



Non-local genotypes of a resident grass species reduce invertebrate species richness

MARTIJN L. VANDEGEHUCHTE,^{1,2} EDUARDO DE LA PEÑA,¹ PETER BREYNE³ and DRIES BONTE¹ ¹Department of Biology, Terrestrial Ecology Unit, Ghent University, Ghent, Belgium, ²Department of Biology and Natural Resource Ecology Laboratory, Colorado State University, Fort Collins, CO, USA and ³Research Institute for Nature and Forest (INBO), Brussels, Belgium

Abstract. 1. Effects of the genotypic identity of a plant can extend beyond the individual phenotype to the community. Because plant material is moved around at an increasing rate, introductions of non-local plant genotypes that are difficult to distinguish from local ones are probably common. Even though such introductions can cause cryptic invasions, their effects on local communities remain largely unexplored.

2. *Ammophila arenaria* is transported and planted throughout the world for dune stabilisation. We used this grass to address the impact of the introduction of non-local genotypes on the diversity of the local invertebrate community. We installed plants from the local population and five introduced populations from regions throughout the natural range in a common environment and identified all naturally colonising aboveground invertebrates.

3. The diversity of the entire invertebrate community, as well as that of herbivores, decreased with increasing geographical distance of the plants' location of origin. Differences between plant populations in predator and detritivore diversity were less consistent with this pattern. Invertebrate species turnover was not related to genetic distance between populations.

4. Our study demonstrates that introduction of non-local genotypes of a resident plant species can negatively affect the invertebrate community. This confirms the idea that caution should be exerted when selecting plant material for restoration or sand stabilisation purposes. Hitherto, explanations for the invasiveness of *A. arenaria* in other continents have been sought in its release from belowground pathogens. Our observation of lower shoot herbivore diversity on non-local plants, however, may indicate a role for release from aboveground enemies.

Key words. *Ammophila arenaria*, community genetics, cryptic invasion, enemy release hypothesis, invertebrate diversity, plant genotype.

Introduction

Genetic variation in plant populations can affect ecological functioning at different levels of organisation, from the individual plant phenotype to the associated ecological community (Crutsinger *et al.*, 2006; Bailey *et al.*, 2009; Madritch *et al.*, 2009). The underlying genotype of a plant can thus produce an extended phenotype that is reflected at the community level, that is a com-

munity phenotype (Whitham *et al.*, 2003, 2006). Different studies have compared the invertebrate fauna of different plant populations or genotypes, often using hybrids (Dungey *et al.*, 2000; Hochwender & Fritz, 2004; Bangert *et al.*, 2005; Hochwender *et al.*, 2005; Wimp *et al.*, 2005, 2007; Tovar-Sánchez & Oyama, 2006; Johnson, 2008; Mooney & Agrawal, 2008; Barbour *et al.*, 2009a,b; Crutsinger *et al.*, 2009; Schadler *et al.*, 2010). The majority of these studies conclude that different plant genotypes harbour different invertebrate communities, often with quantitative differences in species richness.

Given these far-reaching effects of variation among plant genotypes, introducing plants from one spatial population into

Correspondence: Martijn L. Vandegehuchte, Department of Biology, Colorado State University, Fort Collins, CO 80523-1878, USA. E-mail: martijn.vandegehuchte@colostate.edu

another may hold consequences for the larger ecosystem. Such introductions can lead to so-called cryptic invasion, in which invaders cannot, or at least not easily, be recognised from local varieties of the same species. Contrary to the well-studied impacts of invasive plant species (Richardson & Pysek, 2008), the phenomenon of cryptic invasion is much less recognised, but probably very common. Alien genotypes of a local species can become cryptic invaders (Saltonstall, 2002). For example, an introduced European genotype of common reed (*Phragmites australis*) has spread throughout North America, replacing the local genotype with one characterised by a longer lifespan and lower levels of insect herbivory (Saltonstall, 2002; Park & Blossey, 2008).

