

LETTER

Origin matters: widely distributed native and non-native species benefit from different functional traits

Sonja Knapp* and Ingolf Kühn

Department Community Ecology,
UFZ – Helmholtz Centre for
Environmental Research,
Theodor-Lieser-Str. 4, 06120, Halle
(Saale), Germany

*Correspondence: E-mail: sonja.knapp@ufz.de

Abstract

Recently, ecologists debated whether distinguishing native from non-native species is sensible or not. One argument is that widespread and less widespread species are functionally different, whether or not they are native. An opposing statement points out ecologically relevant differences between native and non-native species. We studied the functional traits that drive native and non-native vascular plant species frequency in Germany by explaining species grid-cell frequency using traits and their interaction with status. Native and non-native species frequency was equally driven by life span, ploidy type and self-compatibility. Non-native species frequency rose with later flowering cessation date, whereas this relationship was absent for native species. Native and non-native species differed in storage organs and in the number of environmental conditions they tolerate. We infer that environmental filters drive trait convergence of native and non-native species, whereas competition drives trait divergence. Meanwhile, introduction pathways functionally bias the frequency of non-native species.

Keywords

Alien species, anthropogenic habitats, archaeophytes, community assembly, functional ecology, neophytes, niches, novel ecosystems, species ranges.

Ecology Letters (2012) 15: 696–703

INTRODUCTION

Non-native species have been increasing in floras around the world, and invasive non-native species are recognised as a major threat to biological diversity that can have severe ecological and economic impacts (Vilà *et al.* 2010). Studying non-native species facilitates increased understanding of the characteristics that drive plant species success. Moreover, understanding the impact of non-natives on ecosystem assembly, processes and functions is crucial for a holistic understanding of today's ecosystems (Hulme *et al.* 2011).

The analysis of traits that allow a non-native species to become invasive or that distinguish non-native species from native species has hence been on the research agenda at least for two decades (see meta-analysis by van Kleunen *et al.* 2010b). Still, Davis *et al.* (2011), in a recent comment in *Nature*, argued that ecologists should not 'judge species on their origins'. Indeed, the ecological effects of species should depend on their functional traits rather than whether they originate from one region of the world or another (Thompson & Davis 2011). Accordingly, Thompson *et al.* (1995) previously argued that the most successful non-native species share the same attributes of widespread native species and that the greatest functional differences lie between invasive and non-invasive species.

The comments of Davis *et al.* (2011) and Thompson & Davis (2011) received several responses arguing that the distinction between native and non-native species is helpful (van Kleunen *et al.* 2011) and that the arguments of Thompson & Davis (2011) are fundamentally flawed (Hulme *et al.* 2011). Indeed, some differences have been detected between native and non-native species: e.g. differences in life form (Crawley *et al.* 1996) or in germination speed and reproduction frequency (Chrobok *et al.* 2011). Native and non-native species also differ in habitat preferences. Many non-native species preferably occupy anthropogenic habitats, including both agricultural and urban-industrial areas (Pyšek 1998). Neophytes (plant species introduced/immigrated after the discovery of the

Americas by Columbus) were 2.3 times more frequent in urban than in rural grid-cells in Germany, in a study by Kühn *et al.* (2004a), whereas archaeophytes (introduced/immigrated prior to the discovery of the Americas) were 1.4 times and native plant species only 1.1 times more frequent in urban than in rural grid-cells. The fact that anthropogenic habitats are preferably occupied by non-native species suggests that these more often share a set of traits adapted to disturbance, eutrophication, fragmentation, etc., than do native species. Accordingly, novel species assemblages (Hobbs *et al.* 2006) that are increasingly impacted by humans are likely to have a considerably higher proportion of non-native species than are found in natural and semi-natural habitats. However, differences between the two groups are usually not related to the success of either group (e.g. measured as abundance or frequency of occurrence or occupancy).

Van Kleunen *et al.* (2010a) introduced a thoughtful conceptual framework for major types of comparison between native and non-native species or among non-native species at different stages of the invasion process. They showed that researchers have mainly compared invasive non-native species to either native species or to non-invasive non-native species, doing this either in the introduced or native ranges. However, the comparison needed to test – or rather challenge – the claims made by Thompson & Davis (2011) requires the comparison of both non-native and native species in the introduced range against a common measure of success. This was exemplarily done by van Kleunen *et al.* (2010a) for *Asteraceae* in Germany. To the best of our knowledge, this sort of analyses is still lacking for complete floras across taxonomic groups.

Applying such an approach, one could expect to detect results of two contrasting processes. The concept of environmental filters (Zobel 1997; Grime 2006) suggests that species sharing traits adapted to prevailing environmental conditions will be selected from the regional species pool and will assemble into the same habitat. Consequently, traits converge. However, after passing the filters, traits should diverge to minimise niche overlap between

species, as suggested by the concept of limiting similarity (MacArthur & Levins 1967). Accordingly, non-native species that enter a native community should on the one hand share the traits of native species that are necessary to pass the prevailing environmental filter. On the other hand, to minimise competition, they should differ from native species in traits that enable them to occupy environmental conditions less favoured by native species (cf. Weiher *et al.* 1998; Kühn & Klotz 2007).

