



## HABITAT EFFECTS ON SLUG ASSEMBLAGES AND INTRODUCED SPECIES

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### ABSTRACT

Habitat disturbance alters environmental conditions and can affect biotic exchange. While the process of biotic exchange is difficult to quantify in the field, it affects community assembly and thus species abundance distributions, diversity, faunal homogeneity and biogeographic patterns. Here, we provide the first comprehensive assessment of habitat-specific assemblage structure and turnover in slow, active dispersers, namely slugs (Mollusca: Gastropoda). We compare species richness, densities, assemblage homogeneity and spatial turnover from nine differently disturbed habitat types (total: 729 sites) within an area spanning the border between two major European biogeographic regions, the Atlantic and the Continental Regions. Gardens, mesic open habitats and successions tended to harbour many introduced species. The nonmetric multidimensional scaling plot revealed a gap, rather than a transition, between disturbed habitats (including woody successions) and mature forest stands. This gap indicates a tipping point for slug assemblages related to food sources and microclimate. Anthropogenic disturbance blurred the effect expected from the border between the biogeographic regions. When compared with broadleaved forests as the natural vegetation cover, human disturbance doubled the range before spatial faunal dissimilarity occurred in physically highly fragmented gardens, and more than tripled it in continuously-disturbed habitat types such as mesic open habitats. Our results support the idea that continuously-disturbed habitats are associated with altered passive dispersal and colonization dynamics, distorted biogeographic boundaries and faunal homogenization.

### INTRODUCTION

Anthropogenic disturbance impacts biodiversity and assemblage structure through physical and/or chemical habitat alterations (e.g. Van Dijk *et al.*, 2004; Klimes *et al.*, 2012). However, human disturbance may also increase biotic exchange by increasing dispersal along with the transport of materials (Kappes & Haase, 2012). Dispersal ability in turn determines the scale at which biodiversity patterns and species turnover emerge (Lenoir *et al.*, 2012). Human-driven dispersal allows otherwise dispersal-limited species to access regions beyond their biogeographic boundaries (e.g. Van der Veken *et al.*, 2008; Kappes *et al.*, 2009a; Schilthuisen & Liew, 2009; Winter *et al.*, 2010). Although biotic exchange has received massive attention, Catford *et al.* (2012) conclude that the invasibility of ecosystems has been the focus of much less interest than the invading, or dispersing, species themselves.

Dispersal itself is difficult to quantify in the field, but it indirectly affects local species composition and community structure (Hubbell, 1997; McGill, 2003). The neutral theory of Caswell (1976) and Hubbell (1997, 2001) actually implies that the local

community structure is related to that of the regional community through migration rates. Increases in migration rates increase the ratio between local species richness and the regional species pool (Lenoir *et al.*, 2012). On a site perspective, species abundance distributions (SADs) of core, or resident, species tend to be normally distributed, while rare, difficult to detect, or accidentally entering satellite species introduce a left-skew (Magurran & McGill, 2011).

Dispersal limitation can be assumed for slow, active dispersers such as the Gastropoda, unless they can utilize mobile vectors. The vector that has most accelerated gastropod dispersal in historic times is man (Welter-Schultes, 1998; Kappes & Haase, 2012). We thus hypothesized that the proportion of introduced species and/or rare species may be a function of dispersal properties that are specific for a given habitat type. Consequently, we have studied habitat-type effects on assemblage characteristics within a given taxonomic and functional group (slug-like gastropods) within a larger geographic area. If there is an effect of human disturbance intensity, habitats should differ not only in assemblage composition, but also in SADs and spatial auto-correlations. Among others, the spatial range until distance

decay becomes obvious should differ between habitat types that differ in strength and frequency of anthropogenic disturbance. Under this assumption, we even expect that human-driven faunal homogenization could blur the expected increase of distance decay at the biogeographic border. We test these assumptions with slug assemblages from continental northwestern Europe, a region with a dynamic land-use history (Hurt *et al.*, 2006) and a high human footprint index (Hobbs, Higgs & Harris, 2009).

