Nachrichtenblatt der Ersten Vorarlberger Malakologischen Gesellschaft	7	19 - 30	Rankweil, 30. Sep. 1999

Ecological and zoogeographical comparative study of sand dunes in the Danube-Tisza Valley, Hungary, and in Belgium and the Netherlands.

von KÁROLY BÁBA, Szeged.

Abstract

Snail assemblages in a vegetation successional series on calcareous sand dunes are compared in two regions of contrasting climates. For this, statistical methods and ecological and zoogeographical species groups are used. The malacofauna at the two sites appears identical at the $p<0.001$ level. As vegetation succession proceeds from grasslands to forests, the changes in the proportions of species groups closely follow successional stages and are similar for steppe- and forest dweller, and for omnivorous and herbivorous groups. Climatic influence is reflected in the dominance of subatlantic zoogeographical elements near the sea. It is due to the humid climate that species number, abundance and the length of the successional series increases from east to west.

Zusammenfassung

Schneckenvergesellschaftungen einer Sukzessionsserie auf kalkhältigen Sanddünen in zwei verschiedenen Klimazonen werden verglichen. Diese werden mit statistischen Methoden erfaßt und die ökologischen und zoogeographischen Gruppen verglichen. Die Molluskenfauna der beiden Standorte ist auf der $p< 0,001$ Basis gleich. Bei der Entwicklung der Vegetation von der Rasensteppe zum Wald ändern sich mit den Sukzessionsstadien auch die Artengruppen und zwar in ähnlicher Weise bei Steppen- und Waldbewohnern wie auch bei omnivoren und herbivoren Artengruppen. In Meeresnähe läßt sich der Einfluß des Klimas durch das Hervortreten subatlantischer, zoogeographischer Elemente erkennen. Entsprechend dem humiden Klima steigen Artenzahl, Abundanz und die Länge der Sukzessionsketten.

Introduction

In addition to in-depth surveys of individual phenomena and processes (e.g. succession), ecological research also aims at uncovering similarities and analogous processes. An example for the latter is presented here when successional snail assemblages on calcareous sand dunes are compared in two climatically different regions. In both areas, after a grassland and subsequent scrub stages, vegetation succession terminates in a closed oak woodland climax (Convallario-Quercetum roboris [danubiale-dunense]).

Material and Methods

Samples for this comparison were collected in three countries. In the Netherlands the author visited a total of 20 localities in 6 plant community types in the Westduinepark near The Hague in 1991, 1993 and 1995. From Belgium we used the data of ANTENIUS (1956) obtained in the neighbourhood of De Panne and Onderzoek at altogether 46 sites in 4 community types in 1954 and 1955. In Hungary results from 47 localities in the Danube-Tisza Midregion (BÁBA 1985, 1986, 1997) were compared with the above 66 seashore sites.

For field sampling, squares of 25x25 cm size representing 1 m^2 were used at each locality. Data were analyzed by using statistical tests and also various species groupings. For statistiscs, the Shannon-Wiener diversity, Niclas2 cluster analysis, standardized PCA (PODANI 1988) and chi^2 test (MOORE & al. 1986) were used. For ecological comparisons, we worked with habitat types after LOZEK (1965) and FALKNER (1990), and feeding habit classes (FRÖMMING 1954, KERNEY & al. 1983, GITTENBERGER & al. 1984). The area-analytical zoogeographical classification of species is based on ANT (1963) and BÁBA (1982).

The following species groups were distinguished. Habitat types: steppe dweller (St), riparian ubiquist (RU), bush forest dweller (B), and forest dweller (HF). Feeding habit classes: omnivorous (O), herbivorous (H), and saprophagous (Sp). Zoogeographical fauna groups: with continental climatic character: 1.1 East Siberian, 1.2. West Siberian, 1.3. Euro-Siberian, 1.4. Holarctic, 2.2. Turkestanian, 3. Kaspo-Sarmatian, and 5.3. Ponto-Pannonic; with subatlantic climatic affinity: 5. Ponto-Mediterranean, 5.21. Trasian, 5.22. Illyric-Moesian, 6. Adriato-Mediterranean, 7. Atlanto-Mediterranean, and 8. Holomediterranean.

Relationships between snail assemblages in different successional stages and plant subassociations were studied with the help of chi^2 tests. This procedure is routinely used in the phytocoenological literature: ANTENIUS (1955), DOING (1985) and WESTHOFF & al. (1975) for Belgium and the Netherlands, and SOÓ (1980) and FEKETE (1992) for Hungary. Both extrazonal successional series in this study are characterized by variable humification and complex successional schemes, the latter being valid for both plants (FEKETE 1992) and snails (BÁBA 1986). Plant associations used for this comparison are given in table 1. The subassociations and facies, the number of sample sites and the name of localities are listed below.