Ammophila arenaria (L.) link is a perennial grass native to all coastal dunes of Europe south of latitude 63°N. This species needs regular burial by wind-blown sand to maintain vigorous growth and starts to decline as soon as sand-drift ceases (Huiskes, 1979). Because of its ability to stabilise sand dunes, *A. arenaria* has been used for erosion control for a very long time in Europe (Green, 1965). Because of the success of *A. arenaria* as a sand binder, the species has been introduced in regions across the world, including Australia, New Zealand, South Africa, India, the Falkland Islands and the west coast of the USA (Green, 1965; van der Putten *et al.*, 2005). In Australia (Heyligers, 1985), New Zealand (Hilton *et al.*, 2005) and the USA (Wiedemann & Pickart, 1996), *A. arenaria* is now considered invasive. In South Africa, its spread seems to be limited by water availability (Peter, 2000), although the persistence of the planted populations and the potential for invasion have raised concern and the question for more research (Hertling & Lubke, 2000).

Although the species is not invasive in Europe, cryptic introductions of non-local genotypes into local populations are likely, because *A. arenaria* plants are still used on a large scale for sand stabilisation purposes. For example, in the dunes of Voorne in the Netherlands, 120 ha of foredune ridge has been fortified with *A. arenaria* (van der Putten & Kloosterman, 1991). If non-local genotypes are used for such massive plantings, the consequences could be similar to those of an invasion. Cryptic invasion has already been demonstrated for the North American *A. breviligulata*, where some genotypes used for dune restoration differ from the local genotypes (Fant *et al.*, 2008), and have spread beyond documented restoration areas (Holmstrom *et al.*, 2010).

In a previous study, we demonstrated that seven of 10 common aboveground invertebrate species were less frequently encountered on *A. arenaria* plants from one or several of five introduced European populations than on plants from the local population (Vandegehuchte *et al.*, 2011). These seven species covered the herbivore, predator and detritivore guilds. In contrast, root-feeding nematodes preferentially colonised the non-local populations (Vandegehuchte *et al.*, 2011). In this paper, we assessed whether the species richness of the entire aboveground invertebrate community differed between plant populations of different genotype and whether these differences were more pronounced for herbivores, predators or detritivores. We tested whether the invertebrate species turnover between two plant populations depended on the genetic distance between those two populations and/or the geographical distance between the locations of origin of those two populations.

We suggest that not only introduction of *A. arenaria* into ecosystems where it is absent, but also introduction of *A. arenaria* populations into ecosystems where a local *A. arenaria* population is present can affect the diversity of the local invertebrate community. In our study, genetic distance was correlated with geographical distance between plant populations. We hypothesise that populations from distant locations exert larger effects on the local invertebrate diversity and that species turnover increases with genetic and geographical distance between populations. We specifically address the question whether introduced populations support less herbivore species, because this would point at the possibility of enemy release.

Material and methods

Set-up of field experiment

The field experiment has been described in Vandegehuchte *et al.* (2011). It was conducted in the dunes of the Flemish nature reserve 'Westhoek' in De Panne, at the Belgian coast. In this reserve, large areas of drifting sand can still be found. In these dynamic sand dunes, *A. arenaria* is the dominant plant species, often occurring as monospecific stands.

From 2002 until 2005, seeds of *A. arenaria* were collected each summer from single populations at six locations in Europe, namely Oostvoorne (the Netherlands: 51°53'N, 4°2'O), Het Zwin (Belgium: 51°21'N, 3°21'O), Westende (Belgium: 51°9'N, 2°45'O), De Panne (Belgium: 51°5'N, 2°34'O), São Jacinto (Portugal: 40°39'N, 8°44'W) and Comporta (Portugal: 38°22'N, 8°48'W). These locations were selected to cover a wide range of geographical distances to the field site. At each location, 5–10 spikes were collected from four plants, standing 25 m apart.

Seeds were germinated, and plants were grown according to a standardised procedure. Seventeen months after germination, 10 mature tussocks of each population were taken out of their pots and transplanted to a large open sandy patch in the dunes (51°5' 29.79'N, 2°34' 8.73'E). Plants were randomised in a set-up of six rows of 10 tussocks. They were left in the field from 22 May until 25 September 2008. Details of the growing procedure and characteristics of the plants can be found in Vandegehuchte *et al.* (2011). At harvest, all plants were cut off at ground level and transferred to the laboratory. Leaves were oven dried overnight at 65 °C and weighed.

