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Comparative ecology of the native and alien floras of the British Isles

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SUMMARY

Why do different plant species thrive where they do? This is a difficult question to answer because plants have invaded new niches and subsequently evolved to become better adapted within those niches. Distinguishing the traits that allow successful invasion and those that are evolved adaptations to current environments is not usually possible. We attempt to identify life history components that allow successful invasion by analysing the life history variables and ecological requirements of plant species that have successfully invaded the U.K. in recent years. The British flora is uniquely suited for this analysis because we have precise information on the dates of arrival, rates of spread and final spatial distribution of all our alien vascular plant species. Data on alien plants controls for evolution after invasion because there has been relatively little time for evolution to occur. We use modern phylogenetically-based comparative methods in an attempt to tease apart those components of life histories that have allowed successful invasion (large seeds, tall stature, protracted seed dormancy) from those that are irrelevant (dispersal syndrome, mating system, leaf shape).

1. INTRODUCTION

What are the ecological attributes associated with successful invasion of new habitats? At first glance, it might seem that any search for traits associated with invasive ability would be bound to fail. All species in their native habitats must exhibit the ability to increase when rare (the 'invasion criterion', $dN/dt > 0$ when N is small). If this were not the case, then a species would drift inexorably downwards towards extinction, as one environmental calamity followed another. Since all species must pass the invasion criterion, it is evident that *all* species possess the traits necessary for invasion. It is equally clear that 'competitive ability' is not a species-specific trait; it depends upon the identities of the species with which a plant is competing and upon the environmental conditions under which competition takes place. Likewise a species that was less competitive in one year might be more competitive in a different kind of year (Crawley 1989, 1996). Given these constraints, we would predict that different traits would be associated with different successional stages (e.g. r-strategists with rapid development, wide seed dispersal in space or time and microsite-limited recruitment *vs* K-strategists with large size, long life and seed-limited recruitment), different habitats (e.g. forests *vs* grasslands), and different resource supply rates (e.g. nitrogen-rich *vs* nitrogen-poor soils). We might expect, therefore, that a minimal statistical description of the traits of successful alien plants would involve a high-dimensional model, requiring specification of the abiotic environment, the abundance and specific identity of competitors, herbivores, mutualists and natural enemies, the successional stage, the disturbance regime and the idiosyncrasies of the year in which the attempted invasion occurs. In this paper, we step back from this detailed perspective to take the broadest possible view. We ask what traits distinguish the native and alien members of the British flora? The question of what distinguishes successful and unsuccessful invaders is left for another occasion.

2. METHODS

(*a*) *Definitions*

Natives: plant species that would be present without human intervention (in the case of the British Isles, this means those plants that returned during the first 10000 years after the retreat of the glaciers before humans began mass transport of plants).

Aliens: species introduced by humans after 500 BC. The date is arbitrary, but it allows that recorded Roman introductions are classed as aliens. It also means that many plants associated with human habitats and agricultural fields are classed as natives (much as the house sparrow *Passer domesticus* is classed as a native bird). Continental botanists refer to these ancient, human associated plants as archaeophytes.

Naturalized: aliens with self-replacing populations. For the purposes of this study, the naturalized aliens are defined as those species treated as such by Kent (1992) in his *List of Vascular Plants of the British Isles*. The classification of many species as native or alien, or of aliens as naturalized or not, is highly contentious. This can be seen by comparing the opinions of different modern authors like Stace (1991) in his *New Flora of the*

British Isles and Clement & Foster (1994) in their *Alien Plants of the British Isles*.

Casuals: alien plant species that do not form self-replacing populations, and rely on repeated reintroduction for any semblance of permanence that they might exhibit.

Introduction: the transport (intentional or unintentional) of seeds or viable plant parts from one country to a habitat in another country where the species did not previously occur.

Establishment: the formation of a self-replacing population. Many long-lived introductions (e.g. ornamental trees) give the appearance of establishment but never produce a second generation; such species are best viewed as long-lived casuals.

(*b*) *Data sources*

The identities of the native and alien species are taken from Kent (1992). Information on their phylogeny is extracted from Chase *et al.* (1993) supplemented, where necessary, by the taxonomy used in Stace (1991). Country of origin and mode of introduction were obtained from a wide range of sources, as detailed by Crawley (1997). Distribution and abundance of aliens within British habitats were obtained from more than 100 county floras and from standard works (e.g. Stace 1991; Clapham *et al.* 1962). Data on plant traits come mainly from Grime *et al.* (1988) supplemented with information from the ecological flora database (Fitter & Peat 1994). The analysis of plant traits excluded ferns and horsetails (too little data), but included gymnosperms and a few angiosperm hybrids (where these had a native and an alien parent) and subspecies (where distinctive native and alien members of the same species were identified by Kent (1992)).

