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

4
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9
10 **Keywords: carpological assemblage; carpodeposit; Plant Community Scenario (PCS);**
11 **actuopaleobotany; plant taphonomy**

12 **ABSTRACT**

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

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

44 INTRODUCTION

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

51 Collinson, 1983; Holyoak, 1984; Pierce and Tiffney, 1986; Dunwiddie, 1987; Gastaldo et al., 1987;
52 Spicer and Wolfe, 1987; Mai and Walther, 1988; Tiffney, 1990; Thomasson, 1991; West et al.,
53 1993; Martinetto, 1994; Jechorek, 2000; Kisieliene, 2006; Mercuri et al., 2006; Sadori et al., 2010)
54 and used for the reconstruction of ancient vegetation. However, the relationship between the
55 frequency (or cover) of the diaspore-producing plants in the standing vegetation and their presence
56 in the sediment-transported carpological assemblages only has been investigated in a few cases
57 (Collinson, 1983; Holyoak, 1984; Gastaldo et al., 1986; Thomasson, 1991; Gee et al., 1997; Gee,
58 2005, Sims and Cassara, 2009). There is still a strong need to conduct further studies to improve the
59 interpretation of fossil assemblages.

60 Studies on modern depositional settings, for instance, have demonstrated that the qualitative
61 and quantitative data provided by carpological assemblages can yield more precise information
62 about the composition and community structure of past vegetation (Watts and Winter, 1966;
63 Burrows, 1980; Collinson, 1983; Greatrex, 1983; Thomasson, 1991; Cappars, 1993; Ferguson,
64 1995; Birks and Birks, 2000). Fossil fruits and seeds, like leaves and wood, have an advantage over
65 fossil pollen and spores, because they are usually contemporaneous to the sediments in which they
66 occur (Greatrex, 1983) and less subject to problems related to contamination or long-distance
67 transport (Cappars, 1993; Ferguson, 1995; Gee, 2005). Furthermore it should be noted that plant
68 macrofossils commonly can be assigned with greater certainty to a more precise taxonomic level.
69 Several studies have demonstrated that carpodeposits reflect local plant communities better than
70 assemblages of other plant organs (e.g., Burrows, 1980; Collinson, 1983; Thomasson, 1991;
71 Cappars, 1993; Sims and Cassara, 2009).

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

77 products of the formational process (the fruits and seeds in the assemblage) with the standing
78 vegetation. For this, we apply a simple graphic representation , “Plant Community Scenario” (PCS),
79 recently proposed by Martinetto and Vassio (2010). Using PCSs, the composite set of information
80 provided by a carpological assemblage can be summarized in a single sketch. In this way we obtain
81 a powerful tool for a straightforward comparison of modern and ancient carpological assemblages,
82 which has been applied first for the interpretation of some aspects of Pliocene vegetation in NW
83 Italy (Martinetto and Vassio, 2010), and, more extensively, for Quaternary vegetation (Vassio,
84 2012).

85 GEOGRAPHICAL AND GEOLOGICAL SETTING

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

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

110 METHODS AND MATERIALS

111 Field Methods

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

116 Three sediment samples (Table 1) were collected in the bottom part of the CVB basin (Fig.
117 2B), and only sample (C1I) originates from the upper basin, which is separated from by a steep
118 escarpment. Sample C1H was taken upstream from the confluence of the left tributary of the Ca'
119 Viettone brook, which drains a large vineyard and is associated with mostly abandoned meadows
120 and agricultural fields. The lower CVB sample sites were found to have concentrations of large to
121 middle-sized fruits (*Carpinus* and/or *Corylus*). Three of these fruit concentrations (C1D, C1H,
122 C1L) were deposited in well-sorted sand with bedforms (Fig. 3), and are considered as bedload
123 carpod deposits (cf. Gee, 2005). On the other hand, the sediment matrix of sample C1I is a muddy
124 sand and, at this site, is found at the confluence of a small tributary of the Ca' Viettone brook,
125 where suspension-load sedimentation of fines played a major role in diaspore incorporation. Hence,
126 this assemblage cannot be treated as a typical bedload carpod deposit (sensu Gee, 2005).

