Diversity characteristics of sediment diatom assemblages from lentic freshwaters (Flanders, Belgium): geographic differences and historical changes

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Introduction

Diatoms (Bacillariophyceae) are a speciose group of unicellular algae, occuring in all our fresh waters. Their assemblage composition is closely related to environmental conditions and community diversity has often been related to pollution or other types of stress. In order to asses environmental changes, historical reference data can be obtained from old limnological samples, exsiccata of aquatic macrophytes, sediments, etc.
Here, diversity characteristics of sediment assemblages, as observed in a recent survey of standing waters throughout Flanders, are compared to those of similar assemblages from the period 1852-1943 in a first attempt to address three issues: 1. did increased human impact affect α (inventory) diversity, 2. has ß (differentiation) diversity changed, and 3. are there indications that the differentiation between the major geographic regions of Flanders, as reflected by their diatom communities, may have altered.

Results A: Which region has most taxa and what happened to α diversity?

Species accumulation curves (Fig. 2) and estimates of the number of taxa (Table 1) indicate that taxonomic richness increased in the course of the 20th C, both for Flanders as a whole (ca. 14-22 %), and for most subregions separately. The Campine region has the richest diatom flora, now including some 26 to 40 % more taxa than before. The increase in species richness may amount to 8-26 % for Sandy Flanders, 15-46 % in the Maritime region (dunes & polders) and 6-40 % in the Loam region. Poor representativity and low accuracy due to the limited number of samples may account for the apparent loss of taxa in the Meuse region.
Overall, assemblages are now more diverse than before; dominance decreased (Fig. 3). In the Campine region, local diversity is somewhat lower on average than elsewhere.

Fig. 2. Species accumulation curves.