(*c*) *Analysis*

The need to consider phylogenetic relatedness in comparative studies is widely accepted. At first sight, it might appear that our study provides an exception to this rule. Given that more or less every invader to the U.K. invaded independently, can species be treated as statistically independent? The answer is that they cannot. Aliens are not a phylogenetically random subset of the British flora (e.g. Pinaceae has a high proportion of aliens and Cyperaceae has a low proportion; see Crawley 1997). Because other attributes of organisms obviously tend to covary with phylogeny, aliens will not constitute a random subset of the British flora with respect to these traits either. We should not therefore be surprised to find that attributes, and correlations among them, differ significantly between aliens and natives when species are taken as independent points (see Harvey & Pagel 1991; Harvey *et al.* 1995; Rees 1995 for further discussion).

We have used two comparative methods, both of which map the data from different species on to a phylogeny in order to partition the among-species variance into phylogenetically independent comparisons (technically, linear contrasts) between related taxa. Both methods are derived from Felsenstein (1985). The first (Purvis & Rambaut 1995) compares values of a chosen trait – say, plant height – between one or more native species and one or more related aliens. As many phylogenetically independent contrasts as possible are computed. Under the null hypothesis that native and alien taxa are the same height, we should expect the aliens to be taller than natives in about half of the contrasts: the sign test is used to assess the significance of departures from this expectation. A second procedure (Pagel 1992) is used to test hypotheses involving more than two variables. This computes contrasts in each chosen variable at every node in the phylogeny; multiple regression through the origin is then used to test significance. We used the CAIC package (Purvis & Rambaut 1995) for both methods.

The methods we use require an estimate of phylogeny for all 2684 species in the dataset. Interfamilial relationships were taken from the strict consensus trees in Chase *et al.* (1993), with lower-level relationships according to Stace (1991). Families missing from Chase *et al.* were placed according to Stace (1991). Additionally, some families are paraphyletic or polyphyletic according to Chase *et al.*'s trees; where necessary, we used subfamilial divisions from Clapham *et al.* (1962) to place species in our dataset with their closest relatives in Chase *et al.* We set all branches in the phylogeny to the same length, transforming contrasts whenever they showed marked heterogeneity of variance (Harvey & Pagel 1991).

(*d*) *Statistics*

Statistical analysis was confined to sign tests of the phylogenetically controlled contrasts, based on the null hypothesis of equal representation of positive and negative contrasts between the traits of native and alien plants. In cases where the value of the contrasts showed a trend with the trait score, a contingency table was constructed using the contrasts from the 12 largest and 12 smallest values of the trait score, with significance assessed at the 1% level (>6.64) for a 2×2 table (positive and negative contrasts versus low and high trait scores).

3. RESULTS

(*a*) *Numbers of natives and aliens*

The numbers of alien and native taxa in Kent (1992) are shown in table 1, along with estimates of the numbers of species of plants introduced intentionally and unintentionally to the British Isles (see Crawley 1997 for details). Of the 1169 naturalized alien species, about 70 have become sufficiently widespread in seminatural habitats that a visiting botanist might mistake them for natives. Only about 15 alien species are regarded as problem plants, but even among these species, there is far from unanimous agreement as to their pest status (Williamson 1993). Thus, somewhere between 0.5% and 5% of introduced species have become naturalized, and about 6% of naturalized species behave like natives. By even the most generous

Table 1. *The numbers of native and alien species in the British flora with estimates of the numbers of alien species introduced into the British Isles for various purposes*

(The largest number of introductions was of herbarium specimens; Kew gardens has over 7 million herbarium sheets representing about 80% of the total world flora. About 65000 named taxa are currently sold for horticulture in Britain (Philip & Lord 1995), of which about 14000 represent distinct species grown out of doors. The casual flora runs to more than 6000 species.)

world		250000
brought to Britain	unintentionally 20000 intentionally 200000	220000
grown in Britain	botanic gardens 25000 commercial horticulture 14000 non-cultivated aliens 6000	26000
British flora	native 1515 naturalized 1169	2684
widely naturalized aliens		68
problem plants		15

estimate, well under 0.1% of introduced species have become pests (c.f. Williamson 1993).

