

An analysis of temporal homogenisation and differentiation in Central European village floras

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Abstract

Agriculture and urbanisation shape biodiversity through extirpation of species and facilitation of species introductions. These processes include changes in the functional composition of species assemblages and can result in taxonomic and functional homogenisation. Especially the spread of non-native species has been discussed as a driver of homogenisation. However, no consensus has been reached so far; instead, both homogenisation and differentiation by non-native species have been shown. This inconsistency can partly be attributed to the lack of temporal data: Most homogenisation studies rely on purely spatial analyses, while homogenisation develops over time. We studied vascular plant species occurrences in 59 villages in the West of Germany in the 1980s and twenty years later. Within this period, the villages experienced changes in agriculture and trends towards urbanisation. We asked whether the villages' floras became more similar to each other within the study period, and whether this process differed between selected plant groups. We based plant groups on leaf traits, life form, species native/non-native status, and mode of introduction. This enabled us to discuss changes in the flora in the context of land-use changes. We used Simpson's index of dissimilarity as a measure of β -diversity among villages and calculated species turnover and homogenisation in time. Overall, village floras became more similar to each other within the study period. However, neophytes became less similar to each other across villages. Turnover between sampling periods was largest for species promoted by horticulture and for species with helomorphic leaves (suggesting an effect of habitat loss on turnover). Neophytes will likely continue to differentiate floras on regional scales due to on-going and various introductions.

Zusammenfassung

Landwirtschaft und Urbanisierung beeinflussen die Biodiversität, indem sie das Aussterben von Arten und die Einführung neuer Arten begünstigen. Ein derartiger Artenaustausch kann sowohl Veränderungen in der funktionellen Zusammensetzung von Artengemeinschaften, als auch Homogenisierung auf taxonomischer und funktioneller Ebene nach sich ziehen. Insbesondere die Einführung gebietsfremder Arten wird als Triebfeder von Homogenisierungsprozessen diskutiert. Bislang konnte die Frage, ob gebietsfremde Arten die Angleichung von Artengemeinschaften vorantreiben, allerdings nicht abschließend beantwortet werden, da unterschiedliche Studien einerseits Homogenisierung, andererseits Differenzierung nachgewiesen haben. Zum Teil resultieren diese scheinbar widersprüchlichen Ergebnisse aus dem Mangel an zeitlichen Analysen – obwohl Homogenisierung sich im Laufe der Zeit entwickelt, verwenden die meisten Homogenisierungsstudien räumliche Daten. Wir haben die Entwicklung der Gefäßflora in 59 nordrhein-westfälischen Dörfern zwischen 1980 und 2005 untersucht, einer Zeit, in der die

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Dorfentwicklung von landwirtschaftlichen Veränderungen und Urbanisierungserscheinungen geprägt war. Wir wollten wissen, ob die Dörfer einander floristisch ähnlicher geworden sind und ob sich der Grad des Ähnlicher-Werdens zwischen ausgewählten Artengruppen unterscheidet. Dafür haben wir die Arten anhand ihres floristischen Status, ihrer Einführungsweise, verschiedener Blattmerkmale und ihrer Lebensform in funktionelle Gruppen eingeteilt. So konnten wir Veränderungen der Flora im Licht von Landnutzungsveränderungen diskutieren. Als Maß für Homogenisierung und Arten-Turnover im Lauf der Zeit diente Simpsons Unähnlichkeitsindex. Innerhalb des Untersuchungszeitraums wurden sich die Floren der Dörfer ähnlicher. Dies traf allerdings nicht auf die Gruppe der Neophyten zu; diese wurden einander unähnlicher. Der Arten-Turnover im Untersuchungszeitraum war zum einen für die Arten besonders ausgeprägt, die vom Zierpflanzenanbau profitieren (Gartenflüchtlinge), zum anderen von Arten, die durch eine helomorpe Blattstruktur gekennzeichnet sind, was einen Effekt des Lebensraumverlustes auf den Turnover der Arten andeutet. Da immer wieder verschiedenste neue Neophyten eingeführt oder eingeschleppt werden, werden diese wohl weiterhin differenzierende Effekte auf die Floren regionaler Skalen ausüben.