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

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

164 The last phase of this study was a comparison of the qualitative and quantitative data from
165 both the vegetational surveys and the carpological assemblages using the PCS approach (Martinetto
166 and Vassio, 2010) to obtain a comparable visual rendering of both records. Its application,
167 originally proposed for palaeovegetation reconstructions, has been extended to modern
168 carpodeposits and standing vegetation. PCS represents a standardized way of analyzing floristic
169 quantitative data enriched by qualitative attributes, and consists of a database, calculation sheet, and
170 schematic diagrams in which numbers are translated into simplified and stereotyped pictures. The
171 PCS diagram represents a vegetated transect with four main storeys: the canopy and the arboreal
172 plants, beneath which is are the bushy and herbaceous undergrowth. The position in the
173 vegetational reconstruction attempts to be as realistic as possible, taking into account analogous
174 living plant growth habits. The palaeoenvironmental frame used in the PCSs did not follow the
175 more elaborate scheme of van der Burgh (1983) to minimize subjectivity; this approach does not
176 force the phytosociological interpretation of Neogene taxa based on modern vegetational units. The
177 PCS transect potentially can be subdivided into four main zones representing four principle
178 ecological zones; drawn from the left to the right in the diagram these are: xeric – X, mesic – M,
179 hygrophilous - HY and aquatic – A zones). These zones represent the ecological requirements of
180 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,

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

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

214 RESULTS

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

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

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

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

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

242 Data from the Valtorta basin (Table 2) clearly show the relationship between the cover value
243 of each taxon in the standing vegetation and the frequency of the same taxon in the carpological
244 assemblages. Nearly all taxa with high or medium cover values in the standing vegetation are
245 represented in the two sampled fruit-and-seed accumulations, and this also holds true for most taxa
246 with low cover values. Most of the other commonly taxa occurring only in the life assemblages
247 (vegetation survey) have minuscule cover values. This situation is well documented in the Valtorta
248 deposit-PCSs, because the two reconstructions from carpodeposits (Figs. 8A-B) are not
249 dramatically different from those obtained from the analysis of the standing vegetation (Figs. 8C-
250 D). As a whole, the bias between the deposit-PCSs and the vegetation survey-PCSs is less evident
251 for the Valtorta context (compare Figs. 8A-B and Figs. 8C-D) than for Ca' Viettone (compare Figs.
252 6, 7A and Figs. 7B-D). In particular, the two basins differ greatly in the vegetation closest to the
253 sample sites (Fig. 7B) and along the brook; the carpodeposits *s.l.* better reflect the vegetation of the
254 entire basin (Figs. 7C-D). However, in the PCSs of both basins, major differences emerge when
255 examining the taxonomic diversity associated with the plant symbols, which reflect the PCS-
256 mismatch between the most frequent taxa in the vegetation versus those in the fruit-and-seed
257 accumulations (numerically expressed in the last three columns on the right of Table 2). The PCS-

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

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

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

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

$$287 \quad (X_d - X_v) / X_d * 100.$$

288 Applying the bias index approach to our findings, the overrepresentation of several common taxa in
289 both the Ca' Viettone and Valtorta carpological assemblages can be quantified (i.e., *Alnus*
290 *glutinosa*, *Betula pendula*, *Carex sylvatica*, *Carpinus betulus*, *Polygonum* spp., *Prunus avium*,
291 *Sambucus nigra*). This formula also indicates those species that are underrepresented in both basins
292 (i.e., *Anemone nemorosa*, *Castanea sativa*, *Corylus avellana*, *Fraxinus excelsior*, *Molinia*
293 *arundinacea*, Poaceae, *Quercus* spp., *Robinia pseudoacacia*, *Salix* spp. and *Vaccinium myrtillus*).
294 For those species represented by more than one plant part in the carpodeposit *s.l.*, it is useful to
295 calculate the bias index for each plant part separately (e.g., fruit, seed, immature fruit, utricle,
296 cupule, etc.), because each type of fruit or seed has its own dispersal mode, shape, woodiness, and
297 size (Table 4). The importance of making these distinctions is reflected in *Robinia*, *Alnus*, and
298 *Quercus*, in which the bias indices are quite different for the separate disseminule categories (Table
299 4).

