

Shifty baselines: The landscape factor in archaeological applications of stable carbon and nitrogen isotopes



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ABSTRACT

The carbon (C) and nitrogen (N) stable isotope systems (expressed as $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values) are used extensively in archaeology to study food chains, diet and subsistence practices. However, the variability of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values in different types of landscape is often underestimated leading to calls to consider these values in archaeological contexts as isoscapes. I investigate the relation between landscape characteristics and δC^{13} and δN^{15} values in plants and (human and animal) bones, using a dataset of ~2500 published measurements from modern and past environments in the Netherlands.

Modern sedimentary δC^{13} and δN^{15} values are determined by mixing of terrestrial, riverine, estuarine and marine sediments. Plant $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values vary between different landscape zones depending on , from freshwater wetlands to fully marine settings, depending on factors like the origin of organic matter and soil hydrology.

Archaeological datasets show similar landscape-related variations, with clear differences between plants wild animals and domesticated animals from drylands, freshwater wetlands and marine-influenced wetlands. Plant $\delta^{15}\text{N}$ values (including cereals) can reach levels normally associated with manuring, while herbivore and omnivore $\delta^{15}\text{N}$ values can reach levels normally associated with carnivores. Similarly, humans from different landscape zones have different $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values as well.

This study shows the importance of understanding local and regional food chains when studying subsistence or when making dietary reconstructions - especially in coastal wetlands. Future dietary studies should therefore not rely on standardized universal food chain $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values for plant baselines, herbivores, carnivores and humans. Instead, for each landscape type the food chains and associated isotope values should be determined locally or regionally.

1. Preamble

Some ten years ago, in the special issue of the Journal of Archaeological Science in honour of Richard Klein - and celebrating the 40th anniversary of the journal - two contributions discuss aspects of the use of the carbon (C) and nitrogen (N) stable isotope systems (expressed as $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$): [Makarewicz and Sealy \(2015\)](#) discuss the application of bone collagen stable isotopes to study human diet and mobility, and [Canti and Huisman \(2015\)](#) describe their application in soils and charred plant remains. For the present special issue in honour of Robin Torrence and celebrating the 50th anniversary of the journal of Archaeological Science, I want to revisit these isotope systems in combination with as

geoarchaeology: Following some of the recommendations from [Makarewicz and Sealy \(2015\)](#) and others (e.g. [O'Connell, 2023](#), Guiry et al. 2019), I explore the role of the physical landscape on $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values in the different components in food chains, focussing mostly on wetland and coastal settings.

The main aim of this paper is to explore the relation between of landscape characteristics and $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values in plants and (human and animal) bones. Exploring this spatial aspect will make a connection between bioarchaeological isotope applications and geoarchaeology. As a secondary goal, I will advocate a change in the way $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values in charred plant remains and animal and human bone collagen are often interpreted. This follows from the suggestion of [Makarewicz](#)

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and Sealy (2015) to consider $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values in archaeological contexts as isoscapes - i.e. as having a spatial component – meaning they do not only reflect diet, but also characteristics of the landscape where foodstuffs originated from. Moreover, this study will provide examples and case-studies that can be used as reference, template or inspiration for other archaeological research projects, focussing on differences in isotope values between different types of (wetland and “dry”) landscapes.

I will unpack a dataset of ~2500 published analyses from the Netherlands (and a few from sites in neighbouring Belgium and Germany). This dataset consists of two main groups: One group consists of ~920 $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of sediment, guano, plants and animals that were analysed for biogeochemical and foodweb studies in modern coastal and terrestrial wetland settings. The other dataset consists of ~1530 $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values from charred plants, bone collagen of wild and domesticated animals and humans and charred food crusts from archaeological sites that date from Early Mesolithic to the 19th century AD.

I start with a short introduction on the application of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values in archaeology. A more extensive literature review is available in Digital Supplementary Information 1. Subsequently, I will explore the variability of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ from modern environments, the processes behind this variability and the relation with different types of (wetland) landscapes. This comparison serves to reveal mechanisms causing variability in $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ within and between species in a single ecosystem, as well as differences between ecosystems. This will help to understand the variability in the archaeological data and its spatial scales. I chose to focus on the Netherlands because (1) a large amount of data is already available, (2) the area - though small - includes a range of different environments and (3) the influence of differences in climate are minimal due to the relatively small size of the area.

Next, I discuss $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values from archaeological contexts by following their regional variability in each step of the food chain (from plants to animals to humans), taking into account changes through related to landscape development and human behaviour and subsistence. No attempt will be made to directly compare the modern and archaeological contexts, as the modern data has been affected by major human activities in the last centuries like canalization, dike and polder construction (cf. Digital Supplementary Information 2), intensification of agriculture and environmental measures decreasing nutrient loads (van Beusekom et al., 2019). Finally, I discuss implications of this study for the use and interpretation of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values in archaeological research.

2. Application of stable isotope analyses

2.1. The basis

At the base of the archaeological (and biochemical) applications of stable C and N isotopes lies their fractionation: In a range of biochemical processes and reactions, the lighter isotopes (^{12}C , ^{14}N) are preferred over the heavier ones (^{13}C , ^{15}N). As a result, the reaction products have larger relative amounts of the light isotopes, whereas what is left is enriched in the heavier isotopes. Commonly, the isotope ratios are expressed relative to a standard, with the carbon isotope values expressed as $\delta^{13}\text{C}$ and the nitrogen isotope values as $\delta^{15}\text{N}$ (see Digital Supplementary Information 1 for formulae).

Because of biochemical fractionation processes, $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values in tissues from plants and animals - including humans - can differ as a result of a range of factors, which largely (but not exclusively) fall into four categories:

- (1) The $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values in the carbon and nitrogen compounds assimilated or consumed.
- (2) The relative and absolute amounts of the various assimilated or consumed compounds.

- (3) The way carbon and nitrogen were assimilated or incorporated in plant and animal tissue.
- (4) Growing and living conditions

Key to interpreting the variation in $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values is that they are not only inherited in each trophic step (i.e. from plants to animals, from herbivores to carnivores etc.), but that additional fractionation occurs: Consumers have higher $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values than the consumed food. Although the isotopic increase at each trophic step can vary, they are often roughly estimated at ~1‰ for $\delta^{13}\text{C}$ and ~3–5‰ for $\delta^{15}\text{N}$. Studying $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values in bone collagen and charred plant remains therefore can provide archaeologically relevant information, e.g. on human diet, subsistence and agricultural practices, including animal husbandry and crop cultivation practices. A range of further societal and anthropological information is derived from these basic inferences (cf. O’Connell, 2023). Moreover, methods have been developed to model the relative contribution of different dietary components based on $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values (Fernandes et al., 2014; Hopkins and Ferguson, 2012; Phillips, 2012). For more information on $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ in biochemistry, food-chains and archaeology, see the literature review in Digital Supplementary information 1.

2.2. Criticism

Although the potential of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values for studying human diet, subsistence and agricultural practices is clear, there has been criticism on the way they have been (and are) applied in archaeological research. A major and continuing point of criticism by Makarewicz and Sealy (2015), Guiry (2019) and O’Connell (2023) is the tendency towards too simplistic, black-and-white interpretations. They call for a solid understanding of the food chains, the nutrient dynamics and the variability in $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values in the various compartments of past ecosystems and food sources as a basis for archaeological interpretations. Guiry (2019) indicates that wetland stable carbon and nitrogen isotope values are considerably more complex than often assumed in archaeological studies: The range of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ in freshwater fish bone collagen in ecological literature is much larger than the values commonly anticipated in archaeological palaeodietary interpretation, and encompasses the expected marine values as well. Makarewicz and Sealy (2015) stress the wide and often overlooked or understudied variability (1) at the floral base of food chains (2) between herbivorous taxa (3) due to herbivores’ dietary preferences and availability of food sources throughout the year and (4) the relation between $\delta^{15}\text{N}$ values in diet, different bodily tissues and collagen (see also Phillips et al., 2014). Understanding of such systems can be greatly improved by using data from modern equivalent ecosystems (Lee-Thorpe, 2008).

These points of criticism make it clear that the system of stable C and N isotopes is complex, and that many different variables affect the isotope values within a food chain or ecosystem. Because of this complexity, equifinality (different pathways can lead to the same outcome) is a major concern as well. E.g. high $\delta^{15}\text{N}$ in humans is often equated with marine diets, while high $\delta^{15}\text{N}$ in cereals is often one-on-one interpreted with manuring. However, in both cases there may be other causes for such values. Moreover, there is a tendency to interpret relative small variations (a few ‰) within a population of animals or humans as significant differences in diet, disregarding natural variability. In light of the concerns with too simplistic interpretation of a complex system, a tendency to disregard (traditional) archaeological evidence in the interpretation of isotope values is worrying. Milner et al. (2004), in their critique on Richards et al. (2003a) were probably the first to highlight this. Resolving contradictions between archaeological and isotopic data needs to take into account the wider context of isotope ecology as well as aspects like archaeological context, representativeness and an understanding of the complexity of dietary isotope analyses (see also Milner et al. (2006)). This complexity also affects dietary modelling: Dietary models based on stable isotope values tend to

underestimate not only the complexity of the nitrogen food webs - and therefore $\delta^{15}\text{N}$ values - in many ecosystems, but also of the relation between food, body tissue and collagen $\delta^{15}\text{N}$ values (Makarewicz and Sealy, 2015).

2.3. Outlook

As an alternative method, some researchers advocate the use of additional isotopes (O, S, Zn etc.) to improve the potential for food web reconstruction (e.g. Jaouen et al., 2016; Leach et al., 2003; McCormack et al., 2021; Richards et al., 2003b; Sharpe et al., 2021; Stantis et al., 2021). Others call for a replacement of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ by the compound-specific isotope analyses (CSIA). E.g. $\delta^{15}\text{N}$ values in specific proteins would form a much more reliable indicator for fish consumption (Styring et al., 2010; Webb et al., 2018). However, the more complex nature and (therefore) higher costs prevent the use of these techniques in the numbers that are common in bulk analyses.

If we want to continue using the bulk $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ analyses, the call of Makarewicz and Sealy (2015) to abandon standardized baselines and to use isoscape modelling is highly relevant. Recent significant steps in that direction are publications by Meadows and Fischer (2024) on the specific $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values in the eelgrass biotope, by Prummel et al.

(2024) on the effects of saltmarsh grazing on wild and domesticated herbivores respectively and by Reade et al. (2023) on spatial and temporal variation of $\delta^{15}\text{N}$ in animal bone collagen in the European Late Pleistocene and Early Holocene. The present paper not only can serve as a next step into developing geoarchaeological aspects of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values in food chains and their significance for archaeological applications, but also demonstrates that these analyses can be more useful than sometimes assumed.