## MATERIAL AND METHODS

### *Study sites and sampling*

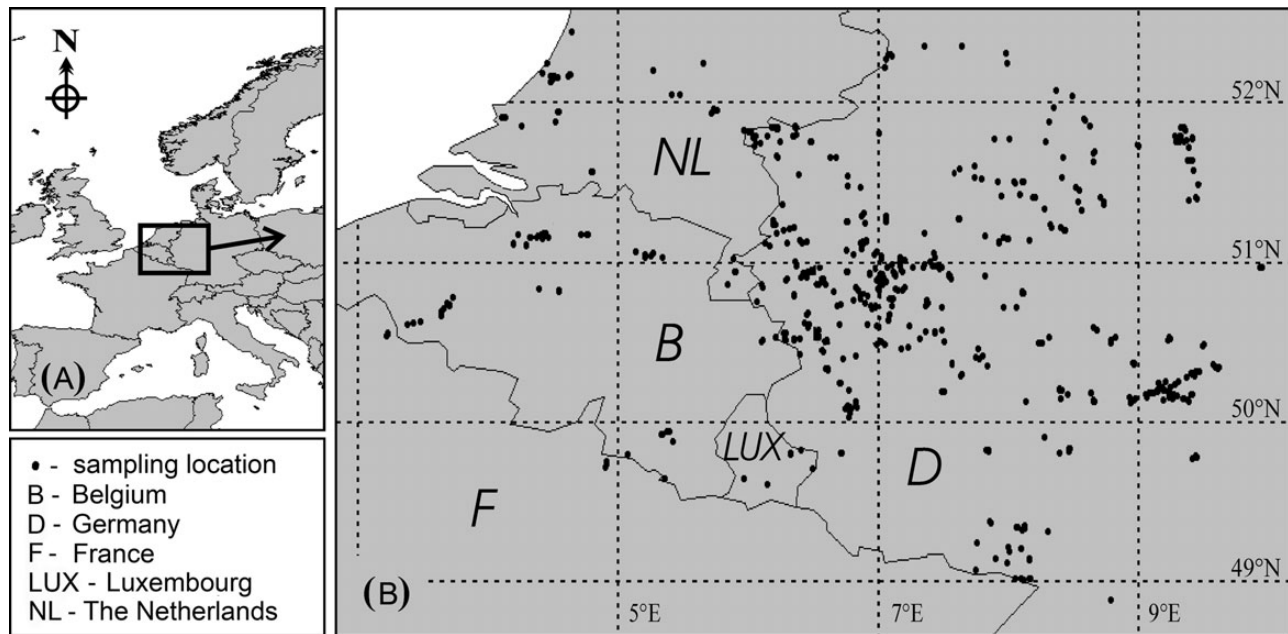
The area covers parts of continental northwestern Europe (Fig. 1) and spans two major biogeographic regions, the Atlantic Region and the Continental Region (European Environmental Agency, 2009). Data acquisition was between 2000 and 2012. The regional clusters in Figure 1 emerged for reasons of accessibility and because several sites were sampled during different specialized surveys. For example, parts of the data were collected in the course of surveys by Kappes (2006) and Kappes *et al.* (2009b), while other datasets were from nature-protection area planning, development and impact assessment reports (H. Kappes, unpubl.). To complement our own sites from southern Rhineland-Palatinate, slug assemblage data from 25 different deciduous forests collected by Studmund (2002) were integrated. Additional sites were surveyed for the present study to fill gaps and to capture regional habitat variability. The complete dataset covers 729 surveys in nine different habitat types: garden-like locations (gardens/parks/cemeteries;  $n = 93$ ), open mesic herb (and grass) stands ( $n = 94$ ), open wet herb and grass stands ( $n = 112$ ), successions (transitional woody areas with shrubs and young trees, either naturally established or planted, without typical forest (soil) properties;  $n = 94$ ), floodplain hardwood forests ( $n = 25$ ), scree forests ( $n = 41$ ), wet deciduous forest ( $n = 40$ ), deciduous forests ( $n = 185$ ) and conifer plantations ( $n = 45$ ). Habitat types were spatially

interspersed with the exception of scree forests. This montane habitat type was geographically restricted to the Continental Region.

Some abiotic and biotic variation within habitat types is based on regional effects (biogeographic and climatic zones). Intra-regional variability within each habitat type was captured as between-survey variability. For example, mesic open habitats can be, or originate from, pastures or mowed areas, some pastures are occasionally mowed and some mowed areas are occasionally grazed upon. In those cases where surveys were performed within a distance of 1 km, the surveyed areas were either in different habitat types, or were designed to capture within-habitat variability.

Sampling was performed when environmental conditions were suitable for slug activity, i.e. when it was moist, but not wet, and when there was no direct sunlight. During the collections, temperatures ranged between 7 and 21°C.

Each survey consisted of quantitative substrate sampling and hand search. Quantitative sampling was performed within a core area that was usually about 400 m<sup>2</sup>, but somewhat larger in continuous habitats such as forests and somewhat smaller in small gardens where no neighbouring garden could be accessed. Usually, eight random subplots covering a minimum of 0.125 m<sup>2</sup> each were sampled, covering a minimum total area of 1 m<sup>2</sup>. In a few sites, more subplots and total areas larger than 1 m<sup>2</sup> were searched (max. 2 m<sup>2</sup>). Where necessary, densities were recalculated to 1 m<sup>2</sup>. This first step captures species that are evenly distributed or at a medium to high abundance. The second step was an additional 30 min search to approach faunal completeness. The number of species that are retrieved depends, among others, on the size of the sampled area and is based on capture probabilities (MacKenzie *et al.*, 2006). Species found during the hand search in a buffer of 10 m around the quantitative plots were thus included in the analysis via a log-based probability score. Scores were as follows: 0.1, 0.2 and 0.5 if one, two or more individuals were found. Provided that the habitat was continuous, a quick search of special microhabitats was performed within a distance of up to 200 m from the quantitative samples and species scored 0.001 (or 0.01) if one (or more)



**Figure 1.** Geographic overview. **A.** Location of the surveyed region in northwestern continental Europe. **B.** Location of the 729 sites; habitat types were spatially interspersed (for details see Supplementary Material).

individuals were found (for further explanation of this method see Kappes *et al.*, 2009b).

Identification follows Kerney, Cameron & Jungbluth (1983), Pinceel *et al.* (2004) and Reise *et al.* (2011). One species, called *Arion lusitanicus* auct. non Mabilie in accordance with this literature, is the subject of ongoing nomenclatural discussions, since the original *A. lusitanicus* is endemic to western Spain (Quinteiro *et al.*, 2005).

### Statistical analysis

Univariate metrics such as species richness and total abundances in the habitat types were compared in an ANOVA with the post-hoc Tukey HSD test for unequal  $n$ . The number of species at a given number of individuals was assessed in a rarefaction analysis using EstimateS (v. 7.5.1; Colwell, 2005). Because this program does not accept densities below 1, all densities were multiplied by 1,000 (accounting for the lowest probability score) and later divided by 1,000 again. Although two habitat types had total densities <200, we selected 200 individuals for comparison between habitats because some curves were intersecting.

