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Are native bluebells (*Hyacinthoides non-scripta*) at risk from alien congenerics? Evidence from distributions and co-occurrence in Scotland

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ABSTRACT

The UK has the highest density of the worldwide distribution of its native bluebell, *Hyacinthoides non-scripta* (Liliaceae), and the prevalence of alien bluebells (hybrids or 'Spanish') has been interpreted as an urgent threat. To assess the potential for competitive and hybridising interactions between natives and alien taxa in the UK, we quantified abundance and co-occurrence in south-central Scotland in relation to physical variables, land cover, and habitat types. To do this we tested the influence of explanatory variables on incidence rates, densities and group sizes at three spatial scales (10 km, 1 km, and records) in selected 10-km squares. We found that (1) natives were nearly 99% of all bluebells recorded, (2) aliens were encountered more frequently than natives though in much smaller maximum numbers per group, (3) increasing rainfall was associated with increasing native and decreasing alien densities, (4) the presence of aliens related to variables correlated with human density, and (5) there was little evidence for habitat exclusivity. Mixed groups accounted for 10% of natives recorded, and over 40% of natives grew within about one kilometre of aliens. These distributions suggest that a high proportion of natives lie within range of potential gene flow via insect pollinators.

1. Introduction

The bluebell *Hyacinthoides non-scripta* (L.) Chouard ex Rothm. is a native lily that holds iconic status in the British Isles. The species is distributed along the coast of western Europe from the Netherlands to northern Spain, but an estimated 25–50% of the world's population is found in the British Isles (Ingrouille, 1995). Though ubiquitous on the scale of 10-km squares (Preston et al., 2002), in 1998 it was listed as specially protected under the Wildlife and Countryside Act (WCA, 1981) in response to commercial over-exploitation; historically populations have also been threatened by land use change and grazing.

More recently, threats posed by introduced and horticultural varieties of bluebell, *Hyacinthoides hispanica* (Mill.) Rothm. and its hybrid with the native *Hyacinthoides x massartiana* Geerinck, have received increasing attention (Pilgrim and Hutchinson, 2004). Both alien taxa have naturalised and the hybrid especially is now widespread (Page, 1987; Preston et al., 2002). The primary conservation concerns include the

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risk that the generally larger alien taxa will outcompete and replace natives as well as the possibility of hybridisation and the loss of genetic integrity of the native species in the UK (Huxel, 1999; Pilgrim and Hutchinson, 2004). Yet to date, reliable data for quantifying these risks have been unavailable (Pearman, 2004; Crawley, 2005; Dines, 2005), and there is a clear need to assess the extent to which *Hyacinthoides* taxa actually and potentially co-occur in the UK.

Co-occurrence on the relevant scale is prerequisite for both competitive and hybridising interactions. This study aimed to determine the distribution of native and alien bluebells on multiple spatial scales using south-central Scotland as a focal region, to address the following questions: (1) How widespread and abundant are alien bluebells, compared to natives? (2) To what extent do natives and aliens co-occur? (3) Are aliens primarily associated with anthropogenic habitats? and (4) Do natives and aliens occupy similar or different niches with respect to climate and habitat? Answers to these questions would provide a basis for understanding the scale and urgency of a threat to the UK's native bluebells.

2. Materials and methods

2.1. *Bluebell taxa and identification*

Alien and native bluebells are spring-flowering, bulbous perennials. The native, *H. non-scripta,* can reach high densities in deciduous woodlands, preferring slightly acidic soil. Reproduction is both by seed and by bulb division (Blackman and Rutter, 1954; Wilson, 1959). It is said to have no (Blackman and Rutter, 1954) to some (Corbet, 1998) self-compatibility, with insect pollinators consisting mainly of *Bombus* species and syrphids. The bulb is entirely renewed annually and as a result flowering and plant size are sensitive to drought and leaf loss experienced in the previous year (Blackman and Rutter, 1954; Littlemore and Barker, 2001). Seeds have no apparent adaptations for dispersal (Knight, 1964) and no dormancy detected beyond the ability to survive their first winter (Thompson and Cox, 1978; Thompson and Grime, 1979). Germination in late autumn responds to seed conditioning at high temperatures followed by a gradual drop in temperature to 11 °C or less (Thompson and Cox, 1978). Seedling survival and establishment are facilitated by mycorrhizal associations (Merryweather and Fitter, 1995).

Non-native bluebells in Britain are highly variable and little is known of their ecological requirements. Turrill (1952) noted that *H. hispanica* "becomes well established under many conditions" in the UK while the hybrid is said to occur wherever the two species meet (Turrill, 1951). However, in addition to spontaneous hybrids, popular commercial cultivars probably represent the source of most alien bluebells in the UK.

Although two alien *Hyacinthoides* taxa occur in the UK, the present survey classified bluebells only as native or alien. Several published keys distinguish two or three taxa (Sell and Murrell, 1996; Rich and Jermy, 1998; Rix, 2004), but in practice classification could be extremely difficult. In this study, to be classed as native bluebells had to possess tubular (parallel-sided) flowers, unilateral inflorescences nodding at the tip, cream-coloured pollen, leaf width <2 cm, and anther heights conspicuously different from each other. Together these criteria accord with accepted field markers for *H. non-scripta*. Any plants not fitting the native description were classed as aliens.

2.2. *Sampling strategy and dependent variables*

A stratified random sampling design was adopted to survey the distribution and abundance of native and alien bluebells. Three transects comprising 17 10-km × 10-km squares (hectads) were chosen (Fig. 1). Two transects each of 5 hectads, running 90 km north–south in western and eastern Scotland, were centred on major cities (Glasgow or Edinburgh) to test the hypothesis of alien dependence on humans while reducing within-transect climate variation. The third transect of 7 hectads ran 190 km east–west to cover the range of temperature and rainfall variation in this part of the UK. Hectads were spaced 10–20 km apart except where the crossing of the east–west and the north–south transects resulted in adjacent hectads being selected. The samples represent a wide range of land uses, climates and anthropogenic impacts (Table 1).

Each hectad was divided into 100 1-km × 1-km cells and 10 of these were selected at random for detailed ground-based survey carried out during flowering in May. A random grid reference in each selected 1-km cell became the starting point for bluebell searches. All bluebells encountered in the course of searches were counted. Because flowers were required for identification, abundance was measured as the number of scapes (erect leafless flower stems growing directly from the ground) even where these likely arose from single genetic individuals.

The search for bluebells was not random but targeted likely bluebell habitats such as woodlands, riparian areas and road verges. Search effort was measured as distance walked in kilometres. Searches were terminated when likely habitat had been investigated and bluebell numbers per km search effort were judged to be approximately constant.