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Introduction

Agriculture and urbanisation are dominant drivers of land-use change and environmental homogenisation (McKinney 2006; Ellis, Goldewijk, Siebert, Lightman, & Ramankutty 2010). The intensification of agricultural production decreased landscape heterogeneity, which in turn decreased species richness (Krebs, Wilson, Bradbury, & Siriwardena 1999). Towns and cities around the world focus on human needs. Consequently, many of them are similar to each other with respect to their built-up structure and climatic conditions such as the urban heat island (McKinney 2006).

The homogenisation of environmental conditions drives the extirpation of mal-adapted species and fosters well-adapted species. Both processes can result in the homogenisation of species assemblages (Winter et al. 2009) with introductions of non-native species being considered a dominant driver of biotic homogenisation (McKinney & Lockwood 1999). However, whether non-native species promote homogenisation or differentiation differs between taxa and scales (Shaw, Spear, Greve, & Chown 2010). For example, Kühn and Klotz (2006), analysing the flora of urban areas in Germany, found that neophytes (i.e. non-native species introduced either deliberately or accidentally after the discovery of the Americas by Columbus in 1492) differentiated the floras of urban areas, while native species homogenised the floras. Similarly, La Sorte et al. (2008) did not find homogenisation by neophytes but differentiation across cities on a European scale.

Given the time-lag between the introduction and establishment of non-native species (Kowarik 1995), they should promote differentiation in early stages of their establishment, not being widely distributed yet, but homogenisation when increasing their ranges (La Sorte & McKinney 2006). Consequently, temporal studies are needed to clarify whether non-native species are dominant drivers of biotic homogenisation or not. However, by now, most homogenisation studies have examined spatial but no temporal patterns (but see Klotz

& Il'minskich 1988; Keith, Newton, Morecroft, Bealey, & Bullock 2009).

As environmental changes affect species functional traits (Lavorel & Garnier 2002), homogenisation and differentiation should be functionally biased. For example, Qian and Guo (2010) demonstrated that short-lived herbaceous species homogenised the floras of North American states, while woody species had differentiating effects. Turning back to the assumption that differentiation and homogenisation are related to species ranges, traits that are characteristic for widespread species should promote homogenisation and traits characterising rare species should promote differentiation.

We analysed changes in the spontaneous flora of 59 German villages between 1980–1984 and 2004–2005. Within this period, villages in Germany experienced de-ruralisation: Many villages formerly dominated by farms became homes of urban commuters (Jetzkowitz, Schneider, & Brunzel 2007), increasing traffic connections among settlements (Aring 2002). The amount of sealed areas increased across European settlements as a consequence of suburbanisation (Scalenghe & Marsan 2009). Trends towards the urbanisation of village floras reflect these developments (Wittig 1998) with neophyte richness increasing in villages dominated by urban commuters (Brunzel, Fischer, Schneider, Jetzkowitz, & Brandl 2009). Moreover, agriculture in the surroundings of villages intensified, changing the regional species pool from which parts of the village flora recruit.

Our questions were:

1. Did the floras of the 59 villages become more similar to each other between 1980/84 and 2004/05?
2. How did the similarity of neophytes among villages change between 1980/84 and 2004/05 in comparison to native species and archaeophytes (non-native species introduced before 1492)?
3. Do the strength of homogenisation/differentiation and the strength of turnover differ among groups of species characterised by specific functional traits?

Materials and methods

Species data

Between 1980 and 1984, the second author mapped the spontaneous vascular flora of 200 villages with old village structures or at least one practising farmer in North-Rhine Westphalia (NRW) in the West of Germany (Wittig & Rückert 1985) in order to detect whether the typical vegetation of old villages was still present. The inventory included all spontaneous plant species (not planted or sown by humans) that grew in accessible public domains within the villages' built areas: along roads, on village squares, market places, footpaths, courtyard entrances, walls, fallow land, and front gardens (there including only weeds that were clearly occurring spontaneously and grew in flower beds or lawns visible from the street). The flora of cemeteries, large parks, ponds, and agricultural or semi-natural areas adjacent to villages was excluded. If a village included remnants of pastures, meadows or forest, only the edges of these habitats were mapped. Each village was mapped once between July and September (Appendix A: Table 1), when most species were flowering, and effects of weeding should be minimal. In the 1980s, it was common that villagers weeded public and private places before the Feast of Corpus Christi in June and the town guards shooting competition in late September (R. Wittig, personal observation). The inventory took place in-between these two feasts. Still, as species were mapped in summer, geophytes and early flowering therophytes are underrepresented.

