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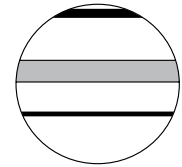
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Abstract

Analyses of pollen, plant macrofossils (seeds, fruits, wood and mosses), molluscs, diatoms and vertebrate (mainly fish) remains allowed a detailed reconstruction of a middle-Holocene alluvial forest and its associated hydrological conditions. The use of multiple proxies resulted in a taxonomically more detailed and environmentally more comprehensive understanding of terrestrial as well as aquatic habitats. The results demonstrate possible biases in palaeoecological reconstructions of alluvial and estuarine environments drawn from single proxies. Many locally occurring woody taxa were underrepresented or remained undetected by pollen analyses. Seeds and fruits also proved to be inadequate to detect several locally important taxa, such as *Ulmus* and *Hedera helix*. Apparently brackish conditions inferred from diatoms, pollen and other microfossils conflicted strikingly with the evidence from molluscs, fish bones and botanical macroremains which suggest a freshwater environment. Brackish sediment (and the microfossil indicators) is likely to have been deposited during spring tides or storm surges, when estuarine waters penetrated more inland than usual. Despite the reworking and deposition of estuarine and saltmarsh sediment well above the tidal node at such events, local salinity levels largely remained unaffected.

Keywords

alluvial forest, Belgium, estuary, macrofossils, microfossils, middle Holocene, multi-proxy, Quercus-Ulmetum, river, Scheldt, sediment transport

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Introduction

Alluvial forests have the highest species richness and productivity as well as structural and successional complexity among temperate forest ecosystems (Bradshaw and Möller, 2004; Schnitzler, 1994a, 1994b; Trémolières et al., 1998; Ward et al., 1999). However, relatively undisturbed alluvial forests have almost become extinct in Europe, and their history and former composition is hardly explored (Bohn et al., 2000; Brown et al., 1997; Wieggers, 1990). Moreover, the few relics of such forests are heavily influenced by the elimination of natural floods because of extensive river management since the Middle Ages, the elm disease (*Ophiostoma ulmi* and *Ophiostoma novo-ulmi*) in the 20th century, forestry activities and by the spread of non-native species during the last few decades (Deiller et al., 2001; Schnitzler, 1994b; Schnitzler et al., 2007; Trémolières et al., 1998; Van Looy et al., 2003).

In addition to their high ecological value, alluvial forests play an important role in the water retention capacity and sedimentation dynamics of river floodplains (Corenblit et al., 2007, 2009), and also perform a range of biogeochemical functions (e.g. Walbridge and Lockaby, 1994). A major target of both biodiversity conservation projects and large-scale flood-risk reduction programmes in NW-Europe is to reinstall more 'natural' riverbeds and valley floors, implying the creation or restoration of alluvial forests (Buijse et al., 2002; Middelkoop et al., 2005; Pedrolí et al.,

2002; Peterken and Hughes, 1995). These river and floodplain rehabilitation programmes generally lack information on the natural baseline (Brown, 2002), and targets are often only based on historical references (Buijse et al., 2002, 2005; Hohensinner et al., 2005; Middelkoop et al., 2005). Compared with historical data, palaeoecological studies can provide insight into more natural situations and reveal the long-term dynamics of specific ecosystems, which are both important elements for restoration and conservation programmes (Birks, 1996; Willis and Birks, 2006). However, our knowledge of pristine alluvial forests in NW-Europe is limited as most such palaeoecological studies refer to a

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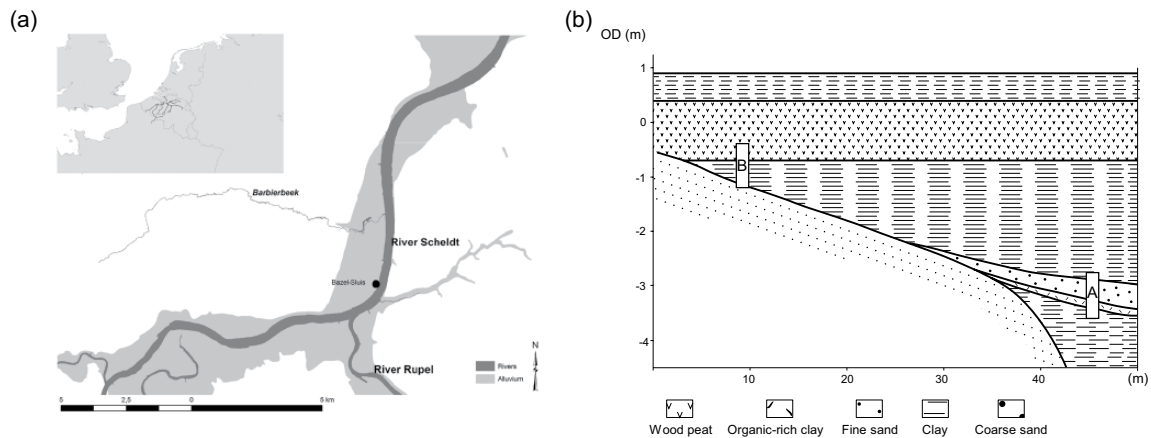


Figure 1. (a) Location of the study site (Bazel-Sluis) and (b) a schematic stratigraphy and position of the sample locations of sequence A and B.

limited number of proxies, hence offering a limited and possibly biased perspective on the former environment. Moreover, many of these studies cover more recent times, thus also reflecting conditions already subjected to important anthropogenic impacts.

Often, palaeoecological studies of Holocene alluvial forest environments rely on fossil coleopteran remains. Although a powerful tool for fine-scale local reconstructions, this only provides indirect information on the vegetation (e.g. Davis et al., 2007; Gandouin and Ponel, 2010). Other studies centred on pollen analysis, but these are limited by low taxonomic precision, little information on entomophilous taxa and problematic identification of the pollen source area (e.g. Pott and Hüppe, 2001). Some studies combine analyses of pollen and coleoptera (e.g. Andrieu-Ponel et al., 2000; Brayshay and Dinnin, 1999; Dinnin and Brayshay, 1999), or pollen and wood remains (e.g. Behre, 1970, 1985, 2004; Van Regteren Altena et al., 1962, 1963a, 1963b). Still, they only provide partial information on the palaeoenvironment. Charred botanical macroremains from anthropogenic structures in floodplain settings imply a risk for bias of certain taxa by human selection (Deforce et al., 2013, 2014). Even less commonly, terrestrial and aquatic proxies are combined, despite the fact that former floodplain environments are very much determined by fluvial dynamics (Ward et al., 2002).

This study uses diatoms, mosses, pollen, seeds and fruits, wood, molluscs and vertebrate remains to reconstruct a middle-Holocene alluvial forest and its associated aquatic environment in lower Belgium. All remains were recovered from clayey and peaty sediments at the foot of a natural levee along the Scheldt River and dated between *c.* 7000 and 5000 cal. yr BP.

Materials and methods

Study area

The river Scheldt is a typical rain-fed lowland river, with a length of 355 km and a catchment area of *c.* 21,863 km² (Meire et al., 2005). Today, the tidal zone extends from the mouth to the city of Ghent, situated 160 km upstream, where sluices block the penetration of tides. The study site is situated in Bazel (51°08'09"N, 4°19'23"E), on the left bank, 84 km upstream from the river mouth and in the present-day oligohaline zone, that is, the zone between mesohaline and freshwater conditions. Currently, salinity ranges from 0.5‰ to 5‰, and the mean tidal range attains 5.2 m (Breine et al., 2008; Meire et al., 2005; Figure 1a). Direct alluvial dynamics are now restricted to the channel and a narrow zone of tidal marsh, as most of the valley floor was reclaimed for agriculture by dike construction. The tidal marsh is dominated by *Phragmites australis* and *Scirpus maritimus* on the lower parts, and *Salix alba*, *Salix caprea*, *Epilobium hirsutum*, *Urtica dioica*

and the exotic invasive plant *Impatiens glandulifera* at higher elevations (Van Braeckel et al., 2008).

Although there was a short period of increased marine influence in the lower valley of the river Scheldt during the middle Holocene (Deforce, 2011; Verbruggen and Denys, 1995), the Scheldt between Ghent and Antwerp was not subjected to tidal influence for most of the Holocene, until the establishment of the Westerscheldt, probably in the 12th century AD (Kiden, 1989). Intensive channel dredging downstream of Antwerp caused an important increase of the tidal amplitude in the last century (Meire et al., 2005).

Sampling and analyses

Samples were taken from alluvial and peaty sediments at the foot of a natural levee, which were exposed in two trenches of an archaeological rescue excavation (Figure 1b). The distance between the two sample locations was *c.* 37 m. Samples for pollen, diatoms and radiocarbon dating were taken from both sediment profiles using monolith tins (sequences A and B). Adjacently, continuous, 5-cm-thick bulk samples were collected for macrofossil analyses (wood, seeds and fruits, mosses, molluscs, vertebrate remains). To increase the sample volume, additional samples for molluscs and vertebrate remains were retrieved from excavation surfaces corresponding to specific levels of sequence A. Sample depths are given relative to the Belgian Ordnance Datum (OD), referring to mean low water level, about 2.3 m below mean sea level.

Subsamples for pollen analysis (*c.* 1 cm³) were taken every 5 cm from both sequences and treated following standard procedures (Moore et al., 1991). The identification of pollen and spores was based on Moore et al. (1991), Beug (2004) and a reference collection of modern pollen and spores. *Pediastrum coenobia* were identified using Komárek and Jankovská (2001), and other non-pollen palynomorphs using van Geel (1978), van Geel et al. (1986) and Pals et al. (1980). At least 500 pollen grains were identified and counted from each sample. Percentages are based on the sum of all terrestrial plants (ΣP). The pollen diagram was subdivided in local pollen assemblage zones (LPAZs) using stratigraphically constrained cluster analysis performed by the program CONISS (Grimm, 1987).

Diatom subsamples were taken every *c.* 10 cm. Samples were treated using standard techniques (Battarbee, 1986) and analysed using light and scanning electron microscopy. At least 200 valves were identified per sample, mostly based on Krammer and Lange-Bertalot (2004) and Witkowski et al. (2000). The nomenclature follows Guiry and Guiry (2013). Taxa are classified according to salinity requirements and life form, based on compilations by Denys (1992) and Van Dam et al. (1994).

Table 1. Radiocarbon dates from Bazel.

Lab code	Sample depth (m below OD)	Sample	Uncal.yr BP	Cal.yr BP (2 σ)	Cal.yr BP (μ)
Beta-343983	52.5–53.5	<i>Urtica dioica</i> (1s), <i>Alnus glutinosa</i> (1c, 4 s, 6 s fr)	4500 \pm 30	5296–5046	5170
KIA-47570	69.5–70.5	<i>Ilex aquifolium</i> (1 s), <i>A. glutinosa</i> (c fr), <i>Quercus</i> sp. (6 b fr)	4575 \pm 35	5447 (12.0%) 5405 5327 (42.3%) 5260 5244 (0.7%) 5236 5224 (0.9%) 5214 5188 (39.5%) 5054	5240
Beta-342273	90.5–91.5	Unidentified (1b, 22 b fr)	4790 \pm 30	5594 (17.3%) 5567 5560 (78.1%) 5470	5521
KIA-47722	110.5–111.5	<i>A. glutinosa</i> (1c)	4660 \pm 30	5468–5314	5400
KIA-47571	279.5–280.5	Betulaceae (2 ct fr), <i>Quercus</i> sp. (1b fr) 2, <i>A. glutinosa</i> (1s)	4950 \pm 35	5744–6201	5674
KIA-47567	312.5–313.5	<i>Tilia</i> sp. (1s)	5035 \pm 35	5898 (90.1%) 5709 5691 (5.3%) 5663	5799
KIA-47720	335.5–336.5	Unidentified twig	6155 \pm 40	7166–6946	7062
KIA-47572	342.5–343.5	<i>Quercus</i> sp. (1s)	6145 \pm 35	7160–6949	7055

OD: Ordnance Datum; s: seed, c: cone, fr: fragment, b: bud, ct: catkin.