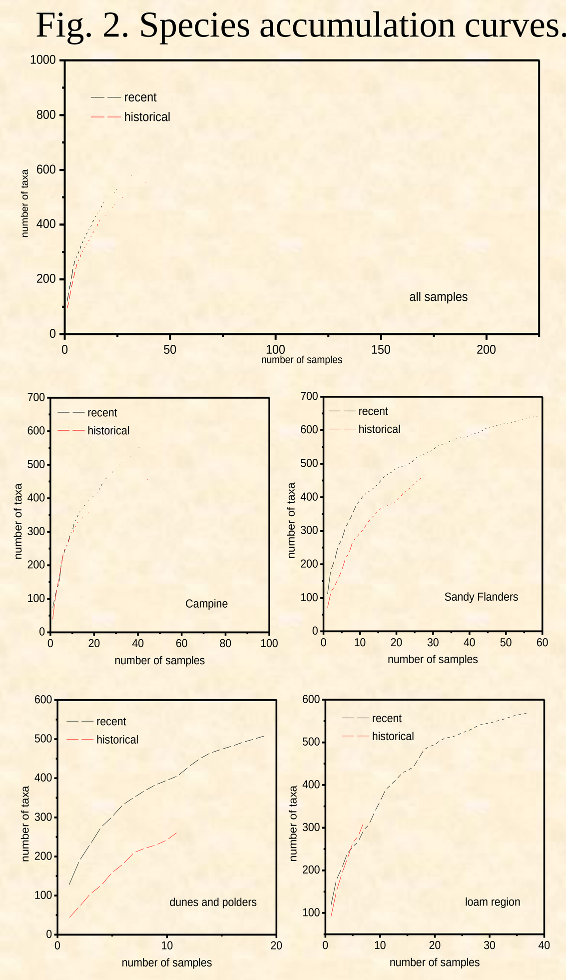
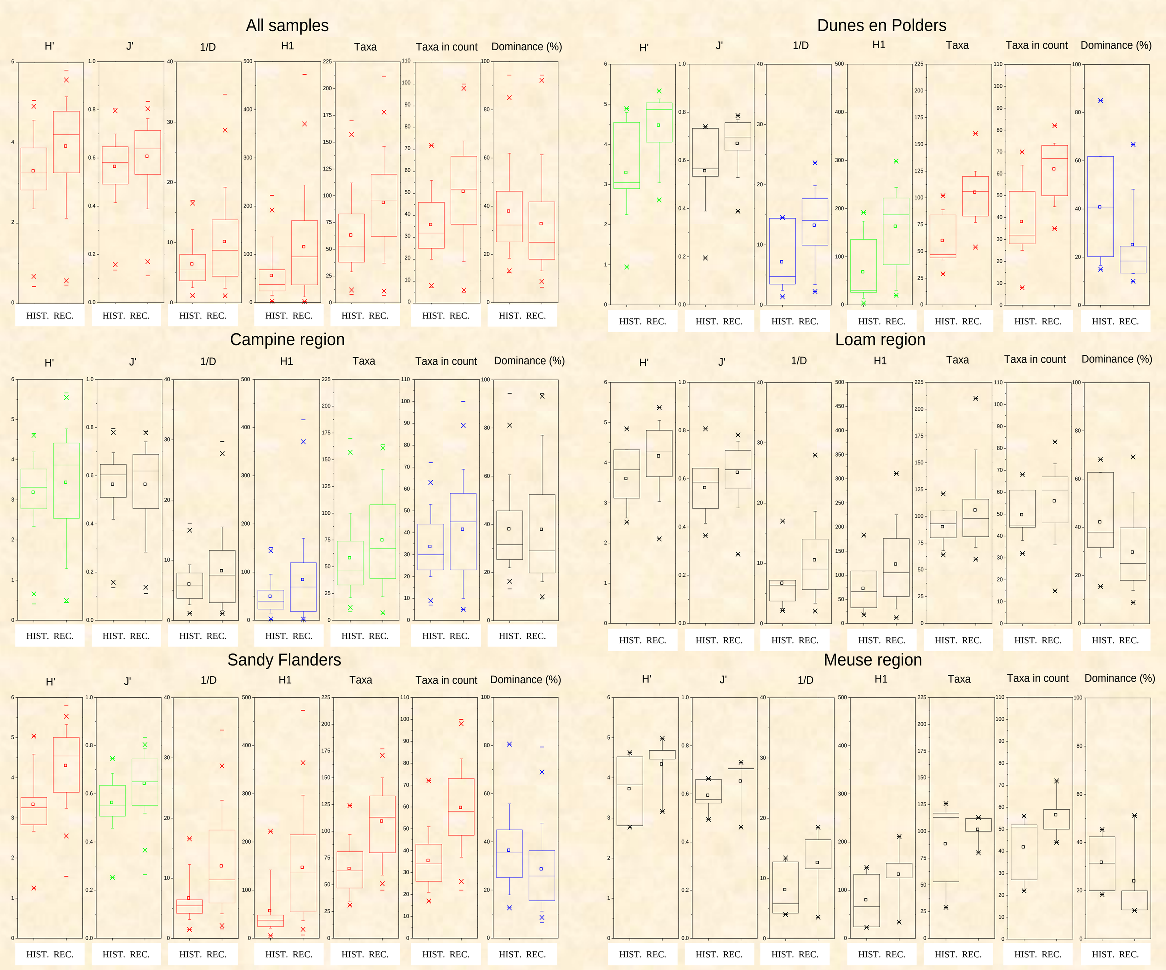


Table 1. Number of taxa.