In 2004 and 2005, the second author again recorded the flora of 200 villages in NRW. This inventory aimed at identifying overall changes in village floras between the 1980s and 2004/05 (not at the comparison of single villages). Thus, villages were chosen randomly (Wittig 2008). All other mapping criteria stayed the same. Still, as several villages had grown in size between the 1980s and 2004/05, for these villages, mapping took longer than in the first study period. In 2004/05, species were mapped between late June and end of August (Appendix A: Table 1). As intensive weeding was not common anymore (R. Wittig, personal observation), the chance of not detecting a species because it was weeded shortly before the inventory should be minimal.

59 of the villages mapped in 2004/05 had also been mapped in 1980/84. We compare the results of the two inventories considering these 59 villages (Fig. 1; see Wittig & Rückert 1985 for details on the study area).

Trait data

The BioFlor database on biological and ecological traits of the German flora provided information on native/non-native status of species and their mode of introduction (Kühn, Durka, & Klotz 2004; <http://www.ufz.de/bioflor>; see Appendix A: Table 2 for trait category definitions). Strictly speaking, native/non-native status and mode of introduction

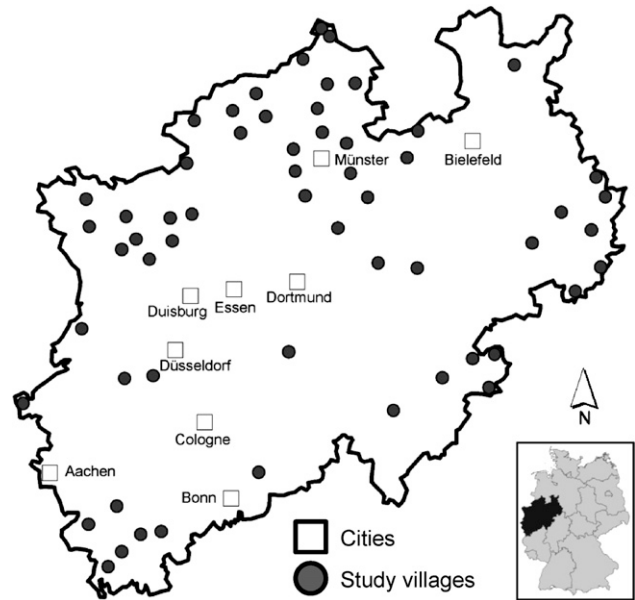


Fig. 1. Location of the 59 study villages in North-Rhine Westphalia. Cities are shown for orientation. The inset shows the location of North-Rhine Westphalia in Germany.

are no traits but descriptions of origin, but we call them traits for simplicity. Species not classified in BioFlor were classified according to Wittig (2008) and Haeupler, Jagel, and Schumacher (2003). Taxa belonging to several status groups were excluded (these were *Alchemilla vulgaris* agg. and *Fragaria* sp., which both comprise several species, some of them being native to Germany and others being non-native in Germany). BioFlor lists 18 questionable archaeophytes for which it is unclear whether they were introduced to Germany or whether they are native. We treated these species as archaeophytes because most of them are agricultural weeds or escaped crop species (Appendix A: Tables 2 and 3), suggesting that they were introduced with early agriculture. We chose native/non-native status to assess the contribution of non-native species to homogenisation in comparison to native species. Modes of introduction were analysed to test whether specific groups of non-native species contribute disproportionately to homogenisation.

Additionally, we chose Raunkiaer's life form, leaf structure, leaf persistence, leaf form, and type of rosette from BioFlor (Appendix A: Table 2). Leaves exchange water, oxygen, and CO₂ with the atmosphere and play a key role within a plant's nutrient regime and heat balance. Accordingly, leaf traits are good indicators for environmental changes (Wright et al. 2005), making them preferable for our study. For example, species with scleromorphic or compound leaves often indicate dry conditions. Raunkiaer's life form classifies species according to the location of their resting buds, which is closely related to climate. Moreover, life form types are indicators of disturbance and land-use changes (Knapp, Kühn, Stolle, & Klotz 2010).

