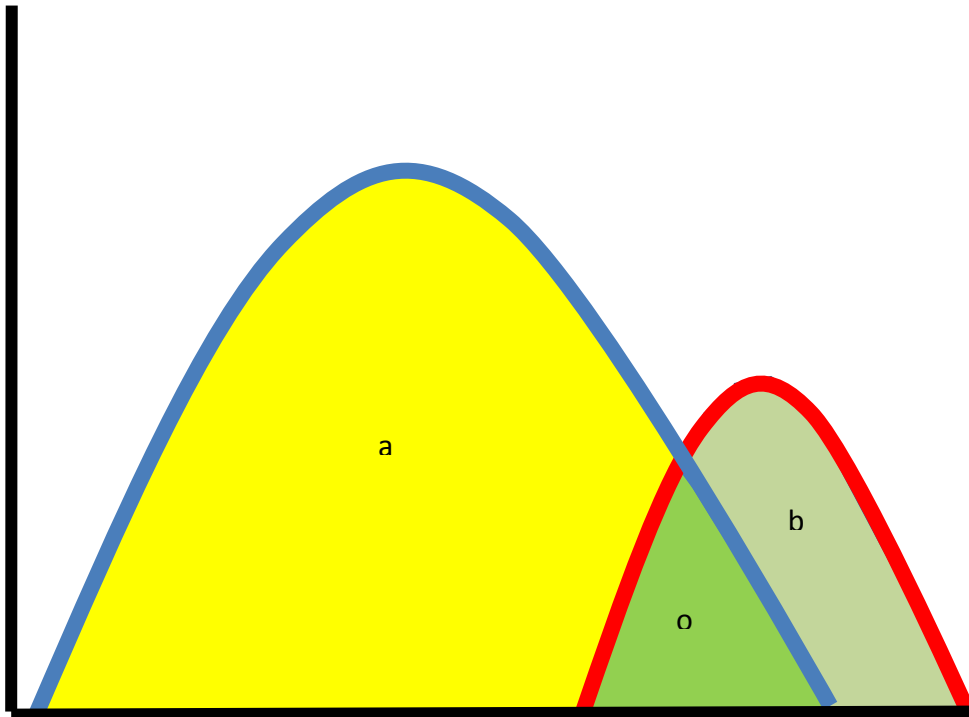**Figure 3 DCA plot produced from analysis of 1438 plots in the National Woodland Survey of Great Britain in 1971. Plots of (a) the 62 most abundant species and (b) the six most significant environmental variables are shown. Species abbreviations follows Hill (1996) and are coded: Woodland specialists = ■; Geographically-restricted woodland specialists = □ ;Other woodland and non-woodland species = X; a full species list is available Corney *et al*. 2006).**