Danube-Tisza Midregion: 1. Brometum tectorum SOÓ 1939, cynodontetosum; Juniperetum communis (secondary), N=3; 2. Festucetum vaginatae danubiale SOÓ 1929, normale, Stipetum sabulosae, Salicetosum rosmarinifoliae, N=7; 3. Junipero populetum albae (ZÓLYOMI 1950) SZODFRIDT 1969, ligustretosum, Polygonetosum latifolii, crataegetosum, populetosum Calamagrostetosum, Caricetosum liparicarpos, N=16; 4. Convallario-Quercetum roboris danubiale SOÓ (1934) 1957, betuletosum, convallarietosum, populetosum, brachypodietosum, N=15; 5. poplar plantation, N=6. (BÁBA 1997)

Seashore dunes: 6. Euphorbio-Agropyretum juncei R. TX 1952, N=12 (Belgium); 7. Euphorbio-Ammophyletum R. TX 1952, N=15 (Belgium); 8. Tortulo-Phlaetum arenarii (MASSART 1908) BR.-BL et DE LEEÜW 1936, N=6 (Belgium) secondary; 9. Hippophao-Sambucetum BEERBOOM 1960, N=1 (Holland); Belgium: 10. Hippophao-Ligustretum BEERBOOM 1960, Holland N=2, typicum, Hippophaoetum N=4, Ligustrum vulgare N=2, Parnassia palustris N=3, Listera ovata N=3, Calamagrostis epigeios N=2, Galium uliginosum N=2, Tortuletosum N=2; 11. Crataego-Betuletum BEERBOOM 1960, N=6 (Belgium & Netherlands), stationary; 12. Convallario-Quercetum roboris dunense DOING 1962, (Holland), eunymetosum N=1, hederetosum N=5, Convallarietosum N=1.

Climatically the two areas are quite unlike. The Danube-Tisza Midregion possesses a dry warm climate with 520-570 mm annual precipitation, while sand dunes in Belgium and the Netherlands receive 526-837 mm precipitation in a year. Soil pH at the studied sites were between 6.1-8.8 in Belgium and the Netherlands, and 6.9-7.8 in Hungary.

Malacofauna

Altogether 56 species were encountered in the two dune-lands. A sum of 6987 individuals belonging to 39 species were collected in Belgium and the Netherlands, while the same figures for the Danube-Tisza Midregion are 4060 and 36, respectively (Table 1). The two malacofaunas are similar at the $p<0.001$ level (chi^2 test). In both regions, the species number increases as succession approaches the climax Convallario-Quercetum community. However, the constant and dominant species in the individual successional stages differ for the two areas.

The constant-dominant species are as follows. Danube-Tisza Midregion (the serial number of plant associations are also given): 1. *Helicopsis striata*, *Cepaea vindobonensis*, 2. *Helicopsis striata*, *Cepaea vindobonensis*, *Pupilla muscorum*, *Chondrula tridens*, 3. *Truncatellina cylindrica*, *Vallonia costata*, *Vitrina pellucida*, *Granaria frumentum*, 4. *Vitrina pellucida*, *Euconulus fulvus*, *Cepaea vindobonensis*, *Vallonia costata*, 5. *Vallonia pulchella*, *Monacha cartusiana*. Seashore dunes: *Candidula intersecta*, *Pupilla muscorum*, 7. *Theba pisana*, 8. *Cernuella jonica*, 9. *Candidula intersecta*, *Trichia hispida*, 10. *Vallonia pulchella*, *Pupilla muscorum*, *Cochlicopa lubrica*, 11. *Vallonia pulchella*, *Pupilla muscorum*, 12. *Oxychilus cellarius*, *Discus rotundus*, *Helix aspersa*. The two sites share the same constant-dominant species for several successional stages.

Species group proportions

Between early and late successional stages, similar tendencies appear at the two sites in the changes of the proportions of different habitat types. Except for secondary vegetation (5, 8), the share of steppe dwellers (St) declines and that of the hygro- and sciophilous forest dwellers (HF) increases - in a complementary way - as succession approaches the forest stage. Simultaneously, bush forest dwellers (B) and riparian ubiquists (RU) also become more abundant (Figure 1). The omnivorous and herbivorous groups also behave reciprocally. In early stages herbivores are dominant. In contrast the saprophagous group (Sp) changes with herbivores (Figure 2). The high proportion of steppe dwellers and herbivores in the two secondary phytocoenoses is remarkable and has serious implications for site management by nature protection authorities.

Except in secondary habitats, species number and diversity increases in both successional series (Figure 3).

The two habitats share the same fauna groups with the exception of the 5.21 Trasian group, which only occurs in the Danube-Tisza Midregion only. However, these groups make up the malacofauna in different proportions in the two localities. This is due to the difference in the distance from dispersal centres for the 2.2. Turkestanian, 3. Ponto-Kaspian, and 5. Ponto-Pannonic groups (all three continental), and for the subatlantic 5.21. Trasian group. Among continental groups, the 1.1. East Siberian and 1.4. Holarctic elements take a dominant role in both successional series (Figure 4). Climatic differences explain that Atlanto-Mediterranean and Illyric-Moesian groups dominate under atlantic climate, while under the dry and warm continental climate Holomediterranean and Trasian elements are the most abundant. The Adriato-Mediterranean class has a subordinate role in both regions (Figure 4), where the Holomediterranean-Trasian class changes reciprocally with the Atlanto-Mediterranean - Holomediterranean class. As vegetation succession proceeds the proportion of subatlantic species increases in the Danube-Tisza Midregion, while that of the continental group becomes higher on seashore dunes (Figure 5).

Successional schemes

Using $p<0.001$ similarity values between plant associations, the course of community succession was detected by following changes in the proportions of steppe dwellers (St), hygrophilous (RU+HF) and mesophilous (B) elements, and in the Shannon-Wiener diversity values (Figure 6). Successional paths are short taking 3-5 and 6-7 stages in continental Hungary and on atlantic dunes, respectively. The increase of characteristic values is trendlike, successional schemes are complex and branching. A similar situation was found for sand and mineralogenic successional series in Hungary (BÁBA 1986, 1997). Both successional series proceed toward a climax along two lines with alternation of habitat drying and wetting. In both series, grassland stages connect to the scrub phase through the *Ligustrum vulgare* stage (Ligustretosum). Stationary phases are the Polygonetosum and Caricetum liparicarpos.