α -, β -, and γ -diversity

For both time spans, we calculated the number of species per village (α -diversity), in all villages (γ -diversity), and γ -diversity of species native to Germany, archaeophytes, and neophytes. We calculated β -diversity between the first and second time span (temporal turnover) for all species and species within trait categories per village. To test whether turnover was functionally biased, we compared turnover rates among a trait's different categories using non-parametric Fisher's pair comparison test (Manly 1991). As each village occurs in both time spans, data are paired and data points are not independent. Fisher's pair comparison test takes this dependency into account. We calculated species temporal turnover with Simpson's index of dissimilarity:

$$\beta_{\text{dissim}} = \sqrt{1 - \left(\frac{a}{(a + \min(b, c))} \right)}$$

which ranges from zero to one (a = number of species shared between two time spans; b and c = number of species unique to a time span). With $\beta_{\text{dissim}} = 1$, two species assemblages have no species in common; with $\beta_{\text{dissim}} = 0$ they have identical species sets. We chose β_{dissim} because it does not reflect differences in species richness between assemblages, unlike other measures of species turnover such as the Jaccard index (Koleff, Gaston, & Lennon 2003). However, the index is problematic if one assemblage is a subset of another; e.g. if assemblage A contains species x , y , z , and assemblage B contains species y and z , $\beta_{\text{dissim}} = 0$, although similarity is incomplete. Therefore, if $\beta_{\text{dissim}} = 0$, we tested whether the communities were really the same or subsets of each other ("subset-cases").

We compared temporal turnover between trait categories once including and once excluding subset-cases. As the exclusion caused a loss of data pairing, we applied the unparametric Mann–Whitney–Wilcox U -test here. Moreover, we excluded trait categories with a mean of ≤ 10 species per village to avoid non-meaningful results (Appendix A: Table 4).

The time of mapping might affect turnover rates (e.g. if a village was mapped in July in 1980/84 but in August in 2004/05). As flowering and non-flowering species and species in early and late life stages were identified, this effect should be small – it would be an issue in spring with many short-lived geophytes, but not in summer. Still, we tested for an effect of mapping time by calculating the difference in time per village (if a village was mapped on the 17th of August in 1980/84, and on the 29th of July in 2004/05, the difference is 19 days). We correlated total species temporal turnover and difference in mapping time (Pearson correlation).

Homogenisation vs. differentiation

Further, we used β_{dissim} to calculate how similar the floras of the 59 villages were to each other in 1980/84 and

how similar they were in 2004/05 (spatial turnover). If similarity in 2004/05 was higher than in 1980/84, homogenisation took place; vice versa, differentiation took place. We calculated homogenisation patterns for all species and within trait categories. Again, we excluded categories with a mean ≤ 10 species per village, and calculated spatial turnover with and without exclusion of subset-cases, using Mann–Whitney–Wilcox U -test in the former and Fisher's pair comparison test in the latter case.

To better understand the effects of neophytes on patterns of homogenisation and differentiation, we additionally calculated spatial turnover for (i) neophytes that became naturalised in Germany before 1850, and neophytes that became naturalised from 1850 onwards, as well as for (ii) escaped ornamental archaeophytes, and escaped ornamental neophytes. We chose the separation by date of naturalisation (taken from BiolFlor) to test whether neophytes that have been present for a long time have contributed to homogenisation, and whether those that have been present for a short time have contributed to differentiation. We chose the year 1850 for separation because this yielded two groups of similar size. Moreover, we decided to separate escaped ornamental species into archaeophytes and neophytes, because ornamental horticulture is a major pathway for the introduction of neophytes (Dehnen-Schmutz, Touza, Perrings, & Williamson 2007) and should therefore be an important driver of homogenisation/differentiation.

Results

α -, β -, and γ -diversity

In 1980/84, the spontaneous flora of the 59 villages (γ -diversity) included 481 species, 310 being native (64.45%), 96 archaeophytes (19.96%), and 74 neophytes (15.38%). One taxon (0.21%) was excluded because it belonged to several status groups. In 2004/05, there were 509 species: 316 native species (62.08%), 95 archaeophytes (18.66%), 96 neophytes (18.86%), and two taxa that were excluded (0.39%) as they belonged to several status groups (Appendix A: Table 3).

Species richness per village increased in 51 villages and decreased in 8 villages (Appendix A: Table 1). It ranged from 44 to 176 species in 1980/84 (mean: 103; Fig. 2) and from 79 to 191 species in 2004/05 (mean: 137.6; Fig. 2). Mean species richness per trait category increased between 1980/84 and 2004/05 in all cases (e.g. neophytes: mean in 1980/84: 9.5; mean in 2004/05: 17.0; escaped ornamental species: mean in 1980/84: 2.7; mean in 2004/05: 8.9; Appendix A: Table 5) except for species with helomorphic leaves (mean in 1980/84: 9.5 species; mean in 2004/05: 8.0 species; Appendix A: Table 5).