We studied the total pool of native and non-native species in Germany available in the database BiolFlor (Klotz *et al.* 2002; Kühn *et al.* 2004b). Our question was whether species success, expressed as the number of grid-cells in which a species is present, is driven by different functional traits for native and non-native species. We based our analysis on Küster *et al.* (2008), who reported traits that characterise successful invaders compared to non-successful ones, using the same set of trait and distribution data. We hypothesised that widespread native and non-native species are both driven by a set of traits that enables them to occupy widespread, disturbed, anthropogenic habitats (for example, reproduction by seeds and short life-span). At the same time, native and non-native species should differ in traits that limit their similarity far enough to decrease competition pressure within these habitats (for example, different flowering phenology to avoid competition, as shown for *Senecio inaequidens* DC. by Lachmuth *et al.* 2011). Moreover, non-native species should differ from native species in traits that are promoted by cultivation or other introduction pathways, such as an early or late flowering period promoted for flowering gardens.

MATERIALS AND METHODS

Species selection

We built our study on the vascular flora of Germany, documented in the FLORKART database (<http://www.floraweb.de>). Therein, occurrences of 3393 species are recorded on the basis of a *c.* 12 × 11 km grid (i.e. 10°longitude × 6°latitude, equal to *c.* 130 km² per grid-cell). FLORKART is maintained at the German Federal Agency for Nature Conservation (Bundesamt für Naturschutz, BfN) on behalf of the German Network for Phytodiversity (NetPhyD, netphyd.floraweb.de). The database consists of > 14 million records of plant occurrences that were acquired by experts and volunteers for three periods: before 1950, 1950–1980 and after 1980. We calculated the number of grid-cells a species occupied after 1950 and the number of grid-cells from which it was absent (data dating earlier than 1950 are less complete than those from 1950 onwards).

The BiolFlor database documents biological and ecological traits of the German flora (Kühn *et al.* 2004b; <http://www.ufz.de/biol-flor>). We chose all species from FLORKART that are assigned to one of three native/non-native status groups in BiolFlor: species native to Germany, archaeophytes and neophytes.

Trait selection

For selected species, we gathered information on those BiolFlor functional traits that had been identified as relevant to the frequency of neophytes in Germany by Küster *et al.* (2008; see Table S1 in Supporting Information). In addition, we included information on whether or not a species is self-compatible and consequently independent of external pollination vectors (potentially relevant for

successful neophytes; Thompson *et al.* 1995). Generally, we concentrated on terrestrial plant species and excluded all species classified as hydrophytes (species with resting buds situated under water) in BiolFlor. We excluded hydrophytes because environmental filters in terrestrial habitats differ from those in aquatic habitats (Roelofs *et al.* 1996). We expect that patterns governed by environmental filters will show up more clearly when distinguishing terrestrial and aquatic habitats.

For the traits, ‘shoot metamorphoses’ and ‘storage organs’, we grouped trait attributes according to mobility: some shoot and storage organs, such as rhizomes, allow the parent plant to place its offspring away from the parent, whereas others, such as bulbs, do not (Table S1 in Supporting Information). The two traits nominally share most of their trait states (i.e. classes) but do not necessarily need to be the same; for example, rhizomes can be both shoots and storage organs but not every rhizome is a storage organ.

‘Affinity to urban areas’ classifies species according to their ability to cope with urban environmental conditions. The concept was introduced by Wittig *et al.* (1985) and distinguishes species that are well adapted to urban environmental conditions (urbanophilic species), species that are indifferent towards urban conditions (urbanoneutral species), and species mal-adapted to urban conditions, which hardly occur in urban areas (urbanophobic species).

The trait ‘number of hemerobic levels’ refers to the concept of hemeroby of the Finish botanist Jalas (1955; cf. Hill *et al.* 2002). Hemerobic levels describe the degree of anthropogenic habitat transformation away from the habitat’s natural state. Levels range from ahemerobic habitats that are not transformed at all to meta-hemerobic habitats that are completely destroyed (e.g. completely sealed; Table S1 in Supporting Information).

Number of habitat types, vegetation formations and vegetation units are closely related to each other. However, the first classifies species according to the abiotic conditions in which they occur (e.g. in bogs or urban-industrial habitats); the second and third classify species according to species composition, with vegetation formations forming the coarser level (e.g. pioneer vegetation on rocks), and vegetation units forming the finer level (e.g. communities of rock and wall crevices or communities of heavy metal soils).

Trait-status interaction models

Simple generalised estimating equations (gee)

We explained the frequency of grid-cells a species occupied by functional traits and their interaction with the species’ native/non-native status. This enabled us to show whether or not the frequency of native species is driven by different trait attributes than the frequency of non-native species. The frequency of potentially occupied grid-cells is limited – a species can neither occur in less than 0 grid-cells, nor can it occur in more than the 2995 grid-cells available in Germany; hence, we logit-transformed species frequency as recommended by Williamson & Gaston (1999).

To first test the effect of each trait-status interaction separately, we applied one generalised estimating equation (R-package ‘gee’; Carey 2011) per trait-status interaction (simple models). Models were run once with a phylogenetic correlation structure based on Brownian Motion, (Freckleton *et al.* 2011) using the functions `corBrownian` and `compar.gee` from R-package ‘ape’, (Paradis *et al.* 2004) and once excluding phylogeny. In the latter case, we applied a fixed correlation structure based on an identity matrix (i.e. analogous to a generalised

linear model). The phylogenetic correlation structure was based on an updated phylogeny of the German flora by Durka *et al.*, published in BiolFlor (Klotz *et al.* 2002) and including branch lengths.

Besides single functional traits, Küster *et al.* (2008) identified three trait interactions as relevant to the frequency of neophytes in Germany (Table S1): the interaction between end of flowering season and ploidy, between end of flowering season and shoot metamorphoses, and between length of flowering season and pollen vector. To test whether or not the effects of these interactions differ between native and non-native species, we applied simple gee-models with triple interactions (native/non-native status * trait 1 * trait 2), again both with and without phylogeny.