(*b*) *Taxonomy*

The aliens and natives were not drawn from species pools with similar taxonomic compositions. Many alien species belong to one of the 40 families not represented in the native British flora, and many families have disproportionately many alien representatives (e.g. Pinaceae, Iridaceae; Kent 1992). It is noteworthy that five of the top 12 over-represented families are phanerophytes (trees and shrubs) and that four of the top 12 are geophytes (bulbs and other plants that perennate underground) . Likewise, there are many British plant families which have no alien representatives (including some large families such as Orchidaceae and Potamogetonaceae) and numerous families that have disproportionately few alien representatives (e.g. Cyperaceae, Juncaceae). The families with no alien members contain many ferns and water plants, two groups with particularly effective long-distance dispersal. The under-represented families contain a preponderance of graminoid monocots like sedges and rushes, more ferns and parasitic plants. The relative paucity of alien Caryophyllaceae is a puzzle.

This non-random species representation makes a phylogenetically controlled approach essential, otherwise counts of species (e.g. chi-squared analysis of contingency tables) might show nothing more than the idiosyncrasies of uneven representation of different plant families.

(*c*) *Life forms of natives and aliens*

The frequency distributions of Raunkiaer's life forms for the native and alien species are shown in figure 1. There is a highly significant difference in the proportional representation of natives and aliens ($\chi^2 = 27.0$, d.f. $= 4$, $P < 0.001$) when species are treated as independent data points; woody plants and geophytes are strongly over-represented amongst the aliens. As we have seen, however, there is a highly significant bias in the taxonomic representation of different alien plant families, and this is determined largely by the horticultural tastes of British gardeners rather than by ecological performance (i.e. gardeners like trees and bulbs). It is unwise, therefore, to interpret the contingency table as showing that different life forms are more or less likely to become established as aliens in

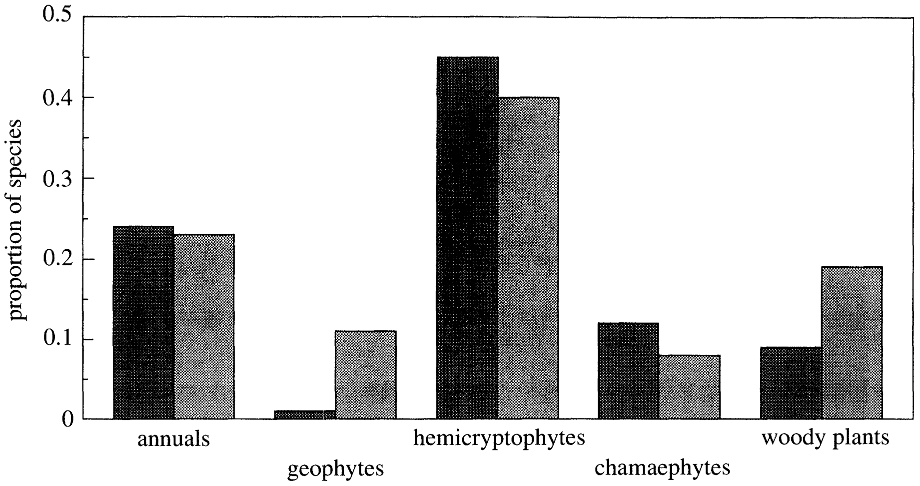

Figure 1. The frequency of different Raunkiaer life forms for natives (dark stippling) and aliens (light stippling). The highly significant preponderance of trees and geophytes amongst the aliens is an artefact of the unequal representation of plant families and the predilection of gardeners for ornamental trees and bulbs.