3. Approach

I use two aggregated datasets of published and reported $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values: One with modern environmental data, and one with archaeology-derived data. The modern environmental data (particulate organic matter or POM, bird guano, primary producers - plants, diatoms, algae - mesofauna, fish and sea mammals) is derived from several study areas within the Netherlands (See Fig. 1A for locations): from the estuaries of the Scheldt (Westerschelde), Rhine, Ems and Elbe rivers (Middelburg and Harman, 2007), from dynamic intertidal mudflats, supratidal salt marshes and uninhabited small islands in the Wadden sea area (Nauta et al., 2023; Reijers et al., 2024) from the intertidal and supratidal landscape of the island of Schiermonnikoog (Schrama et al.,

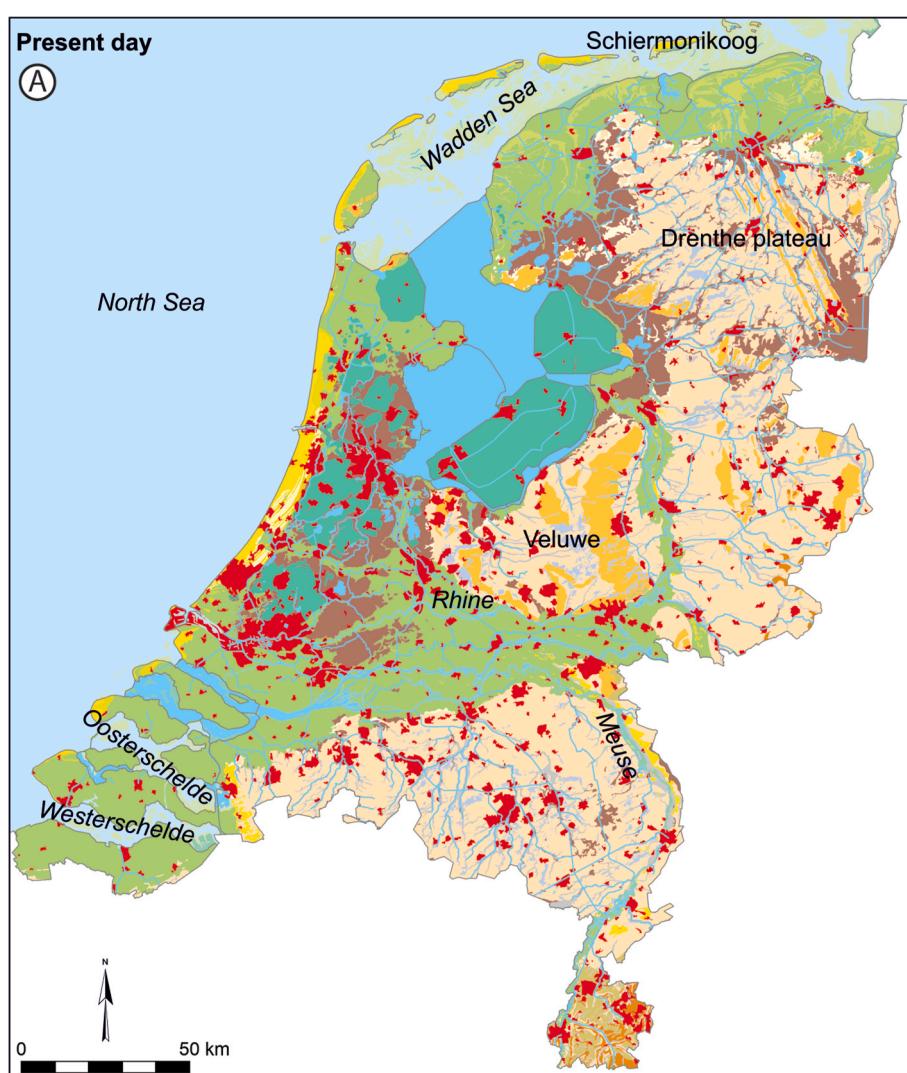
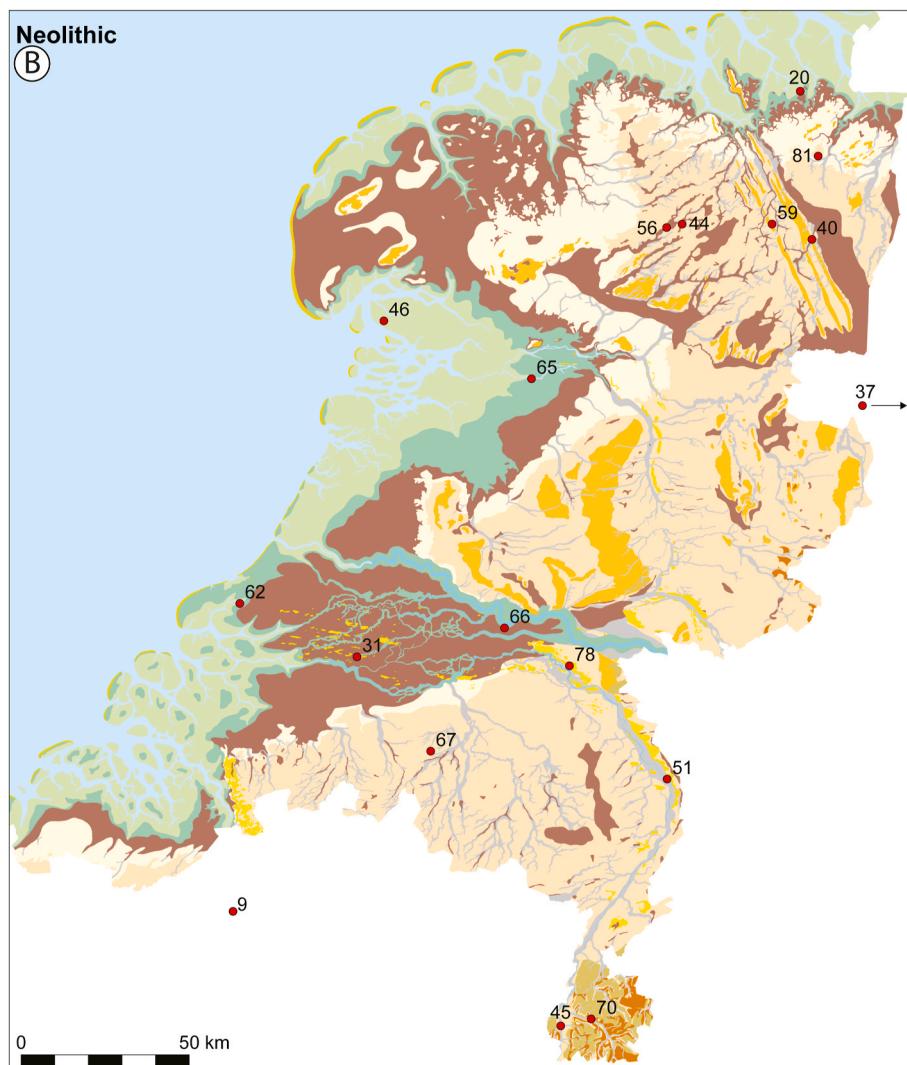


Fig. 1. Maps of the study area. A: Geographic map of the Netherlands, indicating the regions where modern data was derived from, as well as other geographical names used in the text. B: Example of a palaeogeographic map (Neolithic) with the archaeological sites from which data was obtained. (Palaeogeographic map based on Vos et al., 2020). Maps for the other periods can be found in Supplementary information 2.



Holocene landscape

- High dunes
- Beach barriers and low dunes
- Beach plains and dune valleys
- Tidal flats
- Salt marshes and floodplains
- Salt-marsh ridges and tidal levees
- Peat areas
- Ridges in embanked salt marshes and floodplains
- Embanked salt marshes and floodplains
- Reclaimed lake
- Urban areas
- nr Sites

Pleistocene landscape

- Inner water
- Outer water
- Pleistocene sand areas, below 16 m -NAP
- Pleistocene sand areas, 16 - 0 m -NAP
- Pleistocene sand areas, above 0 m NAP
- Floodplains and stream valleys
- River dunes
- Loess area
- Ice-pushed ridges, ice-pushed till and ridges and valleys shaped with flowing land ice
- Areas with Tertiary and older deposits
- Drift-sand areas

Fig. 1. (continued).

2013; Prummel et al., 2024) and from the North Sea (Riera et al., 2002; Jansen et al., 2012). This dataset is available as Digital Supplementary Information 3. Note that some datapoints for plant and animal data are from individual specimens, and others from a mix of multiple specimens. No Suess-correction (to account for recent changes in global atmospheric $\delta^{13}\text{C}$) was applied to this modern data. Not only because no direct comparison is made with the archaeological data: Within the modern dataset, the combinations of different ecosystems and landscapes, makes this correction hazardous to apply (cf. Clark et al., 2020; Dombrosky, 2020; Eide et al., 2017). Note furthermore that the POM estuary data of Middelburg and Harman (2007) was collected between 1996 and 1998, so $\sim 15\text{--}25$ years before the Wadden sea area data, a period with declining nutrient input in the Wadden sea area (van Beusekom et al., 2019). This may limit the potential for comparisons within the modern dataset.