Conclusions

Calcareous sand dunes at the two localities support almost identical malacofaunas and are ecologically very similar in terms of habitat type and feeding habit classes. Zoogeographical differences are mostly due to the contrasting climate of the two regions. Increasing precipitation causes the species number and diversity to increase toward the west. Both successional series proceed toward a climax along two lines with alternating cycles of habitat drying and wetting. Successional paths are short.

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Adress of the author: Dr. Károly Bába, Vár u. 6, H-6720 Szeged, Hungary.

Tab. 1: Species list of the two dune-lands. Abbreviations: Ht=Habitat type, Fh=Feeding habit, Fc=Fauna cycles.

No	Ht	Fh	Fc		Danube-Tisza - Midregion					Sand dunes of Belgium & Netherlands						
				No	1	2	3	4	5	6	7	8	9	10	11	12
				N=	3	7	16	15	6	12	15	6	1	19	6	7
1	St	O	2.2	Cochlicopa lubricella (Rossm. 1834)	3	6	16	15	6	-	-	-	2	-	8	-
2		Sp	8	Truncatellina cylindrica (A. Fer.1807)	-	-	42	27	-	-	-	-	-	16	-	-
3		Sp	1.2	Vertigo pygmaea (Draparnaud 1801)	-	-	-	1	-	-	-	-	-	200	-	-
4		H	5.21	Granaria frumentum (Drap.1801)	14	20	143	16	6	-	-	-	-	-	-	-
5		H	1.1	Pupilla muscorum (Linné 1758)	-	-	498	99	10	4	6	1	1	952	106	-
6		O	1.4	Vallonia costata (O. F. Müller 1774)	-	15	20	-	31	-	-	1	-	118	88	3
7		Sp	1.4	Vallonia pulchella (O. F. Müller 1774)	-	5	6	12	116	-	-	1	1502	168	-	-
8		Sp	1.4	Vallonia excentrica Sterki 1893	-	-	-	-	-	-	-	-	1	136	-	1
9		Sp	8	Chondrula tridens (O. F. Müller 1774)	5	3	938	250	-	-	-	-	-	-	-	-
10		H	7	Candidula unifasciata (Poiret 1801)	-	-	-	-	-	1	-	-	-	-	-	-
11		H	7	Candidula intersecta (Poiret 1801)	-	-	-	-	-	18	23	1	9	111	6	2
12		H	7	Candidula gigaxii (L. Pfeiffer 1850)	-	-	-	-	-	-	-	-	-	-	2	-
13		H	7	Cernuella jonica (Mousson 1854)	-	-	-	-	-	-	-	16	-	-	-	-
14		H	5.3	Xerolenta obvia (Menke 1828)	-	1	3	-	48	-	-	-	-	-	-	-
15		Sp	5.3	Helicopsis striata (O. F. Müller 1774)	26	73	13	-	1	-	-	-	-	-	-	-
16		H	8	Cochlicella acuta (O. F. Müller 1774)	-	-	-	-	-	-	-	2	-	-	-	-
17		H	8	Mon. cartusiana (O. F. Müller 1774)	-	-	1	-	194	-	-	-	1	-	-	1
18		H	8	Monacha cantiana (Montagu 1803)	-	-	-	-	-	-	-	-	-	2	-	-
19		H	8	Theba pisana (O. F. Müller 1774)	-	-	-	-	-	-	487	-	-	25	-	-
20	RU	O	1.2	Succinea oblonga (Draparnaud 1801)	-	-	-	-	12	-	-	2	-	81	39	-
21		H	1.1	Columella edentula (Drap. 1801)	-	-	-	32	-	-	-	-	-	-	-	-
22		Sp	3	Vertigo angustior Jeffreys 1830	-	-	-	8	-	-	-	-	-	804	70	-
23		Sp	1.4	Vertigo antivertigo (Drap. 1801)	-	-	-	-	-	-	-	-	-	11	70	-
24		O	1.4	Zonitoides nitidus (O. F. Müller 1774)	-	-	1	-	-	-	-	-	-	476	10	-
25		O	1.3	Der. reticulatum (O. F. Müller 1774)	-	-	-	1	-	-	-	-	-	-	-	3
26		O	1.3	Deroceras agreste (Linné 1758)	-	-	-	10	23	-	-	-	-	-	-	-
27		H	1.1	Perf. rubiginosa (Rossmässler 1838)	-	-	-	1	-	-	-	-	-	-	1	1
28	B	O	1.4	Cochl. lubrica (O. F. Müller 1774)	-	-	1	12	-	-	-	-	-	445	49	3
29		Sp	1.1	Punctum pygmaeum (Drap. 1801)	-	-	16	36	-	-	-	-	-	49	-	-
30		O	7	Arion ater (Linné 1758)	-	-	-	-	-	-	-	-	-	-	-	8
31		O	1.4	Vitrina pellucida (O. F. Müller 1774)	-	30	17	3	4	-	-	-	1	172	17	5
32		O	5.21	Aegopinella minor (Stabile 1864)	-	-	-	36	-	-	-	-	-	-	-	-
33		O	1.1	Nesovitrea hammonis (Ström 1765)	-	-	-	20	-	-	-	-	-	-	-	-
34		H	7	Tandonia sowerbyi (A. Fer. 1823)	-	-	-	-	-	-	-	-	-	-	-	4
35		O	1.4	Euconulus fulvus (O. F. Müller 1774)	-	-	25	45	32	-	-	-	-	115	6	-
36		H	5.22	Trichia hispida (Linné 1758)	-	-	-	1	-	-	-	-	3	174	57	32
37		H	3	Euomphalia strigella (Drap. 1801)	-	-	-	6	-	-	-	-	-	-	-	-
38		H	3	Cepaea vindobonensis (A. Fer. 1821)	23	22	71	15	22	-	-	-	-	-	-	-
39		H	7	Cepaea nemoralis (Linné 1758)	-	-	-	-	-	-	1	-	1	44	4	-
40		H	7	Helix aspersa O. F. Müller 1774	-	-	-	-	-	-	-	-	-	-	-	52
41		H	5.3	Helix pomatia Linné 1758	4	-	-	16	2	-	-	-	-	-	-	5
42	Hf	Sp	8	Vertigo pusilla O. F. Müller 1774	-	-	-	16	-	-	-	-	-	-	-	-
43		Sp	1.4	Acanth. aculeata (O. F. Müller 1774)	-	-	8	1	-	-	-	-	-	-	-	-
44		H	8	Ena obscura (O. F. Müller 1774)	-	-	-	1	-	-	-	-	-	-	-	-
45		Sp	6	Discus rotundatus (O. F. Müller 1774)	-	-	-	-	-	-	-	-	-	-	1	47
46		O	1.1	Arion subfuscus (Draparnaud 1805)	-	-	-	5	-	-	-	-	-	-	-	-
47		H	7	Arion intermedius Normand 1852	-	-	-	-	-	-	-	-	-	-	-	3
48		O	7	Arion circumscriptus Johnston 1828	-	-	-	1	-	-	-	-	-	-	-	-
49		Sp	6	Vitrea crystallina (O. F. Müller 1774)	-	-	-	1	-	-	-	-	-	-	-	-
50		H	7	Aegopinella nitidula (Drap. 1805)	-	-	-	-	-	-	-	-	-	-	1	26
51		O	7	Oxychilus allarius (Miller 1822)	-	-	-	-	-	-	-	-	2	4	-	9
52		O	7	Oxych. cellarius (O. F. Müller 1774)	-	-	-	-	-	-	-	-	1	4	-	42
53		O	6	Limax cinereoniger Wolf 1803	-	-	-	-	-	-	-	-	-	-	-	2
54		O	1.1	Bradyb. fruticum (O. F. Müller 1774)	-	-	-	8	-	-	-	-	-	-	-	1