As we were interested in differences between native and non-native species only, and not in differences between archaeophytes and neophytes, post-hoc tests were not necessary. We included 'native' as the baseline level in each model, such that the model showed differences between natives and archaeophytes and between natives and neophytes. We set significance levels with $P \geq 0.1$ n.s., $0.1 > P \geq 0.05$ +, $0.05 > P \geq 0.01$ *, $0.01 > P \geq 0.001$ ***, and performed all calculations in R (R Development Core Team 2011).

Multiple models

In the second step, we built a multiple model including all trait-status interactions except for shoot metamorphoses, the number of habitat types and the number of vegetation formations. We excluded these three traits because they are redundant with other traits. Shoot metamorphoses and storage organs are highly collinear. Since 'shoot metamorphoses' focus on morphological origin while 'storage organs' have a stronger focus on functional aspects potentially relevant in the invasion process, we only used the latter in a multiple model. Habitat types, vegetation formations and vegetation units are also correlated to some degree. However, vegetation units, being subclasses of vegetation formations, provide more detailed information than the latter and are also more detailed than habitat types. Accordingly, we kept vegetation units.

For computational reasons, we started off with a generalised linear model (glm). We reduced the fitted model to its minimal adequate version by stepwise backward selection, using Akaike's Information Criterion (AIC; cf. Burnham *et al.* 2011). In this way, we identified important traits while accounting for the presence of other traits.

To account for phylogeny, we transferred the resulting minimal adequate model of the glm into a multiple gee. Again, we included phylogenetic correlation structure in one run of the model and excluded it in another, for better comparability. The gee-model without phylogeny included non-significant interactions. Therefore, we reduced it by backward selection to its minimal adequate version. The model with phylogeny could not be reduced any further. *P*-values for gee-models, excluding phylogeny, were obtained using functions provided by Carl & Kühn (2007).

RESULTS

Phylogenetically uninformed simple generalised estimating equations

In the models including one trait-status interaction each, but excluding phylogeny (Table S2 in Supporting Information), both archaeo-

phytes and neophytes were more frequent than native species with a late-season cessation of flowering. Moreover, archaeophytes and neophytes preferably occurring outside of urban areas (urbanophobic species) were more frequent than urbanophobic native species. Archaeophytes and neophytes were less frequent than native species when the number of hemerobic levels or the number of vegetation units occupied was high. Archaeophytes with rhizomes as shoot metamorphoses were slightly more frequent than native species with rhizomes. Vice versa, archaeophytes with runners as storage organs were less frequent than native species with runners. Archaeophytes were also less frequent than native species when the number of vegetation formations occupied was high. Neophytes with runners or pleiocorms as shoot metamorphoses were more frequent than native species with runners or pleiocorms. Moreover, neophytes with a high affinity to urban areas (urbanophilic species) were more frequent than urbanophilic native species. Vice versa, neophytes occurring with multiple ploidy categories, multiple types of shoot metamorphoses or storage organs or with primary storage roots were less frequent than native species of the same type.

Phylogenetically informed simple generalised estimating equations

When including phylogeny, these relationships did not change except for shoot metamorphoses (Table S2 in Supporting Information): Neophytes with runners were less frequent than the corresponding native species. Neophytes with pleiocorms did not differ from native species. In addition, archaeophytes and neophytes were more frequent than native species with intermediate storage organs (intermediate with respect to dispersal mobility) but less frequent than native species with a long flowering season, biennial or perennial life span and immobile shoot metamorphoses (other than pleiocorm, primary storage roots or bulbs) or when reproducing vegetatively. Generally, many more trait-status interactions were significant in phylogenetically informed models.

Multiple models

The minimal adequate phylogenetically uninformed multiple gee (Table S3 in Supporting Information) kept only the interactions of status with the number of hemerobic levels and of status with number of vegetation units (based on results from the minimal adequate glm; Table S4). However, when phylogeny was included, both archaeophytes and neophytes with a late-season cessation of flowering were more frequent than native species with late cessation of flowering (Table 1, Fig. 1). This relationship is even stronger in phylogenetically uninformed simple models (Fig. S1 in Supporting Information). Moreover, both archaeophytes and neophytes were more frequent than native species when traits included vegetative reproduction or primary storage roots (Table 1). Both archaeophytes and neophytes were less frequent than native species when the number of hemerobic levels occupied was high (Table 1, Fig. 1). However, both groups of non-native species reach similar frequencies as natives at lower numbers of inhabited vegetation units (Table 1, Fig. 1). Archaeophytes were more frequent than native species when traits included pleiocorms as storage organs, but less frequent when traits included runners, bulbs or intermediate storage organs (Table 1). Neophytes were more frequent than native species when traits included immobile storage organs, (other than pleiocorm, primary storage roots or bulbs) but less frequent when traits included

Table 1 Parameter estimates from phylogenetically informed multiple generalised estimating equation (gee) explaining the frequency of archaeophytes and neophytes in comparison to native species (the latter represented by the intercept) in Germany with the interaction of native/non-native status and species traits. Only those variables occurring in the minimal adequate glm (Table S4) were included in the model. *P*-values are denoted with $P \geq 0.1$ n.s., $0.1 > P \geq 0.05$ +; $0.05 > P \geq 0.01$ *; $0.01 > P \geq 0.001$ **; $P < 0.001$ ***

