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Research article

Sweet flowers are slow and weeds make haste: anthropogenic dispersal of plants via garden and construction soil

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Abstract

Anthropogenic activities are increasingly responsible for the dispersal of plants. Of particular concern is anthropogenic dispersal of problematic invasive non-native plants. A common dispersal vector is the movement of soil containing seeds or rhizomes. Housing development and domestic gardening activities cause large quantities of soil to be moved, and understanding the role of these activities is critical for informing policy and management to reduce the spread of problematic plants. Here, by collecting soil samples being moved for housing development and domestic gardening, and observing the species that germinated from these samples, we determined the quantities and invasive status of plants moved. From our samples nearly 2000 individuals representing 90 species germinated. Our results suggest that given the quantity of topsoil needed to cover an average-sized UK garden (190 m^2), there could be 2.2 million and c.2 million viable seeds in soil sourced from housing developments and gardens, respectively. In both housing development and garden samples, native species were more abundant and species-rich than non-native naturalised and invasive species. Buddleia (an invasive) was the most common species overall and in garden samples; this is likely due to multiple traits that adapt it to dispersal, such as prolific seed production. The abundance of invasive and naturalised species was significantly higher in garden than in housing development samples, suggesting that informal movement of soil between gardens poses a greater risk of spreading invasive plants than commercial sources. Consequences for models predicting future distributions of plants, and strategies to mitigate anthropogenic dispersal of problematic plants are considered.

Key words: biodiversity, *Buddleia davidii*, domestic gardens, Japanese knotweed, non-native plants, seed-bank

Introduction

Anthropogenic dispersal, both intentional and unintentional, has long been a factor in determining plant distributions (Thuiller et al. 2006). However, the magnitude and impacts of anthropogenic dispersal are increasing at an unprecedented rate due to growth in global trade and travel (Banks et al. 2015). Anthropogenic activities can move plants within and beyond their native ranges. Some species moved in this way will become invaders with serious ecological and socio-economic impacts (Simberloff et al. 2013).

One of the most important anthropogenic dispersal pathways is the transport of seeds or rhizomes within soil (Hodkinson and Thompson 1997; Hulme et al. 2008). For example, an average of 5.4 seedlings germinated from commercial topsoil samples (120 cm^3) from an arable source in Northern England (Hodkinson and Thompson 1997). Transportation of invasive non-native plants (INNPs) via soil is particularly concerning, given that many INNPs are already capable of high rates of dispersal into disturbed habitat, for example, by prolific seed production (e.g. Buddleia *Buddleia davidii*; Kriticos et al. 2011), which combined with multiple 'release events' increases propagule pressure and the likelihood of that species becoming established (Lockwood, Cassey, and Blackburn 2005). Another way some invasive species disperse is via re-growth from small rhizome fragments (e.g. Japanese knotweed *Fallopia japonica*; van Ham, Genovesi, and Scalera 2013).

Two of the main activities by which soil is translocated are (1) to and from construction sites and (2) between domestic gardens. One study estimated that 0.8 gigatons of earth (soil and rock) is moved annually due to house building in the USA (Hooke 1994); this is likely to increase as global demand for new houses grows. The UK government, for example, plans to build 1 million new homes before 2020 (Prime Minister's Office 2015). Estimating the quantity of soil moved between domestic gardens is difficult but important. In the UK, where ownership of domestic gardens exceeds 20 million and gardening is the country's most popular leisure activity (67% of UK adults list gardening as a hobby; Gross and Lane 2007), the amount of soil transported for gardens is likely to be significant. Traditionally, garden soil was likely obtained from known sources such as friends and family. However, soil is increasingly obtained from a greater variety of sources using 'informal networks', for example, Internet trading sites (e.g. Freecycle™ and Gumtree™) and newspaper adverts. This could result in soil, and therefore potentially seeds and rhizomes, being transported over larger distances.

Despite large quantities of soil being frequently moved due to house construction and gardening, no research has, to our knowledge, empirically studied which species are transported via these methods and in what quantities. Such research is critical for informing policy and management guidelines to reduce the spread of problematic species via such transportation routes. Furthermore, the accuracy of models to predict future distributions of INNP could be greatly improved by better understanding of these species' anthropogenic dispersal mechanisms. Understanding the drivers of INNP distributions is key for identifying high-risk areas, and subsequently to inform management recommendations (Hodkinson and Thompson 1997; Gallardo, Zieritz, and Aldridge 2015).