Also, habitat properties may influence SAD patterns. The curves of the cumulative proportion of species in relation to cumulative proportion of abundance were calculated with the SAD Toolkit (McGill *et al.*, 2007). Binning, such as by log-transformation, creates an artificial distribution mode (Nekola *et al.*, 2008). Yet the shape of the artefact depends on the underlying data structure. This shape has been repeatedly analysed and for example is accounted for by the metric 'logskew' that captures deviations from the lognormal distribution (McGill, 2003). A negative logskew occurs if many species are rare, which can occur under continued individual dispersal into the habitat or low detection probabilities. 'Logskew' is not advised for low abundances (Magurran & McGill, 2011). It thus was computed only for the total abundances per habitat type.

Assemblage turnover between the habitat types was analysed using abundance and presence-absence data. The abundance data were standardized prior to calculating Bray-Curtis similarities. Standardization is advised where the unit of sampling is not tightly controlled (Legendre & Legendre, 1998), as is the case for the combination of quantitative substrate search and semiquantitative hand-search data. The Bray-Curtis similarities have the additional advantage that differences between abundant species and differences between rare species make the same contribution to the index (Legendre & Legendre, 1998). In a second approach, abundances were transformed to presence-absence data and assemblage similarities were calculated as the Sørensen similarity index.

Both Bray-Curtis and Sørensen similarity indices are considered to be semimetrics that are well suited for nonmetric multidimensional scaling (MDS; Legendre & Legendre, 1998). The resulting distance matrices were thus subjected to MDS with 25 repeated runs and displayed in a two-dimensional plot. Analysis of similarities (ANOSIM) with 9,999 replicate permutations was used on the same matrices to test for differences in assemblage composition between habitat types. The multivariate dispersion index (MVDISP) that is based on the index of multivariate dispersion (IMD; Warwick & Clarke, 1993) was additionally calculated, to characterize within-habitat heterogeneity. A MVDISP value below 1 signifies predictable, homogeneous assemblages; a value above 1 indicates less predictable, heterogeneous assemblages. The former may be the result of approaching an equilibrium state under stable conditions (such as from species interactions and habitat filtering), whereas the latter can be the outcome of assemblage decay and dispersing species following disturbances or fragmentation (Warwick & Clarke, 1993). The MDS, ANOSIM and MVDISP were calculated with PRIMER 6 (Primer-E Ltd).

Ecological and genetic studies actually use the same approach such as subsampling discrete units, whether concerned with species, genes or traits (Gregorius, 2010). Spatial assemblage turnover was analysed for the five habitat types with more than 90 sites sampled using SGS v. 1.0d (available at <http://software.bfh-inst2.de/software.html>). This program converts coordinates to distances and allows statistical testing of the results. SGS is usually used for assessing the spatial structure of genotypes and phenotypes. For analysis, the 'genotype' of an assemblage was considered to be its relative species composition. Thus, the proportions of species in the assemblages were entered as the allele frequencies, and genetic distances consequently indicate assemblage turnover. Nei's genetic distances, which have been used in some studies on geographic species turnover (Pokrysko & Cameron, 2005), fail for pairs of sites that have no species in common and thus could not be used. Instead, the distance metric  $D$  was utilized (Gregorius, 1978). Visualization of the spatial autocorrelation was performed in a distogram using Tanimoto's distance  $D$ . Statistical significance was tested in SGS with a Monte-Carlo permutation test that randomly assigns the data to the spatial coordinates (500 runs).

## RESULTS

### Susceptibility of habitat types to introduced species

A total of 25 slug taxa were encountered in the course of the survey. Assemblages differed between habitats, because several species had their highest abundances in just one or a few habitat types (Table 1). Introduced species such as *Milax gagates* and *Tandonia budapestensis* can be considered naturalized in the Atlantic Region, but are not yet frequently found in the wild. Gardens, mesic herb stands and successional areas harboured five to six introduced species, compared with  $\leq 3$  introduced species in (semi-)natural habitats (Table 1). Over one-third of all species recorded from gardens are introduced, compared with less than one-sixth in forested habitats (Table 2). Assemblages from gardens, successions, open mesic stands and floodplain hardwoods were dominated by introduced species. On average, every second garden slug belonged to an introduced species, whereas less than every 50th individual from deciduous forests or conifer plantations was of an introduced species (Table 2).

### Assemblage characteristics in habitat types

Habitat types differed in total species numbers and average species richness per site (Fig. 2). Slug densities were highly variable within each habitat type, resulting in high standard deviations for average densities. Average slug densities, however, were remarkably similar, with the exception of floodplain forests that were somewhat less densely inhabited and conifer plantations with extremely sparse densities (Table 2).

Species richness and densities were correlated ( $r = 0.5247$ ,  $P < 0.001$ ). However, the highest densities were not in the richest sites, but resulted from mass occurrences of single species at intermediate species richness (4–9 species). Densities higher than 10 individuals  $m^{-2}$  were never found in floodplain hardwoods and conifer plantations and only in 12.5% of the sites in wet deciduous forests. In the remaining six habitat types, a consistent 18–25% of the sites had densities higher than 10 individuals  $m^{-2}$ .

Because of the correlation between richness and densities, we ran a rarefaction analysis to compare species richness between habitat types for a set number of 200 individuals  $m^{-2}$ . This analysis indicated that wet open habitats and gardens were comparatively poor in species, whereas successions were comparatively rich in species (Table 2).