Predictor	Estimates
Intercept	-2.70+
Length of flowering season	0.73***
Pollination vector – multiple	0.88***
Pollination vector – selfing	-1.72***
Pollination vector – wind	1.05***
End of flowering season	-0.33***
Vegetative reproduction – seldom	1.21***
Vegetative reproduction – yes	-0.14**
Storage organs – runner	0.51***
Storage organs – rhizome	-0.16*
Storage organs – multiple	0.26***
Storage organs – intermediate	-0.22**
Storage organs – pleiocorm	-0.73***
Storage organs – primary storage organ	0.04 n.s.
Storage organs – immobile else	0.94***
Storage organs – bulb	1.11**
Affinity to urban areas – urbanophilic	-0.08 n.s.
Affinity to urban areas – urbanophobic	-0.34***
Number of hemerobic levels	0.43***
Number of vegetation units	0.56***
Archaeophytes	-1.36*
Neophytes	-1.12**
Length of flowering season: Pollination vector – multiple	-0.11***
Length of flowering season: Pollination vector –selfing	0.38***
Length of flowering season: Pollination vector – wind	-0.35***
Length of flowering season: Archaeophyte	0.43***
Length of flowering season: Neophyte	-0.61***
Pollination vector – multiple: Archaeophyte	2.01***
Pollination vector –selfing: Archaeophyte	4.67***
Pollination vector –wind: Archaeophyte	-0.96 n.s.
Pollination vector – multiple: Neophyte	-0.72**
Pollination vector –selfing: Neophyte	-1.08**
Pollination vector – wind: Neophyte	-1.00*
End of flowering season: Archaeophyte	0.21***
End of flowering season: Neophyte	0.31***
Vegetative reproduction – seldom: Archaeophyte	0.39 n.s.
Vegetative reproduction – yes: Archaeophyte	1.95**
Vegetative reproduction – seldom: Neophyte	-0.21 n.s.
Vegetative reproduction – yes: Neophyte	0.62***
Storage organs – runner: Archaeophyte	-1.79*
Storage organs – rhizome: Archaeophyte	-0.07 n.s.
Storage organs – multiple: Archaeophyte	-0.01 n.s.
Storage organs –intermediate: Archaeophyte	-3.45***
Storage organs – pleiocorm: Archaeophyte	0.57*
Storage organs – primary storage root: Archaeophyte	0.84***
Storage organs – immobile else: Archaeophyte	-1.61 +
Storage organs – bulb: Archaeophyte	-1.07*
Storage organs – runner: Neophyte	0.17 n.s.
Storage organs – rhizome: Neophyte	-0.87***
Storage organs – multiple: Neophyte	-0.71***
Storage organs – intermediate: Neophyte	0.46 +
Storage organs – pleiocorm: Neophyte	-0.91***
Storage organs – primary storage root: Neophyte	1.00***
Storage organs – immobile else: Neophyte	0.35*
Storage organs – bulb: Neophyte	0.49 n.s.
Affinity to urban areas – urbanophilic: Archaeophyte	-0.09 n.s.
Affinity to urban areas – urbanophobic: Archaeophyte	-0.13 n.s.

Table 1 (continued)

Predictor	Estimates
Affinity to urban areas – urbanophilic: Neophyte	-0.39*
Affinity to urban areas – urbanophobic: Neophyte	-1.22***
Number of hemerobic levels: Archaeophyte	-0.94***
Number of hemerobic levels: Neophyte	-0.50***
Number of vegetation units: Archaeophyte	0.26***
Number of vegetation units: Neophyte	0.58***
Length of flowering season: Pollination vector – multiple: Archaeophyte	-0.50***
Length of flowering season: Pollination vector – selfing: Archaeophyte	-1.14***
Length of flowering season: Pollination vector – wind: Archaeophyte	0.42*
Length of flowering season: Pollination vector – multiple: Neophyte	0.36***
Length of flowering season: Pollination vector – selfing: Neophyte	0.45***
Length of flowering season: Pollination vector – wind: Neophyte	0.03 n.s.

rhizomes, pleiocorms or multiple types of storage organs or a high affinity to urban areas (Table 1). The triple interaction of status, length of flowering season and pollination vector turned out to be significant, as well, with archaeophytes being more frequent than native species when wind-pollinated, but neophytes being more frequent than native species when self-pollinated or when multiple pollination vectors have been identified (Table 1).

DISCUSSION

Overall, in phylogenetically informed relationships between species frequencies and effects of different trait-status interactions, there is no difference between native and non-native species when species life span, ploidy type and self-compatibility are considered. On the other hand, native and non-native species differ in frequency according to traits including the end of the flowering season, storage organs, vegetative reproduction, affinity to urban areas, number of vegetation units, number of hemerobic levels and the combination of pollination vector and length of the flowering season. Hence, the results show biological differences in native and non-native species, therefore, the claims of Davis *et al.* (2011) and Thompson & Davis (2011) cannot be supported.

Shared responses of native and non-native species

We can agree with Thompson *et al.* (1995) and Thompson & Davis (2011) that successful species are characterised by traits adapted to anthropogenic and other disturbing impacts. The fact that widespread plant species have a shorter lifespan (Table S2 in Supporting Information) than less widespread species, irrespective of origin, shows that the lifespan results of Küster *et al.* (2008) are not specific to neophytes. Rather, they also apply to native species and archaeophytes. The same is true for effects of self-compatibility on species frequency, which do not differ between native and non-native species. Self-compatibility appears to differ less between native and non-native species than the type of pollination itself. For the latter, archaeophytes and neophytes that are frequent in