In this study we determined the species, invasive status and abundance of plants transported in samples of soil used on housing developments and being swapped between gardens via 'informal networks' in the UK. We explored relationships between status (native, naturalised and invasive) and (1) plant abundance and (2) species richness.

Method

Soil samples were collected throughout west Cornwall, UK from (1) commercial residential housing developments ($n = 15$), which were at different development stages, from land-clearing through to selling properties and (2) being moved between gardens using 'informal networks' ($n = 15$; see Supplementary Material S1 for details). We offered and provided no incentive for samples.

Following piloting studies, data collection began in March 2015. We took 10 samples of 200 cm^3 of soil from a range of depths and locations within each site or mound of soil. Samples were kept under controlled conditions to encourage germination (see Supplementary Material S2 for details). Most plants were identified between 6 and 12 weeks, although any that could not be identified at this stage were grown on until this was possible. Plants were identified to the highest taxonomic level possible, scientific names checked (The Plant List 2016), perennation (annual, biennial and perennial) and native status (native, naturalised or invasive) recorded (Hill, Preston, and Roy 2004) (see Supplementary Material S3 for details). The number of viable seeds in the amount of topsoil needed to cover an average-sized UK garden was calculated (see Supplementary Material S4 for calculations).

Analyses were carried out using R 3.1.3 (R Core Team 2015). Unidentified plants were excluded from statistical analysis. Using a generalised linear mixed model (Poisson distribution) the 'abundance model' explored the effects of the explanatory variables 'source' (housing development or garden), 'native status' and 'perennation' on plant abundance (number of individual plants per sample). Interactions were included in the model and 'species' was added as a random intercept. An observation level random effect was included, as this has been demonstrated to reduce over-dispersion of the type we observed (Harrison 2014). A marginal and conditional R^2 value was calculated for this model (Nakagawa and Schielzeth 2013).

Using a generalised linear model (Poisson distribution), the 'species richness model' explored the relationship between the explanatory variable 'native status' and 'source' (housing development or garden), and the dependent variable of 'species richness' (number of species per sample). It was not possible to include perennation in the species richness model because within the samples were species with multiple perennation strategies. Models were evaluated using R^2 values (using method from Nakagawa and Schielzeth 2013) and Akaike information criterion (AIC). Tukey's honest significant difference (HSD) tests were used for *post hoc* analyses where required.

The alpha and gamma diversity of the samples from both sources were also calculated, using the Gini–Simpson index (Jost 2006). Beta diversity was calculated by dividing gamma by alpha (Whittaker 1960).

Results

When data for garden and housing development samples were pooled, 1828 individual plants of 90 different species germinated, of which 80 species (1817 individuals) were identifiable (Table 1, see Supplementary Material S5 for details). When scaled up, this suggests that in the topsoil needed to cover an average-sized garden of 190 m^2 (Davies et al. 2009), soil sourced from housing developments and gardens contains 2 184 354 (95% CI = 1 456 106–3 028 683) and 1 983 600 (95% CI = 856 039–3 310 717) viable seeds, respectively (see Supplementary Material S6 for details).

In housing development samples, 91.7% ($n = 878$) of individuals were native, 1.5% ($n = 14$) naturalised, 6.5% ($n = 62$) invasive and 0.4% ($n = 4$) were unidentified. In garden samples, 63.3% ($n = 551$) of individuals were native, 7.9% ($n = 69$) naturalised, 27.9% ($n = 243$) invasive and 0.1% ($n = 7$) were unidentified. Buddleia, a non-native invasive, comprised the largest proportion of seedlings in both housing development and garden samples combined (13.9%, $n = 254$) and in garden samples (25.7%, $n = 224$). There was large variation in the abundance of individuals in each sample, particularly within native species (Fig. 1).

