Low α- and high β-diversity in terrestrial isopod assemblages in the Transdanubian region of Hungary

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Abstract

We compiled all published and unpublished isopod distribution data not older than 30 years from the geographical unit of Transdanubia, the western part of Hungary. As a result, records from 758 localities were evaluated according to geographical position (UTM grids), altitude and habitat characteristics (type of vegetation, general moisture conditions within the habitat) by uni- and multivariate statistics. Out of the 57 species known from Hungary, 48 were found in the surveyed region. Overall, species richness varied only slightly, but significantly decreased from natural (undisturbed) wet habitats to disturbed dry habitats. Species composition differed between degraded and natural habitats and, within natural habitats, between highland and lowland sites. Composition of the above-mentioned three habitat classes showed extensive overlap, but species occurrences were associated with species groups found in previous studies for the Hungarian fauna. These results indicate a relatively uniform richness pattern with high compositional turnover according to geographical regions and habitat characteristics. Naturalness (degree of degradation) plays a crucial role in shaping terrestrial isopod assemblages.

Keywords – assemblage type, habitat classification, isopod richness, meta-analysis, spatial scales

Introduction

Basic faunistic data comprise important components of any biogeographical or large-scale conservation biological research (Sutton & Harding, 1989; Taiti & Ferrara, 1989; Schmalfuss, 1998; Sólymos & Fehér, 2005). Faunistic research in the past 30 years provided an increasing data set on terrestrial isopods in Hungary. The results show an impressive increase in the number of species: 15 new species added in the last 10 years (Korsós *et al.,* 2002; Vadkerti & Farkas, 2002; Farkas, 2003, 2004a; Kontschán, 2004; Vilisics, 2005, 2007).

Distribution data are often biased towards the personal preferences of researchers. For instance, targeting specific and mainly protected areas, isopodologists choose woodlands in hilly areas for sampling and seldom collect in dry grasslands or areas heavily modified by human activities. Such localities were rather under-represented in previous publications. Thus, compared to the latest checklist of Forró and Farkas (1998), the species number in Hungary increased from 42 to 57 species.

Habitat quality has major effects on species richness and composition of local assemblages (Warburg, 1993). Thus, besides basic biotic data, we put emphasis on characteristics of the habitats, such as vegetation type, moisture conditions and degradation.

We aimed at (1) exploring the large-scale distribution of the species and species richness (α-diversity) in the Transdanubian region based on field sampling and literature, (2) analysing determinants of local species richness, (3) analysing species composition according to disturbance, vegetation and moisture conditions of the habitats, and (4) validating published species categorisation with the Transdanubian data set.

Material and methods

Database

Transdanubia is the name of the western part of Hungary, covering nearly half of the country. It is bordered by the River Danube in the east, Austria in the west, Slovakia in the north, and Slovenia and