55		H	5,22	Perf. incarnata (O. F. Müller 1774)	-	-	-	1	-	-	-	-	-	-	-	-
56		H	7	Cepaea hortensis (O. F. Müller 1774)	-	-	-	-	-	-	-	-	-	-	-	5
				Σ Number of individuals	75	175	181	696	507	23	517	24	23	544	704	255
				Number of species	6	9	17	30	14	3	4	7	11	21	18	21
				H' diversity (Shannon-Wiener)	2.18	2.46	2.09	3.48	2.73	0.91	0.37	1.75	2.9	3.25	3.25	3.35

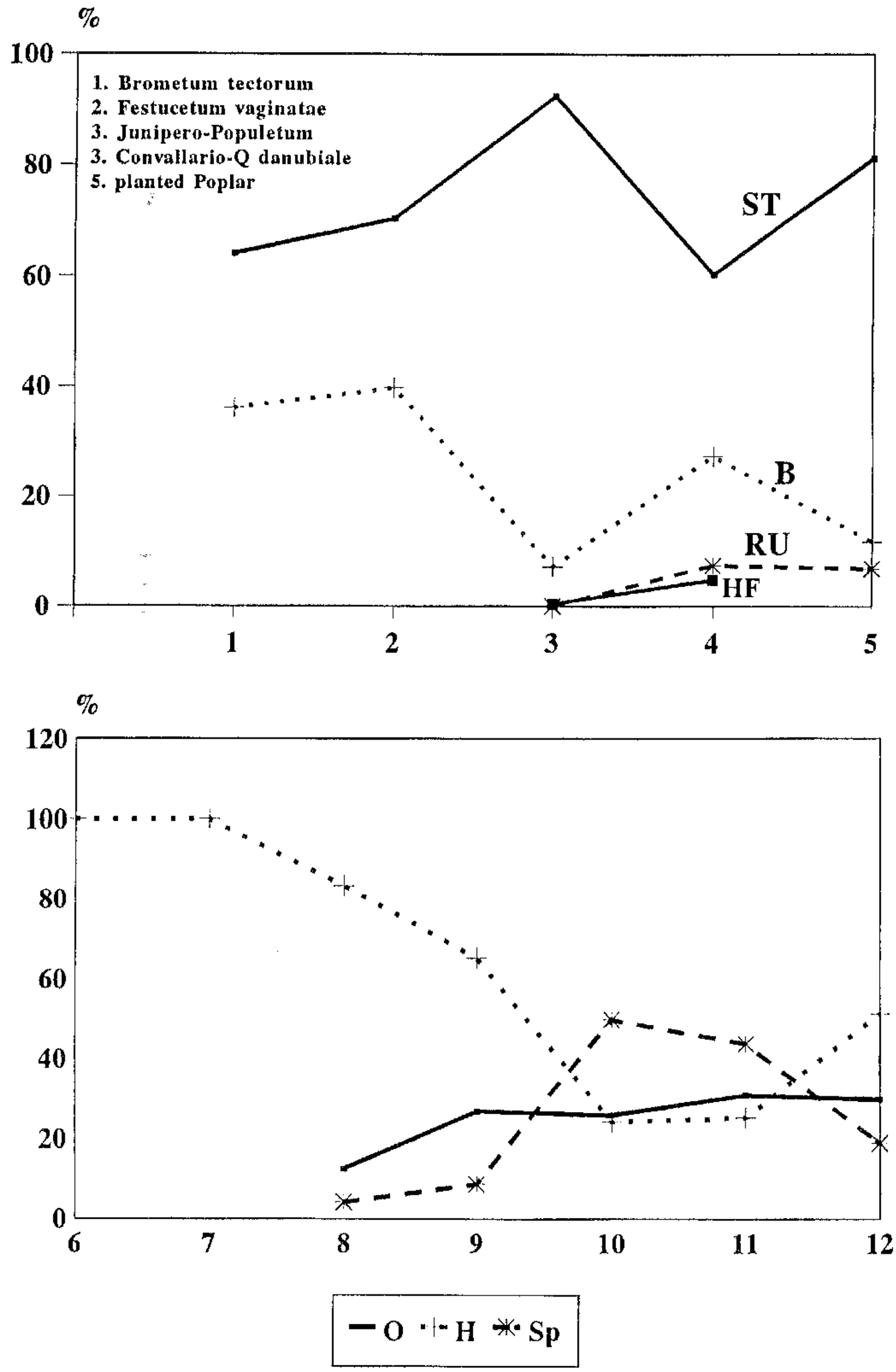

Figure 1 a/b: Changes in habitat types at the two sites. (explanation of abbrevations: see text)

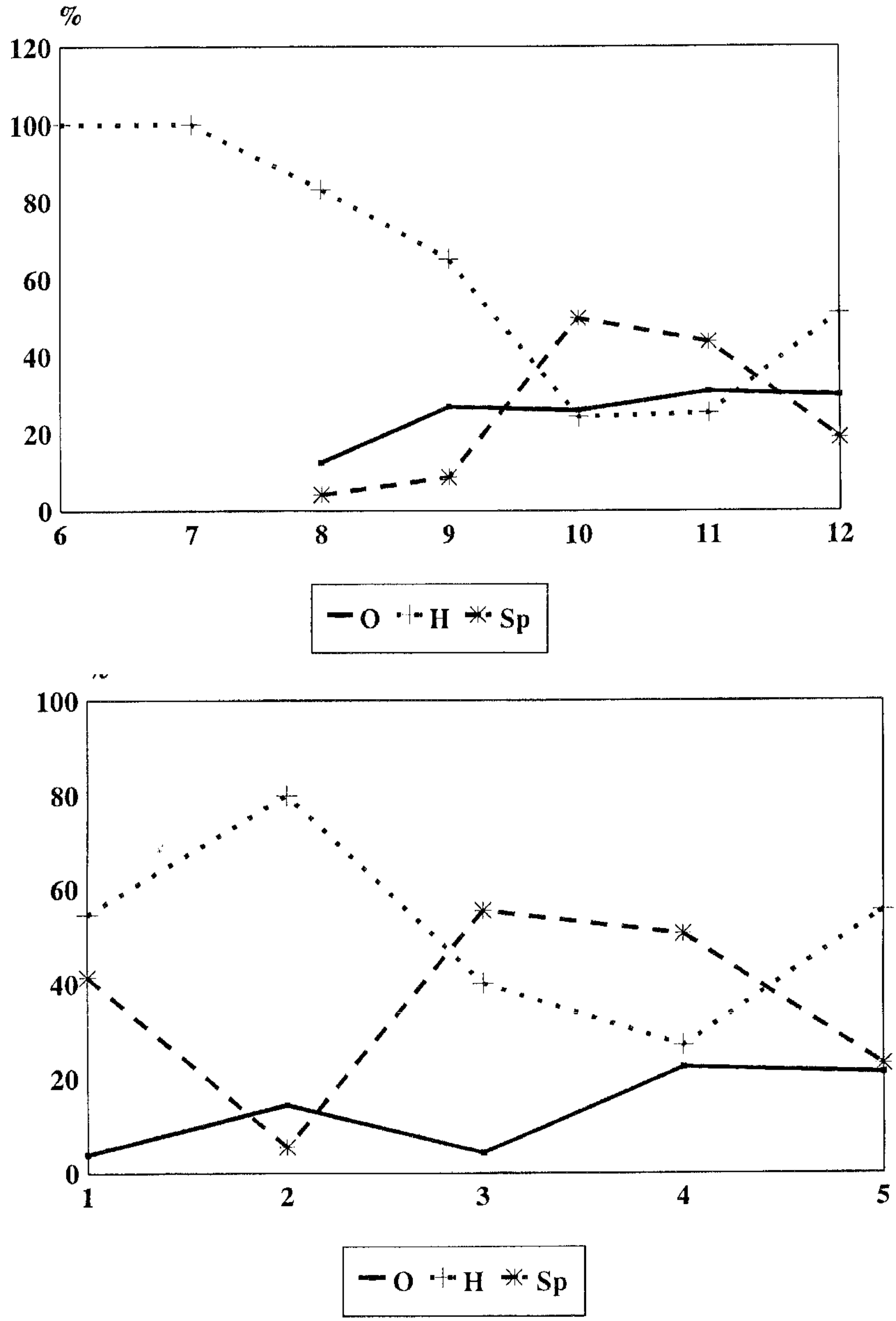

Figure 2: Changes in feeding habit classes in the two dune-lands. (explanation of abbrevations: see text)

