The Coleopterists Bulletin 76(2): 157–174. 2022.

Coleoptera in Floods: Biotic Surveys, Fish Food, Adaptation, Reconstruction of Paleoenvironments, and Preconstruction of Neoenvironments

Michael L. Ferro
Clemson University Arthropod Collection
Department of Plant and Environmental Sciences
277 Poole Agricultural Center
Clemson University, Clemson, SC 29634-0310, USA
spongymesophyll@gmail.com

Abstract

Coleoptera in flood debris are involved in several apparently disparate, but ultimately interrelated disciplines. In some situations, more than 100 beetle species have been collected from debris immediately after a flood and can greatly augment a biotic survey. Beetles entrained in floods represent an important component of terrestrial inputs into lotic systems. Many species of beetles have evolved morphological and behavioral adaptations to avoid or exploit the costs and benefits of flooding and are dependent on floods for habitat formation in the aquatic/terrestrial transition zone along rivers. Quaternary beetle fossils, often found in fluvial deposits, offer a powerful tool to reconstruct past climates and ecosystems, and an important way to better understand the history of a species' distribution. However, the categories above are artificial and overlapping. With rare exception, studies linking these disciplines could not be found. For example, by studying beetles in flood debris today, paleontologists can personally witness the creation of a thanatocoenosis (death assemblage) produced by the same process acting on the same species that left fossils 100,000 years ago. Continued study of the interaction of beetles and floods, especially in light of global climate change, carries the potential to better predict ecosystem-wide changes in the near future.

Keywords: flood refuse, flood drift, inundation, climate change, taphonomy

DOI.org/10.1649/0010-065X-76.2.157

How many species would the Lepidopterist or the Hymenopterist be likely to discover of their favourite groups alive and unimpaired in a tangled bunch of decayed herbage sent in a bag half across a kingdom?

— The coleopterist David Sharp (1894), upon receiving a dripping bag of flood debris in the post

Introduction

During floods, terrestrial beetles can become caught in moving water, concentrated in flood debris, or stranded on surrounding vegetation (Fig. 1). All life stages are involved—eggs, larvae, pupae, and adults may be floating free or attached/clinging to floating material. Terrestrial invertebrates, but especially Coleoptera, entrained in flood debris are associated with four major research areas: 1) faunal checklists; 2) study of terrestrial inputs into lotic systems during floods; 3) adaptations—to flooding itself and/or habitats created by the flood; and 4) paleoenvironmental reconstruction (climate, habitat, and zoogeography) via reconstruction of species' past distribution and habitat.

The purpose of this work is to provide a review of the multiple uses of a single study system and remind (or perhaps *inform*) researchers of its utility. With few exceptions, studies bridging research areas were not found, and a wide variety of unique research topics are available. Flood debris accumulation and associated processes are likely being altered at multiple scales, from localized alteration of water flow (channelization, parking lots, etc.) to global alteration of precipitation events (especially an increase in extreme rain events driven by climate change, for example simulations by Hirabayashi *et al.* (2008) predicted that some parts of the world may begin experiencing "100 year" floods every 30 years!). Therefore, recognizing the relatedness of these seemingly disparate topics will be important in future conservation endeavors.

Nomenclature

In the published English-language literature the mass of material concentrated by floods has been called "flood refuse", "flood debris", "flood drift", "flood rubbish", "freshets", "rejectamenta", and "flotsam" (Table 1). Other terms for "flood" can include "fluvial" (as an adjective) and "inundation" (as a noun). The term "flood debris" is used in preference to others because it is a popular term and has been applied in the most regions. Certainly, a shared vocabulary is preferred. For the most part,

BEETLES IN A FLOOD.

Fig. 1. “Beetles in a Flood” (from Lydekker 1896, facing page 128).

Table 1. English-language terms used to describe organic material entrained and concentrated by flood waters in publications describing collection of insects from that material.

Term	# Pubs.	Dates used	Location (# pubs.)
Flood refuse	38	1873–present	Canada (3), Europe (36)
Flood debris	19	1892–present	Canada (8), Europe (5), New Zealand (2), USA (4)
Flood drift	6	1949–present	Europe (3), New Zealand (1), USA (2)
Flood rubbish	5	1892–1947	Africa (1), Europe (4)
Freshets	4	1884–1947	USA (4)
Rejectamenta	3	1826–1899	Europe (3)
Flotsam	1	2007	USA (1)

non-English language resources were not consulted in this review.

What is a flood? As with any complex subject, it may be that no single definition will satisfy every situation. Beaumont (1975) offered a restricted definition, "…the situation when water discharge is so great that it can no longer be contained within the river channel at a given point.", but this, for example, ignores water rushing across a pasture towards the river channel, or rising water in a lake. A broad definition is found in Webster's Dictionary (Neufeldt 1988), "an overflowing of water on an area normally dry", but land inundated by tides may not be "normally dry". Rojas *et al*. (2013) wrote "…a flood is defined here as the temporary covering of land by water outside its normal confines". What is normal? Additionally, a flood affects more than land; for example, emergent vegetation already on water-covered land can be flooded as water rises. Some authors solve the problem of defining "flood" by ignoring it, or perhaps tactfully leaving the reader to develop their own definition (*e.g.*, Allan and Castillo 2007; Hynes 1970). Functionally, the floods mentioned in this review contain three elements: 1) flowing water, that 2) in a short period of time 3a) covers a substrate that had, just previously, not been covered, and/or 3b) entrains and transports an object (such as a log) that had, just previously, not been at the mercy of the flow. The temporal element is lacking in other definitions but for our purposes is essential—the "flood" comes quickly, and the consequences are as follows.