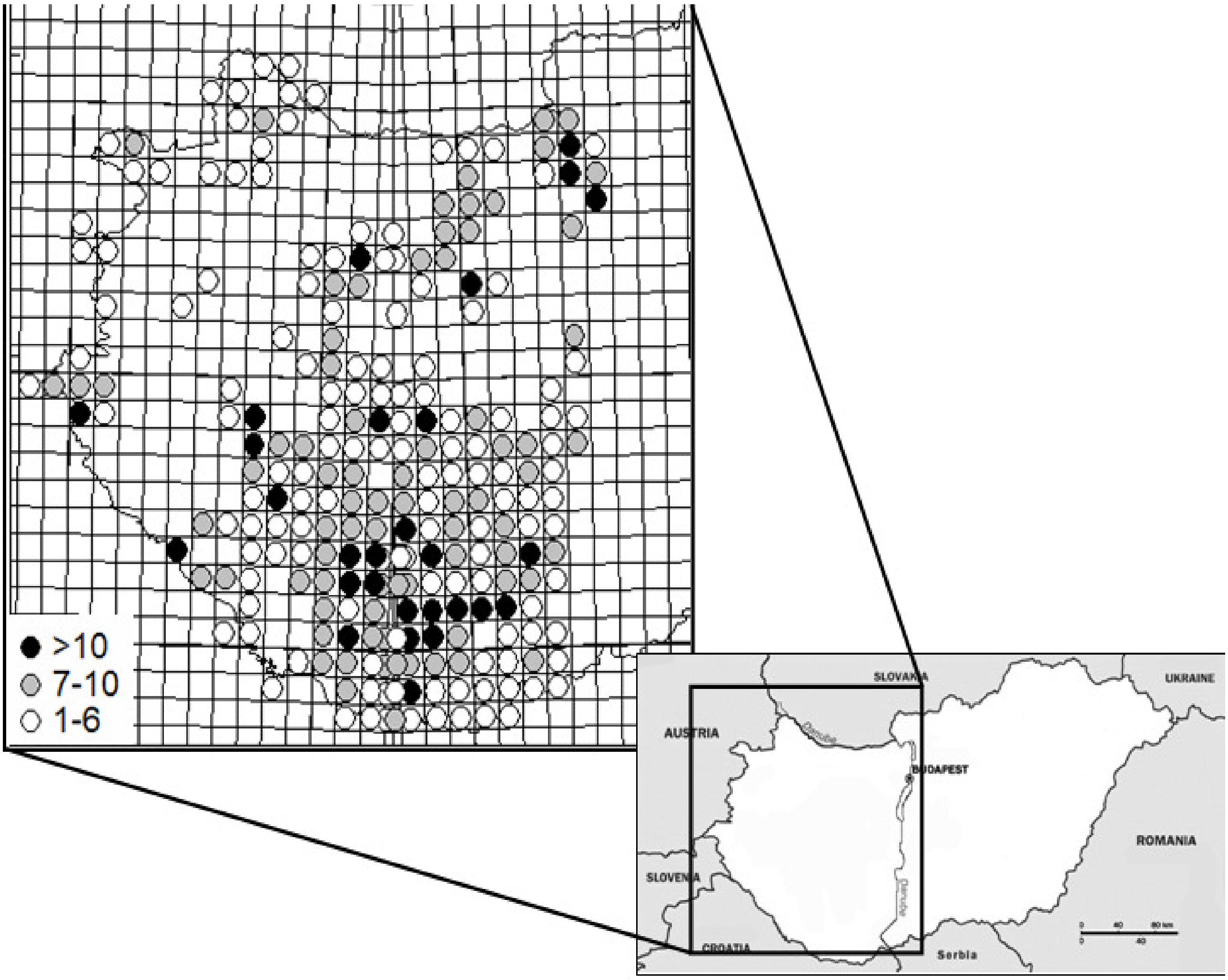

Figure 1. Map of Hungary and the isopods species richness distribution in Transdanubia (10x10 km² UTM grids). Circles and shading refer to species numbers according to legends.

Croatia in the south (Fig. 1). The area forms a biogeographic unit which is influenced by the surrounding southern (Illyric) and western (Alpine) regions. Due to its geographic and biogeographic traits, Transdanubia differs from the Great Hungarian Plain, or the Northern Middle Ranges. The region is constituted by the Lower Alps, the Transdanubian Middle Ranges, the Transdanubian Hills, the Small Plain, and the western edge of the Great Plain.

The Soil Ecology Research Group of the Institute for Biology, at Szent István University (SZIU), began research on ground-dwelling invertebrate species occurrences, applying modern faunistic methods that comprise a designed sampling protocol that includes time-restricted (30 minutes) hand sorting and a datasheet for field assessments (Vilisics *et al.,* 2007), following the example and structure of previously published datasheets (Harding & Sutton, 1985).

For the present analysis, we included all available faunistic data (525 samples) published in the last 30 years (Ilosvay, 1982, 1983; Farkas, 2003, 2004a,b,c, 2005, 2006; Farkas & Vilisics, 2006; Kontschán, 2001a,b,c,d, 2002a,b, 2004; Kontschán & Berczik, 2004; Korsós *et al.,* 2002; Vilisics, 2005, in press; Vilisics & Farkas, 2004) and unpublished field data of the authors (260 samples). Isopod distribution data from the metropolitan city of Budapest were also included in the dataset. Species nomenclature follows Schmalfuss (2003).

Besides species distribution, we registered data on sampling location and environmental factors (e.g. UTM code, Á-NÉR/HGHCS code, vegetation, altitude) available. Assessment of isopod data resulted in a total of 785 records (525 published, 260 unpublished) taken from 243 UTM grid squares (10 km x 10 km). For statistical analyses, 758 records were used: literature data with unidentifiable habitats were not included. Basic faunistic results with a detailed list of species and localities will be given in a separate publication.

For habitat categories, we used HGHCS (Á-NÉR in Hungarian) codes, naturalness, elevation and moisture of localities. HGHCS (Hungarian Generalized Habitat Classification

System) codes (Fekete *et al.,* 1997) primarily contain information on the main Hungarian vegetation types and biotopes. Naturalness of localities refers to the intensity of human disturbance. Natural habitats possess native vegetation and little or no evidence of human disturbance, while degraded localities were towns, villages and farmlands. The altitudes of sampling sites represent two main categories, lowlands and highlands. Samples belonging to highland categories were collected between 300 – 1000 m a.s.l (hilly areas and middle ranges), while most of the lowland areas were located at floodplains of major rivers (Danube, Dráva, Rába). Due to the small number of dry habitats sampled, we used only two categories to characterize moisture conditions. Moist habitats are typically hardwood forests (dominated by oak and elm) and ravines. Wet habitats include riparian willow-poplar forests and alder groves.