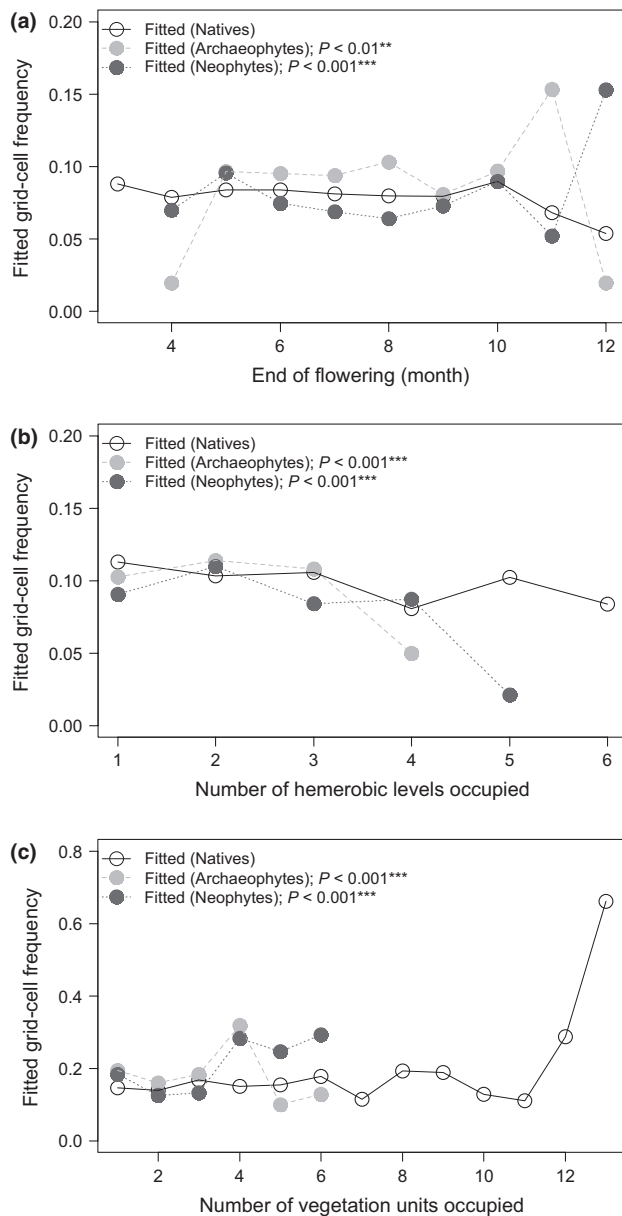


Figure 1 Frequency of vascular plant species native to Germany, archaeophytes, and neophytes, and their relationship to species' traits. Shown are the end of the flowering season (a), number of hemerobic levels occupied by a species (b), and number of vegetation formations occupied (c) in relation to mean fitted (back transformed) estimates of phylogenetically informed multiple gee-models (see Materials & Methods; mean-values were calculated per trait level for each native/non-native status group; e.g. mean of archaeophytes occupying three hemerobic levels). Error probabilities (included in the figure legends) illustrate whether the frequency of archaeophytes and neophytes is driven differently by species' traits than is the frequency of native species: $0.01 > P \geq 0.001^{**}$, $P < 0.001^{***}$. Results excluding phylogenetic relationships among species are illustrated in Fig. S1 in Supporting Information.

Germany rely less on biotic pollination vectors but more on wind, selfing or flexible pollination strategies than do natives. These traits are advantageous for kin founder populations when mating partners are absent or rare (Pyšek *et al.* 2011; van Kleunen *et al.* 2008) or in fragmented anthropogenic habitats where the abundance of pollinating insects is low. (Urbanisation, e.g. drives the extinction of a

range of insect species; Fattorini 2011). An annual life span allows species to rapidly utilise short time periods without disturbance. It may be argued that the invasion of non-native species is driven by disturbance (Davis *et al.* 2000), and that disturbance-related traits should be more important for non-native than for native species. However, at its core, disturbance drives the success of ruderal species, and although a lot of neophytes are ruderal, not all ruderal species are neophytes (Klotz *et al.* 2002). Consequently, both native and non-native species can benefit from being adapted to disturbance.

Differences between native and non-native species

Differences between native and non-native species partly reflect the way non-native species were introduced and the niches they occupy in their introduced range. Late-flowering archaeophytes were more widespread than native species with late flowering. Many archaeophytes are agricultural weeds that occupy a temporal niche: Late in the year, when fields lie fallow or just tilled, agricultural weeds are released from competition with crops. In the German flora, those archaeophytes that finish flowering in late autumn are all characteristic species of field weed communities, pastures, meadows or ruderal weed communities [e.g. *Lamium amplexicaule* L., *Stellaria media* (L.) Vill. s. str., *Tripleurospermum perforatum* (Mérat) Lainz].

The fact that neophyte frequency rose with later-season cessation of flowering can support the hypothesis that the 'late year temporal niche' generally is not fully occupied by native species (cf. Godoy *et al.* 2009). This is not restricted to agricultural habitats. Most species in the German flora flower between June and August (Trefflich *et al.* published in Klotz *et al.* 2002). Consequently, competition pressure decreases towards the end of the year. In the Mediterranean, where many native species stop flowering before the start of the summer dry season, neophytes avoid competition pressure by flowering during summer or later (Celesti-Grapow *et al.* 2003; Godoy *et al.* 2009).

In addition or alternatively, a late flowering season is supported by neophytic introduction pathways: Species that flower when most native species have stopped doing so are more attractive ornamental plants; they prolong the gardening period. Popular examples are several *Aster* species, *Solidago canadensis* L. and *Helianthus tuberosus* L., the latter also used as crop. Propagule pressure from horticulture supports high frequencies of naturalised individuals of these species (Dehnen-Schmutz *et al.* 2007). In contrast, plant species that were introduced accidentally, such as contaminants of transported goods, do not profit from distribution by horticulture (for example, *Senecio inaequidens* DC.). Their successful spread again suggests that non-native species that flower at the end of the year have an advantage because they use a partly vacant niche, irrespective of human preferences (cf. Lachmuth *et al.* 2011).