Table 1: Details of total individual plants and species in all, housing development and garden samples

	Total		Housing development		Garden	
Number of	Individual plants	Species	Individual plants	Species	Individual plants	Species
Total	1828	90	958	67	870	62
Native	1429	60	878	50	551	44
Naturalised	83	12	14	7	69	7
Invasive	305	8	62	6	243	5
No-status (unidentified)	11	10	4	4	7	6

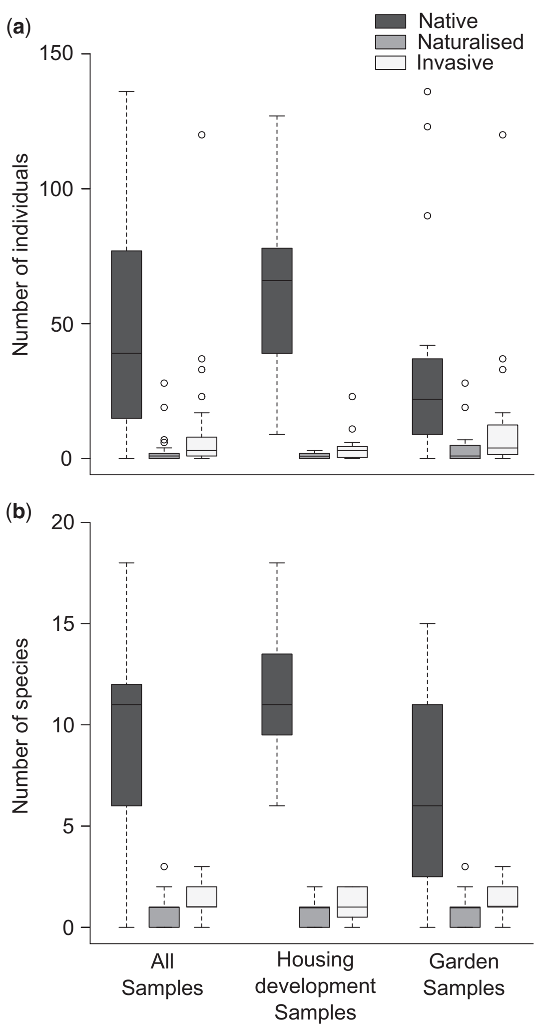

Figure 1: Box and whisker plots for the number of (a) individual plants and (b) species per sample, categorised by source and status.

Native species richness was higher than naturalised species richness, which in turn was higher than invasive species richness (Figs 1 and 2 and Table 1).

Abundance model

Including perennation in the abundance model did not improve parsimony (assessed using AIC), and it was therefore omitted. Species abundance was not significantly different between sources, or between invasive and native plants. However, naturalised species were significantly less abundant than native species overall, and both invasive and naturalised species were more abundant in garden samples than in housing development samples (Table 2a and Fig. 1a). Invasive species appeared more abundant than naturalised; however, this relationship was not statistically significant (Tukey's HSD test: z-value = −1.44, P = 0.312) and was driven by the high abundance of Buddleia.

Species richness model

Garden samples had significantly lower species richness than housing development samples, and both naturalised and invasive plants had significantly lower species richness than native plants (Table 2b and Fig. 1b).

Alpha, beta and gamma diversity

For housing development samples, mean alpha diversity was 0.448, gamma diversity was 0.874 and beta diversity was 1.951. For garden samples, mean alpha diversity was higher at 0.622, gamma was 0.887 and beta diversity was 1.426.

Discussion

This study demonstrates for the first time that large numbers of several native, naturalised and invasive plants are likely being dispersed in soil moved from, to and between housing development sites and gardens. The number of plants that germinated from our samples (nearly 2000 individuals of 90 species), if extrapolated to the quantity of topsoil needed to cover an average-sized garden, would suggest that there could be 2.2 million and c.2 million viable seeds in soil sourced from housing developments and domestic gardens, respectively.

The predominance of Buddleia in our samples was unsurprising considering, it possesses multiple traits typical of invasive species: prolific seed production, fast growth, brief juvenile phase and small seeds (Tallent-Halsell and Watt 2009; Kriticos et al. 2011). The last trait is particularly important for transportation within soil. Conversely, Japanese knotweed, which is regarded as a particularly problematic INNP in the UK, was absent in our samples. Japanese knotweed is considered widespread in the study area and concerns about it spreading via soil are frequently voiced (Bailey 2011; van Ham, Genovesi, and Scalera 2013). However, Japanese knotweed reproduction in the UK is probably entirely vegetative—almost all of the plants known in the UK are female, and fertilisation of flowers is rare; UK summers may also be too cool for effective reproduction by seed (Barney et al. 2006). Transportation within soil is due to rhizome fragments within the soil itself (van Ham, Genovesi, and Scalera 2013). For a soil sample to contain rhizome fragments, it would have to be taken from the rooting zone of a Japanese knotweed plant or have received input from an external source such as river flooding. While soil transportation may be a major factor