1. Flood Debris and Collecting Beetles

Energetic entomologists strike out to collect insects scattered far and wide, while wise entomologists sit deep and let the insects come to them—both are valid strategies. The recommendation to collect beetles from flood debris has largely been lost in the United States. Twenty-four published guides from the United States that include information on how to collect insects were surveyed (1892–2021, data not shown), and only six recommended collecting from flood debris:

1) Riley (1892; updated in Banks 1909): "Freshets usually take place in springtime in most of our rivers and creeks, and furnish the means of obtaining a multitude of Coleoptera, among which there will be many species which can not, or only accidentally, be found otherwise".
2) Gray (1947): "Derbis [sic] left on the shore by a recent flood, freshet, or spring tide, may be simply swarming with insects washed out of their inundated homes. So also may the flotsam caught in a whirlpool or eddy. If an inspection convinces you that such is the case, it will repay you to shovel the derbis [sic] into a burlap bag, drain it, and put it into a separator to extract the creatures, most of which, unlike those taken in sweeping, are likely to be negatively phototrophic".
3) Jaques (1947; reprint 1972): "48. Examine the DEBRIS cast up by RISING STREAMS during a flood or shortly thereafter. You can't beat it for quantity or number of species if you catch it right".
4) White (1983): "Piles of fine grasses and other plant debris often wash up on stream banks during a flood. If you check these piles after a storm or a spring thaw with a heavy snowmelt, you may find that many beetles have been carried to shore along with the debris".
5, 6): Evans (2014, 2021): "Plant debris on the surfaces of streams and rivers contains flying and crawling beetles trapped by floodwaters" (Evans 2014). "Layers of leaves and needles that gather beneath trees, accumulate along streams and rivers as flood debris, or wash up on beaches and lakeshores after storms frequently harbor all kinds of beetles" (Evans 2021).

More recent guides from other parts of the world recommend collection from flood debris: Canada, "flood debris" (Martin 1977); New Zealand, "debris stranded by floods" (Woodward 1951); UK, "flood-refuse" (Cooter and Barclay 2006). While not modern, Samouelle (1826) provides explicit instructions to travelers: "The method of obtaining insects from floods is, to watch the retiring of the waters, and… to gather all the small pieces of wood, floating grass, or other substances, which will be found to be literally covered with insects. At this time, also, the rejectamenta left on the banks of rivers may be examined, and a portion should be collected… As soon as an opportunity occurs the bag should be plunged into boiling water, which will, at once, destroy the lives of the insects thus secured: it should then be emptied, the contents spread on a cloth, or by other means exposed to the sun, or otherwise thoroughly dried…". Samouelle goes on to describe how to preserve the specimens for the trip home. Searching recent flood debris for beetles can be profitable. Eight publications were found that report 100+ species captured from flood debris during a collection event (Table 2). The largest collection was from Easton (1947) who obtained 3,795 specimens representing 327 species from two samples, each "two-thirds of a pailful" in volume, taken in England after two floods.

The importance of flood debris as a collection site is also evident in certain regional checklists (Table 3). Bedwell (1899) reported 34 species collected from "flood refuse" and "rejectamenta" in his list of beetles from Oulton Broad, England. A survey of Coleoptera in the floodplain forests of the Litovelské Pomoraví Protected Landscape Area in the Czech Republic listed 307 species, 117 of which were collected in flood debris (Nakládal 2008). Chandler (1997) reported that a dozen species of Pselaphinae (Staphylinidae) in America north of Mexico have been collected from flood debris. Newton *et al.* (2000) listed seven species of Staphylinidae from flood debris. The following publications reported one or two beetle species from flood debris and are not included in Table 3: Bernhauer and Scott (1931); Denton (2013); Dickason (1949); Donisthorpe (1899); Hamilton (1884); Jennings (1898); Johnson (1982); Majka *et al*. (2010); Murray (1902); Tottenham (1954); Vorst (2009); Vorst *et al*. (2007); Vorst and Johnson (2008); Webster and DeMerchant (2012); Webster *et al.* (2012, 2016); Yates and Hodge (2000).

Despite the usefulness of flood debris as a collecting resource, how samples were chosen, collected, or processed is largely arbitrary. Only one statement about substrate quality was found: "…the most productive of the refuse deposits exhibited a gradient of moisture content which started dry at the top and was saturated at the bottom" (Cooke and Lane 1998). Flood debris was searched for beetles ranging from the day after a flood (Smith 1983) up to 18 days later (Cooke and Lane 1998). At the peak of a flood Joy (1910) collected 30 beetles of a particular species, but two days later only collected five from an equivalent amount of debris. Joy (1910) also speculated that larger beetles were entrained in the middle of the stream and smaller ones on the side after noticing larger beetles in greater numbers in material trapped against the center of a bridge. The most common collection technique reported was to sieve the debris, in the field or at home, and collect the living beetles

Table 2. Research specific to collection of Coleoptera from flood debris.