When bluebells were encountered, the numbers of scapes of each taxon were estimated as a measure of population size. Each loosely-defined group was represented by a separate record. Small groups (<100 scapes) were counted, whereas in larger groups numbers were estimated from counts of each taxon in a random sample of 0.25 m^2 quadrats multiplied by the approximate total area of bluebells. The precision of estimates decreased with increasing numbers, but order of magnitude differences were practical indications of relative abundance. Analyses were conducted as though counts were accurate since it was not possible to quantify the level of error associated with them (e.g. we might expect the coefficient of variation to increase with increasing abundance, but the relationship is unknown and we have not accounted for it in our subsequent analyses). Data were analysed at three different, nested, spatial scales, expressing different qualities of distributions and allowing the influence of different explanatory variables to be explored. From smallest to largest, these spatial scales were: records (raw data of individual groups), points (summing all records obtained on a search around each randomly-generated point, giving data on a scale of 1 km), and hectads (summing data for all points surveyed within each 10-km square). Note that "points" data derived

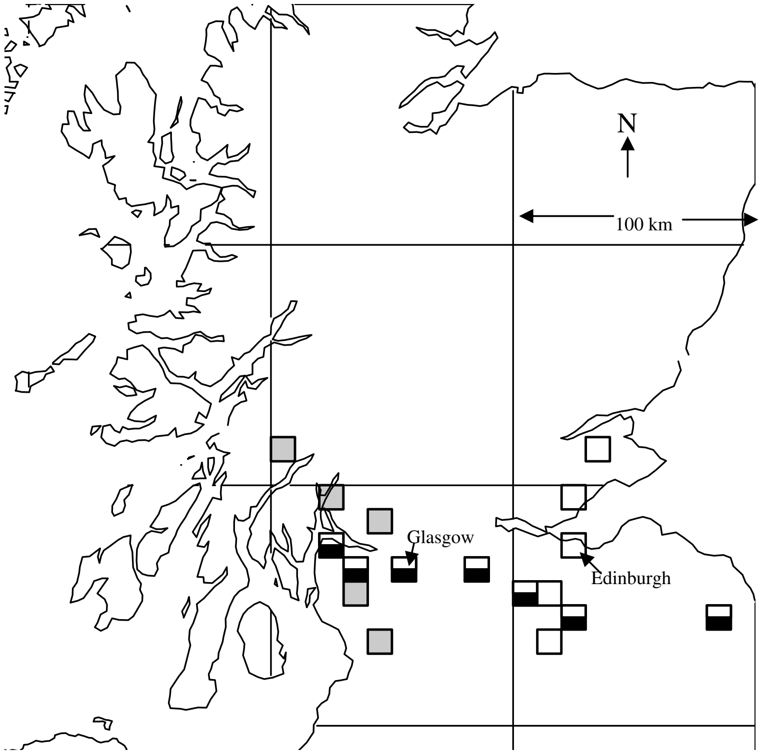

Fig. 1 – Map of the focal area in south-central Scotland. Symbols represent hectads (10-km × 10-km squares) sampled on three transects, two north–south (grey fill in west, white in east) and one east–west (black/white fill). Table 1 summarises climate and land cover attributes.

Table 1 – Attributes of the 17 hectads surveyed. Climate zones varied in rainfall and temperatures. Land cover from LCM (2000).

NGR	Climate zone	Mean elevation, *m* (sd)	% Built	Dominant land cover (%)	2nd Dominant land cover (%)
NN01	West	310 (79.1)	0.07	Heath (58)	Conifer (19)
NS27		157 (127.9)	11.4	Heath (30)	Grass (22)
NS29		277 (172.9)	0.6	Heath (63)	Conifer (18)
NS35		86 (37.5)	6.6	Agriculture (47)	Grass (31)
NS36		120 (41.8)	3.2	Agriculture (36)	Grass (31)
NS43		111 (21.5)	13	Agriculture (70)	Built (13)
NS48		85 (71.3)	0.9	Agriculture (33)	Grass (24)
NS56		27 (12.0)	72	Built (72)	Agriculture (8)
NS86	Central	228 (18.0)	7.1	Agriculture (37)	Grass (18)
NT05		329 (44.5)	0.3	Heath (50)	Bog (16)
NT13		356 (40.7)	0.7	Heath (48)	Agriculture (27)
NT15		382 (98.7)	1.0	Heath (34)	Agriculture (26)
NT24		329 (42.2)	1.4	Heath (36)	Agriculture (27)
NT27	East	46 (23.2)	66.4	Built (66)	Grass (10)
NT29		96 (25.1)	21.8	Agriculture (54)	Built (22)
NO31		69 (30.8)	5.5	Agriculture (79)	Grass (5.5)
NT84		61 (16.2)	0.7	Agriculture (91)	Mixed wood (4)

from irregular areas searched around randomly-generated points rather than from 1-km grid squares.

There were six dependent variables for aspects of abundance. For the hectad (10-km) scale, these were:

(a) the number of points around which each taxon was recorded as present, relative to the total number of points searched (binomial generalised linear model with logit link function) and

(b) the incidence rates of native-only groups, alien-only groups and mixtures, based on the number of records of each group type with search effort distance (log(km)) included as an offset term (a log-linear quasi-Poisson regression model).

On the points (1-km) scale, the response variable was:

(c) the densities of natives and aliens, where present, as log-transformed numbers per km search effort (taxa analysed separately using linear regression).

On the records scale, the response variables considered were:

(d) the frequencies of native-only groups, alien-only groups and mixed groups (analysed using a multinomial regression with logit link function),

(e) estimated numbers of each taxon per group (including mixtures) as log-transformed counts (linear regression), and

(f) the proportion of natives in mixed groups, using the logit of proportion (log(proportion native/(1-proportion native))) as the response variable, rather than the binomial model which could not satisfactorily accommodate the degree of overdispersion (linear regression).

2.3. *Independent variables*

Each group was associated with an elevation (metres), spatial location (distance east and north from a fixed point southwest of all hectads), a habitat type (20 recorded: acid grassland, bog, bracken, coastal deciduous woodland, coastal grassland, coniferous woodland, deciduous woodland, deciduous hedge, riparian deciduous woodland, deciduous scrub, garden, heather, mixed woodland, riparian, road, ruderal, semi-natural grass, tall herb, track, and unimproved grassland), one of nine aspects (eight compass directions plus level ground), a ground cover type (10 recorded: bare, bracken, deciduous scrub, grass, heather, litter, moss/ferns, riparian, semi-natural grass, and tall herb), and one of three light levels (open, light shade, shade). Bracken, heather, riparian, semi-natural grass and tall herb were classes in both the habitat and the ground cover variables. Each record was scored in terms of the presence or absence of buildings, gardens, roads, etc. within 25 m.

Randomly-generated points were characterised by assigning a broad habitat type to a circle 50 m in diameter (10 habitat types: agricultural, bracken, built, coastal, conifer, grassland, heath, mixed woodland (including deciduous), tall herb/semi-natural grass, and 'other', which included the infrequent types bog, open water, waste and ruderal). For hectads, habitat data were derived from the Land Cover Map 2000 (LCM 2000) as total area in hectares occupied by 19 land cover types, amalgamated into eight classes (agricultural (arable + improved grassland), bracken, built, coniferous woodland, grassland (neutral + calcareous), heath (acid grass + shrub heath), mixed woodland (including deciduous), and wet (bog + fen + inland water)). The proportion of habitat types at random points and of land cover types within hectads provided two measures of resource (habitat) availability (see paragraph 4, Section 2.4).