	Historical samples	Recent samples
Observed taxonomic richness		
All samples	762	**944**
Campine region	515	**695**
Sandy Flanders	468	**615**
Dunes & polders	263	**437**
Loam region	312	**513**
Meuse region	**281**	202
Estimated taxonomic richness first-order jackknife (± SD)		
All samples	960.3 ± 24.8	**1149.0** ± 19.4
Campine region	650 ± 26.7	**850.4** ± 21.8
Sandy Flanders	624.2 ± 31.2	**774.2** ± 23.6
Dunes & polders	386.6 ± 33.9	**563.6** ± 18.2
Loam region	458.6 ± 41.0	**641.3** ± 21.1
Meuse region	**426.6** ± 52.2	274.8 ± 8.6
Estimated taxonomic richness second-order jackknife		
All samples	1066.3	**1270.3**
Campine region	709.3	**943.1**
Sandy Flanders	704.9	**864.2**
Dunes & polders	467.7	**617.4**
Loam region	545.6	**708.2**
Meuse region	**509.7**	309.6
Estimated taxonomic richness Chao 2 (± SD)		
All samples	975.9 ± 40.5	**1195.1** ± 47.4
Campine region	634.8 ± 26.9	**889.1** ± 42.2
Sandy Flanders	634.1 ± 34.9	**801.1** ± 39.5
Dunes & polders	481.6 ± 54.4	**551.4** ± 26.1
Loam region	554.3 ± 52.2	**650.2** ± 32.0
Meuse region	**560.2** ± 59.0	312.9 ± 31.3
Estimated taxonomic richness Michaelis Menten Means		
All samples	809	**923.0**
Campine region	569.9	**720.4**
Sandy Flanders	591.8	**635.9**
Dunes & polders	381.0	**532.4**
Loam region	518.2	**550.8**
Meuse region	**710.9**	296.5
Incidence-based coverage estimator (ICE)		
All samples	942.9	**1144.5**
Campine region	637.3	**818.1**
Sandy Flanders	622.8	**777.1**
Dunes & polders	488.9	**568.8**
Loam region	582.4	**626.3**
Meuse region	**611.2**	322.6

Fig. 3. Diversity measures (color indicates significant differences between periods: red $p < 0.001$, green $p < 0.01$, blue $p < 0.05$).



Results B: What about ß diversity?

Table 2. Compositional turnover estimated by DCA and average distances.

	Historical samples	Recent samples
Compositional turn-over (standard deviation units)		
All samples	**8.67**	7.78
Campine region	5.53	**7.96**
Sandy Flanders	**8.36**	6.73
Dunes & polders	**4.64**	4.31
Loam region	**6.46**	4.87
Meuse region	**6.85**	3.50
Average within-group Euclidean distance (x10^{-3})		
All samples	**29.3**	26.4
Campine region	29.7	**29.9**
Sandy Flanders	**28.1**	23.3
Dunes & polders	**30.1**	21.6
Loam region	**32.0**	24.7
Meuse region	**25.9**	22.1
Average within-group Sørensen distance (abundance based)		
All samples	**0.85**	0.84
Campine region	0.85	**0.87**
Sandy Flanders	**0.85**	0.81
Dunes & polders	**0.82**	0.81
Loam region	**0.88**	0.84
Meuse region	**0.86**	0.79
Average within-group Sørensen distance (incidence based)		
All samples	**0.72**	0.65
Campine region	0.72	**0.74**
Sandy Flanders	**0.76**	0.58
Dunes & polders	**0.65**	0.58
Loam region	**0.65**	0.56
Meuse region	**0.76**	0.47

In general, compositional turnover and the average distance between assemblages decreased slightly (Table 2). This also holds at the level of subregions, with exception of the Campine where assemblages nowadays show a wider range of variation. This suggests that habitat heterogeneity represented by the recent dataset is somewhat lower than for the historical samples in most parts of Flanders, but that freshwater conditions became more varied in the Campine region.

Material and methods

This study comprises 213 sediment samples from selected permanent and fresh standing waters collected from 1998 to 2000, and 118 historical sediment samples from this habitat collected between 1852 and 1943 (Fig. 1). Most of the latter were obtained from herbarium macrophytes. All samples were cleaned with concentrated hydrogen peroxyde and permanent slides were prepared using Naphrax®. Exactly 500 valves were counted along random transects, followed by a detailed inventory of the remaining taxa. To allow for optimal comparison with the historical data, some taxa discerned only in the recent samples were lumped to their previous entities. Marine littoral taxa were excluded from all analyses.

