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Trait–environment relationships of plant species at different stages of the introduction process

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Abstract

The success of alien plant species can be attributed to differences in functional traits compared to less successful aliens as well as to native species, and thus their adaptation to environmental conditions. Studies have shown that alien (especially invasive) plant species differ from native species in traits such as specific leaf area (SLA), height, seed size or flowering period, where invasive species showed significantly higher values for these traits. Different environmental conditions, though, may promote the success of native or alien species, leading to competitive exclusion due to dissimilarity in traits between the groups. However, native and alien species can also be similar, with environmental conditions selecting for the same set of traits across species. So far, the effect of traits on invasion success has been studied without considering environmental conditions. To understand this interaction we examined the trait–environment relationship within natives, and two groups of alien plant species differing in times of introduction (archaeophytes vs. neophytes). Further, we investigated the difference between non-invasive and invasive neophytes. We analyzed the relationship between functional traits of 1,300 plant species occurring in 1000 randomly selected grid-cells across Germany and across different climatic conditions and land-cover types. Our results show that temperature, precipitation, the proportion of natural habitats, as well as the number of land-cover patches and geological patches affect archaeophytes and neophytes differently, regarding their level of urbanity (in neophytes negative for all non-urban land covers) and self-pollination (mainly positive for archaeophytes). Similar patterns were observed between non-invasive and invasive neophytes, where additionally, SLA, storage organs and the beginning of flowering were strongly related to several environmental factors. Native species did not express any strong relationship between traits and environment, possibly due to a high internal heterogeneity within this group of species. The relationship between trait and environment was more pronounced in neophytes compared to archaeophytes, and most pronounced in invasive plants. The alien species at different stages of the invasion process showed both similarities and differences in terms of the relationship between traits and the environment, showing that the success of introduced species is context-dependent.

Keywords
archaeophytes, functional traits, GABLIS, indigenous plants, introduced species, invasive species, native species, neophytes

Introduction

Invasive alien species (IAS) have a large ecological impact on the diversity and abundance of native plant species (Vilà et al. 2010; Pyšek et al. 2012). Worldwide, the number of naturalized vascular plant species reaches almost 14,000 with tendencies for further increase (van Kleunen et al. 2015, 2019; Pyšek et al. 2017; Seebens et al. 2019). Consequently, much effort has been invested to identify the main causes of invasiveness. Multiple studies have shown that certain functional plant traits promote invasiveness (e.g. Pyšek and Richardson 2007; Küster et al. 2008; van Kleunen et al. 2010; Tecco et al. 2010; Divíšek et al. 2018). However, a conclusive list of traits that promote successful invasion is lacking mainly due to ambiguous results that can, at least partly, be attributed to the context-dependence of the invasion process (Kueffer et al. 2013). Additionally, propagule pressure and introduction by humans (e.g. cultivation, ornamental purposes) have great effect on invasiveness (Pyšek et al. 2015).

The distribution of alien species is habitat-dependent (Chytrý et al. 2008a, Chytrý et al. 2008b; Dainese and Bragazza 2012), thus functional traits relevant in one type of habitat can become unimportant in another (Divíšek et al. 2018). Therefore, within one habitat the set of traits essential for survival and reproduction should be comparable across different groups of plants (native, non-invasive and invasive alien species). Alien species may thus share some traits with native species which can help them successfully establish under specific environmental conditions (Ordonez et al. 2010), but which may differ among habitats. Yet, alien species exhibit certain dissimilarities to natives, which can be beneficial in the colonization of new environments and reduce competition (Pyšek and Richardson 2007; Divíšek et al. 2018). A meta-analysis by van Kleunen et al. (2010) confirmed that invasive species show significantly higher values for all trait categories analyzed (e.g. size, fitness, growth rate) than native and non-invasive species.

To perform comparative studies of the invasiveness of species, several approaches are possible, as conceptualized by van Kleunen et al. (2010). Of these, the most commonly performed are comparisons of (i) invasive with native species, and (ii) invasive with non-invasive species in the invaded area. However, such comparisons can be performed in both target (introduced) and source area (Parker et al. 2013).