Species characterisation was done according to previous results (Hornung *et al.,* 2007). The categories used for distribution and abundance in Hungary were:

1. "rare" species found in natural habitats (NR), in small, isolated patches. Being mainly relict species (e.g. troglobiont species), they have special ecological demands. They occur in less than 15 UTM 10 km squares in Hungary (e.g. *Mesoniscus graniger, Trichoniscus bosniensis, Calconiscellus karawankianus*).
2. frequent species, in natural habitats, (NF): >15 UTM in Hungary. They are native, widely distributed but not abundant species (e.g. *Orthometopon planum, Protracheoniscus politus*).
3. "rare" species in disturbed, urban/suburban habitats (DR), in small, isolated patches. They have special ecological demands such as co-occurrence with other species (e.g. *Platyarthrus schoblii* with *Lasius neglectus* ant species) or species living only in buildings, in cellars (e.g. *Protracheoniscus major*). They are mainly introduced species, occurring in less than 15 UTMs in Hungary.
4. frequent species connected to disturbed, urban/suburban habitats, mostly anthropogenous ones (DF). >15 UTMs in Hungary. (e.g. *Porcellionides pruinosus, Porcellio scaber*)
5. generalist species –often cosmopolitans– with broad tolerance in a wide variety of habitats (G). >60 (100) UTMs (e.g. *Armadillidium vulgare, Trachelipus rathkii*).
6. uncertain (U) category: too few data; occurrence both in urban and natural habitats; e.g. *Armadillidium versicolor*).

Nomenclature for species characterisation was used according to the terminology proposed by Williamson & Fitter (1996): introduced – found in the wild; established introduced – with a self sustaining population; naturalized. Species that are widely distributed in most continents, like *A. vulgare* (Garthwaite *et al.,* 1995), we considered cosmopolitan. Synanthropic species are connected with human settlements, often using man-made microhabitats as "spring-boards" for adaptation to local conditions before invading other urban and suburban areas. Non-native species are those that went through adaptation and occur in suburban-seminatural fringe areas. Native species are those that are endemic and/or have been established by dispersal/dispersion presumably before historical times.

Statistical analyses

Habitats were classified according to naturalness (natural, degraded), moisture (moist, wet; the two dry habitats were excluded from analyses), altitude (lowland, highland) and vegetation (forest, grassland) based on the Hungarian habitat classification system (Fekete *et al.*, 1997). There were approximately equal numbers of samples within each combination of habitat classes.

We calculated species richness for all 758 localities and used it as a response variable in generalized linear model (GLM) with habitat classes (naturalness, moisture, altitude, vegetation) as factors. Since assumptions of normality were not met, we used Poisson error distribution. The best fit model was selected from the full model in a backward stepwise manner.

Determinants of community composition were analysed by the multivariate regression tree (MRT) method (De'Ath, 2002). We used sum of squares based on the locality/species data matrix as response, and the above factors as independent variables. The best tree was selected by cross-validation. Principal components analysis (PCA) was performed based on the results of the MRT. Localities grouped by terminal nodes of MRT and species were plotted jointly in a PCA biplot to evaluate habitat preferences of the species and identify characteristic species of habitat classes.

The association between species occurrences within species groups and species occurrences due to habitat classification was tested by a Chi-squared test. For data handling we used the MEFA package (http://mefa.r-forge.r-project.org/), for the computations we used the MVPART add-on package (De'Ath, 2002) and the R (2006) software and programming environment.

Results

Field surveys in the Transdanubian region yielded 48 species in the past three decades (Table 1). The final number of species includes 82 % of the known number of terrestrial isopods from Hungary. Species richness on the UTM 10 km squares scale varied between 1 and 28, average richness was 3. Hotspots (>10 species per UTM cell) for native species were located in the Mecsek Mountains (22 species/UTM) and along the River Dráva (16), while hotspots for non-native (mostly introduced) species were located in and around major settlements: Budapest (28), Pécs (24), Kaposvár (21) (Fig. 1).

The distribution of both species richness and species occurrence was skewed, indicating that richness was low in most habitats (<5, mean = 3; Fig. 2A) and most of the species

Table 1. Species occurrence in different habitat types identified by the multivariate regression tree analysis. Species list is sorted according to species groups and decreasing total number of occurrences. Subtotal percentages are calculated for each group separately.