A disadvantage to late cessation of flowering is that seeds may not ripen with winter advancing. This is mediated by the ability to reproduce vegetatively: both groups of non-native species are frequent in Germany if they can produce offspring in the absence of pollinators by using clonal organs. In addition, absence of pollinating insects late in a year is mediated by species' ability to reproduce with the help of selfing or wind-pollination. Thus, the end of the flowering season can be viewed as a surrogate for the end of the active growing season.

In contrast to their frequent occurrence in anthropogenic habitats, non-native species are largely absent from habitats not impacted by humans. These habitats have become rare in central Europe and are mainly restricted to alpine areas, fens and bogs (Sukopp 1969). The entry points of introduced non-native species are mostly located in agricultural areas (archaeophytes) and urban-industrial areas (neophytes), i.e. in habitats highly impacted by anthropogenic activities, where non-native species until now have mainly remained in the environments to which they were introduced (Botham *et al.* 2009). As they occupy the habitats most frequent in Germany (see also Chytrý *et al.* 2009), archaeophytes occurring in vegetation units adapted to agriculture do not need to occupy as many vegetation units as native species to reach the same frequency. The same applies to the occupation of different hemerobic levels when phylogenetic information is excluded (Fig. S1 in Supporting Information).

Introduction pathways bias non-native species success

In general, why do differences occur? If non-native species were a random sample of the originating species pools, the claims of Davis *et al.* (2011) and Thompson & Davis (2011) would certainly be correct and there would be no reason to assume that non-native species differ from native species. The introduction of non-native species, however, is biased, and this affects the functional composition of non-native communities. The majority of non-native plant species have been introduced to new ranges as ornamental species or for other human purposes (52.2% of the naturalised non-native flora of Europe were introduced for ornamental or horticultural reasons; Lambdon *et al.* 2008). These species germinate faster and more often than native species do (Chrobok *et al.* 2011), a logical consequence of selection by cultivation. Non-native species that were not introduced deliberately but immigrated via anthropogenic pathways, such as agricultural weeds or contaminants of transported goods, are partly biased as well. For example, the early plant migrants in central Europe accompanied the migration of agriculture from the Mediterranean and Middle East to the central European countries. Many of these agricultural weeds are still bound to agricultural habitats (e.g. Pyšek 1998). Thus, if non-native species are ecologically different from native species, they should be different because they were selected by humans for a special purpose or because their immigration pathways are biased, and not because they are non-native.

Still, there are also native species that are adapted to the ever-increasing quantity of eutrophic, disturbed or anthropogenic habitats. These native species share a range of functional traits, such as high growth rates, with widespread non-native species. The high frequency of anthropogenic habitats in industrialised countries supports both native and non-native species adapted to anthropogenic conditions but excludes, for example, species that depend on nutrient-poor conditions (Thompson & Davis 2011).

Environmental filters and anthropogenic selection impact species frequency

The scale of 130 km² grid-cells is far too large to identify competitive mechanisms between individual species. Still, the tendency for non-native species to flower late clearly demonstrates their use of a temporal niche. On landscape scales, environmental filters constrain

species occurrence by selecting species that are functionally adapted to the given environmental conditions (Cavender-Bares *et al.* 2009). The high frequency of anthropogenic habitats in Germany selects for species whose short life cycle and flexible reproduction increase their chance to survive disturbance events and to disperse in fragmented landscapes. Whether or not species pass these environmental filters depends solely on their species characteristics, and not on their native/non-native status. After environmental filtering, species that newly enter a flora need to disperse and to compete with species that are already there (Cavender-Bares *et al.* 2009). Widespread native and widespread non-native species that share traits adapted to anthropogenic habitats (Thompson & Davis 2011) need to compete with each other within these habitats. Shifting flowering time to autumn and early winter is not advantageous with respect to pollination and increases the risk of damage by frost. Consequently, it is not the abiotic environment that selects for late flowering. Rather, species with traits interesting for humans, such as a late flowering date that prolongs the flowering season, are selected by humans for ornamental reasons (Kowarik 2005) and disperse to new habitats using anthropogenic vectors (such as agricultural pathways or traffic; Brunzel *et al.* 2009). Within habitats, competitive pressure from the majority of species flowering in early and mid-summer might be an additional selective force, as indicated by the high frequency of archaeophytes and neophytes with a late end of flowering season. However, abundance data and tests on a smaller scale than ours are required to show whether or not temporal niche shifts, as a consequence of competition are visible on scales where competition takes place.

We should not use the distinction between native and non-native species to distinguish 'good species' from 'bad species.' These are associations without ecological relevance and can apply to native (weeds) and non-native species, as well. Rather, the distinction between native and non-native species is valuable for understanding the mechanisms and processes behind species success, such as environmental filters, anthropogenic selection, and niche assembly. Global change strengthens the relevance of research on new species and novel species assemblages (Hobbs *et al.* 2006; Lockwood *et al.* 2011): the introduction of species to regions where they are not native is an imminent part of globalisation and will continue in the future.

ACKNOWLEDGEMENTS

The authors thank the Helmholtz Association for research funding within the core subject 'Land Use Options and Biodiversity' (Seppelt *et al.* 2009). We thank three anonymous referees and Marcel Rejmanek for helpful comments on an earlier version of the text and Dr. Clare Aslan (UC Santa Cruz) for language editing and comments on manuscript structure.

AUTHORSHIP

Both IK and SK agree to the submission of this manuscript; IK conceived the idea; SK analysed the data; SK wrote the first draft of the manuscript; IK and SK substantially revised the first draft.