Functional traits can be used to characterize the success of alien species over natives. Alien species ('exotic' or 'non-native' species) are classified, based on their residence time in the area, into 'archaeophytes' (alien species introduced before 1500 CE), and 'neophytes' (introduced after 1500 CE). Representatives of both groups can be classified according to the stage they reached in the invasion process into casual, naturalized or invasive; the latter term applies if they spread rapidly, become widely distributed (Richardson et al. 2000, Blackburn et al. 2011) and some have an impact on human well-being, ecosystem functioning, biodiversity, or human infrastructure (Vilà et al. 2010). Comparing traits of invasive and non-invasive plant species in their environmental context can help elucidate why some alien species become invasive, and others not (van Kleunen et al. 2010). Considering species at different stages of the invasion process can distinguish between traits that do not confer invasiveness (native vs non-invasive) from those that do (native vs invasive/potential invasive and invasive vs non-invasive) at each individual stage. The influence of traits on invasiveness can be challenging to interpret since it can differ depending on a species' residence time (how much time have alien species spent in their introduced area).

A range of environmental variables such as land cover, climate, and geological bedrock, have been shown to affect native and different groups of non-native species differently, and changes in land cover (providing a proxy for habitat) and/or climatic factors (particularly changes in temperature and rainfall amount and range) may particularly benefit invasive species (Hulme 2009). In Central Europe, both archaeophytes and neophytes prefer similar climatic conditions, reflecting their global environmental preferences, i.e. relatively warm and dry climate possibly due to their origin (Pyšek et al. 2005). Similarly, both groups of alien species are promoted by increasing land use intensity (Chytrý et al. 2008b, 2012; Polce et al. 2011). Accordingly, alien species can be favored when urban or agricultural land cover increases (neophytes and archaeophytes, respectively; Chytrý et al. 2008a). While geological heterogeneity strongly affects native species, this is not the case for archaeophytes, being mainly abundant on arable fields, i.e. homogenous land with fertile soils, while neophytes are strongly related to urban land cover (Kühn et al. 2003, 2004). Additionally, Tecco et al. (2010) showed that climate (temperature, precipitation, and frost), geological variables and land cover had a negative effect mainly on woody alien species and no significant effect on the herbaceous alien plants. Yet, the success of both native and alien species cannot be assessed in isolation from the environmental determinants of their distribution.

The reason why native and alien species may respond differently to environmental factors is often attributed to their functional traits. Wolf et al. (2020) showed a strong pattern of changes in functional composition with respect to environment in a rural–urban gradient. Traits relevant for the success of alien species are related to stress tolerance (i.e. SLA) or environmental disturbance (height, seed size) (Pyšek and Richardson 2008; Gallagher et al. 2015). Further, traits related to competitiveness (e.g. height) can prove beneficial for invasive species (Divíšek et al. 2018). For instance, phenology, in terms of earlier or longer flowering duration can be advantageous. Pyšek et al. (2003) showed that IAS might flower earlier or later than native species as a part of a "try harder" hypothesis. Pollination systems do not show significant links to invasion success (Pyšek and Richardson 2008), but self-pollination tends to support the spread of neophytes more than any other type of pollination (Pyšek et al. 2011). However, the role of pollination in the invasion process is mainly studied without relation to environmental drivers. Kühn et al. (2006), though, showed that pollination types vary spatially and in relation to climatic, geological and land-cover factors.

Evaluating the relationships between the environment and plant functional traits is crucial for understanding the response of species of different origin and different stages in the invasion process to changing environmental conditions (climate change, land-cover change). Here, we quantified the relationships between climate, land cover and bedrock with relevant plant traits using a dataset with 1,300 plant species in Germany. We examined several groups of plants including natives and different subgroups of alien species across 1,000 randomly selected grid cells in Germany. The following questions are addressed: (i) Is there a relationship between plant traits and environment in native and alien species? (ii) How do these relationships depend on the residence time of plant species (with archaeophytes being introduced earlier and neophytes more recently)? (iii) How do these relationships differ between non-invasive and invasive neophytes?

