

# Fit for succession – community structure and life strategies of leafhoppers in urban brownfields

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**Abstract.** 1. Urban brownfields offer an excellent opportunity to study successional processes. Changes in the frequencies of biological traits during succession are of particular interest. They shed light on the general reasons why species emerge and vanish during the course of succession.

2. Leafhopper (Hemiptera: Auchenorrhyncha) occurrence data (3763 species observations) of 194 species were studied. Data was collected on 246 brownfield plots, aged 0–40 years, in two cities in Northern Germany.

3. Four categorical traits were studied: host-plant type, phagy, dormancy, and voltinism. In these traits, two aspects were analysed: (1) changes in trait category frequencies during succession, and (2) distribution of trait categories (i) within the brownfield species pool versus the German species pool and (ii) within species observations.

4. Trait categories showed clear successional trends. Young successional stages were related to feeding on herbs, polyphagy, egg overwintering, and two generations per year.

5. By analysing combinations of two traits, species could be assigned to four functional groups: species associated with young, intermediate and old sites, and one group indifferent to site age. The pioneer group comprised the least number of species, but the highest number of observations.

6. Categories associated with young site age were over-represented in the brownfield species pool. Moreover, within this already biased species pool, species with pioneer trait categories occurred with higher frequency. For the slow colonisers among leafhoppers, brownfields seem to be habitats that are hard to exploit.

**Key words.** Auchenorrhyncha, fourth corner statistic, Hemiptera, hibernation, host-plant specialisation, life-history traits, voltinism.

## Introduction

### *Species traits*

Biological traits are ‘well defined, measurable properties of organisms’ (McGill *et al.*, 2006) that reflect how they live, including growth, feeding, movement, dispersion, and reproduction. More than a century ago, ecologists started to recognise a relationship between the traits of animals and the habitat conditions where they occur (Statzner *et al.*, 2001). Ecologists have long been aware that trade-offs in biological traits enable animals with different trait combinations to settle equally successfully in

the same habitat (Statzner *et al.*, 2001). This led to the idea of *functional groups*, a concept that has recently gained much attention (e.g. Ribera *et al.*, 2001; Dumay *et al.*, 2004). Gitay and Noble (1997) define functional groups as ‘non-phylogenetic groupings of species which perform similarly in an ecosystem, based on a set of common biological attributes’.

Within ecological research, statements about traits give generality and predictability (McGill *et al.*, 2006). One of the objectives of predictive ecology is to know whether species with certain traits will persist under a defined set of environmental conditions (Ribera *et al.*, 2001). In contrast, community ecology, which focuses on species identities, gives valuable and detailed insight, but only into a limited number of species. This species-centred ecology may result in a loss of ecological generality with a tendency towards special cases (McGill *et al.*, 2006). Moreover, it can only study those species that occur with a minimum frequency. In the study of traits, all species may contribute to the picture.

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*Traits and succession*

During the course of succession, species emerge and vanish. However, by solely focusing on the identities of such species, key biological characteristics that cause populations to increase and decline may not be revealed. To this point, the analysis of changes in the frequency of biological traits offers a promising alternative. It sheds light onto which traits, or trait categories, are associated with distinct parts of the successional gradient. Consequently, the latter approach will be used in this paper.

There have already been a number of studies on insects during secondary succession, for example on bees (Steffan-Dewenter & Tschardtke, 2001), butterflies (Steffan-Dewenter & Tschardtke, 1997), beetles (Brown & Hyman, 1986), and leafhoppers (Hollier *et al.*, 1994). From these studies, and also from general ecological theory, a number of hypotheses concerning traits during succession have been formulated and tested: (i) niche breadth will decrease, i.e. host-plant specialisation will increase from polyphagous to monophagous (e.g. Brown & Southwood, 1983; Novotny, 1994; Steffan-Dewenter & Tschardtke, 1997); (ii) the number of generations will decrease [for references, see (i)]; and (iii) overwintering strategy will shift from nymph to adult (to egg) (e.g. Hollier *et al.*, 1994; Nickel, 2003).

*Urban brownfields*

Urban brownfields (derelict land) are increasingly noticed as habitats of conservation significance (Angold *et al.*, 2006). High habitat diversity and a wide range of environmental conditions (Rebele, 1994) provide habitat for species-rich communities (Angold *et al.*, 2006), including rare and endangered species (Eyre *et al.*, 2003). In this respect, it is important to understand whether brownfields can provide habitat equally suitable for all species of the regional species pool, or if only species exhibiting certain traits are able to colonise these habitats. We hypothesise that certain traits may be more frequent than others, since urban brownfields are strongly influenced by successional processes (e.g. Gilbert, 1989), requiring species to constantly track favourable habitats. The existence of brownfields is due to the creation of habitat, for example by demolition of buildings. This new habitat undergoes rapid succession, mostly undirected by man. Typically, young brownfields are dominated by annual herbs, later by perennial herbs and grasses, before, finally, shrubs and trees establish (Brown & Southwood, 1987).

*Aim of the study*

Leafhoppers (Hemiptera: Auchenorrhyncha) are phytophagous insects fairly abundant on brownfield sites (Sanderson, 1992). In the present study, plot-based presence/absence data of leafhoppers were analysed. Data were recorded in urban brownfields of different age and successional state. By analysing four categorical traits (host-plant type, phagy, dormancy, and voltinism), the following questions will be addressed:

- 1 Can trait categories be related to site age in agreement with earlier studies on trait frequencies during succession (regarding host-plant specialisation, number of generations, and overwintering strategy)?
- 2 Do different combinations of trait categories lead to a similar reaction to site age, i.e. are there trade-offs in traits?
- 3 Can combinations of trait categories be used to classify species into functional groups, i.e. groups of species that show the same occurrence pattern along the successional gradient?
- 4 Is the brownfield species pool a representative sample of the potential species pool, with regard to the frequency of trait categories and combinations of trait categories? In other words, do brownfields offer potential habitat for all species?
- 5 Are species with certain trait categories particularly rare or abundant within species observations?

Understanding how changes in traits along the successional gradient of brownfield sites come about may also reveal more general mechanisms of species occurrences regarding other species pools, successional series in different habitats, and/or for different insect groups.