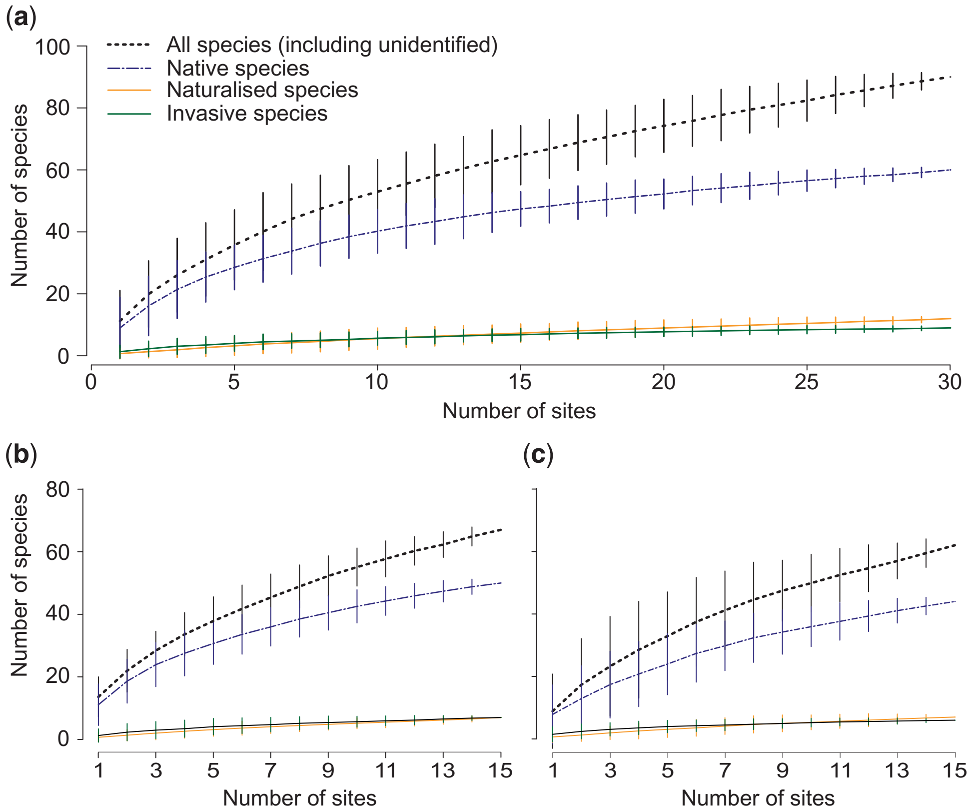

Figure 2: Species accumulation curves for (a) all samples, (b) housing development samples and (c) garden samples, by species status.

Table 2: Results of models exploring (a) species abundance and (b) species richness

	Parameter estimate	Standard error	z-Value	Significance
(a) Effect of source and status on plant abundance				
R^2 marginal = 0.041; R^2 conditional = 0.114				
Intercept	1.02	0.11	9.17	***
Source (garden)	−0.17	0.15	−1.19	NS
Native status (invasive)	−0.31	0.34	−0.9	NS
Native status (naturalised)	−1.08	0.44	−2.46	*
Source (garden) × native status (invasive)	0.88	0.41	2.17	*
Source (garden) × native status (naturalised)	1.45	0.56	2.57	*
(b) Effect of source and status on species richness				
R^2 = 0.098				
Intercept	2.43	0.08	31.65	***
Source (garden)	−0.39	0.12	−3.19	**
Native status (invasive)	−1.99	0.25	−7.83	***
Native status (naturalised)	−2.11	0.31	−6.78	***
Source (garden) × native status (invasive)	0.42	0.36	1.18	NS
Source (garden) × native status (naturalised)	0.39	0.44	0.89	NS

Base categories were housing development and native.
Significance codes:
***<0.001,
**<0.01,
*<0.05, NS, non-significant.

in spreading Japanese knotweed, these findings suggest that the species' propagules are much less widespread within soil samples from gardens and housing development sources than are those of Buddleia.

