Biases in the frequency of fruits and seeds in modern fluvial sediments in NW Italy: the key to interpret analogous fossil assemblages

BIASES IN THE FREQUENCY OF FRUITS AND SEEDS IN MODERN FLUVIAL SEDIMENTS IN NW ITALY: THE KEY TO INTERPRET ANALOGOUS FOSSIL ASSEMBLAGES

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ABSTRACT

To better interpret quantitative and qualitative data from fossilized fruit-and-seed assemblages (carpological assemblages or carpodeposits *s.l.*), extensive taphonomic analyses were undertaken in two modern, small, fluvial catchment basins (Ca' Viettone and Valtorta-Rivara, NW Italy) that are characterized by different vegetation types. Quantitative data from vegetational surveys and carpodeposit analyses were compared using a standardized approach with graphic representation of "Plant Community Scenarios" (PCSs). The contents of the carpodeposits clearly differentiate the different types of vegetation in each basin. Moreover, carpological assemblages from the same basin have a similar signature. Comparison of all samples indicates a relationship between the standing vegetation and the PCS reconstruction based on carpological analysis. The PCS for the Valtorta deposit represents the standing vegetation best, probably because of reduced impact of long-distance dispersal, homogeneity of vegetation, and low anthropogenic influence on the landscape. Three bedload carpodeposits samples from the Ca' Viettone site show similar frequency

values for several taxa, which indicate that bedload transport may homogenize the fruit and seed assemblages. On the other hand, two samples from Valtorta, collected only 200 m apart, are distinctly different, illustrating how carpodeposits can vary due exclusively to sedimentary processes. Such bedload carpodeposits seem to characterize, at least qualitatively, the vegetation of the entire basin rather than just the area adjacent to the sample site. When differences in taxonomic frequency in the standing vegetation and in the carpological assemblages are evaluated, patterns in the over- and underrepresentation of certain types of fruits and seeds become apparent. Such patterns are quantified by a bias index for diaspores of each taxon, derived from empirical observations and applicable to bedload carpodeposits. Factors biasing representation in an assemblage include disseminule size and woodiness. It is found that small diaspore size and absence of diaspore woodiness are associated with taxonomic overrepresentation. Conversely, taxonomic underrepresentation generally is related to large diaspore size and low woodiness. In addition, the mode of dispersal seems to be very important; anemochorous (wind dispersed), endozoochorous (animal dispersal via excrement), and myrmecochorous (ant dispersed) diaspores are clearly overrepresented. Understanding the factors behind the over- and underrepresentation of fruits and seeds in Recent assemblages will certainly be useful in improving the interpretation of analogue fossil assemblages.

INTRODUCTION

Fruits, seeds, and other related reproductive structures (diaspores *s.l.*) often accumulate in association with fluvial sediments, concentrated by water currents (Gee, 2005), to form rich carpological assemblages. These assemblages also are known as carpodeposits *s.l.* or carpodeposits *s.s.* if they are transported as bedload during flood events (bedload carpodeposits; Gee, 2005). Such carpological assemblages, especially from Neogene and Quaternary deposits, have been extensively studied in Europe since the beginning of the 20th Century (e.g., Reid and Reid, 1915; Birks, 1973;

Collinson, 1983; Holyoak, 1984; Pierce and Tiffney, 1986; Dunwiddie, 1987; Gastaldo et al., 1987; Spicer and Wolfe, 1987; Mai and Walther, 1988; Tiffney, 1990; Thomasson, 1991; West et al., 1993; Martinetto, 1994; Jechorek, 2000; Kisieliene, 2006; Mercuri et al., 2006; Sadori et al., 2010) and used for the reconstruction of ancient vegetation. However, the relationship between the frequency (or cover) of the diaspore-producing plants in the standing vegetation and their presence in the sediment-transported carpological assemblages only has been investigated in a few cases (Collinson, 1983; Holyoak, 1984; Gastaldo et al., 1986; Thomasson, 1991; Gee et al., 1997; Gee, 2005, Sims and Cassara, 2009). There is still a strong need to conduct further studies to improve the interpretation of fossil assemblages.

Studies on modern depositional settings, for instance, have demonstrated that the qualitative and quantitative data provided by carpological assemblages can yield more precise information about the composition and community structure of past vegetation (Watts and Winter, 1966; Burrows, 1980; Collinson, 1983; Greatrex, 1983; Thomasson, 1991; Cappers, 1993; Ferguson, 1995; Birks and Birks, 2000). Fossil fruits and seeds, like leaves and wood, have an advantage over fossil pollen and spores, because they are usually contemporaneous to the sediments in which they occur (Greatrex, 1983) and less subject to problems related to contamination or long-distance transport (Cappers, 1993; Ferguson, 1995; Gee, 2005). Furthermore it should be noted that plant macrofossils commonly can be assigned with greater certainty to a more precise taxonomic level. Several studies have demonstrated that carpodeposits reflect local plant communities better than assemblages of other plant organs (e.g., Burrows, 1980; Collinson, 1983; Thomasson, 1991; Cappers, 1993; Sims and Cassara, 2009).

In present study focuses on diaspore taphonomy because of new and promising potential for the interpretation of vegetational signals provided by quantitative carpological datasets. A simple method for comparing standing vegetation and carpodeposits is applied here, and tested in two small catchment basins in NW Italy. Our method does not attempt to factor in all the complex steps involved in the formation of carpological assemblages (Fig. 1) but, instead, compares the end-

products of the formational process (the fruits and seeds in the assemblage) with the standing vegetation. For this, we apply a simple graphic representation , “Plant Community Scenario” (PCS), recently proposed by Martinetto and Vassio (2010). Using PCSs, the composite set of information provided by a carpological assemblage can be summarized in a single sketch. In this way we obtain a powerful tool for a straightforward comparison of modern and ancient carpological assemblages, which has been applied first for the interpretation of some aspects of Pliocene vegetation in NW Italy (Martinetto and Vassio, 2010), and, more extensively, for Quaternary vegetation (Vassio, 2012).