**Methods***Data*

Species occurrence data from urban brownfields in two large cities in Northern Germany were analysed (Strauss & Biedermann, 2006). The cities under study were Bremen (53°05'N, 8°44'E, mean temperature 8.8 °C, mean annual precipitation 694 mm, mean annual precipitation 694 mm), and Berlin (52°30'N, 13°28'E, mean temperature 9.7 °C, mean annual precipitation 560 mm). In both cities, plots of 225 m<sup>2</sup> covered the whole gradient of brownfield successional stages, with 157 plots in Bremen and 89 in Berlin. For each plot, site age was extracted from a time series of aerial photographs. Photographs were available at intervals of 5–10 years. Maximum site age could be inferred from these photographs and was refined to the actual site age by taking into account the vegetation development visible on the photographs, as well as by using additional information from local authorities. On very young sites, inspection of the sites in spring 2003 (Bremen) and 2004 (Berlin) revealed if a site was 0, 1, or 2 years old. Site age ranged from 0 to 40 years, with a median of 6 years.

The data were collected in 2003 (Bremen) and 2004 (Berlin). Sweepnet sampling was carried out four times at monthly intervals between early June and early September. Each sampling procedure consisted of 100 sweeps covering the entire plot. The catch was killed with ethyl acetate and frozen. All male adult individuals were determined to species level (female individuals only for species where determination is possible) (Biedermann & Niedringhaus, 2004).

Samples contained a total of 194 species, with 146 in Bremen and 130 in Berlin. Eighty-two species occurred in both cities. Species numbers per plot ranged from 0 to 32 with a median of 15. Each species was assigned categories concerning four

traits. Each trait was subdivided into two to four categories: (i) host-plant type (herbs, herbs and grasses, grasses, woody plants), (ii) phagy = specialisation in host-plant species (monophagous, oligophagous, polyphagous), (iii) hibernation = overwintering strategy (egg, nymph, adult), and (iv) voltinism = number of generations per year (univoltine, bivoltine). Since very few species feed on herbs *and* grasses, this category was combined with *herbs* for most analysis. Trait information was taken from Nickel and Remane (2002), Nickel (2003), and Biedermann and Niedringhaus (2004).

Two kinds of species data were analysed. First, the species presence/absence data (= observations) on the plots was used, whereby each presence of a species on a plot represents one observation. There were a total of 3763 observations, 2179 in Bremen and 1584 in Berlin. Second, differences between the actual species pool (194 species) and the potential species pool were analysed. To this end, the brownfield species pool was compared to the German species pool, since no information was available for a more regional species pool of the cities under study. For all German species, the trait categories named above were obtained from the same literature sources. Categories that only occurred within the German species pool, but not within the brownfield one, were not analysed.

#### *Relationship between site age and categories of individual traits*

The relationship between trait categories and site age was analysed using the fourth corner method (Legendre *et al.*, 1997). It is based on the inflated data table. This table contains all species observations, their traits, and the corresponding site age. Each row in the table corresponds to the presence of one species on one plot. The aim was to test if any of the trait categories reacted differently from the others in its occurrence along the age gradient. To this end, differences in mean ranks were assessed by calculating the Kruskal–Wallis test statistic ( $H$ ). This global statistic tests if any group behaves differently. In order to establish which categories differed, *a posteriori* testing was carried out by repeating the test for all pairs of groups.  $P$ -values for *a posteriori* testing were corrected for multiple testing using the Hochberg (1988) procedure (Wright, 1992).

For these analyses, the significance of the  $H$ -statistic should not be tested in the standard way (Legendre *et al.*, 1997). Since usually several species were observed at one plot, not all rows of the inflated table were independent, as site age was the same for all species observed on one plot. To overcome this problem, species observations and the corresponding traits were randomised before combining them with site age in the inflated data table. This was done such that the observations for each species were distributed randomly over the plots. This method of permuting species occurrences is based on the environmental control model (Legendre *et al.*, 1997). It assumes that species are found at locations where they encounter appropriate living conditions, and that species do so independently of each other. Since most Auchenorrhyncha guilds in central Europe are considered to not show strong interspecific competition (Nickel, 2003), this assumption is reasonable.

After each randomisation process, the  $H$ -statistic was calculated for the randomised inflated data table. In this case,  $H$  represents a chance value that can be expected if no association between trait categories and site age is present. This procedure was repeated 10 000 times, and each time the resulting chance value for the  $H$ -statistic was compared with the original value.  $P$ -values were derived from the number of times the chance value was smaller than the original value. If 9950 of all 10 000 chance values (= 95%) were smaller than the original value, this corresponds to a  $P$ -value of 0.05 (Legendre *et al.*, 1997; Manly, 2001).

#### *Relationships between site age and category combinations of traits*

*Combinations of two traits.* Next, interactions between traits were examined. A multiple interaction form of the fourth corner statistic, considering more than one trait at a time, does not yet exist (Legendre *et al.*, 1997). Again, the problem of non-independent data (see above) arises. It was found that, when the traits were analysed one at a time, the fourth corner method using a randomisation test (as described above) did not lead to substantially different  $P$ -values than a standard Kruskal–Wallis test (without randomisation). Therefore, to assess the significance of interactions between two traits, standard statistical testing of the inflated data matrix was used, rather than the fourth corner method. We calculated the Wald-type test statistic as suggested by Brunner and Puri (2001), using the SAS procedure PROC MIXED. If the interaction was significant ( $P \leq 0.05$ ), we tested which combinations of trait categories were different from each other. For the latter, *a posteriori* testing was used by applying a Kruskal–Wallis test and the randomisation procedure, as outlined above for individual traits.

*Functional groups.* Each significant interaction between traits allowed the detection of groups of trait combinations that reacted similarly to the age gradient. These groups were assigned the values 1 (group A, youngest average site age), 2 (B, intermediate), or 3 (C, oldest). Groups *in between* were assigned the values 1.5 or 2.5. These numbers were then used to calculate an *average group assignment* for each species. By comparing the group assignments for each trait combination and the average group assignments, species with similar patterns could be detected. It was then tested if these groups of species indeed showed distinct reactions to the age gradient. Groups emerging from this procedure were considered as *functional groups*: groups of species, associated with certain combinations of trait categories, that showed similar reactions to the age gradient.

*Alternative approaches.* The RLQ method (Doledec *et al.*, 1996) offers an alternative way of analysing multivariate environment–trait relationships [see Ribera *et al.* (2001) for an application of the method to ground beetle data]. This three-table ordination technique considers several traits and environmental factors at the same time. However, the output is complex and not as straightforward to interpret as our approach, since several ordination diagrams need to be interpreted simultaneously. An additional cluster analysis is required in order to obtain functional groups (Thuiller *et al.*, 2006).