#	Reference	Location	# beetle spp. or taxa	Taxa
1	Boness 1975	Europe	95+	Coleoptera
2	Cooke and Lane 1998; Lane *et al*. 1999	Europe	283	Coleoptera
3	Cooke and Lane 2001	Europe	160	Coleoptera
4	Corti and Datry 2012	Europe	10 taxa	Coleoptera
5	Day and Murray 1898	Europe	33	Coleoptera
6	Easton 1947	Europe	327	Coleoptera
7	Halbert 1924	Europe	100+	Coleoptera
8	Hewitson 1843	Europe	specimens: "They were in tens of thousands…"	Coleoptera
9	Hoffman 2006	USA	17	Carabidae
10	Hooper 1978	Canada	25	Carabidae
11	LeSage *et al.* 1994	Canada	24	Chrysomelidae
12	Parry 1979	Europe	100+	Coleoptera
13	Sharp 1894	Europe	~100	Coleoptera
14	Shotton and Osborne 1986	Europe	~90	Coleoptera
15	Smith 1983	Europe	38	Coleoptera
16	Steffan 1999	Africa	36+	Coleoptera
17	Townsend 1994	New Zealand	24	Carabidae
18	Washington 2021	Europe	115	Coleoptera
19	Wright and Lane 2012	Europe	300+	Coleoptera

Table 3. Regional checklists that included more than two beetle species collected from flood debris.

#	Reference	Location	# spp.
1	Bedwell 1899	Europe	34
2	Bellstedt and Merkl 1987	Europe	8
3	Champion 1873	Europe	4
4	Crowson 1962	Europe	4
5	Halbert 1895	Europe	4
6	Halbert 1900	Europe	4
7	Janson and Wyse 1924	Europe	4
8	Johnson 1892	Europe	20
9	Keen 1895	Canada	6
10	Nakládal 2008	Europe	117
11	Whitehead 1993	Europe	22

"on the tarsi". For example, Sharp (1894) reported: "My method of capture was to shake out the litter (in a common garden sieve, a few handfuls at a time), over a large white dish with steep sides. A moistened finger-tip transferred the beetles to a laurel bottle and their doom". A Tullgren funnel (Shotton and Osborne 1986) and a Berlese funnel (LeSage *et al*. 1994) have been used as well. Washington (2021) collected 100+ specimens from a shoe entrained in flood debris, collected several hundred specimens from under an old fence post, and then used flotation to collect specimens from wet flood debris; he collected 115 species in total.

The amount of material collected or searched is rarely quantified. Shotton and Osborne (1986) collected 1,573 specimens and 90+ species from a sample with a dry weight of 475 grams. Boness (1975) estimated that one liter of material contained about 600 arthropods (including mites).

Steffan (1999) described an actuo-taphocoenosis (recent death-assemblage) where a variety of recently killed arthropods (36+ spp. of beetles) were found along the shore of saltpan floodplains in Namibia. Some arthropods may have been blown into the area, but the presence of several large dead scorpions and flightless beetles indicated that most specimens were deposited by flood water. The discovery illustrated that, under the right circumstances, specimens of beetles killed during a flood may be readily available weeks or months after the event.

Collection of terrestrial beetles from flowing water not associated with floods has also been reported (Table 4). Barr and Shepard (2017) and Halstead and Haines (1987) seined material from a canal and flume, respectively, over a long period of time and removed large numbers of living and recently dead beetles. Their collections are particularly important because both localities were in mountainous areas and many of the species they collected only live at higher elevations. The collecting technique offered an opportunity to collect species that are otherwise difficult to obtain. McClarin (2007) described what he called "flotsam harvesting", collecting insects from material floating on water that may have been concentrated by wind or rain. Other publications describe collection of beetle species blown onto a body of water and concentrated in a drift line along the shore (*e.g.*, Snow 1902; Tomlin and Sopp 1901; White 1983), but this phenomenon will not be elaborated on further.

Occasionally, terrestrial beetles can be collected *en masse* while seeking refuge on plants and other structures from rapidly rising water (Hoffman 2006; Wright and Lane 2012). Wing (1984) described a spate of Phengodidae larvae in Florida when heavy rains caused them to emerge from the soil *en masse*. Hooper (1978) described the phenomenon: "The exposed parts of the plants will have beetles clinging to them like drowning men clinging [to] trees to get away from rising water". The author experienced a similar situation during 2 August 2014 in Hidalgo Co., New Mexico, USA, when a flash flood created a temporary pond and hundreds of clinging beetles were stranded on the inundated vegetation (Fig. 2). Of the specimens collected, 365 were pinned and deposited in Louisiana State Arthropod Museum (LSAM), Baton Rouge, Louisiana, USA, while the rest were retained in alcohol as bycatch (specimen labels state "sweeping grass in flooded area").

Only one study was found comparing the beetle fauna collected from flood debris with the fauna in the immediate vicinity. During 10 summers of sweep netting at two locations along the Ottawa River in Quebec, Canada, LeSage *et al*. (1994) only collected about 12 species of Chrysomelidae. However, one spring they collected 24 species of Chrysomelidae at the same locations from flood debris!