Identifier	Species	Group	Degraded	Natural	
				highland	lowland
Avul	*Armadillidium vulgare* Latreille, 1804	G	113	104	141
Pcol	*Porcellium collicola* (Verhoeff, 1907)	G	73	105	134
Hrip	*Hyloniscus riparius* (C. Koch, 1838)	G	66	80	148
Trath	*Trachelipus rathkii* (Brandt, 1833)	G	48	56	102
Tnod	*Trachelipus nodulosus* (C. Koch, 1838)	G	37	45	49
Phof	*Platyarthrus hoffmansseggii* Brandt, 1833	G	55	18	44
Tpus	*Trichoniscus pusillus* csoport	G	10	39	49
Hdan	*Haplophthalmus danicus* Budde-Lund, 1880	G	34	20	27
Hmen	*Haplophthalmus mengii* (Zaddach, 1844)	G	17	19	18
Subtotal percentage		G	27	29	43
Ppol	*Protracheoniscus politus* (C. Koch, 1841)	NF	27	144	36
Tratz	*Trachelipus ratzeburgii* (Brandt, 1833)	NF	10	76	45
Lhyp	*Ligidium hypnorum* (Cuvier, 1792)	NF	15	36	21
Lmin	*Lepidoniscus minutus* (C. Koch. 1838)	NF	2	48	5
Lger	*Ligidium germanicum* Verhoeff, 1901	NF	1	34	18
Opla	*Orthometopon planum* (Budde-Lund, 1885)	NF	11	16	0
Subtotal percentage		NF	12	65	2§
Azen	*Armadillidium zenckeri* Brandt, 1833	NR	2	7	49
Hviv	*Hyloniscus vividus* (C. Koch, 1841)	NR	1	18	11
Aopa	*Armadillium opacum* (C. Koch, 1841)	NR	0	18	7
Tste	*Trichoniscus steinboecki* Verhoeff, 1931	NR	0	20	1
Hmon	*Haplophthalmus montivagus* Verhoeff, 1941	NR	4	3	0
Ckar	*Calconiscellus karawankianus* (Verhoeff, 1908)	NR	0	4	2
Pfra	*Protracheoniscus franzi* Strouhal, 1948	NR	0	4	2
Prec	*Porcellium recurvatum* Verhoeff, 1901	NR	0	3	3
Tbos	*Trichoniscus bosniensis* Verhoeff, 1901	NR	0	3	0
Tniv	*Trichoniscus nivatus* Verhoeff, 1917	NR	0	0	2
Apic	*Armadillidium pictum* Brandt, 1833	NR	1	0	0
Taus	*Tachysoniscus austriacus* (Verhoeff, 1908)	NR	0	1	0
Subtotal percentage		NR	5	49	46
Ccon	*Cylisticus convexus* (De Geer, 1778)	DF	58	31	32
Psca	*Porcellio scaber* Laterille, 1804	DF	89	8	7
Ppru	*Porcellionides pruinosus* (Brandt, 1833)	DF	43	7	2
Subtotal percentage		DF	69	17	15

continued

Table 1. *continued*

Identifier	Species	Group	Degraded	Natural	
				highland	lowland
Aros	*Androniscus roseus* (C. Koch, 1838)	DR	19	12	1
Anas	*Armadillidium nasatum* Budde-Lund, 1885	DR	11	1	0
Bcat	*Buddelundiella cataractae* Verhoeff, 1930	DR	7	0	0
Pspi	*Porcellio spinicornis* Say, 1818	DR	5	2	0
Oase	*Oniscus asellus* Linnaeus, 1758	DR	4	1	0
Pmaj	*Protracheoniscus major* (Dollfus, 1903)	DR	4	0	0
Psch	*Platyarthrus schoblii* Budde-Lund, 1885	DR	4	0	0
Pvul	*Proporcellio vulcanius* Verhoeff, 1917	DR	1	2	1
Cste	*Cordioniscus stebbingi* (Patience, 1907)	DR	3	0	0
Rcos	*Reductoniscus costulatus* Kesselyák, 1930	DR	2	0	1
Ttom	*Trichorhina tomentosa* (Budde-Lund, 1893)	DR	3	0	0
Alen	*Agabiformius lentus* (Budde-Lund, 1885)	DR	2	0	0
Pdil	*Porcellio dilatatus* Brandt, 1833	DR	2	0	0
Plae	*Porcellio laevis* (Latreille 1804)	DR	1	0	1
Ccel	*Chaetophiloscia cellaria* (Dollfus, 1884)	DR	1	0	0
Pcoe	*Paraschizidium coeculum* (Silvestri, 1897)	DR	1	0	0
Subtotal percentage		DR	76	20	4
Aver	*Armadillidium versicolor* Stein, 1859	U	10	2	8
Subtotal percentage		U	50	10	40

were rare, with occurrences ranging from 1 to 50 sites out of the studied 758 cases (Fig. 2B).

Species richness was relatively homogeneous across habitat types (Fig. 3), but GLM revealed that richness is significantly higher in natural and wet habitats than in degraded and moist habitats (Table 2, cf. Fig. 3A-B). For the best fit model, residual deviance of the Poisson model was high (906.95, df = 755) compared to null deviance (929.45, df = 757), indicating a low predictive power of the results. However, naturalness and moisture control species richness, although differences are not pronounced (Fig. 3).