The archaeological dataset is aggregated from reported and published $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of charred plant remains, bone collagen (animal and human) and food crusts in ceramics from 82 archaeological sites (Table 1 for sites and sample numbers). Some of these objects have ^{14}C dates, but most are dated by context. Where available, data from single specimen analyses were used, even if averages were used in the original publication. It is not clear in all reports whether single or multiple specimens of charred seeds or plant remains were analysed. This dataset can be found in Digital Supplementary Information 4. For the present study, the results are grouped roughly in 5 groups according to age. These groups were chosen to account for major changes in the landscape as well as in regional subsistence and socio-economic developments:

Mesolithic	(~9500 - 5000 BC)	Hunter-gatherer subsistence Drowning of North Sea area, including Doggerland
Neolithic	(~5000 - 2000BC)	Start of agricultural subsistence Closing of Dutch coast by coastal barrier
Late Prehistoric	(2000-0 BC)	Extensive peat growth
Early Historic	(0-1200 AD)	Increase in economic connections Large-scale peat colonization
Late Historic	(post 1200 AD)	Major erosion events Dike construction Urbanisation

Each site is assigned to a landscape type:

Loess	Loess-covered landscape, restricted to the very South-East of the study area
Coversand	Coversand-covered (Pleistocene) landscape
Riverine floodplains	Valley and upper delta
Riverine wetlands	Lower delta, distal floodbasin fens and swamps
Lakeshore	Only one case: Lake Hüde (D)
Lagoon wetlands	Central Netherlands fens, swamps and tidal fringe lands
Supratidal	Tidal landscape zone: floods only at spring tides or during storms
Coastal barrier	Beach ridge complex with low dunes (ridges), peaty swales and freshwater (rainfall) storage. This zone lies a few kilometre inland of the actual coast with active sandy beach and dunes
Urban	Post 1200 AD cities and monasteries
Dredge finds	Dredge finds from the North Sea

For palaeogeographic maps with the distribution of the sites per period see Digital Supplementary Information 2. The map for the Neolithic is given in Fig. 1B as an example. Sites that are on or close to a boundary of dryland and wetland sites (e.g. between coversand and riverine floodplain) have been assigned to the wetland landscape, assuming that the latter would play a dominant role in food procurement. Two groups are non-spatial: The first group ("Dredge finds") consists of a significant number of bone collagen analyses from material that has been dredged from North Sea floor, mostly as a result of

dredging activity during construction of the "2nd Maasvlakte" and the "Zandmotor" (van der Plicht et al., 2016; van der Plicht and Kuitems, 2022; Kuitems and van der Plicht, 2022). The second group ("Urban") consists of Late Historic larger settlements, cities and monasteries. In some sites (e.g. Groningen), material from two periods fall into two different landscape classes (e.g. Groningen is Supratidal in the Early Historic period and Urban in the Late Historic period).

4. Results: modern environments

4.1. Sediment and particulate matter

Middelburg and Nieuwenhuizen (1998) defined four sedimentary endmembers in particulate organic matter (POM) in the Westerschelde estuary (Fig. 2). The **terrestrial** endmember - representing sediment that washed into the river from surrounding dry land - shows values for $\delta^{15}\text{N}$ (~3.5‰) and $\delta^{13}\text{C}$ (~−26‰) that matches terrestrial C3 plants. **Riverine** and **marine** endmembers both have high $\delta^{15}\text{N}$ values (~9‰) but very different $\delta^{13}\text{C}$ values (riverine ~−30‰, marine ~−9‰). **Estuarine** sediments have $\delta^{13}\text{C}$ values comparable with riverine values (~−29‰) but even higher $\delta^{15}\text{N}$ values (~−15‰) because of high $\delta^{15}\text{N}$ values in particulate organic matter (Middelburg and Nieuwenhuizen, 1998). The origin of relatively high $\delta^{15}\text{N}$ values in the riverine, marine and estuarine end-members may be caused by microbial decay processes of terrestrial organic matter that ends up in a river (cf. Guiry, 2019), but could also be related to primary production by algae (Middelburg and Harman, 2007).

$\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values in suspended matter in Atlantic estuaries from Middelburg and Harman (2007) seem to show mixing of - probably riverine - material (~ $\delta^{13}\text{C}$ −31 to −27‰, $\delta^{15}\text{N}$ 3–9‰) with - probably marine - material with higher values (~ $\delta^{13}\text{C}$ −22 to −18‰, $\delta^{15}\text{N}$ 6–12‰; see Fig. 2). Elevated $\delta^{15}\text{N}$ values can occur on the contact between fresh (riverine) and saline (marine) water, reaching extremely values (12–27‰) in the Westerschelde estuary. These values are attributed to the incorporation by algae of ^{15}N -enriched ammonia (NH_3). The ^{15}N -enriching in the ammonia is caused by redox transformation between NH_3 and oxidized nitrogen species (e.g. NO_x , NO_3^-). This is related to the formation of a stratified water-column, where oxygen-depleted water comes into contact with oxygenated water. This is a regular occurrence in algae blooms during warm seasons (De Brabandere et al., 2006; Dähnke et al., 2022; Middelburg and Harman, 2007). The algae can contribute to higher $\delta^{15}\text{N}$ values in suspended matter, POM and sediments as well, although these values can be diluted by organic matter from other sources. As a result, organic sediments from environments with regular algae blooms and few other sources of organic matter can have high $\delta^{15}\text{N}$ values that may far exceed the expected baselines for primary producers. Whether these conditions are comparable to archaeological settings is debatable: On the one hand, modern algae blooms may be triggered by a heavy loading of riverine, estuarine and coastal waters with human-derived nutrients, despite a significant decrease since the late 1980's (van Beusekom et al., 2019). However, that algae blooms could occur in the deeper past is attested by the occurrence of diatomite deposits in the buried and submerged Neolithic Swifterbant and IJsselmeer lagoonal wetlands (Familetto et al.).

The $\delta^{15}\text{N}$ values in the Wadden Sea sediments (Nauta et al., 2023; Reijers et al., 2024; Schrama et al., 2013), are comparable to those in the Westerschelde, but the $\delta^{13}\text{C}$ values are much higher in Wadden sea sediment (>−12‰). This is probably caused by a large contribution of marine algae and seaweed-derived organic matter to the sedimentary organic matter. It is remarkable that the $\delta^{13}\text{C}$ in Wadden Sea sediment is so different from that of particulate organic matter (POM) – and from the POM-like intertidal and supratidal sediments of Schiermonnikoog as well. Apparently different types of deposits within this area can have very different isotope values, possibly due to the incorporation of different types of organic matter. The $\delta^{13}\text{C}$ values of the Wadden Sea POM and sediments on the Schiermonnikoog tidal flats are lower than those of the

Table 1

List of sites, with region, age and type of sampled material for C,N isotope analyses and literature references. 9 human individuals from Groningen (*) have ages that fall on the transition from Early or Late Historic. These are grouped within the Late Historic age group here and in the graphs.

Site nr.	Site name	Landscape unit	Charred plant remains	Wood charcoal	Foodcrusts	Animal bones and teeth	Human bones and teeth	Data Sources
Mesolithic								
0	Dredge finds				41	37		van der Plicht et al., (2016), Kuitems and van der Plicht (2022), van der Plicht and Kuitems (2022)
7	Balkweg	Coversand			1			Prummel et al. (2024)
38	Jardinga	Coversand			4			Prummel et al. (2024)
43	Lochtenrek	Coversand			1			Prummel et al. (2024)
53	Prikkedam/Tjonger	Coversand			1			van Kruining (2018)
Neolithic								
0	Dredge finds				6	1		van der Plicht et al., (2016), Kuitems and van der Plicht (2022), van der Plicht & Kuitems 2023
9	Bazel (B)	Riverine floodplains			49	1		Meylemans et al., (2016); Crombé et al., 2020;
19	Eenumerhoogte	Supratidal			1			Prummel et al. (2024)
30	Hardinxveld	Riverine wetlands			105	22		Smits and van der Plicht (2009), Brusgaard et al., (2022), Raemaekers <i>in prep</i> Demirci (2022)
37	Huede (D)	Lakeshore		21				Prummel et al. (2024)
39	Kanaal Buinen-Schoonoord	Coversand			1			Prummel et al. (2024)
43	Lochtenrek	Coversand			2			Prummel et al. (2024)
44	Maastricht	Riverine floodplains	1					Brinkkemper et al. (2018)
45	Mienakker	Supratidal	1			1		Brinkkemper et al., (2018), Lanting and van der Plicht (2000)
48	Ooijen/Ooijen-Wanssum	Riverine floodplains		2				Tump (2021), Tump and Kubistal (2023), Tump and Tebbens (2023)
53	Prikkedam/Tjonger	Coversand			2			van Kruining (2018)
56	Rolde-Deurzerbroek	Coversand			1			Prummel et al. (2024)
59	Schippluiden	Coastal barrier			11	39	20	Smits et al., (2010), Smits and van der Plicht (2009), Kamjan et al., (2020)
62	Swifterbant	Lagoon wetlands			110		10	Smits et al., (2010), Brusgaard et al., (2024)
63	Tiel Medel	Riverine floodplains				6		Gron et al. (2023)
63	Tiel Medel	Riverine floodplains	50					Gron et al. (2023)
64	Tilburg - Berkel-Enschot	Coversand		3				Mostert (2021)
67	Valkenburg	Loess	1					Brinkkemper et al. (2018)
75	Wychen	Riverine floodplains	1					Brinkkemper et al. (2018)
78	Zuidbroek	Coversand			1			Prummel et al. (2024)
Late Prehistoric								
0	Dredge finds				7	7		van der Plicht et al., (2016), Kuitems and van der Plicht (2022), van der Plicht & Kuitems 2024
1	Achlum	Supratidal			2			Prummel et al. (2024)
4	Amersfoort	Coversand	1					Brinkkemper et al. (2018)
6	Arkum	Supratidal			2			Prummel et al. (2024)
12	Bovenkarspel	Supratidal	3					Bakels (2018), 2019
14	Boxmeer	Riverine floodplains	1					Bakels (2018), 2019
15	Dalen	Coversand			1			Bakels (2018), 2019
17	Deventer	Coversand	2	1				Brinkkemper et al. (2018)
20	Eigenblok	Riverine floodplains	1					Brinkkemper et al. (2018)
21	Eindhoven	Coversand		1				Kubistal (2023)
23	Englim	Supratidal			4			Prummel et al. (2024)
24	Enkhuizen Haling	Supratidal	1					Bakels (2018), 2019
25	Ezinge	Supratidal			3			Prummel et al. (2024)
32	Helvoirt	Coversand		8				van As and Pieters (2021)
35	Hoogeveen	Coversand			2			Prummel et al. (2024)
40	Leeuwarden	Supratidal			1			De Roller (2020)
48	Ooijen/Ooijen-Wanssum	Riverine floodplains	6	14				Tump (2021), Tump and Kubistal (2023), Tump and Tebbens (2023)
52	Paddepoeel	Supratidal			1			Prummel et al. (2024)
55	Rasquert	Supratidal					1	A. Nijboer, unpublished data
56	Rolde-Deurzerbroek	Coversand			1			Prummel et al. (2024)

(continued on next page)

Table 1 (continued)