An anecdotal comparison of the beetle fauna collected from leaf litter and flood debris was made by the author (Appendix 1). Flood debris was collected along Rock Creek Trail, Kensington, Montgomery Co., Maryland, USA (39.025°, −77.094°) less than one hour following a heavy downpour during 21 April 2017 (Fig. 3). The same day, a sample of leaf litter was taken above the flood line in the immediate area. Both samples were processed in Berlese funnels for 10 days. A total of 103 specimens representing 14 families, 43 genera, and 47 species was collected from the flood debris. Only 15 specimens representing four families, 11 genera, and 11 species were collected from the leaf litter. Three species were common to both samples. For the same amount of effort, flood debris yielded about five times the number of species. Specimens are deposited in the Clemson University Arthropod Collection (CUAC), Clemson, South Carolina, USA.

Table 4. Collection of terrestrial beetles from flowing, non-flood water.

#	Reference	Location	# spp.	Notes
1	Barr and Shepard 2017	USA	343+	general insects seining from a canal
2	Halstead and Haines 1987	USA	160	general insects collected from debris floating down a flume
3	McClarin 2007	USA	"arthropod gold mine"	general Coleoptera, as "flotsam harvesting"

Fig. 2. Jong-Seok Park and Sarah Samson collecting beetles in a temporary pond created by a flash flood in Hidalgo Co., New Mexico, USA during 2 August 2014. Insert: Beetles waiting out the flood.

Only a single publication was found describing emergence (*i.e.*, completion of life cycle) of arthropods from flood debris. Working in Germany, Boness (1975) made collections of arthropods from flood debris over an 18-year period. Mobile specimens were collected immediately, but debris was retained and individuals emergent from eggs or pupae were obtained. From this he collected thousands of individuals and an enormous variety of arthropods, 15 orders, and reported many Diptera and parasitic Hymenoptera. From six samples, Boness (1975) obtained 283 specimens and 95 species of beetles. Of those, 15% were herbivores, 30% predators, and 55% detritivores.

***Conclusion and Recommendations*:** In the immediate aftermath of a flood, beetles clearly are concentrated in flood debris and can be collected *en masse*. While the chance to utilize this collection technique may be serendipitous, the opportunity should not be overlooked by those wishing to contribute to a greater understanding of a local beetle fauna. Additionally, basic information, such as time since flood peak and amount, placement, and description of debris collected, should be recorded.

2. Terrestrial Input of Beetles into Lotic Systems During Floods

Entrainment of terrestrial insects during floods is of interest to stream ecologists because of the effect on allochthonous nutrient and energy inputs on stream dynamics. Most research on invertebrate drift has focused on aquatic taxa during normal flow, but a few studies were found that reference terrestrial taxa during floods.

Whether soil dwelling beetles are entrained during a flood has not been studied. However, Ausden *et al*. (2001) provided an indirect answer to this question. They artificially flooded soil plots (*i.e.*, flood as stagnant inundation) in a grassland in

Fig. 3. Flood debris from which the sample for Appendix 1 was taken: Rock Creek Trail, Kensington, Maryland, USA, 21 April 2017.

England and collected the arthropods as they emerged over time. Collection of arthropods began four days after flooding. Initially few specimens were collected, the number peaked after six days of inundation, then fell to nearly zero after 10 days. The majority of arthropods collected were Staphylinidae (69%) and Coleoptera larvae (12%). The implication is that most sub-soil dwelling beetles will stay in the soil if a flood lasts only a few days and, therefore, beetles entrained in flood waters were originally on or above the surface of the ground.

In France, Corti and Datry (2012) sampled multiple sites along a river for invertebrates entrained within "advancing wetted fronts"—a flow (flood) that rewets a dry riverbed—and compared these with sites along a perennial stream. They found higher terrestrial invertebrate density (200×) and higher species richness (5×) in the advancing wetted front than the perennial stream. They also found that with increasing distance downstream: 1) terrestrial invertebrate density was unaffected; 2) taxonomic richness increased (two taxa every km); and 3) density of living terrestrial invertebrates decreased.

Rosado *et al*. (2014) counted the number of invertebrates on coarse organic particulate matter (CPOM) in a temporary stream in Portugal. Prior to the "first flush event" (first flood of the season), they collected 13 individuals per gram of CPOM in the dry riverbed; during the flood the number of individuals increased to 36 per gram, dropped to 17 five days later, and was seven on day 10. Coleoptera, predominantly Staphylinidae and Carabidae, represented anywhere from 55–87% of the specimens collected.

Anderson and Lehmkuhl (1968) collected drifting invertebrates during the first three spring freshets (floods) on a small Canadian creek. They reported that the terrestrial component was higher during the first freshet than later ones but did not provide any quantitative data.

Tockner and Waringer (1997) began collecting drifting invertebrates from a second-order Austrian stream at flood peak and continued collecting from the same location over seven days as the waters fell. They found that the percentage of terrestrial invertebrates captured was highest during the peak (25%), dropped as the waters receded (4%), and then rose again during a smaller secondary flood peak (23%).

De Jong and Canton (2014) conduced a similar study at two streams in the Desert Southwest of the United States. In both streams, terrestrial invertebrates represented about 65% of the individuals collected 24 hours after flood peak. For one stream, the percent terrestrial was still about 65% 48 hours after peak, but fell to near zero at 96 hours. The proportion of terrestrial taxa in the other stream fell evenly until it was about 20% 168 hours after peak. They collected at least 14 families of terrestrial beetles.