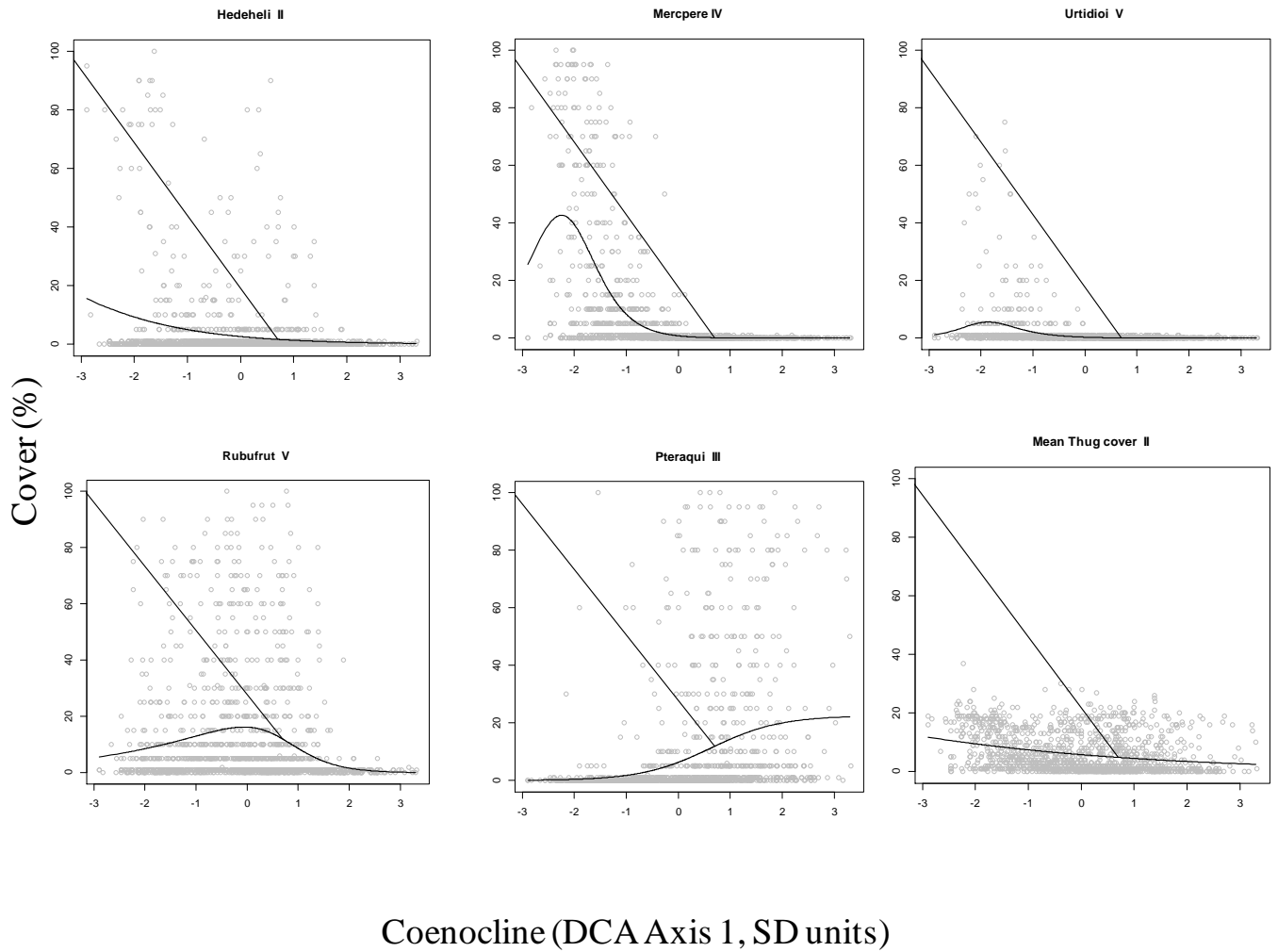**Figure 4 HOF response curves for the four native-dominant species and the averaged response of all five species in the National Woodland Survey of Great Britain in 1971. Species codes: Hedeheli = *Hedera helix*, Mercpere = *Mercurialis perennis*, Pteraqui = *Pteridium aquilinum*, Rubufrut = *Rubus fruticosus* agg., Urtidioi = *Urtica dioica*. Significant fitted HOF model types coded as II, III, IV, V.**
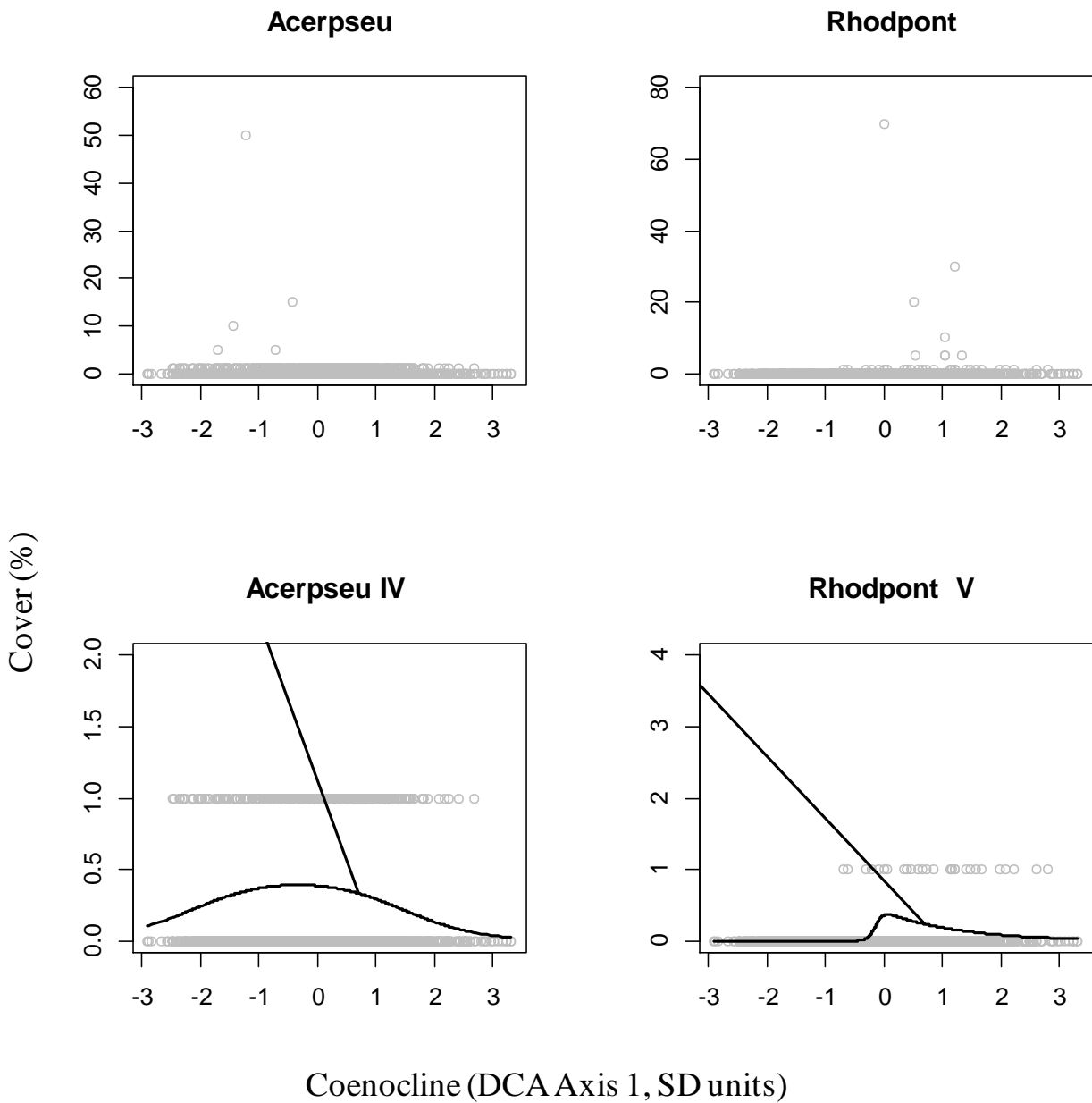