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

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

312 DISCUSSION

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

327 First, the frequency of certain taxa (Table 4) in the fruit-and-seed accumulation (C1G) derived
328 from suspension load is fundamentally different when compared to those same taxa in the bedload
329 carpodeposits. It is clear that some taxa have been favored by flotation and occur in anomalously
330 high percentages; these include *Alnus glutinosa* (30.1%), *Rumex acetosella* (7.7%), *Carex* spp.
331 (6.8%), and *Aruncus dioicus* (4.5%). One taxon, *Alnus glutinosa*, also has a relatively high
332 frequency (36.1%) in the accumulation formed by a combination of bedload transport and
333 suspension-load settling (decantation; C1I). The remaining taxa found in C1I have frequency values
334 very similar to those calculated for the three bedload carpodeposits at Ca' Viettone.

335 To minimize the role of sedimentary processes in determining the composition of carpological
336 assemblages, our analysis of the relationships between standing vegetation and fruit-and-seed
337 accumulations focuses on those deposits that formed under relatively homogeneous conditions, the
338 four bedload carpodeposits *s.s.* (C1D, C1H, C1L – Ca’ Viettone; C2G - Valtorta). As a whole, they
339 show a general disparity (mismatch) between the frequency of a taxon in the vegetational cover and
340 its representation in fruit-and-seed assemblages (Table 2). Some woody plants (e.g., *Castanea*
341 *sativa*, *Corylus avellana*, *Fraxinus excelsior*, *Quercus* spp., *Robinia pseudoacacia*), which are very
342 common (39% total cover VTR, 55% CVB) and produce large fruits, are consistently
343 underrepresented in the bedload carpodeposits, making up a small percentage of each assemblage
344 (< 7%).

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

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

361 study (Martinetto and Vassio, 2010). Therefore, our attention is focused on those factors that can
362 differentiate the response of diaspores to biostratigraphic processes, such as hydrodynamic selection.
363 Holyoak (1984) and Martinetto and Vassio (2010) have assumed that fruit-and-seed size could be
364 an important feature to explain the over- or underrepresentation of any given taxon in a
365 carpodeposit *s.l.* when compared to the standing vegetation. Our studies confirm that diaspore size
366 does play an important role, but also point out a complex interaction with dispersal mode (Fig. 10A)
367 and the degree of woodiness (Fig. 10C), as well. In all Ca' Viettone samples and in C2G (Valtorta),
368 the taxa with large (> 10 mm) fruits or seeds are strongly underrepresented (Fig. 10D) and seem to
369 be negatively affected by their woodiness or dispersal mode (see *Corylus* and *Fraxinus* in Figs.
370 10A, C). Conversely, taxa with small diaspores are usually overrepresented (Fig. 10D). But, the
371 bias index values (Table 4) of several taxa with long-distance dispersal syndromes (anemochory—
372 wind-dispersed, endozoochory—seeds passed through the gut of an animal) are comparable in the
373 two basins (e.g., *Fraxinus excelsior* -365% and -306%, *Rubus gr. fruticosus* 27% and 50%: Table
374 4), which is favorable for the calculation of correction factors in the future. In general,
375 endozoochorous and myrmecochorous (dispersal by ants) taxa tend to be overrepresented (see also
376 Czarnecka, 2005), while autochorous (active or passive dispersal by the plant, itself) and
377 dyszoochorous (seeds consumed by predation) species are mainly underrepresented (Fig. 10A).
378 Diaspore shape seems to be poorly correlated either if a particular taxon is under- and
379 overrepresented (Fig. 10B).

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

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

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

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

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

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

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

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

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

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475

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FIGURES CAPTIONS

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

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

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

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

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

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

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

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

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

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

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

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

538

TABLE CAPTIONS

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

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

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

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

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

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

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