***Conclusion and Recommendations*:** Based on the above glimpses, terrestrial insects on or above dry ground are entrained in greatest numbers at the beginning of a flood, and more species are added the further the flood front proceeds, but the number of species drops as time since the start of the flood increases. However, with so few studies (few, if any, have been repeated), the large number of variables to be measured, and the great variety of flooding/river types, any of the quantifications above may only apply to a single study, location, and/or event. Long-term, repeated studies are needed to help understand the scope of variation in terrestrial beetle inputs during floods.

3. Evolutionary Interaction of Floods and Beetles

The interaction of water bodies, especially lotic systems, and the abutting land is dynamic. Junk *et al.* (1989) proposed the "flood pulse concept" to describe lateral exchange of nutrients between the aquatic/terrestrial transition zone and a river channel. The flood pulse concept also predicts high selective pressures on aquatic and terrestrial organisms to utilize the changing resources in the aquatic/terrestrial transition zone (Junk *et al.* 1989). Species in low-order streams (headwaters) that experience unpredictable floods should show fewer adaptations to floods, while species in higher-order streams with large, predicable flooding should possess many adaptations (Junk *et al.* 1989). Zulka (1994) showed that inundated sites in a river floodplain contained distinct Carabidae species assemblages when compared to sites that did not flood. Species dealt with flooding by: flying away; leaving the meadow to hibernate; climbing trees; remaining attached to woody debris, even up to 40 days after submergence; and in some species of Carabidae individuals on the water surface find the shore by orienting towards vertical silhouettes (Zulka 1994). Lytle and White (2007) found that some aquatic desert-stream insect species actively left the water when rainfall cues indicated an impending flash flood; however, the only beetle they studied, *Gyrinus plicifer* LeConte (Gyrinidae), showed no response. Dawson (1965) recorded several Carabidae species that overwintered among and within stems of tussocks to escape winter flooding. The behavior provided protection but also increased likelihood of flood-related dispersal. While not specific to beetles, Carlson *et al*. (2016) and Hladyz *et al*. (2011) both showed that land-use adjacent to streams, including loss or alteration of native vegetation, affected dispersal of adult aquatic insects and in-stream energy dynamics. Specifically, when woods were replaced with pasture, adult aquatic insects dispersed a shorter distance and there was an increase in autochthonous in-stream energy production, both of which will have wide-ranging effects on the community of beetles in the aquatic/terrestrial transition zone.

Wing morphs and flight potential within beetle populations, hypothesized to be an evolutionary adaptation to flooding, have been studied, especially in Carabidae and Staphylinidae. Using window traps, Bonn (2000) found increased flight of Carabidae after river floods. Bonn and Kleinwachter (1999) collected Carabidae along transects from the edge of the river Elbe to the top of the embankment. They found the proportion of macropterous individuals rose with proximity to the water, peaking at 70% against the water's edge. Wohlgemuth-von Reiche *et al*. (1997) found that smaller, flight-capable species of Staphylinidae were more numerous in habitats with higher inundation risks, while flightless species were more plentiful higher up the bank. Hashimoto and Suzuki (2021) showed that higher rates of macroptery were associated with greater fluctuation of water level in the floodplain-inhabiting beetle *Mecynotarsus niponicus* Lewis (Anthicidae), presumably to facilitate escape during floods.

Aquatic/terrestrial transition-zone invertebrates are affected by flood frequency. Using pitfall trapping, Uetz *et al.* (1979) found that species richness was inversely related to flooding frequency but increased with increasing elevation above the floodplain. Their research included 31 taxa in seven families of beetles. In an extreme example of frequency and unpredictability, hydropeaking for hydroelectric power, which can occur daily, may drive extirpation of aquatic (Kennedy *et al.* 2016) and terrestrial (Tockner *et al*. 2006) insects from affected rivers by destroying eggs or killing emerging adults. At a different scale, by altering flood regimes, hydropeaking can affect morphology of the aquatic/terrestrial transition zone, such as alteration of gravel-bar habitat and substrate embeddedness. Paetzold *et al.* (2008) found that Staphylinidae abundance and richness were negatively affected by loss of gravel bars in rivers impacted by hydropeaking.

A unique extreme is represented by rivers that completely dry up during portions of the year. In some cases, drying is natural; however, in others it is the result of damming and water use for hydroelectric power, irrigation, or human domestic use. Wishart (2000) pitfall trapped in a dry riverbed in Africa. Beetles composed 57% of the individuals captured and 29% of the biomass. Using pitfall traps, Steward *et al*. (2011) compared invertebrates between the riparian zone and the dry riverbed at five sites in Italy and Australia. Using a variety of measures, they found significant differences in invertebrate assemblages between the two habitats and proposed that terrestrial invertebrates occupying a dry riverbed make up a community uniquely different from the riparian community. At all five locations Coleoptera were within the top five most important taxa for determining those differences. Steward *et al*. (2011) noted that many dry riverbed specialist species have inundation-resistance adaptations similar to the desiccation-resistant adaptations of aquatic organisms.

Flooding may create and maintain habitats that are required by terrestrial aquatic/terrestrial transition-zone inhabitants. For example, floods create "litter hovels", aggregations of leaves and debris on overhanging branches, that are heavily used by spiders (Loeser *et al*. 2006). Within tidal marshes some terrestrial beetles require habitats modified by floods—*e.g.*, accumulated debris or bare soil (Desender and Maelfait 1999). In braided rivers, large woody debris entrained and deposited by floods are an important component of the habitat mosaic (Tockner *et al*. 2006).