Methods

Species occurence

Species occurrence data was obtained from FLORKART (Federal Agency for Nature Conservation / Network Phytodiversity Germany; http://www.floraweb.de) for the period 1950–2013. FLORKART includes over 14 million records on species occurrences collected by thousands of volunteers. Species were analyzed at a spatial resolution of grid cells with 10' longitude × 6' latitude (~ on average 130 km^2 ranging from 117 to 140 km^2). A presence/absence matrix was generated for a random sample of 1000 grid cells that contained at least 45 (out of 50) species that can be reasonably assumed to occur in every grid cell and serve as proxy for mapping quality (Kühn et al. 2006). This approach of grid cell selection ensured that chosen grid cells were properly surveyed. Additionally, some grid cells were smaller because they were located at the borders or along the coast. Thus, we excluded cells smaller than 117 km^2 (which is the size of the smallest grid cell that is not truncated by borders or coastlines). Individual matrices were generated for five groups of plants: native (976 species), archaeophytes (168 species) and neophytes (156 species), with 1,300 plant species in total; neophytes were further divided into (i) species featured in the German-Austrian Black List Information System of invasive species (GABLIS; Essl et al. 2011), with 26 species, and (ii) species not included in GABLIS, with 130 plant species. Following GABLIS (Essl et al. 2011), plants were classified into action black list (invasive with limited distribution) and management black list (invasive and widely distributed species). In our paper, we will refer to the species from GABLIS black list (action and management list) as invasive neophytes and to the ones that are not included in GABLIS as non-invasive neophytes.

Traits

Trait data for all plant species were obtained from the Database on Biological and Ecological Traits of the Flora of Germany, BiolFlor (Klotz et al. 2002; Kühn et al. 2004; http://www2.ufz.de/biolflor/index.jsp), and LEDA (Kleyer et al. 2008; https://uol.de/en/landeco/research/leda/data-files). These traits represent morphology, phenology and habitat preferences of all three groups of plant species: SLA, seed mass, height, storage organs, pollination vector, flowering period, urbanity and hemerobic level (Table 1).

Table 1. Functional traits, environmental associations (hemerobic level and urbanity) and invasiveness data (GABLIS list) and sources used for the analysis.

Trait	Values	Units/description	Source
Mean specific leaf area (SLA)	metric	mm^2/mg	LEDA
Seed mass	metric	mg	LEDA
Mean plant height	metric	m	LEDA
Storage organs	yes / no / multiple	Presence Absence Multiple storage organs	BiolFlor
Pollen vector	multiple / insect/ wind / self	Multiple pollination types Wind pollination Self-pollination (including two subgroups: selfing by a neighboring flower and selfing in an unopened flower) Insect pollination	BiolFlor
Flowering period	months	Beginning of flowering period End of flowering period Duration of flowering period	BiolFlor
Urbanity	1–5 values for different states of urbanity	1 – urbanophobic (species grows exclusively outside urban areas) 2 – moderately urbanophobic (species prefers non-urban areas) 3 – urbanoneutral (species has no preference), 4 – moderately urbanophilic (species grows predominantly in urban areas) 5 – urbanophilic (species grow exclusively in urban areas)	BiolFlor
Hemerobic level	level of naturalness with values 1–9	Polyhemerob and α-euhemerob, values 1–2 (species preference for artificial habitats) β-euhemerob and α-mesohemerob, values 3–4 (species prefers altered habitats) β-mesohemerob and α-oligohemerob, values 5–6 (species preference for moderately altered habitats); β-oligohemerob and γ-oligohemerob, values 7–8 (species prefers semi-natural habitats) Ahemerob, value of 9 (species preference for natural habitats)	BiolFlor
GABLIS sublist	no / ML / AL	Neophytes not present on the list Neophytes on the management Black list (ML) Neophytes on the action Black list (AL)	GABLIS

Environmental data

Climate data (temperature, precipitation; Table 2) were obtained from the ALARM project (Fronzek et al. 2012) for the period 1961–1990, land cover (Suppl. material 1: Table S2) data from the CORINE database (Bundesamt für Kartographie und Geodäsie, 2012), and geological data (Table 2) from a map of the German Federal Institute for Geosciences and Natural Resources (Bundesanstalt für Geowissenschaften und Rohstoffe, 1993), all scaled to the same resolution as the floristic maps.