Site nr.	Site name	Landscape unit	Charred plant remains	Wood charcoal	Foodcrusts	Animal bones and teeth	Human bones and teeth	Data Sources
65	Twisk	Supratidal	2					Bakels (2018), 2019
66	Urmond	Riverine floodplains		1				Porreij-Lyklema (2023)
70	Voerendaal	Loess	1					Brinkkemper et al., (2018), Kooistra and Brinkkemper, 2023
72	Weerselo	Coversand	1					Brinkkemper et al. (2018)
73	Westwoud	Supratidal	2					Bakels (2018), 2019
77	Zeist	Coversand	3	3				Brouwer (2021b)
Historic pre 1200 AD								
0	Dredge finds					3	12	van der Plicht et al., (2016), Kuitems and van der Plicht (2022), van der Plicht & Kuitems 2025
1	Achlum	Supratidal				11		Prummel et al. (2024)
5	Anjum	Supratidal				7		Prummel et al. (2024)
6	Arkum	Supratidal				2		Prummel et al. (2024)
8	Baradeel	Supratidal				3	2	Nijboer, unpublished data
11	Blokhuizen	Supratidal					18	McManus et al. (2013)
19	Eenumerhoogte	Supratidal				2		Prummel et al. (2024)
22	Elst G.	Riverine floodplains	1					Brinkkemper et al. (2018)
25	Ezinge	Supratidal				1		Prummel et al. (2024)
28	Groningen	Supratidal				59	110*	Prummel et al., (2024), Huis in 't Veld, 2018
31	Haren	Coversand				5		Prummel et al. (2024)
32	Helvoirt	Coversand		1				van As and Pieters (2021)
33	Hogebeintum	Supratidal					9	Kootker and Heeren (2022)
34	Holwerd	Supratidal				1		Prummel et al. (2024)
35	Hoogeveen	Coversand				1		Prummel et al. (2024)
36	Houten	Riverine floodplains					1	Kootker and Heeren (2022)
40	Leeuwarden	Supratidal				4	1	De Roller (2020)
41	Leiden	Riverine floodplains		11				Meijer and van Dam, 2023
42	Lent	Riverine floodplains					8	Kootker and Heeren (2022)
44	Maastricht	Riverine floodplains	1					Brinkkemper et al. (2018)
48	Ooijen/Ooijen-Wanssum	Riverine floodplains		1				Tump (2021), Tump and Kubistal (2023), Tump and Tebbens (2023)
49	Oosterbeintum	Supratidal				52	43	McManus et al. (2013)
50	Oud Aalden (Coevorden)	Coversand		3				Hendriks and Oude Rengerink, 2021
52	Paddepoel	Supratidal				1		Prummel et al. (2024)
54	Raalte	Coversand	1					Brinkkemper et al. (2018)
55	Rasquert	Supratidal				2	14	A. Nijboer, unpublished data
56	Rolde-Deurzerbroek	Coversand				2		Prummel et al. (2024)
61	Spijkenisse	Riverine floodplains	2					Brinkkemper et al. (2018)
68	Vatrop	Coastal barrier					1	Bartels and Roessingh (2024)
69	Venray	Coversand	1					Brinkkemper et al. (2018)
70	Voerendaal	Loess	21					Brinkkemper et al., (2018), Kooistra & Brinkkemper 2023
71	Voorhuizen	Coversand		3				Brouwer (2021a)
74	Wijnaldum	Supratidal			4		1	Prummel et al., (2024), Nijboer unpublished data
79	Zutphen	River	1					Brinkkemper et al. (2018)
Historic post 1200 AD								
0	Dredge finds	Sea					61	van der Plicht et al., (2016), Kuitems and van der Plicht (2022), van der Plicht & Kuitems 2026
1	Achlum	Supratidal				3		Prummel et al. (2024)
2	Aduard	Urban					20	Schreuder (2023)
3	Alkmaar	Urban				17	25	Schats et al. (2021)
8	Baradeel	Supratidal				2	1	Nijboer, unpublished data
10	Birdaard	Supratidal				1		Prummel et al. (2024)
13	Boven-Tjonger	Coversand				1		Prummel et al. (2024)
16	De Held	Supratidal				11		Prummel et al. (2024)
17	Deventer	Urban	1					Brinkkemper et al. (2018)
18	Dwingeloo	Coversand				4		Prummel et al. (2024)
26	Ferwert	Supratidal				1		Prummel et al. (2024)
27	Goutum	Supratidal				1		Prummel et al. (2024)
28	Groningen	Urban				84	32*	Prummel et al., (2024), Huis in 't Veld, 2018
39	Haarlem	Coversand	1					Aarts (2021)

(continued on next page)

Table 1 (continued)

Site nr.	Site name	Landscape unit	Charred plant remains	Wood charcoal	Foodcrusts	Animal bones and teeth	Human bones and teeth	Data Sources
39	Kanaal Buinen-Schoonoord	Coversand			1			Prummel et al. (2024)
41	Leiden	Urban		6				Meijer and van Dam, 2023
46	Nijmegen (Waal)	Urban	1				154	Willemse (2019)
47	Oldenzaal	Urban			7			Altena et al. (2016)
48	Ooijen/Ooijen-Wanssum	Riverine floodplains		1				Tump (2021), Tump and Kubistal (2023), Tump and Tebbens (2023)
51	Oud Rilland/Reimeswaal	Coastal barrier		1				van de Glind et al. (2021)
55	Rasquert	Supratidal			1			A. Nijboer, unpublished data
57	Rotterdam	Urban	2					Brinkkemper et al. (2018)
58	Schijndel	Coversand		1				Sommers and de Koning (2021)
60	Sint-Michielsgestel	Coversand					3	de Winter (2019)
76	Yesse	Urban			14		11	Bolchini (2020)

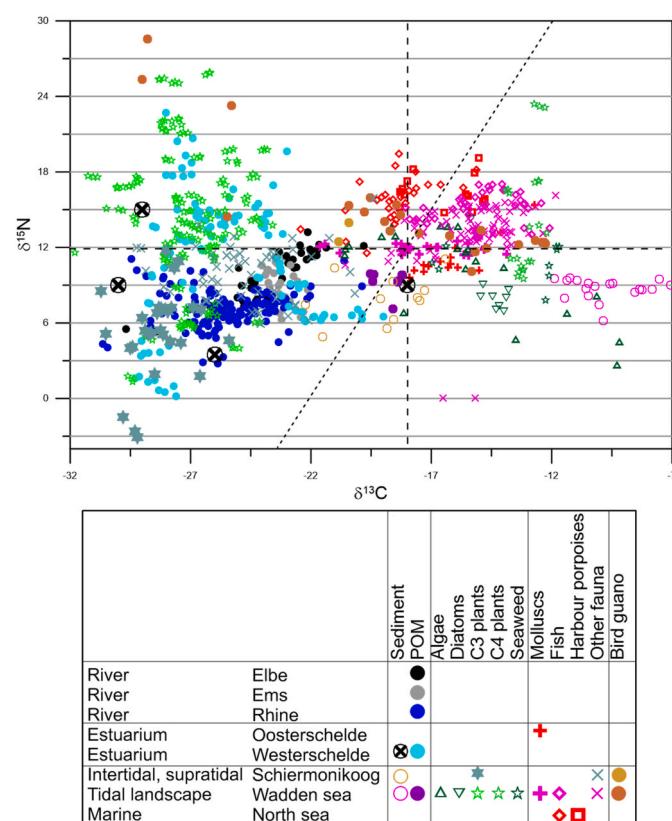


Fig. 2. Plot of $\delta^{13}\text{C}$ - $\delta^{15}\text{N}$ values from modern coastal wetlands. The four sediment endmembers from the Westerschelde estuary are derived from Middelburg and Nieuwenhuize (1998). Particulate organic matter (POM) in estuaries are from Middelburg and Harman (2007). Wadden Sea and Schiermonnikoog data is from Schrama et al. (2013), Nauta et al., 2023, Rijers et al., 2024 and Prummel et al. (2024). Data on marine animals (Oosterschelde and North Sea) are from Riera et al. (2002) and Jansen et al. (2012). The dataset is in Supplementary Information 3, partial graphs of this dataset are in Supplementary Information 5. The slanted broken line indicates a general direction of trophic level steps (1‰ for $\delta^{13}\text{C}$, 3‰ for $\delta^{15}\text{N}$) while the grey horizontal lines are placed at 3‰ $\delta^{13}\text{C}$ intervals. Horizontal and vertical broken lines separate the quadrants as defined by Schulting (2018) for human $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values. For reference, the same slanted broken line, grey horizontal lines and quadrant separators are used in the following graphs in this publication.

Wadden Sea sediments and are mostly higher than those of the marine-influenced parts of the Westerschelde POM (Fig. 2).

4.2. Primary producers

Algae, diatoms and seaweed have considerable ranges in values of $\delta^{13}\text{C}$ (~−20 to −9‰) and $\delta^{15}\text{N}$ (~2–14‰). Moreover, there seems to be a negative correlation, with high $\delta^{13}\text{C}$ correlating with low $\delta^{15}\text{N}$ in the algae. The cause for this is unclear.

Wadden sea plants fall in two separate groups: The C3 plants (including the Schiermonnikoog intertidal and supratidal vegetation) have $\delta^{13}\text{C}$ values of ~−32 to −24‰ whereas C4 plants have $\delta^{13}\text{C}$ values of ~−15 to −12‰. The nitrogen isotope variability is more complex: Most plants have $\delta^{15}\text{N}$ values between ~8 and 14‰, although some C3 plants have lower values (as low as ~−3‰). Schrama et al. (2013) indicate that the higher $\delta^{15}\text{N}$ values occur on lower, more recently formed mudflats that are still regularly inundated (intertidal zone), whereas the lower values are from higher, older landscape elements that flood only now and then (supratidal zone). (Indigenous) C3 and C4 plants from small islands with bird colonies (Rijers et al., 2024), however, reach exceptionally high $\delta^{15}\text{N}$ values, up to ~26‰. This is related to the large amounts of guano that accumulate here, causing a form of natural manuring. The bird guano itself shows massive differences in $\delta^{13}\text{C}$ (from ~−32 to −12‰), most likely resulting from differences in dietary preferences between (mostly carnivorous) bird species. $\delta^{15}\text{N}$ values lie between ~12 and 16‰, but there are a few high outliers that combine low $\delta^{13}\text{C}$ (~−25 to −29‰) with high $\delta^{15}\text{N}$ (~23–29‰).

4.3. Animals

The $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of marine molluscs and other invertebrates, fish and sea mammals from the North Sea and the Oosterschelde estuary in Fig. 2 highlight the close proximity between primary producers and some of the marine species, suggesting that the relatively high $\delta^{15}\text{N}$ levels usually found in marine species are not always caused by long food-chains with many trophic levels (as indicated by Schoeninger and DeNiro, 1984). Rather - at least in these environments - be related as well to high $\delta^{15}\text{N}$ baseline values in primary producers.