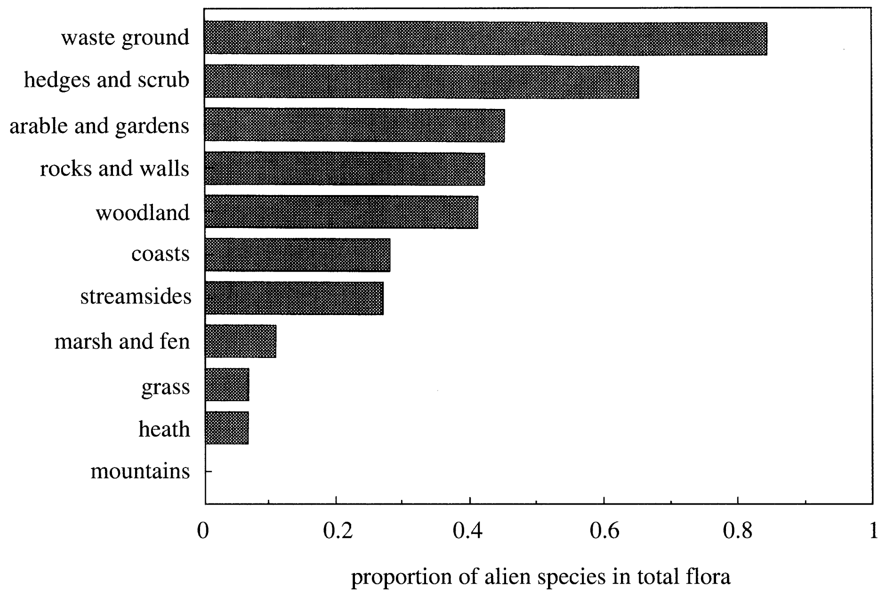

Figure 2. The habitats invaded by aliens in the British Isles, showing the fraction of the total flora of each habitat made up by alien species. Note the strong correlation with human disturbance and the negative relationship with isolation from human activities. These patterns are confounded by the fact that the rate of introduction of suitably pre-adapted alien species declines with isolation and with the difference between the ecological conditions of the target habitat and standard garden conditions (e.g. many more introduced plants are capable of growing in grassy waste ground than on upland cotton grass bogs).

the absence of any control over the rate of introduction of species. Phylogenetically controlled analysis of the life-form data is discussed below.

(*d*) *Mode of introduction*

Most naturalized alien plant species were intentionally introduced. Much the largest category is made up by escaped garden plants, but plantation trees and woody crop plants are well represented. The majority of unintentionally introduced plants are casuals, although several important annual weeds of arable agriculture were unintentionally introduced, probably as contaminants of imported seed. The notion that the most important alien plants arrive as seeds stuck to bootlaces or caught up in trouser turn-ups is wrong. Most of our pernicious plant invaders were originally introduced as garden ornamentals.

(*e*) *Geographic origin of British aliens*

Most British aliens originate from central and southern Europe (Crawley 1997). A log-linear model describing the number of alien species number as a function of four explanatory variables (latitude, area of source country, size of the flora in the original range and great circle distance to the source region) contained significant terms (in order of importance) for latitude (positive), distance (negative) and log(area) (positive). There was no effect of the size of the local flora, presumably because this is well predicted by latitude and log(area). Significant outliers from this model were as follows: Europe, South America and New Zealand had more British aliens than predicted; North America, Turkey and the Middle East, and Mediterranean Europe had fewer British aliens than predicted. The general lack of frost hardiness amongst tropical plant species means that few, if any, tropical species are naturalized in the British Isles. This result draws attention to the asymmetry of exchange of aliens between different countries (e.g. North America received almost the entire European weed flora, but was the source of rather few European aliens; Crawley 1986, 1987).

(*f*) *Invaded habitats within the British Isles*

Alien plant species are non-randomly distributed across habitats (figure 2). Habitats rich in aliens tend to be man-made or highly disturbed by human activities, and to high average cover of bare ground (e.g. waste ground, urban sites, railway lines, walls). Alien species richness is positively correlated with the rate of propagule introduction (e.g. proximity to gardens and allotments, proximity of seed sources like granaries, woollen mills, docks, roadsides and tanneries) and negatively correlated with the isolation of the habitat from urban influence. Thus, mountain tops and remote heathland areas are especially poor in alien species and habitats like coastal sand dunes, that are rich in alien species where they occur close to towns (e.g. in southern England and South Wales), are notably poor in alien plants in more remote areas (e.g. in the Outer Hebrides).

(*g*) *Abundance of alien plants*

Data on the abundance (e.g. population density or biomass) of native plants are extremely scarce; data on the abundance of aliens are even rarer. Most data on plant abundance consist of subjective scores (e.g. Tansley's DAFOR system in which each plant species is allocated to one of the following categories: dominant, abundant, frequent, occasional or rare). There is also a pronounced sampling bias against alien plants because most of the data on plant abundance are gathered by phytosociologists and these people exhibit an unusually high degree of chauvinism about which plant species should, and should not, occur in a given plant community. A small number of modern county floras contain semi-quantitative habitat lists that show no obvious 'anti-alien' prejudice; these data reinforce the impression that alien plant species seldom reach high levels of abundance in British plant communities. Some communities like grazed, mesic grasslands and native *Pinus sylvestris* woodland contain no alien plant species at all (see below). Exceptions, where alien plants comprise a large part of the biomass, include some characteristic communities of waste ground (e.g. *Buddleja davidii* scrub or *Fallopia japonica* thicket where aliens often make up over 90% of the biomass; M. Crawley unpublished observations), plantation woodlands invaded by *Rhododendron ponticum* and chalky sea cliffs in southern England (these support several abundant species including *Centranthus ruber*, *Smyrnium olusatrum*, *Antirrhinum majus*, *Lycium* spp. and *Carpobrotus edulis*).