Total species temporal turnover per village ranged from 0.32 to 0.69 (mean: 0.53). Temporal turnover was not correlated to differences in mapping dates between the first and second time span ($r = -0.04$ n.s.).

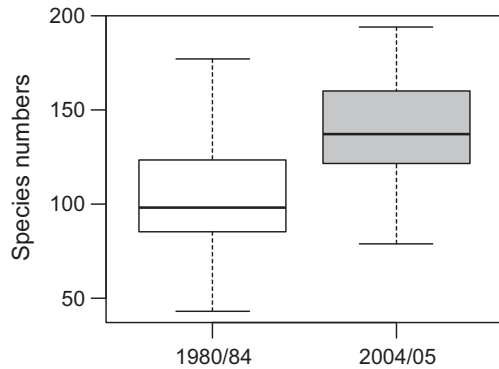


Fig. 2. Species numbers in 1980/84 and 2004/05 in 59 villages in North-Rhine Westphalia, Germany.

Within traits, temporal turnover differed among categories: It was significantly higher for species with helomorphic leaves than for all other leaf structure categories (Table 1). Escaped ornamental species had the highest temporal turnover among all modes of introduction, and neophytes had a higher temporal turnover than natives and archaeophytes. These results did not differ between including and excluding subset-cases (Table 1; see results for all other traits there).

Homogenisation vs. differentiation

The total flora was significantly more similar among villages in 2004/05 than in 1980/84 (Table 2). The same was true for all trait categories, with two exceptions: Among life form types, geophytes showed no changes in similarity. However, when excluding all subset-cases, geophyte similarity increased as well. Among status groups, neophytes were significantly less similar among villages in 2004/05 than in 1980/84 (Fig. 3 and Table 2). Except for geophytes, results did not differ between the inclusion and the exclusion of subset-cases. Homogenisation was mainly driven by species gains, only to a minor extent by species losses (Appendix A: Table

1). Accordingly, many species were distributed across more villages in 2004/05 than in 1980/84. Separating neophytes into those naturalised before 1850 and those naturalised from 1850 onwards yielded no clear results: when including subset-cases, both groups were less similar in 2004/05 than in 1980/84 (Table 2); when excluding subset-cases, both groups were less similar in 1980/84 than in 2004/05. Separating escaped ornamental species into archaeophytes and neophytes showed that the former were more similar to each other among villages in 2004/05 than in 1980/84 (both with and without subset-cases; Table 2). Escaped ornamental neophytes showed no clear results: when including subset-cases, their similarity did not differ between time spans (Table 2); when excluding subset-cases, they were more similar in 2004/05 than in 1980/84. Escaped ornamental archaeophytes had the largest change in similarity between the two time spans (0.38; Table 2), and also the whole group of escaped ornamental species had a high change in similarity (0.10; Table 2).

Discussion

Drivers of homogenisation

Overall, the similarity of village floras increased between 1980/84 and 2004/05, as many species increased their ranges across villages. Range expansion can mainly be attributed to (i) human mobility and (ii) horticulture.

(i) *Human mobility.* Brunzel et al. (2009) showed an increase in the ranges of neophytes across settlements north of Frankfurt/Main, Germany, between 1974 and 2003. Neophytes were more common in settlements, the better the connection to Frankfurt indicating dispersal by traffic. Indeed, both native and non-native species can be dispersed by traffic, including long-distance dispersal (von der Lippe & Kowarik 2007). Consequently, human mobility is one driver of plant species' range expansion.