Data analysis

We analyzed the relationship between traits and environment across native and alien plant species. For each group (natives, archaeophytes, neophytes, non-invasive and invasive neophytes) matrices of species presence/absence × grid cell were created (*S*). Correspondingly, environmental matrices (environment × grid cell, *E*) and trait matrices (traits × species, *T*) for every status group were compiled. To directly associate matrices *S* with *E* and *T*, we used a fourth corner approach as implemented in the function *traitglm*()of mvabund in R (Warton et al. 2015). Fourth corner analysis combines *S* (first–upper-left–corner), *E* (second–lower-left–corner) and *T* (third–upper-right–corner). The fourth (missing–lower right) corner is generated as a matrix that describes the trait-environmental relationships. We checked for collinearity among environmental variables and excluded variables with $r > |0.7|$ (Dormann

Table 2. Environmental variables and their sources used in the 4th corner analyses of trait–environment relationships of plant species in Germany.

Variable	Abbreviation	Categories	Unit	Source
Temperature	tmn tmx	- mean temperature of the coldest month - mean temperature of the warmest month	°C	Fronzek, Carter and Jylhä 2012
Precipitation		- mean annual precipitation - precipitation range of the year	mm	Fronzek Carter and Jylhä 2012
Land cover	arable land (%) natural cover (%) urban cover (%)	Land cover proportion of: - arable land - natural and semi natural areas - urban areas	proportion	Corine Land Cover (CLC)
Number of CLC patches	CLC patches	Total number of land cover patches per grid cell		Corine Land Cover
Geological types		Proportion of subsoils: - calcareous - loess - sand	proportion	Bundesanstalt für Geowissenschaften und Rohstoffe
Number of geological patches	Geological patches	Total number of geological patches per grid cell (regardless of the number of geological types).		Bundesanstalt für Geowissenschaften und Rohstoffe

et al. 2013). The function *manyglm* presents a multivariate extension of GLM (generalized linear model) and calculates the coefficient estimates of GLMs fitted to all (explanatory) variables simultaneously (Wang et al. 2012). Coefficients describe how environmental predictors can be predicted by changes in traits. Further, we used the function *anova.traitglm*() based on bootstrapping with 99 permutations, to test for the statistical significance of trait–environment relationships in predicting presence of only non-native species (for computational reasons, see below) on all sites (Suppl. material 1: Table S1a–d). Since the response matrix *S* was binary multivariate data, we used binomial distribution.

The data analysis was performed using R, version 3.6.1 (R Core Team 2017). The analysis of a larger matrix (e.g. native species) took 19 days on a Dell PowerEdge R930 Server with 4 * CPU E7-8867 v4 2.4 GHz (72 Cores) and 6 TB RAM with Windows 2016.

Results

Overall, there was an increase in the number of prominent trait–environment relationships from native species to non-invasive archaeophytes, non-invasive and invasive neophytes (Fig. 1; Suppl. material 1: Tables S2a).

Native species

Native species in Germany showed high heterogeneity in their functional traits and habitat conditions; thus the relationships between traits and environment were weak (ranging from -0.0003 to 0.01; Suppl. material 1: Table S2a).

Archaeophytes

The frequency of archaeophytes well adapted to urban environmental conditions (urbanity; Fig. 1a; Suppl. material 1: Table S2b) increased with mean temperatures (of both warmest and coldest month), broader precipitation range, across natural and urban areas, and with the number of geological patches. Conversely, their frequency decreased with an increase in annual precipitation, the proportion of calcareous subsoil and total number of Corine Land Cover (CLC) patches per grid cell.

With higher temperatures of the warmest month, species with high seed mass, wind- or self-pollination, high level of naturalness and those beginning to flower early will increase, while those with a long flowering period will decrease. Increasing amounts of precipitation disadvantaged small species that prefer artificial habitats but promoted species with high SLA, seed mass, presence of storage organs and multiple storage, self-pollination, as well as early beginning and late end of flowering.

Neophytes

Mean annual precipitation and number of CLC patches showed a strong positive relationship with multiple storage organs, yet mean temperature of the coldest month negatively affected this trait (Fig. 1b; Suppl. material 1: Tables S2c). Both wind- and self-pollination were negatively influenced by mean annual precipitation, and wind pollination was positively related to temperature (of the coldest and warmest month), sandy substrates and number of geological patches. Increase in the temperature of the warmest month promoted urbanophilic species, while the temperature of the coldest month positively affected the duration and end of the flowering period. Mean annual precipitation showed a negative relationship with plant height, but positive effects on SLA and plants with multiple storage organs.