Since site age is not the only factor driving species occurrence in urban brownfields (Strauss & Biedermann, 2006), the RLQ method seems to be an attractive way to also consider other environmental factors (such as vegetation structure, landscape context, or soil parameters). This study, however, for the sake of clarity, simplicity and comparability to other studies, concentrates on site age alone. Site age is an important factor driving the successional gradient. For example, vegetation structure is highly correlated to successional age, with vegetation changing from scarce and low to dense and high, increasing moss cover, and decreasing proportions of bare soil during the course of succession. Note, however, that sites can vary considerably in the speed of their successional development (Strauss & Biedermann, 2006; Strauss, 2007).

#### *Frequencies of trait categories: brownfield versus potential species pool*

*Categories of individual traits.* To quantify if the brownfield species pool was a representative sample of the potential species pool, it was tested whether trait categories within the brownfield species displayed the same distribution as within all German leafhoppers. For example, 59% of all German species are monophagous, compared with only 47% of the brownfield species. The significance of this difference was assessed by a randomisation test with 10 000 iterations (Manly, 2001). Tests were conducted in Splus 6.1. One hundred and ninety-four species (the number of species present in the brownfield data) were randomly selected from the total of 620 German brownfield species. Next, the proportion of monophagous species within this random selection of species was calculated. This process was repeated 10 000 times. If the actual proportion (47% monophagous species) was smaller than 9950 (95%) of these chance values, the difference between 47 and 59% was considered to be significant with  $P \leq 0.05$ . As before,  $P$ -values were corrected for multiple testing using the Hochberg (1988) procedure.

*Combinations of trait categories.* Next, the categories of all four traits were combined. The frequencies of the 35 combinations that were found in the brownfield species were analysed. The analyses consisted of two steps.

First, it was tested whether any combinations (e.g. of those categories associated with young site age) were more (or less) frequent than would be expected based on the frequencies of individual trait categories. Since such differences may also occur within the German species pool, both the German and the brownfield species pools were tested. Randomisation tests as outlined above were again conducted for the categories of individual traits. To obtain randomised frequencies of category combinations, the trait frequencies within the species pools were used. For each trait, a vector was generated corresponding to the number of species in the pool. Trait frequencies within these vectors were the same as within the original data. The vectors were then randomised and combined into a table. Each line of the resulting table represented a random combination of trait categories. For each combination, its randomised frequency was counted and compared to the true value within the species pool.

Second, we tested for differences in the frequencies of trait combinations between the German and the brownfield species pools. Again, randomisation tests were used. This time, the appropriate number of species (194) was randomly selected from the German species pool. Within this random species selection, the frequencies of combinations were recorded and compared with the observed values.

#### *Frequencies of trait categories: species observations versus species pool*

*Individual traits.* The analyses of the species pool do not take into account the fact that species may occur with different frequencies. We therefore wanted to test if certain trait categories were more (or less) frequent within observations than within the species pool. Here, the randomisation test was conducted by randomly choosing species from the brownfield species pool. The number of species corresponded to the number of observations (3763). Each species might be picked several times. The random frequencies of trait categories were then calculated, and it was tested whether the observed values differed significantly.

*Functional groups.* It was tested whether functional groups (and the combinations comprising them) were more (or less) abundant within species observations than within the species pool. To this end, randomisation tests were conducted as for individual traits, but compared frequencies of functional groups as well as category combinations.

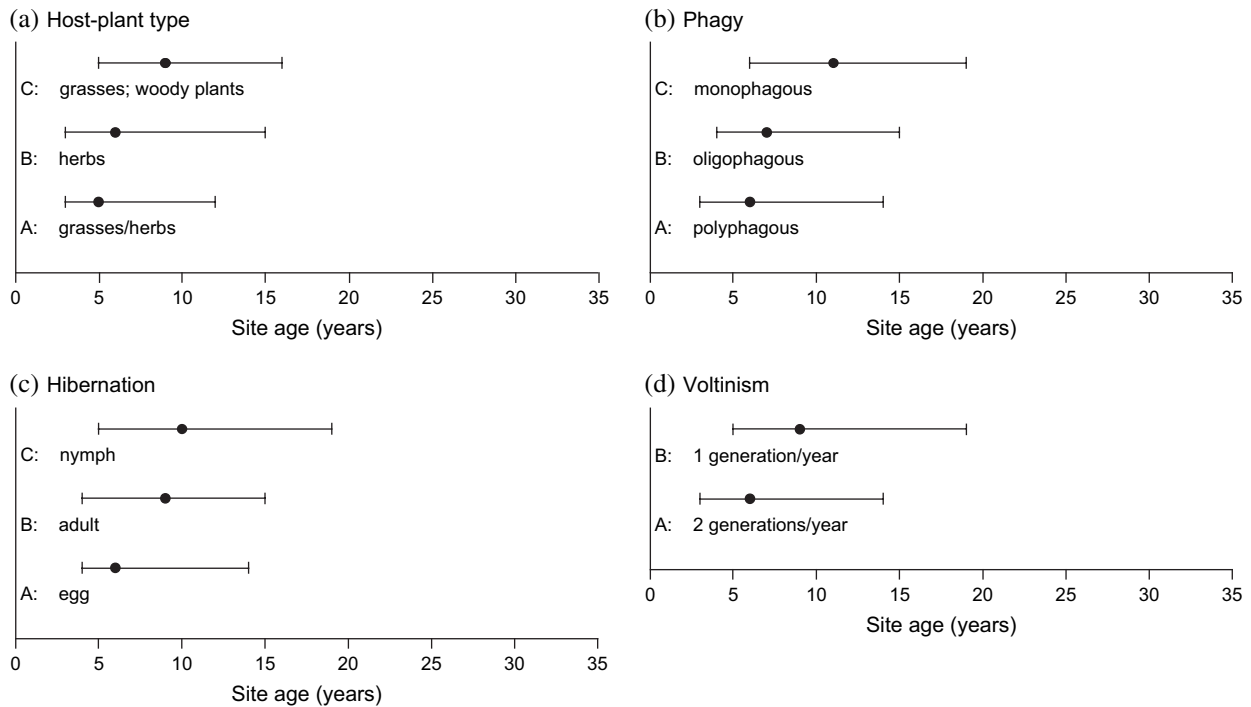
## Results

### *Relating trait categories to site age*

*Individual traits.* For all studied traits, the trait categories differed significantly in their reaction to site age ( $P < 0.001$ ). Each trait category showed a distinct distribution concerning site age. For the trait categories associated with the youngest site age (hereafter: young categories), the median of site age was between 5 and 6 years for all traits (Fig. 1, categories A). For those categories associated with the oldest site age (hereafter: old categories), the median of site age was between 9 and 11 years (Fig. 1, categories C).