5. Results: the archaeological data

5.1. General characteristics

Fig. 3 gives an overview of the aggregated dataset of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values in the various sampled materials from archaeological data. (For plots showing age and landscape zones see Supplementary Information 6). Several apparent groups and outliers are indicated. Of these, the marine animals plot in the same quadrant as the modern fish and

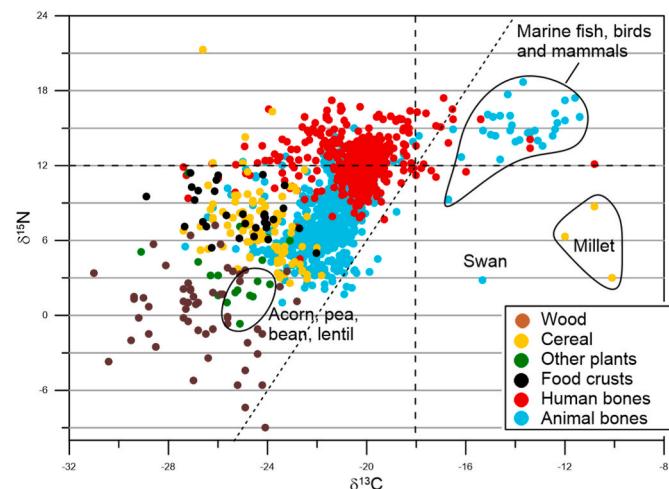


Fig. 3. Plots of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values in the complete archaeological dataset, divided by type of sampled material. Specific groups and samples that stand out in this general plot are indicated separately: Marine fish and mammals; millet as the only C4 plants in the dataset; a group of fabaceae ($n = 5$) and acorns ($n = 2$) and a single swan. This total dataset is shown for reference in light grey in the subsequent plots. See Digital Supplementary Information 4 for this complete archaeological dataset, and Digital Supplementary Information 6A,B for plots showing grouping according to age and landscape.

shellfish (cf. Fig. 2). Of the charred plant analyses, three (iron age) millet samples show the typical high $\delta^{13}\text{C}$ values of C4 plants. Another clear group is formed by pulses and acorns. The low values for the pulses are typical, as obtain their nitrogen compounds from symbiotic bacteria that synthesize them directly from N_2 in air.

The rest of the data in Fig. 3 form a massive cluster, although it is noteworthy that the upper left quadrant is only filled with analyses from Mesolithic and Neolithic age, and the lower left quadrant only with wood charcoal. Further unpicking is done below using graphs in which selections of the data are shown, while the rest of the data are given in light grey symbols in the background.

5.2. Plants

Leaving out the millet analyses, the plant data (Fig. 4A) form two groups: wood charcoal and charred non-woody plants - which are mostly cereals. Within the wood charcoal group, the low $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values from ash and alder probably reflect their natural habitat of nutrient-poor wetlands. The oak charcoal falls into two groups, one with $\delta^{13}\text{C}$ around -25‰ and $\delta^{15}\text{N}$ between -9 and 0‰ , the other with $\delta^{13}\text{C}$ around -28 to -25‰ and $\delta^{15}\text{N}$ between 0 and 6‰ . There is no apparent correlation of these groups with the landscape zones (mostly riverine floodplain, coversand and urban).

Most of the cereal $\delta^{15}\text{N}$ values fall between 3 and 12‰ . These values are in the same range as those of plants with elevated $\delta^{15}\text{N}$ in wetland soils due to reducing conditions – triggered denitrification in their root zone (Fustec et al., 1991; Clément et al., 2003). Within the cereal group, barley tends to have in general slightly lower $\delta^{13}\text{C}$ values than emmer wheat. This may indicate that this more robust type of cereal was grown in wetter conditions, but it could also simply be an interspecies-difference. Recalculating the range of cereal $\delta^{13}\text{C}$ values (~ -23 to -27.4‰) to $\Delta^{13}\text{C}$ values (assuming ambient CO_2 has $\delta^{13}\text{C}_{\text{air}} = 6.4\text{‰}$) give values between 16.7 and 21.5‰ . A comparison with the data in Fabio et al. (2005) and Wallace et al. (2015) shows that these values correlate with wet growing conditions. The variability within the riverine group is high, especially since most of these analyses are from three archaeological soil features on the same site (Tiel-Medel; Gron et al., 2023).

The apparent negative correlation between $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values in

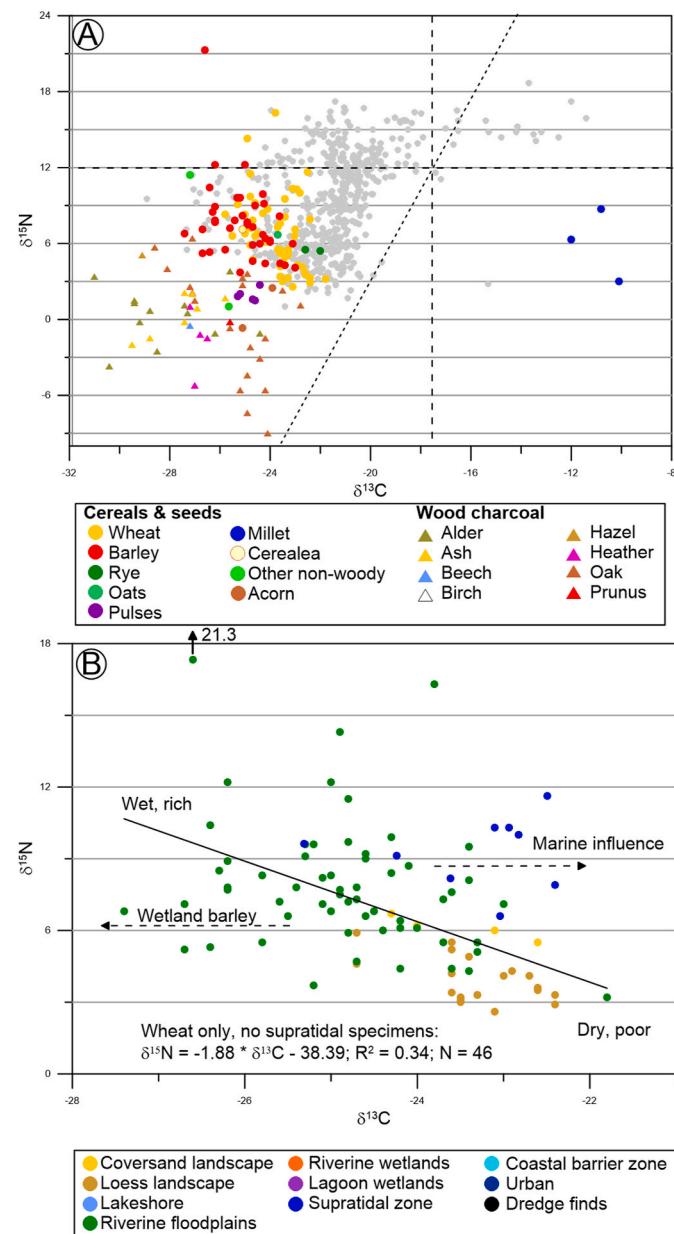


Fig. 4. Plots of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values in charred plant seeds from archaeological sites. A: All plants, woody and non-woody. Plants from wetlands tend to have systematically lower $\delta^{13}\text{C}$ and higher $\delta^{15}\text{N}$ values than plants from dry lands. B: Cut-out from A, only cereals, divided by region. The solid line is a linear regression on the wheat, leaving out the supratidal samples ($\delta^{15}\text{N} = -1.88 * \delta^{13}\text{C} - 38.39$; $R^2 = 0.34$; $N = 46$), indicating a moderate negative correlation. The broken line with arrow indicates a general trend towards higher $\delta^{13}\text{C}$ in supratidal wetlands compared to freshwater wetlands. C: Legend for regions. See also Digital Supplementary Information 6 C.

cereals (esp. wheat; see Fig. 4B) is remarkable. This correlation seems to be related to the landscape setting, with grains from riverine floodplain sites having $\delta^{15}\text{N}$ values from ~ 4 to $>12\text{‰}$ whereas grains from dryland areas (loess, coversand) have $\delta^{15}\text{N}$ below 6‰ . A likely explanation for this is that wet conditions can affect $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ in plants in two ways: Plants with less water stress have lower $\delta^{13}\text{C}$ (Fabio et al., 2005; Wallace et al., 2015) whereas soils with shallow, reducing groundwater conditions provide nitrate with elevated $\delta^{15}\text{N}$ to the plants. An additional factor may be that plants growing on soils that flood more or less regularly receive fine sediment that is rich in nitrogen compounds with elevated $\delta^{15}\text{N}$ values, a process that was apparent in the modern dataset

(see above).

Supratidal sites seem to fall above the general trendline. This can be attributed to higher $\delta^{13}\text{C}$ as a result of inputs of marine organic-rich sediment. With $\delta^{15}\text{N}$ values comparable to plants from riverine floodplains, the wet growing conditions and repeated flooding was probably important in both environments. Overall, the patterns in the analyses of charred plant remains reveal how plant isotope baselines may differ between in different types of landscapes, especially wetlands.

5.3. Wild and domesticated animals

In Fig. 5A, $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values are shown from a range of wild animals: There are clear distinctions in $\delta^{13}\text{C}$ values between freshwater fish, anadromous species and marine fish. Interestingly, the otters also fall in three groups, one group ($N = 6$; Hardinxveld) aligning with freshwater fish, one group ($N = 2$; Hardinxveld and Swifterbant) with the low- $\delta^{13}\text{C}$ anadromous fish and one specimen (Schipluiden) tending even more towards the marine fish group. Of the birds in Fig. 5A, the cormorant falls directly in the marine fish group whereas the swan has a low $\delta^{15}\text{N}$ that is compatible with a herbivorous diet - although the high $\delta^{13}\text{C}$ value (~−15) is unexplained. The ducks - in the lower left quadrant - show a considerable variation. This may be attributed to their potentially variable omnivorous diet. However, the two with the highest $\delta^{13}\text{C}$ (both from Late Historic Oldenzaal) may have been kept - and therefore fed - by humans.

In Fig. 5A, the terrestrial herbivores form a cluster with low $\delta^{15}\text{N}$ (~0–6‰) and $\delta^{13}\text{C}$ (~−24 to −20‰). These values largely overlap with the values in (mostly cultivated) terrestrial plant in Fig. 4A. As a trophic shift would be expected, it is most likely that the animals consumed other (forest?) vegetation that is absent in the available dataset. Fig. 5B shows that within this group there is a tendency for aurochs to be in a range with higher $\delta^{15}\text{N}$ values (~5–7‰), whereas elk tends to have lower values (~2–6‰). This may be related to different feeding habits of these animals. Red deer and roe deer have a much wider range (mostly ~2–7‰) but there are several outliers that fall outside of the terrestrial herbivore group: One (unexplained) low value from Hardinxveld ($\delta^{15}\text{N} = 1.01\text{‰}$) and several high values ($\delta^{15}\text{N} \sim 8–12\text{‰}$) from coastal barrier and supratidal locations (Fig. 5C). These high $\delta^{15}\text{N}$ (and $\delta^{13}\text{C}$) values are most likely the result of the herbivores grazing on plants on inter- and supratidal floodplains (see above and also Prummel et al., 2024). Within the rest of the group, the (Mesolithic) dredged animal bones have somewhat higher collagen $\delta^{13}\text{C}$ values, the riverine ones have lower values, and the riverine wetland and lagoon wetland samples overlap with both. It is hazardous, however, to draw too many conclusions from this because mobility may be an issue here: Sr isotope analyses by Smits et al. (2010) on four red deer from Swifterbant indicated that at least three of them were non-local.