GEOGRAPHICAL AND GEOLOGICAL SETTING

Our study of modern carpological assemblages was carried out in two small catchment basins in the Piedmont region in NW Italy (Fig. 2A): Ca’ Viettone brook (CVB, Fig. 2B) and Valtorta-Rivara (VTR, Fig. 2C). These sites are in the foothills of the Western Alps, at a distance of 2 km from each other, located in a single vegetation belt (Blasi, 2010). Both sites were chosen for their geomorphological characteristics which are considered similar to those of Neogene and Quaternary fossil-bearing basins in the same area (Martinetto and Vassio, 2010; Vassio, 2012). These basins are surrounded by moderately steep hills formed of crystalline rock. An alluvial plain is nearly absent at Valtorta, whereas it is limited to the lower 500 m of the course of the brook at Ca’ Viettone where it erodes soft Pliocene and Quaternary sediments and forms several meanders. The length of each brook was examined between autumn 2008 and summer 2010 to find modern sediments bearing concentrations of fruits and seeds that had accumulated during flood events no more than few months earlier. Different modern fruit-and-seed deposits were found including: either sediment-free accumulations resulting from concentration of buoyant material; or sediment-borne assemblages incorporated into fluvial deposits after bedload transport, for example on point bars. Given the sedimentary context of the fossil deposits, the sediment-borne accumulations were considered as the better analog for plant macrofossil assemblages and have been sampled more extensively.

The two catchment basins differ in their features. The Ca' Viettone (CVB) basin is characterized by a relatively larger size (ca. 4 km in length), lower gradient, patchy vegetation (various types of woodlands, orchard, prairies, meadows, and agricultural fields: Fig. 3) and a strong human influence, which must be kept under careful consideration when interpretating the results of the study. The Valtorta basin is smaller (ca. 1 km in length, Fig. 2C), generally steeper, with relatively homogeneous vegetation (mostly woodland: Fig. 4A) and minor human influence across the landscape.

METHODS AND MATERIALS

Field Methods

The volume of each modern carpological sample (Table 1) used in the study usually corresponds to ~1 dm^3 and is considered the result of a single flood event. Because flood events may occur at different times of the year, we cannot rule out anomalies in the taxonomic abundance data that may be linked to seasonal fruit-and-seed production.

Three sediment samples (Table 1) were collected in the bottom part of the CVB basin (Fig. 2B), and only sample (C1I) originates from the upper basin, which is separated from by a steep escarpment. Sample C1H was taken upstream from the confluence of the left tributary of the Ca' Viettone brook, which drains a large vineyard and is associated with mostly abandoned meadows and agricultural fields. The lower CVB sample sites were found to have concentrations of large to middle-sized fruits (*Carpinus* and/or *Corylus*). Three of these fruit concentrations (C1D, C1H, C1L) were deposited in well-sorted sand with bedforms (Fig. 3), and are considered as bedload carpodeposits (cf. Gee, 2005). On the other hand, the sediment matrix of sample C1I is a muddy sand and, at this site, is found at the confluence of a small tributary of the Ca' Viettone brook, where suspension-load sedimentation of fines played a major role in diaspore incorporation. Hence, this assemblage cannot be treated as a typical bedload carpodeposit (sensu Gee, 2005).

Two samples were collected in rather different settings in the VTR basin. Sample C2E came from a coarse sandy deposit (Fig. 4B-C), that accumulated at the foot of a steep slope (Fig. 4A), and

contained a concentration of plant material generated by bedload transport. However, due to the exceptional concentration of large fruits (e.g., *Castanea:* Fig. 4C), we consider this to be an uncommon type of bedload carpodeposit. Sample C2G was collected 200 m downstream of C2E (Fig. 2C) where the valley bottom is almost flat. Here, the sediment matrix is a medium sand that contained a concentration of only medium-sized fruits (e.g., *Carpinus*); we consider this to be a bedload carpodeposit *s.s.*

Vegetation surveys were carried out in both basins upstream of the carpodeposit *s.l.* sites. Each area was subdivided into different geographic subareas, each possessing a homogeneous vegetation (Fig. 2B, C). Subsequently, subareas with similar vegetation were combined to obtain macro-areas and the term, *weighted mean vegetation,* refers to the entire surveyed area (Table 2). Each drainage clearly exhibits differences in its geomorphology, such as in the width of the brook bed and gradient, and in its vegetation. The vegetated zones along the brook were surveyed along the water course for at least 400 m (Valtorta) and up to 2 km (Ca' Viettone). The orthogonal width of the surveyed area varied from 10 to 100 m on both sides of the brook (Fig. 2B, C).

Finally, a general survey of the vegetation in the entire catchment basin was carried out to estimate the total area covered by the most common plant taxa (Table 2) and the areas covered by the different plant communities (woodlands, meadows, gardens and orchards, etc.: Table 3). Orthophotographs and/or satellite images were used to determine plant cover.