**Table 1.** Mean densities per m<sup>2</sup> in the habitat types.

|   | Wet. decid. forest | Wet open    | Mesic open  | Gardens     | Succ.       | Floodpln forest | Scree forest | Decid. forest | Conifer     |
|---|--------------------|-------------|-------------|-------------|-------------|-----------------|--------------|---------------|-------------|
| <i>Limax cinereoniger</i> Wolf, 1803                        | 0.01               | –           | –           | –           | –           | –               | 0.04         | <b>0.07</b>   | 0.02        |
| <i>Lehmanna marginata</i> (O.F. Müll., 1774)                | –                  | –           | –           | –           | <<0.01      | –               | 0.21         | <b>0.29</b>   | –           |
| <i>Malacolimax tenellus</i> (O.F. Müll., 1774)              | <<0.01             | –           | –           | –           | –           | <<0.01          | 0.15         | <b>0.65</b>   | 0.09        |
| <i>Arion rufus</i> (Linnaeus, 1758)                         | 0.28               | 0.06        | 0.04        | <0.01       | 0.17        | 0.03            | 0.49         | <b>0.91</b>   | 0.26        |
| <i>Arion subfuscus</i> (Draparnaud, 1805)                   | 0.03               | <<0.01      | <0.01       | –           | 0.03        | 0.10            | 0.16         | <b>0.27</b>   | <0.01       |
| <i>Arion silvaticus</i> Lohmander, 1937                     | 0.21               | 0.13        | 0.03        | 0.02        | 0.20        | 0.12            | <b>1.24</b>  | <b>1.73</b>   | 0.04        |
| <i>Tandonia rustica</i> (Millet, 1843)                      | –                  | –           | –           | –           | 0.02        | –               | <b>0.49</b>  | <<0.01        | –           |
| <i>Arion fasciatus</i> (Nilsson, 1823)                      | –                  | 0.04        | 0.01        | –           | 0.02        | <0.01           | <b>0.22</b>  | –             | –           |
| <i>Boettgerilla pallens</i> Simroth, 1912                   | 0.04               | 0.03        | 0.05        | 0.15        | <b>0.37</b> | 0.16            | <b>0.47</b>  | 0.17          | <0.01       |
| <i>Limax maximus</i> Linnaeus, 1758                         | 0.01               | <<0.01      | <<0.01      | 0.04        | <b>0.12</b> | 0.04            | 0.03         | 0.03          | –           |
| <i>Arion lusitanicus</i> auct. non Mab., 1868 <sup>i</sup>  | 0.48               | <b>1.18</b> | <b>1.87</b> | <b>1.82</b> | <b>1.72</b> | <b>1.59</b>     | 0.25         | 0.07          | 0.01        |
| <i>Tandonia budapestensis</i> (Hazay, 1881) <sup>i</sup>    | –                  | –           | –           | –           | <<0.01      | –               | –            | –             | –           |
| <i>Milax gagates</i> (Draparnaud, 1801) <sup>i</sup>        | –                  | –           | <b>0.02</b> | <b>0.02</b> | <b>0.02</b> | –               | –            | –             | –           |
| <i>Arion distinctus</i> J. Mabile, 1868                     | 0.18               | 0.43        | <b>1.17</b> | <b>1.60</b> | <b>1.52</b> | 0.68            | 0.71         | 0.09          | <0.01       |
| <i>Deroceras invadens</i> (Reise et al., 2011) <sup>i</sup> | 0.02               | 0.07        | <b>0.42</b> | <b>0.68</b> | <b>0.45</b> | 0.12            | <<0.01       | <0.01         | –           |
| <i>Arion hortensis</i> A. Férussac, 1819 <sup>(i)</sup>     | –                  | <0.01       | 0.29        | 0.31        | <b>0.69</b> | –               | –            | 0.01          | –           |
| <i>Limacus flavus</i> (Linnaeus, 1758) <sup>i</sup>         | –                  | –           | –           | <b>0.03</b> | –           | –               | –            | –             | –           |
| <i>Lehmanna valentiana</i> (A. Féruss., 1822) <sup>i</sup>  | –                  | –           | 0.01        | <b>0.18</b> | 0.04        | –               | –            | 0.03          | –           |
| <i>Deroceras agreste</i> (Linnaeus, 1758)                   | –                  | <0.01       | <b>0.01</b> | –           | <0.01       | –               | –            | –             | –           |
| <i>Deroceras reticulatum</i> (O.F. Müll., 1774)             | 0.31               | 0.85        | <b>1.70</b> | 0.46        | 0.35        | 0.62            | 0.04         | 0.04          | <0.01       |
| <i>Deroceras sturanyi</i> (Simroth, 1894)                   | <0.01              | –           | <b>0.01</b> | –           | –           | –               | –            | –             | –           |
| <i>Deroceras laeve</i> (O.F. Müller, 1774)                  | <b>1.92</b>        | <b>1.94</b> | 0.03        | 0.04        | <0.01       | 0.31            | –            | <0.01         | –           |
| <i>Arion circumscriptus</i> Johnston, 1828                  | <b>0.29</b>        | 0.17        | 0.03        | <0.01       | 0.04        | 0.05            | <b>0.29</b>  | 0.18          | 0.05        |
| <i>Arion intermedius</i> Normand, 1852                      | <b>1.57</b>        | 0.40        | 0.26        | 0.11        | 0.69        | 0.69            | <b>1.48</b>  | <b>2.11</b>   | 0.58        |
| <i>Arion fuscus</i> (O.F. Müller, 1774)                     | <b>0.43</b>        | <b>0.26</b> | 0.13        | <0.01       | 0.15        | 0.01            | 0.13         | <b>0.29</b>   | <b>0.41</b> |
| No. species with mean densities > 1 m <sup>-2</sup>         | 2                  | 2           | 3           | 2           | 2           | 1               | 2            | 2             | 0           |

Species are sorted by their highest average abundances (indicated by bold numbers) in a habitat type, starting with typical forest species. Decid., deciduous; succ., successions; i, introduced; (i), at least regionally spreading.