Climate data were available as 40-year averages for 5-km × 5-km squares (Meteorological Office, 2005). Climate variables were therefore tested at the point (1-km) scale using values for the 5-km × 5-km square in which the points fell, and at the hectad (10-km) scale by weighting for the number of points in each constituent 5-km square. Distributions with respect to climate were assessed by testing abundances against thirteen rainfall and temperature variables selected a priori for their possible effects on performance at key life stages (Table 2). Rainfall data for different months were highly correlated ($r > 0.98$, df = 15, all $p < 0.001$) as were the selected monthly minimum temperatures, including frost days ($|r| > 0.93$, $p < 0.001$). The correlation between January minimum and July maximum temperatures was 0.47 ($p = 0.06$), and correlations between any one rainfall and one temperature variable were weaker, with $|r| < 0.45$ and p between 0.07 and 0.94.

The three-level factor for climate zone grouped hectads into west (eight 10-km squares less than 20 km from the west coast), east (4 squares less than 20 km from the east coast) and central (5 squares more than 20 km from either coast). Zones differed in monthly rainfalls (west > central and east; $F_{2,14} = 6.7–11.8$ depending on month, all $p < 0.003$) and monthly temperatures, with lower minimum temperatures in the higher-elevation central zone than east and west ($F_{2,14} = 15.2–35.5$, all $p < 0.001$) and July maximum temperatures higher in the east than in central or west ($F_{2,14} = 3.0$, $p \sim 0.08$).

Table 2 – Climate variables selected for their potential influence on bluebell distributions. Meteorological Office (2005) 40-year averages were tested at the points (1-km) and hectads (10-km) scales.

Life stage	Climate variables
Seedling survival, below-ground growth	January minimum temperature January rainfall January days of frost
Emergence, bolting	March rainfall March days of frost
Flowering, pollination	April minimum temperature May hours of bright sun per day
Seed ripening, bulb renewal	July rainfall July maximum temperature
Bulb movement, seed conditioning	September minimum temperature September mean temperature October rainfall October minimum temperature

2.4. Data, statistical models, and analysis

Each of the four questions was addressed both descriptively and statistically. *P* values associated with a particular term of interest were found using an F or Chi-squared test (or, for the multinomial, a likelihood ratio test) to compare a model in which the term was included against the simpler model in which it was removed. Computations were performed using R version 2.4.0 (R Development Core Team, 2006; Crawley, 2002).

Overall distributions were assessed by relating abundance variables to climate zone, relative location east and north, and elevation. Co-occurrence was assessed descriptively as the percentages of samples and of the total numbers of each taxon that were found together in hectads (10-km scale), on point searches (1-km scale) and in mixed groups (records scale). For points, we tested the number around which neither, one, or both taxa were found as a contingency chi-squared. On the records scale, the proportion of natives in mixed groups was investigated to see if processes producing co-occurrence could be inferred from relationships between relative abundance and explanatory variables.

Anthropogenic influence was tested at the hectad scale using as independent variables the area of built land cover and the minimum distance of the hectad from central Edinburgh or Glasgow. In addition, correlations were examined between these two variables and significant climate and land cover variables, and the independent influences of each on aliens were tested in two-variable models in order to disentangle cross-correlations among drivers. On the 1-km scale, densities of the two taxa were compared for those 24 points with "built" habitat type using a Wilcoxon rank sum test. For records, human influence was assessed by the presence/absence of built structures within 25 m.

Climatic influences were tested for hectads and points, since long-term averages were available on the intermediate scale of 5 km. Habitat associations were tested at all three scales using the three different explanatory variables: area of land cover types in hectads, habitat type at the starting point of point searches, and habitat type occupied by the group (modelled using records in the seven habitat types represented more than 20 times each, which included 81% of all natives and 89% of all non-natives recorded). Habitat specificity, using records data, was evaluated for the two taxa using the index for niche breadth, Levins' B′ (Hurlbert, 1978). B′ quantifies the deviation of observed from expected habitat occupancy given variation in abundance of both the taxa and the habitat types (Hurlbert, 1978)

$$B' = X^2 / \left[A \sum (x_i^2 / a_i) \right] \qquad (1)$$

where X is total abundance of the taxon, *A* is total available habitat, x_i is abundance of the taxon in habitat *i* and a_i is the availability of habitat *i*. Habitat availability derived from two sources, (1) LCM, 2000, as hectares of land cover types in the 17 hectads, and (2) number of occurrences of habitat types at the 170 randomly-generated search starting points.

To see whether combinations of variables better explained abundances than single variables, multiple-variable models were built as follows. At the hectad and points scales, full models containing significant single variables (selecting lowest AIC/highest p value among correlated variables) together with interactions were entered into stepwise selection using the "step" procedure in *R*, which chooses the model with the lowest AIC. For records, models were constructed by "step" beginning with the additive effects of all eight independent variables, omitting interactions due to the absence of data in several interaction classes. Minimal adequate models were then constructed by deleting remaining terms that were not significant at $p < 0.05$.

To account for spatial dependence of points within hectads, we re-ran minimal adequate models for points data as mixed effect models (lmer function in *R*), with hectad as a random effect and the environmental variables as fixed effects. At the records scale, spatial autocorrelation was accommodated in all models by including distance east and north as fixed effects.

Finally, the generality of distributions in south-central Scotland was assessed using an independent data set collected by volunteers for Plantlife in 2003 (Pilgrim and Hutchinson, 2004). Plantlife data comprised over 4500 entries recording location, density (three levels), extent (m^2), identity (native, mixed, Spanish), and one of seven habitat types. Over 5% of entries came from Scotland of which 70% occurred in the same four 100 km squares as our survey. Scotland was compared to the rest of the UK for similarity in (1) frequencies of native, "Spanish", and mixed groups, and (2) group type-habitat type associations.

3. Results

Search effort ranged from 0.1 to 5.8 km per point, with a mean of 1.5 (±0.08) km. Eighteen points were inaccessible; thus analysis includes 425 records from 152 points. Habitat types for unaccessed points were obtained from LCM 2000.

Bluebells were found on 68% of point searches. Aliens were found throughout the east–west and north–south ranges sampled at 52% of points, and natives were found in all but the most eastern hectad at 46% of points (Fig 2a). Median and modal numbers per group were comparable for the two taxa, respectively for aliens around 50 and 10 scapes per record, and for natives 100 and 20 scapes (Fig. 2b). The largest numbers for any single group were on the order of 10^3 for aliens and 10^6 for natives (Fig. 2b). Natives comprised nearly 99% of all bluebells recorded and were far more prevalent in the west than in central and eastern zones whether assessed for records, points or hectads (Table 3). Aliens were significantly associated with low elevations (Table 3) even when controlling for human density (*p* to remove elevation from two-variable models <0.02), while the frequency of exclusively native groups varied more between climate zones than did frequencies of alien-only groups and mixtures (Fig. 2c).