Maternal effects should be effectively minimised by the length of time the plants spent in a common environment (Johnson *et al.*, 2006). Moreover, the site of the experiment has been void of any natural vegetation for at least 60 years. The sandy soil did not contain any roots or other fragments and was well homogenised by wind dynamics. Therefore, differences between individual plants because of their environment should have been absent. Furthermore, the random configuration of the plants should have precluded any bias in the effect of plant population caused by spillover of invertebrates to surrounding plants or by influences of the landscape matrix on colonisation patterns. As a consequence, all observed differences between plant populations should be due to broad-sense genetic variation.

Recording of invertebrates

At eight occasions between 4 July and 24 September 2008, all plants were carefully hand searched to assess the presence of aboveground invertebrate species. Adult invertebrates of the orders Araneae, Coleoptera, Collembola, Dictyoptera, Hemiptera, Isopoda, Lepidoptera, Opiliones, Pulmonata and of the family Formicidae of the order Hymenoptera were identified to the species level. Adults of the orders Psocoptera, Dermaptera, Diptera, Acari and Hymenoptera (excluding Formicidae) as well as all larval or nymphal stages were classified into morphospecies. In total, 79 species and 21 morphospecies were recorded. Of those 21 morphospecies, 14 were represented by a single individual. The large majority of invertebrates could thus be identified to the species level.

Invertebrate diversity measures

The alpha diversity of each plant was determined as the number of species recorded on that plant at least once. Similarly, the alpha diversity of a population was equated with the number of species recorded on at least one plant of that population at least once. Whittaker's effective species turnover (β_{Mt-1}) was used as a measure of beta diversity between populations (Tuomisto, 2010a). This is the total or gamma diversity divided by the average population alpha diversity, subtracted by one to set the minimum value to zero. We followed a pairwise approach (Tuomisto, 2010b) by calculating pairwise effective species turnover values between plant populations. Between the six populations, 15 pairwise species turnover values could be calculated.

Each diversity measure was calculated for a full data set of all encountered species and a reduced data set only retaining species with a known ecological association with *A. arenaria*. This way, potential noise in the data caused by the presence of vagrant or transient invertebrate species could be ruled out. We subsequently repeated the calculations for herbivores, for predators and omnivores taken together, and for detritivores from the data set of associated species, to investigate whether diversity patterns differed according to trophic level.

Genetics of the *A. arenaria* populations: Amplification Fragment Length Polymorphism (AFLP) analyses

Details of the AFLP analyses can be found in Data S1.

Statistical analysis

The effects of plant population (categorical), shoot dry mass (continuous) and their interaction on the individual plant alpha diversity were tested with a permutational ANOVA based on 99 999 permutations of residuals under a reduced model, using type III sums of squares (Anderson *et al.*, 2008). Dry mass of the shoot was included as the covariate in the analysis of alpha diversity, because of the expected species-area relationship.

In all analyses, homogeneity of variances was tested with a permutational Levene's test based on 99 999 permutations. It should be noted that for permutational ANOVA, there are no explicit assumptions regarding the distribution of the original variable. Variances were homogeneous (Levene's test, $P > 0.05$) for all variables.

We investigated directional trends in each of the tested variables, by means of an ordered heterogeneity (OH) test (Rice & Gaines, 1994a,b). We ranked the six plant populations in order of geographical distance to the local population. Subsequently, Spearman's rank correlation (r_s) between these distance ranks and the ranks of the means of the tested variable was calculated. The complement of the P -value of the population effect in each of the above-described ANOVAs (P_c) was then multiplied with the obtained Spearman's rank correlation. This measure $r_s P_c$ increases when the heterogeneity among populations increases in a fashion that is consistent with the ordering prescribed on the alternative hypothesis and can be used as a test statistic. Because we did not have any a priori hypothesis about the direction of this ordering, the alternative hypothesis stated that the order of means, be it ascending or descending, was monotonically related to the order of the populations. Therefore, a two-tailed P -value for the $r_s P_c$ statistic was obtained from Rice and Gaines (1994a).