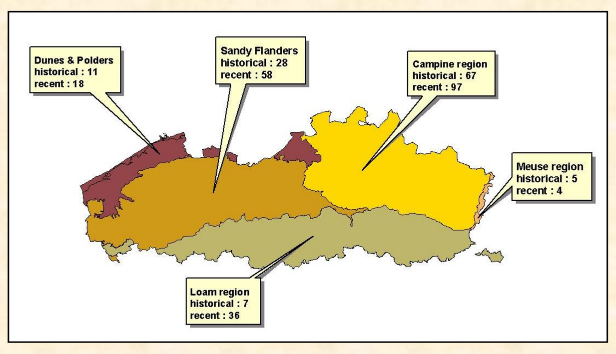


Fig. 1. Delimitation of the five subregions considered in the analyses and number of historical and recent samples in each one of them.

Taxonomic richness measures include the observed number of taxa and incidence-based estimators: first and second-order jackknife, Chao 2, Michaelis Menten Means and Incidence-based coverage (ICE), calculated using EstimateS 6.0b1. In addition to the total number of taxa in the sample, the number of taxa in the count, and the percentage dominance of the most abundant taxon, the folowing *diversity indices* were calculated (Biodiversity Professional Beta, 1997): H' (Shannon-Weaver, log 2 base), J' (evenness), 1/D (reciprocal of Simpson's dominance) and H1 (Hill 1). *Compositional turnover* was estimated as the gradient length of the first axis in Detrended Correspondence Analysis (DCA; CANOCO 4.0). *Average within-group distances*, using Euclidean and Sørensen measures, were also used to asses within-group variation and calculated in Multiple Response Permutation Procedure (MRPP) analyses (PC-Ord 3.2). MRPP was also used to test for significant differences in assemblage composition between regions. From Indicator Species Analysis (PC-Ord 3.2), the proportional within-region abundance relative to the abundance in all samples was used as a measure of *specificity*, while the proportional frequency of a taxon in a group scores *fidelity* (constancy). Both are combined in a general *Indicator Value*, IndVal.
Significance of differences between means was tested by Mann-Whithney *U* tests (Statistica 5.1).

Results C: Do diatoms suggest biogeographic differences and did any changes occur?

MRPP tests on abundance or incidence data of historical and recent samples with subregion as the grouping variable, and applying Euclidean or Sørensen distances, indicate that species composition effectively differs between (some of) the regions.
Pairwise comparisons (Table 3) discriminate the Campine region, and - not surprisingly - dunes and polder area particularly well from the other subregions, but suggest that differences between Sandy Flanders and the Loam region remain limited.
These differences are visualized by DCA ordinations (Fig. 4) of the samples where the subregions are delimited by polygons. The Campine and maritime subregions show the least overlap with the other regions when incidence data are considered, implying that they have more unique, characteristic, taxa. In the analyses of abundance data, the increased degree of overlap between samples from Loam, Meuse, dunes and polders is most notable. In both comparisons, a larger proportion of samples from the Campine region shows a unique species composition in the recent than in the historical dataset.

Table 3. Results of pairwise MRPP; historical data in upper part of matrix, recent data in lower part.

ABUNDANCE-BASED; EUCLIDEAN DISTANCE * p < 0.05, ** p < 0.01; *** p<0.001	Campine region	Sandy Flanders	Dunes & polders	Loam region	Meuse region
Campine region	-	***	***	n.s.	n.s.
Sandy Flanders	***	-	*	n.s.	n.s.
Dunes & polders	***	***	-	n.s.	n.s.
Loam region	***	n.s.	***	-	n.s.
Meuse region	n.s.	n.s.	n.s.	n.s.	-

ABUNDANCE-BASED; SØRENSEN DISTANCE * p < 0.05, ** p < 0.01; *** p<0.001	Campine region	Sandy Flanders	Dunes & polders	Loam region	Meuse region
Campine region	-	***	***	***	n.s.
Sandy Flanders	***	-	*	n.s.	n.s.
Dunes & polders	***	***	-	*	**
Loam region	***	n.s.	***	-	n.s.
Meuse region	*	n.s.	*	n.s.	-

INCIDENCE-BASED; SØRENSEN DISTANCE * p < 0.05, ** p < 0.01; *** p<0.001	Campine region	Sandy Flanders	Dunes & polders	Loam region	Meuse region
Campine region	-	***	***	***	n.s.
Sandy Flanders	***	-	***	*	n.s.
Dunes & polders	***	***	-	***	***
Loam region	***	*	***	-	*
Meuse region	***	***	***	*	-

Fig. 4. DCA ordinations of historical and recent samples along the two principal axes with abundance and incidence data, respectively, and indication of the subregions.