(*h*) *Isolation from human influence*

Very few British alien plant species are established at any great distance away from the direct influence of human activities. Crawley (1997) divides alien species on the basis of the '100 m rule'. Field work by the author (M. J. Crawley, unpublished results) undertaken throughout the British Isles shows that the great majority of naturalized alien plant species are seldom found more than about 10 m from buildings, gardens, walls, waste ground, roadsides or railway lines. Only a handful of species is ever found more than 1000 m away from human disturbance. Of course, it is true that only a tiny fraction of the land area of the British Isles lies more than 1 km from a road or railway (rural roads tend to be about 1 km apart in lowland Britain). Furthermore, isolated areas contain an extremely biased sample of seminatural habitats (mostly heathland, mountain-top, streamside or saltmarsh). The '100 m rule' defines an approximate threshold that separates the small number of thoroughly naturalized aliens that appear not to need direct human intervention for their persistence (e.g. *Mimulus* hybrids, *Epilobium brunnescens*, *Oenothera glazioviana*) from the much larger number of species that appear to be incapable of regeneration in undisturbed seminatural vegetation.

(*i*) *Distribution of alien plants within the British Isles*

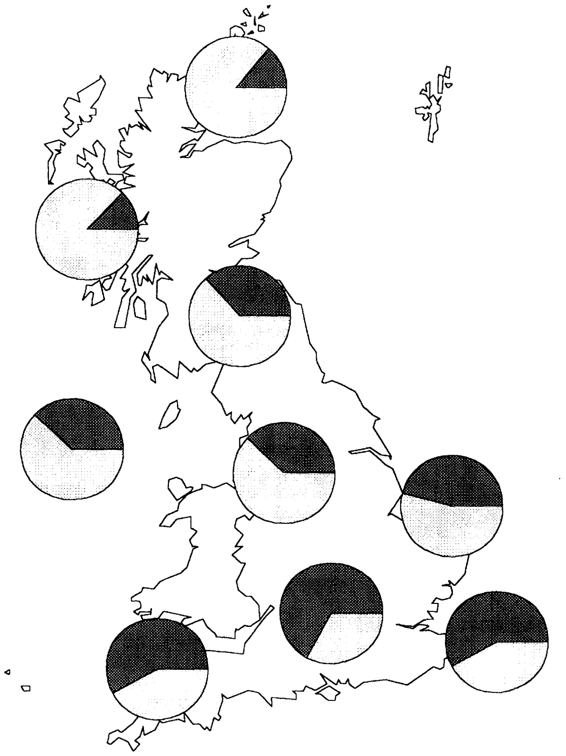

Figure 3. The geographic distribution of alien plant species within the British Isles. The pie diagrams show the proportion of the local flora made up of alien species (dark stippling). There is a pronounced gradient from 67% alien species in southern England to 13% in north-west Scotland. These trends reflect climatic differences (e.g. many frost-sensitive alien species are restricted to the south west of England, Isles of Scilly and the Channel Islands), habitat heterogeneity (there are more habitats per 10 km square in southern England than in northern Scotland) and differences in the rate of propagule introduction (this is probably roughly proportional to human population density, which shows a strong south-east to north-west gradient).

There is a clear trend of declining alien species richness within the British Isles from a maximum in southern England, declining northwards and westwards to a minimum in north-western Scotland (figure 3). Local alien hotspots include the almost frost-free Isles of Scilly off the south-west coast of Cornwall (boosted by escapes of South African and New Zealand plants from the celebrated gardens at Tresco Abbey) and central London (possibly as a result of the warmer climate afforded by the urban 'heat island'). These patterns are consistent with the hypothesis that the most important factor determining the number of alien plant species in a local area is the rate of introduction of propagules by people.

Some alien plant species like *Acer pseudoplatanus* are virtually ubiquitous in their distributions within the British Isles, but the average range of alien plants (as determined by the number of 10 km squares from which they are recorded) is significantly more restricted than the average for natives (Crawley 1997). The most widespread alien, *Matricaria discoidea*, is the 33rd most widespread British species, but the 10th most abundant alien, *Elodea canadensis*, is only the 311th most widespread species.