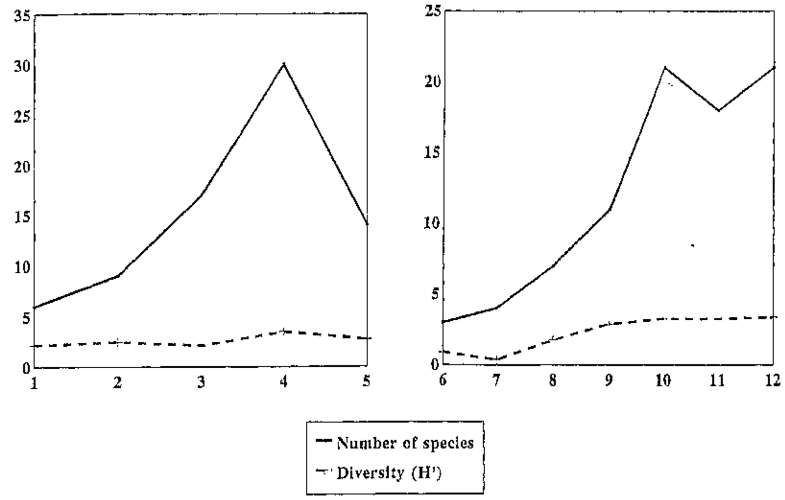

Figure 3: Species number and diversity (H') in the two dune-lands.

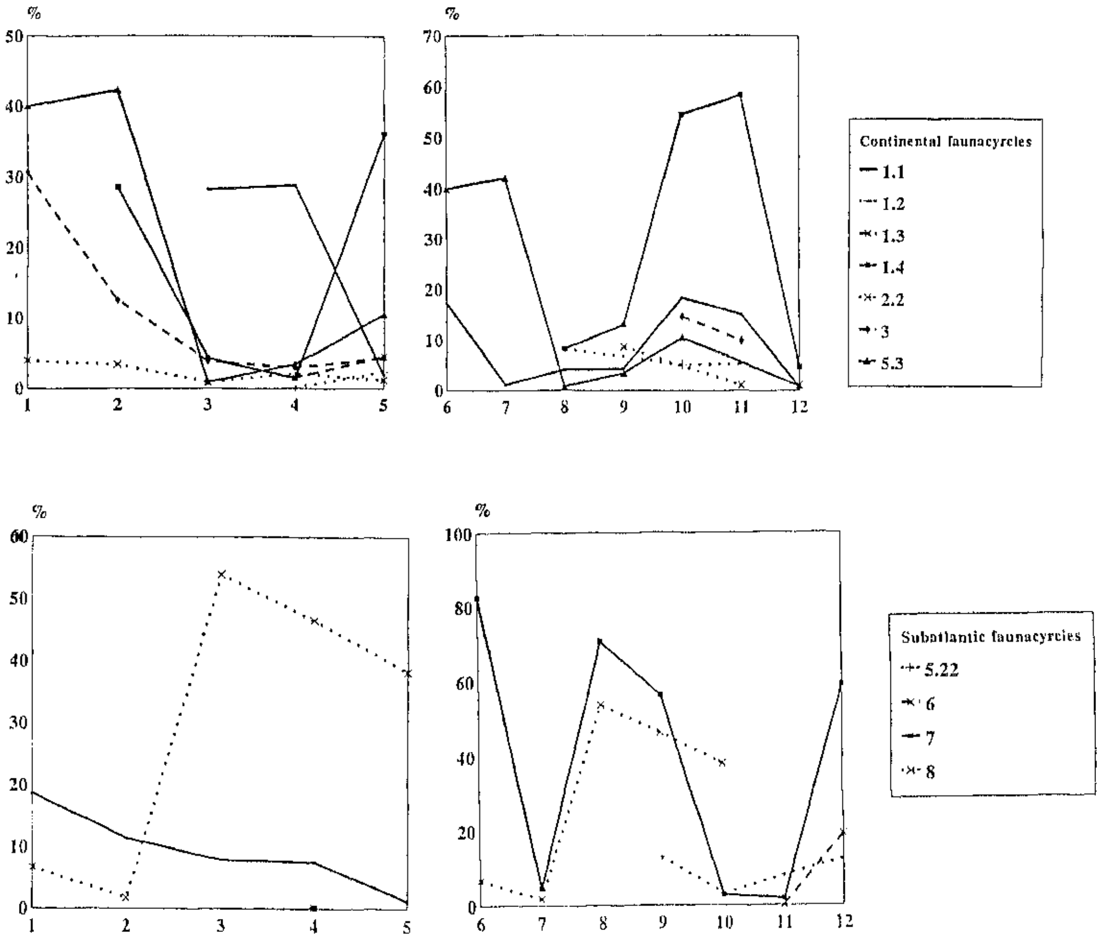

Figure 4: a/b. Proportions of different fauna cycles in the two regions.