Botanical macroremains (seeds, fruits, wood and mosses), molluscs and vertebrate remains were extracted by wet-sieving 2L samples through 4mm, 2mm and 500 μ m mesh sizes, and an additional 2L only through a 4mm mesh sieve. The larger extra samples from sequence A for analyses of molluscs and vertebrate remains were sieved through 2mm mesh size.

Identifications of seeds and fruits were based on the reference collection of the Flanders Heritage Agency and literature, primarily Cappers et al. (2006). The 2 and 0.5mm fractions were only partially analysed and then standardised to equal 4L.

From each sample, 50 wood fragments were randomly selected from the 4mm sieved residue. Transverse, radial and tangential thin sections were cut using a razor blade, mounted in glycerol and studied using a transmitted light microscope (100–400 \times). Identifications are based on Schweingruber (1990).

All moss fragments from the sieved residues were identified using Siebel and During (2006), Smith (2004), Touw and Rubers (1989) and Landwehr (1984) and quantified according to the method described by Van Der Putten et al. (2004). Nomenclature follows Hill et al. (2007).

Molluscs were extracted from a subsample of 70g of the sieved residue. Identification was based on Adam (1960), Cameron (2008) and Kerney and Cameron (1980) for land snails, and Adam (1960), Gittenberger and Janssen (2004), Glöer and Meier-Brook (2003) and Killeen et al. (2004) for aquatic species. The taxonomy follows de Jong (2013). The results are presented as Minimum Number of Individuals (MNI), which for gastropods corresponds to specimens with preserved apex and for bivalves to remains with an umbo. The number of bivalve valves was divided by two. Habitat classifications are based on Gittenberger and Janssen (2004), Kerney and Cameron (1980), Čejka and Hamerlík (2009), Čejka et al. (2008), Davies (2008), Martin and Sommer (2004) and Pišút and Čejka (2002).

Vertebrate remains were sorted from the sieved residues (mesh width > 2mm). The material was identified using the reference collections of the Royal Belgian Institute of Natural Sciences. Insect remains were not studied because of their scarcity in the collected samples.

Botanical macroremains of terrestrial plants were selected for AMS radiocarbon dating from eight levels in the two sequences (Table 1). The results were calibrated using OxCal 4.2 (Bronk Ramsey, 2009) based on atmospheric data from Reimer et al. (2013) and are referred to in the text as the mean values of the calibrated range before present (cal. yr BP), rounded to the nearest 10 years.

Results and interpretation

Lithology and chronology

The lower part of sequence A, up to –3.4m, consists of silty clay with an increasing amount of organic matter towards the top (Figure 2), suggesting deposition near the margin of a river channel with decreasing water depth. Between –3.4 and –3.24m OD, an organic-rich clay with abundant coarse wood fragments represents a decrease in fluvial influence that started at c. 7060 cal. yr BP. At –3.24m OD, a sharp boundary occurs with the next sedimentary unit consisting of coarse sand with wood fragments. Together with the large time interval between the radiocarbon ages of both units (>1000 cal. yr), this suggests a depositional hiatus. The coarse sand must represent an increase in fluvial activity which is likely to have caused partial erosion of the accumulated sediments and the hiatus in the record. From –3.16m OD onwards, clayey layers are sporadically intercalated within this coarse sand and from –3.04m OD onwards, the sediment consists of an alternation of clay and fine sand, once again reflecting decreasing fluvial activity. The top of this sequence is dated around c. 5670 cal. yr BP at –2.8m OD.

The base of sequence B, at –1.20m OD, consists of fine sand with coarse organic detritus which is likely to have been deposited at the margins of a river channel. From –1.14m OD onwards, silty clay with a high organic matter content and many leaf and wood fragments and molluscs was deposited. This process started shortly before 5400 cal. yr BP and corresponds to decreasing fluvial activity at the sampling site. The organic content of the sediment continues to increase, and from c. –0.70m OD onwards, dated at c. 5240 cal. yr BP, wood peat formed. Peat accumulation continued up to 0.28m OD, but because the upper part of the peat was highly humified, samples were only analysed up to –0.48m OD.

Pollen

The pollen diagrams were subdivided into four LPAZs (Figure 2). The lower part of sequence A, LPAZ BASL-1, corresponds to a *Quercus*-dominated dryland vegetation with *Acer*, *Tilia*, *Corylus*, *Ulmus* and *Fraxinus* growing on the levee. The wetland vegetation consists of alder carr with mainly *Alnus*, as well as *Frangula alnus*, *Rhamnus cathartica* and *Salix*. Climbers and epiphytes such as *Hedera helix*, *Humulus* and *Viscum album* are also present. Herbaceous vegetation is hardly represented in this part of the

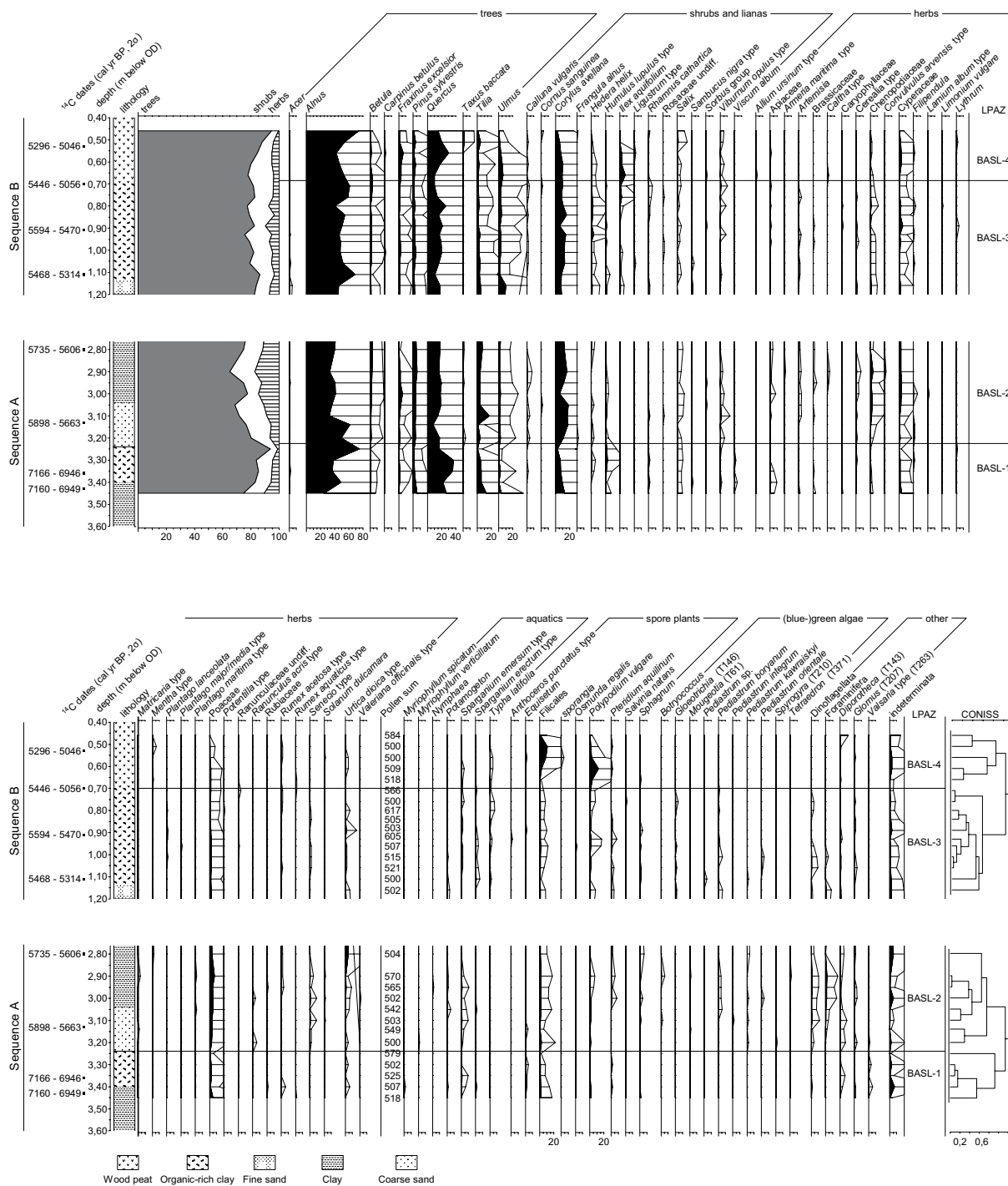


Figure 2. Lithostratigraphy, pollen percentage diagram of selected taxa and cluster analysis diagram for both sequences from Bazel. LPAZ: local pollen assemblage zone; OD: Ordnance Datum.

pollen diagram, with *Apiaceae*, *Cyperaceae*, *Filipendula*, *Lythrum* and *Rumex aquaticus*-type reflecting wet local conditions.

The lowermost part of LPAZ BASL-2 is characterised by a decrease of the total arboreal pollen percentages, mainly of *Alnus* and *Quercus*. This zone is further characterised by the presence of different green algae, such as *Pediastrum*, *Tetraedron* and *Botryococcus*, which occur both in fresh and brackish waters (Matthiessen and Brenner, 1996) and indicate an increase of fluvial influence (Matthiessen et al., 2000). Dinoflagellate cysts and foraminifera also occur in this part of the pollen diagram, and there is an increase of *Chenopodiaceae*, which all reflect an input of estuarine material. The presence of *Armeria maritima*-type

and probably *Artemisia* and *Senecio*-type (including *Aster tripolium*) also indicates an influx of pollen from halophytic vegetation.

LPAZ BASL-3 starts with very similar pollen assemblages as found in the upper part of sequence A. There is a decrease in *Ulmus* around c. 5400 cal. yr BP and an increase of *Ilex aquifolium* at c. 5240 cal. yr BP.

In the lower part of LPAZ BASL-4, which corresponds with the start of the peat accumulation, (possible) marine/estuarine indicators, that is, dinoflagellate cysts, foraminifera, *Artemisia*, *Chenopodiaceae* and *Senecio*-type, decrease or disappear from the pollen record. *Ilex aquifolium* reaches high percentages as do

Polypodium vulgare and other Filicales. *Taxus* occurs in the diagram from c. 5170 cal. yr BP onwards.

Seeds and fruits

Almost all analysed samples contain a large number of woody species, representing c. 50% of the total number of identified taxa. Only the lowermost sample, at -3.6 m OD, is poor in woody species and dominated by *Urtica dioica*, *Alisma* sp., *Mentha aquatica* and *Lycopus europaeus*, which typically reflect the nitrophilous vegetation along a river margin where floating organic material accumulates. *Sambucus nigra* and *Alnus glutinosa*, also present in this sample, may also have grown here, while the nuts of *Corylus avellana* were probably transported by river water or originated from higher up the levee. In the remainder of sequence A, trees and shrubs, including *Tilia cordata* and/or *Tilia platyphyllos*, *Corylus avellana*, *Prunus spinosa*, *Quercus petraea/robur* and *Sambucus nigra*, dominate. This reflects the 'dryland' vegetation on the levee. *Alnus glutinosa* and *Viburnum opulus* occupied the lower part where herbaceous marsh species such as *Lycopus europaeus* and *Alisma* sp. occurred as well.