There are intriguing differences in the spatial distributions of the different life forms (average number of 10 km squares occupied), and natives and aliens show different patterns. For natives, hemicryptophytes have the widest distributions, but alien woody plants and chamaephytes have wider distributions than alien hemicryptophytes. Geophytes have the most restricted

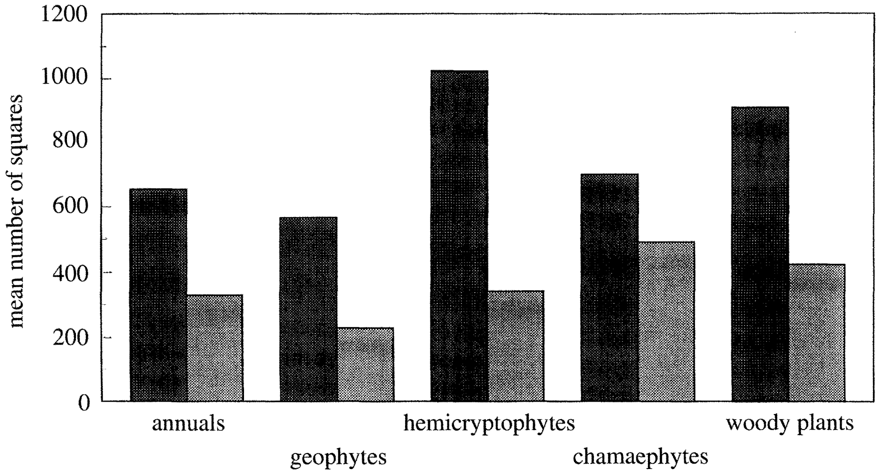

Figure 4. The distribution of native and alien species of different life forms, estimated as the average number of 10 km squares occupied per species. There are intriguing patterns for both natives (dark stippling) and aliens (light stippling). Native hemicryptophytes tend to be more widespread than other life forms, while the most widespread aliens tend to be chamaephytes. Geophytes have the most restricted distributions for both natives and aliens, presumably because they are commonest on warmer soils in southern England. It is interesting that alien hemicryptophytes are proportionately the most restricted when compared with native species, suggesting relatively higher native species saturation than in other life forms like trees.

Table 2. *Phylogenetically controlled contrasts for a variety of traits, comparing native and alien vascular plant species in the British Isles*

(Alien plant species were taller and had larger seeds than the natives. Native plants had more extensive geographical distributions within the British Isles. Seed dispersal syndromes were different; more of the natives were water- or wind-dispersed; more of the aliens were dispersed directly by people or had explosive fruits. Species = the number of species for which data on the trait were available. Contrasts = the number of independent contrasts between natives and aliens in the available data. Signs = number of contrasts in which the native trait was greater than the alien trait/the number of contrasts in which the alien was greater than the native. When there are ties (native = alien), the sum of the positive and negative signs is less than the number of contrasts. Significance = 2-tailed probability of an equal or more extreme distribution of signs (binomial test).

trait	species	contrasts	signs	significance
plant height	1562	134	49/80	0.01
seed weight	782	58	21/37	0.05
distribution	1538	115	97/18	0
dispersal	1669	143	44/25	0.03
life form	1505	143	43/44	n.s.
seedling growth rate	127	6	5/1	n.s.
start flowering	1562	122	45/60	n.s.
end flowering	1556	120	55/52	n.s.
pollination	1508	119	19/25	n.s.
altitude	918	36	21/15	n.s.

distributions for both natives and aliens (figure 4), largely because they are restricted to the warmer, base-rich soils of southern England.

(*j*) ***Ecological traits of alien plants***

Several traits showed no significant differences between native and alien species, but a few traits were strongly and consistently associated with aliens in phylogenetically independent contrasts (table 2). The most clear-cut difference was in plant height; alien plants were taller than their native counterparts in 134 contrasts ($P < 0.01$). Given that plant height and seed size are positively correlated (Rees, this issue), it is not surprising that aliens tended to have larger seeds than their native counterparts. Seed bank dynamics of natives and aliens were significantly different; aliens were less likely to show no seed dormancy and more likely to show protracted (> 20 year) seed dormancy. There was a significant but small tendency for alien plant species to flower relatively early or relatively late in the year comparer with native species, and to be more likely to be pollinated by insects. Within the category of aliens, date of introduction was significantly associated with geographic distribution (not surprisingly, recent introductions had more restricted ranges than did long-established aliens) and more recent introductions were likely to be smaller (and less likely to be trees) than early introductions.