We used separate Mantel tests to assess whether the pairwise effective species turnover between populations was related to either their geographical or genetic distance. All Mantel tests were based on 99 999 permutations.

Results

The alpha diversity of invertebrates associated with a plant, based on all species, differed significantly according to an interaction between shoot dry mass and plant population (Table 1). As expected, the number of species increased with larger shoot biomass, but the strength of this increase differed between plant populations (Fig. 1a). For example, even on plants from Comporta with a large biomass, the number of species remained relatively low. The main effect of plant population was highly significant, even after correction for the effect of shoot biomass. The OH test revealed a significant consistency of the effect with the order of geographical distance from De Panne (Table 2). Plants from Belgian populations supported a larger diversity of invertebrates compared with plants from the Netherlands and Portugal (Fig. 1a). Very similar results were obtained when the analysis was restricted to invertebrate species with a known ecological association with *A. arenaria* (Tables 1 and 2, Fig. 1b). The observed pattern was thus little influenced by the inclusion of transient species from other habitats or species with an unknown host-plant affiliation. These findings confirm our hypotheses that introduced *A. arenaria* populations affect the local invertebrate community associated with this grass and that populations from distant locations exert larger effects.

The effect of shoot dry mass on the alpha diversity of herbivores of *A. arenaria* was significant, as was the main effect of plant population. The interaction between shoot mass and plant population was not significant in this case (Table 1). Again, the number of herbivore species per population decreased in order

Table 1. Results of the ANOVAS testing the effect of shoot dry mass and plant population on the alpha diversity of different groups of species.

Source	d.f.	SS	MS	Pseudo- <i>F</i>	<i>P</i>	Unique perms
Alpha diversity all species						
Mass	1,48	410.33	410.33	66.674	0.00001	90 476
Pop	5,48	162.33	32.467	5.2756	0.0006	95 263
Mass × pop	5,48	173.72	34.744	5.6456	0.0004	95 245
Alpha diversity associated species						
Mass	1,48	305.08	305.08	69.195	0.00001	90 475
Pop	5,48	147.02	29.405	6.6692	0.00008	95 269
Mass × pop	5,48	128.09	25.618	5.8103	0.0003	95 173
Alpha diversity associated herbivores						
Mass	1,48	23.258	23.258	13.5	0.0006	90 386
Pop	5,48	49.384	9.8767	5.733	0.0003	95 197
Mass × pop	5,48	10.771	2.1541	1.2504	0.303	95 210
Alpha diversity associated predators and omnivores						
Mass	1,48	90.525	90.525	59.954	0.00001	90 555
Pop	5,48	27.727	5.5455	3.6727	0.0077	95 234
Mass × pop	5,48	52.008	10.402	6.8889	0.00005	95 217
Alpha diversity associated detritivores						
Mass	1,48	9.7934	9.7934	15.383	0.0002	90 492
Pop	5,48	0.4371	0.087419	0.13731	0.983	95 260
Mass × pop	5,48	7.3129	1.4626	2.2973	0.056	95 267

Mass, shoot dry mass; MS, mean squares; Pop, plant population of origin; SS, sums of squares.

of the population's geographical distance to the field site, so a higher species richness was found on Belgian plant populations (Table 2, Fig. 2a). In other words, plants from more distant populations were visited by a lower number of herbivore species, suggesting these introduced *A. arenaria* populations may experience enemy release.

The alpha diversity of predatory and omnivorous invertebrate species, known to occur in *A. arenaria* stands, increased significantly with shoot dry biomass. The strength of this relationship significantly differed between plant populations (Table 1), but also the main effect of plant population was highly significant. The species richness of predators and omnivores did not correspond well with the order of the geographical distances of the populations to the local population (Table 2). This can be seen in Fig. 2b, where it is clear that for an average shoot weight of 14.7 g, the number of species is highest on plants from São Jacinto, but lowest on plants from Comporta. So even though introduced plant populations clearly affected the diversity of predators and omnivores, this effect was not necessarily negative, as opposed to the effect on herbivore diversity.