For host-plant type, species feeding on grasses and herbs were associated with the youngest site age, followed by those feeding only on herbs (Fig. 1). Species feeding only on grasses did not differ significantly from those feeding on woody plants, both forming the group present at the oldest sites. In terms of host-plant specialisation, polyphagy represented the young category, monophagy the old category, and oligophagy was in between. For dormancy, overwintering as eggs constituted the young category, followed by adults and nymphs. Bivoltine species were associated with the younger sites, univoltine species with the older ones.

*Combinations of two traits.* Four out of the six possible combinations of two traits showed significant interaction: Host plant  $\times$  Phagy ( $P < 0.01$ ), Host plant  $\times$  Overwintering ( $P = 0.01$ ), Phagy  $\times$  Overwintering ( $P < 0.01$ ), and Overwintering  $\times$  Generations ( $P = 0.01$ ). In contrast, Host plant  $\times$  Generations



**Fig. 1.** Boxplots of site age distribution of species occurrences for each trait category. Bars indicate the interquartile range, the median is marked with a dot, whiskers are not shown. All labelled groups (A, B, C) are significantly ( $P \leq 0.05$ ) different from each other.

( $P = 0.22$ ) and Phagy  $\times$  Generations ( $P = 0.09$ ) showed no significant interaction.

Each of the significant combinations exhibited three distinct groups (hereafter: young, intermediate, and old groups); in three cases there was one additional group between two others (Fig. 2). However, some combinations did not differ from most others. This was particularly true for many combinations with adult overwinterers. This category exhibited significant differences only in combination with voltinism. Many groups consisted of more than one combination. Apparently, different combinations of young and old categories led to the same reaction to the age gradient. For example, species feeding on grasses (old category) were assigned to the young group if they were polyphagous. Egg overwinterers (young category) were assigned to the old group if they were monophagous, just as polyphagous nymph overwinterers.

**Functional groups.** Species with similar patterns of group assignment for trait interactions, and with similar average group assignments were grouped. In this way, eight groups could be distinguished. After testing for between-group differences, four discrete groups emerged, which will be referred to as functional groups.

Plots were divided into four age classes (0–2, 3–6, 7–15, and 16–40 years), which may be referred to as the ruderal, early-successional, mid-successional, and late-successional stages, respectively (Brown & Southwood, 1987). For each group, the proportion of observations it contributed to each age class was calculated. Figure 3 shows that group I contributed most (approx. 50%) to age class 1, and then decreased. Group II had its highest proportions in age classes 2 and 3, and

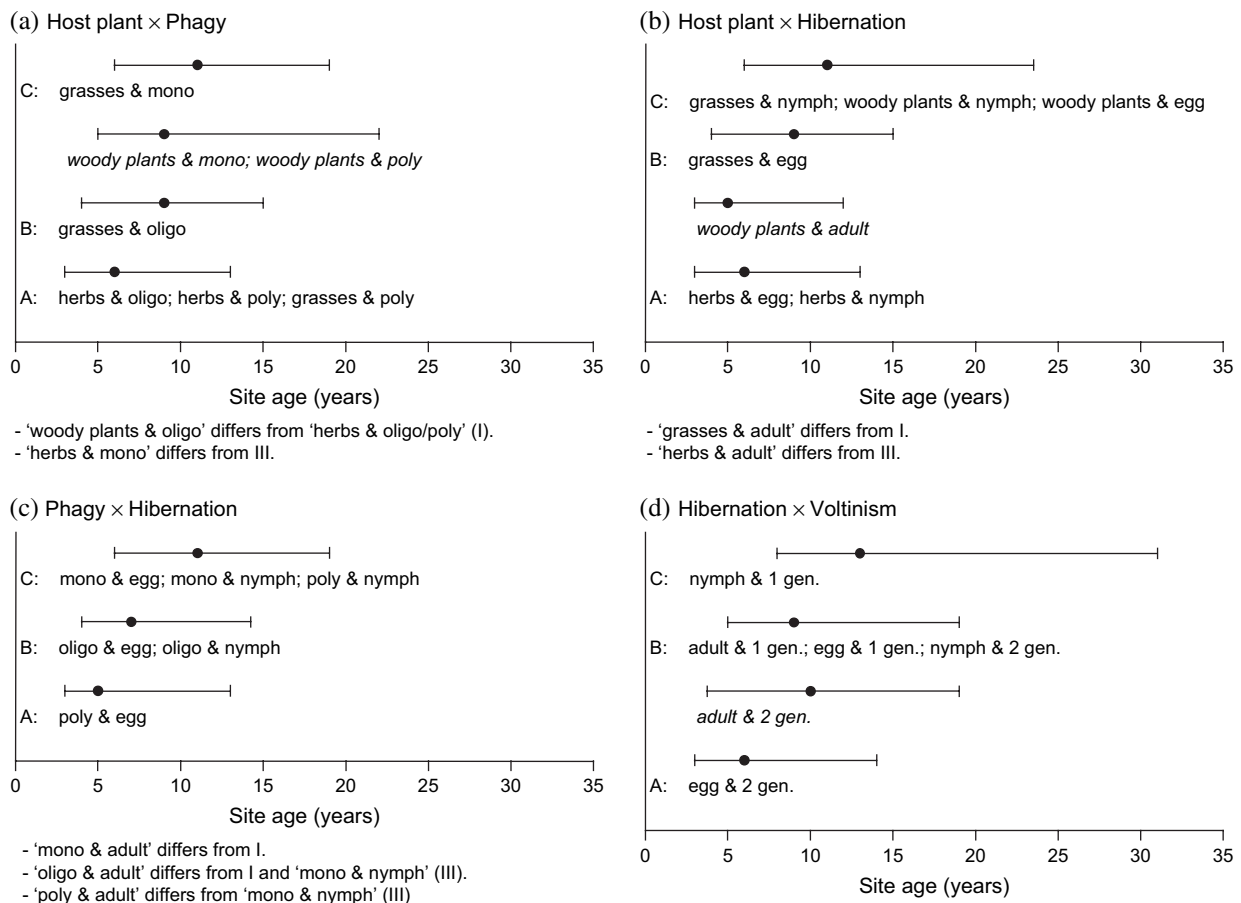
group III in age class 4. Group IV did not show much variation, with low proportions within all age classes.