Analytical Methods

The Recent plant-bearing sediments were processed in the laboratory using the same procedures as those for processing fossil fruits and seeds (Martinetto and Vassio, 2010). A very dilute solution of H_2O_2 (1-3%) was applied to disaggregate the biotic from the abiotic components and facilitate the floatation of the lighter and porous particles, usually fruits and seeds. Subsequently, the floating particles and the heavier materials that settled to the bottom were gently washed and sieved separately. After this material was dried, the fruits and seeds were separated from the sieved residue and sorted by size. Taxa were identified using: atlases of recent fruits and

seeds (Bojňanský and Fargašová, 2007, Ercole et al., 2012); atlases of fossil fruits and seeds (Velichkevich and Zastawniak, 2006, 2009); and by comparison to the Modern Carpological Collection (MCC) at the Department of Earth Sciences (Dipartimento di Scienze della Terra) of Torino University. Finally, these identifications were compiled into a database, and abundance data were generated based on counts of the fruit and seed taxa identified. In the counts, all remains of those plants producing multiple carpological parts were tallied. For *Quercus*, for example, this included isolated mature cupules, immature cupules, acorns, and acorns with cupules. The taxonomic frequencies (%) in each sample were obtained by calculating each taxon's abundance relative to the entire assemblage (Table 2).

The last phase of this study was a comparison of the qualitative and quantitative data from both the vegetational surveys and the carpological assemblages using the PCS approach (Martinetto and Vassio, 2010) to obtain a comparable visual rendering of both records. Its application, originally proposed for palaeovegetation reconstructions, has been extended to modern carpodeposits and standing vegetation. PCS represents a standardized way of analyzing floristic quantitative data enriched by qualitative attributes, and consists of a database, calculation sheet, and schematic diagrams in which numbers are translated into simplified and stereotyped pictures. The PCS diagram represents a vegetated transect with four main storeys: the canopy and the arboreal plants, beneath which is are the bushy and herbaceous undergrowth. The position in the vegetational reconstruction attempts to be as realistic as possible, taking into account analogous living plant growth habits. The palaeoenvironmental frame used in the PCSs did not follow the more elaborate scheme of van der Burgh (1983) to minimize subjectivity; this approach does not force the phytosociological interpretation of Neogene taxa based on modern vegetational units. The PCS transect potentially can be subdivided into four main zones representing four principle ecological zones; drawn from the left to the right in the diagram these are: xeric – X, mesic – M, hygrophilous - HY and aquatic – A zones). These zones represent the ecological requirements of taxa within the carpological assemblage. The presence of these zones in the PCS diagrams is strictly

181 related to the taxa occurring within the carpological assemblage, and each taxon is proportional to
182 the cumulative percent abundance of xeric, mesic, hygrophilous and aquatic plants.
183 The PCS transect usually is represented with a slight slope, while the hygrophilous transect is
184 depicted as flat. If paleomorphology and paleoenvironment of a certain site are well known, it is
185 possible to arrange the PCS profile to better fit with the real or hypothesized spatial context. It is
186 clear that a 2D transect rendition suffers from oversimplification, especially when the modern
187 vegetation is translated into a PCS. But, it seems a good way to obtain homogeneous datasets,
188 easily comparable with the fossil datasets. PCSs represent reconstructions of selected aspects of
189 present or past vegetation in which the quantitative data are expressed by a means of different plant
190 symbols, with an arbitrarily fixed maximum at fifty, for practical and aesthetic reasons (Martinetto
191 and Vassio, 2010). Hence, calculated original taxonomic frequencies are halved. Each plant symbol,
192 instead of representing an individual taxon, represents a definite plant category (the "growth form"
193 of Martinetto and Vassio, 2010), resulting from a combination of features including plant
194 physiognomy (habitus), size (height), leaf seasonality, and environmental requirements (e.g.
195 hygrophilous or aquatic), to obtain a relative small number of component vegetational categories.
196 Moreover plant symbols are represented by acronyms (Fig. 5). As for the width of the different
197 transect zones, the number of each plant symbol drawn in the PCS is proportional to the sum of the
198 occurrence frequencies ("X") of different taxa sharing the same growth form. The repartition of
199 different plant symbols in each ecological zone has been decided to be random. Of course, plant
200 symbols within a PCS can be subsequently re-arranged from a phytosociological perspective as
201 well as the environmental zone, by taking into account information about paleogeomorphological
202 context.
203 Sterile or immature plants (juvenile stages of trees or shrubs) do not contribute to carpological
204 assemblages, nor do plants that reproduce by spores. Hence, a PCS derived from a carpodeposit *s.l.*
205 (deposit-PCS: Figs. 6, 7A and 8A,B) represents only the diaspore-producing plants and, inevitably,

shows an *a priori* difference with the corresponding PCS derived from the standing vegetation, that includes sterile and immature plants (vegetation survey-PCS: Figs. 7B-D and 9C-D).

Taxonomic information about the dominant floristic composition of standing vegetation or of a carpological assemblage is displayed in each PCS by adding 25 taxon (species, genera or family) names which are chosen from amongst the most abundant floristic elements. We consider a taxon to be abundant if it represents > 4% of the relative frequency. These are illustrated once or several more times depending on their percent abundance (i.e., a taxon with a 12% frequency will appear 3 times in the PCS).

RESULTS

Quantitative analyses of the carpodeposits *s.l.* are summarized in Table 2, which also displays the percentage cover of each species in the modern flora of the surveyed areas. The size of vegetational units in the two catchment basins also are estimated (Table 3).

The number of diaspores in each sample varies depending on grain size of the sediment matrix. Higher numbers of diaspores generally are found in medium to fine silty sands; the three richest samples (C1D, CIH and C1L) contain over 1000 specimens per liter (notice that the 0.5 l sample C1D contains 785 specimens). The lowest numbers of diaspores are found in mud (347 in C1I) and coarse sand (239 in C2E). In addition, the sediment-free phytodebris contains fewer fruits and seeds (411 in C1G) than bedload carpodeposits.