REFERENCES

- Botham, M.S., Rothery, P., Hulme, P.E., Hill, M.O., Preston, C.D. & Roy, D.B. (2009). Do urban areas act as foci for the spread of alien plant species? An assessment of temporal trends in the UK. *Divers. Distrib.*, 15, 338–345.

- Brunzel, S., Fischer, S.F., Schneider, J., Jetzkowitz, J. & Brandl, R. (2009). Neo- and archaeophytes respond more strongly than natives to socio-economic mobility and disturbance patterns along an urban-rural gradient. *J. Biogeogr.*, 36, 835–844.
- Burnham, K.P., Anderson, D.R. & Huyvaert, K.P. (2011). AIC model selection and multimodel inference in behavioral ecology: some background, observations, and comparisons. *Behav. Ecol. Sociobiol.*, 65, 23–35.
- Carey, V.J. (2011). *gee: Generalized Estimation Equation solver*. Ported to R by Thomas Lumley and Brian Ripley. Note that maintainers are not available to give advice on using a package they did not author, R package version 4.13–17. Available at: <http://CRAN.R-project.org/package=gee>. Last accessed 2 March 2012.
- Carl, G. & Kühn, I. (2007). Analyzing spatial autocorrelation in species distributions using Gaussian and logit models. *Ecol. Model.*, 207, 159–170.
- Cavender-Bares, J., Kozak, K.H., Fine, P.V.A. & Kembel, S.W. (2009). The merging of community ecology and phylogenetic biology. *Ecol. Lett.*, 12, 693–715.
- Celesti-Grapow, L., Di Marzio, P. & Blasi, C. (2003). Temporal niche separation of the alien flora of Rome (Italy). In: *Plant Invasions: Ecological Threats and Management Solutions* (eds Child, L.E., Brock, J.H., Brundu, G., Prach, K., Pyšek, P., Wade, P.M. & Williamson, M.). Backhuys Publishers Leiden, The Netherlands, pp. 101–111.
- Chrobok, T., Kempel, A., Fischer, M. & van Kleunen, M. (2011). Introduction bias: Cultivated alien plant species germinate faster and more abundantly than native species in Switzerland. *Basic Appl. Ecol.*, 12, 244–250.
- Chytrý, M., Pyšek, P., Wild, J., Pino, J., Maskell, L.C. & Vilà, M. (2009). European map of alien plant invasions based on the quantitative assessment across habitats. *Divers. Distrib.*, 15, 98–107.
- Crawley, M.J., Harvey, P.H. & Purvis, A. (1996). Comparative ecology of the native and alien floras of the British Isles. *Phil. Trans. R. Soc. B*, 351, 1251–1259.
- Davis, M.A., Grime, J.P. & Thompson, K. (2000). Fluctuating resources in plant communities: a general theory of invasibility. *J. Ecol.*, 88, 528–534.
- Davis, M., Chew, M.K., Hobbs, R.J., Lugo, A.E., Ewel, J.J., Vermeij, G.J. *et al.* (2011). Don't judge species on their origins. *Nature*, 474, 153–154.
- Dehnen-Schmutz, K., Touza, J., Perrings, C. & Williamson, M. (2007). The horticultural trade and ornamental plant invasions in Britain. *Conserv. Biol.*, 21, 224–231.
- Fattorini, S. (2011). Insect extinction by urbanization: A long term study in Rome. *Biol. Conserv.*, 144, 370–375.
- Freckleton, R.P., Cooper, N. & Jetz, W. (2011). Comparative Methods as a Statistical Fix: The Dangers of Ignoring an Evolutionary Model. *Am. Nat.*, 178, E10–E17.
- Godoy, O., Castro-Díez, P., Valladares, F. & Costa-Tenorio, M. (2009). Different flowering phenology of alien invasive species in Spain: evidence for the use of an empty temporal niche? *Plant Biology*, 11, 803–811.
- Grime, J.P. (2006). Trait convergence and trait divergence in herbaceous plant communities: Mechanisms and consequences. *J. Veg. Sci.*, 17, 255–260.
- Hill, M.O., Roy, D.B. & Thompson, K. (2002). Hemeroby, urbanity and ruderality: bioindicators of disturbance and human impact. *J. Appl. Ecol.*, 39, 708–720.
- Hobbs, R.J., Arico, S., Aronson, J., Baron, J.S., Bridgewater, P., Cramer, V.A. *et al.* (2006). Novel ecosystems: theoretical and management aspects of the new ecological world order. *Global Ecol. Biogeogr.*, 15, 1–7.
- Hulme, P.E., Pyšek, P. & Duncan, R.P. (2011). Don't be fooled by a name: a reply to Thompson and Davis. *Trends Ecol. Evol.*, 26, 318–318.
- Jalas, J. (1955). Hemerobe und hemerochrome Pflanzenarten. Ein terminologischer Reformversuch. *Acta Soc. Fauna Flora Fenn.*, 72, 1–15.
- van Kleunen, M., Manning, J.C., Pasqualetto, V. & Johnson, S.D. (2008). Phylogenetically independent associations between autonomous self-fertilization and plant invasiveness. *Am. Nat.*, 171, 195–201.
- van Kleunen, M., Dawson, W., Schlaepfer, D., Jeschke, J.M. & Fischer, M. (2010a). Are invaders different? A conceptual framework of comparative approaches for assessing determinants of invasiveness. *Ecol. Lett.*, 13, 947–958.
- van Kleunen, M., Weber, E. & Fischer, M. (2010b). A meta-analysis of trait differences between invasive and non-invasive plant species. *Ecol. Lett.*, 13, 235–245.
- van Kleunen, M., Dawson, W. & Dostal, P. (2011). Research on invasive-plant traits tells us a lot. *Trends Ecol. Evol.*, 26, 317–317.