The number of detritivore species that are associated with *A. arenaria* vegetations was significantly affected by the dry mass of the shoot. No significant main effect of plant population was detected, but the interaction between shoot mass and plant population was marginally significant (Table 1). The steepest increase in detritivore species number with shoot dry mass was observed for the Belgian populations, while this increase was weaker for plants from São Jacinto and Oostvoorne. On plants from Comporta, the number of detritivore species even slightly decreased with increasing shoot biomass (Fig. 2c). The order of the corrected mean numbers of detritivore species matched the order of the populations' distance to the field site perfectly

($r_s = -1$). As a consequence, the OH test yielded a lower *P*-value than the ANOVA. However, the main effect of population still remained non-significant (Table 2). In summary, introduced plants supported a lower detritivore diversity than local plants, and this difference increased with the geographical distance to the local population, but was only visible if plant biomass was relatively high.

For each of the five tested species groupings, Mantel tests revealed that Whittaker's effective species turnover was not significantly correlated with either the genetic or the geographical distance between plant populations. This implies that, contrary to our hypothesis, the difference in invertebrate species' identity was similar between all plant populations, whether these were genetically more or less related.

Discussion

Introduced plant populations clearly supported a lower number of invertebrate species. This effect was most pronounced for herbivores whose species richness decreased with increasing genetic or geographical distance of the introduced genotype. In a previous study of this experiment, we found that of the ten most common aboveground invertebrate species, a majority occurred less frequently on plants from the introduced populations (Vandegehuchte *et al.*, 2011). It thus seems that these single common species' responses are representative of the entire aboveground invertebrate community, including many rare species, resulting in a lower local diversity on introduced plants.

Based on the selectively neutral AFLP markers, an overall genetic isolation by distance of the used plant populations was observed (Data S1). This was mainly because of relatively large

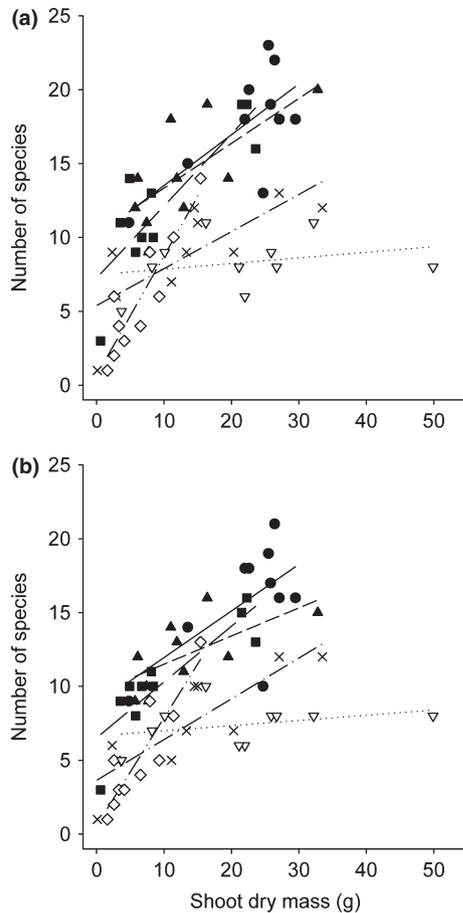


Fig. 1. Relationship between dry shoot mass of a tussock and the number of invertebrate species encountered in that tussock, for six different populations of *A. arenaria*. (a) All invertebrate species included. (b) Data set restricted to invertebrate species with a known ecological association with *A. arenaria*. ● —: De Panne (Belgium), ■ —: Westende (Belgium), ▲ —: Het Zwin (Belgium), × —: Oostvoorne (the Netherlands), ◇ —: São Jacinto (Portugal), ▽ —: Comporta (Portugal).

