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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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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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**

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.

<div align="center">INTRODUCTION</div>

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;

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; Cappers, 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 (Cappers, 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   Cappers, 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 interpretating 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 ~1 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   carpodeposits (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 carpodeposit (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

129 contained a concentration of plant material generated by bedload transport. However, due to the

130 exceptional concentration of large fruits (e.g., *Castanea:* Fig. 4C), we consider this to be an

131 uncommon type of bedload carpodeposit. Sample C2G was collected 200 m downstream of C2E

132 (Fig. 2C) where the valley bottom is almost flat. Here, the sediment matrix is a medium sand that

133 contained a concentration of only medium-sized fruits (e.g., *Carpinus*); we consider this to be a

134 bedload carpodeposit *s.s.*

135   Vegetation surveys were carried out in both basins upstream of the carpodeposit *s.l.* sites.

136 Each area was subdivided into different geographic subareas, each possessing a homogeneous

137 vegetation (Fig. 2B, C). Subsequently, subareas with similar vegetation were combined to obtain

138 macro-areas and the term, *weighted mean vegetation,* refers to the entire surveyed area (Table 2).

139 Each drainage clearly exhibits differences in its geomorphology, such as in the width of the brook

140 bed and gradient, and in its vegetation. The vegetated zones along the brook were surveyed along

141 the water course for at least 400 m (Valtorta) and up to 2 km (Ca' Viettone). The orthogonal width

142 of the surveyed area varied from 10 to 100 m on both sides of the brook (Fig. 2B, C).

143   Finally, a general survey of the vegetation in the entire catchment basin was carried out to

144 estimate the total area covered by the most common plant taxa (Table 2) and the areas covered by

145 the different plant communities (woodlands, meadows, gardens and orchards, etc.: Table 3).

146 Orthophotographs and/or satellite images were used to determine plant cover.

147   Analytical Methods

148   The Recent plant-bearing sediments were processed in the laboratory using the same

149 procedures as those for processing fossil fruits and seeds (Martinetto and Vassio, 2010). A very

150 dilute solution of H_2O_2 (1-3%) was applied to disaggregate the biotic from the abiotic components

151 and facilitate the floatation of the lighter and porous particles, usually fruits and seeds.

152 Subsequently, the floating particles and the heavier materials that settled to the bottom were gently

153 washed and sieved separately. After this material was dried, the fruits and seeds were separated

154 from the sieved residue and sorted by size. Taxa were identified using: atlases of recent fruits 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 <div align="center">RESULTS</div>

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

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 biostratinomic 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 phenomenom 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   authochorous 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.

439 The question remains if and how the vegetation-carpodeposit bias for each taxon, diaspore

440 parameter (e.g., size, degree of woodiness, etc.), or plant category (e.g., trees, herbs, riparian plants,

441 endozoochorous plants, etc.) can be understood and reduced with appropriate corrections. We

442 believe that the Ca' Viettone and Valtorta samples analyzed, to date, do not provide a sufficient

443 statistical basis to propose correction functions that can be applied in the construction of more

444 accurate PCSs based solely on fossil-assemblage data. We suggest that the bias index values may

445 provide only an approximate estimate of the quantitative relationship between a carpodeposit and

446 its source plant community, within a sedimentary setting comparable with the Ca' Viettone and

447 Valtorta contexts.

448   CONCLUSIONS

449 Our initial results are encouraging and we recommend applying the same methodology to

450 different types of vegetation and sedimentary settings to increase the dataset and to collect similar

451 information in a uniform manner. Our actuopalaeobotanical observations provide new information

452 about the transport, preservation potential, and accumulation of diaspores, at the moment limited to

453 small fluvial settings, thus allowing us to interpret some types of carpological assemblages in a new

454 perspective. Bedload carpodeposits found in small catchment basins, seem to provide a rather clear

455 vegetational signal. However, there exists a disparity (mismatch) between the carpodeposit content

456 and the source vegetation exists for most individual taxa.

457 The standardized Plant Community Scenario (PCS) proved to be a useful tool as an objective

458 and easily comprehensible comparison of quantitative data between standing vegetation (survey-

459 PCS) and contemporary carpological assemblages (deposit-PCS). The PCSs obtained from bedload

460 carpodeposits showed that, regardless of the biased frequencies of individual taxa, we can obtain a

461 summary picture of the entire basin's vegetation, which roughly reveals the density of arboreal

462 cover, and the approximate floristic composition of the main vegetational units. The role of the

463 deposit-PCS in reconstructing vegetation is still limited. This is because we have not yet been able

464 to identify the specific statistics necessary for bias correction in carpological assemblages.

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.

475

476   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   calculatation 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. Diapsore 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 Figsures 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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