3.1. Co-occurrence

Assessment of co-occurrence was scale dependent: both taxa were found in 94% of hectads, 30% of point searches (45% of points with bluebells), and 21% of records (Fig 3a). Within searches around points, there was a significant positive association between alien and native taxa ($X^2 = 9.9$, df = 1, $n = 152$, $p < 0.01$). Mixed groups contained 10% of all

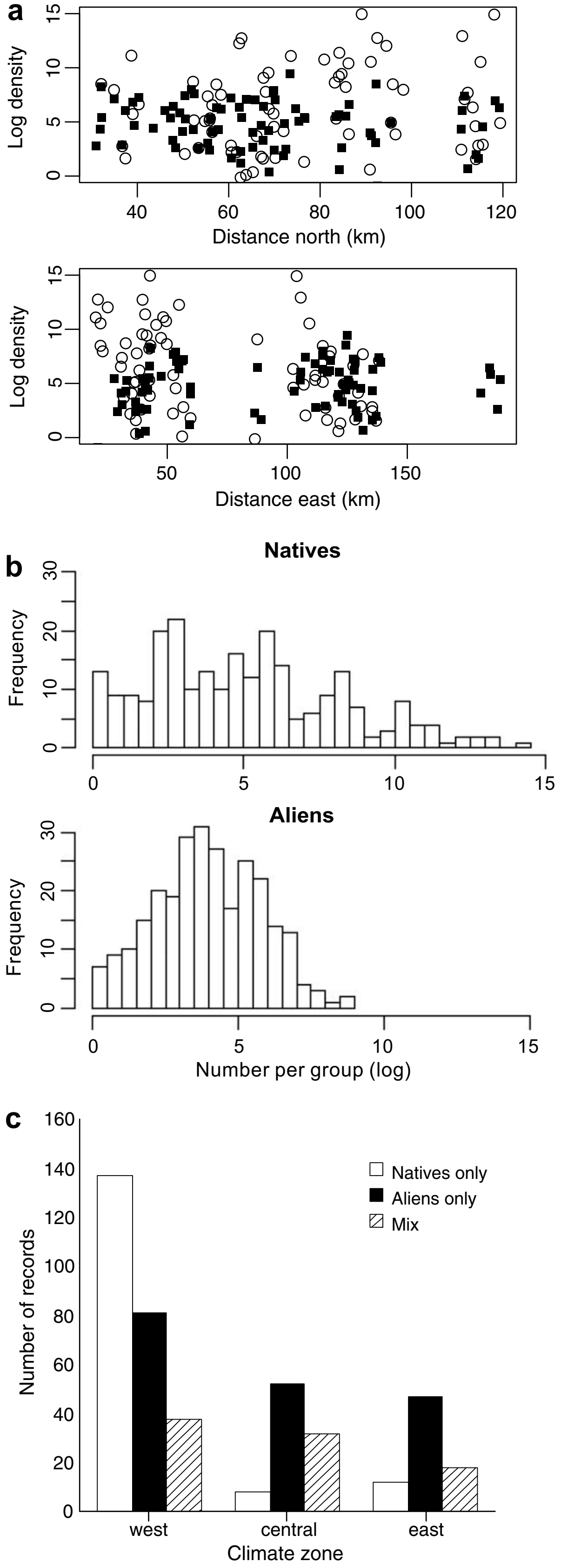

Fig. 2 – Overall spatial distributions. (a) Densities of natives (○) and aliens (■) at 152 points across range sampled from west to east and south to north (zeros omitted, natives $n = 70$, aliens $n = 79$). (b) Frequency distributions of numbers of natives and aliens per group including mixtures (zeros omitted, natives $n = 245$ records, alien $n = 268$; Fisher's exact test for two distributions, $p < 0.001$). (c) Frequencies of native-only and alien-only groups and mixtures in three climate zones ($n = 425$ records).

Table 3 – Overall spatial distributions at three scales. Variables tested singly; tabled values are for P with signs of effects shown for p < 0.20.

Response	Data (scale, *n*)									
	Hectads (10 km, *n* = 17)				Points (1 km, *n* = 152)		Records (*n* = 425)			
	Probability natives	Probability aliens	Incidence native-only groups	Incidence alien-only groups	Density natives (*n* = 70)	Density aliens (*n* = 79)	Group type frequency (*n* = 425)	# Natives per group (ln) (*n* = 245)	# Aliens per group (ln) *n* = 268)	Proportion native in mixtures (*n* = 88)
Explanatory										
Climate zone	<0.001 west > central, east	0.13 (east > west, central)	<0.001 west > central, east	0.52	0.002 west > central, east	0.37	<0.001	<0.001 west > central, east	0.29	0.08 (west > central, east)
km east	<0.001 (−)	0.105 (+)	<0.001 (−)	0.87	0.01 (−)	0.14 (+)	<0.001[a]	<0.001 (−)	0.23	0.01(−)
km north	0.001 (+)	0.86	0.067 (+)	0.58	0.15 (+)	0.20	<0.001[b]	0.80	0.82	0.68
Elevation	0.33	0.003 (−)	0.62	0.048 (−)	0.49	0.28	<0.001[c]	0.07 (−)	0.50	0.99

a Alien-only groups, mixtures > native-only groups.
b Alien-only groups, mixtures < native-only groups.
c Alien-only groups < native-only groups, mixtures.