genetic and geographical distances between the Portuguese and all other populations as well as among the Portuguese populations. At the smaller geographical scale of the North Sea coast, all populations were genetically differentiated from

one another, except for the populations from De Panne and Oostvoorne (Data S1), although of all North Sea populations these were located furthest apart. However, the difference in alpha diversity of the different tested groups of invertebrates was larger between the Oostvoorne population and the Belgian populations than among the Belgian populations. Differences between the North Sea populations in their invertebrate community diversity, therefore, did not correspond well with their genetic differences as revealed by selectively neutral markers. This suggests that genetic differences in quantitative traits under selection rather than neutral shifts in genetic structure are responsible for some of these divergent invertebrate community patterns. Such is also the case for the species richness of the bark-dwelling arthropod community of eucalypt trees in southern Australia, which is tightly linked to genetic variation for the type and quantity of decortivating bark, but does not correlate well with selectively neutral genetic variation (Barbour *et al.*, 2009b). Quantitative traits of *A. arenaria* prone to selection could relate to desiccation resistance, such as root morphology and efficiency, leaf hairs and longitudinal grooves, as well as traits related to defence, such as leaf toughness, silica content or secondary metabolites.

Our expectation that species turnover would increase with genetic distance between the populations was not confirmed. This indicates that differences in the identity of the invertebrate species were similar for all pairs of populations. As in the study of eucalypt arthropods (Barbour *et al.*, 2009b), the genetic similarity rule (Bangert *et al.*, 2006), which states that plants that are genetically more similar (at a molecular level) support more similar communities, is therefore not supported by our results.

Our study demonstrates that introduced populations of *A. arenaria* supported less herbivorous invertebrate species than the local population. Even the introduction of plant populations located at short geographical distances, which are genetically not very differentiated, such as in our case the Oostvoorne population, can reduce the diversity of the local invertebrate community, and in particular that of invertebrate herbivores, substantially. Moreover, our previous study indicated that most of the abundant herbivore species occurred significantly less on plants from at least some of the introduced populations, sometimes even when these originated from locations very nearby (Vandegheuchte *et al.*, 2011).

The probability that cryptic introductions of *A. arenaria* are actually occurring is high. Although this has not been studied directly in Europe, it is a common practice to introduce culms

Table 2. Results of the ordered heterogeneity test for the different diversity metrics.

Diversity metric	d.f.	<i>F</i>	<i>P_F</i>	<i>r_s</i>	<i>r_sP_c</i>	<i>P</i>
Alpha all species	5,48	5.2756	0.0006	−0.8857	−0.8852	0.001
Alpha associated species	5,48	6.6692	0.00008	−0.8857	−0.8856	0.001
Alpha associated herbivores	5,48	5.733	0.0003	−0.7714	−0.7712	0.006
Alpha associated predators and omnivores	5,48	3.6727	0.0077	−0.4286	−0.4253	0.14
Alpha associated detritivores	5,48	0.13731	0.983	−1	−0.017	0.86

r_s, Spearman's rank correlation between the order of plant populations according to their distance to the local population and the means of the tested diversity metric per population. Means were corrected for the shoot dry mass covariate in the model. *P_F*, probability value of the *F*-statistic. *P_c* = 1 − *P_F*. *P*, two-tailed probability value of the *r_sP_c* statistic. The *F*-statistic is from the plant population effect in a permutational ANOVA based on 99 999 permutations.