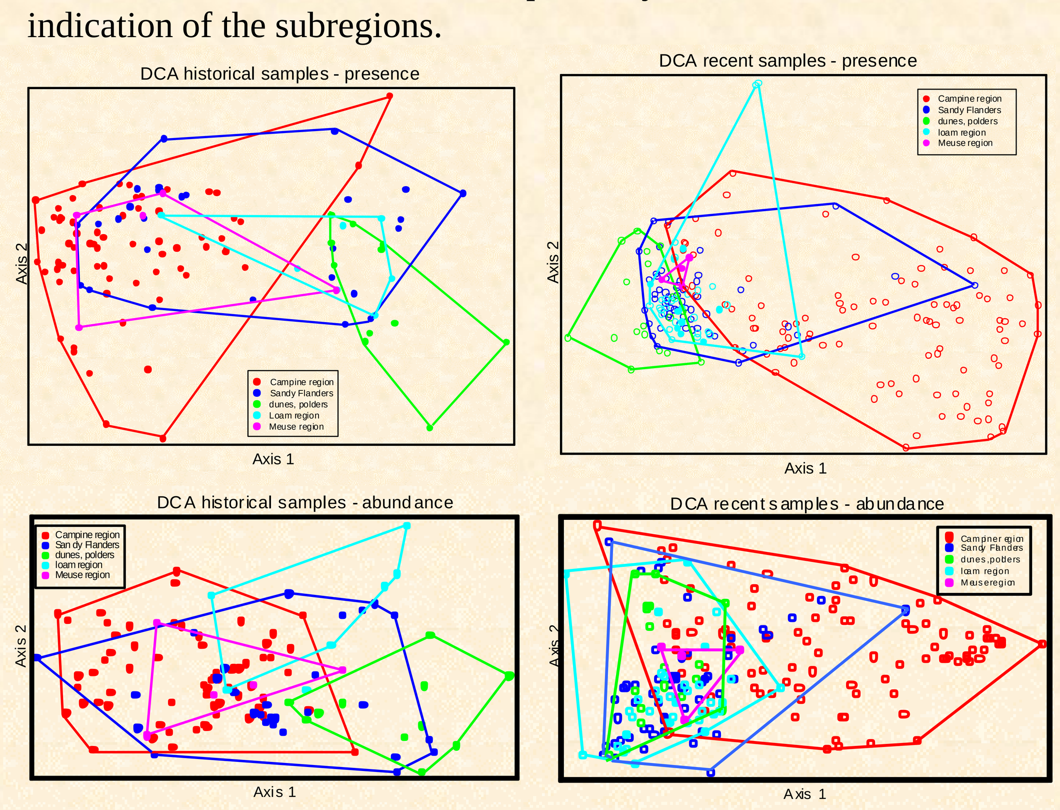


Fig. 5. Relative partitioning of specificity, fidelity and Indval scores over the subregions for historical and recent samples.