**Table 2.** Characteristics of the slug assemblages in the habitat types.

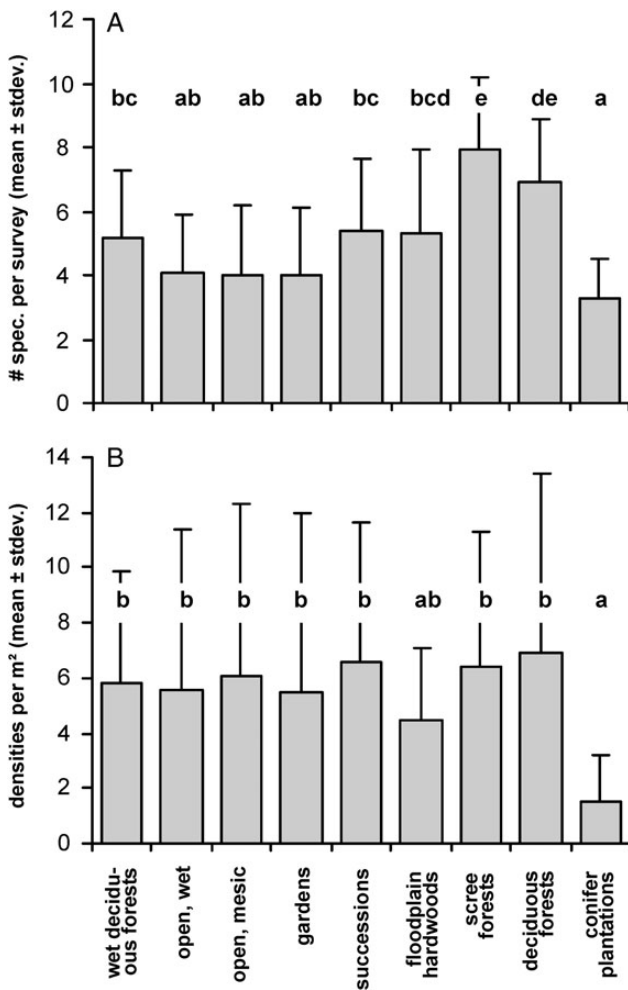
|                       | Sites    | Spec. |     |                  |                   |      | MVDISP | BC    | <i>J</i> | logskew |
|-----------------------|----------|-------|-----|------------------|-------------------|------|--------|-------|----------|---------|
|                       | <i>n</i> | Total | # i | i% <sub>sp</sub> | i% <sub>ind</sub> | r200 | Sør.   |       | Overall  | Overall |
| Wet deciduous forests | 40       | 16    | 2   | 12.5             | 8.5               | 15.7 | 1.194  | 1.118 | 0.688    | –0.296  |
| Open, wet             | 112      | 16    | 3   | 18.8             | 22.6              | 13.5 | 1.113  | 0.999 | 0.679    | –0.799  |
| Open, mesic           | 94       | 19    | 5   | 26.3             | 42.9              | 16.6 | 1.193  | 0.952 | 0.609    | 0.349   |
| Gardens               | 93       | 16    | 6   | 37.5             | 55.3              | 14.4 | 1.091  | 0.947 | 0.650    | –0.144  |
| Successions           | 94       | 21    | 6   | 28.6             | 44.2              | 17.8 | 1.239  | 1.165 | 0.711    | –1.241  |
| Floodplain hardwoods  | 25       | 15    | 2   | 13.3             | 37.9              | n.a. | 1.217  | 1.039 | 0.716    | –0.383  |
| Scree forests         | 41       | 17    | 2   | 11.8             | 3.9               | 16.5 | 0.953  | 1.163 | 0.823    | –2.559  |
| Deciduous forests     | 185      | 19    | 3   | 15.8             | 1.6               | 15.4 | 0.812  | 0.964 | 0.685    | –0.565  |
| Conifer plantations   | 45       | 12    | 1   | 8.3              | 0.8               | n.a. | 1.048  | 1.080 | 0.628    | –0.398  |
| Total                 | 729      | 25    | 7   | 28.0             | 24.2              | n.c. | n.a.   | n.a.  | 0.788    | –1.506  |

# i, number of introduced species; i%<sub>sp</sub>, relative richness of introduced species; i%<sub>ind</sub>, relative abundance of introduced species; r200, rarefaction of species numbers for 200 individuals; *J*, Pielou evenness; MVDISP, multivariate dispersion index for within-habitat type heterogeneity, calculated for the Sørensen (Sør.) and Bray-Curtis (BC) similarities between the sites (the metric 'logskew' accounts for deviations from the lognormal distribution); n.a., not applicable (too few specimens, or cannot be calculated); n.c., not calculated because of computation memory limitation.

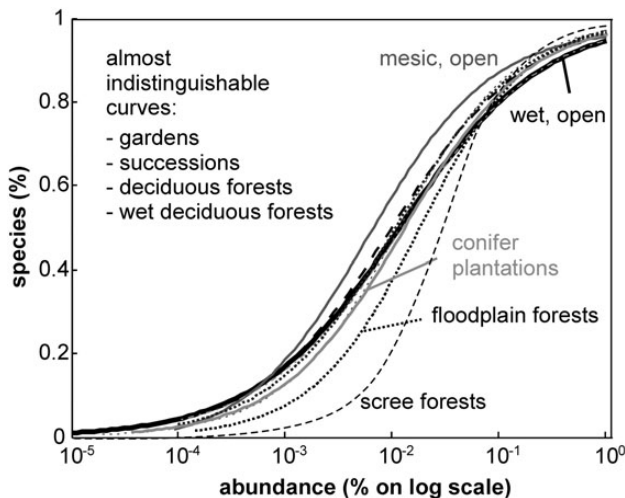
Most habitat types displayed similar patterns in overall relative SAD. However, the overall relative species abundance from the scree forests differed somewhat from the other habitat types, as most species occurred at intermediate abundances (Fig. 3). The curves in Figure 3 correspond to *J*<sub>overall</sub> evenness: mesic open habitats had the lowest, and scree forests the highest, *J*<sub>overall</sub> value (Table 2). A higher evenness was associated with a

more negative logskew ( $J_{\text{overall}} = -0.068 \times \text{logskew} + 0.6421$ ,  $R^2 = 0.8269$ ), i.e. with more uncommon species.