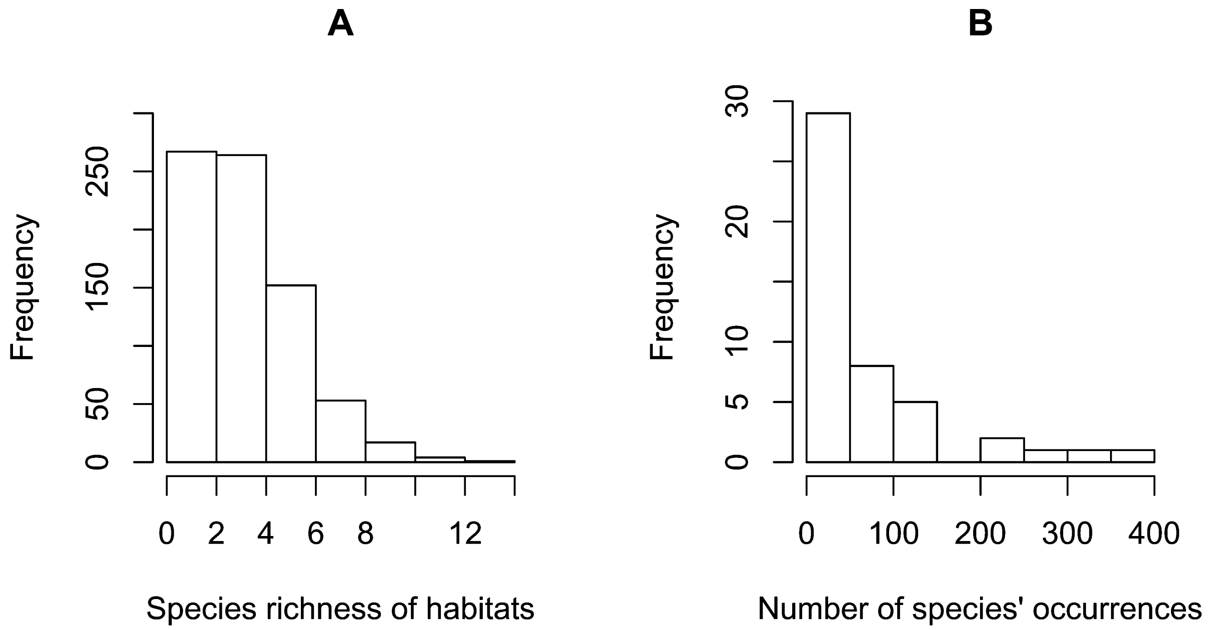

Figure 2. Distribution of species richness (A) and species occurrence (B) in the studied data set of 758 localities and 47 species in the Trans-danubian region of Hungary.

Table 2. Generalized linear modelling with species richness as response variable. To avoid over-parameterisation, only the first levels of factors are represented in the model.

Source of variation	Coefficient ± SE	p
Intercept	1.06 ± 0.05	<0.001
Naturalness: natural	0.09 ± 0.04	<0.05
Moisture: wet	0.19 ± 0.05	<0.001

Based on multivariate regression tree analysis, three groups of sites were identified (Fig. 4) with relatively distinct species composition based on PCA (Fig. 5). Cross-validated relative error rate was high (0.949), indicating low predictive power of the classification based on species composition.

The association between species occurrence within species groups and species occurrence due to habitat classification was significant (Pearson χ^2 test, $\chi^2 = 622.913$, df = 10, $p < 0.0001$, cf. subtotal percentages in Table 1).

Discussion

Our systematic faunistic survey significantly increased the species number of terrestrial isopods known from Hungary. Out of the 57 valid species 48 (84 %) were found from the western part (Transdanubian region) of the country.