The dryland component in the lower part of sequence B includes *Tilia cordata*, *Corylus avellana*, *Quercus petraea/robur*, *Crataegus monogyna*, *Malus sylvestris* subsp. *sylvestris*, *Prunus spinosa*, *Sambucus nigra* and possibly also *Sambucus racemosa*. *Fraxinus excelsior* would have grown on the rather moist soils on the flanks of the levee while the lower, wettest parts supported alder-dominated woodland with *Alnus glutinosa*, *Viburnum opulus* and *Frangula alnus* and/or *Rhamnus cathartica*. The occurrence of *Scirpus lacustris* indicates open water. *A. glutinosa* decreases towards the top while *Cornus sanguinea*, *Frangula alnus* and/or *Rhamnus cathartica* and *Ilex aquifolium* increase. Less continuously present and in low numbers are *Betula alba/pendula*, *Rosa* sp., *Rubus 'fruticosus'*, *Sorbus* sp. and cf. *Viscum album*. The largest number of remains from herbaceous species belongs to *Urtica dioica*, with a maximum at the top of profile B. Herbaceous taxa occurring at more than one level are *Alisma* sp., Apiaceae, *Caltha palustris*, *Carex* sp., *Filipendula ulmaria*, *Lycopus europaeus*, *Ranunculus* sp., *Rumex* sp., *Scirpus lacustris* and *Sparganium erectum*, which all refer to wet conditions, ranging from open water to a productive tall herb community.

Wood

A total of 500 wood fragments were identified, corresponding with at least 16 taxa of trees, shrubs and lianas (Figure 3). Most of the studied wood fragments were twigs with a diameter < 2 cm. Although many samples contained numerous bark fragments originating from large diameter trunks and branches, only a small portion of the preserved wood fragments originated from stems or thick branches, indicating a better preservation of small diameter wood fragments.

Alnus sp. is dominant in all the analysed samples, reflecting the presence of alder-carr vegetation at the foot of the levee. Also *Rhamnus cathartica*, *Frangula alnus*, *Viburnum* sp. and *Salix* sp. must have grown here. Most of the other taxa found prefer drier conditions, and their wood remains are likely to have derived from material falling from higher up the levee. *Ulmus* sp., which is also important in all analysed samples, and *Fraxinus excelsior* prefer moist conditions and are tolerant of temporal inundation. They are more likely to have occurred on the flanks of the levee. *Quercus* and *Tilia* must have occupied the driest spots on the top of the levee. *Corylus avellana* and Pomoideae (including *Malus* sp., *Pyrus* sp., *Crataegus* sp. and *Sorbus* sp.) prefer moist to dry soils and thus most likely formed the shrub layer on the flanks and top of the levee. The wood of trees and shrubs preferring rather

dry soil types was found in sequence A and the lower part of sequence B. Most of these taxa did not occur in the upper half of sequence B where *Alnus* sp., *Ulmus* sp. and *Fraxinus excelsior* were the only trees together with associated shrubs and climbers like *Viburnum*, *Hedera helix* and *Lonicera*. This indicates increasing wetness on the levee. Wood from *Ilex aquifolium* was also present in this part of the sequence.

Mosses

A total of 18 moss taxa were identified. The samples from sequence B show a slightly higher taxonomic diversity than those from sequence A, but this may be a consequence of better preservation conditions. According to shade-tolerance, the identified moss species vary between shade preferring species (mostly less than 5% of relative light availability, for example, *Thamnobryum alopecurum*) and species growing in well-lit places but with partial shade (e.g. *Homalothecium sericeum*). No full light requiring mosses have been found. The moss assemblage indicates both a relatively dry environment (e.g. *Homalothecium sericeum*), as well as shaded and humid conditions (e.g. *Anomodon viticulosus*, *Isothecium myosuroides*, *Neckera crispa*). *Cinclidotus* and *Amblystegium tenax* point to the presence of a frequently inundated zone alongside the river. *Drepanocladus aduncus* is characteristic of waterlogged soils and pools. *Calliergonella cuspidata* has a broader amplitude but also grows on moist soils.

All of the species that are frequent in the analysed samples, for example, *Anomodon viticulosus*, *Homalothecium sericeum*, *Hypnum cupressiforme*, *Isothecium myosuroides*, *Leucodon sciuroides*, *Neckera complanata*, *Thamnum alopecurum* and *Neckera crispa* can grow on a range of different substrates, including rocks and soil, as well as stems and branches of trees. In the absence of rocks, and with several fragments still attached to bark fragments, these moss taxa must have grown mostly as epiphytes on the trees and shrubs that fell in the water. *Thamnobryum alopecurum* and *Oxyrrhynchium hians* often grow on woodland soil and riverbanks, but occur also as epiphytes. These species can form a dense bryophyte carpet in humid forests on the lower part of trees with a base-rich bark such as *Fraxinus excelsior*, *Salix* spp., *Populus* spp., *Acer* spp., *Ulmus* spp. and *Tilia* spp. (Barkman, 1958; BLWG, 2013; Sjögren, 1961). *Hypnum cupressiforme* and *Isothecium myosuroides* prefer moderately acidic substrates and may also have grown on trees with a more neutral or acidic bark like *Quercus robur* or *Alnus glutinosa*, and *Betula* sp. *Habrodon perpusillus*, an exclusive epiphyte, generally grows higher up trees.

Diatoms

No diatoms were preserved in the more organic layers (below -3.24 m OD in sequence A and above -0.70 m OD in sequence B). Two diatom zones are recognised in sequence A, corresponding with the different lithological units (Figures 4 and 5). Except for a peak of brackish (and brackish-fresh) diatoms at -3.10 OD, the coarse sand deposit (-3.24 to -3.04 m OD) is dominated by species characteristic for an alkaline, high-conductivity but essentially fresh environment. The main taxa are *Martyana martyi*, *Karayevia clevei* and small *Cocconeis*, which are all sessile. These species are considered to have lived locally or attached to the coarse sand grains making up this layer. Along with the substrate, this epipsammic assemblage points to deposition in more energetic conditions because of currents or wave disturbance. Common epiphytes (e.g. *Cocconeis placentula*, *Epithemia* spp., *Gomphonema* spp.) are notably absent or only very scarcely represented, suggesting that submerged aquatics and helophytes were also quite sparse. *Cyclotella striata*, a tycho planktonic species of brackish waters, shows a peak at

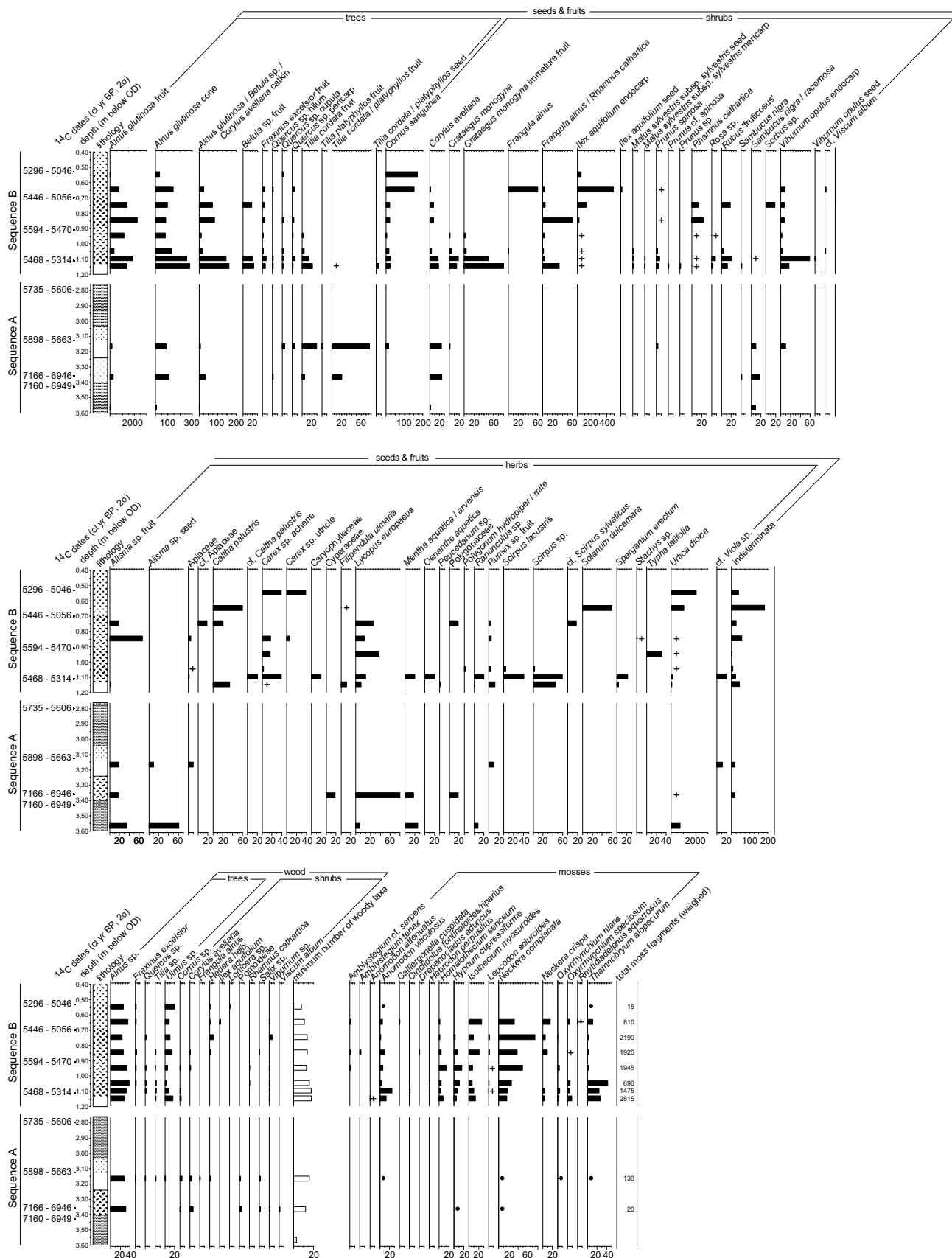


Figure 3. Botanical macrofossil diagram of seeds and fruits, wood and mosses from Bazel. The minimum number of woody taxa is based on the combined data from seeds and fruits and wood identifications. OD: Ordinance Datum.

–3.10 OD, which, combined with small amounts of marine diatoms, indicates the presence of allochthonous remains brought in from the estuary.