Figure 5 HOF response curves for the two neophyte species in the National Woodland Survey of Great Britain in 1971. Species codes: Acerpseu = *Acer pseudoplatanus*, **Rhodpont =** *Rhododendron ponticum*. **Significant fitted HOF model types coded as IV, V. The upper graphs show the entire response and the lower ones illustrate a reduced axis and the fitted lines**.

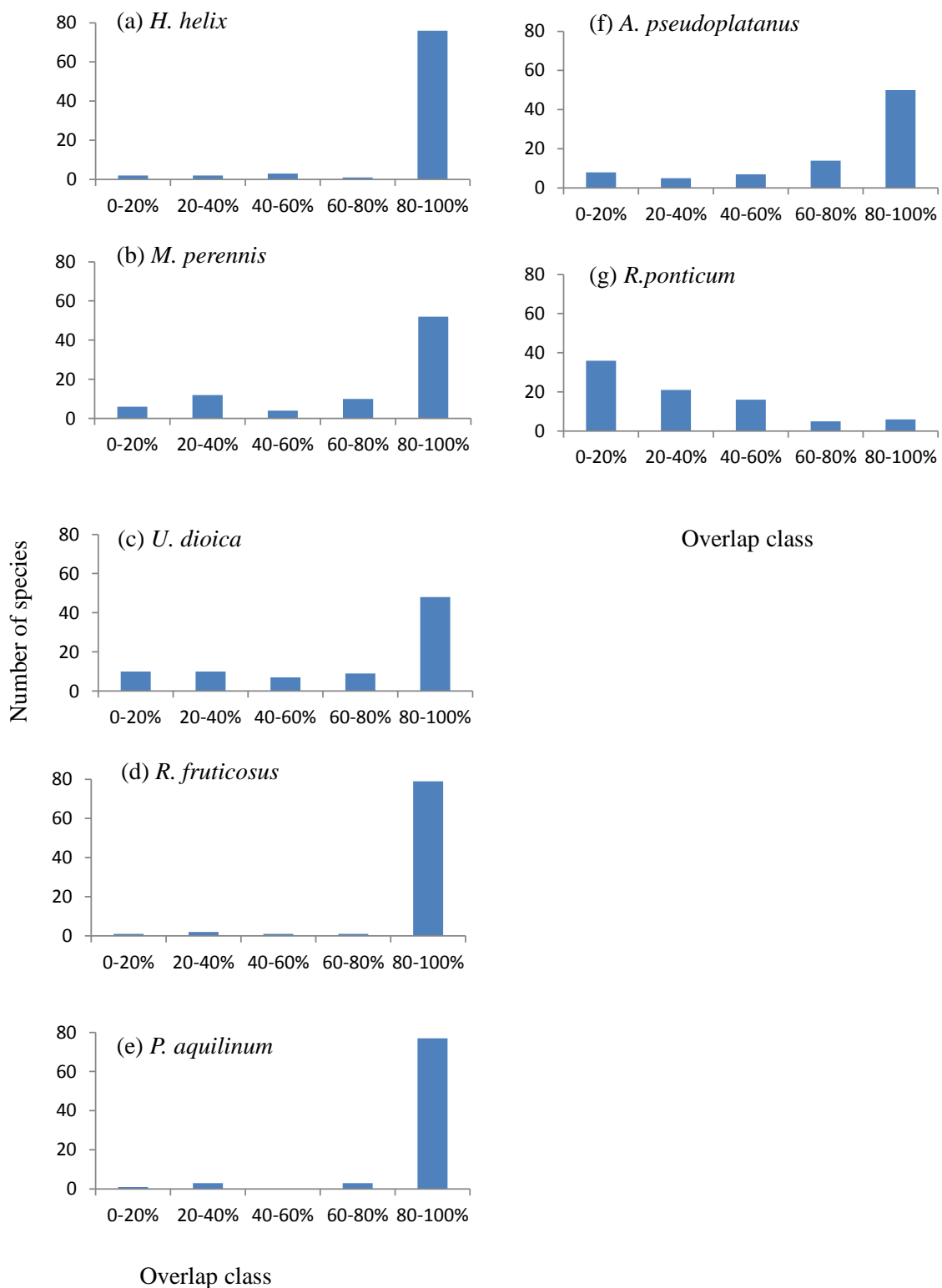**Figure 6 The number of woodland specialist species that are overlapped by the native-dominant and neophyte species derived from HOF species response curves fitted to the primary coenocline of a DCA analysis of the National Woodland Survey of Great Britain in 1971. Species have been grouped into classes <20%, 20-40%, 40-60%, 60-80%, 90-100% of their realized niche that is overlapped by the native-dominant\neophyte.**

E-Appendix I. Woodland specialist species where >80% of the niche range (Impact class = V) is overlapped by a focal native-dominant/neophyte species.