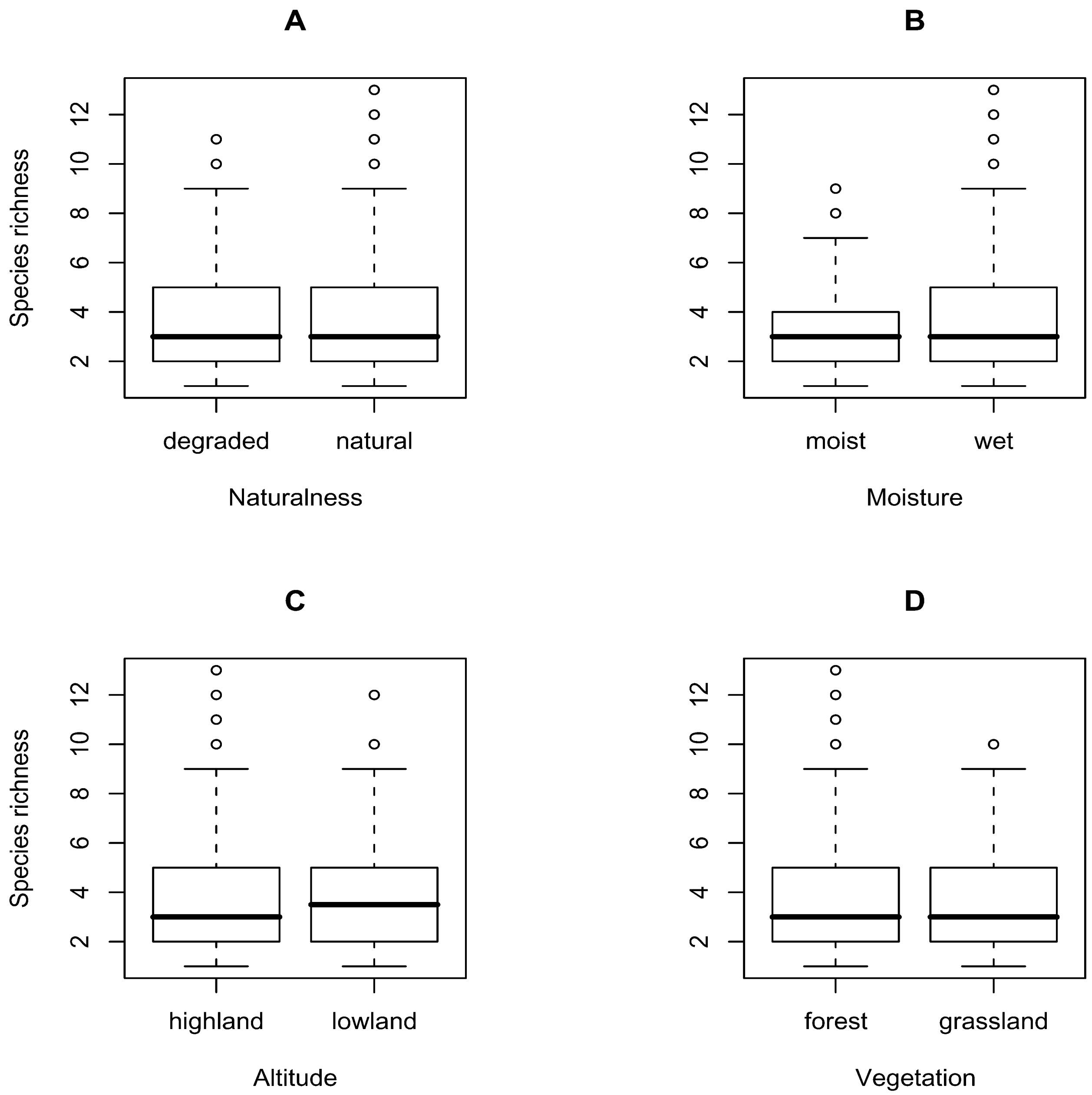

Figure 3. Species richness values within habitat classes based on naturalness (A), moisture (B), altitude (C) and vegetation (D). Boxes indicate inter-quartile range and the median, whiskers indicate minimum and maximum values, and circles stand for outliers.

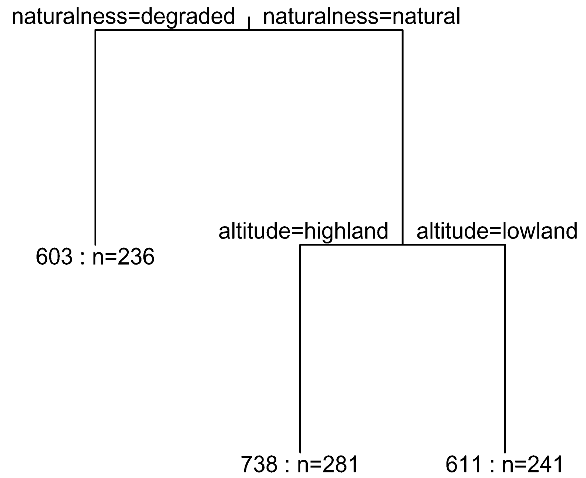

Figure 4. Cross-validated multivariate regression tree based on species/location occurrence data.

The presence of Alpine, Illyric and Balkanic species prove that the region is a diverse biogeographical crossroad for isopods. However, the known species number is lower than in the most adjacent countries. Based on the available –in the most cases not up-to-date– literature, the known species number of Slovenia is 65 (Potočnik, 1979), 60 for Austria (Schmölzer, 1974) and 50 for Slovakia (Databank of Slovak fauna). The number of local native woodlice that occur exclusively in Transdanubia (*Tachysoniscus austriacus, Trichoniscus crassipes, T. steinboecki, T. bosniensis, T. nivatus, Hyloniscus vividus, C. karawankianus, Protracheoniscus franzi, Porcellium recurvatum*) is 16 % of the total Hungarian oniscidean species. In addition, several introduced isopods (*Chaetophiloscia cellaria, Agabiformius lentus, Proporcellio vulcanius, Porcellio laevis, Porcellio dilatatus*) were also found only in the region.