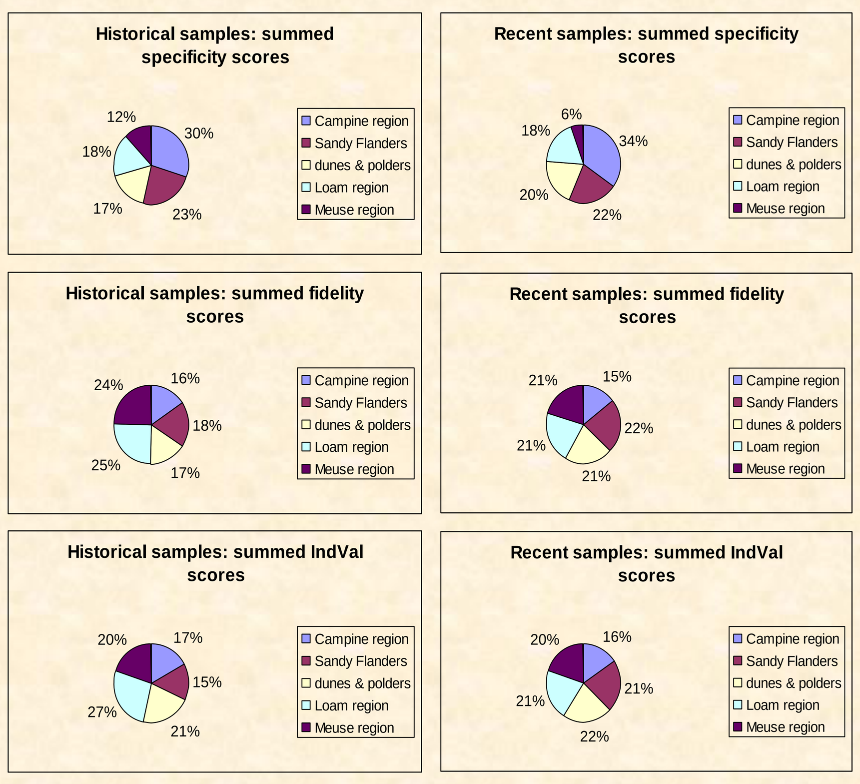
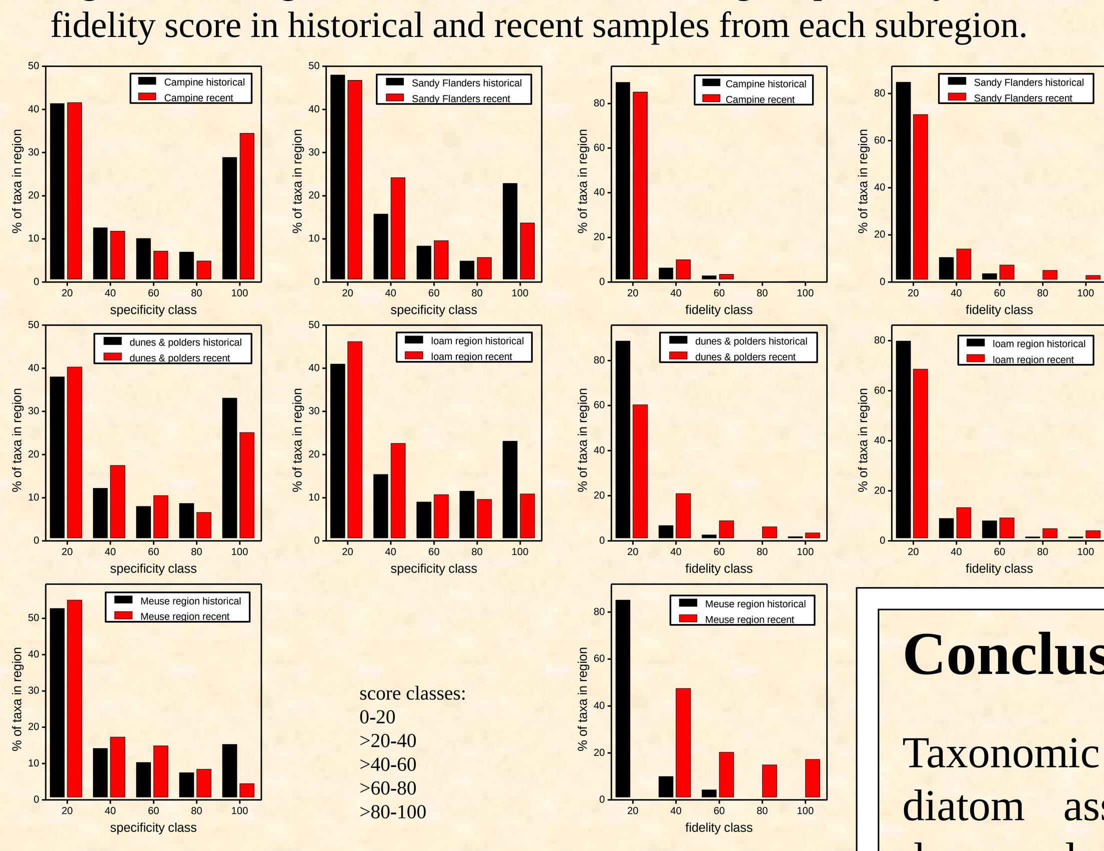