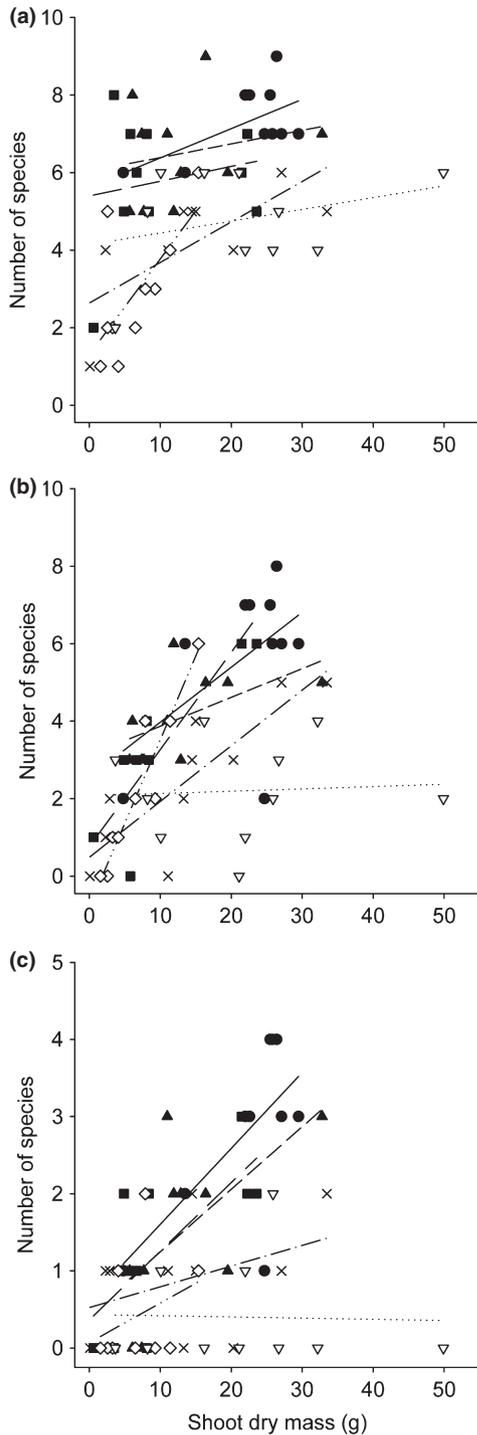


Fig. 2. Relationship between dry shoot mass of a tussock and the number of invertebrate species encountered in that tussock, for six different populations of *A. arenaria*. Only species with a known ecological association with *A. arenaria* are included. (a) Herbivores. (b) Predators and omnivores. (c) Detritivores. ● —: De Panne (Belgium), ■ —: Westende (Belgium), ▲ —: Het Zwin (Belgium), × —: Oostvoorne (the Netherlands), ◇ —: São Jacinto (Portugal), ▽ —: Comporta (Portugal).

of *A. arenaria* for dune stabilisation. In these events, large extensions of dune are planted, presumably not always with plants of the local genotype. In North America, where the congener *A. breviligulata* is applied in the same way, it has been shown that genetically different populations have been introduced for restoration purposes (Fant *et al.*, 2008). Interestingly, the introduced Michigan genotype of *A. breviligulata* that is currently spreading in Minnesota suffers lower levels of insect damage to the panicles than the local plants (Holmstrom *et al.*, 2010). The reduced herbivore load on introduced plant genotypes from other parts of the natural range might thus be a general phenomenon within the genus *Ammophila*.

Our results stress the importance of choosing local *A. arenaria* populations to obtain plant material for the use in dune stabilisation or restoration projects, as cryptic introductions of non-local genotypes of this grass, even at small geographical scales, can have negative impacts on the associated invertebrate community. We thereby confirm the hypothesis of Vander Mijnsbrugge *et al.* (2010) that introduced genotypes can negatively affect local herbivore species, which they consider one reason for choosing local plant material for ecological restoration, apart from better known phenomena such as maladaptation of non-local populations or outbreeding depression caused by hybridisation.

Moreover, studies of belowground organisms yielded little evidence for the enemy release hypothesis as an explanation for the invasiveness of *A. arenaria* in other continents (Beckstead & Parker, 2003; Knevel *et al.*, 2004; van der Putten *et al.*, 2005). Our observation of lower aboveground herbivore diversity on introduced plant genotypes, however, suggests a possibility of aboveground enemy release of *A. arenaria*.

Our experiment furthermore serves as a model system that can provide insight into the effects of introductions at a larger taxonomic and geographical scale, for example the introduction of the European *A. arenaria* into areas of the USA where the local *A. breviligulata* naturally occurs. If similar mechanisms apply to genotypes and species, *A. arenaria* might be experiencing release from aboveground herbivores in the introduced ranges, which could be part of the explanation of the species' invasiveness. Furthermore, given the ever-increasing translocation of organisms around the globe, introductions of non-local genotypes into local communities are expected to increase in frequency. The detection of such cryptic introductions and the investigation of the mechanisms by which they affect communities and ecosystems thus pose new challenges for ecologists.

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Supporting Information

Additional Supporting Information may be found in the online version of this article under the DOI reference: doi: 10.1111/j.1752-4598.2011.00181.x:

Data S1. Details of AFLP analyses.

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