Although average species richness (α-diversity) was usually low (3 species per location on average; see Fig. 3), the composition of species assemblages showed a high rate of turnover in species composition indicating high β- (between site-) diversity (cf. Fig. 5). Assemblage composition was in accordance with the degree of disturbance (disturbed, natural) and altitudinal position (highland, lowland) of habitats on the local scale. Disturbed habitats were clearly distinguished from natural ones on the basis of faunal composition, although the further division of habitats into lowland and highland sites was only found in natural, and not in degraded habitats. This reflects increasing biotic homogenisation along a natural-disturbed gradient.

The most frequent and widely distributed species were *A. vulgare* (from 169 UTM cells), *Hyloniscus riparius* (168), *Porcellium collicola* (164), *Trachelipus rathkii* (127) and *Protracheoniscus politus* (97). Out of these five, the two most frequent species were *Armadillidium vulgare* (358 locality records) and *Porcellium collicola* (312). Both show a rather balanced distribution among the different habitat categories (Tab. 1.). In comparison to the surrounding regions, the climatic conditions and the geographic features of the Carpathian basin seem to provide optimal conditions for the latter species, as it occurs in all main habitat types including natural and degraded, wet and moderately dry ones (Korsós *et al.,* 2002; Farkas, 2004; Vilisics & Farkas, 2004).

In addition to 25 native species, we found 22 introduced, "established introduced", or cosmopolitan species. Therefore, 47 % of the isopods are non-native. Species with a wide distribution that, however, seldom occur in natural habitats but show preference for moderately disturbed –mainly urban-suburban– areas (e.g., *Porcellionides pruinosus, Porcellio spinicornis)* were considered "established introduced". All species of the family Porcellionidae occurred primarily in degraded habitats, suggesting similar ecological requirements among related taxa and the human mediated distribution and migration of the genera in Hungary.

Among the species with more than 50 records, we found *Trachelipus rathkii, Hyloniscus riparius* and *Armadillidium zenckeri* to prefer natural lowland habitats. These areas are mostly riparian poplar-willow or alder forests, but several samples also came from water-meadows. *Trachelipus rathkii* and *H. riparius* were common in settlements, too (e.g. Korsós *et al.,* 2002; Giurginca, 2006; Farkas & Vilisics, 2006; Navrátil, 2007). The latter two are abundant in isopod assemblages of natural habitats of central and eastern Europe (Farkas, 1998; Tuf, 2003).