Table 4. Comparison of average specificity, fidelity and IndVal scores per taxon for the subregions.

* p < 0.05, ** p < 0.01, *** p < 0.001		Campine region	Sandy Flanders	Dunes & polders	Loam region	Meuse region
Average specificity score	**historical**	30.2 ± 38.4	23.3 ± 34.2	17.0 ± 32.7	17.5 ± 31.3	**11.9 ± 25.4**
	recent	**34.6 ± 40.6**	21.8 ± 29.8	**19.8 ± 32.7**	**18.1 ± 27.6**	5.6 ± 15.9
	p, trend	** ↑	n.s.	*** ↑	*** ↑	*** ↓
Average fidelity score	**historical**	7.4 ± 13.1	8.5 ± 12.6	7.7 ± 16.1	11.7 ± 19.5	**11.4 ± 18.1**
	recent	**7.8 ± 12.4**	11.5 ± 19.4	**11.1 ± 19.6**	11.2 ± 19.6	10.8 ± 24.6
	p, trend	* ↑	n.s.	*** ↑	n.s.	*** ↓
Average Indval	**historical**	3.1 ± 6.9	2.6 ± 4.7	3.8 ± 10.3	4.9 ± 10.2	**3.6 ± 8.0**
	recent	3.5 ± 8.1	3.0 ± 5.4	**4.2 ± 9.2**	3.3 ± 6.6	2.9 ± 9.0
	p, trend	n.s.	n.s.	** ↑	n.s.	*** ↓

Fig. 6. Percentage distribution of taxa according to specificity and fidelity score in historical and recent samples from each subregion.



Partitioning of specificity, fidelity and IndVal among subregions has remained fairly stable (Fig. 5). Specificity is now slightly higher for the Campine, but lower for the Meuse samples. Fidelity increased for Sandy Flanders, dunes and polders and Loam region, but only Sandy Flanders improves its position with respect to IndVal. The average specificity of a taxon increased, particularly in the Campine; fidelity is now higher in the Maritime region (Table 4). Whereas the most specific taxa have lost ground in the other regions, a relative increase of this group is observed in the Campine (Fig. 6). Taxa present in a larger proportion of the sites within a particular region are nowadays more numerous in the other parts of Flanders.

Conclusions

Taxonomic richness and local diversity of limnic sediment diatom assemblages increased, but habitat heterogeneity decreased, except in the Campine. The diatom character of the Campine region is now more distinct than before, mainly due to anthropogenic acidification in this area and the loss of nutrient-poor conditions elsewhere. Widely distributed taxa have gained in importance.

Acknowledgements: Data used in this study were obtained in the course of projects funded by the Flemish community through the Institute of Nature Conservation, AMINAL - Natuur and VLINA, and carried out at the Biology Department, University of Antwerpen (RUCA). The National Botanic Garden, KBIN and the universities of Gent, Leuven, Louvain-la-Neuve, Brussel (VUB) and Antwerpen are acknowledged for the use of collections. Thanks are due to the keepers of all collections and to M. Coenen, A. Hendrickx, J. Packet, V. Moons, D. Van Pelt, B. Veraert, L. Weiss for their help in sampling.