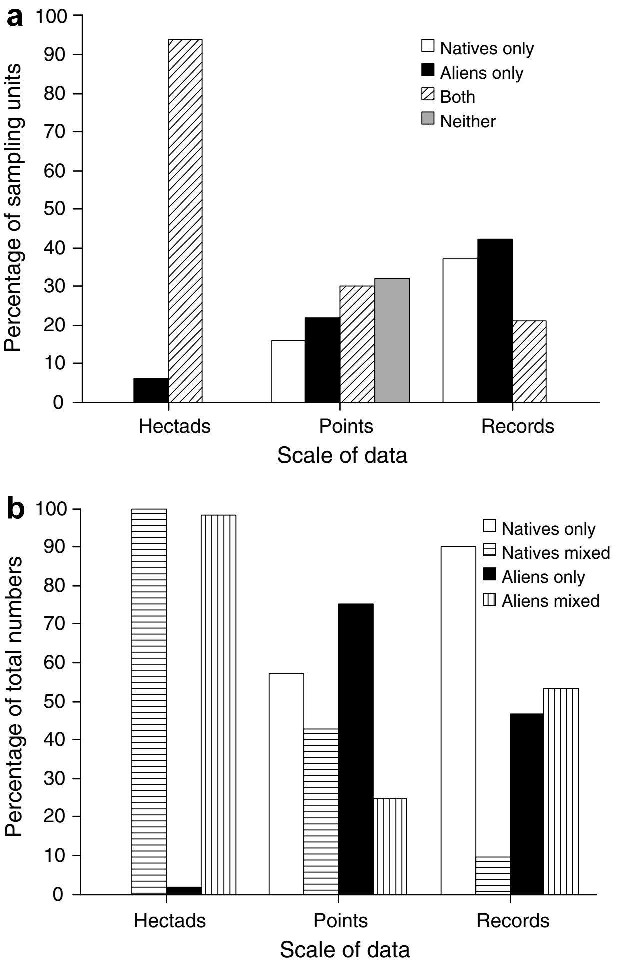

Fig. 3 – Co-occurrence. (a) Percentage of all sampling units in which natives-only, aliens-only, both, or neither were found. (b) Percentage of total estimated numbers of natives and aliens recorded that occurred in alien-only groups, native-only groups and mixtures on the 3 scales. Hectads *n* = 17, points *n* = 152, records *n* = 425. No hectad surveyed contained exclusively natives; records were by definition of occurrences only.

natives and 53% of aliens (Fig. 3b). Mixtures and alien-only groups increased in frequency towards the east and south compared to native-only groups (Table 3), but the incidence rate of mixed groups was not influenced by any variable considered (not shown). Linear regressions showed no relationship between the numbers ($F_{1,86} = 0.004$, $p = 0.95$, $n = 88$ records) or densities ($F_{1,44} = 0.002$, $p = 0.97$, $n = 46$ points) of natives and aliens where they co-occurred. The proportion native in mixed groups declined from west to east ($F_{2,85} = 3.6$, $p \sim 0.01$) and varied significantly with habitat and ground cover (lower in garden and tall herb habitats, $F_{13,74} = 2.1$, $p \sim 0.06$; higher in bracken and litter, $F_{8,79} = 4.4$, $p < 0.001$).

3.2. *Anthopogenic influence*

Aliens were encountered more frequently the greater the total cover of built land in hectads (Table 4) and the closer the hectad was to Edinburgh or Glasgow (the two explanatory vari-

Table 4 – Anthropogenic influence at the hectad and records scales (see text for points scale), p values and effects. Fig. 4 illustrates differences in group type frequencies with proximity to built habitat.

Response	Data (scale, *n*)							
	Hectads(10 km, *n* = 17)					Records (*n* = 425)		
	Probability natives	Probability aliens	Incidence native-only groups	Incidence alien-only groups	Group type frequency (*n* = 425)	# Natives per group (*n* = 245)	# Aliens per group (*n* = 268)	Proportion natives in mixtures (*n* = 88)
Explanatory								
km nearest	0.39	0.005 (–)	0.53	0.067 (–)	–	–	–	–
ha built (ln)	0.43	0.002 (+)	0.42	0.026 (+)	–	–	–	–
25 m of built (yes, no)	–	–	–	–	<0.001	0.12 (yes > no)	0.21	0.13 (no > yes)

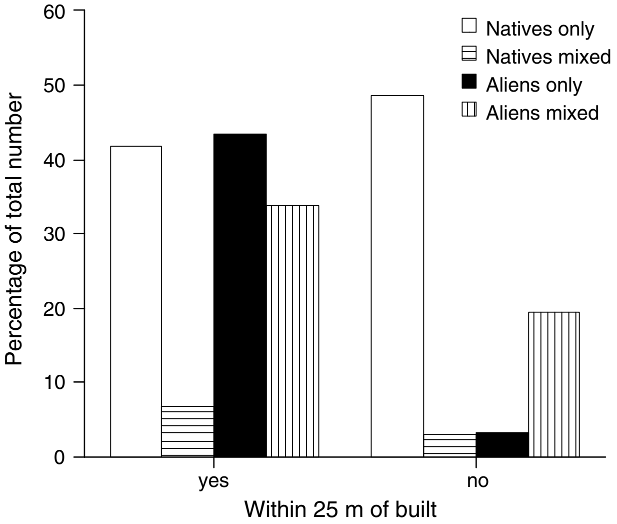

Fig. 4 – Anthropogenic influence on group type. Percentage of total numbers of each taxon that occurred in either single-taxon groups or mixture by proximity of built structures within 25 m.

ables were correlated at $r = -0.70$, $p < 0.02$). The density of aliens was an order of magnitude greater than that of natives where searches centred on built habitat at 10^2 and 10^1, respectively (Wilcoxon rank sign test, $p \sim 0.10$, $n = 24$ points, 11 with natives and 20 with aliens), but alien densities did not differ significantly between searches conducted around built and those around other point habitat types ($F_{7,71} = 0.51$, $p \sim 0.82$ for habitat factor, $n = 79$ points). Lower-elevation hectads, where aliens were most frequent (Table 3), had the greatest proportion of built land cover (correlation between elevation and hectares built (ln) = –0.69, $p = 0.002$, $n = 17$). Within 25 m of built cover, 77% of all aliens were recorded and alien-only groups were the most frequent group type (Fig. 4; $\chi^2 = 77.9$, df = 2, $p < 0.001$), but the number of aliens per record was on the order of 10^1 whether near built habitat or not (Table 4).

3.3. *Climate effects and habitat associations*

Natives were related positively to rainfall and negatively to low temperatures (Table 5, Fig. 5). In contrast, aliens were related negatively to rainfall, varied with temperature minima only in incidence rates and occurred in densities that did

Table 5 – Climate effects at hectad and points scales. Standardised long-term averages tested singly. Tabled values are P with signs of effects to p ~ 0.20. Temperatures and rainfalls were highly correlated among months.

Response	Data (scale, sample size)					
	Hectads (10 km, *n* = 17)				Points (1 km, *n* = 152)	
	Probability natives	Probability aliens	Incidence native-only groups	Incidence alien-only groups	Density natives (*n* = 70)	Density aliens (*n* = 79)
Explanatory						
Minimum °C January	0.031 (+)	0.51	0.018 (+)	0.17 (+)	0.35	0.30
Rainfall mm January	<0.001 (+)	0.016 (–)	0.0015 (+)	0.39	0.0004 (+)	0.08 (–)
Days frost January	0.008 (–)	0.91	0.012 (–)	0.25	0.04 (–)	0.63
Days frost March	0.071 (–)	0.45	0.075 (–)	0.056 (–)	0.46	0.81
Rainfall mm March	<0.001 (+)	0.016 (–)	0.0014 (+)	0.38	0.0003 (+)	0.075 (–)
Minimum °C April	0.21 (+)	0.135 (+)	0.19 (+)	0.032 (+)	0.74	0.76
Sun hours May	0.91	0.22 (+)	0.67	0.22 (+)	0.30	0.48
Rainfall mm July	<0.001 (+)	0.005 (–)	0.0099 (+)	0.16 (–)	0.0012 (+)	0.115 (–)
Maximum °C July	0.395	0.039 +	0.82	0.0047 (+)	0.06 (–)	0.76
Mean °C September	0.86	0.067 (+)	0.61	0.0124 (+)	0.247	0.93
Minimum °C September	0.29	0.13 (+)	0.175 (+)	0.055 (+)	0.87	0.84
Minimum °C October	0.051 (+)	0.40	0.039 (+)	0.17 (+)	0.433	0.578
Rainfall mm October	<0.001 (+)	0.016 (–)	0.0013 (+)	0.46	0.0007 (+)	0.102 (–)