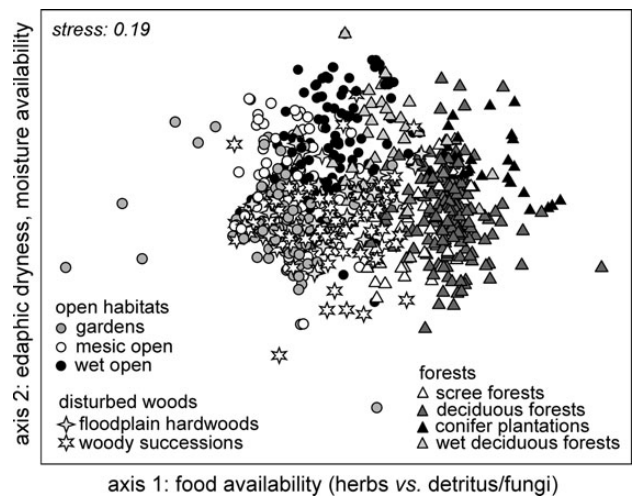
The values of logskew from all sites per habitat type were usually negative, with the exception of mesic open-herb and grass stands in which it was positive (Table 2). Assemblages from the latter habitat type comprise a quite consistent set of three species with average densities > 1 m<sup>-2</sup> (*Arion lusitanicus*,



**Figure 2.** Averages of slug alpha diversity per survey (**A**) and densities per  $m^2$  in the habitat types (**B**). Groups were assigned in an ANOVA approach, using the Tukey HSD test for unequal  $n$ , with  $P < 0.05$ . Shared letters indicate a lack of significance between habitat types.



**Figure 3.** Cumulative proportion of species in relation to per cent abundance, comparing the habitat types in respect of the proportion of species with low, intermediate and high total abundance (e.g. scree forests had many species with intermediate abundances and thus a steep sigmoid increase).



**Figure 4.** Biplot of the nonmetric MDS calculated from the Bray-Curtis Similarities between slug assemblages in the 729 sites. Symbols refer to the different habitat types.

*A. distinctus* and *Deroceras reticulatum*), whereas the other habitat types had only none, one or two species with average densities  $> 1 m^{-2}$  (Table 1).

#### Assemblage turnover between habitat types

Species occurrences were relatively predictable in deciduous forests ( $MVDISP_{Sor.} = 0.812$ ) and most unpredictable in successions and floodplain hardwoods ( $MVDISP_{Sor.} \geq 1.217$ ; Table 2). In contrast, relative abundance composition was more homogeneous for all habitat types;  $MVDISP_{BC}$  varied between 0.947 and 1.165.

Species turnover was visualized in a nonmetric MDS. The two-dimensional MDS had a minimum stress value of 0.19 for the abundance data matrix (Fig. 4; the minimum stress was 0.19 in 20 of 25 runs and 0.20 in the remaining 5 runs) and 0.15 for the presence data matrix (the minimum stress was 0.15 in 11 of 25 runs and  $< 0.19$  in the other runs).

Axis 1 depicted a gradient from herb-rich, open habitats to close-canopy leaf-litter dominated forest sites for both the Bray-Curtis and the Sørensen similarities. Habitat assignments along axis 1 indicate that the major influence is from canopy cover, likely affecting food type and microclimate. Axis 2 of the MDS follows a gradient of edaphic dryness, from constantly moist wetlands to scree forests with quickly-drying, steep slopes and outcrops.

Habitat types covered about 55% of the variability in the abundance data matrix (ANOSIM, global model:  $r = 0.548$ ;  $P < 0.001$ ). Slug assemblages differed between habitat types at probability levels below 0.001, with the exception of two habitat types. Assemblages from gardens and floodplain hardwoods were different, but sporadically overlapped (ANOSIM pairwise comparison:  $r = 0.174$ ;  $P = 0.006$ ). Assemblages from floodplain hardwoods and woody successions largely overlapped (pairwise comparison:  $r = -0.01$ ;  $P = 0.552$ ).

Similarly, habitat type covered about 59% of the variability in the presence-absence data matrix (global model:  $r = 0.592$ ;  $P < 0.001$ ). Slug assemblage composition differed between habitat types with  $P \leq 0.002$ , with the exception of two habitat pairs. Assemblage compositions of floodplain hardwoods and mesic herb stands were only marginally different (ANOSIM pairwise comparison:  $r = 0.098$ ;  $P = 0.028$ ). Floodplain

**Table 3.** Results of the spatial assemblage turnover in the habitat types with >50 sites (see also Fig. 4).

| Habitat type     | Mean between-maximal |          |          |                  |
|------------------|----------------------|----------|----------|------------------|
|                  | Site distance        | Distance | Similar  | Dissimilar       |
| Deciduous forest | 7.4 km               | 492 km   | 0–50 km  | > 150 km         |
| Successions      | 13.5 km              | 435 km   | 0–50 km  | 150–200; >350 km |
| Gardens          | 10.5 km              | 446 km   | 0–100 km | > 250 km         |
| Wet open         | 6.5 km               | 453 km   | 0–50 km  | 200–250 km       |
| Mesic open       | 10.9 km              | 474 km   | 0–50 km  | n.a.             |

Similar or dissimilar refers to values below, or above, the 95% threshold value of random spatial variation, respectively.

hardwoods and woody successions typically shared species compositions (pairwise comparison:  $r = 0.049$ ;  $P = 0.173$ ).