Floristic lists compiled from the carpological assemblages consist of 40 to 60 taxa. This compares to the 70 to 90 taxa that were censused in the modern vegetational surveys, although only about 20 taxa represent a major proportion of the cover. Almost half 46.8% of the taxa identified in the death assemblages were detected in the coeval life assemblage, and 33.4 % of taxa surveyed in the life assemblage also were recovered from the carpodeposits *sl.* These frequencies are closely comparable to those found by Sims and Cassara (2009), which were 45% and 33%, respectively. The reason for this disparity, on one hand, can be partially attributed to the absence of rare species not detected during the vegetation surveys or not identified in the carpodeposits and to the different

taxonomic levels in identification of plants in the two records (surveys and carpodeposits);. On the other hand, explanations must be sought within diaspore production rate and taphonomic effects (see below).

It is evident from the CVB and VTR carpological assemblages (Figs. 7 and 8) that the fruit-and-seed assemblages originating from the two basins can be distinguished readily from one another. Moreover, all samples from the same basin have the same uniform and characteristic signature. Comparison of all samples shows agreement between the modern vegetation and the PCSs reconstructed on the basis of carpological analysis. Carpodeposits *s.l.* seem to better characterize the vegetation from the entire basin area than just the landscape adjacent to the sample site.

Data from the Valtorta basin (Table 2) clearly show the relationship between the cover value of each taxon in the standing vegetation and the frequency of the same taxon in the carpological assemblages. Nearly all taxa with high or medium cover values in the standing vegetation are represented in the two sampled fruit-and-seed accumulations, and this also holds true for most taxa with low cover values. Most of the other commonly taxa occurring only in the life assemblages (vegetation survey) have minuscule cover values. This situation is well documented in the Valtorta deposit-PCSs, because the two reconstructions from carpodeposits (Figs. 8A-B) are not dramatically different from those obtained from the analysis of the standing vegetation (Figs. 8C-D). As a whole, the bias between the deposit-PCSs and the vegetation survey-PCSs is less evident for the Valtorta context (compare Figs. 8A-B and Figs. 8C-D) than for Ca' Viettone (compare Figs. 6, 7A and Figs. 7B-D). In particular, the two basins differ greatly in the vegetation closest to the sample sites (Fig. 7B) and along the brook; the carpodeposits *s.l.* better reflect the vegetation of the entire basin (Figs. 7C-D). However, in the PCSs of both basins, major differences emerge when examining the taxonomic diversity associated with the plant symbols, which reflect the PCS-mismatch between the most frequent taxa in the vegetation versus those in the fruit-and-seed accumulations (numerically expressed in the last three columns on the right of Table 2). The PCS-

mismatch values have been simply calculated by subtracting one half of the percent values for each taxon in the standing vegetation to the halved values of that taxon in the carpodeposit. The PCS-mismatch values are useful for a quick interpretation of the PCSs in the same basin because high positive or negative values immediately point out the different proportions of plant symbols or taxa between the vegetation survey-PCSs versus the deposit-PCSs (Figs. 7 and 8). Furthermore, despite the homogeneous vegetation of the Valtorta basin, when the PCS-mismatch values in both samples (C2E, C2G) from this site are compared, it is found that the two samples contain several taxa in distinctly different quantities (Table 2). For example, *Castanea sativa* and mature fruits of *Corylus avellana* in sample C2E have a positive PCS-mismatch (overrepresented), whereas *Phytolacca americana* has a negative PCS-mismatch (underrepresented). Conversely, *Castanea sativa* and *Corylus avellana* are underrepresented in C2G, whereas *Phytolacca americana* is overrepresented.

A curious phenomenon is the occurrence of a few taxa in the fruit and seed samples, with percentages up to 8% (Table 2), that are either absent or in low frequencies in vegetational surveys (i.e., *Actinidia chinensis, Ficus carica, Fragaria vesca,* Solanaceae). This is probably because these diaspores come from very localized sources (*F. vesca* excepted), and are, for the most part, species cultivated in gardens and orchards. These taxa are all characterized by endozoochorous (seeds passed through the gut of an animal) dispersal, which may involve long-distance transport (cf. Nathan and Muller-Landau, 2000). We ascribe their anomalously high percentage in the carpological assemblages to such a long-dispersal effect. Such an effect contributes to distinct differences between the deposit-PCSs and vegetational survey-PCSs for Ca' Viettone (Fig. 7). It is noteworthy that such species occur with a greater frequency in the more heavily agricultural Ca' Viettone basin, which contains more abundant cultivated fruit trees and vines, and lower values in the Valtorta basin with its more natural flora.

We note that such a PCS-mismatch approach is not suitable for an accurate comparison of similarities in the under-/overrepresentation signal in more than one case in this study. For this purpose, we introduce the concept of a numerical *bias index* (Table 4; Fig. 9), which is calculated

by subtracting the percentage of a species in the standing vegetation. (X_v) from the percentage of the species in a carpodeposit *s.l.,* (X_d). This value then is divided by the percentage of the species in the carpodeposit, and multiplied by 100:

$$(X_d-X_v)/X_d*100.$$

Applying the bias index approach to our findings, the overrepresentation of several common taxa in both the Ca' Viettone and Valtorta carpological assemblages can be quantified (i.e., *Alnus glutinosa*, *Betula pendula*, *Carex sylvatica*, *Carpinus betulus*, *Polygonum* spp., *Prunus avium*, *Sambucus nigra*). This formula also indicates those species that are underrepresented in both basins (i.e., *Anemone nemorosa*, *Castanea sativa*, *Corylus avellana*, *Fraxinus excelsior*, *Molinia arundinacea*, Poaceae, *Quercus* spp., *Robinia pseudoacacia*, *Salix* spp. and *Vaccinium myrtillus*). For those species represented by more than one plant part in the carpodeposit *s.l.*, it is useful to calculate the bias index for each plant part separately (e.g., fruit, seed, immature fruit, utricle, cupule, etc.), because each type of fruit or seed has its own dispersal mode, shape, woodiness, and size (Table 4). The importance of making these distinctions is reflected in *Robinia*, *Alnus,* and *Quercus*, in which the bias indices are quite different for the separate disseminule categories (Table 4).