Woodland specialist species	Focal species							Total
	H. helix	*M. perennis*	*U. dioica*	*R. fruticosus*	*P. aquilinum*	*A. pseudoplatanus*	*R. ponticum*	
Equisetum sylvatica	✓	✓	✓	✓	✓	✓	✓	7
Phyllitis scolopendrium	✓	✓	✓	✓	✓	✓	✓	7
Stachys sylvatica	✓	✓		✓	✓	✓	✓	7
Acer campestris	✓	✓	✓	✓	✓	✓		6
Allium ursinum	✓	✓	✓	✓	✓	✓		6
Bromopsis ramosa	✓	✓	✓	✓	✓	✓		6
Campanula trachelium	✓	✓	✓	✓	✓	✓		6
Carex pendula	✓	✓	✓	✓	✓	✓		6
Carex remota	✓	✓	✓	✓	✓	✓		6
Carex sylvatica	✓	✓	✓	✓	✓	✓		6
Convallaria majalis	✓	✓	✓	✓	✓	✓		6
Crataegus laevigata	✓	✓	✓	✓	✓	✓		6
Elymus caninus	✓	✓	✓	✓	✓	✓		6
Epipactus helliborine	✓	✓	✓	✓	✓	✓		6
Euonymus europaeus	✓	✓	✓	✓	✓	✓		6
Euphorbia amygdaloides	✓	✓	✓	✓	✓	✓		6
Festuca gigantea	✓	✓	✓	✓	✓	✓		6
Fragaria vesca	✓	✓	✓	✓	✓	✓		6
Galium odoratum	✓	✓	✓	✓	✓	✓		6
Geranium robertianum	✓	✓	✓	✓	✓	✓		6
Geum rivale	✓	✓	✓	✓	✓	✓		6
Gymnocarpium dryopteris	✓	✓		✓	✓	✓	✓	6
Hypericum androsaemum	✓	✓	✓	✓	✓	✓		6
Hypericum hirsutum	✓	✓	✓	✓	✓	✓		6
Phegopteris connectilis	✓	✓	✓	✓	✓	✓		6
Polygonatum multiflorum	✓	✓	✓	✓	✓	✓		6
Potentilla sterilis	✓	✓	✓	✓	✓	✓		6
Primula elatior	✓	✓	✓	✓	✓	✓		6
Sanicula europaea	✓	✓	✓	✓	✓	✓		6
Scrophularia nodosa	✓	✓	✓	✓	✓	✓		6
Stachys sylvatica	✓	✓		✓	✓	✓	✓	7
Ulmus glabra	✓	✓	✓	✓	✓	✓		6
Veronica montana	✓	✓	✓	✓	✓	✓		6
Viburnum opulus	✓	✓	✓	✓	✓	✓		6
Vicia sepium.	✓	✓	✓	✓	✓	✓		6
Arum maculatum	✓	✓	✓	✓	✓			5
Ceratocapnos claviculata	✓			✓	✓	✓	✓	5
Cornus sanguinea	✓	✓	✓	✓	✓			5
Melica uniflora		✓	✓	✓	✓	✓		5
Paris quadrifolia	✓	✓		✓	✓	✓		5
Polystichum aculeatum	✓	✓		✓	✓	✓		5
Primula vulgaris	✓	✓	✓	✓	✓	✓		5
Prunus avium	✓		✓	✓	✓	✓		5
Prunus padus	✓		✓	✓	✓	✓		5
Rubus saxatilis	✓	✓		✓	✓	✓		5
Silene dioica	✓	✓	✓	✓	✓			5

Species								
Anemone nemorosa	✓			✓	✓	1		4
Brachypodium sylvaticum	✓	✓		✓	✓			4
Chrysosplenium oppositifolium	✓	✓		✓	✓			4
Conopodium majus	✓			✓	✓	✓		4
Corylus avellana	✓			✓	✓	✓		4
Iris foetidissima	✓	✓	✓	✓				4
Lamiastrum galeobdolon	✓	✓	✓	✓				4
Lathyrus linifolius	✓			✓	✓	✓		4
Listera ovata	✓	✓	✓	✓				4
Moehringia trinervia	✓			✓	✓	✓		4
Polypodium vulgare	✓		✓	✓	✓			4
Rosa spp.	✓	✓		✓	✓			4
Solidago virgaurea	✓		✓	✓	✓			4
Stellaria holostea	✓		✓	✓	✓			4
Tamus communis	✓	✓		✓	✓			4
Valeriana officinalis	✓			✓	✓	✓		4
Athyrium filix-femina	✓			✓	✓			3
Blechnum spicant	✓			✓	✓			3
Hyacinthoides non-scripta	✓			✓	✓			3
Hyacinthoides non-scripta	✓			✓	✓			3
Hypericum pulcrum	✓			✓	✓			3
Ilex aquifolium	✓			✓	✓			3
Lonicera periclymenum	✓			✓	✓			3
Luzula sylvatica	✓			✓	✓			3
Lysimachia nemorum				✓	✓	✓		3
Oreopteris limbosperma	✓			✓	✓			3
Oxalis acetosella	✓			✓	✓			3
Holcus mollis		✓		✓				2
Luzula pilosa				✓	✓			2
Melampyrum pratense	✓				✓			2
Quercus spp.	✓				✓			2
Milium effusum	✓							1
Sorbus aucuparia					✓			1
Vaccinium myrtillus					✓			1
Total number of species	72	50	40	73	73	49	5	