The domesticated herbivores and birds in Fig. 5D, form a clear group, with a wide range of $\delta^{15}\text{N}$ values (~4–15‰) and restricted range in $\delta^{13}\text{C}$ (~−25 to −20‰). This suggest a range of isotopic values in the animal fodder. In the ruminants only plot (Fig. 5E), different $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values are connected to different landscape zones: The group with lowest values ($\delta^{15}\text{N} \sim 6\text{‰}$ and $\delta^{13}\text{C} \sim -25$ to −22‰) are Neolithic animals from freshwater floodplains, i.e. riverine floodplains, riverine wetlands, and lagoonal wetlands. They partially overlap with the wild herbivores in Fig. 5A that for the most part have a riverine floodplain or dryland origin (cf. Fig. 5C). The rest of the group (lagoon wetlands, coastal barrier and supratidal sites from Neolithic to Late Historic) have higher $\delta^{13}\text{C}$ (>~−23‰) and $\delta^{15}\text{N}$ (~4.5–13‰), probably due to their feed coming from soils with shallow groundwater tables and/or regularly flooded areas (see above and Prummel et al., 2024).

The ruminants from lagoon wetlands (the Neolithic Swifterbant sites) fall apart in two groups, a group with high $\delta^{13}\text{C}$ (~−21.5 to −20‰) and $\delta^{15}\text{N}$ (~9–15‰) and a group with low $\delta^{13}\text{C}$ (~−24 to −22‰) and $\delta^{15}\text{N}$ (~2.5–9‰). As both groups are predominantly adults, Brusgaard et al. (2024) indicate that this must have been the result of human

interference: Either one group had a much different dietary regime, or one group was imported and the other locally raised. The overlap with the wild dryland herbivores (Fig. 5A) suggests that the low group could have been imported from e.g. the coversand landscape - but not from the riverine floodplains, as they have even lower $\delta^{13}\text{C}$ values. The $\delta^{15}\text{N}$ values in the high group may reflect the impact of regular flooding, effects of algae blooms and/or denitrification under shallow groundwater tables on plants in the lagoonal wetlands. The specimens from coastal barrier and supratidal landscapes have still higher $\delta^{13}\text{C}$ values than the lagoonal wetland ones - although there is some overlap - reflecting feed from marine-influenced salt-marsh vegetation. It is remarkable that animals from sandy regions largely overlap with this coastal barrier and supratidal group. Closer inspection shows that these are all Historic period animals from the Drenthe plateau (Prummel et al., 2024). This suggests that these animals have been fed with salt marsh plants, e.g. because they were fattened on or imported from the intertidal region bordering the Drenthe plateau, or because fodder was extracted from the salt marshes. The urban animals have similar isotopic values, indicating a role for the supratidal landscape in their feed as well.

Of the $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values in Fig. 5F, (pigs/boar, dogs/wolves, cats), it is often not clear whether we are dealing with wild, domesticated or hybrid animals – especially in the stone age (cf. Erven et al., 2022 for hybridization of neolithic pigs). The dogs/wolves have $\delta^{15}\text{N}$ values that lie around 12‰ - matching well with their role as top-predators - while their $\delta^{13}\text{C}$ values range from ~−25 to ~−17‰. These values fall in the same range as the ones presented by Ewersen et al. (2018), who uses them to discern dogs from wolves by the isotopic indications for fish in the dogs' diets (cf. Digital Supplementary Information Fig. 6F). The $\delta^{13}\text{C}$ values again are related to the region: the highest values (~−20 to −15‰) are from dogs from coastal or intertidal site (Schipluiden, Oosterbeintum, Alkmaar). Dogs from riverine floodplain and riverine wetland sites (Bazel and Hardinxveld) have low values (~−24 to −21‰), whereas the dogs from the Swifterbant lagoonal wetlands lie in between (~−20.5‰). The identification of fish bones in dog coprolites from Swifterbant (Kubiak-Martens and van der Linden, 2022) may indicate that fish played a significant role in the dogs' diets, but the isotope values could also be explained by dogs and wolves feeding on small game from different types of wetlands with different isotope characteristics.

The pigs and boar in Fig. 5F show a pattern very similar to the domesticated herbivores and birds in Fig. 5D, and shows a considerable overlap with them. However, where the herbivores overlap with the left (low $\delta^{13}\text{C}$ values) side of the group of wild herbivores, the pigs and boar overlap more with its right (higher $\delta^{13}\text{C}$ values) side. Moreover, where the herbivores reach $\delta^{15}\text{N}$ values up to ~15‰, pigs do not far exceed a $\delta^{15}\text{N}$ of 12‰. This may indicate that some of the pigs obtained their food from (drier) forests, e.g. from acorns.

5.4. Prepared food: crusts in pots

$\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of charred food crusts in pottery are available only from the Neolithic sites of Hüde and Schipluiden. Although no charred cereal analyses are available from these sites, the food crust $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values (Fig. 6) fall within the general field of freshwater wetland cereals. It is remarkable that the food crusts from (coastal) Schipluiden do not show the elevated $\delta^{13}\text{C}$ values that are seen in cereals from coastal/intertidal sites (cf. Fig. 4C). This may indicate that the Schipluiden cereals were imported from e.g. riverine landscape sites, or that they were grown on plots within the coastal area that did not receive marine sediment input. SEM-based studies and chemical analyses showed that food crust from several other Neolithic sites (Swifterbant, Tiel-Medel, Keinsmerbrug) consist of charred cereal-based porridge that - in addition - often contain fish scales as well as non-cereal plant remains (Raemaekers et al., 2013; Kubiak-Martens and Oudemans, 2023; Oudemans and Kubiak-Martens, 2012). There is also biomarker evidence for fish or animal-derived protein in many of these pots

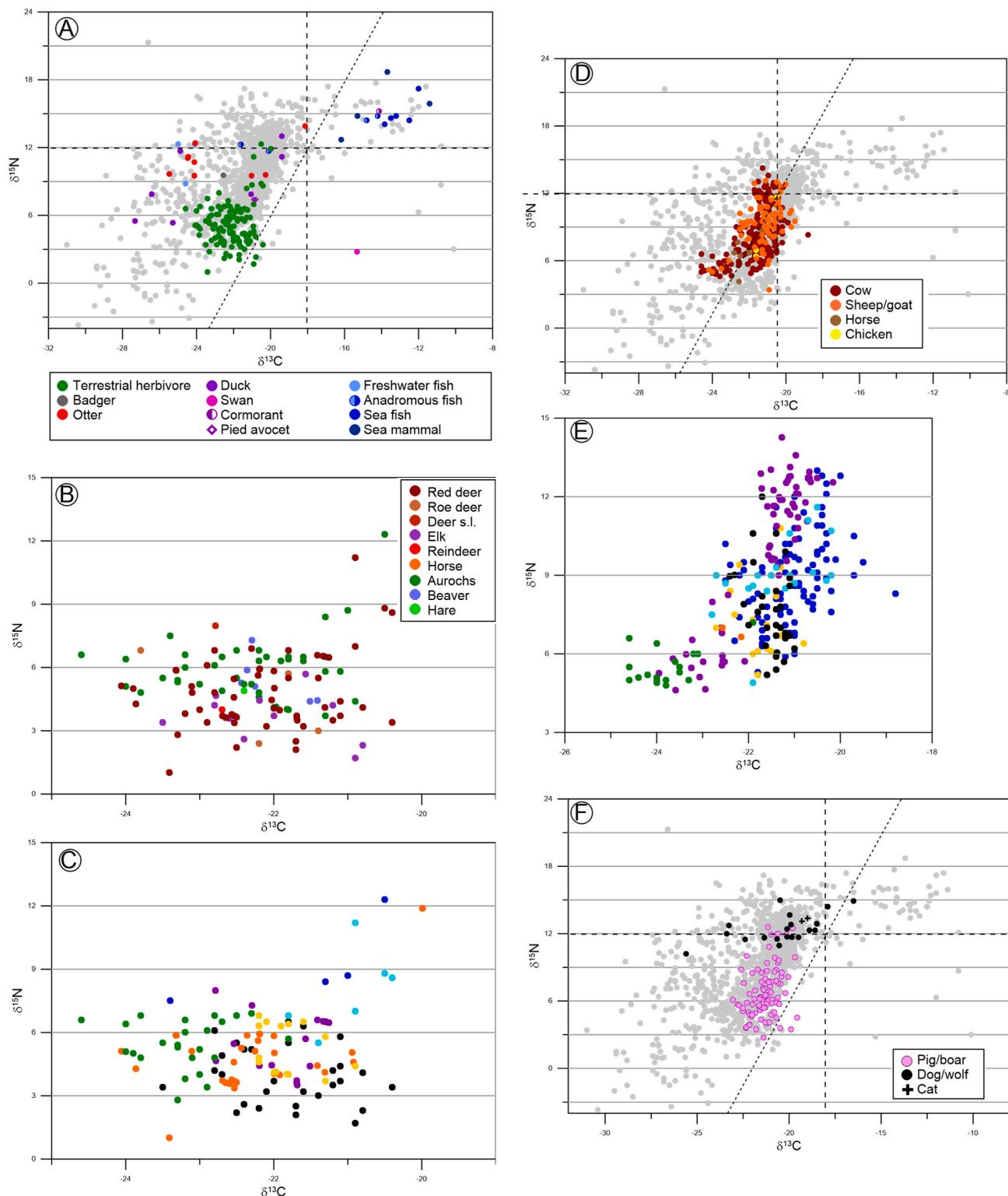


Fig. 5. Plots of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values in various groups of animals. A: All wild/undomesticated animals by species/group. Fish from marine and freshwater environments differ mostly in their $\delta^{13}\text{C}$ values, with anadromous fish having intermediate values. Cormorants have $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values that match with a marine fish diet, but the ducks show a lot of variation that may relate to their omnivorous diet (and maybe human feeding). The swan has low $\delta^{15}\text{N}$ due to a herbivorous diet, but the high $\delta^{13}\text{C}$ is unexplained. The terrestrial herbivores form a tight cluster with few outliers. B: Terrestrial herbivore species colour-coded by species. Within the tight cluster, some differentiation can be seen, probably related to different feeding habits. C: As B but by region; see Fig. 4C for legend. Outliers with high $\delta^{15}\text{N}$ (and $\delta^{13}\text{C}$) values are probably related to grazing on wet soils and/or floodplains where marine flooding occurs regularly. D: Domesticated herbivores and birds. Note the exceptionally high $\delta^{15}\text{N}$ values in a large number of specimens. E: Cut-out of D, with domesticated ruminants by region; legend in Fig. 4C. Specimens from riverine floodplain settings are restricted to the lower left of the plot. Specimens from lagoonal wetlands, coastal barriers and supratidal landscapes show much higher $\delta^{15}\text{N}$, but the lagoonal wetlands tend to have slightly lower $\delta^{15}\text{N}$. F: Omnivores and carnivores. Dog/wolf $\delta^{13}\text{C}$ shows considerable variation that is probably related to differences in the relative amount of marine vs. terrestrial foodstuffs. Pig $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values are comparable to those of the domesticated herbivores. See also Supplementary Information 6 D,E,F. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