In the succeeding layer of (fine) sandy clay, *Cyclotella striata* becomes the main species, indicating an increase in water of estuarine origin, corresponding to an inland extension of the tidal

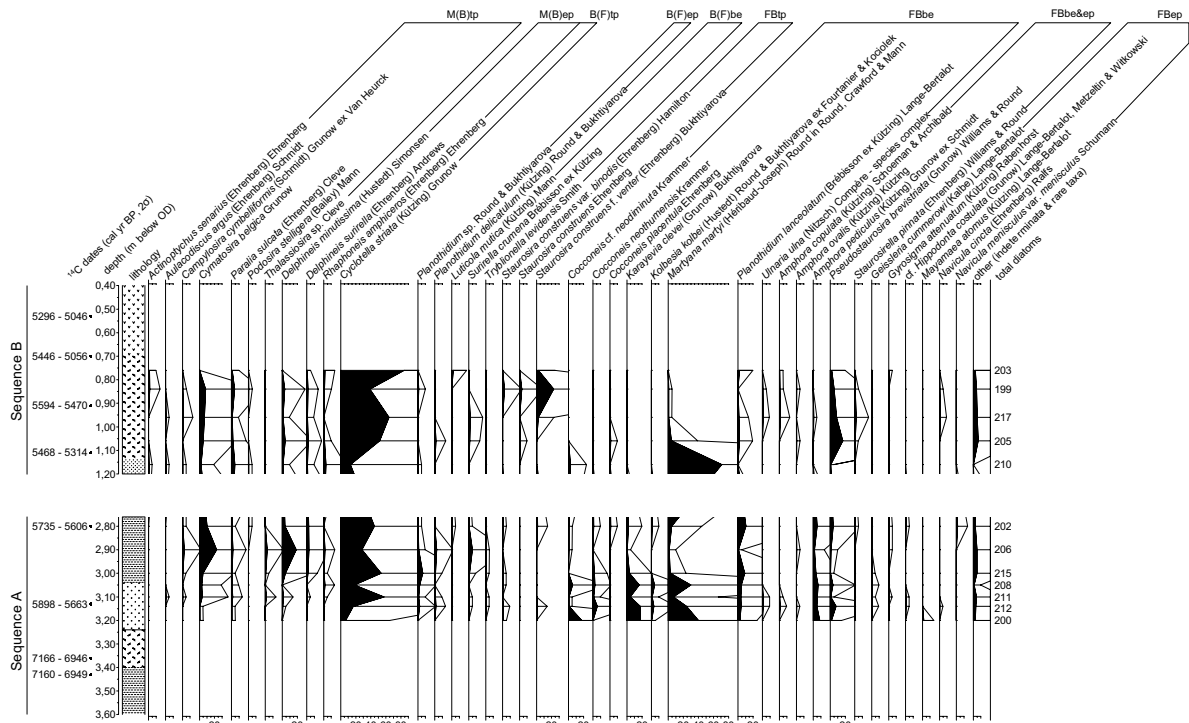


Figure 4. Diatom diagram of sequences A and B from Bazel. Only taxa with more than two valves counted are shown. OD: Ordnance Datum.

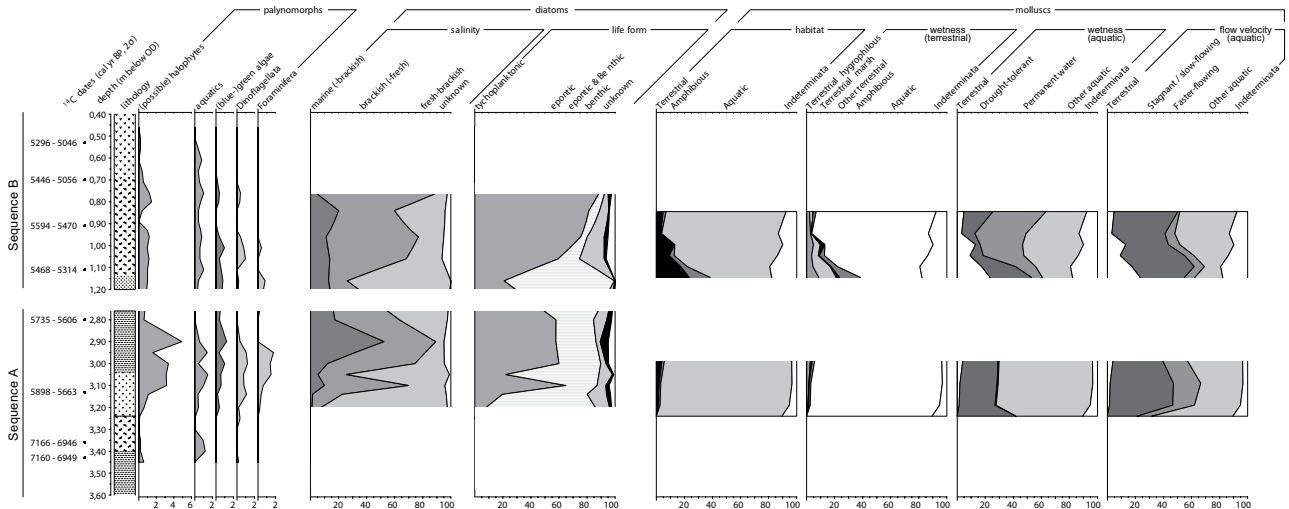


Figure 5. Synthetic diagram of selected palynomorphs, diatoms and molluscs according to their ecological characteristics. Epontic is used for all diatoms adhering closely to a firm substrate. Possible halophytes include *Armeria maritima*-type, *Chenopodiaceae*, *Limonium vulgare*, *Plantago maritima*-type and *Senecio*-type. OD: Ordnance Datum.

prism. This is confirmed by the increased abundance of marine and marine-brackish species (mostly *Cymatosira belgica* and *Delphineis minutissima*). The autochthonous, epipsammic fresh-water flora recorded below -3.05 m is nearly absent in this zone.

The sand at the base of sequence B shows a very different diatom content compared with the top of sequence A. As in the lower part of sequence A, sessile fresh-brackish species are dominant, though mainly represented here by a single species, *Martyna martyi*. The epipsammic assemblage remained present until the onset of clay deposition. Although marine and brackish taxa co-occur in this layer, they remain scarce. The mixture of mainly autochthonous, fresh-brackish, epipsammic

diatoms with allochthonous valves resembles the assemblage composition in the coarse sandy part of sequence A. These levels are not contemporaneous, being separated by a time lapse of several hundred years, but reflect similar substrate conditions.

Cyclotella striata is the most frequent diatom species in the humic clay between -1.14 and -0.70 m OD. Other marine(-brackish) or brackish(-fresh) taxa are less frequent and fresh-brackish taxa are generally poorly represented, except for some *Pseudostaurosira brevistriata* near the base and a modest peak of *Staurorsira construens* f. *venter* at -0.85 m, which possibly reflect the development of some very shallow stagnant water and a reduction in the supply of upstream-transported marine and brackish valves.

Molluscs

Aquatic species dominate all analysed samples (Table 2). These are typical for a well-vegetated freshwater environment with stagnant or slow-flowing water, directly connected to faster flowing water. Terrestrial species are only a minor component of the assemblages and are mostly hygrophilous to strongly hygrophilous (Figure 5; Čejka and Hamerlík, 2009; Martin and Sommer, 2004).

The part of sequence A between -3.24 and -3.00 OD shows higher percentages of aquatic species than sequence B (Figure 5). Many of these aquatic species are desiccation-tolerant though, and only few require permanent water. Sequence A is also characterised by rather high proportions of taxa associated with more fast-flowing water (e.g. *Pisidium amnicum*, *Pisidium supinum*, *Theodoxus fluviatilis*). Overall, the assemblage composition of these deposits indicates a temporarily inundated alluvial environment with running water nearby.

Sequence B shows a higher but decreasing proportion of terrestrial species between -1.15 and -0.85 m OD. Marsh gastropods, such as the terrestrial *Carychium minimum* and the amphibious *Galba truncatula*, also decline. Within the aquatic molluscs, taxa from permanently inundated habitats, such as *Gyraulus crista*, *Hippeutis complanatus*, *Pisidium nitidum* and *Pisidium subtruncatum*, are far more abundant compared with sequence A, and they increase towards the top. The mollusc assemblages of this sequence thus indicate increasing wetness, a more stable water level and more stagnant conditions.

In both sequences, indications of brackish or tidal conditions are lacking; typical species for such environments remain absent (Bruyndoncx et al., 2002). Although *Bithynia tentaculata*, *Planorbis planorbis*, *Radix balthica* and *Theodoxus fluviatilis* tolerate high salinity levels ($>10\%$), these are essentially freshwater species (Gittenberger and Janssen, 2004). Moreover, both sequences yielded species that can only survive at maximum salinities of 0.5% (*Ancylus fluviatilis*, *Omphiscola glabra*, *Pisidium amnicum*, *Pisidium milium*, *Pisidium moitessierianum*, *Pisidium obtusale* and *Segmentina nitida*; Gittenberger and Janssen, 2004).

Vertebrate remains

Most of the vertebrate remains were recovered from the coarse sand and lowermost part of the upper clay deposit of sequence A, dating around 5800 cal. yr BP. The majority comprises skeletal elements of fish ($n=3603$, scales not counted), although some bones of amphibians ($n=5$) and reptiles ($n=3$) were also present (Table 3). Most of the identified fish bones ($n=2894$) are from freshwater fauna, mainly cyprinids. The freshwater species assemblage perfectly matches the oldest comprehensive fish inventory of the lower Scheldt basin (De Selys-Longchamps, 1842, see also Breine et al., 2011) with addition of the wels catfish (*Silurus glanis*), which became locally extinct before the end of the Middle Ages (Van Neer and Ervynck, 2009).

A number of migratory species are represented, again in accordance with de Selys-Longchamps' list (1842). These include the catadromous eel (*Anguilla anguilla*), as well as the catadromous thinlip mullet (*Liza ramada*) and the anadromous sturgeon (*Acipenser* sp., now locally extinct), shad (*Alosa* sp.), smelt (*Osmerus eperlanus*) and salmonids (Salmonidae).

A limited number of clupeids (Clupeidae) and flatfish (Pleuronectidae), including flounder (*Platichthys flesus*), are classified as marine, although these fish have a wide salinity tolerance. All of them occur in brackish and even freshwater (Poll, 1947). Similarly, the freshwater eel and three-spined stickleback (*Gasterosteus aculeatus*) extend into the marine realm (Poll, 1947).

The large majority of the fish species represented in sequence A belong to the 'bream zone' of lowland rivers (Huet, 1959), characterised by maximum water temperatures regularly exceeding

20°C and a stream velocity of $0\text{--}10\text{ cm/s}$ (Aarts and Nienhuis, 2003). Barbel (*Barbus barbus*) and bullhead (*Cottus* sp.) are normally associated with the more upstream 'barbel zone', but it is quite possible that they were derived from smaller, nearby tributaries with faster running water (e.g. the Barbierbeek, a brook joining the Scheldt river near the excavation site, Figure 1). Considering the salinity preferences of individual taxa (Breine et al., 2008), it appears that all may co-occur in the oligohaline zone, at salinities between 0.5% and 5% . Most of the freshwater species are resident, however, while the other taxa are fish that can migrate between the sea and freshwater, so it can be assumed that the assemblage from sequence A represents the 'average' ichthyofauna living near the site.

From sequence B, only a small number of fish remains were recovered from the lowermost part, between -1.1 and -0.8 OD, (Table 3). The species composition is essentially the same as in sequence A, with a predominance of resident freshwater species and a single marine taxon (*Liza ramada*).

The few additional vertebrates, that is, the common frog (*Rana temporaria*) and the grass snake (*Natrix natrix*), indicate the proximity of aquatic habitats. Also the common adder (*Vipera berus*) can be found on the banks of streams (De Witte, 1948).

Discussion

Composition and evolution of the alluvial forest

Throughout the investigated period, alder-dominated woodland persisted at the foot of the levee. However, its local shrub and herb layer as well as the vegetation cover of the higher parts of the levee changed significantly.

Between $c. 7060$ and 5520 cal. yr BP, trees including *Tilia cordata*, *Tilia platyphyllos*, *Quercus*, *Acer*, *Fraxinus excelsior* and *Ulmus*; a rich shrub layer with *Corylus avellana*, *Crataegus monogyna* and *Malus sylvestris* subsp. *sylvestris*; lianas like *Hedera helix* and *Humulus*; and an epiphytic flora of *Viscum album* and various mosses grew on the levee. Comparison with vegetation records from present-day alluvial forests in large European floodplains (Schnitzler, 1994b, 1995) and the geomorphological position of the sampling site indicates a hardwood alluvial forest (Querco-Ulmetum). Except for *Carpinus betulus* which did not occur in N Belgium before $c. 2800$ cal. yr BP (Verbruggen et al., 1996), all woody taxa that are considered characteristic for such an environment (Schnitzler, 1995; Schnitzler et al., 1992), and with a natural distribution including N Belgium (Maes et al., 2006), were present. Such hardwood alluvial forests require very specific hydrodynamic conditions, that is, areas within the floodplain that are only incidentally touched by short-lived inundations (Schnitzler, 1994b; Wolf et al., 1997). More frequent inundation results in replacement by alluvial forests dominated by *Salix* and *Populus* (Schnitzler, 1995).