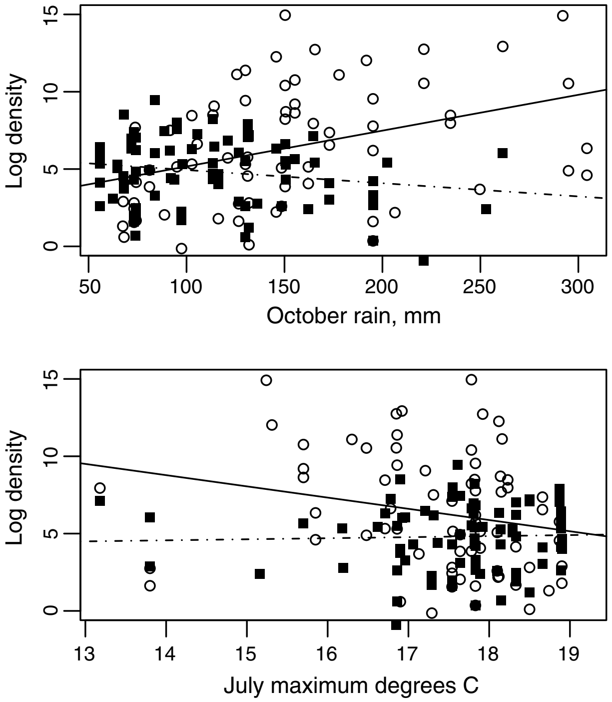

Fig. 5 – Climate effects on taxon densities. Densities of natives (o, solid lines) and aliens (■, dotted lines) across range of October rainfall (native $r^2 = 0.13$, $p \sim 0.001$; alien $r^2 = 0.02$, $p \sim 0.10$) and July maximum temperature (native $r^2 = 0.04$, $p = 0.06$; alien $r^2 = 0.01$, $p = 0.76$). Reanalysis excluding temperatures <14 °C strengthens the negative relationship for natives (giving slope = −0.0176 compared to −0.007 for the complete range of temperatures, $r^2 = 0.16$ compared 0.037, $p = 0.005$ compared 0.06), but has no major effect for aliens (slope = 0.003 compared 0.0006, $r^2 = 0.001$ compared 0.012, $p = 0.34$ compared 0.76).

not vary with temperatures (Table 5, Fig. 5). Both rainfall and temperature variables were correlated with built area in hectads (for rainfalls, $r = (-0.38)$–(-0.42) $p = 0.09$–0.11; for April minimum temperature, $r = 0.57$, $p = 0.02$; for July maximum temperature, $r = 0.47$, $p = 0.06$). The statistical negative influence of rainfall on the probability of encountering aliens remained significant at $p < 0.10$ when controlling for human density, even omitting the Glasgow hectad, but disappeared if either of two other outlier hectads were removed. Taxa showed differing responses to increasing July maximum temperatures, natives declining in density but not varying in incidence rates while aliens increased in incidence but did not vary in density (Table 5). The increasing incidence of alien-only groups with July maximum temperatures held independently of human influence (F to remove from two-variable models >4.86, $p < 0.05$). Both taxa were found throughout the range of July maximum temperatures (Fig. 5).

Climate and habitats were not independent in that taxa occupied more habitat types in western hectads (18 types, not including two coastal habitats) than in central (10) and eastern (7) climate zones. Native density was highest where points fell in (western) coastal habitat, whereas alien density did not vary among the 10 point habitat types (Table 6). For hectads, the coverage of mixed woodland, heath, grassland and bracken all had positive effects on native occurrence, while the strongest effects of land cover types on aliens were negative, relating to heath, conifer and bog (Table 6). The incidence of native- or alien-only groups was not strongly influenced by land cover and statistical relationships were sensitive to the influence of single hectads. For example the incidence rate of native-only groups related negatively to the amount of agricultural land (Table 6), but this depended on one western hectad recording 10^6 natives and 1 alien and disappeared without it ($p = 0.59$).

On the records scale, 14 habitat types were recorded for aliens and 19 for natives. Six types were exclusive to natives (acid grass, bog, coastal deciduous, heather, unimproved grass, and track) but accounted for less than 5% of records and 7% of natives. In 13 of the 20 habitat types both taxa were found, differing in distribution across habitats (Table 6, bottom). For example 64% of aliens recorded were associated with deciduous woodlands and gardens, whereas 34% of natives were found in deciduous habitats and garden and 65% in coastal and bracken habitats.

Habitat type was the best single explanatory variable distinguishing native- and alien-only groups from mixtures as well as numbers of each taxon per group (Table 6). Garden records were dominated by alien-only groups at 82%. Alien-only groups were the most common group type in semi-natural grassland and tall herb habitat at 50% of records in each and were absent in bracken habitat (though aliens were recorded in bracken as mixtures). There was no evidence for habitat exclusivity among the seven common habitat types, which contained substantial proportions of both taxa in either single-taxon groups or mixtures. Native-only groups ranged from 19% of records in semi-natural grassland to 53% of records in deciduous woodlands where they reached their largest numbers per record. Aliens were evenly spread between alien-only groups and mixtures, with their maximum numbers per record in gardens and mixed woodland. Mixtures reached their highest frequency in mixed woodlands at 36% of this infrequent habitat type (less than 6% of all records) and comprised 31% of records in semi-natural grassland and 9% of those under deciduous hedge. Between them semi-natural grass and tall herb typified ground cover in 48% of records (in which, respectively, 40% and 54% of records were alien-only groups), followed by 15% of records each of bare ground (in which 73% of records were alien-only groups) and litter (in which the three group types appeared equally). Both taxa were found associated with all ground cover types apart from heather, which had 2% of native-only groups. All classes of light level and aspect were occupied by both natives and aliens.

Natives exhibited lower niche breadth (higher habitat specificity) than aliens according to the index B′, reflecting large numbers of natives concentrated in few habitat types and aliens more equally apportioned among habitat types. Both data sources for habitat availability gave similar results: (1) hectares of land cover types in hectads gave B′ as 0.04 for natives and 0.28 for aliens, and (2) habitat types recorded at points gave B′ of 0.03 for natives and 0.21 for aliens. Both species exhibited a strong preference for deciduous habitats (Fig. 6) but natives occurred disproportionately in coastal habitats and bracken, while aliens were found disproportionately

Table 6 – Habitat associations at three scales: single variables, p values and signs of effects. For densities, habitat type referred to the point round which search was conducted, not necessarily to bluebell habitats. For groups (records), significant differences within factor variables are listed below table.