Perhaps the most intriguing pattern to emerge from the phylogenetically independent contrasts has to do with Raunkiaer's life form. Ranking species in the sequence of increasing size and longevity (therophyte, geophyte, hemicryptophyte, chamaephyte and phanerophyte) showed no overall distinction between natives and aliens (compare with figure 1 and with Williamson & Fitter 1996), largely because most of the contrasts are between species with the same life form (e.g. all Pinaceae and all Fagaceae are phanerophytes). Nevertheless, there was a significant surfeit of positive contrasts (aliens bigger and longer lived) amongst the long-lived species and a significant surfeit of negative contrasts (aliens smaller and shorter lived) amongst the short-lived species ($\chi^2 = 6.18$; d.f. = 1).

4. DISCUSSION

Given that we had no *a priori* reason to expect that there would be any trait differences between native and alien plants (because all plants must possess traits that allow them to increase when rare), it is extremely interesting to find such a consistent set of relationships in data on the British flora. It looks as if aliens need to 'try harder'; they have bigger seeds and they are taller than comparable native species. These traits are positively correlated, as Rees (this issue) shows. There is evidence that native British communities are not saturated in species and that some life forms (e.g. hemicryptophytes) are more saturated than others (e.g. trees). Vacant niches do exist, but as we shall see, some aspects of the concept of vacant niche are relatively more clear-cut than others. There is no doubt that much clearer patterns will emerge in future, when detailed attention is focused on particular taxa in specified habitats with comparable disturbance regimes.

The first point that needs to be emphasized is that most alien plants were not introduced by accident (the 'seeds in trouser turn-ups' model). The vast preponderance of intentional over unintentional introductions amongst the British alien flora matches the experience from other well-studied floras. In South Africa, for example, government legislation classifies alien plants into two categories of severity: of the 10 spp. of 'declared invaders' which represent a serious threat to native ecosystems, all are woody and all were intentionally introduced. Of the 138 spp. of 'declared weeds', 82% were intentionally introduced, and amongst the 15 unintentionally introduced spp., all were herbaceous, and most were pasture weeds (Henderson 1995).

This last point draws attention to a paradox concerning British grasslands. Grazed, mesic grasslands in Britain support no alien plant species at all, and yet these same grasslands were the source of many of the most pestilential pasture weeds introduced into other parts of the world (*Hypericum perforatum*, *Cirsium arvense*, *Senecio jacobaeae*, *Pilosella officinarum*, *Plantago lanceolata*, *Rumex acetosella*, *Ulex europaeus*, *Cytisus scoparius* and *Hypochoeris radicata* in Australia, South Africa, Pacific islands and the Americas). The probable cause of this asymmetry is the long association between Old World grasslands, people and grazing ungulates, and the importance of introduced domestic livestock as primary agents of disturbance in New World habitats, paving the way for invasion by pre-adapted, grazing tolerant, Old World pasture species when these were introduced in hay and seed mixtures imported by the early European settlers.

A model for the geographic origin of British aliens highlights the importance of proximity and climatic matching. The number of species originating from different regions declines monotonically with increasing difference in latitude (lack of frost-hardiness in tropical and subtropical species is the most obvious cause of this pattern). The strong negative relationship between the number of alien species and distance to the source country (e.g. Europe is the principal source of British aliens) is not a general phenomenon, because Europe is also the principal source of alien plants in distant locations like Australia, New Zealand and South Africa.

Although the British flora is better known than any other flora in the world, there are still a number of potentially serious biases that could influence our interpretation of the comparative ecology of alien plant species in Britain. Knowledge about the abundance of aliens and their ecological function in seminatural habitats is dogged by the tendency of botanists to avoid communities that contain aliens, or to locate their study quadrats in alien-free parts of invaded communities. Worse still is the lack of information on the autecology and ecophysiology of alien plants in sources like the ecological flora database (Fitter & Peat 1994). Despite these difficulties, a few clear patterns have emerged. In phylogenetically independent contrasts, British aliens were larger than their native counterparts, had larger seeds, were more likely to flower very early or very late in year, had long-lived seed banks and were more likely to be pollinated by insects. Some of these traits are internally consistent (e.g. plant height and seed weight are positively associated), but others are not (e.g. large seeds and long seed dormancy are negatively associated in most between-species comparisons; Rees, this issue). Taking these observations together suggests that there are at least two characteristic groups of aliens: those species that are 'more K-strategist' than native K-strategists; and those that are 'more r-strategist' than native r-strategists. Thus, the alien flora contains an abundance of woody and thicket forming species that are capable of excluding native vegetation (*Rhododendron ponticum*, *Symphoricarpos albus*, *Fallopia japonica*) and a group of small, rapidly maturing, long-flowering species that soon succumb to interspecific competition during secondary succession (*Epilobium ciliatum*, *Veronica persica*, *Senecio squalidus*).