By $c. 5520$ cal. yr BP, most taxa indicative of dryland had disappeared from the levee forest, and *Cornus sanguinea*, *Frangula alnus* and *Ilex aquifolium* started to increase, while *Alnus*, *Ulmus* and *Fraxinus excelsior* remained important components of the local vegetation. This evolution is likely to have resulted from the rising groundwater level induced by the relative sea level (RSL) rise (Denys and Baeteman, 1995). From the middle Holocene onwards, peat formation occurred in most of the lower Scheldt valley (Deforce, 2011), and locally, the levees were gradually drowned. Although the diversity of woody taxa decreased considerably during this process (Figure 3), the local vegetation evolved into an alder carr which still included a range of woody species such as *Cornus sanguinea*, *Fraxinus excelsior*, *Frangula alnus*, *Ilex aquifolium*, *Viburnum opulus* and *Ulmus* as well as *Hedera helix* and *Lonicera* on the highest parts of the levee. These locally occurring taxa largely remain absent from the pollen record, while *Ulmus* and *Hedera helix* were not detected by analyses of

Table 2. Minimum Number of Individuals (MNI) of the mollusc remains from Bazel.

Sequence		B	B	B	B	B	B	A	A	A	A
Sample depth (m below OD)		0.845	0.945	0.995	1.045	1.095	1.145	2.99	3.09	3.19	3.24
Terrestrial gastropods											
	Group										
<i>Carychium minimum</i>	T-marsh	2	1	5	13	35	49	–	–	–	–
<i>Carychium tridentatum</i>	T-hygro	1	2	4	2	3	4	–	–	–	–
<i>Carychium</i> sp.	T-hygro	–	1	1	6	–	18	–	–	–	–
<i>Oxyloma elegans</i>	T-marsh	–	–	–	–	–	–	1	–	–	–
<i>Oxyloma</i> sp.	T-marsh	–	–	–	–	–	–	–	–	1	–
Succineidae	T-hygro	1	–	–	–	–	–	4	33	26	–
<i>Cochlicopa lubrica</i>	T-hygro	–	–	–	–	1	–	2	2	2	–
<i>Cochlicopa lubricella</i>	T	–	–	1	–	–	–	–	–	–	–
<i>Columella aspera</i>	T	–	–	–	1	–	–	–	–	–	–
<i>Vertigo moulinsiana</i>	T-marsh	–	–	–	1	–	–	–	–	–	–
<i>Vertigo angustior</i>	T-marsh	1	–	–	–	–	–	–	–	–	–
<i>Vallonia costata</i>	T	–	–	–	–	–	–	–	–	1	–
<i>Vallonia pulchella</i>	T-hygro	–	1	–	1	2	2	–	–	3	–
<i>Punctum pygmaeum</i>	T-hygro	1	–	1	2	4	5	–	1	–	–
<i>Discus rotundatus</i>	T	–	–	2	–	1	3	1	3	5	–
<i>Vitrea crystallina</i>	T-hygro	–	2	–	–	3	6	–	–	–	–
<i>Vitrea</i> sp.	T	–	–	1	–	–	4	–	–	–	–
Oxychilidae	T	–	–	–	–	–	2	–	–	–	–
<i>Aegopinella nitidula</i>	T-hygro	–	–	–	1	–	–	–	2	–	–
<i>Zonitoides nitidus</i>	T-marsh	1	–	1	2	–	2	1	2	5	–
Clausiliidae	T	–	–	–	1	1	–	–	1	2	–
<i>Trochulus hispidus</i>	T	–	–	–	–	–	–	–	–	1	–
<i>Cepaea</i> sp.	T	–	–	–	1	–	–	–	1	1	–
Freshwater gastropods											
<i>Theodoxus fluviatilis</i>	A-flow	–	–	–	–	–	–	5	35	67	–
<i>Bithynia leachii</i>	A-stag-vege	–	–	–	–	–	–	–	1	4	–
<i>Bithynia tentaculata</i>	A	–	1	–	1	2	–	19	119	352	1
<i>Valvata macrostoma</i>	A-drytol-stag	2	2	–	4	2	5	–	7	14	–
<i>Valvata piscinalis</i>	A-stag-vege	7	16	19	48	33	39	62	804	984	4
<i>Valvata cristata</i>	A-drytol-stag	19	2	3	7	2	7	–	–	1	–
<i>Acroloxus lacustris</i>	A-stag	–	–	–	–	–	–	–	–	1	–
<i>Galba truncatula</i>	A-drytol-amphi	3	1	–	12	13	6	4	26	39	–
<i>Lymnaea stagnalis</i>	A-stag-vege	–	–	–	–	–	–	–	1	1	–
<i>Omphiscola glabra</i>	A-drytol-stag-vege	–	–	–	–	–	–	–	–	1	–
<i>Radix auricularia</i>	A-stag-vege	–	–	1	1	–	–	–	23	7	–
<i>Radix labiata/balthica</i> complex	A	9	10	10	5	4	7	15	81	165	–
<i>Stagnicola palustris</i> complex	A-drytol-stag-vege	6	13	1	7	41	42	19	213	431	–
<i>Anisus spirorbis</i>	A-drytol-stag-vege	–	2	–	–	9	5	–	1	4	–
<i>Anisus vortex</i>	A-stag-vege	–	–	–	–	–	–	–	–	1	–
<i>Anisus</i> sp.	A-stag-vege	–	2	–	–	–	–	–	1	–	–
<i>Bathymorphalus contortus</i>	A-permwa-stag-vege	–	–	–	–	–	–	–	2	7	–
<i>Gyraulus crista</i>	A-permwa-stag-vege	19	31	6	39	25	25	–	–	–	–
<i>Gyraulus albus</i>	A	9	12	5	14	4	5	–	6	10	–
<i>Gyraulus laevis</i>	A-stag	3	4	–	2	3	2	–	1	3	–
<i>Gyraulus</i> sp.	A	1	1	1	–	–	–	–	–	1	–
<i>Planorbis planorbis</i>	A-drytol-stag-vege	–	–	–	–	1	–	–	–	3	–
<i>Hipppeutis complanatus</i>	A-permwa-stag-vege	1	8	7	47	11	2	–	–	–	–
<i>Planorbarius corneus</i>	A-permwa-stag-vege	–	–	–	–	–	–	–	–	1	–
<i>Ancylus fluviatilis</i>	A-flow	–	–	–	–	–	–	–	–	3	–
Freshwater bivalves											
<i>Unio pictorum</i>	A	–	–	–	–	–	–	11	45	59	–
<i>Unio tumidus</i>	A	–	–	–	–	–	–	–	8	7	–
<i>Unio</i> sp.	A	–	–	–	1	–	–	–	1	12	–
<i>Anodonta anatina</i>	A	–	–	–	–	–	1	1	3	8	–
<i>Anodonta cygnea</i>	A-stag	–	–	–	–	–	–	–	–	1	–
<i>Anodonta</i> sp.	A	–	–	–	–	–	–	–	1	2	–
<i>Pisidium amnicum</i>	A-flow	–	–	–	–	–	–	3	29	32	1
<i>Pisidium casertanum</i>	A-drytol	–	–	–	2	1	1	34	373	341	8
<i>Pisidium henslowanum</i>	A-flow	1	4	2	4	4	2	3	31	38	–
<i>Pisidium milium</i>	A	–	–	–	–	–	–	–	1	–	–
<i>Pisidium moitessierianum</i>	A-flow	1	11	8	18	17	27	5	25	76	–

(Continued)

Table 2. (Continued)

Sequence		B	B	B	B	B	B	A	A	A	A
<i>Pisidium nitidum</i>	A-permwa	–	1	3	5	3	3	2	13	11	–
<i>Pisidium obtusale</i>	A-drytol-stag	–	–	–	–	–	–	–	–	1	–
<i>Pisidium personatum</i>	A-drytol	–	–	–	–	–	–	–	1	–	–
<i>Pisidium pseudosphaerium</i>	A-stag	–	1	–	–	–	1	–	1	11	–
<i>Pisidium pulchellum</i>	A	–	–	–	–	–	–	–	–	2	–
<i>Pisidium subtruncatum</i>	A-permwa	26	38	21	6	2	1	–	3	9	–
<i>Pisidium supinum</i>	A-flow	–	–	–	–	–	1	24	336	287	1
<i>Pisidium</i> sp.	A	11	19	7	37	4	2	3	24	53	2
Unidentified		11	28	12	46	55	72	8	76	169	2
Total		145	214	122	337	286	405	227	2337	3266	19

OD: Ordnance Datum; A: aquatic species, amph: amphibious species, drytol: dessication-tolerant species, flow: species preferring faster flowing water, hygro: hygrophilous species, marsh: marsh species, permwa: species preferring permanent water, stag: species preferring stagnant or slow-flowing water, T: terrestrial species, vege: species preferring a well-vegetated environment.

Table 3. Inventory of the vertebrate remains from Bazel. In the case of the fish remains, scales were present, but only bone fragments were studied and counted.

Sequence	A	B
Sample depth (m below OD)	3.24–2.99	1.1–0.8
<i>Fish</i>		
<i>Marine</i>		
Sturgeon (<i>Acipenser</i> sp.)	43	–
Shad (<i>Alosa</i> sp.)	30	–
Clupeids (<i>Clupeidae</i> sp.)	8	–
Smelt (<i>Osmerus eperlanus</i>)	71	–
Salmonids (<i>Salmonidae</i> sp.)	1	–
Thinlip mullet (<i>Liza ramada</i>)	2	4
Flounder (<i>Platichthys flesus</i>)	3	–
Flatfish (<i>Pleuronectidae</i> sp.)	20	–
<i>Freshwater</i>		
Eel (<i>Anguilla anguilla</i>)	609	1
Bream (<i>Abramis brama</i>)	4	–
White bream (<i>Blicca bjoerkna</i>)	5	–
Barbel (<i>Barbus barbus</i>)	1	–
Gudgeon (<i>Gobio gobio</i>)	26	–
Roach (<i>Rutilus rutilus</i>)	90	–
Rudd (<i>Scardinius erythrophthalmus</i>)	3	1
Ide (<i>Leuciscus idus</i>)	30	–
Cyprinids (<i>Cyprinidae</i> sp.)	1659	16
Wels catfish (<i>Silurus glanis</i>)	10	–
Pike (<i>Esox lucius</i>)	91	40
Burbot (<i>Lota lota</i>)	1	–
Three-spined stickleback (<i>Gasterosteus aculeatus</i>)	82	2
Bullhead (<i>Cottus</i> sp.)	10	–
Perch (<i>Perca fluviatilis</i>)	52	1
Ruffe (<i>Gymnocephalus cernua</i>)	24	–
Percids (<i>Percidae</i> sp.)	19	–
Unidentified fish (<i>Pisces</i> indet.)	709	25
<i>Amphibians</i>		
Common frog (<i>Rana temporaria</i>)	1	1
Frog (<i>Rana</i> sp.)	3	1
Frog (<i>Anura</i> sp.)	1	–
<i>Reptiles</i>		
Grass snake (<i>Natrix natrix</i>)	2	–
Common adder (<i>Vipera berus</i>)	1	–
Total	3611	92

OD: Ordnance Datum.

seeds and fruits either, and their local occurrence could only be attested to by their wood remains.