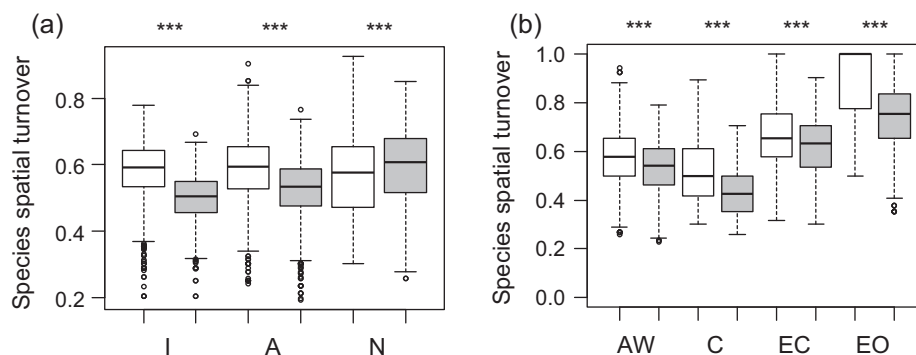


Fig. 3. Species spatial turnover of (a) native/indigenous species (I), archaeophytes (A), and neophytes (N), and (b) agricultural weeds (AW), contaminants (C), escaped crop species (EC), and escaped ornamental species (EO) in 1980/84 (white boxplots) and 2004/05 (grey boxplots) in 59 villages in North-Rhine Westphalia, Germany. Boxplots represent median (line), 25–75% quartiles (boxes), ranges (whiskers) and extreme values (circles).

Table 1. Mean species turnover between 1980/84 and 2004/05 in 59 villages in North-Rhine Westphalia for various plant trait categories. Species turnover was measured as Simpson's index of dissimilarity (0 = complete similarity; 1 = complete dissimilarity). Trait categories with <10 species per village were excluded. Results were calculated once including "subset-cases" using Fisher's pair comparison test, and once excluding "subset-cases" using Mann–Whitney–Wilcoxon *U*-test. The letters given after mean turnover-values denote significant differences ($p \leq 0.05$) among a trait's categories (with a = smallest value, and b–d denoting increasing values).

Traits and trait categories	Mean turnover (incl. subset-cases)	Mean turnover (excl. subset-cases)
Leaf structure		
Helomorphic	0.59c	0.63c
Hygromorphic	0.42a	0.42a
Mesomorphic	0.53b	0.53b
Scleromorphic	0.53b	0.53b
Leaf persistence		
Evergreen	0.50b	0.51a
Summergreen	0.56c	0.56b
Overwintering green	0.45a	0.49a
Leaf form		
Pinnatifid	0.38a	0.43a
Pinnate	0.56c	0.63d
Grass-like	0.54c	0.55c
Long-leaf	0.57c	0.61d
Simple	0.54c	0.54c
Full	0.48b	0.49b
Type of rosette		
Rosette plant	0.37a	0.51a
Hemirosette plant	0.53b	0.53a
Erosulate plant	0.55c	0.55b
Life form		
Geophytes	0.39a	0.56b
Hemicryptophytes	0.50c	0.50a
Phanerophytes	0.36a	0.63b
Therophytes	0.48b	0.48a
Floristic status		
Archaeophyte	0.50a	0.51a
Indigenous	0.52a	0.52a
Neophyte	0.59b	0.59b
Mode of introduction		
Agricultural weed	0.48a	0.52a
Contaminant	0.49a	0.50a
Escaped crop plant	0.51a	0.57ab
Escaped ornamental plant	0.62b	0.78b

Within our study period, commuting became common in North-Rhine Westphalia, and connectivity between villages and cities and among villages increased (Aring 2002). However, although many neophytes increased their ranges across villages (Appendix A: Table 3), they

became less similar during the study period. Additional factors must have affected their occurrence.

- (ii) *Horticulture*. Plant species are more likely to escape from gardens the more often they are sold by nurseries (Dehnen-Schmutz et al. 2007). Indeed, the increasing similarity of ornamental species in our study suggests that a similar pool of cultivated species was used in many villages (as also shown for southern France by Marco, Lavergne, Dutoit, & Bertaudière-Montes 2010). Pre-selection by cultivation should promote the escape from cultivation: In a Swiss study, cultivated non-native species germinated more abundantly than native non-cultivated species (Chrobok, Kempel, Fischer, & van Kleunen 2011). Moreover, changes in gardening preferences between 1980/84 and 2004/05 increased the propagule pressure of several ornamentals (Wittig 2008), e.g. *Cotoneaster* species.

It seems contradictory that neophytes became less similar but escaped ornamentals (with 85% of neophytes) became more similar in the study period. However, our calculations on escaped ornamental archaeophytes and escaped ornamental neophytes showed that the former drove the homogenisation of the whole group of escaped ornamental species while the latter did not. This pattern supports the hypothesis that non-native species contribute to differentiation in early stages of their establishment, while contributing to homogenisation in later stages (La Sorte & McKinney 2006). However, our calculations on neophytes naturalised before 1850 and those introduced from 1850 onwards illustrate that the time it takes until differentiating effects turn into homogenising effects might last much longer than a century.