Response	Data (scale, *n*)									
	Hectads (10 km, *n* = 17)				Points (1 km, *n* = 152)		Records (*n* = 425)			
	Probability natives	Probability aliens	Incidence native-only groups	Incidence alien-only groups	Density natives (*n* = 70)	Density aliens (*n* = 79)	Group type frequency (*n* = 425)	# natives per group (*n* = 245)	# aliens per group (*n* = 268)	Proportion native in mixtures (*n* = 88)
Explanatory										
ha agricultural (ln)	0.27	0.15 (+)	0.101 (−)	0.98	–	–	–	–	–	–
ha mixed wood	0.0004 (+)	0.45	0.20	0.60	–	–	–	–	–	–
ha heath (ln)	0.019 (+)	0.009 (−)	0.31	0.066	–	–	–	–	–	–
ha conifer (ln)	0.58	0.027 (−)	0.41	0.01	–	–	–	–	–	–
ha grass (ln)	<0.001 (+)	0.37	0.16 (+)	0.33	–	–	–	–	–	–
ha bracken (ln)	0.027 (+)	0.95	0.55	0.94	–	–	–	–	–	–
ha bog (ln)	0.36	0.055 (−)	0.72	0.41	–	–	–	–	–	–
Habitat at point (10)	–	–	–	–	0.03 coastal > others	0.82	–	–	–	–
Habitat (7)	–	–	–	–	–	–	<0.001^{a}	<0.001^{e}	0.003^{i}	0.06^{k}
Aspect (9)	–	–	–	–	–	–	<0.001^{b}	0.03^{f}	0.01^{j}	0.33
Light (3)	–	–	–	–	–	–	<0.001^{c}	0.033^{g}	0.59	0.08^{l}
Ground cover (10)	–	–	–	–	–	–	<0.001^{d}	0.003^{h}	0.15	0.0002^{m}

a (Common habitat types only): aliens-only > others in gardens, semi-natural grass, tall herb; natives-only > mixtures in bracken (no alien-only groups); native-only groups > others in deciduous; both aliens-only and natives-only > mixtures under deciduous hedge.

b East: natives-only > aliens-only > mixtures; level: aliens-only > others; NW, W: natives-only > others; SW: aliens-only > others.

c Aliens-only > mixtures in open.

d Aliens-only > others where bare; natives-only > others in grass; alien-only > native-only groups > mixtures in tall herb, semi-natural grass.

e (Common types): deciduous > tall herb, deciduous hedge.

f NE, NW >.

g Shade > open.

h Bracken, litter > others.

i Garden, mixed woodland > other types.

j W < others.

k (All 20 habitat types) garden, tall herb < others.

l Shade > open.

m Bracken, litter > others.

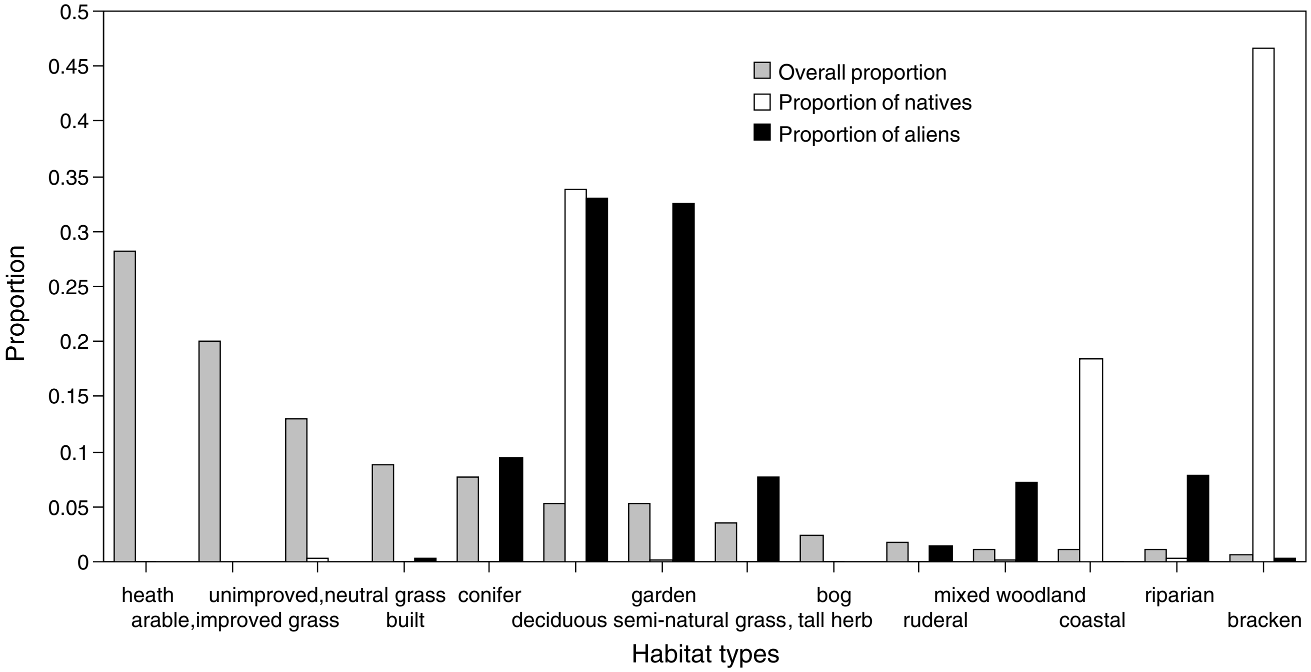

Fig. 6 – Habitat use. Overall proportion of each habitat type (grey bars, from habitat-type data at *n* = 170 random points) in order of decreasing abundance, an indication of habitat availability, and proportion of all natives (white) and aliens (black) recorded in each habitat type.

in garden, mixed woodland and riparian habitats (Fig. 6). Both analyses excluded agricultural land as an available resource, since no bluebells were found in arable or improved grassland.

Comparison of the predictive power of all environmental drivers on bluebell abundance reveal different models for the different taxa, scales and abundance measures (Table 7). At the hectad scale, natives were associated with temperate

Table 7 – Model summary: best single- and multiple-variable models for each abundance variable. A model was considered better than the best single variable if it had lower AIC.