The results from the analyses of pollen, seeds and fruits and wood show that *Tilia* was an important tree in the initial levee forest, be it probably restricted to the highest places. Both the pollen record and the macrobotanical data indicate a local decline of *Tilia* between c. 5800 and 5520 cal.yrBP as a result of increasingly wetter conditions preceding inundation of the levee. Lithological and palynological data illustrate a similar process of valley-floor paludification for a large number of sites in lowland Britain where it provides an alternative explanation to climate change and human impact for the mid-Holocene *Tilia* decline (Grant et al., 2011; Waller, 1994). Our results suggest paludification may also have been an important driving factor for the *Tilia* decline in continental lowland alluvial regions of NW-Europe. Macrobotanical data corroborate firmly that *Tilia* was indeed initially growing within the alluvial area of the Scheldt River and enable its decline to be linked to the RSL rise and subsequent paludification.

The abundance of *Ulmus* must also have been substantial in the local vegetation. Although seeds were completely absent, it is the second most important taxon in the wood remains of deposits dated between c. 5400 and 5170 cal.yrBP. The fluctuations in the pollen percentages of *Ulmus*, including the drop at c. 5400 cal.yrBP, are therefore considered to represent local events, rather than the middle-Holocene *Ulmus* decline. Compared with many other regions in NW-Europe, this event appears to have been less pronounced in N Belgium (Verbruggen et al., 1996).

The high numbers of *Ilex aquifolium* pollen and seeds, both produced sparingly and poorly dispersed, and the occurrence of its wood indicate that this tree or shrub grew as part of the alder-carr vegetation between c. 5520 and 5170 cal.yrBP. This is remarkable, as *Ilex aquifolium* is generally considered intolerant of very wet soils (Peterken and Lloyd, 1967; Weeda et al., 1985). Nevertheless, *Ilex* does occur in alder carr at several English sites (Peterken and Lloyd, 1967), and high *Ilex* pollen values have also been noted in some other studies from similar environments (Scaife, 1988).

The appearance of *Taxus* in the pollen diagram from c. 5170 cal.yrBP onwards correlates with the timing of its occurrence at other sites along the lower Scheldt and many other coastal lowland areas along the southern North Sea (Deforce and Bastiaens, 2007). Although no macroremains of *Taxus* have been found in the samples from Bazel, this tree was most likely part of the local alder-carr vegetation, given that all the contemporary finds of *Taxus* from the region point to its occurrence in carr vegetation on peaty substrates (Branch et al., 2012; Deforce and Bastiaens, 2007).

Potential human impact

Archaeological remains that can be attributed to the Swifterbant-Hazendonk and Michelsberg culture have been found in the vicinity of the sampling site, indicating the presence of temporary hunter-gatherer camps. Therefore, we cannot entirely exclude some local human impact on the vegetation. These cultures correspond with the Mesolithic–Neolithic transition period in the region (Crombé and Vanmontfort, 2007; Louwe Kooijmans, 2007, 2009). In general, there is only limited evidence for (small scale) agricultural activities in the Swifterbant and Hazendonk economies, while hunting, fishing and gathering continued to play a major role (Cappers and Raemaekers, 2008; Deforce et al., 2013; Out, 2008; Rowley-Conwy, 2013; Van Neer et al., 2013). Except for two outliers, all dated archaeological remains fall in the range between *c.* 6950 and 5800 cal. BP, which largely corresponds with the hiatus in the studied sequence. Direct human impact on the local vegetation is thus likely to have been absent or very small in the oldest samples, restricted during the occupation phase which is not covered by the studied sequence, and again virtually absent in the youngest samples.

Some elements in the pollen diagram, such as Cerealia-type and Chenopodiaceae, might however point to human activities in the vicinity of the sampling sites. These occur in levels that are characterised by an important component of allochthonous, mostly brackish and marine microfossils. As Cerealia-type also includes several wild grasses, especially species found growing in littoral environments (Beug, 2004; Joly et al., 2007), and most of the other potential anthropogenic indicators also occur in natural littoral environments, their interpretation as evidence for local crop cultivation or other human disturbance in the vicinity of the site is problematic.

Aquatic environment and fluvial dynamics

With molluscs, fish bones and diatoms being absent, little information is available on the aquatic conditions for the lower part of sequence A, dated around 7060 cal. yr BP. The sedimentology as well as pollen and macrobotanical data do, however, indicate some alluvial influence at the site. Palynomorphs indicative of brackish or marine influence, that is, pollen from halophytic plants, dinoflagellate cysts and foraminifera, are (almost) absent, indicating that the site was situated upstream of the estuary (*sensu* Dalrymple et al., 1992) or situated along a lateral branch that was isolated from the tidal zone. The presence of a hardwood alluvial forest on the levee implies that inundations were ephemeral, occurring no more than a few times a year (Schnitzler, 1994b; Wolf et al., 1997).

Shortly before *c.* 5800 cal. yr BP, marine and brackish palynomorphs increased, with cyanobacteria, green algae and diatoms indicating an influx of estuarine material, originating from brackish conditions. However, molluscs and botanical macroremains which are more likely to represent strictly local conditions do not suggest any salinity increase at the site, whereas the fish fauna indicates slow-flowing water with a salinity level corresponding to the freshwater or the oligohaline zone, that is, <5‰.

There are no indications that the site was within the tidal reach of the Scheldt estuary. With a diurnal tidal regime, the hardwood forest would have been replaced by *Salix*-dominated forest or *Phragmites*. Mollusc species typical of a (freshwater) tidal environment are absent. High numbers of drought-tolerant aquatic taxa and the virtual absence of taxa requiring permanent water, however, point to temporarily inundated conditions.

The most likely setting providing such an assemblage was either at a short distance upstream of the natural tidal limit or along a branch isolated from the part of the river influenced by tides. The presence of marine and brackish microfossils in the alluvial sediments is explained best by the deposition of

sediments during spring tides or storm surges, when estuarine waters penetrated further landward than normal. At such occasions, suspended sediment trapped in the tidal node at the upstream limit of tides following net upstream advection was deposited even further upstream (Wells, 1995). This resulted in the deposition of marine and brackish microfossils and pollen from halophyte vegetation but, according to the other proxies that are more likely to be of local origin, did not result in a significant increase of local salinity levels. It is therefore believed that the recorded pollen from halophyte plants originate from salt marshes much further downstream experiencing erosion at such events.

More clayey deposits with pollen from halophytic plants, dinoflagellate cysts, foraminifera and mesohalobous and polyhalobous diatoms occur at several sites downstream of Bazel at the base of or within peat deposits. These horizons are generally dated between *c.* 6550 and 5650 cal. yr BP (Deforce, 2011; Verbruggen and Denys, 1995; Verhegge et al., 2014). In contrast to Bazel, a decrease of *Alnus* pollen in favour of *Salix* (e.g. Janssens and Ferguson, 1985; Munaut, 1967) or the occurrence of the snail *Mercuria confusa* (Kuijper, 2006) present evidence for freshwater tidal activity at some of these sites, although no actual increase of salinity levels could be inferred.

Upstream of Bazel, peat growth was interrupted by minerogenic sedimentation between *c.* 5820 and 5530 cal. yr BP (Meylemans et al., 2013). Because of the absence of palaeoecological data, it is not yet possible to determine whether this relates to landward penetration of estuarine water during spring tides or increased sediment load of the river.

From 5400 cal. yr BP onwards, the mollusc assemblages indicate increasing wetness. Taxa from permanent water also become more prominent, while inhabitants of faster flowing water recede. Halophyte palynomorphs and marine diatoms continue to be present up to *c.* 5240 cal. yr BP, with brackish diatoms even increasing. Along with the presence of the bones of the marine thinlip mullet (*Liza ramada*), this excludes complete isolation from the river and suggests a connection to the estuary, which was only lost after *c.* 5240 cal. yr BP when peat accumulation restarted.

Present-day hardwood alluvial forests on levees under similar hydrodynamic conditions, that is, which are inundated during spring tides and storm surges, still occur in lowland river valleys in NW-Europe. Their composition is very different from our reconstruction for the middle-Holocene period, however, as these forests are characterised by a low taxonomic diversity and a tree layer dominated by planted taxa such as *Populus x canadensis* and *Salix* spp. (e.g. Wolf et al., 2001). In many of these forests, woodland management was abandoned only recently, and these locations are now rapidly changing into more diverse forest biotopes, with *Quercus*, *Ulmus* and *Fraxinus* colonising the levees (Wolf et al., 1997, 2001).

Conclusion

The use of multiple proxies derived from different habitats and with specific taphonomic properties has enabled a detailed reconstruction of a middle-Holocene alluvial forest and associated hydrological conditions. This forest type was characterised by a very high diversity of woody taxa. It has also been shown that the representation of many of these woody taxa in the pollen record is insufficient to determine their role and dynamics in former alluvial forests communities. Not only for *Fagus sylvatica* and *Populus nigra*, as argued by Brown (2003), but also for *Tilia*, *Ulmus* and *Fraxinus excelsior*, both seeds and wood macrofossils should be considered in addition.

It has also been shown that pollen, diatoms and algae from perimarine fluvial deposits require careful interpretation in terms of tidal activity and palaeosalinity. These microfossils are often used as straightforward palaeosalinity proxies in estuarine

environments (e.g. Byrne et al., 2001; Hijma et al., 2009) but can be transported much further upstream in estuaries than the zone with brackish water or even diurnal tides. This phenomenon has long been recognised (e.g. Simonsen, 1969), but the extent to which such material is incorporated in the depositional record may vary widely with local conditions. In some cases, its predominance may be quite misleading, implying that reliable inferences will usually require supplementary evidence.