Horticulture is also a potential driver of native species range expansion (irrespective of native species being not included in the group of escaped ornamentals): Several native species are frequently cultivated in the villages' gardens and have managed to escape (e.g. *Aquilegia vulgaris* L.). Overall, the high change in escaped ornamental species' similarity between the two time spans illustrates their important contribution to homogenisation in general.

Additionally, the release from herbicides might have contributed to homogenisation. Since 1986, the application of herbicides in areas not used for agriculture, forestry or gardening is forbidden in Germany (Gesetz zum Schutz der Kulturpflanzen/Plant Protection Act §6 (2); date of issue: 15.09.1986). Consequently, herbicide application in public village areas decreased, and a similar decrease can be assumed for private gardens (Wittig 2008). This should promote increased abundance and range expansion for many spontaneous species. However, Brunzel et al. (2009) found that increasing herbicide application increased archaeophyte richness but did not affect native and neophyte richness. As we did not test for the effect of herbicides, we cannot finally conclude that herbicide reduction promoted species range expansion.

Table 2. Homogenisation for the total flora and species within trait categories in 59 villages in North-Rhine Westphalia in 1980/84 vs. 2004/05 was calculated as Simpson's index of dissimilarity (0 = complete similarity; 1 = complete dissimilarity) for all village–village pairs in 1980/84 and in 2004/05. Mean, minimum (min.) and maximum (max.) index-values per time span are given. Differences between 1980/84 and 2004/05 were calculated using Fisher's pair comparison test. "Homogenisation" summarises whether the flora of villages became significantly more (+) similar, less similar (–) or whether there were no significant changes (/). "Mean difference" shows the differences between mean index-values in 1980/84 and 2004/05.

Traits and trait categories	Mean 1980/84	Mean 2004/05	Min. 1980/84	Min. 2004/05	Max. 1980/84	Max. 2004/05	Homogenisation	Mean difference
All species	0.60	0.54	0.26	0.25	0.76	0.71	+	0.06
Leaf structure								
Helomorphic	0.63	0.60	0.00	0.00	1.00	0.94	+	0.03
Hygromorphic	0.48	0.44	0.00	0.00	0.76	0.64	+	0.04
Mesomorphic	0.59	0.52	0.27	0.24	0.76	0.67	+	0.07
Scleromorphic	0.54	0.53	0.00	0.00	0.85	0.74	+	0.01
Leaf persistence								
Evergreen	0.55	0.47	0.00	0.00	0.77	0.66	+	0.08
Summergreen	0.61	0.56	0.24	0.25	0.80	0.75	+	0.05
Overwintering green	0.56	0.46	0.00	0.00	0.85	0.69	+	0.10
Leaf form								
Pinnatifid	0.46	0.38	0.00	0.00	0.80	0.73	+	0.08
Pinnate	0.64	0.58	0.00	0.00	1.00	1.00	+	0.06
Grass-like	0.54	0.44	0.00	0.00	0.93	0.71	+	0.10
Long-leaf	0.64	0.56	0.00	0.00	1.00	0.85	+	0.08
Simple	0.565	0.555	0.00	0.00	0.85	0.80	+	0.01
Full	0.59	0.50	0.00	0.00	0.87	0.74	+	0.09
Type of rosette								
Rosette plant	0.45	0.38	0.00	0.00	1.00	0.75	+	0.07
Hemirosette plant	0.60	0.51	0.29	0.00	0.79	0.72	+	0.09
Erosulate plant	0.62	0.56	0.00	0.31	0.85	0.76	+	0.06
Life form								
Geophytes	0.44	0.43	0.00	0.00	1.00	0.85	/	0.01
Hemicryptophytes	0.59	0.53	0.26	0.23	0.78	0.72	+	0.06
Phanerophytes	0.61	0.50	0.00	0.00	1.00	1.00	+	0.09
Therophytes	0.57	0.50	0.00	0.17	0.81	0.70	+	0.07
Floristic status								
Archaeophyte	0.59	0.53	0.00	0.00	0.90	0.77	+	0.06
Indigenous	0.58	0.50	0.20	0.20	0.78	0.69	+	0.08
Neophyte	0.53	0.58	0.00	0.00	0.93	0.85	–	0.05
Neophytes naturalised before 1850	0.54	0.56	0.00	0.00	1.00	1.00	–	0.02
Neophytes naturalised from 1850 onwards	0.32	0.36	0.00	0.00	1.00	0.87	–	0.04
Mode of introduction								
Agricultural weed	0.57	0.53	0.00	0.00	0.94	0.79	+	0.04
Contaminant	0.42	0.35	0.00	0.00	0.89	0.71	+	0.07
Escaped crop plant	0.64	0.60	0.00	0.00	1.00	0.90	+	0.04
Escaped ornamental plant	0.81	0.71	0.00	0.00	1.00	1.00	+	0.10
Escaped ornamental archaeophytes	0.66	0.28	0.00	0.00	1.00	1.00	+	0.38
Escaped ornamental neophytes	0.78	0.77	0.00	0.00	1.00	1.00	/	0.01