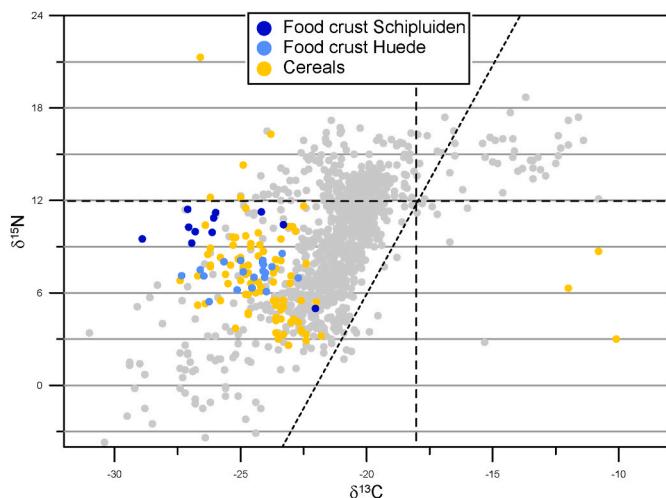


Fig. 6. Isotope plot of the samples from charred food crusts in pottery from two sites, with cereals added for reference. The $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of the charred food crusts fall in the same range as those of charred cereal grains from freshwater wetland sites.

(Demirci, 2022). C/N ratios of the food crusts vary widely (Schipluiden: ~2–33; Smits & Plicht, 2009; Huede: 5–11; Demirci, 2022), indicating variable influence of animal, fish or diary protein. The C/N and $\delta^{15}\text{N}$ values of the Schipluiden and Huede food crusts are comparable with those published in Lucquin et al. (2023) for the lower Rhine basin. They indicated that their foodcrust $\delta^{15}\text{N}$ values had higher values than reference cereals, which would indicate a significant contribution from higher more proteinaceous terrestrial and aquatic animal resources. However, the overlap with the wetland cereal values in our paper demonstrate that caution is needed as some of the stable $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values from freshwater fish and e.g. ducks fall close the range of riverine cereals (cf. Fig. 5A).

5.5. Human diet

Humans (Fig. 7A) show a large variability in their $\delta^{13}\text{C}$ values (~−25 to −13‰) but have less variation in their $\delta^{15}\text{N}$ values (~9–18‰). The $\delta^{15}\text{N}$ value of 4.5‰ from a North Sea Mesolithic individual that was probably incorrectly identified as human (van der Plicht et al., 2016) will not be discussed here further. Based on the divisions made above on plants and wild and domesticated animals, the humans can be divided into four landscape zones: marine, coastal & supratidal, freshwater wetlands & floodplains and terrestrial dry (i.e. rainwater-fed) landscapes. Tentative boundaries are indicated in Fig. 7B. No boundary could be determined between the terrestrial dry areas and the wetlands proper, but it is probably around $\delta^{15}\text{N} = 12\text{‰}$ (i.e. at least one trophic level above dryland wild herbivores; see Fig. 7A–C). Fig. 7B makes clear that the $\delta^{15}\text{N}$ values in themselves cannot be used to discriminate marine from terrestrial diet. For that, the $\delta^{13}\text{C}$ is much more suitable.

The $\delta^{15}\text{N}$ values seem to place all humans in the carnivore group. However the high $\delta^{15}\text{N}$ values in cereals and in food crusts make clear that such values could be reached - at least theoretically - with a plant-only diet that is sourced from various wetland settings with high - $\delta^{15}\text{N}$ plant baselines.

The $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values in humans grouped per period (Fig. 7C) show major changes through time: Of the Mesolithic population, some individuals have a fully marine diet (upper right corner in Fig. 7C) but the larger group aligns with freshwater wetlands and floodplains (upper left corner). Since all these bones are dredge finds, it is unfortunately not possible to correlate these values with the palaeogeography. Still, the large proportion of Mesolithic $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values that fall in the freshwater floodplain group is remarkable. There may be a preservation

bias, however, with human remains from wetlands having a larger chance of survival in the archaeological record than those from dryland settings. Even so, it does support the idea that wetlands – as probably the most productive year-round locations for foragers - provided major sources for subsistence in Mesolithic inhabitants of this area - and probably most of Europe.

The majority of Neolithic individuals analysed (from Swifterbant and Hardinxveld) have a freshwater wetland and floodplain signature. A smaller group with similar $\delta^{15}\text{N}$ and higher $\delta^{13}\text{C}$ (from coast-near Schipluiden and Mienakker) have a coastal barrier/supratidal signature. Another small group - four humans with $\delta^{15}\text{N}$ values ~10‰ - forms a more or less homogeneous separate group from the rest of the Neolithic humans. Remarkably, these four humans are from four different sites (i.e. Swifterbant, Bazel, Hardinxveld and Schipluiden). What is especially interesting is that the Swifterbant individual had non-local Sr isotopes, indicating that it was an immigrant (Smits et al., 2010). No Sr isotopes are available from the other three outliers but of the seven individuals from Schipluiden where oxygen isotope data is available, two were definitively found to be non-locals as well (Smits et al., 2010). These indications for mobility makes it likely that the four outliers with low $\delta^{15}\text{N}$ values are non-locals that came from dry, terrestrial landscapes.

Both during the Mesolithic and the Neolithic, humans have much higher $\delta^{15}\text{N}$ than herbivores, with an apparent human-animal offset $\Delta\delta^{15}\text{N}$ of ~9‰. Concurrently, there does not seem to be a systematic offset in $\delta^{13}\text{C}$. This suggests that large terrestrial herbivores contributed little to human Mesolithic and Neolithic diet. It is very likely that plants were an important component of the diet, and had a major influence on human $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values. However, freshwater waterfowl and fish - with values overlapping with wetland plants - may have had a significant contribution as well. Despite their relatively small role in human diet, large herbivores could still have a cultural importance while their role in food for specific (e.g. feasting) events may still have been significant.

Interestingly, the change in $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values around the Mesolithic - Neolithic transition in our dataset is considerably different in many other parts of Europe (Schulting, 2018; see also Supplementary Information 1): It shows a similar range of Mesolithic $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values during the Mesolithic as is found throughout Europe, although the high $\delta^{13}\text{C}$ values (“Coastal Mesolithic” according to Schulting, 2018) are rare: Most fall in freshwater wetlands & floodplains left quadrants (Fig. 7B). This European “Coastal Mesolithic” probably represents a fully marine-dominated diet, not food from “Coastal barriers and floodplains” or similar landscapes as we have in the Netherlands. This highlights the isotopic difference between a diet based on plants and animals from coastal and intertidal settings and a diet with a large proportion of fish, shellfish or marine mammals. Most important, however, is that the Europe-wide drop in $\delta^{15}\text{N}$ values at the Mesolithic – Neolithic (Schulting, 2018) is lacking in the Netherlands: The $\delta^{15}\text{N}$ values in Neolithic humans from the Netherlands remain at the Mesolithic level, except for the handful of individuals that were probably immigrants (see above). Since there is compelling evidence for widespread agricultural practices during this period (Raemaekers et al., 2023 for an overview) it is most likely that the Dutch data shows evidence for crop cultivation and animal foddering in the freshwater, coastal barrier and supratidal wetlands of the Netherlands. To what extent these practices are comparable to the floodplain cultivation discussed by Bogaard (2004) is open for discussion.

The Dutch Neolithic values are comparable to the Epipaleolithic, Mesolithic and Neolithic values from the Dnieper rapids (Ukraine) (e.g. Lillie et al., 2003; Lillie and Jacobs, 2006) that are often interpreted as showcasing the continuous significant use of fish (Schulting, 2018). Our data shows, alternatively, that these values may represent diets based on a wider range of food sources from freshwater floodplains that may combine fish and waterfowl with a large plant component with wetland $\delta^{15}\text{N}$ values. Similar interpretations may be made about the human diets