Figure 4 depicts another aspect. For each plot, the contribution of each group to the species observations on the plot was calculated. The results are summarised in Fig. 4 as boxplots for each group within each age class. Even though proportions vary considerably within every age class and group, the same trends as described above are nevertheless clearly present. Thus, group I is the youngest functional group, group II the intermediate, group III the oldest, and group IV is indifferent with respect to site age. The groups differed largely in size, with group I comprising 12% of the species, group II 17%, group III 66% and group IV 5%.

Each group consisted of several combinations (Table 1, a), with most combinations (20) assigned to group III. Group I (five combinations) mostly contained polyphagous and bivoltine species. Species feeding on woody plants, monophagous species, and species overwintering as adults were never assigned to that group, no matter which other categories they were combined with. Group II (four combinations) exclusively contained oligophagous species feeding on grasses or woody plants. Species in group IV (six combinations) exclusively fed on herbs.

#### *Frequency of trait categories within the species pool*

**Categories of individual traits.** For all four traits, the category frequencies displayed the same order within the brownfield and the German species pools. However, compared to the German



**Fig. 2.** Boxplots of site age distribution of species occurrences for groups formed by interaction of two traits. For explanation, see Fig. 1. Groups without labels and printed in italics are not significantly different ( $P > 0.05$ ) from the groups they stand in between, but are significantly different from all others. Groups different from only one group or from parts of groups are listed below each plot. gen., generation(s); mono, monophagous; oligo, oligophagous; poly, polyphagous.

species pool, many categories had significantly higher or lower proportions in the brownfield species (Table 2, a). The proportions of species feeding on herbs (18 vs 14%) and on grasses/herbs (4 vs 2%) was slightly, but significantly higher in the brownfield species. There were significantly less monophagous, but more oligophagous and polyphagous species. More egg overwinterers, and fewer adult overwinterers were found. Fewer species were univoltine, more bivoltine (Table 2, a).

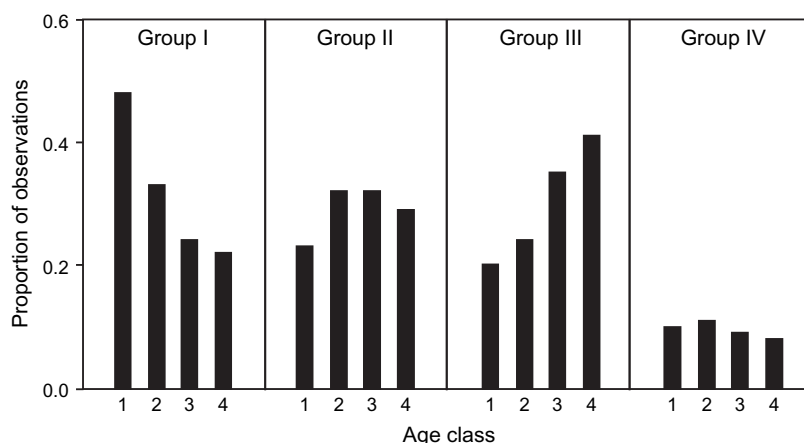
**Co-occurrence of trait categories.** Within the German species pool, a number of category combinations occurred with significantly higher or lower frequency than expected. However, expressed in terms of absolute values, most of these differences were minor (Table 3, columns 'Germ.'). The most pronounced difference was found for the combination *two generations, nymph hibernation, host plant grasses, monophagous*. This combination also occurred more frequently within the brownfield species pool (6.3 vs 1.9%). Most of the time, combinations that deviated significantly from the expected frequencies within the German species showed similar deviations within the brownfield species. However, within the brownfield species, there were additional deviations, with the largest differences occurring for the species

with the trait categories *one generation, egg hibernation, monophagous*. The species with this combination feeding on herbs, and those feeding on grasses, were less frequent (1.5 vs 4.1%; 4.1 vs 7.7%), the ones feeding on woody plant more frequent (14.4 vs 6.7%). The same holds for *two generations, egg hibernation, host plant grasses, oligophagous*.

Frequencies of category combinations differed only slightly between the brownfield species and all German species (Table 3). Most significant differences were small and due to combinations entirely absent from the brownfield species. The largest differences were found for *one generation, egg hibernation, host plant grasses, monophagous* (4.1 vs 13.1% within all German species), *two generations, egg hibernation, host plant grasses, oligophagous* (9.3 vs 3.9%), and *two generations, egg hibernation, host plant herbs, polyphagous* (4.1 vs 1.2%).

#### Frequency of trait categories within species observations

**Categories of individual traits.** With one exception (overwintering as egg), all trait categories had different frequencies



**Fig. 3.** Reaction of functional groups (I–IV) to site age. For each functional group, the proportion (%) of observations the group contributes within each of four age classes, is plotted. Age class 1: 0–2 years (62 plots), age class 2: 3–6 years (60 plots), age class 3: 7–15 years (78 plots), age class 4: 16–40 years (46 plots).

within observations than within the species pool (Table 2, b). In general, categories that were already more common within the species pool (compared to the German species pool), occurred with significantly higher frequencies. However, this did not apply to the overwintering strategy. *Adult* was more frequent in the observations, even though it had been less frequent among the species pool. In addition to the trends found within the species pool, *grasses* as host plant were observed more frequently (52 vs 42%), *woody plants* less frequently (11 vs 36%).

With the exception of hibernation, differences between expected and observed frequencies in species distributions were mostly more substantial than those found between the species pools (Table 2, a and b). For example, monophagous species were far less frequently observed than found in the species pool (22 vs 47%). Polyphagous species, on the other hand, were much more frequent (32 vs 19%), as well as bivoltine species (66 vs 48%).

**Functional groups.** Group frequencies within observations differed significantly from frequencies within the species pool. Species of group I (30% of observations vs 12% in the species pool), group II (31 vs 17%), and group IV (10 vs 5%) were significantly more abundant than within the species pool ( $P < 0.001$ ). Species of group III (29 vs 66%) were observed much less frequently ( $P < 0.001$ ).