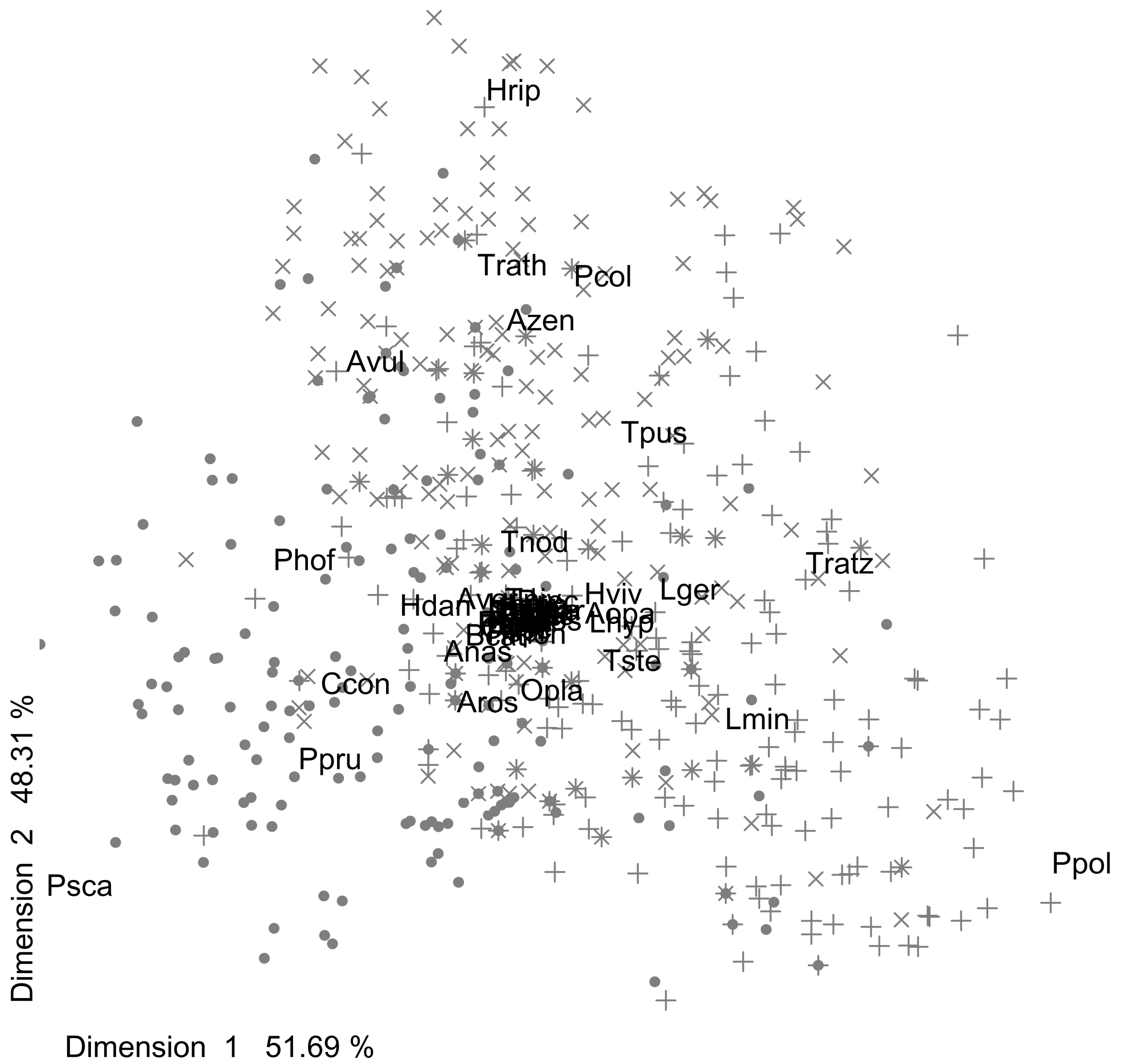

Figure 5. Principal components analysis (PCA) biplot plotted for sample groups identified by multivariate regression tree in Fig. 4, and for species (for full names of abbreviation cf. Table 1). dots: degraded habitats, +: natural highland, x: natural lowland areas.

Species common in Transdanubian natural highlands were *Protracheoniscus politus*, *Trachelipus ratzeburgii* and *Lepidoniscus minutus.* They are similarly typical in other central European deciduous forests (Tuf & Tufová, 2005; Hudáková & Mock, 2006; Mock *et al.,* 2007). Less frequent species of natural highlands, such as *Ligidium germanicum*, *Hyloniscus vividus* and *Trichoniscus steinboecki* are typical of the isopods with local distributions both in Hungary and in the rest of Europe (Gruner, 1966; Schmölzer, 1965; Strouhal, 1958).

In addition to the "big five" (most frequent species mentioned before), the typical woodlice of urban ecosystems and farmlands were *Porcellio scaber*, *Cylisticus convexus* and *Porcellionides pruinosus*. They are common in many parts of the world. *Androniscus roseus* was also found to be a typical, but less common species in Transdanubia, occurring in many types of synanthropic habitats with a range of disturbance levels (Riedel *et al.,* in press).

Our data served as a basis for a quantitative validation of the empirical species characterisation created by Hornung *et al.* (2007). We found significant association between species groups and species occurrence within main habitat classes, although this was not necessarily true for all species found in the region. There were differences between some empirical categories and species occurrence at the habitat level (see Table 1). Possible explanations for such anomalies might be: (1) low disturbance level of the habitats in question, (2) the existence of favourable microhabitats at moderately disturbed sites (*Haplophthalmus montivagus, Ligidium hypnorum, Orthometopon planum*), or (3) connectivity between natural and disturbed (fringe) areas (*Cylisticus convexus*).

Our work demonstrates that compiled data bases of literature and field data on the distribution of terrestrial isopods, along with some very basic attributes of the locations, can serve as a solid basis for further analyses for studies in biogeography, conservation biology and ecology. Species groups –reflecting species-specific affinities to degraded/natural habitats– were successfully validated based on the compiled data-base. We also addressed some questions concerning the overall pattern of species distributions and richness, and main factors influencing the local richness and composition of isopod assemblages. We found that hotspots were different for native (in remote and undisturbed subregions) and non-native species (around major settlements). The fauna of the Transdanubian region is also composed of widely distributed and localized species. Alpine and Illyric biogeographical influences were detected in the occurrences of some localized species. Local richness was primarily influenced by naturalness and moisture conditions, although these differences were not very pronounced. Species composition was primarily influenced by naturalness and altitude. Thus naturalness (disturbance gradient) plays an essential role in shaping local species assemblages.

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