The bias index values obtained from the two sites in the current study are not sufficient to validate this approach and the results of the comparison cannot be considered as statistically significant. However, the quantitative data of Gee et al. (1997) provide a possibility to further test the formulation of the bias index in a different area (NW Germany) that contains several taxa also present in NW Italy. The bias index values were calculated by applying the same formula to the German floristic data, and some interesting results were found (Table 4). For example, *Corylus avellana* is not only overrepresented in our coarse sand deposit (C2E; +33%), but a similar value is calculated (+41%) for the taxon in coarse sand deposits reported by Gee et al. (1997). The same overrepresented state occurs in *Alnus* (extremely overrepresented in VTR samples and +33% in the example of Gee et al., 1997), *Betula* (around +60% - Italy and +70% - Germany), and *Carpinus*

betulus (+70% and +81%). In both the German and Italian floras, *Salix*, *Fraxinus*, and *Quercus* (around -300% and -119%) were found to be underrepresented.

DISCUSSION

Our study of fruits and seeds in sandy sediments (Table 1) and their relationship to extant vegetation was conducted in small catchment areas and very smaller rivers. The results we obtained are certainly useful for the interpretation of fossil assemblages formed in analogous conditions. Yet, we are aware that several fossil carpodeposits are associated to sediments of large and medium-sized rivers, and our results may not represent a good analog for to their interpretation. The advantage provided by the study of small catchment areas consists in an easier detection of the origin of diaspores which are incorporated into fluvial sediments and a better understanding of the effect of sedimentary sorting. However, some of our results are possibly less dependent from the size of the fluvial system, since they concern the processes and factors affecting the frequency of individual fruit and seed taxa in those carpological assemblages which were formed under remarkably different sedimentary conditions: settlement of floating fruits and seeds (C1G), combination of bedload transport and decantation (C1I), and bedload transport alone (C1D, C1H, C1L – Ca' Viettone; C2G - Valtorta), including an anomalous concentration of large fruits (C2E - Valtorta).

First, the frequency of certain taxa (Table 4) in the fruit-and-seed accumulation (C1G) derived from suspension load is fundamentally different when compared to those same taxa in the bedload carpodeposits. It is clear that some taxa have been favored by flotation and occur in anomalously high percentages; these include *Alnus glutinosa* (30.1%), *Rumex acetosella* (7.7%), *Carex* spp. (6.8%), and *Aruncus dioicus* (4.5%). One taxon, *Alnus glutinosa*, also has a relatively high frequency (36.1%) in the accumulation formed by a combination of bedload transport and suspension-load settling (decantation; C1I). The remaining taxa found in C1I have frequency values very similar to those calculated for the three bedload carpodeposits at Ca' Viettone.

To minimize the role of sedimentary processes in determining the composition of carpological assemblages, our analysis of the relationships between standing vegetation and fruit-and-seed accumulations focuses on those deposits that formed under relatively homogeneous conditions, the four bedload carpodeposits *s.s.* (C1D, C1H, C1L – Ca' Viettone; C2G - Valtorta). As a whole, they show a general disparity (mismatch) between the frequency of a taxon in the vegetational cover and its representation in fruit-and-seed assemblages (Table 2). Some woody plants (e.g., *Castanea sativa, Corylus avellana, Fraxinus excelsior, Quercus* spp., *Robinia pseudoacacia*), which are very common (39% total cover VTR, 55% CVB) and produce large fruits, are consistently underrepresented in the bedload carpodeposits, making up a small percentage of each assemblage (< 7%).

On the other hand, other taxa (e.g., *Betula pendula, Carpinus betulus, Sambucus nigra*, and *Vitis vinifera*) are consistently overrepresented to such an extent that they reach a combined percentage of 42% in the Valtorta C2G carpodeposit (Table 2), although their combined cover in the standing vegetation is only 8%. A strong long-distance dispersal effect, possibly enhanced by anthropogenic landscape modification, certainly plays a major role in their overrepresentation. We hypothesize that this is one of the reasons to explain why the PCSs based on bedload carpodeposits look consistently different than the living vegetation of the survey in the Ca' Viettone basin (Fig. 7)**.** The two deposit-PCSs for Valtorta (Figs. 8A-B) correspond well to the standing vegetation, probably because of a reduced impact in the long-dispersal effect. This may explain why *Vitis* seeds account for 3% of the assemblage, but also may be due to the homogeneity of the vegetation and reduced human impact.