With one exception, all combinations of group I were observed more frequently (Table 1, b). The largest difference was found for *two generations, egg hibernation, host plant herbs, polyphagous* (12.3% of observations vs 4.1% of species). Group III contained many species with low prevalence, in particular the combination *one generation, egg hibernation, host plant trees/shrubs, monophagous*. This combination accounted for 14.4% of species versus 3.9% of observations. The most abundant combination was *two generations, egg hibernation, host plant grasses, oligophagous* from group II. It accounted for 20.4% of all observations versus 9.3% of species.

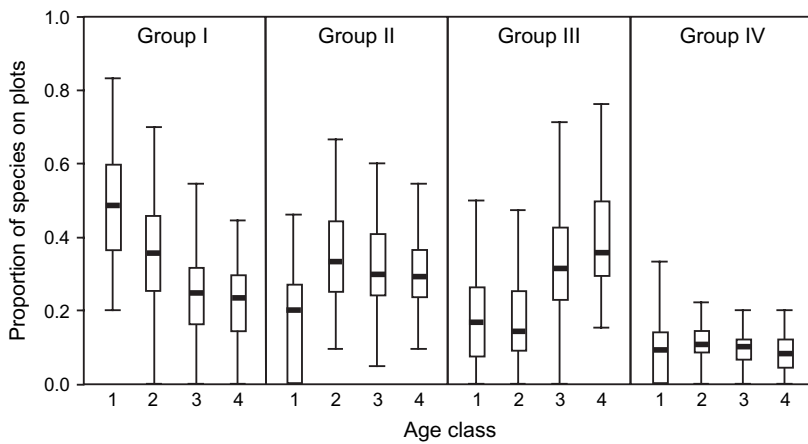
## Discussion

### Traits and successional age

Trait categories that enable species to colonise brownfield sites faster than others could clearly be identified. Polyphagous

species of several phytophagous insect taxa are considered and have been shown to be typical pioneers (e.g. Brown & Southwood, 1983; Hollier *et al.*, 1994; Novotny, 1995; Nickel & Hildebrandt, 2003). Polyphagous species do not rely on the occurrence of particular food plants, thus they can live and reproduce as soon as any vegetation starts to grow. Vegetation succession on brownfield sites typically starts with annual herbs (Brown & Southwood, 1987), thus species feeding on these plants may be quick colonisers. This is even more striking in leafhopper species that can feed both on herbs and grasses, enabling species to make use of most plants growing during early succession. Perennial grasses only occur at later successional stages (Brown & Southwood, 1987), and so do the species feeding on them. Woody plants establish even later in the successional series, thus a time-lag between the occurrence of species feeding on grasses and those feeding on woody plants might be anticipated, but could not be seen in data from the present study. This may be caused by large differences in the pace of tree settlement, depending on soil fertility (Rebele, 1992). The trait *phagy* clearly revealed that the persistence of the host plant influences life histories of phytophagous insects (Denno & Roderick, 1991). Dennis *et al.* (2004) showed that the life strategies of butterflies are correlated to the life strategies of their host plants.

Concerning the overwintering strategy, the results of the present study differed from what others have suggested for leafhoppers. Hollier *et al.* (1994) found that adult and nymph overwinterers were favoured during early succession. Brown (1991) has suggested that adult overwintering may be favourable during early succession, when food resources are limited and individuals have to disperse in order to locate food. Brown (1991) associates nymph overwintering with early and mid successional stages, and egg overwintering with late succession. Nickel (2003) considers the correlation between overwintering stage and successional stage to be uncertain, with weak evidence for a shift from nymph to adult stage. In data from the present study, however, there was strong evidence for a shift from egg to nymph. Species overwintering as nymphs start feeding early in the season, in February or March. Nymphs of egg overwinterers occur in April or May and thus start feeding much later. Hibernation is therefore correlated with the onset of feeding in spring. As young brownfields are dominated by annual plants (Brown & Southwood, 1987), food is provided much



**Fig. 4.** Plot-based observations of species belonging to different functional groups (I–IV). For each plot the proportion (%) of species belonging to each functional group was calculated. These proportions are shown as separate boxplots for each functional group and age class. Boxes show the interquartile range, the line inside the box represents the median, whiskers are drawn to the nearest value not beyond  $1.5 \times$  the interquartile range. Extreme values are not shown.

later than on older brownfields, dominated by perennials. Thus, egg overwintering is a preferable strategy for young brownfields. The trait category *adult hibernation* overall seemed to have less influence than *egg hibernation* and *nymph hibernation*. This may be due to the fact that adults are capable of migrating to suitable habitats for overwintering (Nickel, 2003).

In pioneer insect species, life-cycles are shorter (Brown & Southwood, 1983; Brown, 1991; Frouz *et al.*, 2003). Novotny (1994) found more bivoltine leafhopper species in ephemeral habitats, which is in agreement with results from the present study. Even though some bivoltine leafhopper species show different

levels of flight activity between generations (Nickel, 2003), two generations per year offer twice the chance to spread. Consequently, the second generation might colonise newly emerged habitat that had been free of vegetation only months earlier.

#### Functional groups

Many leafhopper species that have been described as pioneers before were indeed assigned to group I, for example *Cicadella viridis* (L.) or the *Macrosteles* species (Novotny, 1994; Nickel,

**Table 1.** (a) Brownfield species: assignment of trait category combinations to four functional groups (I–IV). Each group represents different occurrence patterns along the successional gradient of urban brownfields. I, early successional stages; II, intermediate; III, late; IV, indifferent reaction. Blank cells: combinations did not occur in the observed species. (b) For each combination, proportion of species pool (%) and proportion of observations (%) are presented.