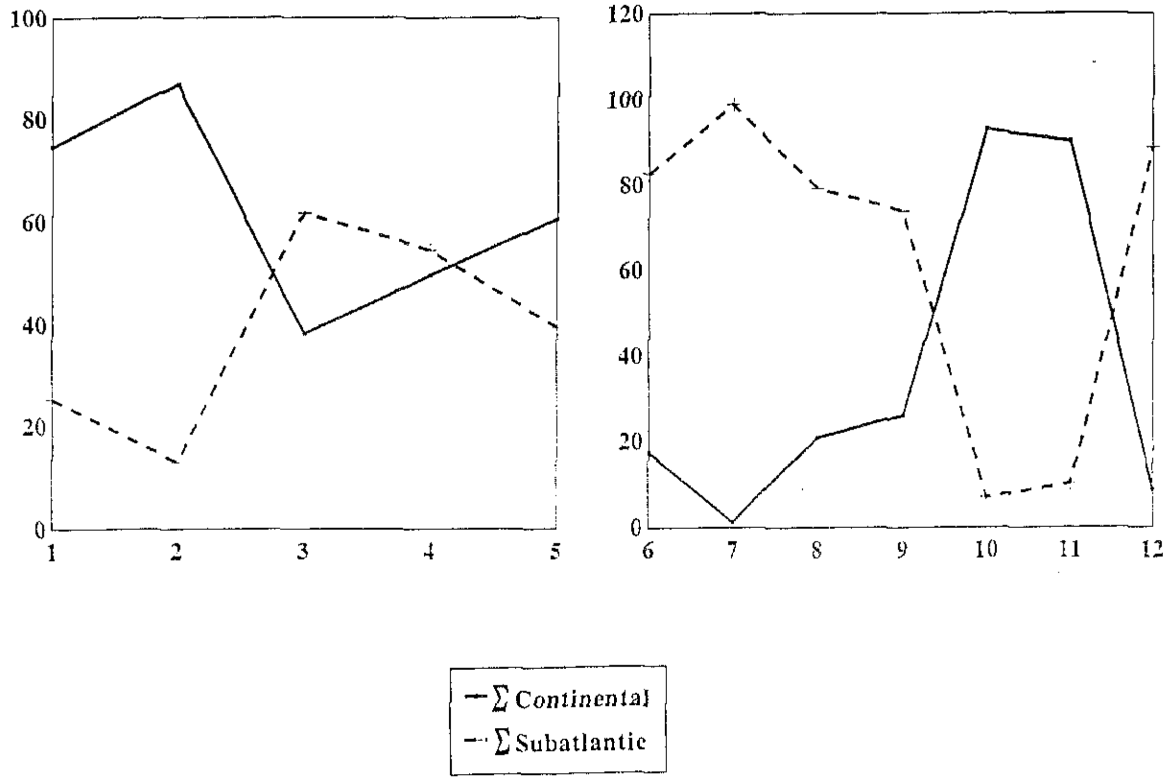

Figure 5: Reciprocal changes in the proportions of continental and subatlantic fauna circle groups during the course of succession.