Non-invasive neophytes

Increasing winter temperature positively affected wind- and self-pollination and flowering duration, whereas tall urbanophilic species were negatively affected (Fig. 1c; Suppl. material 1: Tables S2d). Conversely, high summer temperatures were positively correlated with the frequency of tall urbanophilic non-invasive neophytes, and negatively with long flowering duration or larger SLA and seed size. An increase in the number of CLC patches favored insect-pollinated, urbanophilic plant species with higher SLA, while negatively affecting the abundance of long-flowering, self-pollinated species.

Invasive neophytes

The temperature of the warmest month was positively related to SLA, multiple storage organs, self-pollination and negatively to duration of flowering (Fig. 1d; Suppl. material 1: Tables S2e). In contrast, the temperature of the coldest month was negatively related to SLA and positively to hemeroby. Annual precipitation negatively affected the beginning of flowering, while the precipitation range was positively associated with SLA and self-pollination. The number of CLC patches had a positive relationship with multiple storage organs and a negative one with hemeroby.

Differences among invasive neophytes (black list) were positively associated with land cover and mostly negatively with geological predictors. Neophytes with a limited distribution in Germany (action list) had positive relationships with all three types of land cover and with number of CLC patches and negative associations with calcareous, sandy substrates and number of geological patches.

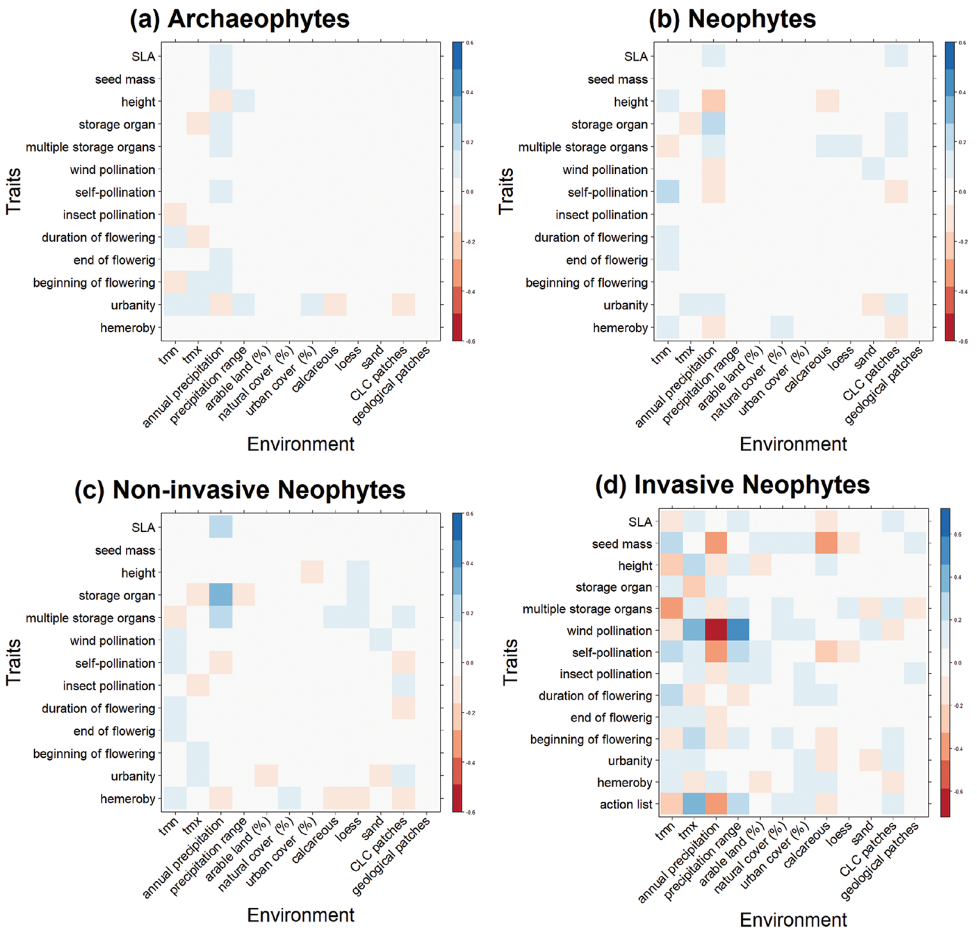

Figure 1. Fourth-corner plots for **a** archaeophytes **b** all neophytes lumped together regardless of status **c** non-invasive neophytes, and **d** invasive neophytes. Figure shows standardized interaction coefficients for plant traits (y-axis) and environmental variables (x-axis). Strong relationships are shown in blue (positive) and red (negative) while color intensity shows interaction strength with coefficient values on log scale. Abbreviations: tmn – mean temperature of the coldest month; tmx – mean temperature of the warmest month; CLC patches – total number of Corine Land Cover patches per grid cell.

Differences among groups

Archaeophytes and neophytes showed several contrasting trait–environment relationships (Fig. 1a, b). Specifically, the frequency of self-pollination in archaeophytes increased with the temperature of the warmest month, mean annual temperature and proportion of loess substrates, while under these conditions the frequency of neophytes diminished. Similarly, in archaeophytes we observed a positive relationship between urbanity and temperature of the coldest month, the proportion of natural areas and number of geological patches, and a negative relationship with annual precipitation and number of land cover patches. Neophytes showed opposing trends.

Further, we observed differences between non-invasive neophytes and invasive neophytes (Fig. 1c, d). While the frequency of invasive neophytes with higher SLA increased with temperature of the warmest month and precipitation range, non-invasive neophytes displayed reversed trends. Similarly, urbanophilic invasive neophytes were promoted by increasing temperature of the coldest month, and insect-pollinated invasives by the number of geological patches and temperature of the warmest month, with contrasting tendency in non-invasive neophytes. Finally, insect-pollinated invasive neophytes benefited from increasing annual precipitation and a high number of land-cover patches, although these variables showed to be disadvantageous for non-invasive neophytes.