- Klotz, S., Kühn, I. & Durka, W. (2002). *BIOLFLOR – Eine Datenbank zu Biologisch-Ökologischen Merkmalen der Gefäßpflanzen in Deutschland*. Bundesamt für Naturschutz, Bonn.
- Kowarik, I. (2005). Urban ornamentals escaped from cultivation. In: *Crop Fertility and Volunteerism: A Threat to Food Security in The Transgenic Era?* (ed. Gressel, J.). Taylor & Francis Boca Raton, Fla., pp. 97–121.
- Kühn, I. & Klotz, S. (2007). From ecosystem invasibility to local, regional and global patterns of invasive species. In: *Biological Invasions* (ed. Nentwig, W.). Springer Berlin, Heidelberg, New York, pp. 181–196.
- Kühn, I., Brandl, R. & Klotz, S. (2004a). The flora of German cities is naturally species rich. *Evol. Ecol. Res.*, 6, 749–764.
- Kühn, I., Durka, W. & Klotz, S. (2004b). BiolFlor – a new plant-trait database as a tool for plant invasion ecology. *Divers. Distrib.*, 10, 363–365.
- Küster, E.C., Kühn, I., Bruehlheide, H. & Klotz, S. (2008). Trait interactions help explain plant invasion success in the German flora. *J. Ecol.*, 96, 860–868.
- Lachmuth, S., Durka, W. & Schurr, F.M. (2011). Differentiation of reproductive and competitive ability in the invaded range of *Senecio inaequidens*: the role of genetic Allee effects, adaptive and nonadaptive evolution. *New Phytol.*, 192, 529–541.
- Lambdon, P.W., Pyšek, P., Basnou, C., Hejda, M., Arianoutsou, M., Essl, F. *et al.* (2008). Alien flora of Europe: species diversity, temporal trends, geographical patterns and research needs. *Preslia*, 80, 101–149.
- Lockwood, J.L., Hoopes, M.F. & Marchetti, M.P. (2011). Non-natives: pluses of invasion ecology. *Nature*, 475, 36–36.
- MacArthur, R. & Levins, R. (1967). Limiting Similarity Convergence and Divergence of Coexisting Species. *Am. Nat.*, 101, 377–385.
- Paradis, E., Claude, J. & Strimmer, K. (2004). APE: analyses of phylogenetics and evolution in R language. *Bioinformatics*, 20, 289–290.
- Pyšek, P. (1998). Alien and native species in Central European urban floras: a quantitative comparison. *J. Biogeogr.*, 25, 155–163.
- Pyšek, P., Jarošík, V., Chytrý, M., Danihelka, J., Kühn, I., Pergl, J. *et al.* (2011). Successful Invaders Co-opt Pollinators of Native Flora and Accumulate Insect Pollinators with Increasing Residence Time. *Ecol. Monogr.*, 81, 277–293.
- R Development Core Team (2011). *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing Vienna, Austria.
- Roelofs, J.G.M., Bobbink, R., Brouwer, E. & Degraaf, M.C.C. (1996). Restoration ecology of aquatic and terrestrial vegetation on non-calcareous sandy soils in The Netherlands. *Acta Bot. Neerl.*, 45, 517–541.
- Seppelt, R., Kühn, I., Klotz, S., Frank, K., Schloter, M., Auge, H. *et al.* (2009). Land Use Options - Strategies and Adaptation to Global Change Terrestrial Environmental Research. *GALA*, 18, 77–80.
- Sukopp, H. (1969). Der Einfluss des Menschen auf die Vegetation. *Vegetatio*, 17, 360–371.
- Thompson, K. & Davis, M.A. (2011). Why research on traits of invasive plants tells us very little. *Trends Ecol. Evol.*, 26, 155–156.
- Thompson, K., Hodgson, J.G. & Rich, T.C.G. (1995). Native and alien invasive plants: More of the same? *Ecography*, 18, 390–402.
- Vilà, M., Basnou, C., Pyšek, P., Josefsson, M., Genovesi, P., Gollasch, S. *et al.* (2010). How well do we understand the impacts of alien species on ecosystem services? A pan-European, cross-taxa assessment. *Front. Ecol. Environ.*, 8, 135–144.
- Weier, E., Clarke, G.D.P. & Keddy, P.A. (1998). Community assembly rules, morphological dispersion, and the coexistence of plant species. *Oikos*, 81, 309–322.
- Williamson, M. & Gaston, K.J. (1999). A simple transformation for sets of range sizes. *Ecography*, 22, 674–680.
- Wittig, R., Diesing, D. & Gödde, M. (1985). Urbanophob Urbanoneutral Urbanophil - Behavior of Species Concerning the Urban Habitat. *Flora*, 177, 265–282.
- Zobel, M. (1997). The relative role of species pools in determining plant species richness: an alternative explanation of species coexistence? *Trends Ecol. Evol.*, 12, 266–269.

SUPPORTING INFORMATION

Additional Supporting Information may be downloaded via the online version of this article at Wiley Online Library (www.ecologyletters.com).

As a service to our authors and readers, this journal provides supporting information supplied by the authors. Such materials are peer-reviewed and may be re-organized for online delivery, but are not copy-edited or typeset. Technical support issues arising from supporting information (other than missing files) should be addressed to the authors.

Editor, Marcel Rejmanek

Manuscript received 3 January 2012

First decision made 25 January 2012

Second decision made 15 March 2012

Manuscript accepted 26 March 2012