The finding that overall native species were more frequent and abundant than non-natives (naturalised and invasive; Fig. 1) and on average more species rich per sample (Table 2b) is consistent with other studies sampling seed banks in the UK (Thompson et al. 2005; Cockel and Gurnell 2012). The three most abundant native species, *Juncus* spp., *Carrex* spp. and *Festuca* spp., were all perennial Graminoids. Graminoids are common in lawns and gardens (Thompson et al. 2005), as well as more generally in the suburban and urban environment (i.e. road verges; Dunnett et al. 1998). Graminoids rapidly colonise disturbed or bare ground (Britton and Fisher 2007) and are often weeds in cultivated beds, so they are likely to be among the most abundant sources of seed. In addition, some are grown ornamentally—the native pendulous sedge (*Carex pendula*) is widely grown in gardens in Cornwall (Preston, Pearman, and Dines 2002, personnal observation). Perennial graminoids have also been found to be amongst the more common species transported in soil on car tyres (Ansong and Pickering 2013).

Given that the abundance of invasive and naturalised species was significantly higher in soil sourced from domestic gardens than from housing developments, informal movement of soil between gardens is more likely to spread INNP than the construction industry. It should be noted that many naturalised species not currently classified as problematic may become so in the future, particularly if their abundance and range is expanded by anthropogenic transportation (Simberloff et al. 2013). In addition to having negative ecological and socio-economic impacts within gardens, INNP species spread via soil might also escape into the wider environment and cause further damage (Dehnen-Schmutz et al. 2007).

The higher number of both individual plants and number of species in housing development samples was interesting given that one would predict that gardens have greater species diversity due to people planting therein. The origin of soil in housing developments is inherently uncertain. This is because in addition to soil being used that has been collected *in situ*, it is also frequently transported between housing developments. We do not have data on the origin of the soil for this study. However, soil imported over greater distances increases the likelihood of introducing new invasive species to a region, and it is possible that the large corporations transport soil over longer distances than do individual people. Recent evidence shows that native species appear to occupy a small proportion of their potential ranges (Bradley, Early, and Sorte 2015). Therefore, soil transportation could move native species into previously unoccupied areas that are environmentally suitable for them, and thus escape habitat loss in their current ranges.

The high alpha diversity (within sample) for garden samples suggests that although gardens harbour many species, the species in each garden are very similar. This could reflect the similar geographic region from which the garden samples were drawn. The lower alpha than beta diversity in housing development samples could be due to the diverse sources of the soil, which could have potentially been obtained far from where samples were collected. A consequence could be that it will be more likely to find a higher number of species not otherwise found in the 'focal region' in housing development than garden samples. The INNP in garden soil, on the other hand, might be better known in the focal region, and so it could be easier to raise awareness about these species amongst garden owners. If messages about the commonly transferred INNP could be clearly and efficiently communicated, it could increase the chances they are identified early, and therefore are more likely to be managed before they become established and spread (Simberloff et al. 2013).

In the UK, a range of regulations and guidelines influence how housing developers move, store, process and dispose of soil (DEFRA 2009; Government Environmental Permits), for example, the EU Waste Framework Directive, Site Waste Management Plans Regulations 2008, and Town and Country Planning Act 1990. Commercial topsoil has to comply with rigorous standards (BSI 2015). Soil moved between gardens is not subject to such restrictions. Expanding the soil movement regulations to include soil transferred between domestic gardens would be extremely difficult to implement and monitor. Therefore, developing incentives for voluntary regulation, such as encouraging recycling soil on site, should be a priority. Furthermore, promoting awareness among domestic garden owners/managers of the need to monitor imported soil for INNPs will help in early identification and allow more effective control (Simberloff et al. 2013).

In further research, it would be interesting to explore explanatory traits driving abundance patterns of particular species across samples, and to alter the method by, for example, chilling soil samples for longer (Thompson et al. 2005). Furthermore, as the species accumulation curves for all species and for native species (Fig. 2) show no indication of asymptotes, it suggests that increased survey effort could have resulted in an increased number of species for both housing developments and garden samples. This would increase estimates of the number of viable seeds in the topsoil covering an average-sized garden.

In conclusion, this study demonstrates new evidence of the scale of anthropogenic plant dispersal. Greater consideration of anthropogenic plant dispersal via soil in models forecasting species range shifts, alongside awareness campaigns to highlight the hazards of moving soil around and the need to monitor what grows from such soil, could mitigate the negative implications of anthropogenic plant dispersal.

Supplementary data

Supplementary data are available at *JUECOL* online.

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Authors' contributions

All authors designed the survey; B.R. collected samples; B.R. and J.B. identified the samples; B.R., J.B., R.I. and R.E. carried out analysis; B.R. drafted the manuscript. All authors edited this and subsequent versions of the manuscript.

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