To the extent that the niches of the resident natives define the niche space occupied by an entire community, it is clear that there will always be vacant niches for alien invaders at 'both ends' of any niche axis. For every ordination of the resident native species (e.g. along an r-K continuum based on time since last disturbance, or on a ranking from most to least nutrient demanding) there are (at least) two possibilities for invasion by an alien species. For example, on a successional niche axis, the alien could grow taller than the native dominant (e.g. alien trees like *Pinus* spp. or *Acacia* spp. overtop and outcompete the native dominant Proteaceae in South African fynbos; Cowling 1992). On an axis of nutrient supply rate, an alien species could invade if it was less demanding in its nutrient requirements than the most tolerant native species (i.e. it had a lower R* sensu; Tilman 1988). We can already see the potential for British invasions of this kind. Given only a modest degree of climatic warming, trees like *Robinia pseudoacacia*, *Ailanthus altissimus* and *Quercus cerris* might begin to replace native dominants, as they have in other parts of Europe (Pysek *et al.* 1995). Similarly, there will always be the possibility of replacement of native early successional species by alien r-strategists that do things more quickly, or disperse their seeds more widely (e.g. *Epilobium ciliatum*, *Conyza sumatrensis*, *Galinsoga parviflora*).

For non-extreme positions on the niche axis, the value of the concept of vacant niche is much less obvious. Does the likelihood of establishment of an alien species 'in between' two native species depend upon their degree of niche separation? Does establishment of an alien species necessarily lead to the greatest reduction in abundance of those native species that are closest to it on a niche axis? Which of the many possible niche axes are predicted to be the most important in explaining or predicting alien invasions ?

Despite the importance of chance and timing in the establishment of alien plants (Crawley 1989), invasions are clearly not completely random events. There are several predictable patterns: (1) weeds in one country are likely to become weeds when introduced to another climatically matched country; (2) invasive crop plants in one country will be invasive in other countries at similar latitudes; (3) the rate of establishment of alien plants will be proportional to the frequency and intensity of disturbance of the habitat (e.g. by alien ungulates); (4) the higher the rate of introduction of propagules and the greater the degree of matching of the ecological attributes of the source and target habitats, the greater the number of alien species is likely to be; and (5) alien plants will grow bigger and have greater ecosystem-level impact than equivalent native plant species as a result of release from their specialist pathogens and herbivores. On the other hand, there appears to be rather little that can be said about the native distribution and abundance of non-weedy plants and their likely performance as aliens. In the case of introduced insects used for the biological control of weeds, there was a positive correlation between the probability of establishment and their distribution and abundance as natives (Crawley 1986, 1987). No such pattern is apparent for British alien plants. In the genus *Impatiens*, for example, the three alien species show an inverse correlation between the extent of their native range and the extent of the alien range within Britain; the most widespread and abundant alien in Britain, *I. glandulifera*, has the most restricted native range.

Most of the differences between the findings of the present analysis and those of earlier studies can be put down to the lack of any attempt at phylogenetic control in works reported in Drake *et al.* (1989), Cowling (1992) and Pysek *et al.* (1995). Their contrary opinions about the importance of life history, seed size and plant height can all be attributed to the problems associated with using chi-squared contingency tables to analyse species count data (Crawley 1993), when there is conspicuously unequal taxonomic representation of natives and aliens (table 1). If the estimate of phylogeny contains non-monophyletic groups, Type I error rates will be elevated. If not all true sister-taxon relationships are shown in the available phylogeny, Type II rates will rise. In the absence of true branch length information, both will rise. These caveats should be borne in mind when considering any of our findings that are near the threshold of significance or based on few contrasts. However, they should not be taken as reasons in favour of analyses treating species as independent; our estimate of phylogeny, however faulty, reflects reality much better than the assumption implicit in such a treatment (namely, that all species radiated instantaneously from a common ancestor). Indeed, simulations show that such cross-species analyses often have wildly elevated Type I error rates, far in excess of any rate found with independent contrasts even when its assumptions are violated (Grafen 1989; Purvis *et al.* 1994).

Finally, the appearance of similar looking 'reconstructed' plant communities made up almost entirely of alien species speaks of the existence of the kind of assembly rules that have proved to be exasperatingly difficult to detect in native vegetation (Wilson 1995). To judge by the few examples studied to date (e.g. mesic grasslands in Hawaii, urban scrublands in Britain), the key parameters are the resource supply rate (this determines the identity of the dominant plant species) and the life history, size and longevity of the dominant alien species (e.g. *Ulex europaeus* in Hawaii, *Buddleja davidii* in Britain). These alien plant communities represent a rich source of natural experiments on community assembly.

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