During floods, terrestrial beetles use litter and wood captured by the flood as a refuge. The number of organisms associated with floating debris can be 20 times higher than in the water column; therefore, removal of debris by dams may have a major impact on riparian species (Tockner *et al*. 2006). Braccia and Batzer (2001) studied invertebrates on woody debris in a flooded upland forest and found that the highest richness occurred during inundation and consisted of terrestrial insects. In their study Coleoptera were the most diverse group collected—25 families.

Transport of terrestrial beetles by floods, especially from one ecozone to another, is poorly studied. Coope (1969) argued that during the Last Glaciation, Britain acted as a refugium from which Coleoptera recolonized Scandinavia via, among other pathways, flood debris washed into the sea during spring thaws. Buckland and Panagiotakopulu (2010) reviewed the biogeography of insect fauna (largely beetles) of North Atlantic islands using subfossils and current collections. Climate models indicate that the presence of refugia on the islands during glaciation is very unlikely and that beetles colonized North Atlantic islands via reintroductions using, but not limited to, Arctic driftwood.

Aware that debris was swept into the ocean during floods on Puerto Rico, Heatwole and Levins (1972) sampled flotsam collected at sea around islands of the Puerto Rican Bank. They collected nearly 300 live adult and larval insects, including 11 families of beetles, from 59 pieces of flotsam. In the Netherlands, Hemminga *et al*. (1990) documented transport of larvae of *Agapanthia villosoviridescens* (DeGeer) (Cerambycidae) in stems of *Aster tripolium* (Jacq.) Dobrocz. (Asteraceae) entrained in flood debris. The larvae were transported among upper and lower saltwater marshes (both ways) in an estuary and Hemminga *et al*. (1990) concluded that this was an essential part of the dispersal mechanism of the species. They also speculated that transport within plant remains may be an important dispersal mechanism for many species. Searching flood debris deposited on a New Zealand beach, Townsend (1994) collected many species of Carabidae swept from low-lying coastal areas. Specimens were plentiful for up to 10 days following the flood, after which the individuals presumably either died or dispersed.

***Conclusion and Recommendations*:** In general, many terrestrial riparian beetle species require habitat/mesohabitat that is created or maintained by floods. Other actions of floods may be important to the life cycle or distribution of particular beetles. These species have evolved a suite of adaptations, many poorly known, that allow them to persist in an otherwise extreme environment. Just as aquatic organisms in lotic systems have evolved strategies to counter the unidirectional aspect of flowing water, riparian species must have as well, but those adaptations are poorly studied. Cultivated landscapes, especially those with flood control or debris removal, may not be able to provide suitable habitat, even for strong-flying species (Zulka 1994).

4. Use of Beetle Fossils from Flood Debris

Flood or fluvial deposits are a common cause of concentration and preservation of beetle fossils (see Table 5). Elias (1994) provided a comprehensive overview of the study of insect fossils including history, methods, use in paleoecology, paleoclimate, zoogeography, and archaeology, and highlighted findings in various regions around the world. In practice, extraction of insect parts is accomplished by washing, sieving, or paraffin flotation of the collected material (Coope 1970; Elias 1994; Kenward *et al.* 1980; Rousseau 2011). Specimens are either retained in alcohol, glued to cards, or encased in DMHF (5,5-dimethylhydantoin formaldehyde resin) or other resins (Coope 1970; Elias 1994). For the most part, beetle fossils from Quaternary deposits are representatives of present-day species and in many cases species-level determination can be achieved by comparison with modern, intact specimens (Coope 1970; Elias 1994; Ponel *et al.* 2003).

Caution should be taken when interpreting insect death assemblages. Kenward (1975, 1976) warned of "background fauna"—airborne insects and insect

Table 5. Select studies using terrestrial invertebrates (generally Coleoptera) from flood deposits to describe past environments.

#	Paper	Country	Time	# beetle taxa
1	Ashworth 1977	Canada	8,600 YBP	81
2	Coope 1968a	UK	Mid-Weichselian	158
3	Coope 1968b	USA	24,000 YBP	21
4	Miller *et al.* 1994	USA	~800,000 YBP	43
5	Morgan *et al.* 1979	USA (Alaska)	Miocene(?)	29
6	Nelson and Carter 1987	USA (Alaska)	Early Holocene	100+
7	Osborne 1980	UK	Cromerian(?)	124
8	Osborne 1996	UK	200 AD	107
9	Ponel *et al.* 2003*	France	Quaternary	394
10	Schwert 1992	USA, 13 sites	Late Wisconsinan	127

*specimens were from a peat bog rather than flood, but this reference is included because of the large number of species reported.

parts in bird droppings—and showed that a sample taken from a highly urbanized area appeared to show an insect death assemblage from an open woodland. Ponel and Richoux (1997) also commented on the difficulty of interpreting fossil assemblages because beetles from a wide range of habitats are brought together by wind or water ("tourist elements"). More studies of contemporary deposits would shed light on these issues. To be most effective, however, they should encompass the entire assemblage, not just a few target taxa.