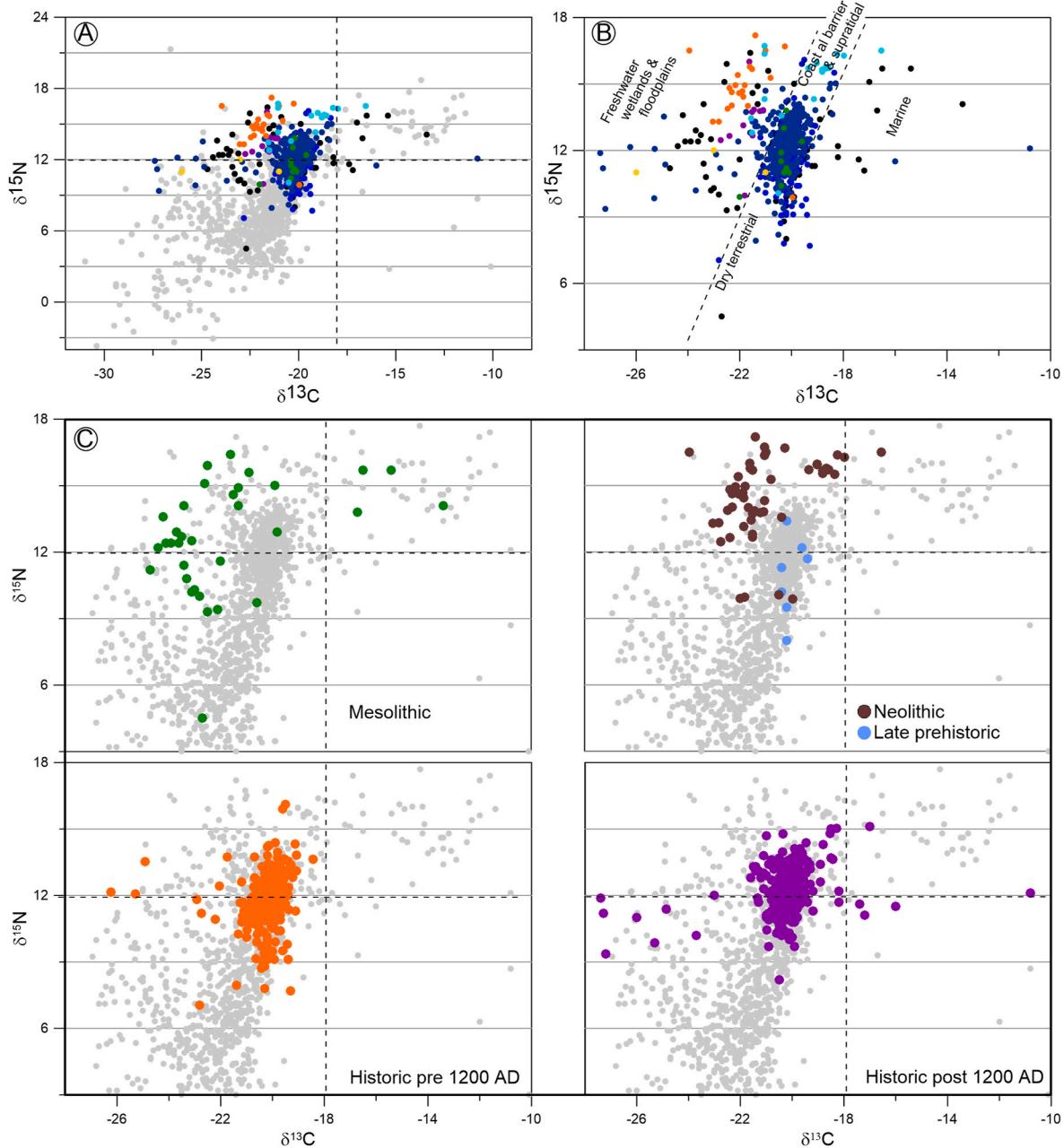


Fig. 7. A: Isotope plot of humans, divided by landscape zone. Legend as in Fig. 4C. The humans clearly fall in the top-predator zone, but there is overlap with the domesticated herbivores. B: Cut-out of A, with landscape zone interpretation added. The broken lines delineate a division into four landscape zones (marine, coastal barriers and supratidal, freshwater wetlands& floodplains, terrestrial dry lands) based on the previously discussed plant and animal isotope values. C: Zoomed-in human isotope plots for each period, demonstrating major changes in $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values.

from Mesolithic and Early Neolithic Danube Iron Gates (Bonsall and Boroneant, 2018) and Early Neolithic Ostorf (Lübbe et al., 2007). $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ analyses on local contemporary charred plants could elucidate this. Based on the above, we may hypothesize that the Europe-wide Mesolithic-Neolithic isotopic shift demonstrated by Schulting (2018) is not as much a hallmark of a change to an agriculture-based diet, but rather of the colonization of the dry, rainwater-fed sand and loess landscape that hitherto had only marginal contributions to human diet.

After the Neolithic, hardly any human, animal or plant isotope values occur that fall in the freshwater wetland and floodplains upper left quadrant: The bulk of the human $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ are now restricted to the Coastal barrier & supratidal and dry terrestrial landscapes (Fig. 7B). This probably reflects the Late Prehistoric expansion of peat over most freshwater wetlands and floodplains. Peat drainage and cutting in later

periods - which started in the Iron Age (Bakker and De Langen, 2023) did not bring back those environments as later (medieval) dike construction put an end to regular flooding in most of the river and intertidal floodplains. Moreover, the digging of ditches for drainage may have lowered groundwater levels to such a degree that nitrate with denitrification-related high $\delta^{15}\text{N}$ values were much less available in the root zones of crops. As a result, post - Neolithic human diet seems to combine food from dry, terrestrial settings and coastal/supratidal landscapes, without much influence from freshwater wetlands.

There is, a considerable amount of outliers in the Historic group with high or low $\delta^{13}\text{C}$ values. High $\delta^{13}\text{C}$ are mostly from dredge finds that fall clearly in the upper right quadrant marine field. These are probably from drowned sailors or fishermen that had a large proportion of marine fish in their diet. The remaining high- $\delta^{13}\text{C}$ and all low- $\delta^{13}\text{C}$ values are

mostly from humans from urban contexts (cities of Groningen and Oldenzaal) but also includes two individuals from the coversand landscape (St. Michielsgestel). These excentric $\delta^{13}\text{C}$ values - and $\delta^{15}\text{N}$ values between 10 and 12 ‰ - overlap largely with those of otters (Fig. 5A), which suggests that these individuals had a diet that was exceptionally rich in fish, while mostly lacking in meat in milk products. The alternative - a diet from wetland plant and animal resources like in the Neolithic - is less likely because those $\delta^{15}\text{N}$ values are considerably higher. The individuals with low $\delta^{13}\text{C}$ values (from Groningen, Oldenzaal and St. Michielsgestel) probably ate mostly freshwater fish, while the ones with high $\delta^{13}\text{C}$ values (from Oldenzaal and Groningen) probably ate mostly marine fish. It is likely that they were clergymen associate with the Saint Plechelmus Basilica (Oldenzaal), the parochial church of St. Michielsgestel or one of several churches in Groningen. A mixed diet of freshwater and marine fish may average out the differences in $\delta^{13}\text{C}$, so there may be more individuals with a fish-dominated diet in the Historic groups. Bones from marine and anadromous fish from (inland) Oldenzaal (included in Fig. 5A) illustrate the importance of fishing fleets providing coastal or marine proteins to inhabitants of the low countries, even inland, during this period.

5.6. Implications

The outcomes of this study have some major implications for the application of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ in archaeological research, and for aspects of past human subsistence and diet. The cases discussed above demonstrate that $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values can differ considerably between different landscapes, due to interaction of physical, chemical and biological processes like sedimentation, denitrification, algae blooms and guano deposition. As a result, similar plant and animal species from different landscapes develop different $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values. This needs to be taken into account before these values can be used as dietary indicators: The $\delta^{13}\text{C}$ values in our dataset differ distinctly in plants, animals and humans between dry-terrestrial, freshwater wetlands, supratidal and backbarrier and fully marine settings. Elevated $\delta^{15}\text{N}$ values from wetland cereals are easily interpreted incorrectly as indicators for manuring, whereas elevated values in the bone collagen of animals or humans with a herbivorous diet are easily mistaken as indicators for a diets rich in animal protein and/or fish.

These findings strengthens the assertion by Mackarewicz and Sealy (2015) that archaeological dietary isotope studies may be better approached using isoscapes. This does, however require the characterization of each step in a food chain in each type of landscape within a region of study. This is a mammoth task that is made even harder because only charred material can be used for the plant component: Bacterial and fungal decay processes alter the $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values in non-charred material, even if well-preserved in waterlogged environments. Moreover, mobility of humans and animals has to be accounted for, e.g. by combining $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ analyses those of e.g. O, S, Sr, Nd and/or Pb.

Dietary modelling requires as input solid information of the isotope ratios in all (potential) foodstuffs. The present study demonstrates that similar foodstuffs from different landscapes can vary significantly in their $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values, and that different foodstuffs from within a single landscape zone may have similar values (e.g. riverine cereals and freshwater fish and birds). This is a source of major potential uncertainties in dietary models that need to be dealt with. Maybe model inputs need to be defined separately for each area of study or each landscape unit. In any case, generic food chains with trophic levels do not suffice, especially not in wetland environments.

6. Conclusions

Our analyses of modern and archaeological data demonstrate how $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values in food chains can vary between landscapes due to sedimentological, chemical and biological differences. This effect is

especially relevant for wetlands. In modern particulate organic matter (POM) and sediments, isotopic variation can be linked to inputs of terrestrial, riverine, marine and estuarine sediments that each contribute different $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values. Sedimentation of particulate organic matter from (^{15}N -enriched) algae blooms and deposition of bird guano are factors that can elevate $\delta^{15}\text{N}$ values in sediments and wetland soils. $\delta^{13}\text{C}$ values in (non-woody) C3 plants vary between different landscape zones, from freshwater wetlands to fully marine settings. Wild and domesticated plant $\delta^{15}\text{N}$ baselines in wetland and floodplains can become further elevated above the (sometimes already elevated) sedimentary baseline in soils with high water tables due to denitrification processes. As a result, plant $\delta^{15}\text{N}$ baselines can differ dependent on their landscape position, with origin of organic matter and soil hydrology as important variables. These high $\delta^{15}\text{N}$ in turn are passed further up the food chain through herbivores and carnivores.

In archaeological datasets, clear differences in $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values between drylands, freshwater wetlands, coastal wetlands and fully marine environments can be seen in plants, wild animals and domesticated animals as well as in humans. Some of these variations have important implications for their application in archaeological contexts. E.g. floodplain and wetland soil plant $\delta^{15}\text{N}$ values can reach (and exceed) levels that have been associated with manuring while floodplain and wetland (wild and domesticated) herbivore and omnivore $\delta^{15}\text{N}$ values can exceed levels that are commonly seen in carnivores. Coastal barrier and supratidal floodplains show similar $\delta^{15}\text{N}$ values in plants and animals as freshwater floodplains, but the marine influence results in elevated $\delta^{13}\text{C}$ values in plants and animals. Humans with a floodplain-based diet inherit these values, including the high $\delta^{15}\text{N}$ values in wetland plants and animals. Because of the high $\delta^{15}\text{N}$ values in plants (including cereals) from floodplains, these levels should not be mistaken for indicators of a high-protein diet.

This study shows the importance of understanding local and regional food chains- and the distribution of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values within them - when studying subsistence or when making dietary reconstructions. Using too simple food chain trophic models while neglecting the spatial component is especially hazardous in the highly variable coastal wetlands, and may lead to incorrect archaeological interpretations. Future dietary studies should therefore not rely blindly on standardized universal food chain isotope values for plant baselines, herbivores, carnivores and humans. Instead, for each landscape unit the food chains and associated isotope values should be determined. Because of the potential presence of remains of non-local animals (and humans) in archaeological records such reconstructions should be accompanied by identification of non-locals within populations, e.g. by additionally analysing stable isotope values of elements like O, Sr, Pb and/or Nd.

Declaration of competing interest

The author declares no conflict of interest.

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Appendix A. Supplementary data

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