#### Spatial turnover in different habitat types

Spatial turnover was only analysed for habitats with more than 50 sites. Slug assemblages within all habitat types displayed a high self-similarity within the first 50 km (Table 3). This pattern was strongest in gardens, where self-similarity persisted up to distances of 100 km and weakest for open wet habitats ( $P < 0.05$ ).

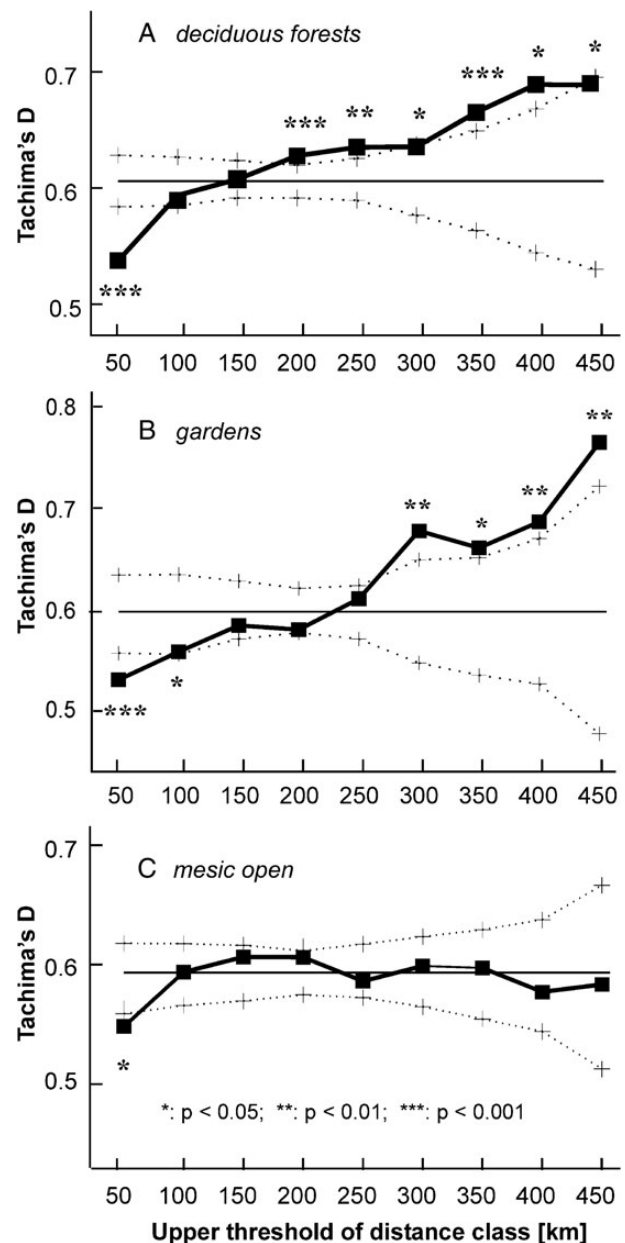
Deciduous forests are the natural vegetation cover in the area under study. Slug assemblages from such forests displayed shifts in assemblages at distances >150 km (Table 3, Fig. 5). This approximately equals the distance from the coastal lowlands to the border of the low mountain ranges (150–200 km) and the distance from the southeastern-most sites to the border between the low mountain ranges and the northwestern lowlands (c. 150–250 km, depending on the site). Successions also displayed a community-change signal at 150–200 km but, in this habitat type, the effect indicates a peculiarity in community assembly in the highly disturbed and heterogeneous centre of the study area (Table 3). Slug assemblages from gardens, wet open and mesic open habitats overcame effects from the biogeographic regions, and displayed turnover at larger scales (Table 3, Fig. 5). Slug assemblages from wet open herb and grass stands displayed a turnover only at intermediate distances (200–250 km). The highly significant signal again indicates a peculiarity in relative assemblage composition in the centre of the study area, because all species in the central sites also occurred in more distal sites. Finally, slug assemblages from mesic open herb and grass stands displayed no signs of regionalization across the studied area (Fig. 5).

## DISCUSSION

#### Invasibility risk of habitat types

Our first assumption, namely that the proportions of introduced and rare species are habitat-type specific, was met. Rare species can hint at dispersal (Loreau & Mouquet, 1999; Magurran & McGill, 2011) but were not synonymous with the level of invasion by nonnative species, since garden-like habitats had only a slight left overall logskew and thus no excessive numbers of rare species. A basically normal distribution suggests some dispersal limitation (Loreau & Mouquet, 1999), which at first glance is in line with the highly fragmented nature of garden habitats.

Nevertheless, transport of plants and materials must have occurred with substantial passive dispersal of slugs. In contrast to assemblages from other habitats, those from gardens were self-similar up to 100 km instead of only within the first 50 km. Also, distance decay was delayed in gardens when compared with



**Figure 5.** Distograms for the slug assemblages. **A.** Deciduous broadleaved forests. **B.** Gardens. **C.** Mesic open habitats. Only the upper value is given for the x-axis (e.g. 50 km should be read 0–50 km). Conventions: thick lines with filled squares, observed values; thin solid line, mean; dotted lines, upper and lower 95% confidence intervals.

deciduous forests. Anthropogenic optimization in terms of soil properties and human-aided dispersal may have fostered this larger-scale assemblage similarity. The latter assumption is supported by the prevalence of introduced slugs, indicating a high invasibility of this habitat type. Introductions and range-filling by both native and nonnative species (and genotypes) provide some upscaling feedback to the regional species pool; introduced slugs seem to spread to mesic herb stands and/or successional areas during naturalization before spreading to the next habitat type such as floodplain hardwoods or fragmented, park-like deciduous forests. However, species of Mediterranean origin need mild winters to survive (Potts, 1975; Peltanová *et al.*, 2012). Thus, climatic suitability differs across northwestern Europe and

most introduced species were found in the Atlantic Region. A head start on climate change, as was illustrated for the much more cared for ornamental plants (Van der Veken *et al.*, 2008), is not that obvious for garden slugs.