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References

- Aarts BG and Nienhuis PH (2003) Fish zonations and guilds as the basis for assessment of ecological integrity of large rivers. *Hydrobiologia* 500: 157–178.
- Adam W (1960) *Faune de Belgique. Mollusques. Tome I: Mollusques terrestres et dulcicoles*. Bruxelles: Patrimoine de l'Institut royal des Sciences naturelles de Belgique.
- Andrieu-Ponel V, Ponel P, Bruneton H et al. (2000) Palaeoenvironments and cultural landscapes of the last 2000 years reconstructed from pollen and Coleopteran records in the Lower Rhône Valley, southern France. *The Holocene* 10: 341–355.
- Barkman JJ (1958) *Phytosociology and Ecology of Cryptogamic Epiphytes Including a Taxonomic Survey and Description of Their Vegetation Units in Europe*. Assen: Van Gorcum & Co.
- Battarbee RW (1986) Diatom analysis. In: Berglund BE (ed.) *Handbook of Holocene Palaeoecology and Palaeohydrology*. Chichester: John Wiley & Sons, pp. 527–563.
- Behre K-E (1970) Die Entwicklungsgeschichte der natürlichen Vegetation im Gebiet der unteren Ems und ihre Abhängigkeit von den Bewegungen des Meeresspiegels. *Probleme der Küstenforschung im südlichen Nordseegebiet* 9: 13–48.
- Behre K-E (1985) Die ursprüngliche Vegetation in den deutschen Marschgebieten und deren Veränderung durch prähistorische Besiedlung und Meeresspiegelsbewegungen. *Verhandlungen der Gesellschaft für Ökologie* 13: 85–96.
- Behre K-E (2004) Coastal development, sea-level change and settlement history during the later Holocene in the clay district of Lower Saxony (Niedersachsen), northern Germany. *Quaternary International* 112: 37–53.
- Beug H-J (2004) *Leitfaden der Pollenbestimmung für Mitteleuropa und angrenzende Gebiete*. München: Verlag Dr. Friedrich Pfeil.
- Birks HJB (1996) Contributions of Quaternary palaeoecology to nature conservation. *Journal of Vegetation Science* 7: 89–98.
- BLWG (2013) BLWG Verspreidingsatlas Planten. Available at: <http://www.verspreidingsatlas.nl/planten> (accessed 13 September 2013).
- Bohn U, Gollub G, Hettwer C et al. (2000) *Karte der natürlichen Vegetation Europas, Maßstab 1:2500000*. Bonn: Bundesamt für Naturschutz.
- Bradshaw RHW and Möller PF (2004) European forest types for biodiversity assessment – A qualitative approach. In: Marchetti M (ed.) *Monitoring and Indicators of Forest Biodiversity in Europe – From Ideas to Operationality: EFI Proceedings 51*. Joensuu: European Forest Institute, pp. 127–133.
- Branch N, Batchelor CR, Cameron NG et al. (2012) Holocene environmental changes in the lower Thames Valley, London, UK: Implications for our understanding of the history of *Taxus* woodland. *The Holocene* 22: 1143–1158.
- Brayshay BA and Dinnin M (1999) Integrated palaeoecological evidence for biodiversity at the floodplain-forest margin. *Journal of Biogeography* 26: 115–131.
- Breine J, Maes J, Stevens M et al. (2008) *Habitat needs to realise conservation goals for fish in estuaries: Case study of the tidal Schelde*. Rapporten van het Instituut voor Natuur- en Bosonderzoek 3. Groenendaal: Instituut voor Natuur- en Bosonderzoek.
- Breine J, Stevens M, Van Den Bergh E et al. (2011) A reference list of fish species for a heavily modified transitional water: The Zeeschelde (Belgium). *Belgian Journal of Zoology* 141: 44–55.
- Bronk Ramsey C (2009) Bayesian analysis of radiocarbon dates. *Radiocarbon* 51: 337–360.
- Brown AG (2002) Learning from the past: Palaeohydrology and palaeoecology. *Freshwater Biology* 47: 817–829.
- Brown AG (2003) Time, space and causality in floodplain palaeoecology. In: Howard AJ, Macklin MG and Passmore DG (eds) *Alluvial Archaeology in Europe*. Lisse: Swets & Zeitlinger, pp. 15–24.
- Brown AG, Harper D and Peterken GF (1997) European floodplain forests: Structure, functioning and management. *Global Ecology and Biogeography Letters* 6: 169–178.
- Bruyndoncx L, Jordaens K, Ysebaert T et al. (2002) Molluscan diversity in tidal marshes along the Scheldt estuary (The Netherlands, Belgium). *Hydrobiologia* 474: 189–196.
- Buijse AD, Coops H, Staras M et al. (2002) Restoration strategies for river floodplains along large lowland rivers in Europe. *Freshwater Biology* 47: 889–907.
- Buijse AD, Klijn F, Leuven RSEW et al. (2005) Rehabilitation of large rivers: References, achievements and integration into river management. *Archiv für Hydrobiologie: Supplement* 155: 1–4.
- Byrne R, Ingram BL, Starratt S et al. (2001) Carbon-isotope, diatom and pollen evidence for late Holocene salinity change in a brackish marsh in the San Francisco estuary. *Quaternary Research* 55: 66–76.
- Cameron R (2008) *Land Snails in the British Isles*. 2nd Edition (Field Studies Council Occasional Publication 79). Shrewsbury: Field Studies Council.
- Cappers RTJ and Raemaekers DCM (2008) Cereal cultivation at Swifterbant? *Current Anthropology* 49: 385–402.
- Cappers RTJ, Bekker RM and Jans JEA (2006) *Digitale zadenatlas van Nederland. Digital seed atlas of the Netherlands*. Groningen: Barkhuis Publishing and Groningen University Library.
- Čejka T and Hamerlík L (2009) Land snails as indicators of soil humidity in Danubian woodland (SW Slovakia). *Polish Journal of Ecology* 57: 741–747.
- Čejka T, Horsák M and Némethová D (2008) The composition and richness of Danubian floodplain forest land snail faunas in relation to forest type and flood frequency. *Journal of Molluscan Studies* 74: 37–45.
- Corenblit D, Steiger J, Gurnell AM et al. (2009) Control of sediment dynamics by vegetation as a key function driving biogeomorphic succession within fluvial corridors. *Earth Surface Processes and Landforms* 34: 1790–1810.
- Corenblit D, Tabacchi E, Steiger J et al. (2007) Reciprocal interactions and adjustments between fluvial landforms and vegetation dynamics in river corridors: A review of complementary approaches. *Earth-Science Reviews* 84: 56–86.
- Crombé P and Vanmontfort B (2007) The neolithisation of the Scheldt basin in western Belgium. In: Whittle A and

- Cummings V (eds) *Going Over: The Mesolithic-Neolithic Transition in North-West Europe: Proceedings of the British Academy 144*. London: British Academy Press, pp. 261–283.
- Dalrymple RW, Zaitlin BA and Boyd R (1992) Estuarine facies models; conceptual basis and stratigraphic implications. *Journal of Sedimentary Research* 62: 1130–1146.
- Davies P (2008) *Snails: Archaeology and Landscape Change*. Oxford: Oxbow Books.
- Davis SR, Brown AG and Dinnin MH (2007) Floodplain connectivity, disturbance and change: A palaeontological investigation of floodplain ecology from south-west England. *Journal of Animal Ecology* 76: 276–288.
- Deforce K (2011) Middle and late Holocene vegetation and landscape evolution of the Scheldt estuary. A palynological study of a peat deposit from Doel (N-Belgium). *Geologica Belgica* 14: 277–288.
- Deforce K and Bastiaens J (2007) The Holocene history of *Taxus baccata* (yew) in Belgium and neighbouring regions. *Belgian Journal of Botany* 140: 222–237.
- Deforce K, Bastiaens J and Crombé P (2014) A reconstruction of middle Holocene alluvial hardwood forests (Lower Scheldt river, N-Belgium) and their exploitation during the Mesolithic-Neolithic transition period (Swifterbant culture, c. 4500–4000 BC). *Quaternaire* 25: 9–21.
- Deforce K, Bastiaens J, Van Neer W et al. (2013) Wood charcoal and seeds as indicators for animal husbandry in a wetland site during the late Mesolithic-early Neolithic transition period (Swifterbant culture, ca. 4600–4000 BC) in NW-Belgium. *Vegetation History and Archaeobotany* 22: 51–60.
- Deiller A-F, Walter J-MN and Trémolières M (2001) Effects of flood interruption on species richness, diversity and floristic composition of woody regeneration in the upper Rhine alluvial hardwood forest. *Regulated Rivers: Research & Management* 17: 393–405.
- De Jong YSDM (2013) Fauna Europaea (Version 2.6.1). Available at: <http://www.faunaeur.org> (accessed 23 August 2013).
- Denys L (1992) *A check-list of the diatoms in the Holocene deposits of the western Belgian coastal plain with a survey of their apparent ecological requirements. I: Introduction, ecological code and complete list*. Belgische Geologische Dienst – Professional paper 246. Brussel: Belgische Geologische Dienst.
- Denys L and Baeteman C (1995) Holocene evolution of relative sea level and local mean high water spring tides in Belgium – A first assessment. *Marine Geology* 124: 1–19.
- De Selys-Longchamps E (1842) Poisons d'eau douce. *Faune Belge* 4: 183–245.
- De Witte GF (1948) *Faune de Belgique. Amphibiens et reptiles*. Bruxelles: Musée royal d'Histoire naturelle de Belgique.
- Dinnin M and Brayshay B (1999) The contribution of a multiproxy approach in reconstructing floodplain development. *Geological Society, London, Special Publications* 163: 179–195.
- Gandouin E and Ponel P (2010) Rivers. In: Dodson J (ed.) *Changing Climates, Earth Systems and Society, International Year of the Planet Earth*. Dordrecht; Heidelberg; London; New York: Springer, pp. 161–175.
- Gittenberger E and Janssen AW (2004) *De Nederlandse zoetwatermollusken. Recente en fossiele weekdieren uit zoet en brak water*. 2nd Edition (Nederlandse Fauna 2). Utrecht: KNNV Uitgeverij.
- Glöer P and Meier-Brook C (2003) *Süßwassermollusken. Ein Bestimmungsschlüssel für die Bundesrepublik Deutschland*. 13th Edition. Hamburg: Deutscher Jugendbund für Naturbeobachtung.
- Grant MJ, Waller MP and Groves JA (2011) The *Tilia* decline: Vegetation change in lowland Britain during the mid and late Holocene. *Quaternary Science Reviews* 30: 394–408.
- Grimm EC (1987) CONISS: A FORTRAN 77 program for stratigraphically constrained cluster analysis by the method of incremental sum of squares. *Computers and Geosciences* 13: 13–35.
- Guiry MD and Guiry GM (2013) *AlgaeBase* (world-wide electronic publication). Galway: National University of Ireland. Available at: <http://www.algaebase.org> (accessed 23 September 2013).
- Hijma MP, Cohen KM, Hoffmann G et al. (2009) From river valley to estuary: The evolution of the Rhine mouth in early to middle Holocene (western Netherlands, Rhine-Meuse delta). *Netherlands Journal of Geosciences* 88: 13–53.
- Hill MO, Preston CD, Bosanquet SDS et al. (2007) *BRYOATT Attributes of British and Irish Mosses, Liverworts and Hornworts*. Cambridge: Centre for Ecology and Hydrology. Available at: <http://www.ceh.ac.uk/products/publications/bryoatt.html> (accessed 29 April 2013).
- Hohensinner S, Jungwirth M, Muhar S et al. (2005) Historical analyses: A foundation for developing and evaluating river-type specific restoration programs. *International Journal of River Basin Management* 3: 87–96.
- Huet M (1959) Profiles and biology of western European streams as related to fish management. *Transactions of the American Fisheries Society* 88: 155–163.
- Janssens W and Ferguson DK (1985) The palaeoecology of the Holocene sediments at Kallo, Northern Belgium. *Review of Palaeobotany and Palynology* 46: 81–95.
- Joly C, Barillé L, Barreau M et al. (2007) Grain and annulus diameter as criteria for distinguishing pollen grains of cereals from wild grasses. *Review of Palaeobotany and Palynology* 146: 221–233.
- Kerney MP and Cameron RAD (1980) *Elseviers slakkengids*. Amsterdam: Elsevier.
- Kiden P (1989) The Late Holocene evolution of the perimarine part of the River Scheldt. In: Henriët JP and De Moor G (eds) *The Quaternary and Tertiary Geology of the Southern Bight, North Sea*. Brussel: Belgische Geologische Dienst, pp. 173–184.
- Killeen I, Aldridge D and Oliver G (2004) *Freshwater Bivalves of Britain and Ireland* (Occasional Publication 82). Shrewsbury: FSC/National Museum of Wales.
- Komárek J and Jankovská V (2001) *Review of the Green Algal Genus Pediastrum; Implication for Pollenanalytical Research* (Bibliotheca Phycologica, Band 108). Berlin; Stuttgart: J. Cramer.
- Krammer K and Lange-Bertalot H (2004) *Die Süßwasserflora von Mitteleuropa 2. Teil 1–4. Nachdruck*. München: Elsevier.
- Kuijper W (2006) Flora en fauna in en rond een Scheldegeul bij Kallo op het einde van het Atlanticum (Beveren, prov. Oost-Vlaanderen). *Relicta* 1: 29–48.
- Landwehr J (1984) *Nieuwe atlas Nederlandse bladmossen*. Zutphen: Thieme.
- Louwe Kooijmans LP (2007) The gradual transition to farming in the Lower Rhine Basin. In: Whittle A and Cummings V (eds) *Going Over: The Mesolithic-Neolithic Transition in North-West Europe*. Oxford: Oxford University Press, pp. 287–309.
- Louwe Kooijmans LP (2009) The agency factor in the process of Neolithisation – A Dutch case study. *Journal of Archaeology in the Low Countries* 1: 27–54.
- Maes B, Bastiaens J, Brinkkemper O et al. (2006) *Inheemse bomen en struiken in Nederland en Vlaanderen*. Amsterdam: Boom.
- Martin K and Sommer M (2004) Relationships between land snail assemblage patterns and soil properties in temperate-humid forest ecosystems. *Journal of Biogeography* 31: 531–545.
- Matthiessen J and Brenner W (1996) Chlorococcalgalgen und Dinoflagellaten-Zysten in rezenten Sedimenten des Greifwalder