Generations	Overwintering	Host-plant type	(a) Functional groups			(b) % observations versus % species								
			Phagy			Phagy								
			Mono	Oligo	Poly	Mono	Oligo	Poly						
One generation	Egg	Herbs	III	IV	I	0.1	1.5	–	2.1	2.1	–	6.4	2.6	–
		Grasses	III	II	IV	2.2	4.1	–	6.0	5.7	–	0.2	0.5	–
		Woody plants	III	III	III	3.9	14.4	–	0.3	2.1	–	1.2	3.6	–
	Nymph	Herbs			III							0.2	0.5	–
		Grasses	III	III		0.1	0.5	–	0.5	2.6	–			
		Woody plants			III							1.4	3.1	–
	Adult	Herbs		IV	IV				1.4	0.5	+	0.5	1.0	–
		Grasses	III	II		2.0	2.1		3.6	1.0	+			
		Woody plants	III	II	III	0.5	2.6	–	0.1	1.0	–	1.3	0.5	+
Two generations	Egg	Herbs	III	I	I	2.2	4.6	–	5.2	3.6	+	12.3	4.1	+
		Grasses	III	II	I	4.0	5.7	–	20.4	9.3	+	5.2	1.0	+
		Woody plants	III	III	III	1.4	5.2	–	0.3	3.1	–	0.7	0.5	
	Nymph	Herbs		IV					4.7	0.5	+			
		Grasses	III	III	III	4.7	6.2	–	1.1	2.1	–	2.0	1.0	+
		Woody plants												
	Adult	Herbs	IV		I	0.8	0.5	+				1.0	0.5	+
		Grasses												
		Woody plants												

+ and – indicate whether proportions within observations are significantly more or less frequent than proportions within the species pool.



**Table 2.** (a) Distribution (%) of trait categories within the species pool and (b) within species observations.

	(a) Species pool within			(b) Species observations on brownfield plots	
	Germany	Brownfields			
Total no. of species/observations	620	194		3763	
Host-plant type					
Herbaceous plants	14	18	+	20	+
Herbaceous plants and grasses	2	4	+	17	+
Grasses	44	42		52	+
Woody plant (shrubs/trees)	38	36		11	–
Phagy (specialisation on plant species)					
Monophagous (one plant species or less than five species of less than five families)	59	47	–	22	–
Oligophagous (one or two plant families or genera)	24	34	+	46	+
Polyphagous	14	19	+	32	+
Hibernation (overwintering strategy)					
Egg	65	74	+	74	
Nymph	19	16		15	–
Adult	15	10	–	11	+
No. of generations/year					
Univoltine (one generation/year)	65	52	–	34	–
Bivoltine (two generations/year)	33	48	+	66	+

+/- indicate significantly ( $P \leq 0.05$ ) higher/lower proportions within the brownfield species pool than within the German species pool (a) or higher/lower proportions within species observations than within the brownfield species pool (b).

2003). In contrast, species like *Javesella pellucida* (F.) or *Laodelphax striatella* (Fall.), considered to be pioneers by others (Nickel, 2003), were placed in group III in the present study. These species are known for their flight activity (Waloff, 1973; della Giustina & Balasse, 1999). Thus, information on flight activity may allow finer grouping. It is obvious that traits influencing dispersal should play an important role during succession, since species need to colonise the newly emerged habitat. Flight capability could be expressed in several ways, for example as the relation of wing surface area and body weight (Nickel, 2003). However, these data are available for only a few species. Therefore, wing dimorphism, i.e. the occurrence of brachypterous individuals, was used as an alternative measure of leafhopper flight capacity by Novotny (1995). In general, brachypterous insect species are expected to increase during succession (Brown & Southwood, 1987; Novotny, 1995; Nickel, 2003). However, the proportions of macropterous and brachypterous individuals within leafhopper species are often variable within and between populations (Nickel, 2003). In addition, flight capability is not necessarily a measure of flight activity, a trait widely unknown for most leafhoppers (but see Waloff, 1973; della Giustina & Balasse, 1999). For this reason, traits concerning dispersal capability were not considered in this study.

The results of the present study show that the pioneer group does not only comprise the *super-pioneer* (two generations, egg hibernation, host plant herbs, polyphagous). Other combinations are apparently also suitable for fast colonisation. For instance, *one generation* is a late category. However, along with the young categories *egg hibernation*, *host plant herbs*, *polyphagous*, it nevertheless allows fast colonisation. Trade-offs in traits enable species with different trait combinations to settle

with equal success in the same habitat (Statzner *et al.*, 2001). Still, in the data from the present study there were comparatively few combinations that allow fast colonisation; the species pool was dominated by combinations that were typical for later successional stages. A possible explanation might be that structural diversity increases during succession (Brown & Southwood, 1987), allowing more strategies.

Even though group I comprised few species, these were very abundant, in particular the combination of all pioneer traits (*two generations*, *egg hibernation*, *host plant herbs*, *polyphagous*). This indicates that the studied brownfields overall represented habitats that were particularly suitable for pioneer species. Group III contained many species with low prevalence. Even though brownfields obviously offer habitat for many of these species, only a small portion of brownfields are suitable for one particular species. This effect was most pronounced with the combination *one generation*, *egg hibernation*, *host plant trees/shrubs*, *monophagous*. This is remarkable, since this combination was particularly frequent within the species pool. Overall, the low occurrence rates of group III members may indicate that these species are more specialised and thus find suitable habitat at only a few locations. Since mainly the mono- and oligophagous members of this group were particularly rare, food-plant limitation to a few sites could indeed be an important factor. In general, species of late successional stages (as group III) have smaller niche breadths (Brown & Southwood, 1983; Steffan-Dewenter & Tschardtke, 2001). Moreover, the species in this group might also be weak dispersers (Strauss, 2007). In this case, these species could only reach sites close to a source habitat. They could not spread over all suitable brownfield habitats within the limited period of time that these habitats persist.

**Table 3.** Combinations of trait categories within the German ('Germ.') and the brownfield ('Brownf.') species pools. For each combination, expected ('Exp.') and observed ('Obs.') frequencies (%) are shown.