Our data suggest that habitats in which the green, plant-based, trophic chain dominates have a high invasibility risk, whereas habitats in which the brown, detritus-based, trophic chain dominates have the lowest invasibility risk. This might be related to the recent dominant pathway of species import along with materials and plants for garden habitats, in which the green trophic chain dominates, i.e. the probability of recent introductions of slug species from the brown trophic chain is low.

#### *Niche-based assembly in open mesic habitats*

The left-side logskew for the totals per habitat was expected. The assemblage metric logskew is known to be sensitive to rare, low-density species (Magurran & McGill, 2011). The number of rare species increases among others with area size (Hanski, 1982; Borda-de-Agua *et al.*, 2012) and spatio-temporal sampling intensity (e.g. McGill, 2003). As a result, the metric logskew tends to become negative when increasing the number of (sub)samples or the area (McGill, 2003). Mesic open herb and grass stands were the exception, in which logskew became positive.

Our result for mesic open habitats parallels that for the tropical forest tree dataset found by McGill (2003), although the spatial extent in our study was much larger (up to 500 km). In our study, assemblages from mesic open habitats lacked distance decay. Historical seasonal livestock migration between pastures has contributed to enlarged distributional ranges of some snails (Dörge *et al.*, 1999) and may have played a role in large-scale homogenization of slug fauna as well. Our results suggest that assemblage similarity across space affected the response of logskew at higher sampling effort.

Three almost equally abundant species occurred in mesic open habitats, with average abundances similar to those in other habitats. These three might be considered as core species. The unimodal distribution in our data thus suggests recent dispersal limitation and niche-based community assembly. Environmental constraints certainly discourage the occurrence of hygrophilous species and species that are sensitive to high microclimatic amplitudes. Livestock trampling and mowing might additionally select for *r*-strategists. Furthermore, the three common slug species of mesic habitats strongly contrast in external appearance, which points to biotic interactions.

However, niche filtering did not protect this habitat type against invasibility. Mesic open habitats have been heavily invaded by *Arion lusitanicus* in recent decades. This invasion is usually followed by a decline and local extinction of the native sibling species *A. rufus* (e.g. Noble & Jones, 1996). The latter species is hardly found in this habitat type any more.

#### *Forest removal and regrowth: a tipping point*

The most heterogeneous slug assemblages were from successional woods, probably reflecting the rapid dynamics and heterogeneous origin of the habitat. Successions grow on abandoned ground that typically was subjected to forest clearance and/or land-use change (Hurt *et al.*, 2006) and thus often stand on disturbed and physico-chemically altered soils. They thus may be considered as a hybrid ecosystem in the sense of Hobbs *et al.* (2009). Some changes in soil chemistry that were introduced to increase soil fertility may be persistent (Van Dijk *et al.*, 2004), even over almost two millennia and after forest conditions have been re-established (Dupouey *et al.*, 2002).

Our study indicated that woody successions equal open habitats rather than forests. The species pool of a successional stand is probably filled at an early stage: successions harboured

forest-associated, open-habitat-associated and introduced slug species, but usually lacked forest specialists. The gap that occurred in the nonmetric MDS plot between mature forests and conifer plantations on the one hand, and the other habitats on the other hand, indicates a tipping point associated with forest cover removal, or forest regrowth.

Scree forests were somewhat intermediate in relation to this tipping point. This habitat type had considerable between-site assemblage heterogeneity and low overall logskew values. The high species richness and high MVDISP value in scree forests are consistent with the habitat heterogeneity hypothesis (MacArthur & Wilson, 1967). Forests on slopes are more susceptible to local gaps in the canopy layer and hence to herb growth. Overall heterogeneity probably relaxed niche-based filtering, but also increased the susceptibility to invading species.

The comparatively high homogeneity of slug assemblages in deciduous forests suggests strong niche-based processes. The tipping point thus might involve the shift between the green and the brown trophic chain. Non-forest-specific snails and slugs persist in woody successions. They can also enter old-growth forests through disturbance-related processes (Kappes, 2006; Kappes *et al.*, 2009a, b). In contrast, forest specialists quickly cease to exist after forest removal and were never found outside forests. Slug assemblages in afforestations may converge towards those of old-growth forests after some 70 years of forest regrowth in the Continental Region (Kappes, 2006), but forest management, climatic suitability and connectivity to other mature forest stands affect faunal resilience after the transition of the tipping point. In the Atlantic Region, forests are highly fragmented, afforestations lack *Limax cinereoniger* among others (H. Kappes, unpubl.) and old forests that are managed have a 50% probability of retrieving this species only if exceeding 1,000 ha (Kappes *et al.*, 2009b).

#### *Conclusions and outlook*

To conclude, land-use changes modify probabilities of passive dispersal and invasibility, and our data indicate that this happens in different compartments of landscapes and regions, to different degrees. Depending of the studied habitat type, a given taxonomic or functional group may display contrasting patterns of dispersal and spatial species turnover, and thus different responses to, e.g. climate change, within a single geographic region. We expect that this differential response can be observed regardless of realm (marine, freshwater or terrestrial) or biome.

#### SUPPLEMENTARY MATERIAL

Supplementary Material is available at *Journal of Molluscan Studies*.

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