- Bodens (suüdlische Ostsee). *Senckenbergiana maritima* 27: 33–48.
- Matthiessen J, Kunz-Pirrig M and Mudie PJ (2000) Freshwater chlorophycean algae in recent marine sediments of the Beaufort, Laptev and Kara Seas (Arctic Ocean). *International Journal of Earth Sciences* 89: 470–485.
- Meire P, Ysebaert T, Van Damme S et al. (2005) The Scheldt estuary: A description of a changing ecosystem. *Hydrobiologia* 540: 1–11.
- Meylemans E, Bogemans F, Storme A et al. (2013) Lateglacial and Holocene fluvial dynamics in the Lower Scheldt basin (N-Belgium) and their impact on the presence, detection and preservation potential of the archaeological record. *Quaternary International* 308–309: 148–161.
- Middelkoop H, Schoor MM, Wolfert HP et al. (2005) Targets for the ecological rehabilitation of the lower Rhine and Meuse based on a historic-geomorphologic reference. *Archiv für Hydrobiologie: Supplement* 155(1–4): 63–88.
- Moore PD, Webb JA and Collinson ME (1991) *Pollen Analysis*. 2nd Edition. Oxford: Blackwell Science.
- Munaut A-V (1967) *Recherches paleo-ecologiques en Basse et Moyenne Belgique*. *Acta Geographica Lovaniensia: Volume* 6. Leuven: Geografisch Instituut, K.U. Leuven.
- Out WA (2008) Neolithisation at the site Brandwijk-Kerkhof, the Netherlands: Natural vegetation, human impact and plant food subsistence. *Vegetation History and Archaeobotany* 17: 25–39.
- Pals JP, Van Geel B and Delfos A (1980) Paleocological studies in the Klokkeweel bog near Hoogkarspel (prov. of Noord-Holland). *Review of Palaeobotany and Palynology* 30: 371–418.
- Pedroli B, De Blust G, Van Looy K et al. (2002) Setting targets in strategies for river restoration. *Landscape Ecology* 17: 5–18.
- Peterken GF and Hughes FMR (1995) Restoration of floodplain rivers in Britain. *Forestry* 68: 187–202.
- Peterken GF and Lloyd PS (1967) *Ilex aquifolium* L. *Journal of Ecology* 55: 841–858.
- Pišút P and Čejka T (2002) Historical development of floodplain site using Mollusca and cartographic evidence. *Ekológia (Bratislava)* 21: 378–396.
- Poll M (1947) *Faune de Belgique. Poissons marins*. Bruxelles: Musée royal d'Histoire naturelle de Belgique.
- Pott R and Hüppe J (2001) *Flussauen- und Vegetationsentwicklung an der mittleren Ems. Zur Geschichte eines Flusses in Nordwestdeutschland* (Abhandlungen aus dem Westfälischen Museum für Naturkunde, vol. 63, iss. 2). Munster: Landschaftsverband Westfalen-Lippe.
- Reimer PJ, Bard E, Bayliss A et al. (2013) IntCal13 and Marine13 radiocarbon age calibration curves 0–50,000 years cal BP. *Radiocarbon* 55: 1869–1887.
- Rowley-Conwy P (2013) North of the frontier: Early domestic animals in Northern Europe. In: Colledge S, Conolly J, Dobney K et al. (eds) *The Origins and Spread of Domestic Animals in Southwest Asia and Europe*. Walnut Creek, CA: Left Coast Press, pp. 283–311.
- Scaife RG (1988) The elm decline in the pollen record of south east England and its relationship to early agriculture. In: Jones M (ed.) *Archaeology and the Flora of the British Isles*. Oxford: Oxford University Committee for Archaeology, pp. 21–33.
- Schnitzler A (1994a) Conservation of biodiversity in alluvial hardwood forests of the temperate zone. The example of the Rhine valley. *Forest Ecology and Management* 68: 385–398.
- Schnitzler A (1994b) European alluvial hardwood forests of large floodplains. *Journal of Biogeography* 21: 605–623.
- Schnitzler A (1995) Successional status of trees in gallery forest along the river Rhine. *Journal of Vegetation Science* 6: 479–486.
- Schnitzler A, Carbiener R and Trémolières M (1992) Ecological segregation between closely related species in the flooded forests of the upper Rhine plain. *New Phytologist* 121: 293–301.
- Schnitzler A, Hale BW and Alsum EM (2007) Examining native and exotic species diversity in European riparian forests. *Biological Conservation* 138: 146–156.
- Schweingruber FH (1990) *Microscopic Wood Anatomy, Structural Variability of Stems and Twigs in Recent and Subfossil Woods from Central Europe*. Birmensdorf: EFWSL.
- Siebel H and During H (2006) *Beknopte mosflora van Nederland en België*. Utrecht: KNNV Uitgeverij.
- Simonsen R (1969) Diatoms as indicators in estuarine environments. *Veröffentlichungen Institut für Meeresforschung zu Bremerhaven* 11: 287–291.
- Sjögren E (1961) Epiphytische Moosvegetation in Laubwäldern der Insel Öland (Schweden). *Acta Phytogeographica Suecica* 44: 1–149.
- Smith AJE (2004) *The Moss Flora of Britain and Ireland*. Cambridge: Cambridge University Press.
- Touw A and Rubers WV (1989) *De Nederlandse Bladmossen*. Utrecht: KNNV Uitgeverij.
- Trémolières M, Sánchez-Pérez JM, Schnitzler A et al. (1998) Impact of river management history on the community structure, species composition and nutrient status in the Rhine alluvial hardwood forest. *Plant Ecology* 135: 59–78.
- Van Braeckel A, Vandevoorde B and Van den Bergh E (2008) *Schorecotopen van de Schelde. Aanzet tot de ontwikkeling van één schorecotopenstelsel voor Vlaanderen en Nederland*. Rapport Instituut voor Natuur en Bosonderzoek 2008/29. Brussel: Instituut voor Natuur en Bosonderzoek.
- Van Dam H, Mertens A and Sinkeldam J (1994) A coded checklist and ecological indicator values of freshwater diatoms from the Netherlands. *Netherlands Journal of Aquatic Ecology* 28: 117–133.
- Van der Putten N, Stieperaere H, Verbruggen C et al. (2004) Holocene palaeoecology and climate history of South Georgia (sub-Antarctica) based on a macrofossil record of bryophytes and seeds. *The Holocene* 14: 382–392.
- Van Geel B (1978) A palaeoecological study of Holocene peat bog sections in Germany and the Netherlands, based on the analysis of pollen, spores and macro- and microscopic remains of fungi, algae, cormophytes and animals. *Review of Palaeobotany and Palynology* 25: 1–120.
- Van Geel B, Klink AG, Pals JP et al. (1986) An upper Eemian lake deposit from Twente, eastern Netherlands. *Review of Palaeobotany and Palynology* 47: 31–61.
- Van Looy K, Honnay O, Bossuyt B et al. (2003) The effects of river embankment and forest fragmentation on the plant species richness and composition of floodplain forests in the Meuse valley, Belgium. *Belgian Journal of Botany* 136: 97–108.
- Van Neer W and Ervynck A (2009) The Holocene occurrence of the European catfish (*Silurus glanis*) in Belgium: The archaeological evidence. *Belgian Journal of Zoology* 139: 70–78.
- Van Neer W, Ervynck A, Lentacker A et al. (2013) Hunting, gathering, fishing and herding: Animal exploitation in Sandy Flanders (NW Belgium) during the second half of the 5th millennium BC. *Environmental Archaeology* 18: 87–101.
- Van Regteren Altena JF, Bakker JA, Clason AT et al. (1962) The Vlaardingen Culture I. *Helinium* 2: 3–35.
- Van Regteren Altena JF, Bakker JA, Clason AT et al. (1963a) The Vlaardingen Culture IV. *Helinium* 3: 39–54.
- Van Regteren Altena JF, Bakker JA, Clason AT et al. (1963b) The Vlaardingen Culture V. *Helinium* 3: 97–120.
- Verbruggen C and Denys L (1995) Early tidal influence on the Lower Schelde, Belgium. In: Gullentops F (ed.) *Wetlands in Flanders: Contributions to Palaeohydrology of the Temperate*

- Zone in the Last 15,000 Years* (Aardkundige Mededelingen 6). Leuven: Leuven University Press, pp. 167–169.
- Verbruggen C, Denys L and Kiden P (1996) Belgium. In: Berglund BE, Birks HJB, Ralska-Jasiewiczowa M et al. (eds) *Palaeoecological Events During the Last 15,000 Years: Regional Syntheses of Palaeoecological Studies of Lakes and Mires in Europe*. Chichester: John Wiley & Sons, pp. 553–574.
- Verhegge J, Missiaen T, Van Strydonck M et al. (2014) Chronology of wetland hydrological dynamics and the Mesolithic-Neolithic transition along the Lower Scheldt: A Bayesian approach. *Radiocarbon* 56: 883–898.
- Walbridge MR and Lockaby BG (1994) Effects of forest management on biogeochemical functions in southern forested wetlands. *Wetlands* 14: 10–17.
- Waller M (1994) Paludification and pollen representation: The influence of wetland size on *Tilia* representation in pollen diagrams. *The Holocene* 4: 430–434.
- Ward JV, Tockner K and Schiemer F (1999) Biodiversity of floodplain ecosystems: Ecotones and connectivity. *Regulated Rivers: Research and Management* 15: 125–139.
- Ward JV, Tockner K, Arscott DB et al. (2002) Riverine landscape diversity. *Freshwater Biology* 47: 517–539.
- Weeda EJ, Westra R, Westra Ch et al. (1985) *Nederlandse oecologische flora*. Hilversum; Haarlem: KNNV uitgeverij.
- Wells JT (1995) Tide-dominated estuaries and tidal rivers. In: Perillo GME (ed.) *Geomorphology and Sedimentology of Estuaries, Developments in Sedimentology*, vol. 53. Amsterdam: Elsevier, pp. 179–206.
- Wiegiers J (1990) Forested wetlands in western Europe. In: Goodall GW, Lugo AE, Brinson M et al. (eds) *Ecosystems of the World 15: Forested Wetlands*. Amsterdam: Elsevier, pp. 407–436.
- Willis KJ and Birks HJB (2006) What is natural? The need for a long-term perspective in biodiversity conservation. *Science* 314: 1261–1265.
- Witkowski A, Lange-Betalot H and Metzeltin D (2000) *Diatom Flora of Marine Coasts I*. Ruggell: A.R.G. Gantner Verlag K.G.
- Wolf RJAM, Stortelder AHF and de Waal RW (2001) *Ooibossen: Bosecosystemen van Nederland Deel 2*. Utrecht: KNNV Uitgeverij.
- Wolf RJAM, Vrieling JG and De Waal R (1997) Riverine woodlands in The Netherlands. *Global Ecology and Biogeography Letters* 6: 287–295.