The crucial point in understanding, and trying to correct for, the bias between the standing vegetation and fruit-and-seed assemblages is the detection of the factors that account for the bias. An important factor that certainly affects under- and overrepresentation is diaspore production rate, often related with the diaspore size (high production associated with small size) and plant size (big dimension associated with high production). But, we have no way to estimate its impact in this

study (Martinetto and Vassio, 2010). Therefore, our attention is focused on those factors that can differentiate the response of diaspores to biostratinomic processes, such as hydrodynamic selection. Holyoak (1984) and Martinetto and Vassio (2010) have assumed that fruit-and-seed size could be an important feature to explain the over- or underrepresentation of any given taxon in a carpodeposit *s.l.* when compared to the standing vegetation. Our studies confirm that diaspore size does play an important role, but also point out a complex interaction with dispersal mode (Fig. 10A) and the degree of woodiness (Fig. 10C), as well. In all Ca' Viettone samples and in C2G (Valtorta), the taxa with large (> 10 mm) fruits or seeds are strongly underrepresented (Fig. 10D) and seem to be negatively affected by their woodiness or dispersal mode (see *Corylus* and *Fraxinus* in Figs. 10A, C). Conversely, taxa with small diaspores are usually overrepresented (Fig. 10D). But, the bias index values (Table 4) of several taxa with long-distance dispersal syndromes (anemochory—wind-dispersed, endozoochory—seeds passed through the gut of an animal) are comparable in the two basins (e.g., *Fraxinus excelsior* -365% and -306%, *Rubus* gr. *fruticosus* 27% and 50%: Table 4), which is favorable for the calculation of correction factors in the future. In general, endozoochorous and myrmecochorous (dispersal by ants) taxa tend to be overrepresented (see also Czarnecka, 2005), while autochorous (active or passive dispersal by the plant, itself) and dyszoochorous (seeds consumed by predation) species are mainly underrepresented (Fig. 10A). Diaspore shape seems to be poorly correlated either if a particular taxon is under- and overrepresented (Fig. 10B).

Another important factor that has been noted by previous authors (Holyoak, 1984; Thomasson, 1991) is the overrepresentation of riparian (riverside) vegetation. In the small basins we studied, there is no real space for riparian vegetation, which is represented by only a few scattered trees of *Alnus glutinosa* and a few patches of herbaceous plants such as *Carex remota, Juncus, Polygonum, Scirpus,* and *Urtica*. Some samples (C1H, C1L, C2G) actually show an overrepresentation of *Alnus glutinosa* and *Polygonum*, which could be explained by the presence of a few of these plants along the banks of the brook, not far from the sample sites. The

overrepresentation of riparian plants also results in a considerable expansion of the hygrophilous belt in the deposit-PCSs (Figs. 7A, 8A-B) when compared to that in the vegetation survey-PCSs (Figs. 7B-D, 8C-D).

Finally, we must point out that under- and overrepresentation of any taxon may radically change within the same deposit, depending to the sampling methodology. In fact, data obtained by preliminary or partial analyses of carpological samples (e.g., Martinetto and Vassio, 2010) cannot be compared with those obtained by a complete analysis of bulk samples. This is because attention is drawn first to the largest fruits and seeds (Gee, 2005), which can be more quickly picked out of the residue. In our samples, taxa with large diaspores make up only a small part of the total carpological remains (e.g., 10.5% in Table 5). Of course, if the analyses were limited to only large diaspores, those taxa with large and usually underrepresented in complete assemblages fruits (i.e., *Castanea, Corylus, Quercus, Robinia*), would become more accurately represented. This is particularly interesting when applying these data to vegetation reconstructions, because our study shows that these taxa may account for a significant part of the vegetational cover (47.4% in the Ca'Viettone basin).

The data in this study, obtained from the quantitative analysis of bulk sediment samples, show that there is generally a very complex and variable relationship between a taxon's frequency in the vegetational cover and its frequency in the seed-and-fruit (carpo)assemblage. An accurate understanding of the sedimentary processes that have produced and influenced the formation of diaspore accumulations is a necessary prerequisite for quantitative carpological analyses. The two Valtorta samples, for instance, illustrate very clearly how much the frequency of a species in a carpological deposit can change solely on the basis of sedimentary processes, despite a homogeneous source of vegetation (see Table 2--*Castanea sativa* and *Corylus avellana).* We interpret this phenomenom as the result of the specific features of the Valtorta C2E deposit; while it is indeed a bedload carpodeposit, it contains an anomalously high concentration of large fruits. This probably is due to its position at a sudden change in the gradient of the Valtorta brook. Similar

situations may, of course, occur in the fossil record and could be easily identified through size analysis of both the diaspores and matrix.

The three samples of medium sand with concentration of medium-sized fruits and seeds (bedload carpodeposits) in the Ca' Viettone basin show similar frequencies for several taxa, which may indicate that bedload transport can homogenize diaspore accumulations. Due to the complex patchy vegetation in Ca' Viettone, we can show that such homogenized bedload carpodeposits do not reflect the vegetation closest to the deposition site. But, rather, provide a record of the vegetation of the entire catchment basin.

In addition, all the bedload carpodeposits (including VTR2C2G of Valtorta-Rivara) show a similar pattern in the over-/underrepresentation of individual taxa, which may be explained by physical parameters in the fruits and seeds and their dispersal mode. Overrepresentation of a taxon may be caused by the small size and overall woodiness of its diaspores. Conversely, underrepresentation of a taxon is linked to large diaspore size and minimal woodiness. Moreover, dispersal mode is also important. This is because there is a general underrepresentation of authochorous and dyszoochorous fruits and seeds, and an overrepresentation of those that are endozoochorous and myrmecochorous. We also observed a long-distance dispersal effect in fruits and seeds of some endozoochorous species (e.g., *Actinidia chinensis*, *Ficus carica*), otherwise rare in the catchment basin, that occur in the sedimentary deposits at consistently higher frequencies.

The modern carpodeposit-PCSs produced by this study are considered to be good analogs for those from ancient fruit and seed-bearing deposits (Martinetto and Vassio, 2010). As a whole, the comparison of all our deposit-PCSs to their respective vegetational survey-PCSs shows that there are biases that would result in serious misinterpretations if an ancient vegetation is reconstructed solely on the abundance of taxa found in a fossil carpodeposit *s.l.* However, the deposit-PCSs derived from bedload carpodeposits generally are representative of the vegetation in the entire catchment basin. Thus, the PCS method would be suitable for application to ancient carpological assemblages of such a type to reconstruct regional, rather than only local, vegetation.