Quaternary beetle fossils offer a powerful tool to reconstruct past climates while simultaneously reconstructing past ecosystems and the relationship between climate change and ecosystem change; see reviews in Elias (1994, 1997, 2006), Porch and Elias (2000), and Walker and Lowe (2007). For example, the Mutual Climatic Range method is used to recreate paleoclimates—temperature and or rainfall—by comparing the modern and past distributions of beetle species based on current and fossil collection data (Elias 1997, 2000). Forbes *et al*. (2020) applied the Mutual Climatic Range method to 88 beetle taxa excavated from the Nunalleq, Alaska archeological site and were able to reconstruct mean summer and winter temperatures from ~1460 AD to the present. Panagiotakopulu (2014) used beetle subfossils to document natural extinction and reintroduction events on North Atlantic islands due to glacial growth and retreat, as well as document more recent human-assisted introductions. Coope and Brophy (1972) highlighted a disconnect between fossil Coleoptera and palynological data in North Wales—both showed temperature oscillations, but at different times. By considering different rates of response between plants and animals they were able to achieve a more accurate description of landscape-wide changes.

There are many more publications on fossil beetles in flood debris than publications on present-day beetles in flood debris. Buckland *et al*. (2020) maintain a bibliography of more than 4,800 publications that use quaternary fossil insects to recreate paleoenvironments. To illustrate the predominance of beetles in the literature, searches within the bibliography were conducted and the number of titles with the following terms were found: chironomid, 406; Coleoptera, 373; beetle, 338; Diptera, 122; Chironomidae, 107; Trichoptera, 29; Hymenoptera, 16; Heteroptera, 6; Hemiptera, 6; Homoptera, 4; Orthoptera, 4; and Lepidoptera, 1.

Buckland and Buckland (2006) also provide the Bugs Coleopteran Ecology Package which is "software based around a database of Coleopteran (beetle) habitat, ecology, distribution and Quaternary fossil records"; it currently contains 11,000+ taxa, 4,400+ references, and 196,000+ fossil records. A search of the database using the term "flood" in "Biology Text" returned 1,778 taxa, "flood debris" returned 802 taxa, and these records were contained in 1,774 publications. Clearly the current review only scratches the surface of available information; however, the records cited in Buckland and Buckland (2006) are predominantly European, so globally there is much more to be discovered.

Beetle fossils can also be used to place the present distribution of a species into a broader context (Elias 1994). Realistically, all of the living specimens that have been collected of a beetle species represent a single snapshot in the history of that species. For example, if a particular species has existed for, say, 100,000 years then all the specimens collected from the year 1700 to the present were obtained during the last 0.003% of its existence. Coope (1970) offered some advice highly relevant to this point (quoted at length):

> *The distribution of a species today cannot be understood purely in terms of the environmental factors governing its existence; historical factors must also be taken into consideration. These historical factors must include past changes in the environment and the associated alterations in the biota as a whole, and also the geographical accidents of space and time that enable a species to take advantage of, or fail to exploit, newly available areas of potential habitat. Although much can be inferred of the past history of a species from studies of its present-day range and recent changes in its distribution, only the fossil record can provide objective data on the past whereabouts of a particular species at any one time.*
>
> *The fossil records shows [sic] that on the larger land masses the present distribution of an insect taxon must be considered as a stage in a dynamic continuum in which the ranges of species and of groups of species are constantly being adjusted in response to changing conditions.*

Unfortunately, incorporation of beetle sub-fossils into species distribution or niche modeling is not regularly applied and current modeling programs do not seem to have a capacity to incorporate sub-fossils or "deep time" into their analyses. Hopefully this will change. Lima-Ribeiro *et al*. (2017) incorporated fossil data in a recent ecological niche model for the jaguar, *Panthera onca* (Linnaeus) (Carnivora: Felidae), and received more optimistic (and, they judged, realistic) conservation scenarios when fossils were included. Pilotto *et al*. (2021) determined that 34% of Swedish red-listed beetles are represented by specimens in the European (sub)fossil record, and are therefore available for long-term niche-modeling analysis by future researchers.

Porch and Elias (2000) and Elias (2006) both provided well designed frameworks for using fossil beetles for future studies on the effect of climate change on ecosystems. A species' past distribution, carbon dating, stable isotope analysis, and ancient DNA can be used to provide robust recreations of past environments. Fossil beetle communities can also help us understand future environments.

The most important aspect of global climate change will be the effect it has on populations of organisms. Studying the effect of past climate change on current species is an important tool that can be used to predict how present climate change will affect those species, and by extension communities and ecosystems. A flood today that entrains and concentrates terrestrial beetles is the exact same process (acting on the same species!) that created a fluvial deposit of beetle fossils 100,000 years ago. There are few opportunities for a paleontologist to personally witness and take part in a thanatocoenosis, but study of beetles in flood debris offers just that. Floods are (somewhat) predictable, easily available, occur all over the world, and offer a kind of repeatability. By making comparisons of beetles entrained in a flood today to the beetles in the surrounding area (species and proportions), we can refine our methods of paleoenvironment reconstruction based on flood deposits, and by extension better preconstruct the neoenvironments of the near future. Amazingly, no research bridging the gap between fossil and modern beetles in flood debris could be found.