Discussion

We did not record any strong trait–environment relationships for native species, which may be due to the heterogeneity of different ecological groups. Preliminary tests (not shown) indicated that this scarcity of trait–environment relationships was not an artifact of the large sample size of native species. This is because (overall) native species colonize a much wider range of environmental conditions in their native range than species alien to that range. Alien species, for example, are rarely found under extreme environmental conditions such as in mountains, seashores, xeric habitats, bogs or fens (Chytrý et al. 2008, Alexander et al. 2011). This means that considering only alien plants makes it more likely to find trait–environment relationships than if all native species or random sets of native species (which are not ecologically selected) are taken into account. Therefore, we suggest analyzing trait–environment relationships of ecologically defined groups of native species. This, however, is beyond the scope of this paper; nevertheless, we report the results of native species to avoid publication bias.

We observed a lower number of strong trait–environment relationships for archaeophytes than neophytes, whereas in invasive neophytes (i.e. those on the GABLIS list) strong relationships were most frequent. Climatic variables had a high explanatory power in all groups. Traits of neophytes were mainly affected by climate and different geological types, and rarely by land cover. Most of the traits of archaeophytes were only affected by climatic conditions, such as temperature and mean annual precipitation (while precipitation range had little effect on their traits) and rarely by other environmental variables. Archaeophytes in Central Europe were predominantly introduced from the Mediterranean and the Middle East (Pyšek et al. 2012b), thus from a smaller range of geographical locations (and hence environmental conditions) than neophytes (introduced from around the globe), and many invasive neophytes originate from different regions and continents, and thus might have adapted to a wider range of environmental factors (Pyšek et al. 2005). This might be the reason why traits of neophytes, in addition to their diverse origin, showed a more pronounced response to climatic and geological factors.

We observed that relationships between environment and traits for different groups of alien species are more often similar rather than contrasting (e.g. height decreases with annual precipitation for both neophytes and archaeophytes; beginning of flowering shifts to earlier months with increasing winter temperature and precipitation for invasive and non-invasive neophytes, etc.). Plant growth (e.g. biomass, height, leaf size) and phenology are directly influenced by temperature (Hatfield and Prueger 2015); for example, extreme temperature (especially summer temperature) can alter the duration and success of the pollination process (Hegland et al. 2009). Furthermore, alien species exhibit traits that allow them to cope better than natives with the recently observed changes in climate or habitats, such as better dispersal ability, higher tolerance to climate change and higher competitiveness (Dukes and Mooney 1999).