The question remains if and how the vegetation-carpodeposit bias for each taxon, diaspore parameter (e.g., size, degree of woodiness, etc.), or plant category (e.g., trees, herbs, riparian plants, endozoochorous plants, etc.) can be understood and reduced with appropriate corrections. We believe that the Ca' Viettone and Valtorta samples analyzed, to date, do not provide a sufficient statistical basis to propose correction functions that can be applied in the construction of more accurate PCSs based solely on fossil-assemblage data. We suggest that the bias index values may provide only an approximate estimate of the quantitative relationship between a carpodeposit and its source plant community, within a sedimentary setting comparable with the Ca' Viettone and Valtorta contexts.

CONCLUSIONS

Our initial results are encouraging and we recommend applying the same methodology to different types of vegetation and sedimentary settings to increase the dataset and to collect similar information in a uniform manner. Our actuopalaeobotanical observations provide new information about the transport, preservation potential, and accumulation of diaspores, at the moment limited to small fluvial settings, thus allowing us to interpret some types of carpological assemblages in a new perspective. Bedload carpodeposits found in small catchment basins, seem to provide a rather clear vegetational signal. However, there exists a disparity (mismatch) between the carpodeposit content and the source vegetation exists for most individual taxa.

The standardized Plant Community Scenario (PCS) proved to be a useful tool as an objective and easily comprehensible comparison of quantitative data between standing vegetation (survey-PCS) and contemporary carpological assemblages (deposit-PCS). The PCSs obtained from bedload carpodeposits showed that, regardless of the biased frequencies of individual taxa, we can obtain a summary picture of the entire basin's vegetation, which roughly reveals the density of arboreal cover, and the approximate floristic composition of the main vegetational units. The role of the deposit-PCS in reconstructing vegetation is still limited. This is because we have not yet been able to identify the specific statistics necessary for bias correction in carpological assemblages.

However, the combined observation of vegetational survey-PCS and deposit-PCS obtained in the present study constitutes a powerful tool to better interpret ancient bedload carpodeposits, from which only the deposit-PCS can be obtained, while the corresponding vegetation-PCS represents the unknown variable.

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FIGURES CAPTIONS

FIGURE 1--Processes involved in the transfer of fruits and seeds from the terrestrial vegetation into the sedimentary deposits, and influences upon these processes. The accumulation of plant macroremains in fluvial sediments implies a selection, and often a concentration, of plant parts from soil-seed assemblages produced by vegetation growing in a catchment basin. Therefore, the number of each diasporetype in a sediment sample has a complex relationship with the cover of their parent plant in the standing vegetation. In fossil assemblages, the source vegetation can be inferred only by the final result of this complex processes ("diaspores in sedimentary deposits"). In modern contexts, all the steps potentially can be investigated. The present study focuses upon the composition of the source vegetation and the content of carpological assemblages in the sediments (the first and the last step of the entire process). The flow chart also shows that the carpological assemblage can be compared to the standing vegetation by means of the Plant Community Scenario (PCS). Flow diagram inspired in part by Nathan and Muller-Landau (2000).

FIGURE 2-- Maps of the study area, within the Piedmont region, in NW Italy. (A) Two, small catchment basins were selected for actuopaleobotanical research: CVB (Ca' Viettone brook), and

VTR (Valtorta-Rivara). (B) Detailed map of the Ca' Viettone basin in which the sample sites, the outline of the vegetational surveys (SWB, surveyed whole basin) and of the catchment basin (CB) are shown. The total area surveyed is further subdivided into smaller zones (not shown in the figure for clarity) including the upper basin (UB) and the lower basin (LB). (C) Detailed map of the Valtorta-Rivara (VTR) basin (CB, catchment basin) subdivided into two main sub-zones (UB, upper basin) within the surveyed area (SWB, surveyed whole basin). Black dots in B and C indicate the sampling points and are shown together with a shortened sample label. Less anthropogenic impact can be seen in C than in B.

FIGURE 3—Point bar sample site of CVB1C1D in the Ca' Viettone brook (arrow). Current ripples are apparent in the sand to the left of the arrow. The narrow open space around the point bar is surrounded by a dense woodland.

FIGURE 4—Features of sampling localities in the Valtorta-Rivara basin. (A) Vegetational context; notice the dense woods and the steep slope directly above the brook. (B) Pool from which sample VTR1C2E was recovered. The dark material to the right of the arrow is mainly composed of large fruits, which have been partly buried by a sandy bedform migrating from right to left. (C) Detailed view of the freshly sampled sediment, appearing to be rich in large fruits of *Castanea* and *Corylus*,and containing smaller, less obvious fruits of *Carpinus* (arrow; scale bar = 1 cm).

FIGURE 5--Acronym, habitus, and plant symbols used for the construction of PCSs. Ecological zones: X, xeric; M, mesic; HY, hygrophilic; A, aquatic. The symbols for herbaceous plants are depicted twice as large as they are drawn in the PCSs for ease of visualization.

FIGURE 6--Plant Community Scenario (PCS) for the CVB1C1D carpodeposit sample. This simplified transect is subdivided into 2 ecological zones, the extents of which are proportional to the cumulative frequency of mesic (M, left) and hygrophilous (HY, right) plants listed in Table 2.