Data (scale, *n*)	Response variable	Best single variable	Other significant single variables	Best multiple variable model
Hectads (10 km, 17)	Probability natives	Rain	East km, north km; min. °C January, January frost days; ha mixed wood, ha heath (ln), ha grass (ln), ha bracken (ln).	Rain + ha mixed wood + ha grass (ln)
	Probability aliens	ha built (ln)	Elevation; km city; rain, max. °C July; ha heath (ln), ha conifer (ln),	Rain + elevation
	Incidence rate native-only groups	km east	Rain, January frost, min. °C January /October	km east + min. °C January
	Incidence rate alien-only groups	maximum °C July	Elevation; ha built (ln), ha conifer (ln); max °C July, min. °C April;	maximum °C July + ha conifer (ln)
Points (1 km, 152)	Density natives (*n* = 70)	Rain (October)	km east; frost days; habitat (10)	Max. °C July + January frost
	Density aliens (*n* = 79)	Rain (ns)	–	–
Records (425)	Group type frequency	Habitat (7)	km east, km north; aspect, habitat, light, ground cover, built25	km east + km north + habitat + built25
	# Natives per group	Habitat (7)	km east, elevation; aspect, habitat, light, ground, built25	km east + habitat
	# Aliens per group	Habitat (7)	Aspect	Habitat + ground cover + (either)aspect or elevation
	Proportion natives in mixtures	Ground (11)	km east, habitat, light	km east + ground cover

areas of mixed woodland and high rainfall whereas aliens were most frequent in drier, lowland regions. At the points scale, native densities showed the importance of climate in the two-variable model, which was robust to spatial autocorrelation (both variables correlated with rainfall at $p < 0.001$: $r = -0.37$ with July maximum °C, $r = -0.31$ January frost days). Alien densities were related weakly only to rainfall. Habitat was of overwhelming importance in trends at the record scale, where natives showed the influence of both large-scale and small-scale drivers and non-natives primarily the effect of local conditions.

The national volunteer survey data showed Scotland to be similar to the rest of the UK. The two regions did not differ in the overall frequencies of group types (chitest, $p = 0.32$), both recording around 75% of occurrences as native and 20–24% as mixtures. Broadleaf woodland was the most frequent habitat type in both regions (55% Scotland, 62% rest of UK), and there were no differences in the frequencies of group types in each of the five main habitats (chitest $p = 0.99$). Mean areas recorded under bluebells were also comparable (t-test of (ln) m^2, $p = 0.75$).

4. Discussion and conclusions

Although *H. hispanica* was introduced into British gardens before 1683 its presence in the wild was noted just 100 years ago, and while the hybrid was first recorded in the wild in 1963 its increasing distribution was only recognised by 1987 (Preston et al., 2002). Thus the naturalisation of the alien taxa is a relatively recent phenomenon and, unlike the native bluebell, current distributions are unlikely to reflect a natural equilibrium with the environment. This poses problems when attempting to identify the environmental drivers leading to invasion by alien species, since the goodness of fit of distribution models can often be poor (Collingham et al., 2000). In any case care must be taken to avoid inferring causality directly from observational studies alone, especially where several explanatory variables are confounded.

Climate, specifically temperature effects on seed germination (Thompson and Cox, 1978), undoubtedly plays a role in deliminating the global distribution of the native and might be expected to play a similar role for aliens. While this study certainly found native and alien taxa exhibited different climate profiles, the distribution of the alien taxa likely reflects introductions and residence time rather than strict climatic limits (Pyšek and Jarošík, 2005). This view is supported by the UK-wide distributions of all three taxa at the eastern, western and southern extremes of the region as well as the presence of the alien in Shetland, the most northern point in the British Isles (Preston et al., 2002). Moreover the broad co-distribution at finer resolutions signifies that a great deal of both UK climate and habitat is good for both taxa. The western coastal climate in particular seemed to enable aliens as well as natives to occupy more habitat types, potentially facilitating colonisation in these areas if aliens are not physiologically constrained by high rainfall.

The small numbers in which aliens occurred is suggestive of repeated recent introductions (Colautti and MacIsaac, 2004), and indeed it appears that the alien distribution is still closely tied to the built environment. This may explain the negative relationships found for aliens with heathland and conifer plantations that are often distant from urban areas, as well as the apparent exclusivity of natives in some coastal, boggy and acidic habitats. However, constant introduction rates alone could realise exponentially increasing distributions (Wonham and Pachepsky, 2006), with cultivation giving aliens the advantages of favourable conditions and opportunities for local adaptation (Mack, 2000; Mack, 2005) as well as dispersal (Hodkinson and Thompson, 1997). In addition, unchecked small groups can make large contributions to an invasion process (Moody and Mack, 1988; Civille et al., 2005). The likelihood of alien species making the transition from naturalised to invasive may be higher for ornamentals than for other deliberate or accidental introductions (Milbau and Stout, 2008), and the availability of alien taxa from gardening nurseries highlights the ongoing risk of human distribution into new areas.

The current distribution of alien *Hyacinthoides* in the UK corresponds to Stage IV (of V) in a neutral framework for determining invasion status (Colautti and MacIsaac, 2004), reflecting evidence that they are established, widespread, and primarily dispersed by humans. Recording of presence on the hectad and tetrad (2-km) scales shows recent increases (Dickson et al., 2000; Preston et al., 2002; Braithwaite et al., 2006). To evaluate the risks this distribution poses to native *H. non-scripta,* examination of co-occurrence is required at more than one spatial scale (Hulme, 2003, 2008); although broadly occupying the same regions (hectads) and landscapes (points), at the records scale co-occurrence is comparatively low.

Clearly the potential for competitive displacement should be assessed at the records scale, where 10% of natives co-occurred with aliens. Natural rates of increase for aliens have yet to be determined, but native *H. non-scripta* transplants in woodlands were found to spread no more than 0.06 my^{-1} over 45 years (van der Veken et al., 2007). If aliens had similar low rates, their natural increase by seeds or bulbs would be slow enough to disqualify them as invasive by some criteria (e.g. Richardson et al., 2000). Nothing is known of bulb interactions that could anticipate the outcome of underground competition. Because aliens are much less numerous than natives and 90% of natives occur in native-only groups, the current risk arising from direct competition may be small.

Hybridisation requires contemporaneous flowering within the range of pollinator flights as well as interfertility, which is widely-assumed despite the absence of primary literature on the subject. Based on bee foraging behaviour (Osborne et al., 1999), considering co-occurrence on the points (1-km) scale may underestimate hybridisation potential. Ellstrand (1992) considered populations to be sympatric or parapatric on a 10-km scale, and in insect-pollinated herbs, >1000 m (e.g. Klinger et al., 1991; Skogsmyr, 1994) and >3000 m (e.g. Westphal et al., 2006) have been used as imperfect isolation distances for genetically modified crops. The smaller alien groups would broadcast relatively little pollen compared to native groups, but their small numbers would promote gene exchange with other groups (Ellstrand, 1992). Thus the presence of over 40% of natives within 1–2 km of aliens could provide considerable opportunities for genetic interactions.

In summary, it is evident that alien *Hyacinthoides* taxa pose a significant potential risk to native *H. non-scripta*. If hybridisation in taxa undifferentiated by habitat could be sufficient to cause assimilation (Wolf et al., 2001), then slow rates of increase and small numbers of aliens could under-represent the scale of eventual change possible in *H. non-scripta*. Understanding the actual impacts of co-occurrence calls for data on demographic rates, competition for space and pollinators (Bjerknes et al., 2007), and the consequences of cross-fertilisation.

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