		Phagy											
		Mono				Oligo				Poly			
Generations	Overwintering	Host-plant type	Germ.	Brownf.	Germ.	Brownf.	Germ.	Brownf.	Germ.	Brownf.	Germ.	Brownf.	
One generation	Egg	Herbs	Obs. 2.7	1.5	-	1.7	2.1	1.5	2.6	1.5	2.1	2.6	
		Grasses	Exp. 4.4	4.1	-	1.9	2.6	0.9	1.5	0.9	1.5	1.5	
		Woody plants	Obs. 13.1	4.1	-	4.6	5.7	0.2	0.5	0.2	0.5	0.5	
	Nymph	Herbs	Exp. 12.1	7.7	+	4.9	5.2	2.4	3.1	2.4	3.1	3.1	
		Grasses	Obs. 11.9	14.4	-	2.6	2.1	2.6	3.6	2.6	3.6	3.6	
		Woody plants	Exp. 10.4	6.7	-	4.3	4.6	2.0	2.6	2.0	2.6	2.6	
		Herbs	Obs. 0.2	0	-	0	0	0.7	0.5	0.7	0.5	0.5	
		Grasses	Exp. 1.2	1.0	-	0.5	0.5	0.2	0.5	0.2	0.5	0.5	
		Woody plants	Obs. 2.9	0.5	-	2.0	2.6	0.2	0	0.2	0	0	
	Adult	Herbs	Exp. 3.4	1.5	-	1.4	1.0	0.7	0.5	0.7	0.5	0.5	
		Grasses	Obs. 0.9	0.0	-	0.7	0.0	-	3.1	3.1	+	3.1	
		Woody plants	Exp. 2.9	1.5	-	1.2	1.0	0.5	0.5	0.5	0.5	0.5	
Herbs		Obs. 0.9	0	-	0.7	0.5	0.9	1.0	0.9	1.0	1.0		
Grasses		Exp. 0.9	0.5	-	0.3	0.5	0.2	0	0.2	0	0		
Woody plants		Obs. 3.1	2.1	+	1.4	1.0	0	0	0	0	0		
Two generations	Egg	Herbs	Exp. 2.6	1.0	+	1.0	0.5	0.5	0.5	0.5	0.5	0.5	
		Grasses	Obs. 4.3	2.6	+	2.2	1.0	0.2	0.5	0.2	0.5	0.5	
		Woody plants	Exp. 2.2	1.0	-	0.9	0.5	0.5	0.5	0.5	0.5	0.5	
		Herbs	Obs. 3.4	4.6	-	2.0	3.6	1.2	4.1	1.2	4.1	4.1	
		Grasses	Exp. 2.4	3.6	-	1.0	2.6	0.5	1.5	0.5	1.5	1.5	
		Woody plants	Obs. 5.3	5.7	-	3.9	9.3	+	1.0	0.7	1.0	1.0	
	Nymph	Herbs	Exp. 6.5	6.7	-	2.7	5.2	1.4	2.6	1.4	2.6	2.6	
		Grasses	Obs. 6.3	5.2	-	2.6	3.1	0.9	0.5	0.9	0.5	0.5	
		Woody plants	Exp. 5.6	6.2	-	2.4	4.1	1.2	2.6	1.2	2.6	2.6	
		Herbs	Obs. 0	0	-	0.2	0.5	0	0	0	0	0	
		Grasses	Exp. 0.7	0.5	+	0.2	0.5	0.2	0.5	0.2	0.5	0.5	
		Woody plants	Obs. 6.3	6.2	+	0.9	2.1	0.3	1.0	0.3	1.0	1.0	
Adult	Herbs	Exp. 1.9	1.5	-	0.7	1.0	0.3	0.5	0.3	0.5	0.5		
	Grasses	Obs. 0.2	0	-	0	0.0	0.3	0	0.3	0	0		
	Woody plants	Exp. 1.5	1.0	-	0.7	1.0	0.3	0.5	0.3	0.5	0.5		
	Herbs	Obs. 0.3	0.5	-	0	0	0.2	0	0.2	0	0		
	Grasses	Exp. 0.5	0.5	-	0.2	0.1	0	0	0	0	0		
	Woody plants	Obs. 0	0	-	0.2	0	0	0	0	0	0		
Two generations	Egg	Herbs	Exp. 1.4	1.0	-	0.5	0.5	0.3	0.5	0.3	0.5		
		Grasses	Obs. 0.2	0	-	0	0	0	0	0	0		
		Woody plants	Exp. 1.2	0.5	-	0.5	0.5	0.2	0	0.2	0		
	Nymph	Herbs	Obs. 0.2	0	-	0	0	0	0	0	0		
		Grasses	Exp. 1.2	0.5	-	0.5	0.5	0.2	0	0.2	0		
		Woody plants	Obs. 1.2	0.5	-	0.5	0.5	0.2	0	0.2	0		

+ and - indicate significant deviation of the observed from the expected values. The second column of + and - for the brownfields indicates significant deviations from the German species pool.

### Trait frequencies within the species pool and within species observations

Within the brownfield species pool, the categories associated with the youngest successional age (*young categories*) were consistently more frequent than within the German species pool. However, in both species pools, the young categories for phagy and voltinism were the least frequent. Therefore, it seems that only few species are adapted to early successional stages, but that these species occur in large numbers.

One might anticipate a co-occurrence of certain categories, for example that young categories combine more frequently than young and old ones. For the German species pool, this was largely not true. The reason for the combination *two generations, nymph hibernation, host plant grasses, monophagous* being particularly frequent remains unclear at this point. It could be possible that grasses provide particularly suitable habitat for nymph hibernation. In the brownfield species pool, co-occurrence of categories was slightly more abundant. Brownfields obviously favour some pioneer combinations (group II: *two generations, egg hibernation, host plant grasses, oligophagous*, group I: *two generations, egg hibernation, herb, polyphagous*). Particularly slow combinations were less common (e.g. group III: *one generation, egg hibernation, host plant grasses, monophagous*). Frequencies within species observations even enhanced this trend: species exhibiting young traits or assigned to the functional groups I and II were much more frequent.

### Conclusions

- 1 For all traits, clear successional trends could be identified. Pioneer categories were: feeding on herbs, polyphagy, bivoltinism, and egg overwintering. The shift from categories associated with young sites to those associated with old ones, occurred during the first 10 years of succession.
- 2 The 35 combinations of trait categories could be assigned to four functional groups. Groups favoured either early, intermediate, or late successional age, one group was indifferent. It is likely that grouping could be refined using information on flight capacity and/or activity. This, however, would require additional, extensive data collection.
- 3 The brownfield species pool was not a representative sample of the total species pool. Even though sites up to 40 years old were considered, species with pioneer trait categories were over-represented. This trend was confirmed by species observations. Most observations were due to only a few category combinations. Thus, even though brownfields offer habitat for many species, most species occur on just a few, mostly older, sites. The variety of trait combinations, and thus species living on older brownfields, is larger than on young ones, where the same sets of traits and species are found on most sites.
- 4 There was no large-scale co-occurrence of trait categories. Remarkable exceptions were high proportions of *two generations, egg hibernation, host plant grasses, oligophagous* and of *one generation, egg hibernation, host plant trees/shrubs,*

*monophagous*. The former seems to be the most successful strategy on brownfields, comprising 20% of the observations. The latter likely stems from high habitat diversity in brownfields, offering a limited amount of habitat for many different, highly specialised species.

- 5 Species with traits that do not allow fast colonisation seem to be less well suited to occupy the potential habitat that brownfields offer.

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