FIGURE 7--PCSs for Ca' Viettone. (A) A deposit-PCS constructed on the basis of mean frequencies of diaspores in three bedload carpodeposits (C1D, C1L, C1H). (B) A vegetation survey-PCS based only on the standing vegetation in the lower portion of the basin. (C) A vegetation

survey-PCS based on the entire area surveyed, which corresponds approximately to one-quarter of the catchment basin. (D) A vegetation survey-PCS based on the estimated percentage cover of each taxon in the entire catchment basin.

FIGURE 8--PCSs for Valtorta. (A) A deposit-PCS constructed on the basis of mean frequencies of diaspores in sample C2E, a coarse bedload carpodeposit. (B) A deposit-PCS based on sample C2G, a bedload carpodeposit. (C) A vegetation survey-PCS based only on the standing vegetation in the lower basin.(D) A vegetation survey-PCS based on the entire area surveyed.

FIGURE 9-- Plots of the mean bias index values (Table 4) for the Ca' Viettone and Valtorta study sites. Underrepresented (below 0) or overrepresented (above 0) selected taxa in the carpodeposits are shown with respect to their abundance based on the vegetational survey. See text for the calculatation of the bias index.

FIGURE 10--Bar charts of the simplified mean bias index values of underrepresented (below 0) and overrepresented (above 0) species in the Ca' Viettone and Valtorta samples. (A) Arrangement by seed dispersal vector (see Table 2: AUTO, autochory; MYRME, myrmechocory; EPI, epizoochory; DYS, dyszoochory; ENDO, endozoochory; ANEMO, anemochory; POLY, polychory) and secondarily by part size. (B) Arrangement by diaspore shape (F, flattened, E, ellipsoidal-elongate; G,globose) and secondarily by part size. (C) Arrangement by degree of diaspore woodiness (L, low; M, medium; H, high) and secondarily by part size. (D) Arrangement by diaspore size. (E) Arrangement by plant habit ("growth form"); see Figure 5 for key to abbreviations. Diapsore size and degree of woodiness seem to be the most important factors influencing carpodeposit occurrence.

TABLE CAPTIONS

TABLE 1--Carpological deposits analyzed in the present study and related geographical, geological, and taphonomical information.

TABLE 2--List of plant taxa recorded in the standing vegetation at the Ca' Viettone brook (CVB) and Valtorta-Rivara (VTR) sites, expressed by the percentage of cover in the surveyed subareas or areas. The occurrence of taxa in the carpological deposits is expressed by frequency. The information on plant habitus and environmental requirements is based on personal observations and taken from the literature (Pignatti, 1982; Fitter and Peat, 1994 - http://www.ecoflora.co.uk; Bojňanský and Fargašová, 2007), and was used to construct the PCSs illustrated in Figsures 6, 7, and 8. The three columns to the right quantify the so-called PCS-mismatch between deposit-PCS and respective vegetation survey-PCS (see text for details). Positive numbers indicate how many more plant symbols are drawn in the deposit-PCS than in the vegetation survey-PCS (e.g., 2.47 for *Actinidia* means two more deciduous climber plant symbols in the deposit-PCS of Ca' Viettone than in the vegetation survey-PCS, see Figs. 7A and D). Negative numbers indicate how many fewer plant symbols are drawn in the deposit-PCS than in the vegetation survey-PCS (e.g., -11.33 for Poaceae means that in the deposit-PCS of Ca' Viettone there are 11 fewer grass medium plant symbols than in the survey-PCS, see Figs. 7A and D). Abbreviations: Se, seed; Fr, fruit; IF, immature fruit; In, infructescence; Ut, utricle; Sc, scale; Cu, cupule; Ac, Achene. In the set of standing vegetation columns, the percentage cover of those species with several types of carpological remains (fruit, seed, cupule, etc.) are repeated and marked in italics; + stands for rare taxa; empty cells indicate absence, while 0.00 indicates values <0.005.

TABLE 3--List of the main vegetational units surveyed, with a rough estimate of their percentage cover in the Ca' Viettone brook (CVB) and Valtorta-Rivara (VTR) catchment basins, obtained by combining field surveys and satellite image data.

TABLE 4--Selection of the most important taxa in the standing vegetation and carpodeposits, with various information related to diaspore characteristics (types of diaspore; dispersal vector, degree of

diaspore woodiness, diaspore shape, part size), plant habitus, and environmental requirements (see also Table 2). Bias-index values for Ca' Viettone brook (CVB) have been calculated as the mean of the three bedload carpodeposits (C1D, C1H, C1L) which reflect relatively similar conditions. Taxa are sorted on the basis of the ascending order of mean bias index values (see text for explanation of bias index: *v* represents species found only in the standing vegetation, while *d* stands for taxa limited to the carpodeposits). Types of diaspore, expressed by abbreviations following taxa names in the first column:Se, seed; Fr, fruit; IF, immature fruit; In, infructescence; Ut, utricle; Sc, scale; Cu, cupule; Ac, Achene. Dispersal vector: AUTO, autochory (passive or active dispersal by the plant); ANEMO, anemochory (wind dispersal); HYDRO, hydrochory (water dispersal); DYS, dyszoochory (seeds consumed by predation); MYRME, myrmecochory (ant dispersal); EPI, epizoochory (dispersal by sticking to an animal's surface); ENDO, endozoochory (dispersal by passage through an animal's gut); POLY, polychory (multiple dispersal mechanisms). Degree of diaspore woodiness: L, low; M, medium; H, high. Diaspore shape: E, ellipsoidal-elongate; F, flattened; G, globose. Environmental requirement: M, mesic; HY, hygrophilous.

TABLE 5 –Taxa with medium to large seeds and fruits (> 5 mm diameter or maximum length) and their percentage cover values in the Ca' Viettone basin and frequency in carpodeposits. The right column shows how frequencies increase when small-sized taxa are excluded.

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