Differences in neophytes vs. archaeophytes

As to the best of our knowledge, no statistical test allows the formal comparison of results across different fourth-corner analyses; we have to interpret differences among the trait-environment responses of different groups qualitatively. Trait-environment relationships were similar (positive or negative, respectively) for archaeophytes and neophytes in 13 cases but differed in seven cases. Primarily, urbanity expressed contrasting relationships, suggesting human-induced propagule pressure as an important driver. Neophytes tend to be more urbanophilic, thus the increase in temperature was positively related to this trait (urban heat island effect; Ricotta et al. 2009). Urban areas facilitate neophytes (Kühn et al. 2004; Kühn and Klotz 2006), and alien species are often associated with cities (Chytrý et al. 2008b; Knapp et al. 2009; Aronson et al. 2014). Some studies showed that neophytes are becoming a dominant group in urban areas (Chocholoušková and Pyšek 2003; Pyšek et al. 2004), while the association of archaeophytes with this type of environment decreased in recent decades, and they are more common in arable landscapes (Botham et al. 2009). Hence, the increase in the proportion of arable and natural land cover affected urbanophytic neophytes negatively, but the increase in the proportion of urban area increased their abundance (and resulted in a reversed trend in archaeophytes). Neophytes are cultivated in gardens and public parks (Reichard and White 2001; Pergl et al. 2016), and their spread is further facilitated by extensive transportation systems (Seebens et al. 2015). Consequently, cities often present harbors for the spread (von der Lippe and Kowarik 2008) and establishment of newly introduced species (Kühn et al. 2017).

The majority of neophytes (especially invasive) are pollinated either by insects or wind, whereas archaeophytes are often self-pollinated (Pyšek et al. 2011). Many agricultural weeds are self-pollinated archaeophytes, possibly due to a lack of suitable pollinators or because of abiotic stress. Further, in archaeophytes, self-pollination is more common with increases in the proportion of loess. This can be due to loess being very fertile and suitable for agriculture, so self-pollination can be an alternative (Kühn et al. 2006), especially with the increasing scarcity of insects in regions of intensive agriculture (Hallmann et al. 2017).

Differences in non-invasive vs. invasive neophytes

Flowering phenology is important for the successful spread of invasive species (Knapp and Kühn 2012). Plant species have evolved in tune to local climatic regimes in their native range or colonized such regions naturally. With increasing temperatures (summer and winter), invasive neophytes finish their flowering period later in the year (with overall shorter duration). However, higher summer temperatures had a negative effect on the duration and higher winter temperature caused invasive neophytes to start flowering earlier. Many invasive species in Germany originate from warmer climates and as a result, an increase in winter temperature can act as a switch to earlier flowering. Earlier flowering of invasive species compared to non-invasive may ensure their reproductive success, and higher summer temperatures prolong the flowering season to late summer (Knapp and Kühn 2012). Low precipitation often impedes flowering, and the species that flower earlier can avoid summer droughts (Godoy et al. 2009). The increase in precipitation range (usually resulting from wet winters and dry summers) decreases the duration of flowering and plants were flowering later in the year. Depending on the origin of invasive neophytes, we can expect different responses to current or future climatic conditions. Provided that climate in the introduced area is the same as in the native area, flowering phenology can stay the same. However, if introduced species are subjected to a different climate, the flowering depends on the capability of invasive species to adapt or respond plastically to new conditions.

Alien plants that have often been introduced for their aesthetic features as ornamental plants can attract pollinators (colorful and fragrant flowers) and divert them from native plants (Bjerknes et al. 2007; Muñoz and Cavieres 2008). The majority of tropical and temperate plants are insect-pollinated (Ollerton et al. 2011), invasive neophytes, though, are primarily insect or self-pollinated. Additionally, many invasive species are annual plants and when suitable pollinators are not available they are able to self-pollinate which can be beneficial for the successful invasion of new areas (van Kleunen et al. 2007).