Conclusion

No doubt the skeptical reader has noticed that the four categories of beetle-flood interactions are artificial and widely overlapping. The flood that washed fresh specimens to the foot of the collector is also the flood that added terrestrial nutrients to the river, drove evolution, created habitat, transported founder populations, and buried fossils. Water (the Grand Idea and all it entails) is changing across the globe—due to specific human intervention such as dams and flood control, and general planetary degradation like global climate change—and any organisms dependent on water or the work of water will be affected. The major research categories outlined above obviously overlap and are ultimately interrelated; however, except in the works of Rosado *et al*. (2014), and to a limited extent Kenward (1975, 1976) and Steffan (1999), little to no integration has occurred. Comparative, quantitative studies of present-day beetles (including all species, not just families of interest) in flood debris that incorporate aspects of the flood itself and the surrounding beetle fauna and environment would go a long way towards bridging the gap between fields.

Hopefully the reader has not been swept away by the flood of information. Perhaps the tide will turn, and scholars will spring forth and plunge headfirst into these fresh waters of research.

Acknowledgments

I thank Robert Anderson, Michael Caterino, Donald Chandler, Matthew Gimmel, Wesley Hall, Curt Harden, Jan Klimaszewski, Gareth Powell, Paul Skelley, and Tim Struyve for help identifying or confirming species identifications. I thank Phil

Buckland and an anonymous reviewer for suggestions that greatly improved the manuscript. I thank Curt Harden for two good references I would never have found. The project would have been greatly diminished without Biodiversity Heritage Library (www.biodiversitylibrary.org) and Resource Sharing (Interlibrary Loan and Scan & Deliver) at Clemson Libraries. This project was partly supported by USDA/NIFA projects SC-1700596. Technical Contribution No. 7052 of the Clemson University Experiment Station (Project # 1700596).

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(Received 11 March 2021; accepted 5 April 2022. Publication date 21 June 2022.)

Appendix 1

Species and number of specimens collected from flood debris and leaf litter from Rock Creek Trail, Kensington, Montgomery Co., Maryland, USA (39.025°, −77.094°) during 21 April 2017 (Fig. 3). See Acknowledgments for list of experts that helped with species identification. Specimens are deposited in Clemson University Arthropod Collection (CUAC).

	Family	Taxon	Flood debris	Leaf litter
1	Carabidae	*Agonum ferreum* Haldeman	4	
2		*Dyschirius globulosus* (Say)	1	
3		*Elaphropus* Motschulsky sp.	4	
4		*Pterostichus sculptus* LeConte	1	
5		*Semiardistomis viridis* (Say)	1	
6		*Trichotichnus fulgens* (Csiki)	2	
7	Ciidae	*Orthocis punctatus* (Mellié)	1	
8	Coccinellidae	*Harmonia axyridis* (Pallas)	2	
9	Curculionidae	*Acalles porosus* Blatchley		1
10		*Anthonomus subfasciatus* LeConte	1	
11		*Barypeithes pellucidus* (Boheman)	5	
12		*Hypothenemus interstitialis* (Hopkins)	1	
13		*Listronotus* Jekel sp.	1	
14		*Pityophthorus liquidambarus* Blackman	1	
15		*Pseudopentarthrum simplex* Casey	1	
16		*Trachyphloeosoma advena* Zimmermann		2
17		*Xyleborinus saxesenii* (Ratzeburg)	1	
18		Gen. sp.	1	
19	Elateridae	*Conoderus bellus* (Say)	1	
20	Histeridae	*Acritus* LeConte sp.	3	
21		*Aeletes politus* LeConte		1
22	Hydrophilidae	*Tectosternum naviculare* (Zimmerman)	1	
23	Laemophloeidae	*Lathropus vernalis* LeConte	1	
24	Monotomidae	*Monotoma americana* Motschulsky	1	
25	Nitidulidae	*Epuraea* Erichson sp.	1	
26		*Stelidota octomaculata* (Say)	1	
27	Phalacridae	*Stilbus* Seidlitz sp.	5	
28	Ptiliidae	*Pteryx* Matthews sp.		2
29	Scarabaeidae	*Ataenius cylindricus* Horn	2	
30		*Ataenius gracilis* Melsheimer	8	
31		*Ataenius spretulus* (Haldeman)	12	
32		*Maladera japonica* (Motschulsky)	1	
33	Silvanidae	*Ahasverus rectus* (LeConte)	5	
34	Staphylinidae	*Acrotona* Thomson sp.	4	
35		*Aloconota* Thomson sp.	2	
36		*Anotylus* Thomson sp.	4	1
37		*Arpedium cribratum* Fauvel	1	
38		*Arthmius* LeConte sp.		1
39		*Baeocera* Erichson sp.		1
40		*Carpelimus gracilis* (Mannerheim)	2	
41		*Cephennodes corporosus* (LeConte)		3
42		*Eleusis pallida* LeConte	1	
43		*Euconnus* Thomson sp. 1	2	
44		*Euconnus* Thomson sp. 2		1
45		*Euconnus* Thomson sp. 3	1	
46		*Hoplandria lateralis* (Melsheimer)	2	
47		*Neobisnius sobrinus* (Erichson)	2	
48		*Oxypoda* Mannerheim sp.	3	
49		*Philonthus* Stephens sp.	2	

(*Continued*)

Appendix 1. (*Continued*)

Family	Taxon	Flood debris	Leaf litter
50	*Platydracus cinnamopterus* (Gravenhorst)	1	
51	*Rhexius schmitti* Brendel	1	1
52	*Scaphisoma* Leach sp.	1	
53	*Scopaeus* Erichson sp.	2	
54	*Thesiastes fossulatus* (Brendel)	2	1