Decreasing similarity of neophytes

Neophytes became less similar within the study period, confirming several spatial studies on biotic homogenisation

(e.g. Kühn & Klotz 2006; La Sorte et al. 2008). Introduction and spread of neophytes are on-going processes: While the pool of native species and archaeophytes is restricted, the pool of neophytes is continually increasing. Consequently, the

chance that archaeophytes and native species that newly enter a village are already present in another village is larger than for neophytes. Indeed, in different villages, different neophytes entered the spontaneous flora after 1984; e.g. *Prunus laurocerasus* L. occurred in only two villages in 2004/05 (Appendix A: Table 3). As time-lags between the introduction of non-native species and their establishment in the spontaneous flora comprise >100 years on average (Kowarik 1995), our study period might be too short to show homogenisation by neophytes. This is also supported by our result that neophytes naturalised before 1850 or from 1850 onwards did not differ in their effect on spatial turnover. Moreover, homogenisation might first be visible on scales larger than the regional scale of our study (Shaw et al. 2010).

Temporal turnover within functional groups

The temporal turnover of species with helomorphic leaves, which was highest among all leaf structure types, can be attributed to habitat loss and the resulting loss of species: Helomorphic species, which are adapted to moist and wet oxygen-deficient habitats (Appendix A: Table 2; such as *Lythrum salicaria* L. or *Ranunculus flammula* L.) are the only trait category that decreased in the study period (not shown). In villages, suitable habitats for helomorphic species can be found, for example, along non-sealed roads or footpaths, where standing water drains slowly. Such habitats were already rare in the 1980s but became even rarer afterwards due to increasing soil sealing as a consequence of suburbanisation (Aring 2002; Scalenghe & Marsan 2009). As we did not map ponds, our results exclude helomorphic species that might occur there.

It has repeatedly been stated that evergreen species increased their abundance and ranges within the last decades as a result of global warming (e.g. Walther et al. 2002). As there are many evergreen species among escaped ornamental species (such as *Mahonia aquifolium* (Pursh) Nutt. or *Alyssum saxatile* L.), villages might give early evidence of the spread of evergreen species, even before these species enter semi-natural habitats. Indeed, several evergreen species increased their ranges across villages between 1980/84 and 2004/05, but as the temporal turnover of evergreen species was not exceptionally high in comparison to other trait groups, we have no evidence that their spread is faster than the spread of species without evergreen leaves.

The high temporal turnover of neophytes and escaped ornamental species illustrates how highly dynamic these groups are. As stated before, whether species escape from cultivation or not largely depends on propagule pressure from cultivation, which is driven by market frequencies and prices (Dehnen-Schmutz et al. 2007) – in other words, horticultural fashions. With changing fashions, turnover is kept high.

Our results on the temporal turnover of overwintering green species, geophytes, and phanerophytes should be interpreted carefully. The two former might not have been

adequately mapped – many geophytes only occur in spring; overwintering green species lose their leaves in spring or early summer. Phanerophytes were often restricted to a small number of villages, causing a high number of subset-cases.

Conclusions

It seems likely that neophytes will continue to have differentiating effects, at least on floras of relatively small, regional scales (Shaw et al. 2010, and references therein). Neophytes that originate from warmer climates than the one of Central Europe should further increase their ranges with increasing temperatures (Kowarik 2005), and the introduction of neophytes will continue. However, given their long time-lags and the fact that most neophytes came to Germany in the 19th and 20th century (Klotz, Kühn, & Durka 2002), many of them might not have expanded their ranges wide enough to homogenise floras on regional scales. This will likely change in the future, with human drivers like traffic and horticulture promoting range expansion and increasing the chance of homogenisation by neophytes.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.baae.2012.06.004>.

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