Climatic factors did not have a different effect on the occurrence of invasive species from the management or action black list. Species on the action list are more likely to be found in all three types of land cover than those from the management list. We can, therefore, expect that species which are invasive but still of limited distribution, will spread, especially as habitats become more fragmented (occurrence of action list species shows an increase with CLC number of patches).

General patterns

Geological bedrocks did not have a major effect on most of the traits in different groups, despite explaining roughly a quarter of plant distribution variability in Germany (Pompe et al. 2008). Archaeophytes often occur on loess, which is highly productive and usually used for intense agriculture. However, in calcareous substrates archaeophytes tend to flower later while invasive neophytes flower earlier and are taller. Species-rich calcareous grasslands used to be common in Germany and are now frequently afforested, suffer from shrub encroachment or are surrounded by agricultural fields (Fischer et al. 1996). Sandy substrates can warm up earlier during winter and spring and can be suitable for neophytes introduced from warmer regions. Additionally, due to its low water-retention property, sandy substrates are frequently colonized by species adapted (i.e. having suitable traits) to drought.

Different land-cover types as well as the number of land-cover patches and geological patches had an effect on most of the traits of invasive neophytes, and very little (or no effect) on archaeophytes. Furthermore, landscape transformation and heterogeneity have an effect on invasive species in different stages of invasion and fragmentation of the landscape may facilitate the spread of invasive species (With 2002). Habitat heterogeneity intensifies invasion and increases dispersal (O'Reilly-Nugent et al. 2016; Dukes and Mooney 1999), and we have recorded a positive relationship with flowering phenology, SLA, height and seed mass of invasive neophytes. However, invasive neophytes with multiple pollination vectors (i.e. having different pollination types) benefited the most whereas wind-pollinated species colonized the least heterogeneous landscapes. These wind-pollinated invasive species are often dependent on specific habitats, for example, *Fraxinus pennsylvanica* or *Acer negundo* are often abundant in riparian or urban habitats (Burton et al. 2005).

Many studies have shown that functional traits of alien species are associated with invasiveness (Hamilton et al. 2005; Pyšek and Richardson 2007; Ordoñez et al. 2010; van Kleunen et al. 2010; Gallagher et al. 2015; Divíšek et al. 2018). However, the results were often ambiguous, possibly due to excluding environmental factors from analyses. In our study, we showed that traits, particularly of invasive neophytes, exhibit a strong relationship with the environment. Native species showed fewer associations with environmental factors as their traits may be more conservative in their native habitat and less likely to fluctuate. Yet, we looked at climatic conditions within a limited period (1961–1990) and native species might show significant changes in their functional traits as climate changes. Similar to native species, archaeophytes, the species that have settled in Germany for a long time, showed the least significant trait-environment relationships among alien species, while the traits of invasive neophytes are greatly affected by climate, geology and land cover. As discussed, this might be due to the fact that many invasive species were introduced from areas with different climatic or geological conditions and respond more flexibly to changes in the environment (Hellmann et al. 2008).

Invasive neophytes mainly show positive trait-environment relationships. Since the values for most of the traits increased with the incorporated environmental factors (especially climatic and land cover variables), we can expect future climate and land-cover change to affect invasive neophytes more strongly than other alien groups. We showed that climate may affect in particular SLA, insect pollination and phenology of invasive species, whereas land cover may mainly influence height, seed mass and wind pollination. Climate change could affect archaeophytes as well. They mainly showed positive relationships with climatic variables, and their values increased with the increase in temperature and precipitation. Future studies on the relationship between functional traits and environment of invasive plants are required in order to examine the effects of climate change or land cover changes. There is evidence that climate change may promote invasiveness (Pyšek et al. 2005), thus distinguishing which traits of alien species are benefiting under different climatic scenarios, can be valuable for management implications.

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Supplementary material 1

Tables S1, S2

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Data type: model output

Explanation note: **Table S1.** Coefficient values from *traitglm* model for (a) native species, (b) archaeophytes, (c) neophytes, (d) non-invasive neophytes, (e) invasive neophytes in Germany. Coefficients describe how traits are related to environmental conditions; values show strength of interaction and direction (positive/negative). **Table S2.** Results of *anova.traitglm* for different groups of non-native species with 99 permutations (probability integral transform residual bootstrap (PIT-trap) block resampling which accounts for correlation in testing).

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