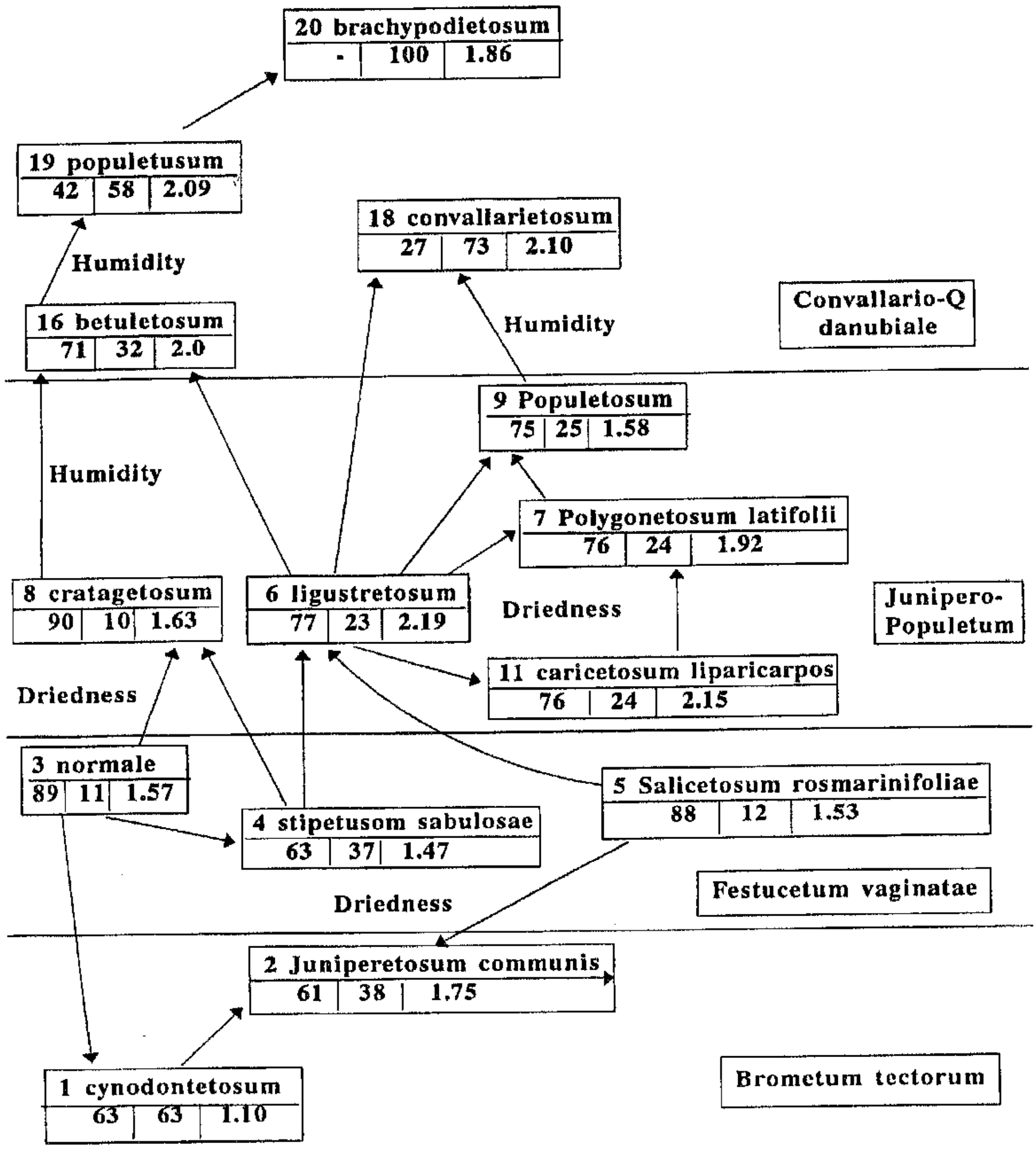

Figure 6/a: Successional scheme for the Danube-Tisza Midregion (based on chi^2 tests at the $p<0.001$ significance level). Changes in the proportions of steppe dwellers (St), hygrophilous RU+HF and mesophilous B species groups indicate habitat drying or wetting. Diversity values are given at the end.

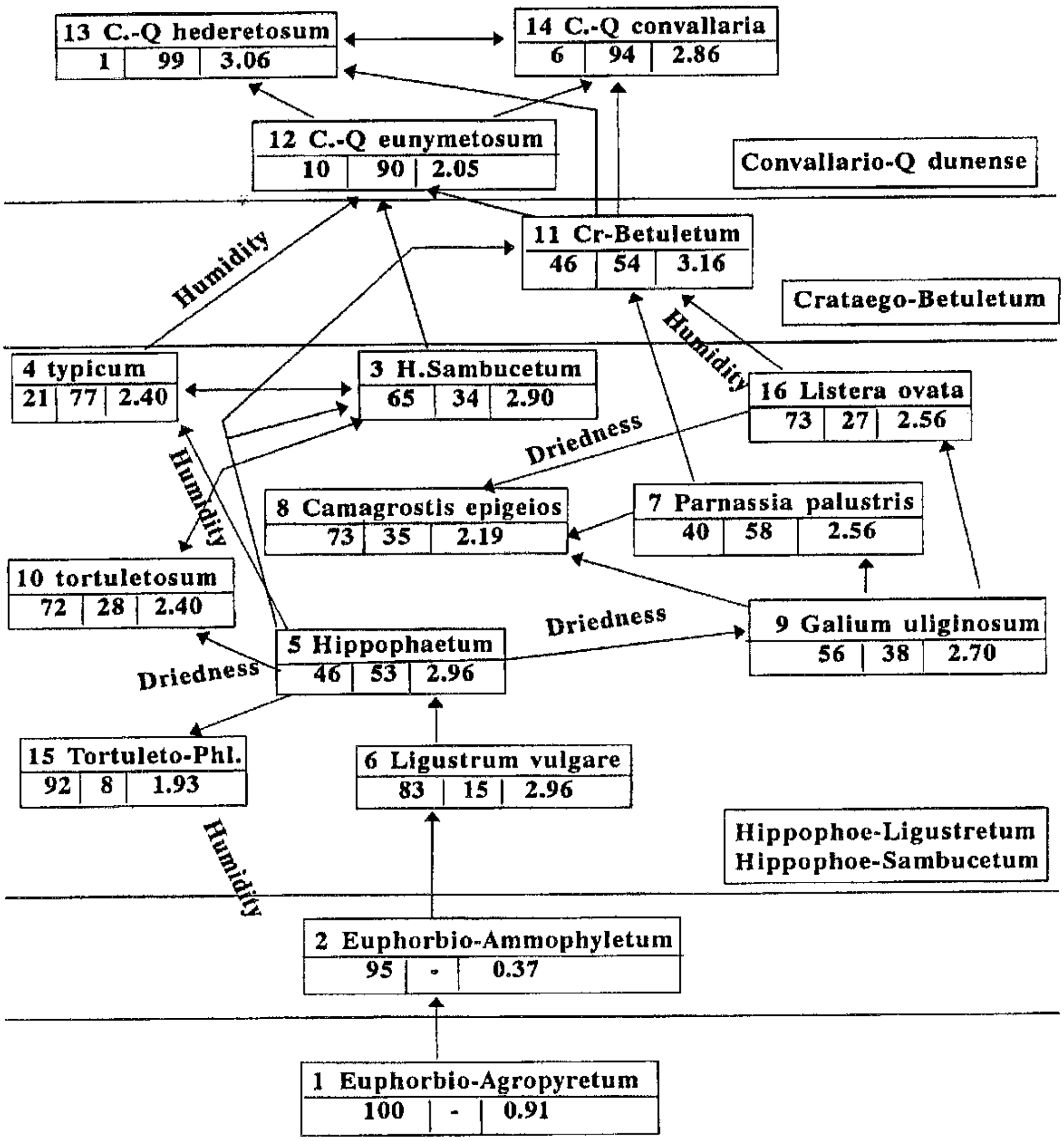

Figure 6/b: Successional scheme for sand dunes in Belgium and Holland (based on chi^2 tests at the $p<0.001$ significance level). Changes in the proportions of steppe dwellers (St), hygrophilous RU+HF and mesophilous B species groups indicate habitat drying or wetting. Diversity values are given at the end.